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Leaf wax lipids in a changing environment: The impact of warming and elevated CO2 on the composition of lipids in the SPRUCE experiment

GEO 511 Master's Thesis

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Abstract

Boreal forests are crucial carbon sinks that regulate the Earth's climate, but their responses to climate change remain uncertain and could potentially turn boreal ecosystems into a source of carbon in the future. Plants have various strategies to cope with environmental change, including the modification of leaf wax lipids to improve protection against water loss. However, how the interaction of warming and elevated CO_2 concentration affects plant lipid composition is poorly understood. Therefore, this study aimed to contribute to research by investigating the effects of whole-ecosystem warming in combination with elevated CO_2 concentrations on lipid composition of six dominant boreal plant species at the SPRUCE (Spruce and Peatland Responses Under Changing Environments) experimental site in Minnesota, USA. Plants in large open-top chambers were exposed to a range of temperature treatments from 0°C to +9°C at ambient and elevated CO_2 concentration (∼900 ppm). Elemental analysis combined with lipid analysis of *n*-alkanes and fatty acids were conducted. This study found that four years of warming and two years of elevated CO_2 treatment had little to no effect on overall foliar carbon content and lipid composition, but did promote a strong increase in foliar nitrogen content. While no significant changes in overall carbon and lipid composition were observed, responses differed between moss, shrubs and trees. Warming increased foliar carbon and nitrogen content and caused a depletion of ^{13}C in shrubs under ambient conditions, while no effect of elevated CO_2 was identified. Results showed that moss was the only plant functional type in which carbon content decreased under ambient conditions, and a strong enrichment in ^{13}C was observed under elevated CO_2. Shrubs showed no changes in lipid composition, while *n*-alkane concentrations of moss and trees increased and more short-chain fatty acids were produced. Over the course of four years, lipid composition of *P.mariana* did not change significantly. However, a strong increase in foliar nitrogen content under ambient and elevated CO_2 was observed in the last sampling year of 2018, along with an enrichment in ^{13}C under ambient conditions. This study demonstrated that moss and trees were more sensitive to warming and elevated CO_2 than shrubs, which may have important implications for the future of boreal ecosystems.

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List of abbreviations

ACL_{alk}	Average chain length of *n*-alkanes
ACL_{fa}	Average chain length of fatty acids
CPI_{alk}	Carbon preference index of *n*-alkanes
CPI_{fa}	Carbon preference index of fatty acids
DCM	Dichloromethane
eCO_2	Elevated CO_2
FA	Fatty acids
GC-FID	Gas chromatography-flame ionization detector
GC-MS	Gas chromatography-mass spectrometry
LME	Linear mixed-effects model
MeOH	Methanol
PFT	Plant functional type
SPRUCE	Spruce and Peatland Responses Under Changing Environments
TLE	Total lipid extract

1 Introduction

The Earth's climate is largely regulated by plants, but despite their global significance it is still uncertain how their responses to increasing temperatures and CO_2 concentrations will affect climate change in the future (Cox *et al.* 2000; Dusenge *et al.* 2019; Nolan *et al.* 2018). It is particularly important to address these uncertainties in boreal ecosystems given the extensive amounts of carbon they have sequestered over time as a result of low temperatures, wet conditions and nutrient-poor soil (Dise 2009; Gorham 1991). These large carbon reservoirs are at risk due to the high rates of warming projected for northern latitudes, which will have a significant impact on vegetation and soil respiration (Collins *et al.* 2013; Dise 2009; Gorham 1991; Stinziano & Way 2014). Changes in boreal vegetation could increase carbon cycling, which may contribute to releasing previously stored carbon and thereby fuel climate change (Malhotra *et al.* 2020; McPartland *et al.* 2020; Norby *et al.* 2019). Recent observations have shown that shifts in plant community composition are occurring in response to warming, whereby vascular shrub cover is increasing to the detriment of important carbon sequestering moss (McPartland *et al.* 2020; Norby *et al.* 2019). Moreover, dominant boreal tree species are showing different capacities to adapt to changes in their environment (Dusenge *et al.* 2020; Warren *et al.* 2021). This could significantly affect carbon cycling above and belowground through changes in productivity, litter composition, and competition between species (Bragazza *et al.* 2013). However, key uncertainties remain about the mechanisms behind the changes in community composition (Bragazza *et al.* 2013), highlighting the need for more research on boreal plant responses to climate change.

When faced with changes in their environment, plants can acclimatize through physiological and phenological adaptations (Richardson *et al.* 2018; Shepherd & Griffiths 2006). An extension of the growing season with earlier onset of budburst and later leaf senescence has been observed in boreal regions under warming (Richardson *et al.* 2018). Furthermore, increases in CO_2 have been found to stimulate photosynthetic activity in plants while warming can have a positive effect on productivity when photosynthesis is below the thermal optimum (Ainsworth & Long 2005; Dusenge *et al.* 2019). Abiotic changes may also bring about nutrient or water limitations, which can result in shifts in biomass allocation, as plants have the ability to invest more biomass to specific organs that will ensure survival during times of stress (Poorter *et al.* 2012). Another defense measure plants can resort to is reducing primary growth and instead synthesizing more secondary metabolites such as lipids (Herms & Mattson 1992; Ohlrogge & Browse 1995). Lipids have diverse functions and are fundamental to various plant structures (Ohlrogge & Browse 1995), including the protective wax coating located on the surface of leaves (Koch & Ensikat 2008; Ohlrogge & Browse 1995; Shepherd & Griffiths 2006). This wax is referred to as the cuticle and forms the boundary between the plant and its surrounding atmosphere and plays a vital role in protecting the plant from foliar water loss and UV radiation (Koch & Ensikat 2008; Ohlrogge & Browse 1995; Riederer & Schreiber 2001; Shepherd & Griffiths 2006). The cuticle consists of the polymer cutin covered by intracuticular wax and an outermost layer referred to as the epicuticular wax (Koch & Ensikat 2008; Kolattukudy 1970; Shepherd & Griffiths 2006). Cuticular waxes are hydrophobic and mainly composed of *n*-alkanes, *n*-fatty acids and *n*-alcohols (Eglinton & Eglinton 2008; Jetter & Riederer 2016; Kolattukudy 1970; Shepherd & Griffiths 2006). Fatty acids and *n*-alkanes can be used as molecular proxies although alkanes are more frequently used by virtue of

their chemical stability over long periods of time (Eglinton & Eglinton 2008; Jansen & Wiesenberg 2017). Applications of such molecular proxies are manifold including paleoecological reconstructions, chemotaxonomy, and source determination in soils (Eglinton & Eglinton 2008; Jansen & Wiesenberg 2017). Importantly, molecular proxies can also be used to trace changes in lipid composition in response to environmental changes (Jansen & Wiesenberg 2017).

Environmental factors such as temperature, CO_2 and drought have been found to affect lipid composition in waxes (Jansen & Wiesenberg 2017). Increasing temperatures, for example, increase chain lengths of *n*-alkanes, in turn making the wax more hydrophobic and improving protection against water loss (Bush & McInerney 2015; Tipple & Pagani 2013). Moreover, increased saturation of fatty acids has been observed with warming, which alters membrane fluidity and improves the thermotolerance of plants (Larkindale & Huang 2004). The effect of CO_2 on lipid composition is not entirely conclusive, with some studies finding no changes in lipid composition, while others observed changes in concentrations of individual compounds (Jansen & Wiesenberg 2017). These findings provide valuable insights into the effects of temperature and CO_2 on lipid composition. However, these two environmental factors are predicted to have interactive effects on plants as highlighted by studies on leaf physiology, where CO_2 can either offset or enhance the effects of warming (Dusenge *et al.* 2019; Way *et al.* 2015). To the best of the author's knowledge, there are currently no studies on the interactive effects of temperature and CO_2 on lipid composition, highlighting the need for more research on this topic.

Studying the interactive effects of temperature and CO_2 is challenging, as existing experimental designs are limited to manipulating one environmental factor at a time (Way *et al.* 2015). A frequently used warming method is the use of field chambers such as open-top chambers that vary in size and function like greenhouses that allow sunlight to enter through the walls but prevent infrared from leaving the chamber, thereby warming the interior (Aronson & McNulty 2009). The use of overhead infrared lamps are another commonly implemented warming method, whereby lamps are suspended above the vegetation and soil (Aronson & McNulty 2009). There are several limitations associated with these methods, such as difficulties in controlling temperatures within chambers and high energy demands of infrared lamps (Aronson & McNulty 2009). Early studies on the effects of CO_2 were conducted under controlled environments using field chambers, but an important limitation is related to the potentially larger effect of the chamber than the CO_2 treatment itself (Ainsworth & Long 2005). As a result, large-scale FACE (free-air CO_2 enrichment) studies have since been used to study the effects of CO_2 (Ainsworth & Long 2005). In these experiments, plants are exposed to elevated CO_2 in their natural environment without confinement and CO_2 is released through vent pipes and dispersed by wind (Ainsworth & Long 2005). While this allows for the effects of elevated CO_2 to be studied in large-scale natural environments, it is difficult to study the interactions of CO_2 with other environmental changes (Ainsworth & Long 2005). These challenges underline the need for experimental designs that allow for multiple environmental factors to be manipulated simultaneously.

The Spruce and Peatland Responses Under Changing Environments (SPRUCE) experiment in Minnesota (USA) is a unique whole-ecosystem warming experiment that is manipulating both temperature and elevated CO_2 over the course of a decade (Hanson *et al.* 2017). The aim of this experiment is to gain insights into the long-term responses

of a vulnerable boreal ecosystem to climatic change (Hanson *et al.* 2017). It seeks to address uncertainties as to whether this region will become a source of carbon in future and thereby exacerbate climate change (Hanson *et al.* 2017). To do this, large open-top enclosures (∼110 m^2) that encompass plants in their entirety are being exposed to above- and belowground warming ranging from 0 °C to +9 °C at ambient and elevated CO_2 concentrations (∼900 ppm) (Hanson *et al.* 2017). At SPRUCE, several studies have been conducted on the response of aboveground vegetation but none have studied leaf waxes so far.

The aim of this thesis was to gain an understanding of the effects of warming and elevated CO_2 concentration on lipid composition of boreal plants in the SPRUCE experiment. More specifically, the following research questions and hypotheses were investigated:

1. How does warming and elevated CO_2 concentration affect plant lipid composition?

   – Based on the findings of previous studies discussed above, an increase in lipid concentration and *n*-alkane chain length are expected.

2. In what way do plant adaptation strategies towards warming and elevated CO_2 differ between plant functional types?

   – In light of evidence presented above, the modification of lipid composition is expected to be more pronounced for moss and trees given that observations suggest they are more susceptible to warming than shrubs.

3. How has lipid composition of *Picea mariana* changed over time following environmental change?

   – With increased duration of warming and elevated CO_2 treatment, *P.mariana* is hypothesized to experience more stress and thus the strongest increases in lipid concentration and *n*-alkane chain lengths in response to warming are expected in the last sampling year of 2018.

2 Study site

The following section is based on Hanson *et al.*'s (2017) paper describing the SPRUCE experimental site and design.

The SPRUCE whole-ecosystem warming experiment is located in the Marcell Experimental Forest in northern Minnesota, USA (47°30.476'N, 93°27.162'W). The climate of this site is sub-humid continental, with mean annual temperatures and precipitation of 3.3 °C and 768 mm, respectively. The area is prone to extreme daily and seasonal temperature fluctuations that can amount to extremes of -38 °C and +30 °C.

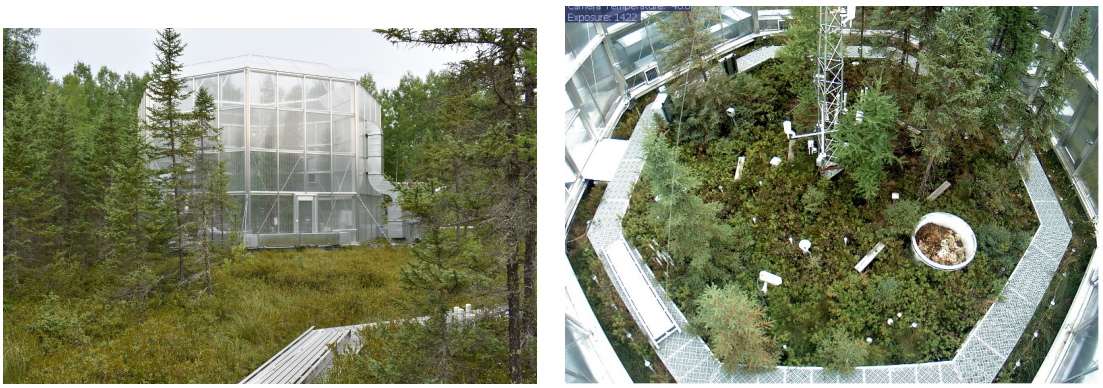
The forest is situated in an ombrotrophic peatland that is dominated by the evergreen conifer *Picea mariana* (black spruce) and the deciduous conifer *Larix laricina* (tamarack). The shrub layer underneath the dominant tree species consists of ericaceous and herbaceous species including *Rhododendron groenlandicum*, *Chamaedaphne calyculata*, *Maianthemum trifolium*, *Rhynchospora alba* and *Eriophorum vaginatum*. Byrophytes cover the peat soil beneath the shrubs and consist of several *Sphagnum* species. The plant community at SPRUCE is depicted in Figure 1, which shows the dominant tree species in 1(a) and the understory made up of shrubs and mosses in 1(b). The peat soil reaches an average depth of 2-3 m and has a perched water table that stems from precipitation, with no input from surrounding groundwater. The microtopography of the soil consists of small mounds and corresponding valleys, which are referred to as hummocks and hollows, respectively.

(a) (b)

Figure 1: Vegetation at the SPRUCE experimental site (photographs taken by Nicholas Ofiti in August 2018).

Ten octagonal open-topped enclosures were established at the site, each 7 meters tall and 12.8 meters in diameter. On average, there are around 18-19 trees per enclosure, which range in height and create a canopy between 5-8 m tall. Figure 2 shows the outer structure of the enclosures and the interior of the enclosure from above. The top of the enclosures are open, with panels angled at 35° to create a frustum that ensures maximum warming efficiency. The chambers are built on a corral that extends 3-4 meters into the sediment beneath the peat, making them hydrologically isolated from the surrounding peat,

which enables enclosure-specific hydrological measurements to be obtained. The following regression-based temperature treatments were assigned randomly to the enclosures: ambient (0 °C), +2.25, +4.5, +6.75 and +9 °C (Figure 3). The two open-topped chambers with no warming treatment (0 °C) are referred to as control plots and are reference plots from which the temperature differentials are calculated from. In addition to these control plots, two further ambient plots were constructed without chambers. For each temperature treatment, there are two enclosures, one at ambient CO_2 concentration and the other treated with elevated CO_2 concentration (-54 ‰) to achieve ∼900 ppm (Figure 3).



(a) (b)

Figure 2: SPRUCE open-top chamber (a) exterior (photograph taken by Nicholas Ofiti in 2018) and (b) interior (PhenoCam Gallery, Seyednasrollah *et al.* 2019).

Belowground warming started in 2014, followed by aboveground warming in 2015 and elevated CO_2 was added in 2016. Aboveground warming heats the air up to six meters in the enclosures and is achieved by drawing air from the middle of the enclosure down to heat exchangers that warm the air to the desired temperature. The warmed air is subsequently distributed through eight diffusers, one located on each wall one meter above the soil. In addition, elevated CO_2 is added to the chambers at four points in the enclosures. To heat the peat, sixty-seven vertical heating elements of 3 m length were installed beneath each enclosure. They are arranged in three circles, the outermost with 48 containing the most heaters, followed by the second inner circle with 12 and the smallest in the center containing 7 heaters. Temperature and relative humidity within the enclosures are measured half-hourly at different heights within the enclosures and peat temperature is measured half-hourly at nine depths. Given that the chambers are open, wind sensors were installed at 10 m above ground level to measure mixing of enclosure air and outside ambient air.

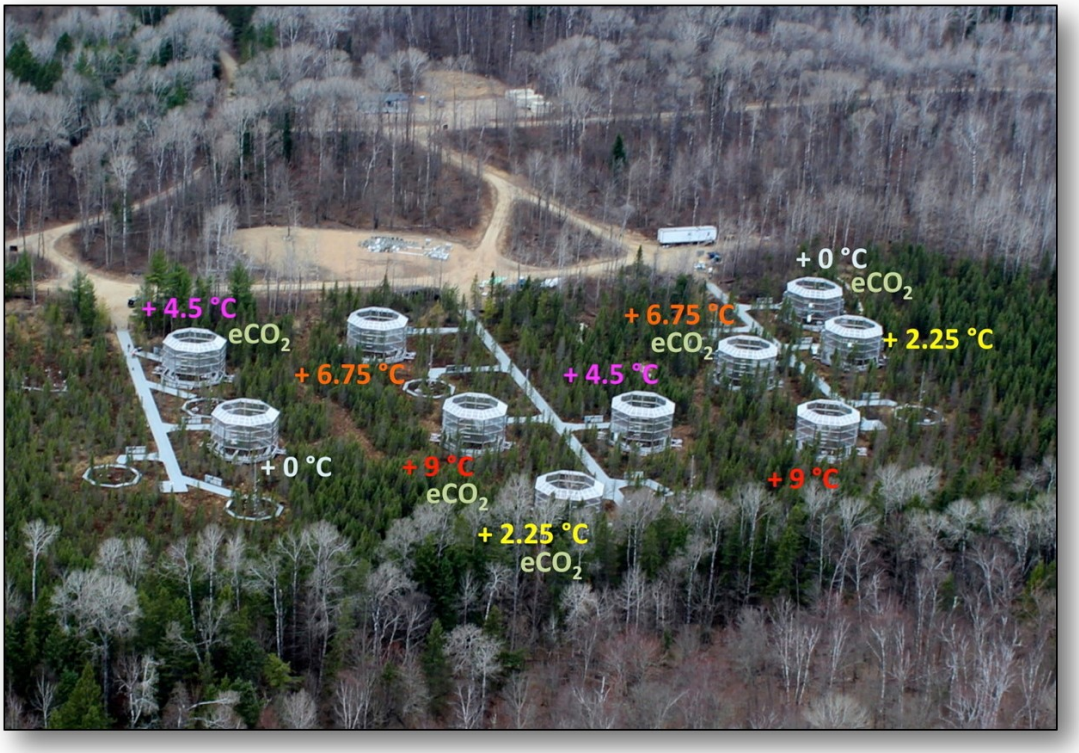


Figure 3: Setup of the SPRUCE experiment showing the ten open-topped chambers and their temperature and CO_2 treatment (Oak Ridge National Laboratory, U.S. Dept. of Energy. n.d., https://mnspruce.ornl.gov/design).

3 Materials and methods

3.1 Sampling and preparation

The samples were collected from the SPRUCE experimental site in August 2018 by members of the Soil and Biogeochemistry group and subsequently brought to the physical Geography laboratory at the University of Zurich. Samples were taken from all ten enclosures and from one unchambered control plot. One sample of each of the following species was collected per enclosure: *Picea mariana*, *Larix laricina*, *Rhododendron groenlandicum*, *Chamaedaphne calyculata*, *Sphagnum* (hollow) and *Sphagnum* (hummock) (Figure 4). Whenever possible, several plants of the same species were sampled within one enclosure to form a mixed sample. After sampling, needles of *P.mariana* were separated into foliar cohorts of 2014, 2016 and 2018. Thus, per enclosure, there was one sample of each species from 2018 (six samples) plus an additional *P.mariana* sample from 2014 and one from 2016, amounting to a total of eight samples per enclosure and an overall total of 88 samples. The samples were freeze-dried and subsequently the leaves were separated from the rest of the plant using tweezers. This separation was possible for all species except for *Sphagnum*, given that differentiation of stem and leaves is more challenging in moss by virtue of its anatomy (Figure 4). Thus, for *Sphagnum*, the separation was focused on removing litter from other species that was mixed into the moss sample. Once separated, the material was milled to ∼1 g of fine powder using a horizontal ball mill with a frequency of 30 s^{-1} for 20-35 seconds depending on the species.

Figure 4: Sample preparation of (a) *C.calyculata*, (b) *L.laricina*, (c) *Sphagnum*, (d) *R.groenlandicum* and (e) *P.mariana* (photographs taken by author).

3.2 Elemental and isotopic analysis

To determine the carbon, nitrogen and δ^{13}C contents of the samples, two analytical replicates of 0.8-1 mg milled material was weighed into tin capsules per sample. A soil reference sample (chernozem) was weighed in after every twelfth sample. Samples were measured using an EA-IRMS Flash 2000-HT Plus linked by Conflo IV to Delta V Plus isotope ratio mass spectrometer. Carbon and nitrogen concentrations are expressed as a percentage, while δ^{13}C is expressed in per mill (‰) and is defined as:

$$\delta^{13}C = \left(\frac{^{13}C/^{12}C_{sample}}{^{13}C/^{12}C_{standard}} - 1 \right) \cdot 10^3 \quad (1)$$

where the standard refers to the international reference standard Vienna Pee Dee Belemnite (VPDB; Dawson *et al.* 2002).

3.3 Lipid analysis

Lipid analysis was conducted following Wiesenberg & Gocke's (2017) method. In a first step, ∼0.3-1 g of milled plant material was extracted via Soxhlet extraction over the course of 24 hours using the solvent mixture DCM:MeOH (93:7,v/v). Figure 5 shows the set-up of the extraction apparatus. Round-bottom flasks filled with solvent were placed in the water bath heated to 54 ± 1 °C. Attached above the flask is the Soxhlet extractor containing the sample, which is connected to a cooler.

After 24 hours, the extracted material in the round-bottom flasks was filtered, filled into vials and left to evaporate until dry and weighed to determine the total lipid extract. An aliquot of the lipid extract was then taken (∼10-15 mg) to further separate lipid extracts into fatty acids and low-polarity lipid fractions. To do this, a glass column filled with 1.5-2 g of KOH-coated silica gel was prepared and the low-polarity fraction was eltued using DCM. This was followed by the elution of the fatty acids using the solvent mixture DCM/formic acid (99:1,v/v). The low-polarity fraction was further separated into aliphatic hydrocarbons, aromatic hydrocarbons and heterocompounds (e.g alcohols and ketones). This was done by adding 5-5.5 cm of activated silica gel to a pasteur pipette prepared with a plug of glass wool. Aliphatic hydrocarbons were eluted using *n*-hexane and aromatic hydrocarbons were eluted using *n*-Hexane:DCM (1:1,v/v). To collect the last fraction of heterocompounds, the mixture DCM:MeOH (93:7, v/v) was used. Before transferring the aliphatic hydrocarbons to GC autosampler vials, 50 µL of the internal standard $D_{50}C_{24}$ was added.

Prior to methylation, an aliquot of the fatty acid fraction was taken (∼1 mg). To methylate the samples, 300 µL of DCM was first added to the sample, followed by 50 µL of the internal standard $D_{39}C_{20}$. After adding 500 µL of boron trifluoride/MeOH, the samples were placed on a heating block at 60 °C for 15 minutes. Once cooled, 500 µL of deionized water was added to the sample and the samples were centrifuged. The lower organic phase of the centrifuged sample was then quantitatively transferred to a glass column filled with 0.5-1 g of sodium sulfate and collected in GC autosampler vials.

Figure 5: Soxhlet extraction apparatus used at the physical Geography laboratory (photograph taken by author)

3.4 Gas chromatography and mass spectrometry

Before measuring *n*-alkanes and fatty acids, the samples were concentrated by reducing the solvent and subsequently transferred into glass micro inserts, which were then placed into GC autosampler vials. Samples were measured using a gas-chromatography flame ionization detector (GC-FID) and for both *n*-alkanes and fatty acids, one sample per species was measured using a gas chromatography mass spectrometer (GC-MS) for compound identification. To measure the alkanes on the GC-FID, 1 μl of sample material was injected with the multi-mode inlet at 70 °C, after which this temperature was held for 4 minutes. At a rate of 5 °C min^{-1}, the temperature was then increased to 320 °C and held for 50 minutes. The temperature for fatty acids was lower (50 °C) and held for 4 minutes, and first ramped up to 150 °C at 4 °C min^{-1} and then to 320 °C at a rate of 3 °C min^{-1} and held for 40 minutes (Wiesenberg & Gocke 2017).

The average chain length (ACL) and carbon preference index (CPI) are frequently used lipid molecular proxies (Bush & McInerney 2013; Wiesenberg & Gocke 2017). The ACL refers to the weighted average of carbon chain lengths of *n*-alkanes and fatty acids and the CPI is the ratio of odd-over-even *n*-alkanes and even-over-odd fatty acids (Wiesenberg & Gocke 2017). An odd-over-even predominance of *n*-alkanes and an even-over-odd predominance for fatty acids is typical for higher plants (Wiesenberg & Gocke 2017). The ACL is often used to differentiate between higher plants and degraded organic matter (Wiesenberg & Gocke 2017), but has also been found to be affected by environmental changes (Bush & McInerney 2015). The proxies were calculated using the following equations

from Wiesenberg & Gocke (2017):

$$ACL = \sum(Z_n \cdot n) / \sum(Z_n) \quad (2)$$

$$CPI_{alk} = \left[\left(\sum C_{21-35\ \text{odd}} / \sum C_{22-32\ \text{even}}\right) + \left(\sum C_{21-35\ \text{odd}} / \sum C_{24-34\ \text{even}}\right)\right] /2 \quad (3)$$

$$CPI_{fa} = \left[\left(\sum C_{20-30\ \text{even}} / \sum C_{21-27\ \text{odd}}\right) + \left(\sum C_{20-30\ \text{even}} / \sum C_{23-29\ \text{odd}}\right)\right] /2 \quad (4)$$

where n refers to the amount of carbons in a compound and Z_n refers to concentration of the compound.

3.5 Statistical analysis

Data was analyzed and visualized using excel and R studio version 1.2.5001 (RStudio Team 2019). For the elemental analysis, a replicate of each sample was prepared and measured, while all other analyses were conducted using a single measurement per sample. The total lipid extract and *n*-alkane and fatty acid concentrations were normalized to total carbon and expressed as $mg\,g^{-1}\,C$ and $\mu g\,g^{-1}\,C$, respectively. Prior to statistical analyses, the species were grouped into plant functional types, which refers to the grouping of species based on similar characteristics and functions (Wullschleger *et al.* 2014). In this study, the plant functional types were defined as moss (*Sphagnum* species), shrubs (*R.groenlandicum and C.calyculata*), and trees (*P.mariana* and *L. laricina*).

A linear mixed-effect model (LME) containing fixed and random effects was used to determine the effect of temperature and CO_2 treatment on parameters of interest with the *nlme* package in R studio. Temperature, CO_2, species, plant functional type and their interactions were defined as the fixed effects and enclosures as the random effects. To test for statistical significance, ANOVA was performed and 5 % was used as the level of significance.

4 Results

4.1 Elemental composition

4.1.1 Carbon, nitrogen and C/N ratio

Carbon, nitrogen and the C/N ratio differed significantly between individual species and plant functional types ($p < 0.01$ for all; Table 1). Overall, carbon (C) content did not show a significant response to warming and CO_2 treatment ($p > 0.05$; $\overline{x} = 46.3 \pm 0.3\,\%$; Table S1; Figure S1). However, temperature was found to be a significant predictor of nitrogen (N) content and C/N ratio ($p = 0.0043$, $p = 0.0145$, respectively). N content ranged from $1.0 \pm 0.1\,\%$ at 0°C to $1.5 \pm 0.1\,\%$ at 9°C under ambient conditions and from $0.9 \pm 0.1\,\%$ at 0°C to $1.3 \pm 0.1\,\%$ at 9°C under elevated CO_2 (eCO_2) conditions. The C/N ratio was found to be 45.8 ± 2.6 at 0°C and 33.4 ± 1.8 at 9°C, and 57.3 ± 4.8 at 0°C and 37.7 ± 2.2 at 9°C in warmed and eCO_2 enclosures, respectively (Table S1; Figure S1).

Temperature treatment significantly affected the C and N content of individual plant functional types (PFTs) ($p = 0.0029$ and $p = 0.0024$, respectively; Figure 6a and b). In addition, the C/N ratio of individual PFTs showed a significant response to both warming treatment ($p = 0.0013$) and CO_2 treatment, individually ($p = 0.0226$; Figure 6c). A strong and significant positive correlation was observed between warming and C content in shrubs and trees under ambient conditions ($R^2 = 0.67$, $p = 0.0013$ and $R^2 = 0.48$, $p = 0.033$; Figure 6a). A different trend was observed in moss, whose C content non-significantly decreased with increasing temperature in ambient enclosures ($R^2 = -0.4$, $p = 0.077$; Figure 6a). In contrast, N content of all PFTs increased linearly and significantly with increasing temperature under ambient conditions (Figure 6b). The same was true for moss and trees under eCO_2 conditions ($R^2 = 0.5$, $p = 0.0024$ and $R^2 = 0.69$, $p = 0.00073$; Figure 6b). In shrubs, however, warming and N content were uncorrelated under eCO_2 conditions ($R^2 = 0.048$, $p = 0.84$; Figure 6b). The C/N ratio decreased significantly with warming in all three PFTs under ambient conditions (Figure 6c). The same was observed under eCO_2 conditions for moss and trees, with a particularly strong response observed in trees ($R^2 = -0.6$; $p = 0.0054$; Figure 6c).

4.1.2 Isotopic signature

Significant differences in $\delta^{13}C$ values were observed between individual species and PFTs ($p < 0.0001$ for both; Table 1). Furthermore, CO_2 treatment was a significant predictor of $\delta^{13}C$ ($p < 0.0001$) and was found to average at $-29.5 \pm 0.2\,‰$ in ambient enclosures compared to $-43.3 \pm 0.4\,‰$ in those treated with eCO_2 (Table S1). When grouped into their respective PFTs, $\delta^{13}C$ showed a significant response to CO_2 treatment ($p < 0.0001$) and warming ($p < 0.0001$), individually. A significant interaction between CO_2 × temperature × PFT was also identified ($p < 0.0001$; Figure 6d). Under ambient conditions, no significant correlation was observed between $\delta^{13}C$ and warming in moss (Figure 6d). In shrubs, a significant negative correlation was observed ($R^2 = -0.48$, $p = 0.032$; Figure 6d), while $\delta^{13}C$ values of trees became significantly less negative ($R^2 = 0.51$, $p = 0.022$; Figure 6d). A strong response to warming under eCO_2 was observed in both moss sub-species, where

δ^{13}C became significantly less negative i.e. more enriched in ^{13}C with increasing temperature ($R^2 = 0.87$, $p < 0.0001$). This effect was not observed for shrubs or trees, whose δ^{13}C values were not significantly affected by warming under eCO_2 conditions (Figure 6d).

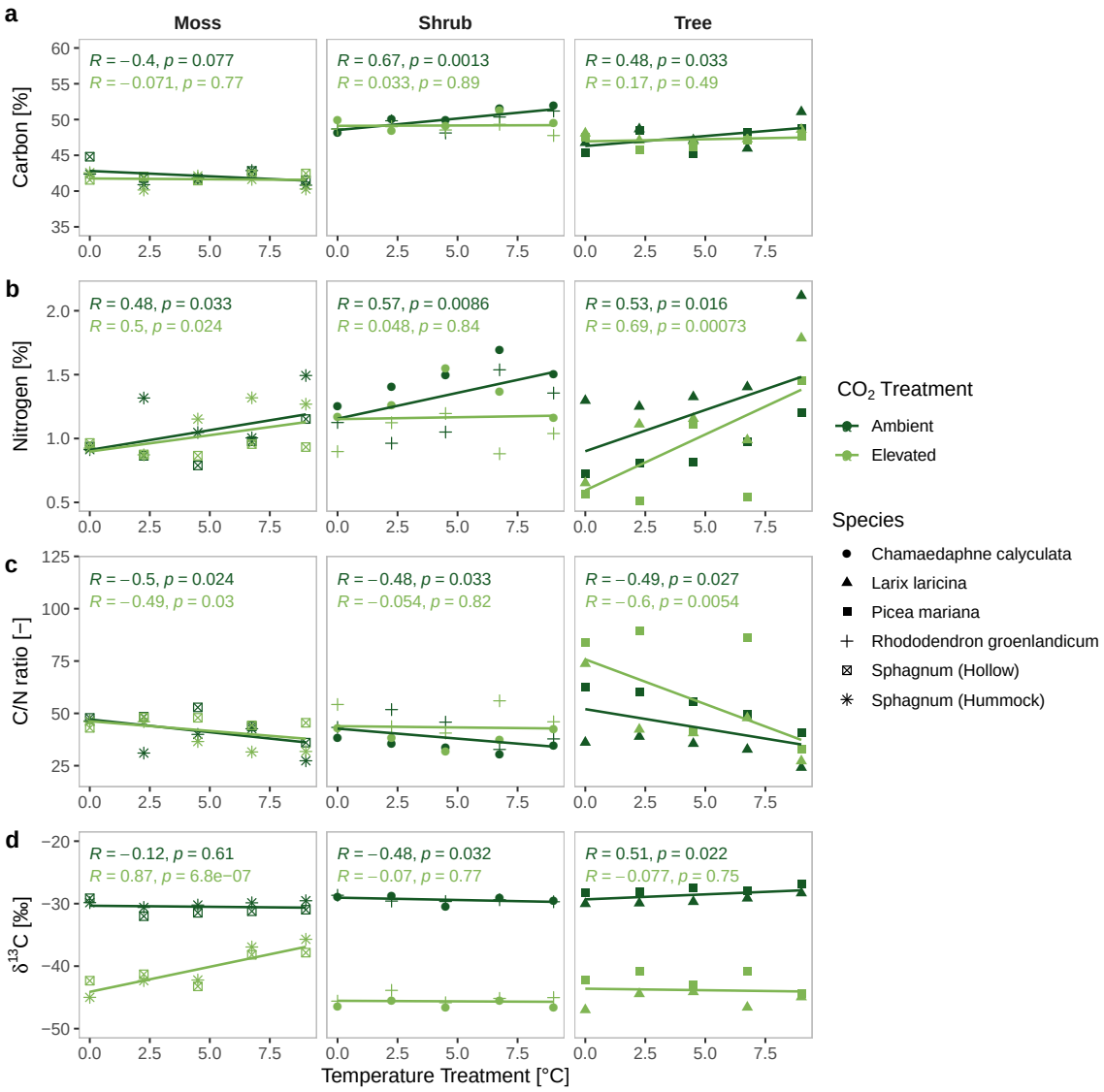


Figure 6: Carbon, nitrogen, C/N ratio and δ^{13}C of plant functional types plotted against temperature treatment under ambient and elevated CO_2 conditions.

Table 1: Carbon, nitrogen, C/N and δ^{13}C values for individual species and plant functional types under ambient and elevated CO_2 treatments, averaged over all temperature treatments (mean ± SE).

		%C		%N		C/N		δ^{13}C	
		Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
Species	*Chamaedaphne calyculata*	50.3 ± 0.5	49.7 ± 0.4	1.5 ± 0.1	1.3 ± 0.1	34.5 ± 0.9	38.6 ± 1.4	-29.4 ± 0.2	-46.1 ± 0.2
	Larix laricina	47.9 ± 0.7	47.6 ± 0.3	1.5 ± 0.1	1.1 ± 0.1	33.5 ± 1.7	46.4 ± 5.1	-29.4 ± 0.2	-45.4 ± 0.4
	Picea mariana	47.2 ± 0.6	46.8 ± 0.4	0.9 ± 0.1	0.8 ± 0.1	53.7 ± 2.7	66.8 ± 8.1	-27.8 ± 0.2	-42.2 ± 0.5
	Rhododendron groenlandicum	49.6 ± 0.5	48.7 ± 0.2	1.2 ± 0.1	1.0 ± 0.0	42.3 ± 2.2	48.1 ± 2.0	-29.4 ± 0.1	-45.1 ± 0.2
	Sphagnum (hummock)	41.8 ± 0.3	41.4 ± 0.4	1.2 ± 0.1	1.1 ± 0.1	37.5 ± 2.4	38.4 ± 2.2	-30.0 ± 0.1	-40.4 ± 1.2
	Sphagnum (hollow)	42.5 ± 0.4	42.0 ± 0.2	0.9 ± 0.0	0.9 ± 0.0	45.8 ± 1.9	45.8 ± 0.7	-31.0 ± 0.3	-40.6 ± 0.7
Plant functional type	Moss	42.1 ± 0.3	41.7 ± 0.2	1.1 ± 0.1	1.0 ± 0.0	41.6 ± 1.8	42.1 ± 1.4	-30.5 ± 0.2	-40.5 ± 0.7
	Shrub	50.0 ± 0.4	49.2 ± 0.2	1.3 ± 0.1	1.2 ± 0.0	38.4 ± 1.5	43.4 ± 1.6	-29.4 ± 0.1	-45.6 ± 0.2
	Tree	47.6 ± 0.4	47.2 ± 0.3	1.2 ± 0.1	1.0 ± 0.1	43.6 ± 2.8	56.6 ± 5.2	-28.6 ± 0.2	-43.8 ± 0.5

4.1.3 Elemental composition of *P.mariana* over time

Carbon content of *P.mariana* did not differ significantly between 2014, 2016, and 2018 ($p > 0.05$; $\overline{x} = 47.3 \pm 0.2\,\%$; Table S3). Nitrogen, C/N ratio and δ^{13}C on the other hand were found to differ significantly between the years ($p < 0.0001$ for all). Nitrogen content of *P.mariana* ranged from 0.6 ± 0.0 % in 2014 to 0.9 ± 0.1 % in 2018 and the C/N ratio was found to decrease from 81.5 ± 3.5 in 2014 to 60.2 ± 4.4 in 2018 (Table S3). The δ^{13}C values ranged from -27.7 ± 0.1 ‰ in 2014 to -27.8 ± 0.2 ‰ in 2018 and from -31.4 ± 0.3 ‰ in 2014 to -42.2 ± 0.5 ‰ in 2018 in ambient and eCO_2 enclosures, respectively (Table S3).

Carbon content of individual years did not show a significant response to warming and eCO_2 treatment ($p > 0.05$). In all years, C content increased linearly with increasing temperatures under ambient conditions and this correlation was significant in 2014 and 2016 (Figure 7a). No significant linear relationship of C content and warming was identified under eCO_2 conditions in any of the years (Figure 7a). Nitrogen content, on the other hand, showed a significant response to warming ($p < 0.0001$). In 2014 and 2016, warming and N content were only weakly correlated under ambient conditions (Figure 7b). However, in 2018, a strong response was observed, whereby warming caused a significant linear increase in N content in ambient enclosures ($R^2 = 0.93$, $p = 0.0001$; Figure 7b). The same trend was observed under eCO_2 conditions; in 2014 and 2016, no significant correlation between warming and N content was observed, while a significant linear increase in N content with warming was observed in 2018 ($R^2 = 0.67$, $p = 0.033$; Figure 7b). The C/N ratio of the individual years showed a significant response to both warming treatment ($p < 0.0001$) and CO_2 treatment ($p = 0.0063$). In 2014, and 2016 no significant correlation between warming and C/N ratio was observed under ambient conditions (Figure 7c). In 2018, however, C/N ratio decreased significantly with increasing temperature ($R^2 = -0.96$, $p = 9.3e\text{-}06$; Figure 7c). Under eCO_2 conditions, C/N decreased with increasing temperature in all years, with the strongest correlation being in 2018 ($R^2 = -0.61$, $p= 0.063$; Figure 7c).

CO_2 treatment had a significant effect on δ^{13}C values of individual years ($p < 0.0001$). In all three years, ambient conditions resulted in less negative δ^{13}C values compared to enclosures treated with elevated CO_2 and over the course of time, the addition of elevated

CO_2 led to a depletion of ^{13}C (Figure 7d). In 2014 and 2016, there was no significant correlation between increasing temperature and $\delta^{13}C$ for either ambient or elevated conditions. However, in 2018, *P.mariana* under ambient conditions became significantly more enriched in ^{13}C with increasing temperature, while the trees under elevated conditions became more depleted in ^{13}C as temperatures rose (R^2 = 0.82, p = 0.0039 and R^2 = -0.43, p = 0.21, respectively; Figure 7d).

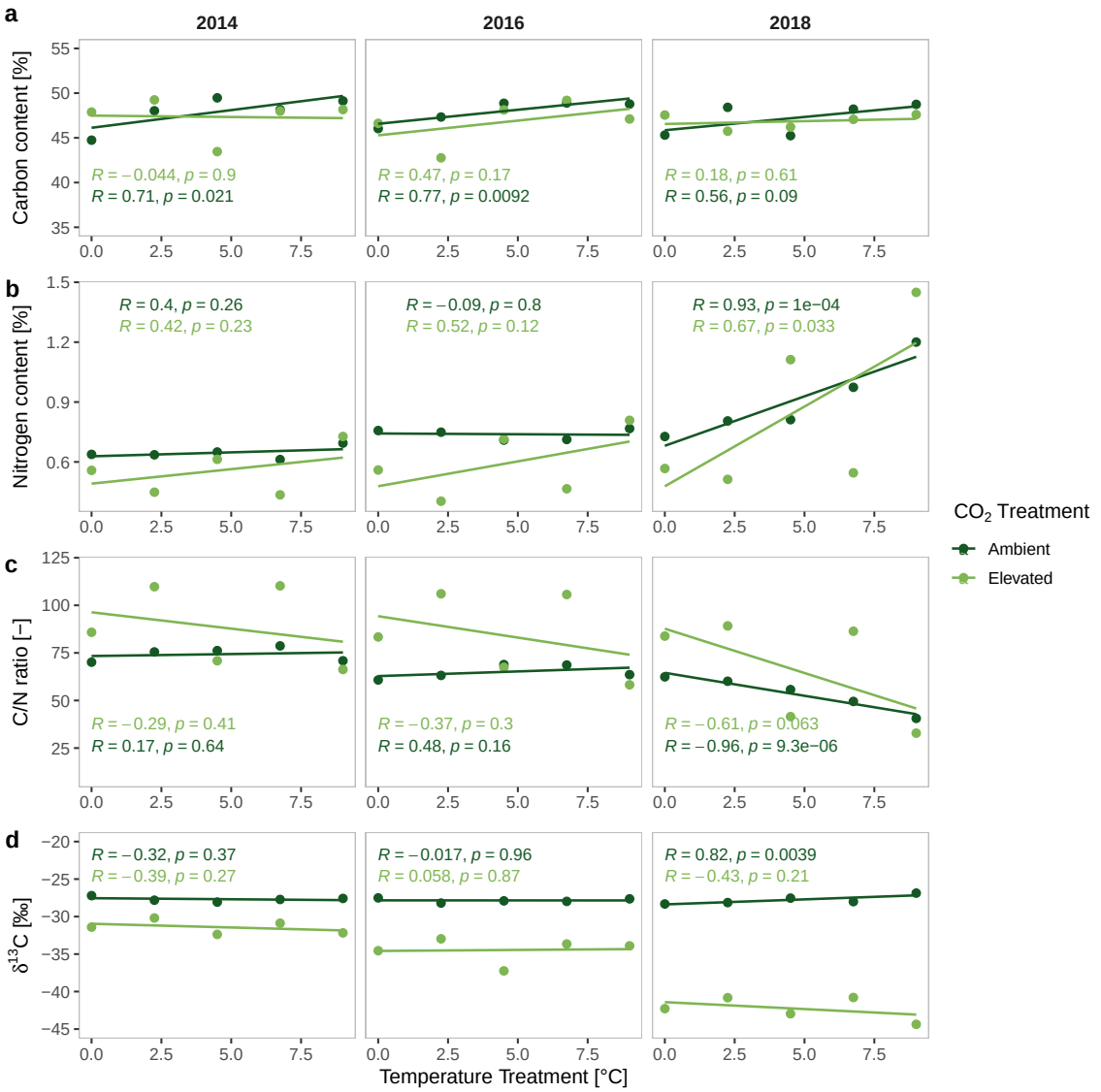


Figure 7: Carbon, nitrogen, C/N and $\delta^{13}C$ of *P.mariana* in 2014, 2016 and 2018, plotted against temperature treatment under ambient and elevated CO_2 conditions.

4.2 Lipids

4.2.1 Total Lipid Extract

Total lipid extract (TLE) differed significantly between species and PFTs ($p < 0.0001$ for both; Table 2). Furthermore, TLE showed a significant response to both temperature and CO_2 treatment ($p = 0.0039$ and $p = 0.0028$, respectively). Under ambient conditions, TLE was found to be 18.7 ± 3.5 mg g^{-1} C at 0°C and 24.2 ± 5.1 mg g^{-1} C at 9°C. In eCO_2 enclosures, TLE was 15.9 ± 3.2 mg g^{-1} C at 0°C and 19.3 ± 3.6 mg g^{-1} C at 9°C (Table S5; Figure S2). Overall, ambient enclosures exhibited higher TLE concentrations than those treated with eCO_2 (21.5 ± 1.8 mg g^{-1} C and 18.7 ± 1.5 mg g^{-1} C, respectively; Table S5).

For plant functional types, only temperature treatment was found to be a significant predictor of TLE ($p = 0.0536$). No significant correlation was observed between warming and TLE concentration of moss under either ambient or eCO_2 conditions (Figure 10a). On a species-specific level, however, a statistically significant linear increase of TLE with warming was identified in *Spagnum (hollow)* under ambient conditions ($R^2 = 0.88$, $p = 0.051$; Figure S3). TLE concentration of shrubs and trees increased linearly with warming under ambient conditions ($R^2 = 0.71$, $p = 0.022$ and $R^2 = 0.62$, $p = 0.055$ respectively; Figure 10a). A similar correlation was observed in trees under eCO_2 conditions ($R^2 = 0.77$, $p = 0.0086$; Figure 10a). The positive correlation between TLE and warming in trees can be mainly attributed to the strong response observed in *L.laricina* under both ambient and elevated conditions ($R^2 = 0.9$, $p = 0.04$ and $R^2 = 0.98$, $p = 0.0039$ respectively; Figure S3). Unlike in trees, TLE and warming were found to be uncorrelated in shrubs under eCO_2 conditions ($R^2 = 0.04$, $p = 0.91$; Figure 10a).

Table 2: Total lipid extract, *n*-alkane and fatty acid concentrations of species and plant functional types under ambient and elevated CO_2 conditions, averaged over all temperature treatments (mean ± SE).

		TLE (mg g^{-1}C)		Concentration$_{alk}$ (μg g^{-1}C)		Concentration$_{fa}$(μg g^{-1}C)	
		Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
Species	*Chamaedaphne calyculata*	29.8 ± 1.9	29.4 ± 1.1	1971.3 ± 447.8	1626.5 ± 164.2	2372.6 ± 319.0	2687.3 ± 276.8
	Larix laricina	29.7 ± 3.4	22.1 ± 2.0	41.2 ± 2.6	38.4 ± 4.4	3794.9 ± 574.2	3189.9 ± 384.9
	Picea mariana	25.6 ± 0.7	22.7 ± 1.1	42.8 ± 7.1	41.2 ± 7.3	2175.5 ± 178.3	2283.0 ± 261.2
	Rhododendron groenlandicum	26.5 ± 1.8	21.4 ± 0.8	3689.4 ± 120.2	2729.4 ± 410.5	1529.7 ± 139.1	1480.3 ± 186.4
	Sphagnum (Hollow)	8.4 ± 0.3	6.8 ± 0.6	169.2 ± 39.9	108.0 ± 27.0	1917.6 ± 182.7	1958.2 ± 263.5
	Sphagnum (Hummock)	9.2 ± 0.7	9.5 ± 0.3	82.4 ± 18.4	66.1 ± 10.0	1873.1 ± 155.5	2393.6 ± 586.8
Plant functional type	Moss	8.8 ± 0.4	8.2 ± 0.5	125.8 ± 25.3	87.1 ± 15.3	1895.3 ± 113.4	2175.9 ± 311.8
	Shrub	28.2 ± 1.3	25.4 ± 1.5	2830.3 ± 360.2	2177.9 ± 227.9	1951.1 ± 216.0	2083.8 ± 255.4
	Tree	27.7 ± 1.8	22.4 ± 1.1	42.0 ± 3.6	39.8 ± 4.0	2985.2 ± 391.4	2736.5 ± 266.3

4.2.2 *n*-Alkane distribution patterns

Carbon chain lengths of C_{21} to C_{35} were identified and while a predominance of odd long-chain *n*-alkanes was observed in all species, the lipid distribution pattern of *n*-alkanes was found to be species-specific (Figure 8). The two shrub species, *R.groenlandicum* and *C. calyculata* were abundant in long chain *n*-alkanes above C_{29} and the dominant chain

length was found to be C_{31} in both, although C_{33} in *R.groenlandicum* was also substantial (Figure 8). *L.laricina* and *P.mariana* in comparison produced more of the shorter and mid chain lengths and peaked at C_{27} and C_{29}, respectively (Figure 8). The *n*-alkane distribution of the two *Sphagnum* species differed in that on the hummocks, C_{31} was the dominant *n*-alkane compared to C_{25} and C_{27} in the hollows (Figure 8). Although *n*-alkane concentrations of *P.mariana* differed between the three years, lipid distribution patterns were similar, with C_{29} being the dominant chain length in all years and no substantial shift in chain lengths. On average, *n*-alkane concentration of all species was higher in ambient enclosures than in elevated CO_2 enclosures and this difference was most pronounced in *Sphagnum (hollow)* and least pronounced in *P.mariana* (Figure 8).

4.2.3 Fatty acid distribution patterns

Fatty acids (FA) of chain lengths C_{14} to C_{30} were identified (Figure 9) and a predominance of even numbered fatty acids was observed in all species. C_{16} was the most abundant in all species, except *C.Calyculata*, in which C_{16} and C_{26} were most abundant. The two *Sphagnum* species had similar distribution patterns of fatty acids, and concentrations of the dominant chain length C_{16} under elevated conditions was higher than under ambient conditions in both species. The distribution patterns of the two shrub species differed substantially, with *R.groenlandicum* concentrations peaking at C_{16} and abundances decreasing from C_{18} to C_{25} for both even and odd chain lengths only to rise again until C_{28}. Fatty acid concentration in *C.calyculata* on the other hand, peaked at C_{16} and even chained FA increased from C_{22} to peak again at C_{26} and decreased again to C_{28} and C_{30}. Differences in distribution patterns were also observed between the two tree species *L.laricina* and *P.mariana*. Although both had a predominance of C_{16}, *L.laricina* was more abundant in long-chain FA from C_{26} to C_{30} compared to *P.mariana*, where concentrations of these FA were low. A noticeable difference was also observed for C_{14}, which was more abundant in *P.mariana* compared to *L.laricina*. Furthermore, in *P.mariana*, C_{16} was more abundant under elevated conditions but more depleted in *L.laricina* compared to ambient conditions. *P.mariana* in 2014, 2016 and 2018 had a peak at C_{16}, which was higher under elevated CO_2 conditions compared to ambient conditions. The concentration of C_{14} decreased from 2014 to 2018, while a noticeable increase in C_{24} occurred under both ambient and elevated CO_2 conditions.

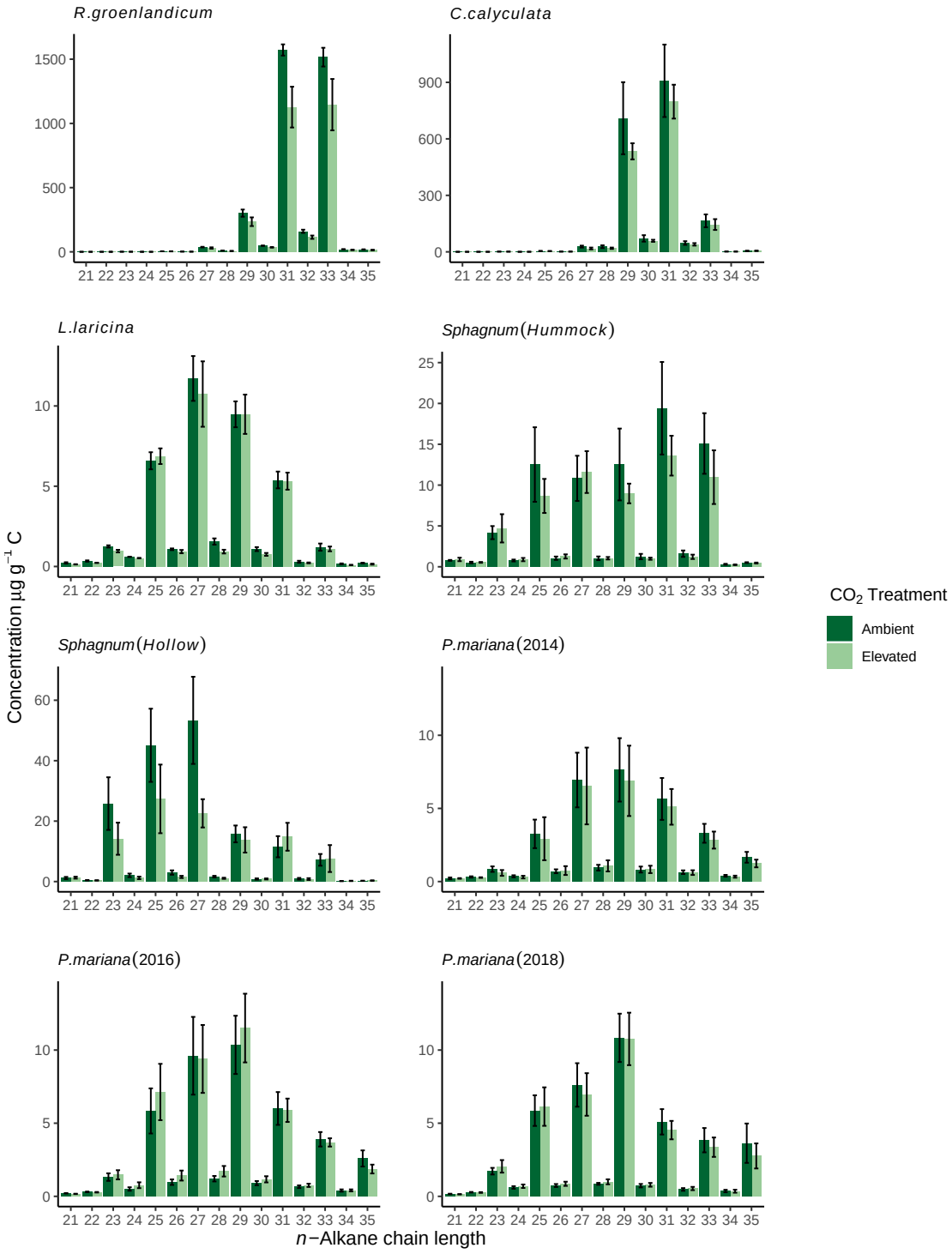


Figure 8: Species-specific n-alkane distribution patterns under ambient and elevated CO_2 conditions (error bars represent the standard error of the mean).

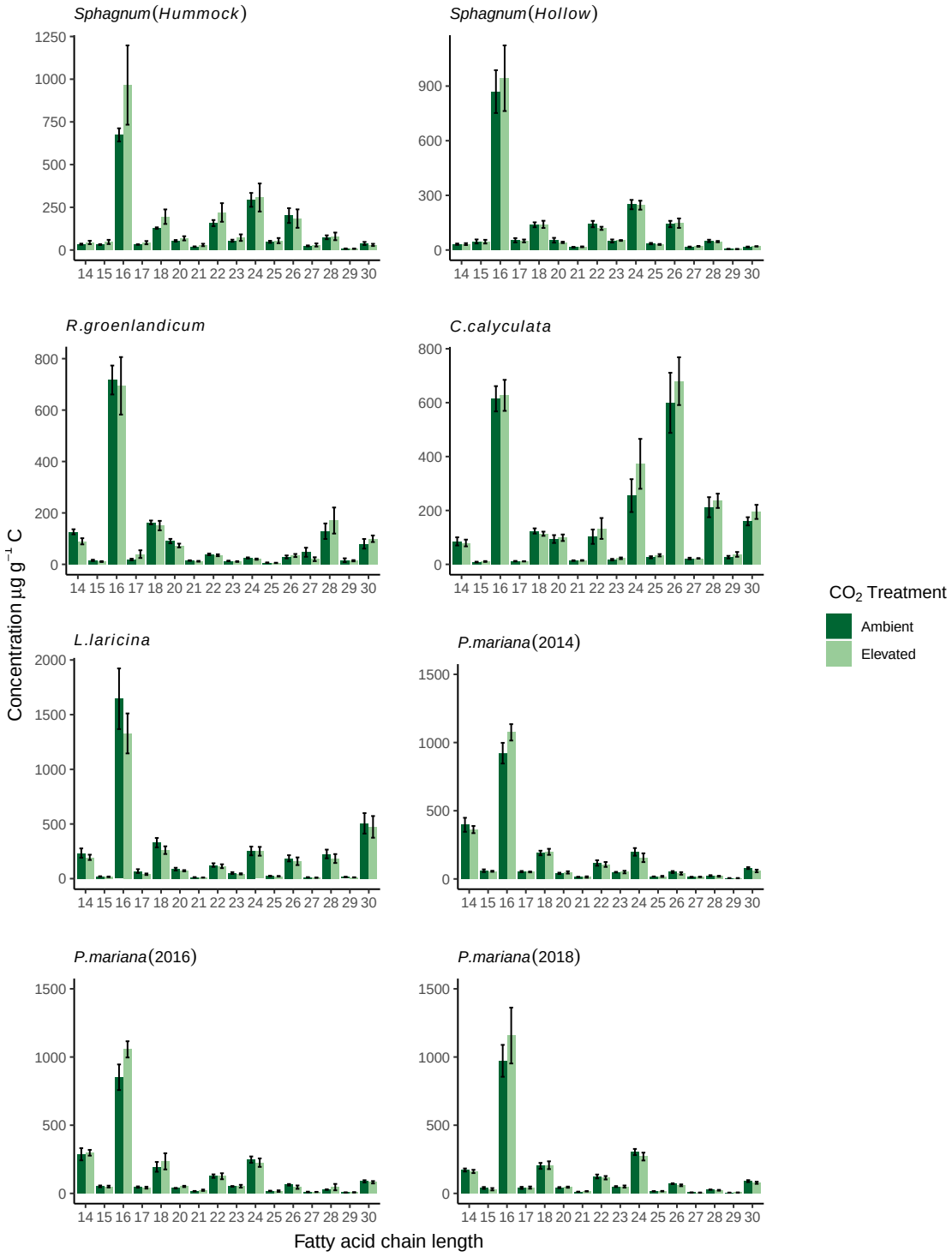


Figure 9: Species-specific fatty acid distribution patterns under ambient and elevated CO_2 conditions (error bars represent the standard error of the mean).

4.2.4 *n*-Alkane and fatty acid content

The overall *n*-alkane concentration of C_{21} to C_{35} was not significantly affected by warming and CO_2 treatments ($p > 0.05$; Table S5; Figure S2) and was found to average at 999.4 ± 267.1 $\mu g\, g^{-1}$ C in ambient enclosures and 768.2 ± 205.6 $\mu g\, g^{-1}$ C in eCO_2 enclosures (Table S5). The high standard error can be explained by the large differences in *n*-alkane concentration between species and between PFTs ($p < 0.0001$; Table 2). The *n*-alkane concentration of *L.laricina* averaged as low as 39.8 ± 2.5 $\mu g\, g^{-1}$ C compared to 3209.4 ± 257.4 $\mu g\, g^{-1}$ C in *R.groenlandicum* (Table S4). When grouped into their respective PFT, *n*-alkane concentration was lowest for trees (40.9 ± 2.6 $\mu g\, g^{-1}$ C) and highest in shrubs (2504.1 ± 233.7 $\mu g\, g^{-1}$ C; Table S4). Neither temperature nor CO_2 treatment had a significant effect on the *n*-alkane concentration of individual PFTs ($p > 0.05$; Figure 10b). In moss and trees, a non-significant linear increase in *n*-alkane concentration with increasing temperature was observed under ambient and eCO_2 conditions (Figure 10b). Conversely, *n*-alkane concentration of shrubs was slightly decreased with warming under both ambient and eCO_2 conditions (Figure 10b). However, none of these correlations were significant ($p > 0.05$; Figure 10b). Notably, the concentration of long-chain *n*-alkanes ($\geq C_{28}$) of moss was strongly correlated with temperature under both ambient and eCO_2 conditions and was mostly attributable to *Sphagnum* on the hollows ($R^2 = 0.58$, $p = 0.082$, $R^2 = 0.79$, $p = 0.0061$; Figure S5). However, when expressed as the mid/long chain ratio, no significant correlation was observed in any of the species (Figure S5).

Fatty acid concentrations were found to vary significantly between species and PFTs ($p < 0.0001$ and $p = 0.0042$, respectively; Table 2). Similar to *n*-alkane concentrations, temperature and CO_2 treatment did not significantly affect FA concentrations of C_{14} to C_{33} ($p > 0.05$; Table S5; Figure S2) and averaged at 2277.2 ± 175.1 $\mu g\, g^{-1}$ C in ambient enclosures and 2332.1 ± 164.3 $\mu g\, g^{-1}$ C in eCO_2 enclosures (Table S5). Temperature and CO_2 treatment were not found to be significant predictors of fatty acid concentration of individual PFTs ($p > 0.05$; Figure 10C). Under ambient conditions, a weak negative correlation between FA concentration and warming was observed in moss and shrubs, while a weak positive correlation was found in trees (Figure 10c). In enclosures treated with eCO_2, FA concentration of trees and moss decreased slightly, and non-significantly with warming (Figure 10c). For shrubs in eCO_2 enclosures, FA concentration was uncorrelated with warming (Figure 10c). When expressed as the ratio of long chain ($\geq C_{20}$) versus short chain ($\leq C_{19}$) fatty acids, a strong negative correlation with temperature was observed in trees and moss under ambient conditions ($R^2 = -0.64$, $p = 0.047$ and $R^2 = -0.58$, $p = 0.076$; Figure S9).

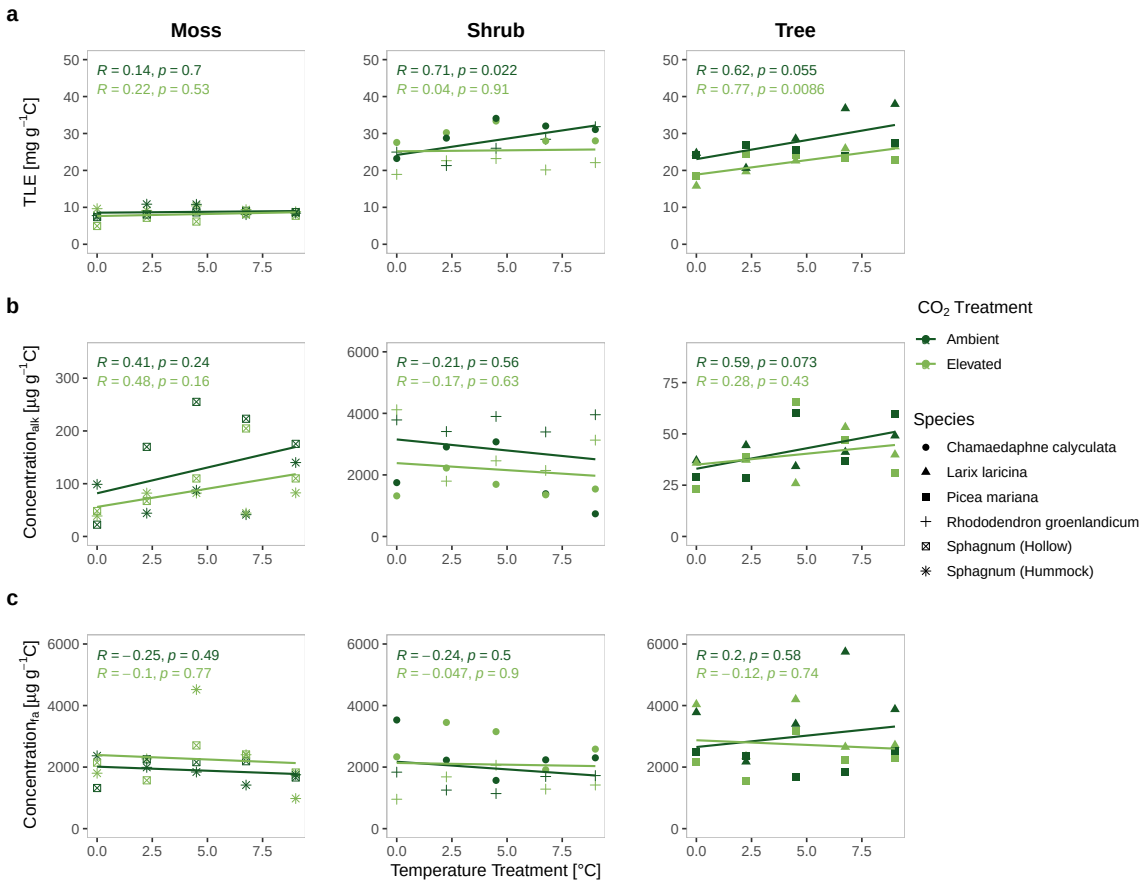


Figure 10: Total lipid extract, *n*-alkane and fatty acid concentrations of plant functional types plotted against temperature treatment under ambient and elevated CO_2 conditions.

4.2.5 Molecular proxies

Average chain length

The average chain length of *n*-alkanes (ACL_{alk}) and fatty acids (ACL_{fa}) differed significantly between both individual species and PFTs ($p < 0.01$ for all; Table 3), but was similar across temperature and CO_2 treatments for both *n*-alkanes and fatty acids ($p > 0.05$; Table S8; Figure S4). Averaged over all species and temperature treatments the ACL_{alk} and ACL_{fa} were found to be ∼29 and ∼20 (respectively) in both ambient and eCO_2 enclosures (Table S8). Furthermore, the ACL_{alk} and ACL_{fa} of individual PFTs were unaffected by warming and CO_2 treatment ($p > 0.05$; Figure 11a and b). In shrubs and trees, no significant change in ACL_{alk} was observed with warming under either CO_2 conditions (Figure 11a). Moss had a non-significant linear decrease in ACL_{alk} with increasing temperatures in the ambient enclosures (R^2 = -0.13, p = 0.72; Figure 11a) and a non-significant increase in elevated CO_2 enclosures (R^2 = 0.29, p = 0.41; Figure 11a). This could be attributable to the fact that the two moss species behaved differently. While ACL_{alk} of both moss species non-significantly increased with warming under eCO_2 (R^2 =

0.18, p = 0.77; R^2 = 0.58, p = 0.31; Figure S6), a non-significant decrease in ACL_{alk} of *Shagnum* on the hollows and a non-significant increase in ACL_{alk} of *Sphagnum (hummock)* was observed with warming under ambient conditions (Figure S6).

The ACL_{fa} of moss decreased with increasing temperature under ambient conditions, but this correlation was not statistically significant (R^2 = -0.52, p = 0.12; Figure 11b). Under elevated CO_2, ACL_{fa} of moss was uncorrelated with increasing temperature (Figure 11b). ACL_{fa} of *R.groenlandicum* and *C.calyculata* did not correlate significantly with increasing temperature when grouped together (Figure 11b). The ACL_{fa} of the two species was tested individually given that their ACL_{fa} differed substantially from each other. However, even when considered individually, ACL_{fa} did not correlate significantly with increasing temperature in either species (Figure S10). For trees, a non-significant decrease in ACL_{fa} with increasing temperature was observed under both ambient and elevated CO_2 conditions (Figure 11b). Of the two tree species, ACL_{fa} of *L.laricina* showed a strong negative and significant correlation with increasing temperature in both ambient and elevated CO_2 enclosures (R^2 = -0.89, p = 0.041 under ambient and R^2 = -0.88, p = 0.048 under elevated CO_2 conditions; Figure S10).

Carbon Preference Index

Significant differences in carbon preference index of alkanes (CPI_{alk}) and fatty acids (CPI_{fa}) were observed between species and PFTs ($p < 0.0001$; Table 3). Neither CPIs changed significantly across temperature and CO_2 treatments ($p > 0.05$; Table S8; Figure S4). The CPI_{alk} and CPI_{fa} were ∼12 and ∼9 (respectively) under both ambient and eCO_2 conditions (Table S8). The CPI_{alk} and CPI_{fa} of PFTs showed no response to warming and CO_2 treatments ($p > 0.05$; Figure 11c and d).

A weak positive correlation was observed between CPI_{alk} and warming in moss in both ambient and eCO_2 enclosures (Figure 11c). CPI_{alk} of shrubs, on the other hand, decreased with warming under both ambient and elevated conditions (Figure 11c). Trees' response differed under ambient and eCO_2 conditions, whereby a weak positive correlation between CPI_{alk} and warming was observed in ambient enclosures, while a weak negative correlation was observed in eCO_2 enclosures (Figure 11c). While no significant response was observed in PFTs, a significant interaction of temperature × species was observed (p = 0.0113). The CPI_{alk} of *R.groenlandicum* showed a strong response to warming in both ambient and elevated CO_2 enclosures, where CPI_{alk} decreased linearly with increasing warming (R^2 = -0.86, p = 0.062, R^2 = -0.67, p = 0.22; Figure S8). The opposite was observed in *Sphagnum* (hollow), where CPI_{alk} increased with increasing temperature, albeit not significantly (Figure S8).

In moss, CPI_{fa} decreased linearly with increasing temperature under ambient conditions, but this correlation was not significant (Figure 11d). Under elevated conditions, a weak positive correlation was identified between CPI_{fa} and warming (Figure 11d). In shrubs, a non-significant linear increase in CPI_{fa} was observed under elevated CO_2 conditions, while a non-significant linear decrease was observed under ambient conditions (Figure 11d). CPI_{fa} of trees in elevated CO_2 enclosures was negatively correlated with increasing temperature, but this correlation was not significant (R^2 = -0.3, p = 0.41; Figure 11d). Under ambient conditions, CPI_{fa} and temperature were uncorrelated in trees (Figure 11d). When regarded on a species-specific level, CO_2 treatment was found to be a significant predictor

of CPI_{fa} (p = 0.0216). A particularly strong response was observed in *L.laricina* under eCO_2 enclosures, where CPI_{fa} decreased significantly with increasing temperature (R^2 = -0.92, p = 0.027; Figure S11).

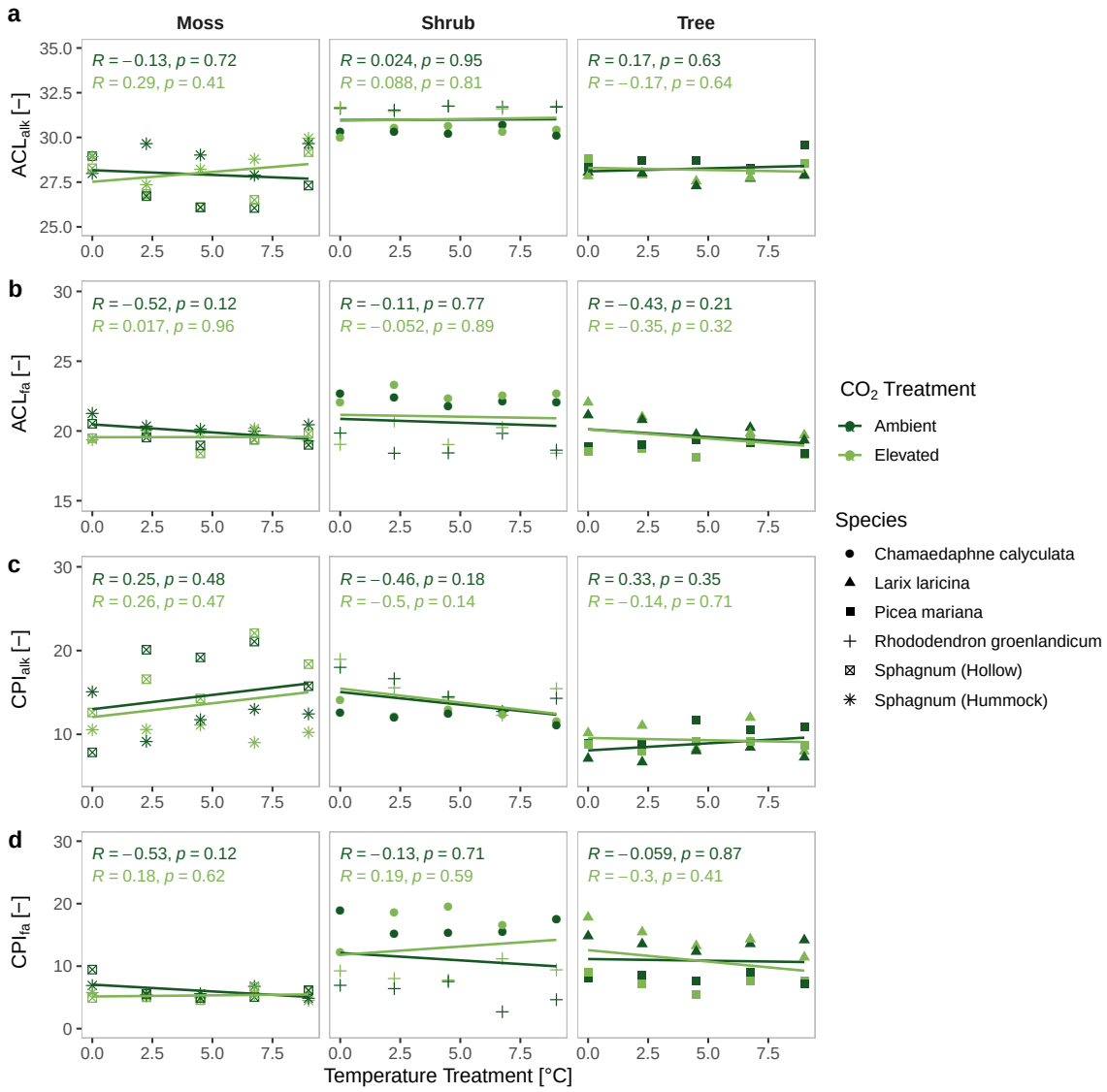


Figure 11: Average chain length and carbon preference index of *n*-alkanes and fatty acids of plant functional types plotted against temperature treatment under ambient and elevated CO_2 conditions.

Table 3: Average chain length and carbon preference index of *n*-alkanes and fatty acids of species and plant functional types under ambient and elevated CO_2 conditions, averaged over all temperature treatments (mean ± SE).

		ACL_{alk}		ACL_{fa}		CPI_{alk}		CPI_{fa}	
		Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
Species	*Chamaedaphne calyculata*	30.3 ± 0.1	30.4 ± 0.1	22.2 ± 0.2	22.6 ± 0.2	12.2 ± 0.3	12.6 ± 0.4	16.5 ± 0.7	16.9 ± 1.3
	Larix laricina	27.8 ± 0.1	27.8 ± 0.1	20.3 ± 0.3	20.5 ± 0.5	7.5 ± 0.3	9.9 ± 0.8	13.7 ± 0.4	14.5 ± 1.1
	Picea mariana	28.7 ± 0.2	28.6 ± 0.1	19.0 ± 0.2	18.6 ± 0.2	10.2 ± 0.6	8.8 ± 0.2	8.1 ± 0.3	7.4 ± 0.6
	Rhododendron groenlandicum	31.7 ± 0.0	31.7 ± 0.1	19.0 ± 0.3	19.5 ± 0.4	15.2 ± 0.9	15.3 ± 1.1	5.6 ± 0.9	9.1 ± 0.6
	Sphagnum (Hollow)	27.0 ± 0.5	27.4 ± 0.6	19.5 ± 0.3	19.4 ± 0.3	16.8 ± 2.4	16.8 ± 1.7	6.2 ± 0.8	5.4 ± 0.4
	Sphagnum (Hummock)	28.8 ± 0.4	28.7 ± 0.4	20.4 ± 0.2	19.8 ± 0.2	12.3 ± 1.0	10.3 ± 0.4	5.9 ± 0.4	5.2 ± 0.2
Plant functional type	Moss	27.9 ± 0.4	28.0 ± 0.4	20.0 ± 0.2	19.6 ± 0.2	14.5 ± 1.4	13.5 ± 1.3	6.1 ± 0.4	5.3 ± 0.2
	Shrub	31.0 ± 0.2	31.0 ± 0.2	20.6 ± 0.6	21.0 ± 0.6	13.7 ± 0.7	14.0 ± 0.7	11.1 ± 1.9	13.0 ± 1.5
	Tree	28.3 ± 0.2	28.2 ± 0.2	19.6 ± 0.3	19.5 ± 0.4	8.8 ± 0.5	9.3 ± 0.4	10.9 ± 1.0	10.9 ± 1.3

4.2.6 Lipid composition of *P.mariana* over time

TLE of *P.mariana* was found to be lowest in 2018 (24.2 ± 0.8 mg g^{-1} C) and highest in 2014 (28.3 ± 1.2 mg g^{-1} C; Table S6). While these differences were found to be significant ($p = 0.0024$), TLE concentration of individual years did not show a significant response to warming, CO_2 treatment or their interaction ($p > 0.05$; Figure 12a). Although a positive relationship between TLE and warming was observed in all years under ambient conditions, these correlations were not statistically significant (Figure 12a). Similarly, under eCO_2, TLE increased with warming in all years, and this correlation was strongest in 2014 ($R^2 = 0.84$, $p = 0.076$; Figure 12a). The *n*-alkane concentration of *P.mariana* differed significantly between the years, while the fatty acid concentration did not ($p = 0.0084$ and $p > 0.05$ respectively; Table S6). Neither *n*-alkane concentration nor FA concentration of the individual years showed a significant response to warming and CO_2 treatment ($p > 0.05$; Figure 12b and c). Under both ambient and eCO_2 conditions, statistically non-significant increases in *n*-alkane concentration with increasing temperature were observed across all years (Figure 12b). Under eCO_2 conditions, a non-significant positive increase in FA concentration with warming was observed in all three years (Figure 12c). Under ambient conditions, no clear trend was observed throughout the three years with FA concentrations increasing very slightly and non-significantly in 2014, only to be uncorrelated in 2016 and decrease slightly and non-significantly in 2018 (Figure 12c).

The ACL_{alk} of *P.mariana* was similar in 2014, 2016 and 2018 ($p > 0.05$; $\overline{x} = 28.8 \pm 0.1$), while the ACL_{fa} was significantly different ($p = 0.0008$; Table S9). Neither ACL_{alk} nor ACL_{fa} of the individual sample years were affected by warming and elevated CO_2 treatment ($p > 0.05$; Figure 13a and b). In 2014, and 2016, a non-significant decrease in ACL_{alk} with increasing temperature was observed under both ambient and elevated CO_2 conditions (Figure 13a). This trend was also observed in 2018 under eCO_2 conditions but not under ambient conditions. Here, a non-significant increase in ACL_{alk} with increasing temperature was observed (Figure 13a). This could be due to the sample at 9°C in the ambient enclosure, which is causing this opposite trend. When this outlier is removed, ACL_{alk} is uncorrelated with temperature (R^2 = -0.0032, $p = 0.97$; Figure S7). Under ambient conditions, ACL_{fa} of *P.mariana* increased with warming in 2014 and 2016 but then decreased slightly with warming in 2018 (Figure 13b). In elevated CO_2 enclosures, ACL_{fa} increased with warming in 2014 and 2016 but then showed no correlation with

warming in 2018 (Figure 13b). None of the above-mentioned correlations were found to be significant (Figure 13b). The CPI_{alk} and CPI_{fa} of *P.mariana* were significantly different between the sample years (p = 0.0001 and p = 0.0053, respectively; Table S9). Neither of the CPIs were significantly affected by temperature and CO_2 treatment ($p > 0.05$; Figure 13c and d). In all years, CPI_{alk} increased with warming under ambient conditions, but these correlations were not statistically significant (Figure 13c). In eCO_2 enclosures, a non-significant positive correlation was observed between CPI_{alk} and warming in 2014 and 2018 compared to a weak and non-significant negative correlation in 2016 (Figure 13c). A significant increase in CPI_{fa} with warming was only observed in 2014 under ambient conditions ($R^2 = 0.88$, p = 0.048; Figure 13d). This was not the case for 2016 and 2018, where a positive correlation and a weak negative correlation was observed between CPI_{fa} and warming, respectively ($p > 0.05$; Figure 13d). Under elevated CO_2, a non-significant decrease in CPI_{fa} was observed with warming in 2014 and 2018, whereas in 2016, a weak and non-significant positive correlation was observed between CPI_{fa} and warming (Figure 13d).

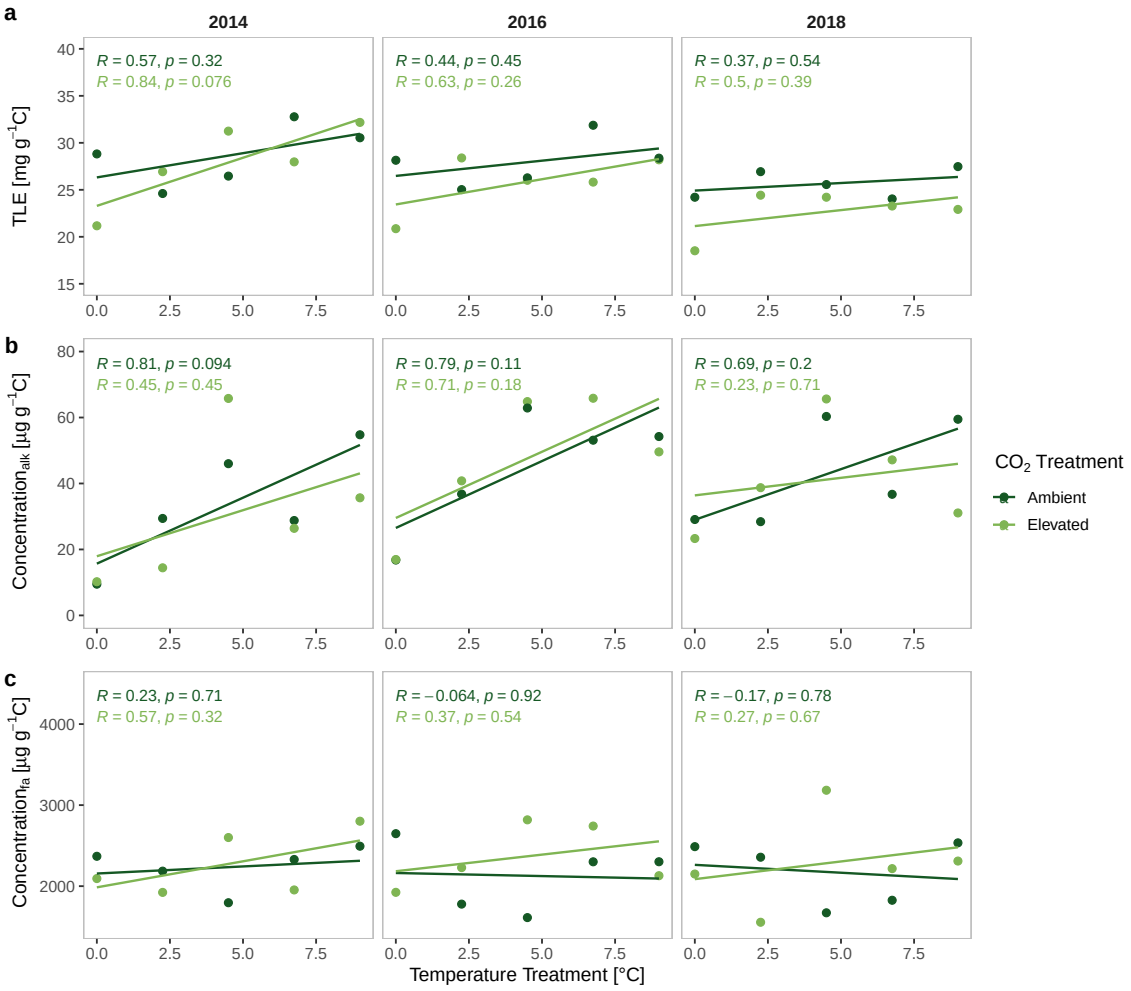


Figure 12: Total lipid extract, *n*-alkane and fatty acid concentrations of *P.mariana* in 2014, 2016 and 2018, plotted against temperature treatment under ambient and elevated CO_2 conditions.

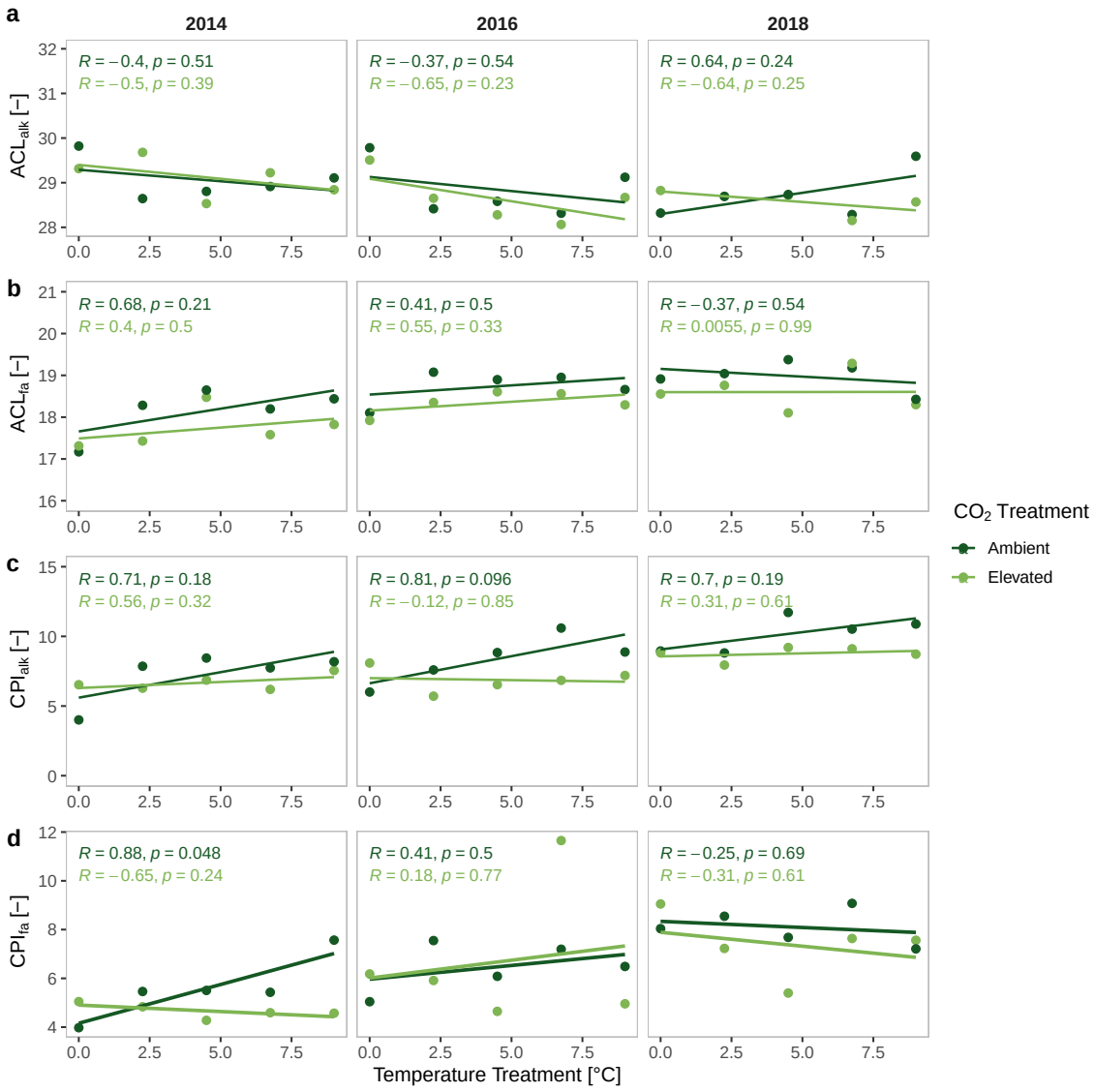


Figure 13: Average chain length and carbon preference index of *n*-alkanes and fatty acids of *P.mariana* in 2014, 2016 and 2018, plotted against temperature treatment under ambient and elevated CO_2 conditions

5 Discussion

5.1 Elemental and lipid composition of species and plant functional types

The carbon content and $\delta^{13}C$ values of *C.calyculata*, *R.groenlandicum L.laricina* and *P.mariana* (Table 1) were comparable to those previously documented at the SPRUCE site (Hobbie *et al.* 2017). In addition, the C content and $\delta^{13}C$ of *Sphagnum* coincided with values found by Asada *et al.* (2005a) and Hobbie *et al.* (2017), respectively. While the nitrogen content and C/N ratios of the two shrub species were found to be similar to Hobbie *et al.* (2017), the two tree species of this study had a higher N content and consequently lower C/N ratios than those reported by the same authors (Table 1). Similarly, the N content of the *Sphagnum* species (Table 1) was slightly higher relative to those reported for several *Sphagnum* species by Asada *et al.* (2005b). The slightly higher N values in this study could be a result of the observed increase in foliar nitrogen with warming, which factored into the average N content of the species.

Total lipid extracts were lower than those reported by Wiesenberg *et al.* (2008) and Srivastava & Wiesenberg (2018) (Table 2). The same authors found differences between individual species and traced these changes back to species-specific epicuticular wax contents caused by varying growth conditions and patterns, which might also explain the discrepancies observed between their values and those of this study. The large variability in *n*-alkane concentrations between species and plant functional types observed in this study, with lowest values of $\sim$40 $\mu g\, g^{-1}$ C in trees (Table 2) is in agreement with average concentrations of gymnosperms (Bush & McInerney 2013). The very high concentrations observed in the shrubs ($>$ 2000 $\mu g\, g^{-1}$ C) are higher than those reported for angiosperms by Bush & McInerney (2013), but high variability has also been observed by Wang *et al.* (2018), which they ascribe to differences in growth habits between plants. Distribution of *n*-alkanes differed significantly between species (Figure 8) and the dominant chain length in shrubs was found to be C_{31}, in line with observations for Ericaceae (Bush & McInerney 2013). For trees, the dominant chain lengths were C_{27} and C_{29}, in part in agreement with Maffei *et al.* (2004), who found that along with C_{27} and C_{29}, C_{31} was the most abundant for Pinales. The two *Sphagnum* species differed in their distribution, a phenomenon also observed in other studies (Diefendorf & Freimuth 2017). In particular, a notable difference has been documented between *Sphagnum* dominated by C_{23} and C_{25} compared to those dominated by C_{31}, often found on hummocks (Diefendorf & Freimuth 2017). This observation was confirmed by this study, where *Sphagnum* on the hummocks was found to peak at C_{31}, compared to C_{25} and C_{27} on the hollows. Distribution patterns of fatty acids showed a strong predominance of C_{16} in all species and an overall even-over-odd dominance (Figure 9), which is typical for higher terrestrial plants (Ohlrogge & Browse 1995; Wiesenberg *et al.* 2008). The ACL_{alk} of shrubs, moss and trees (Table 3) were comparable to those previously reported for evergreen woody angiosperms, mosses and deciduous and evergreen gymnosperms, respectively (Bush & McInerney 2013). Moreover, CPI_{alk} values of the all species were above one (Table 3), which is typical for higher plants and the lowest CPI_{alk} was found in the two tree species, which concurs with the low average CPI value of gymnosperms reported by Bush & McInerney (2013).

5.2 The effect of warming and elevated CO_2 on lipid composition

Temperature was found to be the main driver of leaf nitrogen content under both ambient and eCO_2 conditions (Table S1; Figure S1), most likely attributable to the recent observation at SPRUCE that nutrient availability in the peat is increasing with warming (Malhotra *et al.* 2020). This is in agreement with previous studies that have documented increased mineralization of N in soil under warming, in turn increasing availability for plant uptake (Butler *et al.* 2012; Melillo *et al.* 2011). Elevated CO_2, on the other hand has been observed to cause a decrease in leaf N concentrations as a result of a dilution effect (Xu *et al.* 2013). Consistent with these findings, overall leaf N concentrations were non-significantly lower under eCO_2 conditions. Leaf carbon content was expected to be affected by treatments, given that elevated CO_2 has been found to increase carbon assimilation via increased rates of photosynthesis, and temperature has been found to increase primary productivity if photosynthesis is below the thermal optimum (Ainsworth & Long 2005; Dusenge *et al.* 2019). However, how the interaction of these two environmental factors affects carbon assimilation in plants is still not entirely understood. Ruiz-Vera *et al.* (2013) found that warming inhibited the positive effect of CO_2 on carbon assimilation, while Edwards *et al.* (2017) found that photosynthesis was higher in combined treatments than in CO_2 treatments alone. In this study, neither warming alone nor the combined effect of warming and eCO_2 had an effect on carbon overall (Table S1; Figure S1). A possible explanation for the lack of overall changes in carbon assimilation could be related to the fact that the positive effect of CO_2 and warming on photosynthesis has been found to be inhibited by limiting factors such as water and nutrient availability (Ainsworth & Long 2005; Dusenge *et al.* 2019; Xu *et al.* 2013). Indeed, soil drying has been observed at the SPRUCE experiment (Hanson *et al.* 2020; Malhotra *et al.* 2020) and may have contributed to the lack of overall carbon assimilation. The strong response observed in $\delta^{13}C$ values to CO_2 treatment can be explained by the addition of lighter CO_2 (-54 ‰), resulting in a depletion of ^{13}C in elevated enclosures (Table S1).

Leaf waxes play a crucial role in protecting the plant from abiotic stress and studies have observed changes in wax thickness in response to irradiation, drought, and temperature (Shepherd & Griffiths 2006). In addition to changes in wax content, studies have documented changes in composition and distribution of wax components including *n*-alkanes and fatty acids in response to environmental factors including temperature and CO_2 (Jansen & Wiesenberg 2017). Temperature was found to be a significant predictor of overall TLE concentration under both ambient and elevated CO_2 (Table S5; Figure S2), consistent with Huggins *et al.* (2018). An increase in wax content counteracts water stress by limiting transpiration from leaves (Huggins *et al.* 2018; Shepherd & Griffiths 2006) and thus may indicate that plants at SPRUCE are experiencing a water deficit. The recent finding that plants are responding to soil drying at SPRUCE (Malhotra *et al.* 2020) might explain this response. Overall concentrations and average chain lengths of *n*-alkanes and fatty acids were largely unaffected by warming under both CO_2 conditions, contrary to the first hypothesis of this study (Table S5; Table S8; Figure S2; Figure S4). The lack of a change in *n*-alkane ACL contradicts several studies that have documented that *n*-alkane ACL is positively correlated with increasing temperature, as longer chain lengths increase hydrophobicity of the wax layer, in turn improving protection against water loss (Bush & McInerney 2015; Tipple & Pagani 2013; Wang *et al.* 2018). Another way plants can adapt to higher temperatures is by increasing the saturation of fatty acids, which entails

producing more C_{16} (Larkindale & Huang 2004). The ACL of fatty acids under ambient and eCO_2 conditions did not change significantly with warming (Table S8; Figure S4), indicating that there were no changes in the dominant C_{16} fatty acid chain length and contradicting Larkindale & Huang (2004). The lack in overall changes *n*-alkane and fatty acid concentrations and ACLs might suggest that conditions are still favorable for plants and hence they are investing more in primary metabolism for growth rather than secondary metabolites like lipids for defense (Herms & Mattson 1992; Ohlrogge & Browse 1995). Alternatively, it could also indicate that plants are pursuing other strategies to ensure survival under warming and eCO_2, such as directing biomass allocation to organs that will ensure survival in the face of limiting factors such as a water deficit (Poorter *et al.* 2012). It is important to note that the absence of overall changes in *n*-alkane and fatty acids with warming might also be a result of the lack of replicates taken per sample in this study, in turn limiting statistical power. In addition, this study considered the effect of temperature and CO_2, but given that ecosystems are affected by a multitude of environmental factors, it is difficult to determine whether other factors or their interactions may have influenced the results.

Lipid molecular proxies were found to be similar between ambient and eCO_2 enclosures, while differences in TLE were observed. Under elevated CO_2, an increase in carbon assimilation is expected, in turn increasing carbon-based secondary compounds including lipids (Peñuelas *et al.* 2002). However, studies have not observed such increases, in fact lipid extracts have been found to be similar between ambient and eCO_2 conditions (Peñuelas *et al.* 2002; Wiesenberg *et al.* 2008). On average, ambient enclosures in this study exhibited higher TLE than eCO_2 enclosures (Table S5), contradicting these findings. One possible explanation for this finding may be photosynthetic downregulation under eCO_2 as a result of nutrient or water stress (Peñuelas *et al.* 2002), which is also reflected in the lack of changes in overall carbon content in this study. Peñuelas *et al.* (2002) also highlight the importance of species-specific carbon investment strategies and site-dependency, which might also have contributed to the incongruity of results of this study and their results, as environmental conditions and species at SPRUCE differ vastly from their study (Mediterranean shrubs near a CO_2 spring). Although no significant difference was observed in overall *n*-alkanes concentrations between ambient and eCO_2 enclosures (Table S5; Figure S2), the decrease in TLE may also be related to the trends observed in *n*-alkane chain length abundances of individual species (Figure 8). Under eCO_2, *n*-alkane concentrations of dominant chain lengths were mostly lower than in ambient enclosures, although the extent of this difference was species-specific (Figure 8). Slight decreases in *n*-alkane abundance under eCO_2 were also identified by Wiesenberg *et al.* (2008), which they ascribed to a decrease in the precusors of *n*-alkanes. This could not be confirmed in this study where the overall concentration of fatty acids under eCO_2 was not significantly different from ambient enclosures (Table S5). The ACL of *n*-alkanes and fatty acids were similar between ambient and eCO_2 enclosures, consistent with Huang *et al.* (1999). The same was true for the CPI of *n*-alkanes and fatty acids, inconsistent with Wiesenberg *et al.* (2008), who found species-specific responses in ryegrass and white clover for CPI_{fa} and CPI_{alk}. It might therefore be possible that the boreal plants in this study behave differently than species previously studied. In sum, despite observing differences in TLE concentrations between ambient and eCO_2 enclosures, overall lipid composition was not significantly affected by eCO_2. This implies that the lipid metabolism of plants at SPRUCE was resilient to elevated CO_2, although it is not possible to tell from these results alone whether plants

are using other strategies to cope with eCO_2.

Taken together, the absence of changes in overall carbon and *n*-alkane and fatty acid composition in this study suggests that plants at SPRUCE have not adapted the biosynthesis of lipids and are able to sustain survival with their current metabolism under warming and eCO_2. This contradicts the first hypothesis of this study that plants will invest in changes in lipids to improve protection against abiotic stress. This begs the question of whether plants are using other strategies to deal with the effects of warming and eCO_2. This may be better understood by looking at the responses of individual plant functional types and putting the results of this study into context with other findings at the SPRUCE site.

5.3 Adaptation strategies of plant functional types

Under ambient conditions, shrubs increased their C and N content in response to warming, and showed a depletion in ^{13}C (Figure 6). An increase in C content could be explained by the increase in primary production of shrubs observed at SPRUCE (McPartland *et al.* 2020), which is related to increased rates of photosynthesis and thus carbon assimilation (Dusenge *et al.* 2019). The depletion in ^{13}C at higher temperatures is indicative of reduced water use efficiency and high stomatal conductance (Dawson *et al.* 2002; Moreno-Gutiérrez *et al.* 2012). Shrubs were the only plant functional type whose elemental composition did not show a response under eCO_2 conditions. This could be related to Ward *et al.*'s (2019) finding that photosynthesis of *R.groenlandicum* and *C.calyculata* at SPRUCE acclimated to eCO_2 concentrations. Similarly to elemental composition, an increase in total lipid extracts of shrubs was only observed in ambient enclosures (Figure 10). Concentrations and ACLs of *n*-alkanes and fatty acids were not significantly correlated with warming at either CO_2 level (Figure 10; Figure 11). Taken together, these findings show that shrubs at SPRUCE were more affected by warming than they were by eCO_2. These findings are in line with findings of other studies conducted at SPRUCE that found a larger effect of warming than eCO_2 on plant productivity. Ward *et al.* (2019) for example, found that photosynthetic rates of mature leaves of *R. groenlandicum* and *C.calyculata* were unaffected by eCO_2. In addition, biomass accumulation of shrubs was found to increase under warming, but no change was documented under eCO_2 (McPartland *et al.* 2020). The lack of substantial changes in lipid composition might suggest that conditions under higher temperatures are still favorable for shrubs and that they are investing newly assimilated C for investment in primary metabolism for growth rather than secondary metabolism for defense, of which lipid synthesis is a part of (Herms & Mattson 1992; Ohlrogge & Browse 1995). Another explanation may be that when plants are faced with limiting factors, they are able to allocate carbon to specific organs depending on the limiting factor (Poorter *et al.* 2012). For example, when plants are faced with water stress, they may allocate more C to roots rather than above ground shoots (Poorter *et al.* 2012). This has been observed at SPRUCE, where shrubs are increasing their fine root growth in response to warming and soil drying, more so than trees and graminoids (Malhotra *et al.* 2020).

Similarly to shrubs, carbon and nitrogen content of trees increased under ambient conditions. In contrast to shrubs, however, N content of trees also increased in eCO_2 enclosures (Figure 6). Another difference lies in the response of $\delta^{13}C$, which became significantly more enriched in ^{13}C with warming under ambient conditions as oppose to more depleted

in shrubs (Figure 6). This is typical for plants exposed to limited water resources that respond by increasing water use efficiency through stomatal closure (Dawson *et al.* 2002; Moreno-Gutiérrez *et al.* 2012). Trees were the only PFT to increase TLE with warming at both CO_2 levels (Figure 10). Notably, this correlation was mainly attributed to the very strong response of *L.laricina*, rather than *P. mariana* whose TLE increased with warming but not significantly. Some trends were observed in *n*-alkane and fatty acid composition, but these were not statistically significant, which may be a result of grouping two species together that differ in phenology (deciduous vs. evergreen) and therefore might exhibit diverging responses. A trend towards increasing *n*-alkane concentration with warming was observed under both CO_2 conditions (Figure 10). The ACL_{fa} of both species together decreased with warming under both ambient and eCO_2 (Figure 11) and this was mostly due to *L.laricina's* strong response compared to *P.mariana* whose ACL_{fa} only decreased under ambient conditions (Figure S10). The increase in TLE, production of more short chain fatty acids and increase in *n*-alkane concentration suggest that trees (*L.laricina* in particular) are modifying their lipid composition in response to warming and eCO_2. The synthesis of more short chain fatty acids such as C_{16} may be used to modify the fluidity of leaf membranes, which in turn increases thermotolerance (Larkindale & Huang 2004). However, fatty acids also have several other functions in trees (Hartmann & Trumbore 2016), and thus determining what the precise fate of these short chain fatty acids in this study is, is not possible from these results alone. A recent study at SPRUCE has observed that *L.laricina* is undergoing more hydraulic stress than *P.mariana* (Warren *et al.* 2021), likely explaining its strong contribution to the combined response of trees. Further, hydraulic stress could explain the enrichment in ^{13}C, the increase in TLE and *n*-alkanes as a means to prevent damaging foliar water loss, as has previously been observed in response to water deficit (Dawson *et al.* 2002; Huggins *et al.* 2018; Shepherd & Griffiths 2006). Together with the finding that *L.laricina* is increasing fine root growth in response to soil drying at SPRUCE, while no significant changes were observed for *P.mariana* (Malhotra *et al.* 2020), suggests that *L.laricina* is pursuing strategies to ensure water uptake and prevent water loss from leaves in the face of warming.

The response of moss differed substantially from trees and shrubs in several ways. As opposed to the vascular plants, carbon content of moss declined with warming under ambient conditions (Figure 6). This could be an indication of deteriorating tissue hydration, which is crucial for moss to photosynthesize given they do not have stomata like vascular plants (Weston *et al.* 2015). Soil drying observed with warming at SPRUCE (Hanson *et al.* 2020; Malhotra *et al.* 2020) is likely the driver of this response. Much like trees, N content was significantly correlated with temperature in both CO_2 treatments (Figure 6). A unique response of moss was the very strong enrichment in ^{13}C under eCO_2 conditions (Figure 6). In vascular plants, an enrichment in ^{13}C is associated with increased water use efficiency and reduced stomatal conductance under water stressed situations (Dawson *et al.* 2002; Moreno-Gutiérrez *et al.* 2012) but studies of *Sphagnum* have found that the closer the moss is to the water table and the more productive it is, the more enriched it is in ^{13}C (Deane-Coe *et al.* 2015; Granath *et al.* 2018). Considering that carbon content of *Sphagnum* did not correlate with warming in eCO_2 enclosures and Norby *et al.* (2019) observed declined productivity of *Sphagnum* and desiccation with warming under both CO_2 conditions, it is unlikely that the $\delta^{13}C$ results reflect increased productivity of the moss. Furthermore, FACE experiments across several countries found that biomass of *Sphagnum* was not affected by eCO_2 (Hoosbeek *et al.* 2001). It is more likely that the sampling

process of *Sphagnum* influenced these results. Given that *Sphagnum* growth declined with warming (Norby *et al.* 2019), the same amount of moss collected at higher temperatures likely contained more old stems and branches from before the experiment. As they were submerged in water prior to the experiment, they were more enriched in ^{13}C and thus caused a greater mixing of isotopic signals. This probably occurred in the ambient enclosures as well but is not reflected in the isotopic signature given there was no input with an altered isotopic signal such as the depleted CO_2 added in the eCO_2 enclosures. Total lipid extracts of *Sphagnum* were low and unaffected by temperature and CO_2 (Figure 10), but some trends were observed in lipid composition in *Sphagnum*, although it is important to note that these correlations were not statistically significant. The concentration of *n*-alkanes tended to increase with warming under both CO_2 conditions (Figure 10), and the proportion of short chain fatty acids increased substantially in ambient enclosures (Figure S9), which was also reflected in a decline in ACL_{fa} with warming (Figure 11). Under eCO_2, both *Sphagnum* species produced more C_{16} fatty acids, although this effect was more pronounced in the moss on the hummocks than on the hollows (Figure 9). The CPI_{alk} increased with warming under both CO_2 levels, suggesting synthesis of more odd *n*-alkanes (Figure 11). These findings are likely a response to previously observed water stress in *Sphagnum* caused by warming (Norby *et al.* 2019), as increased *n*-alkane concentrations in leaf waxes are associated with reducing water loss (Huggins *et al.* 2018; Shepherd & Griffiths 2006). The production of more short-chain fatty acids could be used to decrease membrane fluidity and thereby increase thermotolerance (Larkindale & Huang 2004), however it is difficult to say from these results alone what the exact destination of these fatty acids is. In sum, it can be said that *Sphagnum* is modifying its lipid composition in an attempt to defend itself from the stress caused by warming at SPRUCE.

5.4 Lipid composition of black spruce over time

Over time, changes in elemental composition of *P.mariana* needles were observed while lipid composition remained relatively constant. Needle N content responded strongly to warming in 2018 under both ambient and eCO_2 compared to the two previous years (Figure 7), which likely reflects the increase in available nutrients observed at SPRUCE with warming (Malhotra *et al.* 2020). This is in agreement with Nybakken *et al.* (2018) who found an increase in foliar N content of *P.abies* under N rich soils compared to those under control conditions. While the increase in foliar N is often associated with increased C uptake by trees (Nybakken *et al.* 2018), carbon content of *P.mariana* in this study was not found to respond more strongly in 2018 compared to previous years (Figure 7). The depletion of ^{13}C over time reflects the onset of eCO_2 treatment at SPRUCE in 2016. The $\delta^{13}C$ values under ambient and eCO_2 remained unchanged with warming in 2014 and 2016 but in 2018, an enrichment of ^{13}C with warming occurred in ambient enclosures (Figure 7). This may point to increased stress experienced by the trees and reflects the isohydric regulation strategy of the evergreen conifer (Warren *et al.* 2021). According to Warren *et al.* (2021), the strategy to maintain hydraulic safety in *P.mariana* may result in lower carbon uptake by the trees, which would explain the lack of increased C uptake in 2018, despite more nitrogen in needles.

Over the course of the three sampling years, the total lipid extracts of *P.mariana* and concentrations of *n*-alkanes and fatty acids responded similarly to warming under ambient

and eCO_2 conditions (Figure 12). The ACL of *n*-alkanes decreased with warming in 2014 and 2016 under both CO_2 levels. In 2018, the same was true in the eCO_2 enclosures, but the ACL was uncorrelated with warming in ambient enclosures (Figure 13). The ACL of fatty acids did not respond significantly different to warming in any of the years (Figure 13). Taken together, these findings suggest that while elemental composition has changed over time, lipid composition was similar across the sampling years. The lack of a stronger response with time could be due to the fact that the trees are pursuing other strategies to cope with warming and eCO_2. When trees close their stomata, they are able to mobilize non-structural carbohydrates that they have stored over time and use them for osmoregulation, defense or metabolic activities (Hartmann & Trumbore 2016). Balducci *et al.* (2015) found that under warming, *P.mariana* allocated less carbon to cell wall development and thereby produced lower density wood. According to the same authors, this could be due to a change in C allocation, with more C being allocated towards osmoregulation (Balducci *et al.* 2015). Whether this is the case at SPRUCE is currently not known, and how *P.mariana* will adapt to warming and eCO_2 in the long run remains to be answered. The fact that changes in elemental composition were only observed in the last sampling year of 2018, coincides with Norby *et al.*'s (2019) study that found most significant changes to take place in 2017 and 2018. Therefore, given that the experiment is going to run for several more years, changes in lipid composition may still occur in the years to come.

6 Limitations

Sampling and data analysis

One major limitation of this study was the lack of replicates taken per sample, which in turn limited statistical power. This is particularly important as the samples were very heterogeneous, given that per species several plants were sampled within one enclosure to form mixed samples. In addition, during sample preparation it was not possible to distinguish between species or between stem and leaves of the *Sphagnum*, which may have influenced the results.

The grouping of species into plant functional types may also have been problematic as the two tree and shrub species differ in their phenology. Deciduous and evergreen species may respond differently, and so their combined response must be interpreted with caution. In addition, the data was always plotted against the temperature differential (i.e. +0. +2.25, +4.5, +6.75 and +9) and not the actual growing season temperature, which could have implications for correlations and significance.

Experimental design

In this study, the effect of temperature alone and in combination with eCO_2 was analyzed. However, numerous environmental factors affect ecosystems such as precipitation, nutrient status, water table depth, competition and shading of plants and it is therefore difficult to determine whether changes (or lack thereof) observed in this study are a result of temperature and eCO_2 only, or rather caused by the interaction of several factors.

The enclosures at SPRUCE were built on a natural bog, causing heterogeneous conditions within the enclosures. Species composition differs between the enclosures, in terms of abundance and age, potentially influencing community interactions. Furthermore, most likely resource availability is not constant throughout the entire site and so differences are expected within the enclosures, potentially also affecting results.

7 Conclusion and Outlook

This study investigated the effects of whole-ecosystem warming and elevated CO_2 on the lipid composition of six boreal plant species at SPRUCE. The first research question addressed the effect of temperature and eCO_2 on overall plant lipid composition, which showed that contrary to expectations, several years of whole-ecosystem warming and eCO_2 had little to no effect on overall carbon content and lipid composition. However, an increase in overall foliar nitrogen content was observed, likely attributable to the increase in nutrient availability observed in the peat at SPRUCE (Malhotra *et al.* 2020). The second hypothesis of this study was confirmed, as individual plant functional types exhibited divergent responses to warming and eCO_2. Lipid composition of shrubs was largely unaffected by warming and eCO_2, while changes in elemental composition were observed. These changes were predominantly driven by temperature, with little to no effect of eCO_2. The lack of changes in lipid composition could be a result of shrubs pursuing other strategies such as the investment in biomass allocation towards roots, which has been observed at SPRUCE (Malhotra *et al.* 2020). Conversely, moss and trees showed changes in both elemental and lipid composition. A unique response of moss was the decrease in foliar carbon with warming in ambient enclosures, likely reflecting a decline in productivity. In both moss and trees, *n*-alkane concentrations tended to increase and more short-chain fatty acids were produced with warming. The main driver of changes to the lipid composition of *Sphagnum* and trees (*L.laricina* in particular) was most likely water stress previously observed with warming at SPRUCE (Norby *et al.* 2019; Warren *et al.* 2021). Taken together, this study showed that moss and trees are modifying their lipid composition to improve protection against abiotic stress, suggesting that these plant functional types may be more sensitive to whole-ecosystem warming and eCO_2 than shrubs. The lipid composition of *P.mariana* from 2014-2018 was investigated and results showed that while elemental composition changed significantly in 2018, the response of lipid composition to warming remained constant over the course of time. Given that the few changes observed only occurred in 2018, it is possible that changes in lipid composition may occur as the experiment progresses and warrants further research.

This study provided novel insights into how warming and eCO_2 affects the lipid composition of six boreal plant species. The important finding of this study that moss and trees may be more sensitive to warming than shrubs at SPRUCE, adds to a growing body of evidence that suggests this will likely cause shifts in community composition, which will have implications for carbon cycling and potentially turn this ecosystem into a source of carbon and thereby accelerate climate change (Malhotra *et al.* 2020; McPartland *et al.* 2020; Norby *et al.* 2019, Warren *et al.* 2021). This study captured the effect of four years of warming and two years of elevated CO_2. However, the experiment will run for several more years and to gain a more complete picture of how warming and eCO_2 affects plant lipid composition, it is necessary to investigate further leaf wax constituents and to repeat measurements throughout the duration of the experiment. Furthermore, compound-specific stable isotope analysis would shed light on how isotope fractionation during biosynthesis is affected by warming and eCO_2 (Diefendorf & Freimuth 2017). In a wider context, it is imperative to investigate how changes in plant lipid composition at SPRUCE are incorporated in the peat and the implications for soil carbon cycling. This additional research would lead to an improved understanding of the long-term effects of climate warming on boreal plants and the future of this vulnerable ecosystem.

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Appendix: Supplementary results and data

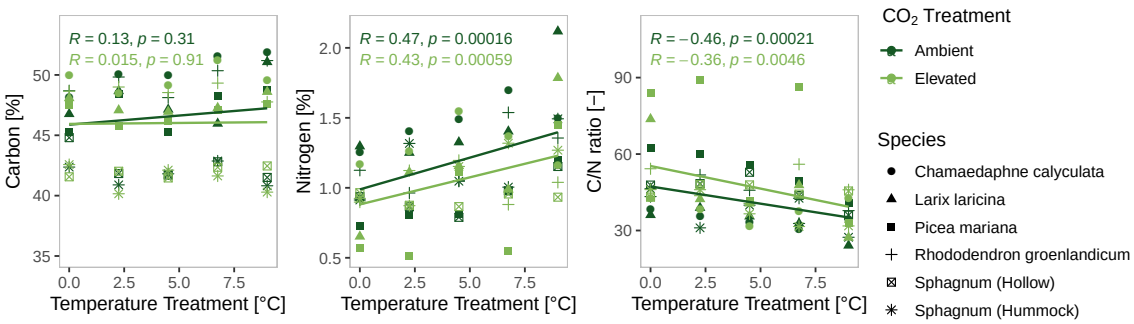

Figure S1: Carbon, nitrogen content and C/N ratio of all samples plotted against temperature treatment under ambient and elevated CO_2 conditions.

Table S1: Carbon, nitrogen, C/N and $\delta^{13}C$ values for each temperature treatment under ambient and elevated CO_2 conditions, averaged over all species (Mean ± SE).

	% C		% N		C/N		‰ $\delta^{13}C$	
Temperature treatment (°C)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0	46.0 ± 0.7	46.4 ± 1.0	1.0 ± 0.1	0.9 ± 0.1	45.8 ± 2.6	57.3 ± 4.8	-29.2 ± 0.2	-44.8 ± 0.6
2.25	46.6 ± 1.2	45.4 ± 1.0	1.1 ± 0.1	1.0 ± 0.1	44.3 ± 3.0	51.3 ± 5.2	-29.8 ± 0.4	-43.0 ± 0.5
4.5	45.7 ± 1.0	45.7 ± 1.0	1.1 ± 0.1	1.2 ± 0.1	44.0 ± 2.5	39.8 ± 1.5	-29.8 ± 0.4	-44.2 ± 0.5
6.75	47.0 ± 1.0	46.5 ± 1.1	1.3 ± 0.1	1.0 ± 0.1	38.7 ± 2.1	50.6 ± 5.4	-29.5 ± 0.3	-42.2 ± 1.1
9	47.5 ± 1.4	46.0 ± 1.0	1.5 ± 0.1	1.3 ± 0.1	33.4 ± 1.8	37.7 ± 2.2	-29.2 ± 0.4	-42.4 ± 1.2
Total	46.6 ± 0.5	46.0 ± 0.4	1.2 ± 0.0	1.1 ± 0.0	41.2 ± 1.2	47.3 ± 2.0	-29.5 ± 0.2	-43.3 ± 0.4

Table S2: Carbon, nitrogen, C/N and $\delta^{13}C$ values of individual species and plant functional types, averaged over all temperature and CO_2 treatments (Mean ± SE).

		% C	% N	C/N
Species	*Chamaedaphne calyculata*	50.0 ± 0.3	1.4 ± 0.0	36.6 ± 0.9
	Larix laricina	47.8 ± 0.4	1.3 ± 0.1	39.9 ± 3.0
	Picea mariana	47.0 ± 0.3	0.9 ± 0.1	60.2 ± 4.4
	Rhododendron groenlandicum	49.1 ± 0.3	1.1 ± 0.1	45.2 ± 1.6
	Sphagnum hummock	41.6 ± 0.2	1.1 ± 0.1	37.9 ± 1.6
	Sphagnum hollow	42.3 ± 0.2	0.9 ± 0.2	45.8 ± 1.0
Plant functional type	Moss	41.9 ± 0.2	1.0 ± 0.0	41.9 ± 1.1
	Shrub	49.6 ± 0.2	1.3 ± 0.0	40.9 ± 1.2
	Tree	47.4 ± 0.3	1.1 ± 0.1	50.1 ± 3.1

Table S3: Carbon, nitrogen, C/N ratio and δ^{13}C values of *P.mariana* in 2014, 2016 and 2018, averaged over all temperature treatments (Mean ± SE).

	% C			% N			C/N			‰ δ^{13}C	
	Ambient	Elevated	Total	Ambient	Elevated	Total	Ambient	Elevated	Total	Ambient	Elevated
2014	47.9 ± 0.6	47.4 ± 0.8	47.6 ± 0.5	0.7 ± 0.0	0.6 ± 0.0	0.6 ± 0.0	74.3 ± 1.3	88.6 ± 6.2	81.5 ± 3.5	-27.7 ± 0.1	-31.4 ± 0.3
2016	48.0 ± 0.4	46.8 ± 0.8	47.4 ± 0.4	0.7 ± 0.0	0.6 ± 0.1	0.7 ± 0.0	65.0 ± 1.1	84.2 ± 6.5	74.6 ± 3.9	-27.8 ± 0.1	-34.5 ± 0.5
2018	47.2 ± 0.6	46.8 ± 0.4	47.0 ± 0.3	0.9 ± 0.1	0.8 ± 0.1	0.9 ± 0.1	53.7 ± 2.7	66.8 ± 8.1	60.2 ± 4.4	-27.8 ± 0.2	-42.2 ± 0.5

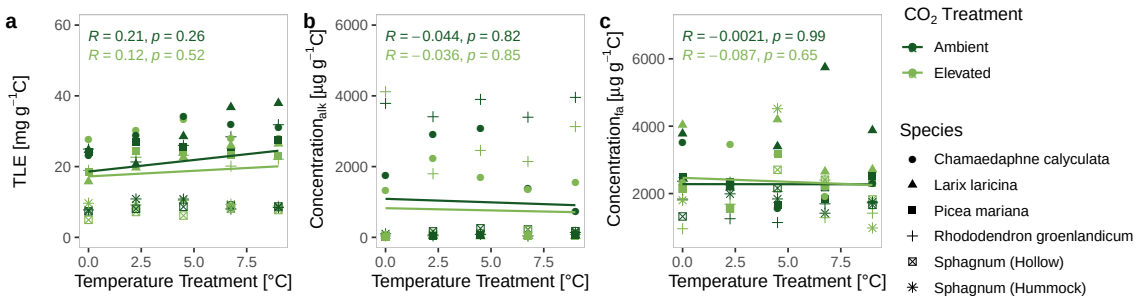

Figure S2: Total lipid extract, *n*-alkane and fatty acid concentrations of all samples plotted against temperature treatment under ambient and elevated CO_2 conditions.

Table S4: Total lipid extract, *n*-alkane and fatty acid concentrations of individual species and plant functional types, averaged over all temperature and CO_2 treatments (mean ± SE).

		TLE (mg g^{-1}C)	Concentration$_{alk}$ (μg g^{-1}C)	Concentration$_{fa}$ (μg g^{-1}C)
Species	*Chamaedaphne calyculata*	29.6 ± 1.0	1798.9 ± 232.1	2530.0 ± 205.9
	Larix laricina	25.9 ± 2.2	39.8 ± 2.5	3492.4 ± 341.1
	Picea mariana	24.2 ± 0.8	42.0 ± 4.8	2229.2 ± 150.1
	Rhododendron groenlandicum	24.0 ± 1.3	3209.4 ± 257.4	1505.0 ± 109.9
	Sphagnum (Hollow)	7.6 ± 0.4	138.6 ± 24.9	1937.9 ± 151.3
	Sphagnum (Hummock)	9.3 ± 0.4	74.2 ± 10.3	2133.3 ± 299.0
Plant functional type	Moss	8.5 ± 0.3	106.4 ± 15.1	2035.6 ± 164.6
	Shrub	26.8 ± 1.0	2504.1 ± 233.7	2017.5 ± 163.5
	Tree	25.0 ± 1.2	40.9 ± 2.6	2860.8 ± 232.1

Table S5: Total lipid extract, *n*-alkane and fatty acid concentrations for each temperature treatment under ambient and elevated CO_2 conditions, averaged over all species (mean ± SE).

	TLE (mg g^{-1}C)		Concentration$_{alk}$ (μg g^{-1}C)		Concentration$_{fa}$ (μg g^{-1}C)	
Temperature treatment (°C)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0	18.7 ± 3.5	15.9 ± 3.2	953.9 ± 631.2	930.3 ± 670.8	2553.4 ± 388.6	2093.4 ± 442.7
2.25	19.4 ± 3.4	18.9 ± 3.7	1100.8 ± 654.4	708.0 ± 415.9	2042.4 ± 165.3	2145.6 ± 297.4
4.5	22.3 ± 4.2	20.0 ± 4.1	1235.2 ± 720.7	739.2 ± 434.1	1963.5 ± 318.3	3303.4 ± 375.1
6.75	23.1 ± 4.9	19.1 ± 3.5	854.3 ± 551.8	641.1 ± 365.6	2518.2 ± 657.5	2146.4 ± 199.3
9	24.2 ± 5.1	19.3 ± 3.6	852.7 ± 629.4	822.6 ± 520.9	2308.6 ± 345.5	1971.5 ± 280.1
Total	21.5 ± 1.8	18.7 ± 1.5	999.4 ± 267.1	768.2 ± 205.6	2277.2 ± 175.1	2332.1 ± 164.3

Table S6: Total lipid extract, *n*-alkane and fatty acid concentrations of *P.mariana* in 2014, 2016 and 2018, averaged over all temperature treatments (mean ± SE).

	TLE (mg g^{-1}C)			Concentration$_{alk}$ (μg g^{-1}C)			Concentration$_{fa}$ (μg g^{-1}C)		
Sample year	Ambient	Elevated	Total	Ambient	Elevated	Total	Ambient	Elevated	Total
2014	28.6 ± 1.4	27.9 ± 2.0	28.3 ± 1.2	33.7 ± 7.8	30.5 ± 9.9	32.1 ± 6.0	2234.6 ± 120.2	2274.5 ± 179.3	2254.6 ± 102.0
2016	27.9 ± 1.2	25.9 ± 1.4	26.9 ± 0.9	44.8 ± 8.2	47.6 ± 9.0	46.2 ± 5.8	2128.3 ± 189.5	2368.6 ± 175.5	2248.5 ± 128.2
2018	25.6 ± 0.7	22.7 ± 1.1	24.2 ± 0.8	42.8 ± 7.1	41.2 ± 7.3	42.0 ± 4.8	2175.5 ± 178.3	2283.0 ± 261.2	2229.2 ± 150.1

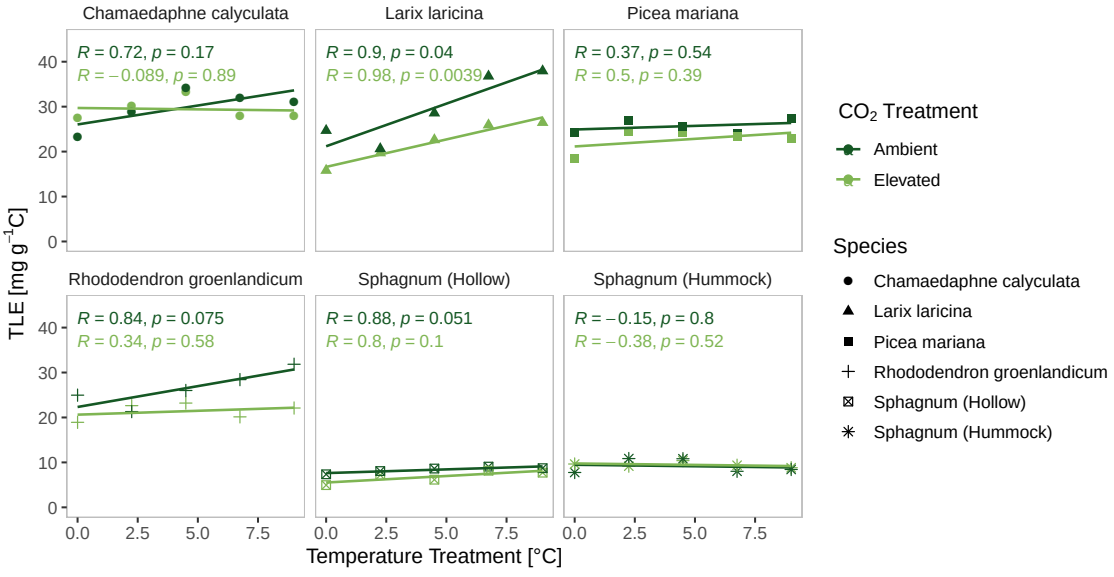

Figure S3: Total lipid extract of individual species plotted against temperature treatment under ambient and elevated CO_2 conditions.

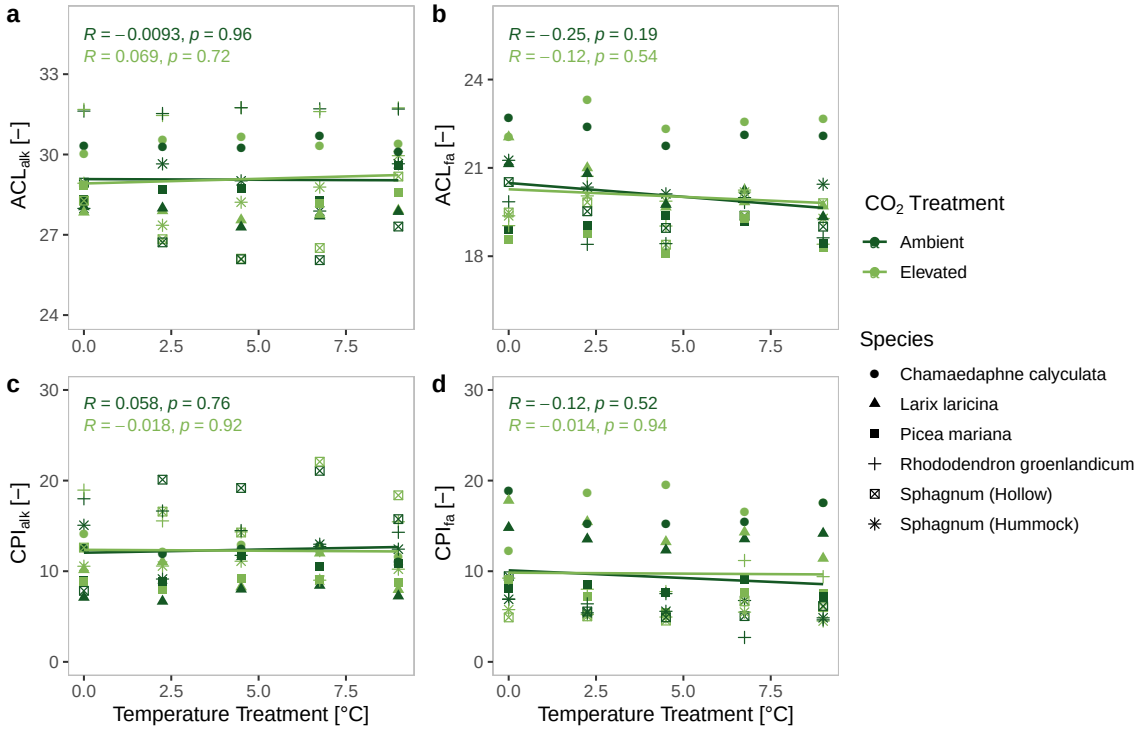

Figure S4: Average chain length and carbon preference index of *n*-alkanes and fatty acids of all samples plotted against temperature treatment under ambient and elevated CO_2 conditions.

Table S7: Average chain length and carbon preference index of *n*-alkanes and fatty acids of individual species and plant functional types, averaged over all temperature and CO_2 treatments (mean ± SE).

		ACL_{alk}	ACL_{fa}	CPI_{alk}	CPI_{fa}
Species	*Chamaedaphne calyculata*	30.4 ± 0.1	22.4 ± 0.1	12.4 ± 3.9	16.7 ± 0.7
	Larix laricina	27.8 ± 0.1	20.4 ± 0.3	8.7 ± 2.8	14.1 ± 0.6
	Picea mariana	28.7 ± 0.1	18.8 ± 0.1	9.5 ± 3.0	7.7 ± 0.3
	Rhododendron groenlandicum	31.7 ± 0.0	19.3 ± 0.3	15.3 ± 4.8	7.4 ± 0.8
	Sphagnum (Hollow)	27.2 ± 0.4	19.4 ± 0.2	16.8 ± 5.3	5.8 ± 0.5
	Sphagnum (Hummock)	28.7 ± 0.3	20.1 ± 0.2	11.3 ± 3.6	5.5 ± 0.3
Plant functional type	Moss	28.0 ± 0.3	19.8 ± 0.1	14.0 ± 1.0	5.7 ± 0.3
	Shrub	31.0 ± 0.2	20.8 ± 0.4	13.8 ± 0.5	12.0 ± 1.2
	Tree	28.2 ± 0.1	19.6 ± 0.2	9.1 ± 0.3	10.9 ± 0.8

Table S8: Average chain length and carbon preference index of *n*-alkanes and fatty acids for each temperature treatment under ambient and elevated CO_2 conditions, averaged over all species (Mean ± SE).

	ACL_{alk}		ACL_{fa}		CPI_{alk}		CPI_{fa}	
Temperature treatment (°C)	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated	Ambient	Elevated
0	29.2 ± 0.6	29.3 ± 0.6	20.7 ± 0.5	20.1 ± 0.6	11.6 ± 1.8	12.5 ± 1.5	10.8 ± 2.0	9.8 ± 1.9
2.25	29.2 ± 0.7	28.8 ± 0.8	20.1 ± 0.6	20.6 ± 0.6	12.2 ± 2.1	12.3 ± 1.3	9.1 ± 1.7	9.9 ± 2.3
4.5	28.9 ± 0.8	28.8 ± 0.8	19.7 ± 0.5	19.6 ± 0.6	12.9 ± 1.5	11.7 ± 1.1	8.9 ± 1.7	9.2 ± 2.5
6.75	28.7 ± 0.9	28.9 ± 0.8	20.1 ± 0.4	20.3 ± 0.5	13.1 ± 1.8	12.8 ± 2.0	8.8 ± 2.0	10.3 ± 1.8
9	29.4 ± 0.7	29.6 ± 0.6	19.7 ± 0.6	19.7 ± 0.7	12.0 ± 1.2	12.1 ± 1.7	9.1 ± 2.2	9.4 ± 1.9
Total	29.1 ± 0.3	29.1 ± 0.3	20.1 ± 0.2	20.0 ± 0.3	12.4 ± 0.7	12.3 ± 0.6	9.3 ± 0.8	9.7 ± 0.9

Table S9: Average chain length and carbon preference index of *n*-alkanes and fatty acids of *P.mariana* in 2014, 2016 and 2018, averaged over all temperature treatments (mean ± SE).

	ACL_{alk}			ACL_{fa}			CPI_{alk}			CPI_{fa}		
Sample year	Ambient	Elevated	Total	Ambient	Elevated	Total	Ambient	Elevated	Total	Ambient	Elevated	Total
2014	29.1 ± 0.2	29.1 ± 0.2	29.1 ± 0.1	18.2 ± 0.3	17.7 ± 0.2	17.9 ± 0.2	7.3 ± 0.8	6.7 ± 0.2	7.0 ± 0.4	5.6 ± 0.6	4.7 ± 0.1	5.1 ± 0.3
2016	28.8 ± 0.3	28.6 ± 0.3	28.7 ± 0.2	18.7 ± 0.2	18.4 ± 0.1	18.5 ± 0.1	8.4 ± 0.8	6.9 ± 0.4	7.6 ± 0.5	6.5 ± 0.4	6.7 ± 1.3	6.6 ± 0.6
2018	28.7 ± 0.2	28.6 ± 0.1	28.7 ± 0.1	19.0 ± 0.2	18.6 ± 0.2	18.8 ± 0.1	10.2 ± 0.6	8.8 ± 0.2	9.5 ± 0.4	8.1 ± 0.3	7.4 ± 0.6	7.7 ± 0.3

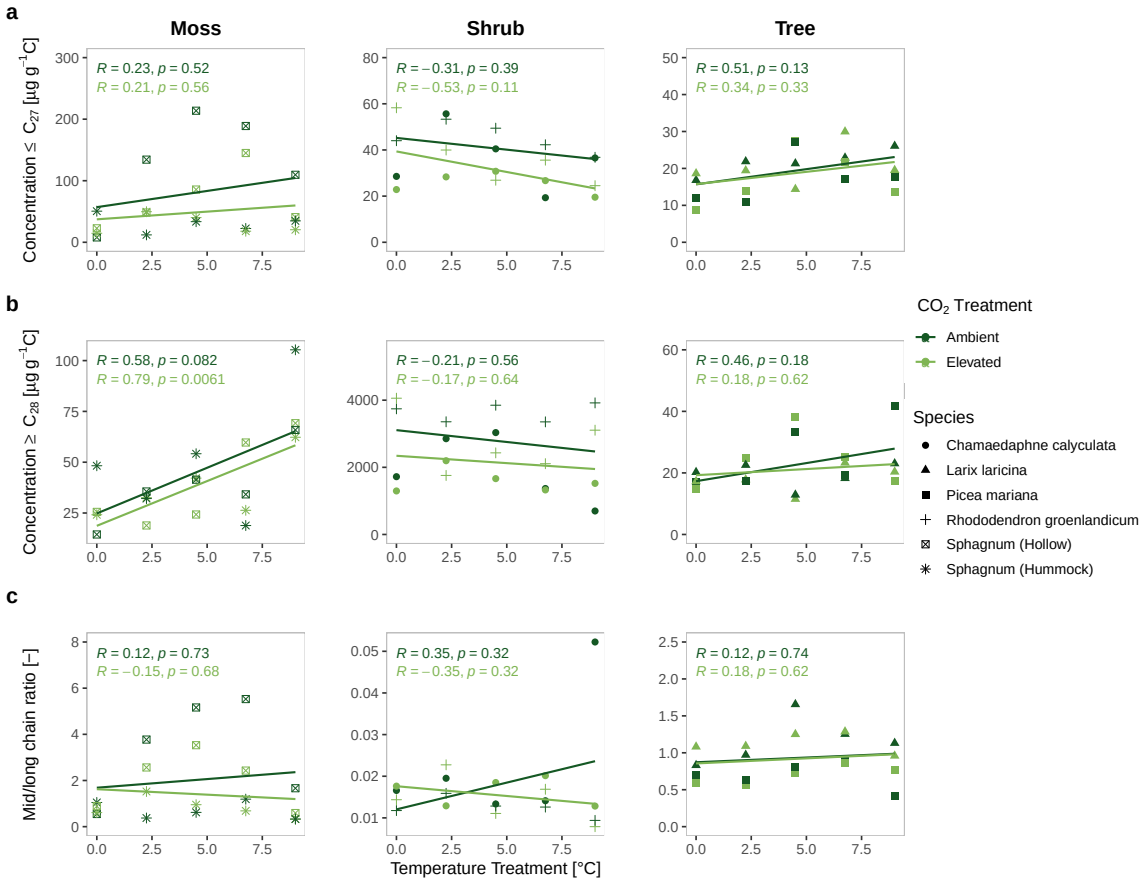

Figure S5: Concentration of mid-chain alkanes ($\leq C_{27}$), long-chain alkanes ($\geq C_{28}$) and mid/long chain ratio of plant functional types plotted against temperature treatment under ambient and elevated CO_2 conditions.

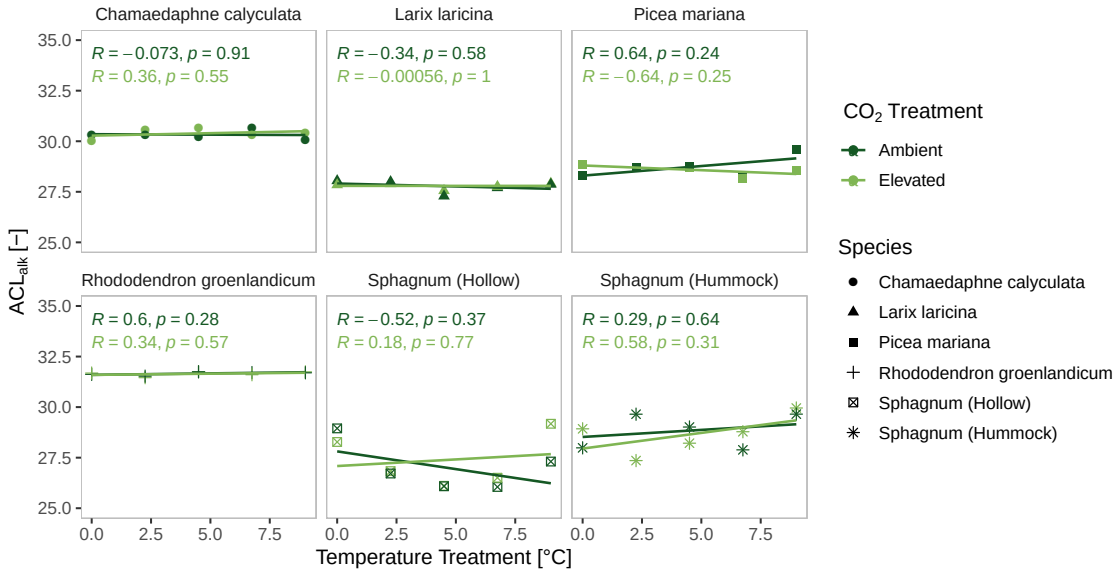

Figure S6: Average chain length of *n*-alkanes of individual species plotted against temperature treatment under ambient and elevated CO_2 conditions.

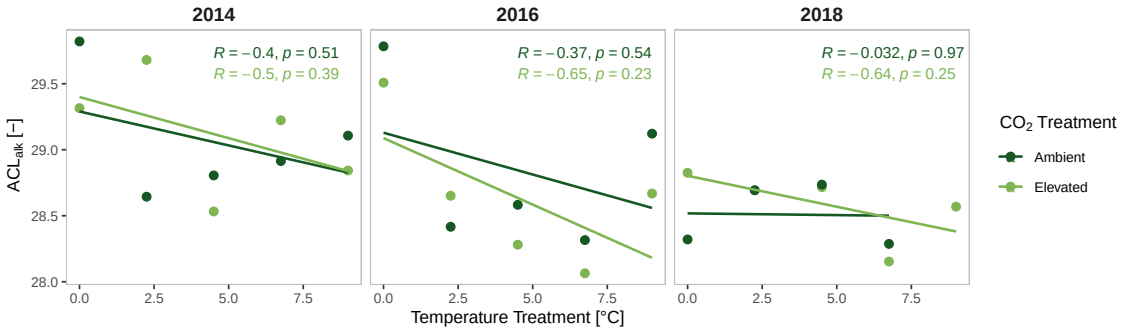

Figure S7: Average chain length of *n*-alkanes of *P.mariana* without sample number 58 at 9°C in the ambient enclosure. Average chain length of *n*-alkanes plotted against temperature treatment under ambient and elevated CO_2.

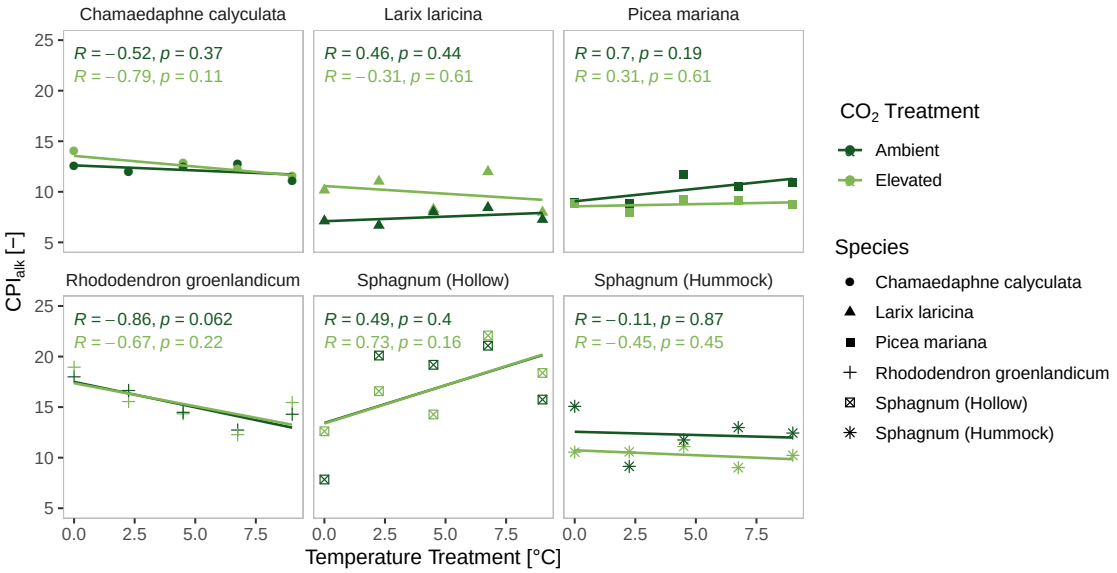

Figure S8: Carbon preference index of *n*-alkanes of individual species plotted against temperature treatment under ambient and elevated CO_2 conditions.

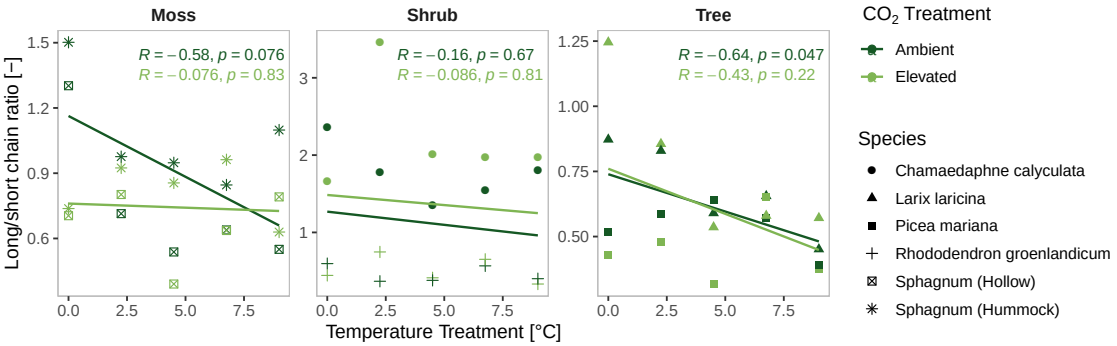

Figure S9: Long chain/short chain ratio of fatty acids of plant functional types plotted against temperature treatment under ambient and elevated CO_2.

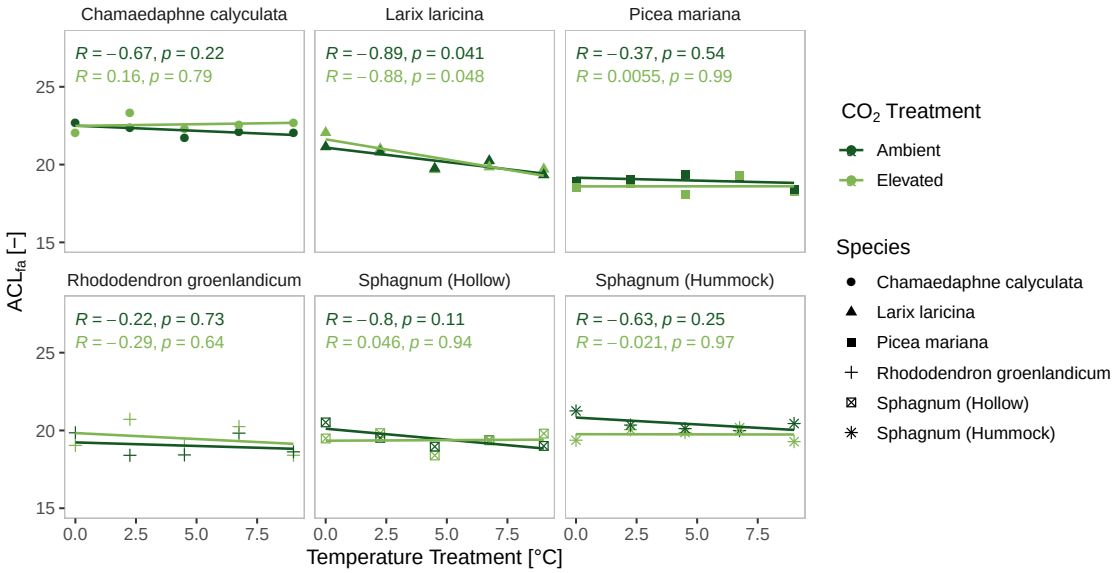

Figure S10: Average chain length of fatty acids of individual species plotted against temperature treatment under ambient and elevated CO_2 conditions.

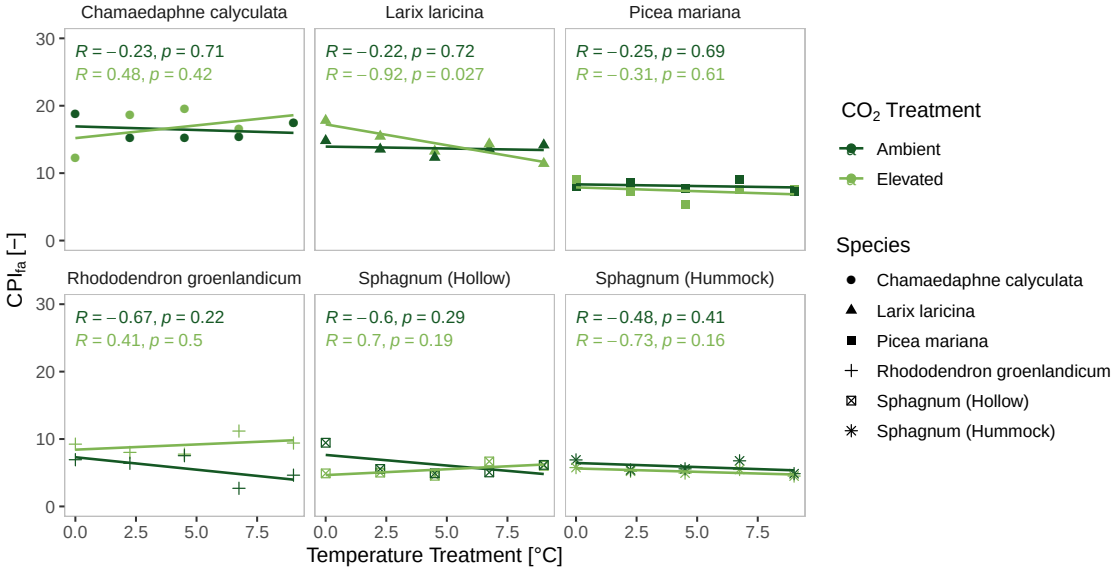

Figure S11: Carbon preference index of fatty acids of individual species plotted against temperature treatment under ambient and elevated CO_2 conditions.

Samplenr	Duplicate	C	N	d13C	Plot	Temperature	CO2	Species	Picea_year	Type
1	a	46.83	1.16	-44.12	Enclosure 4	4.5	Elevated	Larix laricina	0	Tree
1	b	47.07	1.15	-44.12	Enclosure 4	4.5	Elevated	Larix laricina	0	Tree
10	a	45.72	0.77	-28.37	Enclosure 6	0	Ambient	Picea mariana	2018	Tree
10	b	44.90	0.69	-28.26	Enclosure 6	0	Ambient	Picea mariana	2018	Tree
11	a	45.83	0.75	-27.53	Enclosure 6	0	Ambient	Picea mariana	2016	Tree
11	b	46.25	0.77	-27.49	Enclosure 6	0	Ambient	Picea mariana	2016	Tree
12	a	45.02	0.64	-27.20	Enclosure 6	0	Ambient	Picea mariana	2014	Tree
12	b	44.46	0.64	-27.20	Enclosure 6	0	Ambient	Picea mariana	2014	Tree
13	a	47.02	1.07	-28.62	Enclosure 6	0	Ambient	Rhododendron groenlandicum	0	Shrub
13	b	50.35	1.18	-28.70	Enclosure 6	0	Ambient	Rhododendron groenlandicum	0	Shrub
14	a	48.23	1.23	-28.85	Enclosure 6	0	Ambient	Chamaedaphne calyculata	0	Shrub
14	b	48.01	1.27	-29.03	Enclosure 6	0	Ambient	Chamaedaphne calyculata	0	Shrub
15	a	42.29	0.91	-29.84	Enclosure 6	0	Ambient	Sphagnum (Hummock)	0	Moss
15	b	42.44	0.92	-29.83	Enclosure 6	0	Ambient	Sphagnum (Hummock)	0	Moss
16	a	44.97	0.93	-29.07	Enclosure 6	0	Ambient	Sphagnum (Hollow)	0	Moss
16	b	44.64	0.94	-29.21	Enclosure 6	0	Ambient	Sphagnum (Hollow)	0	Moss
17	a	45.66	1.40	-29.16	Enclosure 8	6.75	Ambient	Larix laricina	0	Tree
17	b	46.28	1.40	-29.12	Enclosure 8	6.75	Ambient	Larix laricina	0	Tree
18	a	47.49	0.97	-28.03	Enclosure 8	6.75	Ambient	Picea mariana	2018	Tree
18	b	48.94	0.98	-27.98	Enclosure 8	6.75	Ambient	Picea mariana	2018	Tree
19	a	49.33	0.73	-28.01	Enclosure 8	6.75	Ambient	Picea mariana	2016	Tree
19	b	48.47	0.70	-27.93	Enclosure 8	6.75	Ambient	Picea mariana	2016	Tree
2	a	44.91	1.08	-42.75	Enclosure 4	4.5	Elevated	Picea mariana	2018	Tree
2	b	47.51	1.14	-43.16	Enclosure 4	4.5	Elevated	Picea mariana	2018	Tree
20	a	48.39	0.60	-27.68	Enclosure 8	6.75	Ambient	Picea mariana	2014	Tree
20	b	47.90	0.62	-27.75	Enclosure 8	6.75	Ambient	Picea mariana	2014	Tree
21	a	50.83	1.58	-29.31	Enclosure 8	6.75	Ambient	Rhododendron groenlandicum	0	Shrub
21	b	49.87	1.49	-29.44	Enclosure 8	6.75	Ambient	Rhododendron groenlandicum	0	Shrub
22	a	51.21	1.69	-29.20	Enclosure 8	6.75	Ambient	Chamaedaphne calyculata	0	Shrub
22	b	51.91	1.70	-29.10	Enclosure 8	6.75	Ambient	Chamaedaphne calyculata	0	Shrub
23	a	42.47	1.00	-29.80	Enclosure 8	6.75	Ambient	Sphagnum (Hummock)	0	Moss
23	b	43.27	1.00	-29.93	Enclosure 8	6.75	Ambient	Sphagnum (Hummock)	0	Moss
24	a	43.69	1.00	-31.23	Enclosure 8	6.75	Ambient	Sphagnum (Hollow)	0	Moss
24	b	41.92	0.95	-31.20	Enclosure 8	6.75	Ambient	Sphagnum (Hollow)	0	Moss
25	a	48.27	1.77	-44.94	Enclosure 10	9	Elevated	Larix laricina	0	Tree
25	b	48.94	1.80	-44.96	Enclosure 10	9	Elevated	Larix laricina	0	Tree
26	a	47.52	1.45	-44.29	Enclosure 10	9	Elevated	Picea mariana	2018	Tree
26	b	47.69	1.45	-44.44	Enclosure 10	9	Elevated	Picea mariana	2018	Tree
27	a	46.71	0.81	-34.00	Enclosure 10	9	Elevated	Picea mariana	2016	Tree
27	b	47.51	0.81	-33.80	Enclosure 10	9	Elevated	Picea mariana	2016	Tree
28	a	49.43	0.77	-32.08	Enclosure 10	9	Elevated	Picea mariana	2014	Tree
28	b	46.89	0.69	-32.26	Enclosure 10	9	Elevated	Picea mariana	2014	Tree
29	a	47.63	1.05	-45.01	Enclosure 10	9	Elevated	Rhododendron groenlandicum	0	Shrub
29	b	47.90	1.03	-45.06	Enclosure 10	9	Elevated	Rhododendron groenlandicum	0	Shrub
3	a	47.69	0.68	-37.21	Enclosure 4	4.5	Elevated	Picea mariana	2016	Tree
3	b	48.57	0.74	-37.27	Enclosure 4	4.5	Elevated	Picea mariana	2016	Tree
30	a	49.46	1.20	-46.68	Enclosure 10	9	Elevated	Chamaedaphne calyculata	0	Shrub
30	b	49.67	1.13	-46.69	Enclosure 10	9	Elevated	Chamaedaphne calyculata	0	Shrub
31	a	40.29	1.31	-35.60	Enclosure 10	9	Elevated	Sphagnum (Hummock)	0	Moss
31	b	40.30	1.22	-35.81	Enclosure 10	9	Elevated	Sphagnum (Hummock)	0	Moss
32	a	42.54	0.93	-37.84	Enclosure 10	9	Elevated	Sphagnum (Hollow)	0	Moss
32	b	42.38	0.94	-37.84	Enclosure 10	9	Elevated	Sphagnum (Hollow)	0	Moss
33	a	47.93	1.13	-44.43	Enclosure 11	2.25	Elevated	Larix laricina	0	Tree
33	b	46.22	1.09	-44.44	Enclosure 11	2.25	Elevated	Larix laricina	0	Tree
34	a	44.62	0.51	-40.70	Enclosure 11	2.25	Elevated	Picea mariana	2018	Tree
34	b	46.87	0.52	-40.93	Enclosure 11	2.25	Elevated	Picea mariana	2018	Tree
35	a	43.38	0.40	-32.77	Enclosure 11	2.25	Elevated	Picea mariana	2016	Tree
35	b	42.16	0.41	-33.16	Enclosure 11	2.25	Elevated	Picea mariana	2016	Tree
36	a	49.12	0.44	-30.19	Enclosure 11	2.25	Elevated	Picea mariana	2014	Tree
36	b	49.37	0.45	-30.18	Enclosure 11	2.25	Elevated	Picea mariana	2014	Tree
37	a	49.40	1.17	-43.98	Enclosure 11	2.25	Elevated	Rhododendron groenlandicum	0	Shrub
37	b	48.60	1.08	-43.77	Enclosure 11	2.25	Elevated	Rhododendron groenlandicum	0	Shrub
38	a	49.37	1.31	-45.53	Enclosure 11	2.25	Elevated	Chamaedaphne calyculata	0	Shrub
38	b	47.56	1.22	-45.45	Enclosure 11	2.25	Elevated	Chamaedaphne calyculata	0	Shrub
39	a	41.22	0.88	-42.51	Enclosure 11	2.25	Elevated	Sphagnum (Hummock)	0	Moss
39	b	39.09	0.86	-42.13	Enclosure 11	2.25	Elevated	Sphagnum (Hummock)	0	Moss
4	a	41.74	0.59	-32.38	Enclosure 4	4.5	Elevated	Picea mariana	2014	Tree
4	b	45.18	0.64	-32.38	Enclosure 4	4.5	Elevated	Picea mariana	2014	Tree
40	a	42.17	0.85	-41.21	Enclosure 11	2.25	Elevated	Sphagnum (Hollow)	0	Moss
40	b	41.87	0.90	-41.41	Enclosure 11	2.25	Elevated	Sphagnum (Hollow)	0	Moss
41	a	45.91	1.30	-29.67	Enclosure 13	4.5	Ambient	Larix laricina	0	Tree
41	b	48.36	1.35	-29.72	Enclosure 13	4.5	Ambient	Larix laricina	0	Tree
42	a	44.33	0.80	-27.52	Enclosure 13	4.5	Ambient	Picea mariana	2018	Tree
42	b	46.16	0.82	-27.56	Enclosure 13	4.5	Ambient	Picea mariana	2018	Tree
43	a	48.84	0.71	-27.94	Enclosure 13	4.5	Ambient	Picea mariana	2016	Tree
43	b	48.89	0.70	-27.86	Enclosure 13	4.5	Ambient	Picea mariana	2016	Tree
44	a	49.55	0.67	-28.03	Enclosure 13	4.5	Ambient	Picea mariana	2014	Tree
44	b	49.39	0.63	-28.10	Enclosure 13	4.5	Ambient	Picea mariana	2014	Tree
45	a	48.88	1.07	-29.54	Enclosure 13	4.5	Ambient	Rhododendron groenlandicum	0	Shrub
45	b	47.36	1.03	-29.77	Enclosure 13	4.5	Ambient	Rhododendron groenlandicum	0	Shrub
46	a	49.04	1.47	-30.44	Enclosure 13	4.5	Ambient	Chamaedaphne calyculata	0	Shrub
46	b	50.88	1.51	-30.37	Enclosure 13	4.5	Ambient	Chamaedaphne calyculata	0	Shrub
47	a	41.71	1.02	-30.26	Enclosure 13	4.5	Ambient	Sphagnum (Hummock)	0	Moss
47	b	41.90	1.08	-30.19	Enclosure 13	4.5	Ambient	Sphagnum (Hummock)	0	Moss
48	a	41.71	0.79	-31.55	Enclosure 13	4.5	Ambient	Sphagnum (Hollow)	0	Moss
48	b	41.71	0.79	-31.39	Enclosure 13	4.5	Ambient	Sphagnum (Hollow)	0	Moss
49	a	48.80	1.00	-46.56	Enclosure 16	6.75	Elevated	Larix laricina	0	Tree
49	b	45.73	0.98	-46.64	Enclosure 16	6.75	Elevated	Larix laricina	0	Tree
5	a	48.33	1.18	-45.79	Enclosure 4	4.5	Elevated	Rhododendron groenlandicum	0	Shrub
5	b	48.74	1.21	-45.93	Enclosure 4	4.5	Elevated	Rhododendron groenlandicum	0	Shrub
50	a	47.47	0.53	-40.83	Enclosure 16	6.75	Elevated	Picea mariana	2018	Tree
50	b	46.67	0.56	-40.75	Enclosure 16	6.75	Elevated	Picea mariana	2018	Tree
51	a	49.89	0.47	-33.64	Enclosure 16	6.75	Elevated	Picea mariana	2016	Tree
51	b	48.49	0.46	-33.67	Enclosure 16	6.75	Elevated	Picea mariana	2016	Tree
52	a	47.18	0.43	-30.85	Enclosure 16	6.75	Elevated	Picea mariana	2014	Tree
52	b	48.79	0.44	-30.92	Enclosure 16	6.75	Elevated	Picea mariana	2014	Tree
53	a	49.25	0.88	-45.18	Enclosure 16	6.75	Elevated	Rhododendron groenlandicum	0	Shrub
53	b	49.40	0.88	-45.15	Enclosure 16	6.75	Elevated	Rhododendron groenlandicum	0	Shrub
54	a	51.19	1.38	-45.64	Enclosure 16	6.75	Elevated	Chamaedaphne calyculata	0	Shrub
54	b	51.25	1.36	-45.48	Enclosure 16	6.75	Elevated	Chamaedaphne calyculata	0	Shrub
55	a	41.07	1.31	-36.98	Enclosure 16	6.75	Elevated	Sphagnum (Hummock)	0	Moss
55	b	42.19	1.32	-36.90	Enclosure 16	6.75	Elevated	Sphagnum (Hummock)	0	Moss
56	a	42.60	0.96	-38.21	Enclosure 16	6.75	Elevated	Sphagnum (Hollow)	0	Moss
56	b	42.10	0.95	-38.16	Enclosure 16	6.75	Elevated	Sphagnum (Hollow)	0	Moss
57	a	51.74	2.15	-28.27	Enclosure 17	9	Ambient	Larix laricina	0	Tree
57	b	50.40	2.08	-28.34	Enclosure 17	9	Ambient	Larix laricina	0	Tree
58	a	49.16	1.21	-26.98	Enclosure 17	9	Ambient	Picea mariana	2018	Tree
58	b	48.33	1.19	-26.75	Enclosure 17	9	Ambient	Picea mariana	2018	Tree
59	a	49.26	0.77	-27.68	Enclosure 17	9	Ambient	Picea mariana	2016	Tree
59	b	48.31	0.77	-27.59	Enclosure 17	9	Ambient	Picea mariana	2016	Tree
6	a	49.08	1.63	-46.57	Enclosure 4	4.5	Elevated	Chamaedaphne calyculata	0	Shrub
6	b	49.14	1.47	-46.61	Enclosure 4	4.5	Elevated	Chamaedaphne calyculata	0	Shrub
60	a	49.80	0.67	-27.58	Enclosure 17	9	Ambient	Picea mariana	2014	Tree

60	b	48.46	0.72	-27.57	Enclosure 17	9	Ambient	Picea mariana	2014	Tree
61	a	51.93	1.41	-29.75	Enclosure 17	9	Ambient	Rhododendron groenlandicum	0	Shrub
61	b	50.45	1.30	-29.64	Enclosure 17	9	Ambient	Rhododendron groenlandicum	0	Shrub
62	a	52.20	1.51	-29.45	Enclosure 17	9	Ambient	Chamaedaphne calyculata	0	Shrub
62	b	51.59	1.49	-29.56	Enclosure 17	9	Ambient	Chamaedaphne calyculata	0	Shrub
63	a	40.05	1.44	-29.59	Enclosure 17	9	Ambient	Sphagnum (Hummock)	0	Moss
63	b	41.59	1.54	-29.47	Enclosure 17	9	Ambient	Sphagnum (Hummock)	0	Moss
64	a	41.19	1.15	-31.01	Enclosure 17	9	Ambient	Sphagnum (Hollow)	0	Moss
64	b	41.82	1.16	-30.93	Enclosure 17	9	Ambient	Sphagnum (Hollow)	0	Moss
65	a	47.88	0.65	-47.06	Enclosure 19	0	Elevated	Larix laricina	0	Tree
65	b	48.28	0.65	-46.95	Enclosure 19	0	Elevated	Larix laricina	0	Tree
66	a	46.94	0.57	-42.35	Enclosure 19	0	Elevated	Picea mariana	2018	Tree
66	b	48.16	0.57	-42.19	Enclosure 19	0	Elevated	Picea mariana	2018	Tree
67	a	46.94	0.58	-34.74	Enclosure 19	0	Elevated	Picea mariana	2016	Tree
67	b	46.30	0.54	-34.35	Enclosure 19	0	Elevated	Picea mariana	2016	Tree
68	a	48.23	0.57	-31.30	Enclosure 19	0	Elevated	Picea mariana	2014	Tree
68	b	47.53	0.55	-31.51	Enclosure 19	0	Elevated	Picea mariana	2014	Tree
69	a	48.69	0.87	-45.53	Enclosure 19	0	Elevated	Rhododendron groenlandicum	0	Shrub
69	b	48.61	0.93	-45.68	Enclosure 19	0	Elevated	Rhododendron groenlandicum	0	Shrub
7	a	42.14	1.17	-42.37	Enclosure 4	4.5	Elevated	Sphagnum (Hummock)	0	Moss
7	b	42.09	1.13	-42.07	Enclosure 4	4.5	Elevated	Sphagnum (Hummock)	0	Moss
70	a	49.15	1.15	-46.36	Enclosure 19	0	Elevated	Chamaedaphne calyculata	0	Shrub
70	b	50.82	1.19	-46.44	Enclosure 19	0	Elevated	Chamaedaphne calyculata	0	Shrub
71	a	42.96	0.92	-45.06	Enclosure 19	0	Elevated	Sphagnum (Hummock)	0	Moss
71	b	42.19	0.93	-44.93	Enclosure 19	0	Elevated	Sphagnum (Hummock)	0	Moss
72	a	41.60	0.95	-42.38	Enclosure 19	0	Elevated	Sphagnum (Hollow)	0	Moss
72	b	41.52	0.98	-42.28	Enclosure 19	0	Elevated	Sphagnum (Hollow)	0	Moss
73	a	48.36	1.22	-29.85	Enclosure 20	2.25	Ambient	Larix laricina	0	Tree
73	b	48.97	1.28	-30.00	Enclosure 20	2.25	Ambient	Larix laricina	0	Tree
74	a	48.16	0.80	-28.12	Enclosure 20	2.25	Ambient	Picea mariana	2018	Tree
74	b	48.67	0.82	-28.14	Enclosure 20	2.25	Ambient	Picea mariana	2018	Tree
75	a	48.55	0.77	-28.17	Enclosure 20	2.25	Ambient	Picea mariana	2016	Tree
75	b	46.11	0.73	-28.22	Enclosure 20	2.25	Ambient	Picea mariana	2016	Tree
76	a	47.03	0.62	-27.79	Enclosure 20	2.25	Ambient	Picea mariana	2014	Tree
76	b	49.03	0.65	-27.84	Enclosure 20	2.25	Ambient	Picea mariana	2014	Tree
77	a	49.89	1.00	-29.60	Enclosure 20	2.25	Ambient	Rhododendron groenlandicum	0	Shrub
77	b	49.77	0.93	-29.57	Enclosure 20	2.25	Ambient	Rhododendron groenlandicum	0	Shrub
78	a	51.52	1.45	-28.78	Enclosure 20	2.25	Ambient	Chamaedaphne calyculata	0	Shrub
78	b	48.65	1.35	-28.79	Enclosure 20	2.25	Ambient	Chamaedaphne calyculata	0	Shrub
79	a	40.71	1.31	-30.52	Enclosure 20	2.25	Ambient	Sphagnum (Hummock)	0	Moss
79	b	41.08	1.32	-30.68	Enclosure 20	2.25	Ambient	Sphagnum (Hummock)	0	Moss
8	a	42.41	0.88	-43.30	Enclosure 4	4.5	Elevated	Sphagnum (Hollow)	0	Moss
8	b	40.52	0.85	-43.18	Enclosure 4	4.5	Elevated	Sphagnum (Hollow)	0	Moss
80	a	41.83	0.85	-32.06	Enclosure 20	2.25	Ambient	Sphagnum (Hollow)	0	Moss
80	b	41.84	0.88	-31.96	Enclosure 20	2.25	Ambient	Sphagnum (Hollow)	0	Moss
9	a	45.87	1.24	-29.97	Enclosure 6	0	Ambient	Larix laricina	0	Tree
9	b	47.66	1.35	-30.07	Enclosure 6	0	Ambient	Larix laricina	0	Tree

Samplenr	Plot	Warming treatment	Enclosure	CO2	Species	Picea_year	Type	TLE (mg/gC)
1	Enclosure 4	4.5°C	Yes	Elevated	Larix laricina	0	Tree	22.61
2	Enclosure 4	4.5°C	Yes	Elevated	Picea mariana	2018	Tree	24.21
3	Enclosure 4	4.5°C	Yes	Elevated	Picea mariana	2016	Tree	26.02
4	Enclosure 4	4.5°C	Yes	Elevated	Picea mariana	2014	Tree	31.25
5	Enclosure 4	4.5°C	Yes	Elevated	Rhododendron groenlandicum	0	Shrub	23.20
6	Enclosure 4	4.5°C	Yes	Elevated	Chamaedaphne calyculata	0	Shrub	33.37
7	Enclosure 4	4.5°C	Yes	Elevated	Sphagnum (Hummock)	0	Moss	10.39
8	Enclosure 4	4.5°C	Yes	Elevated	Sphagnum (Hollow)	0	Moss	6.16
9	Enclosure 6	Not heated	Yes	Ambient	Larix laricina	0	Tree	24.68
10	Enclosure 6	Not heated	Yes	Ambient	Picea mariana	2018	Tree	24.21
11	Enclosure 6	Not heated	Yes	Ambient	Picea mariana	2016	Tree	28.15
12	Enclosure 6	Not heated	Yes	Ambient	Picea mariana	2014	Tree	28.82
13	Enclosure 6	Not heated	Yes	Ambient	Rhododendron groenlandicum	0	Shrub	24.96
14	Enclosure 6	Not heated	Yes	Ambient	Chamaedaphne calyculata	0	Shrub	23.22
15	Enclosure 6	Not heated	Yes	Ambient	Sphagnum (Hummock)	0	Moss	7.76
16	Enclosure 6	Not heated	Yes	Ambient	Sphagnum (Hollow)	0	Moss	7.35
17	Enclosure 8	6.75°C	Yes	Ambient	Larix laricina	0	Tree	36.78
18	Enclosure 8	6.75°C	Yes	Ambient	Picea mariana	2018	Tree	24.03
19	Enclosure 8	6.75°C	Yes	Ambient	Picea mariana	2016	Tree	31.87
20	Enclosure 8	6.75°C	Yes	Ambient	Picea mariana	2014	Tree	32.77
21	Enclosure 8	6.75°C	Yes	Ambient	Rhododendron groenlandicum	0	Shrub	28.43
22	Enclosure 8	6.75°C	Yes	Ambient	Chamaedaphne calyculata	0	Shrub	32.02
23	Enclosure 8	6.75°C	Yes	Ambient	Sphagnum (Hummock)	0	Moss	8.02
24	Enclosure 8	6.75°C	Yes	Ambient	Sphagnum (Hollow)	0	Moss	9.06
25	Enclosure 10	9°C	Yes	Elevated	Larix laricina	0	Tree	26.46
26	Enclosure 10	9°C	Yes	Elevated	Picea mariana	2018	Tree	22.92
27	Enclosure 10	9°C	Yes	Elevated	Picea mariana	2016	Tree	28.19
28	Enclosure 10	9°C	Yes	Elevated	Picea mariana	2014	Tree	32.18
29	Enclosure 10	9°C	Yes	Elevated	Rhododendron groenlandicum	0	Shrub	22.10
30	Enclosure 10	9°C	Yes	Elevated	Chamaedaphne calyculata	0	Shrub	28.01
31	Enclosure 10	9°C	Yes	Elevated	Sphagnum (Hummock)	0	Moss	8.82
32	Enclosure 10	9°C	Yes	Elevated	Sphagnum (Hollow)	0	Moss	7.72
33	Enclosure 11	2.25°C	Yes	Elevated	Larix laricina	0	Tree	19.70
34	Enclosure 11	2.25°C	Yes	Elevated	Picea mariana	2018	Tree	24.43
35	Enclosure 11	2.25°C	Yes	Elevated	Picea mariana	2016	Tree	28.39
36	Enclosure 11	2.25°C	Yes	Elevated	Picea mariana	2014	Tree	26.93
37	Enclosure 11	2.25°C	Yes	Elevated	Rhododendron groenlandicum	0	Shrub	22.63
38	Enclosure 11	2.25°C	Yes	Elevated	Chamaedaphne calyculata	0	Shrub	30.23
39	Enclosure 11	2.25°C	Yes	Elevated	Sphagnum (Hummock)	0	Moss	9.17
40	Enclosure 11	2.25°C	Yes	Elevated	Sphagnum (Hollow)	0	Moss	7.17
41	Enclosure 13	4.5°C	Yes	Ambient	Larix laricina	0	Tree	28.57
42	Enclosure 13	4.5°C	Yes	Ambient	Picea mariana	2018	Tree	25.56
43	Enclosure 13	4.5°C	Yes	Ambient	Picea mariana	2016	Tree	26.28
44	Enclosure 13	4.5°C	Yes	Ambient	Picea mariana	2014	Tree	26.46
45	Enclosure 13	4.5°C	Yes	Ambient	Rhododendron groenlandicum	0	Shrub	26.00
46	Enclosure 13	4.5°C	Yes	Ambient	Chamaedaphne calyculata	0	Shrub	34.10
47	Enclosure 13	4.5°C	Yes	Ambient	Sphagnum (Hummock)	0	Moss	10.82
48	Enclosure 13	4.5°C	Yes	Ambient	Sphagnum (Hollow)	0	Moss	8.63
49	Enclosure 16	6.75°C	Yes	Elevated	Larix laricina	0	Tree	25.92
50	Enclosure 16	6.75°C	Yes	Elevated	Picea mariana	2018	Tree	23.27
51	Enclosure 16	6.75°C	Yes	Elevated	Picea mariana	2016	Tree	25.82
52	Enclosure 16	6.75°C	Yes	Elevated	Picea mariana	2014	Tree	27.97
53	Enclosure 16	6.75°C	Yes	Elevated	Rhododendron groenlandicum	0	Shrub	20.14
54	Enclosure 16	6.75°C	Yes	Elevated	Chamaedaphne calyculata	0	Shrub	27.97
55	Enclosure 16	6.75°C	Yes	Elevated	Sphagnum (Hummock)	0	Moss	9.37
56	Enclosure 16	6.75°C	Yes	Elevated	Sphagnum (Hollow)	0	Moss	8.16
57	Enclosure 17	9°C	Yes	Ambient	Larix laricina	0	Tree	37.94
58	Enclosure 17	9°C	Yes	Ambient	Picea mariana	2018	Tree	27.47
59	Enclosure 17	9°C	Yes	Ambient	Picea mariana	2016	Tree	28.37
60	Enclosure 17	9°C	Yes	Ambient	Picea mariana	2014	Tree	30.54
61	Enclosure 17	9°C	Yes	Ambient	Rhododendron groenlandicum	0	Shrub	31.84
62	Enclosure 17	9°C	Yes	Ambient	Chamaedaphne calyculata	0	Shrub	31.07

63	Enclosure 17	9°C	Yes	Ambient	Sphagnum (Hummock)	0	Moss	8.43
64	Enclosure 17	9°C	Yes	Ambient	Sphagnum (Hollow)	0	Moss	8.71
65	Enclosure 19	0°C	Yes	Elevated	Larix laricina	0	Tree	15.80
66	Enclosure 19	0°C	Yes	Elevated	Picea mariana	2018	Tree	18.52
67	Enclosure 19	0°C	Yes	Elevated	Picea mariana	2016	Tree	20.87
68	Enclosure 19	0°C	Yes	Elevated	Picea mariana	2014	Tree	21.17
69	Enclosure 19	0°C	Yes	Elevated	Rhododendron groenlandicum	0	Shrub	18.92
70	Enclosure 19	0°C	Yes	Elevated	Chamaedaphne calyculata	0	Shrub	27.57
71	Enclosure 19	0°C	Yes	Elevated	Sphagnum (Hummock)	0	Moss	9.64
72.	Enclosure 19	0°C	Yes	Elevated	Sphagnum (Hollow)	0	Moss	4.95
73	Enclosure 20	2.25°C	Yes	Ambient	Larix laricina	0	Tree	20.62
74	Enclosure 20	2.25°C	Yes	Ambient	Picea mariana	2018	Tree	26.93
75	Enclosure 20	2.25°C	Yes	Ambient	Picea mariana	2016	Tree	25.02
76	Enclosure 20	2.25°C	Yes	Ambient	Picea mariana	2014	Tree	24.61
77	Enclosure 20	2.25°C	Yes	Ambient	Rhododendron groenlandicum	0	Shrub	21.31
78	Enclosure 20	2.25°C	Yes	Ambient	Chamaedaphne calyculata	0	Shrub	28.75
79	Enclosure 20	2.25°C	Yes	Ambient	Sphagnum (Hummock)	0	Moss	10.85
80	Enclosure 20	2.25°C	Yes	Ambient	Sphagnum (Hollow)	0	Moss	8.08
81	Enclosure 21	Control	No	Control	Larix laricina	0	Tree	17.02
82	Enclosure 21	Control	No	Control	Picea mariana	2018	Tree	20.51
83	Enclosure 21	Control	No	Control	Picea mariana	2016	Tree	26.19
84	Enclosure 21	Control	No	Control	Picea mariana	2014	Tree	21.59
85	Enclosure 21	Control	No	Control	Rhododendron groenlandicum	0	Shrub	22.45
86	Enclosure 21	Control	No	Control	Chamaedaphne calyculata	0	Shrub	28.98
87	Enclosure 21	Control	No	Control	Sphagnum (Hummock)	0	Moss	10.38
88	Enclosure 21	Control	No	Control	Sphagnum (Hollow)	0	Moss	7.92

Sample	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	C31	C32	C33	C34	C35	Plot	Warming	CO2	Species	Picea_year	Type
1	0.17	0.26	0.84	0.50	5.72	0.72	6.17	0.68	5.98	0.54	3.27	0.15	0.66	0.11	0.11	Enclosure 4	4.5°C	Elevated	Larix laricina		Tree
2	0.18	0.36	3.76	1.11	10.38	1.21	10.47	1.39	15.45	1.16	6.42	0.95	5.88	0.75	6.14	Enclosure 4	4.5°C	Elevated	Picea mariana	2018	Tree
3	0.20	0.33	2.35	1.29	11.76	2.00	12.47	2.21	14.48	1.51	6.91	1.05	4.68	0.62	2.96	Enclosure 4	4.5°C	Elevated	Picea mariana	2016	Tree
4	0.27	0.34	1.35	0.65	8.64	1.87	15.57	2.43	15.21	1.70	8.85	1.19	4.86	0.60	2.26	Enclosure 4	4.5°C	Elevated	Picea mariana	2014	Tree
5	0.24	0.32	0.82	0.43	3.39	1.31	20.37	5.56	181.21	32.62	986.90	112.35	1083.52	15.23	13.21	Enclosure 4	4.5°C	Elevated	Rhododendron groenlandicum		Shrub
6	0.34	0.45	1.68	0.66	5.53	1.48	20.61	15.68	441.61	53.65	876.53	48.59	214.07	2.72	10.43	Enclosure 4	4.5°C	Elevated	Chamaedaphne calyculata		Shrub
7	1.14	0.65	5.66	1.17	11.97	1.67	17.83	1.18	11.80	1.18	17.10	1.15	9.20	0.19	0.37	Enclosure 4	4.5°C	Elevated	Sphagnum (Hummock)		Moss
8	2.20	0.56	24.42	2.42	27.58	2.01	26.48	1.26	10.97	0.61	6.83	0.53	3.72	0.16	0.20	Enclosure 4	4.5°C	Elevated	Sphagnum (Hollow)		Moss
9	0.11	0.27	1.10	0.58	5.39	0.93	8.43	1.50	10.06	1.13	5.94	0.23	1.12	0.09	0.16	Enclosure 6	0°C	Ambient	Larix laricina		Tree
10	0.14	0.23	1.89	0.51	4.18	0.55	4.49	0.75	8.28	0.56	3.81	0.32	2.08	0.19	1.10	Enclosure 6	0°C	Ambient	Picea mariana	2018	Tree
11	0.25	0.38	0.78	0.24	0.99	0.30	1.46	0.52	3.42	0.46	2.44	0.46	2.42	0.34	2.32	Enclosure 6	0°C	Ambient	Picea mariana	2016	Tree
12	0.18	0.27	0.44	0.24	0.31	0.27	1.04	0.37	1.24	0.29	1.39	0.36	1.41	0.34	1.33	Enclosure 6	0°C	Ambient	Picea mariana	2014	Tree
13	0.17	0.27	0.63	0.27	3.43	1.60	37.63	9.28	369.25	46.09	1600.72	133.42	1548.24	16.81	18.57	Enclosure 6	0°C	Ambient	Rhododendron groenlandicum		Shrub
14	0.26	0.31	1.04	0.26	2.99	0.72	22.97	26.02	615.05	60.43	837.35	40.54	136.90	1.28	3.49	Enclosure 6	0°C	Ambient	Chamaedaphne calyculata		Shrub
15	0.78	0.37	6.79	0.99	29.76	1.17	10.68	1.03	11.63	1.26	19.57	1.38	12.68	0.23	0.48	Enclosure 6	0°C	Ambient	Sphagnum (Hummock)		Moss
16	0.20	0.19	0.47	0.22	1.81	0.44	4.58	0.60	4.90	0.58	4.94	0.53	2.65	0.09	0.15	Enclosure 6	0°C	Ambient	Sphagnum (Hollow)		Moss
17	0.21	0.32	1.11	0.60	6.81	1.06	12.76	1.26	9.56	0.92	5.06	0.24	0.81	0.20	0.22	Enclosure 8	6.75°C	Ambient	Larix laricina		Tree
18	0.13	0.26	1.51	0.62	5.98	0.69	8.06	0.73	9.42	0.57	3.73	0.31	2.69	0.23	1.79	Enclosure 8	6.75°C	Ambient	Picea mariana	2018	Tree
19	0.15	0.24	0.96	0.36	7.78	1.16	15.60	1.38	12.06	0.84	6.47	0.57	3.66	0.28	1.63	Enclosure 8	6.75°C	Ambient	Picea mariana	2016	Tree
20	0.23	0.33	0.41	0.18	2.04	0.66	7.00	0.91	6.98	0.68	4.98	0.50	2.49	0.33	1.06	Enclosure 8	6.75°C	Ambient	Picea mariana	2014	Tree
21	0.38	0.36	1.07	0.46	4.80	2.41	32.78	9.19	226.88	47.53	1442.76	178.01	1419.44	18.30	11.60	Enclosure 8	6.75°C	Ambient	Rhododendron groenlandicum		Shrub
22	0.00	0.00	1.06	0.00	3.74	0.73	13.79	9.05	349.94	45.68	737.47	44.17	174.26	2.07	5.81	Enclosure 8	6.75°C	Ambient	Chamaedaphne calyculata		Shrub
23	0.60	0.29	3.71	0.48	12.14	0.54	4.68	0.43	3.35	0.52	6.65	0.73	6.63	0.17	0.36	Enclosure 8	6.75°C	Ambient	Sphagnum (Hummock)		Moss
24	1.45	0.55	40.74	2.79	65.13	3.83	74.42	1.90	18.03	0.63	7.97	0.59	4.69	0.15	0.20	Enclosure 8	6.75°C	Ambient	Sphagnum (Hollow)		Moss
25	0.12	0.21	1.26	0.58	7.01	1.02	9.31	1.31	10.38	1.05	5.59	0.31	1.35	0.11	0.25	Enclosure 10	9°C	Elevated	Larix laricina		Tree
26	0.14	0.27	1.60	0.61	4.95	0.67	5.31	0.61	6.98	0.57	3.64	0.42	2.68	0.30	2.32	Enclosure 10	9°C	Elevated	Picea mariana	2018	Tree
27	0.13	0.24	0.87	0.45	5.85	1.39	12.01	1.75	11.73	1.22	6.80	0.81	3.72	0.50	2.09	Enclosure 10	9°C	Elevated	Picea mariana	2016	Tree
28	0.26	0.27	0.57	0.25	2.68	0.78	8.95	1.23	8.70	0.94	5.96	0.63	2.88	0.34	1.22	Enclosure 10	9°C	Elevated	Picea mariana	2014	Tree
29	0.30	0.31	0.54	0.00	2.27	0.95	20.15	6.18	251.82	38.36	1273.00	135.02	1365.15	18.88	17.87	Enclosure 10	9°C	Elevated	Rhododendron groenlandicum		Shrub
30	0.15	0.24	0.62	0.33	2.14	1.22	14.83	21.02	505.09	59.59	763.53	39.32	128.02	1.35	3.84	Enclosure 10	9°C	Elevated	Chamaedaphne calyculata		Shrub
31	0.68	0.60	2.52	0.75	5.48	1.08	9.24	1.36	10.90	1.38	21.37	2.25	24.02	0.40	0.59	Enclosure 10	9°C	Elevated	Sphagnum (Hummock)		Moss
32	0.97	0.26	6.75	0.59	17.61	0.89	13.76	0.76	9.41	1.04	29.45	2.03	25.44	0.45	0.62	Enclosure 10	9°C	Elevated	Sphagnum (Hollow)		Moss
33	0.11	0.23	0.90	0.51	6.83	0.78	10.06	0.75	8.91	0.63	5.54	0.24	1.47	0.11	0.17	Enclosure 11	2.25°C	Elevated	Larix laricina		Tree
34	0.14	0.22	1.61	0.65	5.16	0.80	5.43	1.17	11.74	0.86	4.71	0.56	3.48	0.30	1.90	Enclosure 11	2.25°C	Elevated	Picea mariana	2018	Tree
35	0.14	0.25	1.23	0.73	5.65	1.22	5.92	1.73	10.95	1.24	5.50	0.81	3.63	0.35	1.44	Enclosure 11	2.25°C	Elevated	Picea mariana	2016	Tree
36	0.20	0.26	0.24	0.17	0.79	0.26	1.77	0.42	2.82	0.42	3.34	0.42	2.25	0.25	0.81	Enclosure 11	2.25°C	Elevated	Picea mariana	2014	Tree
37	0.17	0.26	1.23	0.39	5.88	1.75	30.30	5.67	181.35	28.16	813.36	69.05	646.24	6.67	7.33	Enclosure 11	2.25°C	Elevated	Rhododendron groenlandicum		Shrub
38	0.34	0.33	1.15	0.35	3.46	1.28	21.41	25.50	640.93	78.33	1148.13	63.04	231.40	2.17	6.98	Enclosure 11	2.25°C	Elevated	Chamaedaphne calyculata		Shrub
39	1.61	0.60	11.10	1.50	15.27	2.03	17.52	1.31	9.91	0.92	11.51	0.93	7.47	0.17	0.35	Enclosure 11	2.25°C	Elevated	Sphagnum (Hummock)		Moss
40	1.09	0.30	8.48	0.71	14.27	1.20	22.35	0.85	8.22	0.46	6.03	0.38	2.61	0.13	0.19	Enclosure 11	2.25°C	Elevated	Sphagnum (Hollow)		Moss
41	0.25	0.31	1.37	0.64	8.26	1.01	9.49	1.04	6.42	0.70	3.48	0.17	0.71	0.14	0.22	Enclosure 13	4.5°C	Ambient	Larix laricina		Tree
42	0.17	0.26	2.52	0.92	9.73	1.03	12.43	0.95	13.20	0.82	5.88	0.60	4.98	0.52	6.31	Enclosure 13	4.5°C	Ambient	Picea mariana	2018	Tree
43	0.20	0.30	1.90	0.85	10.13	1.42	14.34	1.50	13.04	1.17	7.02	0.92	4.89	0.68	4.52	Enclosure 13	4.5°C	Ambient	Picea mariana	2016	Tree
44	0.11	0.22	0.90	0.48	6.04	0.99	10.61	1.17	10.02	1.04	6.60	0.78	3.75	0.53	2.76	Enclosure 13	4.5°C	Ambient	Picea mariana	2014	Tree
45	0.17	0.23	1.03	0.37	4.52	2.28	40.83	9.95	249.25	46.21	1638.15	180.25	1677.80	24.79	23.23	Enclosure 13	4.5°C	Ambient	Rhododendron groenlandicum		Shrub
46	0.44	0.40	1.49	0.51	3.82	1.75	32.06	46.04	1226.04	115.92	1359.62	63.35	214.86	2.07	6.55	Enclosure 13	4.5°C	Ambient	Chamaedaphne calyculata		Shrub
47	0.75	0.47	4.27	0.82	8.85	1.48	16.83	1.25	13.42	1.23	19.50	1.66	16.18	0.34	0.60	Enclosure 13	4.5°C	Ambient	Sphagnum (Hummock)		Moss
48	2.37	0.69	49.33	3.73	70.64	4.77	82.19	2.19	18.45	0.69	11.19	0.84	7.71	0.13	0.20	Enclosure 13	4.5°C	Ambient	Sphagnum (Hollow)		Moss
49	0.12	0.22	0.82	0.52	8.59	1.29	18.40	1.07	13.47	0.83	6.38	0.22	1.12	0.09	0.11	Enclosure 16	6.75°C	Elevated	Larix laricina		Tree
50	0.13	0.23	1.78	0.70	7.55	1.14	10.33	1.24	13.37	0.91	5.13	0.44	2.55	0.18	1.47	Enclosure 16	6.75°C	Elevated	Picea mariana	2018	Tree
51	0.18	0.33	2.07	1.11	11.05	2.22	14.48	2.49	17.17	1.50	7.28	0.71	3.46	0.32	1.46	Enclosure 16	6.75°C	Elevated	Picea mariana	2016	Tree
52	0.19	0.28	0.38	0.29	1.75	0.64	4.80	0.96	5.85	0.84	5.69	0.61	2.89	0.29	0.93	Enclosure 16	6.75°C	Elevated	Picea mariana	2014	Tree
53	0.23	0.22	0.73	0.33	3.09	1.26	29.72	6.68	198.96	33.64	881.97	111.62	849.10	15.30	11.13	Enclosure 16	6.75°C	Elevated	Rhododendron groenlandicum		Shrub
54	0.24	0.27	1.25	0.60	5.57	2.21	16.58	17.60	472.86	51.62	650.07	28.97	100.55	1.10	3.68	Enclosure 16	6.75°C	Elevated	Chamaedaphne calyculata		Shrub
55	0.58	0.47	2.40	0.59	5.09	0.87	8.01	0.79	6.47	0.79	9.25	1.01	7.44	0.21	0.38	Enclosure 16	6.75°C	Elevated	Sphagnum (Hummock)		Moss
56	1.83	0.53	29.19	2.02	70.74	2.72	38.01	1.76	30.46	1.46	21.74	0.60	3.34	0.08	0.26	Enclosure 16	6.75°C	Elevated	Sphagnum (Hollow)		Moss
57	0.37	0.50	1.44	0.61	5.49	1.24	16.42	2.09	11.15	1.33	6.26	0.33	1.47	0.15	0.28	Enclosure 17	9°C	Ambient	Larix laricina		Tree
58	0.16	0.35	1.43	0.58	5.56	0.90	8.65	1.07	16.07	1.15	8.17	0.78	6.53	0.61	7.46	Enclosure 17	9°C	Ambient	Picea mariana	2018	Tree
59	0.22	0.31	0.95	0.35	4.48	1.12	10.89	1.53	14.61	1.26	9.18	0.84	5.10	0.42	2.98	Enclosure 17	9°C	Ambient	Picea mariana	2016	Tree
60	0.45	0.48	1.11	0.34	3.66	0.97	11.12	1.54	14.22	1.49	10.24	1.06	5.25	0.54	2.29	Enclosure 17	9°C	Ambient	Picea mariana	2014	Tree
61	0.25	0.35	0.87	0.43	3.50	1.72	29.69	9.07	308.48	53.19	1677.25	182.36	1648.07	22.74	17.81	Enclosure 17	9°C	Ambient	Rhododendron groenlandicum		Shrub
62	0.38	0.37	1.37	0.49	5.94	2.08	25.90	14.42	275.26	28.15	313.45	15.38	50.58	0.61	1.58	Enclosure 17	9°C	Ambient	Chamaedaphne calyculata		Shrub
63	0.89	0.79	4.36	1.03	8.98	1.46	17.26	1.74	28.49	2.44	39.83	3.05	28.62	0.51	0.62	Enclosure 17	9°C	Ambient	Sphagnum (Hummock)		Moss
64	1.12	0.42	21.65	1.99	44.86	2.71	36.87	1.71	20.71	1.68	24.95	2.02	14.11	0.28	0.42	Enclosure 17	9°C	Ambient	Sphagnum (Hollow)		Moss
65	0.15	0.21	0.96	0.52	6.20	0.82	9.76	0.82	8.68	0.72	5.80	0.20	0.89	0.04	0.08	Enclosure 19	0°C	Elevated	Larix laricina		Tree
66	0.13	0.24	1.50	0.38	2.64	0.46	3.28	0.55	6.25	0.43	2.75	0.30	2.22	0.21	1.97	Enclosure 19	0°C	Elevated	Picea mariana	2018	Tree
67	0.18	0.24	0.82	0.22	1.35	0.27	2.08	0.40	3.20	0.35	2.93	0.37	2.94	0.23	1.39	Enclosure 19	0°C	Elevated	Picea mariana	2016	Tree
68	0.14	0.20	0.40	0.16	0.78	0.20	1.58	0.31	1.84	0.25	1.70	0.22	1.30	0.18	0.96	Enclosure 19	0°C	Elevated	Picea mariana	2014	Tree
69	0.30	0.34	0.67	0.32	5.46	2.00	49.18	8.61	359.25	42.66	1679.30	143.04	1786.16	18.92	20.44	Enclosure 19	0°C	Elevated	Rhododendron groenlandicum		Shrub
70	0.23	0.32	1.11	0.38	3.37	0.97	16.48	16.09	608.19	50.66	549.11	18.92	51.15	0.49	1.56	Enclosure 19	0°C	Elevated	Chamaedaphne calyculata		Shrub
71	0.47	0.38	1.85	0.39	5.57	0.65	5.37	0.58	5.80	0.66	8.81	0.75	6.70	0.24	0.60	Enclosure 19	0°C	Elevated	Sphagnum (Hummock)		Moss
72	0.37	0.24	2.04	0.36	6.59	0.84	12.28	0.78	9.84	0.73	10.04	0.56	2.96	0.26	0.37	Enclosure 19	0°C	Elevated	Sphagnum (Hollow)		Moss
73	0.18	0.31	1.23	0.59	6.98	1.12	11.46	1.90	10.20	1.34	6.21	0.52	1.93	0.25	0.20	Enclosure 20	2.25°C	Ambient	Larix laricina		Tree
74	0.23	0.30	1.24	0.41	3.85	0.52	4.44	0.78	7.22	0.54	3.89	0.35	2.91	0.25	1.50	Enclosure 20	2.25°C	Ambient	Picea mariana	2018	Tree
75	0.22	0.30	1.99	0.72	5.80	0.85	5.75	1.10	8.63	0.79	4.93	0.51	3.44	0.26	1.50	Enclosure 20	2.25°C	Ambient	Picea mariana	2016	Tree
76	0.12	0.27	1.37	0.56	4.24	0.63	4.93	0.75	5.71	0.61	5.03	0.50	3.61	0.23	0.86	Enclosure 20	2.25°C	Ambient	Picea mariana	2014	Tree
77	0.00	0.47	1.20	0.59	5.95	2.31	42.80	9.70	352.96	45.77	1499.92	126.39	1286.65	16.16	18.72	Enclosure 20	2.25°C	Ambient	Rhododendron groenlandicum		Shrub
78	0.36	0.44	1.62	0.63	5.67	2.11	44.81	41.86	1081.54	106.81	1293.36	71.19	247.24	2.56	7.89	Enclosure 20	2.25°C	Ambient	Chamaedaphne calyculata		Shrub

79	0.90	0.69	1.78	0.52	2.86	0.60	4.66	0.73	5.73	0.79	11.52	1.19	11.37	0.27	0.50	Enclosure 20	2.25°C	Ambient	Sphagnum (Hummock)		Moss
80	0.74	0.31	16.77	1.54	43.03	3.18	68.69	1.76	16.73	0.64	8.57	0.68	6.75	0.15	0.31	Enclosure 20	2.25°C	Ambient	Sphagnum (Hollow)		Moss
81	0.18	0.25	0.68	0.34	3.17	0.77	6.35	1.73	10.22	1.43	7.17	0.29	1.31	0.14	0.20	Enclosure 21	Control	Control	Larix laricina		Tree
82	0.29	0.66	4.02	1.27	4.28	1.63	4.63	1.36	8.30	1.03	4.00	0.80	3.57	0.37	1.87	Enclosure 21	Control	Control	Picea mariana	2018	Tree
83	0.21	0.31	0.98	0.30	1.61	0.47	2.50	0.77	4.49	0.70	3.30	0.70	2.86	0.37	1.81	Enclosure 21	Control	Control	Picea mariana	2016	Tree
84	0.20	0.24	0.51	0.26	1.05	0.34	2.03	0.53	2.88	0.54	2.75	0.58	2.37	0.37	1.53	Enclosure 21	Control	Control	Picea mariana	2014	Tree
85	0.46	0.46	0.98	0.63	8.27	4.00	56.57	13.19	317.28	55.91	1527.05	166.07	1437.59	19.41	17.37	Enclosure 21	Control	Control	Rhododendron groenlandicum		Shrub
86	0.62	0.37	1.68	0.73	4.97	2.00	46.61	39.28	706.68	80.08	983.71	52.52	186.20	2.02	5.58	Enclosure 21	Control	Control	Chamaedaphne calyculata		Shrub
87	1.61	0.41	7.96	0.79	7.43	0.55	7.83	0.56	5.39	0.30	4.70	0.23	1.81	0.00	0.00	Enclosure 21	Control	Control	Sphagnum (Hummock)		Moss
88	2.80	0.58	12.06	1.41	19.31	2.18	29.77	1.45	11.10	0.69	7.29	0.41	3.02	0.12	0.34	Enclosure 21	Control	Control	Sphagnum (Hollow)		Moss

Sample	C14	C15	C16	C17	C18	C20	C21	C22	C23	C24	C25	C26	C27	C28	C29	C30	Plot	Warming	CO2	Species	Picea_year	Type
1	257.87	13.52	2018.68	67.54	376.61	74.53	12.52	116.42	52.85	329.55	28.76	175.54	8.84	190.66	10.64	464.88	Enclosure 4	4.5°C	Elevated	Larix laricina		Tree
2	148.38	5.10	1891.76	72.24	298.46	32.94	20.04	145.91	78.30	293.98	21.91	63.54	4.63	23.04	6.70	76.71	Enclosure 4	4.5°C	Elevated	Picea mariana	2018	Tree
3	308.47	49.90	1284.95	67.99	196.75	52.56	39.61	134.32	89.61	337.37	33.18	81.13	10.07	28.20	10.51	94.02	Enclosure 4	4.5°C	Elevated	Picea mariana	2016	Tree
4	350.36	44.31	1158.38	59.21	189.56	48.60	30.90	130.81	74.82	254.14	31.02	71.37	21.65	30.67	10.05	94.45	Enclosure 4	4.5°C	Elevated	Picea mariana	2014	Tree
5	119.98	11.28	1080.71	31.70	214.58	95.90	17.05	48.94	15.90	28.16	8.15	37.14	22.96	172.57	22.18	133.44	Enclosure 4	4.5°C	Elevated	Rhododendron groenlandicum		Shrub
6	105.59	10.09	777.21	16.99	138.58	116.30	15.98	178.31	22.94	416.72	36.46	866.98	26.09	236.96	16.44	170.95	Enclosure 4	4.5°C	Elevated	Chamaedaphne calyculata		Shrub
7	80.57	91.66	1839.37	76.11	348.12	136.72	55.51	402.04	142.06	596.14	109.69	376.71	61.00	148.87	10.96	43.73	Enclosure 4	4.5°C	Elevated	Sphagnum (Hummock)		Moss
8	46.01	84.83	1556.60	74.98	182.70	44.92	25.35	131.42	59.91	240.34	30.90	123.50	27.86	50.41	6.33	18.57	Enclosure 4	4.5°C	Elevated	Sphagnum (Hollow)		Moss
9	201.10	11.88	1453.84	39.87	310.92	72.20	10.29	127.51	54.38	255.41	25.51	227.73	15.43	310.19	20.14	641.37	Enclosure 6	0°C	Ambient	Larix laricina		Tree
10	191.82	32.85	1192.94	27.61	193.91	46.28	15.50	149.61	57.38	320.46	18.26	82.68	5.37	30.09	7.91	115.10	Enclosure 6	0°C	Ambient	Picea mariana	2018	Tree
11	452.27	75.76	1059.93	52.62	332.80	42.31	22.66	120.75	56.07	202.68	19.47	50.59	18.72	23.69	7.88	109.84	Enclosure 6	0°C	Ambient	Picea mariana	2016	Tree
12	586.44	66.94	1004.05	54.93	234.94	36.42	14.05	97.20	41.16	103.50	13.10	22.22	19.66	9.32	4.27	60.56	Enclosure 6	0°C	Ambient	Picea mariana	2014	Tree
13	147.29	10.24	788.03	20.55	183.75	96.90	16.44	47.98	16.12	30.48	9.05	50.05	41.69	217.24	18.44	141.47	Enclosure 6	0°C	Ambient	Rhododendron groenlandicum		Shrub
14	116.03	8.88	763.26	13.71	150.18	139.48	18.03	205.11	28.06	479.95	40.27	980.47	26.03	318.40	42.24	200.93	Enclosure 6	0°C	Ambient	Chamaedaphne calyculata		Shrub
15	40.93	32.24	695.63	35.99	141.57	68.21	22.29	190.76	65.62	448.13	62.34	372.97	32.20	93.47	12.98	52.37	Enclosure 6	0°C	Ambient	Sphagnum (Hummock)		Moss
16	21.66	9.49	426.12	11.48	104.71	105.12	8.21	196.83	20.83	192.87	27.90	83.84	14.14	65.26	7.50	24.29	Enclosure 6	0°C	Ambient	Sphagnum (Hollow)		Moss
17	334.00	28.23	2525.22	115.72	467.07	132.78	21.31	184.08	79.31	383.70	35.84	268.00	17.63	331.54	22.48	798.11	Enclosure 8	6.75°C	Ambient	Larix laricina		Tree
18	140.90	25.63	794.32	35.19	167.60	32.12	11.72	92.88	38.07	281.17	14.10	65.86	4.74	27.70	4.69	89.53	Enclosure 8	6.75°C	Ambient	Picea mariana	2018	Tree
19	251.35	47.67	962.61	56.09	182.63	38.33	16.48	119.28	53.00	315.73	22.74	78.50	8.53	34.75	7.72	105.31	Enclosure 8	6.75°C	Ambient	Picea mariana	2016	Tree
20	349.48	38.84	1059.64	65.34	199.66	34.01	16.29	97.45	50.94	200.32	18.87	54.04	13.45	29.96	6.06	95.36	Enclosure 8	6.75°C	Ambient	Picea mariana	2014	Tree
21	130.87	13.86	755.47	16.54	164.34	68.14	13.48	33.24	11.18	19.77	7.14	30.30	112.58	184.41	43.73	89.43	Enclosure 8	6.75°C	Ambient	Rhododendron groenlandicum		Shrub
22	85.37	7.13	641.23	13.56	130.78	90.96	13.27	63.65	16.62	143.84	20.58	534.98	22.62	279.48	31.67	140.84	Enclosure 8	6.75°C	Ambient	Chamaedaphne calyculata		Shrub
23	24.17	24.83	561.15	34.54	122.45	40.99	12.45	87.22	32.95	207.75	26.65	173.91	14.99	33.93	3.78	14.39	Enclosure 8	6.75°C	Ambient	Sphagnum (Hummock)		Moss
24	31.60	65.21	1023.30	67.06	149.50	36.41	20.15	124.24	60.83	282.14	41.42	184.13	22.81	56.66	8.02	17.35	Enclosure 8	6.75°C	Ambient	Sphagnum (Hollow)		Moss
25	171.47	18.22	1276.36	40.09	220.30	69.17	12.55	98.63	37.39	193.26	20.54	116.22	7.75	132.08	12.88	285.79	Enclosure 10	9°C	Elevated	Larix laricina		Tree
26	132.44	15.43	1257.16	37.65	236.10	52.25	15.81	97.12	44.67	277.24	14.56	54.65	2.56	15.92	6.05	50.40	Enclosure 10	9°C	Elevated	Picea mariana	2018	Tree
27	296.46	24.44	960.09	36.28	182.32	49.82	24.95	110.62	56.69	219.75	21.02	51.28	9.67	22.35	7.50	56.17	Enclosure 10	9°C	Elevated	Picea mariana	2016	Tree
28	463.68	55.05	1237.89	46.27	286.09	80.04	20.46	164.38	72.21	210.22	25.61	51.78	14.09	25.46	7.16	41.35	Enclosure 10	9°C	Elevated	Picea mariana	2014	Tree
29	80.96	8.62	795.91	16.25	162.61	85.23	13.82	32.28	11.66	17.66	3.39	17.56	6.56	85.32	9.07	71.15	Enclosure 10	9°C	Elevated	Rhododendron groenlandicum		Shrub
30	102.97	8.42	627.37	10.16	119.19	82.58	12.72	70.29	19.11	287.07	26.56	667.17	19.23	268.56	44.82	218.45	Enclosure 10	9°C	Elevated	Chamaedaphne calyculata		Shrub
31	20.30	17.18	453.24	16.31	93.77	28.00	14.99	70.59	27.83	107.26	20.08	56.37	9.88	26.12	4.11	13.01	Enclosure 10	9°C	Elevated	Sphagnum (Hummock)		Moss
32	30.02	33.62	784.50	40.37	130.20	48.68	18.92	107.33	49.65	272.15	32.07	187.98	18.87	43.05	6.22	21.05	Enclosure 10	9°C	Elevated	Sphagnum (Hollow)		Moss
33	133.25	10.24	927.93	26.34	167.69	51.10	7.80	83.71	34.05	191.61	15.63	119.01	6.57	139.53	10.21	423.40	Enclosure 11	2.25°C	Elevated	Larix laricina		Tree
34	146.66	38.05	706.95	26.17	132.73	36.92	12.50	84.12	33.68	173.97	11.38	43.06	6.63	18.80	4.98	78.21	Enclosure 11	2.25°C	Elevated	Picea mariana	2018	Tree
35	278.18	62.22	1034.63	40.99	160.16	49.80	25.84	103.61	47.26	225.67	19.78	54.36	9.09	22.40	7.50	87.57	Enclosure 11	2.25°C	Elevated	Picea mariana	2016	Tree
36	321.65	59.04	949.41	58.98	166.71	37.97	6.91	74.31	33.74	97.58	12.35	26.29	10.89	12.84	3.40	51.20	Enclosure 11	2.25°C	Elevated	Picea mariana	2014	Tree
37	99.29	9.78	611.84	96.24	145.56	64.12	10.72	36.56	11.30	22.18	6.61	49.23	47.64	345.59	15.05	110.48	Enclosure 11	2.25°C	Elevated	Rhododendron groenlandicum		Shrub
38	91.68	11.06	561.30	10.54	99.32	105.78	17.21	270.87	27.17	723.18	48.28	837.57	23.57	294.12	60.29	269.04	Enclosure 11	2.25°C	Elevated	Chamaedaphne calyculata		Shrub
39	36.74	48.63	872.97	41.67	178.19	77.72	31.58	224.51	70.66	289.29	53.77	176.13	27.81	94.23	8.93	34.34	Enclosure 11	2.25°C	Elevated	Sphagnum (Hummock)		Moss
40	22.53	34.88	672.07	34.85	107.19	32.48	16.62	109.39	54.11	232.07	29.85	123.80	19.71	56.55	5.26	19.25	Enclosure 11	2.25°C	Elevated	Sphagnum (Hollow)		Moss
41	187.70	18.97	1569.48	52.20	310.60	81.08	10.41	115.75	52.98	287.49	24.23	185.52	7.12	175.28	8.84	313.19	Enclosure 13	4.5°C	Ambient	Larix laricina		Tree
42	164.83	29.88	652.31	26.65	145.66	33.93	11.69	93.30	46.79	253.97	14.46	64.08	4.11	28.91	5.99	94.96	Enclosure 13	4.5°C	Ambient	Picea mariana	2018	Tree
43	272.40	37.65	575.51	30.27	128.29	30.62	15.01	88.64	44.75	189.14	15.40	56.38	7.29	28.51	7.63	84.91	Enclosure 13	4.5°C	Ambient	Picea mariana	2016	Tree
44	311.47	40.17	686.45	36.84	145.22	33.48	14.35	84.07	48.71	182.31	17.01	54.26	10.52	28.05	7.13	95.87	Enclosure 13	4.5°C	Ambient	Picea mariana	2014	Tree
45	98.72	12.60	561.37	9.87	143.82	91.15	13.24	29.08	10.62	19.28	4.42	17.53	10.74	64.52	6.94	46.34	Enclosure 13	4.5°C	Ambient	Rhododendron groenlandicum		Shrub
46	75.11	5.82	482.74	10.01	92.48	48.32	9.81	61.62	10.18	164.68	18.29	284.70	9.87	119.69	23.82	150.47	Enclosure 13	4.5°C	Ambient	Chamaedaphne calyculata		Shrub
47	37.05	36.80	721.22	29.97	119.56	54.84	22.64	163.60	48.90	269.63	47.04	157.18	23.60	76.86	6.83	24.34	Enclosure 13	4.5°C	Ambient	Sphagnum (Hummock)		Moss
48	42.19	71.05	1085.38	68.13	138.28	39.35	17.15	127.95	61.69	244.93	37.92	141.48	15.08	47.78	5.76	16.73	Enclosure 13	4.5°C	Ambient	Sphagnum (Hollow)		Moss
49	165.18	12.65	1219.11	35.81	245.95	83.67	8.22	89.40	34.46	171.24	15.67	95.97	4.18	118.49	9.15	343.01	Enclosure 16	6.75°C	Elevated	Larix laricina		Tree
50	198.25	49.08	883.78	43.68	167.07	54.57	18.12	143.43	56.45	350.50	20.52	82.64	8.99	33.49	9.62	96.38	Enclosure 16	6.75°C	Elevated	Picea mariana	2018	Tree
51	368.51	52.06	1035.56	25.57	470.64	66.56	16.23	205.16	33.64	194.48	0.00	5.39	14.66	139.51	10.17	103.69	Enclosure 16	6.75°C	Elevated	Picea mariana	2016	Tree
52	353.94	53.93	926.65	45.69	168.04	31.47	5.60	87.40	36.23	102.96	13.56	28.42	16.80	16.57	4.38	61.88	Enclosure 16	6.75°C	Elevated	Picea mariana	2014	Tree
53	99.10	6.95	518.92	40.82	111.87	62.23	8.33	27.53	7.06	13.88	4.97	44.25	17.03	191.91	15.40	114.36	Enclosure 16	6.75°C	Elevated	Rhododendron groenlandicum		Shrub
54	75.57	7.28	456.60	10.68	93.69	62.95	10.25	58.58	13.09	206.28	24.99	564.63	20.78	151.27	15.44	141.98	Enclosure 16	6.75°C	Elevated	Chamaedaphne calyculata		Shrub
55	46.10	44.39	886.07	42.08	204.93	74.50	26.58	238.79	69.63	337.46	56.60	193.71	35.04	93.42	9.05	42.44	Enclosure 16	6.75°C	Elevated	Sphagnum (Hummock)		Moss
56	43.30	46.49	1131.16	61.04	190.76	50.34	13.84	146.57	53.04	317.41	37.89	223.95	20.95	46.05	4.66	22.74	Enclosure 16	6.75°C	Elevated	Sphagnum (Hollow)		Moss
57	330.62	21.67	1855.94	105.70	357.42	90.56	11.07	107.09	36.98	158.20	17.39	130.26	10.99	179.67	15.53	448.09	Enclosure 17	9°C	Ambient	Larix laricina		Tree
58	158.13	63.15	1272.47	65.76	264.49	46.70	9.68	122.66	52.60	278.02	15.86	69.11	10.02	24.47	4.85	76.67	Enclosure 17	9°C	Ambient	Picea mariana	2018	Tree
59	275.76	53.08	977.39	53.74	181.17	40.44	14.81	165.48	57.96	260.18	20.15	76.01	11.45	30.07	6.59	77.23	Enclosure 17	9°C	Ambient	Picea mariana	2016	Tree
60	315.33	62.79	1059.76	58.30	212.76	60.42	14.60	194.73	50.83	269.13	19.70	59.00	9.45	27.79	6.36	72.16	Enclosure 17	9°C	Ambient	Picea mariana	2014	Tree
61	146.91	14.62	865.60	29.61	173.82	118.45	18.21	43.34	16.51	28.35	7.62	26.69	46.73	90.54	10.53	86.96	Enclosure 17	9°C	Ambient	Rhododendron groenlandicum		Shrub
62	115.37	7.43	554.85	12.83	131.45	101.72	14.01	103.54	15.18	282.17	25.79	614.91	24.29	165.71	13.70	118.67	Enclosure 17	9°C	Ambient	Chamaedaphne calyculata		Shrub
63	28.91	28.29	613.42	26.55	136.85	59.05	22.19	176.04	61.52	263.68	51.25	141.31	26.82	70.89	7.05	36.39	Enclosure 17	9°C	Ambient	Sphagnum (Hummock)		Moss

64	26.19	37.09	848.46	43.88	117.51	36.56	12.15	96.83	39.03	198.74	24.14	132.96	11.27	26.00	2.21	10.23	Enclosure 17	9°C	Ambient	Sphagnum (Hollow)	Moss
65	246.65	28.21	1198.74	32.27	292.18	83.01	9.06	180.92	59.84	365.61	29.39	289.28	16.83	339.32	15.76	850.31	Enclosure 19	0°C	Elevated	Larix laricina	Tree
66	179.32	45.02	1047.67	32.78	199.23	51.22	11.22	103.04	37.97	254.89	12.30	53.89	5.74	23.73	4.11	87.80	Enclosure 19	0°C	Elevated	Picea mariana 2018	Tree
67	239.17	61.36	964.98	40.13	165.31	36.82	9.88	75.16	35.97	150.36	11.12	36.73	8.42	17.64	3.71	67.43	Enclosure 19	0°C	Elevated	Picea mariana 2016	Tree
68	320.66	67.91	1101.89	45.88	183.42	40.89	6.28	73.97	34.87	113.34	10.23	24.31	11.17	12.81	3.39	42.87	Enclosure 19	0°C	Elevated	Picea mariana 2014	Tree
69	48.74	16.91	464.15	13.58	118.73	58.08	9.54	31.48	8.53	18.67	4.25	23.73	6.02	56.45	8.51	68.58	Enclosure 19	0°C	Elevated	Rhododendron groenlandicum	Shrub
70	32.23	16.70	695.30	13.42	119.12	134.16	17.40	105.61	30.76	257.47	38.53	421.25	22.15	197.52	16.97	215.74	Enclosure 19	0°C	Elevated	Chamaedaphne calyculata	Shrub
71	37.33	34.37	776.21	38.97	150.05	102.30	19.52	162.89	51.52	206.60	34.77	116.90	13.91	36.39	3.75	16.22	Enclosure 19	0°C	Elevated	Sphagnum (Hummock)	Moss
72	33.90	48.77	956.40	63.57	156.09	54.79	21.38	168.05	76.14	282.24	35.80	130.24	22.79	57.86	5.83	31.77	Enclosure 19	0°C	Elevated	Sphagnum (Hollow)	Moss
73	116.19	17.06	821.34	33.14	200.61	59.46	5.95	87.92	33.24	182.12	16.53	118.48	9.74	133.35	9.57	329.04	Enclosure 20	2.25°C	Ambient	Larix laricina	Tree
74	202.41	49.32	948.31	48.14	237.33	53.57	12.58	162.49	56.31	383.40	16.98	73.45	8.78	25.45	4.44	74.38	Enclosure 20	2.25°C	Ambient	Picea mariana 2018	Tree
75	183.50	44.81	682.96	40.09	148.61	40.87	12.56	139.92	46.41	270.70	15.32	54.03	8.09	21.82	4.86	64.14	Enclosure 20	2.25°C	Ambient	Picea mariana 2016	Tree
76	422.41	92.48	800.53	52.58	158.29	40.22	13.33	111.01	55.91	236.54	17.55	63.13	17.50	24.26	6.00	73.72	Enclosure 20	2.25°C	Ambient	Picea mariana 2014	Tree
77	109.27	25.46	614.33	17.48	149.57	77.46	11.60	39.80	11.59	26.12	4.33	19.61	23.70	87.75	0.00	35.23	Enclosure 20	2.25°C	Ambient	Rhododendron groenlandicum	Shrub
78	34.19	13.41	629.99	8.57	114.63	89.14	14.04	79.28	17.23	204.73	26.55	582.19	25.28	177.11	22.13	187.72	Enclosure 20	2.25°C	Ambient	Chamaedaphne calyculata	Shrub
79	39.47	36.66	777.60	32.69	121.17	46.34	17.21	169.48	62.93	278.62	52.88	162.82	23.59	97.70	7.50	64.57	Enclosure 20	2.25°C	Ambient	Sphagnum (Hummock)	Moss
80	37.71	51.87	965.18	77.14	182.39	50.69	18.85	166.31	65.05	328.49	44.02	170.83	20.99	53.91	4.39	15.00	Enclosure 20	2.25°C	Ambient	Sphagnum (Hollow)	Moss
81	128.90	23.31	796.02	27.56	176.12	39.70	4.30	79.43	33.68	155.04	12.97	89.17	5.83	89.24	4.98	256.68	Enclosure 21	Control	Control	Larix laricina	Tree
82	222.77	41.27	956.78	31.27	202.62	51.50	14.99	124.37	44.47	255.17	12.31	48.78	5.90	25.83	4.13	83.79	Enclosure 21	Control	Control	Picea mariana 2018	Tree
83	408.77	47.78	996.81	41.84	170.46	39.33	11.03	85.20	40.30	147.92	11.42	30.70	6.62	17.87	3.70	63.94	Enclosure 21	Control	Control	Picea mariana 2016	Tree
84	434.15	79.09	819.92	40.45	138.84	30.93	7.39	70.15	34.66	102.67	10.14	27.45	9.24	15.02	3.55	57.54	Enclosure 21	Control	Control	Picea mariana 2014	Tree
85	142.23	11.66	639.59	21.52	144.58	91.28	17.93	39.78	14.69	30.15	9.90	46.62	26.93	155.77	24.04	198.08	Enclosure 21	Control	Control	Rhododendron groenlandicum	Shrub
86	70.99	10.69	564.10	12.87	119.99	338.19	26.25	276.73	26.72	427.28	47.59	688.45	28.55	251.58	29.11	238.44	Enclosure 21	Control	Control	Chamaedaphne calyculata	Shrub
87	36.11	57.63	976.26	39.56	125.42	40.44	12.91	90.93	43.39	144.15	19.64	65.22	11.27	17.41	2.44	4.65	Enclosure 21	Control	Control	Sphagnum (Hummock)	Moss
88	34.59	45.76	748.20	40.41	152.75	45.49	17.87	116.28	51.45	174.18	27.92	95.42	14.61	38.66	3.86	14.95	Enclosure 21	Control	Control	Sphagnum (Hollow)	Moss

Personal declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

Zurich, March 28, 2021