

1 Dear Editor and Reviewers,  
2 Thank you very much for all your time involved and for reviewers' constructive comments  
3 concerning our manuscript. These comments are all valuable and helpful for improving our  
4 manuscript. Point-by-point responses to the reviewers are listed below. We have combined the  
5 answers in one document since we refer to both reviewers in each response. The response to  
6 reviewer #2 starts on page 13.

7  
8 **RESPONSES TO REVIEWER #1**  
9 Manuscript ID bg-2022-179

10  
11 First of all, thank you very much for your thoughtful review of our manuscript. We appreciate your  
12 positive feedback that "The results provide interesting context for understanding biocrust  
13 physiology worldwide". The comments you raised are very helpful and constructive for improving  
14 our work. All authors have carefully discussed the comments. Below, we provide detailed responses  
15 that correspond to each of your comments (highlighted in bold and italics). We hope that our  
16 responses and explanations (directly after the corresponding comment in normal font, blue and  
17 italics for new text in the revised manuscript) can fully address all points.

18  
19 ***Comments to the Author: the presentation needs work for simplicity and clarity.***

20  
21 Thank you for your time in reviewing such a long manuscript. The length is required since our  
22 research used two modeling approaches to study the carbon balance at six different sites, which  
23 required a comprehensive methods section, and a long discussion section for explaining the various  
24 results at different sites. However, we have tried our best to clarify and shorten the sections  
25 according to the comments. In the response, we elaborate in more detail on several specific  
26 comments.

27  
28 ***Abstract: more quantitative if possible. This extends to the introduction starting especially on line***  
29 ***50 where the text could benefit from numeric values to help the reader understand the magnitude***  
30 ***of C stocks and fluxes that biocrusts interact with.***

31 Thanks for the suggestion, we agree and have added to the abstract both the reasonable carbon  
32 balance number at D1 and also the unrealistic one at T2. The abstract has been rewritten also based  
33 on the comments of reviewer #2 (see below). Furthermore, in the revised introduction, we have  
34 added the carbon balance numbers in L50 and 51 as follows:

35 *An annual carbon budget of 21.49 g C m<sup>-2</sup> based on measured field data was reported in the study*  
36 *of Lange (2003b) on the crustose lichen Lecanora muralis growing on a rock surface in a*  
37 *temperate climate of southern Germany. Furthermore, Büdel et al. (2018) estimated an annual C*  
38 *balance of 1.7 g C m<sup>-2</sup> based on measurements on cyanobacteria-dominated biocrust in an Australian*  
39 *dry savannah ecosystem.*

40 ***Line 69: when environmental conditions are in an optimal range vascular plant would usually be***  
41 ***favored, so what constitutes 'optimal' for biocrusts here?***

42 Thank you for pointing this out. ‘optimal’ here means an ideal situation where each environmental  
43 factor is in its optimal range for the growth of biocrusts, as determined in the laboratory  
44 measurements. The optimal conditions are species-specific. For instance, based on our measured  
45 data in D1, the optimal amount of water input for photosynthesis of biocrust dominated by  
46 *Diploschistes diacapsis* is around 0.37 mm precipitation equivalent, while for biocrust dominated  
47 by moss *Didymodon rigidulus* it is 2.55 mm precipitation equivalent. The optimal water condition  
48 for biocrusts in the field then corresponds to a rainfall pattern that leads to frequent saturation in the  
49 optimal range, and that may differ from the optimal rainfall for vascular plants. We revised this  
50 sentence as: “*While highest values of productivity in biocrusts under field conditions are achieved*  
51 *when the environmental factors are in the range that is optimal for the specific biocrust, it has been*  
52 *found that biocrusts are also able to achieve metabolic activity and thus, potential productivity,*  
53 *under sub-optimal conditions of temperature and light.*”

54 **Line 92: ‘a Q10 relationship’**

55 Thank you for pointing this out, we have corrected it accordingly.

56 **Regarding longwave radiation, I question somewhat the use of the ERA5 data if avoidable; were**  
57 **local surface temperature data available at any of the sites and if so how closely do these data**  
58 **align with the ERA5 data? Reading on to line 127, if surface temperature are available, avoiding**  
59 **ERA5 in the model would be advisable.**

60 Thank you very much for the suggestion. First of all, we cannot compare our measured local surface  
61 temperature data of biocrusts to the ERA5 data, since our ERA5 data set does not contain surface  
62 temperature. In the original version, we tried to explain this in L136-L141, but made it clearer in the  
63 revised manuscript, and also shifted the text upwards to the end of section 2.2.1 as follows: “*...long-*  
64 *wave radiation and snowfall, which were taken from ERA5 dataset*  
65 *(<https://www.ecmwf.int/en/forecasts/datasets/reanalysis-datasets/era5>). Although directly measured*  
66 *surface temperature data are available for all sites, we use ERA5-based down-welling long-wave*  
67 *radiation instead to simulate surface temperature on biocrusts. This is necessary since, in our*  
68 *model, calculations of photosynthesis and respiration require not only surface temperature, but*  
69 *also depend on water saturation of biocrusts (affecting activity). However, we do not have water*  
70 *saturation data available at most sites. Therefore, we instead simulate the dynamic water saturation*  
71 *of biocrusts based on climate, via processes such as evaporation, rainfall, and dew. The calculation*  
72 *of evaporation and dew automatically includes the computation of a surface temperature that*  
73 *emerges from solving the surface energy balance, thereby including down-welling long-wave*  
74 *radiation. Since the simulated surface temperature that is connected to simulated water saturation*  
75 *slightly deviates from the observed surface temperature (see Fig. 1 and S1), we do not directly use*  
76 *the observed surface temperature as input in the modeling approach, to avoid inconsistencies.*”

77 **Line 127 should be in the previous section.**

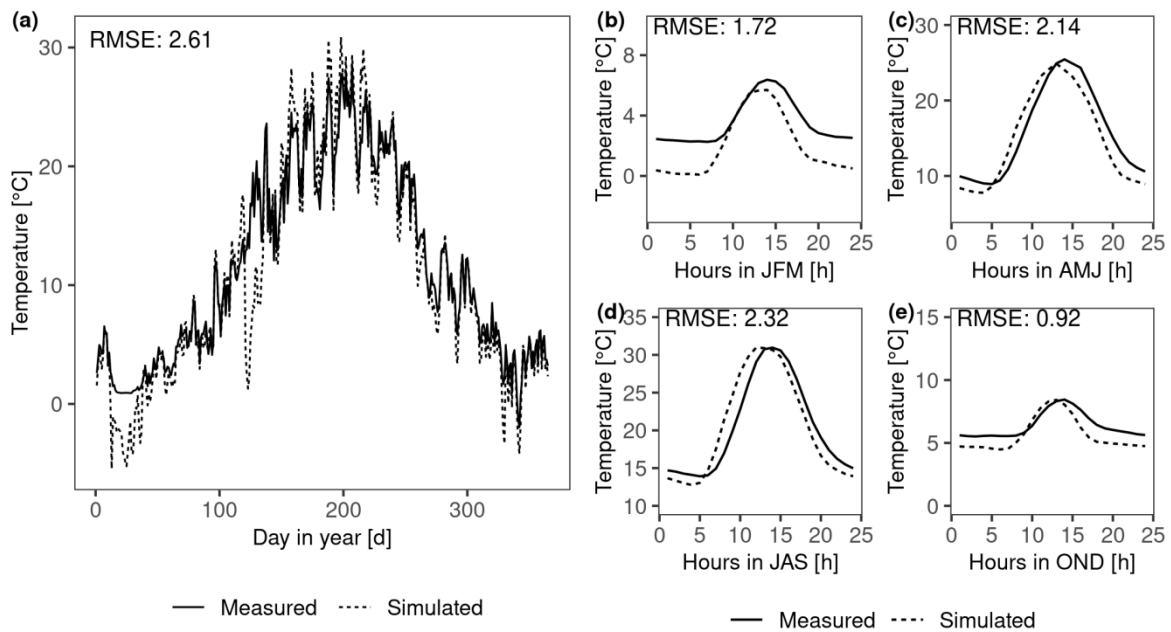
78 Thank you for the suggestion, we have changed this in the revised version.

79 **On line 174, something more than a visual comparison is necessary. In Fig. 1 a-d (should be b-e**  
80 **because the left panel should be a), the consistent early peak in the simulated temperatures**  
81 **should be corrected for if possible because the heat capacity that entered the model is obviously**

82 *incorrect. I'm not sure how this interacts with the discussion 188 if temperature was*  
83 *approximated. When is the temperature approximated and when was it modeled?*

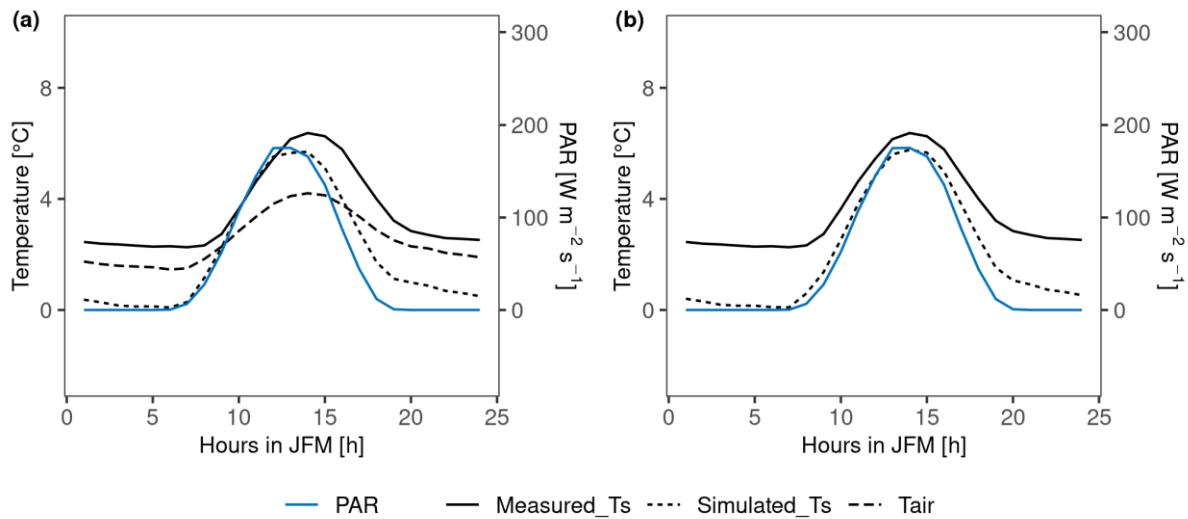
84 Thank you for the comment. We now use RMSE to quantify the calibration in the revised  
85 manuscript and we have updated the curve fitting as follows:

86 We have first checked the measured surface temperature at sites that show an early peak (A1, T1,  
87 T2), and corrected the measured surface temperature data at half-hourly resolution since the data  
88 was shifted due to an improper gap-filling method we have used previously. In the raw dataset at  
89 these sites, we only have dates and not times corresponding to the data, and there are a few days  
90 where data are missing for some time points. We initially filled these gaps by shifting the data  
91 afterward, which caused an overall advance in some of the data points. Now we corrected the  
92 dataset by filling each gap with the average value of the data points at the same hour of the previous  
93 and the following day and also the previous and following 1.5-hour interval of the same day. This  
94 improves the calibration results, but notably only at site T2 (as Fig. 1 shows).



95 Figure 1: Calibration results of abiotic parameters of the data-driven model by fitting the daily (a)  
96 and diurnal (b-e) patterns of surface temperature at site T2. (b) to (e) represent the patterns of  
97 average hourly surface temperature from January to March (JFM), April to June (AMJ), July to  
98 September (JAS), and October to December (OND), respectively.

99 However, the early peak still exists, for instance, from January to March at site T2 (Fig. 1 (b)). This  
100 may result from the measured diurnal patterns of PAR or air temperature at 2m being inconsistent  
101 with the measured surface temperature. We compared the diurnal patterns of the measured PAR,  
102 surface temperature (Measured\_Ts) and air temperature at 2m (Tair), and simulated surface  
103 temperature (Simulated\_Ts) from January to March, and found the different measured climate  
104 variables might have uncertainties against each other. For instance, Tair has an earlier increase than  
105 Measured\_Ts, which is unusual, and also is always lower than Measured\_Ts, even at night, which  
106 could partly explain the underestimated surface temperature there (Fig. 2 (a)). When we shifted the  
107 PAR data to 1 hour later, we found that the early peak of simulated surface temperature is corrected  
108 (Fig. 2 (b)).



109 Figure 2: The diurnal patterns of PAR, measured surface temperature (Measured\_Ts), measured air  
 110 temperature at 2m (Tair), and simulated surface temperature (Simulated\_Ts) from January to March  
 111 at site T2. (a): The patterns of original measurements and simulation. (b): the patterns of measured  
 112 variables and simulated surface temperature when PAR was shifted to 1 hour later.

113 In the model, we do not calibrate the surface heat capacity, since it strongly depends on the dynamic  
 114 surface water content which in turn is controlled by many biotic and abiotic factors in the model.  
 115 We calibrated instead the soil heat capacity and thermal conductivity in the model. However, the  
 116 soil parameters do not have a strong influence on the timing of the peak in surface temperature. In  
 117 addition, a sensitivity analysis of soil thermal conductivity has been conducted at T1 to check  
 118 whether the bias in calibrated boundary parameters can have a large impact on the carbon balance  
 119 of biocrusts. The results showed that changing soil thermal conductivity does not prevent a negative  
 120 carbon balance value in the model (change from  $-42.8$  to  $-37.1$  and to  $-50.9 \text{ g C m}^{-2} \text{ yr}^{-1}$ ,  
 121 respectively, for lichen-dominated biocrust when soil thermal conductivity increased or decreased 5  
 122 times). This point has been added in the Supplement.

123 The statement at line 188 does not refer to the measured or simulated surface temperature, but to the  
 124 ambient temperature in the laboratory when carrying out the gas exchange measurements to identify  
 125 the optimum temperature of photosynthesis. This is an essential parameter for estimating the  
 126 photosynthesis rate and carbon balance, but has little impact on the simulation of surface  
 127 temperature on biocrusts. We have made this clearer in the revised manuscript: “... *Since the  
 128 ambient temperature range that was applied in the laboratory for samples from all sites except D2  
 129 was too small to capture the optimum temperature of photosynthesis reliably, we approximated the  
 130 optimum temperature from the measured data set as the average surface temperature during active  
 131 periods.*”

132 *Section 2.3.2 needs improvement also on line 204 regarding the negative photosynthesis rate.  
 133 This could be a negative net C flux or the Rd parameter exceeding carbon uptake, but  
 134 photosynthesis itself isn't negative.*

135 Thank you for the suggestion. Yes, the measured net C flux is negative, and the response curves that  
 136 are shown in Fig. 2 are net photosynthesis rates, not gross photosynthesis. We have corrected this in  
 137 the revised manuscript.

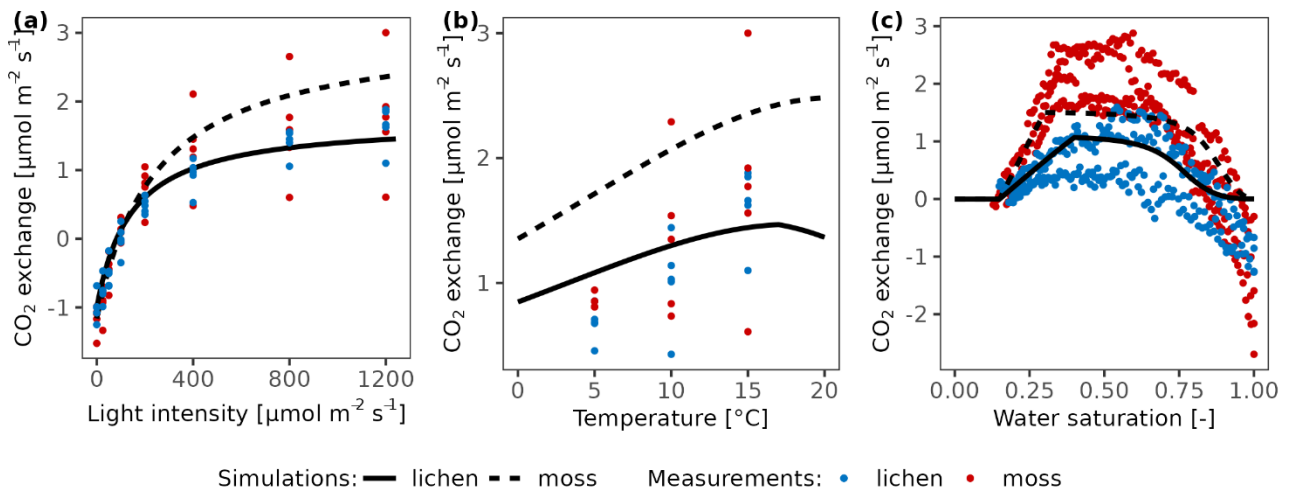
138 Moreover, we intended to re-calibrate the model to reduce the net photosynthesis rate at high water  
139 saturation by reducing the parameter minimum CO<sub>2</sub> diffusivity. The new calibration results for site  
140 T1 are shown below (Fig. 3). We improved the calibration, especially at D2. However, we can only  
141 reduce the net photosynthetic rate close to 0 at high water saturation, but it is impossible to fit the  
142 strongly negative net C flux there.

143 The reason are the CO<sub>2</sub> diffusion pathways implemented in our data-driven model. We assume that  
144 CO<sub>2</sub> only leaves the thallus through the same route as it enters. Furthermore, we assume that the net  
145 flux between the interior of a lichen/bryophyte and the atmosphere has the same magnitude as the  
146 flux (respiration minus photosynthesis; see Fig.4). This “steady-state” assumption is similar to  
147 vascular vegetation models and is justified by the comparably small internal space for CO<sub>2</sub> storage  
148 which prevents long-term (meaning minutes) maintenance of photosynthesis under insufficient  
149 influx of CO<sub>2</sub>. These assumptions do not allow the simulation of a negative net C flux under the  
150 relatively high light of the response curve setup (see also Fig. 4 (a)). As the measured response  
151 curves show, the net C flux of one sample of lichen-dominated biocrust at high water saturation  
152 (Fig. 3 (c)) is similar to the dark respiration rate obtained from the light-response curve (Fig. 3 (a)),  
153 meaning that, for this sample, the flux of CO<sub>2</sub> out of the thallus to the atmosphere at high water  
154 saturation is likely similar in magnitude to respiration rate. In this case, the gross photosynthesis  
155 rate of the sample is likely approximately zero. But, in the model, the CO<sub>2</sub> concentration inside the  
156 thallus needs to be larger than the atmospheric CO<sub>2</sub> (400 ppm) in order to achieve a negative net  
157 flux. The relatively high CO<sub>2</sub> concentration together with the ambient light level of 400 μmol/m<sup>2</sup>/s  
158 in the experimental setup of the water response curve, force the modelled gross photosynthesis rate  
159 to markedly exceed zero, and therefore it is impossible to achieve a large negative net C flux with  
160 the model.

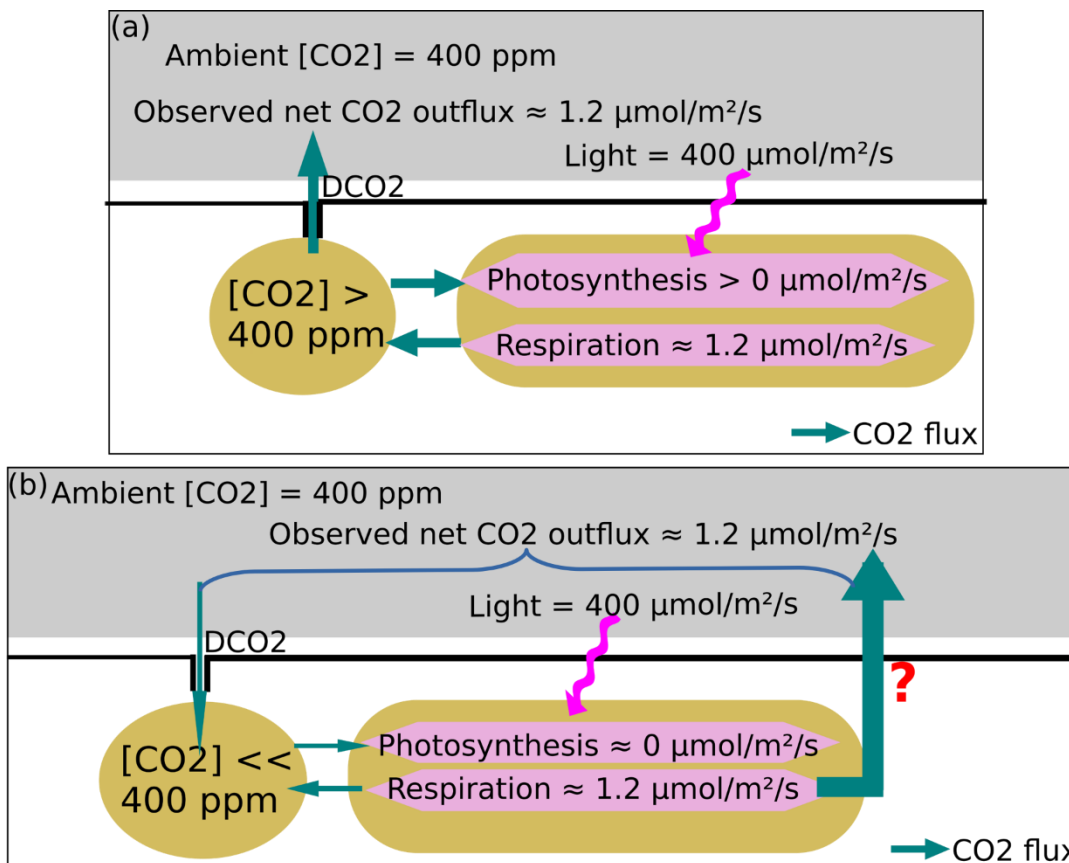
161 The only way to simulate a negative net C flux under light is to assume that the largest part of CO<sub>2</sub>  
162 leaves the thallus via a different route (Fig. 4 (b)). In this case, the small flux of CO<sub>2</sub> from the  
163 atmosphere into the thallus at high water saturation and further into the chloroplasts, which leads to  
164 little gross photosynthesis, is overcompensated by a much larger respiration flux that directly enters  
165 the atmosphere through a different route. However, this is highly uncertain and also a bit  
166 questionable for most lichens and bryophytes. It may be possible in a lichen if the organism has a  
167 high amount of fungal biomass located above the photobionts that contain the chloroplasts, but  
168 without detailed information on the morphology, this would represent an arbitrary parametrization.  
169 Alternatively, we would have to assume that respiration of the sample in Fig. 3 (c) is substantially  
170 higher than in Fig. 3 (a), but this seems arbitrary, too.

171 We have clarified this in the revised manuscript as follows from L203-208: “*However, the water*  
172 *responses were least well-fitted, especially at high water contents. The measured net photosynthesis*  
173 *response rate was negative in some cases at high water saturation, but it is not possible to*  
174 *reproduce this negative net photosynthesis rates with our adapted Farquhar photosynthesis model*  
175 *for the light and CO<sub>2</sub> conditions of the laboratory setup. Under these conditions, gross*  
176 *photosynthesis is larger than respiration and thus CO<sub>2</sub> is required to diffuse from the atmosphere*  
177 *into the thallus, not out of it. Even under low diffusivity, caused by high water saturation, there will*  
178 *be no net diffusion of CO<sub>2</sub> from the thallus into the ambient air assuming that inward and outward*  
179 *flows of CO<sub>2</sub> share the same pathway and that diffusion of CO<sub>2</sub> between atmosphere and thallus is*

180 *in steady-state with the flux (respiration minus gross photosynthesis). For details please see the*  
 181 *Supplement.”*



182 Figure 3: Calibration of photosynthesis parameters of the model by fitting photosynthesis response  
 183 curves of moss- and lichen-dominated biocrust samples to measurements at site T1. (a): net  
 184 photosynthesis rate in response to light at optimum water content and 15 °C. (b): net photosynthesis  
 185 rate in response to temperature at 1200 μmol m<sup>-2</sup> s<sup>-1</sup> light and optimal water content. (c): net  
 186 photosynthesis rate in response to relative water saturation at 400 μmol m<sup>-2</sup> s<sup>-1</sup> light and 15 °C.



187  
 188 Figure 4: The schematic diagram of the CO<sub>2</sub> diffusion pathways. (a): the pathway in the data-driven  
 189 model, which makes it impossible to fit a strongly negative net C flux. (b): The pathway that allows  
 190 a simulation of strongly negative net C flux. Please note that the figure only shows CO<sub>2</sub> fluxes.



191 Contrary to vascular plants, CO<sub>2</sub> and water exchange are not coupled in lichens and mosses, due to  
192 lack of stomata. The model thus calculates water fluxes independently based on the surface energy  
193 balance.

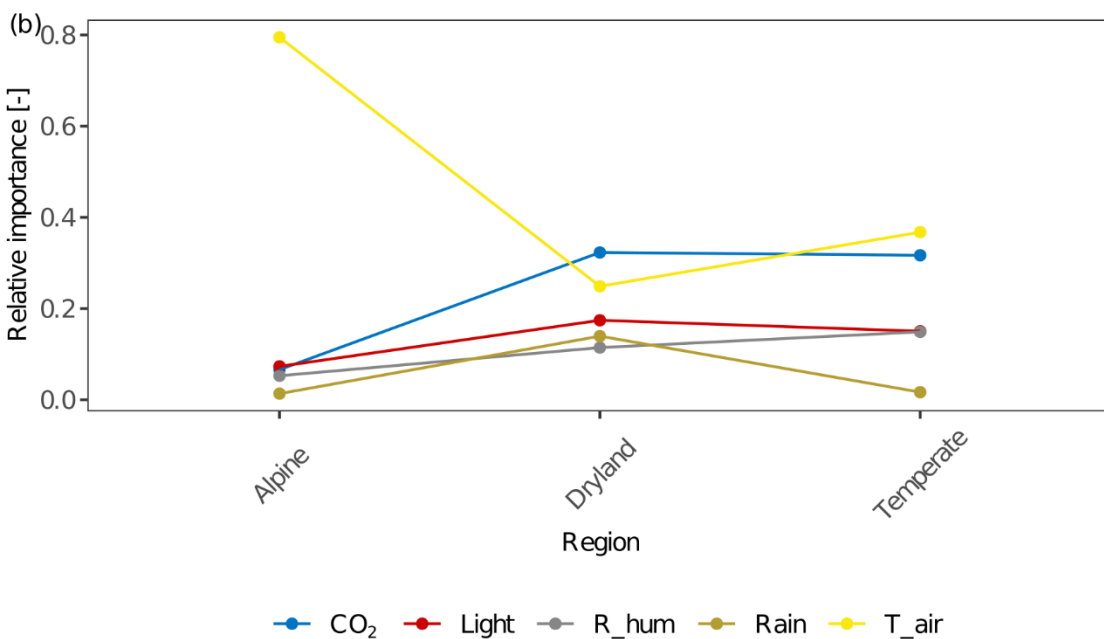
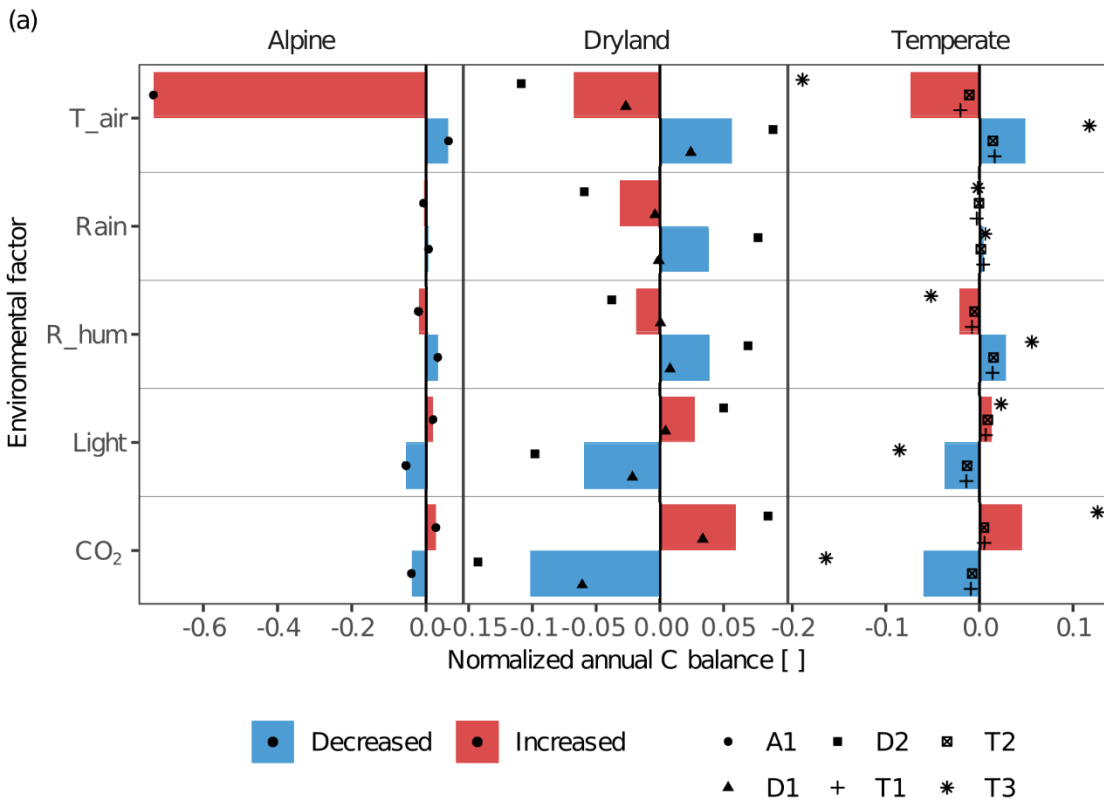
194 Moreover, the carbon balance estimates are affected by uncertainty in physiological parameters that  
195 were calibrated based on measurements of photosynthesis response curves. We thus conducted a  
196 sensitivity analysis of the following physiological parameters: *metabolic respiration cost per*  
197 *surface area (Resp\_main), Q10 value of respiration (q10), the optimum temperature for gross*  
198 *photosynthesis (Topt), respiration cost of RuBisCO enzyme (Rub\_ratio), light absorption fraction in*  
199 *cells (ExtL), minimum saturation for activation (Sat\_act0), and minimum saturation for full*  
200 *activation (Sat\_act1) to examine to what extent the physiological parameters can affect the carbon*  
201 *balance of biocrusts at all study sites. The detailed procedure and results were described in the*  
202 *responses to reviewer #2 below. This additional analysis has been contained in the revised*  
203 *manuscript.*

204 *I'm not entirely convinced about the usefulness of section 2.5 and its description was rather*  
205 *meandering. That being said Fig. 6a is interesting but I wish that the normalization was done*  
206 *differently as a normalized value of < - 10 (for the case of air temperature) is difficult to discern.*

207 Thank you for this comment. In the original section 2.5, the sensitivity of the annual carbon balance of  
208 biocrusts among the study sites with regard to both abiotic factors and also seasonal acclimation  
209 of physiological parameters was described, which indeed was a bit unfocused. Based on the  
210 comments of reviewer #2, we now conducted an additional sensitivity analysis on the effects of  
211 individual physiological parameters on the carbon balance, which makes the topic of section 2.5  
212 more consistent. In the revised manuscript, we added a summary paragraph at the beginning of  
213 section 2.5 to have an overview of the sensitivity analyses that have been performed, and shortened  
214 the description of the normalization procedure and sensitivity analysis of acclimation (see below).

215 Regarding the normalization method, we normalized the annual C balance value for environmental  
216 factors between different climatic zones. The normalized C balance values are now more  
217 meaningful, and also comparable among factors and sites.

218 The new results of the sensitivity analysis of environmental factors are presented as follows:



219

220 Section 2.5 in the new version of the manuscript reads as follows:

221 *2.5 Sensitivity analyses*

222 *To investigate the role of environmental factors, physiological properties, and also seasonal*  
 223 *acclimation for the simulated annual carbon balance of biocrusts, we conducted three sensitivity*  
 224 *analyses using our data-driven model. With this setup, we intend to put into context the effects of*  
 225 *environmental conditions and the uncertainty associated with the physiological properties that were*  
 226 *used to parameterize the model. We additionally explore the impact of seasonally acclimatized*



227 *physiological properties on carbon assimilation at site T1, since variation between seasons*  
228 *represents additional uncertainty in the estimation of the carbon balance.*

### 229 *2.5.1 Effects of environmental factors*

230 *To investigate the role that environmental factors, namely air temperature ( $T_{air}$ ), light intensity*  
231 *(Light), ambient  $CO_2$  concentration ( $CO_2$ ), and different types of water sources play in regulating*  
232 *the C balance of biocrusts, sensitivity analyses were conducted for lichen-dominated biocrusts from*  
233 *all study sites. The different types of water sources include rainfall (Rain) and non-rainfall water*  
234 *inputs such as dew and water vapor, which are determined by relative air humidity ( $R_{hum}$ ). All*  
235 *the environmental factors were reduced and increased by half (+/- 50%), except for  $T_{air}$  and*  
236  *$R_{hum}$ . The  $T_{air}$  differences varied by 5 K and  $R_{hum}$  by 20%. Moreover, relative humidity was*  
237 *constrained between 0 and 100% when the varied relative humidity exceeded this range.*

238 *The annual C balance for each modified environmental factor was then normalized following Eq.*  
239 *(1), and normalized again among different environmental factors within each climatic zone for*  
240 *comparing the relative importance of environmental factors:*

$$241 \text{ Normalized C balance} = \frac{C_{ij} - C_j}{|C_j|}, \quad (1)$$

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

243 *A positive normalized C balance demonstrates an increase in annual C balance when certain*  
244 *environmental factors change, and a larger magnitude of the normalized C balance number*  
245 *demonstrates a larger effect of this environmental factor compared to a factor with a smaller value.*

### 246 *2.5.2 Effect of physiological parameters*

247 *The sensitivity analysis of physiological parameters was conducted for lichen-dominated biocrust at*  
248 *all study sites. The original parameter values were obtained by calibration to measured net*  
249 *photosynthesis response curves. We then varied the values of the following physiological*  
250 *parameters by a consistent range for all sites: metabolic respiration cost per surface area*  
251 *( $Resp_{main}$ ),  $Q_{10}$  value of respiration ( $q_{10}$ ), the optimum temperature for gross photosynthesis*  
252 *( $T_{opt}$ ), respiration cost of RuBisCO enzyme ( $Rub_{ratio}$ ), and light absorption fraction in cells*  
253 *( $ExtL$ ), minimum saturation for activation ( $Sat_{act0}$ ), and minimum saturation for full activation*  
254 *( $Sat_{act1}$ ). Specifically, we increased or decreased  $Resp_{main}$ ,  $ExtL$ ,  $q_{10}$ ,  $Sat_{act0}$  by 30%,*  
255  *$Rub_{ratio}$  and  $Sat_{act1}$  by 20%, and  $T_{opt}$  by 5 K. These parameters are chosen since they are*  
256 *closely related to the response of photosynthesis and respiration to water, light, and temperature.*  
257 *These ranges of different parameters were determined based on the observed bounds of the*  
258 *photosynthetic response curves of all replicates, which have large deviations between each other at*  
259 *most sites as shown in Fig. 2 and Fig. S2. The effects of the varied physiological parameters on the*  
260 *carbon balance were then normalized using the same normalization method as for the*  
261 *environmental factors (in Sect. 2.5.1) for comparison among parameters and climatic zones.*

### 262 *2.5.3 Effect of seasonal acclimation*

263 *Another sensitivity analysis was performed for site T1 to investigate the impact of seasonally*  
264 *acclimatized physiological properties on the carbon balance. We analyzed the lichen- and moss-*  
265 *dominated biocrusts at site T1 as an example, because the measured time-series of activity showed*

266 *that in temperate sites such as T1, the organisms were active most of the time, and thus the C*  
267 *balance would be more sensitive to seasonally varying properties.*

268 *In the analysis, rather than keeping all calibrated parameters fixed throughout the simulation*  
269 *period of the data-driven model, the physiological parameters metabolic respiration cost per*  
270 *surface area (Resp\_main), light absorption fraction in cells (ExtL), and the ratio of Jmax to Vcmax*  
271 *(jvratio) were set to another set of values in the winter months in order to adapt to the climatic*  
272 *conditions, since biocrusts at sites T1 were collected in summer months. These new, “dynamic”*  
273 *parameters were applied in an additional simulation and the resulting carbon balance was*  
274 *compared to the original simulation based on the “fixed” parameters. The dynamic parameters*  
275 *were chosen and varied based on the literature: Respiration of lichens was found to acclimate to*  
276 *seasonal changes in temperature (Lange and Green, 2005). Moreover, under low light, organisms*  
277 *showed shade-adapted physiological characteristics with low PAR compensation and saturation*  
278 *points (LCP and LSP; Green and Lange, 1991). These properties can be expressed by certain*  
279 *parameters of the data-driven model. For instance, the respiration rate is determined by the*  
280 *parameter Resp\_main; LCP and LSP can be affected by changing the slope of the photosynthesis-*  
281 *light relations through the parameter ExtL; LCP and LSP can also be modified via the parameter*  
282 *jvratio as it influences the value of light use efficiency at unsaturated light.*

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

287 ***How does the data driven model in 2.3 differ from LiBry in 2.6 especially given that LiBry***  
288 ***doesn't fit the observations well as described in 3.2? Was there an effort to improve LiBry given***  
289 ***the results of the study?***

290 Thanks for the questions. The data-driven model was used to directly estimate carbon balance of  
291 biocrusts based on measured photosynthesis response curves, while the LiBry model was used to  
292 estimate the carbon balance of a potential biocrust community at each site that is well adapted to  
293 local climate. It was used to identify missing processes and therefore LiBry was not calibrated by  
294 measurements on purpose.

295 More specifically, the data-driven model aims at estimating the carbon balance of biocrusts in the  
296 field based on parameters that determine their response to environmental conditions. These  
297 parameters include hydration and physiological properties that are either measured or obtained by  
298 calibration based on measurements such as net photosynthesis response curves to light, water and  
299 temperature. In contrast, the LiBry model simulates the responses of a large number of  
300 physiologically and morphologically different strategies to environmental conditions. Each strategy  
301 is defined by a unique combination of parameter values and thus represents a group of functionally  
302 identical individuals. At the level of functional properties (traits), several similar strategies together  
303 may represent a species, thereby accounting for intra-specific trait variation. The LiBry model  
304 simulates environmental filtering of strategies for given environmental conditions to mimic natural  
305 selection and to predict trait distributions of lichen and bryophyte communities. A strategy can  
306 survive in the LiBry model if it can maintain a positive carbon balance in the long-term. Therefore,  
307 the mismatch of LiBry model simulations to observations indicates that the observed species with

308 its parameter combination cannot have a positive carbon balance in LiBry, which is consistent with  
309 the carbon loss of parameterized biocrusts estimated by the data-driven model in T1 and T2.

310 Our study can help to improve the LiBry model. We found that the missing seasonal acclimation of  
311 physiological parameters could be a source of bias in estimating the carbon balance. Therefore, in  
312 the future development of the LiBry model, seasonal acclimation of parameters should be  
313 considered to achieve more accurate predictions.

314 We have included these points in the Discussion and Supplement in the revised manuscript (see also  
315 answers to reviewer #2).

316 *Line 362: not the moisture required to give them the ability to be active?*

317 Thank you for the comments. Yes, moisture is crucial for the activity and CO<sub>2</sub> diffusivity of  
318 biocrusts and thus an essential factor for the carbon balance, this is also the reason why rainfall and  
319 relative humidity are environmental factors we chose. As discussed in L464-L466, the rainfall  
320 amounts of most events at temperate and alpine sites are always comparably large, thus the decrease  
321 of rainfall in the sensitivity analysis would not entirely avoid a long activity period for biocrusts.  
322 Therefore, moisture might be less relevant in these regions.

323 *The Fig. 7 legend could use more detail. I had to search what the “fixed” and “dynamic”*  
324 *parameters meant. They were detailed in section 2.5, where these terms could have been more*  
325 *clearly defined.*

326 Thank you for pointing this out. We have defined the term “fixed” and “dynamic” parameters in  
327 section 2.5.3 (see above) as names for two simulations in this sensitivity analysis. Moreover, the  
328 legend has been improved as follows:

329 *“Figure 7: Comparison of accumulated annual C balance between two simulations in the sensitivity*  
330 *analysis of seasonal acclimation of physiological properties. In the simulation “fixed parameters”,*  
331 *all parameters that have been calibrated or measured remained constant throughout the simulation*  
332 *year. For the simulation “dynamic parameters” at site T1, parameter metabolic respiration cost*  
333 *per surface area (Resp\_main) was reduced by half, light absorption fraction in cells (ExtL) was*  
334 *doubled but restricted to one, the ratio of Jmax to Vcmax (jvratio) was increased by two times from*  
335 *September to February to adapt to the winter climates. For the other months, the “fixed” values*  
336 *were used.”*

337 *Line 422 and elsewhere: subscripting (here in CO<sub>2</sub>) is inconsistent, used correctly here but not*  
338 *in other places.*

339 Thanks for pointing this out, the subscription has been checked carefully and corrected accordingly.

340 *For precipitation, how is dewfall and other factors that are important to biocrusts considered? In*  
341 *line 477 and elsewhere, is vapor pressure deficit not a more physiologically consistent approach*  
342 *for estimating stomatal function than relative humidity and/or is relative humidity mostly a*  
343 *surrogate for the surface being sufficiently wet for biocrust function to proceed?*

344 Thank you for the comment. In addition to rainfall, the model considers dew as water input as well  
345 via the energy balance approach (negative energy balance leads to condensation at the surface).  
346 Moreover, rainfall and dew can affect the biocrust annual carbon balance differently. For example,

347 the daily dew amount is usually lower than an individual rainfall event, but it is more likely in the  
348 optimal water range for the photosynthesis of biocrusts. Furthermore, dew is more frequent than  
349 rainfall events. Hence dew is likely relevant for the carbon balance of biocrusts. In addition to liquid  
350 water in the form of rainfall and dew, water vapor uptake is also a water source that can activate  
351 biocrusts (if the primary photoautotroph is not a cyanobacterium). The effects of liquid or vapor  
352 uptake on the photosynthesis of biocrusts are different (Lange, 2001).

353 Vapor pressure deficit is a consistent approach, and we also use vapor pressure deficit as a factor in  
354 the calculations of evaporation and dewfall in the data-driven model. Unlike vascular plants that  
355 have stomata, biocrusts are poikilohydric, and cannot actively control water exchange. Uptake (or  
356 loss) of water from (or to) the air in the model depends on the difference between saturation water  
357 vapor pressure at the surface corrected by water potential inside the biocrust thallus and the  
358 atmospheric water vapor pressure which is related to relative humidity. The relative humidity is  
359 used in the model as climate forcing data also because it is commonly monitored by weather  
360 stations at our study sites. We have clarified this in the Supplement of the revised manuscript in the  
361 “Details about the LiBry model”.

362 *Line 569 and elsewhere: wasn't there just one alpine site such that a more accurate summary*  
363 *would be “at an alpine site”?*

364 Thank you for the suggestion, we have corrected all the phrase “at alpine sites” to “*at an alpine*  
365 *site*” or “*at the alpine site*” thoroughly in the revised version of the manuscript.

366 *Line 570: “obvious” is subjective.*

367 Thanks for pointing this out, this phrase has been deleted.

3

4 Thank you very much for your thoughtful and comprehensive review of our paper. We appreciate  
5 your positive feedback (“I like this study and commend the authors for an ambitious undertaking”).  
6 All comments you raised are very valuable and helpful for improving our research. All authors have  
7 seriously and carefully discussed all these comments. Below we provide the detailed responses that  
8 correspond to each of your comments (highlighted in bold and italics). We hope that our responses  
9 and explanations (directly after the corresponding comment in normal font, blue and italics for new  
10 text in the revised manuscript) can fully address all your concerns.

11

12 **GENERAL COMMENTS**

13 *This is a paper that endeavors to simulate carbon balance in biocrusts. The approach is very nice*  
14 *and has high potential, but the model does fail in some cases and the authors should be more up*  
15 *front about this. Fortunately, in my view, the places where the model fails are interesting and can*  
16 *be discussed. The title and abstract should reflect that a model was constructed and tested and did*  
17 *not work in all cases, and the reasons should be enumerated and explored. This is done for one*  
18 *source of uncertainty, the environmental conditions; however, it is done inadequately for what is*  
19 *likely the larger source of error: the physiological parameters of the biocrusts.*

20 Thank you very much for the detailed review and acknowledgment of our approach. The data-  
21 driven model is used to estimate species-specific responses to environmental conditions that are  
22 governed by physiological parameters. Therefore, we totally agree that not only environmental  
23 conditions, but also physiological parameters may cause biases in estimating the carbon balance.  
24 Consequently, we now also take into account the physiological parameters as a source of error, in  
25 addition to the already previously tested impacts of seasonal change of several physiological  
26 parameters on annual carbon balance.

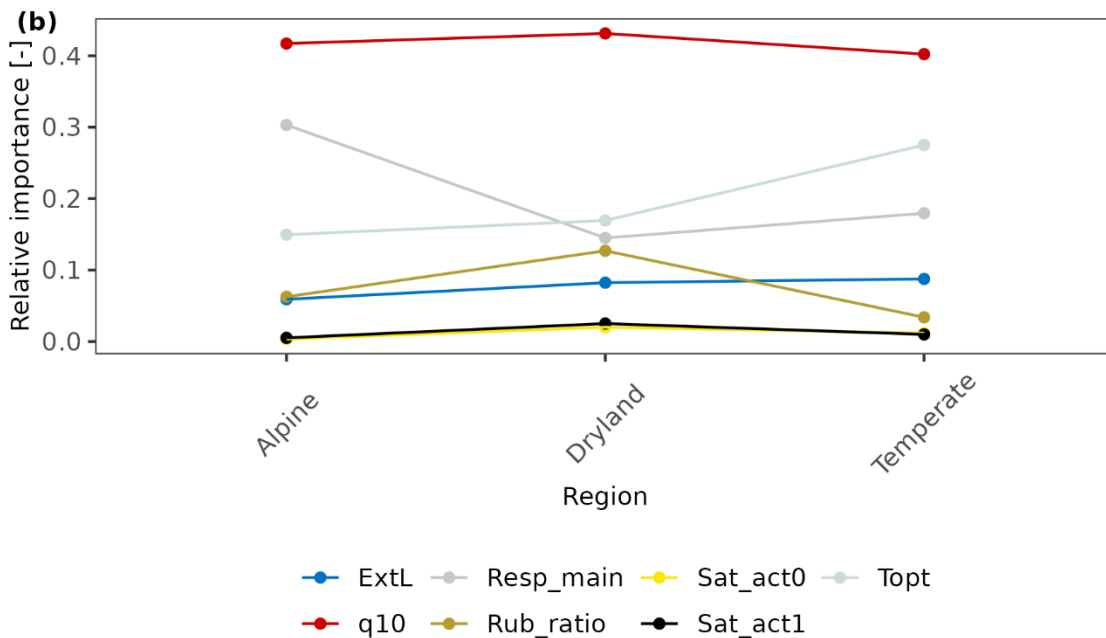
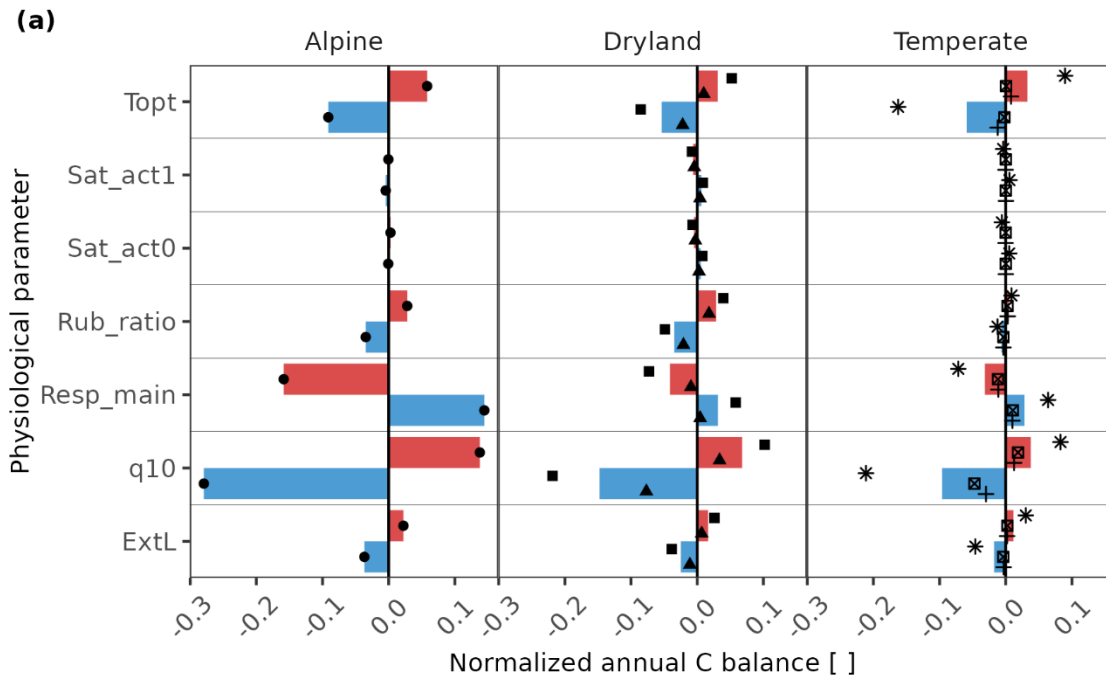
27 In the revised manuscript, we included a new section (see also our answer to reviewer #1):

28 *2.5.2 Effect of physiological parameters*

29 *The sensitivity analysis of physiological parameters was conducted for lichen-dominated biocrust at*  
30 *all study sites. The original parameter values were obtained by calibration to measured net*  
31 *photosynthesis response curves. We then varied the values of the following physiological*  
32 *parameters by a consistent range for all sites: metabolic respiration cost per surface area*  
33 *(Resp\_main), Q10 value of respiration (q10), the optimum temperature for gross photosynthesis*  
34 *(Topt), respiration cost of RuBisCO enzyme (Rub\_ratio), and light absorption fraction in cells*  
35 *(ExtL), minimum saturation for activation (Sat\_act0), and minimum saturation for full activation*  
36 *(Sat\_act1). Specifically, we increased or decreased Resp\_main, ExtL, q10, Sat\_act0 by 30%,*  
37 *Rub\_ratio and Sat\_act1 by 20%, and Topt by 5 K. These parameters are chosen since they are*  
38 *closely related to the response of photosynthesis and respiration to water, light, and temperature.*  
39 *And the ranges of different parameters were determined based on the observed bounds of the*  
40 *photosynthetic response curves of all replicates, which have large deviations between each other at*  
41 *most sites as shown in Fig. 2 and Fig. S2. The effects of the varied physiological parameters on the*

42 carbon balance were then normalized using the same normalization method as for the  
 43 environmental factors (in Sect. 2.5.1) for comparison among parameters and climatic zones.

44 The results are shown in the following figure:



45  
 46 *Figure New1: (a) The effects of physiological parameters – metabolic respiration cost per surface*  
 47 *area (Resp\_main), Q10 value of respiration (q10), the optimum temperature for gross*  
 48 *photosynthesis (Topt), respiration cost of RuBisCO enzyme (Rub\_ratio), light absorption fraction in*  
 49 *cells (ExtL), minimum saturation for activation (Sat\_act0), and minimum saturation for full*



50 *activation (Sat\_act1) – on the annual C balance of lichen-dominated biocrusts in different climate*  
51 *regions. The parameters decreased or increased based on the measured deviation in photosynthesis*  
52 *response curves of replicates. The altered annual C balance resulting from increasing or*  
53 *decreasing parameters is normalized by the original C balance. The colored columns indicate the*  
54 *average value of the normalized C balance at sites with similar climate conditions. Various styles of*  
55 *black points indicate different sites. (b) Relative importance of each physiological parameter*  
56 *compared to other parameters across the climatic regions. Larger relative importance implies a*  
57 *more important effect the parameter has on the C balance compared to other parameters in the*  
58 *given climatic region, and vice versa.*

59 In the Results section of the revised version of the manuscript, we have described the results in the  
60 following way: “*We found that physiology plays an important role in all regions. In particular, the*  
61 *respiration-related parameters such as q10, Resp\_main, and Topt have a notably higher impact on*  
62 *carbon balance estimation (Fig. New1). Furthermore, the relative importance of several*  
63 *physiological parameters showed similar patterns across climatic zones: in all regions, q10 is the*  
64 *most essential parameter, Sat\_act0 and Sat\_act1 play little roles in affecting C balance. Other*  
65 *parameters showed slightly different patterns among regions. Metabolic respiration cost*  
66 *(Resp\_main), for instance, plays a more important role than optimum temperature for gross*  
67 *photosynthesis (Topt) at the alpine site, while the optimum temperature is more essential in*  
68 *drylands and temperate regions (Fig. New1(b)).*”

69 ***Carbon balance numbers should be listed and emphasized in the abstract, both the believable and***  
70 ***unbelievable ones.***

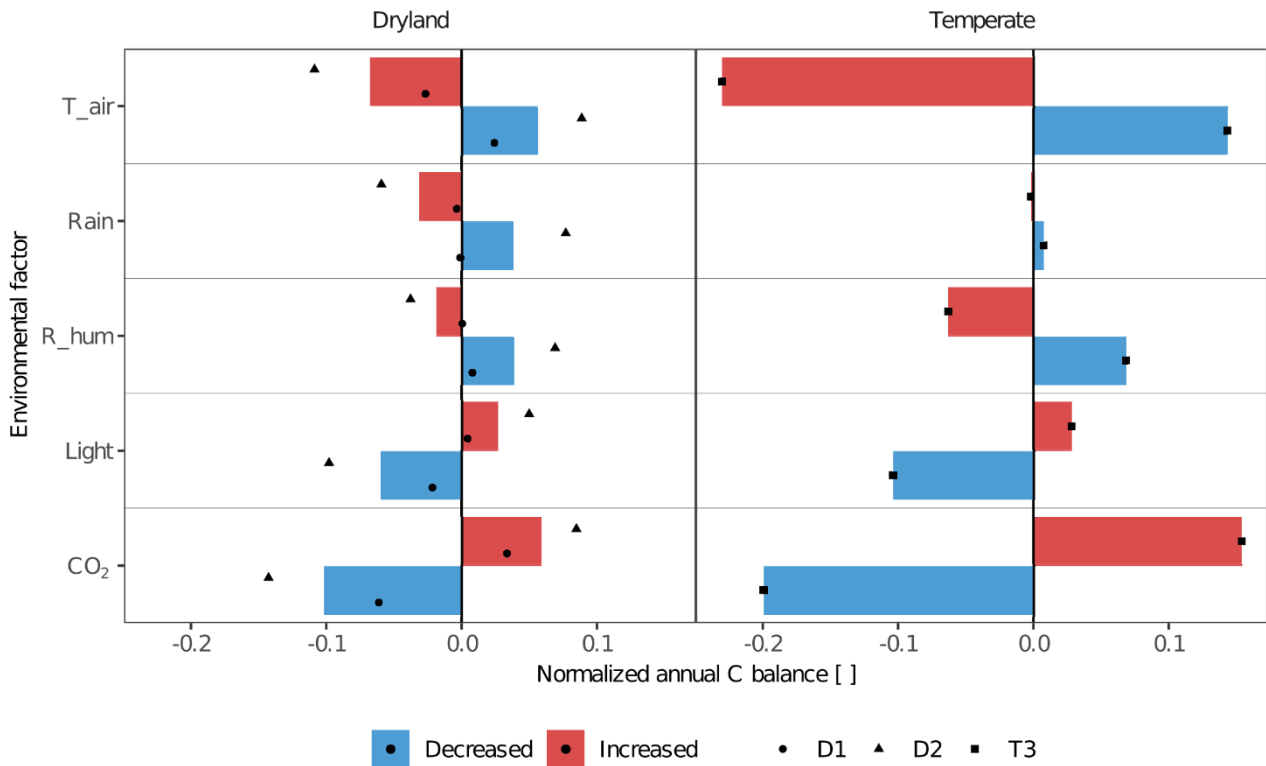
71 Thank you for your suggestion, we have described the carbon balance numbers at D1 and T2 in the  
72 abstract. The rewritten abstract is copied below.

73 ***As the model does not always work, the claims about uncovering drivers and mechanisms should***  
74 ***be substantially reduced to maybe a speculative hint here or there, not proffered as major claims***  
75 ***in the title and abstract.***

76 Thank you for the suggestion. In the revised manuscript, we made it clearer that we aim to explore  
77 the biocrust carbon balance and its drivers across different climatic zones, both environmental and  
78 physiological ones, and that we test potential underlying mechanisms, such as acclimation, rather  
79 than providing precise estimates of carbon fluxes for each climate region.

80 We compared the relative importance of various environmental factors and physiology in the  
81 carbon balance of biocrusts among climatic zones. We think even though the data-driven model  
82 failed to estimate the carbon balance at some sites, the comparison of different sites is valid since  
83 the measurement procedure is consistent. Moreover, the patterns of relative importance remain  
84 similar when excluding the sites with strongly negative carbon balance (T1, T2, and A1). The  
85 effects of environmental factors at remaining sites are shown in the following figure (Fig. New2),  
86 and we added it to Discussion and Supplement in the revised manuscript as well:





87

88 *Figure New2: The effects of environmental factors - CO<sub>2</sub> concentration (CO<sub>2</sub>), relative air humidity*  
 89 *(R\_hum), rainfall amount (Rain), air temperature (T\_air) and light intensity (Light) on the annual*  
 90 *C balance of lichen-dominated biocrusts at different sites with reasonable carbon balance estimates*  
 91 *(excluding site T1, T2 and A1 with strongly negative C balance). The colored columns indicate the*  
 92 *average value of the normalized C balance at sites with similar climate conditions. Various styles of*  
 93 *black points indicate different sites.*

94 Therefore, the conclusions regarding the comparison of the relative importance of the  
 95 environmental factors across climatic conditions may be valid. The title and abstract in the revised  
 96 version of the manuscript can be found below.

97 *A question I am left with is: after seeing the failure at some sites to estimate a positive C balance,*  
 98 *does this mean the dryland ones are also wrong and giving what might be a right number for the*  
 99 *wrong reason, or does the model genuinely work better at those sites and if so why. These things*  
 100 *are touched on but should be the main focus of the discussion.*

101 Thank you for this good question. We elaborated on this point in the subsection “Uncertainties of  
 102 long-term C balance simulated by the data-driven model” of the discussion in the revised  
 103 manuscript (also see below):

104 *In comparison to the unrealistic C balance numbers at T1, T2, and A1, we estimated more*  
 105 *reasonable values in drylands and at T3. However, we do not make a definitive statement about*  
 106 *whether or not the model predicts an accurate carbon balance in drylands, since the measured*  
 107 *climate data and photosynthesis response curves that were used for calibrating land surface*  
 108 *properties and various physiological parameters represent only samples of the large physiological*  
 109 *and climatic variation. A higher accuracy would be more likely to be expected in drylands as these*

110 *regions have a more uniform climate throughout the year regarding temperature and light levels*  
111 *than temperate regions that show substantial seasonality. Additionally, variation in light conditions*  
112 *is slightly more relevant for the simulated carbon balance than variation in moisture (see Fig. 6)*  
113 *because the organisms are able to become inactive, meaning that the dry season in drylands does*  
114 *not have a decisive effect on the carbon balance, while low light in winter in temperate climate does*  
115 *since organisms have to be active then. Furthermore, the longer inactive period in drylands could*  
116 *reduce the error in the magnitude of the simulated carbon balance caused by incorrectly estimated*  
117 *physiological parameter values. We estimated a smaller absolute change in annual carbon balance*  
118 *in drylands with varied physiological parameters in the sensitivity analysis (for instance, the C*  
119 *balance changed by 34.6 g C m<sup>-2</sup> yr<sup>-1</sup> for parameter T<sub>opt</sub> at T1, while it changed only by 1.5 g C m<sup>-2</sup>*  
120 *yr<sup>-1</sup> at D1).*

121 *Generally, I want to emphasize again that physiological parameters being a likely source of*  
122 *uncertainty needs more attention above and beyond the possible effects of seasonal acclimation.*

123 Yes, we totally agree that the physiological parameters are likely a large source of uncertainty. We  
124 have performed sensitivity analyses to explore the role of physiological parameters in the carbon  
125 balance estimation of biocrusts at different sites under contrasting climatic conditions. The results  
126 are shown in the figure above, and we reported this in the revised version of the manuscript.

127

## 128 **SPECIFIC COMMENTS**

129 *Title: going back and re-reading the title, I think it is not accurate to say 'drivers are determined'*  
130 *for sites where the authors later explain that some of the C balance numbers are quite unrealistic*  
131 *(eg -96 g/m2/yr).*

132 Thank you for the suggestion. We have improved the title, accordingly, showing the role of both  
133 environmental factors and physiological uncertainties in estimating the carbon balance of biocrusts  
134 under different climatic conditions. The title in the revised manuscript reads as follows:

135 *Exploring environmental and physiological drivers of the annual carbon budget of biocrusts from*  
136 *various climatic zones with a mechanistic data-driven model*

## 137 **Abstract**

138 *L22. 'along a climatic gradient' is pretty vague at this point in the abstract and I am having*  
139 *trouble following what was done. How big is this gradient?*

140 Thank you for this point. The climate gradient has not been quantified, it is used to demonstrate that  
141 the six study sites are located in different climatic zones with contrasting climatic conditions,  
142 especially in rainfall amounts. The climatic gradient here is mainly a moisture input gradient from  
143 high in the snow-free season of the alpine region and temperate regions to low in arid regions. We  
144 do not use the term “climate gradient” but “different climatic conditions” in the revised manuscript.  
145 The rewritten abstract is below.

146 *L25. effects on what? Looks from context like carbon balance, but I had to go back to previous*  
147 *sentences to figure this out.*

148 Thank you for pointing this out. It is indeed the effect on the annual carbon balance of biocrusts.  
149 We have clarified it in the abstract of the revised manuscript (see below).

150 *The last sentence of the abstract indicates that the key conclusions are methodological while the*  
151 *title and introductory section suggests there will be new mechanistic insights. The previous*  
152 *sentence about climate change came as a surprise since climate change was not mentioned*  
153 *before that and the stated conclusion in this sentence is also vague and unsatisfying. With this*  
154 *mix of basic system function, applied stuff like climate change, and methodological issues, the*  
155 *abstract leaves the impression that the study will be unfocused. [Note: upon reading the whole*  
156 *paper, it is more focused than I thought it would be; thus, I recommend the abstract be rewritten*  
157 *to reflect this.]*

158 Thanks for the suggestions. The conclusions related to climate change and giving methodological  
159 suggestions are based on the results of sensitivity analyses. We agree that these conclusions deviate  
160 from our main topic. Therefore, the conclusions have been revised to be more consistent with the  
161 main topic of the manuscript, which is the use of a modeling approach to estimate the carbon  
162 balance of biocrusts at sites across different climatic conditions, and the sensitivity of the carbon  
163 balance of biocrusts to environmental factors and physiological parameters. The examined  
164 sensitivity can provide insight into the potential reasons why the data-driven model succeeds or fails  
165 to estimate biocrust carbon balance under different climatic conditions. The new conclusions were  
166 rewritten in the new version of the Abstract (see below).

167 *Having read further in the paper, making it clear early in the abstract that this paper is mainly*  
168 *based on a modeling approach is recommended. I recommend to include something like "While*  
169 *there is a lot of empirical field data on biocrusts, rarely have these been assembled into a*  
170 *comprehensive modeling framework. Here we use such a framework to explore factors such as*  
171 *biocrust C balance in contrasting climates" I recommend to say this before talking about the*  
172 *environmental factors and gradients and it will make more sense to readers. Also I would back*  
173 *way off saying the 'key drivers are determined' based on what follows.*

174 Thanks for these very constructive suggestions. In the revised abstract, the data-driven model for  
175 estimating biocrust carbon balance has been highlighted at the beginning of the abstract, and we  
176 then introduced the objective of the study, which is to explore the effects of environmental factors  
177 and physiological parameters on the carbon balance of biocrusts in different climate regions. The  
178 conclusions have been rewritten in the way as stated in the response to the previous comment.

179 The revised Abstract is as follows:

180 *Biocrusts are a worldwide phenomenon, contributing substantially to ecosystem functioning. Their*  
181 *growth and survival depend on multiple environmental factors, including climatic ones, and the*  
182 *relations of these factors to physiological processes. Responses of biocrusts to individual*  
183 *environmental factors have been examined in a large number of field and laboratory experiments.*  
184 *These observational data, however, rarely have been assembled into a comprehensive, consistent*  
185 *framework that allows quantitative exploration of the roles of multiple environmental factors and*  
186 *physiological properties for the performance of biocrusts, in particular across climatic regions.*  
187 *Here we used a data-driven mechanistic modeling framework to simulate the carbon balance of*  
188 *biocrusts, a key measure of their growth and survival. We thereby assessed the relative importance*

189 *of physiological and environmental factors for the carbon balance at six study sites that differ in*  
190 *climatic conditions. Moreover, we examined the role of seasonal acclimation of physiological*  
191 *properties using our framework, since the effects of this process on the carbon balance of biocrusts*  
192 *are poorly constrained so far. We found substantial effects of air temperature, CO<sub>2</sub> concentration,*  
193 *and physiological parameters that are related to respiration on biocrust carbon balance, which*  
194 *differ, however, in their patterns across regions. The ambient CO<sub>2</sub> concentration is the most*  
195 *important factor for biocrusts from drylands while air temperature has the strongest impact at*  
196 *alpine and temperate sites. Metabolic respiration cost plays a more important role than optimum*  
197 *temperature for gross photosynthesis at the alpine site; this is not the case, however, in drylands*  
198 *and temperate regions. Moreover, we estimated a small annual carbon gain of 1.5 g m<sup>-2</sup> yr<sup>-1</sup> by*  
199 *lichen-dominated biocrust and 1.9 g m<sup>-2</sup> yr<sup>-1</sup> by moss-dominated biocrust at a dryland site, while the*  
200 *biocrusts lost a large amount of carbon at some of the temperate sites (e.g., -92.1 for lichen- and -*  
201 *74.7 g m<sup>-2</sup> yr<sup>-1</sup> for moss-dominated biocrust). These strongly negative values contradict the*  
202 *observed survival of the organisms at the sites and may be caused by the uncertainty in*  
203 *environmental conditions and physiological parameters, which we assessed in a sensitivity analysis.*  
204 *Another potential explanation for this result may be the lack of acclimation in the modeling*  
205 *approach since the carbon balance can increase substantially when testing for seasonally varying*  
206 *parameters in the sensitivity analysis. We conclude that the uncertainties in air temperature, CO<sub>2</sub>*  
207 *concentration, respiration-related physiological parameters, and the absence of seasonal*  
208 *acclimation in the model for humid temperate and alpine regions may be a relevant source of error*  
209 *and should be taken into account in future approaches that aim at estimating the long-term biocrust*  
210 *carbon balance based on ecophysiological data.*

## 211 **Introduction**

212 *The first paragraph is an overgeneralized description of biocrusts and their function leaving me*  
213 *not sure where the paper is going. I recommend to hone in more clearly on setting up the*  
214 *modeling approach and discussion of the biocrust role in ecosystem C balance to set up the later*  
215 *material. The second paragraph is much better, setting up the importance of long-term C balance*  
216 *in biocrusts.*

217 Thank you for the suggestion. We designed the first paragraph to serve for setting up the  
218 importance of exploring the survival and long-term carbon balance of biocrusts in the second  
219 paragraph by describing the wide distribution of biocrusts and their important ecosystem  
220 functioning. However, we have revised the first paragraph as you recommended to more clearly  
221 show readers what our manuscript is about. We highlighted biocrusts, their importance, and  
222 different methodologies to explore them, including the cited empirical and modeling work, which is  
223 well connected to the further description of the different methodologies in the subsequent  
224 paragraph. Furthermore, we deleted the first two sentences of the second paragraph (L44 - L46) to  
225 adapt to the revised first paragraph, and the first paragraph now reads as follows:

226 *Non-vascular photoautotrophs, such as lichens, mosses, eukaryotic algae, and cyanobacteria,*  
227 *together with heterotrophic microorganisms, form biological soil crusts (biocrusts) which occur in*  
228 *various environments across the globe and provide a wide range of important ecosystem functions,*  
229 *such as build-up of soil organic carbon and nutrients (Chamizo et al., 2012; Dümig et al., 2014;*  
230 *Belnap et al., 2016; Ferrenberg et al., 2018). Due to the importance of biocrusts in ecosystem*

231 *functioning, their growth and survival have been extensively studied, through different*  
232 *methodological approaches (e.g., Ladrón de Guevara et al., 2018; Lange et al., 2006; Porada et*  
233 *al., 2019). An established measure to quantify the growth of biocrusts is their long-term carbon*  
234 *balance (hereafter, C balance), which corresponds to the (accumulated) net carbon flux across the*  
235 *system boundaries including all relevant carbon gains and losses.*

236 ***Finally by the end of the introduction I understand what the paper is about. It is a modeling***  
237 ***study exploring C balance in biocrusts over a range of conditions. This needs to be MUCH more***  
238 ***clear in the title and abstract.***

239 Thank you for the suggestion. We have highlighted this topic in the title and abstract as stated  
240 above.

241 Moreover, the last two paragraphs of Introduction have been modified in the revised manuscript to  
242 adapt to the main focus that the effects of environmental factors and physiological parameters on  
243 the carbon balance of biocrusts in different climate regions, as follows:

244 *Most studies on the relationships between C balance and environmental factors for biocrusts are*  
245 *based on laboratory experiments (e.g., Coe et al., 2012; Cowan et al., 1992; Lange et al., 1998a) or*  
246 *direct field measurements in situ over short periods of time (e.g., Brostoff et al., 2005; Lange et al.,*  
247 *1994). From this work cited above, it has been recognized that the C balance of biocrusts is*  
248 *strongly influenced by factors such as water supply, temperature, radiation, and CO<sub>2</sub> concentration*  
249 *and the complex relations of these factors to physiological processes such as photosynthesis and*  
250 *respiration. While the highest values of productivity under field conditions are achieved when the*  
251 *environmental factors are in the range that is optimal for the specific biocrust, it has been found*  
252 *that biocrusts are also able to achieve activity and thus, potential productivity, under sub-optimal*  
253 *conditions of temperature and light (Colesie et al., 2016; Raggio et al., 2017, 2014). It is largely*  
254 *unknown, however, which relative importance each of these environmental factors and*  
255 *physiological parameters has for the long-term C balance of biocrusts under natural field*  
256 *conditions, and if the importance of factors/parameters shows a spatial and temporal pattern. In*  
257 *addition, seasonal acclimation of photosynthetic and respiratory properties of species to intra-*  
258 *annually varying climate factors found by several studies ...*

259 *Here, we applied a mechanistic data-driven model to (a) complement empirical estimates of the*  
260 *annual C balance of biocrusts and (b) to address the knowledge gaps concerning the relative*  
261 *importance of different environmental factors and physiological parameters for the C balance*  
262 *along climatic gradients, thereby accounting for the role of seasonal acclimation. The advantage of*  
263 *this modeling approach is that it can predict at high temporal resolution the dynamic C balance of*  
264 *biocrust organisms for given locations by simulating the physiological processes driven by*  
265 *environmental factors. The model allows for a deeper mechanistic understanding of the C balance*  
266 *of biocrusts through factorial experiments and sensitivity analyses regarding physiological*  
267 *parameters and individual environmental factors ...*

268 ***2.1. I recommend that instead of making the case that the sites were chosen because they are the***  
269 ***only sites with these data in the world (a dubious claim in my opinion - I can think of several***  
270 ***other well-studied biocrust-focused sites that probably have enough data to take a similar***  
271 ***approach), the authors should make the case that the sites were chosen to enhance the work done***



272 *by the authors at these sites, which would be an adequate justification. The one exception to this*  
273 *might be the innovative 'activity measurements' the authors mention. If this is the case, I*  
274 *recommend to be more clear about this and explain why other proxies of activity (soil moisture*  
275 *perhaps) could not work at other sites.*

276 Thank you for the suggestions. We elaborated on this point in the following way:

277 *... These sites were chosen based on data availability for carbon balance estimation, and because*  
278 *they cover a broad range of climatic conditions. The field and laboratory measurements conducted*  
279 *at all sites were following a similar protocol, which allows comparing the simulation results among*  
280 *sites. The necessary empirical data for C balance estimation regarding climatic conditions, species*  
281 *physiological characteristics, and status especially in terms of moisture such as water content or*  
282 *activity, have been monitored in a relatively small number of experiments, so far, and the six study*  
283 *sites chosen here to provide a good opportunity to utilize these data for an extended modeling*  
284 *approach. In this context, activity measurements are more suitable than soil moisture records since*  
285 *they are direct, non-invasive and they do not show deviations in the temporal patterns at high*  
286 *resolution, which may occur with soil moisture time series.*

287 ***L143. Soil-surface boundary layer CO<sub>2</sub> is often higher than this due to diffusion from soil. This***  
288 ***should be mentioned and the ramifications considered.***

289 Thank you for the comment. We agree that the release of CO<sub>2</sub> from soil may increase the soil-  
290 surface CO<sub>2</sub> concentration, and thus influence the C balance estimation. However, all our study  
291 sites are open sites, meaning that the CO<sub>2</sub> diffused from the soil may spread quickly. Hence, we are  
292 not sure how large the increase in surface CO<sub>2</sub> concentration is, as we did not monitor the surface  
293 CO<sub>2</sub> concentration.

294 We will add a sentence to mention this point in L143: *“The CO<sub>2</sub> concentration at the soil surface*  
295 *may be higher than 400 ppm due to the flux of respired CO<sub>2</sub> from the soil. Since our study sites are*  
296 *on open ground, we do not assume substantial accumulation of CO<sub>2</sub> in the near-surface boundary*  
297 *layer. We discuss the effect of uncertainties in CO<sub>2</sub> concentration below in Sect. 4.2”.*

298 Moreover, we discussed this point in the subsection “Uncertainties of long-term C balance  
299 simulated by the data-driven model” of the discussion in the revised manuscript as follows:

300 *As the results (Fig. 6) show, CO<sub>2</sub> concentration is an essential factor for the annual C balance of*  
301 *biocrusts, especially at dryland and some temperate sites. Therefore, uncertainty in the CO<sub>2</sub>-value*  
302 *prescribed in the model may be a source of error. The CO<sub>2</sub> concentration at the surface boundary*  
303 *might exceed the value of 400 ppm that was prescribed in the model because of CO<sub>2</sub> diffusion from*  
304 *soil, which may lead to an underestimated C balance (Fig. 6a). However, with enhanced CO<sub>2</sub>*  
305 *concentration in the sensitivity analysis (600 ppm) at site T1, for instance, the estimated carbon*  
306 *balance increased only slightly, and is still strongly negative (-37.0 g C m<sup>-2</sup> yr<sup>-1</sup> for lichen and -30.2*  
307 *g C m<sup>-2</sup> yr<sup>-1</sup> for moss). Hence, the lower CO<sub>2</sub> concentration can partially contribute to the strongly*  
308 *negative C balance at T1 and T2, but is not a major factor.*

309 ***L144. Were these intact biocrusted soils or were the biocrusts removed from the soil and***  
310 ***measured in an enclosed chamber separate from the soil column? Same question for L149-160.***

311 The CO<sub>2</sub> exchange measurements at L144 as well as L149-160 were for biocrust samples where the  
312 soil underneath the sample was removed up to the amount necessary to preserve the physical  
313 structure of the biocrusts. There may be small amounts of soil still attached to the samples at some  
314 sites, but no significant differences were found between dark respiration rates (Raggio et al, 2018),  
315 which indicates little influence of the remaining soil on gas exchange rates of biocrusts. The CO<sub>2</sub>  
316 exchange rates of clean biocrusts samples were then measured using the GFS 3000 Photosynthesis  
317 System. We have included this information in L145 in the revised version of our manuscript:  
318 “(lichen- and moss- and also cyano-dominated biocrusts removed from surplus soil ...”; and in  
319 L152: “*Before measurements, the soil underneath these biocrust samples was removed up to the*  
320 *amount necessary to preserve the physical structure of the biocrusts*”.

321 *L153. For poikilohydric biocrust organisms, time since hydration is a big factor in how these C*  
322 *balance values will look. It may be in the cited papers, but it should be discussed here too. The*  
323 *whole conclusions of the study could hinge on differences between, say, 1 hour vs. 4 hr vs. 24*  
324 *hour wet-up periods for the biocrusts examined. Whether this has been adequately taken into*  
325 *account or not, it should be described how this issue was handled.*

326 Thank you for this important comment. Before CO<sub>2</sub>-exchange measurements for biocrusts from  
327 sites were carried out, the samples were rehydrated in a climate chamber. At site T1, T2, A1 and  
328 D1, for instance, dry biocrust samples were wetted once daily for three days (Raggio et al., 2018).  
329 This is an accepted working protocol for reactivating lichens and mosses. We have added this point  
330 to L152: “... *The samples were subjected to reactivation for at least two days (D2) or three days*  
331 *(T1, T2, D1, A1). At T1, T2, A1 and D1, for instance, samples were kept at 12°C under 12 h dark*  
332 *and 12 h light (100 μmol m<sup>-2</sup> s<sup>-1</sup>) conditions for three days and wetted once a day.*”

333 In water content response curve measurements, samples were hydrated to the maximum water  
334 content, and then measured while drying down. The length of the activity period since hydration  
335 allowing net photosynthesis is determined in the model by the simulated water saturation that  
336 depends on the climatic forcing as well as two calibrated parameters (Sat\_act0 and Sat\_act1) that  
337 determine the minimum water saturation for activation and full activation, respectively.

338 Furthermore, regarding the potential impacts of the revitalization period or the range of water  
339 saturation that allows activity in the model on the respiration and carbon balance estimation, we  
340 included respiration-related parameters and parameters on activity estimation (Sat\_act0 and  
341 Sat\_act1) in the sensitivity analysis of physiological parameters. We have added this point in the  
342 revised manuscript.

343 *Table 1. 110 mm is pretty low. I'd probably call that arid rather than semiarid. If the*  
344 *determination is based on something else like aridity index, that should be reported.*

345 Thanks for the suggestion, we defined the climate type based solely on the annual rainfall, not the  
346 aridity index. And we have modified the type from ‘semi-arid’ to ‘arid’.

347 *Table 2. 96 is a big loss of C. The dryland values are in line with what I would expect--small*  
348 *positive fluxes. These data are really valuable and this is a nice contribution of this study. Not a*  
349 *lot of people try to calculate these as carefully as done here. A selection of these numbers should*  
350 *be in the abstract to make the goals and findings of the study more concrete up front.*



351 Thank you for your support on the methodology and the suggestion. The specific carbon balance  
352 number at sites D1 and T2 have been demonstrated in the abstract to present examples for  
353 reasonable and unrealistic estimates. The abstract in the revised manuscript is copied above.

354 However, due to the comments from reviewer #1, we have reduced the parameter minimum CO<sub>2</sub>  
355 diffusivity to improve the fitting of the water-response curves at all sites and re-calibrated some  
356 physiological parameters. The estimated C balance values decreased a bit at some sites, but there  
357 are still some reasonable values in drylands and T3, and strongly negative values at T1, T2. The  
358 new results are shown in the following table (Table 2):

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

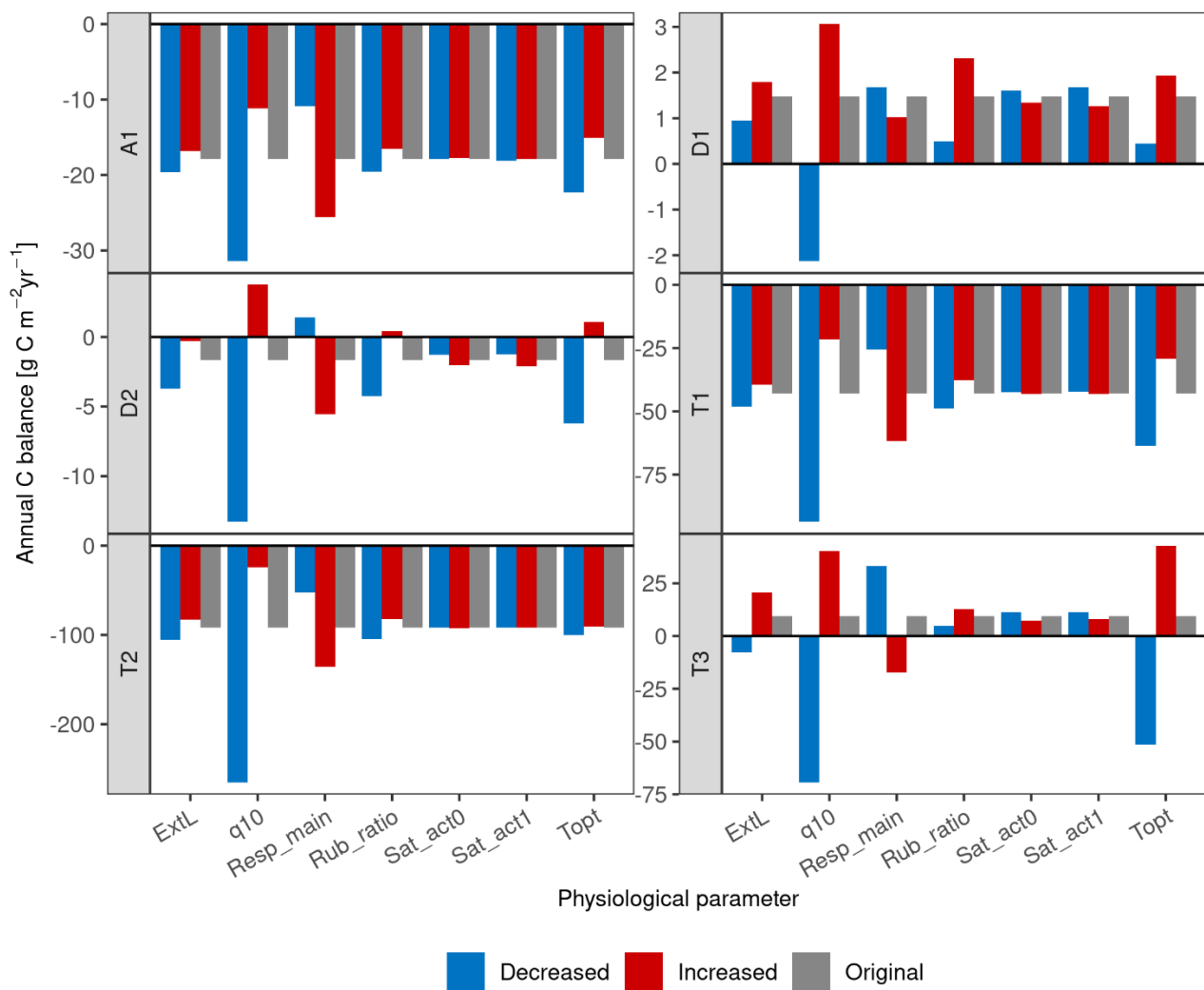
|                     | Lichen                               | Moss                                 | Cyanocrust                           |
|---------------------|--------------------------------------|--------------------------------------|--------------------------------------|
|                     | g C m <sup>-2</sup> yr <sup>-1</sup> | g C m <sup>-2</sup> yr <sup>-1</sup> | g C m <sup>-2</sup> yr <sup>-1</sup> |
| D1 (Almeria)        | 1.5                                  | 1.9                                  |                                      |
| D2 (Soebatsfontein) | -1.7                                 | 3.1                                  | -8.3                                 |
| T1 (Gössenheim)     | -42.8                                | -39.4                                |                                      |
| T2 (Öland)          | -92.1                                | -74.7                                |                                      |
| T3 (Linde)          | 9.4                                  | 18.7                                 |                                      |
| A1 (Hochtor)        | -17.9                                | -6.8                                 |                                      |

360 We also revised the corresponding descriptions in the Results and Discussion sections of the revised  
361 version of manuscript.

362 *Sensitivity of the environmental factors is fine and appears to be well done, but what about*  
363 *sensitivity to the estimates of the biocrust physiological parameters? Those are the ones that*  
364 *likely have much more substantial errors in my view. The high variability in these parameters*  
365 *among individually measured biocrusts is even noted by the authors. What if the light response*  
366 *or moisture curve or temp response is misshapen, have intercepts at 0 that are slightly off, etc?*

367 This is a crucial point, thanks for the suggestion. We performed sensitivity analyses of  
368 physiological parameters as described in the responses above. The results of the relative importance  
369 of physiology are also interpreted in the figure above (Fig. New1). Since the same gas exchange  
370 methodology has been used for sites T1, T2, A1, and D1, differences in the simulated C balance  
371 among these regions likely result from variation in the species-specific interactions between climate  
372 and physiological processes. This point is also included in the discussion section of the revised  
373 version of manuscript.

374 Moreover, we added a figure (Fig. New3) in the Supplement to support the results (in the Results  
375 section) that *“even though physiology plays an important role in all regions, the C balance did not*  
376 *become positive when the physiological parameters were varied reasonably, that is the parameters*  
377 *were varied to relatively cover the deviation of response curves of replicates. Furthermore, the*  
378 *change in C balance value is much smaller in drylands compared to other regions.”*



379

380 *Figure New3: the C balance number estimated by the data-driven model without changing the*  
 381 *parameters (Original), and with increasing and decreasing physiological parameters (Increased*  
 382 *and Decreased, respectively). The changed parameters are respiration cost of RuBisCO enzyme*  
 383 *(Rub\_ratio), light absorption fraction in cells (ExtL), metabolic respiration cost per surface area*  
 384 *(Resp\_main), the optimum temperature for gross photosynthesis (Topt), Q10 value of respiration*  
 385 *(q10), minimum saturation for activation (Sat\_act0) and minimum saturation for full activation*  
 386 *(Sat\_act1). Resp\_main, ExtL, q10, Sat\_act0 increased or decreased by 30%, Rub\_ratio and*  
 387 *Sat\_act1 by 20%, and Topt by 5 K.*

388 *L398-407. Good discussion and I agree this aspect of the model throws really reasonable values,*  
 389 *just from first principles. A shrubland that might be found in a 100-300 mm MAP ecosystem*  
 390 *typically has an NPP on the order of 100 g/m2/yr and I would expect biocrusts to be an order of*  
 391 *magnitude or two below that given their size, amount of chlorophyll, etc.*

392 Thank you, we do appreciate this acknowledgment.

393 *L410-413. This needs to be further unpacked. It of course makes no sense for them to lose as*  
 394 *much carbon per year as a shrubland grows. Which part of the model is responsible for this*  
 395 *nonsensical result?*

396 Thank you for pointing this out. We have explained the potential reasons for the unrealistic carbon  
397 balance numbers at these two temperate sites in section 4.3, but in the revised manuscript, we  
398 switched the order of subsection 4.2 (The effects of environmental and physiological parameters on  
399 carbon balance; see below for the revised version) and the subsection “Uncertainties of long-term C  
400 balance simulated by the data-driven model”, in which we combined the subsection 4.3 and 4.5 and  
401 expanded the explanations for the unrealistic numbers based on the uncertainties in environmental  
402 factors and physiology including our answer to other points, as follows:

#### 403 *4.2 Uncertainties of long-term C balance simulated by the data-driven model.*

404 *The data-driven model simulated relatively reasonable C balance values in drylands but*  
405 *unrealistic, negative values at temperate sites T1 and T2. Since the same or similar gas exchange*  
406 *methodology has been used for all sites, differences in the simulated C balance among these*  
407 *regions likely result from variation in the species-specific interactions between climate and*  
408 *physiological processes, including seasonal variation in physiological properties due to*  
409 *acclimation.*

410 *As the results (Fig. 6) show, CO<sub>2</sub> concentration is an essential factor for the annual C balance of*  
411 *biocrusts, especially at dryland and some temperate sites. Therefore, uncertainty in the CO<sub>2</sub>-value*  
412 *prescribed in the model may be a source of error. The CO<sub>2</sub> concentration at the surface boundary*  
413 *might exceed the value of 400 ppm that was prescribed in the model because of CO<sub>2</sub> diffusion from*  
414 *the soil, which may lead to an underestimated C balance (Fig. 6a). However, with enhanced CO<sub>2</sub>*  
415 *concentration in the sensitivity analysis (600 ppm) at site T1, for instance, the estimated carbon*  
416 *balance increased only slightly, and is still strongly negative (-37.0 g C m<sup>-2</sup> yr<sup>-1</sup> for lichen and -30.2*  
417 *g C m<sup>-2</sup> yr<sup>-1</sup> for moss). Hence, the lower CO<sub>2</sub> concentration can partially contribute to the strongly*  
418 *negative C balance at T1 and T2, but is not a major factor.*

419 *Furthermore, the negative C balance at temperate and alpine sites may result from the*  
420 *uncertainties in physiology, which were also observed between replicates (see Fig. 2 and Fig. S2).*  
421 *An overestimation of dark respiration rates of the photoautotrophs in the biocrust may result from*  
422 *including a small amount of heterotrophic respiration. The overestimated respiration rate then*  
423 *leads to an overestimation of the parameter metabolic respiration cost per surface area*  
424 *(Resp\_main) and might also cause an underestimated Q<sub>10</sub> value calculated from the respiration*  
425 *rates. The uncertainties of these two parameters reduce the estimated C balance largely (Fig.*  
426 *New1). Additionally, the optimum temperature (T<sub>opt</sub>), which is also the reference temperature for*  
427 *calculating the respiration rate, cannot be well constrained by the limited measured temperature*  
428 *response data set. Thus, T<sub>opt</sub> may be underestimated. The larger difference in surface temperature*  
429 *to T<sub>opt</sub> results in a larger respiration rate, and lower gross photosynthesis, which leads to a lower*  
430 *C balance.*

431 *Although the uncertainty in individual physiological parameters may not lead to the markedly*  
432 *negative C balance estimates, as indicated by still negative values upon variation of these*  
433 *parameters, additive effects of all parameters combined with long-term unfavorable environmental*  
434 *conditions may cause a large amount of carbon lost over a year. The optimal conditions are rare*  
435 *within a year, which was also described by Lange (2003b). Thus, the overestimated respiration rate*  
436 *leads to a lower carbon gain during the relatively optimal conditions, which may not be sufficient to*  
437 *compensate for exaggerated C losses under long-term harsh conditions, such as autumn and winter*

438 *at site T1, for instance. For this reason, the simulated C balance of mosses and lichens in temperate*  
439 *humid regions was mostly negative.*

440 *In addition to the uncertainty in the values of physiological parameters, seasonal acclimation of*  
441 *these physiological traits to the current climatic conditions may play an important role in*  
442 *regulating the C balance at humid sites where the organisms are active throughout the year, such*  
443 *as site T1 (Fig. 7). It was observed, for instance, that the respiration of lichens shows acclimation*  
444 *to seasonal changes in temperature, and the maximum CO<sub>2</sub> exchange rate of the organisms remains*  
445 *steady throughout the year (Lange and Green, 2005). Gauslaa (2006) found a higher chlorophyll*  
446 *a/b ratio in forest lichens with increasing light. Moreover, depression in quantum efficiency in*  
447 *summer under extremely dry conditions has been observed (Vivas et al., 2017). These varied*  
448 *physiological properties of organisms within a year may result in different photosynthesis and*  
449 *respiration rates, and thus different C balances in comparison to the ones that cannot acclimate to*  
450 *the seasonal climate. The missing seasonal acclimation of physiological traits may explain why the*  
451 *data-driven model estimated a negative C balance for biocrusts in humid regions.*

452 *Another limitation of the modeling approach may be the lack of separate responses of respiration*  
453 *and photosynthesis to metabolic activity. Both photosynthetic activity and respiration reach their*  
454 *maximum in the model once the water saturation reaches the optimum value for net photosynthesis*  
455 *(Wopt<sub>np</sub>). In some cases, however, respiration rate may reach the maximum value only at a higher*  
456 *saturation than Wopt<sub>np</sub> (Lange, 1980), indicating that the model may overestimate respiration in*  
457 *the long-term.*

458 *In comparison to the unrealistic C balance numbers at T1 and T2, we estimated more reasonable*  
459 *values in drylands and at T3. However, we do not make a definitive statement about whether or not*  
460 *the model predicts an accurate carbon balance in drylands. since the measured climate data and*  
461 *photosynthesis response curves that were used for calibrating land surface properties and various*  
462 *physiological parameters represent only samples of the large physiological and climatic variation.*  
463 *A higher accuracy would be more likely to be expected in drylands as these regions have a more*  
464 *uniform climate throughout the year than temperate regions that show substantial seasonality.*  
465 *Additionally, variation in light conditions is slightly more relevant for the simulated carbon balance*  
466 *than variation in moisture (see Fig. 6) because the organisms are able to become inactive, meaning*  
467 *that the dry season in drylands does not have a decisive effect on the carbon balance, while low*  
468 *light in winter in temperate climate does since organisms have to be active then. Furthermore, the*  
469 *longer total inactive period in drylands could reduce the bias in the magnitude of the simulated*  
470 *carbon balance caused by incorrectly estimated physiological parameter values. We estimated a*  
471 *smaller absolute change in annual carbon balance in drylands with varied physiological*  
472 *parameters in the sensitivity analysis (for instance, the C balance changed by 34.6 g C m<sup>-2</sup> yr<sup>-1</sup> for*  
473 *parameter T<sub>opt</sub> at T1, while it changed only by 1.5 g C m<sup>-2</sup> yr<sup>-1</sup> at D1).*

474 *Furthermore, the estimated C balance may be inaccurate due to the potential bias in estimated*  
475 *relative water saturation, which partly depends on prescribed MWC obtained by measurements.*  
476 *However, the outcome of the sensitivity analysis of MWC at T1 revealed that the annual carbon*  
477 *estimation is robust to the uncertainties with regard to the prescribed MWC (details in the*  
478 *Supplement). Another factor that potentially affects the accuracy of C balance estimates is*  
479 *interannual climatic variability. While the model estimated unrealistic C balance values of lichen-*

480 *dominated biocrusts at T1 and T2 for current conditions, the C balance may have been different in*  
481 *other years. Therefore, the simulation of annual C balance based on multi-year climate data is*  
482 *worthy of future study to understand the long-term C balance better. Moreover, the estimated*  
483 *negative C balance of certain lichen and moss species may not be generalizable and representative*  
484 *for the overall situation in the field due to the large variation in physiological adaptation strategies*  
485 *to climate. There could be other organisms that form cryptogamic covers, for instance, that show a*  
486 *different degree of depression in net photosynthesis at high water content (Lange et al., 1995), and*  
487 *thus have more reasonable C balance values.*

488 ***L419. This is a key point of the paper. I recommend the authors discuss it here, not below.***

489 Thank you for the suggestion. In this part of the discussion, we only wanted to address the  
490 limitations and uncertainties of the LiBry model. The objective of LiBry is to evaluate the negative  
491 carbon balance estimated by the data-driven model that we constructed for the study. The  
492 inconsistency of the response curves between the functional types predicted by the LiBry model for  
493 the sites and the observed species indicates that the physiological parameters that are necessary to  
494 maintain a positive carbon balance are not compatible with those of the sampled biocrusts. In other  
495 words, our measured biocrusts cannot obtain a positive carbon balance when they are represented in  
496 the LiBry model. Since LiBry is based on the same processes as the data-driven model, this is in  
497 line with the negative values of our data-driven model simulations.

498 We have modified the paragraph on LiBry in the revised manuscript, while the main discussion on  
499 uncertainties of physiological parameters was located in the new section 4.2 (see above).

500 *“The mismatches between strategies predicted via selection by the LiBry model for the sites and the*  
501 *collected species with regard to their net photosynthesis response curves indicate that the*  
502 *physiological parameter values that would be necessary to maintain a positive carbon balance in*  
503 *LiBry are not compatible with those of the sampled biocrusts. This is in line with the results of the*  
504 *data-driven model, which also simulates a negative C balance and is based on the same*  
505 *physiological processes as LiBry. This also applies to the lack of seasonal acclimation in both*  
506 *modeling approaches, since the strategies in LiBry are assumed to have constant functional*  
507 *properties throughout the simulation.”*

508 ***L436. There are a number of field manipulations showing exactly this in Spain and USA. Could***  
509 ***be worthwhile to cite here.***

510 Thank you for the suggestion, we cited the related empirical papers in the revised manuscript  
511 (L437):

512 *The consistent effects of warming on C balance of biocrusts are found in various field studies (e.g.,*  
513 *Darrouzet-Nardi et al., 2015; Ladrón de Guevara et al., 2014; Li et al., 2021; Maestre et al., 2013).*

514 ***L436-504. This section on abiotic factors is long and includes a lot of speculation. For example,***  
515 ***the paragraph on humidity goes through a lot of hypotheticals and discussion when to me the***  
516 ***humidity didn't stick out as a huge factor in the earlier parts of the paper, with the authors saying***  
517 ***that co2 and air temperature were more relevant.***

518 Thank you for the suggestions. In fact, we found that all examined environmental factors were  
519 relevant, but CO<sub>2</sub> and air temperature were relatively more important. We discussed humidity and



520 rainfall in such depth because we found it interesting that they have differing effects on the carbon  
521 balance, although being both related to water input, and even the same factor may have different  
522 effects on carbon balance in different climate zones. Furthermore, moisture-related factors are  
523 usually assumed to be crucial for biocrust ecophysiology, which is why we explain our findings in  
524 detail here to avoid misunderstandings. However, we have focused the discussion on the more  
525 relevant factors and findings to shorten and simplify this subsection.

526 Moreover, we also added the discussion on the importance of physiological parameters to this  
527 subsection following the environmental factors. The subsection will read as follows in the revised  
528 manuscript:

#### 529 *4.3 Potential factors influencing the C balance.*

530 *Despite diverse climatic conditions, we found similarities regarding the dominant environmental*  
531 *factors and physiological parameters controlling the C balance. Thereby, CO<sub>2</sub> and air temperature*  
532 *were the two most important environmental factors at all sites. Relative air humidity, partly*  
533 *rainfall, and light intensity were also relevant for the estimation of the C balance. In terms of*  
534 *physiological parameters, the respiration-related parameters were the most important drivers,*  
535 *while parameters that affect V<sub>cmax</sub> and thus the light-independent CO<sub>2</sub> assimilation rate were*  
536 *relevant, too.*

537 *The relative importance of these factors/parameters varied slightly among climatic regions.*  
538 *Regarding the comparison between environmental factors, we cannot rule out that the magnitudes*  
539 *of changes in environmental factors that we applied in the sensitivity analysis were not balanced,*  
540 *which may have led to an overestimation of the relative importance of certain factors, such as air*  
541 *temperature, for instance, compared to the others. The spatial patterns across climate regions of a*  
542 *given environmental factor, however, are not affected by this, which means that differences between*  
543 *climatic regions for a given factor are most likely robust. Hence, air temperature is more relevant*  
544 *at the alpine site and relative air humidity has a higher impact in temperate than in other regions,*  
545 *CO<sub>2</sub> and rainfall are likely to have the largest effect on C balance in drylands. Even though the*  
546 *data-driven model failed to estimate reasonable C balance at some sites, the comparison of the*  
547 *relative importance of the environmental factors across climatic regions may be valid since the*  
548 *measurement procedure is consistent. Moreover, the patterns of relative importance remain similar*  
549 *when excluding the sites with strongly negative carbon balance (T1, T2, and A1; as shown in the*  
550 *Fig. New2 in the Supplement). Nevertheless, we only studied the sensitivity of the C balance of*  
551 *biocrusts dominated by the lichen *Psora decipiens* and *Cladonia furcata* (at T3), and there are*  
552 *variations between lichens of different growth forms and between biocrust types. For example,*  
553 *cyanolichens increase in abundance with increasing rainfall, but trebouxoid lichens have their*  
554 *physiological optimum in drier conditions (Phinney et al., 2021). Moreover, the impact of*  
555 *precipitation on isidiate lichens is weaker than that of temperature (Phinney et al., 2021).*

#### 556 *4.3.1 Environmental factors*

557 *Our results suggest that warming can result in a large amount of carbon loss at all sites, with a*  
558 *particularly large effect in the alpine region. The consistent effects of warming on C balance of*  
559 *biocrusts are found in various field studies (e.g., Darrouzet-Nardi et al., 2015; Ladrón de Guevara*  
560 *et al., 2014; Li et al., 2021; Maestre et al., 2013). This can be explained by the overall less optimal*

561 *water and temperature conditions associated with warming. The simulated increasing respiratory*  
562 *costs with warming overcompensate gains in gross photosynthesis.*

563 *Ambient CO<sub>2</sub> concentration affects the gross photosynthesis rate to a large extent in the model.*  
564 *Although the intra-annual change in air CO<sub>2</sub> concentration may be small in the field compared to*  
565 *other environmental factors, the increase of CO<sub>2</sub> in the atmosphere in recent decades (IPCC 2021)*  
566 *may alter the long-term C balance substantially. However, this beneficial effect of elevated CO<sub>2</sub> on*  
567 *photosynthesis and C balance may be reduced in reality due to future limitation of growth by*  
568 *nitrogen (Coe et al., 2012), which is not considered in the model, or also due to shortened activity*  
569 *periods resulting from warmer and drier future climatic conditions.*

570 *Light intensity has the third largest effect on C balance, slightly larger than moisture. Light is one*  
571 *of the essential factors for photosynthesis as simulated by our model, and it is a limiting factor of*  
572 *photosynthetic carbon assimilation, in particular in winter at temperate and alpine sites (the mean*  
573 *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*  
574 *site). Hence, increasing light intensity can promote carbon accumulation.*

575 *Factors that determine water supply are rainfall and non-rainfall inputs such as dew and water*  
576 *vapor that are related to relative humidity. The relative importance of different moisture factors in*  
577 *mediating C balance varies in the model. Relative humidity plays a more important role in*  
578 *mediating the C balance than rainfall amount. This may be due to the timing of dew or water vapor*  
579 *uptake, which is greatest before sunrise (Chamizo et al., 2021; Ouyang et al., 2017) and prolongs*  
580 *the activated periods in the early morning when the organisms start assimilating carbon (Veste and*  
581 *Littmann, 2006). This may result in a markedly increased annual C balance in the model. Rainfall*  
582 *amount was not a key factor affecting the simulated biocrust performance at one of the arid sites,*  
583 *which is consistent with another study (Baldauf et al., 2020). At the other dryland site (D2),*  
584 *however, this was not the case. Moreover, we found that the effect of the amount of rainfall is small*  
585 *in humid temperate and alpine regions as well. The differing effects of rainfall on the C balance*  
586 *depend on the change in relative water saturation that follows from rainfall event sizes and patterns*  
587 *throughout the year (Reed et al., 2012). In some cases, decreased rainfall leading to lower water*  
588 *saturation of biocrusts may facilitate photosynthetic carbon gain via increasing the CO<sub>2</sub> diffusivity*  
589 *from the atmosphere into the chloroplast (Lange et al., 1997). Nevertheless, reducing water*  
590 *saturation below a certain value can cause a decline in the duration of activity (Proctor, 2001;*  
591 *Veste et al., 2008) which thus reduces carbon accumulation. Thus, there may be a rain threshold*  
592 *below which decreasing rain may start having a negative effect on biocrust C balances. The*  
593 *threshold is likely species-specific as it is associated with the water-holding capacity of the*  
594 *organism. Our simulation results thus highlight the need for the combined application of field*  
595 *experiments and data-driven modeling to improve our understanding of differential responses to*  
596 *variation in precipitation.*

#### 597 *4.3.2 Physiological parameters*

598 *The parameter  $q_{10}$  is a key parameter that substantially affects respiration.  $\text{Resp}_{\text{main}}$  is the dark*  
599 *respiration rate at a reference temperature that is linked in the model to  $V_{\text{cmax}}$ , the maximum rate*  
600 *of carboxylation of RuBisCO in the Calvin Cycle of photosynthesis (Walker et al., 2014).  $T_{\text{opt}}$  is a*  
601 *parameter that controls gross photosynthesis as well as respiration as it is also the reference*  
602 *temperature for calculating respiration rates.  $\text{Rub}_{\text{ratio}}$  can affect  $V_{\text{cmax}}$  and hence the maximum*



603 *CO<sub>2</sub> assimilation rate, while ExtL regulates the light using efficiency under limited light conditions.*  
604 *Sat\_act0 and Sat\_act1 are two parameters that determine the range of water saturation for initial*  
605 *activation and full metabolic activity. They have the smallest effects on the C balance of lichen-*  
606 *dominated biocrusts at all sites.*

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

615 *L511. Here we get back more to what I care about: why did those estimates come out with big*  
616 *losses? An idea is suggested, which is that the long periods of suboptimal conditions are the*  
617 *problem. I would bet it goes something like this: the net C flux field/lab measurements slightly*  
618 *overestimate the C losses because of the timing of the respiration measurements with respect to*  
619 *hydration or the stresses of an incubation or a number of other factors. Plus, it's hard to*  
620 *separate crust from heterotrophs so you always get some heterotroph signal in those*  
621 *physiological measurements. Then this slightly exaggerated C loss gets multiplied by all the times*  
622 *when the conditions are not great (most of the year) and it looks like a ton of carbon is lost.*  
623 *Maybe my narrative of what went wrong here is itself quite wrong, but I think if sensitivity to*  
624 *physiological parameters is added and then a more complete post mortem of what happened with*  
625 *these calculations is done, the whole study will make more sense. I want to see a story like this,*  
626 *but that the authors provide to the best of their ability.*

627 Thank you for the very helpful and reasonable suggestions. The relative importance of various  
628 environmental factors and physiological parameters has been examined. We now discuss the  
629 potential reasons leading to unrealistic carbon losses of biocrusts especially at T1 and T2 from two  
630 perspectives, namely environmental factors and physiological parameters including seasonal  
631 acclimation, in the revised manuscript in subsection 4.3 (see above).

632 *L515-525. Seasonal acclimation sure, but what about inaccurate estimates of physiological*  
633 *parameters? It's always a possibility. These things are very hard to measure. I see that the LiBry*  
634 *model is being used here as a talking point for why the numbers are not correct. I am not totally*  
635 *sure I buy the seasonal acclimation argument. It could be a factor but I think it is a lot more than*  
636 *that on the physiological side of things.*

637 Thank you for the comments. We agree that the physiological parameters, which are hard to be  
638 measured directly and are calibrated from measured photosynthesis response curves of biocrusts,  
639 are quite uncertain. If the data-driven model is sensitive to these physiological parameters, the  
640 parameters are likely to be the reason for the failure of the model simulation. We have included this  
641 point in the revised version of the manuscript (see above).

642 However, the seasonal variation of the physiological parameters is also relevant, since adapting a  
643 parameter to a constant value throughout the year usually does not solve problems with the C

644 balance estimation. If, for instance, the model underestimated the physiological parameter  
645 Rub\_ratio slightly, the increase of this parameter for the whole year would not make the annual  
646 carbon balance positive in the sensitivity analysis, because increased light use efficiency in winter is  
647 compensated by reduced efficiency in summer.

648 *L559-560. Ok yes this is what I have been saying for the whole review! The authors are aware of*  
649 *this. It needs to be discussed MUCH more thoroughly throughout. It doesn't make sense to*  
650 *exhaustively turn over all the abiotic variables when the physiology is very possibly the biggest*  
651 *source of error. Ideally it would be sensitivity-tested like the environmental variables. How*  
652 *sensitive is the model to parameter estimates on light response curve, A-Ci curve, temp response,*  
653 *respiration q10, etc.*

654 Thank you for the suggestions. We have expanded accordingly the analyses of the impacts of  
655 physiological parameters on carbon balance estimation by the data-driven model as described  
656 above. The relative importance of environmental factors has been considered as an argument for  
657 another possible source of error rather than the main findings of the study. The procedure, results,  
658 and discussion in terms of the relative importance of individual physiological parameters as well as  
659 their uncertainties that may lead to unrealistic C balance numbers were all described in the above  
660 answers.

661 *L563. This I agree with. It's a very nice approach, I think it just needs a more complete*  
662 *explanation for the modeling shortfalls. It is fine that it fails, it just has to be better described*  
663 *why, with quantitative information. The acclimation piece is a start, but I have a feeling the*  
664 *shortcomings of the physiological estimates are a lot greater than just lack of accounting for*  
665 *acclimation. Various physiology numbers are probably slightly wrong and the model is likely*  
666 *sensitive to this.*

667 Thank you very much for the support of the approach we constructed. Yes, in addition to  
668 environmental factors and acclimation as the sources of error in carbon balance estimation, we have  
669 performed sensitivity analyses of physiological parameters to have a more comprehensive  
670 assessment of which factors or parameters are more relevant to the simulated carbon balance by the  
671 data-driven model and might thus cause the model simulation to fail.

672 *L569. This paper has multiple sites, but does not have an explicit spatial component so I would*  
673 *not use this word here.*

674 Thanks for the suggestion, we considered alternative expressions: *distinct patterns of their relative*  
675 *impacts across climate regions.*

676 *L571. I do not find it particularly insightful to say rainfall is relevant in drylands. This is a given.*  
677 *Also I don't follow the argument about CO2 and question the assumed value used (400 ppm). I*  
678 *would focus the conclusion on where the model succeeds and why and vice versa.*

679 Thanks for the suggestions. The conclusions drawn from the results have been modified to focus  
680 more on the data-driven model estimation of biocrust carbon balance and its sensitivity to  
681 environmental factors and physiological parameters in different climatic zones.

682 The Conclusion section in the revised manuscript read as follows:

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

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

704 **L581-585. This paragraph doesn't add much and can be removed.**

705 Thank you for the suggestion, we have deleted this paragraph in the revised manuscript.

706

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