Life Sciences und Facility Management
IUNR Institut für Umwelt und Natürliche Ressourcen

WSL-Institut für Schnee- und Lawinenforschung SLF

Vegetation and soil microbial diversity along alpine elevation and snow gradients

Master thesis | Environment and Natural Resources

January 13, 2022

Sabrina Keller

Picture: S. Keller

Supervisors:

Prof. Dr. Jürgen Dengler |
Dr. Daniel Hepenstrick
ZHAW Life Sciences und Facility Management Institut für Umwelt und Natürliche Ressourcen
Grüentalstrasse 14
8820 Wädenswil

Dr. Christian Rixen
Mountain Ecosystems
WSL Institute for Snow and Avalanche Research SLF
Flüelastrasse 11
7260 Davos

Abstract

Along elevation gradients, effects of changing environmental conditions can be observed and predicted, with plants being commonly used as bioindicators. The relationship between plant alpha diversity and elevation depends on the sampling design and shows unimodal or decreasing patterns, whereas there are inconsistent or even contradictory findings for soil microbes (bacteria, fungi, protists). I examined plant and microbial diversity indices (species richness, Shannon index, Shannon evenness index) along alpine elevation and snow gradients in Switzerland, using the snow gradient to represent seasonal variation and soil moisture. To determine the effect of both gradients on diversity indices and test their relationship, I conducted linear mixed-effect models (LME) and correlation tests. In structural equation models (SEM), I examined the (in-) direct effect of elevation and snow gradient, pH, and plant species richness on microbial diversity. All diversity indices of plants and microbes showed a unimodal relationship along the elevation gradient, while species richness of fungi was influenced by the interaction of both gradients and showed increasing and decreasing linear patterns along the snow gradient. The species richness of protists showed no relationship with elevation but was highest in plots under snow cover. I could not detect an effect of plant species richness on microbial diversity indices in the SEM. Both gradients, as well as pH, had shown a direct influence, whereby their effects differed between microbial groups and indices. Even though plant species richness did not significantly affect microbial diversity in my analyses, at least a link between plant and bacterial diversity is to be expected, because they follow the same unimodal curve and are positively correlated. Thus, further research is needed, for example based on functional groups, to explore these relationships.

Keywords: alpha diversity, Alps, drivers, elevation gradient, pH, plants, microbes, rRNA sequencing, species richness, snow gradient, structural equation model SEM

Content

Introduction **5**

Methods **9**

Study area and sampling design *9*

Vegetation and soil field sampling *10*

Soil processing *11*

Microbial RNA extraction, reverse-transcription, library preparation and sequencing *12*

Microbial sequence analyses: filtering and identification *12*

Data preparation *13*

Data analysis *13*

Results **16**

Effects of elevation and snow gradient on plant and microbial diversity indices *16*

Correlation between plant and microbial diversity indices *18*

(In-) direct effects on microbial diversity indices *19*

Discussion **22**

Inconsistent patterns of plant and microbial diversity along elevation and snow gradient *22*

Diversity indices correlate only between plants and bacteria *23*

No indirect effects of elevation, snow gradient and pH on microbe diversity *24*

Conclusion and outlook *25*

Acknowledgement **26**

Bibliography **27**

Appendix **37**

General characterization of all sampled plots *37*

Identified plant species at species level *39*

Author contribution: Performed work by year and person *41*

Chi^2 and p-Values of LME models, explaining the diversity indices as a function of elevation and treatment (snow gradient) *42*

Correlation matrix between plant and microbial diversity indices (species richness, Shannon index, evenness index) 44

Correlation coefficients between plant and microbial diversity indices 45

SEM variable selection: Correlation coefficients for plant diversity indices 46

SEM variable selection: Correlation coefficients for bacteria diversity indices 47

SEM variable selection: Correlation coefficients for fungi diversity indices 48

SEM variable selection: Correlation coefficients for protist diversity indices 49

Chi^2 and p-Values of LME models, explaining the drivers of plant and microbial diversity indices 50

Individual variable contribution in SEM for microbial species richness 52

Individual variable contribution in SEM for microbial Shannon index 53

Individual variable contribution in SEM for microbial evenness index 54

Introduction

The study of diversity patterns along elevational gradients has a long tradition (Linnaeus 1781) because environmental conditions alter drastically within short spatial distances (Yao *et al.* 2017). This involves not only broadening ecological understanding, but also to predict the effects of environmental change, which includes climate warming, on terrestrial ecosystems (Lomolino 2001; Rahbek 2005; Malhi *et al.* 2010; Grytnes *et al.* 2014). Thus, elevational gradients serve as natural experimental base to study these effects (Körner 2007; Siles & Margesin 2017). One of these effects is the climate-induced decrease in snow cover in mountainous regions (IPCC 2013), which in turn affects alpine biotic communities (Lazzaro *et al.* 2015; Rixen & Wipf 2017). Alpine regions are expected to respond particularly strongly to global warming (Pepin *et al.* 2015) for example, because of the snow-albedo feedback mechanism (Giorgi *et al.* 1997). This is critical because these regions exhibit high plant diversity and provide important ecosystem services, such as carbon storage in permafrost soils (Körner 2003).

Changes in plant (Bruun *et al.* 2006; Baniya *et al.* 2012; Grytnes *et al.* 2014) and microbial (Fierer *et al.* 2011; Ni *et al.* 2018; Tian *et al.* 2021) community diversity along elevational gradients are often studied, with research on microbial diversity lagging behind for a long time due to lack of technical methods (Dunbar *et al.* 2002; Griffiths *et al.* 2011; Hol *et al.* 2013). The findings regarding the diversity patterns of plant communities exhibit two different patterns: diversity decreases with increasing elevation (Theurillat *et al.* 2003; Vittoz *et al.* 2010; Pauli *et al.* 2012; Bässler *et al.* 2016) in arid to moderate humid biomes and a grain size of $1m^2$ or shows a maximum at middle elevations in alpine arid (Bryant *et al.* 2008; Namgail *et al.* 2012) or suboceanic (Bruun *et al.* 2006;) biomes. Compared to plants, less is known about elevational diversity patterns of microbes (bacteria, fungi, protists) (Shen *et al.* 2013), with inconsistent or even contradictory findings. Therefore, it is important to contextualize the interpretation of diversity patterns. The extent of the gradient (Field *et al.* 2009; Siefert *et al.* 2012), the plot size (Baumann *et al.* 2016; Talebi *et al.* 2021), the taxonomic resolution (Polyakova *et al.* 2016; Dembicz *et al.* 2021), and the biome (Echeverría-Londoño *et al.* 2018; Testolin *et al.* 2021) in which the study was conducted must be considered.

Bryant *et al.* (2008) demonstrated a monotonic decrease of bacteria diversity at phylum level with increasing elevation in the alpine to sub-nival zone (920 m vertical distance) in a semi-arid biome. Because pH decreases along this elevation gradient (Bryant *et al.* 2008), Shen *et al.* (2014) criticized this study that only diversity of the phylum *Acidobacteria*, which are sensitive to changes in pH (Jones et al. 2009), was considered; therefore, the decreasing bacterial diversity related to pH rather than elevation gradient. Furthermore, the taxonomic resolution is not as detailed as in a later study by Fierer *et al.* (2011), so the diversity pattern found may be biased. Fierer *et al.* (2011) in turn found no significant changes along an elevational gradient (200 m a.s.l to 3400 m a.s.l) for the species richness of bacteria at phylum level in the humid climate of eastern Andes of Peru, with Singh *et al.* (2012)

criticizing this study for having a too wide range of geologies to detect patterns. The elevation gradient also showed no significant relationship with bacterial diversity at phylum level in the study by Wu *et al.* (2017), who collected their data along a lower elevation gradient between 500 m a.s.l and 1900 m a.s.l in a moderately humid biome. Shen *et al.* (2013) also found no consistent patterns for bacterial diversity at phylum level, although they did find significant differences between specific elevation levels along a gradient from 530 m a.s.l. to 2200 m a.s.l in an arid biome in temperate to subalpine forests. Singh *et al.* (2012) or Peay *et al.* (2017) on the other hand, found clear patterns for bacterial diversity at phylum level which describe the highest species richness at mid-elevations levels , and this despite the fact that they conducted their studies at different elevations (Singh *et al.* 2012: 1000 m a.s.l to 3600 m a.s.l; Peay *et al.* 2017: 50 m a.s.l to 1000 m a.s.l) and biomes (Singh *et al.* 2012: mesic; Peay *et al.* 2017: tropical).

Studies also come to contradictory results regarding fungal diversity patterns. The study by Shen *et al.* (2014), conducted along the same gradient as Shen *et al.* (2013), did not demonstrate any correlation with the elevation gradient for the diversity of fungi at phylum level. Surprisingly, Ping *et al.* (2017) found in the same study area as Shen *et al.* (2013) and Shen *et al.* (2014), significant differences in fungal diversity at genus level: Richness and evenness index decreased with increasing elevation, whereas Shannon index first decreased and then increased at higher elevations. However, Ping *et al.* (2017) examined a much shorter elevation gradient between 699 m a.s.l. and 1177 m a.s.l than Shen *et al.* (2013) and Shen *et al.* (2014) (530 m a.s.l. to 2200 m a.s.l). A similar pattern was shown by Ni *et al.* (2018) and Nottingham *et al.* (2018), who observed a decrease in fungal alpha diversity at phylum level along the elevational gradient. Ni *et al.* (2018) found these patterns in the same study area as Shen *et al.* (2013, 2014), and Ping *et al.* (2017), but on a higher gradient between 2000 m a.s.l. and 2500 m a.s.l, whereas Nottingham *et al.* (2018) conducted their study in a tropical biome following a very long gradient from 194 m a.s.l. to 3644 m a.s.l. This again contradicts the study of Peay *et al.* (2017), conducted in a tropic biome, which found an increase in fungal richness at phylum level with increasing elevation.

The least is known about the elevation-related diversity patterns of protists compared to bacteria or fungi (Boenigk *et al.* 2018; Rahbek *et al.* 2019; Burki *et al.* 2021). There is no consensus on whether elevation has any effect on protists at all, because in certain studies, it is not even considered as a driver (Malard *et al.* 2021). For particular groups within protists, Seppey *et al.* (2019) demonstrated a positive, negative or unimodal influence of elevation, although these patterns did not emerge when overall protist diversity was considered. Mazel *et al.* (2021) were able to show that the composition of the functional groups changes along an elevation gradient. The latter two studies were both conducted in the Swiss Western Alps, with a shorter gradient (1500 m) for Seppey *et al.* (2019) than for Mazel *et al.* (2021) which measures 2600 m.

Further knowledge gaps exist about the relationships between plant and microbial diversity along elevational gradients (Porazinska *et al.* 2018), including their response to climate change (Hagedorn *et al.* 2019; Winkler *et al.* 2019). To provide evidence of changing ecological conditions, plants are often used as bioindicators because they respond to shifts in their environment (Rixen & Wipf 2017; Steinbauer *et al.* 2018). Microbes perform important ecosystem functions (Rillig *et al.* 2002; Monson *et al.* 2006; Carney *et al.* 2007) and influence global carbon fluxes (Singh *et al.* 2010; Caron *et al.* 2017; Fierer 2017). Therefore, it is important to know whether plant community diversity can be used as proxy for microbial diversity to predict their response to altering environmental conditions (Hooper *et al.* 2000; De Deyn & Van der Putten 2005; Gao *et al.* 2013). Either there is a positive correlation, as increased plant diversity leads to more micro-niches for microbes, or it is linked to the predominant evolution of bacteria from highly productive specific taxa, leading to an overall decrease in microbial diversity (Goberna *et al.* 2016). To date, it has not been possible to identify any consistent patterns. As a supporting rationale for a positive correlation between plant and microbial diversity, Broughton & Gross (2000), Kowalchuk *et al.* (2002), Millard & Singh (2010) and Eisenhauer *et al.* (2011) cite the heterogeneous resource availability of litter and root exudates, which leads to increased microbial diversity. Dassen *et al.* (2017) and Porazinska *et al.* (2018) both found a positive correlation between species richness of plants and fungi, with this pattern not confirmed for bacteria and protists in the study of Dassen *et al.* (2017). On the other hand, a positive correlation was found for species richness for bacteria and plants (Porazinska *et al.* 2018; Sun *et al.* 2019) and for functional plant diversity and bacteria species richness (Shigyo *et al.* 2019). Prober *et al.* (2014) and Zverev *et al.* (2021) indeed concluded that alpha diversity of plants and alpha diversity of bacteria and fungi are largely decoupled.

A snow gradient, as in my study, represents the seasonal variations in microbial communities due to changing soil moisture conditions (Lipson & Schmidt 2004; Buckeridge & Grogan 2010; Ernakovich *et al.* 2014). The influence of seasonal change differs among microbial groups, with bacteria showing the highest diversity at the time of snowmelt and in summer, whereas it is highest for fungi under winter snow cover (Lazzaro *et al.* 2015). Among protists, the highest diversity is expected at the time of snowmelt (Fiore-Donno *et al.* 2019).

Soil pH is considered as an important driver of diversity patterns of plants (Vonlanthen *et al.* 2006), as well as microbes (Dassen *et al.* 2017; Tian *et al.* 2021). Plant diversity shows a unimodal relationship with pH (Palpurina *et al.* 2017; Dembicz *et al.* 2020). The impact of pH on the diversity of microbes depends on the phylum studied, so the effect can be positive or negative (Fierer & Jackson 2006; Lauber *et al.* 2009; Chu *et al.* 2010). This effect could be demonstrated on all scales (Lauber et al. 2009; Chong *et al*. 2010) in arctic and alpine ecosystems (Zinger *et al.* 2009; Chu *et al.* 2010). Furthermore, Ren *et al.* (2018) demonstrated a direct and indirect effect of pH via other environmental variables on the diversity patterns of microbes.

As described, studies come to conflicting conclusions regarding the effect of elevation on microbial diversity and the relationship between plant and microbial diversity. Therefore, the aim of my Master thesis is (i) to determine the influence of alpine elevation and snow gradient on the alpha diversity of microbes (bacteria, fungi, protists) and to compare these with the diversity patterns of vascular plants. Further, I want (ii) to test if correlations exist between plant and microbial alpha diversity indices. Finally, I am interested in (iii) whether elevation and snowmelt patterns effect microbes directly or indirectly via plant diversity and the role of soil pH as a driver of these patterns.

I hypothesize that the elevational gradient affects plant, as well as microbial alpha diversity, with different patterns expected within microbes. I anticipate the largest plant and bacterial diversity at mid elevations. The elevation gradient is likely to have a negative effect on the diversity of fungi and protists. The snow gradient affects the alpha diversity of bacteria, fungi, and protists positive or negative. For plant diversity, I do not expect any influence of snow gradient, because the studied plots are spatially close. Although there is conflicting evidence on the correlation between plant and microbial alpha diversity, I expect high plant alpha diversity to correlate positively with bacterial and fungal diversity. Finally, I assume that the elevation and snow gradient effect all microbial groups directly and indirectly through alpha plant diversity. Since soil pH is cited in many studies as a driver of plant and microbial alpha diversity, I expect that it also affects microbes directly and indirectly.

I investigate plant and microbial diversity along three elevation gradients in the Swiss Eastern Central Alps, where each elevational level includes a snow gradient. Vegetation surveys and microbial RNA analyses provide the basis for the calculation of diversity indices. My thesis is a part of the multiyear Postdoc project of Anna Maria Fiore-Donno (University of Cologne) and a further development of the Bachelor thesis of Fiona Schwaller (ETH Zurich), conducted in 2020. Therefore, data collection, processing and analysis were carried out by different persons and took place over two years (author contribution Table 4, Appendix).

Methods

Study area and sampling design

The study area is located in the Eastern Central Alps in the Swiss canton of Grisons, on the mountains Wannengrat (Chörbschhorn), Jakobshorn and Schwarzhorn near Davos at an elevation between 1972 and 2816 m a.s.l (Figure 1). The climate normals at Davos Weissfluhjoch (2691 m a.s.l, 2'780'616 / 1'189'634) are characterized by a mean annual temperature of -1.9 ºC, 262 days of frost, a total annual precipitation of 1411 mm and snowfall on 119 days a year (Bundesamt für Meteorologie und Klimatologie 2021). The mineral bedrock is composed of acidic rocks: Gneiss and mica schist at Wannengrat; metagranitoids, moraine, gneiss, mica schist and amphibolites at Jakobshorn; and gneiss, mica schist and metagranitoids at Schwarzhorn (Bundesamt für Landestopografie 2021a). Alpine farming is practiced in the study area, with certain areas considered unproductive (Bundesamt für Landestopografie 2022).

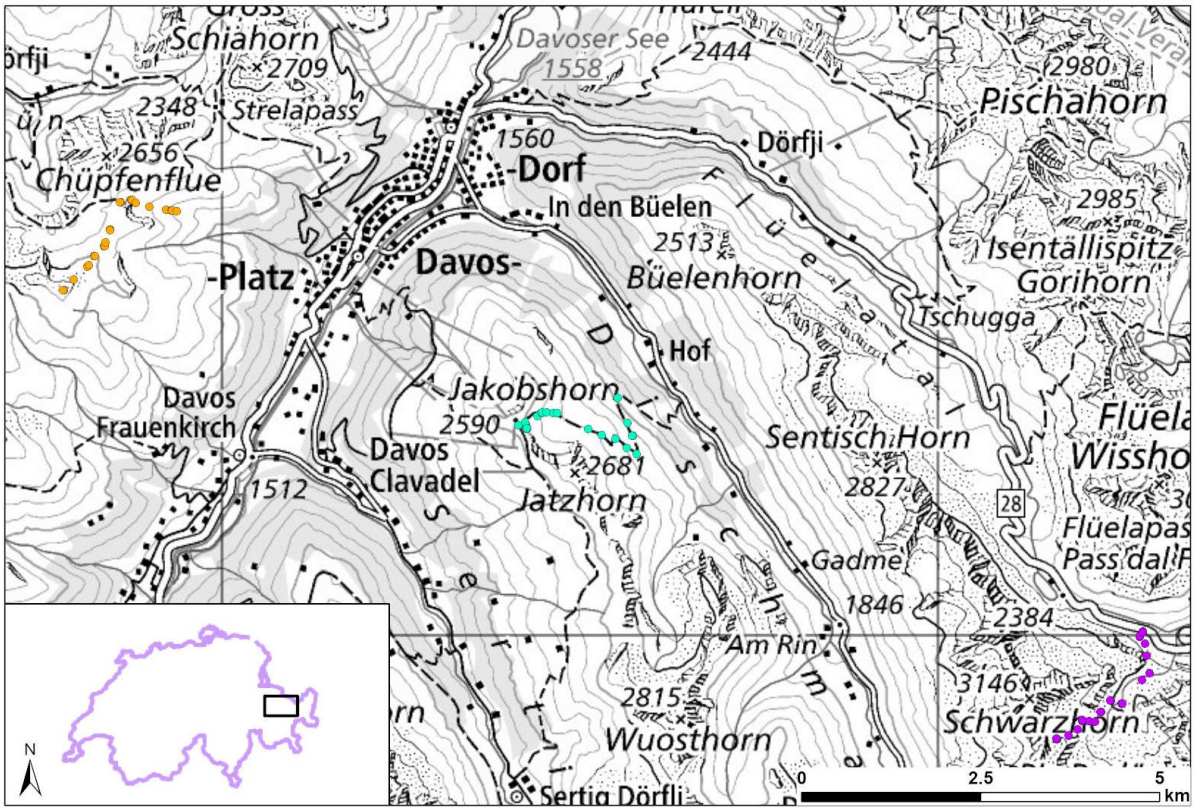

Figure 1 The study area is located in the Davos region with plots along elevation gradients on Wannengrat (orange), Jakobshorn (turquoise) and Schwarzhorn (purple). (1:60'000; map: Bundesamt für Landestopografie (2021b), edited)

On each of the three studied mountains, an elevation gradient with 15 to 16 sites was established (Schwarzhorn & Wannengrat each *n*= 15; Jakobshorn *n*= 16). These gradients are located at Wannengrat between 2160 m a.s.l and 2639 m a.s.l, at Jakobshorn between 1972 m a.s.l and 2557 m a.s.l and at Schwarzhorn 2323 m a.s.l and 2815 m a.s.l. The sites within the gradients are separated by

a mean vertical distance of 38.29 m, with a maximum of 100.24 m and a minimum of 4.71 m, both at Jakobshorn. The horizontal distance between the sites is maximum 378.29 m (Jakobshorn) and minimum 50.33 m (Wannengrat). The slope of the studied sites ranges from 7 ° to 45 ° at Wannengrat, from 0° to 44° on Jakobshorn, and from 0° to 50° at Schwarzhorn, with average slightly steeper sites at Jakobshorn and Schwarzhorn (both 21°) than at Schwarzhorn (19°). The sites at Jakobshorn are oriented northeast on average (81°; min: 5 °, max: 320 °); and southeast on Wannengrat (132°; min: 20 °, max: 330 °) and Schwarzhorn (96°; min: 5 °, max 355 °).

A site consists of three plots with a diameter of 40 cm, resulting in a total of 138 plots. In spring 2020, the location of plots within a site was laid out so that one plot is under a snow patch (Sn), one plot is at its edge (Ed), and one plot is 1 m away from it (1 m). The three plots per site represent a factorial snow gradient to track changes in soil microbes during snowmelt (Figure 2). *Treatment* stands in the following as a synonym for snow gradient.

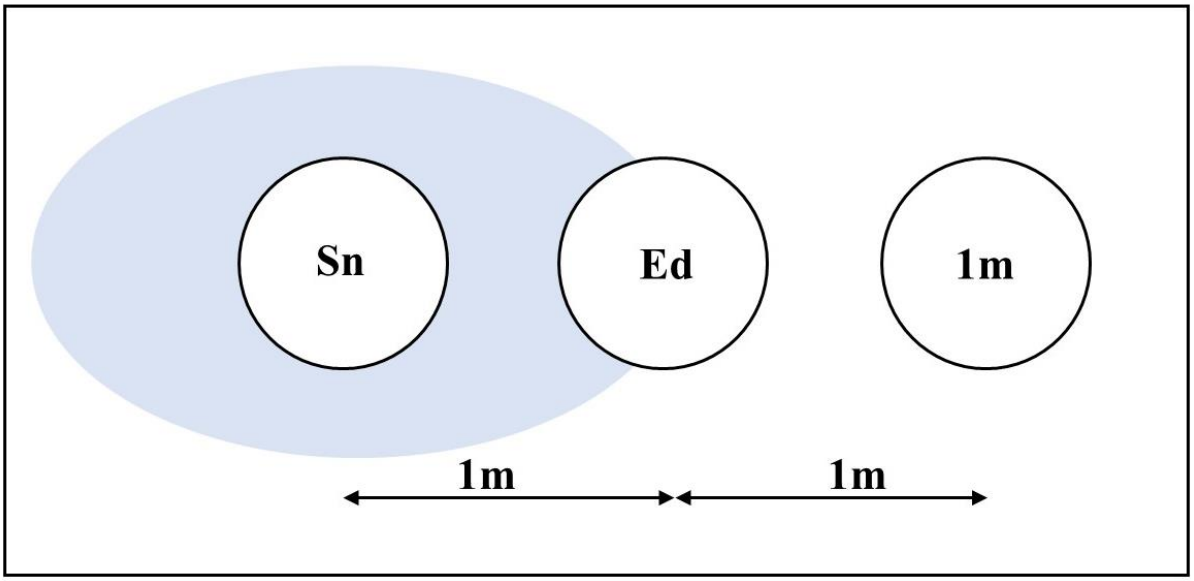

Figure 2 A site consists of three plots, which are about 1 m apart. One plot (Sn) was under a snow patch (light blue) in spring 2020, one was at its edge (Ed), and one was 1 m from the edge (1 m).

Vegetation and soil field sampling

The coordinates and *Elevation (m a.s.l)* of the plots were recorded in 2020 using a Trimble Geo XH 6000 (precision 0.1/ 0.01 m). The plot center was fixed in the ground by small metal plate with two screws. In 2021, all plots were re-located with a Stonex S800 (precision 0.01 m) at an antenna height of 2 m to replace missing tags.

Vegetation surveys took place between June and August in 2020 (n= 72) by Fiona Schwaller and 2021 (n= 66) by me. *Vascular plants* rooted in a plot were identified and their *cover (%)* estimated, with nomenclature referring to the checklist of Juillerat *et al.* (2017). For *bryophytes* and *lichens*, total cover

(%) was estimated. To ensure a similar phenology, the vegetation surveys were first carried out at lower elevations. Cover *(%)* of *rocks and gravel*, *open ground* and *litter* was estimated. These six ground cover values together add up to 100%. In addition, the following environmental and structural parameters were measured for each plot: *Aspect (°)* was measured with a mobile phone compass and *slope (°)* with the White Risk App (Institut für Schnee- und Lawinenforschung SLF 2021). *Mean vegetation height (cm)* was measured with a double meter at four regularly spaced locations at the edge of the plot and one in the center. The height of the five plants closest to the double meter was measured without raising them. In addition, the *maximum vegetation height (cm)* was measured, and its *phenology* was determined. Four measurements with a soil corer at the edge of the plot gave the *mean soil depth (cm)*. According to Dengler *et al.* (2016), *maximum microrelief (cm)* was measured where it showed the largest difference in relief perpendicular to a stick, placed on the soil surface.

Soil sampling (n=138) took place 2020 at the time of snowmelt in May at Wannengrat and Schwarzhorn and in June and in July at Schwarzhorn. A square of about 30 cm per side of the vegetation layer was removed with a spade. 300 g soil was collected from the upper layer (to about 5 cm depth) with clean gloves and a metal spoon and placed in a plastic bag. After collection, the soil samples were stored at 5 °C.

In September 2019, at ten sites per transect temperature loggers were buried in a depth of 5 cm and measured soil temperature every two hours for one year. This gives the *mean annual soil temperature (°C)* per site. The *soil temperature at soil sampling (°C)* was measured during the soil sampling in 2020.

Soil processing

The *water content (%),* which represents the soil moisture during snowmelt, was calculated of about 4 g of soil from each plot was dried in an oven at 60 °C for 48 hours as soon as possible after their collection and then reweighed. From each soil sample, circa 4 g of sieved dry soil was rewetted with 40 ml of distilled water for one hour before measuring the *pH Value* with a pH meter.

Soil samples were prepared using the fumigation-extraction method (Vance *et al.* 1987; Witt *et al.* 2000; Voroney *et al.* 2008). Two subsamples of 4 g each were collected from fresh soil sample. The first subsample was shaken immediately in 20 ml of 0.5 Mol potassium sulfate solution (K_2SO_4) for one hour, then centrifuged at 4500 rounds per minute for 10 minutes and thereafter filtered through Watman 595 filter paper. Soil extracts were analyzed using Analytik Jena Multi N/C 2100s analyzer (Analytik Jena AG) and the amounts of *Total organic carbon TOC (mg/g dry soil)* and *Total dissolved nitrogen TDN (mg/g dry soil)* were determined. The second subsample was fumigated with 50 ml of ethanol-free chloroform for 24 hours. After fumigation, the same procedure as for the first subsample was performed. To calculate *Microbial carbon MC (µg/g dry soil)* and *Microbial nitrogen MN (µg/g dry soil)*, the non-fumigated TOC and TDN were subtracted from the fumigated TOC and TDN. The *microbial CN* ratio

is obtained by dividing MC by MN. The results of MN and MC were corrected by dividing by extraction efficiency factors. A factor of 0.45 was used for MC (Vance *et al.* 1987) and a factor of 0.54 was used for MN (Brookes *et al.* 1985).

Microbial RNA extraction, reverse-transcription, library preparation and sequencing

In 19 of the 138 plots examined, microbial RNA extraction could not be performed due to unsuitable soil quality. Prior starting the following steps, great care was taken to work in a RNAse-free environment, notably by treating all object that would come in contact with the samples with RNaseZap, RNase decontamination solution (Sigma-Aldrich, MO, USA). The tubes containing the soil samples in Life Guard were unfrozen, centrifuged and the buffer removed. Circa 1 g of wet soil was removed with a spatula to be put in the tubes of the RNeasy PowerSoil Total RNA kit (Qiagen GmbH, Hilden, Germany). The manufacturers' protocol was strictly followed, apart for the disruption step, which was carried on a MP Biomedicals FastPrep-24 homogenizer for 30 s at 5 m/sec. The RNA was eluted in 50 ml of the buffer SR7, with the addition of 1 ml of recombinant RNasin ribonuclease inhibitor (Promega, Madison, WI, USA). Quantity and quality were roughly evaluated on an agarose gel. DNAs were digested with DNAse I (New England BioLabs, MA, USA) following the manufacturers' protocol. DNase was not inactivated, since we proceeded immediately to remove proteins and small RNAs using the Megaclear kit (Invitrogen, CA, USA), following the manufacturers' protocol. Samples were eluted with 50 ml of preheated elution buffer, and quantified using a Qubit 30 Fluorometer (Invitrogen, CA, USA) using 2 ml of the RNA in the high sensitivity buffer. Quality was estimated for some samples with a 2100 Bioanalyzer (Agilent, CA, USA) using the Prokaryote Total RNA Nano assay. Sample's whit a concentration below 11 ng/ml were precipitated with 1:10 volume of 5 M Ammonium Acetate and washed with ethanol, following the protocol of the Megaclear kit. Samples with a RNA concentration >10ng/µL were further processed. Libraries were prepared using the NEBNext Ultra II Directional RNA Library Prep Kit (New England Biolabs, Ipswich, MS, USA) with no removal of rRNAs or selection of mRNAs. The first strand cDNA synthesis incubation time at 42°C was increased from 15 to 50 min. To select fragments of cDNA (after the second strand synthesis) of 370-600 bp, the fragmentation time was reduced to 10 min. The library size selection option "400bp" was chosen and the final libraries were amplified with 12 PCR cycles. Libraries were sequenced with a single complete run of NovaSeq SP FC (Illumina Inc., San Diego, CA, US), length of paired reads of 250 bp at the Cologne Genomic Centre, University of Cologne, Germany.

Microbial sequence analyses: filtering and identification

The obtained forward and reverse reads were paired using FLASH (Magoč & Salzberg 2011), with the default parameters modified as follows: maximum allowed ratio between the number of mismatched base pairs and the overlap length of 0.10 (instead of 0.25, thus more stringent), minimum overlap of 15,

maximum overlap of 251. Reads were preprocessed with PRINSEQ (Schmieder & Edwards 2011), to exclude any reads with low-quality bases ("N"), minimum and maximum length of 250 and 450 bp, respectively, a mean minimum quality of 30, and deleting poly-Gs larger than 9 pb. The fragments of the SSU rRNA gene belonging to archaea, bacteria and eukaryotes were then selected using sortmeRNA (Kopylova *et al.* 2012), with the following Silva databases as references: silva-euk-18s-id95, silva-bac-16s-id90, silva-arc-16s-id95, silva-euk-28s-id98, silva-bac-23s-id98, silva-arc-23s-id98. Search was conducted with a e-value of 0.1 and keeping only the first match. The prokaryotes SSUs taxonomic identity was assessed using phyloFlash (Gruber-Vodicka *et al.* 2020) the provided database. Eukaryotic reads were identified to the genus level against the PR2 database (Guillou *et al.* 2013), using Blast + (Camacho *et al.* 2009) with a e-value of $1E^{-10}$ and keeping only one best hit. Unicellular eukaryotes were classified as protists, and additional information was added about lifestyle (free-living, plant or animal parasite) and nutrition (heterotroph, autotroph or mixotroph), whenever possible, using (Adl *et al.* 2012) as reference.

Data preparation

I used the VEGEDAZ program (Küchler 2020) to calculate *species richness* (number of identified species per plot), *Shannon index* (Shannon 2001), and *Shannon evenness index* (Pielou 1966; hereafter evenness index), as well as the following eight weighted indicator values for the vascular plants per plot: *Temperature Value, Continentality Value* and *Light Value, Moisture Value, Reaction Value* (soil acidity)*, Nutrient Value, Humus Value* and *Air content Value* (Landolt *et al.* 2010).

For the bacteria, protists and fungi I calculated *species richness*, *Shannon index* (Shannon 2001) and *evenness index* (Pielou 1966) using the R packages `dplyr` (Wickham *et al.* 2021), `tidyverse` (Wickham *et al.* 2019) and `vegan` (Oksanen *et al.* 2020). For all microbe groups, *species richness* is the number of genus-level mRNA fragments per soil sample.

Data analysis

All statistical analyses were performed using the software R version 4.1.1 (R Core Team 2021). To test whether plant and microbial diversity indices were determined by elevation and the snow gradient, I used linear mixed-effects models (LME) from the `lme4` package (Bates *et al.* 2015). I included elevation, the quadratic term of elevation (to account for non-linear effects), snow gradient (3 levels; Sn, Ed, 1 m) and the interaction of snow gradient with the linear and the quadratic term of elevation as fixed factors and *Transect* and *Site* as random factor. The significance of the variables was derived using likelihood-ratio tests comparing models with and without the factor of interest. I stepwise removed non-significant terms from the model so that the final model contained only significant terms. In case of a significant interaction, the individual contribution of the variable was determined by removing the interaction from the model. Model estimates and 95% confidence intervals were obtained

with the `effects` package (Fox & Weisberg 2019). For each term I extracted numerator degrees of freedom (NumDF) and denominator degrees of freedom (DenDF) with the package `lmerTest` (Kuznetsova *et al.* 2020) to present the model structure. For each model, graphical model validation was done to visually inspect for normality and independence of errors using the package `DHARMa` (Hartig 2021). Outliers in the residuals of the final models were removed if a value was four standard deviations above the mean. For the visualization of the final models the packages `ggplot2` (Wickham 2016) was used.

Pearson's correlation coefficients between diversity indices of microbes and plants were calculated method within the `Hmisc` package (Frank E & Charles 2021) and visualized in a matrix with `GGally` (Schloerke *et al.* 2021).

To understand the drivers of plant and microbial diversity, I conducted structural equation models (SEM) like Yuan *et al.* (2016) or Shigyo *et al.* (2019). The main questions of my SEM were whether elevation (a) and snow gradient (b) affect plants species richness and microbial diversity (species richness, Shannon index, evenness index) and whether the effects of elevation and snow gradient on microbial diversity can be indirectly explained by effects via plant species richness (c). I was also interested in whether plant and microbial diversity depended on soil pH (d) and whether it had an indirect effect on microbes via plant species richness (c). To answer these questions, I created a literature based hypothetical SEM (Figure 3) for plant and microbial diversity indices and their potential drivers (SEM variables), calculated correlation tests, and linear-mixed-effect models. In the first step of variable selection for the SEM I calculated Pearson's correlation coefficients for plant and microbial diversity indices and their potential drivers, which I determined through literature review. Then I used the significant variables ($p \leq 0.05$) as predictors in linear-mixed-effect models unless they were not correlated ($|r| < 0.7$; Table 7 - Table 10, Appendix), to determine which variables are included in the SEM. Subsequently I implemented the SEM statistically with the package `lavaan` (Rosseel *et al.* 2021), scaling all numeric variables to a mean of zero and a standard deviation of one (Grace 2006). For all residuals to be normally distributed, I used the natural logarithm (ln) of the pH. As I wanted to account for non-linear relationships between elevation and the other variables, I included elevation as a composite variable of the linear and the squared term of elevation. This composite variable can be interpreted as the effect of elevation as a whole, not distinguishing between the contribution of the linear and quadratic terms. Two interaction terms were included in the SEM: Treatment (snow gradient) and elevation respectively treatment and squared elevation, to test whether the effect of elevation on plant and microbial diversity depends on the snow gradient. I visually implemented the relationships between response and predictor variables in the final SEM by multiplying the estimates of each term by 20, which then represented the arrow thickness.

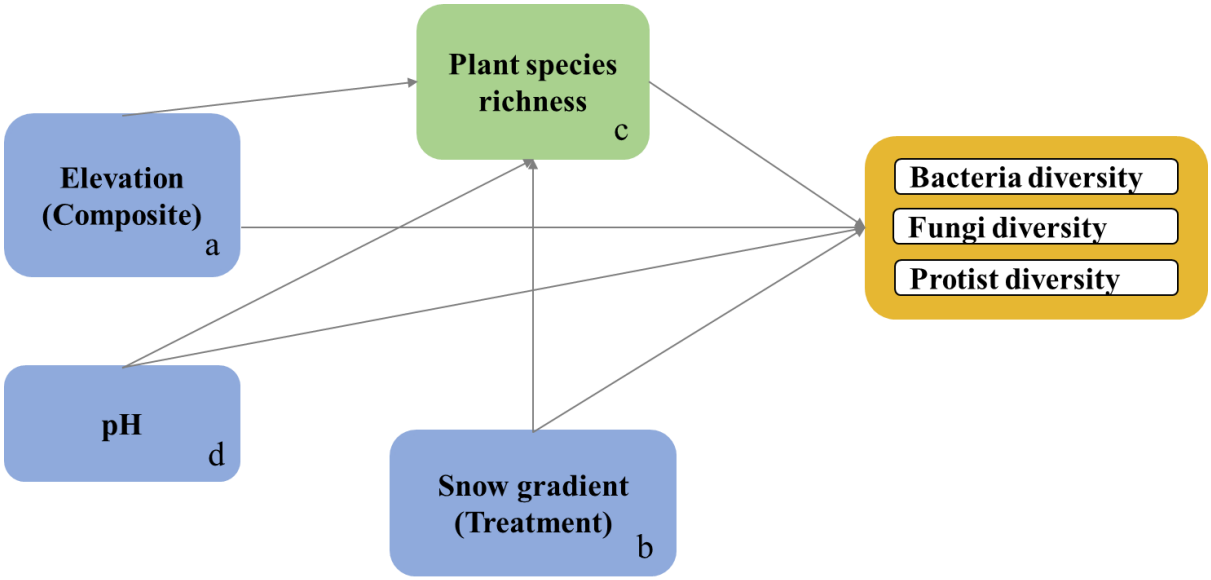

Figure 3 Hypothetical SEM shows possible direct (a, b, d) and indirect (c) drivers of plant species richness and microbial diversity indices (species richness, Shannon index, evenness index). Elevation and squared elevation (composite term), pH and snowmelt pattern (treatment) could affect microbial diversity direct or indirectly via plant species richness.

Results

In total, I identified 109 vascular plant species and three bryophyte species at species level with species richness at the plot level ranging from four to 29. Within the microbial groups, I found the most different RNA fragments at genus level for bacteria, namely 3649 and a count per plot between 878 and 1639. For fungi, the total is 1862 and the RNA pieces per plot ranges from 176 to 596. I identified 1737 different RNA segments for protists, with the range per plot being similar to fungi, ranging from 198 to 539. The soil pH was in the acidic range between 3.52 and 6.28 (more details Table 2 and Table 3, Appendix).

Effects of elevation and snow gradient on plant and microbial diversity indices

The fitted LME models for plant species richness showed a significant (p = 0.004) hump-shaped relationship with elevation (elevation and squared elevation term) and peaked at 2300 m a.s.l with 15 species, while it was lowest at 2800 m a.s.l with six species. The Shannon index and evenness index of the plants also showed unimodal patterns with elevation (Figure 4 a-c). The snow gradient did not explain any of the three plant diversity measures (Table 5, Appendix).

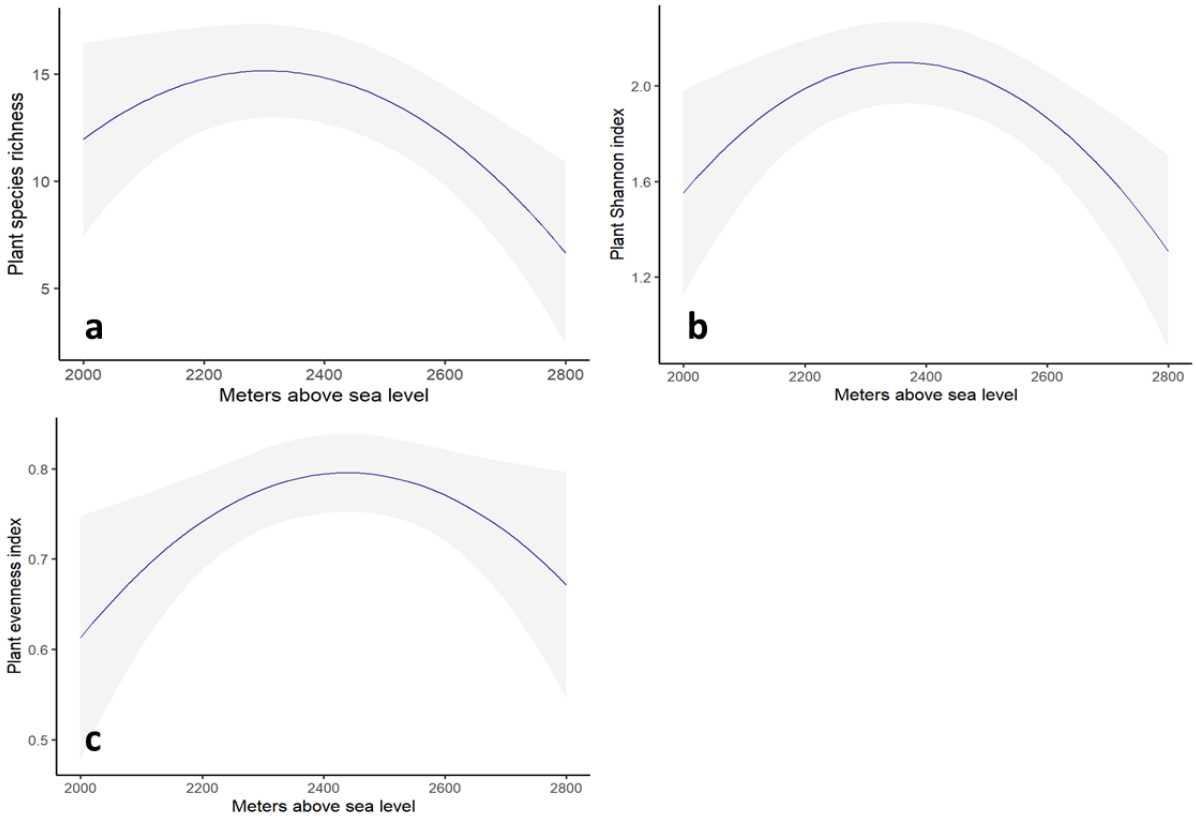

Figure 4 The fitted LME models for plant diversity indices (a: species richness, b: Shannon index; c: evenness index), show a significant unimodal relationship along the elevation gradient with the highest diversity at middle elevations. The blue line showy the fitted index, the gray area the standard deviation.

All three indices of bacterial diversity showed a unimodal relationship with elevation (Figure 5; all *p*-values Table 5, Appendix) in the fitted LME models. The interaction of elevation and snow gradient significantly affected species richness (Figure 5a), but not Shannon index and evenness index. On these indices the term of elevation and squared elevation showed significant impacts (Figure 5b-c). The Sn plots, which were still under a snow patch when sampled, harbored the largest species richness of 1140 species at 2320 m a.s.l. The fewest species (1049 RNA fragments) were located in a snow-free (1 m) plot at 2800 m a.s.l.

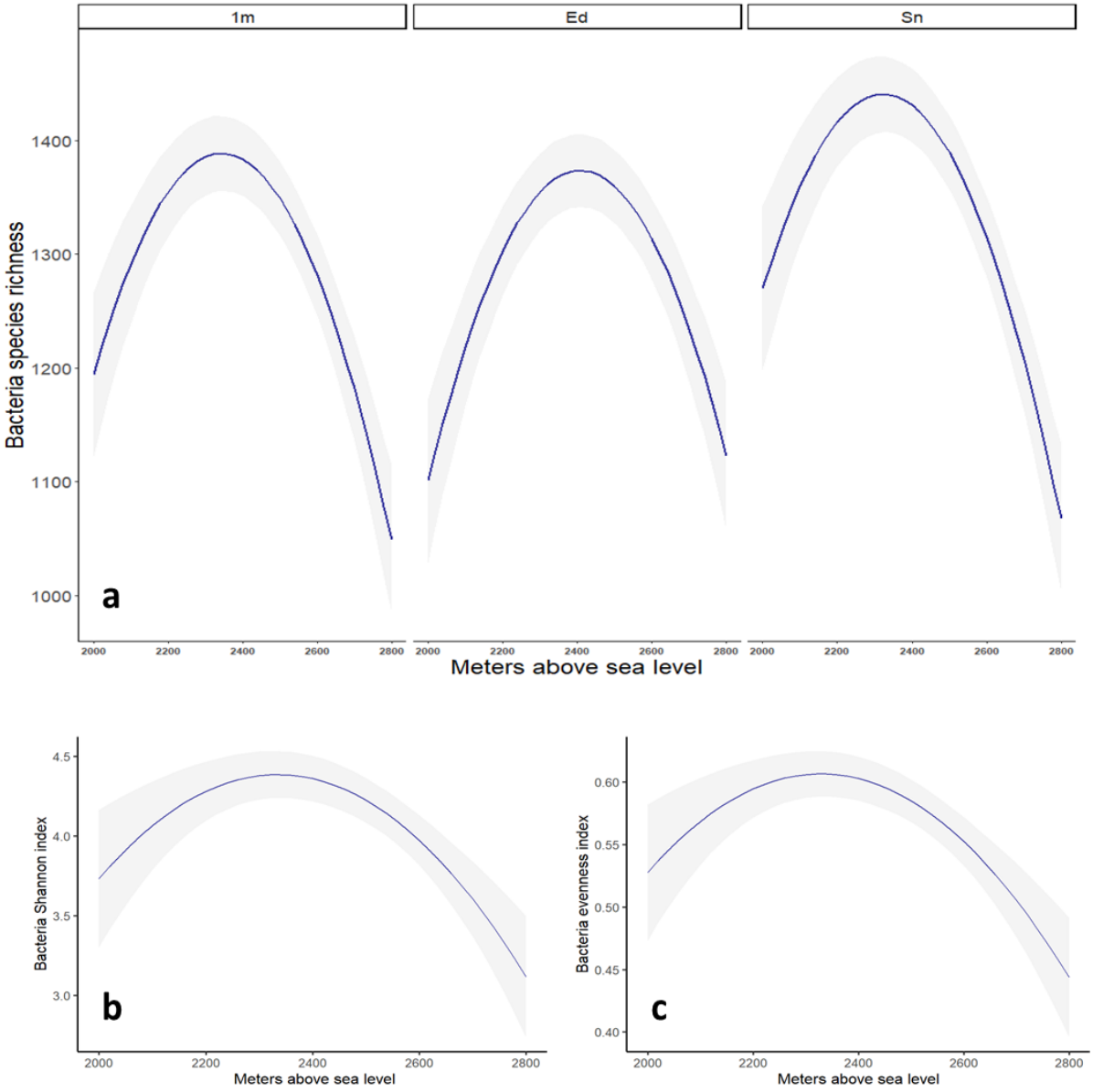

Figure 5 The fitted LME models for bacteria diversity indices (a: species richness, b: Shannon index; c: evenness index), show a significant unimodal relationship along the elevation gradient with the highest diversity at middle elevations. Only the species richness could be explained by the interaction of elevation and snow gradient. The blue line shows the fitted index, the gray area the standard deviation.

In interaction with snow gradient, the fungal species richness decreased in the snow-free (1 m) and snow covered (Sn) plots along the elevation gradient whereas it increased in the Ed plots (Figure 6a). The Shannon index and evenness index of fungi were not significantly affected by either elevation or snow gradient (all *p*-values Table 5, Appendix). The most (426 at 2000 m a.s.l.) and least (304 at 2800 m a.s.l.) RNA fragments at genus level were identified in the Sn plots, which means that these plots cover the widest range of fungal species richness. The elevation gradient had no effect on protist diversity (Figure 6b). Only the snow gradient alone had a significant effect on species richness of protists, with this being highest (363 RNA fragments) in the Sn plots, as it was for bacteria and fungi (all *p*-values Table 5, Appendix).

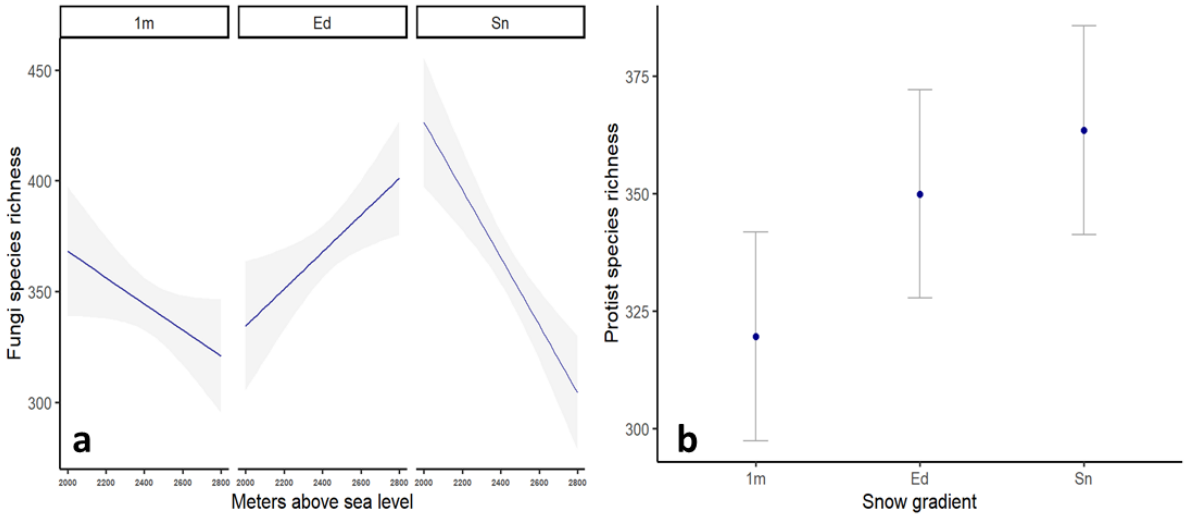

Figure 6 Fitted LME models for fungal species richness (a) and protist species richness (b). The interaction of elevation and snow gradient affects fungal species richness while protist species richness can only be explained by snow gradient. The blue line respectively dot for the protists shows the fitted species richness, and the gray area respectively bar shows the standard deviation.

Correlation between plant and microbial diversity indices

Species richness of plants was significantly positively correlated with species richness, Shannon index, and evenness index of bacteria (all at least $p < 0.005$). For the plant evenness index, on the other hand, I did not observe any significant correlations with the microbial diversity indices. I also found positive correlations between the Shannon index of plants and all three indices of bacterial diversity, although they were less strong than when plant species richness was considered (Table 1). There was no correlation between the diversity of plants and fungi. These correlations were all non-significant and showed a positive or negative relationship (all *r*- and *p*- Values Table 6 and Figure 10, Appendix). There was no correlation between plant and protist diversity indices in my data.

Table 1 Pearson correlation coefficients (r) showed significant (p < 0.05) positive relationships between plant species richness respectively Shannon index and all bacteria diversity indices.

Index I	**Index II**	***r***	***p***
Plant species richness	Bacteria Shannon index	0.368	**<0.001**
Plant species richness	Bacteria evenness index	0.372	**<0.001**
Plant species richness	Bacteria species richness	0.254	**0.005**
Plant Shannon index	Bacteria Shannon index	0.308	**0.001**
Plant Shannon index	Bacteria evenness index	0.314	**0.001**
Plant Shannon index	Bacteria species richness	0.196	**0.032**

(In-) direct effects on microbial diversity indices

The correlation tests as the first step of variable selection for SEM showed that pH had a significant positive effect on plant evenness index (p= 0.019), bacteria species richness (p= 0.035), bacteria Shannon index (p= 0.011), bacteria evenness index (p= 0.016), protist species richness (p= 0.009) and a negative effect on fungi species richness (p= 0.029) (Table 7- Table 10, Appendix).

In the second step of SEM variable selection, the LME models with the significant uncorrelated ($|r| <$ 0.7) variables from the correlation tests showed that pH explained the Shannon index (p= 0.02) and evenness index (p= 0.023) of the plants. The Shannon index (p= 0.001) and evenness index (p= 0.001) of the bacteria could also be explained by pH. For the diversity indices of fungi and protists, pH showed no significance (Table 11 Appendix).

The SEM for microbial species richness (*test statistic*= 16.12, *df*=11, p= 0.137) showed no indirect effects of elevation and snow gradient on the species richness of all microbe groups (Figure 7). The composite term of elevation (elevation and elevation squared) had a significant negative effect on the species richness of plants (p< 0.001) and bacteria (p< 0.001). The ln(pH) had a direct positive effect on the species richness of bacteria (p= 0.013) and protists (p= 0.007), but negative effect on fungal species richness (p= 0.014). The contribution of all variables included can be found in Table 12 in the Appendix.

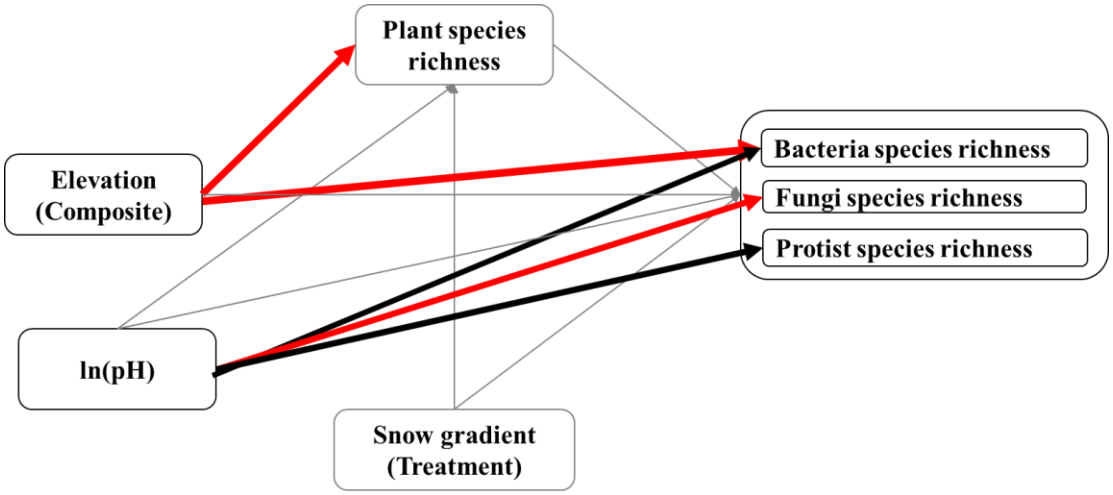

Figure 7 Structural Equation Model (SEM) showed direction and strength (arrow thickness) of expected (grey) and calculated (black: positive; red: negative) effects of the composite term of elevation (elevation and elevation squared), snow gradient and ln(pH) on plant and microbial species richness. Bacterial species richness was directly negative effected by elevation. The ln(pH) had a direct positive (bacteria, protist) or negative (fungi) effect on microbial species richness.

The SEM for microbial Shannon index (*test statistic*=10.628, *df*=11, *p*=0.475) showed only direct effects. The bacterial Shannon index was negatively effected by the composite term of elevation (elevation and squared elevation; $p < 0.001$) and positively effected ($p < 0.001$) by the ln(pH). No predictor used in the model showed an effect on the Shannon index of fungi or protists (Figure 8). The contribution of all variables included can be found in Table 13 in the Appendix.

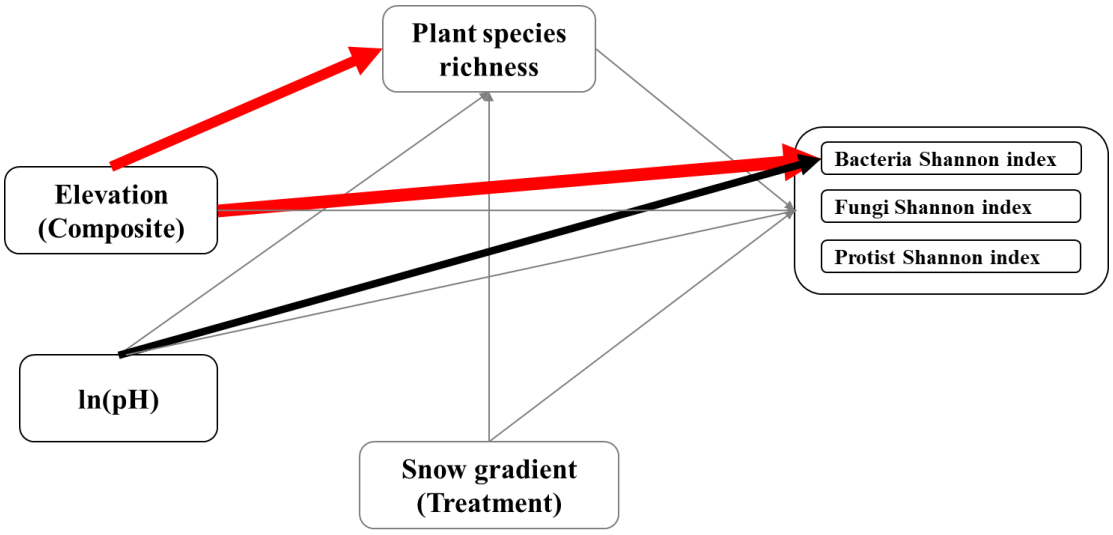

Figure 8 Structural Equation Model (SEM) showed direction and strength (arrow thickness) of expected (grey) and calculated (black: positive; red: negative) effects of the composite term of elevation (elevation and elevation squared), snow gradient and ln(pH) on plant species richness and microbial Shannon indices. There was no indirect effect of elevation, snow gradient or ln(pH) via plant species richness on Shannon microbial indices. Only the Shannon index of bacteria was effected by elevation (negative) and ln(pH) (positive).

As for the two previous SEM, the microbial evenness indices (*test statistic*= 9.442, *df*=11, *p*= 0.581) were only directly influenced by the predictors (Figure 9). The composite term of elevation (elevation and elevation squared) had a negative effect on the bacteria evenness index (*p*< 0.001) and plant species richness (p< 0.001), but a positive effect on fungal evenness index (*p*= 0.034). The evenness index of the bacteria was also positively influenced by the ln(pH) (p< 0.001). The contribution of all variables included can be found in Table 14 in the Appendix.

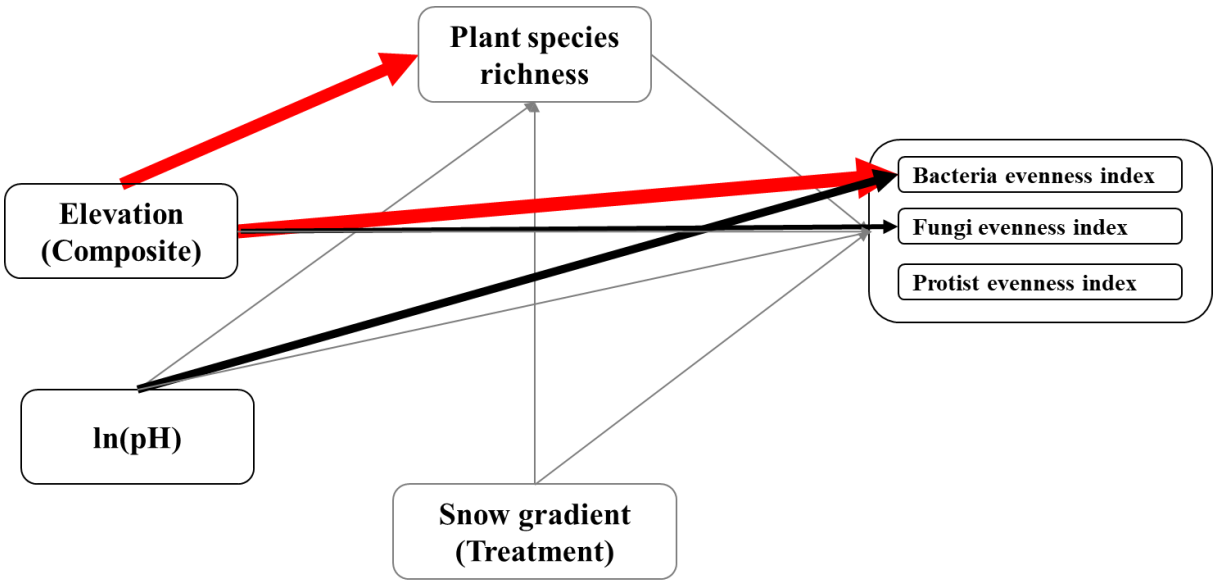

Figure 9 Structural Equation Model (SEM) showed direction and strength (arrow thickness) of expected (grey) and calculated (black: positive; red: negative) effects of the composite term of elevation (elevation and elevation squared), snow gradient and ln(pH) on plant species richness and microbial evenness index. Evenness index of bacteria is positively effected by ln(pH) but negatively effected by elevation. In contrast, the fungal evenness index showed a positive influence of elevation.

All three SEMs showed only direct effects of elevation, snow gradient and ln(pH) on all microbial diversity indices (species richness, Shannon index, evenness index). The composite term of elevation had a negative impact on all diversity indices of bacteria, but a positive effect on the evenness index of fungi. Snow gradient had no effect on either plant or microbial diversity. The ln(pH) was the only predictor that influenced all microbial groups, namely in the SEM for species richness. It had a positive effect on bacteria and protists, but a negative effect on fungi.

Discussion

Inconsistent patterns of plant and microbial diversity along elevation and snow gradient

My hypothesis was confirmed that plant diversity indices followed a unimodal pattern along the elevation gradient, resulting in the highest diversity occurring at middle elevations at 2300 m a.s.l. These findings are consistent with a number of other studies, along lower (Yu 2004; Bruun *et al.* 2006; Grytnes *et al.* 2006), higher (Namgail *et al.* 2012) and equidistant (Bryant *et al.* 2008) gradients as in my thesis, whereas in these studies the broader grain size was considered. Other studies found an effect of snow accumulation on plant diversity (Elumeeva *et al.* 2013; Winkler *et al.* 2019), I did not find an impact of snow gradient their diversity indices, as anticipated. It was probably because the snow gradient in my study is so small-scale, that there was no difference in plant diversity in it.

As with plants, I expected bacteria to have the highest diversity at intermediate elevations, and an additional positive or negative effect of snow gradient. For species richness, this conjecture was true because it showed a significant relationship with the interaction of elevation and snow gradient, with this effect being highest in the snow plots (Sn). My results are in line with the findings of Peay *et al.* (2017) and Nottingham *et al.* (2018), which showed the highest bacterial diversity at mid elevations in humid biomes, whereas the investigated gradients were longer than in my thesis. A possible explanation for this peak is the intermediate stress hypothesis (Huston 1994): Beyond the tree line, environmental conditions are less favorable for bacteria, resulting in less competition and greater species richness. At the highest elevation, environmental conditions are so extreme that diversity decreases again (Singh *et al.* 2012). The highest species richness in the snow covered plots can be explained by seasonal variations in microbial biomass (Schmidt *et al.* 2015), which peaks under early spring snowpack (Schadt *et al.* 2003; Ley *et al.* 2004; Lipson & Schmidt 2004). There, the highest sustained soil moisture is reached (Ley *et al.* 2004; Monson *et al.* 2006; Freeman *et al.* 2009), which limits microbial activity (King *et al.* 2008). This fits with the findings of the Bachelor's thesis of Schwaller (2020), which demonstrated in the same study area that the highest microbial activity is in the snow covered plots.

Regarding the patterns of fungal diversity, my hypothesis was partially confirmed, as I was only able to detect the expected decrease in diversity with increasing elevation for species richness in the snow free and snow covered plots. In the plots at the edge of the snow patch (Ed), in contrast, it increased, highlighting the influence of the snow gradient on fungal diversity. These inconsistent patterns, fit with the studies conducted so far: Although the studies by Ni *et al.* (2018), Nottingham *et al.* (2018) and Shen *et al.* (2020) were conducted in different biomes and the transects were of different lengths as in my thesis, they confirmed a decrease in fungal diversity along the elevational gradient, whereas Peay *et al.* (2017) found an increase. The taxonomic level at which diversity patterns are examined is considered a possible rationale for these differences (Yeh *et al.* 2018), with them being more apparent

at lower levels (Looby *et al.* 2016). Therefore, when comparing my results, it must be considered that I calculated the diversity indices of the microbes at the genus level, whereas the results of the cited studies refer to the phylum level. In addition, it is likely that niche differentiation occurs along the elevational gradient within different taxa (Prosser *et al.* 2007) and that other environmental factors interact with elevation to influence fungal diversity (Peay *et al.* 2017).

Contrary to my hypothesis, I was unable to demonstrate an effect of elevational gradient on protist diversity, which was also the finding of Grossmann *et al.* (2016) or Teittinen *et al.* (2016) who carried out their studies in alpine and subarctic biomes, respectively. Other studies, however, demonstrated an effect of elevation on protist diversity (Seppey *et al.* 2019; Mazel *et al.* 2021) in alpine biomes. Only the snow gradient showed a significant effect on species richness, which is highest in the snow covered plots and lowest in the snow free plots. Since the snow gradient represents the soil moisture which is an important driver (Zinger *et al.* 2009; Bates *et al.* 2013), the condition in the Sn plots seem to be most favorable. That could be because the highest sustained soil moisture is under early spring snow packs (Ley *et al.* 2004; Monson *et al.* 2006; Freeman *et al.* 2009).

Diversity indices correlate only between plants and bacteria

I demonstrated a strong positive correlation between plant and bacterial alpha diversity indices, which is in line with Nottingham *et al.* (2018), Porazinska *et al.* (2018) and Sun *et al.* (2019). Contrary to my expectations, this pattern did not occur for fungi, which was also found in the studies of Prober *et al.* (2014) or Zverev *et al.* (2021). That correlations only occur between plant and bacterial diversity may indicate that biotic interactions between these groups are stronger than between plants and fungi (Nottingham *et al.* 2018), due to plant carbon inputs (Lange *et al.* 2015) and alteration of microhabitats (Prober *et al.* 2014). The correlation between plant and fungal diversity indices is strongest when they can be explained by the same predictors (Yang *et al.* 2017). I have shown that the species richness of plants can be explained by elevation and that of fungi by the interaction between elevation and snow gradient. This fact may be one reason why fungal diversity is not correlated with plant diversity in my data. The general inconsistencies regarding the correlation between plant and microbial diversity are explained by Prober *et al.* (2014) with the different spatial scales with which the studies are conducted. At small scales, patterns are visible, which disappear at larger scales as they become masked by environmental factors (Tedersoo *et al.* 2014). Furthermore, it should be emphasized that microbe sampling in spring, as in my case, is only a snapshot of their community diversity. Since the diversity of microbes shows seasonal variations (Lazzaro *et al.* 2015), sampling in summer could lead to different results.

No indirect effects of elevation, snow gradient and pH on microbe diversity

To disentangle the direct and indirect effects of elevation, snow gradient and pH on microbial diversity I calculated SEMs and expected, that all mentioned environment parameters would have a direct and indirect impact via plant species richness on the diversity indices of microbes. The SEMs showed that there are no indirect impacts of elevation, snow gradient and pH on microbial diversity and that the effects differ by index and by microbe group.

It is surprising that only direct effects of the elevation gradient are visible in my data, because many environmental factors are associated with it and change along the gradient (Fierer *et al.* 2011). Presumably, indirect effects would have been visible if other environmental factors, for example total carbon or total nitrogen (Ni *et al.* 2018; Nottingham *et al.* 2018; Shen *et al.* 2020), had been in the model in addition to plant species richness. The elevation gradient showed a negative effect on all indices of bacteria and on species richness of plants. On the other hand, the fungal evenness index was slightly positively explained by elevation, which is in line with Peay *et al.* (2017). The direct effects of elevation on bacteria (Nottingham *et al.* 2018), fungal (Shen *et al.* 2020) and protist (Seppey *et al.* 2019) diversity are well documented compared to the indirect impact. In contrast to my results, Tang *et al.* (2020) were able to determine a direct and indirect effect of elevation on bacterial diversity, although it was not plant species richness that was involved in SEM, but rather the degree of plant cover. Shigyo *et al.* (2019) found that elevation negatively affects bacterial diversity directly and indirectly through plant functional diversity (C/N leaf ratio), with results differing slightly between the depth of soil layers. Since taxonomic plant diversity did not affect bacterial diversity in their study, this suggests the importance of the C/N ratio of plant communities as a driver along elevational gradients.

Although the snow gradient, and the soil moisture it represents, is considered as driver of microbial diversity (Zinger *et al.* 2009; Bates *et al.* 2013), it did not have a significant effect in my SEMs. It is possible that the effect is overridden by the predictors elevation and pH because their influence on the diversity indices is mostly highly significant (Table 12-Table 14, Appendix).

In my SEMs, pH was positively associated with all diversity indices of bacteria and species richness of protists, and negatively associated with species richness of fungi. It is not surprising that all microbial groups are influenced by pH, as it is considered an important driver along with elevation (Shen *et al.* 2013, 2019, 2020; Wang *et al.* 2015). My results of a positive effect of pH on bacteria diversity indices are in line with the study of Tripathi *et al.* (2012). In contrast to my findings, Ping *et al.* (2017) and Shen *et al.* (2014) found a positive relationship between pH and fungal diversity. For protist diversity Malard *et al.* (2021) demonstrated a hump-shaped relationship with pH while I demonstrated a positive relationship. Probably there was no indirect impact of pH on plant species richness, because of the narrow acidic range (3.52 to 6.28) in my study area.

Conclusion and outlook

With this thesis, I was able to demonstrate that elevation and snow gradient differentially affect plant and microbial diversity indices. Furthermore, I found positive correlations between plant and bacterial diversity indices. By conducting structural equation models, I showed that there were no indirect effects of elevation and snow gradient, as well as pH, trough plant species richness on microbial diversity indices. In comparison with previously conducted studies, the inconsistent diversity patterns among microbes stand out. This may be due to the fact that they were conducted on different scales (Schmidt *et al.* 2015), geological substrates (Singh *et al.* 2012) and transect lengths (Shen *et al.* 2020). Although I could not explain microbial diversity by plant diversity, it cannot be ruled out that this is not possible in principle. Further research is needed to determine these relationships: Additional indices could be included to characterize microbial diversity, such as Operational Taxonomic Unit OTU as in Barberán *et al.* (2015), Yang *et al.* (2017) and Duan *et al.* (2021) or Chao1 as in Shen *et al.* (2014), Siles & Margesin (2017) and Ni *et al.* (2018). Another extension would be to compare community composition and use Sörensen similarity index as Kivlin *et al.* (2017) did. It would be interesting to analyze the diversity indices at different systematic levels to reveal patterns of individual families or functional groups within bacteria, fungi, and protists. But at too coarse level, it is quite possible that certain patterns will be lost (Yeh *et al.* 2018). For plants, functional groups as de Mesquita *et al.* (2017) or plant traits as Delgado-Baquerizo *et al.* (2018) could also be used as predictors of microbial diversity. In conclusion, it can be said that research on the plant-microbe relationship still has great potential, as knowledge gaps and inconsistent findings persist.

Acknowledgement

I received a lot of support in the work process of my master thesis. Therefore, I would like to thank the following people:

A big thanks goes to **Christian Rixen**, who advised me on methodological, practical, and analytical issues and made sure that the focus of the work was not lost. Thanks also for the support during the fieldwork and the tricks on how to distinguish vegetative alpine *Poaceae*.

Thanks to **Jürgen Dengler** and **Daniel Hepenstrick** for having taken time for meetings and for proofreading my thesis.

Anne Kempel and **Alessandra Bottero** took time for my statistical questions and showed me that working with R can actually be fun. Thank you for this insight and your support.

Thank you, **Anna Maria Fiore Donno**, for answering my microbiology questions, processing your data, and sharing them with me.

Field work is better in pairs! Thank you, **Alex**, **Agathe, Manu** and **Vera** for spending rainy, windy, stormy but also sunny hours with me on the mountain.

The **WSL Institute of Snow and Avalanche Research SLF** enabled me to stay in Davos for six months, which facilitated the field and office work enormously. Many thanks for this!

Bibliography

Adl, S.M., Simpson, A.G.B., Lane, C.E., Lukeš, J., Bass, D., Bowser, S.S., Brown, M.W., Burki, F., Dunthorn, M. & (…) & Spiegel, F.W. (2012). The revised classification of eukaryotes. *The Journal of Eukaryotic Microbiology*, 59, 429–493.

Baniya, C., Solhøy, T., Gauslaa, Y. & Palmer, M. (2012). Richness and Composition of Vascular Plants and Cryptogams along a High Elevational Gradient on Buddha Mountain, Central Tibet. *Folia Geobotanica.*, 47, 135–151.

Barberán, A., McGuire, K.L., Wolf, J.A., Jones, F.A., Wright, S.J., Turner, B.L., Essene, A., Hubbell, S.P., Faircloth, B.C. & Fierer, N. (2015). Relating belowground microbial composition to the taxonomic, phylogenetic, and functional trait distributions of trees in a tropical forest. *Ecology Letters*, 18, 1397–1405.

Bässler, C., Cadotte, M.W., Beudert, B., Heibl, C., Blaschke, M., Bradtka, J.H., Langbehn, T., Werth, S. & Müller, J. (2016). Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. *Ecography*, 39, 689–698.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.

Bates, S.T., Clemente, J.C., Flores, G.E., Walters, W.A., Parfrey, L.W., Knight, R. & Fierer, N. (2013). Global biogeography of highly diverse protistan communities in soil. *The ISME Journal,* 7, 652–659.

Baumann, E., Weiser, F., Chiarucci, A., Jentsch, A. & Dengler, J. (2016). Diversity and functional composition of alpine grasslands along an elevational transect in the Gran Paradiso National Park (NW Italy). *TUEXENIA*, 36, 337–358.

Boenigk, J., Wodniok, S., Bock, C., Beisser, D., Hempel, C., Grossmann, L., Lange, A. & Jensen, M. (2018). Geographic distance and mountain ranges structure freshwater protist communities on a European scale. *Metabarcoding and Metagenomics*, 2, 1-14.

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 Biology and Biochemistry*, 17, 837–842.

Broughton, L.C. & Gross, K.L. (2000). Patterns of diversity in plant and soil microbial communities along a productivity gradient in a Michigan old-field. *Oecologia*, 125, 420–427.

Bruun, H., Moen, J., Virtanen, R., Grytnes, J.A., Oksanen, L. & Angerbjörn, A. (2006). Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*, 17, 37–46.

Bryant, J.A., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J. & Green, J.L. (2008). Microbes on mountainsides: Contrasting elevational patterns of bacterial and plant diversity. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, 105, 11505–11511.

Buckeridge, K.M. & Grogan, P. (2010). Deepened snow increases late thaw biogeochemical pulses in mesic low arctic tundra. *Biogeochemistry*, 101, 105–121.

Bundesamt für Landestopografie. (2022). *Vereinfachte Bodennutzung*. *geo.admin.ch*. Available at: https://map.geo.admin.ch/?lang=de&topic=ech&bgLayer=ch.swisstopo.pixelkarte-farbe&layers=ch.swisstopo.zeitreihen,ch.bfs.gebaeude_wohnungs_register,ch.bav.haltestellen-oev,ch.swisstopo.swisstlm3d-wanderwege,ch.astra.wanderland-sperrungen_umleitungen,ch.bfs.arealstatistik-hintergrund&layers_opacity=1,1,1,0.8,0.8,0.75&layers_visibility=false,false,false,false,false,t

rue&layers_timestamp=18641231,,,,,&E=2782712.03&N=1183356.29&zoom=5. Last accessed 9 January 2022.

Bundesamt für Landestopografie. (2022). *Vereinfachte Bodennutzung*. *geo.admin.ch*. Available at: https://map.geo.admin.ch/?lang=de&topic=ech&bgLayer=ch.swisstopo.pixelkarte-farbe&layers=ch.swisstopo.zeitreihen,ch.bfs.gebaeude_wohnungs_register,ch.bav.haltestellen-oev,ch.swisstopo.swisstlm3d-wanderwege,ch.astra.wanderland-sperrungen_umleitungen,ch.bfs.arealstatistik-hintergrund&layers_opacity=1,1,1,0.8,0.8,0.75&layers_visibility=false,false,false,false,false,true&layers_timestamp=18641231,,,,,&E=2782712.03&N=1183356.29&zoom=5. Last accessed 9 January 2022.

Bundesamt für Landestopografie. (2021a). *Geologie 500*. *geo.admin.ch*. Available at: https://map.geo.admin.ch/?lang=de&topic=ech&bgLayer=ch.swisstopo.pixelkarte-farbe&layers=ch.bav.haltestellen-oev,ch.swisstopo.swisstlm3d-wanderwege,ch.bafu.biogeographische_regionen,ch.bafu.permafrost,ch.blw.bodeneignung-naehrstoffspeichervermoegen,ch.bafu.flora-weltensutter_atlas,ch.bafu.wald-wasserverfuegbarkeit_pflanzen,ch.bafu.landesforstinventar-wirtschaftsregionen,ch.swisstopo.geologie-geocover.metadata,ch.swisstopo.geologie-generalkarte-ggk200.metadata,ch.swisstopo.geologie-geologischer_atlas.metadata,ch.swisstopo.geologie-geocover,ch.swisstopo.geologie-gisgeol-flaechen-10to100km2,ch.swisstopo.geologie-geologische_karte&layers_opacity=1,0.8,0.75,0.75,0.75,0.75,0.7,1,0.75,1,1,1,0.75,0.5&layers_visibility=false,false,false,false,false,false,false,false,false,false,false,false,false,true&E=2792489.80&N=1179154.33&zoom=7&catalogNodes=532,533&layers_timestamp=,,,,,,2018,,,,,,. Last accessed 20 October 2021.

Bundesamt für Landestopografie. (2021b). *Web Map Tiling Services WMTS: Verfügbare Dienste und Daten*. *Geoadminch - Geoportal Bundes*. Available at: https://www.geo.admin.ch/de/geo-dienstleistungen/geodienste/darstellungsdienste-webmapping-webgis-anwendungen/web-map-tiling-services-wmts.html. Last accessed 15 December 2021.

Bundesamt für Meteorologie und Klimatologie. (2021). *Klimadiagramme und Normwerte pro Station*. *Klima-Normwerte*. Available at: https://www.meteoschweiz.admin.ch/home/klima/schweizer-klima-im-detail/klima-normwerte/klimadiagramme-und-normwerte-pro-station.html?station=wfj. Last accessed 20 October 2021.

Burki, F., Sandin, M.M. & Jamy, M. (2021). Diversity and ecology of protists revealed by metabarcoding. Current Biology, 31, R1267–R1280.

Camacho, C., Coulouris, G., Avagyan, V., Ma, N., Papadopoulos, J., Bealer, K. & Madden, T.L. (2009). BLAST+: architecture and applications. *BMC Bioinformatics*, 10, 1-9.

Carney, K.M., Hungate, B.A., Drake, B.G. & Megonigal, J.P. (2007). Altered soil microbial community at elevated CO_2 leads to loss of soil carbon. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, 104, 4990–4995.

Caron, D.A., Alexander, H., Allen, A.E., Archibald, J.M., Armbrust, E.V., Bachy, C., Bell, C.J., Bharti, A., Dyhrman, S.T. & (…) & Worden, A.Z. (2017). Probing the evolution, ecology and physiology of marine protists using transcriptomics. *Nat. Rev. Microbiol.*, 15, 6–20.

Chong, C., Pearce, D., Convey, P., Tan, G.Y., Wong, R. & Tan, I.K.-P. (2010). High levels of spatial heterogeneity in the biodiversity of soil prokaryotes on Signy Island, Antarctica. *Soil Biology & Biochemistry*, 42, 601-610.

Chu, H., Fierer, N., Lauber, C.L., Caporaso, J.G., Knight, R. & Grogan, P. (2010). Soil bacterial diversity in the Arctic is not fundamentally different from that found in other biomes. *Environ Microbiol*, 12, 2998–3006.

Dassen, S., Cortois, R., Martens, H., Hollander, M., Kowalchuk, G., Putten, W. & Deyn, G.B. (2017). Differential responses of soil bacteria, fungi, archaea and protists to plant species richness and plant functional group identity. *Molecular Ecology.*, 26, 1-14.

De Deyn, G.B. & Van der Putten, W.H. (2005). Linking aboveground and belowground diversity. *Trends in Ecology & Evolution*, 20, 625–633.

Delgado-Baquerizo, M., Fry, E.L., Eldridge, D.J., de Vries, F.T., Manning, P., Hamonts, K., Kattge, J., Boenisch, G., Singh, B.K. & Bardgett, R.D. (2018). Plant attributes explain the distribution of soil microbial communities in two contrasting regions of the globe. *New Phytologist*, 219, 574–587.

Dembicz, I., Velev, N., Boch, S., Janišová, M., Palpurina, S., Pedashenko, H., Vassilev, K. & Dengler, J. (2020). Drivers of plant diversity in Bulgarian dry grasslands vary across spatial scales and functional-taxonomic groups. *Journal of Vegetation Science*, 32, 1-14.

Dengler, J., Boch, S., Filibeck, G., Chiarucci, A., Dembicz, I., Guarino, R., Henneberg, B., Janišová, M., Marcenò, C. & (…) & Biurrun, I. (2016). Assessing plant diversity and composition in grasslands across spatial scales: the standardised EDGG sampling methodology. *Bulletin of the Eurasian Dry Grassland Group*, 32, 13–30.

Duan, Y., Lian, J., Lilong, W., Wang, X., Luo, Y., Wang, W., Wu, F., Zhao, J., Ding, Y. & (…) & Li, Y. (2021). Variation in Soil Microbial Communities Along an Elevational Gradient in Alpine Meadows of the Qilian Mountains, China. *Frontiers in Microbiology*, 12, 1-14.

Dunbar, J., Barns, S.M., Ticknor, L.O. & Kuske, C.R. (2002). Empirical and Theoretical Bacterial Diversity in Four Arizona Soils. *Applied and Environmental Microbiology,* 68, 3035-3045.

Echeverría-Londoño, S., Enquist, B.J., Neves, D.M., Violle, C., Boyle, B., Kraft, N.J.B., Maitner, B.S., McGill , B., Peet, R.K. & (…) & Kerkhoff , A.J. (2018). Plant Functional Diversity and the Biogeography of Biomes in North and South America. *Frontiers in Ecology and Evolution*, 6, 1-12.

Eisenhauer, N., Milcu, A., Sabais, A.C.W., Bessler, H., Brenner, J., Engels, C., Klarner, B., Maraun, M., Partsch, S. & (…) & Scheu, S. (2011). Plant Diversity Surpasses Plant Functional Groups and Plant Productivity as Driver of Soil Biota in the Long Term. *PLOS ONE*, 6, 1-11.

Elumeeva, T., Onipchenko, V., Egorov, A.V., Khubiev, A.B., Tekeev, D.K., Soudzilovskaia, N. & Cornelissen, J. (2013). Long-term vegetation dynamic in the Northwestern Caucasus: Which communities are more affected by upward shifts of plant species? *Alpine Botany*, 123, 77–85.

Ernakovich, J.G., Hopping, K.A., Berdanier, A.B., Simpson, R.T., Kachergis, E.J., Steltzer, H. & Wallenstein, M.D. (2014). Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology*, 20, 3256–3269.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G. & (…) & Turner, J.R.G. (2009). Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, 36, 132–147.

Fierer, N. (2017). Embracing the unknown: disentangling the complexities of the soil microbiome. *Nature Reviews Microbiology*, 15, 579–590.

Fierer, N., McCain, C.M., Meir, P., Zimmermann, M., Rapp, J.M., Silman, M.R. & Knight, R. (2011). Microbes do not follow the elevational diversity patterns of plants and animals. *Ecology*, 92, 797–804.

Fierer, N. & Jackson, R.B. (2006). The diversity and biogeography of soil bacterial communities. *PNAS Proceedings of the National Academy of Sciences of the United States of America*, 103, 626–631.

Fiore-Donno, A.M., Richter-Heitmann, T., Degrune, F., Dumack, K., Regan, K.M., Marhan, S., *et al.* (2019). Functional Traits and Spatio-Temporal Structure of a Major Group of Soil Protists (Rhizaria: Cercozoa) in a Temperate Grassland. *Frontiers in Microbiology*, 10, 1-12.

Fox, J. & Weisberg, S. (2019). *An R Companion to Applied Regression*. 3rd edn. Sage, Thousand Oaks CA.

Frank E, H. & Charles, D. (2021). *Hmisc: Harrell Miscellaneous*. R package version 4.6-0.

Freeman, K., Pescador, M., Reed, S., Costello, E., Robeson, M. & Schmidt, S. (2009). Soil CO_2 flux and photoautotrophic community composition in high-elevation, "barren" soil. *Environmental microbiology*, 11, 674–86.

Gao, C., Shi, N.-N., Liu, Y.-X., Peay, K.G., Zheng, Y., Ding, Q., Mi, X.-C., Ma, G.-P., Wubet, T. & (…) & Guo, L.-D- (2013). Host plant genus-level diversity is the best predictor of ectomycorrhizal fungal diversity in a Chinese subtropical forest. *Molecular Ecology*, 22, 3403–3414.

Giorgi, F., Hurrell, J.W., Marinucci, M.R. & Beniston, M. (1997). Elevation Dependency of the Surface Climate Change Signal: A Model Study. *Journal of Climate*, 10, 288–296.

Goberna, M., Navarro-Cano, J.A. & Verdú, M. (2016). Opposing phylogenetic diversity gradients of plant and soil bacterial communities. *Proceedings of the Royal Society B: Biological Sciences*, 283, 1-6.

Grace, J.B. (2006). *Structural Equation Modeling and Natural Systems*. Cambridge University Press, Cambridge.

Griffiths, R.I., Thomson, B.C., James, P., Bell, T., Bailey, M. & Whiteley, A.S. (2011). The bacterial biogeography of British soils. *Environmental Microbiology*, 13, 1642–1654.

Grossmann, L., Jensen, M., Pandey, R., Jost, S., Bass, D., Psenner, R. & Boenigk, J. (2016). Molecular investigation of protistan diversity along an elevation transect of alpine lakes. *Aquatic Microbial Ecology*, 78, 25-37.

Gruber-Vodicka, H.R., Seah, B.K.B. & Pruesse, E. (2020). phyloFlash: Rapid Small-Subunit rRNA Profiling and Targeted Assembly from Metagenomes. *mSystems*, 5, e00920-20.

Grytnes, J.A., Heegaard, E. & Ihlen, P. (2006). Species richness of vascular plants, bryophytes, and lichens along an altitudinal gradient in western Norway. *Acta Oecologica-international Journal of Ecology - ACTA OECOL*, 29, 241–246.

Grytnes, J.-A., Kapfer, J., Jurasinski, G., Birks, H.H., Henriksen, H., Klanderud, K., Odland, A., Ohlson, M., Wipf, S. & Birks, H.J.B. (2014). Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography*, 23, 876–884.

Guillou, L., Bachar, D., Audic, S., Bass, D., Berney, C., Bittner, L., Boutte, C., Burgaud, G., de Vargas, C. & (…) & Christen, R. (2013). The Protist Ribosomal Reference database (PR2): a catalog of unicellular eukaryote small sub-unit rRNA sequences with curated taxonomy. *Nucleic Acids Research*, D597-604.

Hagedorn, F., Gavazov, K. & Alexander, J.M. (2019). Above- and belowground linkages shape responses of mountain vegetation to climate change. *Science*, 365, 1119–1123.

Hartig, F. (2021). *DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models*. R package version 0.4.4.

Hol, W.H.G., Bezemer, T.M. & Biere, A. (2013). Getting the ecology into interactions between plants and the plant growth-promoting bacterium Pseudomonas fluorescens. *Frontiers in Plant Science*, 4, 1-9.

Hooper, D.U., Bignell, D.E., Brown, V.K., Brussard, L., Dangerfield, J.M., Wall, D.H., Wardle, D., Coleman, D.C., Giller, K.E. & (…) & Wolters, V. (2000). Interactions between Aboveground and Belowground Biodiversity in Terrestrial Ecosystems: Patterns, Mechanisms, and Feedbacks. *BioScience*, 50, 1049–1061.

Huston, M. (1994). Biological Diversity: *The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.

Institut für Schnee- und Lawinenforschung SLF. (2021). *White Risk*. WSL Institut für Schnee und Lawinenforschung SLF, Davos.

IPCC. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jones, R.T., Robeson, M.S., Lauber, C.L., Hamady, M., Knight, R. & Fierer, N. (2009). A comprehensive survey of soil acidobacterial diversity using pyrosequencing and clone library analyses. *The ISME Journal*, 3, 442–453.

Juillerat, P., Bäumler, B., Bornand, C., Gygax, A., Jutzi, M., Möhl, A., *et al.* (2017). *Flora Helvetica Checklist 2017: der Gefässpflanzen der Schweiz*. InfoFlora, Genf.

King, A., Meyer, A.F. & Schmidt, S. (2008). High levels of microbial biomass and activity in unvegetated tropical and temperate alpine soils. *Soil Biology and Biochemistry*, 40, 2605–2610.

Kivlin, S., Lynn, J., Kanzenel, M., Beals, K. & Rudgers, J. (2017). Biogeography of plant-associated fungal symbionts in mountain ecosystems: A meta-analysis. *Diversity and Distributions*, 23, 1067–1077.

Kopylova, E., Noé, L. & Touzet, H. (2012). SortMeRNA: fast and accurate filtering of ribosomal RNAs in metatranscriptomic data. *Bioinformatics*, 28, 3211–3217.

Körner, C. (2003). *Alpine Plant Life. Functional Plant Ecology of High Mountain Ecosystems*. 2nd edn. Springer, Berlin.

Körner, C. (2007). The use of 'altitude' in ecological research. Trends Ecol Evol 22: 569-574. *Trends in ecology & evolution*, 22, 569–74.

Kowalchuk, G.A., Buma, D.S., de Boer, W., Klinkhamer, P.G.L. & van Veen, J.A. (2002). Effects of above-ground plant species composition and diversity on the diversity of soil-borne microorganisms. *Antonie Van Leeuwenhoek*, 81, 509-520.

Küchler, M. (2020). *VEGEDAZ-Editor, Datenbank, Analyse und Zeigerwerte für Vegetationsaufnahmen*. WSL, Birmensdorf.

Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B. & Jensen, S.P. (2020). *lmerTest: Tests in Linear Mixed Effects Models*. R package version 3.1-3.

Landolt, E., Bäumler, B., Erhardt, A., Hegg, O., Klötzli, F., Lämmler, W., Nobis, N., Rudmann-Maurer, K., Schweingruber, F.-H. & (…) & Wohlgemuth, T. (2010). *Flora indicativa. Ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. Ecological indicators values and biological attributes of the flora of Switzerland and the Alps*. 1st edn. Haupt, Bern.

Lange, M., Eisenhauer, N., Sierra, C.A., Bessler, H., Engels, C., Griffiths, R.I., Mellado-Vázquez , P.G., Malik, A.A., Roy, J. & (…) Gleixner, G. (2015). Plant diversity increases soil microbial activity and soil carbon storage. *Nature Communications*, 6, 1-8,.

Lauber, C.L., Hamady, M., Knight, R. & Fierer, N. (2009). Pyrosequencing-Based Assessment of Soil pH as a Predictor of Soil Bacterial Community Structure at the Continental Scale. *Applied and Environmental Microbiology,* 75, 5111-5120.

Lazzaro, A., Hilfiker, D. & Zeyer, J. (2015). Structures of Microbial Communities in Alpine Soils: Seasonal and Elevational Effects. *Frontiers in Microbiology*, 6, 1-13.

Ley, R.E., Williams, M.W. & Schmidt, S.K. (2004). Microbial population dynamics in an extreme environment: controlling factors in talus soils at 3750 m in the Colorado Rocky Mountains. *Biogeochemistry*, 68, 297–311.

Linnaeus, C. (1781). On the increase of the habitable earth. *Amoenitates Academicae,* 2, 17–27.

Lipson, D.A. & Schmidt, S.K. (2004). Seasonal Changes in an Alpine Soil Bacterial Community in the Colorado Rocky Mountains. *Applied and Environmental Microbiology*, 70, 2867–2879.

Lomolino, M.V. (2001). Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10, 3–13.

Looby, C.I., Maltz, M.R. & Treseder, K.K. (2016). Belowground responses to elevation in a changing cloud forest. *Ecology and Evolution*, 6, 1996–2009.

Magoč, T. & Salzberg, S.L. (2011). FLASH: fast length adjustment of short reads to improve genome assemblies. *Bioinformatics*, 27, 2957–2963.

Malard, L., Mod, H., Guex, N., Broennimann, O., Yashiro, E., Lara, E., Mitchell, E.A.D., Niculita-Hirzel, H. & Guisan, A. (2021). Comparative analysis of diversity and environmental niches of soil bacterial, archaeal, fungal and protist communities reveal niche divergences along environmental gradients in the Alps. *Research Square,* no volume, no page.

Malhi, Y., Silman, M., Salinas, N., Bush, M., Meir, P. & Saatchi, S. (2010). Introduction: Elevation gradients in the tropics: laboratories for ecosystem ecology and global change research. *Glob. Global Change Biology*, 16, 3171–3175.

Mazel, F., Malard, L., Niculita-Hirzel, H., Yashiro, E., Mod, H.K., Mitchell, E.A.D., Singer, D., Buri, A., Pinto, E., & (…) & Guisan, A. (2021). Soil protist function varies with elevation in the Swiss Alps. *Environmental Microbiology,* no volume, no page.

de Mesquita, C.P.B., Knelman, J., King, A., Farrer, E., Porazinska, D., Schmidt, S., & Suding, K. (2017). Plant colonization of moss-dominated soils in the alpine: Microbial and biogeochemical implications. *Soil Biology and Biochemistry*, 111, 135–142.

Millard, P. & Singh, B. (2010). Does grassland vegetation drive soil microbial diversity? *Nutrient Cycling in Agroecosystems*, 88, 147–158.

Monson, R., Lipson, D., Burns, S., Turnipseed, A., Delany, A., Williams, M. & Schmidt, S. (2006). Winter Forest Soil Respiration Controlled by Climate and Microbial Community Composition. *Nature*, 439, 711–714.

Namgail, T., Rawat, G.S., Mishra, C., van Wieren, S.E. & Prins, H.H.T. (2012). Biomass and diversity of dry alpine plant communities along altitudinal gradients in the Himalayas. *Journal of Plant Research*, 125, 93–101.

Ni, Y., Yang, T., Zhang, K., Shen, C. & Chu, H. (2018). Fungal Communities Along a Small-Scale Elevational Gradient in an Alpine Tundra Are Determined by Soil Carbon Nitrogen Ratios. *Frontiers in Microbiology*, 9, 1-9.

Nottingham, A.T., Fierer, N., Turner, B.L., Whitaker, J., Ostle, N.J., McNamara, N.P., Bardgett, R.D., Leff, J.W., Salinas, N. & (…) & Meir, P. (2018). Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes. *Ecology*, 99, 2455–2466.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L. & (…) & Wagner, H. (2020). *vegan: Community Ecology Package*. R package version 2.5-7.

Palpurina, S., Wagner, V., von Wehrden, H., Hájek, M., Horsák, M., Brinkert, A., Hölzel, N., Wesche, K., Kamp, J. & (…) Chytrý, M. & (2017). The relationship between plant species richness and soil pH vanishes with increasing aridity across Eurasian dry grasslands. *Global Ecology and Biogeography*, 26, 425–434.

Pauli, H., Gottfried, M., Dullinger, S., Abdaladze, O., Akhalkatsi, M., Benito Alonso, J.L., Coldea, G., Dick, J., Erschbamer, B. & (…) & Grabherr, G. (2012). Recent Plant Diversity Changes on Europe's Mountain Summits. *Science*, 336, 353–5.

Peay, K.G., von Sperber, C., Cardarelli, E., Toju, H., Francis, C.A., Chadwick, O.A., Vitiusek, P.M. (2017). Convergence and contrast in the community structure of Bacteria, Fungi and Archaea along a tropical elevation–climate gradient. *FEMS Microbiology Ecology*, 93, 1-12.

Pepin, N., Bradley, R.S., Diaz, H.F., Baraer, M., Caceres, E.B., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M.Z. & (…) & Yang, D.Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, 5, 424–430.

Pielou, E.C. (1966). The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology*, 13, 131–144.

Ping, Y., Han, D., Wang, N., Hu, Y., Mu, L. & Feng, F. (2017). Vertical zonation of soil fungal community structure in a Korean pine forest on Changbai Mountain, China. *World J. Microbiol. Biotechnol.*, 33, 1-10.

Polyakova, M.A., Dembicz, I., Becker, T., Becker, U., Demina, O.N., Ermakov, N., Filibeck, G., Guarino, R., Janišová, M. & (…) & Dengler, J. (2016). Scale- and taxon-dependent patterns of plant diversity in steppes of Khakassia, South Siberia (Russia). *Biodiversity and Conservation*, 25, 2251–2273.

Porazinska, D.L., Farrer, E.C., Spasojevic, M.J., de Mesquita, C.P.B., Sartwell, S.A., Smith, J.G., White, C.T., King, A.J., Suding, K.N. & Schmidt S.K. (2018). Plant diversity and density predict belowground diversity and function in an early successional alpine ecosystem. *Ecology*, 99, 1942–1952.

Prober, S.M., Leff, J.W., Bates, S.T., Borer, E.T., Firn, J., Harpole, W.S., Lind, E.M., Seabloom, E.W., Adler, P.B. & (…) & Fierer, N. (2014). Plant diversity predicts beta but not alpha diversity of soil microbes across grasslands worldwide. *Ecology Letters*, 18, 85–95.

Prosser, J.I., Bohannan, B.J.M., Curtis, T.P., Ellis, R.J., Firestone, M.K., Freckleton, R.P., Green, J.L., Green, L.E., Kilham, K. & (…) & Young, J.P.W. (2007). The role of ecological theory in microbial ecology. *Nature Reviews Microbiology*, 5, 384–392.

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Wien.

Rahbek, C. (2005). The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8, 224–239.

Rahbek, C., Borregaard, M., Colwell, R., Dalsgaard, B., Holt, B., Morueta-Holme, N., Nogués-Bravo , D., Whittaker, R. & Fjeldså, J. (2019). Humboldt's enigma: What causes global patterns of mountain biodiversity? *Science*, 365, 1108–1113.

Ren, B., Hu, Y., Chen, B., Zhang, Y., Thiele, J., Shi, R., Liu, M. & Bu, R. (2018). Soil pH and plant diversity shape soil bacterial community structure in the active layer across the latitudinal gradients in continuous permafrost region of Northeastern China. *Scientific Reports*, 8, 1-11.

Rillig, M.C., Wright, S.F., Shaw, M.R. & Field, C.B. (2002). Artificial Climate Warming Positively Affects Arbuscular Mycorrhizae but Decreases Soil Aggregate Water Stability in an Annual Grassland. *Oikos*, 97, 52–58.

Rixen, C. & Wipf, S. (2017). Non-equilibrium in Alpine Plant Assemblages: Shifts in Europe's Summit Floras. In: *High Mountain Conservation in a Changing World*, Advances in Global Change Research (eds. J. Catalan, J.M. Ninot & M.M. Aniz). Springer International Publishing, Cham, pp. 285–303.

Rosseel, Y., Jorgensen, T.D., Rockwood, N., Oberski, D., Byrnes, J., Vanbrabant, L., Savalei, V., Merkle, E., Hallquist, M. & (…) & Du, H. (2021). *lavaan: Latent Variable Analysis*. R package version 0.6-9.

Schadt, C.W., Martin, A.P., Lipson, D.A. & Schmidt, S.K. (2003). Seasonal Dynamics of Previously Unknown Fungal Lineages in Tundra Soils. *Science*, 301, 1359–1361.

Schloerke, B., Cook, D., Larmarange, J., Briatte, F., Marbach, M., Thoen, E., Elberg, A., Toomet, O., Crowley, J. & (…) & Wickham, H. (2021). *GGally: Extension to "ggplot2."*. R package version 2.1.2.

Schmidt, S.K., King, A.J., Meier, C.L., Bowman, W.D., Farrer, E.C., Suding, K.N., Nemergut, D.R. (2015). Plant–microbe interactions at multiple scales across a high-elevation landscape. *Plant Ecology & Diversity*, 8, 703–712.

Schmieder, R. & Edwards, R. (2011). Quality control and preprocessing of metagenomic datasets. *Bioinformatics*, 27, 863–864.

Schwaller, F. (2020). Vegetation and microbial biomass along elevational gradients: effects of snow cover and other environmental parameters. Bachelor thesis, Eidgenössische Technische Hochschule ETH, Zürich.

Seppey, C., Broennimann, O., Buri, A., Yashiro, E., Pinto-Figueroa, E., Singer, D., Blandenier, Q., Mitchell, E., Hirzel, H. & (…) & Lara, E. (2019). Soil protist diversity in the Swiss western Alps is better predicted by topo-climatic than by edaphic variables. *Journal of Biogeography*, 47, 1-13.

Shannon, C.E. (2001). A mathematical theory of communication. *Bell System Technical Journal*, 5, 3–55.

Shen, C., Gunina, A., Luo, Y., Wang, J., He, J.-Z., Kuzyakov, Y., Hemp, A., Classen, A.T. & Ge, Y. (2020). Contrasting patterns and drivers of soil bacterial and fungal diversity across a mountain gradient. *Environmental Microbiology*, 22, 3287–3301.

Shen, C., Shi, Y., Fan, K., He, J.-S., Adams, J.M., Ge, Y. & Chu, H. (2019). Soil pH dominates elevational diversity pattern for bacteria in high elevation alkaline soils on the Tibetan Plateau. *FEMS Microbiology Ecology*, 95, 1-9.

Shen, C., Liang, W., Shi, Y., Lin, X., Zhang, H., Wu, X., Xie, G., Chain, P. & Chu, H. (2014). Contrasting elevational diversity patterns between eukaryotic soil microbes and plants. *Ecology*, 95, 3190–3202.

Shen, C., Xiong, J., Zhang, H., Feng, Y., Lin, X., Li, X., Liang, W. & Chu, H. (2013). Soil pH drives the spatial distribution of bacterial communities along elevation on Changbai Mountain. *Soil Soil Biology and Biochemistry*, 57, 204–211.

Shigyo, N., Umeki, K. & Hirao, T. (2019). Plant functional diversity and soil properties control elevational diversity gradients of soil bacteria. *FEMS Microbiology Ecology*, 95, 1-10.

Siefert, A., Ravenscroft, C., Althoff, D., Alvarez-Yépiz, J.C., Carter, B.E., Glennon, K.L., Heberling, J.M., Jo, I.S., Ponters, A. & (…) & Fridley, J.D. (2012). Scale dependence of vegetation–

environment relationships: a meta-analysis of multivariate data. *Journal of Vegetation Science*, 23, 942–951.

Siles, J.A. & Margesin, R. (2017). Seasonal soil microbial responses are limited to changes in functionality at two Alpine forest sites differing in altitude and vegetation. *Scientific Reports*, 7, 1-16.

Singh, B.K., Bardgett, R.D., Smith, P. & Reay, D.S. (2010). Microorganisms and climate change: terrestrial feedbacks and mitigation options. *Nature Reviews Microbiology*, 8, 779–790.

Singh, D., Takahashi, K., Kim, M., Chun, J. & Adams, J.M. (2012). A Hump-Backed Trend in Bacterial Diversity with Elevation on Mount Fuji, Japan. *Microbial Ecology*, 63, 429–437.

Steinbauer, M.J., Grytnes, J.-A., Jurasinski, G., Kulonen, A., Lenoir, J., Pauli, H., Rixen, C., Winkler, M., Bardy-Durchhalter, M. & (…) Wipf, S. (2018). Accelerated increase in plant species richness on mountain summits is linked to warming. *Nature*, 556, 231–234.

Sun, Y.-Q., Wang, J., Shen, C., He, J.-Z. & Ge, Y. (2019). Plant evenness modulates the effect of plant richness on soil bacterial diversity. *Science of The Total Environment*, 662, 8–14.

Talebi, A., Attar, F., Naqinezhad, A., Dembicz, I. & Dengler, J. (2021). Scale-dependent patterns and drivers of plant diversity in steppe grasslands of the Central Alborz Mts., Iran. *Journal of Vegetation Science*, 32, 1-15.

Tang, M., Li, L., Wang, X., You, J., Li, J. & Chen, X. (2020). Elevational is the main factor controlling the soil microbial community structure in alpine tundra of the Changbai Mountain. *Scientific Reports*, 10, 1-16.

Tedersoo, L., Bahram, M. & Dickie, I.A. (2014). Does host plant richness explain diversity of ectomycorrhizal fungi? Re-evaluation of Gao et al. (2013) data sets reveals sampling effects. *Molecular Ecology*, 23, 992–995.

Teittinen, A., Kallajoki, L., Meier, S., Stigzelius, T. & Soininen, J. (2016). The roles of elevation and local environmental factors as drivers of diatom diversity in subarctic streams. *Freshwater Biology*, 61, 1509–1521.

Testolin, R., Attorre, F., Borchardt, P., Brand, R.F., Bruelheide, H., Chytrý, M., De Sanctis, M., Dolezal, J., Finckh, M. & (…) & Jiménez-Alfaro, B. (2021). Global patterns and drivers of alpine plant species richness. *Global Ecology and Biogeography*, 30, 1218–1231.

Theurillat, J.-P., Schlüssel, A., Geissler, P., Guisan, A., Velluti, C. & Wiget, L. (2003). Vascular Plant and Bryophyte Diversity along Elevation Gradients in the Alps. *Alpine Biodiversity in Europe* (eds. L. Nagy, C. Körner & D.B.A. Thompson*)*, pp. 85–193, Springer, Heidelberg.

Tian, Q., Jiang, Y., Tang, Y., Wu, Y., Tang, Z. & Liu, F. (2021). Soil pH and Organic Carbon Properties Drive Soil Bacterial Communities in Surface and Deep Layers Along an Elevational Gradient. *Frontiers in Microbiology*, 12, 1-15.

Tripathi, B.M., Kim, M., Singh, D., Lee-Cruz, L., Lai-Hoe, A., Ainuddin, A.N., Go, R., Rahim, R.A., Husni, M.H.A. & (…) & Adams, J.M. (2012). Tropical soil bacterial communities in Malaysia: pH dominates in the equatorial tropics too. *Microbial ecology* 64, 474–84.

Vance, E.D., Brookes, P.C. & Jenkinson, D.S. (1987). An extraction method for measuring soil microbial biomass C. *Soil Biology and Biochemistry*, 19, 703–707.

Vittoz, P., Camenisch, M., Mayor, R., Miserere, L., Vust, M. & Theurillat, J.-P. (2010). Subalpine-nival gradient of species richness for vascular plants, bryophytes and lichens in the Swiss Inner Alps. *Botanica Helvetica*, 120, 139–149.

Vonlanthen, C.M., Kammer, P., Eugster, W., Bühler, A. & Veit, H. (2006). Alpine vascular plant species richness: The importance of daily maximum temperature and pH. *Plant Ecology.*, 184, 13–25.

Voroney, P.R., Brookes, P.C. & Beyaert, R.P. (2008). Soil Microbial Biomass C, N, P and S. In: *Soil Sampling and Methods of Analysis* (eds. M.R. Carter. & E.G Gregorich). CRC Press Taylor & Francis, Boca Raton, pp. 637–653.

Wang, J.-T., Cao, P., Hu, H.-W., Li, J., Han, L.-L., Zhang, L.-M., Zheng, Y.-M. & He, J.-Z. (2015). Altitudinal distribution patterns of soil bacterial and archaeal communities along mt. Shegyla on the Tibetan Plateau. *Microbial Ecology*, 69, 135–145.

Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer, New York.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L. & (…) & Yutani, H. (2019). Welcome to the Tidyverse. *Journal of Open Source Software*, 4, 1-6.

Wickham, H., François, R., Henry, L. & Müller, K. (2021). *dplyr: A Grammar of Data Manipulation*. R package version 1.0.7.

Winkler, D.E., Lubetkin, K.C., Carrell, A.A., Jabis, M.D., Yang, Y. & Kueppers, L.M. (2019). Responses of alpine plant communities to climate warming. In: *Ecosystem Consequences of Soil Warming* (ed. J.E.Mohan). Academic Press, pp. 297–346.

Witt, C., Gaunt, J., Galicia, C., Ottow, J. & Neue, H.-U. (2000). A rapid chloroform-fumigation extraction method for measuring soil microbial biomass carbon and nitrogen in flooded rice soils. *Biology and Fertility of Soils*, 30, 510–519.

Wu, J., Anderson, B.J., Buckley, H.L., Lewis, G. & Lear, G. (2017). Aspect has a greater impact on alpine soil bacterial community structure than elevation. *FEMS microbiology ecology*, 93, 1-11.

Yang, T., Adams, J., Shi, Y., He, J.-S., Jing, X., Chen, L., Tedersoo, L. & Chu, H. (2017). Soil fungal diversity in natural grasslands of the Tibetan Plateau: Associations with plant diversity and productivity. *New Phytologist*, 215, 1-10.

Yao, F., Yang, S., Wang, Z., Wang, X., Ye, J., Wang, X., De Bruyn, J.M., Feng, X., Jiang, Y. & Li, H. (2017). Microbial Taxa Distribution Is Associated with Ecological Trophic Cascades along an Elevation Gradient. *Front. Microbiol.*, 8, 1-17.

Yeh, C.-F., Soininen, J., Teittinen, A. & Wang, J. (2018). Elevational patterns and hierarchical determinants of biodiversity across microbial taxonomic scales. *Molecular Ecology*, 28, 1-14.

Yu, H. (2004). Distribution of plant species richness along elevation gradient in Hubei Province, China. *International Institute for Earth System Science (ESSI)*, no volume, no number.

Yuan, X., Knelman, J.E., Gasarch, E., Wang, D., Nemergut, D.R. & Seastedt, T.R. (2016). Plant community and soil chemistry responses to long-term nitrogen inputs drive changes in alpine bacterial communities. *Ecology*, 97, 1543–1554.

Zinger, L., Shahnavaz, B., Baptist, F., Geremia, R. & Choler, P. (2009). Microbial diversity in alpine tundra soils correlates with snow cover dynamics. *The ISME journal*, 3, 850–9.

Zverev, A., Kichko, A., Pinaev, A., Provorov, N. & Andronov, E. (2021). Diversity Indices of Plant Communities and Their Rhizosphere Microbiomes: An Attempt to Find the Connection. *Microorganisms*, 9, 1-11.

Appendix

General characterization of all sampled plots

Table 2 Minimum, maximum, mean, and standard deviation of all metric parameters over all 138 sampled plots.

Environmental- and structural parameters	Min	Max	Mean	Std. deviation
Elevation (m a.s.l)	1972.4	2816.25	2410.49	182.57
Aspect (°)	5	355	103.09	81.47
Slope (°)	0	50	20.6	10
Mean vegetation height (cm)	0.5	20.6	5.85	3.9
Maximum vegetation height (cm)	6	45	16.7	8.09
Maximum microrelief (cm)	0.5	13.5	4.82	2.68
Covers				
Vascular plants (%)	10	96.8	63.13	20.25
Bryophytes (%)	0	45	7.44	9.39
Lichens (%)	0	35	3.55	5.9
Rocks & Gravel (%)	0	78.4	6.9	10.36
Open ground (%)	0	62	13	13.11
Litter (%)	0	32.9	5.97	6.13
Soil properties				
Mean soil depth (cm)	1.13	45.25	14.83	8.68
Mean annual soil temperature (°C)	0.55	5.3	2.81	0.99
Soil temperature at sampling (°C)	0.13	19.80	4.41	5.00
Water content (%)	17.00	91.00	48.66	13.86
pH	3.52	6.28	4.09	0.43
Microbial Carbon MC (µg/g dry soil)	43.96	1178.44	508.02	215.25
Microbial Nitrogen MN (µg/g dry soil)	3.51	402.06	77.62	50.44
Microbial CN ratio	1.55	16.24	7.31	1.88
Total organic carbon TOC (mg/g dry soil)	0.01	0.66	0.32	0.12
Total dissolved nitrogen TDN (mg/g dry soil)	0.01	0.23	0.06	0.03
Indicator Values				
Temperature Value	1	2.36	1.56	0.33
Continentality Value	1.07	3.78	2.73	0.5
Light Value	3.09	5	4.17	0.4
Moisture Value	2.17	3.98	3.06	0.3
Reaction Value	1.27	3.19	2.14	0.26
Nutrients Value	1.22	3.82	2.23	0.39
Humus Value	2.88	4.63	3.3	0.39
Air content Value	1.02	3.9	2.3	0.56
Diversity Indices				
Plant Shannon index	0.54	3.02	1.95	0.47
Plant evenness index	0.18	0.95	0.76	0.15
Plant species richness	4	29	14	4.81
Bacteria Shannon index	2.31	5.04	4.14	0.50

Bacteria evenness index	0.34	0.69	0.57	0.06
Bacteria species richness	878.00	1639.00	1336.19	144.43
Fungi Shannon index	1.84	4.52	3.62	0.47
Fungi evenness index	0.33	0.80	0.62	0.08
Fungi species richness	176.00	596.00	357.91	73.19
Protist Shannon index	1.22	4.82	4.14	0.48
Protist evenness index	0.21	0.84	0.71	0.08
Protist species richness	198.00	539.00	344.18	79.69
Protists functional groups				
Lifestyle not known (%)	0.06	6.08	1.29	0.95
Animal parasite, symbiont, protistan parasite (%)	0.29	52.28	6.67	9.54
Free-living (%)	46.83	98.92	89.59	9.97
Plant/ algal parasite (%)	0.00	27.99	2.45	4.56
Nutrition not known (%)	0.17	6.29	1.78	0.97
Heterotroph (%)	35.28	97.47	88.40	9.47
Autotroph (%)	0.72	62.72	7.58	9.31
Mixotroph (%)	0.25	9.87	2.25	1.79

Identified plant species at species level

Table 3 Identified plant species (vascular plants n= 109, bryophytes n=3) at species level during field work in 2020 and 2021 in alphabetic order.

Aconitum napellus subsp. *vulgare* Rouy & Foucaud
Adenostyles alliariae (Gouan) A. Kern.
Agrostis alpina Scop.
Agrostis capillaris L.
Agrostis rupestris All.
Agrostis schraderiana Bech.
Alchemilla vulgaris aggr.
Anthoxanthum alpinum Á. Löve & D. Löve
Arenaria biflora L.
Arnica montana L.
Avenella flexuosa (L.) Drejer
Calluna vulgaris (L.) Hull
Campanula barbata L.
Campanula scheuchzeri VilL.
Cardamine alpina Willd.
Cardamine resedifolia L.
Carex capillaris L.
Carex curvula AlL.
Carex flava aggr.
Carex paupercula Michx.
Carex sempervirens VilL.
Cerastium cerastoides (L.) Britton
Cirsium spinosissimum (L.) Scop.
Coeloglossum viride (L.) Hartm.
Crocus albiflorus Kit.
Deschampsia cespitosa (L.) P. Beauv.
Diphasiastrum alpinum (L.) Holub
Doronicum clusii (AlL.) Tausch
Empetrum nigrum subsp. *hermaphroditum* (Hagerup) Böcher
Epilobium anagallidifolium Lam.
Erigeron uniflorus L.
Euphrasia minima Schleich.
Festuca ovina aggr.
Festuca quadriflora Honck.
Festuca rubra aggr.
Festuca violacea aggr.
Galium anisophyllon Vill.
Gentiana acaulis L.
Gentiana bavarica L.
Gentiana orbicularis Schur
Gentiana punctata L.
Geum montanum L.
Gnaphalium supinum L.
Gnaphalium sylvaticum L.
Helictotrichon versicolor (Vill.) Pilg.
Hieracium alpinum L.
Hieracium piliferum aggr.
*Homogyne alpina (*L.*)* Cass.
*Huperzia selago (*L.*)* Schrank & Mart.
Juncus jacquinii L.
Juniperus communis subsp. *alpina* Celak.
Leontodon helveticus Mérat
Leontodon hispidus L.
*Leucanthemopsis alpina (*L.*)* Heywood
*Ligusticum mutellina (*L.*)* Crantz
*Loiseleuria procumbens (*L.*)* Desv.
Lotus alpinus (DC.) Ramond
Luzula alpina Hoppe
Luzula alpinopilosa (Chaix) Breistr.
Luzula lutea (All.) DC.
Luzula multiflora aggr.
Luzula spicata (L.) DC.
Lycopodium annotinum L.
Minuartia sedoides (L.) Hiern
Myosotis alpestris F. W. Schmidt
Myosotis nemorosa Besser
Nardus stricta L.
Oreochloa disticha (Wulfen) Link
Phleum alpinum aggr.
Phleum rhaeticum (Humphries) Rauschert
Phyteuma betonicifolium Vill.
Phyteuma globulariifolium subsp. *pedemontanum* (Rich. Schulz) Bech.
Phyteuma hemisphaericum L.
Pinguicula vulgaris L.
Plantago alpina L.
Poa alpina L.
Polygonum viviparum L.
Potentilla aurea L.
Primula integrifolia L.
Prunella vulgaris L.
Pulsatilla alpina (L.) Delarbre
Pulsatilla alpina subsp. *apiifolia* (Scop.) Nyman
Ranunculus glacialis L.
Ranunculus kuepferi Greuter & Burdet

Ranunculus montanus aggr.
Rhododendron ferrugineum L.
Sagina saginoides (L.) H. Karst.
Salix herbacea L.
Salix retusa L.
Salix serpillifolia Scop.
Saxifraga stellaris L.
Sedum alpestre Vill.
Selaginella selaginoides (L.) Schrank & Mart.
Sempervivum montanum L.
Senecio incanus subsp. *carniolicus* (Willd.) Braun-Blanq.
Sibbaldia procumbens L.
Silene acaulis (L.) Jacq.
Silene rupestris L.
Silene vulgaris (Moench) Garcke
Soldanella alpina L.
Soldanella pusilla Baumg.
Solidago virgaurea subsp. *minuta* (L.) Arcang.
Thesium pyrenaicum Pourr.
Trifolium alpinum L.
Trifolium pratense L.
Vaccinium gaultherioides Bigelow
Vaccinium myrtillus L.
Vaccinium vitis-idaea L.
Veratrum album L.
Veronica alpina L.
Veronica bellidioides L.
Viola biflora L.

Author contribution: Performed work by year and person

Table 4 Overview of performed work by year and person (AF= Anna Maria Fiore-Donno, CR= Christian Rixen, CRo= Christoph Rosinger, FS= Fiona Schwaller, SK= Sabrina Keller, MBD= Mathilde Borg Dahl).

	Year	Person
Field survey & measurements		
Set up sampling design	2019, 2020	AF, CR
Bury temperature loggers	2019	AF, CR
Vegetation survey	2020, 2021	FS, SK, CR
Soil sampling	2020	AF
Elevation (m a.s.l)	2020, 2021	FS, SK
Aspect (°)	2020, 2021	FS, SK
Slope (°)	2020, 2021	FS, SK
Mean vegetation height (cm)	2020, 2021	FS, SK
Maximum vegetation height (cm)	2021	SK
Maximum microrelief (cm)	2021	SK
Vascular plants (%)	2020, 2021	FS, SK
Bryophytes (%)	2020, 2021	FS, SK
Lichens (%)	2020, 2021	FS, SK
Rocks & Scree (%)	2020, 2021	FS, SK
Open ground (%)	2020, 2021	FS, SK
Litter (%)	2020, 2021	FS, SK
Mean soil depth (cm)	2021	SK
Soil temperature at soil sampling (°C)	2020	AF
Water content (%)	2020	AF
Lab work		
RNA extraction	2021	AF
pH	2020	AF
Microbial carbon MC (µg/g dry soil)	2020	CRo
Microbial nitrogen MN (µg/g dry soil)	2020	CRo
Microbial CN ratio	2020	CRo
Total organic carbon TOC (mg/g dry soil)	2020	CRo
Total dissolved nitrogen TDN (mg/g dry soil)	2020	CRo
Office Work		
Processing RNA data	2021	AF, MBD

Chi² and *p*-Values of LME models, explaining the diversity indices as a function of elevation and treatment (snow gradient)

*Table 5 Chi2, p-values, numerator (NumDF) and denominator (DenDF) degrees of freedom for plant and microbial diversity in dependence of elevation and treatment (snow gradient) calculated in LME models with 1| Site/Transect as random factor. Significant terms (p-value < 0.05) of the final models are in bold. The (squared) elevation significantly influenced all diversity indices of plants and bacteria. Species richness of fungi and protists was influenced by the interaction of elevation*treatment, and by treatment, respectively.*

Plant diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi²	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**
Elevation	**7.617**	**0.006**	1	30.932	**11.407**	**0.001**	1	22.896	**5.952**	**0.015**	1	43.001
Elevation²	**8.409**	**0.004**	1	42.984	**11.927**	**0.001**	1	41.300	**5.823**	**0.016**	1	43.001
Treatment	1.602	0.449	2	86.000	1.747	0.417	2	86.000	3.973	0.137	2	86.000
Elevation x Treatment	2.094	0.351	2	86.000	2.585	0.275	2	86.000	1.845	0.398	2	86.000
Elavtion² x Treatment	0.205	0.902	2	86.000	2.605	0.272	2	86.000	4.97	0.083	2	86.000
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	10.529	3.245			0.097	0.312			0.010	0.100		
Transect	2.243	1.498			0.010	0.098			0	0		

Bacteria diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi²	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**
Elevation	16.507	0	1	29.672	**18.647**	**0**	1	15.823	**18.329**	**0**	1	13.277
Elevation²	**17.045**	**0**	1	39.276	**19.684**	**0**	1	30.642	**19.415**	**0**	1	28.642
Treatment	7.759	0.021	2	48.611	3.295	0.193	2	73.054	3.782	0.151	2	73.088
Elevation x Treatment	**8.338**	**0.015**	2	74.585	2.860	0.239	2	73.090	2.885	0.236	2	73.124
Elavtion² x Treatment	0.462	0.794	2	72.402	3.17	0.205	2	73.034	2.222	0.329	2	73.067
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	7273.000	85.280			0.112	0.335			0.002	0.043		
Transect	1607.000	40.080			0.001	0.032			< 0.001	0.001		

Fungi diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi^2	***p***	**NumDF**	**DenDF**	**Chi^2**	***p***	**NumDF**	**DenDF**	**Chi^2**	***p***	**NumDF**	**DenDF**
Elevation	2.506	0.113	1	19.579	1.231	0.267	1	29.652	2.156	0.142	1	27.998
$Elevation^2$	2.682	0.101	1	91.207	1.400	0.237	1	91.275	2.413	0.120	1	91.114
Treatment	4.133	0.127	2	75.357	0.862	0.650	2	73.105	2.008	0.366	2	73.175
Elevation x Treatment	**10.933**	**0.004**	2	75.336	3.810	0.149	2	73.172	3.301	0.192	2	73.241
$Elavtion^2$ x Treatment	0.272	0.873	2	73.312	0.677	0.713	2	73.040	0.384	0.825	2	73.109
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	1632.800	40.408			0.056	0.237			0.002	0.041		
Transect	24.760	4.976			0.017	0.129			< 0.001	0.019		

Protist diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi^2	***p***	**NumDF**	**DenDF**	**Chi^2**	***p***	**NumDF**	**DenDF**	**Chi^2**	***p***	**NumDF**	**DenDF**
Elevation	0.473	0.492	1	31.053	1.592	0.207	1	28.301	2.382	0.123	1	36.494
$Elevation^2$	0.107	0.743	1	101.208	1.456	0.228	1	83.594	2.244	0.134	1	83.339
Treatment	**12.267**	**0.002**	2	77.315	0.779	0.677	2	73.223	0.401	0.818	2	72.967
Elevation x Treatment	5.844	0.054	2	73.177	0.890	0.641	2	73.313	0.904	0.636	2	73.054
$Elavtion^2$ x Treatment	3.94	0.139	2	73.083	0.369	0.832	2	73.132	1.452	0.484	2	72.816
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	2298.000	47.940			0.010	0.098			0.001	0.023		
Transect	1070.000	32.720			0.010	0.100			< 0.001	< 0.001		

Correlation matrix between plant and microbial diversity indices (species richness, Shannon index, evenness index)

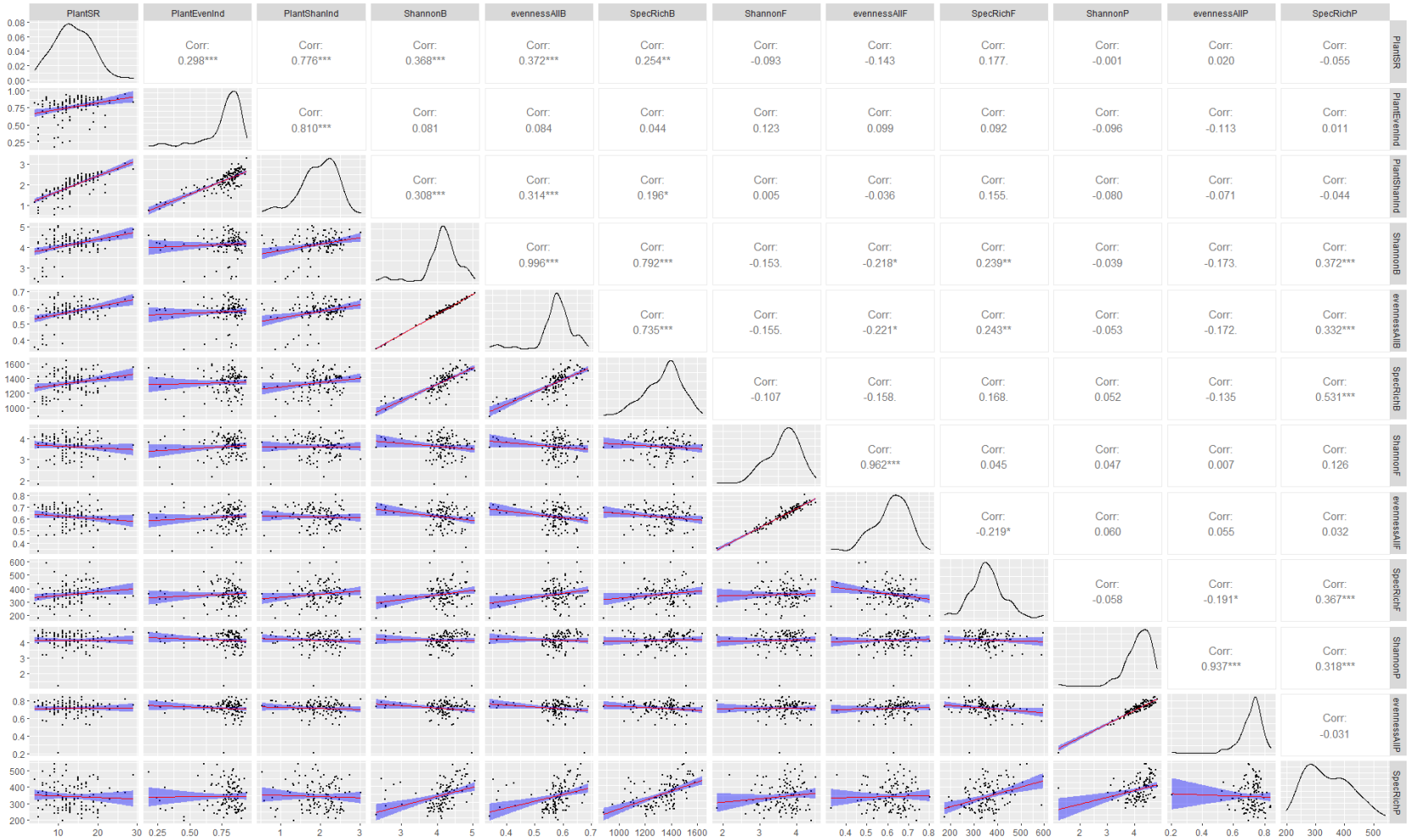

*Figure 10 Correlations between plant and microbial diversity indices (species richness, Shannon index, evenness index) showing direction and strength of the correlation (Corr) and the significance (*** < 0.001, ** < 0.01, * < 0.05). There are only positive correlations between plant and bacterial diversity. Between the microbe's indices there are significant positive (e.g., species richness protists - bacteria, r= 0.531) and negative (e.g., Evenness index fungi - bacteria, r=-0.221).*

Correlation coefficients between plant and microbial diversity indices

Table 6 Pearson's Correlation Coefficient (r) and p-Value (p) between plant and microbial diversity indices showed that species richness and Shannon index of plants and bacteria are positively correlated. Significant p-values (<0.05) in bold.

Index I	Index II	*r*	*p*
Plant species richness	**Bacteria Shannon index**	0.368	**<0.001**
Plant species richness	**Bacteria evenness index**	0.372	**<0.001**
Plant species richness	**Bacteria species richness**	0.254	**0.005**
Plant species richness	Fungi Shannon index	-0.093	0.313
Plant species richness	Fungi evenness index	-0.143	0.121
Plant species richness	Fungi species richness	0.177	0.055
Plant species richness	Protist Shannon index	-0.001	0.989
Plant species richness	Protist evenness index	0.020	0.831
Plant species richness	Protist species richness	-0.055	0.552
Plant Shannon index	**Bacteria Shannon index**	0.308	**0.001**
Plant Shannon index	**Bacteria evenness index**	0.314	**0.001**
Plant Shannon index	**Bacteria species richness**	0.196	**0.032**
Plant Shannon index	Fungi Shannon index	0.005	0.960
Plant Shannon index	Fungi evenness index	-0.036	0.694
Plant Shannon index	Fungi species richness	0.155	0.093
Plant Shannon index	Protist Shannon index	-0.080	0.387
Plant Shannon index	Protist evenness index	-0.071	0.445
Plant Shannon index	Protist species richness	-0.044	0.632
Plant evenness index	Bacteria Shannon index	0.081	0.380
Plant evenness index	Bacteria evenness index	0.084	0.363
Plant evenness index	Bacteria species richness	0.044	0.633
Plant evenness index	Fungi Shannon index	0.123	0.183
Plant evenness index	Fungi evenness index	0.099	0.282
Plant evenness index	Fungi species richness	0.092	0.318
Plant evenness index	Protist Shannon index	-0.096	0.301
Plant evenness index	Protist evenness index	-0.113	0.220
Plant evenness index	Protist species richness	0.011	0.902

SEM variable selection: Correlation coefficients for plant diversity indices

Table 7 Pearson's correlation coefficients (r) and their significance (p) for potential SEM predictors of plant diversity indices showing direction and strength of the correlation. Significant variables highlighted in bold. The pH value had a significant positive effect on plant evenness index (p=0.019).

Plant diversity index	Predictor	*r*	*p*
Species richness	pH	0.012	0.886
Species richness	Aspect	-0.084	0.327
Species richness	Slope	0.141	0.100
Species richness	Litter	-0.054	0.529
Species richness	**Elevation**	-0.411	**<0.001**
Species richness	**Soil temperature**	0.561	**<0.001**
Species richness	**Mean soil depth**	0.169	**0.048**
Species richness	**Maximum micro relief**	0.191	**0.025**
Species richness	**Bryophyte cover**	-0.169	**0.047**
Species richness	Lichen cover	-0.053	0.540
Species richness	**TOC**	0.368	**<0.001**
Species richness	**TDN**	0.291	**0.001**
Shannon index	pH	0.146	0.088
Shannon index	Aspect	-0.089	0.302
Shannon index	Slope	0.153	0.074
Shannon index	Litter	-0.119	0.163
Shannon index	**Elevation**	-0.207	**0.015**
Shannon index	**Soil temperature**	0.300	**0.008**
Shannon index	**Mean soil depth**	0.228	**0.007**
Shannon index	Maximum micro relief	0.126	0.142
Shannon index	Bryophyte cover	-0.087	0.310
Shannon index	Lichen cover	-0.087	0.312
Shannon index	**TOC**	0.207	**0.015**
Shannon index	**TDN**	0.185	**0.030**
Evenness index	**pH**	0.200	**0.019**
Evenness index	Aspect	-0.083	0.334
Evenness index	Slope	0.094	0.271
Evenness index	**Litter**	-0.173	**0.043**
Evenness index	Elevation	0.070	0.412
Evenness index	Soil temperature	-0.030	0.794
Evenness index	**Mean soil depth**	0.201	**0.018**
Evenness index	Maximum micro relief	-0.012	0.886
Evenness index	Bryophyte cover	0.021	0.811
Evenness index	Lichen cover	-0.068	0.428
Evenness index	TOC	-0.042	0.624
Evenness index	TDN	0.007	0.934

SEM variable selection: Correlation coefficients for bacteria diversity indices

Table 8 Pearson's correlation coefficients (r) and their significance (p) for potential SEM predictors of bacteria diversity indices showing direction and strength of the correlation. Significant variables highlighted in bold. The pH showed significant positive correlations with species richness (p=0.035), Shannon index (p=0.011) and evenness index(p=0.016).

Bacteria diversity index	Predictor	*r*	*p*
Species richness	**pH**	0.193	**0.035**
Species richness	**Soil temperature**	0.283	**0.018**
Species richness	Soil temperature sampling	-0.161	0.080
Species richness	**Mean soil depth**	0.248	**0.007**
Species richness	**Litter**	0.219	**0.017**
Species richness	**Water content**	0.268	**0.004**
Species richness	TOC	-0.005	0.957
Species richness	TDN	0.063	0.501
Species richness	**Total plant cover**	0.219	**0.017**
Species richness	Elevation	-0.180	0.051
Shannon index	**pH**	0.232	**0.011**
Shannon index	**Soil temperature**	0.457	**<0.001**
Shannon index	Soil temperature sampling	-0.155	0.092
Shannon index	**Mean soil depth**	0.298	**0.001**
Shannon index	**Litter**	0.242	**0.008**
Shannon index	**Water content**	0.491	**<0.001**
Shannon index	TOC	0.142	0.124
Shannon index	**TDN**	0.232	**0.012**
Shannon index	**Total plant cover**	0.438	**<0.001**
Shannon index	**Elevation**	-0.331	**<0.001**
Evenness index	**pH**	0.221	**0.016**
Evenness index	**Soil temperature**	0.473	**<0.001**
Evenness index	Soil temperature sampling	-0.149	0.105
Evenness index	**Mean soil depth**	0.295	**0.001**
Evenness index	**Litter**	0.238	**0.009**
Evenness index	**Water content**	0.507	**<0.001**
Evenness index	TOC	0.165	0.074
Evenness index	**TDN**	0.248	**0.007**
Evenness index	**Total plant cover**	0.457	**<0.001**
Evenness index	**Elevation**	-0.347	**<0.001**

SEM variable selection: Correlation coefficients for fungi diversity indices

Table 9 Pearson's correlation coefficients (r) and their significance (p) for potential SEM predictors of fungal diversity indices showing direction and strength of the correlation. Significant variables highlighted in bold. The pH showed a significant negative correlation (p= 0.029) with species richness.

Fungal diversity index	Predictor	*r*	*p*
Species richness	**pH**	-0.201	**0.029**
Species richness	Litter	-0.064	0.486
Species richness	Elevation	-0.112	0.226
Species richness	Soil temperature	0.093	0.450
Species richness	Soil temperature sampling	-0.174	0.058
Species richness	Mean soil depth	0.160	0.081
Species richness	Water content	0.155	0.097
Species richness	TOC	0.093	0.316
Species richness	TDN	-0.035	0.710
Species richness	Total plant cover	0.176	0.056
Shannon index	pH	0.086	0.352
Shannon index	Litter	-0.167	0.070
Shannon index	Elevation	0.152	0.098
Shannon index	Soil temperature	-0.083	0.497
Shannon index	Soil temperature sampling	-0.030	0.743
Shannon index	Mean soil depth	-0.073	0.433
Shannon index	Water content	-0.054	0.561
Shannon index	TOC	-0.029	0.754
Shannon index	TDN	-0.020	0.831
Shannon index	Total plant cover	-0.135	0.144
Evenness index	pH	0.154	0.095
Evenness index	Litter	-0.134	0.147
Evenness index	**Elevation**	0.191	**0.037**
Evenness index	Soil temperature	-0.124	0.309
Evenness index	Soil temperature sampling	0.009	0.920
Evenness index	Mean soil depth	-0.114	0.216
Evenness index	Water content	-0.085	0.367
Evenness index	TOC	-0.075	0.418
Evenness index	TDN	-0.025	0.790
Evenness index	**Total plant cover**	-0.187	**0.042**

SEM variable selection: Correlation coefficients for protist diversity indices

Table 10 Pearson's correlation coefficients (r) and their significance (p) for potential SEM predictors of protists diversity indices showing direction and strength of the correlation. Significant variables highlighted in bold. The pH showed significant positive correlation (p= 0.009) with species richness.

Protist diversity index	Predictor	*r*	*p*
Species richness	**pH**	0.239	**0.009**
Species richness	Elevation	0.002	0.986
Species richness	Soil temperature	-0.032	0.793
Species richness	Soil temperature sampling	-0.149	0.105
Species richness	Mean soil depth	-0.020	0.829
Species richness	Litter	0.025	0.785
Species richness	Water content	0.064	0.497
Species richness	**TOC**	-0.393	**<0.001**
Species richness	**TDN**	-0.217	**0.018**
Species richness	Total plant cover	-0.172	0.061
Shannon index	pH	-0.083	0.371
Shannon index	Elevation	-0.083	0.370
Shannon index	Soil temperature	-0.077	0.530
Shannon index	Soil temperature sampling	0.019	0.834
Shannon index	Mean soil depth	-0.071	0.441
Shannon index	Litter	0.054	0.562
Shannon index	Water content	-0.149	0.110
Shannon index	TOC	-0.064	0.488
Shannon index	TDN	0.011	0.909
Shannon index	Total plant cover	-0.118	0.203
Evenness index	pH	-0.172	0.061
Evenness index	Elevation	-0.090	0.331
Evenness index	Soil temperature	-0.069	0.574
Evenness index	Soil temperature sampling	0.079	0.392
Evenness index	Mean soil depth	-0.072	0.439
Evenness index	Litter	0.051	0.585
Evenness index	**Water content**	-0.184	**0.048**
Evenness index	TOC	0.077	0.410
Evenness index	TDN	0.093	0.318
Evenness index	Total plant cover	-0.058	0.534

Chi² and *p*-Values of LME models, explaining the drivers of plant and microbial diversity indices

Table 11 Chi², p-values, numerator (NumDF) and denominator (DenDF) degrees of freedom for the drivers of plant and microbial diversity calculated in LME models with 1| Site/Transect as random factor. Significant terms (p<0.05) are in bold. The pH significantly positively affects plant and bacterial Shannon index (p=0.02; p= 0.001) and evenness index (p= 0.023; p= 0.001). On the diversity indices of fungi and protists, pH showed no significant effect.

Plant diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi²	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**
Elevation	**7.027**	**0.008**	1	58.170	**10.517**	**0.001**	1	55.100	**5.171**	**0.023**	1	59.207
Elevation²	**7.864**	**0.005**	1	125.237	**11.194**	**0.001**	1	117.217	**5.147**	**0.023**	1	113.849
Treatment	1.642	0.440	2	98.630	1.114	0.573	2	95.967	3.073	0.215	2	92.582
Elevation x Treatment	2.255	0.324	2	86.289	3.603	0.165	2	85.953	2.440	0.295	2	85.939
Elavtion² x Treatment	0.156	0.925	2	86.247	2.595	0.273	2	86.102	5.005	0.082	2	86.210
pH	1.190	0.275	1	104.105	**5.455**	**0.020**	1	87.520	**5.199**	**0.023**	1	76.672
Mean soil depth	1.340	0.247	1	111.696	1.356	0.244	1	110.316	1.353	0.245	1	108.279
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	11.423	3.380			0.103	0.321			0.010	0.102		
Transect	1.137	1.066			0.001	0.036			0.000	0.000		

Bacteria diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi²	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**
Elevation	16.501	0.000	1	58.920	**18.448**	**0**	1	65.611	**18.041**	**<0.001**	1	65.362
Elevation²	**17.045**	**0**	1	99.755	**19.698**	**0**	1	106.933	**19.333**	**<0.001**	1	106.965
Treatment	7.759	0.021	2	81.727	2.426	0.297	2	97.332	3.581	0.167	2	97.130
Elevation x Treatment	**8.338**	**0.015**	2	72.471	2.76	0.252	2	72.271	2.784	0.249	2	72.047
Elavtion² x Treatment	0.515	0.773	2	72.366	5.213	0.074	2	71.687	4.008	0.135	2	71.475
pH	2.949	0.086	1	66.980	**11.495**	**0.001**	1	93.668	**10.867**	**0.001**	1	93.052
Mean soil depth	1.227	0.268	1	103.501	0.612	0.434	1	106.310	0.595	0.441	1	106.322
TDN	2.776	0.096	1	67.231	0.574	0.448	1	92.426	0.227	0.633	1	91.493
Water content	1.174	0.279	1	95.864	**5.991**	**0.014**	1	102.856	**5.882**	**0.015**	1	102.977
Total plant cover	0.092	0.761	1	106.944	0.027	0.870	1	106.627	0.049	0.824	1	106.661
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	6773.000	82.300			0.103	0.321			0.002	0.041		
Transect	1830.000	42.780			0	0			0	0.000		

Fungi diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi²	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**
Elevation	3.356	0.067	1	57.309	1.231	0.267	1	54.133	2.156	0.142	1	53.769
Elevation²	3.495	0.062	1	89.528	1.400	0.237	1	89.983	2.413	0.120	1	89.130
Treatment	4.690	0.096	2	70.789	0.806	0.668	2	70.473	2.033	0.362	2	69.587
Elevation x Treatment	**10.933**	**0.004**	2	73.593	4.434	0.109	2	73.066	4.086	0.130	2	73.067
Elavtion² x Treatment	0.201	0.904	2	73.358	0.751	0.687	2	72.807	0.441	0.802	2	72.809
pH	3.088	0.079	1	52.917	0.275	0.600	1	52.693	1.666	0.197	1	51.734
Total plant cover	0.142	0.707	1	92.778	0.494	0.482	1	95.931	0.261	0.610	1	94.940
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	1340.000	36.610			0.053	0.230			0.001	0.038		
Transect	0	0			0.024	0.153			0.001	0.024		

Protist diversity	**Species richness**				**Shannon index**				**Evenness index**			
	Chi²	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**	**Chi²**	***p***	**NumDF**	**DenDF**
Elevation	3.714	0.054	1	41.484	1.448	0.229	1	35.640	0.472	0.492	1	37.224
Elevation²	3.351	0.067	1	93.190	1.309	0.253	1	80.120	1.888	0.169	1	80.851
Treatment	2.736	0.255	2	72.338	0.549	0.760	2	56.430	0.286	0.867	2	57.809
Elevation x Treatment	5.120	0.077	2	69.746	0.88	0.644	2	68.505	0.758	0.685	2	69.093
Elavtion² x Treatment	3.024	0.221	2	69.789	0.415	0.813	2	68.346	1.306	0.520	2	68.956
pH	1.685	0.194	1	55.385	0.399	0.528	1	40.954	2.387	0.122	1	41.988
TOC	**16.150**	**0**	1	55.385	0.329	0.566	1	40.953	0.800	0.371	1	41.987
Random factor	**Variance**	**Std. dev**			**Variance**	**Std. dev**			**Variance**	**Std. dev**		
Site:Transect	1675.700	40.940			0.013	0.114			0.001	0.025		
Transect	941.300	30.680			0.012	0.108			0	0		

Individual variable contribution in SEM for microbial species richness

Table 12 Contribution of each variable in SEM for plant and microbial species richness, showing the estimates of the scaled variables, standard errors (Std. Err), z- values, p- values, results where the latent variable has a variance of one (Std.lv), and results where the latent and observed variable have a variance of one (Std.all). To account for nonlinear relationships of elevation with the other variables, it is included as a composite variable (elevation and squared elevation). The interaction between (squared) elevation and treatment (snow gradient) was tested to determine whether the effect of elevation on diversity indices depends on snow gradient. Significant variables are in bold. The ln(pH) showed a significant positive effect on species richness of bacteria (p= 0.013) and protists (p= 0.007), but a negative effect for fungi (p= 0.014).

	Estimate	Std.Err	z-value	p- value	Std.lv	Std.all
Plant species richness ~						
Elevation comp.	**-0.242**	**0.056**	**-4.283**	**<0.001**	**-0.495**	**-0.482**
Treatment	0.02	0.103	0.191	0.849	0.02	0.019
Elevation x Treatment	-0.059	0.082	-0.718	0.473	-0.059	-0.058
Elevation^2 x Treatment	0.017	0.059	0.291	0.771	0.017	0.029
ln(pH)	0.035	0.08	0.431	0.667	0.035	0.035
Bacteria species richness ~						
Elevation comp.	**-0.255**	**0.059**	**-4.305**	**<0.001**	**-0.523**	**-0.525**
Treatment	0.12	0.094	1.278	0.201	0.12	0.12
Elevation x Treatment	-0.046	0.076	-0.611	0.541	-0.046	-0.047
Elevation^2 x Treatment	-0.014	0.054	-0.254	0.8	-0.014	-0.024
ln(pH)	**0.182**	**0.074**	**2.471**	**0.013**	**0.182**	**0.188**
Plant species richness	-0.01	0.084	-0.12	0.904	-0.01	-0.01
Fungi species richness ~						
Elevation comp.	-0.079	0.05	-1.598	0.11	-0.162	-0.163
Treatment	0.107	0.108	0.99	0.322	0.107	0.106
Elevation x Treatment	-0.076	0.086	-0.881	0.378	-0.076	-0.077
Elevation^2 x Treatment	0.021	0.061	0.335	0.737	0.021	0.036
ln(pH)	**-0.206**	**0.084**	**-2.449**	**0.014**	**-0.206**	**-0.213**
Plant species richness	0.092	0.096	0.964	0.335	0.092	0.095
Protist species richness ~						
Elevation comp.	-0.027	0.048	-0.56	0.575	-0.055	-0.055
Treatment	0.126	0.107	1.169	0.243	0.126	0.125
Elevation x Treatment	-0.013	0.086	-0.154	0.877	-0.013	-0.013
Elevation^2 x Treatment	0.077	0.061	1.268	0.205	0.077	0.135
ln(pH)	**0.225**	**0.084**	**2.683**	**0.007**	**0.225**	**0.233**
Plant species richness	-0.096	0.096	-1.005	0.315	-0.096	-0.099

Individual variable contribution in SEM for microbial Shannon index

Table 13 Contribution of each variable in SEM for plant species richness and microbial Shannon index, showing the estimates of the scaled variables, standard errors (Std. Err), z- values, p- values, results where the latent variable has a variance of one (Std.lv), and results where the latent and observed variable have a variance of one (Std.all). To account for nonlinear relationships of elevation with the other variables, it is included as a composite variable (elevation and squared elevation). The interaction between (squared) elevation and treatment (snow gradient) was tested to determine whether the effect of elevation on diversity indices depends on snow gradient. Significant variables are in bold. The ln(pH) only effected bacterial Shannon index (p< 0.001).

	Estimate	Std.Err	z-value	p-value	Std.lv	Std.all
Plant species richness~						
Elevation comp.	**-0.337**	**0.062**	**-5.408**	**<0.001**	**-0.525**	**-0.51**
Treatment	0.017	0.101	0.167	0.868	0.017	0.016
Elevation x Treatment	-0.06	0.081	-0.747	0.455	-0.06	-0.059
Elevation^2 x Treatment	0.018	0.057	0.306	0.76	0.018	0.03
ln(pH)	0.055	0.079	0.7	0.484	0.055	0.055
Bacteria Shannon index~						
Elevation comp.	**-0.401**	**0.064**	**-6.214**	**<0.001**	**-0.623**	**-0.621**
Treatment	0.063	0.083	0.753	0.452	0.063	0.062
Elevation x Treatment	-0.052	0.067	-0.785	0.432	-0.052	-0.052
Elevation^2 x Treatment	-0.037	0.047	-0.778	0.436	-0.037	-0.064
ln(pH)	**0.239**	**0.065**	**3.67**	**<0.001**	**0.239**	**0.245**
Plant species richness	0.038	0.075	0.508	0.612	0.038	0.039
Fungi Shannon index~						
Elevation comp.	0.106	0.067	1.578	0.115	0.164	0.165
Treatment	-0.046	0.111	-0.412	0.681	-0.046	-0.045
Elevation x Treatment	-0.155	0.089	-1.745	0.081	-0.155	-0.156
Elevation^2 x Treatment	0.043	0.063	0.685	0.493	0.043	0.075
ln(pH)	0.092	0.086	1.067	0.286	0.092	0.095
Plant species richness	-0.021	0.1	-0.21	0.834	-0.021	-0.022
Protist Shannon index~						
Elevation comp.	0.05	0.068	0.731	0.465	0.077	0.077
Treatment	0.048	0.113	0.425	0.671	0.048	0.048
Elevation x Treatment	0.058	0.091	0.637	0.524	0.058	0.059
Elevation^2 x Treatment	0.021	0.064	0.323	0.747	0.021	0.036
ln(pH)	-0.073	0.089	-0.828	0.408	-0.073	-0.076
Plant species richness	0.039	0.103	0.381	0.703	0.039	0.04

Individual variable contribution in SEM for microbial evenness index

Table 14 Contribution of each variable in SEM for plant species richness and microbial evenness index, showing the estimates of the scaled variables, standard errors (Std. Err), z- values, p- values, results where the latent variable has a variance of one (Std.lv), and results where the latent and observed variable have a variance of one (Std.all). To account for nonlinear relationships of elevation with the other variables, it is included as a composite variable (elevation and squared elevation). The interaction between (squared) elevation and treatment (snow gradient) was tested to determine whether the effect of elevation on diversity indices depends on snow gradient. Significant variables are in bold. Significant variables are in bold. The ln(pH) showed a significant positive effect on the evenness index of bacteria (p< 0.001).

	Estimate	Std.Err	z-value	p-value	Std.lv	Std.all
Plant species richness~						
Elevation comp.	**-0.351**	**0.063**	**-5.536**	**<0.001**	**-0.528**	**-0.513**
Treatment	0.016	0.101	0.163	0.871	0.016	0.016
Elevation x Treatment	-0.061	0.081	-0.751	0.453	-0.061	-0.059
$Elevation^2$ x Treatment	0.018	0.057	0.308	0.758	0.018	0.03
ln(pH)	0.059	0.079	0.744	0.457	0.059	0.059
Bacteria evenness index~						
Elevation comp.	**-0.415**	**0.065**	**-6.348**	**<0.001**	**-0.624**	**-0.622**
Treatment	0.052	0.083	0.63	0.529	0.052	0.052
Elevation x Treatment	-0.052	0.067	-0.776	0.438	-0.052	-0.052
$Elevation^2$ x Treatment	-0.039	0.047	-0.82	0.412	-0.039	-0.067
ln(pH)	**0.231**	**0.065**	**3.549**	**<0.001**	**0.231**	**0.237**
Plant species richness	0.042	0.076	0.549	0.583	0.042	0.043
Fungi evenness index~						
Elevation comp.	**0.145**	**0.068**	**2.125**	**0.034**	**0.219**	**0.22**
Treatment	-0.051	0.108	-0.468	0.639	-0.051	-0.051
Elevation x Treatment	-0.138	0.087	-1.596	0.11	-0.138	-0.14
$Elevation^2$ x Treatment	0.029	0.061	0.476	0.634	0.029	0.051
ln(pH)	0.157	0.085	1.85	0.064	0.157	0.162
Plant species richness	-0.042	0.098	-0.424	0.671	-0.042	-0.043
Protist evenness index~						
Elevation comp.	0.065	0.07	0.933	0.351	0.098	0.098
Treatment	0.002	0.112	0.015	0.988	0.002	0.002
Elevation x Treatment	0.059	0.09	0.652	0.515	0.059	0.059
$Elevation^2$ x Treatment	-0.005	0.064	-0.082	0.935	-0.005	-0.009
ln(pH)	-0.158	0.088	-1.791	0.073	-0.158	-0.163
Plant species richness	0.076	0.102	0.744	0.457	0.076	0.079