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Can Antarctic lichens acclimatize to changes in temperature?

Claudia Colesie[1] | Burkhard Büdel[2] | Vaughan Hurry[1] | Thomas George Allan Green[3,4]

[1]Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, Umeå, Sweden

[2]Department of Plant Ecology and Systematics, University of Kaiserslautern, Kaiserslautern, Germany

[3]Departamento de Biologia Vegetal II, Facultad de Farmacia, Universidad Complutense, Madrid, Spain

[4]Department of Biological Sciences, University of Waikato, Hamilton, New Zealand

Correspondence
Claudia Colesie, Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, Umeå, Sweden.
Email: Claudia.colesie@googlemail.com

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Abstract

The Antarctic Peninsula, a tundra biome dominated by lichens and bryophytes, is an ecozone undergoing rapid temperature shifts. Such changes may demand a high physiological plasticity of the local lichen species to maintain their role as key drivers in this pristine habitat. This study examines the response of net photosynthesis and respiration to increasing temperatures for three Antarctic lichen species with different ecological response amplitudes. We hypothesize that negative effects caused by increased temperatures can be mitigated by thermal acclimation of respiration and/or photosynthesis. The fully controlled growth chamber experiment simulated intermediate and extreme temperature increases over the time course of 6 weeks. Results showed that, in contrast to our hypothesis, none of the species was able to down-regulate temperature-driven respiratory losses through thermal acclimation of respiration. Instead, severe effects on photobiont vitality demonstrated that temperatures around 15°C mark the upper limit for the two species restricted to the Antarctic, and when mycobiont demands exceeded the photobiont capacity they could not survive within the lichen thallus. In contrast, the widespread lichen species was able to recover its homoeostasis by rapidly increasing net photosynthesis. We conclude that to understand the complete lichen response, acclimation processes of both symbionts, the photo- and the mycobiont, have to be evaluated separately. As a result, we postulate that any acclimation processes in lichen are species-specific. This, together with the high degree of response variability and sensitivity to temperature in different species that co-occur spatially close, complicates any predictions regarding future community composition in the Antarctic. Nevertheless, our results suggest that species with a broad ecological amplitude may be favoured with on-going changes in temperature.

KEYWORDS
Antarctica, biological soil crusts, climate warming, lichen, net photosynthesis, thermal acclimation, *Usnea aurantiaco-atra*

1 | INTRODUCTION

The rates at which organisms process carbon and nutrients via biogeochemical cycling, photosynthesis (P) and respiration (R) are temperature sensitive. Understanding the biological mechanisms that regulate carbon exchange rates and their response to climate change is among the most urgent scientific challenges for ecosystem ecologists to assess terrestrial carbon cycle–climate feedbacks (Bardgett, Freeman, & Ostle, 2008). Many ecophysiological studies have addressed the question of how the absolute rates, and the balance between P and R, will change in response to climate change (e.g. Atkin et al., 2015; Drake et al., 2016; Karhu et al., 2014; Wang et al., 2014). It is known that the increases in temperature will directly affect photosynthesis and respiration and, traditionally,

simplified climate models have assumed that both will rise exponentially with short-term changes in temperature (King, Gunderson, Post, Weston, & Wullschleger, 2006), generating a positive climate-ecosystem carbon feedback (Davidson & Janssens, 2006) with the potential to accelerate climate warming by up to 1.4 times (Cox, Betts, Jones, Spall, & Totterdell, 2000). In recent years, studies on vascular plants are leading to a re-evaluation of the model assumptions because many plants show physiological, structural and biochemical adjustments that mitigate the effects of temperature increases (Körner, 2006; Vanderwel et al., 2015). This effect is referred to as thermal acclimation (Davidson & Janssens, 2006; Luo, Wan, Hui, & Wallace, 2001; Oechel et al., 2000). Acclimation of R to colder growth temperatures results in increased respiratory CO_2 release measured at a chosen standard temperature (RmT). Conversely, acclimation to high growth temperature results in lower RmT (Atkin, Bruhn, Hurry, & Tjoelker, 2005). Understanding and characterising the ecophysiological response of major contributors to ecosystem respiration is highlighted as an essential research priority to help predict accurately how warming will affect carbon efflux across different ecosystems (Heinemeyer et al., 2012). There is sound documentation of thermal acclimation for vascular plants (e.g. Reich, Tjoelker, Machado, & Oleksyn, 2006), their mycorrhizal symbionts (Heinemeyer, Ineson, Ostle, & Fitter, 2006) and free-living ectomycorrhizal fungi grown in agar (Malcolm, López-Gutiérrez, Koide, & Eissenstat, 2008). For heterotrophic soil microbes, the topic is controversial (Carey et al., 2016; Crowther & Bradford, 2013; Min, Lehmeier, Ballantyne, & Billings, 2016).

While these better understood global carbon players (vascular plants and their mycorrhizal symbionts) have a major role in wet, moist and temperate terrestrial biomes, 35% of the Earth`s land mass is permanently or seasonally arid (accounting for the largest terrestrial biome, Peel, Finlayson, & McMahon, 2007) and vascular plants are excluded or diminished by low water availability or low temperatures. These environments are often dominated by biological soil crusts (BSC, Pointing & Belnap, 2012). These inconspicuous communities, composed of several poikilohydric organisms (lichens, bryophytes, cyanobacteria, algae, bacteria and microfungi) have only recently been described to make a small but significant (equal to annual anthropogenic carbon input) contribution to global CO_2 uptake (Elbert et al., 2012; Porada, Weber, Elbert, Pöschl, & Kleidon, 2014). The habitats that are dominated by BSC, hot and cold deserts, drylands, badlands, polar regions (Belnap, Weber, & Büdel, 2016; Pointing & Belnap, 2012) are also suggested to be the first, and most severely affected, by predicted temperature increases (IPCC report, 2014).

Lichens are a key component in late successional stage BSC (Rosentreter, Eldridge, Westberg, Williams, & Grube, 2016). Compared to other BSC components, their proportionate biomass is high so that the ecophysiological response of a soil-crust lichen can be considered an appropriate proxy for the response of the entire crust (Lange, 2003). Lichens are fungi (mycobiont) symbiotic with photosynthetic green algal or cyanobacterial partners (photobiont). The mycobiont composes the major part of the lichen and contributes the majority of the respired CO_2. In instantaneous measurements of lichen CO_2 exchange, the respiration increases exponentially with increasing temperature, whilst gross photosynthesis increases up to about 30°C before beginning to decline. As a consequence, lichen *net* photosynthesis has an optimal temperature above which further increases in respiration depress net carbon gain, and it has been shown that net CO_2 exchange can become negative at moderately elevated temperatures (Green & Lange, 1994). Lethal temperatures for photosynthesis in active, hydrated lichens are not high, usually around 30–35°C (Chiarucci, Calderisi, Casini, & Bonini, 2008; Lange, 1965; Maphangwa, Musil, Raitt, & Zedda, 2014; Smith, 1981).

Because lichens, as poikilohydric organisms, often become hydrated overnight due to dew, fog or rain, the ecophysiological response to increased temperatures overnight are of special interest. While night-time hydration at *moderate* temperatures stimulated growth and resulted in thallus extension (Bidussi, Gauslaa, & Solhaug, 2013), it has been suggested that being hydrated during *warm* nights results in exceptionally poor carbon balance and that this may exclude lichens from some habitats (Lange, 2000). However, these assumptions are only valid if the instantaneous responses of P and R remain stable with respect to temperature and no acclimation occurs to mitigate these effects.

To date, the processes that underpin acclimation to increasing temperature are poorly understood for BSC communities and lichens (Green & Proctor, 2016). Larson and Kershaw (1975) reported species-specific acclimation with some species showing seasonal changes in the net photosynthetic (NP) capacity with constant respiration and others responding in a manner similar to the process of cold hardening found in higher plants (Larson & Kershaw, 1975). Therefore, the responses of the two processes (NP and R) should be considered separately to better understand the lichens response to changing climate. Although NP and R have different temperature sensitivities, both processes have been described to acclimate with changing seasons under natural conditions (Lange & Green, 2005; MacKenzie, MacDonald, Dubois, & Campbell, 2001). While acclimation of lichen R seems to be species-specific and can show full acclimation to temperature (Lange & Green, 2005), seasonal acclimation of lichen NP (electron transport rate and gross photosynthesis) is triggered by two factors, temperature and light availability (MacKenzie et al., 2001). The underlying physiological mechanisms are yet to be understood, and the response of lichens to environmental change is additionally confounded by their longevity through many seasonal cycles and by their slow growth rates (Lindsay, 1973; Sancho, Green, & Pintado, 2007).

In polar regions, lichens form a major part of the vegetation and are dominant in biological soil crusts (Williams, Borchhardt, et al., 2017; Figure 1a). Here, studies emphasising acclimation processes and the corresponding risk assessment are expected to be particularly useful because colder climates are considerably more responsive to increased ambient temperatures compared with warmer regions (Carey et al., 2016). The Antarctic Peninsula, especially, serves as an early warning system in understanding species and ecosystem responses to climate change because it recently experienced

FIGURE 1 Study site and lichen species. (a) Overview of the vegetation near Juan Carlos 1 Base, on Livingston Island. (b) *Stereocaulon alpinum* in natural appearance, Glove as scale. (c) *Usnea aurantiaco-atra*. (d) *Placopsis contortuplicata*

relatively fast regional climate changes (Turner et al., 2014). At present, temperatures are, at least temporary, declining (Turner et al., 2016) and this complicates the already complex response of the local biodiversity to a changing climate (Convey, 2011), for example, through "snowkill" as an additional threat to local lichen populations (Sancho et al., 2017). An important aspect of recent climate change scenarios overall is the increasing frequency of extreme events such as heat waves (>5°C above daily temperature for at least 5 consecutive days) (IPCC report, 2007). Such infrequent warming events might have significant and long-lasting impacts on local communities (Walther et al., 2002). In the Antarctic, for example, the extraordinarily warm summer 2001–2002 in Taylor Valley, continental Antarctica, had a disproportionally large impact on the local invertebrate community (Courtright, Wall, & Virginia, 2001), and provides a case study for projecting how above- and below-ground ecosystems may respond in the future (Wall, 2007). The most drastic change from this warming event was water availability, with significant influences that persisted for several years (Barrett et al., 2008). This demonstrates the strong interconnection between the thermal and the hydric environment in the Antarctic and underlines the need for accurate experimental testing and monitoring.

This study aims to describe potential acclimation processes of R and NP to changing temperatures in polar lichens with special regard to differences in thermal acclimation within these symbiotic organisms. To isolate the temperature effect, we chose an experimental approach that allows maximum control and monitoring of conditions (water availability, light regime). The two following hypotheses are tested:

1. Lichens show thermal acclimation of respiration in a manner similar to patterns known from vascular plants, mitigating the effects of higher temperatures, while photosynthetic rates and the lichen thallus morphology remain more or less unaffected.
2. The degree of acclimation and the rates at which lichens acclimate to new temperatures will be species-specific. We expect species with broader distribution patterns and ecophysiological amplitudes to acclimate both faster and more complete, than species with very specific physiological adjustments to their surrounding environment.

2 | MATERIALS AND METHODS

2.1 | Species selection

We chose three different lichen species collected on Livingston Island in the maritime Antarctic. The lichens were selected to cover a variety of different growth forms, distribution patterns and photobionts with possible differences in their individual acclimation potential. For example, a cyanobacterial photobiont might contribute to a lichen's ability to adapt to temperature, as shown for the tropical lichen *Dictyonema glabratum* (Lange, Büdel, Zellner, Zotz, & Meyer, 1994), the epilithic lichen *Peltula capensis*, from South Africa (Wessels & Kappen, 1993) and *Collema tenax*, a typical soil-crust lichen in arid lands (Lange, Belnap, & Reichenberger, 1998). Because of the low photobiont diversity in the Antarctic, both for green algal photobionts (Domaschke, Fernández-Mendoza, A. García, Martín, & Printzen, 2012) and cyanobionts (Wirtz et al., 2003), we distinguish between these two functional groups rather than specific photobiont strains. To minimize covariation, each of the three traits (growth form, distribution pattern, photobiont) overlapped within two of the selected lichen species.

Stereocaulon alpinum Laurer is a member of the group of circumarctic-alpine lichens that are found bipolar and also in the alpine environments of the temperate regions (Øvstedal & Smith, 2001). *Stereocaulon alpinum* also occurs in the dry cool boreal zone, where mean summer temperature reaches up to 13.8°C (Coxson & Marsh, 2001). *Stereocaulon alpinum* is a fruticose lichen (Figure 1b), circa 5–7-cm high, with cephalodia that contain cyanobacteria of the genus *Nostoc* as an additional cyanobiont, in addition to the trebouxioid primary

green algal photobiont. Due to its broader distribution and its tripartite composition, this lichen is considered to have a relatively wide ecological amplitude. *Usnea aurantiaco-atra* (Jacq.) Bory is a dominant component in vegetation communities of the maritime Antarctic and Alpine subantarctic regions (Øvstedal & Smith, 2001). *Usnea aurantiaco-atra* has a fruticose, erect growth form with many apothecia (Figure 1c). It contains a trebouxoid green algal photobiont and can be considered to be highly specialized to Antarctic climate conditions (Laguna-Defior, Pintado, Green, Blanquer, & Sancho, 2016). *Placopsis contortuplicata* I. M. Lamb, in contrast to the first two species, grows foliose to effigurate (Figure 1d) but shares the feature of having cephalodia containing *Nostoc* as a cyanobiont with *S. alpinum*. The distribution of *P. contortuplicata* is restricted to the southernmost South America, the Subantarctic Islands and the Antarctic Peninsula (to at least 70°S), a distribution that it shares with *U. aurantiaco-atra*.

2.2 | Sample collection

All lichen samples were collected in January 2015 in the vicinity of Juan Carlos I base (62°39 S; 60°23 W), which is located in the South Bay of Livingston Island, Antarctica. Mean annual temperatures are −2.8 °C with summer mean monthly temperatures above freezing, and the maximum mean monthly temperature is 4.3 °C. Mean annual precipitation is 444.5 mm, with 75% falling in summer and autumn (Bañón, Justel, Velázquez, & Quesada, 2013). The bedrock of Livingston Island is a low-grade metamorphic turbidite sequence with volcanic to volcanoclastic rocks, intruded by igneous bodies (Arche, López-Martínez, & Martínez de Pisón, 1992; Moura, Francelino, Schaefer, Simas, & de Mendonça, 2012). Besides two native flowering plant species (*Deschampsia antarctica* Desv. and *Colobanthus quitensis* (Kunth) Bartl.), 110 lichen and 50 bryophyte species have been reported from the vicinity of Juan Carlos I base (Sancho, Schulz, Schroeter, & Kappen, 1999).

Four intact thalli of each species were collected: *S. alpinum*, *U. aurantiaco-atra* and *P. contortuplicata*. Identification was based on morphological and anatomical features using appropriate determination keys (Øvstedal & Smith, 2001). Samples were dried at room temperature, frozen at −20°C and transported to the laboratory, where they were stored in the frozen state until used. Frozen storage is described as being suitable for long-term storage of lichens for experimental studies (Honegger, 2003).

2.3 | Experimental design

Because most biological processes in Antarctica operate at the scale of the organism and their microclimate, we chose temperatures that are likely to occur under natural conditions in the lichens microclimate. The overall design of this study was to incubate the lichens at three different temperatures (one control plus two treatments with elevated temperatures) and to track changes in photosynthesis and respiration rates over time. The control group is represented by a set of samples incubated at 5°C as this temperature approximates the mean temperature when the organisms are active under natural conditions (Schlensog, Green, & Schroeter, 2013). The 15 °C treatment was considered to reflect moderately "increased" temperatures as this temperature is 5°C above the recorded maximum thallus temperature when the organisms were active at Livingston Island (Schroeter, Green, Pintado, Türk, & Sancho, 2017). A 23°C treatment was chosen to reflect an "extreme" but still reasonable change. Temperatures up to 26°C were recorded as maximum thallus temperature while the organisms were active on Leonie Island, Antarctica (Schroeter et al., 2017). Our treatment aims to increase the duration of exposure to such temperature extremes to simulate a "heat wave" (De Boeck, Dreesen, Janssens, & Nijs, 2010). The treatments at the three temperatures will be referred to as control (C_5), 15 degrees (T_{15}) and 23 degrees (T_{23}). Three replicates each for the three selected species were used and, to avoid sample-dependent presetting (such as microhabitat-dependent acclimation), each thallus was divided into three parts, with each part allocated to a different temperature treatment.

After the start of the treatments, CO_2 exchange (NP, net photosynthesis and R, respiration) was measured for all lichen samples at 5, 15 and 23°C and this was repeated at 1-week intervals. A standardized label was allocated to each measured sample: for example, $C_{5,5}$ = control samples measured at 5°C, $T_{23,15}$ = samples in the 23°C treatment measured at 15°C. The aim was to detect any acclimation to the treatment temperature and the instantaneous response to the other two temperatures.

2.3.1 | Sample treatment

Prior to the experiment, the intact lichen samples underwent a reactivation procedure composed of 2 days dry storage at 4°C in the dark and 24 h at 4°C and 200 μmol photons m^{-2} s^{-1}, before they were divided and fixed in CO_2-inert wire-mesh baskets. This procedure was found to be suitable for previous gas exchange studies on polar lichens and biological soil crusts (Colesie, Green, Haferkamp, & Büdel, 2014) and removes problems of water condensation on the sample and re-saturation respiration that is known to differ both in amplitude and in time required to reach steady state after an initial burst in respiration (Sundberg, Ekblad, Näsholm, & Palmqvist, 1999). Initial test experiments showed that gas exchange rates were in the same order of magnitude as during field measurements from other studies (Green, Schroeter, Kappen, Seppelt, & Maseyk, 1998) indicating no physiological consequences from storage at −20°C. Nine baskets (3 species × 3 replicates) were put into a 30 cm × 20 cm plexiglass box with the lid slightly open, together with a temperature and humidity logger (HOBO, Onset). Three of these boxes were prepared and each of them allocated to a growth cabinet at 5 (control), 15 or 23°C (Total number of samples: 3 species × 3 replicates × 3 treatment temperatures). Each box was arranged in a way that 150–200 μmol photons m^{-2} s^{-1} reached the lichen surface. For reactivation of lichen metabolism, the samples were sprayed with water until water saturation (external water droplets remaining on the lichens' surface). The activity of the lichens in the incubation boxes was monitored using an Imaging chlorophyll fluorometer (Imaging PAM, Walz, Germany). The lichens were then allowed to slowly desiccate

in the boxes and once they had dried out and became inactive (Yield of PSII below 0.2) they were kept in this stage for 1 day until the next reactivation. This treatment was chosen to mimic natural conditions because lichens as poikilohydric organisms often repeatedly undergo hydration-desiccation cycles under natural conditions (Green, Sancho, & Pintado, 2011) and similar treatments were shown to optimize lichen cultivation in growth chambers (Gauslaa, Alam, & Solhaug, 2016). Each hydration-desiccation cycle took about 3–4 days so that assays of photosynthesis and respiration rates were on a weekly basis. Total incubation time was 6 weeks.

2.3.2 | Assays

Carbon dioxide gas exchange measurements were conducted under controlled laboratory conditions using a mini cuvette system (CMS400, Walz Company, Effeltrich, Germany). Relative humidity of the incoming air was adjusted using a cold trap and was kept stable at 90% for all measurements. Net photosynthesis (NP) was measured under saturating light levels at 500 μmol photons m^{-2} s^{-1} and rates of dark respiration (R) were obtained by shading the cuvette completely (until the ΔCO_2 signal had stabilized). Assay temperatures were adjusted to those of the treatments and each sample was measured at all three temperatures (5, 15, and 23 °C; total number of readings: 3 species × 3 replicates × 3 treatment temperatures × 3 assay temperatures). To minimize any effects due to the assay temperature being different to the treatment temperature, the measurements at assay temperatures were made randomly and samples immediately replaced in their treatment temperature after the assays. The CO_2 exchange of the samples was related to chlorophyll content. Chlorophyll contents were determined by extracting the samples twice with dimethyl-sulfoxide (DMSO) at 60°C for 90 min and measuring the absorption at standard wavelengths (Ronen & Galun, 1984).

2.4 | Microscopy

Visualization of the internal thallus structure and anatomical properties was performed with a light microscope equipped with differential interference contrast (Axioskop, Carl Zeiss, Jena, Germany). Thin sections of the lichen thalli before and after the treatment were prepared using a freezing microtome (Leitz, Wetzlar, Germany). Pictures were taken using the Axio-Vision software.

2.5 | Calculations and statistics

The occurrence of acclimation over the time course of the experiment was investigated by presenting the results in three different ways.

First, the rates of net photosynthesis (NP), respiration (R) and the ratio of net photosynthesis to respiration (NP/R), measured at their respective incubation temperatures ($C_{5,5}$, $T_{15,15}$, and $T_{23,23}$), were plotted over the time course of the experiment with the objective of detecting changes over time (Figure 3). The ratio of net photosynthesis to respiration (NP/R) was calculated to approximate whole lichen homoeostasis. A value of 1 indicates that both processes compensate each other, while values below 1 indicate a high fraction of respiration compared to net photosynthesis and vice versa. Statistical testing was based on regression analysis using the Sigma Plot software (Systat Software GmbH, San Jose, USA). All linear regression lines are based on data that passed normality tests (Shapiro–Wilk) and tested for significance with $\alpha = 0.05$. For each plot, regression lines were fit to the data, the null hypothesis (slope equal to zero, $p > .05$) tested, and the coefficient of determination (r^2) calculated. Effects of temperature were analysed using a single factor GLM (General Linear Model) repeated measure procedure for each species separate. Effects of time were analysed using a single factor GLM repeated measure procedure for each species at each temperature separate. The species*temperature effect was tested with a two factor GLM repeated measure procedure (SPSS, IBM Analytics, New York). The low sample size did not permit the necessary degrees of freedom to test the interaction term between time and other main effects.

Second, to see whether the instantaneous response to elevated temperature remains stable and whether *growing* at warmer temperatures reduces the negative effects resulting from this, we assessed comparisons between $C_{5,5}$ and $C_{5,15}$, with those between $C_{5,5}$ and $T_{15,15}$. For the $C_{5,5}$ vs. $C_{5,15}$ comparison, we expect respiration rates to increase when measured at a higher temperature, but net photosynthesis rates to decrease because 15°C is above the optimal temperature (Lange & Kappen, 1972). As a consequence, a line linking $C_{5,5}$ to $C_{5,15}$ would have a negative slope for both processes. Any acclimation to new, warmer growing conditions ($C_{5,5}$ vs. $T_{15,15}$ comparison) reduces the magnitude of this negative effect and results in a flattening of the negative slope. This means, that if acclimation occurs, the slope between $C_{5,5}$ and $T_{15,15}$ should be less than the slope between $C_{5,5}$ and $C_{5,15}$. Slopes were calculated from a linear equation at the beginning of the experiment and at the end. Means were compared by a two-way repeated measure ANOVA (SPSS, IBM Analytics, New York) using a significance level of $p < .05$ to check for differences between species and treatment temperature. Where ANOVA indicated significant results, the treatment effect was assessed for each species.

Third, physiological rates (NP and R) of organisms grown at elevated temperature (15°C), but measured at the standard, control temperature ($T_{15,5}$) were analysed. Acclimation to higher growth temperatures results in decreasing rates when measured back at colder, standard temperatures. To demonstrate this decrease, mean values from the beginning of the experiment were compared to those gathered after 6-week treatment and between the species by a two-way repeated measure ANOVA (SPSS, IBM Analytics, New York) using a significance level of $p < .05$.

3 | RESULTS

3.1 | Incubation conditions

During the experiment, treatment temperatures remained stable with only a small discrepancy from the intended treatment temperatures (5, 15, and 23°C, Table 1). Active time was inversely proportional to

TABLE 1 Incubation conditions. Overall climatic conditions during the incubation and the count of hours that lichens were active after a hydration event. Given are mean values ± standard deviation

Incubation setup (code)	Air temperature (°C)	Humidity when active (%)	Active time after hydration (h)
Control	5.9 ± 2.6	89.3 ± 13.9	42.2 ± 4.3
Increased	14.6 ± 3.4	80.4 ± 8.2	35.4 ± 2.7
Extreme	21.9 ± 4.3	79.1 ± 29.3	28.8 ± 1.9

the water vapour pressure deficit VPD (Figure 2; $p = .0022$) and such relationships were previously described to appropriately simulate heat wave events (De Boeck et al., 2010).

3.2 | Change in NP, R, and their ratio over time

Control samples incubated and measured at 5°C showed stable net photosynthesis and respiration that did not change over the time course of the experiment (black lines, Figure 3). All repeated measure GLMs showed no significant effects of time ($p > .05$). This stability under control conditions indicated that our control conditions were suitable for the stable maintenance of all three lichens selected for this study.

3.2.1 | Net photosynthesis

For all species, the net photosynthetic rates were similar for the control and 15°C treatments at the start of monitoring (Figure 3; 1.93 vs. 2.14 μmol CO_2 g^{-1} s^{-1} for *S. alpinum* ($p = .53$), 0.85 vs. 1.0 μmol CO_2 g^{-1} s^{-1} for *U. aurantiaco-atra* ($p = .80$), 1.41 vs 1.69 μmol CO_2 g^{-1} s^{-1} for *P. contortuplicata* ($p = .58$)). However, during the treatments they changed significantly ($F_{3/4} = 8.25$ and $p = .035$ for *S. alpinum*; $F_{2/5} = 8.21$ and $p = .026$ for *P. contortuplicata*). At 15°C (red lines, Figure 3), NP increased for *S. alpinum* ($p = .0002$, $r^2 = .5925$, slope = 0.3229, $t = 4.8940$), remained stable for *U. aurantiaca-atra* ($F_{2/1} = 0.75$ and $p = .632$)) and decreased to near zero for *P. contortuplicata* ($p = .0103$, $r^2 = .3855$, slope = −0.4847, $t = -2.9637$). When exposed to extreme temperatures (23°C, green lines, Figure 3), already at the start of the experiment, only *S. alpinum* showed NP rates similar to control and 15°C treatments. For *U. aurantiaco-atra* and *P. contortuplicata*, this was close to zero or even negative. Over time, under the extreme temperature regime, net photosynthesis declined significantly for *S. alpinum* ($p = .0044$, $r^2 = .6120$, slope = −1.3899, $t = -3.7740$) and *U. aurantiaco-atra* ($p = .0220$, $r^2 = .5509$, slope = −1.6229, $t = -2.9302$) with a similar trend for *P. contortuplicata* ($p = .0536$, $r^2 = .4342$, slope = −0.7583, $t = -2.3177$). However, all species ceased to show a NP response to light after 3 or 4 weeks indicating that the photobiont was dead and that treatment at 23°C exceeded their survival capacity at least within the local population.

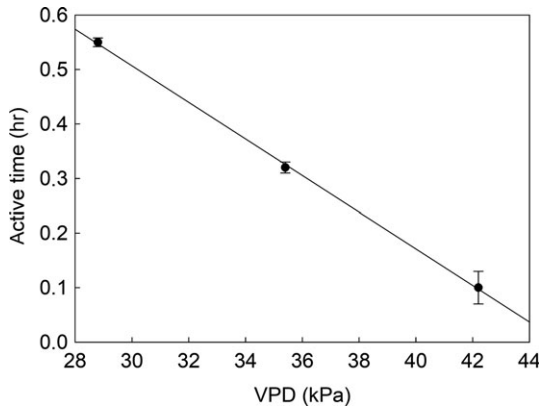

FIGURE 2 Active time of lichen samples in the experiment plotted against VPD in the experiment boxes

3.2.2 | Respiration

Respiration rates were significantly increased by treatment temperature ($F_{2/6} = 14.34$, $p = .005$ for *S. alpinum*, $F_{2/6} = 11.605$, $p = .009$ for *U. aurantiaco-atra*; $F_{2/4} = 105.99$, $p < .001$ for *P. contortuplicata*) and were at least double that of the controls (Figure 3). Nevertheless, these rates did not change over the time course of the experiment ($F_{3/4} = 0.58$, $p = .65$ for *S. alpinum*, $F_{1/5} = 1.06$, $p = .344$ for *U. aurantiaco-atra*; $F_{2/5} = 0.18$, $p = .84$ for *P. contortuplicata*), indicating no thermal acclimation of these processes. Respiration rates were highest at 23°C for the first 3 or 4 weeks (green lines, Figure 3) but after this period the 23°C samples did not show a reaction to changing light and the photobionts were therefore considered dead and the samples excluded from further analysis.

3.2.3 | NP/R ratio

NP/R ratios were different between the different temperature treatments ($F_{6/8} = 67.220$, $p < .001$ for *S. alpinum*; $F_{2/6} = 35.76$, $p < .001$ for *U. aurantiaco-atra*; $F_{2/6} = 165.12$, $p < .001$ for *P. contortuplicata*). The NP/R ratio for the control groups of all three species indicated that NP rates at 5°C were at least double R rates during the whole experiment. At 15°C, the NP/R ratio was lower and close to 1 at the start of the treatments but as the experiment progressed (red lines, Figure 3), the ratio recovered to control levels for *S. alpinum* ($p = .0010$, $r^2 = .7170$, slope = 0.2120, $t = 5.5859$), remained stable around 1 for *U. aurantiaca-atra* ($F_{2/1} = 4.68$ and $p = .311$)) and declined to below 1 after 3 weeks for *P. contortuplicata* ($p = .0325$, $r^2 = .2868$, slope = −0.1881, $t = -2.3730$). At the extreme temperature (23°C, green lines, Figure 3) NP/R ratios were below 1 for all samples and, as the experiment progressed, showed significant decreases for *S. alpinum* ($p = .0010$, $r^2 = .7170$, slope = −0.5331, $t = -4.7751$) and *U. aurantiaco-atra* ($p = .0002$, $r^2 = .8727$, slope = 0.4309, $t = -6.9282$). For *P. contortuplicata*, NP/R ratio at 23 °C was stable around zero during the latter half of the experiment.

3.3 | Changes in the response to high temperatures

According to our suggestion any acclimation to new, warmer growing conditions should entail a lesser negative slope at the end of the

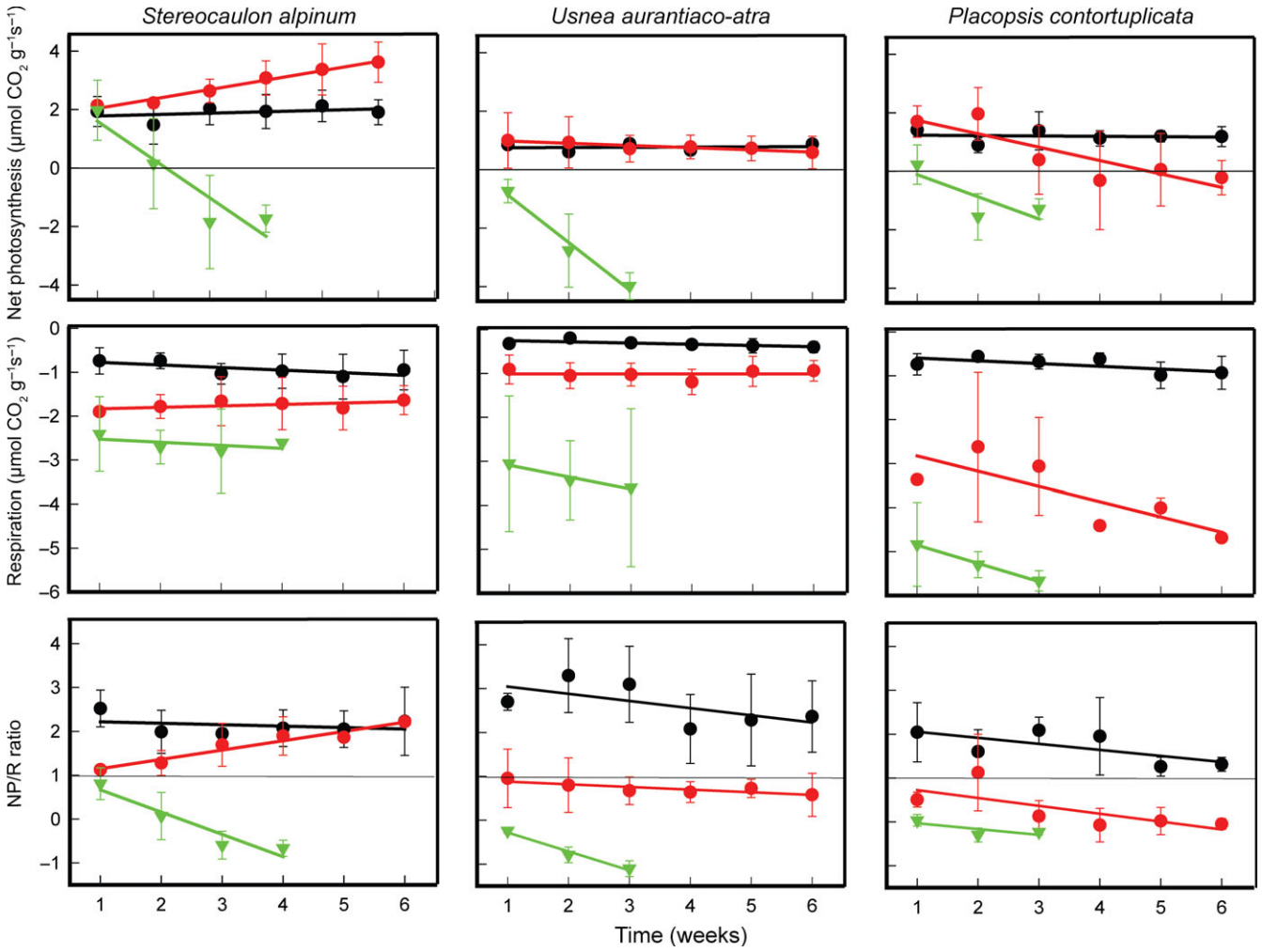

FIGURE 3 Changes in net photosynthesis (upper graphs), respiration rates (middle graphs) and NP/R ratio (lower graphs) during incubation at different temperatures. Shown are mean values (n = 3) ± standard deviation of samples treated at different temperatures and measured at their respective treatment temperature. • and black line = controls (5°C) measured at 5 °C assay temperature ($C_{5,5}$); ● and red line = increased (15°C) measured at 15 °C assay temperature ($T_{15,15}$); ▲ and green line = extreme (23°C) measured at 23°C ($T_{23,23}$)

experiment (grey bars, Figure 4) when compared to the start (black bars, Figure 4). For the controls, no such decline occurred for any species, either for net photosynthesis (Figure 4a–c) or for respiration (Figure 4d–f), showing that the immediate response to increased temperatures was stable and consistent during the whole experiment for the controls. However, growth at elevated temperatures (15°C) had significant effects that were different between the species ($F_{2/3}$ = 95.03, p = .002 for NP; $F_{2/3}$ = 88.88, p = .002 for R). For NP of *S. alpinum* (Figure 4a), positive slopes indicated that NP rates increased when measured at 15°C, which shows that the optimal temperature for this species was above 5°C from the beginning of the experiment. After growing at 15°C for 6 weeks, the slope between $C_{5,5}$ and $T_{15,15}$ was significantly increased (p = .039), indicating that the temperature optimum had shifted to even higher temperatures and the species had acclimated to the new warmer growing temperature. No such changes occurred for respiration in *S. alpinum* (Figure 4d) indicating that growing at elevated temperatures did not change the response of respiration to higher temperatures and there was no acclimation of R to the warmer growing temperature. For *U. aurantiaco-atra* (Figure 4b,e), the treatment had no significant effect on the slopes. For *P. contortuplicata* (Figure 4c,f), the changes were most drastic. Here, net photosynthesis for $T_{15,15}$ at the end of the experiment was lower than it was at the start and compared to the control group, resulting in a significantly increased negative slope that indicated that these samples suffered from severe thermal stress and the 15°C treatment already exceeded their photobiont survival capacity. Respiration also increased significantly (p = .019, Figure 4f) for the treatment at the end of the experiment, indicating that the lichens carbon balance tipped strongly into the negative.

3.4 | Changes in response to control temperature

Net photosynthesis rates $T_{15,5}$ varied significantly between the species ($F_{2/1}$ = 345, p = .038) with the highest rates for *S. alpinum*. Additionally, NP rates for all species decreased when compared

between the beginning and the end of the experiment (Figure 5; $F_{2/1} = 1470$, $p = .018$). This indicated that initial rates could not be maintained in the treatment and most possibly the temperature optimum had shifted for these species. It also implied that key traits (high NP rates at low temperatures) were lost during the experiment. For *P. contortuplicata*, NP rates were close to zero and negative so that these were excluded from the analysis.

Respiration rates measured at the 5°C control temperature (Figure 5) did not differ between the species ($F_{2/1} = 2.77$, $p = .39$) and also showed no change from the start to the end of the experiment ($F_{2/1} = 13.98$, $p = .186$). This indicated that the temperature response of respiration did not change during the experiment and initial rates were preserved.

3.5 | Morphological changes

Visual effects of the incubation at 15°C varied drastically between the species. In untreated samples of *S. alpinum*, the green algal photobiont was located in small bundles underneath the upper cortex (Figure 6a). After 6 weeks of incubation at 15°C, the photobiont layer appeared less constricted than before but remained vividly green (Figure 6b). In *U. aurantiaco-atra*, the photobionts did not occur in a compact layer but were spread in small clusters between the outer cortex and the central string (Figure 6c). These algal clusters could still be found after the 15°C treatment (Figure 6d), but some of them only contained dead cell material (Figure 6e). In *P. contortuplicata*, the green algal photobiont originally formed a dense layer underneath the upper cortex (Figure 6f) but after the incubation at 15°C only dead, brown cell material was present indicating that the photobiont inside this lichen species did not survive the treatment (Figure 6g).

4 | DISCUSSION

In the present study, we have provided experimental evidence that polar macro-lichens exposed to warmer growing conditions are unable to rapidly reduce their resulting respiration losses via thermal acclimation of respiration. For all tested species, an *extreme* increase in temperature exceeded their photobiont survival capacity at the latest after 3 or 4 weeks. At a more moderate *increased* temperature, we found a high degree of response variability and sensitivity between the species. Most interestingly, a widely distributed lichen species (*S. alpinum*) was capable of restoring its energy homoeostasis via an increase in net photosynthesis. In contrast, the specialized species, that were naturally growing in the same environment and spatially close, did not show this type of acclimation (*P. contortuplicata*), or showed it less obviously (*U. aurantiaco-atra*). Significant effects on photobiont vitality indicated that any acclimation processes in lichens are subject to complicated interplays between the two symbionts and strongly depend on their individual acclimation potential. Our finding emphasizes species-specific sensitivity to changes in temperature in this pristine environment and underlines the fragility of the vegetation community composition.

Based on extensive studies in higher plants, thermal acclimation of respiration is a common biological feedback to long-term temperature

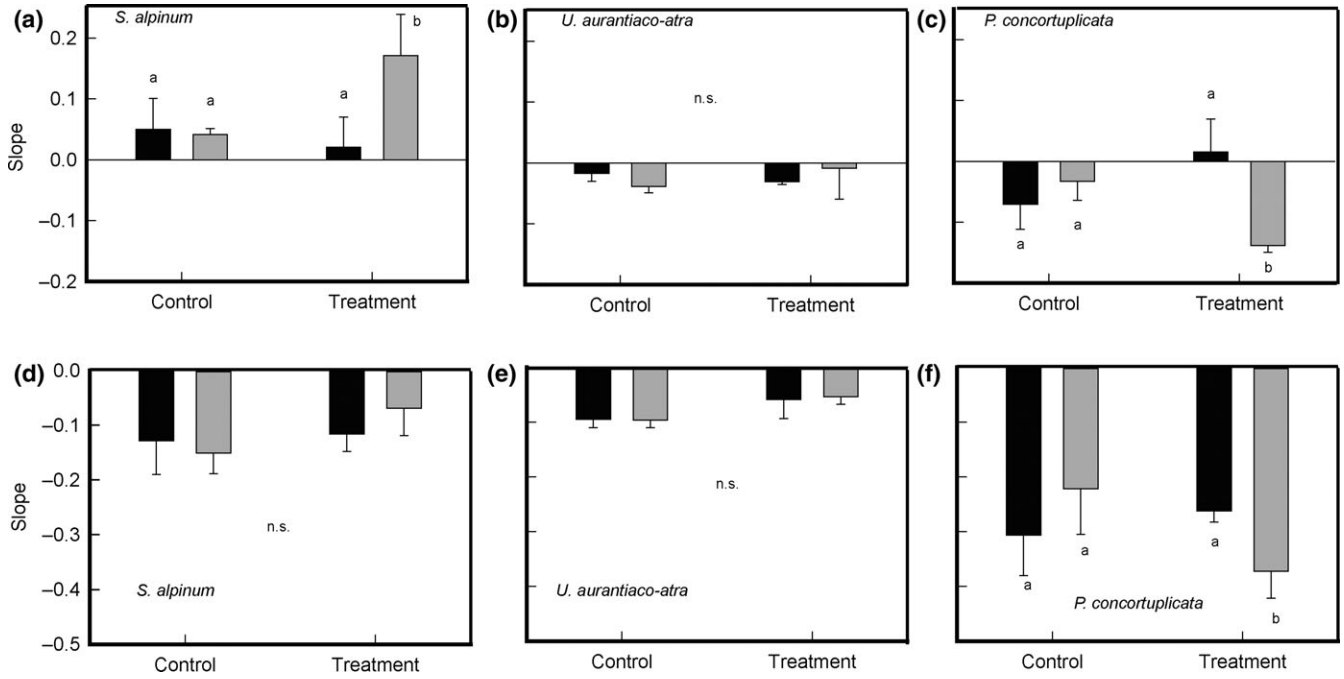

FIGURE 4 Responses to elevated temperature (15°C) for the control group and the 15°C treatment. Slopes from linear equations between $C_{5,5}$ vs. $C_{5,15}$ and $C_{5,5}$ vs. $T_{15,15}$ are compared from the beginning (black bars) and the end of the experiment (grey bars). Data are presented separately for changes in net photosynthesis (a,b,c) and respiration (d,e,f). Shown are mean values ($n = 3$) ± standard deviation and results from post hoc tests, with different letters indicating significant differences between the means

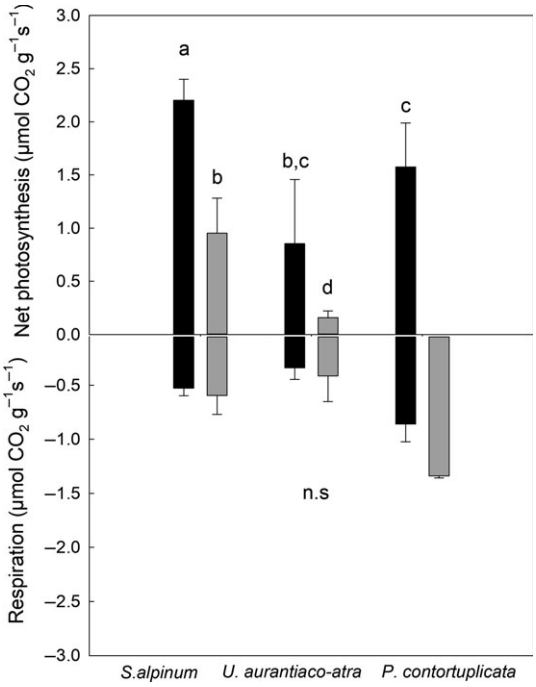

FIGURE 5 Rmt and NPmt. Net photosynthesis and respiration of organisms grown at elevated temperature (15°C), but measured back at the standard, control temperature ($T_{15,5}$) from the beginning (black bars) and the end of the experiment (grey bars). Shown are mean values ± standard deviation and results from post hoc tests, with different letters indicating significant differences between the means

increases (e.g. Atkin et al., 2015). If lichens have a similar capacity to acclimate their energy metabolism in response to changes in their thermal environment, then we would expect that the respiration rates of lichens held at higher temperatures would show a decrease in respiration losses over time. Our results show that, as expected, respiration shows an immediate increase when all species were activated at higher temperatures (Figures 3 and 4). However, the increased R at the higher temperatures (Figure 3) did not show any down-regulation with time over the 6 weeks of the experiment, suggesting that no thermal acclimation of respiration occurred in any of three selected lichen species in this study. We can support this assumption with three lines of evidence. Firstly, respiration rates remained at the same level over the time course of the experiment (Figure 3). Secondly, the responses of respiration to higher temperatures remain stable during the treatment (Figure 4). Thirdly, organisms that were exposed to warmer growing conditions did not show any down-regulation of respiration when measured at the standard, control temperature (Figure 5). This finding is in line with a study on soil respiration in the Antarctic, where it has been shown that both the biomass-specific respiration rate and the overall rate of SOC mineralization increased with temperature and this was interpreted as respiration by soil micro-organisms not down-regulating relative to temperature (Laudicina et al., 2015). One explanation for this finding might be that, unlike autotrophic counterparts, heterotrophic organisms do not gain any evolutionary advantage from physiological down-regulation in response to increased temperature (Hartley, Heinemeyer, & Ineson, 2007). In agreement with this, it is known that Antarctic invertebrates rely on life history traits that allow them to remain dormant throughout most of the year whilst taking advantage of short-term favourable (warmer) conditions (Convey, 1996, 1997). Such survival strategies enhance the performance of the native biota under current climate conditions and are discussed to be an important factor influencing soil invertebrate communities (Nielsen & Wall, 2013). Nevertheless, this finding is unexpected, especially because lichens were previously described to acclimate respiration rates within seasons under natural conditions (Lange & Green, 2005). In contrast to the study from Lange and Green (2005), we applied drastic and abrupt changes rather than a continuous change in conditions. The severity of changes we applied was necessary to provoke significant responses in a reasonable amount of time and to simulate a heat wave stimulus. The advantage of this approach is that we have experimentally focused on one effect and can exclude factors that potentially cover temperature effects.

In addition to these negative effects of increased temperature on lichen respiration, one important factor in this study is the deleterious effect of the higher temperatures on the photobionts (Figure 6). All three species showed a collapse in NP/R when incubated at 23°C (Figure 3). This collapse appears to be due to photobiont death and is also shown at 15°C for *P. contortuplicata*, and to a lesser degree for *U. aurantico-atra* (Figure 6). The death of the photobionts within the thallus has also previously been described for *Psora decipiens*, when cold and wet acclimated thalli were transplanted to hot desert conditions and vice versa (Williams, Colesie, et al., 2017). It indicates that 23°C is well above the survival temperature for all the photobionts in this study and 15°C is about the upper limit for the two highly specialized lichen species, which only occur with a narrow distribution range in the Antarctic. The finding is in line with other studies indicating a possible adaptation of Antarctic photobionts to colder growing conditions (Balarinová, Váczi, Barták, Hazdrová, & Forbelská, 2013). Photobiont death makes it difficult to interpret changes in NP/R, especially at 23°C, but also partly at 15°C for the two temperature-sensitive lichen species. Only *S. alpinum*, which is a lichen species with a wider distribution range, is robust enough to acclimate (Figure 3).

Surprisingly, and in contrast to our hypothesis, the recovery of the NP/R ratio in *S. alpinum* resulted from increased net photosynthesis rates, rather than acclimation of respiration. This finding is clearly substantiated by a significantly lowered NPmT at the end of the experiment (Figure 5) and the shift of the NP temperature optimum (Figure 4). In lichens, there are two mechanisms available for acclimating photosynthesis to changing growth temperatures. The first would be by changing the number of photobiont cells in the thallus (Tretiach, Bertuzzi, Carniel, & Virgilio, 2013). Domaschke, Vivas, Sancho, and Printzen (2013) demonstrated this option for *Cetraria aculetata*, where temperate populations of the same lichen species had a significantly higher NP and number of photobionts cell per mg dry weight than their polar counterparts. The second option would be through acclimation of the macromolecular composition to different environmental conditions within an existing photobiont cell (MacKenzie et al., 2001). It has been shown that within a nearly stable, non-dividing algal cell population in *Lobaria pulmonaria*, the key photosynthetic proteins

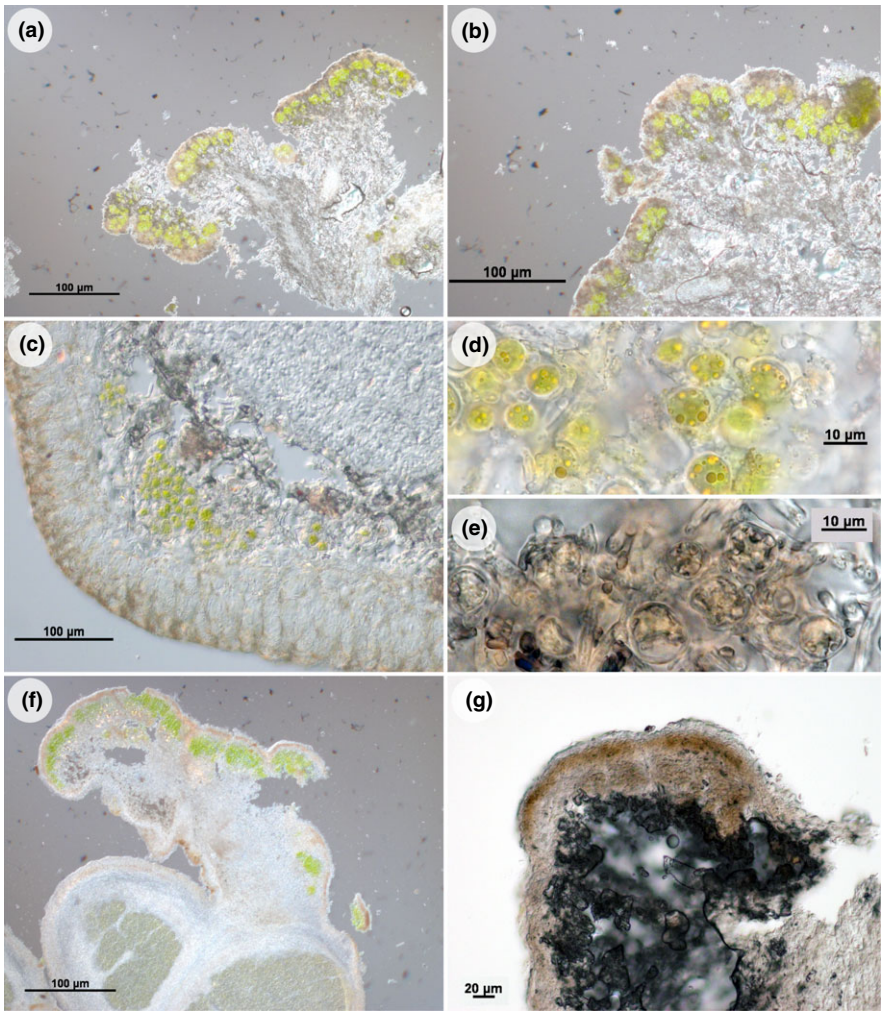

FIGURE 6 Microscopic comparison of lichen morphology. Pictures on the left show cross sections of the lichen before the incubation (a: *Stereocaulon alpinum*, c: *Usnea aurantiaco-atra*, f: *Placopsis contortuplicata*). On the right side, pictures from after the 15°C incubation. b: *S. alpinum* the green algal photobiont in vivid green colour, d: trebuxioid photobiont in *U. aurantiaco-atra*, e: dead cell material in the photobiont layer of *U. aurantiaco-atra*, g: thalli of *P. contortuplicata* after the treatment

showed significant seasonal acclimation (Schofield, Campbell, Funk, & MacKenzie, 2003). This second mechanism may be similar to findings in vascular plants, where the Rubisco enzyme content and activation is a key component of thermal acclimation of photosynthesis (e.g. Hurry, Strand, Tobiaeson, Gardeström, & Öquist, 1995).

To estimate the relevance of acclimation processes in lichens under natural conditions, it is also important to know the actual rate at which such acclimation process occurs. Such an assessment can be done by checking when the NP/R homoeostasis was restored. For *S. alpinum*, NP/R ratio of warm incubated samples already equals that of the controls after 3 weeks. This equates to only about 106 active hours and reflects a fast rate of acclimation, supporting the suggestion of acclimation via changes in the macromolecular composition because this rate of change is higher than the described turnover rate of photobionts in lichens (Hill, 1992). It also indicates how quickly lichens can respond to environmental temperature change and suggests that although lichens are slow-growing organisms, this does not mean that their metabolic processes are less responsive than in other organisms. For example, thermal acclimation by plants (Atkin & Tjoelker, 2003), animals (Seebacher, White, & Franklin, 2015) or fungi (Crowther & Bradford, 2013) manifests itself over time frames ranging from days to weeks.

Nevertheless, such acclimation of NP seems to be a species-specific trait. In general, broadly distributed, or species from variable temperature environments are likely to be more capable of acclimating than species experiencing a limited thermal range (Crowther & Bradford, 2013; Seebacher et al., 2015). If so, thermal acclimation as a species-specific trait in lichens can be suitable for environmental risk assessment and interpretation of the ecological spectrum of a species. Species with high acclimation potential are considered to be at less at risk than ones with narrow ecophysiological amplitudes. In our study, the two species with restricted distribution in the Antarctic showed little acclimation potential; in fact, *P contortuplicata* did not show any signs of acclimation for R nor NP and died during the incubation at higher temperatures. *U. aurantiaco–atra* did not show increasing rates of NP with time but both the decreasing NPmT (Figure 5) and the marginally lowered slope (Figure 4b) points towards some potential acclimation processes. Therefore, we interpret the widely distributed lichen *S. alpinum* to be at less risk than highly adapted Antarctic restricted species such as *P. contortuplicata* or *U. aurantiaco–atra*.

Our findings provide mechanistic insight into why lichen biodiversity could decline and the lichen community composition shift to more dominant generalist species in the maritime Antarctic. This phenomenon is already described for the Arctic tundra (Lang et al.,

2012). Such community shifts could lead to regional-scale biotic homogenization, which is a threat for Antarctic ice-free habitats (Lee et al., 2017) and could alter ecosystem functioning and productivity (Clavel, Julliard, & Devictor, 2011). However, we stress that the response of individual organisms cannot fully reflect the entire community response for the selected ecozone. Future studies should address three important topics: the first concerns the potential for acclimation process in lichen photobionts. It is clear from our study that the photobionts in the studied lichens were not able to survive elevated temperatures that were maintained for extended periods (weeks). In one species even temperatures as low as 15°C were lethal in this study. Differential adaptive and acclimatize mechanisms appear to exist in phototrophic microorganisms residing in low-temperature environments although these are also described to be understudied (Morgan-Kiss, Priscu, Pocock, Gudynaite-Savitch, & Huner, 2006). Secondly, the effects of increased temperature on the lichen and the biochemical mechanisms underlying this response should be studied in greater detail. Thirdly, future studies need to combine laboratory studies with in situ site performance.

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ORCID

Claudia Colesie http://orcid.org/0000-0003-1136-0290

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