



Climate change leads to higher NPP at the end of the century in the Antarctic Tundra: Response patterns through the lens of lichens

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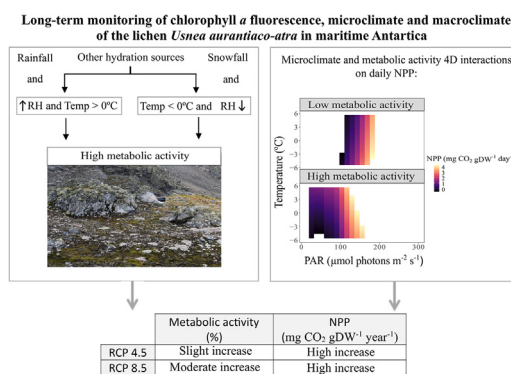
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HIGHLIGHTS

- Macroclimate is a poor predictor of NPP in cryptogams from tundra.
- The hydration sources available throughout the year explain the seasonal metabolic response pattern.
- Temperature seems to be the main driver for NPP and metabolic activity.
- RCP 4.5 and RCP 8.5 predict positive effects on metabolic activity duration at the end of the century.
- Climate warming leads to an NPP increase at the end of the century for species with similar physiological response ranges.

GRAPHICAL ABSTRACT



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ABSTRACT

Poikilohydric autotrophs are the main colonizers of the permanent ice-free areas in the Antarctic tundra biome. Global climate warming and the small human footprint in this ecosystem make it especially vulnerable to abrupt changes. Elucidating the effects of climate change on the Antarctic ecosystem is challenging because it mainly comprises poikilohydric species, which are greatly influenced by microtopographic factors. In the present study, we investigated the potential effects of climate change on the metabolic activity and net primary photosynthesis (NPP) in the widespread lichen species *Usnea aurantiaco-atra*. Long-term monitoring of chlorophyll *a* fluorescence in the field was combined with photosynthetic performance measurements in laboratory experiments in order to establish the daily response patterns under biotic and abiotic factors at micro- and macro-scales. Our findings suggest that macroclimate is a poor predictor of NPP, thereby indicating that microclimate is the main driver due to the strong effects of microtopographic factors on cryptogams. Metabolic activity is also crucial for estimating the NPP, which is highly dependent on the type, distribution, and duration of the hydration sources available throughout the year. Under RCP 4.5 and RCP 8.5, metabolic activity will increase slightly compared with that at present due to the increased precipitation events predicted in MIROC5. Temperature is highlighted as the main driver for NPP projections, and thus climate warming will lead to an average increase in NPP of 167–171% at the end of the century. However, small changes in other drivers such as light and relative humidity may strongly modify the metabolic activity patterns of poikilohydric

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autotrophs, and thus their NPP. Species with similar physiological response ranges to the species investigated in the present study are expected to behave in a similar manner provided that liquid water is available.

1. Introduction

Since the second half of the 20th century, the Antarctic Peninsula has experienced among the fastest rates of regional warming throughout the world (Vaughan et al., 2003). In particular, temperatures have increased by 0.54 °C per decade since the 1950s, with initial warming by 0.32 °C per decade until 1997, followed by cooling at 0.47 °C per decade until 2014 (Turner et al., 2016; Oliva et al., 2017; Gonzalez and Fortuny, 2018). Therefore, there is great concern about the implications of climate change for this biome and the vulnerability of the species that inhabit the area (Turner et al., 2005; Thomas et al., 2009; Sancho et al., 2017). Furthermore, the relative simplicity of this ecosystem (Convey, 2013) makes maritime Antarctica one of the most suitable areas for elucidating the potential effects of climate change.

The Antarctic terrestrial vegetation is assembled in extensive tufts over 0.3% of the permanent ice-free surface (Convey et al., 2020). The main components are lichens, which comprise 65% of the total species identified (Casanovas et al., 2015). The successful survival of this group is facilitated by their poikilohydric nature because their hydration status tends to be in equilibrium with the environment, where they are metabolically active when hydrated and dormant when dry. Dormancy constitutes an abiotic stress avoidance strategy that ensures the survival of these species (Green et al., 2018). This response trait (any trait that varies in response to changes in environmental conditions according to Violle et al. (2007)) is widespread in various organisms, such as mosses, nematodes, tardigrades, rotifers, and collembolans (Convey et al., 2020).

Despite the large amount of fresh water present in Antarctica, it is biologically unavailable because it is in the form of ice. Therefore, the different available hydration sources and their regimes in Antarctica restrict the presence of poikilohydric autotrophs to habitats where water is useable (Pannowitz et al., 2003). Liquid water is supplied in the forms of rainfall and meltwater (mostly during the austral summer; Kappen et al., 1995; Schlenz et al., 2013), but also from snowfall, permanent snow, and ice banks (Robinson et al., 2003), which might only be available during a few days or even weeks per year (Kennedy, 1993). Thus, refuges such as rock crevices or drainage basins are considered essential for providing protection against harsh conditions, including dehydration (Sadowsky et al., 2016), thereby highlighting the important effects of microclimate on terrestrial biota (Sancho et al., 2016).

Understanding the spatial and temporal variations in the Antarctic terrestrial ecosystem (Chown and Convey, 2007) requires investigations of the metabolic response traits of poikilohydric autotrophs at different scales. At the spatial scale, Guglielmin et al. (2012) concluded that the effect of the air temperature on the soil surface temperature changes seasonally in maritime Antarctica. During the winter, its effect is drastically reduced because of the protection provided by snow cover. However, this cover melts during the summer and the air temperature has a greater impact on the soil surface temperature. Schroeter et al. (2010) observed that in spite of the 16 °C difference in mean air temperature between maritime and continental Antarctica, lichens were metabolically active at almost identical microclimatic temperatures (ca. 2 °C), thereby indicating convergence at a microclimatic scale. At the temporal scale, the opportunistic responses of poikilohydric autotrophs to transient periods of favorable microclimatic conditions have been demonstrated in several biomes, thereby highlighting the need for investigations at high temporal resolution (Insarov and Schroeter, 2002).

The activation of metabolism in poikilohydric autotrophs initiates processes such as photosynthesis that do not occur in a dormant state. Therefore, the duration of metabolic activity is essential for modeling the productivity of cryptogams (Schroeter et al., 2000). In maritime Antarctica, net primary photosynthesis (NPP) is restricted to the four to

six warmer months of the year (Block et al., 2009) when the temperature and radiation are sufficiently high to allow the release of liquid water and promote carbon gain.

In the present study, we evaluated how the main abiotic factors in maritime Antarctica might modulate the metabolic activity and NPP in lichens in order to predict the effects of climate change. Assessing these changes is important for obtaining a better understanding of changes in the global carbon cycle because the contribution of poikilohydric autotrophs to the global NPP is estimated at about 3.9 Pg C year⁻¹ (7% of the NPP by terrestrial vegetation) (Elbert et al., 2012; Porada et al., 2013, 2014), and 20% comes from biomes similar to maritime Antarctica, such as polar desert and alpine tundra.

In the present study, long-term microclimate, macroclimate, and metabolic activity monitoring were conducted for *Usnea aurantiaco-atra* (Jacq.) Bory, which is one of the most common lichens in maritime Antarctica (Øvstedal and Smith, 2001). Modeling was performed to evaluate the effects of different regional (micro- and macroclimate) and temporal (intra- and inter-annual fluctuations) scales. In this study, we determined: (i) the interaction between the effects of photosynthetically active radiation (PAR), temperature, relative humidity (RH), and precipitation on the metabolic activity and NPP of lichens; (ii) the vulnerability of lichens to the climate change scenarios predicted by the Intergovernmental Panel on Climate Change (IPCC); (iii) whether NPP could be predicted using macroclimate rather than microclimate; and (iv) whether NPP is overestimated if metabolic activity is not included in the models.

We hypothesized that the NPP of lichens would increase under climate change scenarios due to global warming. This hypothesis was also suggested in previous studies, such as those by Smith (1999), Xiong et al. (2000), and Singh et al. (2018), based on experimental observations that the current temperature and PAR in maritime Antarctica do not allow many cryptogams to achieve their maximal net photosynthesis. The environmental conditions that these species experience are widely known as “suboptimal conditions”.

2. Methods

2.1. Research site

The research site is located near the Juan Carlos I Spanish Antarctic Station in an ice-free area of South Bay, Livingston Island, South Shetland Islands, maritime Antarctica (62°39'46"S, 60°23'20"W). Most of Livingston Island is of volcanic origin but the study area comprises sedimentary rocks, with a sequence of shale and turbiditic deposits. Due to its location at the northernmost tip of the Antarctic Peninsula, the region is exposed to mild or cold air masses (Gonzalez and Fortuny, 2018). The effects of the sea and almost continuous cloud cover lead to small daily and annual temperature oscillations in maritime Antarctica (Bargagli, 2005). The temperature often remains close to freezing point even during the winter (AEMET, 2019). The radiation also exhibits strong seasonal variations (AEMET, 2019).

2.2. Gas exchange analysis

Photosynthesis data for *Usnea aurantiaco-atra* were obtained from laboratory measurements acquired by Kappen (1985) using an infrared gas analyzer (Bios, Firma Leybold Heraeus, Hanau). This system provides accurate interpretations of the effects of changing environmental conditions on gas exchange processes (Midgley et al., 1997). The system comprises a temperature and humidity controlled Plexiglas cuvette, with fan-operated air circulation, and flow meters to maintain a constant airstream

of 0.5 l h^{-1} (Kappen, 1983). The response of the net photosynthesis ($\text{mg CO}_2 \text{ gDW}^{-1} \text{ h}^{-1}$) to incident light was determined at five light intensities ($0, 50, 130, 290$ and $470 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and six different temperatures ($-5, 0, 5, 10, 15$, and 20°C) at an air CO_2 content of 350 ppm .

Due to the minimum photosynthetic threshold detectable by the infra-red gas analyzer, photosynthetic rates under -6°C were set to zero. Previous field measurements of $0.008 \text{ mg CO}_2 \text{ gDW}^{-1} \text{ h}^{-1}$ at -10°C in Antarctica support this assumption (Kappen, 1989; Schroeter et al., 1995).

2.3. Metabolic activity monitoring

We obtained long-term photosystem II activity measurements using a PAM monitoring system (MoniDA, Gademann Instruments, Germany). MoniDA is a non-invasive and automatic system that measures chlorophyll *a* fluorescence and reports it to a database via satellite or local networks (Murchie and Lawson, 2013; Raggio et al., 2016).

The MoniDA central unit recorded data from two probes placed close to the samples, which were on a rock colonized with lichens near Juan Carlos I Spanish Antarctic Station. Each probe contained a single optical fiber for fluorescence measurements, as well as microclimatic sensors for measuring PAR ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and temperature ($^\circ\text{C}$). The sensors were located ca. 3 mm from the *U. aurantiaco-atra* thalli, and metabolic activity and microclimatic data were recorded simultaneously at hourly intervals from January 2009 to December 2014. The activity or inactivity of the photosynthetic systems was determined using a saturation pulse method (Schreiber et al., 1986). Basal fluorescence (*F*) was measured by irradiating the samples with a low intensity-modulated light ($0.025 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$), which was sufficiently low to not induce electron transport through photosystem II but sufficiently high to obtain a minimum chlorophyll fluorescence value. The samples were then subjected to a saturating pulse of actinic light (for about 1 s at $4000 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$) to induce a maximum fluorescence value (*Fm'*) and shut down the photosystem II reaction centers. The light absorbed by photosystem II (the effective photosynthetic yield of photosystem II or yield) was calculated as $(Fm' - F) / Fm'$ (Schreiber and Bilger, 1993; Maxwell and Johnson, 2000; Fracheboud, 2004). Yield values of zero indicated inactivity of photosystem II, and thus the samples were considered to be metabolically inactive, whereas yields greater than zero indicated the activity of photosystem II (Raggio et al., 2014). The metabolic activity (%) was calculated on a daily basis as the number of records when the yield was greater than zero divided by the total number of records.

The harsh environmental conditions in Antarctica resulted in several gaps in our dataset, and thus, which made it necessary to check and validate the measurements. As a consequence, the measurement period used for this study was a 41-month period comprising valid data from January 2009 to July 2011, and from February 2014 to December 2014. The total dataset included 58,010 hourly records, which correspond to one of the longest field dataset for Antarctica.

2.4. Climate data

2.4.1. Macroclimate

Macroclimatic data at hourly intervals were obtained from the Spanish Meteorological Agency (AEMET; <https://antartida.aemet.es/>). The automatic weather station (Campbell CR 1000) was located in an open area about 500 m from the study area (AEMET, 2019).

Mean air temperature ($^\circ\text{C}$), solar radiation (W m^{-2}), precipitation (mm), and relative humidity (%) data were downloaded for two different time periods at hourly intervals: (i) from 2000 to 2009 corresponding to the same time period as the Historical scenario, and (ii) from 2009 to 2014 corresponding to the same time period as the long-term chlorophyll *a* fluorescence measurements.

According to the conversion method described by Sager and Mc Farlane (1997), solar radiation in W m^{-2} was transformed into PAR in $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ assuming that 50% of the total incident solar energy was PAR (Papaioannou et al., 1993).

2.4.2. Global climate model

Model for Interdisciplinary Research on Climate 5 (MIROC5; Watanabe et al., 2010) is a coupled general circulation model (CGCM) developed for the fifth phase of the Coupled Model Intercomparison Project (CMIP5) used in the IPCC Fifth Assessment Report (AR5). The projections were generated using climate forcing data derived from the first ensemble member (r1i1p1). Data are publicly available from the Earth System Grid Federation website (<https://esgf-node.llnl.gov/projects/cmip5/>). Near surface mean air temperature (K), mean surface downwelling shortwave radiation in the air (W m^{-2}), precipitation (mm), and near-surface relative humidity (%) data were all downloaded with daily resolution (the maximum resolution available). Climate change scenarios were designed to operate at decade scales in order to increase their robustness (Flato et al., 2013).

Two representative concentration pathways (RCP 4.5 and RCP 8.5; Collins et al., 2013) were selected for the middle (years 2040 to 2049) and end of the century (years 2090 to 2099). RCP 4.5 describes a global scenario where carbon emissions increase and stabilize at 538 ppm CO_2 before the year 2100, temperature increases by 1.1°C to 2.6°C , and radiative forcing reaches 4.5 W m^{-2} . RCP 8.5 is the most aggressive global scenario and it is characterized by greenhouse gas emissions increasing to 936 ppm by the year 2100, temperature increasing by 2.6°C to 4.8°C , and radiative forcing of 8.5 W m^{-2} . The Historical scenario from 2000 to 2009 was also considered in order to compare the climate change simulations with the real macroclimatic conditions.

2.4.3. Statistical scaling

In order to correct the bias related to climate change scenarios (Historical scenario, RCP 4.5, and RCP 8.5), the delta change method was applied to the following predictors: PAR, relative humidity, and temperature (Maraun, 2016; Fang et al., 2015). Therefore, the “deltas” (anomalies) were calculated as the differences between the simulated Historical scenario and the real macroclimatic conditions from 2000 to 2009 for each variable and on a daily basis. Absolute differences were used for temperatures and relative changes for precipitation (Navarro-Racines et al., 2020). The delta changes were then subtracted from the RCPs and the Historical scenario.

Downscaling of the climate change scenarios to microclimate was then also performed using the delta change method for PAR and temperature at daily intervals (Navarro-Racines et al., 2020; Hülber et al., 2016). The delta changes were calculated as the differences between the real macroclimatic conditions from 2009 to 2014 and the microclimatic measurements in the same time period, which were then subtracted from the climate change scenarios.

The precipitation rates obtained from simulated climate change scenarios are still controversial and among their main weaknesses (Turner et al., 2007). Therefore, in order to reduce the dependence of the model on precipitation rates and analyze how metabolic activation changed under different hydration sources, precipitation was represented as a categorical factor with three levels: “rainfall,” “snowfall,” and “non-precipitation events.” “Rainfall” was defined as records of precipitation occurring at temperatures at or above 0°C . “Snowfall” was defined as records of precipitation occurring at temperatures below 0°C (Marks et al., 2013). “Non-precipitation events” were defined as periods when no precipitation occurred but the species was active. These categorical factors allowed us to test how different forms of precipitation were distributed throughout the year but without altering the total annual precipitation, and the roles of rainfall and snowfall as metabolic activation triggers.

2.5. Generalized additive model (GAM)

GAM was used to model nonlinear trends in the time series, such as seasonal or within year variation. We performed three sequential GAM analyses to investigate how macro- and microclimatic patterns might affect the relationship between metabolic activity and NPP. The GAMs were implemented using the mgcv package in R (Wood, 2019). A cubic spline smoothing function was used for each predictor and the tensor product for

interaction effects between predictors. In both cases, the k-dimensions were optimized by cross validation. Stepwise model selection was used to select the predictors to retain in the model according to the best deviance reduction (Akaike information criterion). GAM multi-dimensional smoothing effects plots were visualized using mgcviz (Fasiolo et al., 2020). A P-value < 0.05 was considered as the minimum level of significance.

The first GAM (GAM 1; Fig. S1) modeled the response pattern of the net photosynthesis relative to temperature and PAR under laboratory conditions. This response pattern was used to estimate the NPP based on the long-term monitoring dataset from 2009 to 2014. NPP was estimated at two different geographic scales (micro- and macroclimate). Moreover, the effect of metabolic activity as a biotic driver was evaluated at each geographic scale. To evaluate it, two different situations were modeled: (i) considering only the periods when the lichen was metabolically active, and (ii) assuming that the lichen was always active (Table 1). The long-term monitoring dataset at hourly intervals was divided into four different datasets for the analysis (Table 1). The response variable for each dataset was the net photosynthetic rate. The smoothing terms were temperature ($k = 9$), and PAR ($k = 9$). The tensor product was the two-way interaction between temperature and PAR ($k = 27$).

A second GAM (GAM 2) was performed in order: (i) to determine how the main macroclimatic factors influenced the daily metabolic activity pattern from 2009 to 2014, and (ii) to predict the metabolic activity for RCP 4.5 and RCP 8.5 in the middle and at the end of the century. The response variable was metabolic activity. The smoothing terms were macroclimatic temperature ($k = 9$), macroclimatic PAR ($k = 9$), macroclimatic relative humidity ($k = 9$), and precipitation ($k = 3$, using “fs” as a penalized smoothing basis). The tensor product was the three-way interaction between temperature, PAR, and relative humidity according to each precipitation category (“rainfall,” “snowfall,” and “non-precipitation events;” $k = 124$).

A third GAM was required (GAM 3) due to the temporal mismatch between the long-term monitoring data from 2009 to 2014 (at hourly intervals) and the RCP simulations (at daily intervals). This model allowed us: (i) to determine how the main microclimatic drivers and metabolic activity influenced the daily NPP; and (ii) to predict the NPP based on RCP 4.5 and RCP 8.5. In the analysis, the microclimatic temperature, microclimatic PAR, and metabolic activity were averaged, and the NPP was summed. The response variable was daily NPP. The smoothing terms were the microclimatic temperature ($k = 9$), microclimatic PAR ($k = 9$), and metabolic activity ($k = 9$). The tensor product was the three-way interaction between temperature, PAR, and metabolic activity ($k = 103$).

3. Results

3.1. Climate conditions from 2009 to 2014

The microclimatic and macroclimatic data are presented in Table 2. On average, the microclimatic temperature was 1.5°C higher than the air temperature (Fig. S2a). Among the total microclimatic and macroclimatic temperature records, 7.3% and 10.3% were lower than -6°C , respectively. Complete darkness occurred in 57% of the total microclimatic PAR records (Table 2). The average annual mean microclimatic PAR was $155\ \mu\text{mol photons m}^{-2}\text{ s}^{-1}$ lower than the average macroclimatic PAR (Table 2 and Fig. S2b). This difference was higher from November to March when it reached $240\ \mu\text{mol photons m}^{-2}\text{ s}^{-1}$.

Table 1

Summary of the datasets used to model the daily net primary photosynthesis (NPP) of *U. aurantiaco-atra* at Livingston Island (maritime Antarctica) from 2009 to 2014.

Datasets	Climatic conditions	Metabolic activity	Output matrix
Dataset 1	Microclimate	Included	Microclimatic PAR and temperature, metabolic activity and the associated net photosynthetic rate.
Dataset 2	Microclimate	It was assumed that lichens were always active	Microclimatic PAR and temperature, and the associated net photosynthetic rate.
Dataset 3	Macroclimate	Included	Macroclimatic PAR and temperature, metabolic activity and the associated net photosynthetic rate.
Dataset 4	Macroclimate	It was assumed that lichens were always active	Macroclimatic PAR and temperature, and the associated net photosynthetic rate.

Table 2

Summary of the microclimatic and macroclimatic conditions measured from 2009 to 2014 at Livingston Island (maritime Antarctica). The 25%, 50% and 75% quantiles are represented as $Q_{25\%}$, $Q_{50\%}$ and $Q_{75\%}$, respectively.

	Microclimate		Macroclimate		
	Temperature ($^{\circ}\text{C}$)	PAR ($\mu\text{mol photons m}^{-2}\text{ s}^{-1}$)	Temperature ($^{\circ}\text{C}$)	PAR ($\mu\text{mol photons m}^{-2}\text{ s}^{-1}$)	RH (%)
Mean \pm standard deviation	-0.3 ± 3.9	30 ± 106	-1.2 ± 3.6	185 ± 339	82 ± 10
Minimum	-14.9	0	-17.4	0	32
$Q_{25\%}$	-2.9	0	-3.2	6	75
$Q_{50\%}$	-0.2	0	-0.6	16	84
$Q_{75\%}$	2.4	15	1.3	212	91
Maximum	23.4	2065	9.4	2961	100

The mean annual precipitation was 373 mm, with larger amounts in the summer months (Fig. S2d).

3.2. NPP from 2009 to 2014

The NPP estimates obtained based on the microclimate and considering when the lichen was metabolically active (“Dataset 1” in Table 1) exhibited a similar annual pattern for the four years monitored from 2009 to 2014 (Fig. 1).

The mean daily NPP (\pm standard deviation) was $0.25 \pm 0.09\text{ mg CO}_2\text{ gDW}^{-1}\text{ day}^{-1}$. The mean NPP during the warmest months from November to March was $0.7 \pm 0.2\text{ mg CO}_2\text{ gDW}^{-1}\text{ day}^{-1}$, and $-0.08 \pm 0.07\text{ mg CO}_2\text{ gDW}^{-1}\text{ day}^{-1}$ during the coldest months from April to October (Fig. 1).

The mean monthly NPP was positive during the warmest months and negative during the coldest months (Fig. 1), thereby indicating carbon gain and loss, respectively. The highest NPP occurred in February 2014 ($42.7\text{ mg CO}_2\text{ gDW}^{-1}\text{ month}^{-1}$) and the lowest in July 2014 ($-15\text{ mg CO}_2\text{ gDW}^{-1}\text{ month}^{-1}$) (Fig. 1).

The mean annual NPP over the 42-month period was $92.2\text{ mg CO}_2\text{ gDW}^{-1}\text{ year}^{-1}$. The mean NPP was $366.3\text{ mg CO}_2\text{ gDW}^{-1}$ in the warmest months and $-61.1\text{ mg CO}_2\text{ gDW}^{-1}$ in the coldest months.

Compared with the NPP modeling results based on microclimate and metabolic activity as main drivers (“Dataset 1” in Table 1), the other three datasets employed to estimate the NPP (“Dataset 2,” “Dataset 3,” and “Dataset 4” in Table 1) obtained the following overestimates (Fig. 2): (i) the NPP estimates based on microclimate and assuming that the species was always metabolically active were overestimated by 3.8 times, reaching $356.2\text{ mg CO}_2\text{ gDW}^{-1}\text{ year}^{-1}$; (ii) the NPP estimates based on macroclimate and including the metabolic activity were overestimated by 4.4 times, reaching $409\text{ mg CO}_2\text{ gDW}^{-1}\text{ year}^{-1}$; and (iii) the NPP estimates based on macroclimate and assuming that the species was always metabolically active were overestimated 9.8 times, reaching $906.6\text{ mg CO}_2\text{ gDW}^{-1}\text{ year}^{-1}$.

Comparison of the NPP estimates obtained at micro- and macro-scales showed that the monthly NPP values based on macroclimate were positive for all months throughout the year, whereas those based on microclimate were negative from May to October (Fig. 2). The NPP estimates were higher when the model was based on macroclimatic data.

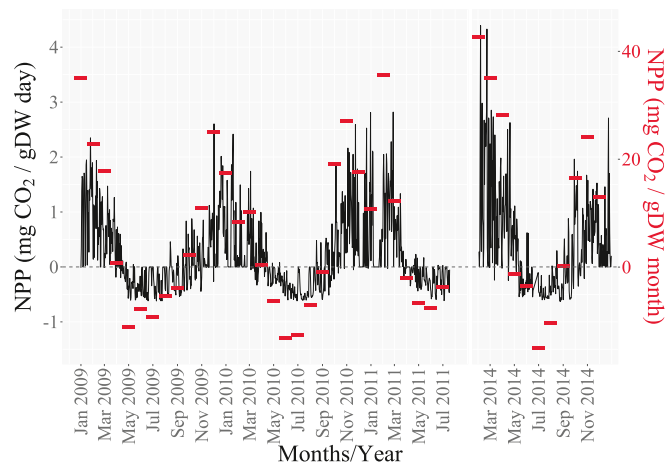


Fig. 1. Net primary productivity (NPP) from 2009 to 2014 of *U. aurantiaco-atra* at maritime Antarctica at daily (black lines) and monthly (red horizontal lines) intervals. The NPP estimations were based on microclimate and considering only the periods when the species was metabolically active. Negative values represent carbon losses and positive values represent carbon gains.

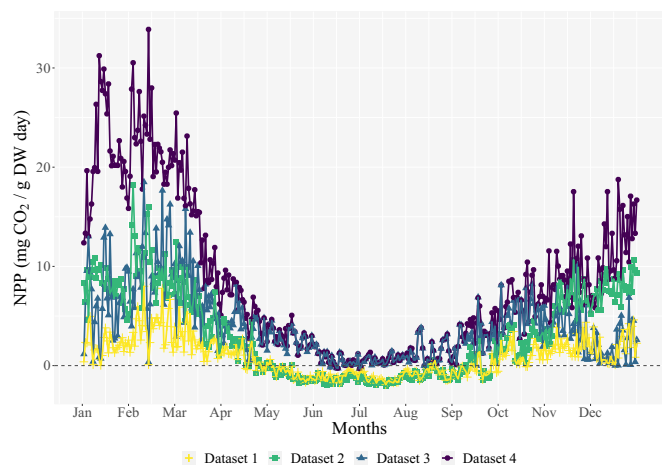


Fig. 2. Daily net primary productivity (NPP) of *U. aurantiaco-atra* at maritime Antarctica as the mean from 2009 to 2014. The NPP estimations were based on microclimate and considering only the periods when the species was metabolically active ('Dataset 1'); on microclimate but assuming that the species were always active ('Dataset 2'); on macroclimate and considering only the periods when the species was metabolically active ('Dataset 3'); and on macroclimate but assuming that the species were always active ('Dataset 4'). Negative values represent carbon losses and positive values represent carbon gains.

The response pattern of the NPP was analyzed with GAM 3, where the model had an R^2 value of 0.89 and it explained 90% of the total deviance. The significant variables according to GAM 3 are shown in Table 3. The graphic output of the model shown in Fig. 3 illustrates how the NPP changed according to both the abiotic factors and metabolic activity. The most important results in Fig. 3 are as follows: (i) temperature was a crucial driver when the species was metabolically active for long periods of time; and (ii) during shorter metabolic activity periods, higher PAR values and lower temperatures were required to maximize the NPP (Fig. 3 and Table 3).

3.3. Metabolic activity from 2009 to 2014

The long-term measurements of chlorophyll *a* fluorescence obtained in the field indicated that the mean annual metabolic activity (\pm standard

Table 3

Significance of the smoothing terms obtained from the generalized additive model (GAM 3), in which the effect of microclimate and metabolic activity on the daily net primary photosynthesis (NPP) of *U. aurantiaco-atra* at Livingston Island (maritime Antarctica) from 2009 to 2014 is evaluated. The edf corresponds to the estimated degrees of freedom. P value <0.05 is considered as the minimum level of significance.

Smoothing terms	edf	F-test	P-value
s(PAR)	6.93	0.27	0.969
s(Temperature)	6.23	25.7	<2e-16
s(Metabolic activity)	1	0.69	0.407
s(PAR, Metabolic activity, Temperature)	87.8	29.1	<2e-16

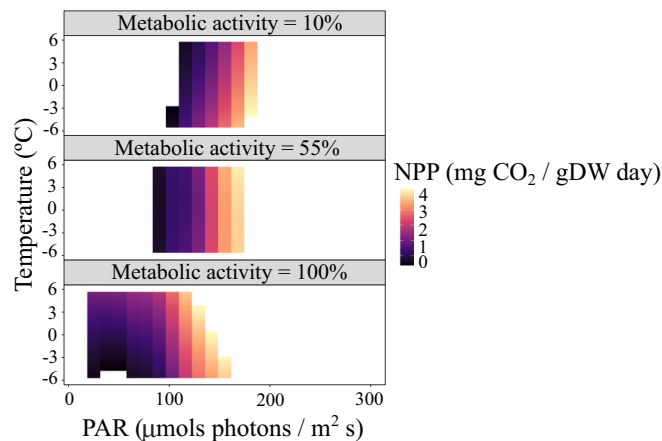


Fig. 3. Four-way interaction between daily microclimate (temperature and PAR), metabolic activity, and net primary productivity (NPP) from 2009 to 2014 of *U. aurantiaco-atra* at maritime Antarctica. The four-way interaction has been visualized as a contour plot of three-way interactions between daily microclimatic (temperature and PAR), and NPP at one different metabolic activity level (10, 55, and 100%). The colour gradient corresponds to the response variable, in which high NPP is shown in light orange and low NPP in black.

deviation) was $67.4 \pm 26.4\%$ from 2009 to 2014. The mean metabolic activity (\pm standard deviation) was $48.8 \pm 34.4\%$ in the warmest months and $80.1 \pm 20.9\%$ in the coldest months (Fig. S3).

Rainfall and snowfall caused metabolic activation in 4.3% and 0.28% of the total records, respectively. The other records where rainfall or snowfall were not recorded but the species was metabolically active ("non-precipitation events") comprised 95.4% of the total records.

The metabolic activity response pattern was analyzed with GAM 2, where the model had an R^2 value of 0.58 and it explained 60% of the total deviance. The significant variables according to GAM 2 are shown in Table 4. The graphic output from the model presented in Fig. 4 shows how the metabolic activity changed according to the abiotic factors. The

Table 4

Significance of the smoothing terms obtained from the generalized additive model (GAM 2), in which the effect of macroclimate on the daily metabolic activity of *U. aurantiaco-atra* at Livingston Island (maritime Antarctica) from 2009 to 2014 is evaluated. The edf corresponds to the estimated degrees of freedom. P value <0.05 is considered as the minimum level of significance.

Smoothing terms	edf	F-test	P-value
s(PAR)	1.00	2.49	0.11
s(Temperature)	6.24	2.49	0.02
s(RH)	2.35	0.73	0.51
s(Precipitation)	0.00	0.00	0.37
te(Temperature, PAR, RH): non precipitation events	34.96	3.86	0.00
te(Temperature, PAR, RH): rainfall	11.22	2.39	0.00
te(Temperature, PAR, RH): snowfall	8.49	1.33	0.21

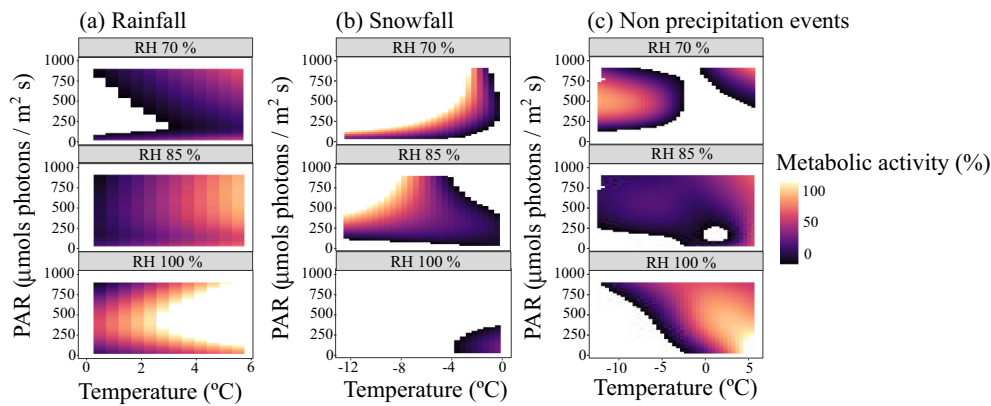


Fig. 4. Four-way interaction between daily macroclimatic (temperature, PAR, and relative humidity (RH)) and metabolic activity according to the hydration source (rainfall, snowfall, and non-precipitation events) of *U. aurantiaco-atra* at maritime Antarctica. The four-way interaction has been visualized as a contour plot of three-way interactions between daily macroclimatic (temperature and PAR), and metabolic activity at one different relative humidity level (70, 85, and 100%). The colour gradient corresponds to the response variable, in which high metabolic activity is shown in red and no metabolic activity in blue.

most important results in Fig. 4 are as follows: (i) the hydration sources (“rainfall,” “snowfall,” and “non-precipitation events”) had different effects on the metabolic activity pattern; (ii) the high relative humidity when it was raining and low relative humidity when it was snowing led to metabolic activity with a longer duration; (iii) when non-precipitation events were recorded but species were metabolically active, small changes in any driver led to greater changes in the duration of metabolic activity; and (iv) temperature was the main driver related to the metabolic activity response pattern (Fig. 4 and Table 4).

3.4. Metabolic activity and NPP predictions under climate change scenarios

The mean metabolic activity patterns were similar according to the RCPs and field measurements (Fig. 5), with high and relatively stable metabolic activity from May to October, and low rates from November to April. The metabolic activity was predicted to increase slightly under both RCP

scenarios (RCP 4.5 and RCP 8.5), especially at the end of the century. The mean metabolic activity was predicted to increase from 67.4% at present to 71.9/70.4% under RCP 4.5 and to 71.3/72.9% under RCP 8.5 for the middle/end of the century, respectively. In the warmest months (from November to March), the metabolic activity was predicted to increase from 48.8% at present to 56.9/57.3% and 56.9/60% under RCP 4.5 and RCP 8.5 for the middle/end of the century, respectively.

The mean NPP was predicted to increase under both RCPs in the middle and at the end of the century (Fig. 6). In the middle of the century, NPP was predicted to increase by 167% ($154 \text{ mg CO}_2 \text{ gDW}^{-1} \text{ year}^{-1}$) under RCP 4.5 and by 153% ($141 \text{ mg CO}_2 \text{ gDW}^{-1} \text{ year}^{-1}$) under RCP 8.5. At the end of the century, the NPP was predicted to stabilize under RCP 4.5 and to increase by 189% ($174 \text{ mg CO}_2 \text{ gDW}^{-1} \text{ year}^{-1}$) under RCP 8.5. The current five months of negative NPP were predicted to decrease to four months under both RCPs by the middle of the century and to three months under RCP 8.5 by the end of the century.

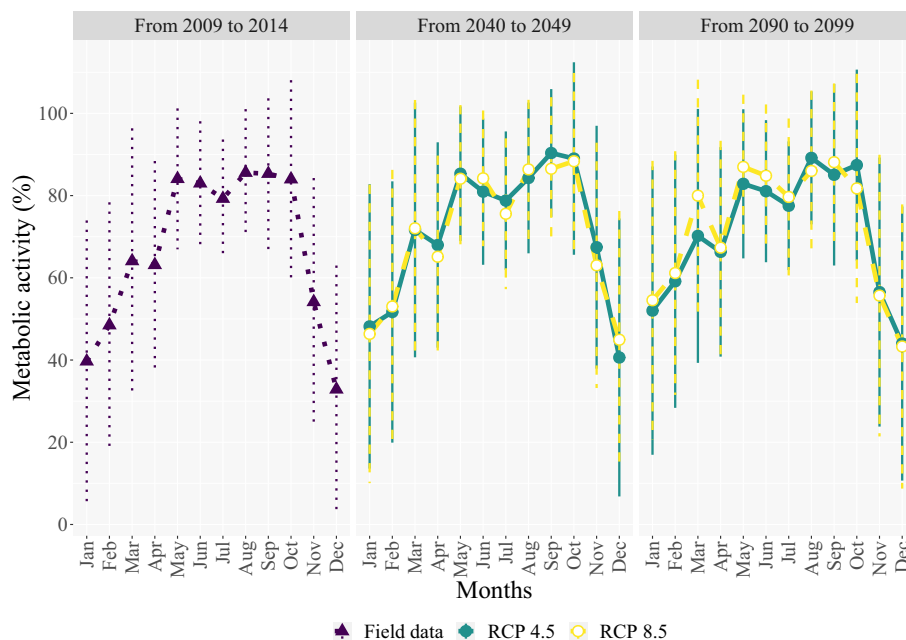


Fig. 5. Monthly mean of metabolic activity of *U. aurantiaco-atra* at maritime Antarctica for three different periods of time. The metabolic activity from 2009 to 2014 corresponds to the field measurements. The metabolic activity in the middle (2040 to 2049) and in the end (2090 to 2099) of the century corresponds to the projected values for the RCP 4.5 and RCP 8.5 scenarios. Vertical lines represent the standard error values.

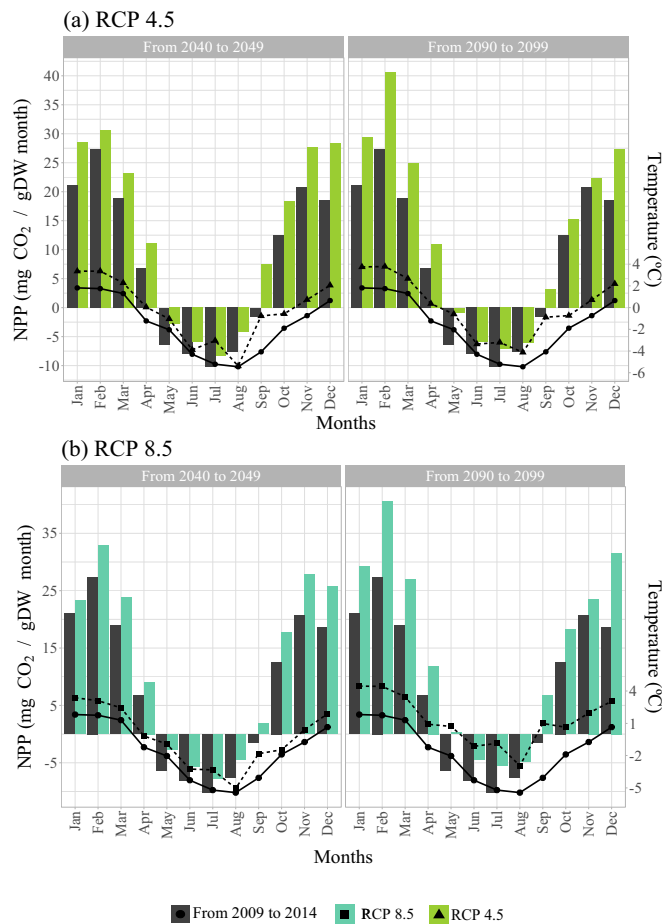


Fig. 6. Projection of the monthly net primary photosynthesis (NPP) at the middle and the end of the century for (a) RCP 4.5 and (b) RCP 8.5 of *U. aurantiaco-atra* at maritime Antarctica. Black bars represent the NPP from 2009 to 2014. Negative values represent carbon losses and positive values represent carbon gains. The black lines are the monthly mean of macroclimatic temperature for the present time and for the RCPs.

4. Discussion

4.1. Baseline for predictions under climate change: suboptimal conditions and spatial resolution in dormant species

Modeling the effect of climate change on the physiological performance of poikilohydric autotrophs is a complex problem because they are highly dependent on the microtopographic factors and are normally subjected to suboptimal environmental conditions.

The mismatch between the spatial scale of the models and organisms needs to be adjusted (Potter et al., 2013). The macroclimate-based NPP model showed that even when metabolic activity was included as a biotic driver, the NPP was overestimated by 4.4 times (Fig. 2) probably due to the macroclimatic PAR was six times greater than the microclimatic PAR. In fact, our findings showed that the NPP was higher when PAR was higher (Fig. 3). Quantifying the error incurred when modeling the NPP using micro- or macroclimate highlights the importance of the microtopographic conditions, which are highly heterogeneous and might diverge strongly from the surrounding macroclimate (Schroeter et al., 2017; Holmes and Dingle, 1965). Therefore, models established based on macroclimate are poor predictors of the NPP because microclimate is the main driver. Determining the effects of geographic scales on both the metabolic activity and NPP can allow a baseline to be established to elucidate the potential effects of climate change on the global carbon cycle in tundra biomes such as maritime Antarctica.

The ability of cryptogams to entry into dormant status is determined by the climatic conditions. The benefits of dormancy include allowing species to increase their resistance to freezing and water shortage, as well as avoiding the need to cope with high PAR and temperature conditions (Green et al., 2007). In general, the microclimatic temperatures when lichens are metabolically active in maritime Antarctica range from 1.1 °C to 4 °C (Schroeter et al., 2010; Schlensoeg et al., 2013; Raggio et al., 2016; Schroeter et al., 2017), which is around 10 °C lower than the optimal temperature for net photosynthesis measured under laboratory conditions (Kappen, 1985; Harrison et al., 1986, 1989; Harrison and Rothery, 1988; Kappen and Redon, 1987; Kappen et al., 1988; Schroeter et al., 1995; Laguna-Defior et al., 2016a). Our findings demonstrated that the duration of metabolic activity was a crucial biotic driver to model the NPP in dormant species, where the NPP was overestimated by 3.8 times when metabolic activity was not considered in the predictive models (Fig. 2).

4.2. Longer duration of metabolic activity during the summer under climate change

The response patterns of lichens to climate trends are highly dependent on their physiological tolerance range. In particular, their characteristic poikilohydry means that the capacity for survival is associated with the hydration sources available in a niche.

We found that the metabolic activity patterns changed according to the available hydration sources, which varied throughout the seasons. Rainfall mainly occurs during the Antarctic summer and high relative humidity appeared to be essential for delaying the dehydration process, thereby maximizing the metabolic activity (Fig. 4a). By contrast, snowfall led to high metabolic activity when the relative humidity was low (Fig. 4b). The effect of snowfall was not statistically significant (Table 4) but both rainfall and snowfall events appeared to trigger metabolic activation of the study species (Fig. 4). The metabolic activity detected when no precipitation events were recorded may have been due to the extension of metabolic activity after rainfall and snowfall events (Schroeter et al., 2010) because the species could remain wet for several hours under the low temperatures and high humidity recorded in maritime Antarctica (Barták et al., 2005). In these conditions, hydration could be extended for up to 20 h (Kappen and Schroeter, 1997).

The occurrences of metabolic activity when no precipitation events were recorded may also have been due to a wide variety of potential hydration sources, such as meltwater and snow cover. Small changes in any driver led to large changes in the duration of metabolic activity and temperature was the most important driver (Fig. 4c). Similar to rainfall events, high relative humidity led to high metabolic activity at temperatures above 0 °C (Fig. 4c). This effect can be explained by meltwater in the early summer, which has been established as another hydration source that is available for short periods of time to morphotypes attached tightly to rocks (Kappen, 2000; Barták et al., 2005). When temperatures dropped below 0 °C, high metabolic activity was dependent on PAR and it only occurred when the relative humidity was low (Fig. 4c). This pattern was suggested previously by Kappen et al. (1995) who concluded that lichens covered by snow layers could be metabolically active during the colder months. Some radiation may penetrate through the snow layer to melt the ice crystals closest to the lichen thalli and activate them (Kappen et al., 1995).

Relative humidity plays an indirect role in Antarctica (Fig. 4, Table 4) by prolonging the duration of metabolic activity rather than promoting metabolic activation (Green and Proctor, 2016). Hydration by humid air appears to be a slow process, and thus complete hydration of the lichen thalli may take a long time (Lange et al., 1988). However, it has been demonstrated that epiphytic species such as *Usnea dasopoga* may exhibit full reactivation under humid conditions (ca. 50 min; Phinney et al., 2018).

The seasonal metabolic activity patterns are not expected to change greatly by the end of the century. The metabolic activity response pattern highlights the effects of precipitation events, which are concentrated in the summer and spring seasons (AEMET, 2019; Vignon et al., 2021), and

freezing temperatures and low water availability do not imply a dormant state of metabolic inactivity during the Antarctic winter (Fig. 5; Robinson et al., 2003). Metabolic activity may increase from 67.4% to 70.4% and 72.9% at the end of the century under RCP 4.5 and RCP 8.5, respectively (Fig. 5). We hypothesize that the pronounced predicted increase during the warmest months is related to increases in the amount of the precipitation events and changes in the hydrological regimes (Lee et al., 2017; Vignon et al., 2021). However, the high metabolic activity found under the RCPs may be also explained by: (i) the accumulation of snow predicted at the end of the century in Antarctica providing protection to the species (Ye and Mather, 1997); and (ii) the ice melt predicted for coastal regions (Lee et al., 2017).

Therefore, under climate change conditions, lichens in tundra biomes with similar physiological tolerance ranges to the model species will exhibit increased periods of metabolic activity provided that liquid water is available. Furthermore, understanding how the response patterns of lichens are modulated by different hydration sources is crucial for assessing the potential effects of climate change on the survival of cryptogams due to the passive dependence of poikilohydric autotroph species on surrounding water.

4.3. Higher NPP under RCP 4.5 and RCP 8.5 due to climate warming

Under climate change scenarios, the projected increase in temperature will lead to increases in NPP of 167% and 189% under RCP 4.5 and RCP 8.5 at the end of the century, respectively (Fig. 6). These increases are supported by the significant effect of microclimatic temperature on NPP (Table 4), which we found was greater at high metabolic activity levels (Fig. 3). Therefore, extending the duration of metabolic activity will lead to higher NPP values at temperatures above 0 °C. However, the maximum NPP will be reached only if PAR is around 100–200 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, which corresponds to the mean PAR value when poikilohydric autotrophs are metabolically active in maritime Antarctica (Schroeter et al., 2017). NPP appears to be modulated by the ability of species to compensate for carbon losses at low PAR values, which is related to adaptation to the suboptimal conditions present in Antarctica (e.g., Kappen and Redon, 1987; Schroeter et al., 1995; Pannowitz et al., 2006).

The mean microclimatic temperature of -0.29 °C and PAR of 30 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ found on Livingston Island are markedly lower than the conditions needed to maximize NPP. The temperature at which *U. aurantiaco-atra* achieves its maximum net photosynthesis has been established as ca. 12.7 °C (Laguna-Defior et al., 2016). The NPP exceeded two times the mean NPP on 22.5% of the days from 2009 to 2014, which highlights that exceptional microclimatic conditions lead to an extra carbon gain. This opportunistic behavior in response to optimal transient periods is considered a strategy for maximizing the NPP and it may be related to rapid metabolic reactivation of the species (Kappen, 1985). Higher NPP values were predicted under climate change scenarios but the opportunistic response is unpredictable due to the low temporal resolution of RCPs, which are designed to operate at decade scales.

Therefore, according to our models, the effects of climate change on the NPP will be highly positive due to global warming. The synergy among abiotic conditions appears to be highly dependent on the species and its habitat (Colesie et al., 2018). However, the response to the CO_2 concentration has been investigated rarely in Antarctic cryptogams. Previous studies in other biomes showed that the tolerance of lichens to high CO_2 concentrations is dependent on the species (e.g., Lange et al., 1999; Lange, 2002), thereby demonstrating the need to produce better models for understanding the NPP response patterns of tundra biome species to climate change.

Changes in the NPP might affect the Antarctic landscape structure and community composition. Thus, the current biomes in the sub-Antarctic area such as Navarino Island (Southern Chile) could provide a good control model for the expected changes because they have similar macroclimatic conditions to those projected by RCPs for maritime Antarctica at the end

of the century. Previous studies of the same model species showed that the annual metabolic activity was lower on Navarino Island than maritime Antarctica (only 42.9%; Laguna-Defior, 2016) but the photosynthetic performance was similar in both areas (Laguna-Defior, 2016). It has been suggested that climate change will lead to the expansion of ice-free areas by about 25% (Lee et al., 2017), thereby providing more niches for colonization and increasing the connectivity between terrestrial vegetation patches. These changes could lead to biotic homogenization at a regional scale (Lee et al., 2017) and favor the best adapted species, but also lead to the extinction of less competitive species. New species might invade the ice-free areas, including colonization by mosses (Walther et al., 2002) or by invasive species such as *Poa annua* (Molina-Montenegro et al., 2016). Moreover, two higher plants that are present in Antarctica (*Colobanthus quitensis* and *Deschampsia antarctica*) might undergo rapid expansion in terms of both their extent and number (Smith, 2001). The invasion by *P. annua* might be explained by its high productivity, which is greater than that of the native *D. antarctica* (Green et al., 2007). In fact, the NPP of the native vascular plants in maritime Antarctica (Edwards and Smith, 1988) has been estimated as higher than those of bryophytes (e.g., Baker, 1972; Collins and Callaghan, 1980; Davis, 1981; Ino, 1983; Davey, 1997) and lichens (Hooker, 1980; Smith, 1984; Kappen, 1985, 1988; Schroeter et al., 1995; Schroeter, 1997).

5. Conclusion

Predicting how climate change will impact the terrestrial vegetation in Antarctica is challenging because the predominant terrestrial vegetation is symbiotic, poikilohydric, and strongly influenced by microtopographic factors. Therefore, considering drivers such as microclimate and metabolic activity is essential to avoid overestimating the NPP, thereby allowing a baseline to be established for elucidating the potential effects of climate change in tundra biomes such as maritime Antarctica. Under climate change conditions, metabolic activity is predicted to increase due to the greater availability of water sources, as well as, the NPP due to climate warming. Therefore, species with similar physiological ranges to the species investigated are expected to maintain similar behavior at the end of the century.

CRedit authorship contribution statement

Núria Beltrán-Sanz: Conceptualization, Methodology, Investigation, Resources, Writing – original draft, Writing – review & editing. **José Raggio:** Investigation, Writing – review & editing. **Sergi Gonzalez:** Formal analysis, Writing – review & editing. **Francesco Dal Grande:** Formal analysis, Writing – review & editing. **Stefan Prost:** Writing – review & editing. **Allan Green:** Supervision, Writing – original draft, Writing – review & editing. **Ana Pintado:** Investigation, Writing – review & editing. **Leopoldo García Sancho:** Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.155495>.

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