Plant Soil
https://doi.org/10.1007/s11104-026-08455-1

RESEARCH ARTICLE

# Understanding the links between functional performance and environment in cold desert ecosystems through the flagship biocrust forming moss *Syntrichia caninervis*

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Received: 30 September 2025 / Accepted: 27 February 2026

**Abstract**
*Background and aims* Biocrust communities shape the soil surface in drylands, regulating important ecosystem properties. Despite this, few works address key functional attributes in these poikilohydric photosynthetic communities, including the length of metabolic activity in the field and its relationship with microclimate. We aim to disentangle the links between functional performance of a keystone biocrust species and environment in drylands, in order to better understand ecosystem functioning and services provided to the soil by these organisms.
*Methods* We developed a 23 months monitoring experiment using very high resolution measurements of chlorophyll *a* fluorescence and microclimate in the field, comparing habitats with soils of different particle size composition and microclimatic conditions for the flagship biocrust moss *Syntrichia caninervis* on the Colorado Plateau, Utah, USA.
*Results* While growing in soils of different composition did not impair the functional performance of the species, the sun/shade plasticity did affect key physiological attributes. Our results quantified a strategy based on avoidance of the most extreme environmental conditions, where metabolic activity only occur during 19.9% of the total time monitored. Relative humidity was the best microclimatic predictor of metabolic activity, and the annual length of metabolically active periods showed strong convergences with other drylands of the world.
*Conclusions* These results collectively suggest a strong control of the environment over the ecosystem services provided by biocrusts. Our results include evidence for an improved understanding of the plasticity of *S. caninervis* to its variety of habitats, and its response to potential threats under different climate change scenarios.

**Keywords** Cryptogamic vegetation · Chlorophyll a fluorescence · Microclimate · Lichen and moss ecophysiology · Photosynthesis · Plant-soil interactions

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Responsible Editor: Amandine Erktan.

**Supplementary Information** The online version contains supplementary material available at https://doi.org/10.1007/s11104-026-08455-1.

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## Introduction

Plant life in drylands must cope a well-known set of environmental stress conditions, such as low water availability, high potential evaporation, long periods of dryness, big temperature drifts in short time periods, and strong solar radiation. Water availability and its variability, together with how water is accessible and useful for primary producers, are determining factors in these ecosystems, supporting important paradigms in desert plant ecology (Noy-Meir 1973; Reynolds et al. 2004).

Plants have managed to inhabit drylands using different general strategies that can be either structural or physiological. The environmental conditions could reduce plant functionality, but the reality is that there is high diversity in plant forms, functions, and metabolic pathways for optimizing photosynthesis in these ecosystems (Ehleringer 1995; Gibson 1998; Maestre et al. 2021). This apparent contradiction has been defined as the "functional paradox of drylands" (Maestre et al. 2021).

Drylands research in the last few decades has emphasized the importance of a less visible group of heterogenic organisms grouped under the term biocrusts, formed by mosses, lichens, liverworts, cyanobacteria, algae, fungi, and heterotrophic bacteria living in the uppermost centimetres of the soil surface (refer to Belnap et al. 2016). Despite being small and often inconspicuous, increasing knowledge about biocrusts is aiding in forming a more complete understanding of drylands functioning. The services that biocrusts provide to ecosystems are linked to their intimate association with the soil, covering a wide spectrum from soil erosion and water control to the promotion of soil biodiversity (Sancho et al. 2014; Xiao et al. 2022). When biocrusts are present, normally in habitats where vascular plants coverage is constrained, carbon fluxes between soil and atmosphere are strongly influenced by these organisms (Sancho et al. 2016).

The relevance of studying mosses inside the biocrust community has been recently reviewed by Ladrón de Guevara and Maestre (2022), demonstrating their importance in dryland ecosystems. Biocrust forming mosses often dominate communities in later stages of biocrust successional processes, promoting the development of more complex plant communities in drylands (Lan et al. 2021). Using moss dominated biocrusts to prevent soil erosion has shown to be successful, and its photosynthetic efficiency (in terms of carbon fixation) at optimum water contents is the highest among the biocrust community (Ladrón de Guevara and Maestre 2022). Further, Eldridge et al. (2023) have recently shown that biocrust mosses are huge carbon reservoirs worldwide, supporting ecosystem multifunctionality in areas where vascular plant cover is low.

The species chosen for this work, the biocrust forming moss *Syntrichia caninervis* Mitt, is a flagship species in biocrust research. It is a drought-resistant moss that is widely distributed through drylands of the Northern Hemisphere (Pan et al. 2016), and it probably is the most studied biocrust species in hotspots for drylands research such as the Colorado Plateau in the United States of America (USA) and the Gurbantünggüt Desert in China. Previous research from Tao and Zhang (2012) and Pan et al. (2016) showed morphological adaptations of the species in the form of a tiny hairs at the tip of each leaf that allows for the capture of three different types of water sources (high humid atmosphere -water vapour-, fog –suspended liquid water- and liquid water –free water in the moss surface-), linking morphology and functionality for living in deserts. The importance of precipitation pulses over the C balance of *S. caninervis* has been deeply studied (Barker et al. 2005; Coe et al. 2012; Wu et al. 2015; Young et al. 2025), with results showing increases in mortality of the species linked to changes in summer precipitation patterns (Reed et al. 2012; Phillips et al. 2022). Furthermore, *S. caninervis* has been analysed from different perspectives such as its physiological and cytological tolerance to desiccation and UV radiation (Ekwealor et al. 2021; Zhang et al. 2011), exploration of linkages between desiccation tolerance and climate change (Clark 2020), and its performance under snow cover in the field (Yin et al. 2021; Zhang and Zhang 2020). All this available knowledge combined with its wide distribution through the northern hemisphere, makes *S. caninervis* as an excellent model species for dryland research focused on biocrusts.

This study aims to enhance our understanding of potential patterns of ecological plasticity and the influence of soil type on the ecosystem functioning of *Syntrichia caninervis*. We focus on detailed, daily physiological performance measurements in the field and explore how these are linked to environmental conditions. As a poikilohydric organism, *S. caninervis* is only metabolically active when hydrated, which serves as a stress-avoidance strategy, allowing the moss to quickly desiccate and thus avoid damage during extreme climatic conditions (Green and Proctor 2016). This avoidance strategy is key to its ability to survive in harsh environments such as drylands (Green et al. 2011). Long-term monitoring of chlorophyll *a* fluorescence alongside microclimate data provides valuable insight into these avoidance strategies (Schroeter et al. 2011). These tools help quantify the percentage of time the organism is metabolically active under varying environmental conditions, which is a key indicator of field-level functional performance. Additionally, although they have not been quantified, both photosynthetic and respiratory activity situations are included in the monitoring, which are critical to assessing the potential carbon balance of these photosynthetic organisms (Schroeter et al. 2000; Beltrán-Sanz et al. 2022). By analyzing the evolution of the metabolic activity periods together with microclimate, we can assess the degree of environmental stress in each habitat. A low percentage of metabolic activity often reflects the organism's strategy to remain dormant during average conditions, becoming active only during select, milder periods (Green et al. 2007; Green and Proctor 2016). Our central hypothesis is that *S. caninervis* exhibits a functional pattern consistent with long periods of metabolic inactivity during the more extreme climatic situations, and reduced periods of metabolic activity during milder environmental conditions. We also propose that the species' ecological plasticity across the study area is supported by distinct functional strategies associated with the different microhabitats examined.

Here, we present findings from 23-month field investigation of *S. caninervis* physiology on the Colorado Plateau, USA. We measured the percentage of metabolic activity in a temporal basis along with key physiological traits, specifically, quantum Yield, maximum photochemical efficiency (Fv/Fm), and electron transport rate of Photosystem II. Additionally, we monitored essential microclimate variables, including moss surface temperature, relative moisture and photosynthetic active radiation. Data were collected across two separate experiments (experiment I and experiment II) to assess environmental and physiological dynamics over time. The area chosen is an important and representative site of cold deserts and continental drylands worldwide, and an important location for biocrust research (Finger-Higgens et al. 2022). Several researchers have proposed that the species is physiologically plastic and widely distributed in different niches of the Colorado Plateau (Bowker et al. 2000; Clark 2020). Thus, a wide monitoring of different microhabitats can help to cover a comprehensive distributional pattern of the species. Altogether, this research contributes to building a comprehensive understanding of *Syntrichia caninervis*' responses to environmental change. Such insights are valuable for informing models that project a potential 25–63% decline in the species' productivity under future climate scenarios (Coe & Sparks 2014). By identifying periods of metabolic activity and assessing physiological performance during those times, this study also advances our understanding of the ecological services *S. caninervis* provides to these widespread dryland ecosystems.

## Material and methods

### Sites and species description

This study was conducted at two field sites on the Colorado Plateau, USA. The first site was located near Castle Valley, Utah, approximately 30 km northeast of Moab (38.67448° N, −109.41492° W), at an elevation of 1,350 m above sea level. The area has a mean annual temperature of 13 °C and receives about 269 mm of precipitation annually (Darrouzet-Nardi et al. 2015). Soils are calcareous sandy loam Aridisols of the Rizno series, composed of 61% sand, 21% silt, and 15% clay (Darrouzet-Nardi et al. 2015). The vascular plant community includes *Achnatherum hymenoides*, *Pleuraphis jamesii*, *Bromus tectorum*, and *Atriplex confertifolia*. Biocrusts are dominated by *Syntrichia caninervis*, *Microcoleus vaginatus*, and the cyanolichens *Collema tenax* and *Collema coccophorum*, with maximum crust cover reaching up to 40% and average values around 26% (Darrouzet-Nardi et al. 2015). The second site was located on the outskirts of Moab, Utah (38.55663° N, −109.50657° W), at 1,227 m elevation, with a mean annual temperature of 13.3 °C and annual precipitation of 229 mm (Geiger et al. 2023). Dominant vascular plants species include *Ephedra viridis*, *Artemisia filifolia*, and *Coleogyne ramosissima*. Biocrusts at this site are mainly composed of *S. caninervis* and *M. vaginatus*, with no lichen-dominated communities present. Biocrust cover at the Moab site is lower than at Castle Valley, averaging around 15% (Geiger et al. 2023). Soils are Aridisols with a sandy composition (86% sand, 6% silt, 6% clay; Geiger et al. 2023). Both sites are situated in a semi-arid, cool desert climate characterized by cold, snowy winters and a bimodal precipitation regime, with peaks in winter–spring and during the summer monsoon season (Belnap 2002). The Moab site, being closer to developed areas, experiences greater human disturbance compared to the more remote Castle Valley location. *S. caninervis* has a wide distribution in deserts and basins of the southwest of the USA, and is properly described morphologically and ecologically in Bowker et al. (2000). The species tolerates different elevations and different microhabitats such as exposition to full sun and more shaded sites, then with different degrees of radiation and soil water content (Bowker et al. 2000; Stark et al. 2005).

## Experimental design

For experiment I, three patches separated by at least 1 m of *S. caninervis* were monitored at each of the two research sites (Castle Valley and Moab sites; total of six samples monitored) from October 4th 2016 to May 29th 2017, completing 236 consecutive days of comparison between the two. The aim of the experiment was to compare the functional performance of the species in two field sites that are different regarding biocrust cover, diversity and soil texture. The monitoring ended on the last date mentioned due to equipment failure. For experiment II, three different patches were monitored at two different microsites in the Moab site (total of six samples monitored) from September 29th 2018 to December 31 st 2019, completing 15 months of consecutive measurements. The two microsites chosen were the understory (shade microsites) of the most abundant shrubs in the area, *Ephedra viridis*, and free interspaces clearly separated from vascular vegetation (sun microsites), coinciding with microsites types selected in past experiments (Bowker et al. 2000; Clark 2020; Stark et al. 2005). We also were careful to obtain full sun protection for the monitoring probes.

For both experiments, we carried out chlorophyll *a* fluorescence monitoring and microclimate measurements. The equipment chosen for the approach was a HexPAM fluorometer (Gademann Instruments, Germany), a Pulse Amplitude Modulated (PAM) device based on the saturation pulse methodology (refer to Schreiber et al. 1995). Each piece of equipment had a central unit linked to several independent probes, with each of them including a non-invasive fiber optic cable for detecting chlorophyll *a* fluorescence, and three microclimatic sensors for detecting air relative moisture (RM, analogue to air relative humidity), temperature and photosynthetic active radiation (PAR), all placed only a few cm from the monitored sample location. The RM sensor was placed in the bottom part of the probe, exposed to the air and only a few cm away and at similar height compared with the place where the fiber optic was pointing to the biocrust for the fluorescence monitoring, allowing that way similar microhabitats between both points.

The relative moisture (RM) and air temperature data recorded at each measuring point were used to calculate the Vapour Pressure Deficit (VPD). VPD is defined as the difference between the saturated vapour pressure at a given air temperature and the actual vapour pressure of the air (e.g., Jones 2014). It represents the evaporative demand of the atmosphere and is a key ecophysiological variable because it integrates temperature and relative humidity into a single metric directly related to plant transpiration. We calculated atmospheric VPD as the difference between the saturated vapour pressure ($P_{sat}$, kPa) and the actual vapour pressure ($P_{air}$, kPa). First, $P_{sat}$ was calculated using the updated formulation of the Buck equation for water surfaces (Buck 1981, 1996):

$$P_{sat} = EF_w \times 0.61121 \times \exp\left(\frac{(18.678 - T/234.5)T}{257.14 + T}\right)$$

where $T$ is air temperature (°C).

The enhancement factor $EF_w$, which corrects for non-ideal behaviour of moist air as a function of atmospheric pressure, was calculated as:

$$EF_w = 1 + 10^{-4}\left[7.2 + P\left(0.0320 + 5.9 \times 10^{-6}T^2\right)\right]$$

where $P$ is atmospheric pressure (we used an standard value of 101.325 kPa).

Second, the actual vapour pressure ($P_{air}$, kPa) was obtained following Tetens (1930):

$$P_{air} = P_{sat} \times \frac{RM}{100}$$

where $RM$ is relative moisture (%).

Measurements of all variables were scheduled each 15 min, being automatically recorded by the equipment after a saturation pulse and then sent to a website through modem connection immediately after data acquisition. This methodology allowed us to obtain four key physiological variables that are indirect indicators of the photosynthetic process. As such, the following functional traits were obtained: (i) Φ of PSII, that is the quantum Yield of Photosystem II, that will be summarized along the text and graphs as the term "Yield". This value is calculated as the ratio between the maximum fluorescence (Fm´) and steady-state fluorescence ($Ft'$) under illuminated conditions using a saturating light pulse and a weak measuring light, respectively (Yield PSII = (Fm′ – Ft′)/Fm′; refer to Raggio et al. 2023). This parameter reflects the efficiency with which absorbed light is used in the photochemical pathway when the sample is exposed to illumination (environmental PAR > 0), and when all three competitive mechanisms that disperse incident light in a photosynthetic organism (fluorescence, heat dissipation, and photochemical pathway) are active (Maxwell and Johnson 2000). (ii) Maximum photochemical efficiency (Fv/Fm), which is calculated with the same methodology as Yield PSII but in dark conditions (PAR = 0). This important difference implies that Yield and Fv/Fm have different functional meanings, with the latter being an indicator of the state of the health of the PSII, and, in extension, and indicator of the exposure to stress conditions in photosynthetic organisms. Optimal unstressed ranges for this indicator in mosses normally falls between 0.76 and 0.83 (Proctor 2003). The Fv/Fm values provided in our analyses are daily means of all the nighttime period evaluated each 15 min, providing then a big amount of activity data points under complete dark conditions. This guarantees a strongly reliable perspective for complete dark adaptation values in the field for the moss monitored. A value of Fv/Fm bigger than 0 indicates that there is variable fluorescence (Fv) in the sample monitored, that is the rest between the maximum and the minimum fluorescence (Fm-Fo, see Maxwell and Johnson 2000). This variable fluorescence is an indicator of metabolic activity (biocrust is obtaining water). (iii) Electron Transport Rate (ETR), was calculated by multiplying the Yield PSII by the incident PAR under conditions of illumination and correction factors ($ETR = Yield\ PSII \times PAR \times 0.5 \times 0.84$) and is a proxy indicator of photosynthetic productivity. In this work we use ETR as a qualitative approach to photosynthetic productivity, indicating that the situations with higher ETR accumulated in a time period should be more productive from a photosynthetic perspective, but without assuming risks of related with extrapolations to quantitative C fixation. Following the formula, the ETR is always 0 in absence of PAR, and needs illumination to be calculated. (iv) Percentage of metabolic activity, which calculates the length of the active periods. This was calculated on a daily basis as the number of total points recorded with metabolic activity divided by the amount of total points recorded (which are 96 points every day, with measurements every 15 min as stated above). All recorded points with Yield PSII > 0, or Fv/Fm > 0 were considered as situations where the biocrusts were hydrated at different extents, and were thus recorded as metabolic activity situations, allowing for the separation of metabolically active and inactive periods. The ability of cryptogams to rapidly switch metabolic activity on and off in response to hydration status is central to their survival strategy, in contrast to vascular plants, which lack this desiccation-tolerant capability.

### Data management and statistical analyses

From here on we will refer to treatments as the different situations evaluated in each Experiment (i.e. Experiment I: higher—Castle Valley site—vs lower—Moab site—biocrust diversity and Experiment II: shade versus sun microsites).

During the time span of both experiments, the equipment manifested certain technical problems or measurement errors that led to the records containing missing entries in microclimatic variables. Summarizing, the amount of missing data was dependent of each of the three microclimatic sensors at each probe that was monitoring each sample. For example, one probe could have two sensors working properly, and one missing data during a certain period. The most usual percentage of missing data for all the sensors and probes together was between 2.4% and 7.5% from the total amount of data recorded, with peaks in some probes and sensor of 46.6% and 67% (refer to Online resource 1, Table S1 for all the percentages by sensor and microclimatic parameter). It should be noted that the frequency of our recordings, every 15 min over 23 months for two experiments, implies that tens of thousands of data entries were recorded for each of the variables and sample, providing a robust data set for understanding microclimatic and functional patterns in the species, despite some erroneous readings.

Despite of the big amount of data available for all the parameters monitored during the study, the existing gaps already mentioned create statistical constraints when we aim to establish comparisons between treatments in both experiments I and II. In order to solve this issue, we have imputed missing data and fill in the gaps, following the methodology proposed by Moreno et al. 2022, where they applied this approach in an experiment with similar structure to the one reported here. To estimate missing values in sensor *y* for microclimatic variable *z* at time *t*, we identified a corresponding sensor *x* (with no missing data for *z* at time *t*) that best met the following criteria: (i) highest percentage of shared complete observations for variable *z* between sensors *x* and *y*, (ii) strongest correlation of those shared observations, and (iii) similarity in experimental treatment between sensors. To quantify this selection, we calculated a selection score ($S_x$) for each candidate sensor *x* using the following expression:

$$Sx = \%VC_{x,} + \left(R^2_{x,} \cdot 100\right) + \left\{100,\ if\ treatment_x = treatment_y\ or\ 0, otherwise\right\}$$

where sx, that ranges from 0 and 300, represents the selection score of the sensor x; $\%VC_{x,}$ is the percent of complete observations (i.e., have no missing values) that are shared between sensors x and y; $r^2_{x,y}$ is the Pearson's $R^2$ of the complete observations for x and y sensors; and $treatment_x$ and $treatment_y$ are the respective treatment of the x and y sensors for the experiment I and II. During data interpretation, the sensor *x* used as predictor to estimate the missing value in the sensor y was selected according to the higher selection score. The missing value in the sensor y was then estimated with the linear model (y ~ x) fitted with the complete observations between x and y sensors of the microclimatic variable z.

To assess the main effects of the corresponding treatment of each experiment on ecophysiological (% of activity, Yield, Fv/Fm, and ETR) and microclimatic (temperature, RM, and PAR) response variables, we fitted repeated-measures mixed-effect models. Two models were constructed independently for each experiment and response variable, one for the day periods and another for the night periods, separating periods using an incident PAR threshold of 0 µmol $m^{-2}$ $s^{-1}$. Variables were averaged daily for each sensor and period, with Yield and Fv/Fm averaged only across positive values to reflect active metabolic periods.

In each model, treatment was included as a fixed factor and moss replicates as random factors to account for repeated measurements. Additionally, seasonal effects were modelled using a categorical variable combining treatment, season, and year (IntFac), where each level represents a unique treatment × season × year combination, allowing evaluation of seasonal differences both within and between treatments while accounting for interannual variation. Pairwise differences among levels were assessed using Tukey contrasts post-hoc.

The model family was chosen according to the response variable distribution:

> Percentage of activity was analysed using binomial GLMMs. For each sensor and day, the response was the number of hours with metabolic activity (n_Y) out of the total monitored hours per day (n_hours), with n_hours used as binomial weights.
>
> Relative humidity was expressed as a proportion (RM/100) and modelled using beta GLMMs with a logit link. No values of exactly 0 or 1 were present.

PAR and ETR were modelled using gamma GLMMs with a log link and including only positive values

The remaining variables (temperature, Yield and Fv/Fm) were analysed with linear mixed-effect models, as assumptions were met.

To evaluate microclimatic conditions during moss activity, temperature, RM, and PAR were averaged daily for each sensor and period only for days with Yield or Fv/Fm > 0 and analysed with the same model framework. Additionally, three GLMMs were fitted for Experiment II to assess the effect of temperature, RM and VPD on % activity of *S. caninervis*, including lineal or quadratic and treatment interaction terms as fixed factors, and moss replicates as random factors. Dependent and fixed variables were daily-averaged, and binomial distributions were used.

The packages dplyr (Wickham et al. 2021), lme4, (Bates et al. 2015), glmmTMB (Brooks et al. 2017), multcomp (Hothorn et al. 2008), MuMIn (Barton 2020) and ggplot2 (Wickham 2016) were used for data analysis and graph preparation in R version 4.0.5 (R Core Team 2021).

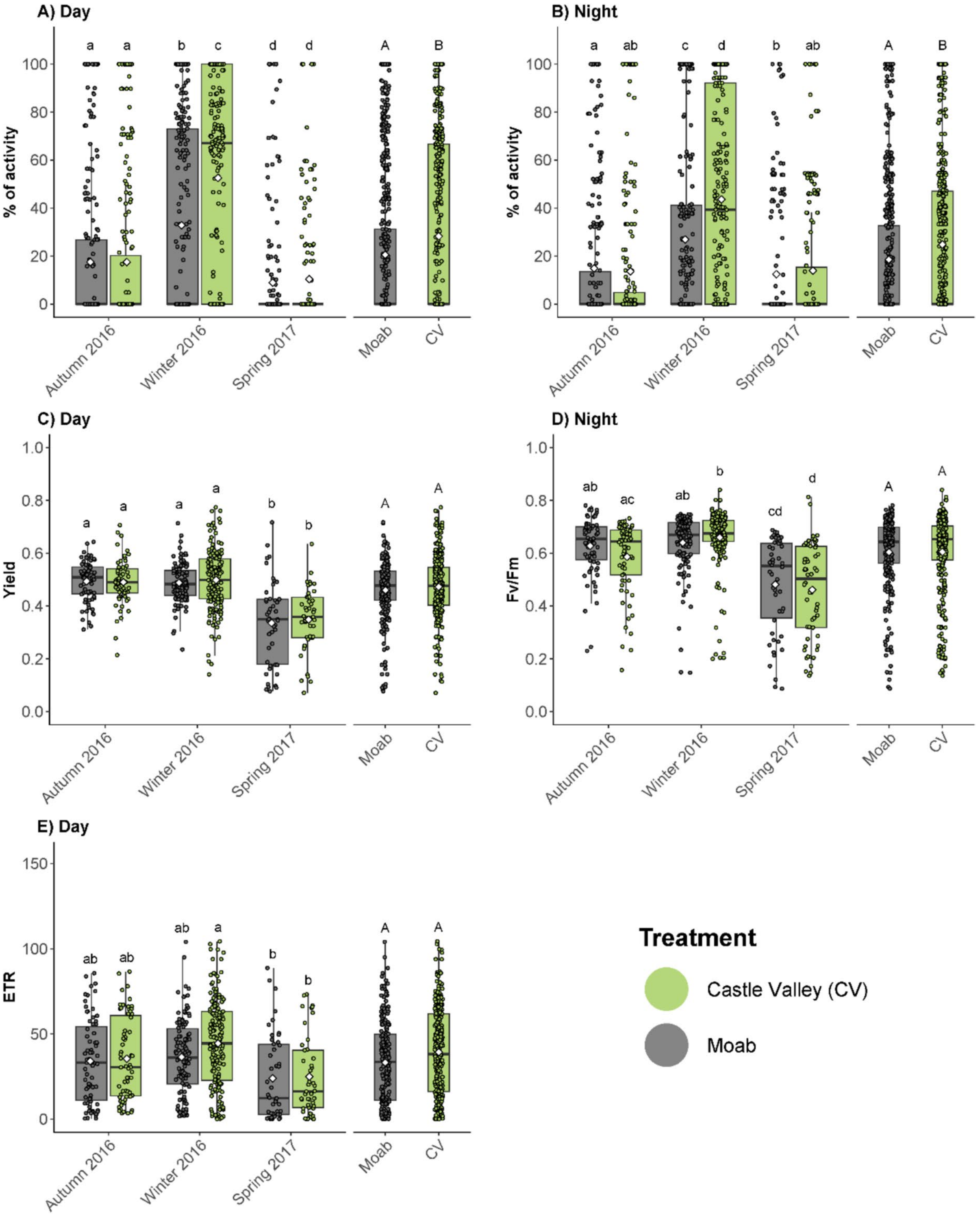
## Results

### Experiment I: Comparison between areas with different biocrust diversity and cover

The first experiment aimed to compare the functional performance and the microclimate of *S. caninervis* in two areas of the Colorado Plateau that differ in biocrust diversity, cover, vascular plant composition, and soils texture. Analyses of the main ecophysiological indicators found a similar trend between sites for Yield, Fv/Fm and ETR, but not for the percentage of metabolic activity, which was significantly higher in Castle Valley, with the winter season accounting for the majority of the general difference observed (Fig. 1). The spring showed a drastic reduction in the % of metabolic activity, accompanied by a smoother reduction of Yield and Fv/Fm (Fig. 1). When microclimatic conditions were analysed over the total measurement period of experiment I, including both active and inactive periods, more statistically significant differences between sites were observed. Specifically, nighttime temperature and daytime relative moisture (RM) were significantly higher at the Castle Valley site (Online Resource 2, Fig. S1). Conversely, when microclimate was analysed for only activity periods, we observed a different and more homogeneous pattern, with only RM during day showing statistical differences between sites, being higher again in the Castle Valley site. All the other microclimatic variables showed no statistical differences between sites (temperature during day and night, RM during night and PAR, Online Resource 2, Fig. S2). Finally, the seasonal comparisons regarding microclimate showed broader ranges and more differences among seasons for RM, temperature and PAR when all the monitoring periods were included (Online Resource 2, Fig. S1), and narrower ranges and less variability among seasons regarding the same variables when data are analysed only during activity (Online Resource 2, Fig. S2).

### Experiment II: sun and shade microsite comparisons

The percentage of daily activity (all activity situations with PAR > 0, Fig. 2A) trended to be higher in the shade compared to the sun microsites in all seasons, supported with a statistically significant difference in favour of the shade over the complete period (Fig. 2A). The autumn and the winter showed clearly higher percentages of activity compared with the spring, followed by the summer, which appear to be the most restrictive seasons for metabolic activity. The percentage of activity during the night (PAR = 0, Fig. 2B) followed a similar trend to that observed during the day. However, the higher activity observed in the shade microsite was less pronounced and not statistically significant over the entired period when compared to the sun microsite. An inverse pattern was observed for the analysis of Yield and Fv/Fm, that was higher in both cases for the sun microsites, but only statically significant in the long-term in the case of the Yield (Figs. 2C and 2D). A similar pattern as the one detailed in Fig. 2A was observed for the seasonal evolution of Yield and Fv/Fm, that are higher during autumn and winter and decreases in spring and mainly in summer, the season where both variables reach their minimum. The ETR (Fig. 2E) was higher and significant in the sun microsites and was lower in spring and summer compared with autumn and winter, despite the less amount of light available in these periods of the year.


A) Day
B) Night
C) Day
D) Night
E) Day
% of activity
Yield
Fv/Fm
ETR
Autumn 2016
Winter 2016
Spring 2017
Moab
CV
a a b c d d A B
a ab c d b ab A B
a a a a b b A A
ab ac ab b cd d A A
ab ab ab a b b A A
Treatment
Castle Valley (CV)
Moab

◂**Fig. 1** Box plots showing the daily distribution of moss **A – B**) % of activity, **C**) yield, **D**) Fv/Fm and **E**) ETR for the day (PAR > 0; left panels) and night (PAR = 0; right panels) periods in experiment I. Each panel represents distribution for the Moab and Castle Valley (CV), Utah, sites conditions grouped by season and for the complete data series. Coloured dots and colour diamonds represent daily records and mean values respectively of each variable by treatment and season. Letters above each box plot indicate significant differences ($p < 0.05$, Tukey Contrasts post-hoc test) after a mixed-effect model. Daily yield and Fv/Fm values result from averaging only positive values (i.e., reflecting the situations where the moss is metabolically active)

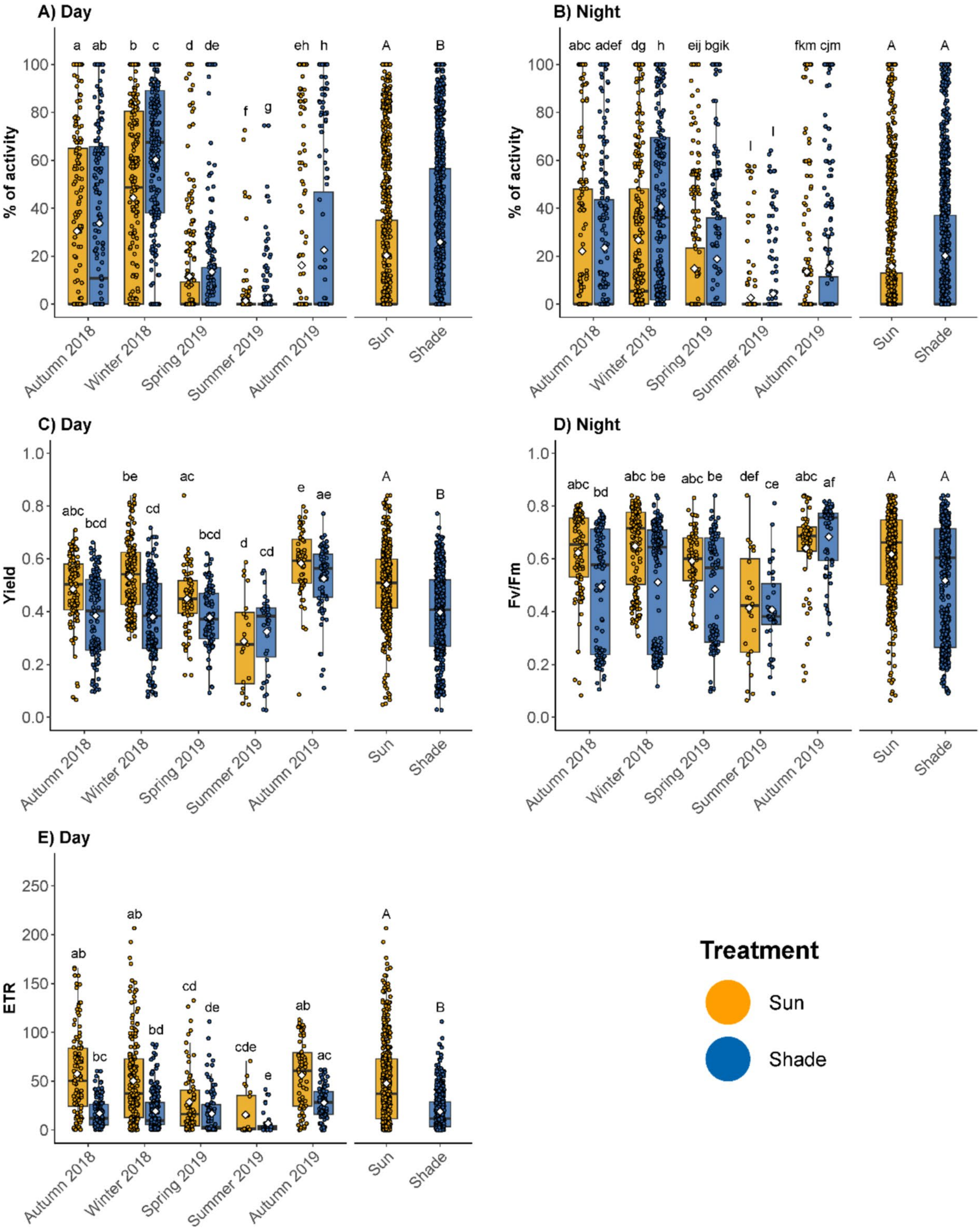
A similar comparison was tested for the main microclimatic parameters analysed in the experiment during all the measuring period (Fig. 3). As expected, T on the surface of *S. caninervis* followed a macro environmental pattern, being higher in the summer and lower in winter, and showing a statistically significant difference in the long term in favour of the sun microsite during the day period (Fig. 3A). The RM showed an inverse pattern compared with T in relation with the values obtained at each of the seasons, being lower in the sun, but with non-statistical difference in the long term (Fig. 3C). The PAR is notably higher and significant in the sun vs the shade treatments and follows a clear macro environmental pattern across the year (Fig. 3D). During activity (Fig. 4), the microclimatic conditions differed considerably from those measured during all the recordings (Fig. 3), and showed also less differences among seasons in comparison (refer to Fig. 3 vs Fig. 4). Specifically, there were less statistically significant differences considering all the seasons together in the microclimate when active (Fig. 4A-4D) compared with the microclimate that considers activity and inactivity situations (Figs. 3A-3D).

Continuous monitoring of both microclimate conditions and sample functional performance allowed for the establishment of predictive models of metabolic activity (Fig. 5 and Online Resource 2, Table S1). Both microclimatic temperature and RM were individually good predictors of the percentage of metabolic activity, with RM showing stronger predictive power. Specifically, RM alone had a statistically significant coefficient of determination ($R^2 = 0.71$), outperforming temperature as a predictor (Online Resource 2, Table S1). Metabolic activity saturated at temperatures above 10 °C (Fig. 5A), indicating that activity predominantly occurs under cooler conditions. In contrast, Fig. 5B reveals that RM values below 30% suppress activity entirely, while maximum activity occurs at RM levels between 75 and 80%, with a plateau maintained at higher RM levels. Finally, Fig. 5 also shows the relationships between VPD and the % of activity (Fig. 5C). It can be observed how it has a strong and similar predictive power as RM over % of activity, with and $R^2 =$ to 0.67, but with a negative lineal relationship for both treatments (sun and shade) that creates a collapse of metabolic activity at values slightly over 1.5 kPa of VPD.

Functional performance understood as Yield and Fv/Fm of the moss was restricted to certain windows of microclimatic situations, with narrow ranges between 0 °C and 20 °C in the case of day temperature and broader ones between 25 and 100% in the case of RM (Online Resource 2, Fig. S4). Figure S4 reinforces the information provided by Fig. 5, but in this case showing direct relationships between microclimate and other important physiological parameters, different to % of activity, such as Yield and Fv/Fm.

Consistent results were observed across experiments I and II, with both showing an average of approximately 20% metabolic activity across all conditions analyzed (Table 1). During periods of metabolic activity, mean microclimatic temperature was roughly half (or even less) of the mean temperature observed across the full measurement period. In contrast, RM values during active periods were at least 20% higher than the overall mean. Similarly, photosynthetically active radiation (PAR) levels were consistently lower during active periods, though specific ranges varied by experiment.

Mean Yield values during periods of activity (calculated as the average of Yield during the day and Fv/Fm during the night) were close to 0.5, for instance, 0.57 for the sun treatment in Experiment II, 0.48 for the shade treatment in Experiment II, and 0.56 for both Moab and CV sites in Experiment I (Table 1). While these values are lower than those expected under optimal, unstressed conditions (typically 0.7–0.8), they represent averages across the entire monitoring period, encompassing a wide range of environmental conditions that may induce physiological stress.


A) Day
% of activity
0
20
40
60
80
100
a
ab
b
c
d
de
f
g
eh
h
A
B
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
B) Night
% of activity
abc
adef
dg
h
eij
bgik
l
l
fkm
cjm
A
A
C) Day
Yield
0.0
0.2
0.4
0.6
0.8
1.0
abc
bcd
be
cd
ac
bcd
d
cd
e
ae
A
B
D) Night
Fv/Fm
abc
bd
abc
be
abc
be
def
ce
abc
af
A
A
E) Day
ETR
0
50
100
150
200
250
ab
bc
ab
bd
cd
de
cde
e
ab
ac
A
B
Treatment
● Sun
● Shade

◂**Fig. 2** Box plots showing the daily distribution of moss **A** – **B**) % of activity, **C**) yield, **D**) Fv/Fm and **E**) Electron Transport Rate (ETR) for the day (PAR > 0; left panels) and night (PAR = 0; right panels) periods in experiment II. Each panel represents distribution for sun (yellow columns) and shade (blue columns) conditions grouped by season and for the complete measured period. Coloured dots and coloured diamonds represent daily records and mean values respectively of each variable by treatment and season. Letters above each box plot indicate significant differences ($p < 0.05$, Tukey Contrasts post-hoc test) after a repeated measures mixed-effect model. Daily yield, Fv/Fm and ETR values result from averaging only positive values (i.e., reflecting the situations where the moss is metabolically active)

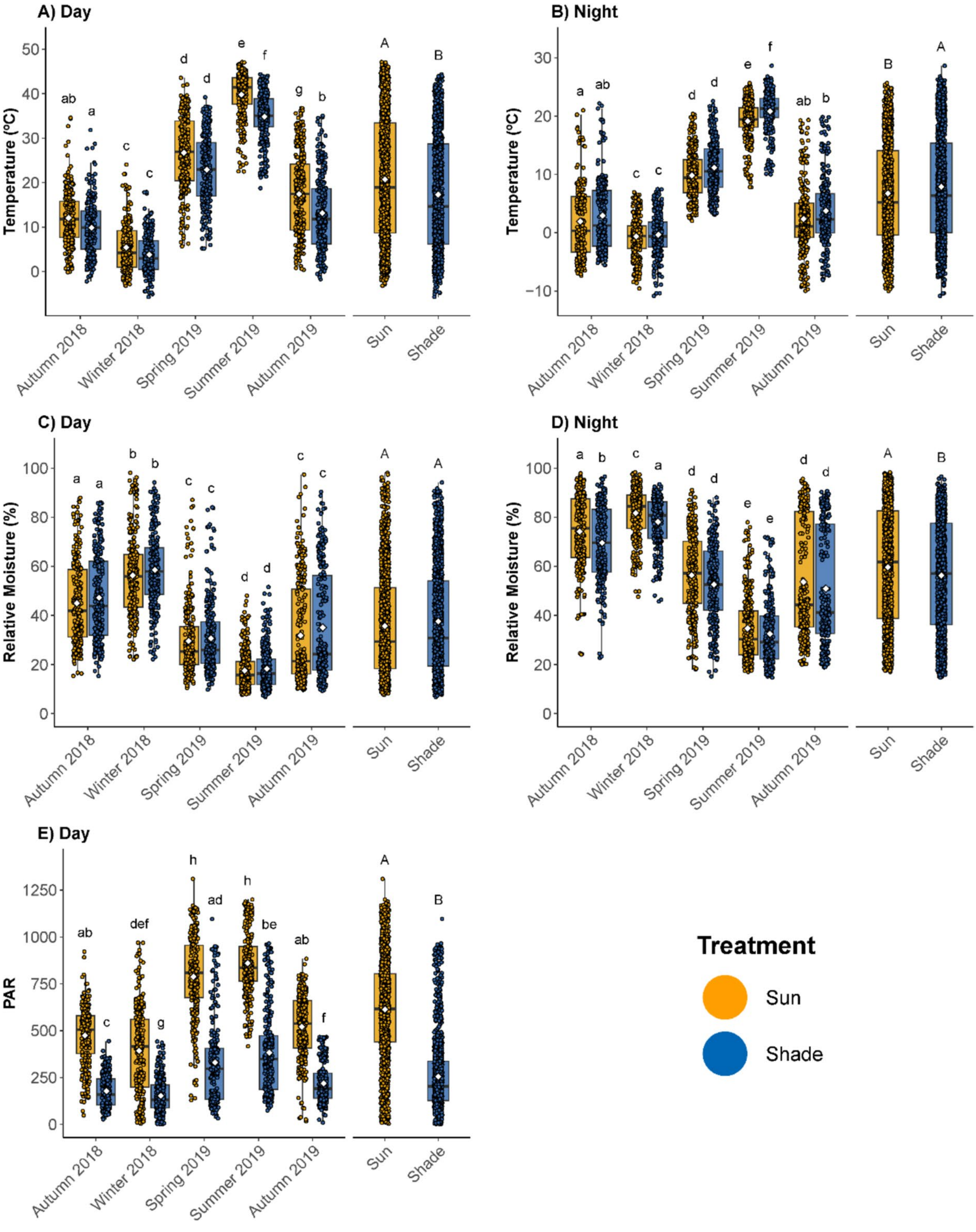
## Discussion

The results obtained from the two experiments provide insights into the strong linkages between physiology and environmental conditions for the biocrust moss *S. caninervis*, underlining the importance of its poikilohydric nature. Overall, experiment I showed similar patterns between Castle Valley (CV) and Moab among the different parameters monitored (Fig. 1, Online Resource 2, Fig. S1 and S2). Physiological indicators showed a higher percentage of metabolic activity in Castle Valley compared to Moab, both during the day and at night (Fig. 1). This difference may be explained by the higher mean RM in the daytime throughout the measuring period (Online Resource 2, Fig. S1), as RM is a strong indicator of water availability (Raggio et al. 2017), an important factor explaining metabolic activity in this organism.

Despite the longer duration of activity in Castle Valley, no significant differences were observed between sites in terms of photosynthetic efficiency, as measured by Yield and Fv/Fm (Fig. 1). This indicates that the lower activity found in Moab does not adversely affect the photosynthetic apparatus of *Syntrichia caninervis*. Similarly, no statistical differences were found in electron transport rate (ETR) between sites, indicating comparable photosynthetic productivity, an important consideration for understanding long-term carbon balance. Although ETR can become decoupled from net $CO_2$ assimilation rate under stressful situations (Flexas et al. 1999) and may indicate photorespiration under some circumstances (Proctor and Smirnoff 2011), it still provides a useful links with C gain in vascular plants (Flexas and Carriquí 2020; Sun et al. 2023) and mosses (Green et al 1998).

The higher percentage of metabolic activity in Castle Valley during experiment I appears to be primarily driven by winter conditions, which was the period with the highest contrast between the two sites. Variations in snow cover duration and/or soil water content during this season may explain the observed contrast. In general, our results indicate that the species, *S. caninervis*, is well adapted to both sites, with healthy indicators for potential growth. This means that while soil texture might influence biocrust biodiversity and coverage, it does not appear to impose significant functional constraints on existing biocrust communities. Moreover, although Moab is closer to urban areas and potentially subject to greater human disturbance, no negative physiological effects were detected in the samples from this site.

The aim of experiment II was to disentangle the ability of *S. caninervis* to perform in sun and shade microhabitats in the Colorado Plateau (Bowker et al 2000; Clark 2020) from an ecophysiological perspective. Compared to experiment I, physiological responses in this experiment showed greater variability and impairment, with clear differences between treatments. Notably, while shade-exposed samples exhibited a significantly higher overall percentage of metabolic activity during the day, sun-exposed samples showed significantly higher Yield and ETR (Fig. 2). These results indicate a divergence in functional strategy between microhabitats. The microclimate conditions support these findings, with sun microsites showing significantly higher temperature and photosynthetically active radiation (PAR) throughout the monitoring period (Fig. 3). These conditions likely increased desiccation rate and reduced the amount of field conditions with simultaneous water availability and suitable light conditions for activating photosynthesis. This pattern can be harmful for biocrust physiology and impair growth (Maphangwa et al. 2012; Raggio et al. 2023), but no other functional indicator supported this hypothesis. On the contrary, Yield and ETR were significantly higher in the sun microhabitats, clearly indicating that the amount of incident light using the photochemical pathway and the overall photosynthetic productivity respectively were higher in the sun. Rather than a deficiency or limitation, the reduced activity in the sun has an important consequence, that is avoiding more stressful situations in the field, something seemingly


A) Day
Temperature (°C)
0
10
20
30
40
50
ab
a
c
c
d
d
e
f
g
b
A
B
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
B) Night
Temperature (°C)
−10
0
10
20
30
a
ab
c
c
d
d
e
f
ab
b
B
A
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
C) Day
Relative Moisture (%)
0
20
40
60
80
100
a
a
b
b
c
c
d
d
c
c
A
A
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
D) Night
Relative Moisture (%)
0
20
40
60
80
100
a
b
c
a
d
d
e
e
d
d
A
B
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
E) Day
PAR
0
250
500
750
1000
1250
ab
c
def
g
h
ad
h
be
ab
f
A
B
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
Treatment
Sun
Shade

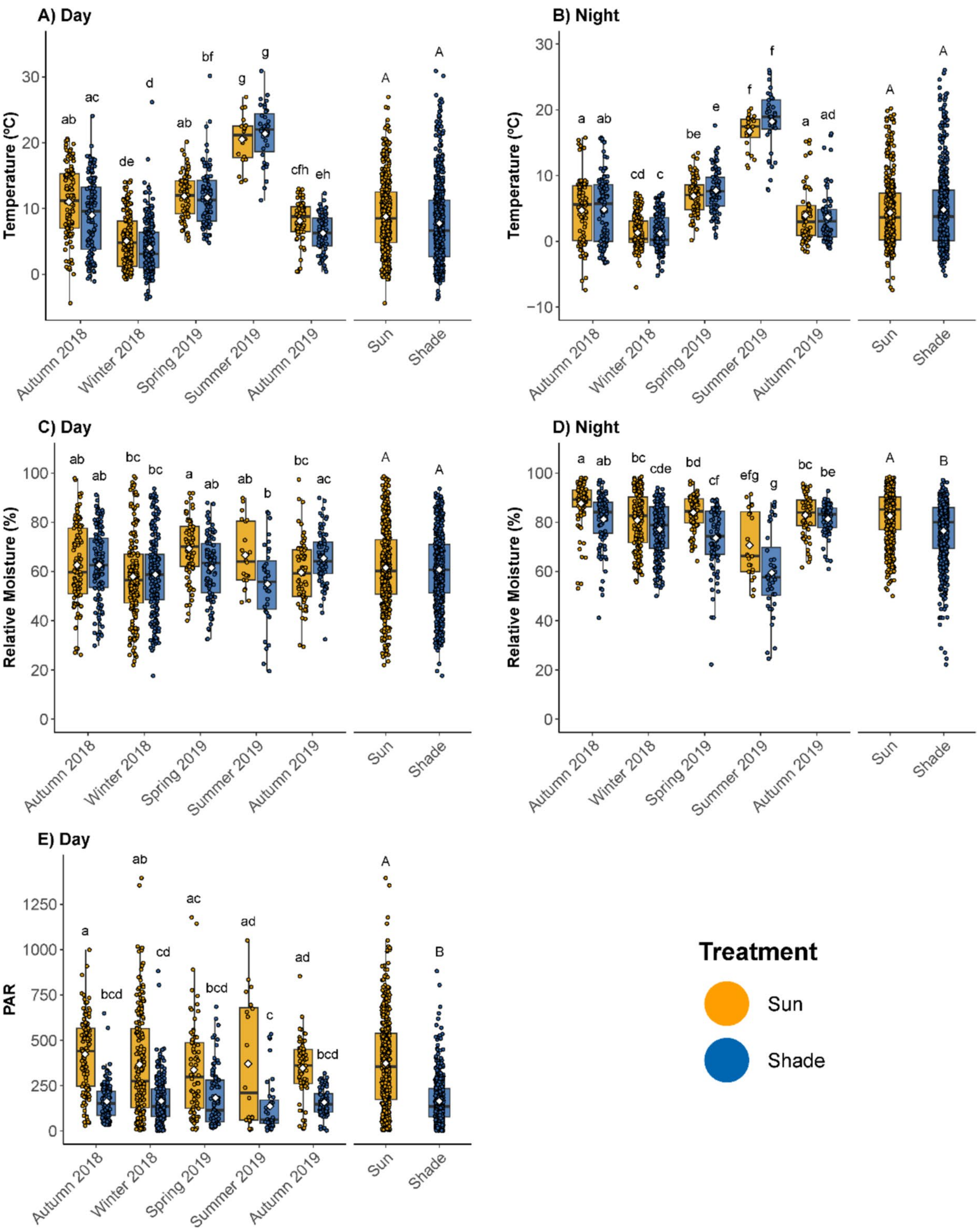
◂**Fig. 3** Box plots showing the daily distribution of moss surface **A – B**) temperature (ºC), **C – D**) relative moisture (%) and **E**) photosynthetically active radiation (PAR, µmol $m^{-2}$ $s^{-1}$) for day ($PAR > 0$; left panels) and night ($PAR = 0$; right panels) periods in experiment II. Each panel represents distribution for light (yellow columns) and shade (blue columns) conditions grouped by season and for the complete data series. Coloured dots and colour diamonds represent daily records and mean values respectively of each variable by treatment and season. Letters above each box plot indicate significant differences ($p < 0.05$, Tukey Contrasts post-hoc test) after a repeated measures mixed-effect model

common in biocrusts (Green and Proctor 2016). An example of this pattern is seen with the microclimatic temperature while active, where ranges were strongly reduced compared with the general microclimatic temperature (refer to Fig. 3 vs Fig. 4 in the temperature subgraphs and Online Resource 2 Fig S4). Additionally, differences between sun and shade (Fig. 3) diminish when only biocrust activity periods were considered for temperature effects (Fig. 4). The pattern observed indicates that biocrust response to temperature may be controlled by an avoidance strategy of the most extreme situations, with a resulting uncoupling of metabolic activity from mean macro environmental conditions (Schlensog et al. 2013). It seems that the species of moss selects for more moderate and stable micro environmental conditions for activity, thus avoiding extremes such as below zero and hot temperatures, regardless of the microhabitat where it grows (Online Resource 2, Fig. S4, same pattern can be observed in Fig.S3 for exp I).

Regardless of some of the physiological similarities across microclimates, we found that living in the sun or shade does matter for *S. caninervis*. The species appears to be sun-adapted, exhibiting optimal physiological performance, particularly in Yield and ETR, under high light conditions (Fig. 2). However, it also maintains an adequate physiological performance in shaded microhabitats, likely due to extended periods of daytime metabolic activity (Fig. 2A), which provides an important resource advantage. Our findings challenge the expectations of the "islands of fertility" hypothesis (Charley and West 1975; Walker et al. 2001), which suggests that shaded areas beneath shrubs in drylands promote plant growth through microclimatic buffering. In contrast, our results show that *S. caninervis* employs distinct and successful physiological strategies across both microhabitats. In fact, the species' strong photoprotection mechanisms (Ekwealor et al. 2021; Robinson and Waterman 2014) allow it to function competitively under full sun. Moreover, the presence of shrub roots beneath the biocrust may negatively impact moss hydration by extracting water from already moisture-limited soils, a pattern supported by lower RM values at the moss surface during night activity periods in shaded microsites (Fig. 4D).

Seasonal trait analysis in experiment II further emphasizes the importance of environmental context. Winter was the season with the highest—and statistically significant—percentage of metabolic activity, followed by autumn, while spring and summer showed much lower activity levels (Fig. 2A). Interestingly, the pattern of optimal performance during the winter gets extended for other key functional traits related to photosynthesis and C balance, such as Yield, Fv/Fm, and even ETR during this season. Although the lower percentage of activity during the spring indeed gets compensated by higher PAR and temperature in relation to Yield and ETR (Fig. 2C and 2E), our results support the strong importance of the winter for biocrust annual functionality (also supported by the results of experiment I, Fig. 1), indicating that intermittent winter snow covers serves as an additional water source. Our results are aligned with earlier evidence in other studies (Belnap 2002; Coe et al. 2012; Zhang and Zhang 2020).

Given the importance that the percentage of metabolic activity plays in determining biocrust functional patterns and their contribution to ecosystem services in drylands, improving our understanding and modeling of its predictors is essential. While total microclimatic mean daily temperature is an acceptable predictor of the daily percentage of metabolic activity, the microclimatic mean daily RM was a better (and stronger) predictor variable (Fig. 5, Online Resource 2, Table S1). This finding support former evidences with different biocrust types (Baldauf et al. 2021; Büdel et al. 2018; Raggio et al. 2017) that consider that this microclimatic predictor of activity is stronger because it encompasses all the water availability in different forms that can be used by biocrusts (liquid water, snow, dew, fog, water vapour, soil water Green et al. 2011; Lange 2001), and, thus, is the bottleneck of any physiological process in poikilohydric organisms. As such, RM reflects the primary environmental


A) Day
Temperature (°C)
0
10
20
30
ab
ac
de
d
ab
bf
g
g
cfh
eh
A
A
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
B) Night
Temperature (°C)
−10
0
10
20
30
a
ab
cd
c
be
e
f
f
a
ad
A
A
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
C) Day
Relative Moisture (%)
0
20
40
60
80
100
ab
ab
bc
bc
a
ab
ab
b
bc
ac
A
A
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
D) Night
Relative Moisture (%)
0
20
40
60
80
100
a
ab
bc
cde
bd
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efg
g
bc
be
A
B
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
E) Day
PAR
0
250
500
750
1000
1250
a
bcd
ab
cd
ac
bcd
ad
c
ad
bcd
A
B
Autumn 2018
Winter 2018
Spring 2019
Summer 2019
Autumn 2019
Sun
Shade
Treatment
Sun
Shade

◂**Fig. 4** Box plots showing the daily distribution of moss surface in **A** – **B**) temperature (ºC), **C** – **D**) relative moisture (%) and **E**) photosynthetically active radiation (PAR, µmol $m^{-2}$ $s^{-1}$) **in activity** for day ($PAR > 0$; left panels) and night ($PAR = 0$; right panels) periods in experiment II. Each panel represents distribution for light (yellow columns) and shade (blue columns) conditions grouped by season and for the complete data series. Coloured dots and colour diamonds represent daily records and mean values respectively of each variable by treatment and season. Letters above each box plot indicate significant differences ($p < 0.05$, Tukey Contrasts post-hoc test) after a mixed-effect model

factor for physiological processes in these organisms. Importantly, the predictive strength of mean daily RM appears to be independent of the dominant biocrust organism type, reinforcing the notion that environmental moisture availability exerts a stronger influence than species-specific traits on functional performance. Our data also reveal critical microclimatic thresholds for three physiological variables central to *S. caninervis* functionality: the percentage of metabolic activity (Fig. 5A), Yield, and Fv/Fm (Online Resource 2, Figs. S3, S4). The highest values of all three tend to occur at mean daily T around or below 10–12 ºC, with temperature slightly below 0 ºC marking the lower thermal limit for optimal functional performance. A critical functional window emerges between 30% and 75–80% mean daily RM, within which all three physiological indicators reach or approach their maximum values on a substantial number of days. However, high RM values alone do not ensure activity, particularly during winter conditions when temperatures fall well below 0 °C and biocrusts remain frozen, leading to inactivity despite high moisture availability. The relationship between VPD and % of activity (Fig. 5C) encompass both RM and temperature in one combined variable. This combination creates a strongly intuitive and inverse direct relationship with % of activity collapsing at values of VPD over 1.5 kPa. This threshold coincides with that found in other studies, where stomatal conductance of vascular plants declines markedly when VPD exceeds approximately 1.5–2.0 kPa (Oren et al. 1999; Novick et al. 2016). Its powerful prediction ability over metabolic activity points to it as an excellent variable for predicting metabolic activity in biocrusts communities. These identified microclimatic thresholds for temperature, RM and VPD may be considered tipping points from above or below which the physiological performance of this species could be damaged under possible climate change scenarios in the area.

By combining data from both experiments, this study presents a comprehensive 684-day continuous monitoring dataset covering 12 patches *Syntrichia caninervis* samples, providing valuable insight into the species' functional ecology (Table 1). A key finding is that the mean daily temperature during active periods is approximately half the mean daily temperature across the full monitoring period. This pattern is consistent across all monitored microclimatic variables, reinforcing the notion that *S. caninervis* selectively activates metabolism under mild, favorable conditions. The overall percentage of metabolic activity, including both light and dark periods, was 19.9%, supporting the interpretation that avoidance of environmental extremes is a central physiological strategy for *S. caninervis* survival in the Colorado Plateau. This value appears to be ecologically meaningful rather than incidental. Strikingly similar activity percentages were reported in long-term biocrust monitoring studies from the Tabernas Desert, SE Spain, Europe's driest region (Lázaro et al. 2008), by Pintado et al. (2010) and Raggio et al. (2014). These convergent findings across geographically and taxonomically distinct biocrust systems underscore a common trait among drylands: a narrow, environmentally driven window of physiological activity.

These insights deepen our understanding of *S. caninervis* strategies in dryland environments, but also have broader implications for ecosystem-level processes. The high-resolution physiological profiles obtained in this study can inform carbon balance assessments, particularly when integrated with field and laboratory gas exchange data. Since metabolic activity is the driver behind many biocrust-provided ecosystem services, such as nutrient (N and P) cycling, erosion control, and microhabitat formation, understanding the timing and duration of these active periods is crucial. Moreover, *S. caninervis* has maintained stable cover in the Colorado Plateau over the past 25 years, even as warming trends have negatively affected nitrogen-fixing lichens in the region (Finger-Higgins et al. 2022). The detailed linkages established here between microclimate and functional performance offer a valuable framework for exploring the differential impacts of climate change on biocrust communities. They also provide a foundation for predictive models that can inform land management

**Fig. 5** Relationships between the daily % of activity and moss surface **A**) temperature (ºC), **B**) relative moisture (%), and **C**) Vapour Pressure Deficit (VPD) in Experiment II. Observations are shown for light (orange dots) and shade (blue dots) conditions. The size of dots represents the proportion of observations at each temperature or relative moisture. The solid lines represent the smoothed trend fitted by a local polynomial regression fitting (LOESS) under light (orange lines) and shade (blue lines) conditions

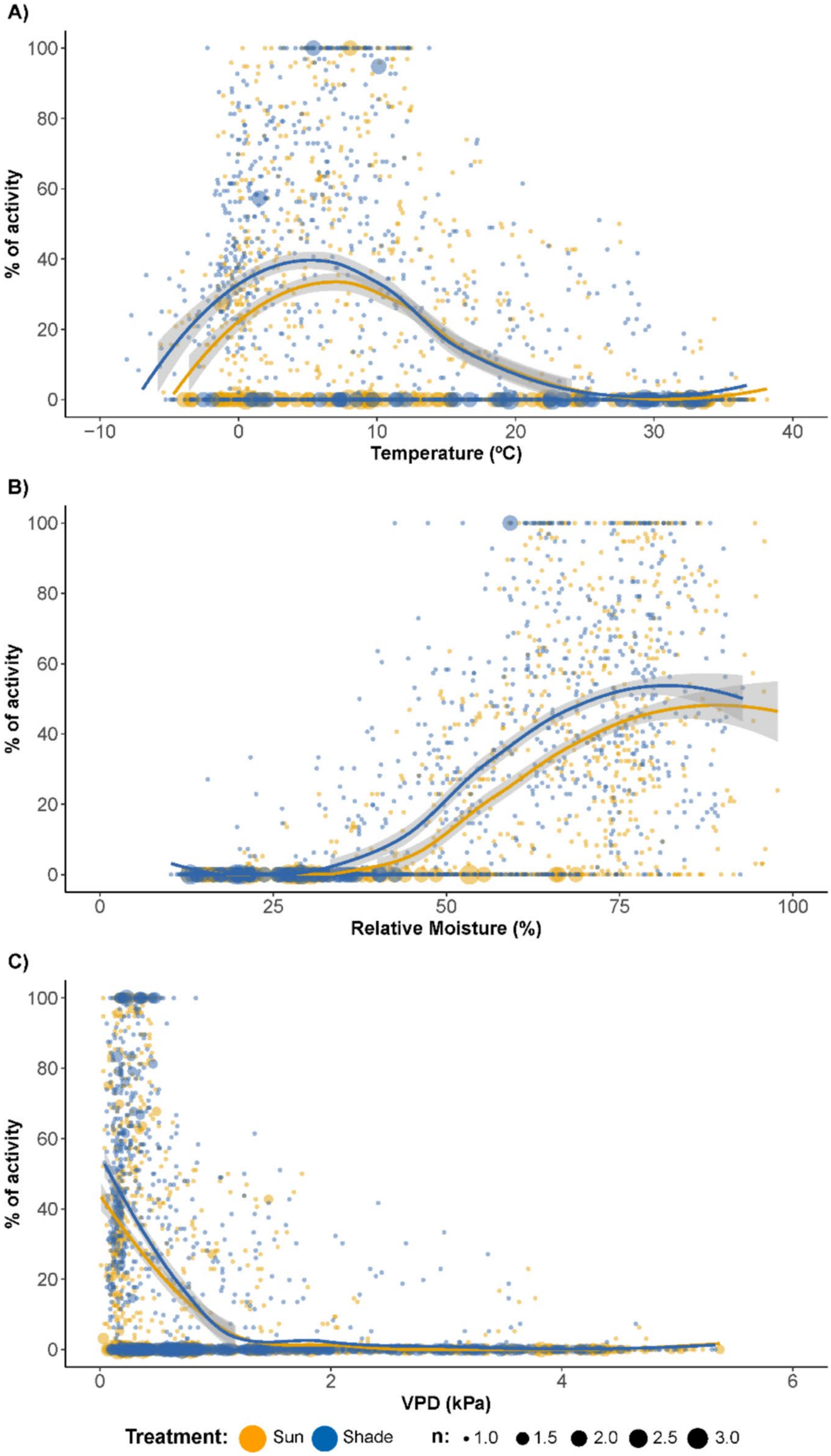

**Table 1** Summary of moss surface microclimatic and ecophysiological variables observed under treatment of two experiments (i.e. Moab and Castle Valley (CV), Utah, for experiment I and sun and shade conditions for experiment II). Temp. – average temperature (ºC), RM – average relative moisture (%), PAR – photosynthetically active radiation. Treat. is type of treatment in the study. In the column "Days", the words "Act." imply means of situations when metabolic activity was detected during all the monitoring, excluding inactive situations. When a number appears in that column, it refers to means of active and inactive situations during the amount of days shown. The standard deviation is included after all the means provided. Measurements correspond to all the monitoring explained in the methodology section

| Treat | Days | Mean Temp. ± sd | Mean RM ± sd | Mean PAR ± sd | Mean Yield in Act. ± sd | Mean % Act | Sum ETR |
|---|---|---|---|---|---|---|---|
| **Exp I** | | | | | | | |
| MOAB | 237 | 10.5 ± 11.8 | 48.9 ± 28.5 | 248 ± 425 | 0.11 ± 0.23 | 18.50 | 109,587 |
| CV | 237 | 11.3 ± 12.7 | 50.3 ± 28.9 | 239 ± 417 | 0.15 ± 0.26 | 24.80 | 153,402 |
| MOAB | Act | 5.81 ± 5.25 | 71.7 ± 23.9 | 156 ± 279 | 0.56 ± 0.16 | - | - |
| CV | | 5.45 ± 5.46 | 70.7 ± 24.6 | 163 ± 290 | 0.56 ± 0.156 | - | - |
| **Exp II** | | | | | | | |
| Sun | 447 | 14.3 ± 16.2 | 47 ± 29 | 324 ± 547 | 0.10 ± 0.23 | 16.6 | 304,325 |
| Shade | 447 | 13.1 ± 13.7 | 46.2 ± 26.8 | 137 ± 324 | 0.11 ± 0.22 | 21.3 | 149,349 |
| Sun | Act | 6.76 ± 6.03 | 71.6 ± 21.1 | 219 ± 375 | 0.57 ± 0.16 | - | - |
| Shade | | 5.93 ± 5.88 | 69.2 ± 18.2 | 98.8 ± 213 | 0.48 ± 0.21 | - | - |
| **Exp I + Exp II** | | | | | | | |
| All | 684 | 12.69 ± 14.15 | 47.65 ± 28.25 | 235.05 ± 446.33 | 0.11 ± 0.23 | 19.9 | 358,332 |
| All | Act | 6.03 ± 5.76 | 70.57 ± 21.50 | 154.56 ± 295.25 | 0.54 ± 0.18 | - | - |

and conservation strategies aimed at sustaining soil function and ecosystem resilience in dryland environments.

**Acknowledgements** We acknowledge the USGS Ecosystem Mission Area Land Change Science Program, and the research projects CRIPTOCOVER and POLAR ROCKS (CTM2015-64728-C2-1-R and PID2019-105469RB-C21 respectively) from the Spanish Government for the funding provided for developing this research. We want to acknowledge also to Dr. Ana Pintado Valverde and USGS reviewers for their internal revision of the manuscript and helpful comments prior to submission. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

**Authors contribution** **Jose Raggio**: conceptualization, investigation, methodology, data curation, writing; **David Sánchez-Pescador**: investigation, data curation, statistical analyses, review and edit; **Ed Grote:** methodology, data curation, administration of the project in the long term; **Leopoldo García-Sancho**: funding acquisition, conceptualization, investigation, review and edit. **Rebecca Finger-Higgens**: investigation, data curation, review and edits **Jayne Belnap**: funding acquisition, conceptualization, investigation.

**Funding** Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This study was funded by the USGS Ecosystem Mission Area Land Change Science Program, and by the research projects CRIPTOCOVER and POLAR ROCKS (CTM2015-64728-C2-1-R and PID2019-105469RB-C21 respectively) funded by the Spanish Government.

**Data availability** R scripts and all data used for developing this research will be made available in Figshare at DOI: https://doi.org/10.6084/m9.figshare.25888654

## Declarations

**Competing interest** The authors have no financial interests to disclose.

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