Emissions of biogenic volatile organic compounds from arctic shrub litter are coupled with changes in the bacterial community composition

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Highlights

- Changes in volatile emission patterns during decomposition vary between plant species.
- Volatile emissions differ between high arctic and low arctic litter.
- Bacterial community changes correlate with volatile emission changes for *Salix* litter.

Abstract

Emissions of biogenic volatile organic compounds (BVOCs) from natural ecosystems impact atmospheric chemistry as well as biological interactions and even soil biogeochemical processes. Plant litter emits substantial amounts of BVOCs. These emissions may contribute to total ecosystem emissions especially in the Arctic where the living plant biomass is low and the amount of litter is expected to increase as the deciduous shrubs expand in response to a warmer climate. Here, we incubated in the laboratory litter from the evergreen *Cassiope tetragona* and deciduous *Salix* spp. from a high arctic and a low arctic location. The 8-week-long incubation was conducted with temperature increasing from 5 °C to 26 °C, mimicking the transition from winter to summer. BVOC emissions from the decomposing litter were sampled weekly in adsorbent cartridges and analyzed using gas chromatography–mass spectrometry, and the bacterial communitycomposition was investigated by sequencing of PCR amplified 16S rRNAgene fragments. Our results showed that litter from *C. tetragona*, which is a terpenoid storing species, had higher BVOC emission rates (mainly terpenoids) than the *Salix* litter, which does not have specialized BVOC storing compartments. The *C. tetragona* litter emissions were higher in the high arctic than the low arctic samples. The emission rates from the *C. tetragona* litter increased during the incubation period, whereas emission rates from the *Salix* litter decreased, suggesting that the emissions originated from different sources and/or processes. The bacterial community composition in the *Salix* litter, but not in the *C. tetragona* litter,

changed in parallel with the changes in the BVOC emissions during the incubation period. Therefore, we suggest that bacteria may be more important for the BVOC emissions from decomposing *Salix* litter than *C. tetragona* litter.

1. Introduction

Emissions of biogenic volatile organic compounds (BVOCs) from natural ecosystems have significant impact on chemical and physical properties of the atmosphere and therefore also affect the climate (Atkinson and Arey, 1998, Shindell et al., 2009, IPCC, 2013, Ehn et al., 2014, Scott et al., 2014). Most attention has been given to emissions from plants and whole ecosystems and far less to the litter and soil. This is despite the fact that a wide range of BVOCs can be emitted in substantial amounts from both litter and soil (Leff and Fierer, 2008, Gray et al., 2010, Aaltonen et al., 2011, Mäki et al., 2017). In particular, aboveground litter BVOC emissions can be significant, especially during spring and autumn when monoterpenes can emitted in high amounts from pine litter (Hellén et al., 2006, Aaltonen et al., 2011, Peñuelas et al., 2014, Mäki et al., 2017). Other BVOCs emitted in substantial amounts from leaf litter are methanol, acetone and acetaldehyde(Gray et al., 2010). Even though we know that aboveground litter BVOC emissions might be important, we lack understanding of different mechanisms controlling the litter emissions, such as the effect of temperature, litter types and the microbiome of the litter.

Emissions of BVOCs may influence the climate by changing the atmospheric concentrations of important greenhouse gasses. For instance, in the presence of atmospheric nitrogen oxides, the breakdown of BVOCs can lead to the formation of NO_2, which, in turn, can be photodissociated to form tropospheric ozone (Atkinson and Arey, 1998, Peñuelas and Staudt, 2010). Furthermore, if BVOCs react with hydroxyl radicals it will decrease the oxidation capacity of the atmosphere and thereby prolong the lifetime of methane (Laothawornkitkul et al., 2009, Peñuelas and Staudt, 2010). The atmospheric breakdown of BVOCs may also increase the formation of secondary organic aerosols and cloud condensation nuclei, which can lead to increased cloud cover and radiative reflection (Shindell et al., 2009, IPCC, 2013, Scott et al., 2014).

Emissions of BVOCs do not only influence processes in the atmosphere but also several belowground biogeochemical processes related to the decomposition of organic matter. For instance, by acting as substrate for microorganisms, monoterpenes have been suggested to increase microbial N (nitrogen) immobilization and thereby decrease the net N mineralization rate (White, 1994, Paavolainen et al., 1998, Smolander et al., 2006). Monoterpenes have also been suggested to decrease the rate of nitrification(White, 1986, White, 1988, White, 1991, Ward et al., 1997, Paavolainen et al., 1998), and this may e.g. be a consequense of ammonia monooxygenaseinhibition (White, 1988, White, 1994) or decreased net N mineralization (White, 1994, Paavolainen et al., 1998). Furthermore, it has been proposed that different BVOCs can promote or restrain bacterial and fungal growth (Effmert et al., 2012, Peñuelas et al., 2014) and function as signaling molecules between belowground organisms (Wheatley, 2002, Bending et al., 2006, Schmidt et al., 2015, Tyc et al., 2017). Many BVOCs are also released without having any known specific function, for instance isopropanol, isoprene and different ketones may be emitted as

intermediate products of microbial metabolism (Korpi et al., 2009, Insam and Seewald, 2010). In particular, a wide range of BVOCs are emitted under anaerobic conditions as products of fermentation processes (Insam and Seewald, 2010, Seewald et al., 2010, Faubert et al., 2011). Litter emissions associated with microbial decomposition of organic matter are quantitatively more important than abiotic emissions (Leff and Fierer, 2008, Gray et al., 2010, Gray and Fierer, 2012, Wu and Wang, 2015). Here, BVOCs can be released from microorganisms, from extracellular biochemical processes in the organic matter or directly from the substrate (Korpi et al., 2009). The quantity and composition of the emissions depend both on the type of litter and on the composition of the decomposer community (Insam and Seewald, 2010, Peñuelas et al., 2014). Additionally, a range of different parameters in the environment such as temperature, pH, oxygen level, the availability of nutrients and soil moisture can change both the consumption and the emissions of BVOCs (Insam and Seewald, 2010). In particular, temperature is highly important since it changes the volatility of BVOCs and the transport resistance along the diffusion path out of the litter (Kesselmeier and Staudt, 1999). Furthermore, temperature may also change the emissions by altering the activity and community composition of the decomposing microorganisms (Kirschbaum, 1995, Deslippe et al., 2012, Rinnan et al., 2014).

Global warming is proceeding strongly in the Arctic with the predicted temperature increase of 2.2–2.4 times the global average (IPCC, 2013). In addition to the direct temperature effect on litter BVOC emissions, global warming will also increase plant biomass and alter the composition of vegetation. Especially the biomass of deciduous shrubs and leaf litter is expected to increase in the Arctic (Walker et al., 2006, Elmendorf et al., 2012a, Elmendorf et al., 2012b). Furthermore, changes in plant species composition are likely to change litter emissions since different plant litter types emit different BVOC emission profiles (Leff and Fierer, 2008, Gray et al., 2010, Gray and Fierer, 2012).

The aim of this work was to assess how BVOC emissions from arctic leaf litter change during spring as temperature increases and microbial community potentially changes. We measured emissions of BVOCs (size range: 5C-25C) from aboveground litter of common arctic species during an eight-week-long laboratory incubation, where temperature was stepwise raised, mimicking typical spring soil surface temperatures in the Arctic. Litter of three species grown under different climatic conditions was used in order to assess differences between plant litter types. We used litter from *Salix glauca* collected from a low arctic location, *Salix arctica* collected from a high arctic location and *Cassiope tetragona* which was collected from both a low and a high arctic location. *C. tetragona* is an evergreen dwarf shrub that is characterized by having glandular trichomes on the leaf surface (Schollert et al., 2015) which are specialized storage structures for BVOCs (Laothawornkitkul et al., 2009, Loreto and Schnitzler, 2010). The *Salix*species are deciduous shrubs and trees with high isoprene emission capacity and no specialized BVOC storage structures (Fineschi et al., 2013). Changes in the bacterial community during the course of the experiment were assessed in parallel with the BVOC measurements. We hypothesized 1) that litter with BVOC storage structures would have higher emission rates than litter without the known storage structures, 2) that the release of BVOCs from litter would decrease over time due to a faster decomposition of the more labile litter constituents at the beginning of the decomposition and due to a depletion of BVOCs inside the plant

tissue as the litter decomposes, 3) that BVOC emissions would be higher from high arctic *C. tetragona* litter than from low arctic *C. tetragona* litter because the density of terpenoid storing trichomes have been found to be higher on plants grown under colder conditions and 4) that the BVOC emission profiles would change in the course of incubation parallel with microbial community changes.

2. Materials and methods

2.1. Plant litter collection

Leaf litter of *Salix glauca* L. coll and *C. tetragona* (L.) D. Don was collected at Low Arctic Disko Island (69°14′N, 53°32′W) with an annual accumulated precipitation of 436 mm (1991–2004; Hansen et al., 2006) and mean annual temperature of −1.7 °C (1992–2013). Litter of *Salix arctica* P. Pallas and *C. tetragona* was collected in High Arctic Zackenberg Valley (74°30′N, 20°30′W) with mean annual temperature of −9.1 °C and mean annual accumulated precipitation of approximately 205 mm (2003–2013; Mylius et al., 2014). The litter was a composite of samples collected from tens of individual plants growing on an area of appr. 100 × 100 m in each location. Litter from Zackenberg was collected in August with a mean temperature of 5.4 °C and litter from Disko Island was collected in September with a mean temperature of 3.5 °C. *Salix* leaf litter was collected by taking senescent leaves that were still loosely attached to the stem or collected from the ground within 7 days of litter fall. *C. tetragona* litter was collected by taking the brown parts of the braches between the green and grey parts. Litter samples were stored at 5 °C during transport to Denmark (9 days for Zackenberg samples and 12 days for Disko Island samples), where they were stored at −18 °C.

2.2. Experimental set-up for laboratory incubation

The litter samples were prepared at −10 °C. *Salix* litter was cut into pieces of 0.5 cm × 0.5 cm and the needle-like *C. tetragona* litter into 0.5 cm long pieces. This procedure was done to enhance homogeneity of material for DNA extractions, but it may also have led to higher BVOC emissions and decomposition rates. Approximately 1.3 g dry weight of *Salix* litter and 2.7 g dry weight of *C. tetragona* litter from each location were used per 210 ml glass jar. This corresponded to 2.5 g fresh weight for *Salix* and 3.3 g fresh weight for *C. tetragona*. Litter for each location and species was weighed into six glass jars, giving six replicates per species and location. In addition, six empty 210 ml glass jars were used as experimental blanks. The whole experimental setup thus consisted of 30 glass jars.

Prior to the experiment, all litter samples were pre-conditioned to equal water holding capacity by placing the 210-ml glass jars into larger glass containers containing deionized water and a relative humidity in headspace of 95%. The glass jars were open, while the larger containers were covered with Parafilm and stored in dark at 5 °C. Parafilm allows diffusion of O_2 and CO_2 but still maintains the stable relative humidity inside the jars. The pre-conditioning period was started 18 days before the first BVOC measurements and the set-up was maintained during the entire experiment, except during sampling. Empty glass jars used as experimental blanks were treated in a similar way.

During the experiment, the glass jars were incubated in the dark and the temperature was stepwise increased from 5 °C to 26 °C. The temperature was increased by 7 °C every 14 days, giving incubation temperatures of 5 °C, 12 °C, 19 °C, and 26 °C. At each temperature, BVOC emissions were measured twice, approximately one and two weeks after each temperature adjustment. A 200-mg fresh weight subsample for DNA isolation and microbial community composition assessment was obtained after the second BVOC measurement at each incubation temperature. Each time, the remaining litter in the sample was carefully weighed.

At the end of the experiment, litter samples were oven dried at 65 °C to determine the final dry weight and then grounded for chemical analyses. Total carbon (C) and N concentrations were analyzed using a LECO TruSpec Carbon Nitrogen Analyzer. Near infrared reflectance (NIR) spectra were measured on an Antaris II NIR-analyzer (Thermo Fisher Scientific, Waltham, MA, USA) taking three measurements per sample with re-packing.

2.3. BVOC measurements

BVOC emissions were sampled in dark after placing a lid with Teflon fittings for in- and outflow on the 210 ml glass jar. Air filtered free of BVOCs and particles by a charcoal filter and of ozone by a copper tubing coated with potassium iodide was pushed into the jar at a rate of 200 ml min^{-1}. Air was pulled out of the jar through a stainless steel adsorbent tube packed with 150 mg Tenax TA and 200 mg Carbograph 1 TD at a rate of 200 ml min^{-1}. At 5 °C and 12 °C the sampling time was 1 h and at 19 °C and 26 °C it was 45 min. Different sampling times were used to ensure large enough sample volumes considering the expected lower biological activity at lower temperatures. Blank samples were collected in parallel with litter measurements by sampling from the empty glass jars. The used adsorbent tubes trap compounds in the range C5-C25.
The adsorbent tubes were analyzed following thermal desorption by gas chromatography-mass spectrometry as by Vedel-Petersen et al. (2015). Identification of BVOCs was done using pure standards for toluene, 1-octen-3-ol, nonanal, 2-methylfuran, isoprene, α-pinene, camphene, 1,8-cineole, limonene, γ-terpinene and α-humulene and the mass spectra in the NIST library. Only BVOCs identified with a MS match of more than 85% were used for further data processing. For BVOC quantification where pure standards were not available α-pinene was used for monoterpenes, 1,8-cineole for oxygenated monoterpenes, α-humulene for sesquiterpenes and toluene for all other BVOCs. BVOCs captured in blank measurements were subtracted from the dataset. Emission rates were calculated as ng g^{-1} (dry weight) h^{-1}(Ortega and Helmig, 2008) and BVOCs were categorized into terpenoids, halogenated compounds, benzenoids, acids and esters, aldehydes, ketones, alcohols, ethers, alkenes and alkanes. These categories were prioritized in the mentioned order, with terpenoids having the highest priority and alkanes the lowest. Compounds belonging to more than one of the categories were assigned the category with the highest priority.

2.4. Bacterial community composition

In order to investigate changes in the litter microbial community composition, a sub-sample of ca. 200 mg fresh weight was taken from each litter jar after 14 day long incubation at each temperature. Sub-samples were immediately frozen in liquid nitrogen and placed at −80 °C for later analysis. The DNA was extracted using PowerLyzer™ PowerSoil® DNA Isolation Kit (MoBio, Carlsbad, CA, USA). PCR and qPCR using the primers ITS4 (White et al., 1990) and gITS7 (Ihrmark et al., 2012) targeting the fungal ITS2 region were unsuccessful, and therefore we only investigated the community structure of bacteria.

2.4.1. Sequencing library preparation

Sequencing library was prepared as described previously (Bang-Andreasen et al., 2017). Primer pair 515f/806r targeting bacterial V4 region of the 16S rRNA gene was used for PCR amplification (515f: 5′-GTGCCAGCMGCCGCGGTAA-3'; 806r: 5′-GGACTACHVGGGTWTCTAAT-3' (Caporaso et al., 2012)). PCR amplifications were performed with primers containing a template-specific sequence consisting of a 2-nucleotide linker and a 4-6-nucleotide barcode. Each of three independent 10-µl reactions per DNA sample contained 2 µl 5x PCRBIO Reaction Buffer (PCR Biosystems Ltd, London, UK), 3 µl bovine serum albumin (BSA) (Bioron, Ludwigshafen, Germany), 0.2 µl dNTP (10 mM), 0.5 µl dual-labeled, 0.1 µl PCRBIO HIFI Polymerase (PCR Biosystems Ltd, London, UK), 0.5 µl DNA template, and 5.2 µl ddH_2O. The cycling conditions were the following: 95 °C for 1 min, followed by 30 cycles at 95 °C for 15 s, 50 °C for 20 s, 72 °C for 20 s, and then 72 °C for 5 min. The resulting PCR amplicons from the technical triplicates were pooled, and amplification was verified by agarose gel electrophoresis. Amplicons were purified using HighPrep™ PCR clean up system (Magbio Genomics, Gaithersburg, MD, USA), DNA concentration was quantified by Qubit® HS DNA assay (Life Technologies, Darmstadt, Germany), and samples were equimolarly pooled. Ligation of Illumina adapters was performed using TruSeq DNA PCR-free LT Sample Preparation Kit (Illumina, San Diego, CA, USA) following a modified protocol. The final library was subjected to sequencing on Illumina MiSeq 2 × 250 bp paired-end platform at the National High-throughput DNA Sequencing Centre (Copenhagen, Denmark).

2.4.2. Sequence data analysis

Illumina sequencing data were processed using the pipeline SEED (Vetrovsky and Baldrian, 2013). Pair-end reads were merged using fastq-join (Aronesty, 2013). Sequences were clustered at 97% similarity level using UPARSE (Edgar, 2013) - chimeric sequences were discarded during clustering. Singleton sequences were removed from the dataset and consensus sequences were constructed for each operational taxonomic unit(OTU). Closest hits were identified using SILVA database (Quast et al., 2013). Sequence data have been deposited in the MGRAST public database (http://metagenomics.anl.gov/) with the numbers 4765510.3, 4765511.3, 4765512.3 and 4765513.3.

2.5. Statistics

General Linear Model Repeated Measures Analysis of Variance (RM-ANOVA) was used to test for effects on BVOC emissions of the within-subjects factors: “Temperature/time” and “Measurement” (difference between the first and second measurement at each temperature). The between-subject

factor (“Location”) was used to test for the difference between the litter from the Low Arctic or the High Arctic. The model tested for main effects and all combinations of interactions between the three factors. One sample was identified as an outlier and was replaced with the average of the corresponding replicates. Data were transformed if needed to meet the presumptions of RM-ANOVA. No model was run for emissions of BVOC categories where homogeneity of variance could not be obtained. General Linear Model Analysis of Variance (ANOVA) was used to test for differences between locations in regards to % C, % N and C:N ratio. All models tested *Salix* and *C. tetragona* litter separately. Analyses were conducted in IBM SPSS Statistics 19.0.0 (SPSS Inc. IBM Company, Armonk, NY, USA). Effects were considered significant if $P < 0.05$.

The multivariate datasets (emission rates of individual BVOCs, the microbial community composition and NIR spectra) were subjected to principal component analyses (PCA) using SIMCA 13.0.3 (Umetrics, Umeå, Sweden) separately for *Salix* and *C. tetragona* litter. For NIR spectra, the data were preprocessed by standard normal variate transformation to remove scatter and centered.

BVOC and bacterial data were mean centered and scaled to unit-variance to let compounds have equal importance in the analysis. For the bacterial community composition, OTUs contributing less than 1% to the total number of OTUs in less than four samples were disregarded from the analysis. For BVOCs, compounds appearing in less than 70% of the samples were disregarded from the analysis. Outliers were removed from all PCAs when relevant.

3. Results

3.1. BVOC emissions from Salix litter

We found a total of 84 different BVOCs emitted from the *Salix* litter. The emissions were dominated by benzenoids and terpenoids (on average 32% and 28% of the total emissions, respectively), followed by alkenes and alkanes (Fig. 1a). The single most emitted BVOC from the *Salix* litter was cic-linalool-oxide (Supplementary Table S1, Table S2). The emission of this compound was almost twice as high as the second most emitted BVOC, which was dodecane (Supplementary Table S1, Table S2).

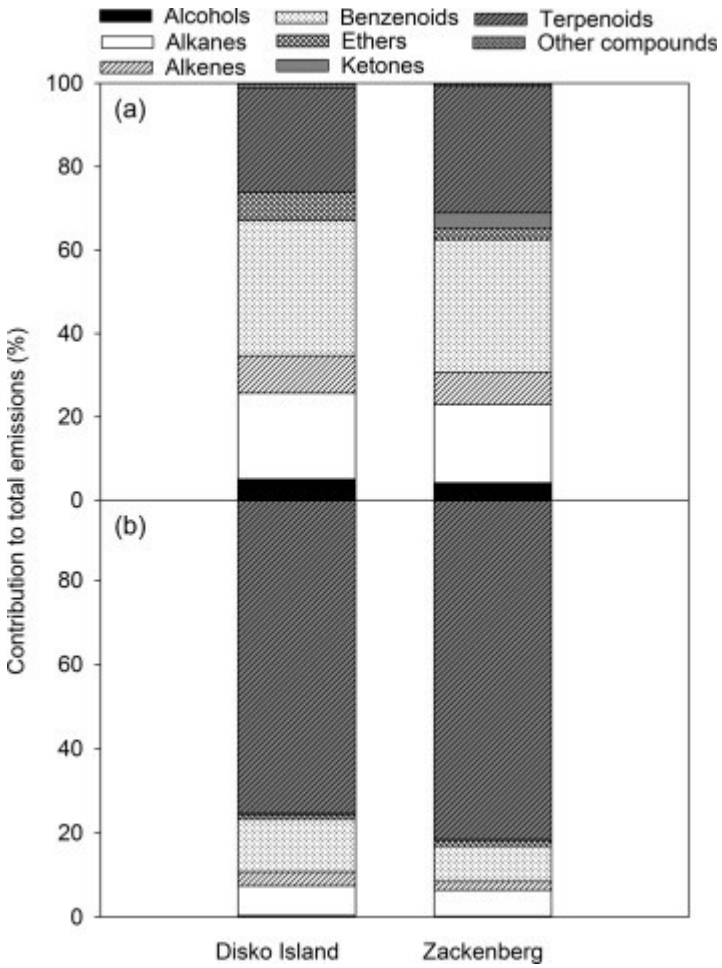

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Fig. 1. Contribution of different BVOC categories emitted from (a) *Salix* litter and (b) *C. tetragona* litter collected from low arctic Disko and high arctic Zackenberg to total emissions. Data shown are averages of 8 measurements (n = 48) taken during an eight week incubation period at increasing temperatures.

The development of the BVOC emissions during the incubation period varied depending on the BVOC categories (Fig. 2). Emissions of terpenoids, benzenoids, alkanes, alkenes and the total emission rates were significantly affected by temperature/time (Fig. 2a, b, c, d and h). The emission rates of benzenoids, alkanes, ethers, ketones and the total emissions were highest at the lowest temperatures in the beginning of the incubation period (Fig. 2b, c, e, g and h). In contrast, alkenes had the highest emissions rates towards the end of the incubation period where the temperature was highest (Fig. 2d).

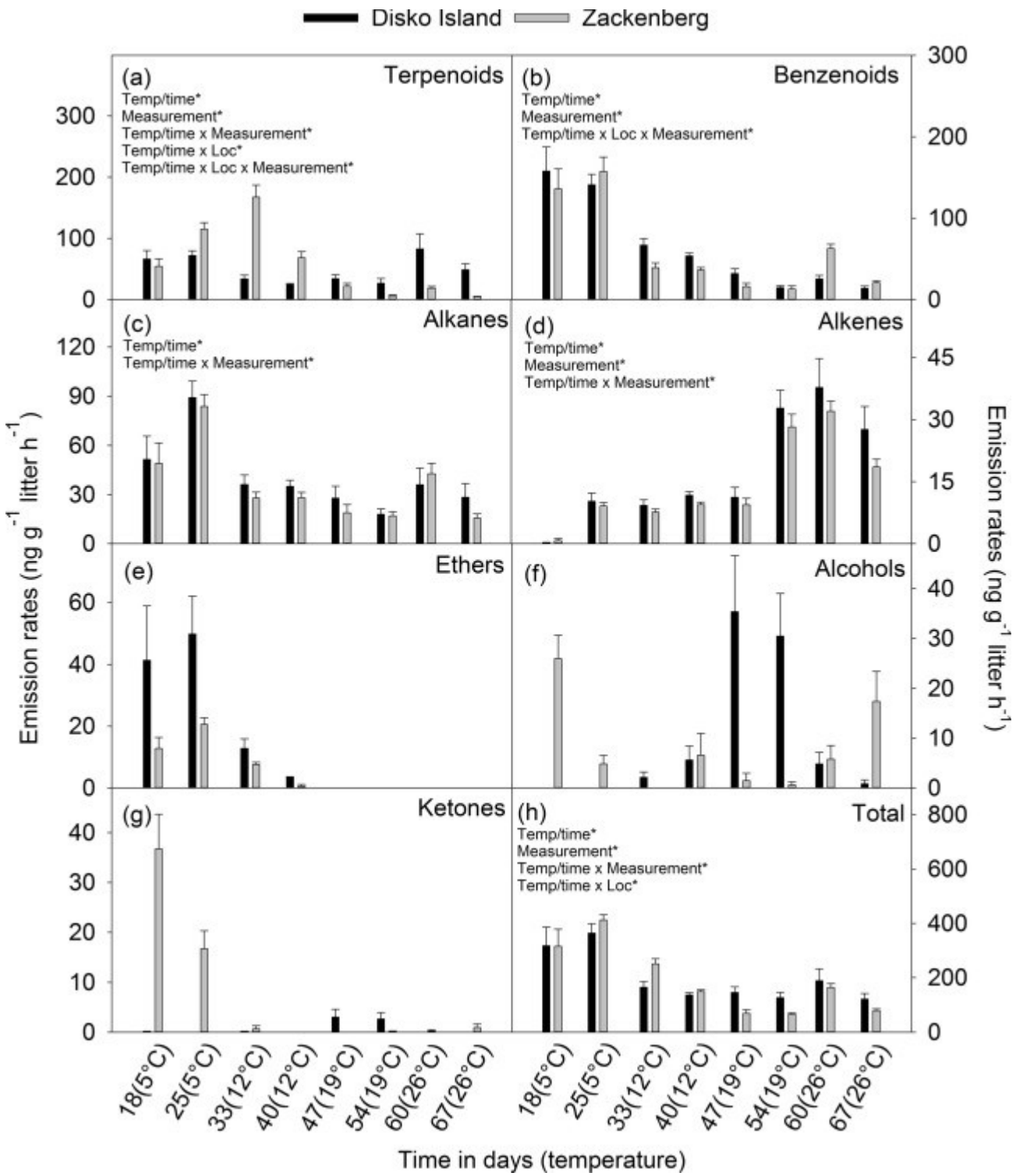

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Fig. 2. Emissions of (a) terpenoids, (b) benzenoids, (c) alkanes, (d) alkenes, (e) ethers, (f) alcohols, (g) ketones and (h) total BVOCs from *Salix* litter during an eight week incubation with stepwise temperature increase from 5 °C to 26 °C. Emission rates are shown as: ng g (dry weight)$^{-1}$ h^{-1}. Two measurements were made at each temperature. The bars show mean + SE (n = 6). Statistically significant effects of the study period (Temp/time), differences between the first and second measurement at each temperature (Measurement), and differences between the low arctic Disko Island (*S. glauca*) and the high arctic Zackenberg (*S. arctica*) (Location) and interactions hereof are shown to the top left of each graph as * (Repeated Measures Analysis of Variance; $P \leq 0.05$). No statistical test was run for

emissions of ethers, alcohols, and ketones since homogeneity of variance for these BVOC categories could not be obtained with data transformations.

The emission profile of *S. glauca* litter changed from the first to the second measurement at 5 °C, 19 °C and 26 °C, and the emission profile of *S. arctica*litter changed between the two measurements at 5 °C, 12 °C and 26 °C (Supplementary Fig. S1a and b). Furthermore, the emission rates of terpenoids, benzenoids, alkenes and the total emissions were significantly different between the two measurements (Fig. 2a, b and d). For terpenoids, alkenes, and total emission rates this effect depended significantly on the temperature/time (Fig. 2a, d and h). Here, the emissions at the lower temperatures were in general higher during the second measurement than during the first, whereas at the higher temperatures the emissions were highest during the first measurement at each temperature. There were only few significant differences between the two *Salix* species grown at the different locations. These were expressed as interactions with temperature/time for the terpenoids, alkanes and total emissions (Fig. 2a, c and h) and as three factor interactions between temperature/time, measurement and location for terpenoids and benzenoids (Fig. 2a and b).

3.2. BVOC emissions from C. tetragona litter

The *C. tetragona* litter emitted a total of 129 different BVOCs. Terpenoids comprised on average 79% of the total emissions, followed by benzenoids, alkanes, alkenes, and ethers (Fig. 1b). The single most emitted BVOC from the *C. tetragona* litter was 1.8-cineole that had emission rates almost twice as high as *cis*-linalool oxide, which was the second most emitted BVOC (Supplementary Table S3 and Table S4).

We found significant effect of temperature/time for all the BVOC categories that we tested statistically (Fig. 3). The total emissions and the emissions of terpenoids and alkenes generally increased during the study period, except for the last measurement day where these emissions decreased again (Fig. 3a and d). The emission of benzenoids and ether were, in general, lowest in the beginning and in the end of the incubation period and highest during measurements at 12 °C and 19 °C (Fig. 3b and e). None of the BVOC categories that we tested statistically had highest emission rates at the low temperatures in the beginning of the incubation period.

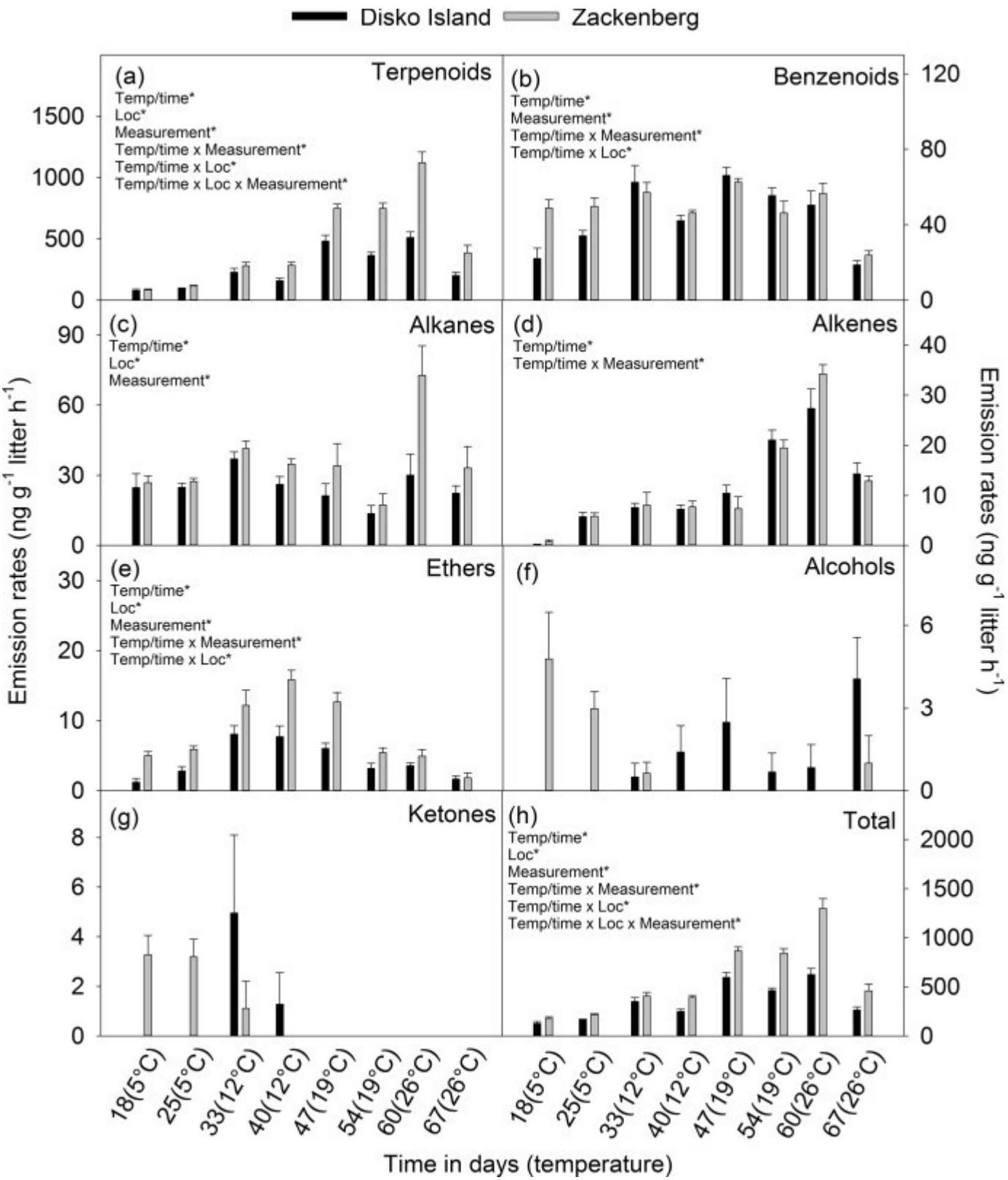

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Fig. 3. Emissions of (a) terpenoids, (b) benzenoids, (c) alkanes, (d) alkenes, (e) ethers, (f) alcohols, (g) ketones and (h) total BVOCs from *Cassiope tetragona* litter during an eight week incubation with stepwise temperature increase from 5 °C to 26 °C. Emission rates are shown as: ng g (dry weight)$^{-1}$ h^{-1}. Two measurements were made at each temperature. The bars show mean + SE (n = 6). Statistically significant effects of the study period (Temp/time), differences between the first and second measurement at each

temperature (Measurement), and differences between the low arctic Disko Island (*S. glauca*) and the high arctic Zackenberg (*C. tetragona*) (Location) and interactions hereof are shown to the top left of each graph as * (Repeated Measures Analysis of Variance; $P \leq 0.05$). No statistical test was run for emissions of ethers, alcohols, and ketones since homogeneity of variance for these BVOC categories could not be obtained with data transformations.

The emissions from the *C. tetragona* litter differed significantly between the two locations for several of the BVOC categories; the emissions of terpenoids, alkanes, ether and total emissions were significantly higher from high arctic Zackenberg litter than from low arctic Disko Island (Fig. 3a, c, e and h). Furthermore, for the terpenoid and total emissions, the higher emissions from the Zackenberg litter were significantly more pronounced towards the end of the study period (Fig. 3a and h). In contrast, the higher emissions of benzenoids and ether from the Zackenberg litter were significantly less pronounced during that same period (Fig. 3b).

The emission profile of *C. tetragona* litter from Zackenberg changed from the first to the second measurement at 5 °C, 19 °C and 26 °C but for the Disko Island *C. tetragona* litter it only changed between the two measurements at 26 °C (Supplementary Fig. S1c and d). Furthermore, the emission rates of terpenoids, benzenoids, alkanes and total emissions were significantly lower during the second measurement compared to the first at most temperatures (Fig. 3a, b, c and h). In all cases these emissions decreased most from 19 °C to 26 °C.

3.3. Litter mass loss and chemistry

The mass loss during the incubation period was 37% for *Salix glauca* litter from Disko Island and 52% for *Salix arctica* litter from Zackenberg, while it was 17% and 12% for *C. tetragona* from Disko Island and Zackenberg, respectively.

After the incubation period, the % C and C:N ratio in the *S. glauca* litter from Disko Island were significantly higher than those in *S. arctica* litter from Zackenberg (Table 1). Furthermore, the PCA on the NIR spectra showed a clear difference in the litter chemistry between the two *Salix* species along the principal component 1 (PC 1), which explained 97.9% of the variance in the data (Supplementary Fig. S2a). The loading plot for the PC 1 showed that the spectral regions most characteristic for the Zackenberg litter were at 5150 cm^{-1} and the region towards 4000 cm^{-1}, potentially indicating differences in the content of water and polysaccharides, respectively (Supplementary Fig. S1b).

Table 1. Elemental analysis of carbon (C), nitrogen (N) and C:N ratio of *Salix glauca*and *Cassiope tertagona* litter from low arctic Disko Island and *Salix arctica* and *Cassiope tetragona* litter from high arctic Zackenberg at the end of the eight-week incubation period (mean ± SE, n = 6).

	Disko Island	Zackenberg	Statistical significance
Salix			
C content (%)	50.1 ± 0.1	47.2 ± 0.1	<0.001
N content (%)	0.9 ± 0.0	0.9 ± 0.0	0.399
C:N	56.5 ± 1.4	51.7 ± 1.0	0.020
C. tetragona			

	Disko Island	Zackenberg	Statistical significance
C content (%)	58.1 ± 0.2	56.2 ± 0.1	<0.001
N content (%)	1.00 ± 0.0	1.3 ± 0.0	<0.001
C:N	58.7 ± 2.1	45.0 + 1.0	<0.001

Statistically significant differences between litter from the two locations are shown (General Linear Model Analysis of Variance (ANOVA)). *Salix* and *C. tetragona* were tested in separate models.

The % C and C:N ratio were significantly higher and the % N significantly lower for *C. tetragona* from Disko Island compared to *C. tetragona* from Zackenberg (Table 1). In accordance with this, the NIR spectra showed that the chemistry of *C. tetragona* litter from the two locations was partly distinct (Supplementary Fig. S1c).

3.4. Bacterial community composition

After quality filtering and chimera removal, the dataset encompassed 1,629,811 DNA sequences. Each *C. tetragona* sample was represented by 2200 ± 336 (average ± standard error of the mean) sequences, and each *Salix* sample was represented by 4211 ± 518 sequences. In the *C. tetragona*litter samples, we found a total of 995 different OTUs of which 586 were assigned to 294 different genera (including 12 candidate genera), while in the *Salix* litter samples we detected 915 different OTUs of which 575 were assigned to 225 different genera (including 9 candidate genera). The Shannon Diversity Index was 2.54 ± 0.14 for the *C. tetragona* samples and was lower for the *Salix* samples at 1.86 ± 0.20. Richness and Shannon Diversity Index decreased during the experiment for both *Salix* and *C. tetragona* litter and for both locations (Supplementary Tables S5-S6). At phylum level, the bacterial community in the *Salix* litter was dominated by Actinobacteria, which increased their dominance during the course of the experiment (Fig. 4a and b). Actinobacteria were mainly represented by two OTUs, i) an OTU assigned to *Kitasatospora* (within Streptomycetaceae), which increased dramatically in the Disko samples during the experiment, but were stable throughout the Zackenberg samples, and ii) an OTU assigned to *Frigoribacterium* (within Microbacteriaceae) mainly in the Disko Island samples at 5–19 °C. A list of the dominant OTUs in the *Salix* and *C. tetragona*litter and their phylogenetic affiliation is presented in Supplementary Tables S7-S8.

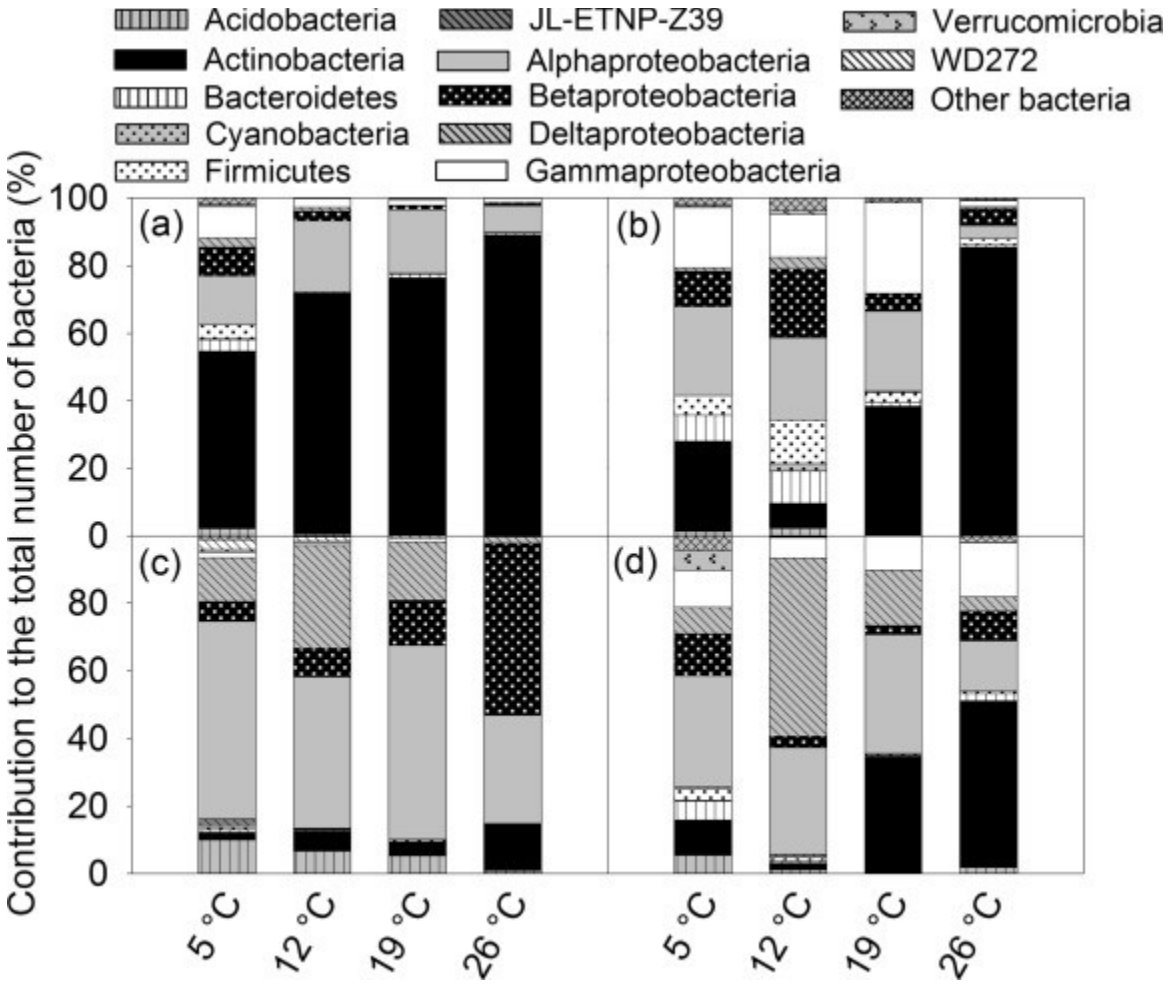

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Fig. 4. Contribution of acidobacteria, actinobacteria, bacteroidetes, cyanobacteria, firmicutes, JL-ETNP-239, alphaproteobacteria, betaproteobacteria, deltaproteobacteria, gammaproteobacteria, verrucomicrobia, WD272 and other bacteria the total number of bacteria in (a) *Salix glauca* litter from low arctic Disko Island, (b) *Salix arctica* litter from high arctic Zackenberg and in *Cassiope tetragona* litter from (c) Disko Island and (d) Zackenberg. The litter was incubated for eight weeks with stepwise increase in temperature (5 °C, 12 °C, 19 °C and 26 °C). The bacterial community structure was determined at each temperature (n = 6).

Even though Actinobacteria did not dominate the *C. tetragona* litter to the same extent as the *Salix* litter (Fig. 4c and d), the OTU assigned to *Kitasatospora* was the fourth most abundant in *C. tetragona* litter. This OTU increased during the experiment in the Disko Island samples but not in the Zackenberg samples. In contrast to the *Salix* litter, the *C. tetragona* litter was in general dominated by Proteobacteria represented by a large number of OTUs assigned to Alpha-, Beta-, Delta- and Gammaproteobacteria. A search for the closest relative to the numerically dominant OTUs did not reveal any hits in a database on bacteria known to produce BVOCs (http://bioinformatics.charite.de/mvoc/).

3.5. Linking the volatile and microbial fingerprints

The PCA performed on emissions from *Salix* litter dispersed according to temperature/time showing that the BVOC emission profiles changed during the course of the experiment (Fig. 5a). The

differences between temperatures were most pronounced in the beginning of the experiment where the temperatures were lowest (Fig. 5a). The corresponding loading plot showed that benzenoids, and especially undecane, oxylene and 1,2,3-trimethylbenzene were characteristic for the lowest temperatures (Supplementary Fig. S3). There was no clear separation between the emission profiles of the high arctic *S. arctica* and the low arctic *S. glauca* (Fig. 5a). The PCA performed on the relative abundance of bacteria in the *Salix*litter showed a pattern similar to the PCA for the BVOC emissions, with samples being dispersed according to temperature/time (Fig. 5b). However, in contrast to the BVOC emission profiles, the abundance of bacteria was most clearly temperature/time separated towards the end of the study period were the temperatures were highest (Fig. 5b). This PCA further showed a separation of the two *Salix* species from the two different locations, indicating that the community structure of bacteria in the two *Salix* species were distinct.

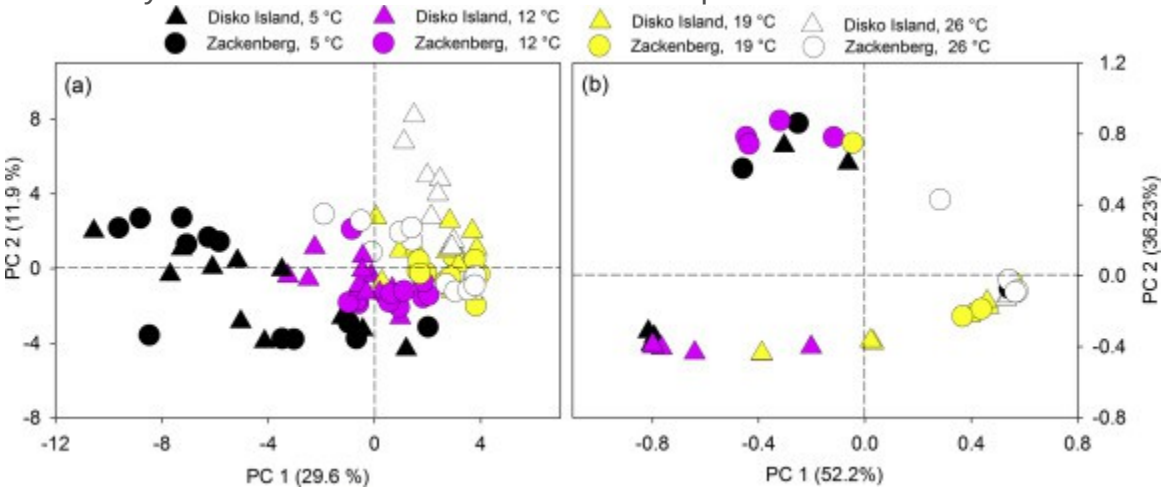

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Fig. 5. Score plots from principal component analyses on (a) emission of individual BVOCs and (b) the relative abundance of bacteria on *Salix glauca* litter from low arctic Disko Island and *Salix arctica* litter from high arctic Zackenberg during an eight-week incubation study with increasing temperature simulating the transition from early spring to summer. The variance explained by each principal component (PC) is shown in parentheses.

The PCA on the BVOC emissions from *C. tetragona* had a clear separation according to temperature/time for both locations, showing that the relative contribution of individual compounds changed during the course of the experiment (Fig. 6a). The corresponding loading plot showed that especially terpenoids were relatively more abundant at the later stages of decomposition where the temperatures were higher (Supplementary Fig. S4). In contrast, benzenoids like 1,2-diethylbenzene and 4-ethyl-1,2-dimethylbenzene were relatively more abundant at the colder temperatures.

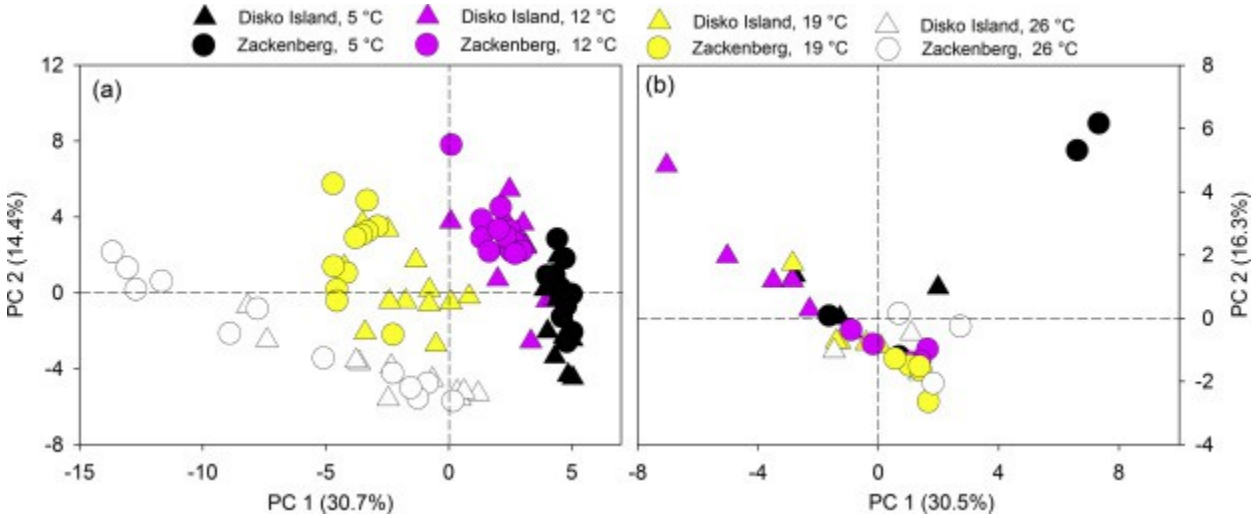

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Fig. 6. Score plots from principal component analyses on (a) emission of individual BVOCs and (b) the relative abundance of bacteria on *C. tetragona* litter from low arctic Disko Island and high arctic Zackenberg during an eight-week incubation study with increasing temperature simulating the transition from early spring to summer. The variance explained by each principal component (PC) is shown in parentheses.

The emission profiles from high arctic Zackenberg litter were not clearly distinct from those from the low arctic Disko Island (Fig. 6a). There was no separation between bacterial communities in the *C. tetragona* litter at the different temperatures (Fig. 6b). Furthermore, the litter bacterial community structure in high arctic Zackenberg and low arctic Disko Island only separated clearly at 12 °C. At all other temperatures, the bacterial community structure in the *C. tetragona* litter from the two locations were similar (Fig. 6b).

4. Discussion

4.1. Litter BVOC emissions

Throughout the incubation period we found terpenoids to constitute a large part of the total emission from the *C. tetragona* litter. Since *C. tetragona* is a species storing terpenoids (Rinnan et al., 2014, Schollert et al., 2015), it is likely that the majority of the terpenoids originated from storage pools being released as the litter decomposed. This suggestion is in accordance with a range of other studies, which have detected significant terpenoid emissions from aboveground plant litter of terpenoid-storing species (Hellén et al., 2006, Gray et al., 2010, Aaltonen et al., 2011, Gray and Fierer, 2012, Greenberg et al., 2012, Mäki et al., 2017). The lack of specialized terpenoid storage structures in *Salix* spp. most likely explains the much lower terpenoid emissions from this litter. We can therefore confirm our hypothesis suggesting that litter with BVOC storage structures have higher emission rates than litter without storage structures. However, we have used a technique that detects only C5-C25 BVOCs. Therefore, it is important to note that we cannot assess differences in the low molecular weight compounds typical for litter emissions, such as methanol, acetone and acetaldehyde (Gray et al., 2010). This may be significant since methanol has

been shown to constitute around 95% of BVOC emissions from decomposing litter from various plant species (Gray et al., 2010).

We observed that the total emissions from the *C. tetragona* litter in general increased during the incubation period, whereas the total emissions from the *Salix* litter generally decreased. We could therefore confirm our second hypothesis suggesting that the release of BVOCs from litter would decrease over time only for *Salix*. Only few studies have examined temporal patterns of BVOC emissions from incubated litter. However, Gray et al. (2010) and Gray and Fierer (2012) measured leaf litter BVOC emissions from 12 different plant species during 20 day- and 125 day incubation periods, respectively. These studies observed distinct temporal emission patterns for the different litter types, however suggesting no clear difference between evergreen and deciduous species (Gray et al., 2010, Gray and Fierer, 2012). We speculate that the distinct temporal pattern for *C. tetragona* and *Salix* litter in the present study is due to differences in the decomposition rate. Across leaf litter types from numerous different shrub species, those that are evergreen generally decompose slower than those that are the deciduous (Cornelissen, 1996, Cornelissen et al., 2007). Thus, in contrast to the deciduous *Salix*species, it may take longer time before cell walls and BVOC storage structures break and release the contents in the evergreen *C. tetragona,*which could explain why this litter had highest emissions towards the end of the incubation. However, another explanation may be that the emissions from *Salix* and *C. tetragona* litter were derived from different processes. By far the highest contribution to the total emissions from the *C. tetragona* litter were the mono- and sesquiterpenes, of which the majority came from storage compartments. These emissions may have been highly temperature dependent because warmer conditions increase the decomposition rate of the storage compartments and the BVOC volatilization rates (Laothawornkitkul et al., 2009). In contrast, BVOC emissions from the *Salix*litter, which does not contain specific BVOC storage compartments, is likely dominated by newly produced BVOCs released from processes associated with the microbial decomposition. The BVOC emissions from the *Salix* litter may have been highest during the earlier stages of the incubation because a larger fraction of labile components in the fresh litter allowed for a faster decomposition rate (Wang et al., 2004).

We found numerous significant changes in BVOC emissions from the first to the second measurement at the same temperature, suggesting that the changes in the BVOC emissions during the incubation period, at least to some extent, were driven by the effect of time. This is in line with other studies that observed that litter BVOC emission changed over time at stable temperature (Gray et al., 2010, Gray and Fierer, 2012). Our results showed considerable variation in the direction of change depending on litter type and BVOC category, except for at 26 °C where the emissions, almost consistently, decreased from the first to the second measurement. We suggest that a higher fraction of resilient plant parts at this later decomposition stage have slowed down decomposition rate which, in turn, has decreased the emissions. Furthermore, a depletion of stored BVOCs during the incubation period may have contributed further to the lower emissions. We hypothesized that the release of BVOCs from litter would decrease over time. We observed that the different BVOC categories developed differently but if we consider only the total emissions we could confirm this

hypothesis for the *Salix* litter. Since the total emissions decreased only on the last day for the *C. tetragona*litter, the hypothesis could not be fully confirmed for this species.
The *C. tetragona* litter emissions of several BVOC categories were higher from the high arctic Zackenberg than from Disko Island. In contrast, there were no differences between the *Salix* litter from the two locations. This suggests that either the *C. tetragona* litter or the microorganisms inhabiting the litter differed. Since the bacterial communities on the *C. tetragona* litter from the two locations were similar but the C:N ratio and the NIR spectra of the litter were different, the litter chemical composition was likely responsible for the different emissions. We hypothesized that BVOC emissions from *C. tetragona* litter, which stores BVOCs inside trichomes in the leaves, would be higher from high arctic litter than from low arctic litter, due to higher density of trichomes on plants grown under colder conditions (Hartikainen et al., 2014, Schollert et al., 2015). Since we measured higher *C. tetragona* emissions from the high arctic litter than from the low arctic litter, most likely due to differences in the chemical composition of the litter, not the microorganisms, our data supports this hypothesis. However, under field conditions the higher emission potential of the litter from higher latitudes may be counteracted by the typically lower temperatures, which reduce volatility. The suggestion that it was the trichome density which was causing the different emissions rates in the *C. tetragona* litter is further supported by the fact that the emission rates from the *Salix* litter, which does not contain trichomes, was similar from the two locations.

4.2. Coupling between litter BVOC emissions and the microbial community structure

During the incubation period we detected a change in the relative abundance of bacteria in the *Salix* litter with a general increase of *Actinobacteria* that are known to have a K-selected lifestyle (Fierer et al., 2007). Higher relative abundance of *Actinobacteria* later in the incubation period is likely to reflect more decomposed litter which had a higher fraction of resilient plant parts (Wang et al., 2004). We also found a change in the BVOC emissions from the *Salix* litter during the incubation period: the emission of alkenes generally increased but that of benzenoids and alkanes decreased. These different temporal emission patterns suggest that different factors may have controlled the emissions of these compounds as the decomposition progressed. The succession-like changes in the bacterial community allow us to speculate that bacteria could have played a role for the different emission patterns since we know that different bacteria can produce or take up different types of BVOCs (Insam and Seewald, 2010) and may increase the release of BVOCs from the litter during the degradation of plant cells. In accordance with our results, Seewald et al. (2010) observed parallel changes in soil BVOC emissions and the fungal community composition with the application of different types of fertilizers. Since we for unknown reasons could not amplify fungal DNA, we can only attempt to assess the relationship between bacterial community composition and BVOC emissions. The dominant OTU on *Salix* litter and the fourth most dominant OTU on *C. tetragona* litter was assigned to *Kitasatospora* within the family *Streptomycetaceae.* Little is known about the ecology of *Kitasatospora* spp. but the mycelial morphology of *Kitasatospora* spp. (Girard et al., 2014) resembles that of strains of the closely related *Streptomyces*. These branching hyphal filaments assist the bacteria in adhering to and penetrating leaf litter and other organic remains, which are then

decomposed by a large repertoire of hydrolytic exoenzymes to provide nutrients (Schrempf, 2007). Members of S*treptomycetaceae* produce numerous BVOCs (Rabe et al., 2013) and *Streptomyces* is the best studied of the three genera within *Streptomycetaceae* in terms of BVOC production (Tyc et al., 2017). Many *Streptomyces* spp. are known to produce a wide range of BVOCs, e.g. different terpenoids (Peñuelas et al., 2014, Yamada et al., 2015), and Kitasatospora *setae* possesses several gene clusters presumably involved in production of sequiterpenes and other BVOCs (Ichikawa et al., 2010, Citron et al., 2012). The increase in emission of terpenoids from the *C. tetragona*litter over time was concomitant with an increase in the relative abundance of the OTU assigned to *Kitasatospora* on the Disko Island samples. However, a similar pattern was not observed for the *Salix* litter causing us to be cautious about linking terpenoid emission to production by this OTU.

The emission profiles of *C. tetragona* litter also changed during the course of the incubation. However, we did not find clear succession-like changes in the bacterial community in this litter except for a decrease in diversity and richness during the experiment.

On the other hand, the bacterial community on the *C. tetragona* litter was dominated by a number of OTUs assigned to different lineages of *Proteobacteria* with members known to produce or transform BVOCs. For example, species within *Myxococcales* (Dickschat et al., 2004, Dickschat et al., 2005, Yamada et al., 2015) and *Burkholderia* (Yamada et al., 2015, Weisskopf and Bailly, 2013) are able to produce different BVOCs, and several *Sphingomonas* spp. have the capacity to transform a range of terpenoids (Grishko et al., 2014). While these OTUs may influence the BVOC emission profile by opening plant cells, by processing BVOCs released from the litter and by producing BVOCs, we are not able to directly link emission of specific groups of BVOCs to the relative abundance of the dominating OTUs. Instead, the *C. tetragona* emissions might have been driven by other factors, such as temperature, as we previously suggested. Terpenoids, which were highly emitted from the *C. tetragona* litter, are known to have microbial growth inhibiting properties (Junker and Tholl, 2013). More specifically, a screening of 80 vascular plant extracts for their antimicrobial properties showed that *C. tetragona* was one of two species expressing moderate to very strong antimicrobial activity (Paudel et al., 2014) and this may explain the inconsistent changes in relative abundance of bacteria during the incubation period on this litter.

Our fourth hypothesis that the BVOC emission profiles would change in the course of incubation parallel with bacterial community changes, could only be confirmed for the *Salix* litter. Therefore, bacteria may be more important for the BVOC emissions from decomposing *Salix* litter than from decomposing *C. tetragona* litter.

4.3. Conclusions

This study showed that BVOC emissions from decomposing shrub litter from common arctic plant species changed during the course of the experiment and that the temporal emission pattern varied between species. These emission changes were caused by both the increase in temperature and litter decomposition over time. Arctic field measurements are typically done during the summer period (Schollert et al., 2014, Kramshøj et al., 2016, Lindwall et al., 2016, Svendsen et al., 2016).

However, our study showed that emissions of some BVOCs peaked during the early stages of decomposition at temperature of 5 °C, especially for the *Salix* litter. Our study also showed that litter of the BVOC-storing *C. tetragona* had higher BVOC emissions than the *Salix* litter, which does not have specific storage structures for BVOCs. Therefore, these results suggest that the importance of future arctic BVOC emissions from litter to the atmosphere highly depend on the dominant plant species. Climate warming is expected to cause changes in the arctic plant species composition (Sturm et al., 2001, Walker et al., 2006). For instance, deciduous shrubs will likely become more dominant, especially in the warmer regions of the Arctic (Walker et al., 2006, Elmendorf et al., 2012a). Since we found that litter emissions from the evergreen *C. tetragona* were higher for the high arctic than low arctic litter, we suggest that also plant phenotypic responses to a warmer climate can influence future litter emissions. To our knowledge, this is the first study to couple litter BVOC emissions with the litter-associated bacterial community. We observed parallel changes for the *Salix* litter but not for the *C. tetragona* litter and we therefore speculate that the importance of bacteria for litter BVOC emissions may depend on the litter type.

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