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

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Abstract. Biocrusts are a worldwide phenomenon, contributing substantially to ecosystem functioning. Their growth and survival depend on multiple environmental factors, including climatic conditions. While the physiological responses of biocrusts to individual environmental factors have been examined in laboratory experiments, the relative importance of these factors along climatic gradients is largely unknown. Moreover, it is not fully understood how acclimation of biocrusts may alter the relative impacts of certain factors. We aim here at determining the relative effects of environmental factors on biocrusts along climatic gradients, using the carbon balance of biocrust organisms as a measure of their performance. 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 CO₂ 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) (Belnap et al., 2016). Biocrusts occur in various environments across the globe and are especially ubiquitous in environments where low water availability inhibits the development of vascular plants (Belnap et al., 2004; Lange et al., 1998a; Samolov et al., 2020). They provide a wide range of important ecosystem functions, such as build-up of soil organic carbon and nutrients (Chamizo et al., 2012; Düsing et al., 2014; Ferrenberg et al., 2018). Biocrusts contribute substantially to ecosystem carbon fluxes at the global scale (Elbert et al., 2012). Especially in desert ecosystems, biocrusts can be a major contributor to the annual CO₂ uptake (Tucker et al., 2019; Wohlfahrt et al., 2008). Cyanobacteria, which are common components of biocrusts, either free-living or associated with mosses and lichens, facilitate biotic nitrogen fixation and may subsequently increase carbon sequestration by enhancing the concentration of photosynthesis-related enzymes in top soils (Ackermann et al., 2012; Evans and Lange, 2003).

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

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

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

2 Material and Methods

We simulated the C balance of biocrusts from six climatically different study sites in a semi-empirical way using a data-driven model. The model simulates photosynthetic rate based on the Farquhar photosynthesis model developed by Farquhar and von Caemmerer (1982) and respiration rate based on Q10 relationship. The C balance is computed as the difference of
photosynthesis and respiration accumulated over a given time period. In the model, both photosynthesis and respiration depend on surface temperature, relative water saturation, and the activity of the biocrust, which are all simulated in a coupled way via the surface energy balance as a function of climate input data. Photosynthesis additionally depends on ambient CO₂ concentration.

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

2.1 Study sites

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

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

We did not directly use the observed surface temperature and activity as forcing data for the model since these properties are strongly linked to water saturation (and CO₂ 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, the time-series of surface temperature and water saturation data at all sites were estimated based on a simulation of the energy and water balance. The activity of the organisms was then approximated via the empirical equations describing the link between water saturation and metabolic activity (see Porada et al., 2013). Furthermore, ambient CO₂ concentration was assumed to be constant at 400 ppm.

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

### 2.2.3 Photosynthesis response and water storage

For all sites, CO₂ exchange measurements under controlled conditions in the laboratory or in the field (site T3) were conducted using a mobile gas exchange system GFS 3000 (Walz GmbH, Effeltrich, Germany) with an infrared-gas analyzer to explore the physiological characteristics of samples of different biocrust types (same as those measured for validation; main species see Table 1; Diez et al., 2019; Raggio et al., 2018; Tamm et al., 2018). Net photosynthesis was measured at different ranges of light intensity, water content, and temperature. Light response curves, for instance, were determined at 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, and A1 (Raggio et al., 2018). Moreover, the maximum water storage capacity (MWC) of the samples was quantified in the
laboratory for samples from sites D1, T1, T2, and A1 (Raggio et al., 2018), whereas the MWC at site D2 was approximated as the maximum value when measuring water response curves (Tamm et al., 2018; Weber et al., 2012). MWC at site T3 was estimated as the value of the same genus measured in Hamburg, Germany (*Cladonia portentosa* and *Polytrichum formosum*, Petersen et al., in prep.). MWC was acquired since it is one of the essential parameters of the model to convert the specific water content in mm to relative water saturation required by the model used here.

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

<table>
<thead>
<tr>
<th>Site</th>
<th>Code</th>
<th>Climate</th>
<th>Measured annual rainfall [mm]</th>
<th>Dominant species at the site</th>
<th>Data for Calibration</th>
<th>Data for Validation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Laboratory CO₂ exchange response curves</td>
<td></td>
</tr>
<tr>
<td>Almeria, Spain</td>
<td>D1</td>
<td>semi-arid</td>
<td>110</td>
<td><em>Psora decipiens, Didymodon rigidulus</em></td>
<td>Light, water, temperature</td>
<td>Surface temperature</td>
</tr>
<tr>
<td>Soebatsfontein, South Africa</td>
<td>D2</td>
<td>semi-arid</td>
<td>141</td>
<td><em>Psora decipiens,</em> <em>Psora crenata,</em> <em>Ceratodon purpureus,</em> <em>Collema coccophorum</em></td>
<td>Light, water, temperature</td>
<td>Water content</td>
</tr>
<tr>
<td>Gössenheim, Bavaria, Germany</td>
<td>T1</td>
<td>Temperate</td>
<td>424</td>
<td><em>Psora decipiens,</em> <em>Trichostomum crispulum</em></td>
<td>Light, water, temperature</td>
<td>Activity</td>
</tr>
<tr>
<td>Öland, Sweden</td>
<td>T2</td>
<td>Temperate</td>
<td>441</td>
<td><em>Psora decipiens,</em> <em>Tortella tortuosa</em></td>
<td>Light, water, temperature</td>
<td></td>
</tr>
<tr>
<td>Linde, Brandenburg, Germany</td>
<td>T3</td>
<td>Temperate</td>
<td>449</td>
<td><em>Cladonia furcata,</em> <em>Polytrichum piliferum</em></td>
<td>Light, water, temperature</td>
<td></td>
</tr>
<tr>
<td>Hochtor, Austria</td>
<td>A1</td>
<td>Alpine</td>
<td>744</td>
<td><em>Psora decipiens,</em> <em>Tortella rigens</em></td>
<td>Light, water, temperature</td>
<td></td>
</tr>
</tbody>
</table>


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.

The set of parameters that corresponded to minimum differences between simulated and measured values (visual assessment) was used in the data-driven model. The calibration results of surface temperature and the photosynthesis response curves at 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 S2.

The daily surface temperature was simulated accurately (visual comparison) except for site T3 where the temperature during cold seasons was underestimated, and at site D1 the peak temperature within a day in hot seasons was underestimated (Fig. S1). The peak in surface temperature occurred too early by around 3 hours at site T1 and T2, but the magnitude of the peak corresponded well to the measured data (Fig. 1 and S1). Therefore, in general, the fitting of the surface temperature patterns was satisfactory.
Figure 1: Calibration results of abiotic parameters of the data-driven model by fitting the daily (left panel) and diurnal (right panel) patterns of surface temperature at site T2. Right: (a) to (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, reference maintenance respiration rate, and the $Q_{10}$ value of respiration. Since the temperature range at all sites except D2 was too small to capture the optimum temperature reliably, it was approximated 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 ($V_{c\text{max}}$, $V_{o\text{max}}$), respiration cost of RuBisCO enzyme ($p_{rr}$), and water saturation at which organisms become active ($sat_{\text{min}}$).
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, especially at high water contents, because the measured photosynthesis response rate can become negative at high water saturation, but it is impossible to simulate negative photosynthesis rates with the Farquhar photosynthetic model for the light and CO$_2$ conditions of the laboratory setup. Under these conditions, photosynthesis is larger than respiration. Thus, 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. 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 CO₂ 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

2.5.1 Effects of environmental factors

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

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

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

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

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

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

\[
N_{ab} = |N_{ab}(\text{increase})| + |N_{ab}(\text{decrease})|, \quad (2)
\]
Relative importance = \frac{N_{ab}}{\sum_{b=1}^{N} N_{ab}}, \quad (3)

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

### 2.5.2 Effect of seasonal acclimation

Another sensitivity analysis was performed for site T1 to investigate the impact of seasonally acclimatized properties on carbon assimilation. The properties were varied based on the literature. Respiration of lichens was found to acclimate to seasonal changes in temperature (Lange and Green, 2005). Moreover, under low light, organisms showed shade-adapted physiological characteristics with low PAR compensation and saturation points (LCP and LSP; Green and Lange, 1991). Thus, under low light conditions, the organisms have a stronger ability to utilize low light intensities for photosynthesis.

These properties can be expressed by certain parameters of the data-driven model. For instance, the respiration rate is determined by the parameter metabolic respiration cost per surface area (Resp\_main); LCP and LSP can be affected by changing the slope of the photosynthesis-light relations through light absorption fraction in cells (extL); LCP and LSP can also be modified via the ratio of Jmax to Vcmax (jvratio) as it influences the value of light use efficiency at unsaturated light.

With higher efficiency, the light required to reach the saturated light level declines. Jmax is a crucial parameter quantifying the maximum rate of electron transport in the light-dependent reactions of photosynthesis, Vcmax describes the maximum rate of carboxylation of RuBisCO in the Calvin Cycle of photosynthesis (Walker et al., 2014). Accordingly, rather than keeping all parameters fixed throughout the simulation period of the data-driven model, in the sensitivity analysis, the physiological parameters were set to another set of values in the winter months. We analyzed the lichen- and moss-dominated biocrusts at site T1 as an example, because the measured time-series activity showed that in temperate sites such as T1, the organisms were active most of the time, and thus the C balance would be more sensitive to the modifying properties.

In the sensitivity analysis, these calibrated physiological parameters of the data-driven model were varied for the non-growing months to adapt to the climatic conditions because the organisms at site T1 were collected in their growing seasons.

Specifically, in an hourly simulation during September and December, January, and February, the parameter Resp\_main was reduced to half to lighten the respiratory cost for the samples collected at site T1. The size of extL was doubled to increase the slope of photosynthesis-light relations. In addition, the parameter jvratio was doubled as well to enhance the light use efficiency.

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

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

3 Results
3.1 Data-driven model
3.1.1 Validation of the data-driven model
Figure 3: Validation of the estimated daily (left panel) and diurnal (right panel) 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: (a) to (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 CO₂ 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 CO₂ exchange rate at high water content was overestimated compared to the measurements. Moreover, there were large variations in measurements of respiration and CO₂ exchange rate as water content was low and thus simulated CO₂ 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 and 0.65 mm for cyanocrust), the accuracy of the model predictions was improved (root 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).
Furthermore, the simulations were similar to measurements in magnitude. Therefore, despite the large variation, we are confident about the general validity of the model.

**Figure 4**: Validation of the photosynthesis and respiration scheme of the data-driven model through comparison of modelled and measured CO₂ 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 sites showed a small positive value. Moreover, a cyanocrust additionally measured at site D2 showed a small net release of carbon in the model.

<table>
<thead>
<tr>
<th></th>
<th>Lichen</th>
<th>Moss</th>
<th>Cyanocrust</th>
</tr>
</thead>
<tbody>
<tr>
<td>D1 (Almeria)</td>
<td>3.8</td>
<td>3.2</td>
<td></td>
</tr>
<tr>
<td>D2 (Soebatsfontein)</td>
<td>0.7</td>
<td>6.3</td>
<td>-2.0</td>
</tr>
<tr>
<td>T1 (Gössenheim)</td>
<td>-27.3</td>
<td>-28.6</td>
<td></td>
</tr>
</tbody>
</table>
Furthermore, according to these data-driven model simulations, despite the C balance of two biocrust types being positive at site T3, a large amount of carbon was lost at the sites T1 and T2 in temperate humid regions. These results imply that according to the data-driven model, the biocrusts would not survive in the long-term at most of the temperate humid research sites. At the alpine site A1, the moss-dominated biocrust showed a small positive C balance, whereas the lichen crust lost carbon in a year with long periods of ice cover.

3.2 Dominant strategies selected by the LiBry Model

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

![Figure 5](https://doi.org/10.5194/bg-2022-179)

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).
Figure 6: (a) The effects of environmental factors - CO$_2$ concentration (CO$_2$), relative air humidity (Rhum), rainfall amount (Rain), air temperature (Tair) 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 0.04 for rainfall and 0.44 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 larger impact than rainfall amount at D1 while similar at D2. 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 temperate regions. 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 sites, the normalized C balance increased with enhanced 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 alpine site A1, C balance decreased strongly as air temperature raised by 5 K (normalized C balance of -13.59), and at all sites, the direction of the effect remained constant, namely, warming decreased the C balance and vice versa.
3.3.2 Acclimation of physiological properties

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

![Graph comparing accumulated annual C balance between simulations with dynamic parameters and fixed ones for lichens and mosses at site T1.](image)

*Figure 7*: Comparison of accumulated annual C balance between simulations with dynamic parameters and fixed ones of lichens and mosses at site T1. For the simulation with the fixed parameters, all parameters that have been calibrated or measured remained constant throughout the simulation year. For the simulation with dynamic parameters at site T1, parameter metabolic respiration cost per surface area (Resp\_main) was reduced by half, light absorption fraction in cells (extL) was doubled but restricted to one, the ratio of Jmax to Vcmax (jvratio) was increased by two times from September to February. The values remained the same in other months as the ones prescribed in the simulation with fixed parameters.

4 Discussion

4.1 Simulated C balance of data-driven model
The data-driven model aims to provide observation-based estimates of the carbon fluxes of non-vascular photoautotrophs which may serve as approximation for the C balance of vegetation in biocrust-dominated ecosystems. At the two dryland sites, the lichen- and moss-dominated biocrusts were estimated to be carbon sinks on an annual basis. As shown in the results, 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.

The estimated C balance at the two dryland sites is consistent with the magnitude of the annual C balance of different biocrust types reported by various studies in arid habitats. Feng et al. (2014) recorded that the biocrusts composed of lichens, 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 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 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 fluctuate relatively largely, but the magnitude is consistent with the simulated results by the data-driven model at D1 and D2.

For biocrust lichens growing on rock surface in a temperate grassland, Lange (2003b) measured an annual carbon gain of 21.49 g C m\(^{-2}\). Additionally, several studies estimated the carbon budget in humid tundra habitats. An amount of \(\sim12\text{–}70\) g C m\(^{-2}\) yr\(^{-1}\) carbon was fixed by moss-dominated biocrust, for instance (Schuur et al., 2007). The magnitude of these values corresponds to the estimation of the C balance at T3. However, the estimated annual carbon losses of lichens and mosses by the data-driven model in temperate regions T1 and T2 should actually lead to the death of these organisms, which is not consistent with their dominant abundance in the field and is much lower than published by previous studies.

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

4.2 Potential factors influencing the C balance

Despite diverse climatic conditions, we found similarities regarding the dominant environmental factors controlling the C balance. As shown in the results, CO\(_2\) and air temperature were two most important factors at all sites that impact C balances in the model. Relative air humidity, partly precipitation, and light intensity were also essential for C balance. The relative importance of these factors varied slightly among climatic regions and the effects of these factors on the C balance were different in direction among sites. We cannot rule out that the magnitudes of changes in environmental factors that we applied in the sensitivity analysis were not balanced, which may have led to an overestimation of the relative importance of certain factors, such as air temperature, for instance, compared to the others. The spatial patterns across climate regions of a given environmental factor, however, are not affected by this, which means that differences between climatic regions for a given factor are most likely robust. Hence, rainfall and CO\(_2\) are likely to have the largest effect on C balance in drylands.
compared to other regions, while air temperature is more relevant in alpine regions and light and relative air humidity have a higher impact in temperate than in other regions. Nevertheless, we only studied the sensitivity of the C balance of biocrusts dominated by the lichen *Psora decipiens* and *Cladonia furcata* (at T3), and there are variations between lichens of different growth forms and between biocrust types. For example, cyanolichens increase in abundance with increasing rainfall, but trebouxiod 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).

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

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 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.

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

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

Moreover, the reduced evaporation mitigates effects of drying and inactivity of organisms that occur especially at midday. These two processes consequently result in a markedly increased annual C balance in the model.

However, the beneficial impact of the increased humidity is not common in all drylands. At site D2, our results showed an apparent decrease in annual C balance with increased humidity. This could result from the different calculated reference respiratory costs of the investigated organisms at these two sites from their photosynthesis in response to temperature data. During nights with higher humidity, the surface temperature of organisms increases due to less evaporative cooling, which
increases the respiratory carbon loss at night. Moreover, higher humidity increases the activity and activates organisms that are otherwise inactive at night (annual mean humidity at night is 66% at D1 and 70% at D2). Thus, more carbon will be lost due to longer periods of respiration in the dark or at low light. The reference respiratory cost of the measured organisms at D2 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 than D1 under similar temperature conditions. This is supported by our results that also showed a larger yearly mean respiration 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 °C at D1 and D2, respectively). Therefore, although more carbon is assimilated during the day due to higher humidity in both 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 organisms at D2 have a higher respiration rate than at D1. This may explain the decrease of the annual C balance with increased air humidity at site D2 in the model.

4.3 Estimated negative C balance using the data-driven model

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

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

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

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

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

Additionally, the ability of the model to capture seasonality variations of C balance, which have been shown by other studies (Büdel et al., 2018; Lange, 2003a; Zhao et al., 2016), could not be evaluated here since the monitoring of C balance in the field 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 CO₂ 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 to estimate the annual carbon budget. Additionally, integration of acclimation of physiological traits in models can improve the accuracy in C balance estimation.

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

Code and Data Availability Statement. Source code of the data-driven model, LiBry modelling results, R-scripts to run the analysis in this manuscript are available in Zenodo repository at https://doi.org/10.5281/zenodo.6971250. Field and laboratory data are available in the corresponding publications cited in the manuscript and also from the corresponding author upon request.
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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