



1 Key drivers of the annual carbon budget of biocrusts from various 2 climatic zones determined with a mechanistic data-driven model

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15 **Abstract.** Biocrusts are a worldwide phenomenon, contributing substantially to ecosystem functioning. Their growth and
16 survival depend on multiple environmental factors, including climatic conditions. While the physiological responses of
17 biocrusts to individual environmental factors have been examined in laboratory experiments, the relative importance of these
18 factors along climatic gradients is largely unknown. Moreover, it is not fully understood how acclimation of biocrusts may
19 alter the relative impacts of certain factors. We aim here at determining the relative effects of environmental factors on
20 biocrusts along climatic gradients, using the carbon balance of biocrust organisms as a measure of their performance.
21 Additionally, we explore the role that seasonal acclimation plays in the carbon balance of biocrusts. We applied a data-
22 driven mechanistic model at six study sites along a climatic gradient to simulate the annual carbon balance of biocrusts
23 dominated by different lichen and moss species. Furthermore, we performed several sensitivity analyses to investigate the
24 relative importance of driving factors, thereby including the impacts of acclimation. Our modelling approach suggests
25 substantial effects of light intensity and relative humidity in temperate regions, while air temperature has the strongest
26 impact at alpine sites. In drylands, ambient CO₂ concentration and also the amount of rainfall are important drivers of the
27 carbon balance of biocrusts. Seasonal acclimation is a key feature, mostly in temperate regions, affecting biocrust
28 functioning. We conclude that climate change, which may lead to warmer and, in some regions, drier air, will potentially
29 have large effects on long-term carbon balances of biocrusts at global scale. Moreover, we highlight the key role of seasonal



30 acclimation, which suggests that the season and timing of collecting and monitoring biocrusts should be given additional
31 consideration in experimental investigations, especially when measurements are used as the basis for quantitative estimates
32 and forecasts.

33 **1 Introduction**

34 Non-vascular photoautotrophs, such as lichens, mosses, eukaryotic algae and cyanobacteria, together with heterotrophic
35 microorganisms form biological soil crusts (biocrusts) (Belnap et al., 2016). Biocrusts occur in various environments across
36 the globe and are especially ubiquitous in environments where low water availability inhibits the development of vascular
37 plants (Belnap et al., 2004; Lange et al., 1998a; Samolov et al., 2020). They provide a wide range of important ecosystem
38 functions, such as build-up of soil organic carbon and nutrients (Chamizo et al., 2012; Dümig et al., 2014; Ferrenberg et al.,
39 2018). Biocrusts contribute substantially to ecosystem carbon fluxes at the global scale (Elbert et al., 2012). Especially in
40 desert ecosystems, biocrusts can be a major contributor to the annual CO₂ uptake (Tucker et al., 2019; Wohlfahrt et al., 2008).
41 Cyanobacteria, which are common components of biocrusts, either free-living or associated with mosses and lichens,
42 facilitate biotic nitrogen fixation and may subsequently increase carbon sequestration by enhancing the concentration of
43 photosynthesis-related enzymes in top soils (Ackermann et al., 2012; Evans and Lange, 2003).

44 Owing to their importance in ecosystem functioning, studies on growth and survival of biocrusts are crucial. Growth depends
45 on the long-term carbon balance (hereafter, C balance), which corresponds to the (accumulated) net carbon flux across the
46 system boundaries including all relevant carbon gains and losses. In order to ensure survival, any species needs to achieve a
47 positive C balance in the long-term, while negative values may occur for short periods. Acknowledging the importance of C
48 balance, an increasing number of studies have investigated the long-term C balance of individual non-vascular organisms as
49 well as biocrust communities, and their environmental drivers. An annual carbon budget based on measured field data was
50 reported in the study of Lange (2003b) on the crustose lichen *Lecanora muralis* growing on a rock surface in a temperate
51 climate of southern Germany. Furthermore, Büdel et al. (2018) measured the annual C balance for a cyanobacteria-
52 dominated biocrust in an Australian dry savannah ecosystem. Several other studies obtained long-term, large-scale values of
53 the C balance by scaling up short-term, local measurements of CO₂ exchange rate under natural field conditions (Lange et al.,
54 1994; Zotz et al., 2003). For an estimation of the global C balance of cryptogamic covers, which include biocrusts,
55 conversion factors based on the maximum photosynthesis rate have been suggested as a best-guess solution (Elbert et al.,
56 2012). However, there are some drawbacks to these approaches for acquiring a C balance at both organism and community
57 scale. First, the measurement of the long-term continuous CO₂ exchange rate of an individual organism or biocrust
58 community has technical limitations and is highly time- and resource-consuming. Second, upscaling via extrapolation may
59 result in bias in annual C balance estimation if the length and the frequency of sampling cannot capture the full variability of
60 CO₂ exchange throughout the year (Bader et al., 2010). Moreover, using empirical approaches alone, it is difficult to



61 understand the underlying mechanisms of how climatic conditions affect individual physiological processes, and
62 consequently which role these processes play in the observed changes in C balance and growth at the individual as well as
63 community level. Such approaches are thus subject to large uncertainty when used for projections of C balance under climate
64 change.

65 Most studies on the relationships between C balance and environmental factors for biocrusts are based on laboratory
66 experiments (e.g. Coe et al., 2012; Cowan et al., 1992; Lange et al., 1998a) or direct field measurements in situ over short
67 periods of time (e.g. Brostoff et al., 2005; Lange et al., 1994). From this work cited above, it has been recognized that the
68 type and temporal pattern of water supply, temperature, radiation, and also CO₂ concentration are among the factors that are
69 crucial for the C balance of biocrusts. While highest values of productivity in biocrusts are achieved when the environmental
70 factors are in their optimal range, it has been found that biocrusts under field conditions are also able to achieve maximum
71 activity and thus, potential productivity, under sub-optimal conditions of temperature and light (Colesie et al., 2016; Raggio
72 et al., 2017, 2014). It is largely unknown, however, which relative importance each of these factors has for the long-term C
73 balance of biocrusts under natural field conditions, and if the importance of factors shows a spatial and temporal pattern. In
74 addition, seasonal acclimation of photosynthetic and respiratory properties of species to intra-annually varying climate
75 factors found by several studies (e.g. Gauslaa et al., 2006; Lange and Green, 2005; Wagner et al., 2014) may substantially
76 affect biocrust C balance, thus leading to further complexity in the spatio-temporal relations between C balance and
77 environmental factors. One of the few experimental studies investigating biocrust acclimation potential to changing
78 temperatures has found threshold temperatures for the survival of lichen species (Colesie et al., 2018) but the overall extent
79 of the impact is poorly understood.

80 Here, we applied a mechanistic data-driven model to (a) complement empirical estimates of the annual C balance of
81 biocrusts and (b) to address the knowledge gaps concerning the relative importance of different environmental factors for the
82 C balance along climatic gradients, thereby accounting for the role of seasonal acclimation. The advantage of this modelling
83 approach is that it can predict at high temporal resolution the dynamic C balance of biocrust organisms for given locations by
84 simulating the physiological processes driven by environmental factors. The model allows for a deeper mechanistic
85 understanding of the C balance of biocrusts through factorial experiments and sensitivity analyses regarding parameters and
86 individual environmental factors, which would be impractical to realize in field or laboratory experiments. To complement
87 our analyses using the data-driven model, a process-based dynamic non-vascular vegetation model, called LiBry, was
88 employed as an supporting tool (Porada et al., 2013).

89 **2 Material and Methods**

90 We simulated the C balance of biocrusts from six climatically different study sites in a semi-empirical way using a data-
91 driven model. The model simulates photosynthetic rate based on the Farquhar photosynthesis model developed by Farquhar
92 and von Caemmerer (1982) and respiration rate based on Q₁₀ relationship. The C balance is computed as the difference of



93 photosynthesis and respiration accumulated over a given time period. In the model, both photosynthesis and respiration
94 depend on surface temperature, relative water saturation, and the activity of the biocrust, which are all simulated in a coupled
95 way via the surface energy balance as a function of climate input data. Photosynthesis additionally depends on ambient CO₂
96 concentration.

97 To calibrate the model, we first determined soil and land surface properties that are required for the coupled energy and
98 water balance in the model through fitting simulated to measured surface temperature patterns. Then, we parameterized the
99 physiological properties of the organisms using measured relationships between net photosynthesis and light intensity, water
100 content, and temperature. Finally, we validated the model with regard to the water content or activity patterns of biocrusts
101 and compared the modelled CO₂ assimilation rate to measured values. The data sets used for calibration and validation of the
102 model as well as basic climate conditions of each site are described in Table 1. Sites were listed in ascending order of total
103 annual precipitation based on measured data.

104 2.1 Study sites

105 In our study we considered six sites, namely two dryland sites at Almeria (Spain) and Soebatsfontein (South Africa;
106 hereafter D1 and D2); three temperate sites at Gössenheim (Germany), Öland (Sweden), and Linde (Germany; Hereafter T1,
107 T2, and T3); and one alpine site at Hochtort (Austria; Hereafter A1) (Table 1). These sites were chosen based on data
108 availability and because they cover a broad range of different climatic conditions. To our knowledge, the necessary empirical
109 data regarding climatic conditions, species physiological characteristics, and status such as activity, which is used to estimate
110 C balance, have been monitored in only a small number of experiments, including the six study sites chosen here.

111 Sites D1 and D2 are characterized by a semi-arid climate with mean annual precipitation of less than 250 mm, but a wet
112 winter season (Büdel et al., 2014; Haarmeyer et al., 2010). Sites T1, T2, and T3 have a temperate climate. The mean
113 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
114 region with a mean annual precipitation between 1750 and 2000 mm, of which more than 70% are snowfall; the A1 site is
115 covered by snow for at least 200 days per year (Büdel et al., 2014). More detailed site descriptions are provided in the
116 corresponding studies cited above.

117 2.2 Observational Data

118 2.2.1 Climatic variables

119 The proposed data-driven model for estimating the annual C balance of dominant biocrust types at each site was forced by
120 hourly microclimatic variables. The forcing data sets of the data-driven model include photosynthetically active radiation
121 (PAR), long-wave radiation (near-infrared), relative air humidity, air temperature, wind speed, rainfall, and snowfall. All the
122 microclimatic variables were measured on-site by climate stations with a temporal resolution of 10 min (5 min in A1 and D1;
123 data available at <http://www.biota-africa.org>; Raggio et al., 2017; M. Veste, unpublished data), except for long-wave



124 radiation and snowfall, which were taken from ERA5 dataset ([https://www.ecmwf.int/en/forecasts/datasets/reanalysis-](https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5)
125 [datasets/era5](https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5)). Then all these microclimate data were aggregated to data with hourly temporal resolution.

126 **2.2.2 Dynamic biocrust variables**

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

136 We did not directly use the observed surface temperature and activity as forcing data for the model since these properties are
137 strongly linked to water saturation (and CO₂ diffusivity). Input data of water saturation, however, were not available at most
138 sites. Although the overall patterns of simulated and observed surface temperature match well (see below, Sect. 2.3),
139 inconsistencies would likely occur at hourly resolution if simulated dynamic water content was used in the model together
140 with observed temperature and activity. Hence, the time-series of surface temperature and water saturation data at all sites
141 were estimated based on a simulation of the energy and water balance. The activity of the organisms was then approximated
142 via the empirical equations describing the link between water saturation and metabolic activity (see Porada et al., 2013).
143 Furthermore, ambient CO₂ concentration was assumed to be constant at 400 ppm.

144 For validation of C balance, we used data of the on-site CO₂-exchange rate of different biocrust types (lichen- and moss- and
145 also cyano-dominated biocrusts; the latter composed of cyanolichen and cyanobacteria) that were measured by a portable
146 gas exchange system at several time intervals from November 4th to 8th at site D2 (Tamm et al., 2018). For the other sites,
147 additional field measurements of CO₂-exchange were not available.

148 **2.2.3 Photosynthesis response and water storage**

149 For all sites, CO₂ exchange measurements under controlled conditions in the laboratory or in the field (site T3) were
150 conducted using a mobile gas exchange system GFS 3000 (Walz GmbH, Effeltrich, Germany) with an infrared-gas analyzer
151 to explore the physiological characteristics of samples of different biocrust types (same as those measured for validation;
152 main species see Table 1; Diez et al., 2019; Raggio et al., 2018; Tamm et al., 2018). Net photosynthesis was measured at
153 different ranges of light intensity, water content, and temperature. Light response curves, for instance, were determined at
154 optimum water saturation and 15 °C, water response curves were measured at 400 μmol m⁻² s⁻¹ and 15 °C at sites D1, T1, T2,
155 and A1 (Raggio et al., 2018). Moreover, the maximum water storage capacity (MWC) of the samples was quantified in the



156 laboratory for samples from sites D1, T1, T2, and A1 (Raggio et al., 2018), whereas the MWC at site D2 was approximated
 157 as the maximum value when measuring water response curves (Tamm et al., 2018; Weber et al., 2012). MWC at site T3 was
 158 estimated as the value of the same genus measured in Hamburg, Germany (*Cladonia portentosa* and *Polytrichum formosum*,
 159 Petersen et al., in prep.). MWC was acquired since it is one of the essential parameters of the model to convert the specific
 160 water content in mm to relative water saturation required by the model used here.

161 **Table 1:** Properties of the study sites and data which are available (+ sign) for calibration and validation of the data-driven
 162 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	<i>Psora decipiens</i> , <i>Didymodon rigidulus</i>	<i>Psora decipiens</i> , <i>Psora crenata</i> , <i>Ceratodon purpureus</i> , <i>Collema coccophorum</i>	<i>Psora decipiens</i> , <i>Trichostomun crispulum</i>	<i>Psora decipiens</i> , <i>Tortella tortuosa</i>	<i>Cladonia furcata</i> , <i>Polytrichum piliferum</i>	<i>Psora decipiens</i> , <i>Tortella rigens</i>	
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
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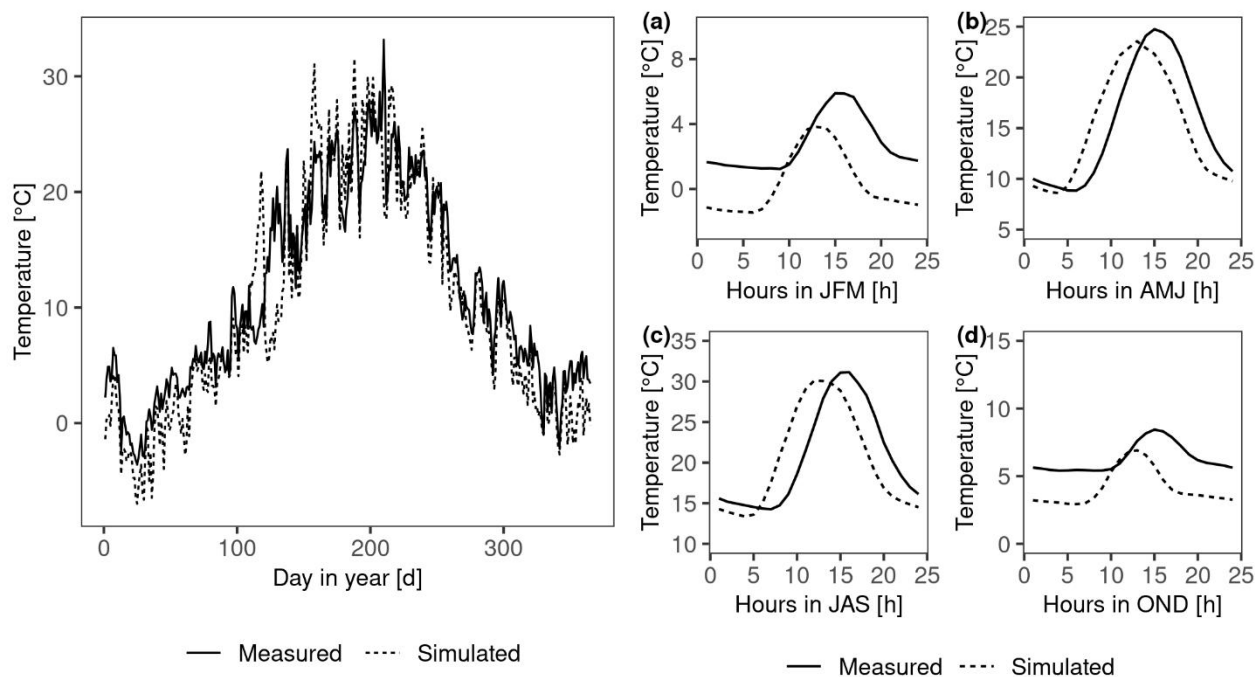
163 **2.3 Parameterization of the data-driven model**

164 **2.3.1 Abiotic surface properties**

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

170 The set of parameters that corresponded to minimum differences between simulated and measured values (visual assessment)
171 was used in the data-driven model. The calibration results of surface temperature and the photosynthesis response curves at
172 site T2 are shown in Fig. 1 and Fig. 2, respectively. The results of dominant species at other sites are shown in Fig. S1 and
173 S2.

174 The daily surface temperature was simulated accurately (visual comparison) except for site T3 where the temperature during
175 cold seasons was underestimated, and at site D1 the peak temperature within a day in hot seasons was underestimated (Fig.
176 S1). The peak in surface temperature occurred too early by around 3 hours at site T1 and T2, but the magnitude of the peak
177 corresponded well to the measured data (Fig. 1 and S1). Therefore, in general, the fitting of the surface temperature patterns
178 was satisfactory.

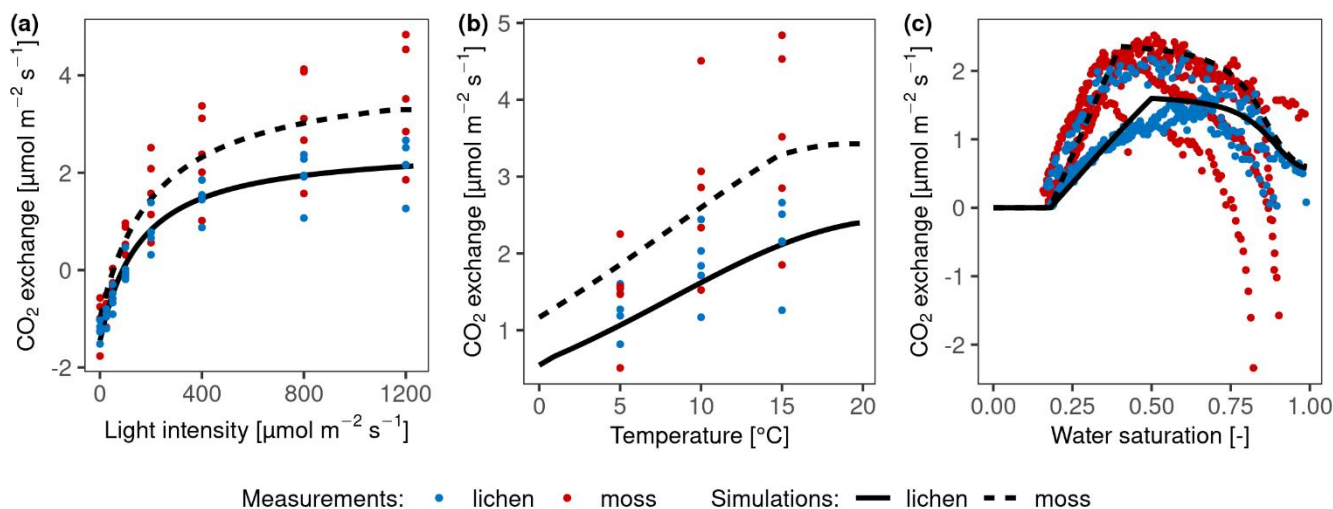


179

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

184 2.3.2 Biocrust physiological properties

185 Furthermore, several parameters required by the Farquhar photosynthesis scheme and the respiration scheme were directly
186 measured or calculated from gas exchange data sets, such as MWC of the thallus, optimum water content, the optimum
187 temperature for gross photosynthesis, reference maintenance respiration rate, and the Q_{10} value of respiration. Since the
188 temperature range at all sites except D2 was too small to capture the optimum temperature reliably, it was approximated
189 from the measured data set as the average surface temperature during active periods. In addition, the optimum temperature
190 was also constrained by fitting the Farquhar equations to photosynthesis curves, as related to environmental factors light,
191 water content, and temperature. Such fitting method was also used to obtain some other photosynthesis-related parameters of
192 organisms, such as molar carboxylation and oxygenation rate of RuBisCO (V_{cmax} , V_{omax}), respiration cost of RuBisCO
193 enzyme (p_{rr}), and water saturation at which organisms become active ($satmin$).



194

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

199 Since the measured values between replicates showed large variation, in particular the water and temperature-dependent data,
200 as illustrated by the coloured points in Fig. 2, we fitted the curves to the average values of all replicates. The calibration
201 results showed that visually and overall, the photosynthetic curves could be parameterized to fit the measurements well,
202 given that different samples were used for measuring responses to different driving factors, and considering the
203 methodological differences between light and water response curve measurements. However, the water responses were least
204 well-fitted, especially at high water contents, because the measured photosynthesis response rate can become negative at
205 high water saturation, but it is impossible to simulate negative photosynthesis rates with the Farquhar photosynthetic model
206 for the light and CO₂ conditions of the laboratory setup. Under these conditions, photosynthesis is larger than respiration.
207 Thus, even under low diffusivity, caused by high water saturation, there will be no net diffusion of CO₂ from the thallus into
208 the ambient air. Furthermore, matching the simulated temperature-response of net photosynthesis to the measured data under
209 cool conditions turned out to be difficult for samples from site T1 and A1 (Fig. S2). There were too few data points in the
210 measured temperature response data set to constrain the optimum temperature and temperature relation (see Fig. 2), but the
211 fitting turned out well because the simulated optimum temperature for net photosynthesis at site T1 was coincidentally close
212 to the value of 17 °C reported by Colesie et al. for this site. (2014; see Fig. S2).

213 2.4 Validation of the data-driven model



214 The water saturation and activity estimated by the data-driven model were validated by comparing with the daily and diurnal
215 patterns of measured activity (5 sites, not at site D2) and water content data (only at D2). Furthermore, the C balance
216 estimated by the data-driven model was validated by comparison to the in situ measured net CO₂ exchange rate of moss,
217 lichen, and cyanocrust-dominated biocrusts. These data were sampled at site D2 by removing the soil respiration rate,
218 predicted by means of a fitted regression (Weber et al., 2012). Since data on water saturation were available, measured PAR,
219 surface temperature, and water content were used to simulate the C balance using the data-driven model, in contrast to the
220 setup described above. The activity, however, was calculated in the same way as described in the setup. Moreover, the
221 parameters of the model were the same as the calibrated ones of the corresponding biocrust types.

222 2.5 Sensitivity analysis

223 2.5.1 Effects of environmental factors

224 To investigate the role that environmental factors, namely air temperature (T_{air}), light intensity (Light), ambient CO₂
225 concentration (CO₂), and different types of water sources play in regulating the C balance of biocrusts, sensitivity analyses
226 were conducted using our data-driven model for lichen-dominated biocrusts from all study sites. The different types of water
227 sources include rainfall (Rain) and non-rainfall water inputs such as dew and water vapor, which are also determined by
228 relative air humidity (R_{hum}).

229 All the environmental factors were reduced and increased by half (+/- 50%), except for air temperature and relative humidity.
230 The air temperature differences varied by 5 K and relative humidity by 20%. Moreover, relative humidity was constrained
231 between 0 and 100% when the varied relative humidity exceeded this range. The annual C balance with changing
232 environmental factors was then normalized for comparing the relative importance of factors among climate zones following
233 Eq. (1):

$$234 \text{ Normalized C balance} = \frac{C_{ij} - C_j}{|C_j|}, \quad (1)$$

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

236 Then the positive normalized C balance would show an increased annual C balance with varying environmental factors, and
237 thus more carbon accumulation. Moreover, the size of the normalized C balance is proportional to the magnitude of change
238 of the C balance when certain environmental factors change. Therefore, a larger normalized C balance also demonstrates a
239 larger change in annual C balance, and thus a larger effect of this environmental factor.

240 To interpret the spatial distribution of the importance of different environmental factors on C balance, the relative
241 importance of each factor in the given climatic region was calculated following Eq. (2) and Eq. (3):

$$242 N_{ab} = |N_{ab}(\text{increase})| + |N_{ab}(\text{decrease})|, \quad (2)$$



243
$$\text{Relative importance} = \frac{N_{ab}}{\sum_{a=1}^n N_{ab}}, \quad (3)$$

244 where N_{ab} (increase) and N_{ab} (decrease) are the normalized C balance of increasing or decreasing the environmental factor a
245 in climatic region b, respectively. N_{ab} is thus the change amplitude of normalized C balance of environmental factor a in
246 climatic region b.

247 2.5.2 Effect of seasonal acclimation

248 Another sensitivity analysis was performed for site T1 to investigate the impact of seasonally acclimatized properties on
249 carbon assimilation. The properties were varied based on the literature. Respiration of lichens was found to acclimate to
250 seasonal changes in temperature (Lange and Green, 2005). Moreover, under low light, organisms showed shade-adapted
251 physiological characteristics with low PAR compensation and saturation points (LCP and LSP; Green and Lange, 1991).
252 Thus, under low light conditions, the organisms have a stronger ability to utilize low light intensities for photosynthesis.
253 These properties can be expressed by certain parameters of the data-driven model. For instance, the respiration rate is
254 determined by the parameter metabolic respiration cost per surface area (Resp_main); LCP and LSP can be affected by
255 changing the slope of the photosynthesis-light relations through light absorption fraction in cells (extL); LCP and LSP can
256 also be modified via the ratio of J_{max} to V_{max} (jvratio) as it influences the value of light use efficiency at unsaturated light.
257 With higher efficiency, the light required to reach the saturated light level declines. J_{max} is a crucial parameter quantifying
258 the maximum rate of electron transport in the light-dependent reactions of photosynthesis, V_{max} describes the maximum
259 rate of carboxylation of RuBisCO in the Calvin Cycle of photosynthesis (Walker et al., 2014). Accordingly, rather than
260 keeping all parameters fixed throughout the simulation period of the data-driven model, in the sensitivity analysis, the
261 physiological parameters were set to another set of values in the winter months. We analyzed the lichen- and moss-
262 dominated biocrusts at site T1 as an example, because the measured time-series activity showed that in temperate sites such
263 as T1, the organisms were active most of the time, and thus the C balance would be more sensitive to the modifying
264 properties.

265 In the sensitivity analysis, these calibrated physiological parameters of the data-driven model were varied for the non-
266 growing months to adapt to the climatic conditions because the organisms at site T1 were collected in their growing seasons.
267 Specifically, in an hourly simulation during September and December, January, and February, the parameter Resp_main was
268 reduced to half to lighten the respiratory cost for the samples collected at site T1. The size of extL was doubled to increase
269 the slope of photosynthesis-light relations. In addition, the parameter jvratio was doubled as well to enhance the light use
270 efficiency.

271 2.6 LiBry Model



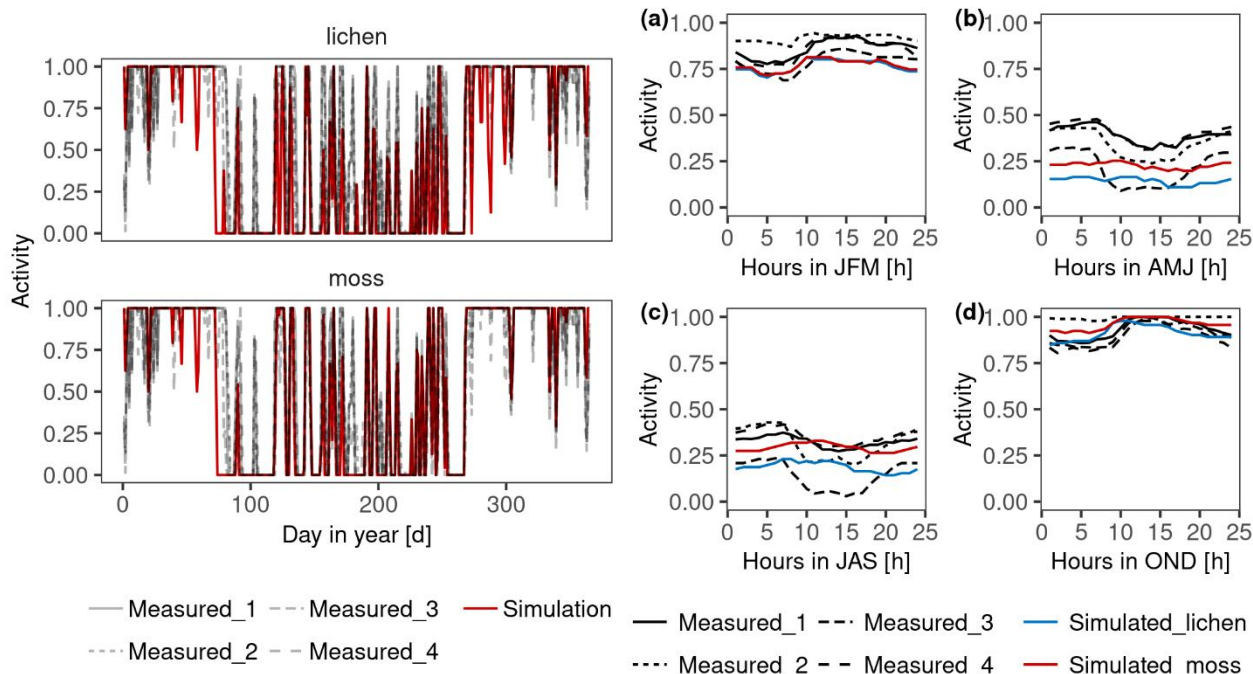
272 LiBry is a process-based dynamic global vegetation model (DGVM) specific to non-vascular vegetation. The model mimics
273 environmental filtering in the real world by simulating many different functional strategies and selecting those which
274 maintain a positive C balance under the respective climatic conditions. The strategies are characterized by a combination of
275 11 physiological and morphological parameters. More information about the model is briefly described in the Appendix, and
276 a full detailed description can be found in Porada et al. (2013, 2019). For this study, the LiBry model was run for 300 years
277 with repeated microclimate forcing data of one year from the six study sites, calibrated abiotic parameters same as the data-
278 driven model, and initially generated 1000 strategies. C balance and dynamics of the surface cover of the strategies were
279 simulated until a steady state was reached, so that the final successful strategies were those where long-term biomass values
280 were positive. Moreover, at the end of the simulation, the average values of functional traits were estimated by weighting all
281 surviving strategies based on their relative cover. The (hypothetical) strategy characterized by these average values is called
282 average strategy. The strategy with the largest cover area is called dominant strategy.

283 Furthermore, we compared the physiological parameters of the average strategy and the selected dominant strategies to the
284 ones of organisms in the field by means of their respective photosynthesis response curves. This comparison can verify the C
285 balance estimated by the data-driven model from a reversed perspective as the strategies were freely selected by the LiBry
286 model based on their C balance, without prescribing values based on site level observations.

287 **3 Results**

288 **3.1 Data-driven model**

289 **3.1.1 Validation of the data-driven model**



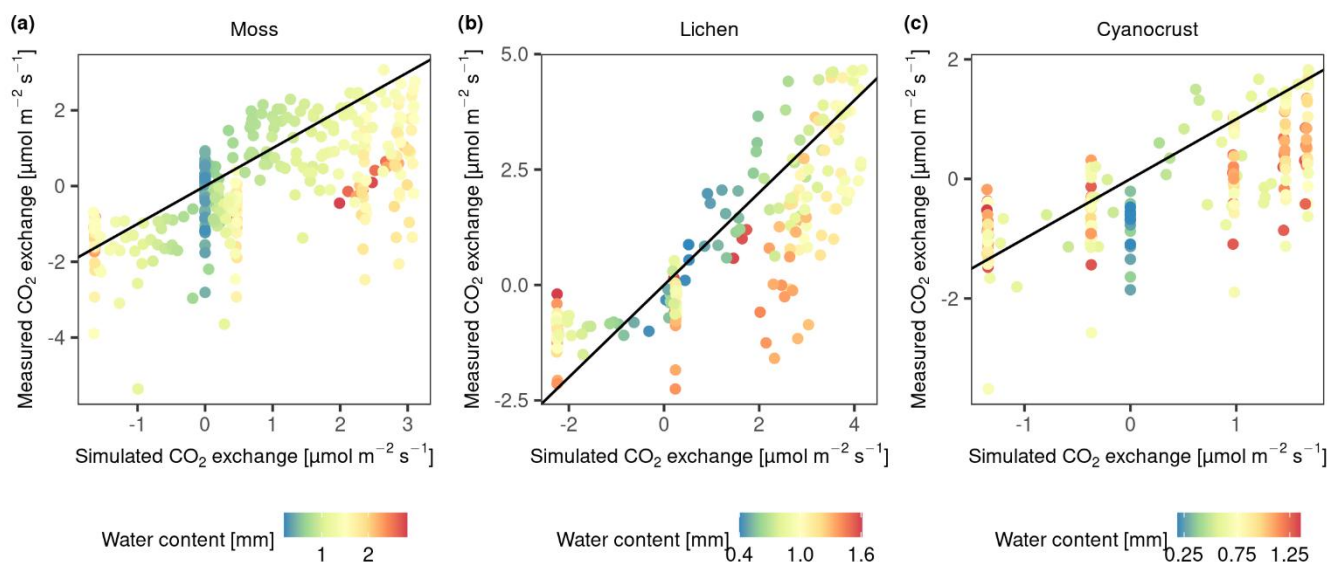
290
 291 **Figure 3:** Validation of the estimated daily (left panel) and diurnal (right panel) patterns of activity of lichen- and moss-
 292 dominated biocrusts at site T3. The simulated patterns of activity were compared to measured data by four sensors at
 293 different locations. Right: (a) to (d) represent the patterns of average hourly activity from January to March (JFM), April to
 294 June (AMJ), July to September (JAS), and October to December (OND), respectively.

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

302 The comparison of simulated and on-site measured CO₂ exchange rates of three biocrust types (moss, lichen, and cyanocrust
 303 composed of cyanolichens and cyanobacteria) at site D2 showed mismatches, especially when water saturation was at both
 304 ends of the gradient (Fig. 4). The CO₂ exchange rate at high water content was overestimated compared to the measurements.
 305 Moreover, there were large variations in measurements of respiration and CO₂ exchange rate as water content was low and
 306 thus simulated CO₂ exchange rate was zero. Excluding the values at both ends of water content (0.58 and 1.74 mm for moss;
 307 0.22 and 0.68 mm for lichen; 0.26 and 0.65 mm for cyanocrust), the accuracy of the model predictions was improved (root
 308 mean square error (rmse) decreased from 1.45 to 1.36 for moss, 1.27 to 0.71 for lichen, and 0.92 to 0.87 for cyanocrust).



309 Furthermore, the simulations were similar to measurements in magnitude. Therefore, despite the large variation, we are
 310 confident about the general validity of the model.



311
 312 **Figure 4:** Validation of the photosynthesis and respiration scheme of the data-driven model through comparison of modelled
 313 and measured CO₂ exchange rate of moss, lichen, and cyanocrust given the measured water content, surface temperature,
 314 PAR, and calculated activity. Observational data were collected in November in 2013 at site D2. The 1:1 line is shown in
 315 black.

316 3.1.2 Estimated C balance by data-driven model

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

320 **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)	3.8	3.2	
D2 (Soebatsfontein)	0.7	6.3	-2.0
T1 (Gössenheim)	-27.3	-28.6	

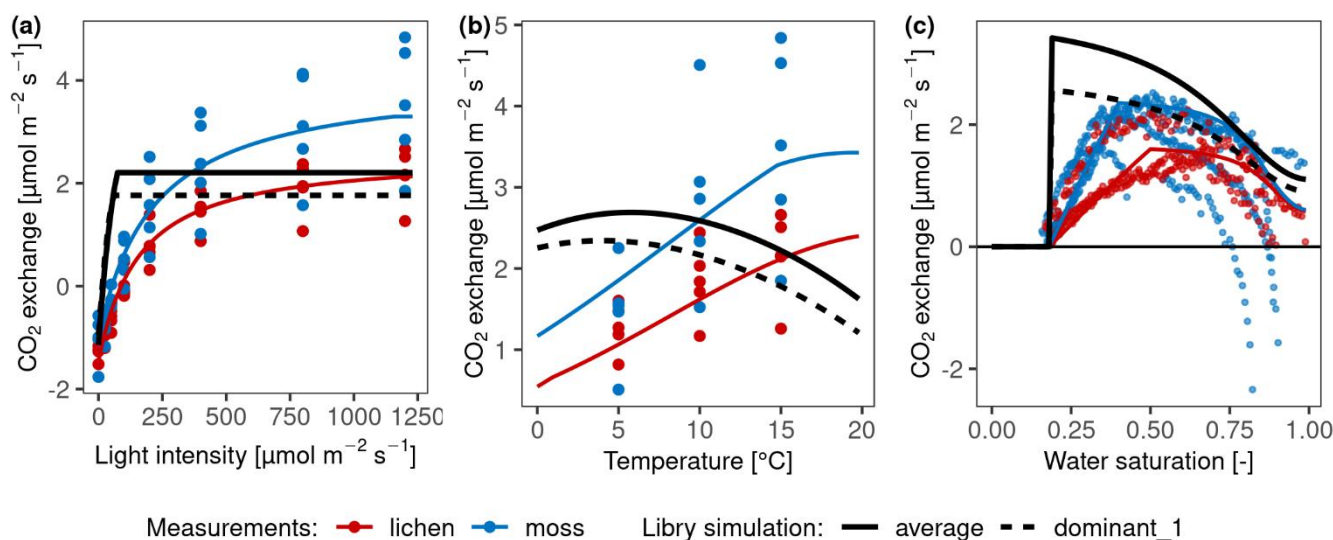


T2 (Öland)	-96.0	-63.9
T3 (Linde)	7.1	13.3
A1 (Hochtor)	-11.4	6.2

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

326 3.2 Dominant strategies selected by the LiBry Model

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



335 **Figure 5:** Comparison of net photosynthesis response of measured samples with simulated selected dominant and average
 336 strategies of LiBry at site T2. (a): light response curve; (b): temperature response curve; (c): water response relation. The



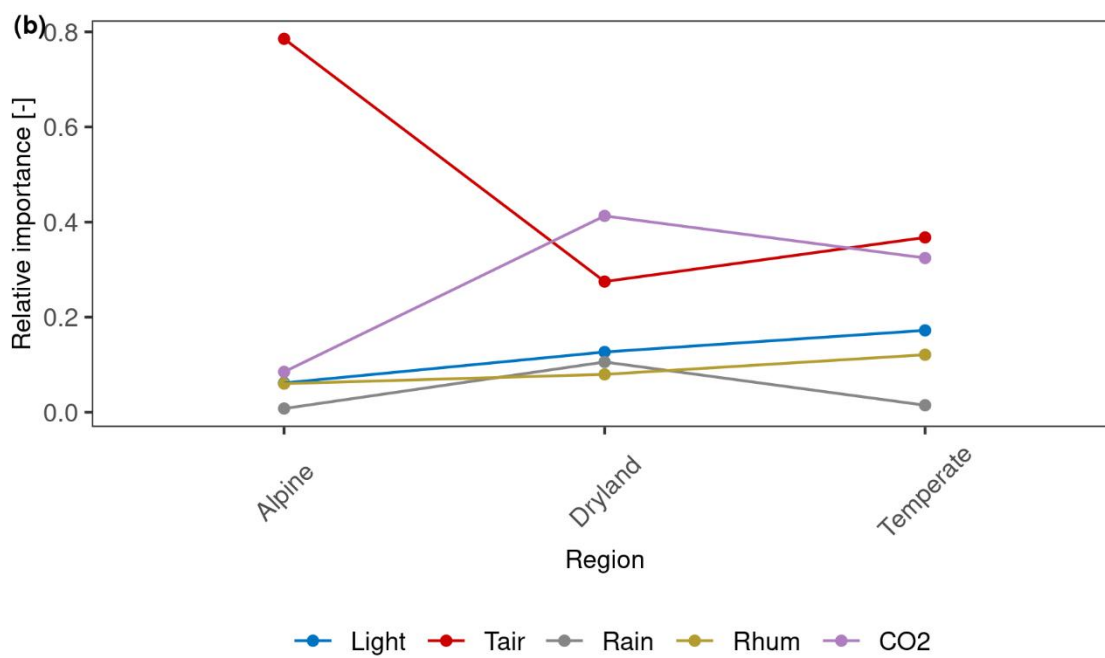
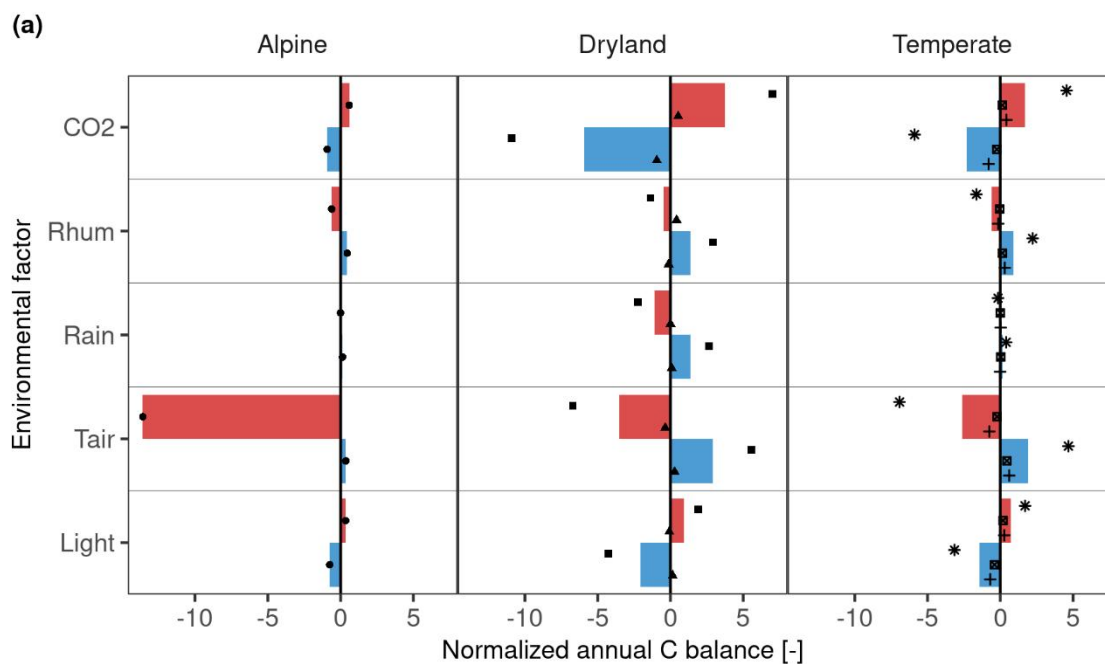
337 colored points represent the measured CO₂ exchange rates of moss and lichen, and the coloured lines correspond to the data-
338 driven model. The black lines show the photosynthesis response of the dominant strategy selected by the LiBry model
339 (dashed) and the average strategy (solid). The parameter values of the average strategy correspond to the average of all
340 surviving strategies.

341 **3.3 Driving factors of variation of the C balance**

342 **3.3.1 Environmental factors**

343 The environmental factors light intensity, CO₂ concentration, air temperature, and various water sources, had different
344 effects on the C balance of lichens in different climate zones (Fig. 6). For all sites within a given climate zone, the effects of
345 different environmental factors on C balance were overall similar but showed an apparent larger variation at the temperate
346 site T3 in contrast to the other two temperate sites, and at site D2 compared to D1 (Fig. 6a). This may be due to
347 physiological differences of the investigated biocrust species between these sites and consequently variations in the
348 responses of net photosynthesis rate to temperature, water, and light between them (Fig. 2 and S2).

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





352 **Figure 6:** (a) The effects of environmental factors - CO₂ concentration (CO₂), relative air humidity (Rhum), rainfall amount
353 (Rain), air temperature (T_{air}) and light intensity (Light) on the annual C balance of lichens in different climate regions. The
354 altered annual C balance resulting from increasing or decreasing environmental factors is normalized by the C balance under
355 original environmental conditions. The colored columns indicate the average value of the normalized C balance at sites with
356 similar climate conditions. Various styles of black points indicate different sites. Positive normalized C balance implies that
357 the annual C balance increases with varying environmental factors and more carbon was accumulated in a year at the site,
358 and vice versa. A larger normalized C balance reflects that the C balance is more sensitive to the altering environmental
359 factor, and thus the environmental factor has a larger effect on C balance. (b) Relative importance of each environmental
360 factor compared to other factors across the climatic regions. Larger relative importance implies a more important effect the
361 factor has on the C balance compared to other factors in the given climatic region, and vice versa.

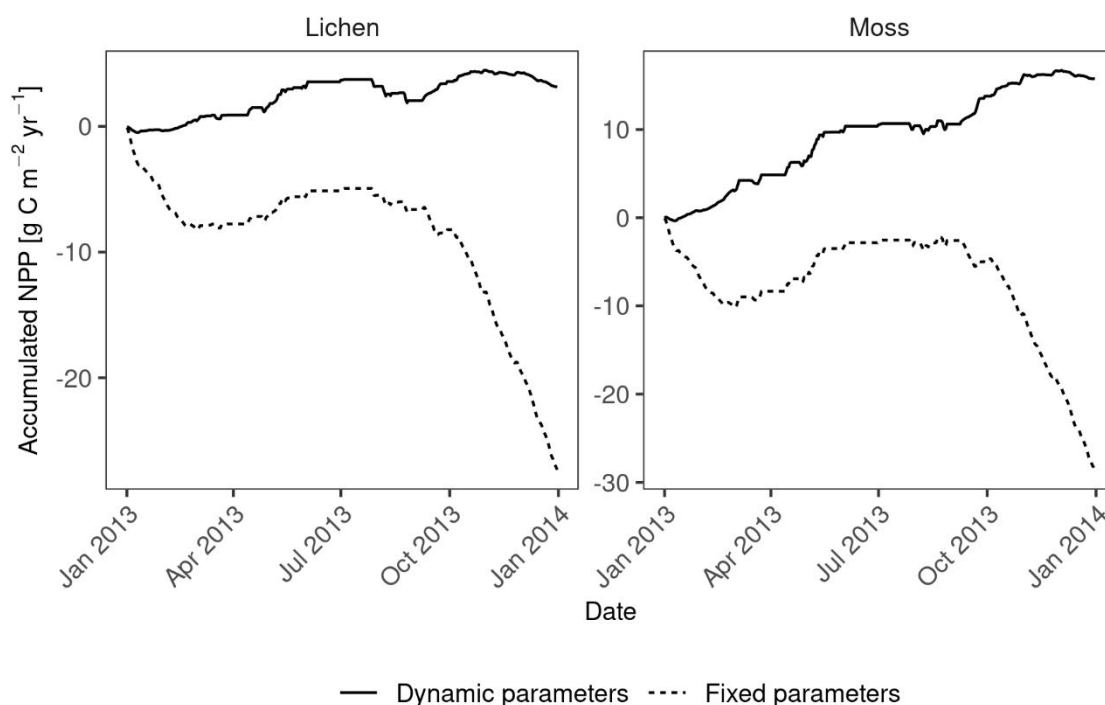
362 In general, air temperature and CO₂ concentration were the most important drivers for C balance of biocrust organisms
363 between climate zones. Light intensity and relative humidity played a relevant role in impacting the C balance as well.
364 Rainfall amount had lower relative importance at all sites except dryland D2, where the effect of rainfall on C balance was
365 similar to other factors (Fig. 6a). Therefore, rainfall amount showed a maximum in relative importance in drylands,
366 compared to other regions. In general, the effect of the other water source, relative air humidity, was moderate but notable at
367 all climate zones, and is slightly larger in temperate region in comparison to other climate zones. Furthermore, the humidity
368 had a slightly larger impact on C balance in comparison to rainfall amount at all temperate and alpine sites (e.g., change
369 amplitude was 0.04 for rainfall and 0.44 for humidity at T1). Moreover, reduced humidity can have a positive effect on C
370 accumulation in these regions (e.g., the normalized C balance was 0.3 at T1 when relative humidity was reduced). In
371 drylands, however, the impacts of water sources on C balance varied between sites. The results showed that relative
372 humidity had a larger impact than rainfall amount at D1 while similar at D2. Reducing relative humidity had a positive effect
373 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
374 when relative humidity decreases).

375 The ambient CO₂ concentration was an essential factor for the C balance at all sites especially in drylands, resulting in
376 positive effects on C balance with increasing CO₂. Furthermore, light intensity had a marked impact on the C budget at all
377 sites except for dryland D1, and it was relatively more important in temperate regions. At site T2, for example, the
378 normalized C balance was changed to -0.39 and to 0.19 for half and doubled light intensity, respectively. At these sites, the
379 normalized C balance increased with enhanced light intensity. At site D1, however, the values did not vary largely, and even
380 slightly more carbon was lost as the light levels increased (0.16 and -0.08 for half and doubled light intensity). Air
381 temperature had a large impact on C balance at all sites. Especially at alpine site A1, C balance decreased strongly as air
382 temperature raised by 5 K (normalized C balance of -13.59), and at all sites, the direction of the effect remained constant,
383 namely, warming decreased the C balance and vice versa.



384 3.3.2 Acclimation of physiological properties

385 The sensitivity analysis for acclimation showed a marked increase in annual productivity of lichen- and moss-dominated
386 biocrusts at site T1 (Fig. 7) when the seasonal acclimation of several physiological parameters was included in the model
387 (from -27.3 to 3.1 $\text{g C m}^{-2} \text{yr}^{-1}$ and from -28.6 to 15.7 $\text{g C m}^{-2} \text{yr}^{-1}$).



388

389 **Figure 7:** Comparison of accumulated annual C balance between simulations with dynamic parameters and fixed ones
390 of lichens and mosses at site T1. For the simulation with the fixed parameters, all parameters that have been calibrated
391 or measured remained constant throughout the simulation year. For the simulation with dynamic parameters at site T1,
392 parameter metabolic respiration cost per surface area (Resp_main) was reduced by half, light absorption fraction in
393 cells (extL) was doubled but restricted to one, the ratio of J_{max} to V_{cmax} (j_{vratio}) was increased by two times from
394 September to February. The values remained the same in other months as the ones prescribed in the simulation with
395 fixed parameters.

396 4 Discussion

397 4.1 Simulated C balance of data-driven model



398 The data-driven model aims to provide observation-based estimates of the carbon fluxes of non-vascular photoautotrophs
399 which may serve as approximation for the C balance of vegetation in biocrust-dominated ecosystems. At the two dryland
400 sites, the lichen- and moss-dominated biocrusts were estimated to be carbon sinks on an annual basis. As shown in the results,
401 lichens took up 3.8 and 0.7 g C m⁻² yr⁻¹, and mosses accumulated 3.2 and 6.3 g C m⁻² yr⁻¹ at site D1 and D2, respectively.

402 The estimated C balance at the two dryland sites is consistent with the magnitude of the annual C balance of different
403 biocrust types reported by various studies in arid habitats. Feng et al. (2014) recorded that the biocrusts composed of lichens,
404 mosses, 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
405 larger carbon gain by lichen biocrust of 11.7 g C m⁻² yr⁻¹ in the Mojave Desert, USA. For cyanobacteria, an annual carbon
406 uptake of 0.02 to 2.3 g C m⁻² was reported for deserts (Jeffries et al., 1993). The estimated C balance values in drylands
407 fluctuate relatively largely, but the magnitude is consistent with the simulated results by the data-driven model at D1 and D2.

408 For biocrust lichens growing on rock surface in a temperate grassland, Lange (2003b) measured an annual carbon gain of
409 21.49 g C m⁻². Additionally, several studies estimated the carbon budget in humid tundra habitats. An amount of ~12–70 g C
410 m⁻² yr⁻¹ carbon was fixed by moss-dominated biocrust, for instance (Schuur et al., 2007). The magnitude of these values
411 corresponds to the estimation of the C balance at T3. However, the estimated annual carbon losses of lichens and mosses by
412 the data-driven model in temperate regions T1 and T2 should actually lead to the death of these organisms, which is not
413 consistent with their dominant abundance in the field and is much lower than published by previous studies.

414 The mismatches of trait values between strategies selected by the LiBry model and collected species indicate that strategies
415 corresponding to the collected species could not maintain a positive long-term C balance, and thus were not able to survive
416 in the LiBry model. This is consistent with the results of the data-driven model, which also simulates a negative C balance
417 for those trait values. Nevertheless, there are some uncertainties in the model simulation. A bias in model estimates could
418 result, for instance, from missing physiological processes and trade-offs. Potential reasons for the inconsistency between
419 models and observations are discussed further below.

420 **4.2 Potential factors influencing the C balance**

421 Despite diverse climatic conditions, we found similarities regarding the dominant environmental factors controlling the C
422 balance. As shown in the results, CO₂ and air temperature were two most important factors at all sites that impact C balances
423 in the model. Relative air humidity, partly precipitation, and light intensity were also essential for C balance. The relative
424 importance of these factors varied slightly among climatic regions and the effects of these factors on the C balance were
425 different in direction among sites. We cannot rule out that the magnitudes of changes in environmental factors that we
426 applied in the sensitivity analysis were not balanced, which may have led to an overestimation of the relative importance of
427 certain factors, such as air temperature, for instance, compared to the others. The spatial patterns across climate regions of a
428 given environmental factor, however, are not affected by this, which means that differences between climatic regions for a
429 given factor are most likely robust. Hence, rainfall and CO₂ are likely to have the largest effect on C balance in drylands



430 compared to other regions, while air temperature is more relevant in alpine regions and light and relative air humidity have a
431 higher impact in temperate than in other regions. Nevertheless, we only studied the sensitivity of the C balance of biocrusts
432 dominated by the lichen *Psora decipiens* and *Cladonia furcata* (at T3), and there are variations between lichens of different
433 growth forms and between biocrust types. For example, cyanolichens increase in abundance with increasing rainfall, but
434 trebouxoid lichens have their physiological optimum in drier conditions (Phinney et al., 2021). Moreover, the impact of
435 precipitation on isidiate lichens is weaker than that of temperature (Phinney et al., 2021).

436 Our results suggest that warming can result in a large amount of carbon loss at all sites, with a particular large effect in the
437 alpine region. This can be explained by the overall less optimal water and temperature conditions associated with warming.
438 The simulated increasing respiratory costs with warming overcompensate gains in gross photosynthesis.

439 Ambient CO₂ concentration affects the gross photosynthesis rate to a large extent in the model. Although the intra-annual
440 change in air CO₂ concentration may be small in the field compared to other environmental factors, the increase of CO₂ in
441 the atmosphere in recent decades (IPCC 2021) may alter the long-term C balance substantially.

442 Light intensity is one of the essential factors for photosynthesis as simulated by our model. According to our climate forcing
443 data, the mean value of radiation maxima in January is 244 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at T1 and 245 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the alpine site. During
444 wintertime in temperate and alpine regions, light intensity may be lower than the light saturation point (Fig.2 and S2).
445 Therefore, light intensity is a limiting factor of photosynthetic carbon assimilation in these regions, and increasing light
446 intensity can thus promote carbon accumulation. However, the higher light intensity can raise the surface temperature and
447 thus lead to more evaporation. More water loss would result in lower water saturation and activity especially in drylands,
448 which could limit the net photosynthesis rate. Therefore, at dryland D1, the increasing light intensity has the opposite impact
449 compared with other sites.

450 Biocrust water content is regulated by both rainfall and non-rainfall water inputs. The relative importance of different water
451 sources in mediating C balance varies in the model. Precipitation amount was not a key factor affecting the simulated
452 biocrust performance at one of the arid sites, which is consistent with another study (Baldauf et al., 2020). Our results
453 suggest that at the other dryland site D2, however, the precipitation amount is very closely associated with the C balance of
454 lichens. Moreover, we found that the effect of the amount of precipitation is small in relative humid temperate and alpine
455 regions. The effect of precipitation on C balance depends on the change in relative water saturation that follows from
456 precipitation event sizes and patterns. In some cases, decreased precipitation leading to a lower water saturation of biocrusts
457 may facilitate photosynthetic carbon gain via increasing the CO₂ diffusivity from the atmosphere into the chloroplast (Lange
458 et al., 1997). Nevertheless, reducing water saturation below a certain value can cause a decline in the duration of activity
459 (Proctor, 2001; Veste et al., 2008) which thus reduces carbon accumulation. Thus, there may be a rain threshold below which
460 decreasing rain may start having a negative effect on biocrust C balances. The threshold is likely species-specific as it is
461 associated with the water holding capacity of the organism. At arid region D1, despite the number of rainfall events being



462 lower, the size of many single events is still large. When rainfall input is varied in the model (decreased by half), the activity
463 and water saturation patterns of the studied organisms are similar to the ones with original rainfall (Fig. S5a and S5b). At the
464 temperate and alpine sites, although the reduction in rainfall lowered the saturation as well as the activity at many time
465 points (Fig. S5c and S5d), the organisms still remained active during most of the time (active 56% to 52% of the time during
466 one year as rainfall decreased by half) and even still fully active, since there was frequent and considerable rainfall in the
467 year of data collection. Thereby, the negative impact induced by reduced activity can be compensated by the positive impact
468 caused by reduced saturation. Thus, in the model, the impact of precipitation amount is small on C balance in these regions.

469 Moreover, the difference in effects of precipitation between two drylands may result from the different precipitation patterns.
470 The precipitation events are more evenly distributed throughout the year in D2 compared to D1, and many single events are
471 small in size. Decreasing the amount of precipitation alters the activity and water saturation patterns of the investigated
472 organisms to a larger extent in D2 as compared to D1 (Fig. S5e and f). Therefore, the amount of precipitation has a relatively
473 larger impact on the simulated C balance at site D2. Several studies found strong effects of variations in the precipitation
474 pattern on biocrust C balance (such as Reed et al., 2012). Our simulation results thus highlight the need for combined
475 application of field experiments and data-driven modelling to improve our understanding of differential responses to
476 variation in precipitation.

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

491 However, the beneficial impact of the increased humidity is not common in all drylands. At site D2, our results showed an
492 apparent decrease in annual C balance with increased humidity. This could result from the different calculated reference
493 respiratory costs of the investigated organisms at these two sites from their photosynthesis in response to temperature data.
494 During nights with higher humidity, the surface temperature of organisms increases due to less evaporative cooling, which



495 increases the respiratory carbon loss at night. Moreover, higher humidity increases the activity and activates organisms that
496 are otherwise inactive at night (annual mean humidity at night is 66% at D1 and 70% at D2). Thus, more carbon will be lost
497 due to longer periods of respiration in the dark or at low light. The reference respiratory cost of the measured organisms at
498 D2 is much larger than at D1 (1.2 and 2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at D1 and D2, respectively), so the respiration rate at D2 will be
499 larger than D1 under similar temperature conditions. This is supported by our results that also showed a larger yearly mean
500 respiration rate during the night at D2 (0.35 and 1.04 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at D1 and D2, respectively; the yearly air temperature is
501 12.5 and 14 °C at D1 and D2, respectively). Therefore, although more carbon is assimilated during the day due to higher
502 humidity in both drylands, more carbon is also lost during the night. The higher carbon loss at night at site D2 is larger than
503 at D1, since the organisms at D2 have a higher respiration rate than at D1. This may explain the decrease of the annual C
504 balance with increased air humidity at site D2 in the model.

505 **4.3 Estimated negative C balance using the data-driven model**

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

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

526 **4.4 Validation of the data-driven model**



527 The validation results of the model showed an overall good fit of daily and diurnal patterns of water content and activity (Fig.
528 3 and S3), and C balance at D2 (shown in Fig. 4) given the uncertainties in the data used to parameterize and evaluate the
529 model. This indicates that the data-driven model may be a reliable tool for C balance estimation, provided that a sufficient
530 amount of suitable forcing data is available.

531 A potential explanation for the general underestimation of activity at night and morning during several periods in a year is
532 the larger prescribed MWC and satmin of organisms in the model compared to those of the samples from the activity
533 measurements. Consequently, simulated saturation was lower, but minimal saturation for being active was higher than the
534 samples. Thus, the activity may have been underestimated at small water inputs such as dew and water vapor, which occur
535 mainly during the night and in the morning hours (Fig. S6). Moreover, underestimated activity in April and June at site T1
536 (Fig. S3 F(b)) may have resulted from a gap in rainfall measurements during this period. Not only rainfall amount but also
537 timing and frequency of rainfall events are essential for the physiological responses of biocrust communities (Belnap et al.,
538 2004; Coe et al., 2012; Reed et al., 2012). Therefore, although the measured annual total amount of rainfall is reasonable
539 (424 mm at site T1), the missing rainfall during a series of days in summer at site T1 would lead us to incorrectly predict that
540 the biocrusts remain inactive on these days.

541 Moreover, the mismatch between modelled and observed CO₂ assimilation rates at low or high water contents at site D2 (Fig.
542 4) may have partly resulted from the calibration procedure. In the calibration the simulated CO₂ exchange rates were higher
543 than measurements when the saturation exceeded the optimum saturation and hardly showed any negative values at high
544 saturation (Fig. S2 f). In turn, the simulated CO₂ exchange rates of biocrusts with an extremely low water content were zero
545 while the measurements showed negative values (see Fig. S2 f), pointing at a certain degree of metabolic activity in natural
546 conditions. Furthermore, the samples used for validation were different from the ones for calibration, which can also lead to
547 inaccuracies.

548 Additionally, the ability of the model to capture seasonality variations of C balance, which have been shown by other studies
549 (Büdel et al., 2018; Lange, 2003a; Zhao et al., 2016), could not be evaluated here since the monitoring of C balance in the
550 field and collection of samples used for photosynthesis performance measurements were conducted only during October and
551 early November.

552 **4.5 Uncertainties of long-term C balance simulated by the data-driven model**

553 Apart from the missing seasonal acclimation of physiological traits in the data-driven model, the estimated C balance may be
554 inaccurate due to potential bias in estimated relative water saturation, which partly depends on prescribed MWC, a
555 morphological model parameter that is obtained by measurements. We varied the MWC of lichen-dominated biocrust from
556 site T1 by half (+/- 50%) to examine how important uncertainty in this parameter is for the estimation of the C balance. The
557 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
558 MWC). Therefore, the annual carbon estimation is robust to the uncertainties with regard to the prescribed MWC.



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

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

567 **5 Conclusions**

568 While all environmental factors that were examined in our study may act as key drivers for the C balance of biocrusts, they
569 show distinct spatial patterns of their relative impacts. At alpine sites, air temperature is likely the most relevant factor.
570 Relative humidity and light may be relevant for the C balance mainly in humid temperate sites, which is not obvious. In
571 drylands, rainfall and also ambient CO₂ are found to be additional relevant factors. Furthermore, the direction of effect of
572 relative humidity may vary between dryland and humid sites: the higher humidity can be beneficial for the C balance in arid
573 regions, whereas it induces carbon loss in humid temperate and alpine sites. However, these patterns in drylands depend on
574 the species characteristics and microclimatic conditions of the habitat. Therefore, for the generalization of the roles of water
575 types in various climatic zones, a larger number of different organisms at multiple sites needs to be studied.

576 Our study suggests that a better, more detailed understanding of the seasonal variation of physiological traits is necessary, as
577 acclimation may affect the C balance substantially. The season and timing of collecting and monitoring the species should be
578 considered in experimental studies, especially when the characteristics of species are the basis for further analyses and
579 forecasts to estimate the annual carbon budget. Additionally, integration of acclimation of physiological traits in models can
580 improve the accuracy in C balance estimation.

581 Mechanistic models, as an add-on to experimental approaches, are well suited to explore the responses of the C balance of
582 biocrusts to separate environmental factors, and the underlying mechanisms. In turn, models need to be constrained by
583 measurements. As a result, we recommend combining experiments, field investigations, and modelling approaches to acquire
584 a comprehensive understanding from all perspectives of how biocrusts respond to climate and, potentially, future climate
585 change.

586 *Code and Data Availability Statement.* Source code of the data-driven model, LiBry modelling results, R-scripts to run the
587 analysis in this manuscript are available in Zenodo repository at <https://doi.org/10.5281/zenodo.6971250>. Field and
588 laboratory data are available in the corresponding publications cited in the manuscript and also from the corresponding
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590 *Author Contributions.* YM and PP designed the study, BW, AK, MV and JR provided the observational data. YM did the
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