Soil Biology and Biochemistry 138 (2019) 107569

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

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

Plant expansion drives bacteria and collembola communities under winter climate change in frost-affected tundra

Eveline J. Krab[a,b,*], Sylvain Monteux[b], James T. Weedon[c,d], Ellen Dorrepaal[b]

[a] Swedish University of Agricultural Sciences, Department of Soil and Environment, SE-750 07, Uppsala, Sweden
[b] Climate Impacts Research Centre, Department of Ecology and Environmental Science, Umeå University, SE-981 07, Abisko, Sweden
[c] Department of Ecological Science, VU Amsterdam, De Boelelaan 1085, 1081 HV, Amsterdam, Netherlands
[d] Centre of Excellence PLECO, University of Antwerp, Universiteitsplein 1, Wilrijk, 2610, Belgium

ARTICLE INFO

Keywords:
Arctic
Global warming
Microbes
Snow
Shrub encroachment
Soil fauna

ABSTRACT

At high latitudes, winter warming facilitates vegetation expansion into barren frost-affected soils. The interplay of changes in winter climate and plant presence may alter soil functioning via effects on decomposers. Responses of decomposer soil fauna and microorganisms to such changes likely differ from each other, since their life histories, dispersal mechanisms and microhabitats vary greatly.

We investigated the relative impacts of short-term winter warming and increases in plant cover on bacteria and collembola community composition in cryoturbated, non-sorted circle tundra. By covering non-sorted circles with insulating gardening fibre cloth (fleeces) or using stone walls accumulating snow, we imposed two climate-change scenarios: snow accumulation increased autumn-to-late winter soil temperatures (−1 cm) by 1.4 °C, while fleeces warmed soils during that period by 1 °C and increased spring temperatures by 1.1 °C. Summer bacteria and collembola communities were sampled from within-circle locations differing in vegetation abundance and soil properties.

Two years of winter warming had no effects on either decomposer community. Instead, their community compositions were strongly determined by sampling location: communities in barren circle centres were distinct from those in vegetated outer rims, while communities in sparsely vegetated patches of circle centres were intermediate. Diversity patterns indicate that collembola communities are tightly linked to plant presence while bacteria communities correlated with soil properties.

Our results thus suggest that direct effects of short-term winter warming are likely to be minimal, but that vegetation encroachment on barren cryoturbated ground will affect decomposer community composition substantially. At decadal timescales, collembola community changes may follow relatively fast after warming-driven plant establishment into barren areas, whereas bacteria communities may take longer to respond. If shifts in decomposer community composition are indicative for changes in their activity, vegetation overgrowth will likely have much stronger effects on soil functioning in frost-affected tundra than short-term winter warming.

1. Introduction

Global biodiversity is changing rapidly in response to environmental changes, especially in arctic ecosystems (IPCC, 2013; Sala et al., 2000). In these ecosystems, the soil hosts undoubtedly the largest reservoir of diversity, even though its full magnitude is still unknown (Heywood and Watson, 1995). Changes in soil diversity may affect soil functioning, as a large part of the soil biota is involved in carbon (C) and nitrogen (N) turnover during decomposition (Heemsbergen, 2004; Strickland et al., 2009). For example microbial decomposers mineralize C and N by enzymatic breakdown of larger organic molecules, while invertebrate decomposers promote decomposition by grazing on microbes and by facilitating microbial growth through transforming particulate detritus into matter that breaks down more easily (Lavelle, 1997). Decomposer soil fauna and microorganisms vary greatly in life histories, dispersal mechanisms and microhabitats, and therefore likely respond in different ways to environmental changes. Increases in summer temperature often induce profound effects on soil communities and decomposition rates (e.g. Aerts, 2006). At high latitudes, however, soils are frozen or covered with snow for the largest part of the year and climatic changes are expected to be most dramatic during winter (e.g. IPCC, 2013; Thompson and Wallace, 2001). So far, the consequences of

* Corresponding author. Swedish University of Agricultural Sciences, Department of Soil and Environment, SE-750 07, Uppsala, Sweden.
E-mail addresses: eveline.krab@slu.se, e.j.krab@gmail.com (E.J. Krab).

https://doi.org/10.1016/j.soilbio.2019.107569
Received 16 January 2019; Received in revised form 12 August 2019; Accepted 18 August 2019
Available online 19 August 2019

winter climate change for soil decomposer communities, and if these differ between soil biota, remains poorly investigated (but see Mannisto et al., 2013; Morgado et al., 2016; Semenova et al., 2016; Sjursen et al., 2005).

It is increasingly recognized that altered snowfall patterns in cold regions can affect soil processes (e.g. Blankinship and Hart, 2012; Wipf et al., 2015) and directly induce changes in decomposer communities (Bokhorst et al., 2012; Semenova et al., 2016). Fungal communities have been shown to respond to experimental snow manipulation in northern ecosystems (Christiansen et al., 2017; Semenova et al., 2016), while bacteria communities in arctic peatlands are less responsive to changes in winter soil temperatures (Weedon et al., 2017). Soil fauna community composition also seems to be relatively robust to changes in (winter) climate (Alatalo et al., 2015; Bokhorst et al., 2012), although it has been suggested that the timing and nature of winter climate change phenomena, rather than their magnitude, might be more important determinants of changes to soil biota and their effects on ecosystem functioning (Olsson et al., 2003). Warmer autumns, or earlier snowfall, may, for example, prolong decomposer activity around plant senescence, whereas warmer springs may advance the timing of activity and microbial regime shifts (Edwards et al., 2006). Given the importance of seasonal shifts in decomposer communities for the retention of C and N (Bardgett et al., 2005; Zak et al., 1990), any disruption of these patterns could have far-reaching implications for the functioning of arctic ecosystems.

Changes in snow cover thickness and altered winter soil temperatures may not only directly affect soil decomposer communities, but also indirectly via their effects on plants (Frost et al., 2013; Krab et al., 2018). Soil organisms are likely to respond to vegetation changes, although its impact may differ between soil fauna and microbes. Microbial communities differ greatly between different vegetation types in arctic ecosystems (e.g. Wallenstein et al., 2007), but within arctic heathlands at least, spatial variability in microbial community composition seems generally low (Hill et al., 2016; Ushio et al., 2013), suggesting only a weak direct relationship between plant identity and microbial communities. Soil fauna, in contrast, are highly sensitive to plant identity (Coulson et al., 2003; Nielsen and Wall, 2013), litter quality (Krab et al., 2013) and root presence (Eo and Nakamoto, 2008; Pollierer et al., 2007). Further, both microbes and soil fauna are reported to be sensitive to changes in soil properties, such as pH, soil fertility and porosity (Beylich et al., 2010; Siciliano et al., 2014), which in longer-term may follow after vegetation cover changes. Direct, short-term winter warming effects on decomposer activity and carbon release may thus be amplified or mitigated by the indirect effects of restructuring of the decomposers' habitats (Hicks Pries et al., 2015; Sistla et al., 2013).

About 30% of the global permafrost region consists of partly barren, cryoturbated (frost-disturbed) soils, which contribute greatly to long-term C accumulation and play a critical role in the source-sink status of the arctic (Hugelius et al., 2014; Koven et al., 2011; Lundin et al., 2016). This is driven by burial of organic matter through frost-induced soil movement during the cold season, which likely makes these ecosystems particularly sensitive to changes in winter climate. Aerial observations indicate that cryoturbated soils in the subarctic region have been increasingly overgrown by vegetation in the past 50 years, a change that indeed has been attributed to climate warming (Becher et al., 2013; Frost et al., 2013). It is likely that winter processes have played an important role in this gradual overgrowth, by relieving plants from severe frost damage, prolonging seasonal growth and reducing damage to roots due to decreasing cryoturbation (Frost et al., 2013; Krab et al., 2018). As our knowledge on decomposer communities in cryoturbated soils is virtually non-existent (but see Gittel et al., 2014) it is still unclear which decomposers are present and how their communities may respond to changes in winter soil temperatures and vegetation cover changes. Changes in decomposer communities may ultimately lead to changes in ecosystem functioning (e.g. Cragg and Bardgett, 2001; Eisenhauer et al., 2012; Heemsbergen, 2004; Maron et al., 2018; Trivedi et al., 2016). We therefore require a better understanding of both direct and indirect mechanisms by which climate change may act on soil decomposer communities in these important landscapes.

We investigated how community composition of bacteria and collembola, are affected by winter climate change and plant establishment into cryoturbated tundra, specifically non-sorted circle (NSC) tundra. Collembola are considered a keystone faunal decomposer and are generally found in great abundance in arctic heaths (Seastedt, 1984; Alatalo et al., 2015) whereas bacteria are likely the most abundant microbial component in topsoils of cryoturbated ecosystems (Gittel et al., 2014, Makoto et al., unpublished data). Non-sorted circles are a common type of cryoturbated tundra, characterized by a dynamic pattern of patches of barren and vegetated soil. Due to the interplay of wind, frost heave and the lack of vegetation preventing accumulation of snow in the barren circle centres, NSCs are insulated with only shallow snow cover in winter and thus exposed to strong soil frost and repeated freeze-thaw cycles. Non-sorted circles provide natural gradients of vegetation presence and SOM build-up: the barren inner domains and recently overgrown inner domains both consist of (mainly) mineral soil but differ substantially in vegetation cover, whereas the overgrown areas of NSC inner domains are similar in vegetation community composition to the outer domains that have a well-established organic soil layer relative to the inner domain (e.g. Makoto and Klaminder, 2012). Additionally, NSCs provide gradients in harshness of winter climate, where inner domain soils are generally colder and more exposed to freeze thaw cycles than outer domains (Väisänen et al., 2017).

We subjected NSCs in alpine tundra in subarctic Sweden to two winters of increased winter insulation, by simulating two short-term winter warming scenarios: 1) we accumulated snow on NSCs by using snow walls, increasing soil temperatures from late autumn to late winter, and 2) we covered NSCs with gardening fleeces, thereby warming soils from early autumn to late spring. Bacteria and collembola communities were sampled in barren areas in inner domains, sparsely vegetated areas in inner domains and in fully vegetated outer domains of NSCs, to represent the effects of plant cover on decomposer communities. We assessed to what extent winter warming and potential habitat changes represented by plant cover alter decomposer community structure by assessing β-diversity and operational taxonomic units (OTUs)/species relative abundances. We hypothesized that both the direct effects of winter climate change and effects via vegetation cover and its associated changes in soil properties will lead to altered summer community composition of bacteria and collembola. Considering the natural differences in winter soil microclimate between inner and outer domains (Väisänen et al., 2017), short-term increases in winter soil temperatures will most likely lead to convergence of decomposer community composition towards outer domain community composition. Moreover, we hypothesized the relative impact of winter climate change and vegetation cover-driven effects to differ between bacteria and collembola. As bacteria seem to be less directly affected by plant presence and identity than collembola in arctic tundra (Coulson et al., 1993; Hill et al., 2016; Ushio et al., 2013) we expected bacteria communities to show a larger response to direct abiotic effects of winter climate change, in particular to the more extensive fleece manipulation via spring-warming effects on microbial community turnover. In contrast, we expected collembola community composition to be more strongly related to vegetation cover. Additionally, we take advantage of the decoupled gradients in soil properties and vegetation presence between (newly overgrown) NSC centres and outer domains. These gradients allow to test whether bacteria and collembola community composition changes related to potential plant establishment into NSCs are more tightly linked to vegetation presence or to vegetation-induced changes to soil properties, such as organic matter build-up. Together, this set of treatments do not only provide us with baseline knowledge on decomposer communities in frost-affected soils, but also give us a

perspective of how winter climate change and changes in vegetation cover may affect these communities in cryoturbated tundra.

2. Methods

2.1. Site description

The study was conducted in subarctic-alpine cryoturbated tundra in Northern Sweden at approximately 860 m a.s.l. (68°30′ N, 19°11′E). The site is located 20 km southeast of Abisko (385 m a.s.l.), with mean annual air temperature and precipitation (1990–2013) of 0.3 °C and 337 mm, respectively (Abisko Station Meteorological Data). A comparable higher-altitude nearby site is Latnjajaure (981 m a.s.l.), that has a mean annual air temperature of −2.0 °C (Björk et al., 2007). Snow on the experimental site is typically present from November to May. The site is located in a zone of discontinuous permafrost, the active layer is > 2 m, and bedrock starts at about 1 m depth (*unpublished data*). The site is characterized by an abundance of NSCs with high cryogenic activity (Klaus et al., 2013). Non-sorted circles can be observed as partially vegetated to barren circular/elongated patches with a diameter of 1–3 m (Fig. S1a), which are in part covered by crustose lichens and contain spots with loose lying rocks, pebbles and disturbed silt without lichen cover (henceforth referred to as “inner domains”) (Makoto and Klaminder, 2012). These circles are surrounded by heath vegetation dominated by mosses, the evergreen dwarf shrubs *Empetrum nigrum* L. and *Vaccinium vitis-idaea* L. and the deciduous dwarf shrubs *Betula nana* L. and *Vaccinium uliginosum* L. (“outer domains”) (Makoto and Klaminder, 2012).

2.2. Experimental setup

We created two winter climate change scenarios by subjecting individual NSCs to two winters of increased experimental winter insulation: 1) We accumulated snow on NSCs by using stone walls, increasing soil temperatures from late autumn to late winter (~6 months, Table S1, n = 3), and 2) we covered NSCs by gardening fleeces from early autumn until late spring, warming soils for a longer period (~8 months, Table S1, n = 6). To do this, we selected fifteen NSCs (1–2 m diameter) in an area of about 100 m × 150 m that showed signs of cryogenic activity. The chosen NSCs were spatially arranged into six blocks, each located at least 10 meters apart. Blocks 1, 2 and 3 contained one replicate of each winter climate change treatment (3 circles per block), while block 4, 5 and 6 only contained a replicate of the control and fleece treatments (2 circles per block). At one randomly selected NSC in block 1, 2 and 3, we constructed stone walls from local rocks along the upwind side (westerly) of each circle and its vegetated outer domain, to trap snow and experimentally increase snow depth during the snow-covered season. These walls were max. 60 cm high, 2 m long, and had a crescent-shaped form (Fig. S1ac). The number of replicates of this treatment was practically constrained by the availability of rocks of suitable sizes at the site, while building walls or fences with other materials was prevented by the high cryogenic activity. In all six blocks, one randomly selected NSC was completely covered (including parts of the outer domains) with rectangular, 4-layered polypropylene fleece fabric (Nelson Garden, Sweden; 17 g/m^2) to increase winter soil insulation from early autumn (2012: September 28th; 2013: September 18th) to late spring (2013: May 31st; 2014: June 3rd, about two weeks after the natural snowmelt). Fleeces were kept in place with ropes and small rocks around the edges (Fig. S1b). One further circle in each of six blocks served as a control and received no treatment.

2.3. Effects of treatments on snow depth and soil temperature

Snow depth was measured in all treatments in both years at the peak of snow accumulation (late March/early April) at 50-cm intervals along a west-east transect across each plot (i.e. perpendicular to the stone walls). In 2014, an additional snow depth measurement was made at the end of April, following a period of heavy snowfall. The snow accumulation treatment increased snow cover depth across the NSCs by an average of 7 cm (average depth over two years 10 ± 13 cm in the snow treatment, and 3 ± 5 cm in the control treatment) (Table S2). Snow depth increase was larger close to the stone wall, as most snow accumulated directly behind the walls (Figs. S1c and S2), but this did not lead to soil temperatures differences between inner and outer domains (*unpublished data*; 2014–2016).

In each NSC, soil temperature was logged in the inner domain (1 cm depth) using temperature loggers with external sensors (Tiny Tag Talk 2, Intab Interface-Teknik AB, Sweden) installed in autumn 2012 and 2013 and removed in late spring (in 2014 soil temperatures were also recorded in summer until the 21st of July). For better understanding of the effects of the treatments, temperature data were split into five sub-seasons with characteristic patterns of temperature, daylight, and snow conditions: i.e. autumn, midwinter, late winter, spring and summer (Table S1). In both years, mean soil temperatures during the coldest periods of the winter season (autumn, midwinter, late winter) were 0.6–1.3 °C warmer in the fleece treatment and 0.9–1.8 °C warmer in the snow treatment than in the control plots (Fig. S3, Table S3). Our treatments, however, slightly differed in their effects on soil temperatures in some sub-seasons (Tables S4 and S5). Both fleece and snow treatments had equally strong positive effects on soil temperatures in autumn (1.0–1.7 °C increase, Table S3) and mid-winter (0.8–1.9 °C increase, Table S3), while only the snow treatment significantly increased soil temperatures in the coldest part of the winter, the late-winter sub-season (with 0.9–1.4 °C, Table S3). In spring, only the fleece treatment had an effect on soil temperatures (1.3 °C warmer, Table S3). Summer soil temperatures (only measured in 2014) were unaffected by our treatments (Fig. S2, Table S3). Our treatments thus induced comparable temperature increases to previous snow manipulation studies (Dorrepaal et al., 2004; Johansson et al., 2013). Moreover, our obtained spring warming corresponded to observed warming trends during springtime in the Arctic of 1–2 °C per decade in the last 20 years (Rigor et al., 2000); and is therefore a realistic simulation of future climate change predictions for the coming decades.

2.4. Field sampling

To analyse diversity of soil fauna and microbes, and differences in soil properties, soil cores were taken from the experimentally manipulated and control NSCs in July 2014. Cores were taken in (i) the non-vegetated barren NSC inner domain, (ii) sparsely vegetated parts in the NSC inner domain and (iii) the vegetated outer domain just outside the NSCs (henceforth ‘sampling domains’). Vegetation cover on soil cores taken from the outer domains was > 80%, vegetation cover on cores taken from the barren inner domains was < 5%, whereas cores taken from the sparsely vegetated inner domains were intermediate between the two extremes, on average 34 ± 6% (average ± s.e.) vegetation cover ($P < 0.001$, Table 2, Fig. 4a). Samples taken from NSCs that were manipulated using a stone wall were taken from the western side of the circles (for outer domains > 10 cm from the walls), which received the most additional snow (29 ± 19 cm increase directly after the stone wall – 10 ± 8 cm increase 50 cm east of stone wall; Fig. S2). Samples from control and fleece treated NSCs were taken in a randomly assigned direction but at similar spots along the gradient; i.e. for inner domains in the circle centre, and for outer domains at a similar distance from the inner domain ‘border’ (~25 cm).

In each sampling domain, one soil core was taken to investigate abundance and diversity of the soil fauna (collembola) community, 10-cm in diameter and approximately 8-cm deep. Further, two smaller soil samples (from 1 cm to 8 cm depth) were taken immediately adjacent to these soil cores using ethanol-cleaned forceps/spatula and transferred into separate 2 mL tubes, to determine bacterial diversity and to be able to relate the bacteria to the collembola community. The soil fauna cores

were transferred into PVC containers directly after collection in the field and photographed from above for vegetation cover estimate of sampling domains in NSCs. Photos were overlain by a grid (digitally) and grid cells containing vegetation were counted and expressed as a percentage of the total surface. Three additional cores of 2.5 cm diameter (8 cm deep) were taken in each sampling domain 2 days prior to the sampling of collembola and bacteria. These three cores were taken within 30–50 cm of the decomposer sampling location in each domain, and pooled after sampling. While disturbance associated with this sampling on the decomposer communities is consistent across the treatments and likely minimal, care should be taken when comparing our communities with other studies. All cores were stored at 4°C for 24 h before extraction, except for samples for bacterial analyses, which were stored directly at −80 °C until further analyses.

2.5. Collembola extraction

Collembola were extracted from their cores for 17 days using a Tullgren heat extractor (Van Straalen and Rijninks, 1982) that created a within-core temperature gradient of 30 °C (top) −16 °C (bottom) (Krab et al., 2015). Collembola were collected in 70% ethanol and determined with a microscope to species level using the keys of Fjellberg (1998, 2007) and counted for each core separately, after which densities (ind. L^{-1}) were determined using the stone-corrected volume of each core.

2.6. Bacterial DNA extraction, PCR, clean-up and sequencing

Bacterial community profiles were generated for each sample using amplicon sequencing of 16S RNA genes from DNA extracts. DNA was extracted from 0.25 to 0.40 g of soil, using a PowerSoil DNA Extraction Kit (MoBio), according to the manufacturer's instructions. Presence and quality of DNA was checked on a Nanodrop 1000 spectrophotometer (Thermo Scientific) and concentrations ranged from 2.3 to 168.7 ng/μL, then DNA templates were diluted to 5 ng/μL, or in a 1:1 ratio if concentration was too low, to reduce the concentration of PCR inhibitors.

The V3 region of the 16S ribosomal RNA was targeted in PCR amplification to characterize bacterial diversity (Bartram et al., 2011) (PCR details and primers in Table S6). PCR products were cleaned using AMPure XP Bead Clean-up (Beckman-Coulter) according to manufacturer's instructions. Clean PCR products from each sample were then quantified using Nanodrop 1000 Spectrophotometer, and pooled together in equimolar ratios. Three 20 μL subsamples from this clean pooled library were subsequently ran through a 1.5% agarose electrophoresis gel for size selection and gel extractions with a QIAquick Gel Extraction Kit (Qiagen) was performed according to the manufacturer's instructions. The resulting gel-extracted library was quantified on a Qubit 3.0 Fluorometer (Thermo Scientific), diluted to 4pM and sequenced on a MiSeq platform (Illumina) using V2 chemistry with 2 × 150 cycles. Samples were then demultiplexed using MiSeq Reporter GenerateFASTQ workflow with default parameters, and paired reads were uploaded to ENA (study number PRJEB26326).

2.7. Bioinformatics pipeline

Only a short summary of the bioinformatics processing is described here, while details of commands used are available as a Jupyter notebook linked to this article at figshare.com. Paired-end reads were merged together using VSEARCH v2.3.0 (Rognes et al., 2016) keeping only perfect matches (*-fastq_maxdiffs 0*). Primers were removed using a custom-made *awk* script prior to quality-filtering (maximum expected error threshold of 0.05; *-fastq_maxee 0.05*), then dereplicated sequences were clustered into Operational Taxonomic Units (OTUs) with a 97% identity using VSEARCH *-cluster_size* algorithm. Presence of chimeric OTUs was then checked with the UCHIME algorithm (Edgar et al., 2011) against the Broad Institute GOLD database. OTUs were mapped to the original reads using VSEARCH with a 97% similarity cut-off to create an OTU table. The OTU table was imported in R (v 3.1.3) to remove OTUs present in the DNA extraction and PCR technical control samples (i.e. putative contaminants). Technical controls had very low numbers of reads (830 and 1033); only one biological sample had fewer (476) reads and had failed to amplify. Three OTUs each represented more than 5% of the reads in the technical control samples, but only 0.47% of the total reads in all samples combined (8030 out of 1694153). The low number of reads from technical control samples, and low abundance of their dominant OTUs in other samples, therefore suggests negligible amounts of contamination. For further analyses, the three OTUs that predominated in technical control samples were removed from the combined dataset. The updated OTU table was analyzed subsequently in QIIME (v1.9.1, Caporaso et al., 2010) OTUs that were not present in at least 10% of the samples were discarded, and representative sequences for the remaining OTUs were aligned using PyNAST v1.2.2 (Caporaso et al., 2010). A phylogenetic tree was constructed using FastTree v2.13 (Price et al., 2010) and taxonomy was assigned to the OTUs using the RDP naïve Bayesian classifier v2.2 (Wang et al., 2007) and the Greengenes 13_8 database (McDonald et al., 2012). Finally, the OTU table was normalized by rarefaction to 2000 sequences per sample (Kuczynski et al., 2010), and weighted UniFrac phylogenetic distance matrixes were computed (Lozupone et al., 2011) for further statistical analyses (see below).

2.8. Soil properties

Soil for measuring soil properties was sieved through a 2-mm mesh. We used 10 g of the sieved soil for determining soil organic matter % (g organic material/g dry weight) by loss on ignition (6 h at 500 °C). We measured pH (Mettler Toledo MP220) after adding 50 ml of demineralized water to 10 g of sieved soil and 2 h of shaking at 250 rpm on an orbital shaker. Soil bulk density (g soil/cm^3) and volumetric water content (cm^3 H_2O/cm^3 core) were calculated by weighing the soil invertebrate cores before soil fauna extraction and measuring the exact height of the core. After soil fauna extraction, the volume and weight of stones were determined and removed, and the cores were dried at 70 °C for 48 h and weighed again.

2.9. Data and statistical analyses

All statistical analyses were performed using the R software (v.3.2.3).

To visualize dissimilarity patterns, nonmetric multidimensional scaling (NMDS) was carried out for bacteria (deep (8 cm) and surface (1 cm) communities combined (Fig. 1) as well as separately (Fig. S4)), and for collembola. For assessing how diversity patterns are related to vegetation cover and soil properties (pH, SOM%, bulk and volumetric soil moisture) we projected the latter variables onto the NMDS ordination, and tested their correlation with the ordination space using the envfit() function in the vegan package (Oksanen, 2015).

To test if the community compositions of bacteria and collembola were affected by the winter climate treatments and depended on sampling domains, we performed permutation tests for multifactorial multivariate analysis of variance (Two-way PERMANOVA, no. of permutations: 999, Anderson, 2001). Dissimilarity matrixes were created using commonly used indices for each decomposer group that account for relative 'species' abundances: 'Bray-Curtis' for collembola (Bray and Curtis, 1957) and 'weighted Unifrac' dissimilarity for bacteria (Lozupone et al., 2011). Fixed factors in these analyses were 'winter climate treatment' and 'sampling domain,' experimental block was added as random factor to account for spatial dependency of observations, as community composition in the different domains within a given block could be expected to be non-independent. As PERMANOVA analyses do not perform well on unbalanced experimental designs (i.e. different numbers of replicates per treatment combination) (Anderson and Walsh, 2013), separate analyses were carried out for the control

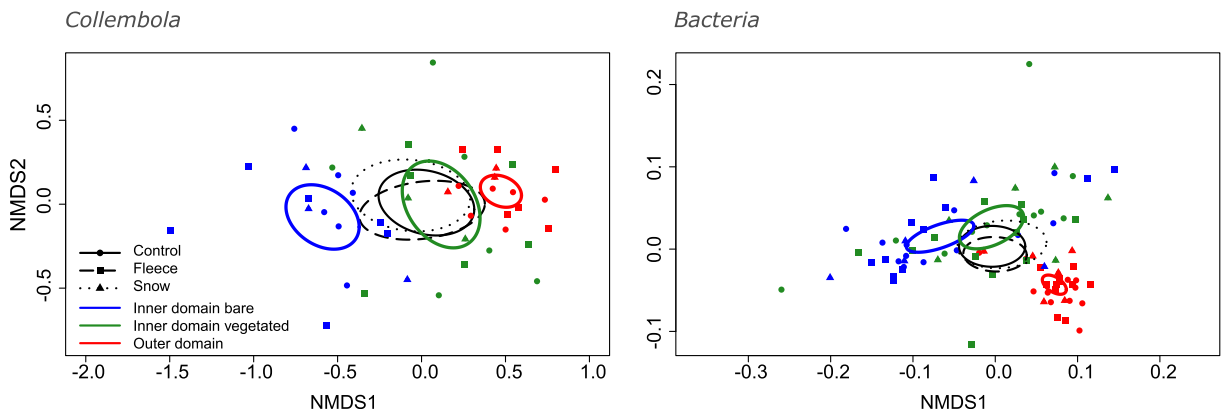

Fig. 1. NMDS ordination plots of collembola species composition and bacteria OTUs composition in non-sorted circles. Ellipses represent 95% confidence areas based on the standard errors of the average of the axis scores. The coloured ellipses are averaged across all treatments. Black ellipses are averaged across all sampling domains. Dissimilarities between communities are shown by a larger separation in the NMDS-1 and NMDS-2 score space. Stress for collembola ordination was 0.16, stress for bacteria ordination 0.11. Each point depicted in this ordination depicts one sampled community; microbial communities contain both 'surface communities' (−1 cm) and 'deep communities' (−8 cm).

and fleece treatment (n = 6) and for all three treatments including only the blocks where all treatments were present (block, 1–3, n = 3). These analyses were carried out for the deeper- and surface-living bacteria and for the collembola community separately. To identify the differences between levels of domain factors we performed pairwise PERMANOVA analyses followed by P-value adjustment (Holm correction) to maintain an overall alpha value of 0.05 (Martinez Arbizu, 2017). To test the degree of correspondence between bacterial and collembola diversity patterns, we performed a Procrustes test.

Effects of winter warming treatment and sampling domain on vegetation cover and soil properties were analysed by linear mixed models, As these tests were run on the full (unbalanced) dataset, block could not be included as random factor (see Krab et al., 2018), instead Circle ID was added as random factor to account for spatial dependency of observations. Data were transformed where needed to fit the assumptions of normality and homoscedasticity of residuals. Post-hoc tests were conducted using least square means using the difflsmeans() function from the package lmerTest (Kuznetsova et al., 2017).

3. Results

3.1. Decomposer community composition

Collembola and bacteria communities were not affected by the winter climate treatments but strongly responded to sampling domains (Fig. 1, Table 1). The responses of bacteria and collembola showed similar patterns, as NMDS ordinations of the collembola and bacteria communities were significantly correlated (procrustes sum of squares 0.79/0.64, correlation = 0.46/0.60, significance = 0.001, for collembola vs. surface/deep bacteria communities).

Collembola and bacteria communities differed strongly between sampling domains with different plant cover (Fig. 1; Permanova $P < 0.01$, Table 1 (test A-F)). Both collembola and bacteria communities in the barren inner domains were significantly different from communities found in the outer domains (Fig. 1 (no overlap of the blue and red markers and ellipses); Table S7). Communities from sparsely vegetated inner domain patches were intermediate between the barren inner domains and outer domains (Fig. 1), indicating that these communities form a transition between the two other communities. These patterns were consistent when surface- and deeper-living bacteria communities were analysed separately (Fig. S4). Interestingly, collembola communities in the vegetated inner domain showed a larger resemblance with outer domain communities (Fig. 1; Table S7 (post-hoc tests A)), whereas the surface bacteria communities in vegetated inner domains were more similar to those in the barren inner domain (Fig. 1, Fig. S4; Table S7 (post-hoc tests C/D)). Deep living bacteria communities differed significantly between all sampling domains (Table S7 (post hoc test E/F)). No interaction between treatment and sampling domain was found, indicating that the lack of response of the communities to short-term winter climate change was consistent among the sampling domains.

3.2. Patterns in taxonomic composition

Most collembola species were more abundant in vegetated inner and outer domains than in the barren inner domains, except for *Folsomia quadrioculata* and *Tetracanthella wahlgreni*. These species showed (relatively) high abundances in all sampling domains; from 42.6 ± 17.7% in outer domains in the control treatment to 89.5 ± 43.2% in barren inner domains in the fleece treatment for *F. quadrioculata* (average ± se, Fig. 2), and for *T. walghreni* from 2.4 ± 0.8% in barren inner domains in the fleece treatment to 27.9 ± 23.2% in vegetated inner domains in the snow treatment (average ± se, Fig. 2). However these species were less clearly associated with the outer domain in the ordination (Fig. 3a), as their relative abundances in vegetated domains was lower compared to other species (except for *T. walghreni* in the snow treatments, Fig. 2). *Folsomia quadrioculata* contributed on average 84.8 ± 18.1% of the total relative abundance in barren inner domains, but only 47.3 ± 6.6% in the inner and 44.3 ± 9.9% in the outer domains with vegetation (average over control and treatments ± s.e). The species *Isotomiella minor* was rarely found in the barren inner domains (1.2 ± 0.8%) but formed approximately 25% of the community in the vegetated inner domains (23.2 ± 6.9%) and outer domains (25.1 ± 6.7%) (average over control and treatments ± s.e). The gradient in increasing vegetation cover corresponded to an increase in collembola species richness across sampling domains (Fig. S5). When correlating taxonomic information to community dissimilarity in our ordination (Fig. 3a), most (low abundance) species were positively associated with the outer domain.

Sequences assigned to the phyla Proteobacteria, Acidobacteria and Actinobacteria were most abundant in the NSCs (Fig. 2). There were no clear differences in relative abundance of phyla between treatments but outer domains contained relatively more Actinobacteria and fewer Chloroflexi and Cyanobacteria than inner domains (Fig. 2) and estimates of OTU diversity varied between sampling domains (Fig. S5). When correlating taxonomic information with community dissimilarity in our ordination, communities in (barren) inner domains were associated with higher abundances of WPS2, Verrucomicrobia, A3 and Gemmatimonadetes, and vegetated outer domains with Acidobacteria, Actinobacteria and Proteobacteria that are the most abundant phyla

Table 1
Effects of winter warming treatments (control, fleece and snow addition) and sampling domain (Inner domain barren, Inner domain vegetated and Outer domain) on community composition (β-diversity) of collembola (0–8 cm depth) and bacteria communities (at 1 and 8 cm depth) in NSCs, analysed by PERMANOVA models with only the control and fleece treatments (n = 6, test ***A*** for collembola, test ***C*** and ***E*** for bacteria) or with all treatments (n = 3, test ***B*** for collembola, test ***D*** and ***F*** for bacteria). Statistically significant effects (P < 0.05) are in bold font.

		dF	Resid.	F_{MODEL}	R^2	Pr (> F)
***Collembola* (0–8 cm)**						
A: Treatments →	Treatment	1	30	1.171	0.027	0.303
Control & Fleece (n = 6)	**Domain**	2	30	4.658	0.216	**0.001**
	Treatment x Domain	2	30	1.307	0.061	0.237
B: Treatments→	Treatment	2	18	0.834	0.055	0.558
Control, Fleece & Snow (n = 3)	**Domain**	2	18	2.953	0.195	**0.004**
	Treatment x Domain	4	18	1.176	0.155	0.245
***Bacteria* (-1 cm)**						
C: Treatments →	Treatment	1	29	0.763	0.016	0.594
Control & Fleece (n = 6)	**Domain**	2	29	7.539	0.315	**0.001**
	Treatment x Domain	2	29	1.538	0.064	0.150
D: Treatments →	Treatment	2	17	0.976	0.062	0.490
Control, Fleece & Snow (n = 3)	**Domain**	2	17	4.183	0.267	**0.001**
	Treatment x Domain	4	17	1.016	0.130	0.465
***Bacteria* (-8 cm)**						
E: Treatments →	Treatment	1	27	1.078	0.019	0.318
Control & Fleece (n = 6)	**Domain**	2	27	15.212	0.510	**0.001**
	Treatment x Domain	2	27	0.580	0.019	0.812
F: Treatments →	Treatment	2	18	0.561	0.024	0.737
Control, Fleece & Snow (n = 3)	**Domain**	2	18	12.591	0.539	**0.001**
	Treatment x Domain	4	18	0.611	0.052	0.801

Table 2
Linear mixed model results testing the effects of winter warming treatments (control, fleece and snow), sampling domain (Inner domain barren, Inner domain vegetated and Outer domain), and their interactions on vegetation cover (%) and soil properties in NSCs. Soil properties tested are: soil organic matter content (SOM %), bulk density, pH and moisture. Data for vegetation cover were rank-transformed and for SOM% log-transformed transformed prior to analysis. Statistically significant effects (P < 0.05) are shown in bold.

	Num DF	Den DF	F_{MODEL}	Pr (> F)
Vegetation cover %				
Treatment	2	12	1.52	0.349
Domain	2	24	106.45	< **0.001**
Treatment x Domain	4	24	1.43	0.256
SOM %				
Treatment	2	12	5.47	**0.02**
Domain	2	24	139.43	< **0.001**
Treatment x Domain	4	24	3.29	**0.028**
Bulk density				
Treatment	2	12	0.12	0.890
Domain	2	24	163.99	< **0.001**
Treatment x Domain	4	24	3.61	**0.019**
pH				
Treatment	2	12	0.97	0.407
Domain	2	24	56.97	< **0.001**
Treatment x Domain	4	24	4.16	**0.011**
Soil moisture				
Treatment	2	36	0.33	0.720
Domain	2	36	14.62	> < < **0.001**
Treatment x Domain	4	36	1.71	0.169

overall (Fig. 3b).

3.3. Soil properties

Sampling domain was by far the strongest driver of variation in all measured soil properties (all P < 0.001, Table 2, Fig. 4). Most soil properties differed between each sampling domain; the inner domain with vegetation was normally an intermediate between the barren inner domain and outer domain (except for soil moisture). Especially for SOM % and pH, barren and vegetated inner domains were somewhat similar (although still significantly different from each other) and both differed substantially from the outer domain, reflecting the mineral nature of the soil in inner domains (Fig. 4bd). There were no overall main effects of the winter climate manipulation treatments on any of the soil properties during the summer. However, there were treatment effects on SOM% in vegetated inner domains (3.5 ± 0.9% in control, 2.8 ± 0.5% in fleece and 1.4% ± 0.5% in the snow treatment) and vegetated outer domains (32.6 ± 4.4% in control, 25.9 ± 4.7% in the fleece and 10.2 ± 3.0% in the snow treatment), and on bulk density in barren inner domains (1.5 g cm-3 ± 0.1 $g\,cm^{-3}$ in control, 1.3 $g\,cm^{-3}$ ± 0.1 $g\,cm^{-3}$ in fleece and 1.1 $g\,cm^{-3}$ ± 0.1 $g\,cm^{-3}$ in the snow treatment), all showing a decline due to the fleece and snow treatment (Fig. 4bc).

3.4. Community composition related to vegetation cover and soil properties

Only vegetation cover, pH and soil moisture content were significantly associated with collembola dissimilarity patterns, of which vegetation cover correlated most strongly (R^2 = 0.63, $P < 0.05$, Fig. 3c). In contrast, all (soil) properties were significantly correlated with bacterial community dissimilarity, of which bulk density (R^2 = 0.53, $P < 0.001$, Fig. 3d) and SOM % (R^2 = 0.51, $P < 0.001$) correlated most strongly and primarily with the differences between inner and outer domain. Microbial communities in inner barren domains seemed to separate from those in vegetated inner domains driven by other soil properties rather than vegetation presence in the barren

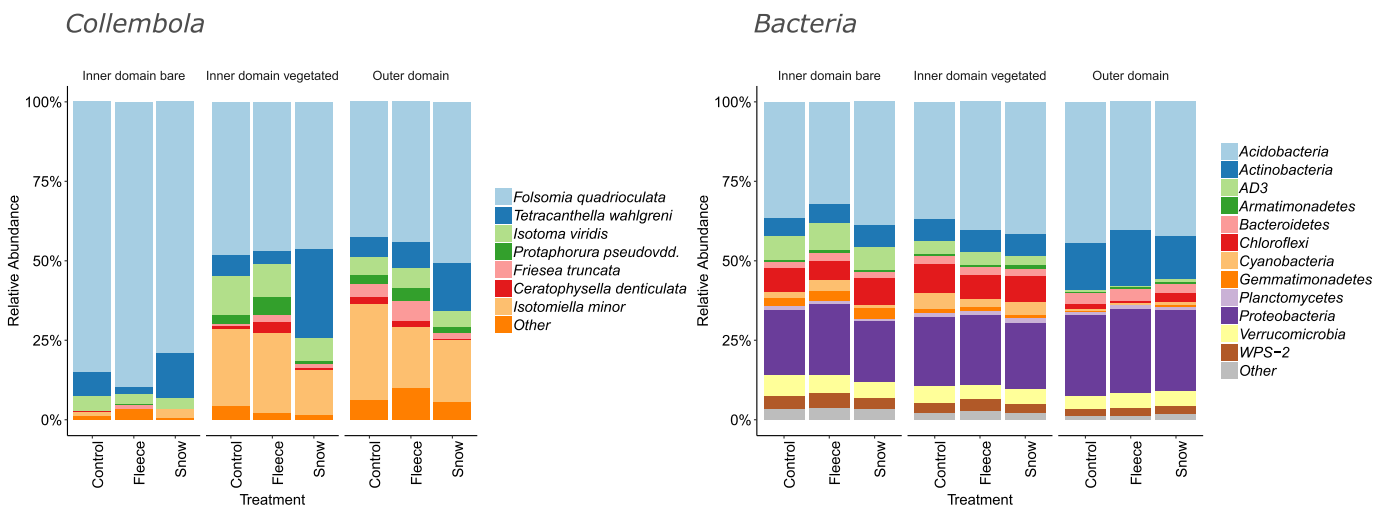

Fig. 2. Average relative abundance (%) of collembola species and bacterial phyla (based on relative abundance of OTUs) in three sampling domains of non-sorted circles: 'inner domain barren', 'inner domain vegetated' and 'outer domain'; and for the three different winter warming treatments: 'control', 'fleece' and 'snow'. N = 6 for the control and fleece treatments and n = 3 for the snow treatment for collembola communities. N = 12 for the control and fleece treatments and n = 6 for the snow treatment for bacteria, for which communities are averaged over both sampling depths.

inner domains (Fig. 3d).

4. Discussion

We studied the effects of short-term winter climate change and plant establishment in cryoturbated soils on microbial and faunal decomposers, by manipulating winter soil temperature for two years, and effects of vegetation cover changes across NSCs. We predicted that both winter climate and vegetation cover changes would impact decomposers, and that bacteria would more strongly respond to direct effects of altered winter climate (treatment), whereas collembola communities would be more affected by changes in vegetation cover of

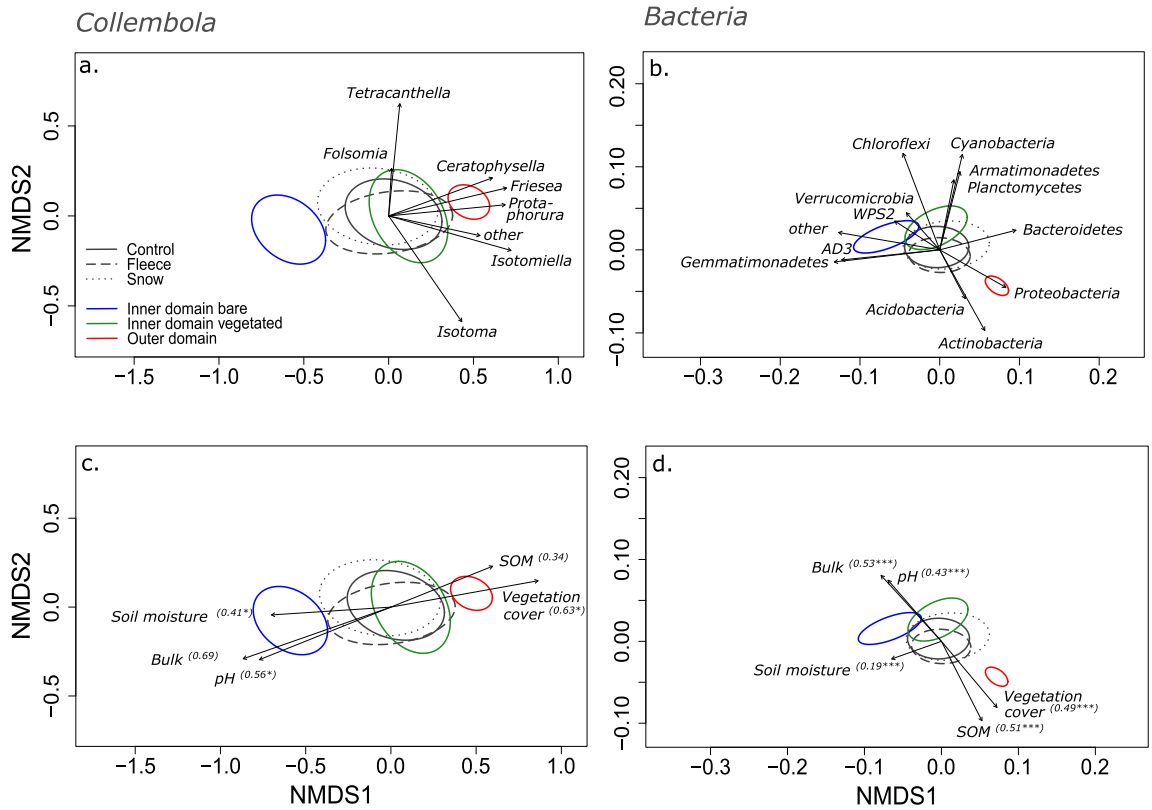

Fig. 3. NMDS ordination plots of collembola species composition and bacteria OTUs in non-sorted circles with a) vectors for collembola species abundance of the most abundant species (only genus name is represented in figure), b) relative abundance of the most abundant bacteria phyla and c) vectors of the measured explaining environmental variables plotted onto the NMDS ordination for collembola and d) for bacteria. The projections of points onto the vectors have maximum correlation with species/phyla (relative) abundance in the community (a and b) and corresponding environmental variables (c and d). Numbers and asterisks in brackets represent R^2 values and statistical significance of correlations with the ordination space (envfit, significance codes: '***' 0.001; '*' 0.05). Ellipses and vectors are plotted on ordinations as presented in Fig. 1.

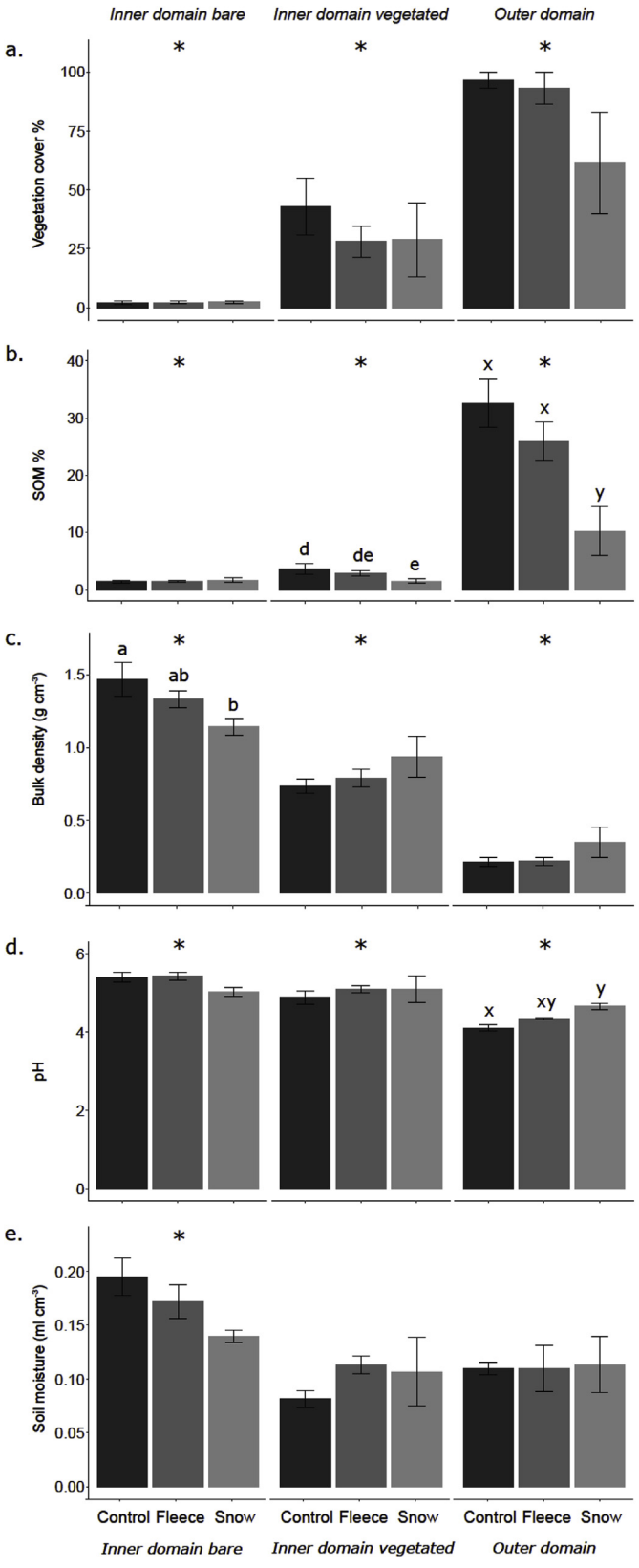

Fig. 4. Effects of winter warming treatments ('control', 'fleece' and 'snow' (grey scales)) on soil properties (b-e, mean ± s.e.) in three sampling domains of non-sorted circles ('inner domain barren', 'inner domain vegetated' and 'outer domain'); and the corresponding vegetation cover (a). Soil properties are: b) soil organic matter % (SOM), c) bulk density, d) pH, and e) soil moisture. Sampling domains with asterisks above the bars differ statistically significantly ($P < 0.05$; Post-hoc tests) from other domains with or without asterisk for the respective soil property. Different letters above bars indicate statistically significant differences between winter treatments ($P < 0.05$; Post-hoc tests) within each sampling domain. N = 6 for the 'control' and 'fleece' treatment, n = 3 for the 'snow' treatment.

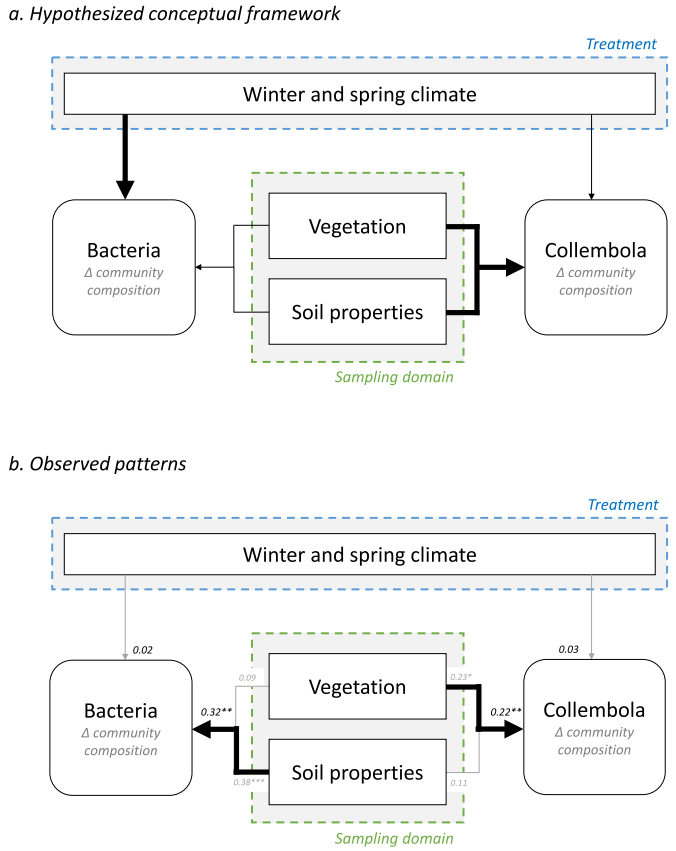

Fig. 5. Conceptual figure explaining a) the hypothesized relative importance of short-term direct effects of winter climate change (Treatment) vs. vegetation cover and soil property changes (Sampling domain) on bacteria and collembola community composition (β-diversity) in NSCs. And b) the suggested importance of these drivers based on the results of this study. Direct short-term effects of winter climate change on vegetation and soil properties, as well as interactions between bacteria and collembola have been omitted from this framework. Arrows indicate hypothesized (a) or observed statistically significant (b) correlations, arrow size and line thickness indicate relative importance of the drivers, and grey arrows (in (b)) non-significant effects. Black numbers represent correlation coefficients (R^2) from the model testing the effect of treatment and sampling domain (Table 1, Model A and C) whereas the grey numbers represent correlation coefficients testing the effects of separate sampling domains (Table S7, Model A and C). Note that these correlation coefficients are obtained by carrying out separate tests for bacteria and collembola: relative differences should thus only considered per coefficient (or arrow/line) pair: within decomposer groups and within coefficient colour (grey/black). N = 6, Stars indicate significant effects of drivers: * = $P < 0.05$, ** $P < 0.001$. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

NSCs, represented by sampling domain (Fig. 5a). However, increased winter (and spring) soil temperatures had no significant effect on composition of both collembola and bacteria summer communities, and did thus not make the communities of the inner domains more similar to outer domain communities. Instead, community composition of both decomposer groups was strongly determined by presence of vegetation and associated soil properties. Such consistent lack of response of

bacteria and collembola communities to short-term winter warming, and strong response to plant presence in NSCs are not in accordance with our expectation that bacteria would be more strongly affected by our short-term climate manipulations than collembola. Still, we found indications that differences in collembola community composition are most strongly associated with vegetation presence, while shifts in bacteria community assemblage are mostly related to differences in soil properties (Fig. 5b). Below we will further discuss the potential causes and implications of these findings.

4.1. No effect of short-term winter warming on decomposer community composition

Short-term winter warming imposed by snow addition and gardening fleeces affected neither bacterial nor collembola community composition during the summer. Microbial communities in cold soils may experience strong community shifts during spring (Schadt, 2003; Buckeridge et al., 2013 *but see* Wallenstein et al., 2007), and winter warming could therefore be expected to affect bacterial community composition especially in late winter/early spring. It has further been suggested that later during the growing season, not only direct legacy effects, but also effects of spring warming on the timing of the bacterial community shift might cause small shifts in microbial communities, as were observed in an alpine peat bog after one winter of snow manipulation (Robroek et al., 2013). Also, it cannot be excluded that decomposer communities may respond to somewhat stronger short-term soil winter warming when a certain soil temperature threshold is exceeded, or that year to year variation in soil temperatures may overrule their sensitivity to the subtle treatment effects. However, no significant (small) shifts were observed here. This may indicate that either the communities did not respond to the increased winter soil temperatures, or that potential effects during winter and/or spring were not captured by our sampling.

The lack of response of the decomposer communities was surprising, because 2 years of experimental winter warming did induce some changes in soil properties and vegetation in NSCs, which persisted throughout the growing season. Most notably, snow addition lead to a decrease in SOM % in the vegetated inner and outer domains and a decrease in bulk density in the barren inner domains. An increase in decomposition rates required to cause the observed changes in SOM% would likely have been reflected in the decomposer community and was thus not supported by our data, although we cannot exclude possible shifts in the fungal community or in total decomposer abundance. However, a recent study using our experiment revealed no substantial differences in SOM extracellular enzyme activity and microbial respiration due to the snow treatment (Väisänen et al., 2018). We therefore suggest that the decrease in SOM and increase in bulk density were potentially a result of physical changes to the soil such as changes in SOM burial rates or flushing out of dissolvable organic matter during snowmelt, which may especially occur under the increased snow cover simulated by the snow addition treatment. However, considering the magnitude of the changes in SOM dynamics and bulk density, the observed effect is most likely overestimated by the low number of replicates. Further, another study using this experiment showed that shrub growth, phenology and gross ecosystem production were affected by winter warming (Krab et al., 2018; Väisänen et al., 2017). This may have induced changes in plant physiology during the growing season (e.g Wheeler et al., 2016) leading to changes in C-supply to decomposers via root exudates. However, these observed effects on soil properties and vegetation that persisted throughout the growing season did not lead to consistent changes in bacteria and collembola community composition. This implies that in contrast to what has been suggested in earlier work (e.g. Wookey et al., 2009), impacts of winter warming on soil abiotic properties or vegetation do not seem to cascade through to at least part of the soil decomposer system of tundra ecosystems.

4.2. Decadal NSC overgrowth and changing soil properties strongly affect decomposer communities

An Increase in vegetation cover in the barren cryoturbated tundra systems, has been considered a longer-term effect of climate change that could be specifically linked to altered winter climate (Frost et al., 2013; Kade et al., 2005; Klaus et al., 2013; Krab et al., 2018; Tape et al., 2012). Our sampling locations in NSCs could thus be considered natural gradients of vegetation presence and SOM build-up, where the vegetated inner domains and outer domains with established organic soil layer could be seen as long-term effects of winter climate change. Our results suggest that vegetation establishment into NSCs and associated changes in soil properties as a response to long-term climate change (Becher et al., 2013) will cause considerable changes in both the bacterial and collembola community (Fig. 5b).

Collembola communities were generally more diverse in sampling domains that included vegetation. This is mostly characterized by a relative decrease in dominance by *F. quadrioculata,* and a relative increase in abundance of *I. minor* and *C. denticulata.* The relatively high abundance of *F. quadrioculata* in the more disturbed inner domains may be ascribed to a high degree of phenotypical plasticity, as its adaptability to harsh conditions has been documented (Sengupta et al., 2016). However, similar phenotypic plasticity may simply be undocumented for other species. Alternatively, the higher occurrence of other species in vegetated areas may be more related to food sources and vertical stratification preference. *Folsomia quadrioculata* is a mid- to surface-living species documented as primary decomposer (Chahartaghi et al., 2005) and fungal feeder (Ferlian et al., 2015), whereas *I. minor* lives generally in deeper soil layers feeding predominantly on bacteria (Ferlian et al., 2015). *Ceratophysella denticulata*, mostly absent from the barren inner domains is suggested to feed on other soil fauna such as nematodes (von Saltzwedel et al., 2016) that may be more abundant in the vegetated domains. The barren inner domains of NSC may thus simply not provide both the habitable space and preferable food sources for these species. The similarity between collembola community composition in vegetated inner domains and outer domains and the large difference in SOM percentages between these sampling domains suggests that specifically the presence of plants, and not their effect on SOM and pH, might be driving collembola community composition.

In contrast, the relative abundance of certain bacterial phyla differed between inner and outer domains. Bacteria communities in barren inner domains were relatively similar to vegetated inner domains and both differed from outer domains, thus following the patterning of SOM % and soil pH. This suggests that bacterial community composition is mostly driven by differences in soil properties rather than plant presence alone. The presence of roots is known to have a positive influence on collembola species richness and abundance (Fujii et al., 2014), since root litter, root exudates and root-associated fungi form an important food source for collembola (Pollierer et al., 2007; Rusek, 1998). Following establishment, plant presence increases SOM quality, nutrient availability and lowers soil pH, which are widely considered to be the major drivers of microbial community composition (Siciliano et al., 2014; Stark et al., 2012).

Our data suggest that, at least for longer-term effects of winter climate change via plant establishment in cryoturbated soils, the drivers of the changes in collembola and bacteria communities are different.

4.3. Ecological implications at different scales

This study aimed to disentangle the relative importance of short-term winter climate change and vegetation cover on decomposer community composition in cryoturbated tundra. Our results suggest that winter soil warming of approximately 1 °C did not affect decomposer communities in short-term, but such temperature changes may, on a longer-tem in response to indirect effects of climate change through plant establishment into formerly barren cryoturbated areas,

cause strong changes in decomposer communities The speed at which this happens will likely be different for bacteria and collembola, because they respond differently to vegetation presence and changes in soil properties that follow sometime after plant establishment. Collembola have the ability to disperse relatively fast to resource-rich patches when plants establish (Hertzberg, 1997). In these patches they may feed on plant-associated microbes, such as mycorrhizal fungi, that may actually be the first soil biota to respond (or even precede) plant establishment. Even though bacteria communities have short generation times and undergo rapid seasonal community shifts, their community composition seems to be dependent on soil properties that change more slowly after plant establishment, such as the buildup of SOM and N, which typically limit plant and microbial growth in early succession (Tscherko et al., 2004; Wardle et al., 2004).

On a landscape scale, increases in vegetation cover in cryoturbated soils will decrease habitat heterogeneity, which will likely strongly affect the structuring of soil communities (Ettema and Wardle, 2002; Rantalainen et al., 2005). Decomposer communities associated with barren soils, or occurring specifically at the edge of barren domains, may disappear. For collembola, species richness peaks in fully vegetated domains (Fig. S5), and communities in barren domains are a subset of this diversity. Therefore, no net changes in species richness on a landscape scale would be expected. For bacteria, however, it cannot be excluded that diversity of 'species' particularly related to the more alkaline mineral surface soils of barren cryoturbated tundra or those related specifically to habitat edges, will disappear and that total landscape bacterial diversity may decrease.

An important future step would thus be to understand how vegetation establishment into cryoturbated areas will alter decomposer community composition more specifically, and to identify if these changes (and potential discrepancies between microbial and soil fauna responses) translate into functional changes. In the case of soil fauna, a functional trait approach seems promising for this purpose (Heemsbergen, 2004; Makkonen et al., 2011). For example documented feeding preferences of the species found in vegetated domains seemed to be more diverse than those in inner domains. This implies that increases in these species may have consequences for the functioning of lower trophic levels. However, the success of using trait approaches still largely depends on the availability of trait records for documented species and records of their relative species abundances, as performing trait measurements directly on sampled communities is extremely laborious or practically impossible. For bacteria, making predictions of how environmental changes may affect community composition specifically and how these changes may consequently affect ecosystem functioning, remains highly speculative at present (but see Oliverio et al., 2017). The observed clear shifts in decomposer community composition related to long-term increases in plant presence over NSCs can be expected to alter ecosystem functioning (Balser and Firestone, 2005; Heemsbergen, 2004; Strickland et al., 2009), even though there might be a high degree of redundancy in soil communities (Prosser, 2012; Schimel and Schaeffer, 2012). Temporal mismatches in the response of different parts of the decomposer food-web to vegetation establishment may lead to altered decomposer interactions and consequently to changes in their combined activity. In this respect, incorporating fungal responses to vegetation establishment would be needed to more fully assess consequences for the decomposer food-web. Plant establishment in frost-affected soils will induce substantial changes in the ecosystem C-dynamics through increased quantity and quality of C inputs, but the net effects of these changes will depend on the extent of functional changes of the decomposer community. If the observed shifts in decomposer community composition are indeed indicative for changes in their activity, vegetation overgrowth will likely have much stronger effects on soil functioning in frost-affected tundra than short-term winter warming.

Authors' contribution

E.D designed and established the winter manipulation experiment. E.J.K and E.D. maintained the winter manipulation experiment; E.J.K. planned measurements and design for this study and E.J.K and S.M conducted all field and laboratory work; E.J.K., S.M. and J.T.W analysed the data; E.J.K. wrote the manuscript with substantial input from all co-authors.

Data accessibility

Bioinformatics and figure-generating scripts used in this publication are available online from figshare: https://doi.org/10.6084/m9.figshare.9730760. DNA sequences used in this publication have been deposited at the European Nucleotide Archive (ENA, study accession number PRJEB26326).

Acknowledgements

We thank Jan Borgelt, Suzanne Korf and Laurenz Teuber for assistance in the field, Adèle Binetruy for collembola identification and counting, and Erik Lundin for assistance in the laboratory. We thank the research group of Sarah Lebeer at University of Antwerp for hosting the molecular work. Thanks also go to the Swedish Polar Research Secretariat most specifically the staff of the Abisko Scientific Research Station for their hospitality and offering logistic support, to the members of the CIRC 'writing club' for useful comments on earlier versions of this manuscript and to Maria Väisänen for kindly sharing background data needed for revising this paper. Marina Becher, Gesche Blume-Werry, Frida Keuper and Kobayashi Makoto have been involved in the set-up of experimental design and/or its maintenance. This research was financially supported by grants from VR (621-2011-5444), Formas (214-2011-788), and a Wallenberg Academy Fellowship (2012.0152) to E.D. and Formas (2017-01182) to E.J.K.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2019.107569.

References

Aerts, R., 2006. The freezer defrosting: global warming and litter decomposition rates in cold biomes: *Global warming and litter decomposition*. Journal of Ecology 94, 713–724. https://doi.org/10.1111/j.1365-2745.2006.01142.x.

Alatalo, J.M., Jagerbrand, A.K., Cuchta, P., 2015. Collembola at three alpine subarctic sites resistant to twenty years of experimental warming. Scientific Reports 5, 18161. https://doi.org/10.1038/srep18161.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26, 32–46.

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecological Monographs 83, 557–574. https://doi.org/10.1890/12-2010.1.

Balser, T.C., Firestone, M.K., 2005. Linking microbial community composition and soil processes in a California annual grassland and mixed-conifer forest. Biogeochemistry 73, 395–415. https://doi.org/10.1007/s10533-004-0372-y.

Bardgett, R.D., Bowman, W.D., Kaufmann, R., Schmidt, S.K., 2005. A temporal approach to linking aboveground and belowground ecology. Trends in Ecology & Evolution 20, 634–641. https://doi.org/10.1016/j.tree.2005.08.005.

Bartram, A.K., Lynch, M.D.J., Stearns, J.C., Moreno-Hagelsieb, G., Neufeld, J.D., 2011. Generation of multimillion-sequence 16S rRNA gene libraries from complex microbial communities by assembling paired-end illumina reads. Applied and Environmental Microbiology 77, 3846–3852. https://doi.org/10.1128/AEM.02772-10.

Becher, M., Olid, C., Klaminder, J., 2013. Buried soil organic inclusions in non-sorted circles fields in northern Sweden: age and Paleoclimatic context. Journal of Geophysical Research: Biogeosciences 118, 104–111. https://doi.org/10.1002/jgrg.20016.

Beylich, A., Oberholzer, H.-R., Schrader, S., Hoeper, H., Wilke, B.-M., 2010. Evaluation of soil compaction effects on soil biota and soil biological processes in soils. Soil and Tillage Research 109, 133–143. https://doi.org/10.1016/j.still.2010.05.010.

Björk, R.G., Klemedtsson, L., Molau, U., Harndorf, J., Odman, A., Giesler, R., 2007. Linkages between N turnover and plant community structure in a tundra landscape.

Plant and Soil 294, 247–261. https://doi.org/10.1007/s11104-007-9250-4.
Blankinship, J.C., Hart, S.C., 2012. Consequences of manipulated snow cover on soil gaseous emission and N retention in the growing season: a meta-analysis. Ecosphere 3https://doi.org/10.1890/ES11-00225.1. UNSP 1.
Bokhorst, S., Phoenix, G.K., Bjerke, J.W., Callaghan, T.V., Huyer-Brugman, F., Berg, M.P., 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. Global Change Biology 18, 1152–1162. https://doi.org/10.1111/j.1365-2486.2011.02565.x.
Bray, J., Curtis, J., 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27, 326–349.
Buckeridge, K.M., Banerjee, S., Siciliano, S.D., Grogan, P., 2013. The seasonal pattern of soil microbial community structure in mesic low arctic tundra. Soil Biology and Biochemistry 65, 338–347. https://doi.org/10.1016/j.soilbio.2013.06.012.
Caporaso, J.G., Kuczynski, J., Stombaugh, J., Bittinger, K., Bushman, F.D., Costello, E.K., Fierer, N., Pena, A.G., Goodrich, J.K., Gordon, J.I., Huttley, G.A., Kelley, S.T., Knights, D., Koenig, J.E., Ley, R.E., Lozupone, C.A., McDonald, D., Muegge, B.D., Pirrung, M., Reeder, J., Sevinsky, J.R., Tumbaugh, P.J., Walters, W.A., Widmann, J., Yatsunenko, T., Zaneveld, J., Knight, R., 2010. QIIME allows analysis of high-throughput community sequencing data. Nature Methods 7, 335–336. https://doi.org/10.1038/nmeth.f.303.
Chahartaghi, M., Langel, R., Scheu, S., Ruess, L., 2005. Feeding guilds in Collembola based on nitrogen stable isotope ratios. Soil Biology and Biochemistry 37, 1718–1725. https://doi.org/10.1016/j.soilbio.2005.02.006.
Christiansen, C.T., Haugwitz, M.S., Prieme, A., Nielsen, C.S., Elberling, B., Michelsen, A., Grogan, P., Blok, D., 2017. Enhanced summer warming reduces fungal decomposer diversity and litter mass loss more strongly in dry than in wet tundra. Global Change Biology 23, 406–420. https://doi.org/10.1111/gcb.13362.
Coulson, S., Hodkinson, I.D., Strathdee, A., Bale, J.S., Block, W., Worland, M.R., Webb, N.R., 1993. Simulated climate change: the interaction between vegetation type and microhabitat temperatures at Ny \AAlesund, Svalbard. Polar Biology 13, 67–70.
Coulson, S.J., Hodkinson, I.D., Webb, N.R., 2003. Microscale distribution patterns in high Arctic soil microarthropod communities: the influence of plant species within the vegetation mosaic. Ecography 26, 801–809.
Cragg, R.G., Bardgett, R.D., 2001. How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. Soil Biology and Biochemistry 33, 2073–2081.
Dorrepaal, E., Aerts, R., Cornelissen, J.H., Callaghan, T.V., Van Logtestijn, R.S., 2004. Summer warming and increased winter snow cover affect Sphagnum fuscum growth, structure and production in a sub-arctic bog. Global Change Biology 10, 93–104.
Edgar, R.C., Haas, B.J., Clemente, J.C., Quince, C., Knight, R., 2011. UCHIME improves sensitivity and speed of chimera detection. Bioinformatics 27, 2194–2200. https://doi.org/10.1093/bioinformatics/btr381.
Edwards, K.A., McCulloch, J., Kershaw, G.P., Jefferies, R.L., 2006. Soil microbial and nutrient dynamics in a wet Arctic sedge meadow in late winter and early spring. Soil Biology and Biochemistry 38, 2843–2851. https://doi.org/10.1016/j.soilbio.2006.04.042.
Eisenhauer, N., Reich, P.B., Isbell, F., 2012. Decomposer diversity and identity influence plant diversity effects on ecosystem functioning. Ecology 93, 2227–2240. https://doi.org/10.1890/11-2266.1.
Eo, J., Nakamoto, T., 2008. Spatial relationships between roots and soil organisms under different tillage systems. European Journal of Soil Biology 44, 277–282. https://doi.org/10.1016/j.ejsobi.2008.02.003.
Ettema, C.H., Wardle, D.A., 2002. Spatial soil ecology. Trends in Ecology & Evolution 17, 177–183.
Ferlian, O., Klarner, B., Langeneckert, A.E., Scheu, S., 2015. Trophic niche differentiation and utilisation of food resources in collembolans based on complementary analyses of fatty acids and stable isotopes. Soil Biology and Biochemistry 82, 28–35. https://doi.org/10.1016/j.soilbio.2014.12.012.
Fjellberg, A., 1998. The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha. Brill, Leiden, Boston, Köln.
Fjellberg, A., 2007. The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona. Brll, Leiden, Boston.
Frost, G.V., Epstein, H.E., Walker, D.A., Matyshak, G., Ermokhina, K., 2013. Patterned-ground facilitates shrub expansion in Low Arctic tundra. Environmental Research Letters 8, 015035. https://doi.org/10.1088/1748-9326/8/1/015035.
Fujii, S., Saitoh, S., Takeda, H., 2014. Effects of rhizospheres on the community composition of Collembola in a temperate forest. Applied Soil Ecology 83, 109–115. https://doi.org/10.1016/j.apsoil.2014.03.018.
Gittel, A., Barta, J., Kohoutova, I., Schnecker, J., Wild, B., Capek, P., Kaiser, C., Torsvik, V.L., Richter, A., Schleper, C., Urich, T., 2014. Site- and horizon-specific patterns of microbial community structure and enzyme activities in permafrost-affected soils of Greenland. Frontiers in Microbiology 5, 541. https://doi.org/10.3389/fmicb.2014.00541.
Heemsbergen, D.A., 2004. Biodiversity effects on soil processes explained by interspecific functional dissimilarity. Science 306, 1019–1020. https://doi.org/10.1126/science.1101865.
Hertzberg, K., 1997. Migration of Collembola in a patchy environment. Pedobiologia 41, 494–505.
Heywood, V., Watson, R.T., 1995. Global Biodiversity Asssesment, United Nations Environment Programme. Cambridge University Press, Cambridge, New York, USA.
Hicks Pries, C.E., van Logtestijn, R.S.P., Schuur, E.A.G., Natali, S.M., Cornelissen, J.H.C., Aerts, R., Dorrepaal, E., 2015. Decadal warming causes a consistent and persistent shift from heterotrophic to autotrophic respiration in contrasting permafrost ecosystems. Global Change Biology 21, 4508–4519. https://doi.org/10.1111/gcb.13032.
Hill, R., Saetnan, E.R., Scullion, J., Gwynn-Jones, D., Ostle, N., Edwards, A., 2016. Temporal and spatial influences incur reconfiguration of Arctic heathland soil bacterial community structure. Environmental Microbiology 18, 1942. https://doi.org/10.1111/1462-2920.13017.
Hugelius, G., Strauss, J., Zubrzycki, S., Harden, J.W., Schuur, E.A.G., Ping, C.-L., Schirrmeister, L., Grosse, G., Michaelson, G.J., Koven, C.D., O'Donnell, J.A., Elberling, B., Mishra, U., Camill, P., Yu, Z., Palmtag, J., Kuhry, P., 2014. Estimated stocks of circumpolar permafrost carbon with quantified uncertainty ranges and identified data gaps. Biogeosciences 11, 6573–6593. https://doi.org/10.5194/bg-11-6573-2014.
IPCC, 2013. In: Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (Eds.), 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, pp. 1535. https://doi.org/10.1017/CBO9781107415324. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
Johansson, M., Callaghan, T.V., Bosio, J., Akerman, H.J., Jackowicz-Korczynski, M., Christensen, T.R., 2013. Rapid responses of permafrost and vegetation to experimentally increased snow cover in sub-arctic Sweden. Environmental Research Letters 8, 035025. https://doi.org/10.1088/1748-9326/8/3/035025.
Kade, A., Walker, D.A., Raynolds, M.K., 2005. Plant communities and soils in cryoturbated tundra along a bioclimate gradient in the Low Arctic, Alaska. Phytocoenologia 35, 761–820. https://doi.org/10.1127/0340-269X/2005/0035-0761.
Klaus, M., Becher, M., Klaminder, J., 2013. Cryogenic soil activity along bioclimatic gradients in northern Sweden: insights from eight different proxies: cryogenic soil activity along bioclimatic gradients. Permafrost and Periglacial Processes 24, 210–223. https://doi.org/10.1002/ppp.1778.
Koven, C.D., Ringeval, B., Friedlingstein, P., Ciais, P., Cadule, P., Khvorostyanov, D., Krinner, G., Tarnocai, C., 2011. Permafrost carbon-climate feedbacks accelerate global warming. Proceedings of the National Academy of Sciences of the United States of America 108, 14769–14774. https://doi.org/10.1073/pnas.1103910108.
Krab, E.J., Berg, M.P., Aerts, R., van Logtestijn, R.S.P., Cornelissen, J.H.C., 2013. Vascular plant litter input in subarctic peat bogs changes Collembola diets and decomposition patterns. Soil Biology and Biochemistry 63, 106–115. https://doi.org/10.1016/j.soilbio.2013.03.032.
Krab, E.J., Cornelissen, J.H.C., Berg, M.P., 2015. A simple experimental set-up to disentangle the effects of altered temperature and moisture regimes on soil organisms. Methods in Ecology and Evolution 6, 1159–1168. https://doi.org/10.1111/2041-210X.12408.
Krab, E.J., Roennefarth, J., Becher, M., Blume-Werry, G., Keuper, F., Klaminder, J., Kreyling, J., Makoto, K., Milbau, A., Dorrepaal, E., 2018. Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions. Journal of Ecology 106, 599–612. https://doi.org/10.1111/1365-2745.12872.
Kuczynski, J., Liu, Z.Z., Lozupone, C., McDonald, D., Fierer, N., Knight, R., 2010. Microbial community resemblance methods differ in their ability to detect biologically relevant patterns. Nature Methods 7, 813–U867. https://doi.org/10.1038/nmeth.1499.
Kuznetsova, A., Brockhoff, P.B., Christensen, R.H.B., 2017. lmerTest package: tests in linear mixed effects models. Journal of Statistical Software 82 (13), 1–26. https://doi.org/10.18637/jss.v082.i13.
Lavelle, P., 1997. Faunal activities and soil processes: adaptive strategies that determine ecosystem function. In: In: Begon, M., Fitter, A.H. (Eds.), Advances in Ecological Research, vol. 27. Academic Press Ltd-Elsevier Science Ltd, London, pp. 93–132.
Lozupone, C., Lladser, M.E., Knights, D., Stombaugh, J., Knight, R., 2011. UniFrac: an effective distance metric for microbial community comparison. The ISME Journal 5, 169–172. https://doi.org/10.1038/ismej.2010.133.
Lundin, E.J., Klaminder, J., Giesler, R., Persson, A., Olefeldt, D., Heliasz, M., Christensen, T.R., Karlsson, J., 2016. Is the subarctic landscape still a carbon sink? Evidence from a detailed catchment balance. Geophysical Research Letters 43, 1988–1995. https://doi.org/10.1002/2015GL066970.
Makkonen, M., Berg, M.P., van Hal, J.R., Callaghan, T.V., Press, M.C., Aerts, R., 2011. Traits explain the responses of a sub-arctic Collembola community to climate manipulation. Soil Biology and Biochemistry 43, 377–384. https://doi.org/10.1016/j.soilbio.2010.11.004.
Makoto, K., Klaminder, J., 2012. The influence of non-sorted circles on species diversity of vascular plants, bryophytes and lichens in Sub-Arctic Tundra. Polar Biology 35, 1659–1667. https://doi.org/10.1007/s00300-012-1206-3.
Mannisto, M.K., Kurhela, E., Tiirola, M., Haggblom, M.M., 2013. Acidobacteria dominate the active bacterial communities of Arctic tundra with widely divergent winter-time snow accumulation and soil temperatures. FEMS Microbiology Ecology 84, 47–59. https://doi.org/10.1111/1574-6941.12035.
Maron, P.-A., Sarr, A., Kaisermann, A., Leveque, J., Mathieu, O., Guigue, J., Karimi, B., Bernard, L., Dequiedt, S., Terrat, S., Chabbi, A., Ranjard, L., 2018. High microbial diversity promotes soil ecosystem functioning. Applied and Environmental Microbiology 84https://doi.org/10.1128/AEM.02738-17. UNSP e02738-17.
Martinez Arbizu, P., 2017. Pairwise Adonis: pairwise multilevel comparison using adonis. R Package Version 0. 0.1.
McDonald, D., Price, M.N., Goodrich, J., Nawrocki, E.P., DeSantis, T.Z., Probst, A., Andersen, G.L., Knight, R., Hugenholtz, P., 2012. An improved Greengenes taxonomy with explicit ranks for ecological and evolutionary analyses of bacteria and archaea. The ISME Journal 6, 610–618. https://doi.org/10.1038/ismej.2011.139.
Morgado, L.N., Semenova, T.A., Welker, J.M., Walker, M.D., Smets, E., Geml, J., 2016. Long-term increase in snow depth leads to compositional changes in arctic ectomycorrhizal fungal communities. Global Change Biology 22, 3080–3096. https://doi.org/10.1111/gcb.13294.
Nielsen, U.N., Wall, D.H., 2013. The future of soil invertebrate communities in polar

regions: different climate change responses in the Arctic and Antarctic? Ecology Letters 16, 409–419. https://doi.org/10.1111/ele.12058.
Oksanen, J., 2015. Multivariate Analysis of Ecological Communities in R: Vegan Tutorial.
Oliverio, A.M., Bradford, M.A., Fierer, N., 2017. Identifying the microbial taxa that consistently respond to soil warming across time and space. Global Change Biology 23, 2117–2129. https://doi.org/10.1111/gcb.13557.
Olsson, P.Q., Sturm, M., Racine, C.H., Romanovsky, V., Liston, G.E., 2003. Five stages of the Alaskan Arctic cold season with ecosystem implications. Arctic Antarctic and Alpine Research 35, 74–81. https://doi.org/10.1657/1523-0430(2003)035[0074:FSOTAA]2.0.CO;2.
Pollierer, M.M., Langel, R., Körner, C., Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10, 729–736. https://doi.org/10.1111/j.1461-0248.2007.01064.x.
Price, M.N., Dehal, P.S., Arkin, A.P., 2010. FastTree 2-approximately maximum-likelihood trees for large alignments. PLoS One 5, e9490. https://doi.org/10.1371/journal.pone.0009490.
Prosser, J.I., 2012. Ecosystem processes and interactions in a morass of diversity. FEMS Microbiology Ecology 81, 507–519. https://doi.org/10.1111/j.1574-6941.2012.01435.x.
Rantalainen, M.L., Fritze, H., Haimi, J., Pennanen, T., Setala, H., 2005. Species richness and food web structure of soil decomposer community as affected by the size of habitat fragment and habitat corridors. Global Change Biology 11, 1614–1627. https://doi.org/10.1111/j.1365-2486.2005.00999.x.
Rigor, I.G., Colony, R.L., Martin, S., 2000. Variations in surface air temperature observations in the Arctic, 1979-97. Journal of Climate 13, 896–914. https://doi.org/10.1175/1520-0442(2000)013<0896:VISATO>2.0.CO;2.
Robroek, B.J.M., Heijboer, A., Jassey, V.E.J., Hefting, M.M., Rouwenhorst, T.G., Buttler, A., Bragazza, L., 2013. Snow cover manipulation effects on microbial community structure and soil chemistry in a mountain bog. Plant and Soil 369, 151–164. https://doi.org/10.1007/s11104-012-1547-2.
Rognes, T., Flouri, T., Nichols, B., Quince, C., Mahe, F., 2016. VSEARCH: a versatile open source tool for metagenomics. Peerj 4, e2584. https://doi.org/10.7717/peerj.2584.
Rusek, J., 1998. Biodiversity of Collembola and their functional role in the ecosystem. Biological Conservation 7, 1207–1219.
Sala, O.E., Chapin, F.S., Armesto, J.J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L.F., Jackson, R.B., Kinzig, A., Leemans, R., Lodge, D.M., Mooney, H.A., Oesterheld, M., Poff, N.L., Sykes, M.T., Walker, B.H., Walker, M., Wall, D.H., 2000. Biodiversity - global biodiversity scenarios for the year 2100. Science 287, 1770–1774. https://doi.org/10.1126/science.287.5459.1770.
Schadt, C.W., 2003. Seasonal dynamics of previously unknown fungal lineages in tundra soils. Science 301, 1359–1361. https://doi.org/10.1126/science.1086940.
Schimel, J.P., Schaeffer, S.M., 2012. Microbial control over carbon cycling in soil. Frontiers in Microbiology 3, 348. https://doi.org/10.3389/fmicb.2012.00348.
Seastedt R., T., 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29, 25–46. https://doi.org/10.1146/annurev.en.29.010184.000325.
Semenova, T.A., Morgado, L.N., Welker, J.M., Walker, M.D., Smets, E., Geml, J., 2016. Compositional and functional shifts in arctic fungal communities in response to experimentally increased snow depth. Soil Biology and Biochemistry 100, 201–209. https://doi.org/10.1016/j.soilbio.2016.06.001.
Sengupta, S., Ergon, T., Leinass, P.H., 2016. Genotypic differences in embryonic life history traits of Folsomia quadrioculata (Collembola: isotomidae) across a wide geographical range. Ecological Entomology 41, 72–84. https://doi.org/10.1111/een.12270.
Siciliano, S.D., Palmer, A.S., Winsley, T., Lamb, E., Bissett, A., Brown, M.V., van Dorst, J., Ji, M., Ferrari, B.C., Grogan, P., Chu, H., Snape, I., 2014. Soil fertility is associated with fungal and bacterial richness, whereas pH is associated with community composition in polar soil microbial communities. Soil Biology and Biochemistry 78, 10–20. https://doi.org/10.1016/j.soilbio.2014.07.005.
Sistla, S.A., Moore, J.C., Simpson, R.T., Gough, L., Shaver, G.R., Schimel, J.P., 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. Nature 497, 615. https://doi.org/10.1038/nature12129.
Sjursen, H., Michelsen, A., Holmstrup, M., 2005. Effects of freeze–thaw cycles on microarthropods and nutrient availability in a sub-Arctic soil. Applied Soil Ecology 28, 79–93. https://doi.org/10.1016/j.apsoil.2004.06.003.
Stark, S., Eskelinen, A., Mannisto, M.K., 2012. Regulation of microbial community composition and activity by soil nutrient availability, soil pH, and herbivory in the tundra. Ecosystems 15, 18–33. https://doi.org/10.1007/s10021-011-9491-1.
Strickland, M.S., Lauber, C., Fierer, N., Bradford, M.A., 2009. Testing the functional significance of microbial community composition. Ecology 90, 441–451.
Tape, K.D., Hallinger, M., Welker, J.M., Ruess, R.W., 2012. Landscape heterogeneity of shrub expansion in arctic Alaska. Ecosystems 15, 711–724. https://doi.org/10.1007/s10021-012-9540-4.
Thompson, D.W.J., Wallace, J.M., 2001. Regional climate impacts of the Northern Hemisphere annular mode. Science 293, 85–89. https://doi.org/10.1126/science.1058958.
Trivedi, P., Delgado-Baquerizo, M., Trivedi, C., Hu, H., Anderson, I.C., Jeffries, T.C., Zhou, J., Singh, B.K., 2016. Microbial regulation of the soil carbon cycle: evidence from gene-enzyme relationships. The ISME Journal 10, 2593–2604. https://doi.org/10.1038/ismej.2016.65.
Tscherko, D., Hammesfahr, U., Marx, M.C., Kandeler, E., 2004. Shifts in rhizosphere microbial communities and enzyme activity of Poa alpina across an alpine chronosequence. Soil Biology and Biochemistry 36, 1685–1698. https://doi.org/10.1016/j.soilbio.2004.07.004.
Ushio, M., Makoto, K., Klaminder, J., Nakano, S., 2013. CARD-FISH analysis of prokaryotic community composition and abundance along small-scale vegetation gradients in a dry arctic tundra ecosystem. Soil Biology and Biochemistry 64, 147–154. https://doi.org/10.1016/j.soilbio.2013.05.002.
Väisänen, M., Krab, E.J., Dorrepaal, E., 2017. Carbon dynamics at frost-patterned tundra driven by long-term vegetation change rather than by short-term non-growing season warming. Biogeochemistry 136, 103–117. https://doi.org/10.1007/s10533-017-0385-y.
Väisänen, M., Gavazov, K., Krab, E.J., Dorrepaal, E., 2018. The legacy effects of winter climate on microbial functioning after snowmelt in a subarctic tundra. Microbial Ecology. https://doi.org/10.1007/s00248-018-1213-1.
Van Straalen, N., Rijninks, P., 1982. The efficiency of Tullgren apparatus with respect to interpreting seasonal changes in age structure of soil arthropod populations. Pedobiologia 24, 197–209.
von Saltzwedel, H., Scheu, S., Schaefer, I., 2016. Founder events and pre-glacial divergences shape the genetic structure of European Collembola species. BMC Evolutionary Biology 16, 148. https://doi.org/10.1186/s12862-016-0719-8.
Wallenstein, M.D., McMahon, S., Schimel, J., 2007. Bacterial and fungal community structure in Arctic tundra tussock and shrub soils. FEMS Microbiology Ecology 59, 428–435. https://doi.org/10.1111/j.1574-6941.2006.00260.x.
Wang, Q., Garrity, G.M., Tiedje, J.M., Cole, J.R., 2007. Naive Bayesian classifier for rapid assignment of rRNA sequences into the new bacterial taxonomy. Applied and Environmental Microbiology 73, 5261–5267. https://doi.org/10.1128/AEM.00062-07.
Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setala, H., van der Putten, W.H., Wall, D.H., 2004. Ecological linkages between aboveground and belowground biota. Science 304, 1629–1633. https://doi.org/10.1126/science.1094875.
Weedon, J.T., Kowalchuk, G.A., Aerts, R., Freriks, S., Roling, W.F.M., Bodegom, P.M., 2017. Compositional Stability of the Bacterial Community in a Climate-Sensitive Sub-Arctic Peatland, vol. 8. pp. 317.
Wheeler, J.A., Cortes, A.J., Sedlacek, J., Karrenberg, S., van Kleunen, M., Wipf, S., Hoch, G., Bossdorf, O., Rixen, C., 2016. The snow and the willows: earlier spring snowmelt reduces performance in the low-lying alpine shrub Salix herbacea. Journal of Ecology 104, 1041–1050. https://doi.org/10.1111/1365-2745.12579.
Wipf, S., Sommerkorn, M., Stutter, M.I., Wubs, E.R.J., van der Wal, R., 2015. Snow cover, freeze-thaw, and the retention of nutrients in an oceanic mountain ecosystem. Ecosphere 6, 207. https://doi.org/10.1890/ES15-00099.1.
Wookey, P.A., Aerts, R., Bardgett, R.D., Baptist, F., BråThen, K.A., Cornelissen, J.H.C., Gough, L., Hartley, I.P., Hopkins, D.W., Lavorel, S., Shaver, G.R., 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. Global Change Biology 15, 1153–1172. https://doi.org/10.1111/j.1365-2486.2008.01801.x.
Zak, D.R., Groffman, P.M., Pregitzer, K.S., Christensen, S., Tiedje, J.M., 1990. The vernal dam- plant microbe competition for nitrogen in northern hardwood forests. Ecology 71, 651–656. https://doi.org/10.2307/1940319.