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RESEARCH ARTICLE

# Lichen bleaching as a response to long-term experimental warming in the High Arctic

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## Abstract

1. Lichens are an important component of Arctic ecosystems. Studies have indicated a decline in the abundance of Arctic lichens during recent decades, which is often attributed to competitive pressure from vascular plants. However, the direct effects of warming on the lichen symbiosis have rarely been explored, particularly in the High Arctic, where shrubification is less pronounced than in the Low Arctic, and where warming might hence have more direct effects on the growth and survival of lichens.
2. Here, we investigated the physiological responses of *Cetrariella delisei*, a widespread circumpolar lichen species, to almost a decade of experimental warming with open-top chambers.
3. We found that *C. delisei* physiologically deteriorated in response to the warming treatment, with the myco- and photobiont differing in their sensitivities to warming. Symbiotic deterioration was manifested in a 2.4-fold reduction in net photosynthesis, an approximate doubling in maximum respiration rate, and a loss of 60% of the algal photobiont and a 30% decline in chlorophyll concentration, which caused bleaching of the lichen thallus. These changes resulted in a negative thallus carbon balance and a loss of photosynthetic capacity at low temperatures.
4. Our findings, which advance mechanistic understanding of symbiotic breakdown and lichen bleaching, shed new light on the physiological impacts of warming on polar lichens. We show that photobionts have high sensitivity to increases in mean and maximum daily summertime air temperatures of 1 and 4°C, respectively. These are early warning signals that the mat-forming lichen *C. delisei* is under threat in the rapidly warming Arctic.

KEYWORDS
bleaching, *Cetrariella delisei*, dysbiosis, High Arctic, lichen, net photosynthesis, thermal acclimation

## 1 | INTRODUCTION

Dysbiosis, the breakdown of symbiotic relationships caused by physiological stress, is one of the many observed effects of global warming (Kiers et al., 2010). A well-known example of climate change-induced dysbiosis is coral bleaching, which has large and cascading consequences for entire marine ecosystems (Helgoe et al., 2024). However, in the terrestrial realm, the impacts of climate warming on symbiotic breakdown are less apparent, although recent observations suggest that lichens, which are frequent and widespread in terrestrial ecosystems (Asplund & Wardle, 2017), may be prone to dysbiosis caused by rising temperatures (Colesie et al., 2018; Meyer et al., 2022, 2024; Raggio et al., 2023; Stanton et al., 2023). The lichen symbiosis is an integrated association between a fungus (mycobiont) and a green alga and/or cyanobacterium (photobiont; Spribille et al., 2022) and can include more partners such as secondary mycobionts or multiple photobionts, yeasts, bacteria, or protists (Hawksworth & Grube, 2020). Lichens provide important ecosystem services, such as carbon sequestration, nitrogen fixation, or protection from soil erosion (Asplund & Wardle, 2017; Porada et al., 2014). They are especially important in environments where vascular plant growth is limited, such as semi-arid, arid and polar habitats, where they dominate vegetation (Armstrong, 2017; Colesie et al., 2014), form the basis of the trophic chains (Finne et al., 2023), and contribute significantly to biodiversity (Øvstedal et al., 2009).

The success of lichens lies in poikilohydry, allowing dormancy during dry periods and rapid metabolic reactivation when hydrated (Kranner et al., 2008). Lichens process carbon through fixation via photosynthesis by the photobiont and energy expenditure through respiration, most of which is attributable to the mycobiont (Palmqvist, 2000). Both partners in the lichen symbiosis maintain their individual physiological characteristics such as activation thresholds or relationships with temperature (Meyer et al., 2024; Palmqvist, 2000). For example, with increasing temperature, respiration rate increases, while net photosynthesis (NP) peaks at an optimum (Kappen & Lange, 1972; Lange & Green, 2005; Palmqvist, 2000; Sundberg et al., 1999). Beyond this optimum temperature, NP decreases due to photorespiration and a disproportionate increase in respiration (Palmqvist, 2000). Because of these physiological asymmetries, any differences in the responses of the mycobiont and photobiont to changes in environmental conditions potentially put the symbiosis under strain.

Lichens can show thermal acclimation in response to temperature changes (Colesie et al., 2018). Acclimation occurs when an organism adjusts its phenotypic expression through physiological, biochemical or structural traits in response to temperature changes (Atkin & Tjoelker, 2003; Zhou et al., 2007). In response to seasonal temperature variation, lichens can acclimatize by adjusting their chlorophyll content (MacKenzie et al., 2001), photobiont population density (Tretiach et al., 2013) or photosynthetic efficiency (Macfarlane & Kershaw, 1982; Vivas et al., 2017). Respiration can also acclimatize seasonally through the downregulation of respiration rates (Lange & Green, 2005). Lichens also acclimatize to specific environments across spatial scales through altering physiological and morphological traits such as maximum NP rates, optimal temperature for photosynthesis, chlorophyll content or the proportion of photobiont to mycobiont (Domaschke et al., 2013; Sun & Friedmann, 2005).

Successful thermal acclimation is assumed to be a relatively rapid process, but can only happen while the lichen is active (Colesie et al., 2018; Lange & Green, 2005). This is crucial, because either in hot and dry climates (e.g. deserts) or extremely cold climates (e.g. polar environments), lichens often remain dormant for extended periods (Raggio et al., 2016; Schroeter et al., 2000), potentially restricting their acclimation capacity. Climate warming may further constrain this capacity by shortening active periods. Rising vapour pressure deficit (VPD), which increases atmospheric drying (Grossiord et al., 2020), can reduce hydration opportunities and thereby limit the duration of physiological activity (Colesie et al., 2018). If rapid warming occurs during the dormant phase, upon rehydration, lichens may then be exposed to stressful conditions without the opportunity to gradually acclimate.

Still, even when lichens are active, acclimation is not a universal trait. Firstly, warming must remain within physiological thresholds, since excessive heat during active periods can cause thermal damage (Gauslaa, 2023; Kraft et al., 2022; Osyczka & Myśliwa-Kurdziel, 2024). Secondly, if warming exceeds the rate at which symbiotic partners can physiologically adjust, respiration can surpass carbon gain and lead to overall carbon loss. Over time, this imbalance can lead to carbon starvation. In winter, premature reactivation under low or no light can cause net carbon loss through respiration (Bokhorst et al., 2016), while in summer, shortened active periods can limit photosynthetic carbon gain (Raggio et al., 2023), preventing recovery of lost carbon reserves, ultimately impeding acclimation. The risk of carbon starvation might be amplified in environments where climate warming happens and lichens are predominantly dormant, such as the Arctic. There is mixed evidence for whether individual lichen populations and different species in cold extreme environments can thermally acclimate to temperature increases in situ (Stanton et al., 2023) as only a few physiological studies have addressed rapid climate change scenarios (Bokhorst et al., 2016; Colesie et al., 2018; Meyer et al., 2022; Raggio et al., 2023; Schipperges et al., 1995).

In the Arctic, long-term monitoring and experimental warming treatments show negative effects of warming on lichen cover, richness or diversity, with the main causal mechanism—particularly in the low Arctic—being an increase in vascular plant canopy cover and associated litter deposition, which contribute to shading and the competitive exclusion of lichens (Alatalo et al., 2017; Fraser et al., 2014; Lang et al., 2012). Although some studies (e.g. Betway-May et al., 2025; Cornelissen et al., 2001) have shown mixed, or no, effects of warming, particularly in drier sites, the general trend is that warming has a negative effect on lichen abundance. The High Arctic typically has lower plant cover compared to lower latitudes (Cornelissen et al., 2001), so any effects of warming are more likely to arise from direct physiological impacts on lichens, rather than competition from vascular plants (Paquette & Hargreaves, 2021). However, despite the urgent need to study warming effects on

Arctic lichens, studies focusing on lichen physiological functioning in response to warming in the region are still scarce.

The aim of this research is to contribute to understanding the potential of acclimation to climate change in a lichen population on Svalbard in the High Arctic, where air temperatures are rising seven times faster than the global mean (Nordli et al., 2020). We studied the mat-forming lichen *C. delisei* (Bory ex Schaer.) Kärnefelt & Thell, a fruticose lichen species with a wide distribution across Arctic tundra and alpine regions, which forms an important part of the diet of Svalbard reindeer, one of the principal vertebrate herbivores inhabiting the archipelago (Cooper & Wookey, 2001). We compared samples that were exposed to 9 years of experimental warming in plots covered with open-top chambers (OTCs) with samples from unchambered plots for traits related to carbon balance, NP and respiration rates, chlorophyll content and photobiont-to-mycobiont ratio. Long-term experiments are essential to allow extremely slow-growing lichens to acclimatize to warming treatments. If the lichen acclimatized to warming, we expected the symbiotic relationships to be adjusted and to show an increase in photosynthetic rate and/or a downregulation of respiration rate, in accordance with the current understanding of thermal acclimation (e.g. Colesie et al., 2018; Lange & Green, 2005; MacKenzie et al., 2001). Higher rates of NP could be manifested through downregulation of respiration, or an increase in PS efficiency, such as through higher chlorophyll content, and/or an increase of photobiont cells, resulting in a change to photobiont-to-mycobiont ratio (Domaschke et al., 2013; Schipperges et al., 1995; Sun & Friedmann, 2005).

## 2 | MATERIALS AND METHODS

### 2.1 | Study site and open-top chamber experiment

The OTC experiment was set up in September 2014 at Kongsfjordneset on the Brøgger Peninsula, Svalbard (Figure 1a,b; 78°57.997′ N, 11°28.545′ E; Newsham et al., 2022). It comprises 48 plots, 24 of which were covered with fibreglass OTCs constructed from PALSUN (Palram Industries Ltd., Doncaster, UK), and which are hereafter referred to as 'treatment plots'. The other 24 plots are unchambered and are hereafter referred to as 'control plots'. PALSUN has high transmittance in the visible spectrum (~87%–91%) and blocks UV radiation. The average summer temperature at Kongsfjordneset is 3.7°C, while the winter average drops to −12.7°C with an annual average of −5.7 ± 3.5°C. Annual precipitation is 550 mm, summer rainfall is 82 mm, and snow typically melts by early June and returns in mid-September (Hanssen-Bauer et al., 2019). The landscape consists of rocky terrain with patterned ground and frost boils (Newsham et al., 2022). Vegetation cover

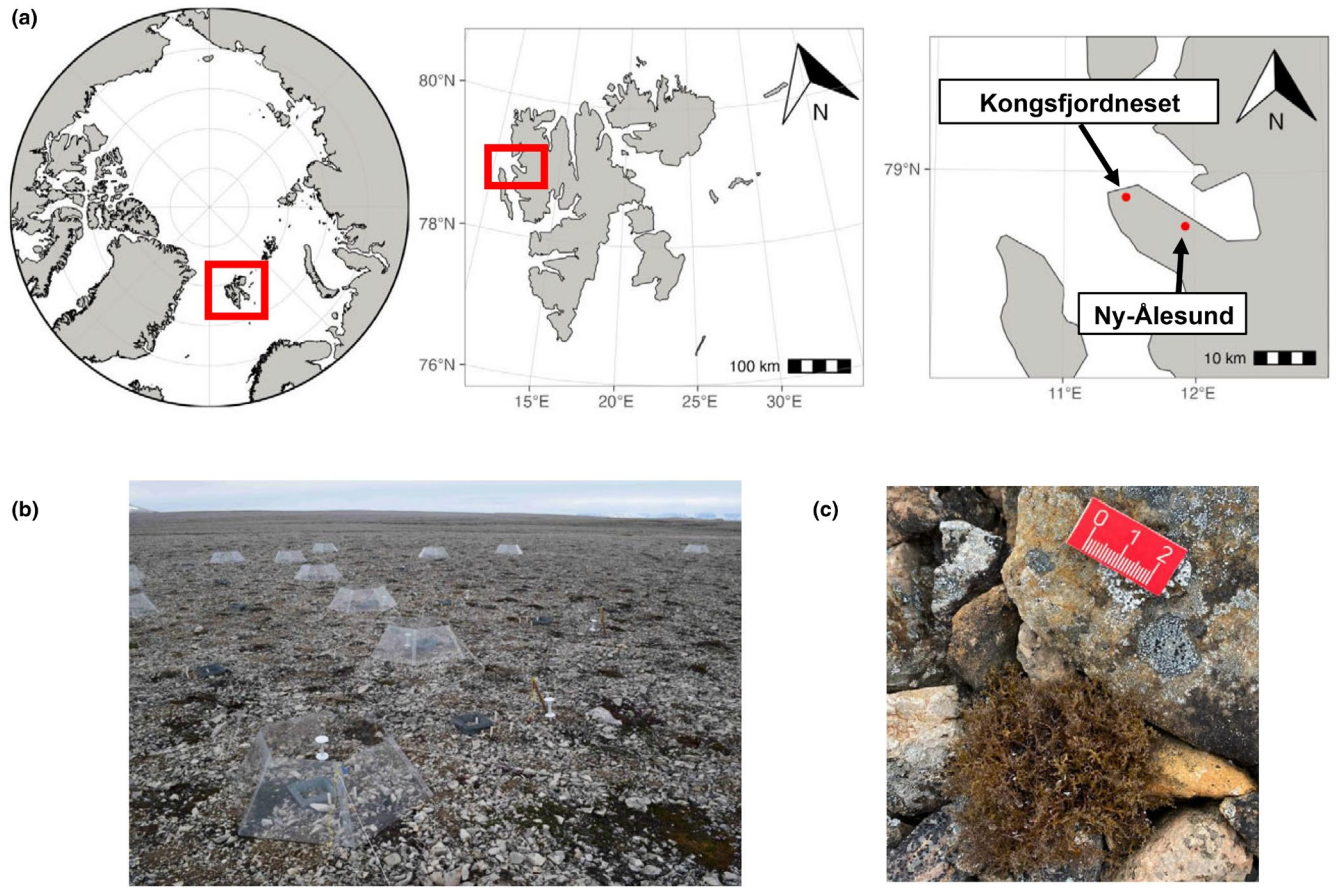


FIGURE 1 (a) Location of the study site at Kongsfjordneset relative to the research settlement at Ny-Ålesund. The position of Svalbard is shown in the red box in the left-hand panel. (b) OTC experiment with microclimate loggers. (c) The lichen *C. delisei* in a control plot, with scale bar in centimetres.

is sparse and is characterized by mosses (*Sanionia*, *Polytrichastrum* and *Dicranum* spp.), lichens (*C. delisei*, *Flavocetraria nivalis* and *Ochrolechia frigida*) and low-growing vascular plant species (*Bistorta vivipara*, *Salix polaris* and *Saxifraga oppositifolia*; Newsham et al., 2022).

## 2.2 | Microclimate characteristics

The OTC experiment was installed for a total of 9 years before our collection. We measured climate data from 3 months of the growing season 2023 to illustrate that the OTCs indeed had a warming effect. We installed three pairs of TMS-4 data loggers (Wild et al., 2019) to monitor surface air temperature at ~1 cm above ground level every 15 min during the main growing season from 29 June to 30 August 2023. Additionally, to calculate the vapour pressure deficit (VPD), three pairs of Thermochron iButtons (Analog Devices, Dallas, USA) were used to track surface air temperature (°C) and relative humidity (RH; %) inside and outside OTCs at the lichen surface layer (Figure 1b) from 20 July 2023 to 30 August 2023. For all microclimate parameters (surface air temperature, RH and VPD), we calculated daily means ± standard deviation, maxima and minima. For calculating VPD, we used the *RHtoVPD* function from the *plantecophys* package in R (Duursma, 2015).

Additionally, we measured photosynthetic photon flux density (PPFD) inside and outside five OTCs at each plot's cardinal points and the plot's centre close to solar noon on an overcast day during summer (30 August 2023) using a PAR Sensor (Skye, Powys, UK). We calculated mean PPFD for each plot and performed a Student's *t*-test to test for differences in light conditions inside and outside the OTCs.

## 2.3 | Species sampling

Samples of *C. delisei* (Figure 1b,c) were collected in June 2022 and August 2023 (Permit: RiS ID 6921, granted by Governor of Svalbard) from inside and outside OTCs. We identified the species by its morphological features, and through nucleotide BLAST analysis (https://blast.ncbi.nlm.nih.gov/) of ribosomal DNA internal transcribed spacer region sequences (deposited in GenBank under accession code PX240394), which matched at >99% sequence identity and 99% query coverage with sequences of *C. delisei*. After collection, the lichens were air-dried at room temperature and were subsequently stored at −20°C.

## 2.4 | Replication statement

| Scale of inference | Scale at which the factor of interest is applied | Number of replicates at the appropriate scale |
|---|---|---|
| Lichen thallus | Plot | 4 control, 4 treatment[a] |
| Lichen thallus | Plot | 10 control, 9 treatment[b] |

[a] For light and temperature response, carbon use efficiency and relative proportion of photobiont to mycobiont.

[b] For chlorophyll content.

## 2.5 | Sample preparation

The samples were thawed in a dark fridge at 4°C for 24 h. Subsequently, they were cleaned of any adhering material, rewetted and exposed to low light conditions (200 μmol photons $m^{-1} s^{-2}$) at 4°C for 24 h at room temperature. Specimens were stored in the fridge between measurements to prevent acclimation to laboratory conditions. The samples were fully hydrated before each measurement by generously spraying them with mineral water. Excess water was removed by shaking and blotting with a paper towel.

## 2.6 | Gas exchange measurements

We conducted $CO_2$ exchange measurements under controlled temperature, light and moisture conditions using a compact minicuvette system (CMS400, Walz GmbH, Effeltrich, Germany). The relative humidity in the cuvette was kept above 90% and the flow rate was set to 500 mL $min^{-1}$. The mean ambient $CO_2$ level over the measurement period was 410 ± 12.3 ppm. Four control and four treatment samples from different plots were used. Measured $CO_2$ exchange rates were converted to rates of NP and DR (dark respiration) using the equation of Farquhar and von Caemmerer (1982). All NP and DR calculations were standardized by dry weight (48 h at 60°C).

## 2.7 | Light response

To evaluate whether OTCs influenced the physiological response of the samples to light availability, we calculated light saturation points (LSPs), that is, the light intensity (μmol photons $m^{-2} s^{-1}$) when NP is light saturated and additional increases in light intensity do not increase photosynthetic rate ($n = 4$ per treatment and $n = 4$ per control). LSPs were extracted from light response curves (LRCs), which were measured by exposing hydrated samples to light intensities of 0, 25, 50, 100, 200, 400, 600, 800, 1000 and 1200 μmol photons $m^{-1} s^{-2}$. To test if the light responses were influenced by temperature, LRCs were repeated at different temperatures (0, 5, 10, 15, 20 and 25°C). LRCs were fitted using standard least-squares non-linear regression using the *fit_AQ_curve* function in R (Tomeo, 2019). To test the effect of OTCs on light saturation points, we fitted a linear mixed-effects model with temperature step (a factor of 0, 5, 10, 15, 20 or 25°C) as a random effect.

## 2.8 | Temperature response

To determine the effect of warming on NP and DR rates between control and treatment samples, we recorded carbon flux at 0, 5, 10, 15, 20 and 25°C (with steps randomized to prevent acclimation) at intervals from hydration to desiccation, alternating light (750 μmol photons $m^{-1} s^{-2}$ for NP) and dark conditions (0 μmol photons $m^{-1} s^{-2}$ for DR), and weighing the lichen at each interval (see Figure S1 for

desiccation curves). We extracted the peak NP and peak DR values for each sample at each temperature and performed non-parametric bootstrapping to construct temperature response curves using the *rTPC* and *nls.multstart* packages in R (Padfield et al., 2021). Code for bootstrapping and figures to create temperature curve plots was adapted from Padfield et al. (2021). In the model selection process, as our data included negative NP values, we chose models that spanned negative values above and below optimal temperature, and selected the best model fit using the lowest AICc values. We chose a quadratic model (Montagnes et al., 2008), used the non-parametric bootstrapping method and extracted 95% confidence intervals (CIs). For NP rates, we extracted estimated model means and 95% CIs for each control and treatment temperature response. In addition, we extracted optimal temperature for photosynthesis ($T_{opt}$, i.e. the temperature at which NP was the highest), maximum net photosynthesis ($NP_{max}$), thermal breadth ($T_{breadth}$, i.e. the range of temperatures over which a curve's rate is at least 0.8 of its peak), critical thermal minimum ($CT_{min}$, i.e. the temperature at which the rate is 5% of the minimum rate), critical thermal maximum ($CT_{max}$, i.e. the temperature at which the rate is 5% of the maximum rate) and thermal tolerance ($T_{tol}$; $CT_{max}$-$CT_{min}$). $T_{breadth}$, $CT_{min}$ and $CT_{max}$ were adapted from Padfield et al. (2021). For DR rates, we modelled the temperature responses and calculated the maximum mean respiration prediction and associated 95% CIs.

## 2.9 | Carbon use efficiency at peak NP

Carbon use efficiency (CUE) is a dimensionless ratio and represents the proportion of assimilated carbon utilized for new biomass production after accounting for respiratory loss (Choudhury, 2000; Manzoni et al., 2012). Values below 50% indicate more carbon lost through respiration than gained through photosynthesis. We calculated carbon use efficiency (CUE = NP/(NP + DR)) at each temperature step. CUE values were determined at points at the peak NP interval and the corresponding DR at that time to reflect the sample's best instantaneous performance. Since all treatment samples at 0°C, one at 20°C, and two at 25°C yielded negative assimilation values, they were assigned CUE values of 0%.

## 2.10 | Relative proportion of photobiont to mycobiont

Lichen thallus cross-sections ($n = 30$ for control and $n = 34$ for treatment) were prepared from a separate set of samples ($n = 4$ for control and $n = 4$ for treatment). Since algal cells are not homogeneously distributed in a thallus, and to ensure that we used comparable portions of thalli, only top branches were selected for these analyses as they usually contain the majority of the algal cells (Domaschke et al., 2013). Thalli were hydrated and cut to 15 μm thickness using a freezing microtome (Leica CM1900, Leica). Subsequently, we used a digital camera (Leica DFC 420C, Leica) attached to a microscope (Leica DMLP Polarizing Light Microscope, Leica) to capture thallus images at ×200 magnification. Using ImageJ software (Rueden et al., 2017), we manually highlighted algal cells in the thallus and the total area of each cross-section and subsequently calculated the relative proportion of photobiont to mycobiont within each thallus cross-section. We fitted a linear mixed-effects model (*lme4* package in R; Bates et al., 2003) with each sampled thallus as a random effect to determine the effect of OTCs on the photobiont-to-mycobiont ratio.

## 2.11 | Chlorophyll concentration

The concentration of chlorophyll was measured in another set of fresh samples ($n = 10$ for control and $n = 9$ for treatment). The samples underwent two rounds of extraction in dimethyl-sulfoxide (DMSO) at 60°C in a water bath for 60 min. Chlorophyll concentration was determined using the protocol of Ronen and Galun (1984) using absorbance values at 648 nm, 665 nm and 700 nm. Differences between treatments and controls were compared using Student's *t*-tests.

## 2.12 | Data analyses

Statistical analyses were conducted in R (version 4.3.2, R Core Team, 2023). Normality and equal variances tests were performed using functions from the *rstatix* package (Kassambara, 2021). Figures were generated using the *ggplot2* package (Wickham & Grolemund, 2016).

# 3 | RESULTS

## 3.1 | Microclimate

Between 29 June and 30 August 2023, the mean (±SD) surface air temperatures inside and outside the OTCs were 10.6 ± 3.9°C and 9.4 ± 3.2°C, respectively. Mean daily maximum surface air temperature was also higher inside than outside OTCs, at 15.5 ± 4.6°C and 12.8 ± 3.5°C, respectively. All 62 daily maximum and minimum temperatures were higher inside the OTCs than outside (Figure 2a). The maximum temperature recorded inside OTCs was 24.3°C, compared to 20.1°C in the control plots. Mean RH inside and outside the OTCs was similar, at 87.9 ± 13.2% and 85.7 ± 14.8%, respectively. Relative humidity reached 100% during rainfall events, but only the control desiccated fully (RH 0%), with RH only dropping to 28.1% inside OTCs (Figure 2b). The mean VPD was also higher inside OTCs than outside (0.252 ± 0. 0.004 and 0.167 ± 0.001 kPa, respectively; Figure 2c). Maximum VPD inside OTCs was 4.72 kPa, whereas that outside the chambers was 2.47 kPa. Photosynthetic active radiation did not differ between the inside and the outside of the OTCs ($t = 2.31$, $p = 0.051$; $n = 5$). All microclimatic values are summarized in Tables S1 and S2.

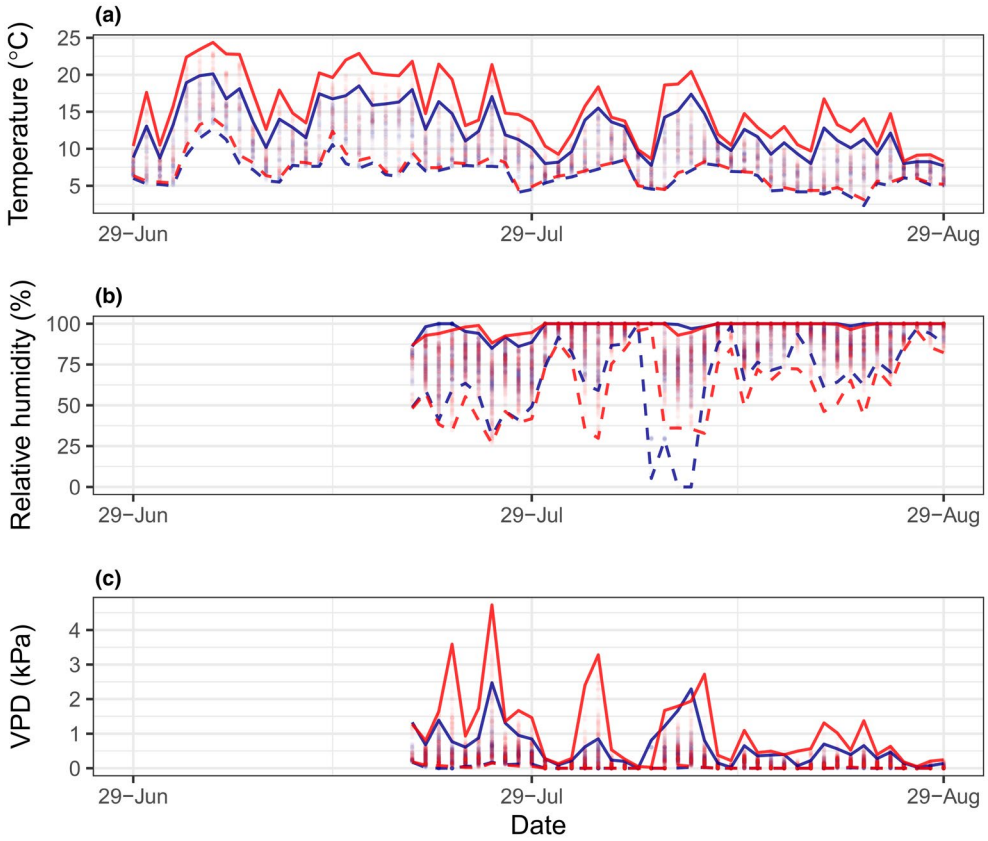


FIGURE 2 (a) Temperature (°C). (b) relative humidity (%). (c) and vapour pressure deficit (VPD; kPa) recorded inside (red lines) and outside (blue lines) OTCs. Solid and dashed lines represent maximum daily values and minimum daily values, respectively. Points show individual measurements recorded every 15 min.

### 3.2 | Thallus morphological comparison

Thalli of *C. delisei* bleached in response to the OTC treatment. Treated thalli were visually less brown than those sampled from outside chambers (Figure 3; Figure S2), with sections of thalli from OTCs showing strong decreases in the abundance of live green algae and less homogeneous distributions of cells (Figure 3; Figure S2).

### 3.3 | Light responses

Light response curves showed a typical response for high light environments, saturating at a PPFD of around 750 µmol photons $m^{-2} s^{-1}$ (Figure S3). After 9 years of treatment, light responses remained unchanged, with no differences in LSP values across temperatures between control and treatment samples (Table S3 and Figure S4; estimate = −36.37, SE = 67.92, $t = -0.54$, $p = 0.595$).

### 3.4 | Temperature responses

The shape of the curve for the responses of NP to temperature was similar for both control and treatment samples. NP curves for control and treatment samples increased from 0°C, peaked at optimal temperature (11.6°C for control and 12.5°C for treatment), above which NP declined (Figure 4a, Tables S4 and S5). The absolute rate of NP, however, was significantly higher for the control samples, at least up to 23°C, when both curves started to overlap (Figure 4a; Table S4). Moreover, NP rates for control samples yielded positive NP throughout the experiment, while this was only the case over a narrower temperature range for the treatment samples (1.1–23.9°C; Figure 4a). Temperature responses are summarized in Figure 4a and Table S5. Mean $NP_{max}$ estimates were significantly higher for the control samples than the treatment samples (2.398 µmol photons $g^{-1} s^{-1}$; 95% CI: 2.043–2.398 and 0.981 µmol photons $g^{-1} s^{-1}$; 95% CI: 0.595–1.574, respectively). Similarly, $T_{breadth}$ was also significantly higher for control samples than for treatment samples (13.4°C, 95% CI: 12.3–15.3 and 10.2°C, 95% CI: 9.1–11.9, respectively), as was $T_{tol}$ (30°C, 95% CI: 26.9–34.1 and 22.8°C, 95% CI: 20.1–26.3, respectively). In contrast, $CT_{min}$ was significantly lower for control samples than treatment samples (−6.3°C, 95% CI: −1.7–−3.4 and 1.1°C, 95% CI: 0.0–2.5, respectively). $T_{opt}$ did not differ between control and treatment samples (11.6°C, 95% CI: 10.3–12.5 and 12.5°C, 95% CI: 10.9–14.9, respectively), and $CT_{max}$ was also the same for control and treatment samples (26.5°C, 95% CI: 24.9–28.1 and 23.9°C, 95% CI: 21.3–28.9, respectively). The response of maximum DR to temperature showed an increasing exponential

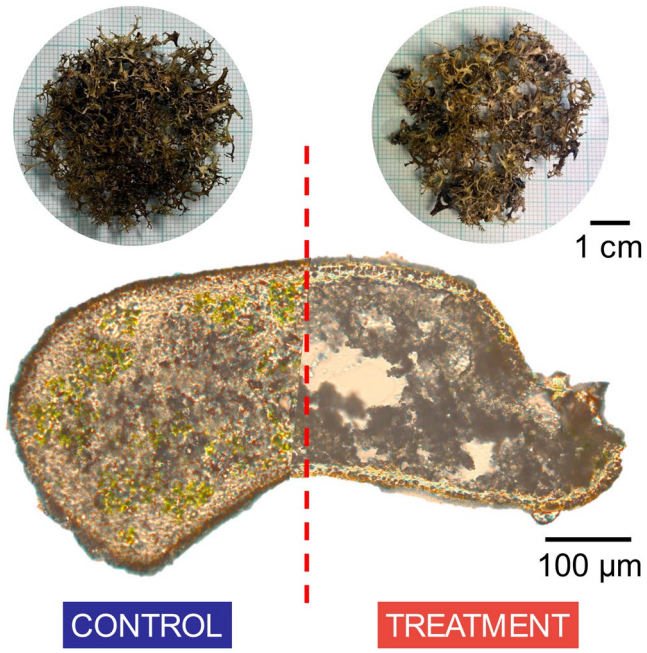


FIGURE 3 Macro- (top) and microscopic (bottom) comparison of *C. delisei* thalli sampled from outside (left) and inside (right) OTCs showing that treated thalli had a paler outer cortex than control specimens, which were browner. Thallus sections (bottom) showing that treated lichens lost most of their algal photobionts from their tissues (bleaching), and the outer cortex is paler compared to control samples.

trend with increasing temperature for both control and treatment groups (see mean estimate and 95% CI in Figure 4b and Table S4), with mean estimates reaching maximum values of 4.43 μmol photons $g^{-1}s^{-1}$ (95% CI: 3.61–5.24) for control samples and 6.31 μmol photons $g^{-1}s^{-1}$ (95% CI: 5.77–6.47) for treatment samples at 25°C (Figure 4b). From 6°C onwards, the mean DR rate for treated samples was consistently higher than that of control samples (Figure 4b).

### 3.5 | Carbon use efficiency at peak NP

The response of CUE to temperature differed strongly between the control and treated samples. For the former, CUE exceeded 50% at temperatures ≤15°C but declined to 14%–38% at ≥20°C. For the treated samples, CUE was <50% at all temperatures except 10°C, at which CUE peaked (Figure 5).

### 3.6 | Photobiont-to-mycobiont ratio and chlorophyll concentration

Treated samples had a significantly reduced proportion of photobiont to mycobiont compared with control samples (estimate = −8.94, SE = 2.53, $t = -3.53$, $p = 0.009$; $n = 4$ for control and $n = 4$ for treatment; Table S6). The mean proportion of photobiont in the thallus for control samples was 13.96%, as opposed to 5.03% for treatment samples. We found a significant reduction in mean (±SE) chlorophyll concentration in treatment compared with control samples (86.05 ± 7.68 and 123.12 mg $g^{-1}$ ± 4.23, respectively; $t = 4.35$, $p < 0.001$; $n = 10$ for control and 9 for treatment).

## 4 | DISCUSSION

Our results indicate that 9 years of passive warming with OTCs in the High Arctic caused the lichen *C. delisei* to bleach and exhibit signs of dysbiosis, which were manifested in multiple physiological changes. Three lines of evidence indicate the breakdown of the symbiosis. Firstly, carbon uptake rates were lower for experimentally warmed thalli. Secondly, no signs of thermal acclimation of respiration were recorded for treated thalli, resulting in significant carbon loss. Thirdly, treated thalli had lower chlorophyll concentrations and lost a significant amount of their photobionts. This deterioration of symbiosis bears remarkable similarities to coral bleaching processes, which are associated with the loss of photobionts (Helgoe et al., 2024). Our study advances current understanding of lichen responses to experimental warming by showing that photobionts are apparently highly sensitive to increases in mean and maximum daily summertime air temperatures of 1–4°C.

### 4.1 | Evidence of dysbiosis from unbalanced photosynthesis and respiration rates

Thermal acclimation to long-term warming, which is well documented in higher plants (Atkin & Tjoelker, 2003; Zhou et al., 2007), could have occurred in *C. delisei* through increases in photosynthetic rates (Schipperges et al., 1995), or downregulation of respiration rates to a new thermal optimum (Colesie et al., 2018; Lange & Green, 2005). However, we observed no sign of thermal acclimation as the physiological optima ($T_{opt}$) did not shift with warming (Figure 4a). Instead of acclimation, NP rates and $NP_{max}$ were lower for treated than control thalli across all temperatures (Figure 4a). Rather than acclimatizing by downregulation, the respiration rates of treated samples increased exponentially from 6°C onwards (Figure 4b), a pattern that has also been observed in other lichen experimental warming studies (e.g. Colesie et al., 2018; Meyer et al., 2022; Williams et al., 2017). This rise may reflect thermal stress-induced respiration (Kappen & Lange, 1972; Kraft et al., 2022; Williams et al., 2017), though whether it remains an active stress response after 9 years is unclear. Still, no thermal acclimation of lichens was reported in previous studies in diverse ecosystems, including Antarctica (Bokhorst et al., 2016; Colesie et al., 2018), temperate continental regions (Meyer et al., 2022) and warm arid environments (Ferrenberg et al., 2015; Maphangwa et al., 2012; Pirintsos et al., 2011). Nonetheless, it was surprising not to see any thermal acclimation of respiration as reported by Lange and Green (2005). However, as the heterotroph in the relationship, the mycobiont does not theoretically gain any advantage

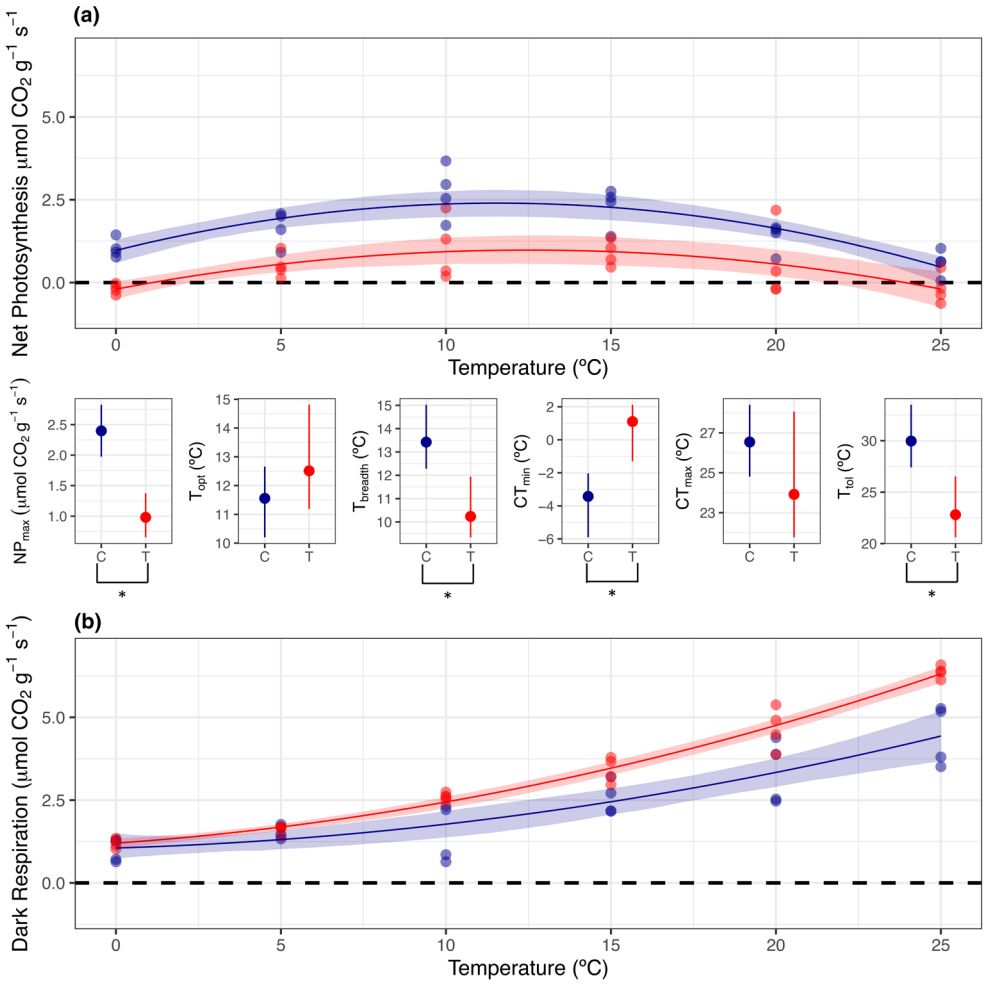


FIGURE 4 Treatment samples (red lines and symbols or T; $n = 4$ at each temperature) showed decreased NP performance, and higher DR values compared to control specimens (blue lines and symbols or C; $n = 4$ at each temperature). (a) Treatment samples showed deterioration of photosynthetic parameters but no shift in optimal temperature ($NP_{max}$ = maximum photosynthesis; $T_{opt}$ = thermal optimum; $T_{breadth}$ = thermal breadth; $CT_{min}$ = critical minimal temperature; $CT_{max}$ = critical maximal temperature; $T_{tol}$ = thermal tolerance). Asterisks below individual figures represent significant differences between the variables. (b) DR increased exponentially with temperature. The relationship was steeper for treatment samples. Points show measured values of NP or DR, solid lines represent the mean model fit, and the associated bands represent 95% confidence intervals.

through the downregulation of respiration (Hartley et al., 2007). Lower or complete inhibition of respiration could also result from extreme temperature stress or functional death (Meyer et al., 2022; Osyczka & Myśliwa-Kurdziel, 2024), complicating the interpretation of thermal responses in experimental treatments.

The treated samples also lost the ability to effectively photosynthesize at lower temperatures (see $CT_{min}$ in Figure 4a), without compensatory gains at higher temperatures (see $T_{breadth}$ and $CT_{max}$ in Figure 4a). Carbon uptake of these samples was insufficient to offset respiration below 1.1°C and above 23.9°C, leading to negative NP (Figure 4a). In practice, the narrower $T_{breadth}$ and $T_{tol}$ of these samples limits their operational temperature range compared to controls. Having a narrower thermal tolerance could be especially harmful when carbon uptake is limited by non-optimal light conditions in colder periods. *C. delisei*, alongside other lichens, is known to often operate at sub-optimal light conditions such as under spring snow and temperatures below 0°C (Raggio et al., 2016; Schroeter et al., 2000; Uchida et al., 2006). Therefore, losing the ability to effectively photosynthesize at low temperatures negatively affects the overall carbon budget of the lichen, by limiting its ability to acquire carbon during periods of lower respiration outside the winter months.

The imbalance between respiration and photosynthesis was further evident in the CUE results (Figure 5). For treatment samples, CUE remained below 50% (except at 10°C), indicating that carbon loss through respiration dominated over photosynthesis. Since low CUEs generally mean reduced carbon stabilization (Manzoni et al., 2012), the treatment samples lost more carbon than they gained. Accordingly, control samples maintained CUEs of ~70%, at least at 0–10°C, but temperatures above ~17°C resulted in CUEs below 50% (Figure 5). This observation indicates that optimal carbon partitioning is linked to temperature. This is expected, since higher

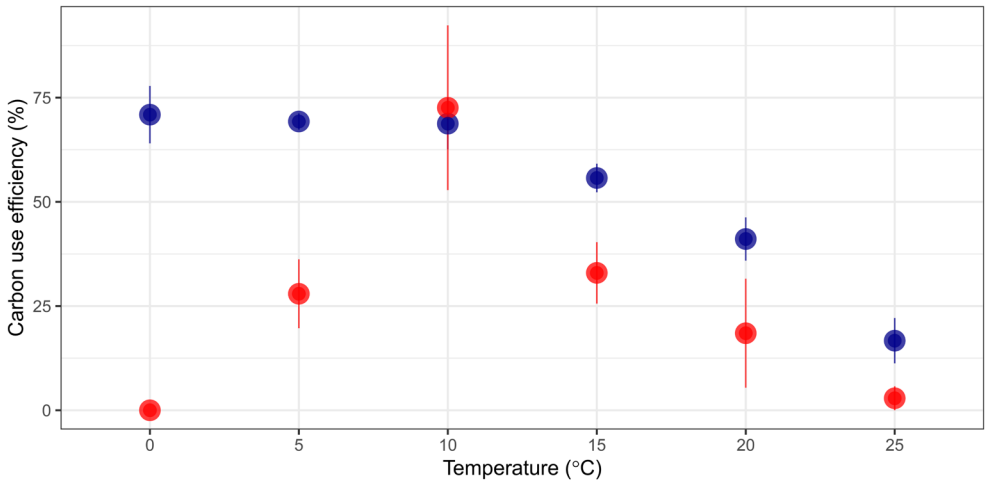


FIGURE 5 Carbon use efficiency (%) of control (blue circles) and treatment (red circles) samples at 0–25°C. Note that photosynthesis and respiration dominate when CUE is higher than and less than 50%, respectively. Control samples showed a CUE response favouring photosynthesis from 0 to 15°C, which fell below 50% at 20–25°C, favouring respiration, whereas treatment samples only functioned well around an optimal temperature of 10°C. Values are means ± SE ($n = 4$). Samples that did not reach a positive NP were assigned to 0%.

than optimal temperatures reduce CUE due to disproportionately increased respiration (Gemal et al., 2022; Manzoni et al., 2012). For mosses, other studies have found CUE to be 62%–81% in the sub-Arctic (Street et al., 2013) and ~70% at optimal temperature in the Antarctic (Gemal et al., 2022).

The impaired physiological balance between photosynthesis and respiration is owing to both photobiont and mycobiont. Since NP declined in treatment samples at 0–5°C while respiration did not differ (Figure 4), the reduction stems from impaired photosynthesis. At higher temperatures (15–25°C), the imbalance of CUE was driven by increased respiration (Figures 4 and 5), hence the mycobiont's inability to acclimatize. Altogether, the lack of thermal acclimation and the divergence between photosynthetic and respiratory responses reinforce the onset of dysbiosis, the decoupling of the symbiotic relationship as partners display distinct ecophysiological thresholds and thermal sensitivities.

## 4.2 | Algal loss and chlorophyll degradation as additional evidence for dysbiosis

Although lichens can respond to changes in temperature by adjusting their photobiont-to-mycobiont ratio (Domaschke et al., 2013; Sun & Friedmann, 2005; Tretiach et al., 2013) and chlorophyll concentration (MacKenzie et al., 2001), our results indicate that such an adjustment did not occur, and that instead both photobiont-to-mycobiont ratio and chlorophyll concentration decreased in treated thalli. These could be the first signs of lichen bleaching because both parameters generally correlate with the photosynthetic capacity of lichen thalli (Domaschke et al., 2013). Similar losses of chlorophyll or photosynthetic efficiency following warming have been recorded in other studies (Colesie et al., 2018; Meyer et al., 2022; Pirintsos et al., 2011; Pisani et al., 2007). Visually, the loss of the algal symbiont was also documented through microscopy (Figure 3). Although differing in their exposure times and warming magnitude, other studies have similarly documented the visual loss of algae from lichen thalli as a result of long periods under snow (Benedict, 1990; Bokhorst et al., 2016), warming treatments (Bokhorst et al., 2016; Colesie et al., 2018; Meyer et al., 2022) or transplantation (Williams et al., 2017). In these studies, photobiont loss, recorded as either a decrease in the proportion of photobiont to mycobiont or chlorophyll content, seems to be a common endpoint for temperature-stressed lichens, but whether photobiont loss occurs or not likely depends on the severity of the temperature increase as well as the active exposure duration.

An alternative explanation for the loss of chlorophyll and photobionts could be a change in light exposure due to the OTCs. Depending on the material used, OTCs can, for example, screen UV light and have significant shading effects on lichens and plants, resulting in shade adaptation (Gemal et al., 2022). However, in the present study, light levels in OTCs and control plots were not significantly different, and LSPs did not differ between treated and control samples (Table S3), suggesting that light limitation was not a major factor causing the physiological changes to the lichen. Furthermore, UV radiation was partially screened by the OTCs, not enhanced, and hence, UV-driven chlorophyll degradation (Gauslaa & Solhaug, 2000) is unlikely to explain the bleaching observed in chambered lichens. Additionally, shading typically leads to an increase, not a decrease, in photobiont abundance and chlorophyll content in lichens (Gauslaa & Solhaug, 1996), further reducing the likelihood that reduced UV exposure caused the observed loss of photobionts.

Interestingly, the mycobiont also exhibited signs of pigmentation changes, with the outer cortex of treated thalli appearing paler than that of thalli sampled from outside the OTCs (Figure 3). Although

we have no quantitative measurements of cortex pigmentation, this likely reflects a reduction in brown melanin pigments. Melanin serves as protection against UV damage and its production is stimulated by UV exposure (Solhaug et al., 2003). We offer two potential explanations for this pigment reduction. Firstly, OTCs may have reduced UV exposure, lowering the need for photoprotection and thus melanin production. Secondly, pigment reduction could result from impaired melanin production or its degradation following carbon starvation. Melanin synthesis is energetically expensive, and lichens are known to degrade sun-screening pigments such as usnic acid to access additional energy under stressed conditions (Beckett et al., 2015). Similarly, reductions in other protective pigments, such as carotenoids, have been observed after lichen transplantation to warmer environments (Pirintsos et al., 2011). However, the precise cause of the observed cortex paling remains unclear and further experimental studies are needed to confirm the underlying mechanisms responsible for this morphological response. Importantly, because the physiological response to light did not differ significantly between the treatment and the control, any potential OTC-related light effects were either minimal or masked by other factors. Consequently, the consistent differences observed between treated and control thalli are more likely to have been driven by temperature effects rather than changes in light conditions.

### 4.3 | Potential drivers of observed change

Over 9 years of exposure to elevated temperatures and increased VPD, *C. delisei* may have gradually depleted its carbon reserves through several interacting mechanisms. The most likely mechanism is through increased respiratory losses during winter and spring when lichens are light-limited (Bokhorst et al., 2016). OTCs may increase snow trapping and induce warmer conditions (Bokhorst et al., 2016). All lichen samples had a negative carbon balance under low light in cold conditions (see LRCs in Figure S3), hence, they would have lost energy when light limited. Therefore, if dormancy was interrupted under snow or at times of low light conditions, gradual depletion of carbon reserves of treatment samples might have happened through increased respiratory losses under warmer conditions. In addition, earlier snowmelt outside the OTCs may have allowed control lichens to resume photosynthesis sooner than those within the treatment plots, limiting time for carbon fixation (Benedict, 1990; Bokhorst et al., 2016). Secondly, the 51% increase in mean VPD induced by OTCs during summer (Figure 2, Table S2) could have shortened windows for possible photosynthesis, despite otherwise favourable light conditions (Raggio et al., 2016). As the physiological activity of *C. delisei* on the Brøgger Peninsula ceases quickly after rainfall due to rapid desiccation (Uchida et al., 2006), higher VPD likely accelerated drying, reducing active periods for carbon fixation even when light conditions were optimal (Colesie et al., 2018; Ferrenberg et al., 2015; Maphangwa et al., 2012; Meyer et al., 2022; Raggio et al., 2016). Thirdly, a limited capacity for thermal acclimation likely complemented carbon starvation (Colesie et al., 2018; Meyer et al., 2022). Thermal acclimation can occur rapidly (*c.* 14 days; Colesie et al., 2018), but the organism needs to actively experience new conditions. Reduced periods of hydration and activity under warmer summer conditions may have prevented gradual acclimation, limiting an adjustment of photosynthetic efficiency to match increased respiratory demands. Together, these processes likely contributed to the carbon starvation and physiological stress observed in *C. delisei*, which were manifested in dysbiosis and bleaching.

### 4.4 | Lichen bleaching in a warmer Arctic

Our study highlights the vulnerability of a dominant Arctic lichen to increases of 1–4°C in mean and maximum daily summertime air temperatures. Given the 1.7°C decade$^{-1}$ rise in air temperature recorded on Svalbard between 1991 and 2018 (Nordli et al., 2020), and the important role of *C. delisei* and other fruticose lichens, such as *Flavocetraria nivalis*, *Cetraria islandica*, *Alectoria nigricans* and *Cladonia* spp., in the diet of the most abundant vertebrate herbivore on the archipelago (Cooper & Wookey, 2001), our observations indicate that rapidly rising air temperatures could have significant implications for Arctic terrestrial food webs. As for coral bleaching under thermal stress (Helgoe et al., 2024), lichen bleaching apparently arises from a lack of acclimation due to a disruption in carbon balance between energy input and expenditure. We suggest a definition of lichen bleaching as a dysbiosis state marked by photobiont loss, with measurable impacts on physiology and survival. Insights from coral research, particularly mechanisms of algal loss following stress events, may inform our understanding of lichen bleaching. For example, whether carbon starvation in lichens triggers algal loss through parasitism or 'mycoaggressions' by the mycobiont via mechanical or chemical means (Bokhorst et al., 2016; Gannutz, 1970; Sanders, 2023; Williams et al., 2017) as observed in corals (for review of symbiophagy see Helgoe et al., 2024) remains to be experimentally tested and should be the focus for future research.

Future climate projections for Svalbard and the Arctic indicate continued rising temperatures (Rantanen et al., 2022) and a shift in precipitation patterns toward a higher rain-to-snow ratio (Bintanja & Andry, 2017; Hanssen-Bauer et al., 2019). Since lichens are strongly affected by the interactions between temperature, light and hydration patterns, it is vital to establish more long-term in situ acclimation studies with integrated physiological activity, microclimate and gas exchange measurements (Raggio et al., 2023). Knowing under which abiotic conditions the lichen is metabolically active and loses or gains carbon over the long term is essential because lichens may enter dormancy under extreme conditions such as heatwaves (Osyczka & Myśliwa-Kurdziel, 2024). Plus, quantifying how much carbon is lost during increased rainfall events during light-limited warmer periods is vital as it can intensify carbon starvation and cause increased mortality (Gauslaa, 2023). Finally, further acclimation studies across the Arctic are necessary to determine whether lichen responses are universal or species-specific, as some species may exhibit greater

acclimation potential than others (Bokhorst et al., 2016; Colesie et al., 2018; Stanton et al., 2023).

Thus far, lichen decline in the Arctic has been attributed mainly to competition from expanding vascular plants (e.g. Cornelissen et al., 2001; Fraser et al., 2014; Lang et al., 2012). Our findings, however, show that abiotic changes alone, through direct physiological impacts such as increased temperature and VPD, can drive lichen dysbiosis independently of vascular plant competition. Arctic lichens may be more vulnerable to bleaching from carbon starvation as they might have fewer opportunities for acclimation than lichens from lower latitudes because of long dormancy periods. Even if summertime acclimation occurs, activation triggered by warmth or rain-on-snow events during winter could drive overall carbon respiration losses without any opportunity for photosynthesis, although this link remains hypothetical and requires further study. If these negative responses are widespread across lichen taxa and biomes, the resulting declines could impair ecosystem services, including habitat and food provision for herbivores, soil stabilization or carbon and nitrogen sequestration (Asplund & Wardle, 2017).

## AUTHOR CONTRIBUTIONS

Jiří Šubrt conceived the initial idea, designed the methodology, collected samples, performed laboratory analyses and wrote the manuscript. Mariana García Criado provided supervision and comments for shaping the analyses and the manuscript. Kevin K. Newsham set up and maintained the field experiment, deployed loggers and conducted fieldwork. Claudia Colesie conceived the initial idea, designed the methodology, performed laboratory analyses, collected samples and provided supervision. All authors contributed to the drafts, comments and gave approval for publication.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data and code for this study are freely available to download at https://zenodo.org/records/19484347 (Šubrt, 2026) and https://github.com/JiriSubrt/Lichen_bleaching_OTC_paper.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Figure S1.** Desiccation curves used to extract peak NP and DR values to construct temperature response curves. Note that the top four rows are control samples and the bottom four rows are treatment samples. Green and brown lines represent NP and DR measurements, respectively, and each point represents one measurement. Plots show assimilation (*y*-axis) over time in minutes (x-axis).

**Figure S2.** (a) Photos of lichens showing that treatment samples (on red background) bleached compared to control samples (on blue background). (b) Sections of thalli showing that control samples contain more algal photobiont in their tissues, and have a browner outer cortex than treatment samples.

**Figure S3.** Light response curves across a temperature gradient from 0 to 25°C. Control samples are shown in blue, and treatment samples in red. Net photosynthesis was measured at irradiances of 0, 25, 50, 100, 200, 400, 600, 800, 1000 and 1200 μmol photons $g^{-1}s^{-1}$. Curves were fitted using standard least-squares non-linear regression. The *y*-axis intercept at NP of 0 μmol $g^{-1}s^{-1}$ represents a line below which NP is negative. Light response curves showed a weaker photosynthetic response for treatment samples.

**Figure S4.** Breakdown of light saturation points (the irradiance, measured in μmol photons $m^{-2}s^{-1}$, at which additional increases in light do not increase photosynthetic rate) extracted from light response curves ($n = 4$ per temperature). Panels show light saturation points at temperatures of 0, 5, 10, 15, 20 and 25°C.

**Table S1.** Microclimate summary (means ± standard errors) for surface temperature, surface relative humidity, VPD, and light levels, measured outside (control) and inside (treatment) the OTCs. Wilcoxon rank tests were performed as data were not normally distributed, except for light levels, where a Student's *t*-test was performed.

**Table S2.** Maximum and minimum values of surface air temperature, relative humidity and vapour pressure deficit measured from 20 July–30 August 2023 (RH and VPD) and 29 June–30 August 2023 (temperature).

**Table S3.** Model output from a linear mixed effect model with a random effect of temperature, exploring the effect of OTCs on light saturation points.

**Table S4.** Estimated means and 95% confidence intervals for extracted bootstrapped parameters from temperature response curves for net photosynthesis. Treatment and control samples were collected from inside and outside OTCs, respectively. $n = 4$ for each group.

**Table S5.** Estimated means and 95% confidence intervals for extracted bootstrapped parameters from temperature response curves for net photosynthesis. Treatment and control samples were collected from inside and outside OTCs, respectively. $n = 4$ for each group.

**Table S6.** Model output from a linear mixed effect model with a random effect of sample (due to multiple measurements on individual samples), exploring the effect of OTCs on the proportion of photobiont to mycobiont (percentage algal cell cover in thallus section).

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