1 ~~Key drivers of the annual carbon budget of biocrusts from various~~
2 ~~climatic zones determined with a mechanistic data-driven model~~
3 Exploring environmental and physiological drivers of the annual
4 carbon budget of biocrusts from various climatic zones with a
5 mechanistic data-driven model

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18 **Abstract.** Biocrusts are a worldwide phenomenon, contributing substantially to ecosystem functioning. Their growth and
19 survival depend on multiple environmental factors, including climatic ones, and the relations of these factors to physiological
20 processes ~~conditions~~. ~~While the physiological r~~Responses of biocrusts to individual environmental factors have been examined
21 in a large number of field and laboratory experiments.~~, the relative importance of these factors along climatic gradients is~~
22 ~~largely unknown. Moreover, it is not fully understood how acclimation of biocrusts may alter the relative impacts of certain~~
23 ~~factors. We aim here at determining the relative effects of environmental factors on biocrusts along climatic gradients, using~~
24 ~~the carbon balance of biocrust organisms as a measure of their performance.~~ These observational data, however, rarely have
25 been assembled into a comprehensive, consistent framework that allows quantitative exploration of the roles of multiple
26 environmental factors and physiological properties for the performance of biocrusts, in particular across climatic regions. Here
27 we used a data-driven mechanistic modeling framework to simulate the carbon balance of biocrusts, a key measure of their
28 growth and survival. We thereby assessed the relative importance of physiological and environmental factors for the carbon
29 balance at six study sites that differ in climatic conditions. Moreover, we examined the role of seasonal acclimation of
30 physiological properties using our framework, since the effects of this process on the carbon balance of biocrusts are poorly
31 constrained so far. We found substantial effects of air temperature, CO_2 concentration, and physiological parameters that are
32 related to respiration on biocrust carbon balance, which differ, however, in their patterns across regions. The ambient CO_2
33 concentration is the most important factor for biocrusts from drylands while air temperature has the strongest impact at alpine

and temperate sites. Metabolic respiration cost plays a more important role than optimum temperature for gross photosynthesis at the alpine site; this is not the case, however, in drylands and temperate regions. Moreover, we estimated a small annual carbon gain of 1.5 g m^{-2} yr^{-1} by lichen-dominated biocrust and 1.9 g m^{-2} yr^{-1} by moss-dominated biocrust at a dryland site, while the biocrusts lost a large amount of carbon at some of the temperate sites (e.g., -92.1 for lichen- and -74.7 g m^{-2} yr^{-1} for moss-dominated biocrust). These strongly negative values contradict the observed survival of the organisms at the sites and may be caused by the uncertainty in environmental conditions and physiological parameters, which we assessed in a sensitivity analysis. Another potential explanation for this result may be the lack of acclimation in the modeling approach since the carbon balance can increase substantially when testing for seasonally varying parameters in the sensitivity analysis. We conclude that the uncertainties in air temperature, CO_2 concentration, respiration-related physiological parameters, and the absence of seasonal acclimation in the model for humid temperate and alpine regions may be a relevant source of error and should be taken into account in future approaches that aim at estimating the long-term biocrust carbon balance based on ecophysiological data.

Additionally, we explore the role that seasonal acclimation plays in the carbon balance of biocrusts. We applied a data-driven mechanistic model at six study sites along a climatic gradient to simulate the annual carbon balance of biocrusts dominated by different lichen and moss species. Furthermore, we performed several sensitivity analyses to investigate the relative importance of driving factors, thereby including the impacts of acclimation. Our modelling approach suggests substantial effects of light intensity and relative humidity in temperate regions, while air temperature has the strongest impact at alpine sites. In drylands, ambient CO_2 concentration and also the amount of rainfall are important drivers of the carbon balance of biocrusts. Seasonal acclimation is a key feature, mostly in temperate regions, affecting biocrust functioning. We conclude that climate change, which may lead to warmer and, in some regions, drier air, will potentially have large effects on long-term carbon balances of biocrusts at global scale. Moreover, we highlight the key role of seasonal acclimation, which suggests that the season and timing of collecting and monitoring biocrusts should be given additional consideration in experimental investigations, especially when measurements are used as the basis for quantitative estimates and forecasts.

1 Introduction

Non-vascular photoautotrophs, such as lichens, mosses, eukaryotic algae and cyanobacteria, together with heterotrophic microorganisms, form biological soil crusts (biocrusts) which occur in various environments across the globe and provide a

61 wide range of important ecosystem functions, such as build-up of soil organic carbon and nutrients (Belnap et al., 2016;

62 Chamizo et al., 2012; Dümig et al., 2014; Ferrenberg et al., 2018). Due to the importance of biocrusts in ecosystem functioning,

63 their growth and survival have been extensively studied, through different methodological approaches (e.g. Ladrón de Guevara

64 et al., 2018; Lange et al., 2006; Porada et al., 2019). An established measure to quantify the growth of biocrusts is their long-

65 term carbon balance (hereafter, C balance), which corresponds to the (accumulated) net carbon flux across the system

66 boundaries including all relevant carbon gains and losses.(Belnap et al., 2016). Biocrusts occur in various environments across

67 the globe and are especially ubiquitous in environments where low water availability inhibits the development of vascular

68 plants (Belnap et al., 2004; Lange et al., 1998a; Samolov et al., 2020). They provide a wide range of important ecosystem

69 functions, such as build-up of soil organic carbon and nutrients (Chamizo et al., 2012; Dümig et al., 2014; Ferrenberg et al.,

70 2018). Biocrusts contribute substantially to ecosystem carbon fluxes at the global scale (Elbert et al., 2012). Especially in

71 desert ecosystems, biocrusts can be a major contributor to the annual CO_2 uptake (Tucker et al., 2019; Wohlfahrt et al., 2008).

72 Cyanobacteria, which are common components of biocrusts, either free-living or associated with mosses and lichens, facilitate

73 biotic nitrogen fixation and may subsequently increase carbon sequestration by enhancing the concentration of photosynthesis-

74 related enzymes in top soils (Ackermann et al., 2012; Evans and Lange, 2003).

75 Owing to their importance in ecosystem functioning, studies on growth and survival of biocrusts are crucial. Growth depends

76 on the long-term carbon balance (hereafter, C balance), which corresponds to the (accumulated) net carbon flux across the

77 system boundaries including all relevant carbon gains and losses. In order to ensure survival, any species needs to achieve a

78 positive C balance in the long-term, while negative values may occur for short periods. Acknowledging the importance of C

79 balance, an increasing number of studies have investigated the long-term C balance of individual non-vascular organisms as

80 well as biocrust communities, and their environmental drivers. An annual carbon budget of 21.49 g C m^{-2} based on measured

81 field data was reported in the study of Lange (2003b) on the crustose lichen *Lecanora muralis* growing on a rock surface in a

82 temperate climate of southern Germany. Furthermore, Büdel et al. (2018) estimated an annual C balance of 1.7 g C m^{-2} based

83 on measurements on measured the annual C balance for a cyanobacteria-dominated biocrust in an Australian dry savannah

84 ecosystem. Several other studies obtained long-term, large-scale values of the C balance by scaling up short-term, local

85 measurements of CO_2 exchange rate under natural field conditions (Lange et al., 1994; Zotz et al., 2003). For an estimation

86 of the global C balance of cryptogamic covers, which include biocrusts, conversion factors based on the maximum

87 photosynthesis rate have been suggested as a best-guess solution (Elbert et al., 2012). However, there are some drawbacks to

88 these approaches for acquiring a C balance at both organism and community scale. First, the measurement of the long-term

89 continuous CO_2 exchange rate of an individual organism or biocrust community has technical limitations and is highly time-

90 and resource-consuming. Second, upscaling via extrapolation may result in bias in annual C balance estimation if the length

91 and the frequency of sampling cannot capture the full variability of CO_2 exchange throughout the year (Bader et al., 2010).

92 Moreover, using empirical approaches alone, it is difficult to understand the underlying mechanisms of how climatic

93 conditions affect individual physiological processes, and consequently which role these processes play in the observed

94 changes in C balance and growth at the individual as well as community level. Such approaches are thus subject to large

95 uncertainty when used for projections of C balance under climate change.

96 Most studies on the relationships between C balance and environmental factors for biocrusts are based on laboratory

97 experiments (e.g. Coe et al., 2012b; Cowan et al., 1992; Lange et al., 1998) or direct field measurements in situ over short

98 periods of time (e.g. Brostoff et al., 2005; Lange et al., 1994). From this work cited above, it has been recognized that the C

99 balance of biocrusts is strongly influenced by factors such as water supply, temperature, radiation, and CO_2 concentration and

100 the complex relations of these factors to physiological processes such as photosynthesis and respiration. ~~the type and temporal~~

101 ~~pattern of water supply, temperature, radiation, and also CO2 concentration are among the factors that are crucial for the C~~

102 ~~balance of biocrusts.~~ While the highest values of productivity ~~in biocrusts~~ under field conditions are achieved when the

103 environmental factors are in the range that is optimal for the specific biocrust~~their optimal range~~, it has been found that

104 biocrusts ~~under field conditions~~ are also able to achieve metabolic ~~maximum~~ activity and thus, potential productivity, under

105 sub-optimal conditions of temperature and light (Colesie et al., 2016; Raggio et al., 2017, 2014). It is largely unknown,

106 however, which relative importance each of these environmental factors and physiological parameters has for the long-term C

107 balance of biocrusts under natural field conditions, and if the importance of factors/parameters shows a spatial and temporal

108 pattern. In addition, seasonal acclimation of photosynthetic and respiratory properties of species to intra-annually varying

109 climate factors found by several studies (e.g. Gauslaa et al., 2006; Lange and Green, 2005; Wagner et al., 2014) may

110 substantially affect biocrust C balance, thus leading to further complexity in the spatio-temporal relations between C balance

111 and environmental factors/physiological parameters. One of the few experimental studies investigating biocrust acclimation

112 potential to changing temperatures has found threshold temperatures for the survival of lichen species (Colesie et al., 2018)

113 but the overall extent of the impact is poorly understood.

114 Here, we applied a mechanistic data-driven model to (a) complement empirical estimates of the annual C balance of biocrusts

115 and (b) to address the knowledge gaps concerning the relative importance of different environmental factors and physiological

116 parameters for the C balance ~~along climatic gradients~~in contrasting climates, thereby accounting for the role of seasonal

117 acclimation. The advantage of this modeling approach is that it can predict at high temporal resolution the dynamic C balance

118 of biocrust organisms for given locations by simulating the physiological processes driven by environmental factors. The

119 model allows for a deeper mechanistic understanding of the C balance of biocrusts through factorial experiments and sensitivity

120 analyses regarding physiological parameters and individual environmental factors, which would be impractical to realize in

121 field or laboratory experiments. To complement our analyses using the data-driven model, a process-based dynamic non-

122 vascular vegetation model, called LiBry, was employed as an supporting tool (Porada et al., 2013).

123 **2 Material and Methods**

124 We simulated the C balance of biocrusts from six climatically different study sites in a semi-empirical way using a data-driven

125 model. The model simulates photosynthetic rate based on the Farquhar photosynthesis model developed by Farquhar and von

126 Caemmerer (1982) and respiration rate based on a Q10 relationship. The C balance is computed as the difference of

127 photosynthesis and respiration accumulated over a given time period. In the model, both photosynthesis and respiration depend

128 on surface temperature, relative water saturation, and the activity of the biocrust, which are all simulated in a coupled way via

129 the surface energy balance as a function of climate input data. Photosynthesis additionally depends on ambient CO_2

130 concentration.

131 To calibrate the model, we first determined soil and land surface properties that are required for the coupled energy and water

132 balance in the model through fitting simulated to measured surface temperature patterns. Then, we parameterized the

133 physiological properties of the organisms using measured relationships between net photosynthesis and light intensity, water

134 content, and temperature. Finally, we validated the model with regard to the water content or activity patterns of biocrusts and

135 compared the modelled CO_2 assimilation rate to measured values. The data sets used for calibration and validation of the model

136 as well as basic climate conditions of each site are described in Table 1. Sites were listed in ascending order of total annual

137 precipitation based on measured data.

2.1 Study sites

139 In our study we considered six sites, namely two dryland sites at Almeria (Spain) and Soebatsfontein (South Africa; hereafter

140 D1 and D2); three temperate sites at Gössenheim (Germany), Öland (Sweden), and Linde (Germany; Hereafter T1, T2, and

141 T3); and one alpine site at Hochtor (Austria; Hereafter A1) (Table 1). These sites were chosen based on data availability for C

142 balance estimation, and because they cover a broad range of different climatic conditions. The field and laboratory

143 measurements conducted at all sites were following a similar protocol, which allows comparing the simulation results among

144 sites. To our knowledge, Tthe necessary empirical data for C balance estimation regarding climatic conditions, species

145 physiological characteristics, and status especially in terms of moisture such as water content or such as activity, which is used

146 to estimate C balance, have been monitored in only a relatively small number of experiments, so far, and including the six

147 study sites chosen here to provide a good opportunity to utilize these data for an extended modeling approach. In this context,

148 activity measurements are more suitable than soil moisture records since they are direct, non-invasive and they do not show

149 deviations in the temporal patterns at high resolution, which may occur with soil moisture time series.

150 Sites D1 and D2 are characterized by an semi-arid climate with mean annual precipitation of less than 250 mm, but a wet

151 winter season (Büdel et al., 2014; Haarmeyer et al., 2010). Sites T1, T2, and T3 have a temperate climate. The mean

152 precipitation in these three sites is around 550 mm (Büdel et al., 2014; Diez et al., 2019). Site A1 is located in a humid alpine

153 region with a mean annual precipitation between 1750 and 2000 mm, of which more than 70% are snowfall; the A1 site is

154 covered by snow for at least 200 days per year (Büdel et al., 2014). More detailed site descriptions are provided in the

155 corresponding studies cited above.

2.2 Observational Data

2.2.1 Climatic variables

The proposed data-driven model for estimating the annual C balance of dominant biocrust types at each site was forced by hourly microclimatic variables. The forcing data sets of the data-driven model include photosynthetically active radiation (PAR), long-wave radiation (near-infrared), relative air humidity, air temperature, wind speed, rainfall, and snowfall. All the microclimatic variables were measured on-site by climate stations with a temporal resolution of 10 min (5 min in A1 and D1; data available at http://www.biota-africa.org; Raggio et al., 2017; M. Veste, unpublished data), except for long-wave radiation and snowfall, which were taken from ERA5 dataset (https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5). Although directly measured surface temperature data are available for all sites, we use ERA5-based down-welling long-wave radiation instead to simulate surface temperature on biocrusts. This is necessary since, in our model, calculations of photosynthesis and respiration require not only surface temperature, but also depend on water saturation of biocrusts (affecting activity). However, we do not have water saturation data available at most sites. Therefore, we instead simulate the dynamic water saturation of biocrusts based on climate, via processes such as evaporation, rainfall, and dew. The calculation of evaporation and dew automatically includes the computation of a surface temperature that emerges from solving the surface energy balance, thereby including down-welling long-wave radiation. Since the simulated surface temperature that is connected to simulated water saturation slightly deviates from the observed surface temperature (see Fig. 1 and S1), we do not directly use the observed surface temperature as input in the modeling approach, to avoid inconsistencies. Then all these microclimate data were aggregated to data with hourly temporal resolution.

2.2.2 Dynamic biocrust variables

~~Surface temperature data are available for all sites.~~ Besides the surface temperature, ~~b~~Biocrust activity was either monitored directly (binary: active or not active) using a continuous chlorophyll fluorescence monitoring system (Raggio et al., 2014, 2017), or indirectly via the electrical conductivity of the substrate (BWP, Umweltanalytische Produkte GmbH, Cottbus, Germany; Weber et al., 2016; M. Veste, unpublished data). For site D2, the biocrust water content was calculated instead of activity based on electrical conductivity. Due to snow covering the measuring instruments, data of site A1 only covers the time from August to October. Samples from both lichen- and also moss-dominated biocrusts were measured at all sites, except for site T3 where four BWPs were mostly located in moss-dominated biocrusts. At site D2, additionally cyanolichen- and cyanobacteria-dominated biocrusts were monitored. The measured surface temperature, water content, and activity data at all sites were then aggregated to data with a temporal resolution of one hour.

As explained in Sect. 2.2.1, ~~W~~we did not directly use the observed surface temperature and activity (or water content) as forcing data for the model, ~~since these properties are strongly linked to water saturation (and CO_2 diffusivity). Input data of water saturation, however, were not available at most sites. Although the overall patterns of simulated and observed surface temperature match well (see below, Sect. 2.3), inconsistencies would likely occur at hourly resolution if simulated dynamic water content was used in the model together with observed temperature and activity. Hence,~~ but estimated the time-series of

6

189 surface temperature and water saturation data at all sites ~~were estimated~~ based on a simulation of the energy and water balance.

190 The activity of the organisms was then approximated via the empirical equations describing the link between water saturation

191 and metabolic activity (see Porada et al., 2013). Furthermore, ambient CO_2 concentration was assumed to be constant at 400

192 ppm. The CO_2 concentration at the soil surface may be higher than 400 ppm due to the flux of respired CO_2 from the soil.

193 Since our study sites are on open ground, we do not assume substantial accumulation of CO_2 in the near-surface boundary

194 layer. We discuss the effect of uncertainties in CO_2 concentration below in Sect. 4.2.

195 For validation of C balance, we used data of the on-site CO_2-exchange rate of different biocrust types (lichen- and moss- and

196 also cyano-dominated biocrusts removed from surplus soil; the latter composed of cyanolichen and cyanobacteria) that were

197 measured by a portable gas exchange system at several time intervals from November 4th to 8th at site D2 (Tamm et al., 2018).

198 For the other sites, additional field measurements of CO_2-exchange were not available.

2.2.3 Photosynthesis response and water storage

200 For all sites, CO_2 exchange measurements under controlled conditions in the laboratory or in the field (site T3) were conducted

201 using a mobile gas exchange system GFS 3000 (Walz GmbH, Effeltrich, Germany) with an infrared-gas analyzer to explore

202 the physiological characteristics of samples of different biocrust types (same as those measured for validation; main species

203 see Table 1; Diez et al., 2019; Raggio et al., 2018; Tamm et al., 2018). Before measurements, the soil underneath these biocrust

204 samples was removed up to the amount necessary to preserve the physical structure of the biocrusts. And the samples were

205 subjected to reactivation for at least two days (D2) or three days (T1, T2, D1, A1). At T1, T2, A1 and D1, for instance, samples

206 were kept at 12°C under 12 h dark and 12 h light (100 µmol m^{-2} s^{-1}) conditions for three days and wetted once a day. Net

207 photosynthesis was measured at different ranges of light intensity, water content, and temperature. Light response curves, for

208 instance, were determined at optimum water saturation and 15 °C, water response curves were measured at 400 µmol m^{-2} s^{-1}

209 and 15 °C at sites D1, T1, T2, and A1 (Raggio et al., 2018). Moreover, the maximum water storage capacity (MWC) of the

210 samples was quantified in the laboratory for samples from sites D1, T1, T2, and A1 (Raggio et al., 2018), whereas the MWC

211 at site D2 was approximated as the maximum value when measuring water response curves (Tamm et al., 2018; Weber et al.,

212 2012). MWC at site T3 was estimated as the value of the same genus measured in Hamburg, Germany (*Cladonia portentosa*

213 and *Polytrichum formosum*, Petersen et al., in prep.). MWC was acquired since it is one of the essential parameters of the

214 model to convert the specific water content in mm to relative water saturation required by the model used here.

215 **Table 1**: Properties of the study sites and data which are available (+ sign) for calibration and validation of the data-driven

216 model.

Site	Almeria, Spain	Soebatsfontein, South Africa	Gössenheim, Bavaria, Germany	Öland, Sweden	Linde, Brandenburg, Germany	Hochtor, Austria
Code	D1	D2	T1	T2	T3	A1
Climate	~~semi-~~arid	~~semi-~~arid	Temperate	Temperate	Temperate	Alpine

Measured annual rainfall [mm]		110	141	424	441	449	744
Dominant species at the site		*Psora decipiens, Didymodon rigidulus*	*Psora decipiens, Psora crenata, Ceratodon purpureus, Collema coccophorum*	*Psora decipiens, Trichostomun crispulum*	*Psora decipiens, Tortella tortuosa*	*Cladonia furcata, Polytrichum piliferum*	*Psora decipiens, Tortella rigens*
Data for Calibration	Laboratory CO_2 exchange response curves	Light, water, temperature	Light, water, temperature	Light, water, temperature	Light, water, temperature	Light, temperature	Light, water, temperature
	Surface temperature	+	+	+	+	+	+
Data for Validation	Water content	-	+	-	-	-	-
	Activity	+	-	+	+	+	+
	CO_2 exchange on site	-	+	-	-	-	-
References		Raggio et al., 2018	Tamm et al., 2018; Weber et al., 2012	Raggio et al., 2018	Raggio et al., 2018	Veste, unpublished data; Diez et al. 2019	Raggio et al., 2018

2.3 Parameterization of the data-driven model

2.3.1 Abiotic surface properties

Several abiotic parameters of the data-driven model describing soil and land surface properties, such as roughness length or soil thermal conductivity, were required to simulate the energy and water balance. These parameters were obtained by fitting the daily and diurnal surface temperature patterns of lichen-dominated biocrust at all sites except for site T3. At site T3, we compared the surface temperature patterns of simulated moss-dominated biocrusts to data collected by sensors in four locations.

224 The set of parameters that corresponded to minimum differences between simulated and measured values (visual

225 assessment) was used in the data-driven model. The calibration results of surface temperature and the photosynthesis

226 response curves at site T2 are shown in Fig. 1 and Fig. 2, respectively. The results of dominant species at other sites are

227 shown in Fig. S1 and S2.

228 The daily surface temperature was simulated accurately (the maximum value of root mean square error (RMSE) at all sites is

229 3.78)(visual comparison) except for site T3 where the temperature during cold seasons was underestimated, and at site D1 the

230 peak temperature within a day in hot seasons was underestimated (Fig. S1). The peak in surface temperature occurred too early

231 by around 1-23 hours at site D1, A1, T1 and T2, but the magnitude of the peak corresponded well to the measured data (Fig.

232 1 and S1). Therefore, in general, the fitting of the surface temperature patterns was satisfactory. The mismatches may result

233 from the measured climate variables such as PAR or air temperature at 2 m being inconsistent with the measured surface

234 temperature (detailed descriptions are in Appendix) and bias in the calibrated soil properties such as soil thermal conductivity

235 since it may affect the surface temperature difference between morning and evening. A sensitivity analysis of soil thermal

236 conductivity to C balance is shown in the Appendix.

237
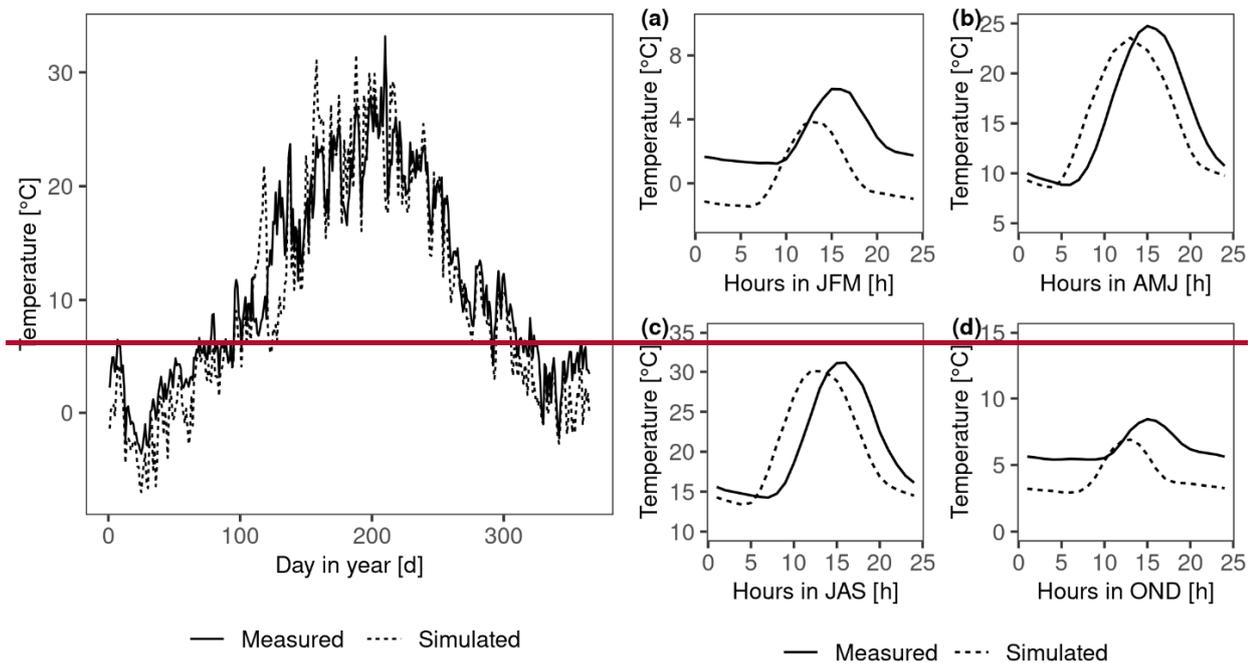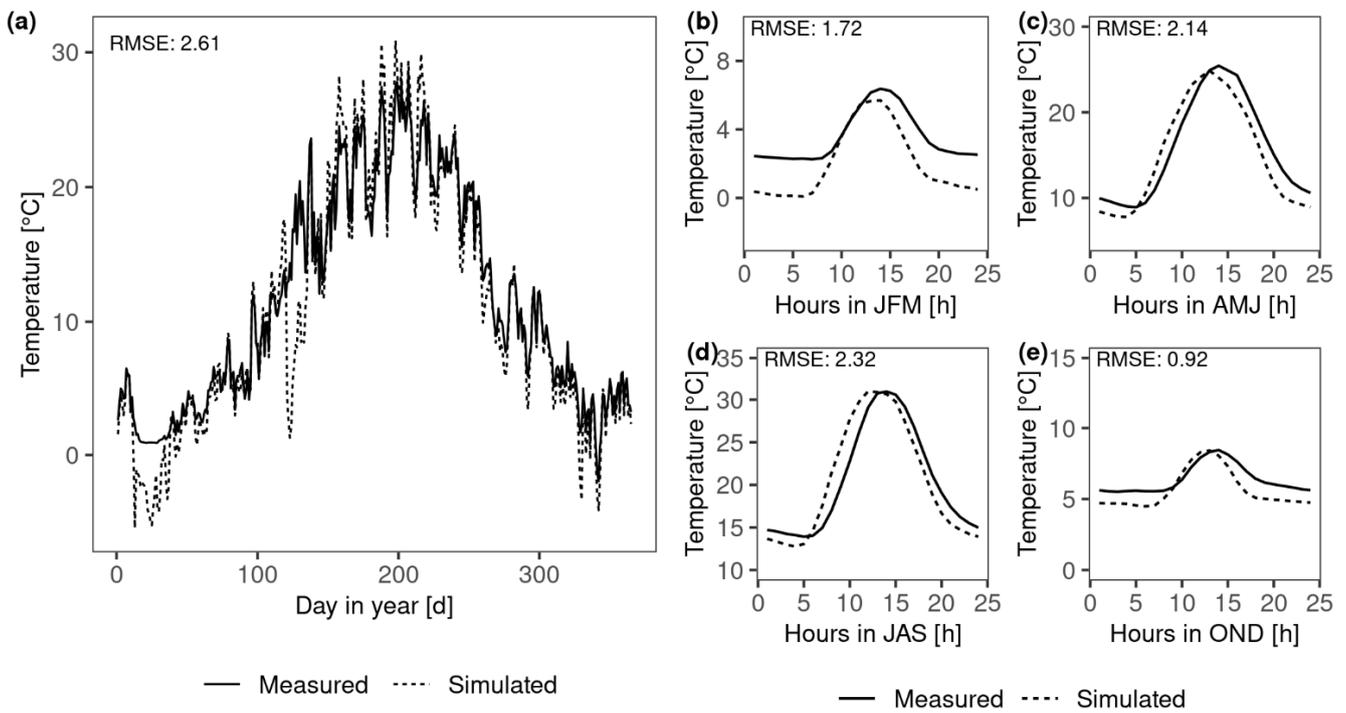
9

Figure 1: Calibration results of abiotic parameters of the data-driven model by fitting the daily (a~~left panel~~) and diurnal (b-
e~~right panel~~) patterns of surface temperature of lichen-dominated biocrusts at site T2. ~~Right:~~ (b~~a~~) to (e~~d~~) represent the patterns
of average hourly surface temperature from January to March (JFM), April to June (AMJ), July to September (JAS), and
October to December (OND), respectively.

2.3.2 Biocrust physiological properties

Furthermore, several parameters required by the Farquhar photosynthesis scheme and the respiration scheme were directly
measured or calculated from gas exchange data sets, such as MWC of the thallus, optimum water content, the optimum
temperature for gross photosynthesis, metabolic respiration cost~~reference maintenance respiration rate~~, and the Q_{10} value of
respiration. Since the ambient temperature range that was applied in the laboratory for samples from ~~at~~ all sites except D2 was
too small to capture the optimum temperature of photosynthesis reliably, ~~it was~~we approximated the optimum temperature
from the measured data set as the average surface temperature during active periods. In addition, the optimum temperature
was also constrained by fitting the Farquhar equations to photosynthesis curves, as related to environmental factors light, water
content, and temperature. Such fitting method was also used to obtain some other photosynthesis-related parameters of
organisms, such as molar carboxylation and oxygenation rate of RuBisCO (V_{cmax}, V_{omax}), respiration cost of RuBisCO
enzyme (~~p_rr_~~Rub_ratio), and minimum saturation for activation ~~water saturation at which organisms become active~~
(Sat_act0~~satmin~~).

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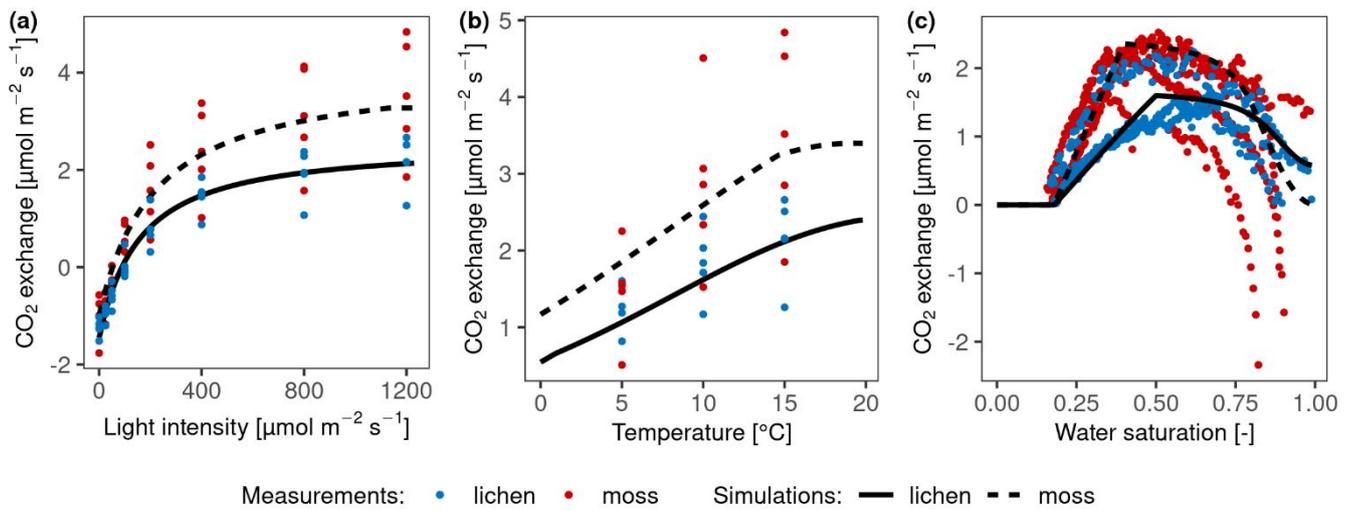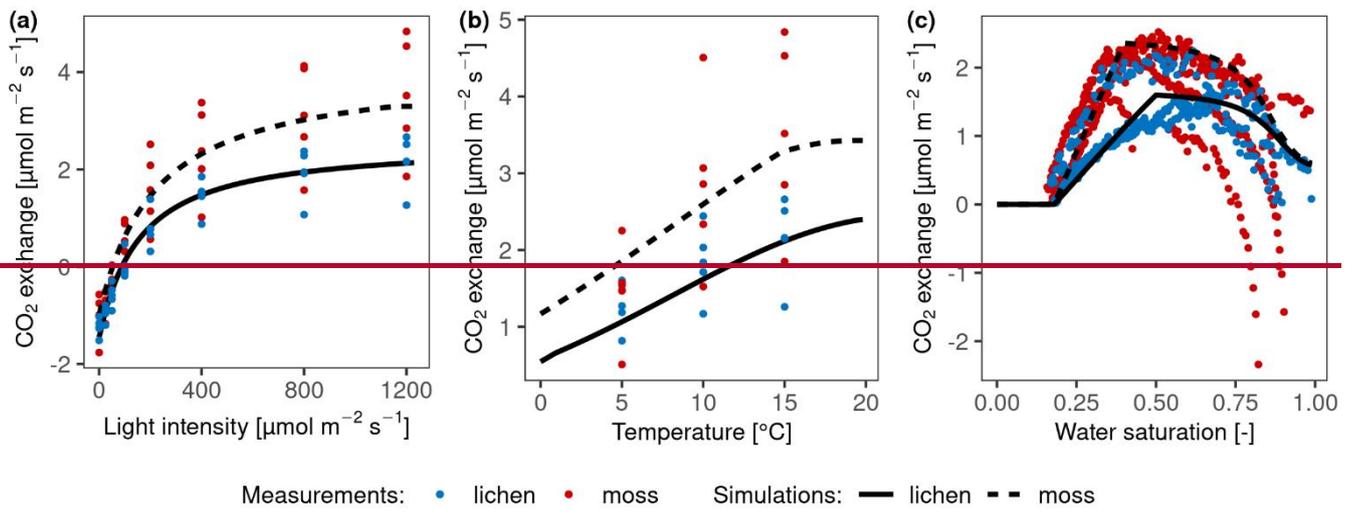
Figure 2: Calibration of photosynthesis parameters of the model by fitting photosynthesis response curves of moss- and lichen-dominated biocrust samples to measurements at site T2. (a): net photosynthesis rate in response to light at optimum water content and 15 °C. (b): net photosynthesis rate in response to temperature at 1200 μmol m^{-2} s^{-1} light and optimal water content. (c): net photosynthesis rate in response to relative water saturation at 400 μmol m^{-2} s^{-1} light and 15 °C.

Since the measured values between replicates showed large variation, in particular the water and temperature-dependent data, as illustrated by the coloured points in Fig. 2, we fitted the curves to the average values of all replicates. The calibration results showed that visually and overall, the photosynthetic curves could be parameterized to fit the measurements well, given that different samples were used for measuring responses to different driving factors, and considering the methodological differences between light and water response curve measurements. However, the water responses were least well-fitted,

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especially at high water contents~~., because t~~The measured net photosynthesis response rate ~~can become~~ was negative in some cases at high water saturation, but it is ~~impossible~~ not possible to ~~simulate~~ reproduce this negative net photosynthesis rates with ~~the~~ our adapted Farquhar photosynthetic model for the light and CO_2 conditions of the laboratory setup. Under these conditions, gross photosynthesis is larger than respiration and thus CO_2 is required to diffuse from the atmosphere into the thallus, not out of it. ~~Thus, e~~Even under low diffusivity, caused by high water saturation, there will be no net diffusion of CO_2 from the thallus into the ambient air assuming that inward and outward flows of CO_2 share the same pathway and that diffusion of CO_2 between atmosphere and thallus is in steady-state with the flux (respiration minus gross photosynthesis). For details please see Appendix. Furthermore, matching the simulated temperature-response of net photosynthesis to the measured data under cool conditions turned out to be difficult for samples from site T1 and A1 (Fig. S2). There were too few data points in the measured temperature response data set to constrain the optimum temperature and temperature relation (see Fig. 2), but the fitting turned out well because the simulated optimum temperature for net photosynthesis at site T1 was coincidentally close to the value of 17 °C reported by Colesie et al. for this site. (2014; see Fig. S2).

2.4 Validation of the data-driven model

The water saturation and activity estimated by the data-driven model were validated by comparing with the daily and diurnal patterns of measured activity (5 sites, not at site D2) and water content data (only at D2). Furthermore, the C balance estimated by the data-driven model was validated by comparison to the in situ measured net CO_2 exchange rate of moss, lichen, and cyanocrust-dominated biocrusts. These data were sampled at site D2 by removing the soil respiration rate, predicted by means of a fitted regression (Weber et al., 2012). Since data on water saturation were available, measured PAR, surface temperature, and water content were used to simulate the C balance using the data-driven model, in contrast to the setup described above. The activity, however, was calculated in the same way as described in the setup. Moreover, the parameters of the model were the same as the calibrated ones of the corresponding biocrust types.

2.5 Sensitivity analysis

To investigate the role of environmental factors, physiological properties, and also seasonal acclimation for the simulated annual C balance of biocrusts, we conducted three sensitivity analyses using our data-driven model. With this setup, we intend to put into context the effects of environmental conditions and the uncertainty associated with the physiological properties that were used to parameterize the model. We additionally explore the impact of seasonally acclimatized physiological properties on carbon assimilation at site T1, since variation between seasons represents additional uncertainty in the estimation of the C balance.

2.5.1 Effects of environmental factors

To investigate the role that environmental factors, namely air temperature (T_air~~Tair~~), light intensity (Light), ambient CO_2 concentration (CO_2), and different types of water sources play in regulating the C balance of biocrusts, sensitivity analyses

297 were conducted ~~using our data-driven model~~ for lichen-dominated biocrusts from all study sites. The different types of water

298 sources include rainfall (Rain) and non-rainfall water inputs such as dew and water vapor, which are ~~also~~ determined by relative

299 air humidity (R_hum~~Rhum~~). All the environmental factors were reduced and increased by half (+/- 50%), except for T_air and

300 R_hum~~air temperature and relative humidity~~. The T_air ~~air temperature~~ differences varied by 5 K and R_hum ~~relative humidity~~

301 by 20%. Moreover, relative humidity was constrained between 0 and 100% when the varied relative humidity exceeded this

302 range.

303 The annual C balance ~~with changing~~for each modified environmental factors was then normalized following Eq. (1), and

304 normalized again among different environmental factors within each climatic zone for comparing the relative importance of

305 environmental factors: ~~normalized for comparing the relative importance of factors among climate zones following Eq. (1):~~

306 $$Normalized\ C\ balance = \frac{c_{ij} - c_j}{|c_j|},\qquad\qquad(1)$$

307 where C_{ij} is the C balance of factor j under operation i, and C_j is the original C balance of factor j.

308 A positive normalized C balance demonstrates an increase in annual C balance when certain environmental factors change,

309 and a larger magnitude of the normalized C balance number demonstrates a larger effect of this environmental factor compared

310 to a factor with a smaller value.

311 ~~Then the positive normalized C balance would show an increased annual C balance with varying environmental factors, and~~

312 ~~thus more carbon accumulation. Moreover, the size of the normalized C balance is proportional to the magnitude of change of~~

313 ~~the C balance when certain environmental factors change. Therefore, a larger normalized C balance also demonstrates a larger~~

314 ~~change in annual C balance, and thus a larger effect of this environmental factor.~~

315 ~~To interpret the spatial distribution of the importance of different environmental factors on C balance, the relative importance~~

316 ~~of each factor in the given climatic region was calculated following Eq. (2) and Eq. (3):~~

317 ~~$N_{ab} = |N_{ab}(increase)| + |N_{ab}(decrease)|,$~~ ~~(2)~~

318 ~~$Relative\ importance = \frac{N_{ab}}{\sum_{a=1}^{n} N_{ab}},$~~ ~~(3)~~

319 ~~where Nab (increase) and Nab (decrease) are the normalized C balance of increasing or decreasing the environmental factor a~~

320 ~~in climatic region b, respectively. Nab is thus the change amplitude of normalized C balance of environmental factor a in~~

321 ~~climatic region b.~~

322 **2.5.2 Effect of physiological parameters**

323 The sensitivity analysis of physiological parameters was conducted for lichen-dominated biocrust at all study sites. The original

324 parameter values were obtained by calibration to measured net photosynthesis response curves. We then varied the values of

325 the following physiological parameters by a consistent range for all sites: metabolic respiration cost per surface area

326 (Resp_main), Q10 value of respiration (q10), the optimum temperature for gross photosynthesis (Topt), respiration cost of
327 RuBisCO enzyme (Rub_ratio), and light absorption fraction in cells (ExtL), minimum saturation for activation (Sat_act0), and
328 minimum saturation for full activation (Sat_act1). Specifically, we increased or decreased Resp_main, ExtL, q10, Sat_act0 by
329 30%, Rub_ratio and Sat_act1 by 20%, and Topt by 5 K. These parameters are chosen since they are closely related to the
330 response of photosynthesis and respiration to water, light, and temperature. These ranges of different parameters were
331 determined based on the observed bounds of the photosynthetic response curves of all replicates (see calibration results with
332 varied parameters at all sites in Fig. S5-S10), which have large deviations between each other at most sites as shown in Fig. 2
333 and Fig. S2. The effects of the varied physiological parameters on the C balance were then normalized using the same
334 normalization method as for the environmental factors (in Sect. 2.5.1) for comparison among parameters and climatic zones.

335 **2.5.2 2.5.3 Effect of seasonal acclimation**

336 Another sensitivity analysis was performed for site T1 to investigate the impact of seasonally acclimatized physiological
337 properties on the carbon assimilation C balance. We analysed the lichen- and moss-dominated biocrusts at site T1 as an
338 example, because the measured time-series of activity showed that in temperate sites such as T1, the organisms were active
339 most of the time, and thus the C balance would be more sensitive to seasonally varying properties.

340 In the analysis, rather than keeping all calibrated parameters fixed throughout the simulation period of the data-driven model,
341 the physiological parameters metabolic respiration cost per surface area (Resp_main), light absorption fraction in cells (ExtL),
342 and the ratio of Jmax to Vcmax (jvratio) were set to another set of values in the winter months in order to adapt to the climatic
343 conditions, since biocrusts at sites T1 were collected in summer months. These new, "dynamic" parameters were applied in an
344 additional simulation and the resulting C balance was compared to the original simulation based on the "fixed" parameters.
345 The dynamic parameters were chosen and varied based on the literature: The properties were varied based on the literature.
346 Respiration of lichens was found to acclimate to seasonal changes in temperature (Lange and Green, 2005). Moreover, under
347 low light, organisms showed shade-adapted physiological characteristics with low PAR compensation and saturation points
348 (LCP and LSP; Green and Lange, 1991). Thus, under low light conditions, the organisms have a stronger ability to utilize low
349 light intensities for photosynthesis. These properties can be expressed by certain parameters of the data-driven model. For
350 instance, the respiration rate is determined by the parameter metabolic respiration cost per surface area (Resp_main); LCP and
351 LSP can be affected by changing the slope of the photosynthesis-light relations through light absorption fraction in cells
352 (ethrough the parameter ExtL); LCP and LSP can also be modified via the parameter ratio of Jmax to Vcmax (jvratio) as it
353 influences the value of light use efficiency at unsaturated light. With higher efficiency, the light required to reach the saturated
354 light level declines. Jmax is a crucial parameter quantifying the maximum rate of electron transport in the light dependent
355 reactions of photosynthesis, Vcmax describes the maximum rate of carboxylation of RuBisCO in the Calvin Cycle of
356 photosynthesis (Walker et al., 2014). Accordingly, rather than keeping all parameters fixed throughout the simulation period
357 of the data-driven model, in the sensitivity analysis, the physiological parameters were set to another set of values in the winter

364 Accordingly, in an hourly simulation during September and December, January, and February, the parameter Resp_main was

365 reduced to half to lighten the respiratory cost for the samples collected at site T1. The size of EextL was doubled to increase

366 the slope of photosynthesis-light relations. In addition, the parameter jvratio was doubled as well to enhance the light use

367 efficiency.

2.6 LiBry Model

369 LiBry is a process-based dynamic global vegetation model (DGVM) specific to non-vascular vegetation. The model mimics

370 environmental filtering in the real world by simulating many different functional strategies and selecting those which maintain

371 a positive C balance under the respective climatic conditions. The strategies are characterized by a combination of 11

372 physiological and morphological parameters. More information about the model is briefly described in the Appendix, and a

373 full detailed description can be found in Porada et al. (2013, 2019).

374 For this study, the LiBry model was run for 300 years with repeated microclimate forcing data of one year from the six study

375 sites, calibrated abiotic parameters same as the data-driven model, and initially generated 1000 strategies. C balance and

376 dynamics of the surface cover of the strategies were simulated until a steady state was reached, so that the final successful

377 strategies were those where long-term biomass values were positive. Moreover, at the end of the simulation, the average values

378 of functional traits were estimated by weighting all surviving strategies based on their relative cover. The (hypothetical)

379 strategy characterized by these average values is called average strategy. The strategy with the largest cover area is called

380 dominant strategy.

381 Furthermore, we compared the physiological parameters of the average strategy and the selected dominant strategies to the

382 ones of organisms in the field by means of their respective photosynthesis response curves. This comparison can verify the C

383 balance estimated by the data-driven model from a reversed perspective as LiBry model is based on the same processes as the

384 data-driven model, but the strategies were freely selected by the LiBry model based on their C balance, without prescribing

385 values based on site level observations.

3 Results

3.1 Data-driven model

15

3.1.1 Validation of the data-driven model
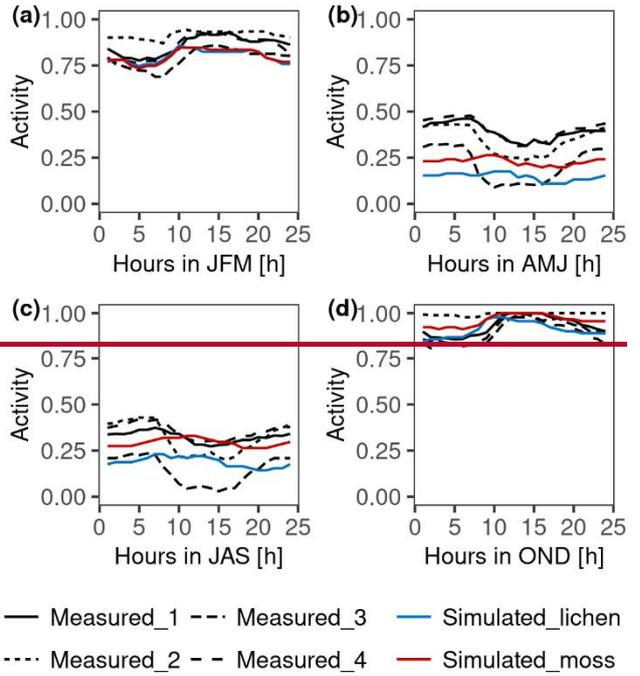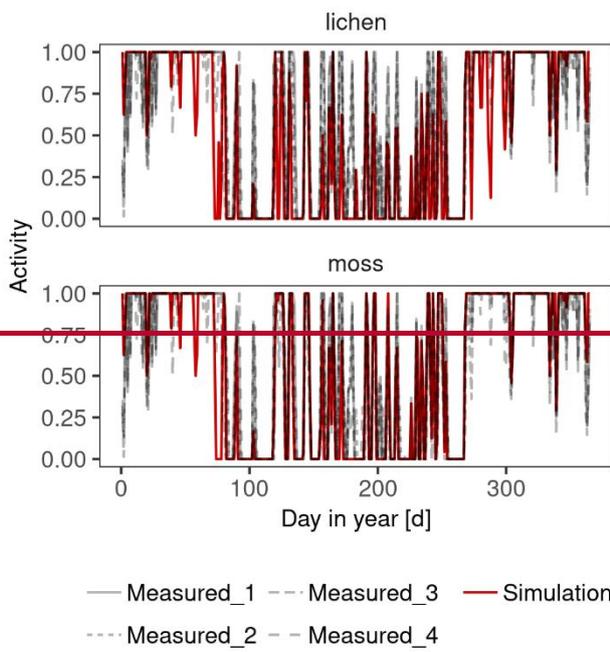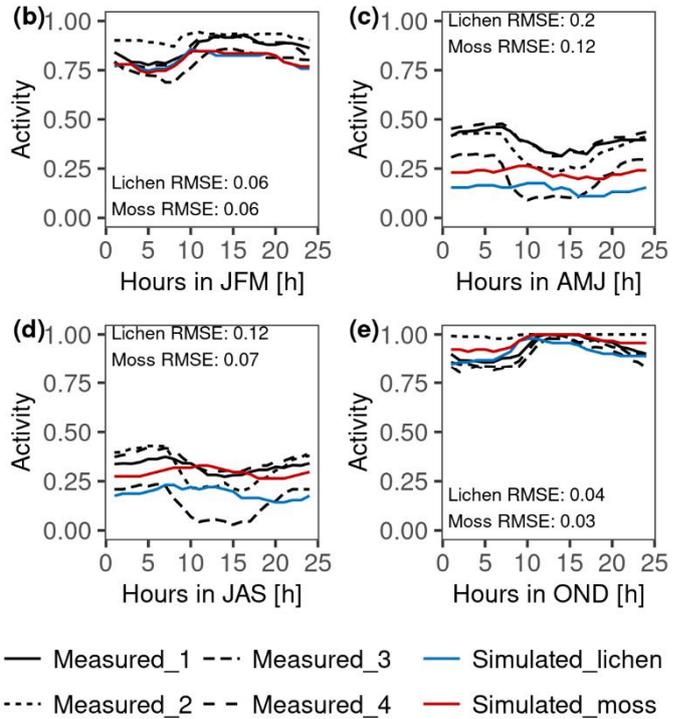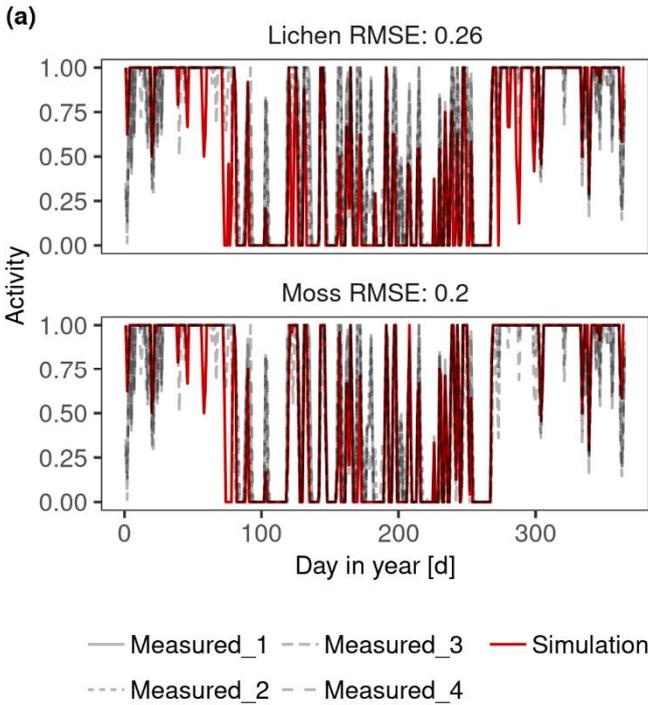
Figure 3: Validation of the estimated daily (~~left panel~~a) and diurnal (~~right panel~~b-e) patterns of activity of lichen- and moss-dominated biocrusts at site T3. The simulated patterns of activity were compared to measured data by four sensors at different locations. ~~Right:~~ (~~b~~a) to (~~e~~d) represent the patterns of average hourly activity from January to March (JFM), April to June (AMJ), July to September (JAS), and October to December (OND), respectively.

In general, the simulated daily and diurnal patterns of activity (water content at site D2) fit the measurements reasonably well in magnitude (Fig. 3 and Fig. S3). However, our fitting resulted in a more dampened diurnal activity pattern simulated by the model, and the activity at night and in the morning was underestimated during several seasons at sites D1, T1, T2 and A1. In addition, both the daily and diurnal activity during April and June at site T1 were underestimated. Furthermore, water content was overestimated for moss-dominated biocrust, especially when there was a large amount of water input at D2, although the patterns corresponded well to the measured data for all three biocrust types (Fig. S3). This overestimation may have resulted from the bias in measured MWC of samples used for constraining the water content in the model.

The comparison of simulated and on-site measured CO_2 exchange rates of three biocrust types (moss, lichen, and cyanocrust composed of cyanolichens and cyanobacteria) at site D2 showed mismatches, especially when water saturation was at both ends of the gradient (Fig. 4). The CO_2 exchange rate at high water content was overestimated compared to the measurements. Moreover, there were large variations in measurements of respiration and CO_2 exchange rate as water content was low and thus simulated CO_2 exchange rate was zero. Excluding the values at both ends of water content (0.58 and 1.74 mm for moss; 0.22 and 0.68 mm for lichen; 0.26~~5~~ and 1.24~~0.65~~ mm for cyanocrust), the accuracy of the model predictions was improved (root mean square error (RMSE~~rmse~~) decreased from 1.4~~45~~ to 1.36 for moss, 1.27 to 0.65~~71~~ for lichen, and 0.79~~0.92~~ to 0.77~~0.87~~ for cyanocrust). Furthermore, the simulations were similar to measurements in magnitude. Therefore, despite the large variation, we are confident about the general validity of the model.

17
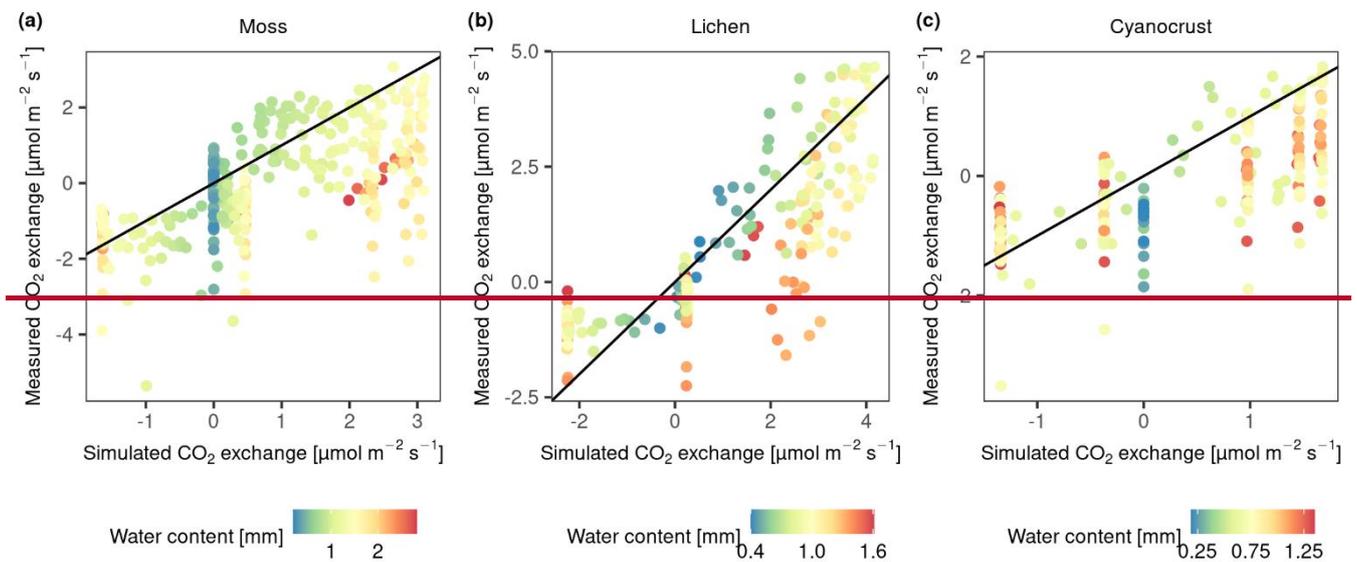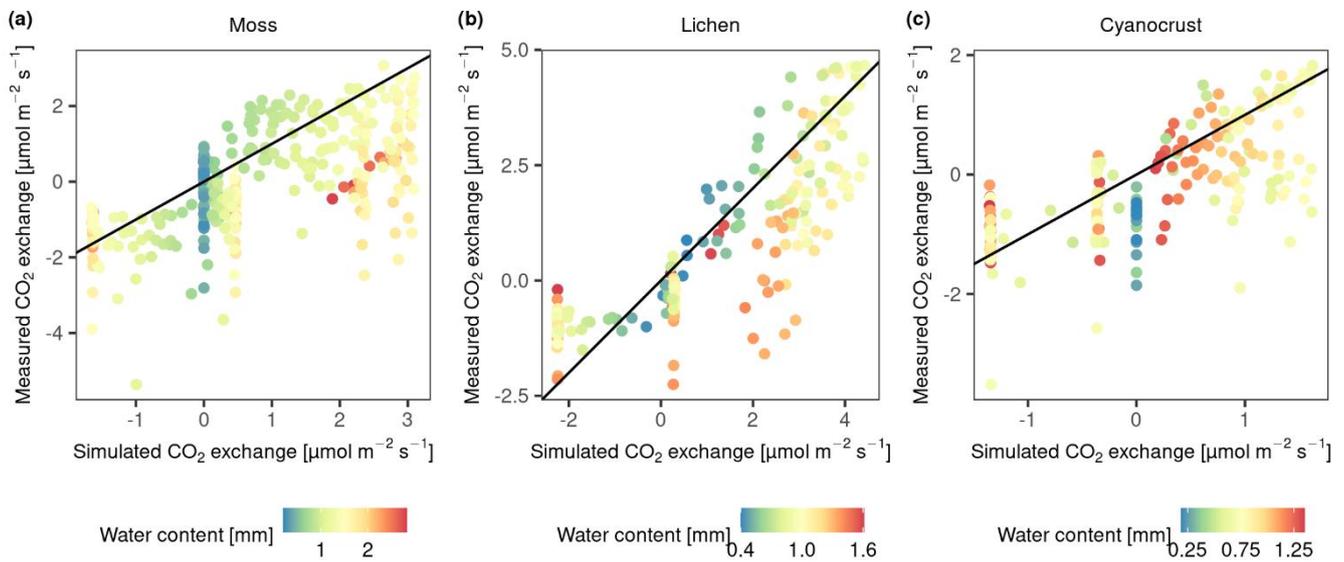
Figure 4: Validation of the photosynthesis and respiration scheme of the data-driven model through comparison of modelled and measured CO_2 exchange rate of moss, lichen, and cyanocrust given the measured water content, surface temperature, PAR, and calculated activity. Observational data were collected in November in 2013 at site D2. The 1:1 line is shown in black.

3.1.2 Estimated C balance by data-driven model.

The simulated annual C balance of each collected biocrust type at each site is listed in Table. 2. The annual C balance of lichen- and moss-dominated biocrusts at ~~two~~ dryland D1 ~~sites~~ showed a small positive value. Moreover, the moss-dominated biocrust at dryland D2 gained small amount of carbon while lichen-dominated biocrust and a cyanocrust additionally measured at site D2 showed a small net release of carbon in the model.

Table 2: Simulated annual carbon budgets of each biocrust type at all sites.

	Lichen	Moss	Cyanocrust
	g C m^{-2} yr^{-1}	g C m^{-2} yr^{-1}	g C m^{-2} yr^{-1}
D1 (Almeria)	1.5~~3.8~~	1.9~~3.2~~	
D2 (Soebatsfontein)	-1~~0~~.7	3.1~~6.3~~	-8.3~~2.0~~
T1 (Gössenheim)	-42.8~~27.3~~	-39.4~~28.6~~	
T2 (Öland)	-92.1~~96.0~~	-74.7~~63.9~~	
T3 (Linde)	9.4~~7.1~~	18.7~~13.3~~	

18

| A1 (Hochtor) | -17.9 ~~11.4~~ | -6.8 ~~6.2~~ |

422 Furthermore, according to these data-driven model simulations, despite the C balance of two biocrust types being positive at
423 site T3, a large amount of carbon was lost at the sites T1 and T2 in temperate humid regions. These results imply that according
424 to the data-driven model, the biocrusts would not survive in the long-term at most of the temperate humid research sites. At
425 the alpine site A1, ~~the~~ both lichen- and moss-dominated biocrust ~~showed a small positive C balance, whereas the lichen crust~~
426 lost carbon in a year with long periods of ice cover.

3.2 Dominant strategies selected by the LiBry Model

428 In general, the photosynthesis response curves of dominant and average strategies selected by the LiBry model did not fit well
429 to the measurements, especially at temperate site T2 (Fig. 5; the results for the other sites with negative C balance are shown
430 in Fig. S4). Specifically, the selected physiological traits which determine water and light acquisition of the dominant and
431 average strategies in LiBry differed from those of the collected samples at all sites. Compared to the measured samples, the
432 LiBry strategies showed markedly higher efficiency at low light intensity and faster activation. By design, the LiB~~b~~ry model
433 selected strategies with a positive C balance in the long-term run, and thus the mismatches are consistent with the fact that the
434 data-driven model simulated negative C balances.

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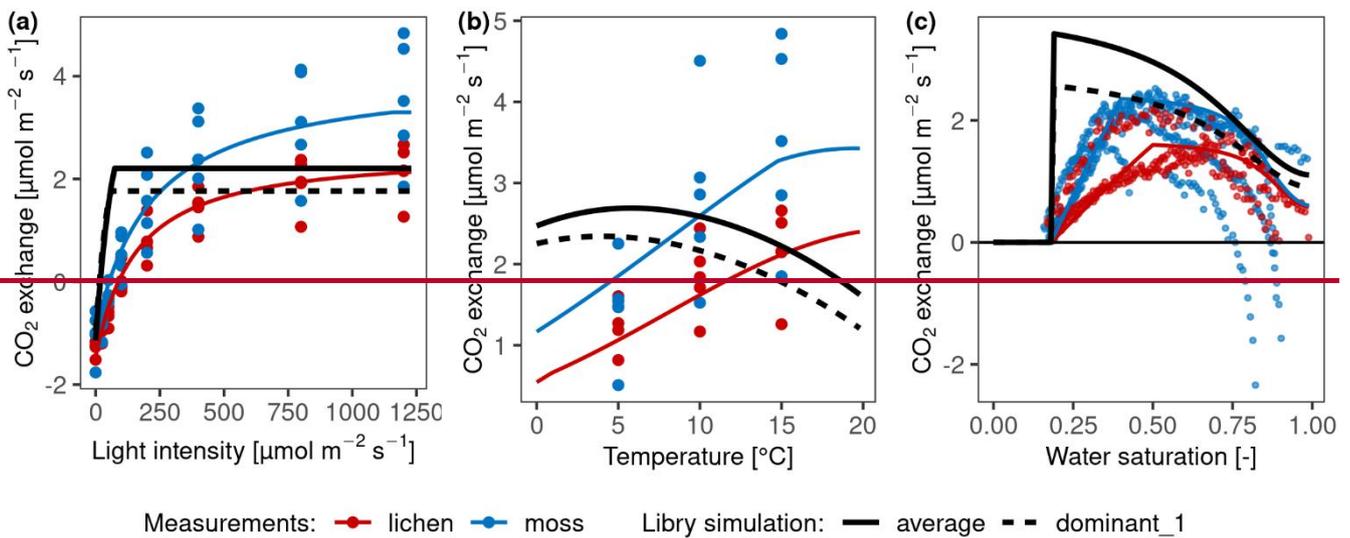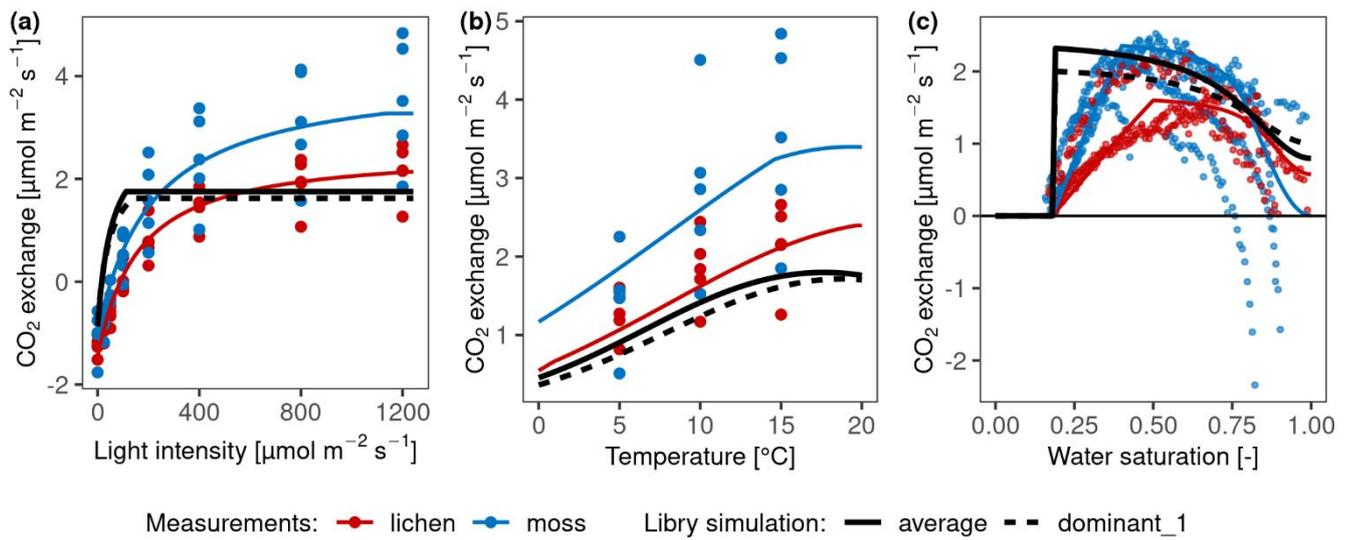
Figure 5: Comparison of net photosynthesis response of measured samples with simulated selected dominant and average strategies of LiBry at site T2. (a): light response curve; (b): temperature response curve; (c): water response relation. The colored points represent the measured CO_2 exchange rates of moss and lichen, and the coloured lines correspond to the data-driven model. The black lines show the photosynthesis response of the dominant strategy selected by the LiBry model (dashed) and the average strategy (solid). The parameter values of the average strategy correspond to the average of all surviving strategies.

3.3 Driving factors of variation of the C balance

3.3.1 Environmental factors

The environmental factors light intensity, CO_2 concentration, air temperature, and various water sources, had different effects on the C balance of lichens in different climate zones (Fig. 6). For all sites within a given climate zone, the effects of different environmental factors on C balance were overall similar but showed an apparent larger variation at the temperate site T3 in contrast to the other two temperate sites, and at site D2 compared to D1 (Fig. 6a). This may be due to physiological differences of the investigated biocrust species between these sites and consequently variations in the responses of net photosynthesis rate to temperature, water, and light between them (Fig. 2 and S2).

Furthermore, the spatial patterns of the relative importance of different environmental factors show that the factors which have the strongest effects differ between climatic regions (Fig. 6b).

20

(a)

(b)

(a)

(b)
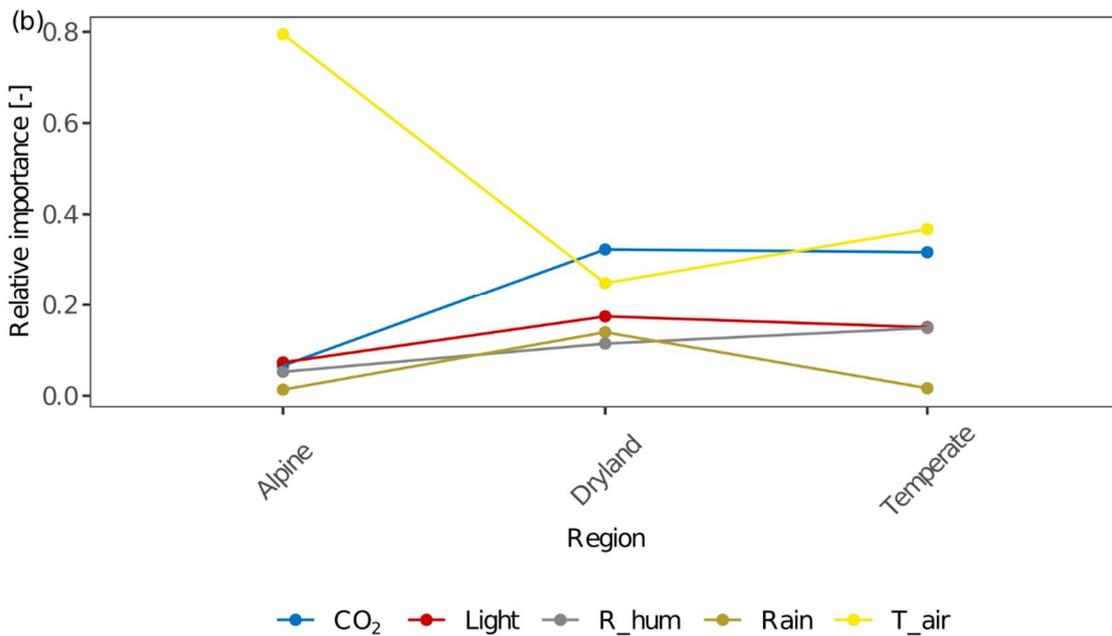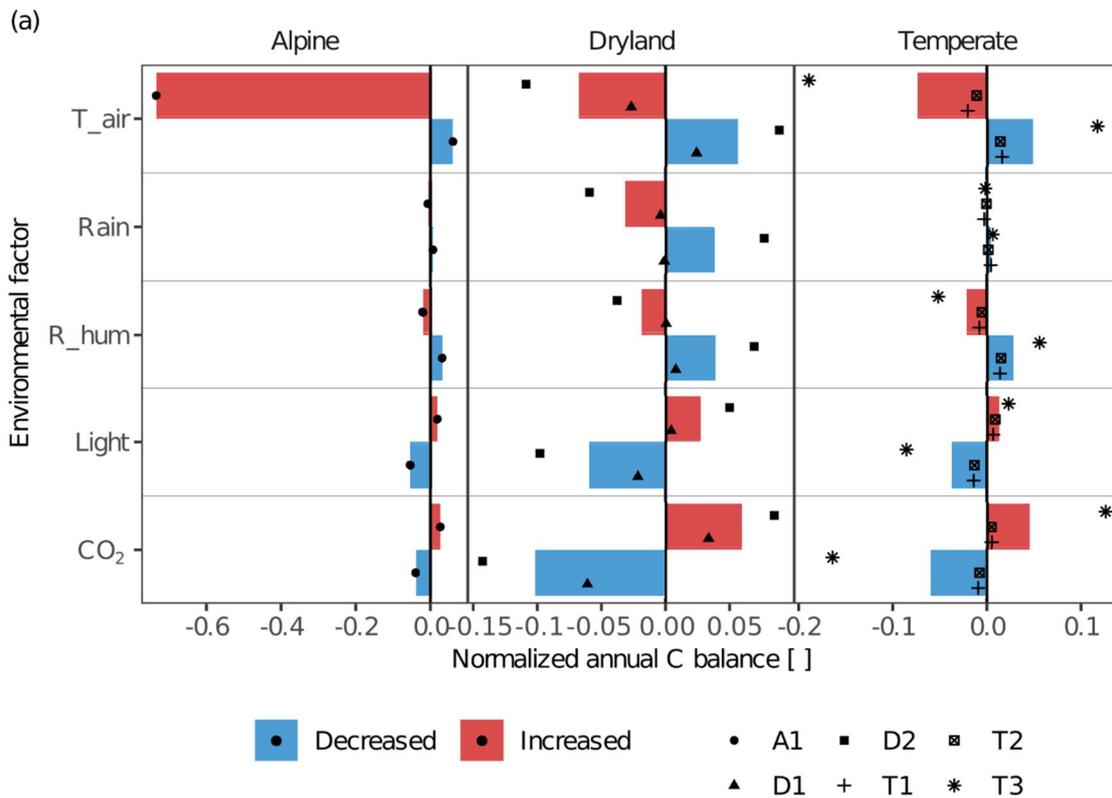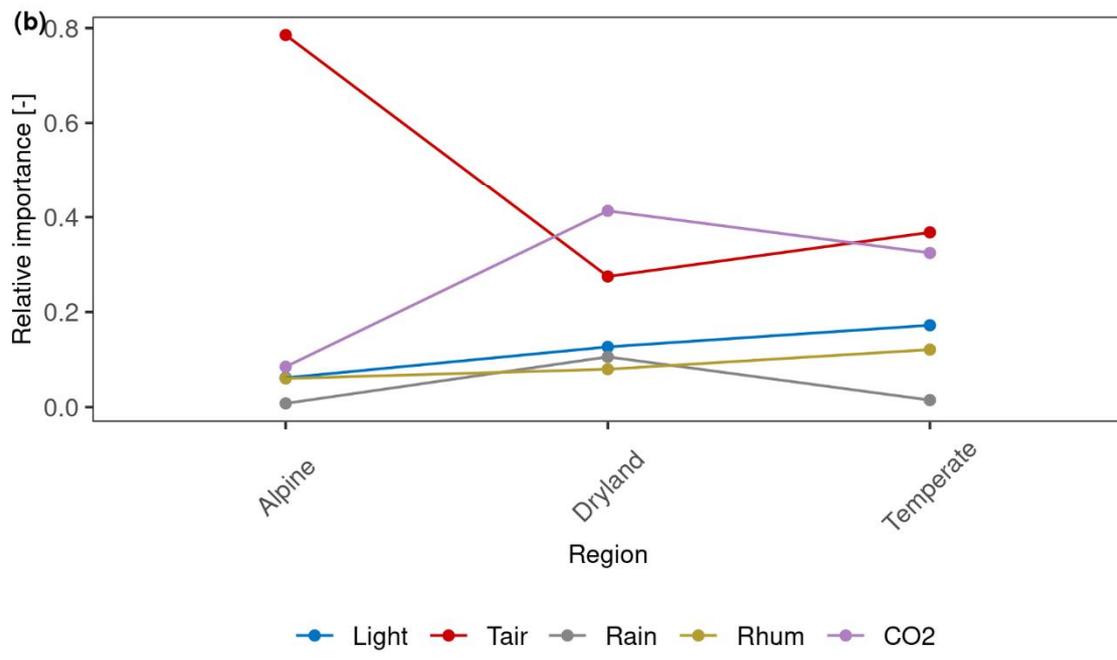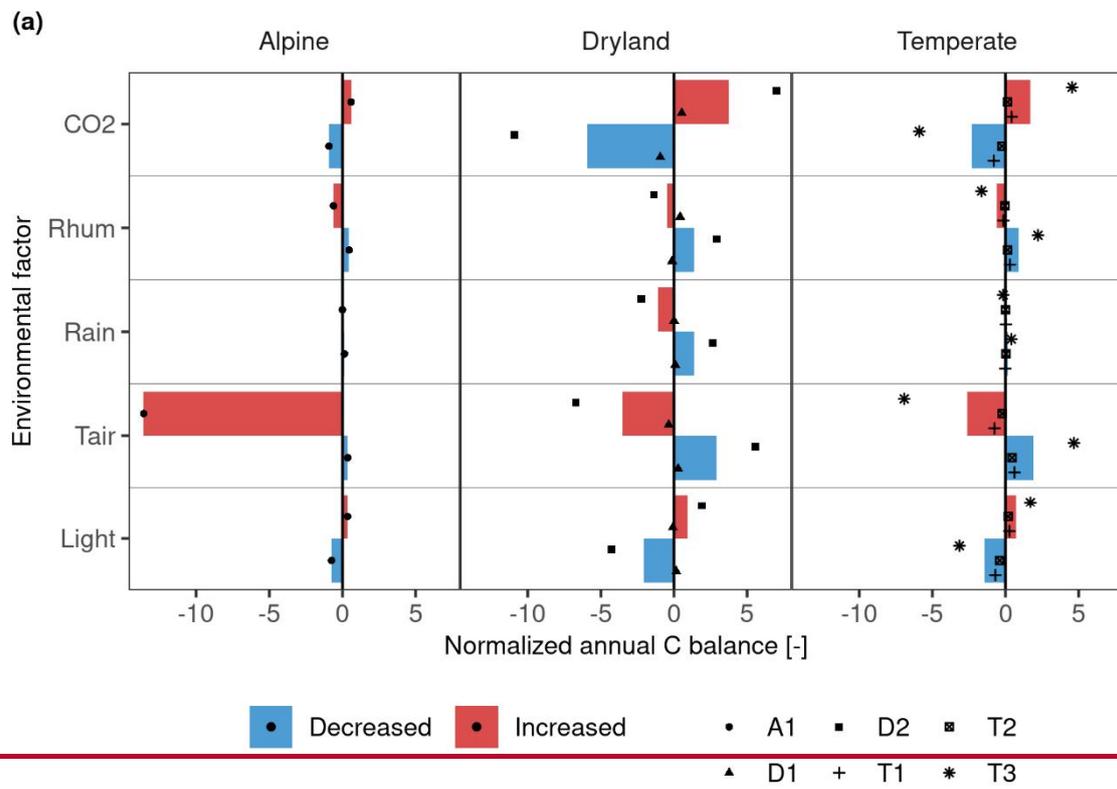
Figure 6: (a) The effects of environmental factors - CO_2 concentration (CO_2), relative air humidity (R_hum), rainfall amount (Rain), air temperature (T_air) and light intensity (Light) on the annual C balance of lichens in different climate regions. The altered annual C balance resulting from increasing or decreasing environmental factors is normalized by the C balance under original environmental conditions. The colored columns indicate the average value of the normalized C balance at sites with similar climate conditions. Various styles of black points indicate different sites. Positive normalized C balance implies that the annual C balance increases with varying environmental factors and more carbon was accumulated in a year at the site, and vice versa. A larger normalized C balance reflects that the C balance is more sensitive to the altering environmental factor, and thus the environmental factor has a larger effect on C balance. (b) Relative importance of each environmental factor compared to other factors across the climatic regions. Larger relative importance implies a more important effect the factor has on the C balance compared to other factors in the given climatic region, and vice versa.

In general, air temperature and CO_2 concentration were the most important drivers for C balance of biocrust organisms between climate zones. Light intensity and relative humidity played a relevant role in impacting the C balance as well. Rainfall amount had lower relative importance at all sites except dryland D2, where the effect of rainfall on C balance was similar to other factors (Fig. 6a). Therefore, rainfall amount showed a maximum in relative importance in drylands, compared to other regions. In general, the effect of the other water source, relative air humidity, was moderate but notable at all climate zones, and is slightly larger in temperate region in comparison to other climate zones. Furthermore, the humidity had a slightly larger impact on C balance in comparison to rainfall amount at all temperate and alpine sites (e.g., change amplitude was 0.007 for rainfall and 0.021 for humidity at T1). ~~Moreover, reduced humidity can have a positive effect on C accumulation in these regions (e.g., the normalized C balance was 0.3 at T1 when relative humidity was reduced).~~ In drylands, however, the impacts of water sources on C balance varied between sites. The results showed that relative humidity had a slightly larger impact than rainfall amount at D1 while ~~similar~~ smaller at D2 (the change in amplitude at D2 was 0.108 for humidity and 0.137 for rainfall). ~~Reducing relative humidity had a positive effect on C accumulation at D2 while C accumulation was reduced at D1 (normalized C balance is 2.90 at D2 and -0.13 at D1 when relative humidity decreases).~~

The ambient CO_2 concentration was an essential factor for the C balance at all sites especially in drylands, resulting in positive effects on C balance with increasing CO_2. Furthermore, light intensity had a marked impact on the C budget at all sites ~~except for dryland D1~~, and it was relatively more important in drylands and temperate regions than the alpine site. ~~At site T2, for example, the normalized C balance was changed to -0.39 and to 0.19 for half and doubled light intensity, respectively.~~ At ~~these~~ all sites, the normalized C balance increased with enhanced light intensity and vice versa (e.g. normalized C balance at T2 are -0.013 and 0.008 for half and doubled light intensity). ~~At site D1, however, the values did not vary largely, and even slightly more carbon was lost as the light levels increased (0.16 and -0.08 for half and doubled light intensity).~~ Air temperature had a large impact on C balance at all sites. Especially at the alpine site A1, C balance decreased strongly as air temperature raised by 5 K (normalized C balance of -0.735 ~~-13.59~~), and at all sites, the direction of the effect remained constant, namely, warming decreased the C balance and vice versa.

23

3.3.2 Physiological parameters

We found that physiology plays an important role in all regions. In particular, the respiration-related parameters such as q10, Resp_main, and Topt have a notably higher impact on C balance estimation (Fig. 7). Furthermore, the relative importance of several physiological parameters showed similar patterns across climatic zones: in all regions, q10 is the most essential parameter, Sat_act0 and Sat_act1 play little roles in affecting C balance. Other parameters showed slightly different patterns among regions. Metabolic respiration cost (Resp_main), for instance, plays a more important role than optimum temperature for gross photosynthesis (Topt) at the alpine site, while the optimum temperature is more essential in drylands and temperate regions (Fig. 7b).

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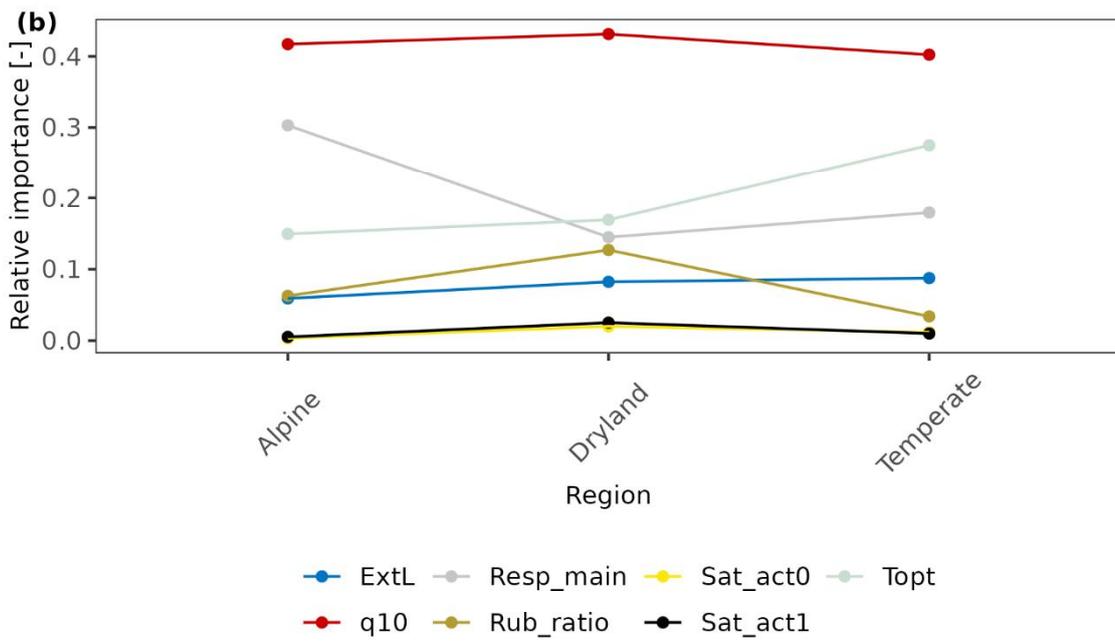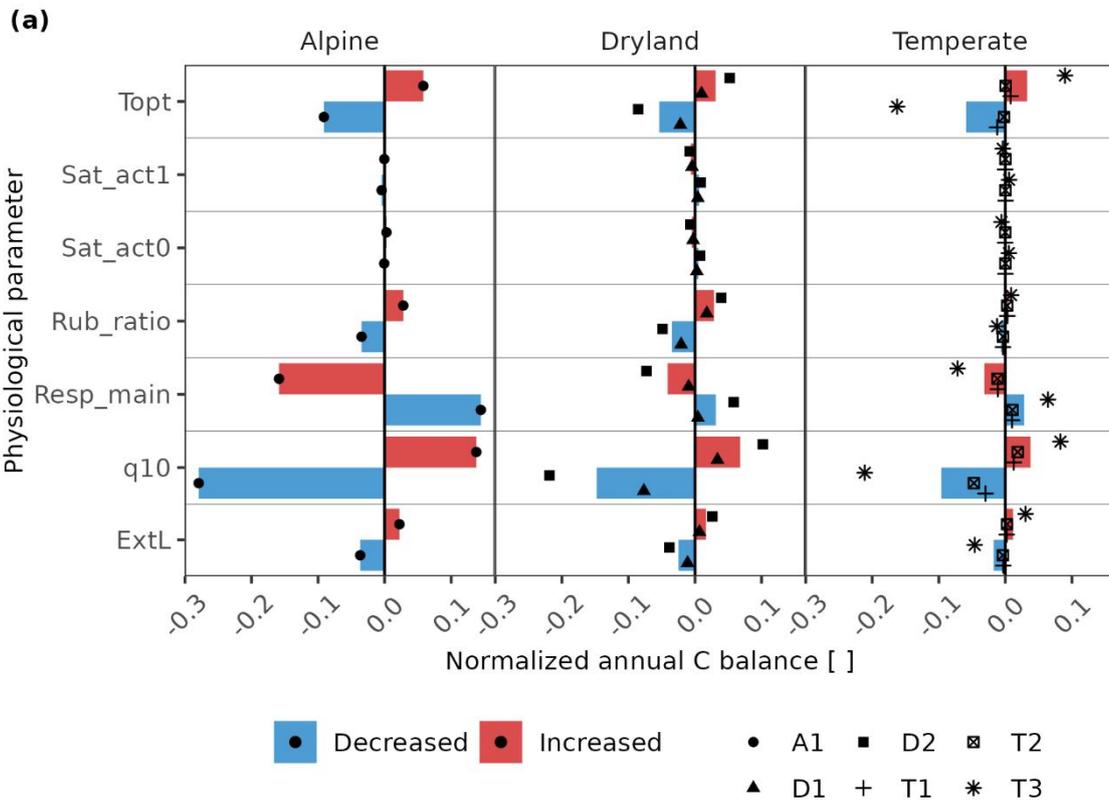
498 Figure 7: (a) The effects of physiological parameters – metabolic respiration cost per surface area (Resp_main), Q10 value of
499 respiration (q10), the optimum temperature for gross photosynthesis (Topt), respiration cost of RuBisCO enzyme (Rub_ratio),
500 and light absorption fraction in cells (ExtL), minimum saturation for activation (Sat_act0), and minimum saturation for full
501 activation (Sat_act1) – on the annual C balance of lichen-dominated biocrusts in different climate regions. The parameters
502 decreased or increased by a consistent range for all sites based on the measured deviation in photosynthesis response curves
503 of replicates. The altered annual C balance resulting from increasing or decreasing parameters is normalized by the original C
504 balance. The coloured columns indicate the average value of the normalized C balance at sites with similar climate conditions.
505 Various styles of black points indicate different sites. (b) Relative importance of each physiological parameter compared to
506 other parameters across the climatic regions. Larger relative importance implies a more important effect the parameter has on
507 the C balance compared to other parameters in the given climatic region, and vice versa.

508 However, even though physiology parameters play an important role in all regions, the C balance at T1, T2 and A1 did not
509 become positive when the physiological parameters were varied reasonably, that is the parameters were varied to relatively
510 cover the deviation of response curves of replicates. Furthermore, the change in C balance value is much smaller in drylands
511 compared to other regions (as shown in Fig. S11 in Appendix).

512 ~~3.3.2~~3.3.3 **Acclimation of physiological properties**

513 The sensitivity analysis for acclimation showed a marked increase in annual productivity of lichen- and moss-dominated
514 biocrusts at site T1 (Fig. 8~~7~~) when the seasonal acclimation of several physiological parameters was included in the model
515 (from -~~27.3~~42.8 to -15.5~~3.1~~ g C m^{-2} yr^{-1} and from -~~39.4~~28.6 to -4.2~~15.7~~ g C m^{-2} yr^{-1}).
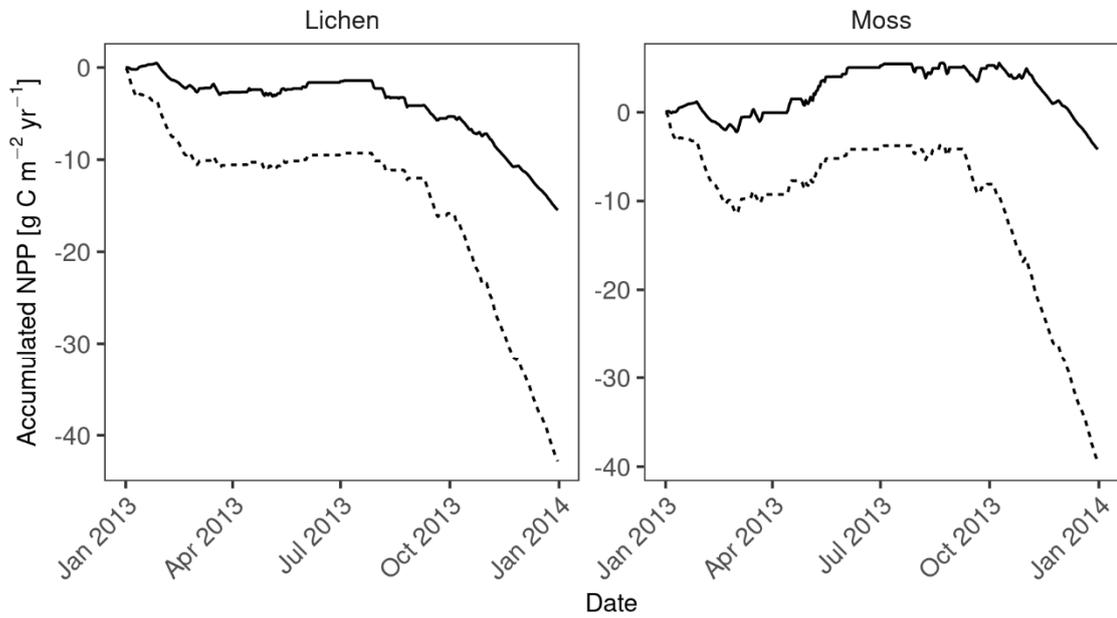
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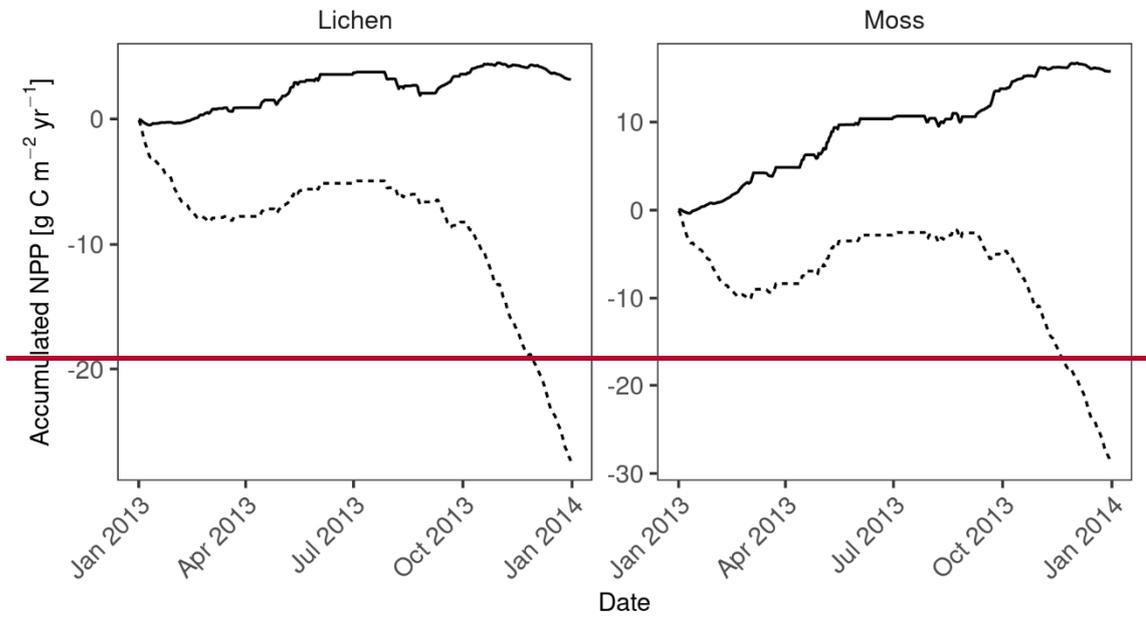
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518 **Figure ~~7~~8**: Comparison of accumulated annual C balance between <u>two simulations in the sensitivity analysis of seasonal</u>
519 <u>acclimation of physiological properties. In the simulation "fixed parameters",</u> ~~simulations with dynamic parameters and fixed~~
520 ~~ones of lichens and mosses at site T1. For the simulation with the fixed parameters,~~ all parameters that have been calibrated or
521 measured remained constant throughout the simulation year. <u>For the simulation "dynamic parameters" at site T1,</u> ~~For the~~
522 ~~simulation with dynamic parameters at site T1~~, parameter metabolic respiration cost per surface area (Resp_main) was reduced
523 by half, light absorption fraction in cells (<u>E</u>~~e~~xtL) was doubled but restricted to one, the ratio of Jmax to Vcmax (jvratio) was
524 increased by two times from September to February <u>to adapt to the winter climates. For the other months, the "fixed" values</u>
525 <u>were used.</u>~~The values remained the same in other months as the ones prescribed in the simulation with fixed parameters~~.

526 **4 Discussion**

527 **4.1 Simulated C balance of data-driven model**

528 The data-driven model aims to provide observation-based estimates of the carbon fluxes of non-vascular photoautotrophs
529 which may serve as approximation for the C balance of vegetation in biocrust-dominated ecosystems. At the two dryland sites,
530 the ~~lichen and~~ moss-dominated biocrusts were estimated to be carbon sinks on an annual basis<u>, and lichen-dominated biocrust</u>
531 <u>can also be a carbon sink at one of the dryland sites</u>. As shown in the results, ~~lichens took up 3.8 and 0.7 g C m⁻² yr⁻¹, and~~ mosses
532 accumulated <u>1.9</u>~~3.2~~ and <u>3.1</u>~~6.3~~ g C m⁻² yr⁻¹ at site D1 and D2, respectively<u>, and lichens accumulated 1.5 g C m⁻² yr⁻¹ at site D1</u>.

533 The estimated C balance at the two dryland sites is consistent with the magnitude of the annual C balance of different biocrust
534 types reported by various studies in arid habitats. Feng et al. (2014) recorded that the biocrusts composed of lichens, mosses,
535 and cyanobacteria of the Mu Us Desert in China took up 3.46 to 6.05 g C m⁻² yr⁻¹. Brostoff et al. (2005) estimated a larger
536 carbon gain by lichen biocrust of 11.7 g C m⁻² yr⁻¹ in the Mojave Desert, USA. For cyanobacteria, an annual carbon uptake of
537 0.02 to 2.3 g C m⁻² was reported for deserts (Jeffries et al., 1993). The estimated C balance values in drylands fluctuate
538 relatively largely, but the magnitude is consistent with the simulated results by the data-driven model at D1 and D2.

539 For biocrust lichens growing on rock surface <u>without soil attached underneath</u> in a temperate grassland, Lange (2003b)
540 measured an annual carbon gain of 21.49 g C m⁻². Additionally, several studies estimated the carbon budget in humid tundra
541 habitats. An amount of ~12–70 g C m⁻² yr⁻¹ carbon was fixed by moss-dominated biocrust, for instance (Schuur et al., 2007).
542 The magnitude of these values corresponds to the estimation of the C balance at T3. However, the estimated annual carbon
543 losses of lichens and mosses by the data-driven model in temperate regions T1 and T2 should actually lead to the death of
544 these organisms, which is not consistent with their dominant abundance in the field and is much lower than published by
545 previous studies.

546 The mismatches of trait values between strategies <u>predicted via selection</u> ~~selected~~ by the LiBry model <u>for the sites</u> and <u>the</u>
547 collected species <u>with regard to their net photosynthesis response curves</u> indicate that <u>the physiological parameter values that</u>
548 <u>would be necessary to maintain a positive C balance in LiBry are not compatible with those of the sampled biocrusts.</u> ~~strategies~~

28

549 ~~corresponding to the collected species could not maintain a positive long-term C balance, and thus were not able to survive in~~

550 ~~the LiBry model.~~ This is ~~consistent~~ in line with the results of the data-driven model, which also simulates a negative C balance

551 and is based on the same physiological processes as LiBry. This also applies to the lack of seasonal acclimation in both

552 modeling approaches, since the strategies in LiBry are assumed to have constant functional properties throughout the

553 simulation. ~~for those trait values. Nevertheless, there are some uncertainties in the model simulation. A bias in model estimates~~

554 ~~could result, for instance, from missing physiological processes and trade-offs. Potential reasons for the inconsistency between~~

555 ~~models and observations are discussed further below.~~

4.2 Uncertainties of long-term C balance simulated by the data-driven model.

557 The data-driven model simulated relatively reasonable C balance values in drylands but unrealistic, negative values at

558 temperate sites T1 and T2. Since the same or similar gas exchange methodology has been used for all sites, differences in the

559 simulated C balance among these regions likely result from variation in the species-specific interactions between climate and

560 physiological processes, including seasonal variation in physiological properties due to acclimation.

561 As the results (Fig. 6) show, CO_2 concentration is an essential factor for the annual C balance of biocrusts, especially at dryland

562 and some temperate sites. Therefore, uncertainty in the CO_2-value prescribed in the model may be a source of error. The CO_2

563 concentration at the surface boundary might exceed the value of 400 ppm that was prescribed in the model because of CO_2

564 diffusion from the soil, which may lead to an underestimated C balance (Fig. 6a). However, with enhanced CO_2 concentration

565 in the sensitivity analysis (600 ppm) at site T1, for instance, the estimated C balance increased only slightly, and is still strongly

566 negative (-37.0 g C m^{-2} yr^{-1} for lichen and -30.2 g C m^{-2} yr^{-1} for moss). Hence, the lower CO_2 concentration can partially

567 contribute to the strongly negative C balance at T1 and T2, but is not a major factor.

568 Furthermore, the negative C balance at temperate and alpine sites may result from the uncertainties in physiology, which were

569 also observed between replicates (see Fig. 2 and Fig. S2). An overestimation of dark respiration rates of the photoautotrophs

570 in the biocrust may result from including a small amount of heterotrophic respiration. The overestimated respiration rate then

571 leads to an overestimation of the parameter metabolic respiration cost per surface area (Resp_main) and might also cause an

572 underestimated Q10 value (q10) calculated from the respiration rates. The uncertainties of these two parameters reduce the

573 estimated C balance largely (Fig. 7). Additionally, the optimum temperature (Topt), which is also the reference temperature

574 for calculating the respiration rate, cannot be well constrained by the limited measured temperature response data set. Thus,

575 Topt may be underestimated. The larger difference in surface temperature to Topt results in a larger respiration rate, and lower

576 gross photosynthesis, which leads to a lower C balance.

577 Although the uncertainty in individual physiological parameters may not lead to the markedly negative C balance estimates,

578 as indicated by still negative values upon variation of these parameters (Fig. S11), additive effects of all parameters combined

579 with long-term unfavourable environmental conditions may cause a large amount of carbon lost over a year. The optimal

29

580 conditions are rare within a year, which was also described by Lange (2003b). Thus, the overestimated respiration rate leads
581 to a lower carbon gain during the relatively optimal conditions, which may not be sufficient to compensate for exaggerated C
582 losses under long-term harsh conditions, such as autumn and winter at site T1, for instance. For this reason, the simulated C
583 balance of mosses and lichens in temperate humid regions was mostly negative.

584 In addition to the uncertainty in the values of physiological parameters, seasonal acclimation of these physiological traits to
585 the current climatic conditions may play an important role in regulating the C balance at humid sites where the organisms are
586 active throughout the year, such as site T1 (Fig. 8). It was observed, for instance, that the respiration of lichens shows
587 acclimation to seasonal changes in temperature, and the maximum CO_2 exchange rate of the organisms remains steady
588 throughout the year (Lange and Green, 2005). Gauslaa (2006) found a higher chlorophyll a/b ratio in forest lichens with
589 increasing light. Moreover, depression in quantum efficiency in summer under extremely dry conditions has been observed
590 (Vivas et al., 2017). These varied physiological properties of organisms within a year may result in different photosynthesis
591 and respiration rates, and thus different C balances in comparison to the ones that cannot acclimate to the seasonal climate.
592 The missing seasonal acclimation of physiological traits may explain why the data-driven model estimated a negative C
593 balance for biocrusts in humid regions.

594 Another limitation of the modeling approach may be the lack of separate responses of respiration and photosynthesis to
595 metabolic activity. Both photosynthetic activity and respiration reach their maximum in the model once the water saturation
596 reaches the optimum value for net photosynthesis (Wopt_np). In some cases, however, respiration rate may reach the maximum
597 value only at a higher saturation than Wopt_np (Lange, 1980), indicating that the model may overestimate respiration in the
598 long-term.

599 In comparison to the unrealistic C balance numbers at T1 and T2, we estimated more reasonable values in drylands and at T3.
600 However, we do not make a definitive statement about whether or not the model predicts an accurate C balance in drylands.
601 since the measured climate data and photosynthesis response curves that were used for calibrating land surface properties and
602 various physiological parameters represent only samples of the large physiological and climatic variation. A higher accuracy
603 would be more likely to be expected in drylands as these regions have a more uniform climate throughout the year than
604 temperate regions that show substantial seasonality. Additionally, variation in light conditions is slightly more relevant for the
605 simulated C balance than variation in moisture (see Fig. 6) because the organisms are able to become inactive, meaning that
606 the dry season in drylands does not have a decisive effect on the C balance, while low light in winter in temperate climate does
607 since organisms have to be active then. Furthermore, the longer total inactive period in drylands could reduce the bias in the
608 magnitude of the simulated C balance caused by incorrectly estimated physiological parameter values. We estimated a smaller
609 absolute change in annual C balance in drylands with varied physiological parameters in the sensitivity analysis (for instance,
610 the C balance of lichens changed by 34.6 g C m^{-2} yr^{-1} for parameter Topt at T1, while it changed only by 1.5 g C m^{-2} yr^{-1} at
611 D1).

612 Furthermore, the estimated C balance may be inaccurate due to the potential bias in estimated relative water saturation, which

613 partly depends on prescribed MWC obtained by measurements. However, the outcome of the sensitivity analysis of MWC at

614 T1 revealed that the annual carbon estimation is robust to the uncertainties with regard to the prescribed MWC (details in

615 Appendix). Another factor that potentially affects the accuracy of C balance estimates is interannual climatic variability. While

616 the model estimated unrealistic C balance values of lichen-dominated biocrusts at T1 and T2 for current conditions, the C

617 balance may have been different in other years. Therefore, the simulation of annual C balance based on multi-year climate

618 data is worthy of future study to understand the long-term C balance better. Moreover, the estimated negative C balance of

619 certain lichen and moss species may not be generalizable and representative for the overall situation in the field due to the

620 large variation in physiological adaptation strategies to climate. There could be other organisms that form cryptogamic covers,

621 for instance, that show a different degree of depression in net photosynthesis at high water content (Lange et al., 1995), and

622 thus have more reasonable C balance values.

623 **4.2~~4.3~~ Potential factors influencing the C balance**

624 Despite diverse climatic conditions, we found similarities regarding the dominant environmental factors and physiological

625 parameters controlling the C balance. ~~As shown in the results,~~ Thereby, CO_2 and air temperature were the two most important

626 environmental factors at all sites ~~that impact C balances in the model~~. Relative air humidity, partly precipitation, and light

627 intensity were also ~~essential~~ relevant for the estimation of the C balance. In terms of physiological parameters, the respiration-

628 related parameters were the most important drivers, while parameters that affect Vcmax and thus the light-independent CO_2

629 assimilation rate were relevant, too.

630 The relative importance of these factors/parameters varied slightly among climatic regions. ~~and the effects of these factors on~~

631 ~~the C balance were different in direction among sites.~~ Regarding the comparison between environmental factors, ~~w~~We cannot

632 rule out that the magnitudes of changes in environmental factors that we applied in the sensitivity analysis were not balanced,

633 which may have led to an overestimation of the relative importance of certain factors, such as air temperature, for instance,

634 compared to the others. The spatial patterns across climate regions of a given environmental factor, however, are not affected

635 by this, which means that differences between climatic regions for a given factor are most likely robust. Hence, air temperature

636 is more relevant at the alpine site and relative air humidity has a higher impact in temperate than in other regions, rainfall and

637 CO_2 are likely to have the largest effect on C balance in drylands. Even though the data-driven model failed to estimate

638 reasonable C balance at some sites, the comparison of the relative importance of the environmental factors across climatic

639 regions may be valid since the measurement procedure is consistent. Moreover, the patterns of relative importance remain

640 similar when excluding the sites with strongly negative C balance (T1, T2, and A1; as shown in the Fig. S12 in Appendix).

641 ~~compared to other regions, while air temperature is more relevant in alpine regions and light and relative air humidity have a~~

642 ~~higher impact in temperate than in other regions.~~ Nevertheless, we only studied the sensitivity of the C balance of biocrusts

643 dominated by the lichen *Psora decipiens* and *Cladonia furcata* (at T3), and there are variations between lichens of different

31

growth forms and between biocrust types. For example, cyanolichens increase in abundance with increasing rainfall, but trebouxioid lichens have their physiological optimum in drier conditions (Phinney et al., 2021). Moreover, the impact of precipitation on isidiate lichens is weaker than that of temperature (Phinney et al., 2021).

4.3.1 Environmental factors

Our results suggest that warming can result in a large amount of carbon loss at all sites, with a particular large effect in the alpine region. The consistent effects of warming on C balance of biocrusts are found in various field studies (e.g., Darrouzet-Nardi et al., 2015; Ladrón de Guevara et al., 2014; Li et al., 2021; Maestre et al., 2013). This can be explained by the overall less optimal water and temperature conditions associated with warming. The simulated increasing respiratory costs with warming overcompensate gains in gross photosynthesis.

Ambient CO_2 concentration affects the gross photosynthesis rate to a large extent in the model. Although the intra-annual change in air CO_2 concentration may be small in the field compared to other environmental factors, the increase of CO_2 in the atmosphere in recent decades (IPCC 2021) may alter the long-term C balance substantially. However, this beneficial effect of elevated CO_2 on photosynthesis and C balance may be reduced in reality due to future limitation of growth by nitrogen (Coe et al., 2012a), which is not considered in the model, or also due to shortened activity periods resulting from warmer and drier future climatic conditions.

Light intensity has the third largest effect on C balance, slightly larger than moisture. Light is one of the essential factors for photosynthesis as simulated by our model, and it is Light intensity is one of the essential factors for photosynthesis as simulated by our model. According to our climate forcing data, the mean value of radiation maxima in January is 244 μmol m⁻² s⁻¹ at T1 and 245 μmol m⁻² s⁻¹ at the alpine site. During wintertime in temperate and alpine regions, light intensity may be lower than the light saturation point (Fig.2 and S2). Therefore, light intensity is a limiting factor of photosynthetic carbon assimilation, in particular in winter at temperate and alpine sites (the mean value of radiation maxima in January is 244 μmol m^{-2} s^{-1} at T1 and 245 μmol m^{-2} s^{-1} at the alpine site). Hence, increasing light intensity can promote carbon accumulation. in these regions, and increasing light intensity can thus promote carbon accumulation. However, the higher light intensity can raise the surface temperature and thus lead to more evaporation. More water loss would result in lower water saturation and activity especially in drylands, which could limit the net photosynthesis rate. Therefore, at dryland D1, the increasing light intensity has the opposite impact compared with other sites.

Factors that determine water supply are rainfall and non-rainfall inputs such as dew and water vapor that are related to relative humidity. The relative importance of different moisture factors in mediating C balance varies in the model. Relative humidity plays a more important role in mediating the C balance than rainfall amount. This may be due to the timing of dew or water vapor uptake, which is greatest before sunrise (Chamizo et al., 2021; Ouyang et al., 2017) and prolongs the activated periods in the early morning when the organisms start assimilating carbon (Veste and Littmann, 2006). This may result in a markedly increased annual C balance in the model. Rainfall amount was not a key factor affecting the simulated biocrust performance

at one of the arid sites, which is consistent with another study (Baldauf et al., 2021). At the other dryland site (D2), however, this was not the case. Moreover, we found that the effect of the amount of rainfall is small in humid temperate and alpine regions as well. The differing effects of rainfall on the C balance depend on the change in relative water saturation that follows from rainfall event sizes and patterns throughout the year (Reed et al., 2012). In some cases, decreased rainfall leading to lower water saturation of biocrusts may facilitate photosynthetic carbon gain via increasing the CO_2 diffusivity from the atmosphere into the chloroplast (Lange et al., 1997). Nevertheless, reducing water saturation below a certain value can cause a decline in the duration of activity (Proctor, 2001; Veste et al., 2008) which thus reduces carbon accumulation. Thus, there may be a rain threshold below which decreasing rain may start having a negative effect on biocrust C balances. The threshold is likely species-specific as it is associated with the water-holding capacity of the organism. Our simulation results thus highlight the need for the combined application of field experiments and data-driven modeling to improve our understanding of differential responses to variation in precipitation.

Biocrust water content is regulated by both rainfall and non-rainfall water inputs. The relative importance of different water sources in mediating C balance varies in the model. Precipitation amount was not a key factor affecting the simulated biocrust performance at one of the arid sites, which is consistent with another study (Baldauf et al., 2020). Our results suggest that at the other dryland site D2, however, the precipitation amount is very closely associated with the C balance of lichens. Moreover, we found that the effect of the amount of precipitation is small in relative humid temperate and alpine regions. The effect of precipitation on C balance depends on the change in relative water saturation that follows from precipitation event sizes and patterns. In some cases, decreased precipitation leading to a lower water saturation of biocrusts may facilitate photosynthetic carbon gain via increasing the CO2 diffusivity from the atmosphere into the chloroplast (Lange et al., 1997). Nevertheless, reducing water saturation below a certain value can cause a decline in the duration of activity (Proctor, 2001; Veste et al., 2008) which thus reduces carbon accumulation. Thus, there may be a rain threshold below which decreasing rain may start having a negative effect on biocrust C balances. The threshold is likely species-specific as it is associated with the water holding capacity of the organism. At arid region D1, despite the number of rainfall events being lower, the size of many single events is still large. When rainfall input is varied in the model (decreased by half), the activity and water saturation patterns of the studied organisms are similar to the ones with original rainfall (Fig. S5a and S5b). At the temperate and alpine sites, although the reduction in rainfall lowered the saturation as well as the activity at many time points (Fig. S5c and S5d), the organisms still remained active during most of the time (active 56% to 52% of the time during one year as rainfall decreased by half) and even still fully active, since there was frequent and considerable rainfall in the year of data collection. Thereby, the negative impact induced by reduced activity can be compensated by the positive impact caused by reduced saturation. Thus, in the model, the impact of precipitation amount is small on C balance in these regions.

Moreover, the difference in effects of precipitation between two drylands may result from the different precipitation patterns. The precipitation events are more evenly distributed throughout the year in D2 compared to D1, and many single events are

708 small in size. Decreasing the amount of precipitation alters the activity and water saturation patterns of the investigated
709 organisms to a larger extent in D2 as compared to D1 (Fig. S5e and f). Therefore, the amount of precipitation has a relatively
710 larger impact on the simulated C balance at site D2. Several studies found strong effects of variations in the precipitation
711 pattern on biocrust C balance (such as Reed et al., 2012). Our simulation results thus highlight the need for combined
712 application of field experiments and data-driven modelling to improve our understanding of differential responses to variation
713 in precipitation.

714 Furthermore, our findings indicate that relative humidity plays an important role in mediating the C balance of lichens in arid
715 regions, which is consistent with the results of Baldauf et al. (2020). Our results also imply that relative humidity is a crucial
716 factor at humid sites. However, in contrast to rainfall, the non-rainfall water inputs, such as water vapor and dew, that depend
717 on relative humidity have contrasting impacts on the simulated C balances of temperate, alpine, and dryland biocrusts (Fig. 6).
718 Whereas the increase in relative humidity can reduce the annual carbon gain in temperate regions, it causes an increase at D1.
719 The possible reason for this opposite direction of effect could be that the effect of air humidity depends on the moisture
720 conditions of the site. Higher relative air humidity could enhance water vapor and dew uptake and reduce evaporation. At
721 humid temperate and alpine sites, this yields larger water saturation and more periods with extremely high saturation at sub-
722 optimal, light limited conditions. However, in drylands, the non rainfall water uptake in the form of dew or water vapor is
723 greatest before sunrise (Chamizo et al., 2021; Ouyang et al., 2017). Especially in coastal deserts (like the Succulent Karoo)
724 increased fog and nocturnal dewfall in combination with higher humidity and shading mainly lead to prolonged activated
725 periods in the early morning when the organisms start assimilating carbon (Veste and Littmann, 2006). Moreover, the reduced
726 evaporation mitigates effects of drying and inactivity of organisms that occur especially at midday. These two processes
727 consequently result in a markedly increased annual C balance in the model.

728 However, the beneficial impact of the increased humidity is not common in all drylands. At site D2, our results showed an
729 apparent decrease in annual C balance with increased humidity. This could result from the different calculated reference
730 respiratory costs of the investigated organisms at these two sites from their photosynthesis in response to temperature data.
731 During nights with higher humidity, the surface temperature of organisms increases due to less evaporative cooling, which
732 increases the respiratory carbon loss at night. Moreover, higher humidity increases the activity and activates organisms that
733 are otherwise inactive at night (annual mean humidity at night is 66% at D1 and 70% at D2). Thus, more carbon will be lost
734 due to longer periods of respiration in the dark or at low light. The reference respiratory cost of the measured organisms at D2
735 is much larger than at D1 (1.2 and 2.5 µmol m 2 s 1 at D1 and D2, respectively), so the respiration rate at D2 will be larger
736 than D1 under similar temperature conditions. This is supported by our results that also showed a larger yearly mean respiration
737 rate during the night at D2 (0.35 and 1.04 µmol m 2 s 1 at D1 and D2, respectively; the yearly air temperature is 12.5 and 14
738 °C at D1 and D2, respectively). Therefore, although more carbon is assimilated during the day due to higher humidity in both
739 drylands, more carbon is also lost during the night. The higher carbon loss at night at site D2 is larger than at D1, since the

34

740 organisms at D2 have a higher respiration rate than at D1. This may explain the decrease of the annual C balance with increased
741 air humidity at site D2 in the model.

742 4.3 Estimated negative C balance using the data-driven model

743 Under climate change conditions, the individual environmental factors will likely interact with each other to affect organisms
744 (e.g. Rillig et al., 2019). The critical role of the combination of optimal air temperature, water content, and light intensity for
745 the growth of biocrusts is also observed in various other studies (Büdel et al., 2018; Lange, 2003a; Lange et al., 1998b).
746 Overall, optimal conditions are always rare within a year, which was also described by Lange (2003b). In some cases, carbon
747 gains during the relatively optimal conditions may not be sufficient to compensate for losses under long-term harsh conditions,
748 such as autumn and winter at site T1, for instance. For this reason, the simulated C balance of mosses and lichens in temperate
749 humid regions was mostly negative. Given their survival under field conditions, there may be some unconsidered mechanisms
750 in the model that allow real biocrusts to persist under these unfavourable environmental conditions.

751 Seasonal acclimation of physiological traits to the current climatic conditions may play an important role in regulating the C
752 balance at humid sites where the organisms are active throughout the year, such as site T1 (Fig. 7). It was observed, for instance,
753 that the respiration of lichens shows acclimation to seasonal changes in temperature, and the maximum CO2 exchange rate of
754 the organisms remains steady throughout the year (Lange and Green, 2005). Gauslaa (2006) found a higher chlorophyll a/b
755 ratio in forest lichen with increasing light. Moreover, depression in quantum efficiency in summer under extremely dry
756 conditions has been observed (Vivas et al., 2017). These varied physiological properties of organisms within a year could result
757 in different photosynthesis and respiration rates, and thus different C balances in comparison to the ones that cannot acclimate
758 to the seasonal climate. The missing seasonal acclimation of physiological traits may explain why the data driven model
759 estimated a negative C balance for biocrusts in humid regions. Also, the LiBry model does not account for seasonal acclimation
760 since the strategies are assumed to have constant functional properties throughout the simulation. Therefore, this can partly
761 account for the mismatch of traits of selected strategies by LiBry and observations.

762 **4.3.2 Physiological parameters**

763 The parameter q10 is a key parameter that substantially affects respiration. Resp_main is the dark respiration rate at a reference
764 temperature that is linked in the model to Vcmax, the maximum rate of carboxylation of RuBisCO in the Calvin Cycle of
765 photosynthesis (Walker et al., 2014). Topt is a parameter that controls gross photosynthesis as well as respiration as it is also
766 the reference temperature for calculating respiration rates. Rub_ratio can affect Vcmax and hence the maximum CO_2
767 assimilation rate, while ExtL regulates the light using efficiency under limited light conditions. Sat_act0 and Sat_act1 are two
768 parameters that determine the range of water saturation for initial activation and full metabolic activity. They have the smallest
769 effects on the C balance of lichen-dominated biocrusts at all sites.

770 Our modeling results give insights into the relative effects of individual physiological parameters on annual C balance across
771 different climatic zones. However, the impacts of physiology on biocrust C balance are complex since they always arise from
772 combinations of these physiological parameters. Thereby, different parameter combinations that correspond to different
773 relative impacts on the C balance may lead to the same response curves. Hence, we cannot directly link individual physiological
774 parameters to the underlying mechanisms since we do not have enough data to distinguish multiple possible parameter
775 combinations from each other, in case they produce the same response curves.

776

777 **4.4 Validation of the data-driven model**

778 The validation results of the model showed an overall good fit of daily and diurnal patterns of water content and activity (Fig.
779 3 and S3), and C balance at D2 (shown in Fig. 4) given the uncertainties in the data used to parameterize and evaluate the
780 model. This indicates that the data-driven model may be a reliable tool for C balance estimation, provided that a sufficient
781 amount of suitable forcing data is available.

782 A potential explanation for the general underestimation of activity at night and morning during several periods in a year is the
783 larger prescribed MWC and Sat_act0satmin of organisms in the model compared to those of the samples from the activity
784 measurements. Consequently, simulated saturation was lower, but minimal saturation for being active was higher than the
785 samples. Thus, the activity may have been underestimated at small water inputs such as dew and water vapor, which occur
786 mainly during the night and in the morning hours (Fig. S136). Moreover, underestimated activity in April and June at site T1
787 (Fig. S3 F(b)) may have resulted from a gap in rainfall measurements during this period. Not only rainfall amount but also
788 timing and frequency of rainfall events are essential for the physiological responses of biocrust communities (Belnap et al.,
789 2004; Coe et al., 2012b; Reed et al., 2012). Therefore, although the measured annual total amount of rainfall is reasonable (424
790 mm at site T1), the missing rainfall during a series of days in summer at site T1 would lead us to incorrectly predict that the
791 biocrusts remain inactive on these days.

792 Moreover, the mismatch between modelled and observed CO_2 assimilation rates at low or high water contents at site D2 (Fig.
793 4) may have partly resulted from the calibration procedure. In the calibration the simulated CO_2 exchange rates were higher
794 than measurements when the saturation exceeded the optimum saturation and hardly showed any negative values at high
795 saturation (Fig. S2 f). In turn, the simulated CO_2 exchange rates of biocrusts with an extremely low water content were zero
796 while the measurements showed negative values (see Fig. S2 f), pointing at a certain degree of metabolic activity in natural
797 conditions. Furthermore, the samples used for validation were different from the ones for calibration, which can also lead to
798 inaccuracies.

799 Additionally, the ability of the model to capture seasonality variations of C balance, which have been shown by other studies
800 (Büdel et al., 2018; Lange, 2003a; Zhao et al., 2016), could not be evaluated here since the monitoring of C balance in the field

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and collection of samples used for photosynthesis performance measurements were conducted only during October and early November.

4.5 Uncertainties of long-term C balance simulated by the data-driven model

Apart from the missing seasonal acclimation of physiological traits in the data-driven model, the estimated C balance may be inaccurate due to potential bias in estimated relative water saturation, which partly depends on prescribed MWC, a morphological model parameter that is obtained by measurements. We varied the MWC of lichen-dominated biocrust from site T1 by half (+/- 50%) to examine how important uncertainty in this parameter is for the estimation of the C balance. The outcome revealed that MWC has little effect on C balance (-25.0, -27.3, -28.3 g C m^{-2} yr^{-1} for reduced, original and increased MWC). Therefore, the annual carbon estimation is robust to the uncertainties with regard to the prescribed MWC.

Furthermore, the C balance estimated by the data-driven model could be affected by a bias in calibrated physiological parameters for organisms from photosynthesis response curves. Not all organisms forming cryptogamic covers show the same degree of depression in net photosynthesis at high water content. For instance, among lichens, there is a wide variation in responses of net photosynthesis to water saturation (Lange et al., 1995), also between individuals (Fig. 2 and S2).

Despite potential bias, this approach provides possibilities to predict the long-term C balance of biocrusts in the field across various climate zones, and it enables us to analyse the mechanisms driving C balance. However, in the future, the model needs to be calibrated with a larger number of samples collected and measured in various seasons to take the acclimation of physiological properties into account.

5 Conclusions

While all environmental factors that were examined in our study may act as key drivers for the C balance of biocrusts, they show distinct spatial patterns of their relative impacts. At alpine sites, air temperature is likely the most relevant factor. Relative humidity and light may be relevant for the C balance mainly in humid temperate sites, which is not obvious. In drylands, rainfall and also ambient CO_2 are found to be additional relevant factors. Furthermore, the direction of effect of relative humidity may vary between dryland and humid sites: the higher humidity can be beneficial for the C balance in arid regions, whereas it induces carbon loss in humid temperate and alpine sites. However, these patterns in drylands depend on the species characteristics and microclimatic conditions of the habitat. Therefore, for the generalization of the roles of water types in various climatic zones, a larger number of different organisms at multiple sites needs to be studied.

Our study suggests that a better, more detailed understanding of the seasonal variation of physiological traits is necessary, as acclimation may affect the C balance substantially. The season and timing of collecting and monitoring the species should be considered in experimental studies, especially when the characteristics of species are the basis for further analyses and forecasts

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830 ~~to estimate the annual carbon budget. Additionally, integration of acclimation of physiological traits in models can improve~~
831 ~~the accuracy in C balance estimation.~~
832 ~~Mechanistic models, as an add-on to experimental approaches, are well suited to explore the responses of the C balance of~~
833 ~~biocrusts to separate environmental factors, and the underlying mechanisms. In turn, models need to be constrained by~~
834 ~~measurements. As a result, we recommend combining experiments, field investigations, and modelling approaches to acquire~~
835 ~~a comprehensive understanding from all perspectives of how biocrusts respond to climate and, potentially, future climate~~
836 ~~change.~~

Our data-driven model provides possibilities to predict the long-term C balance of biocrusts in the field across various climate zones, and it enables us to analyse mechanisms that drive the C balance, despite marked uncertainties in the parametrization. We simulated reasonable C balance values in drylands but unrealistic ones at temperate sites with substantial seasonality. Uncertainties in environmental factors and respiration rate are likely to be the source of error for the C balance estimation since (1) all environmental factors that were examined in our study may act as relevant drivers for the C balance of biocrusts and (2) respiration-related parameters had the largest impacts compared to other physiological parameters, such as water relations or parameters solely related to Vcmax. CO_2 and air temperature showed the strongest effects among environmental factors and at the alpine site, the air temperature was most relevant. Compared to environmental factors, the relative impacts of physiological parameters are rather equal across climate regions. The optimum temperature may be slightly more relevant in temperate regions, while metabolic respiration cost is most important at the alpine site. Due to the importance of respiration-related physiological parameters, more studies to improve their accuracy are warranted in the future application of C balance modeling approaches.

Our study suggests that a better, more detailed understanding of the seasonal variation of physiological traits is necessary, as the more realistic estimations in drylands compared to temperate sites could be due to the weaker climate seasonality. The model needs to be calibrated with a larger number of samples collected and measured in various seasons to take the acclimation of physiological properties into account. Additionally, the integration of acclimation of physiological traits in process-based models may improve their accuracy in C balance estimation.

Author Contributions. YM and PP designed the study, BW, AK, MV and JR provided the observational data. YM did the data processing, ran the model, YM, PP, CC, BW and MB did the data analysis and interpretation, YM wrote the manuscript and all authors revised it.

Conflict of Interest. The authors have no conflict of interest to declare.

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References

Ackermann, K., Zackrisson, O., Rousk, J., Jones, D. L. and DeLuca, T. H.: N2 Fixation in Feather Mosses is a Sensitive Indicator of N Deposition in Boreal Forests, Ecosystems, 15(6), 986–998, doi:10.1007/s10021-012-9562-y, 2012.

Bader, M. Y., Zotz, G. and Lange, O. L.: How to minimize the sampling effort for obtaining reliable estimates of diel and annual CO2 budgets in lichens, Lichenologist, 42(1), 97–111, doi:10.1017/S0024282909990338, 2010.

Baldauf, S., Porada, P., Maestre, F. T. and Tietjen, B.: Relative humidity predominantly determines long-term biocrust-forming lichen cover in drylands under climate change, J. Ecol., 109(3), 1370–1385, doi:10.1111/1365-2745.13563, 2021.

Belnap, J., Phillips, S. L. and Miller, M. E.: Response of desert biological soil crusts to alterations in precipitation frequency, Oecologia, 141, 306–316, doi:10.1007/s00442-003-1438-6, 2004.

Belnap, J., Weber, B. and Büdel, B.: Biological Soil Crusts as an organizing principle in drylands, in Biological soil crusts: an organizing principle in drylands, pp. 3–13, Springer International Publishing., 2016.

Brostoff, W. N., Rasoul Sharifi, M., Rundel, P. W., Sharifi, M. R. and Rundel, P. W.: Photosynthesis of cryptobiotic soil crusts in a seasonally inundated system of pans and dunes in the western Mojave Desert, CA: Field studies, Flora, 200(6), 592–600, doi:10.1016/j.flora.2005.06.008, 2005.

Büdel, B., Colesie, C., Green, T. G. A., Grube, M., Lázaro Suau, R., Loewen-Schneider, K., Maier, S., Peer, T., Pintado, A., Raggio, J., Ruprecht, U., Sancho, L. G., Schroeter, B., Türk, R., Weber, B., Wedin, M., Westberg, M., Williams, L. and Zheng, L.: Improved appreciation of the functioning and importance of biological soil crusts in Europe: The Soil Crust International Project (SCIN), Biodivers. Conserv., 23(7), 1639–1658, doi:10.1007/s10531-014-0645-2, 2014.

Büdel, B., Williams, W. J. and Reichenberger, H.: Annual net primary productivity of a cyanobacteria-dominated biological

891 soil crust in the Gulf Savannah, Queensland, Australia, Biogeosciences, 15, 491–505, doi:https://doi.org/10.5194/bg-15-491-
892 2018, 2018.

893 Chamizo, S., Cantón, Y., Miralles, I. and Domingo, F.: Biological soil crust development affects physicochemical
894 characteristics of soil surface in semiarid ecosystems, Soil Biol. Biochem., 49, 96–105, doi:10.1016/j.soilbio.2012.02.017,
895 2012.

896 Chamizo, S., Rodríguez-Caballero, E., Moro, M. J. and Cantón, Y.: Non-rainfall water inputs: A key water source for biocrust
897 carbon fixation, Sci. Total Environ., 792, 148–299, doi:10.1016/j.scitotenv.2021.148299, 2021.

898 Coe, K. K., Belnap, J., Grote, E. E. and Sparks, J. P.: Physiological ecology of desert biocrust moss following 10 years exposure
899 to elevated CO2: Evidence for enhanced photosynthetic thermotolerance, Physiol. Plant., 144(4), 346–356,
900 doi:10.1111/j.1399-3054.2012.01566.x, 2012a.

901 Coe, K. K., Belnap, J. and Sparks, J. P.: Precipitation-driven carbon balance controls survivorship of desert biocrust mosses,
902 Ecology, 93(7), 1626–1636, doi:10.1890/11-2247.1, 2012b.

903 Colesie, C., Green, T. G. A., Haferkamp, I. and Bu, B.: Habitat stress initiates changes in composition , CO 2 gas exchange
904 and C-allocation as life traits in biological soil crusts, ISME J., 8, 2104–2115, doi:10.1038/ismej.2014.47, 2014.

905 Colesie, C., Green, T. G. A., Raggio, J. and Büdel, B.: Summer Activity Patterns of Antarctic and High Alpine
906 Lichendominated Biological Soil Crusts — Similar But Different?, Arctic, Antarct. Alp. Res., 48(3), 449–460,
907 doi:10.1657/AAAR0015-047, 2016.

908 Colesie, C., Büdel, B., Hurry, V. and Green, T. G. A.: Can Antarctic lichens acclimatize to changes in temperature?, Glob.
909 Chang. Biol., 24(3), 1123–1135, doi:10.1111/gcb.13984, 2018.

910 Cowan, I. R., Lange, O. L. and Green, T. G. A. A.: Carbon-dioxide exchange in lichens: determination of transport and
911 carboxylation characteristics, Planta, 187(2), 282–294, doi:10.1007/BF00201952, 1992.

912 Darrouzet-Nardi, A., Reed, S. C., Grote, E. E. and Belnap, J.: Observations of net soil exchange of CO2 in a dryland show
913 experimental warming increases carbon losses in biocrust soils, Biogeochemistry, 126(3), 363–378, doi:10.1007/s10533-015-
914 0163-7, 2015.

915 Diez, M., Wachendorf, M. and Stefan, T.: Modelling photosynthesis and carbon fluxes of moss-and lichen-dominated
916 biological soil crusts in temperate dry acid grasslands in Brandenburg., 49th Annual Meeting of the Ecological Society of
917 Germany, Austria and Switzerland, Münster, Germany, doi: 10.13140/RG.2.2.27244.51849, 2019.

918 Dümig, A., Veste, M., Hagedorn, F., Fischer, T., Lange, P., Spröte, R. and Kögel-Knabner, I.: Organic matter from biological
919 soil crusts induces the initial formation of sandy temperate soils, Catena, 122, 196–208, doi:10.1016/j.catena.2014.06.011,

920   2014.

921   Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andreae, M. O. and Pöschl, U.: Contribution of cryptogamic

922   covers to the global cycles of carbon and nitrogen, Nat. Geosci., 5(7), 459–462, doi:10.1038/ngeo1486, 2012.

923   ~~Evans, R. D. and Lange, O. L.: Biological Soil Crusts and Ecosystem Nitrogen and Carbon Dynamics, in Biological Soil~~

924   ~~Crusts: Structure, Function, and Management, edited by J. Belnap and O. L. Lange, pp. 263–279, Springer Berlin Heidelberg,~~

925   ~~Berlin, Heidelberg., 2003.~~

926   Farquhar, G. D. and von Caemmerer, S.: Modelling of Photosynthetic Response to Environmental Conditions, in Physiological

927   Plant Ecology II, edited by O. L. Lange, pp. 549–587, Springer, Berlin, Heidelberg., 1982.

928   Feng, W., Zhang, Y., Wu, B., Qin, S. and Lai, Z.: Influence of Environmental Factors on Carbon Dioxide Exchange in

929   Biological Soil Crusts in Desert Areas, Arid L. Res. Manag., 28(2), 186–196, doi:10.1080/15324982.2013.835006, 2014.

930   Ferrenberg, S., Faist, A. M., Howell, A. and Reed, S. C.: Biocrusts enhance soil fertility and Bromus tectorum growth, and

931   interact with warming to influence germination, Plant Soil, 429(1–2), 77–90, doi:10.1007/s11104-017-3525-1, 2018.

932   Gauslaa, Y., Lie, M., Solhaug, K. A. and Ohlson, M.: Growth and ecophysiological acclimation of the foliose lichen Lobaria

933   pulmonaria in forests with contrasting light climates, Oecologia, 147(3), 406–416, doi:10.1007/s00442-005-0283-1, 2006.

934   Green, T. G. A. and Lange, O. L.: Ecophysiological adaptations of the lichen genera pseudocyphellaria and sticta to south

935   temperate rainforests, Lichenol., 23(3), 267–282, doi:10.1017/S0024282991000427, 1991.

936   Haarmeyer, D. H., Luther-Mosebach, J., Dengler, J., Schmiedel, U., Finckh, M., Berger, K., Deckert, J., Domptail, S. E.,

937   Dreber, N., Gibreel, T., Grohmann, C., Gröngröft, A., Haensler, A., Hanke, W., A., H., Husted, L. B., N., K. F., M., K., Krug,

938   C. B., Labitzky, T., Linke, T., Mager, D., Mey, W., Muche, G., Naumann, C., Pellowski, M., Powrie, L. W., Pröpper, M.,

939   Rutherford, M. C., Schneiderat, U., Strohbach, B. J., Vohland, K., Weber, B., Wesuls, D., Wisch, U., Zedda, L., Büdel, B.,

940   Darienko, T., Deutschewitz, K., Dojani, S., Erb, E., Falk, T., Friedl, T., Kanzler, S.-E., Limpricht, C., Linsenmair, K. E., Mohr,

941   K., Oliver, T., Petersen, A., Rambold, G., Zeller, U., Austermühle, R., Bausch, J., Bösing, B. M., Classen, N., Dorendorf, J.,

942   Dorigo, W., Esler, K. J., Etzold, S., G., A., G., L., Hecht, J., Hoyer, P., Kongor, R. Y., Lang, H., Lieckfeld, L. A. B., Oldeland,

943   J., Peters, J., Röwer, I. U., September, Z. M., Sop, T. K., van Rooyen, M. W., Weber, J., Willer, J. and Jürgens, N.: The BIOTA

944   Observatories., in Biodiversity in southern Africa. Volume I: Patterns at local scale - the BIOTA Observatories, edited by N.

945   Jürgens, D. H. Haarmeyer, Luther-Mosebach, D. J., M. J., Finckh, and U. Schmiedel, pp. 6–801, Klaus Hess Publisher,

946   Göttingen & Windhoek., 2010.

947   IPCC, 2021: Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment

948   Report of the Intergovernmental Panel on Climate Change, edited by: Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors,

949   C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K.

Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, In press, doi:10.1017/9781009157896, 2021.

Jeffries, D. L., Link, S. O. and Klopatek, J. M.: CO_2 fluxes of cryptogamic crusts: I. Response to resaturation, New Phytol., 125(2), 163–173, doi:10.1111/j.1469-8137.1993.tb03891.x, 1993.

Ladrón de Guevara, M., Lázaro, R., Quero, J. L., Ochoa, V., Gozalo, B., Berdugo, M., Uclés, O., Escolar, C. and Maestre, F. T.: Simulated climate change reduced the capacity of lichen-dominated biocrusts to act as carbon sinks in two semi-arid Mediterranean ecosystems, Biodivers. Conserv., 23(7), 1787–1807, doi:10.1007/s10531-014-0681-y, 2014.

Ladrón de Guevara, M., Gozalo, B., Raggio, J., Lafuente, A., Prieto, M. and Maestre, F. T.: Warming reduces the cover, richness and evenness of lichen-dominated biocrusts but promotes moss growth: insights from an 8 yr experiment, New Phytol., 220(3), 811–823, doi:10.1111/nph.15000, 2018.

Lange, O. L.: Moisture content and CO_2 exchange of lichens - I. Influence of temperature on moisture-dependent net photosynthesis and dark respiration in Ramalina maciformis, Oecologia, 45(1), 82–87, doi:10.1007/BF00346710, 1980.

Lange, O. L.: Photosynthetic productivity of the epilithic lichen Lecanora muralis: Long-term field monitoring of CO_2 exchange and its physiological interpretation. II. Diel and seasonal patterns of net photosynthesis and respiration, Flora, 198, 55–70, doi:10.1078/0367-2530-00100, 2003a.

Lange, O. L.: Photosynthetic productivity of the epilithic lichen Lecanora muralis: Long-term field monitoring of CO_2 exchange and its physiological interpretation. III. Diel, seasonal, and annual carbon budgets, Flora, 198(4), 277–292, doi:10.1078/0367-2530-00100, 2003b.

Lange, O. L. and Green, T. G. A.: Lichens show that fungi can acclimate their respiration to seasonal changes in temperature, Oecologia, 142(1), 11–19, doi:10.1007/s00442-004-1697-x, 2005.

Lange, O. L., Meyer, A., Zellner, H. and Heber, U.: Photosynthesis and Water Relations of Lichen Soil Crusts: Field Measurements in the Coastal Fog Zone of the Namib Desert, Funct. Ecol., 8(2), 253, doi:10.2307/2389909, 1994.

Lange, O. L., Reichenberger, H. and Meyer, A.: High thallus water content and photosynthetic CO_2 exchange of lichens. Laboratory experiments with soil crust species from local xerothermic steppe formations in Franconia, Germany, Flecht. Follmann Contrib. to Lichenol. honour Gerhard Follmann. Geobot. Phytotaxon. Study Group, Univ. Köln, Köln, 139–153, 1995.

Lange, O. L., Belnap, J., Reichenberger, H. and Meyer, A.: Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: Role of water content on light and temperature responses of CO_2 exchange, Flora, 192(1), 1–15, doi:10.1016/S0367-2530(17)30749-1, 1997.

Lange, O. L., Belnap, J. and Reichenberger, H.: Photosynthesis of the cyanobacterial soil-crust lichen Collema tenax from arid lands in southern Utah, USA: Role of water content on light and temperature responses of CO2 exchange, Funct. Ecol., 12(2), 195–202, doi:10.1046/j.1365-2435.1998.00192.x, 1998.

~~Lange, O. L., Hahn, S. C., Meyer, A. and Tenhunen, J. D.: Upland tundra in the foothills of the Brooks Range, Alaska, U.S.A.: Lichen long term photosynthetic CO2 uptake and net carbon gain, Arct. Alp. Res., 30(3), 252–261, doi:10.2307/1551972, 1998b.~~

Lange, O. L., Allan Green, T. G., Melzer, B., Meyer, A. and Zellner, H.: Water relations and CO2 exchange of the terrestrial lichen Teloschistes capensis in the Namib fog desert: Measurements during two seasons in the field and under controlled conditions, Flora - Morphol. Distrib. Funct. Ecol. Plants, 201(4), 268–280, doi:https://doi.org/10.1016/j.flora.2005.08.003, 2006.

Li, X., Hui, R., Zhang, P. and Song, N.: Divergent responses of moss- and lichen-dominated biocrusts to warming and increased drought in arid desert regions, Agric. For. Meteorol., 303(February), doi:10.1016/j.agrformet.2021.108387, 2021.

Maestre, F. T., Escolar, C., de Guevara, M. L., Quero, J. L., Lázaro, R., Delgado-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B. and Gallardo, A.: Changes in biocrust cover drive carbon cycle responses to climate change in drylands, Glob. Chang. Biol., 19(12), 3835–3847, doi:10.1111/gcb.12306, 2013.

Ouyang, H., Lan, S., Yang, H. and Hu, C.: Mechanism of biocrusts boosting and utilizing non-rainfall water in Hobq Desert of China, Appl. Soil Ecol., 120, 70–80, doi:10.1016/j.apsoil.2017.07.024, 2017.

Phinney, N. H., Gauslaa, Y., Palmqvist, K. and Esseen, P. A.: Macroclimate drives growth of hair lichens in boreal forest canopies, J. Ecol., 109(1), 478–490, doi:10.1111/1365-2745.13522, 2021.

Porada, P., Weber, B., Elbert, W., Pöschl, U. and Kleidon, A.: Estimating global carbon uptake by lichens and bryophytes with a process-based model, Biogeosciences, 10, 6989–7033, doi:10.5194/bg-10-6989-2013, 2013.

Porada, P., Tamm, A., Kleidon, A., Pöschl, U. and Weber, B.: Global NO and HONO emissions of biological soil crusts estimated by a process-based non-vascular vegetation model, Biogeosciences, 16(9), 2003–2031, 2019.

Proctor, M.: Patterns of desiccation tolerance and recovery in bryophytes, Plant Growth Regul., 35(2), 147–156, doi:10.1023/A:1014429720821, 2001.

Raggio, J., Pintado, A., Vivas, M., Sancho, L. G., Büdel, B., Colesie, C., Weber, B., Schroeter, B., Lázaro, R. and Green, T. G. A.: Continuous chlorophyll fluorescence, gas exchange and microclimate monitoring in a natural soil crust habitat in Tabernas badlands, Almería, Spain: Progressing towards a model to understand productivity, Biodivers. Conserv., 23(7), 1809–1826, doi:10.1007/s10531-014-0692-8, 2014.

Raggio, J., Green, T. G. A., Sancho, L. G., Pintado, A., Colesie, C., Weber, B. and Büdel, B.: Metabolic activity duration can be effectively predicted from macroclimatic data for biological soil crust habitats across Europe, Geoderma, 306, 10–17, doi:10.1016/j.geoderma.2017.07.001, 2017.

Raggio, J., Green, T. G. A., Pintado, A., Sancho, L. G. and Büdel, B.: Environmental determinants of biocrust carbon fluxes across Europe : possibilities for a functional type approach, Plant Soil, 429, 147–157 [online] Available from: https://doi.org/10.1007/s11104-018-3646-1, 2018.

Reed, S. C., Coe, K. K., Sparks, J. P., Housman, D. C., Zelikova, T. J. and Belnap, J.: Changes to dryland rainfall result in rapid moss mortality and altered soil fertility, Nat. Clim. Chang., 2(10), 752–755, doi:10.1038/nclimate1596, 2012.

Rillig, M. C., Ryo, M., Lehmann, A., Aguilar-Trigueros, C. A., Buchert, S., Wulf, A., Iwasaki, A., Roy, J. and Yang, G.: The role of multiple global change factors in driving soil functions and microbial biodiversity, Science, 366(6467), 886–890, doi:10.1126/science.aay2832, 2019.

Samolov, E., Baumann, K., Büdel, B., Jung, P., Leinweber, P., Mikhailyuk, T., Karsten, U. and Glaser, K.: Biodiversity of algae and cyanobacteria in biological soil crusts collected along a climatic gradient in chile using an integrative approach, Microorganisms, 8(7), 1–28, doi:10.3390/microorganisms8071047, 2020.

Schuur, E. A. G., Crummer, K. G., Vogel, J. G. and MacK, M. C.: Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra, Ecosystems, 10(2), 280–292, doi:10.1007/s10021-007-9024-0, 2007.

Tamm, A., Caesar, J., Kunz, N., Colesie, C., Reichenberger, H. and Weber, B.: Ecophysiological properties of three biological soil crust types and their photoautotrophs from the Succulent Karoo, South Africa, Plant Soil, 429(1–2), 127–146, doi:10.1007/s11104-018-3635-4, 2018.

Tucker, C. L., Ferrenberg, S. and Reed, S. C.: Climatic Sensitivity of Dryland Soil CO2 Fluxes Differs Dramatically with Biological Soil Crust Successional State, Ecosystems, 22(1), 15–32, doi:10.1007/s10021-018-0250-4, 2019.

Veste, M. and Littmann, T.: Dewfall and its Geo-ecological Implication for Biological Surface Dewfall and its Geo-ecological Implication for Biological Surface Crusts in Desert Sand Dunes (North-western Negev , Israel), J. Arid L. Stud., 16(3), 139–147, 2006.

Veste, M., Heusinkveld, B. G., Berkowicz, S. M., Breckle, S.-W., Littmann, T. and Jacobs, A. F. G.: Dew formation and activity of biological soil crusts, in Arid Dune Ecosystems – The Nizzana Sands in the Negev Desert, Ecological Studies 200, edited by S.-W. Breckle, A. Yair, and M. Veste, pp. 305–318, Springer., 2008.

Vivas, M., Pintado, A. and Sancho, L. G.: F v / F m acclimation to the Mediterranean summer drought in two sympatric Lasallia species from the Iberian mountains, Lichenol., 49(2), 157–165, doi:10.1017/S0024282917000032, 2017.

Wagner, S., Zotz, G. and Bader, M. Y.: The temperature acclimation potential of tropical bryophytes, Plant Biol., 16(1), 117–124, doi:10.1111/plb.12037, 2014.

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., Scales, J. C., Wohlfahrt, G., Wullschleger, S. D., Woodward, F. I. and Walker, A. P.: The relationship of leaf photosynthetic traits – V cmax and J max – to leaf nitrogen , leaf phosphorus , and specific leaf area : a meta-analysis and modeling study, Ecol. Evol., 4(16), 3218–3235, doi:10.1002/ece3.1173, 2014.

Weber, B., Graf, T. and Bass, M.: Ecophysiological analysis of moss-dominated biological soil crusts and their separate components from the Succulent Karoo, South Africa, Planta, 236(1), 129–139, doi:10.1007/s00425-012-1595-0, 2012.

Weber, B., Berkemeier, T., Ruckteschler, N., Caesar, J., Heintz, H., Ritter, H. and Braß, H.: Development and calibration of a novel sensor to quantify the water content of surface soils and biological soil crusts, Methods Ecol. Evol., 7(1), 14–22, doi:10.1111/2041-210X.12459, 2016.

~~Wohlfahrt, G., Fenstermaker, L. F. and Arnone III, J. A.: Large annual net ecosystem CO2 uptake of a Mojave Desert ecosystem, Glob. Chang. Biol., 14(7), 1475–1487, doi:10.1111/j.1365-2486.2008.01593.x, 2008.~~

Zhao, Y., Zhang, Z., Hu, Y. and Chen, Y.: The seasonal and successional variations of carbon release from biological soil crust-covered soil, J. Arid Environ., 127, 148–153, doi:10.1016/j.jaridenv.2015.11.012, 2016.

Zotz, G., Schultz, S. and Rottenberger, S.: Are tropical lowlands a marginal habitat for macrolichens? Evidence from a field study with Parmotrema endosulphureum in Panama, Flora, 198(1), 71–77, doi:10.1078/0367-2530-00077, 2003.