

RESEARCH ARTICLE

Modelling the carbon balance in bryophytes and lichens: Presentation of PoiCarb 1.0, a new model for explaining distribution patterns and predicting climate-change effects

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Abstract

Premise: Bryophytes and lichens have important functional roles in many ecosystems. Insight into their CO₂-exchange responses to climatic conditions is essential for understanding current and predicting future productivity and biomass patterns, but responses are hard to quantify at time scales beyond instantaneous measurements. We present PoiCarb 1.0, a model to study how CO₂-exchange rates of these poikilohydric organisms change through time as a function of weather conditions.

Methods: PoiCarb simulates diel fluctuations of CO₂ exchange and estimates long-term carbon balances, identifying optimal and limiting climatic patterns. Modelled processes were net photosynthesis, dark respiration, evaporation and water uptake. Measured CO₂-exchange responses to light, temperature, atmospheric CO₂ concentration, and thallus water content (calculated in a separate module) were used to parameterize the model's carbon module. We validated the model by comparing modelled diel courses of net CO₂ exchange to such courses from field measurements on the tropical lichen *Crocodia aurata*. To demonstrate the model's usefulness, we simulated potential climate-change effects.

Results: Diel patterns were reproduced well, and the modelled and observed diel carbon balances were strongly positively correlated. Simulated warming effects via changes in metabolic rates were consistently negative, while effects via faster drying were variable, depending on the timing of hydration.

Conclusions: Reproducing weather-dependent variation in diel carbon balances is a clear improvement compared to simply extrapolating short-term measurements or potential photosynthetic rates. Apart from predicting climate-change effects, future uses of PoiCarb include testing hypotheses about distribution patterns of poikilohydric organisms and guiding conservation strategies for species.

KEYWORDS

bryophytes, carbon balance, climate change, CO₂ exchange, *Crocodia aurata*, epiphytes, gas exchange, lichens, modelling, photosynthesis, photosynthetic response curves

Bryophytes (mosses, liverworts, and hornworts) and lichens are important components of many ecosystems, where they play vital and varying roles in regard to productivity and biomass accumulation, nitrogen fixation (DeLuca et al., 2002; Adams and Duggan, 2008; Markham and Fernández Otárola, 2021), nutrient and water cycling (Cornelissen et al., 2007; Porada et al., 2014; Ah-Peng et al., 2017), plant–animal interactions, and

facilitation or competition with vascular plants (Zamfir, 2000; Gornall et al., 2011). While we lack detailed knowledge of current responses to interacting environmental drivers, ongoing climate change brings even more uncertainty about the future of these organisms and, consequently, the ecosystems they inhabit.

An ecophysiologicaly relevant feature that bryophytes and lichens have in common is poikilohydry (Blum, 1973).

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Poikilohydric organisms passively equilibrate their water content with the environment. Their hydration status can thus fluctuate strongly, influencing rates of CO₂ exchange. At the dry end, low water content limits metabolic activity (first photosynthesis, then dark respiration); at the wet end, for many species, a surplus of water can lead to suprasaturation depression of photosynthesis due to a diffusion limitation of CO₂ uptake (e.g., Lange et al., 1993). Therefore, a positive carbon balance (i.e., a net carbon gain over a certain duration) can only be achieved by poikilohydric organisms when the right water content (neither too low nor too high) coincides with favorable light and temperature conditions long enough to allow sufficient carbon gain via photosynthesis to compensate for any nightly carbon loss. As a result, in some habitats, photosynthetic carbon gain during the day frequently fails to exceed losses through dark respiration due to short or poorly timed activity times (Lechowicz, 1981; Nash et al., 1982; Titus et al., 1983; Lange et al., 1994), which ultimately restricts biomass gain (Palmqvist and Sundberg, 2000). Hydration and CO₂-exchange patterns are thus highly critical to the growth of bryophytes, lichens, and other poikilohydric autotrophs in many terrestrial habitats.

Given that constantly changing microclimatic conditions in the field have a much stronger impact on poikilohydric organisms than on homoiohydric ones, carbon budgets would ideally be determined through very frequent, regular, long-term in situ CO₂-exchange measurements (Bader et al., 2010). Such long-term time series are exceedingly rare, with the longest records available for a lichen species, *Protoparmeliopsis muralis* (Lecanoraceae), which was studied during 15 months with a semi-automated cuvette (Lange, 2002, 2003a, 2003b). With the same type of cuvette, Büdel et al. (2018) recorded CO₂ exchange in a biological soil-crust community in Australia for 1 year. All other available data sets are restricted to just a few days or weeks (e.g., Zotz et al., 1997, 2003; Lange et al., 2000, 2004, 2006; Reiter et al., 2008; Raggio et al., 2014; Colesie et al., 2016). A few valuable long-term field studies of the photosynthetic activity of lichens used fluorescence signals (e.g., Leisner et al., 1996; Lange et al., 1999), but did not assess CO₂ exchange. Analyzing the *Protoparmeliopsis muralis* data set, Bader et al. (2010) concluded that the extrapolation of diel carbon budgets does not provide sufficiently accurate estimates of long-term budgets unless the number of days sampled is impractically large and the temporal frequency of individual measurements is high (every 1.5 h for annual budgets, every 0.5 h for diel budgets).

Since such detailed measurements are not really an option in most cases, models are an alternative to estimate long-term carbon balances. The simplest model, converting maximum photosynthesis rates into annual balances based on some fixed conversion factor (based on average activity times and rates across ecosystems), has been used for global carbon-gain estimates (Elbert et al., 2012). While this approach produces a useful, though highly uncertain, first estimate of long-term carbon balances at the global level, such an approach cannot provide insights into geographic patterns or climatic dependencies, nor into day-to-day variation in CO₂ exchange. Because of the strong temporal fluctuations in metabolic

activity in poikilohydric plants, their carbon balance cannot be estimated with models developed for “normal” homoiohydric plants, for which the highest rate of net photosynthesis is indeed a reliable predictor of integrated diel carbon gain (Zotz and Winter, 1993). Therefore, the development of a CO₂-exchange model for poikilohydric plants seems the only viable option to obtain reliable estimates of diel, seasonal, and longer-term carbon balances for these organisms.

To date, several attempts to develop models aiming to quantify the net productivity of bryophytes and lichens have been published. Lange et al. (1977) developed a model for the desert lichen *Ramalina maciformis* (Ramalinaceae). By following the model structure suggested by Schulze et al. (1976), they reproduced diel variation in CO₂-exchange rates quite well. However, in their study, as well as in more recent ones for boreal epiphytic lichens (Sundberg et al., 1996) and subarctic bryophytes (Street et al., 2012), measured thallus water content was an input to the models. Water content, however, is not easily monitored and itself strongly depends on climatic conditions. Ideally, a carbon-balance model should thus also include a water-dynamics module. Such a module was implemented by Rice et al. (2011) when studying trade-offs between water retention and photosynthesis in relation to moss canopy structure, with a simplified carbon module assuming saturating light conditions. For lichens, simple biophysical hydration models have also been developed and applied in a statistical modelling of growth rates (Jonsson et al., 2008; Jonsson-Čabrčić et al., 2010). None of these studies, however, aimed at mechanistically determining long-term carbon balances in situ in natural habitats. For other studies that aimed to model bryophyte carbon balances at the ecosystem (Frolking et al., 2002; DeLucia et al., 2003) or global level (LiBry model; Porada et al., 2013), validation of the results is obviously difficult due to a lack of field data. Application of the mechanistic LiBry model, originally conceived as a dynamic global vegetation model (Porada et al., 2013), at more local scales (Baldauf et al., 2021; Ma et al., 2022) is giving promising insights into the climatic controls on lichen and bryophyte carbon balances, although its parameterization at the local scale is very challenging. For understanding distributional and biomass patterns and climate-change effects on carbon balances of poikilohydric organisms, species-specific and more empirically based modelling approaches are needed to overcome these limitations.

Here we aimed to develop a carbon balance model for bryophytes and lichens that can simulate their performance under different measured or simulated microclimatic conditions. Specifically, the model, named PoiCarb (for poikilohydric and carbon balance) simulates fluctuations of CO₂ exchange (net photosynthesis and dark respiration) based on observed responses of water and CO₂ exchange to environmental variation projected on time courses of climatic conditions and atmospheric CO₂ concentrations, as a tool to estimate long-term carbon balances.

A similar approach was presented by Uchida et al. (2002) and later applied by Osaki and Nakatsubo (2021) to terrestrial pioneer mosses and most recently by Ma et al. (2022) for

biocrusts. PoiCarb generalizes that approach and offers a solution that is easy to understand and use with a flexible application to different settings and species and climate data with different temporal resolutions. Our model can be used to explore mechanistic explanations of current regional distribution patterns of bryophytes and lichens and to predict and understand their responses to future climate change. Using the model, we can disentangle how increased air temperatures, changes in precipitation patterns, and increased atmospheric CO₂ levels will likely impact carbon balances, with implications for species distributions, community composition, and ecosystem productivity.

Here, we present the model with a validation test case based on 15 days of CO₂-exchange data from Lange et al. (2004) and the data from the green-algal lichen *Crocodia aurata* (Peltigeraceae, published as *Pseudocyphellaria aurata*, nomenclature changed by Moncada et al. [2014]). However, PoiCarb can be used for other groups of poikilohydric organisms, given the availability of the correct parameters. We also present a simple experiment (“modelling exercise”) that illustrates how the model can be used to study climate-change effects on the long-term carbon balance of a lichen species.

MATERIALS AND METHODS

Model description

We based our model description loosely on the ODD (overview, design, details) format suggested for individual-based models by Grimm et al. (2006, 2010, 2020), because several sections of this format are also useful for other model types. The overview and details are presented here, and the design concepts are presented in the introduction. The model was implemented in R version 4.1.2 (R Core Team, 2021).

Model purpose

The direct purpose of PoiCarb is to calculate long-term carbon balances of poikilohydric organisms by simulating diel fluctuations of CO₂ exchange based on empirically determined responses of water and CO₂ exchange (net photosynthesis and dark respiration) to environmental conditions, projected on time courses of current and future atmospheric CO₂ concentrations ([CO₂]) and microclimatic conditions. The scientific purpose of calculating these carbon balances is to understand how these organisms respond to environmental variation, be it in space (distribution patterns, habitat preferences) or in time (e.g., seasonality, climate change).

Model structure, variables, and processes

PoiCarb consists of two modules: a carbon-dynamics module and a water-dynamics module. In the water-dynamics module, the change in water content (WC, in % of the dry mass) in the

bryophyte or lichen thallus is calculated for each time step through rates of water gain and loss, which depend on precipitation (water gain, i.e., wetting) and vapor-pressure deficit (water loss, i.e., drying; in PoiCarb 1.0, rehydration at low VPD is not implemented). Precipitation can be rain, but it can also be, e.g., fog or dew, if data are available on such water inputs. In the carbon-dynamics module, the net carbon gain per time unit (in $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$) is calculated through rates of CO₂ exchange, which depend on thallus water content (from the water-dynamics module), light (photosynthetically active radiation [PAR]) level, air temperature, and [CO₂].

The carbon-dynamics module is based on empirically determined responses of net photosynthesis and dark respiration to environmental factors. We assume that there are no interactive effects of these factors. As a base rate, the model uses the CO₂-exchange rate at a given light level (from the climatic input data), calculated from the light-response curve. This curve should be determined at an optimal water content and at a standard temperature and [CO₂]. These conditions then define 100% CO₂ exchange in the respective response curves, which are thus standardized to express CO₂-exchange rate as a percentage rather than in the original units. These curves should be determined under the same standard conditions (except for the variable factor, of course) and with saturating light. At conditions deviating from these standards, the CO₂-exchange rate is then modified accordingly by multiplying the base rate with each of the respective correction factors. For example, if a low water content allows only 50% of the maximum photosynthesis rate and a suboptimal temperature allows only 80%, the base rate taken from the light-response curve is multiplied by 0.5×0.8 . This method is relatively simplistic but effective for treating the joint action of the controlling environmental factors (Lange, 2002). Dark-respiration rates are calculated similarly based on the respiration base rate (i.e., CO₂ exchange in the dark) from the light-response curves, corrected for temperature and water content (i.e., temperature- and water-response curves of CO₂ exchange in the dark). For net photosynthesis at light levels below the light compensation point but above 0, when there is a net CO₂ release, the model uses the correction factors from the dark-respiration curves, since dark respiration dominates these exchange rates. The instantaneous net photosynthesis or respiration rates are then integrated over the desired time intervals, which depend on the temporal resolution of the climatic input data, yielding the carbon budget per time step. These are then summed up to give daytime, nightly, diel, or long-term carbon balances.

Model parameters

Model parameters characterizing the photosynthetic response curves and drying speed of different species are needed to run the model. These can be obtained from measured responses of CO₂-exchange rates (net photosynthesis and dark respiration) to different light, temperature, and [CO₂] levels and to changes in lichen or bryophyte water content and from measured

maximum water contents and drying speeds at different temperatures and humidities.

The equations used for the response curves can be chosen by the user to best fit a particular data set. For the validation data set, we selected the following nonlinear regression equations (nls function in R) to fit them to the empirical data (Figure 1) and to estimate the parameters needed for the model:

The light-response curve (Figure 1A; Potvin et al., 1990) was described by:

$$A = a_1 \left[1 - e^{-b_1(\text{PAR}-c_1)} \right], \quad (1)$$

where A is the instantaneous CO_2 -exchange rate in $\text{nmol g}^{-1} \text{s}^{-1}$ and PAR is the photosynthetically active radiation in $\mu\text{mol m}^{-2} \text{s}^{-1}$. Parameters a_1 , b_1 , and c_1 characterize the

light-response curve. Parameter a_1 corresponds to the maximum rate of net CO_2 exchange (light-saturated rate of photosynthesis, A_{max} in $\text{nmol g}^{-1} \text{s}^{-1}$), b_1 corresponds to the apparent quantum yield, and c_1 is the light compensation point (LCP in $\mu\text{mol m}^{-2} \text{s}^{-1}$).

An equivalent equation (Appendix S1) was used for the CO_2 -response curve (Figure 1B) and the water-content-response curve for dark respiration (Figure 1E).

The water-content-response curve for net photosynthesis (Figure 1C; Wagner et al., 2013) was described by:

$$A = \left(a_{\text{wc}}^2 \text{WC} \right) / \left(\text{WC}^2 + a_{\text{wc}} b_{\text{wc}} \right) + c_{\text{wc}}, \quad (2)$$

where WC is the thallus water content in % of dry mass. Parameters a_{wc} , b_{wc} , and c_{wc} characterize the response

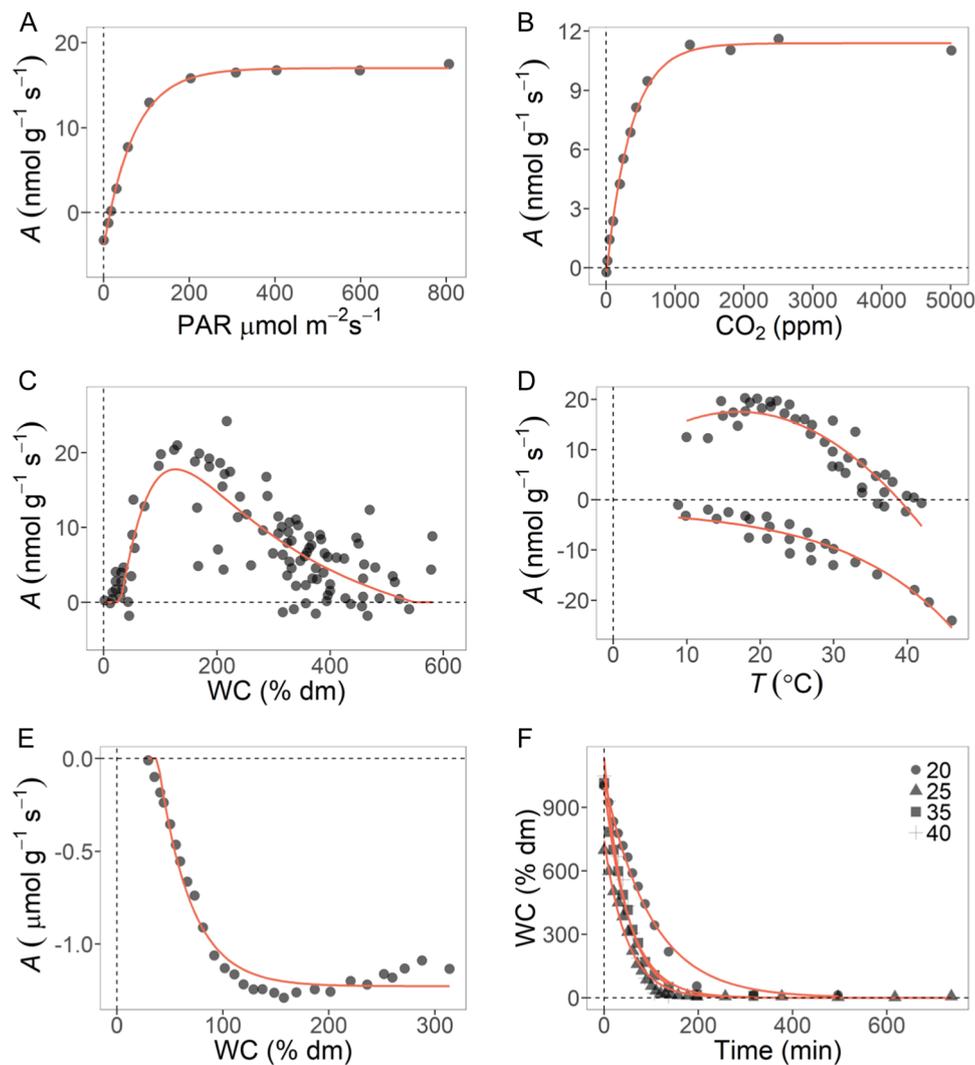


FIGURE 1 Environmental response curves (red lines) of CO_2 exchange used for the parameterization of our carbon-balance model for bryophytes and lichens (A–E): (A) light-response curve; (B) CO_2 -response curve; (C), (E) water-content-response curve under saturating light level (net photosynthesis) and in the dark (dark respiration); (D) temperature-response curve under saturating light level (net photosynthesis) and in the dark (dark respiration). Data (points) are for the lichen *Crocodia aurata* (Lange et al., 2004), except the CO_2 -response and water-content-response curve in the dark, which are based on data for the lichen *Lecanora muralis* (Lange, 2002). (F) Example of drying speed curves at different air temperatures (symbols, in $^{\circ}\text{C}$) for the tropical bryophyte *Bryopteris flicina* (authors' unpublished data). Similar curves with different parameter values are expected for other poikilohydric autotrophs.

curve, with a_{wc} and b_{wc} affecting the position and width of the optimum water content and c_{wc} adjusting the height of the curve.

This equation was additionally restricted to avoid negative values. We are aware that, in fact, water-content-response curves should include a small section with negative values when the water content is very low but not yet 0, when respiration exceeds gross photosynthesis (see e.g., Figure 5 of Zotz et al., 2000). However, this section is often not resolved in available response curves, and we assume that it represents only a very small fraction of the active time of most bryophytes and lichens. We therefore ignored this section (i.e., set it to zero) in this case, but it is possible for the user to include this section of negative A values explicitly in the model.

The temperature-response curves for net photosynthesis and respiration (Figure 1D; Wagner et al., 2013) were described by:

$$A = a_T - b_T T_{air} (c_T - T_{air}),$$

(3 temperature response with light)

$$A = -(a_{TRd} T_{air} + b_{TRd}),$$

(4 temperature response in the dark)

where T_{air} is the air temperature in °C and a_T , b_T , c_T , are coefficients of the photosynthesis curve, with a_T indicating the rate of net photosynthesis at 0°C, and b_T and c_T affecting the strength of the changes in A with changes in temperature and optimal temperature, respectively. The coefficients for the dark-respiration curve, a_{TRd} and b_{TRd} manipulate the increase in R_d (dark respiration) per increase in temperature (functioning in a similar way as the Q_{10}) and indicate the R_d at 0°C, respectively.

The drying speed parameters were determined by fitting an exponential decay function:

$$WC = WC_{max} e^{(-DCt)},$$

(5)

where t is the time in minutes needed for the sample to complete drying, DC is the coefficient describing the decaying constant and WC_{max} is the coefficient corresponding to the maximum water content, at the beginning of the measurement. To include the effects of temperature and humidity conditions, as expressed by the vapor-pressure deficit (VPD), on drying speed, the DC should be determined at different VPDs (e.g., by varying the temperature) and can then be predicted by the VPD using a linear regression model. Similarly, drying speeds depend on the size of the sample (e.g., Gauslaa and Solhaug, 1998; Merinero et al., 2014), and these relationships need to be established if there is large size variation between individuals. Methods for collecting drying-speed data were discussed by Wang and Bader (2018). Alternatively, physical models may be used to predict dehydration and hydration rates as functions of environmental conditions and/or

thallus size and structure (e.g., Jonsson et al., 2008; Jonsson-Čabrčić et al., 2010; Ma et al., 2022).

Model validation

For model validation, a good set of response curves plus data for a sufficient number of diel CO_2 -exchange patterns, plus the corresponding microclimatic conditions and diel fluctuations in the water content are needed for comparison with the modelled diel patterns and carbon balances. Such data sets are extremely rare, but we found one suitable study, which we used for validation. We used 15 days of data of in situ CO_2 -exchange measurements on the broad-lobed lichen *Crocodia aurata* from a montane rainforest (at ca 1200 m a.s.l.) in Panama (Lange et al., 2004). The data set also included values for air temperature, PAR, and most importantly, lichen water content, determined at the same time as the CO_2 -exchange measurements. Response curves for temperature, light, and water content were also available (Figure 1). In that study, no CO_2 -response curves for photosynthesis or water-content-response curves for dark respiration were provided, so that we used the curves available for the crustose lichen *Protoparmeliopsis muralis* (Lange, 2002), which had dark-respiration rates similar to those observed in *C. aurata*. A detailed description of the measurement of environmental response curves can be found in the original publications (Lange, 2002; Lange et al., 2004). Since the data set did not include data on atmospheric $[CO_2]$ in the lichen microhabitat, we used a fixed value of 350 ppm CO_2 (average atmospheric concentration at the time of the measurements in 1993), for which the effect of the CO_2 -response curve in the model was set to 1, i.e., had no effect on the C-exchange rate. Still, the CO_2 -response curve was needed in the model to allow using PoiCarb for experiments that simulate increased atmospheric $[CO_2]$ (see below).

Because the validation data set did not contain drying curves, air humidity, or rain events, we used the water content data from the diel courses to estimate the necessary parameters and to infer rain events—a modelling step that is unnecessary with more complete data sets. We calculated the water loss between each measurement and related the loss rate to the air temperature to obtain the temperature dependence of the DC . Value for WC_{max} was taken from the most common maximum reached at rewetting in the measured diel curves. A rain event was inferred whenever the lichen water content was raised by 47% or more (an empirically determined threshold that yielded the best correspondence of modelled and measured water-content fluctuations), and these events were added to the climate input data. Although not ideal, this method allowed us to reproduce the observed water-content dynamics sufficiently to reproduce the observed CO_2 -exchange patterns. With the availability of drying curves and environmental moisture data, this model module should perform even better.

The model was validated by comparing modelled and observed values and patterns for instantaneous CO_2 -exchange rates and for daytime, nightly, diel, and long-term (as long as

possible, here, 15-day) carbon balances. Daytime balances were calculated between 06:00 and 18:00 hours, nightly between 18:00 and 06:00 hours, corresponding to the tropical day and night hours, and integrated to diel balances. To evaluate the water-dynamics module and its effects on the overall model outcome, we also modelled the carbon balance based on observed water contents and compared observed and modelled water contents and the CO₂-exchange patterns and balances based on observed vs. modelled water contents. We evaluated the fit of the modelled values (rates or balances) using linear regression models, with observed values as the explanatory variable and modelled values as the response variable. For an unbiased fit, the model slope would be 1, the intercept would be 0, and for a perfect fit the R^2 would be 1. We tested the no-bias null hypothesis using the P value for the slope and the confidence interval for the intercept.

Since we did not have access to the original data that we used for validation (response curves, diel CO₂-exchange patterns, and climate data from Lange et al. [2004]), we used the WebPlotDigitizer (Rohatgi, 2020) for extracting data points from the published data visualizations.

Elasticity analysis

We estimated the effects of the input parameters on the carbon-balance output for the model by performing a local elasticity analysis. The analysis was carried out by proportionally changing one of the parameters at a time, while keeping all others constant, and determining which parameters cause the largest changes in the output. Each of the parameters was changed by the following percentages: -50%, -25%, -10%, -5%, -1%, +1%, +5%, +10%, +25%, +50%. We expressed elasticity as the ratio of model outputs for the changed vs. the original parameters.

To be able to interpret these elasticities in terms of the observed variation in the parameters among species and data sets, we collected published photosynthetic response curves from 10 papers (Harley et al., 1989; Green et al., 1997; Zotz et al., 1997; Romero et al., 2006; Waite and Sack, 2010; Wagner et al., 2013, 2014b; Song et al., 2015; Wang et al., 2017; Wang and Bader, 2018), complemented with our unpublished data from five tropical bryophyte species from Costa Rica and 11 from Ecuador (L. Guérot and M. Y. Bader, unpublished data), and extracted parameter values for a total of 106 species from various ecosystems globally (Appendix S2). Using this information plus the results of the elasticity analysis, we evaluated which parameters are most critical to a reliable model output to guide measurement efforts for parameter estimation in future studies.

Model experiments

As an example of the potential use of PoiCarb, we performed a simple climate-change experiment using the model to differentiate warming effects on drying speed

from direct effects on metabolic rates, and to study the potential of increased [CO₂] to compensate for negative warming effects. We ran the model with the same climate input used for model validation and then again with air temperature increased by +3 K and +6 K (corresponding to moderate to strong global climate warming predictions for the current century; IPCC, 2021). To isolate the effects of changes in metabolic rates from those of faster drying, we calculated the water content with the original temperatures and only the carbon module was run with the changed temperatures. These results were compared with a model run with increased temperatures influencing both water dynamics and CO₂ exchange. Additionally, we increased [CO₂] by 300 ppm, using the scenario with full temperature effects, to study to what extent this could compensate the anticipated negative effect of the increased temperatures. We simplified the modelling by assuming no acclimation to higher temperatures, since no empirical information to the contrary is available for tropical species. Paired t -tests were run to test for differences in the changes in diel carbon balances resulting from the three scenarios (warming affecting metabolic rates only vs. warming affecting metabolic rates plus drying; warming with or without increased [CO₂]; warming with increased CO₂ vs. no warming to test whether CO₂ compensates for warming).

RESULTS

Model testing (validation)

Comparing the modelled and observed CO₂-exchange rates (A_m and A_o) of the lichen *Crocodia aurata* shows that the general shape of the diel patterns was reproduced well, although the exact values did not always match (Figure 2; Appendix S3, Figure S1). In particular, the observed and the modelled water content (WC_o and WC_m), although following very similar patterns, showed some notable deviations concerning the maxima reached on some days (Figures 2 and 3A).

The biases in the modelled CO₂-exchange rates changed little when using WC_o or WC_m (Figure 3B, C); i.e., the regression models did not differ in their slope (model-coefficient confidence intervals overlap) and hardly in their intercept (Table 1), but with WC_m , the variation increased (and the R^2 of the model decreased from 0.9 to 0.6 for instantaneous rates; Figure 3B, C). For both models, the slope of the relationship was <1 (Table 1), while the intercept was at or near 0; i.e., at higher rates, the model tended to underestimate the exchange rates. This underestimation was due to rates being measured in the diel courses that were above the A_{max} determined during the photosynthetic response curves. The higher variation when using modelled water contents was clearly due to an accumulation of inaccuracies from the water and carbon modules. Although the modelled water content correlated

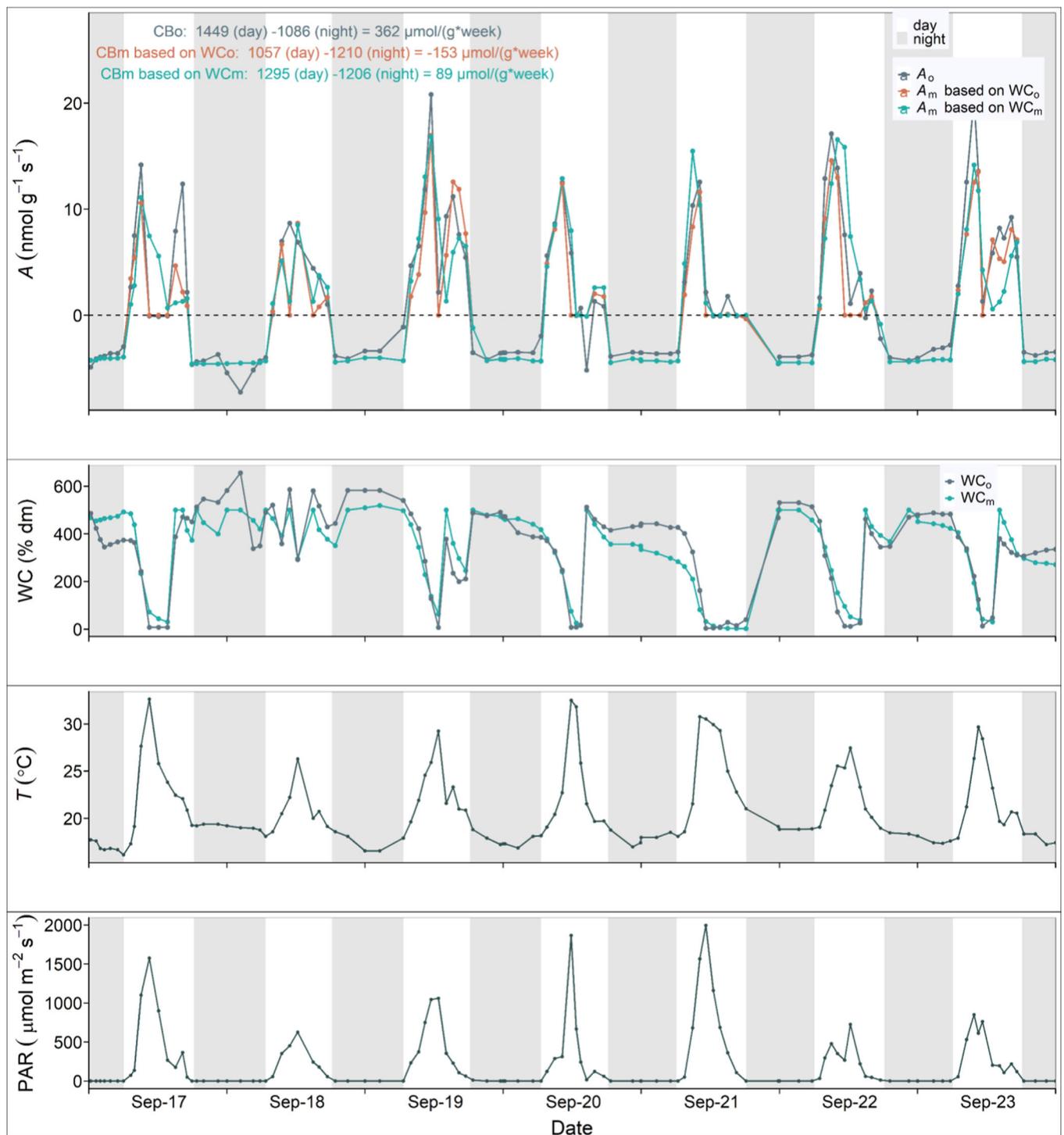


FIGURE 2 Validation of the carbon balance model: modelled assimilation (A_m) for the lichen *Crocodia aurata* using modelled water content (A_m based on WC_m , turquoise line; WC_m , turquoise line) or using the observed water content (A_m based on WC_o , orange line; WC_o , grey line) compared with the observed assimilation (A_o , grey line). Total carbon balances (in μmol) during the daytime (12 h light) and night (12 h dark) are shown in the left upper corner (CB_o , observed carbon balance, CB_m , modelled carbon balance based on WC_m , CB_m based on WC_o). Observed assimilation and water content data and climate input data (PAR, T) are from Lange et al. (2004). Grey areas represent the nights. The plot shows the first week (17 to 23 September 1993) of 15 recorded days. The remaining 8 days are shown in Appendix S3, Figure S1.

strongly with the observed water content (Figure 3A), the remaining variation adds uncertainty to the carbon model, highlighting the importance of reliable water content data for the overall performance of the model.

Like the instantaneous rates, the modelled diel carbon balances were clearly positively related to the observed diel carbon balances but were generally lower, either due to a lower mean, when using WC_o (Figure 4A), or to an increasing

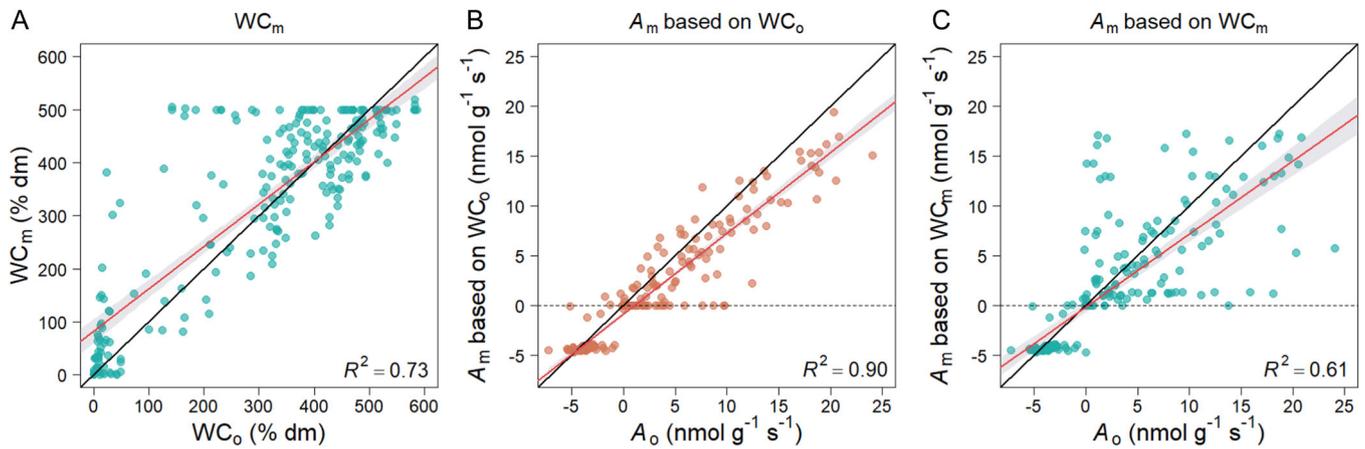


FIGURE 3 Model validation based on the instantaneous water contents and CO_2 -exchange rates observed and modelled for the lichen *Crocodia aurata* with data recorded on average every 90 min for 15 days, 17 September to 1 October 1993 (Lange et al. 2004). (A) Modelled water content compared to observed water content; (B) modelled assimilation rates using the observed water content compared to the observed assimilation rates; and (C) modelled assimilation rates using the modelled water content compared to observed assimilation rates. Black lines are the 1:1 theoretical optimal fits. Red lines are linear regressions, with the goodness-of-fit of the models shown in the bottom right corner in each plot.

TABLE 1 Results of the linear regression models of modelled water content (WC_m) and modelled assimilation (A_m) and carbon balances (CB_m) of the lichen *Crocodia aurata* as functions of the observed values (WC_o , A_o , and CB_o) graphically presented in Figures 3–5. Shown are the estimated coefficients for intercept and slope. An unbiased model fit would have an intercept of 0 and a slope of 1 (i.e., the 1:1 line). The 95% confidence interval (between the lower and upper limits, CI-L and CI-U) indicates whether the intercept and slope include 0 and 1, respectively (indicated in bold when this is the case, i.e., when the model does not differ significantly from the unbiased 1:1 line, as also indicated by high P values in case of the intercepts).

Model info	Model fit	Est.	CI-L 2.5%	CI-U 97.5%	t	P
Figure 3A Dependent variable: WC_m	$F_{1,234} = 632$, $P < 0.001$ $R^2 = 0.73$ (Intercept) WC_o	82 0.80	60 0.74	105 0.86	7.30	<0.001
Figure 3B Dependent variable: A_m (based on WC_o)	$F_{1,234} = 2130$, $P < 0.001$ $R^2 = 0.90$ (Intercept) A_o	-0.8 0.81	-1.1 0.78	-0.6 0.85	-6.79	<0.001
Figure 3C Dependent variable: A_m (based on WC_m)	$F_{1,234} = 366.23$, $P < 0.001$ $R^2 = 0.61$ (Intercept) A_o	-0.2 0.73	-0.7 0.66	0.4 0.81	-0.55	0.58
Figure 4A Dependent variable: Diel CB_m (based on WC_o)	$F_{1,13} = 55.39$, $P < 0.001$ $R^2 = 0.81$ (Intercept) Diel CB_o	-68.8 0.7	-88.2 0.52	-49.4 0.94	-7.66	<0.001
Figure 4B Dependent variable: Nightly CB_m (based on WC_o)	$F_{1,13} = 58.55$, $P < 0.001$ $R^2 = 0.82$ (Intercept) Nightly CB_o	-64.6 0.7	-93.1 0.49	-36.1 0.88	-4.89	<0.001
Figure 4C Dependent variable: Daytime CB_m (based on WC_o)	$F_{1,13} = 47.06$, $P < 0.001$ $R^2 = 0.78$ (Intercept) Daytime CB_o	-14.9 0.8	-63.8 0.52	34.0 0.99	-0.66	0.52
Figure 4D Dependent variable: Diel CB_m	$F_{1,13} = 12.76$, $P < 0.001$ $R^2 = 0.50$ (Intercept) Diel CB_o	-34.7 0.6	-65.1 0.22	-4.3 0.88	-2.47	0.03
Figure 4E Dependent variable: Nightly CB_m	$F_{1,13} = 54.82$, $P = 0.00$ $R^2 = 0.81$ (Intercept) Nightly CB_o	-70.1 0.7	-98.2 0.46	-42.0 0.85	-5.40	<0.001
Figure 4F Dependent variable: Daytime CB_m	$F_{1,13} = 15.34$, $P < 0.001$ $R^2 = 0.54$ (Intercept) Daytime CB_o	30.2 0.7	-44.2 0.29	104.6 1.02	0.88	0.40

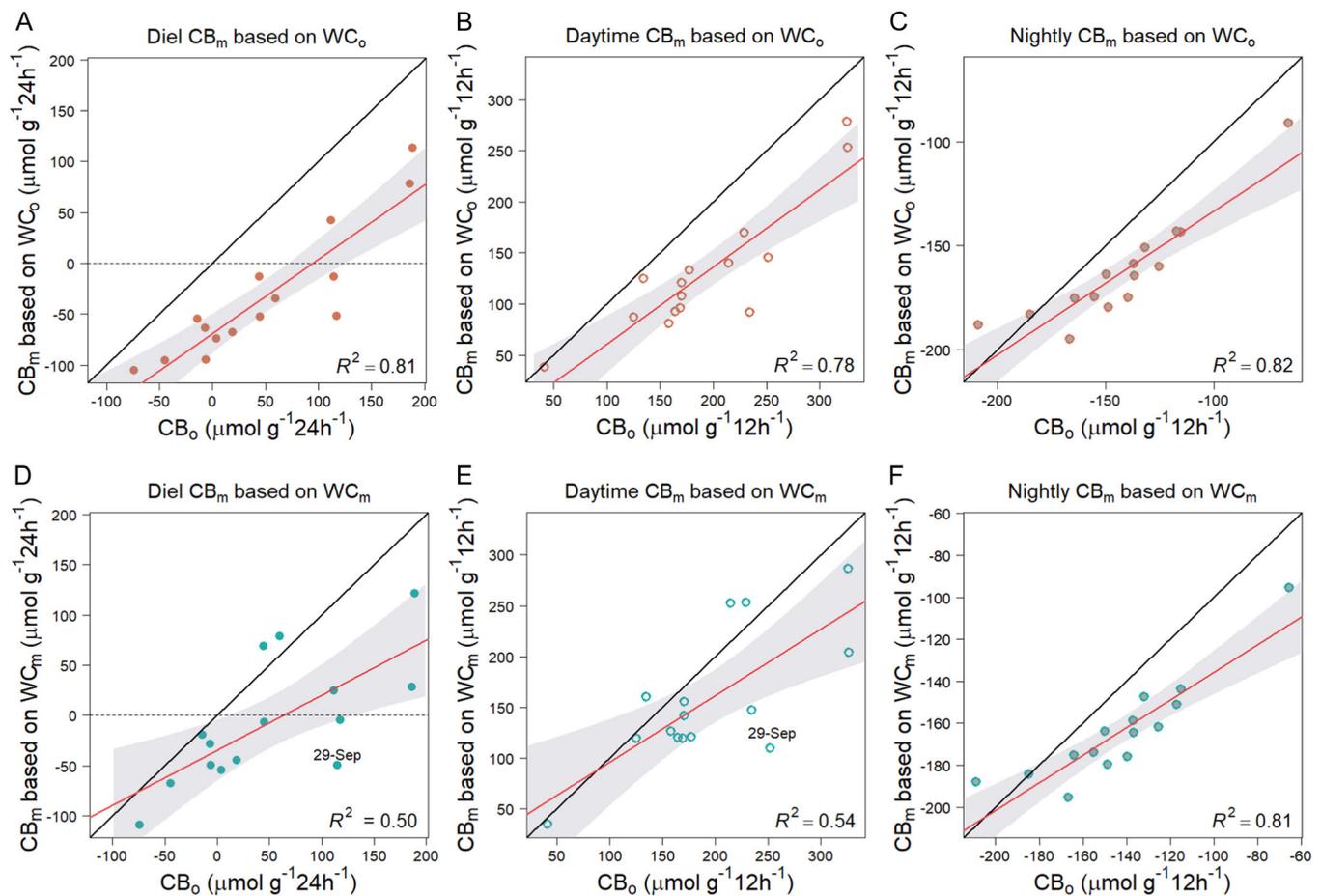


FIGURE 4 Modelled carbon balances (CB_m) of the lichen *Crocodia aurata* compared to the observed carbon balances (CB_o). (A–C) Modelled carbon balances based on the observed water content (WC_o): (A) Diel (24-h) balances (orange circles); (B) daytime (06:00–18:00 hours) balances (open orange circles); (C) nightly (18:00–06:00 hours) balances (gray-shaded orange circles). (D–F) Modelled carbon balances based on the modelled water content (WC_m): (D) Diel (24-h) balances (turquoise circles); (E) daytime (06:00–18:00 hours) balances (open turquoise circles; (F) nightly (18:00–06:00 hours) balances (grey-shaded turquoise circles). Black lines are 1:1 optimal fits. Red lines represent the linear models, with the goodness-of-fit of the models shown in the bottom right corners. Model coefficients and their confidence intervals are shown in Table 1.

deviation with increasing diel balance when using WC_m (Figure 4D). Again, when the observed water contents were used, the variation was lower ($R^2 = 0.81$ vs. 0.50 when using WC_m), but relationships did not differ significantly from each other (large overlap in confidence intervals for the model coefficients; Table 1). Thereby, both daytime and the nightly carbon balances were underestimated, especially in the higher ranges (Figure 4, Table 1). Only for daytime balances calculated with WC_m (Figure 4E) did the regression line not differ significantly from the 1:1 line, but this lack of a significant difference was arguably due to the larger variation rather than due to a better fit. The overall underestimation was primarily caused by one day (29 September) with an unrealistically high measured daytime carbon balance at $252 \mu\text{mol g}^{-1} 12 \text{ h}^{-1}$, compared to just $110 \mu\text{mol g}^{-1} 12 \text{ h}^{-1}$ according to the model. The strong mismatch could be due to a measuring problem because the CO_2 -exchange rates measured on this particular day were unusually high, with points that were substantially above the maximum value of the light-response curve

measured under optimal conditions (see Appendix S3, Figure S1 and Figure 1A).

Elasticity analysis

Changing the parameters of the environmental response curves of net photosynthesis and respiration by up to 50% above and below the original value for *Crocodia aurata* yielded up to 25-fold higher or 50-fold lower carbon balances for the 15-day validation period (Figure 5). The elasticity analysis based on a fixed change in the parameter alone does not, however, necessarily reveal which parameters are most critical. How critical they are also depends on the variability of the parameters among species and on the error range inherent to common measurement techniques. When considering the range of possible values found in studies on different bryophytes and lichens (Figure 6), some parameters (b_{TRd} and b_{wCRd}) are highly variable among measured response curves and are therefore more

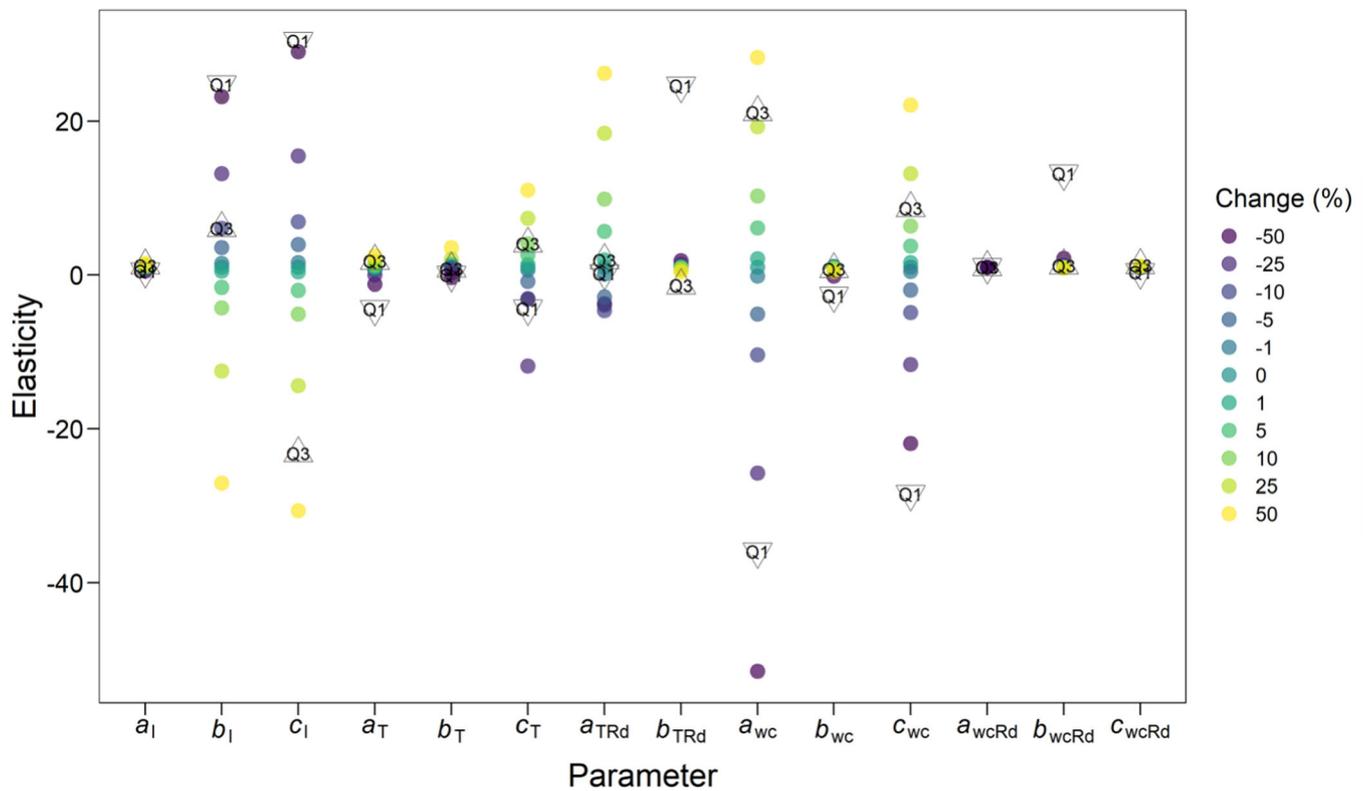


FIGURE 5 Elasticity analysis; parameters of the carbon-dynamics module (x -axis) changed by different percentages (% change) from the values for *Crocodia aurata* and set to the 25 and 75% percentiles (first and third quantiles, Q1 and Q3) of parameter values found in published data (see also Figure 6). Elasticity is expressed as the ratio of the model output (net total carbon balance over the 15 days used in model validation; see Figure 2 and Appendix S3, Figure S1) with the single parameter changed and the output derived from the original parameters.

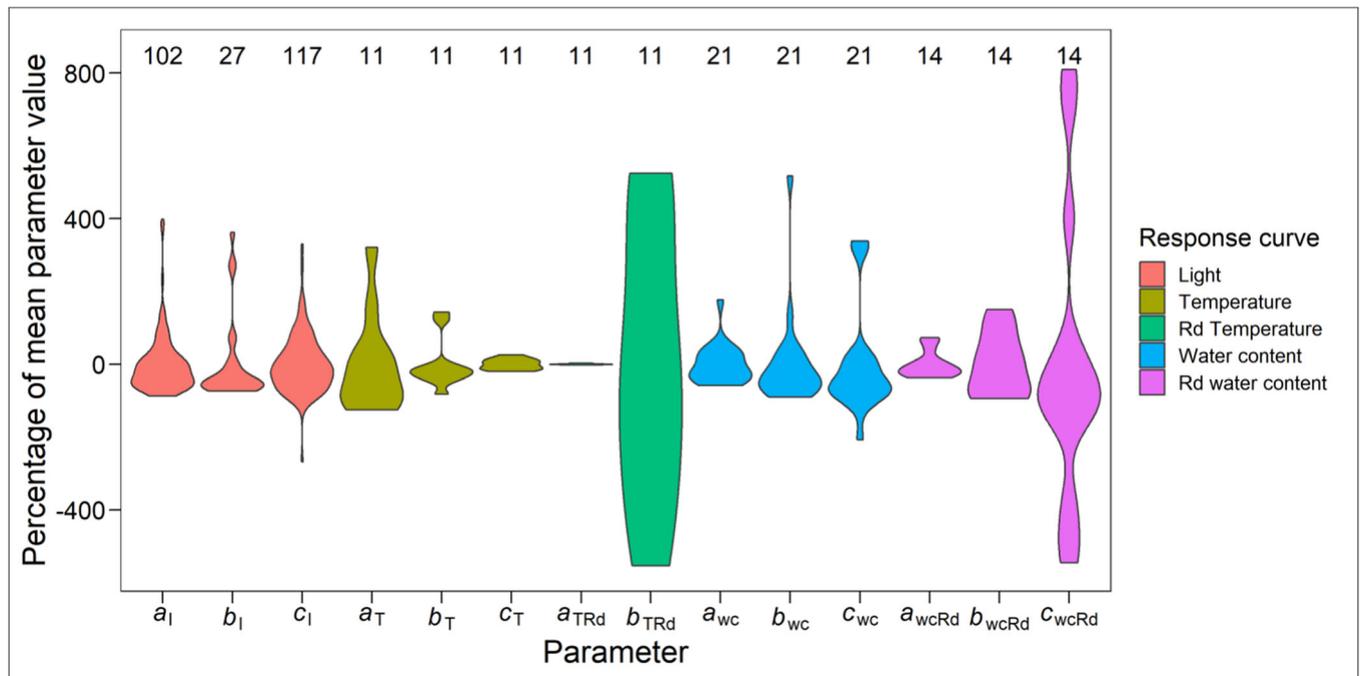


FIGURE 6 Violin plot of the standardized parameter values (difference from mean divided by the mean and multiplied by 100) derived from light (a_l , b_l , c_l), water (a_{wc} , b_{wc} , c_{wc}) and temperature (a_T , b_T , c_T) photosynthesis response curves, as well as from the water (a_{wcRd} , b_{wcRd} , c_{wcRd}) and temperature (a_{TRd} , b_{TRd}) dark-respiration response curves of different bryophytes and lichen species derived from published data. The number of parameters found in the literature (n) is shown on top. Raw (nonstandardized) parameter values and references are given in Appendix S2, Table S1. Nonstandardized means, standard deviations and extremes are shown in Appendix S4, Table S1.

influential than the elasticity analysis alone suggests. Others have very little influence according to both the elasticity analysis and within the range that is commonly found (a_1 , b_T , b_{WC} and a_{WCrd} , c_{WCrd}), while still others are not very variable between measured curves and have less effect within their common range than predicted by the elasticity analysis (e.g., c_T , a_{TRd}). The most critical parameters, given the ranges of values found in the literature (25% to 75% percentiles, Q1 to Q3 in Figure 6), are the light compensation point (c_l), and the water-content-response curve parameters a_{WC} and c_{WC} . These may all result in a >30-fold change in carbon balance if changed from the first to the third quartile. For most parameters, the parameter values for *C. aurata* lay within the middle two quantiles of reported values. However, for b_1 , the value was relatively high so that even the 75% percentile of all reported values included in our survey (Figure 6) lay below the value used, explaining the shift of the quartiles relative to the +50% and -50% ranges (Figure 5).

Model experiments

A temperature increase in the carbon-dynamics module alone led to a considerable decline in daytime net carbon gain (-22% for +3 K; -50% for +6 K) and to higher nightly respiratory losses (-15% for +3 K; -34% for +6 K), resulting in an overall negative carbon balance (Figure 7; Appendix S3, Figure S3; Table 2). Unsurprisingly, the +6 K warming had a more negative effect in this scenario, i.e., without calculating faster drying or an increase in $[CO_2]$ (Figure 8).

Increased air temperatures would also affect the drying speed. Including this effect in the water-dynamics module did not change the mean diel carbon balances, neither for the +3 K scenarios [$t(14) = 0.39$, $P = 0.70$] nor for the +6 K

scenarios [$t(14) = 0.05$, $P = 0.96$; Figures 8 and 9; Table 2; Appendix S3, Figures S2 and S4]. However, even though the mean effect of warming on diel balances stayed similar, adding the effect of drying increased the variation of the warming effects, which even became positive on a few days (Figure 8). The variation caused by changes in drying speed was so large that there was hardly a correlation between the modelled diel balance without warming and the modelled diel balance with the full warming effects, as expressed in the very low R^2 of the relationships ($R^2 = 0.34$ for +3 K and 0.20 for +6 K; Figure 8). A pronounced negative effect of faster drying was observed on days with reduced time available for photosynthesis. The resulting narrower peaks of net photosynthesis usually occurred in the morning, at lower light levels. Since the lichen dried out before maximum light levels were reached at noon, faster drying inevitably lowered carbon gain. This effect can be seen particularly well on 17 and 19 September (Figure 9). A positive effect of faster drying was observed when the lichen went into a state of metabolic inactivity before the end of the night, so that part of the nighttime there was little or no dark respiration. This effect can be seen well at +6 K warming on 21 and 24 September (Figure 9).

Adding 300 ppm CO_2 with the warming resulted in significantly higher mean diel carbon balances compared to warming without the CO_2 addition, both at +3 K warming [$t(14) = -9.30$, $P < 0.001$] and +6 K warming [$t(14) = -6.26$, $P < 0.001$]. At +3 K warming, CO_2 addition could compensate for the negative effects of warming [$t(14) = 0.31$, $P = 0.76$: no difference compared to no warming], but at +6 K warming it could not [$t(14) = -3.91$, $P < 0.01$; Figures 8 and 10; Table 2; Appendix S3, Figure S2]. For daytime carbon balances, the extra CO_2 even overcompensated for the negative +3 K warming effect (mean daytime change of +27 $\mu mol g^{-1} d^{-1}$), while the nightly losses were

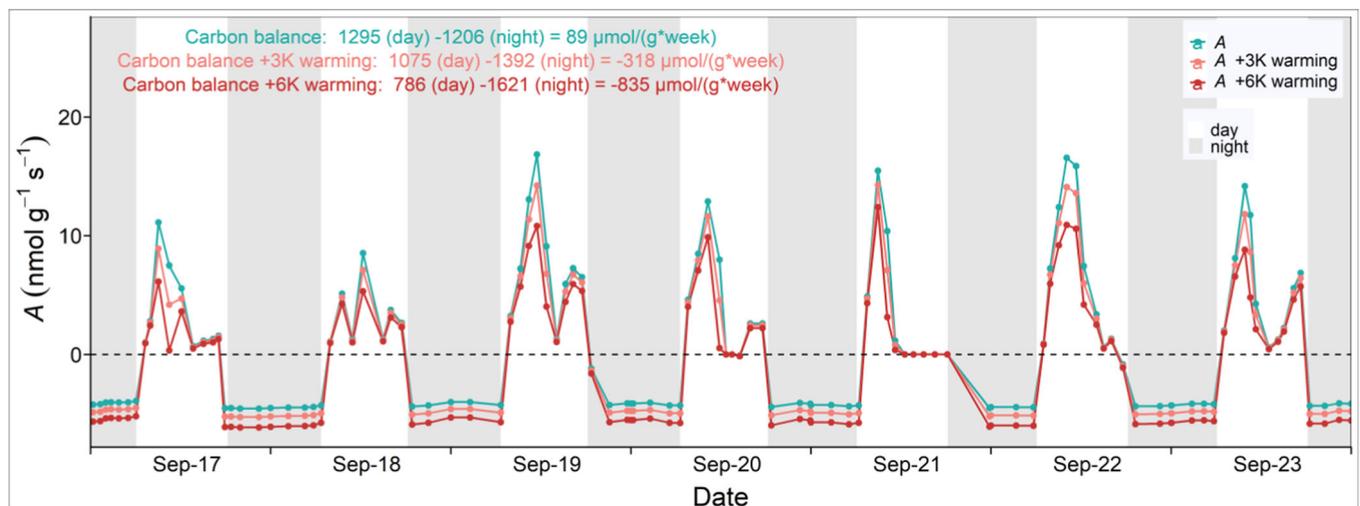


FIGURE 7 Model experiment 1. Effect of warming on CO_2 -exchange rates in the lichen *Crocodia aurata* with exchange rates affected only via the metabolic temperature response without faster drying. Modelled assimilation based on original microclimate input data (turquoise line) and modelled assimilation with temperature increased by 3 K (light red line) and 6 K (dark red line). Grey areas represent the nights. The plot shows the first week (17 to 23 September 1993) of 15 days of microclimatic data. The last 8 days are shown in Appendix S3, Figure S3.

TABLE 2 Summary of the results of warming and CO₂ addition on modelled diel carbon balances in the lichen *Crocodyla aurata* (experiments 1 and 2). Warming by either 3 K or 6 K was applied either only to the carbon-exchange module, affecting rates of CO₂ exchange but not drying rates (scenario 1a), or also affecting drying rates (scenario 1b). In addition to scenario 1b, [CO₂] was increased by 300 ppm (scenario 2). A negative change implies a lower net carbon gain, i.e., during the night it implies a stronger carbon loss. The % change for day and night combined (the diel change) is particularly large, since in most scenarios the daytime and nightly negative effects add up but also because the reference balances were small (balancing daytime gains and nightly losses).

Warming level	Model scenario	Change daytime (%)	Change night (%)	Change diel (%)	Change (μmol g ⁻¹ d ⁻¹) daytime	Change (μmol g ⁻¹ d ⁻¹) night	Change (μmol g ⁻¹ d ⁻¹) diel
+3 K	1a. Warming (no effect on drying)	-22	-15	-797	-33.8	-25.3	-59.0
	1b. Warming total effect	-20	-13	-714	-31.1	-21.7	-52.8
	2. Warming with increased [CO ₂]	+17	-12	+91	+26.9	-20.3	+6.7
+6 K	1a. Warming (no effect on drying)	-50	-34	-1807	-77.3	-56.4	-133.7
	1b. Warming total effect	-59	-25	-1795	-91.6	-41.2	-132.8
	2. Warming with increased [CO ₂]	-35	-24	-1269	-54.5	-39.4	-93.9

not affected, resulting in an overall similar diel carbon balance as without warming or added CO₂ (Figure 10; Table 2; Appendix S3, Figures S2 and S5). Overall, variation was high, and on many days, the total effect of +3 K warming plus increased [CO₂] was positive (Figure 8A).

DISCUSSION

Our PoiCarb model aims to calculate long-term carbon balances in bryophytes and lichens based on the environmental response curves of CO₂ exchange using microclimatic data. The validation shows that the diel courses in CO₂ exchange are reproduced quite well, although with the data used here, the model tended to underestimate both diel and weekly carbon balances compared to those derived directly from field measurements. More important than the mere quantitative results obtained by the model are the insights into the conditions that are favorable or unfavorable for carbon gain in bryophytes and lichens with different physiological traits, expanding use of the model beyond the quantitative estimation of long-term carbon balances. Because the model reproduces diel variation of CO₂ exchange based on microclimate, it can be used to assess which types of weather lead to more positive long-term carbon balances. Likewise, it can be used to characterize suitable microhabitats for different life-forms or species for which response curves to environmental factors are available.

Priorization of future data collection

The paucity of validation data sets in the form of measured diel or longer-term bryophyte CO₂-exchange data, which limited our options for model validation, is related to the large effort involved in gathering such data in the field and indicates how urgently a model is needed to improve our estimates and understanding of long-term carbon balances and the responses of these organisms to changing climates (Bader et al., 2010). PoiCarb is relatively simple and requires a manageable set of response curves to define the parameters and climatic factors as input. It is therefore applicable even with relatively basic ecophysiological and microclimatic data sets. Response curves of CO₂ exchange to environmental variables are available for a limited number of bryophyte and lichen species, with light-response curves being most frequently reported, followed by water-content-response curves, while temperature- and CO₂-response curves are rarer. Fortunately, our elasticity analysis shows that some parameters, those that are either similar between species or have little impact on the model output, can be estimated based on similar species with existing response curves or by taking a reasonable guess from the range of published parameters. Conveniently, these less critical parameters include those related to temperature and CO₂-response curves. However, the

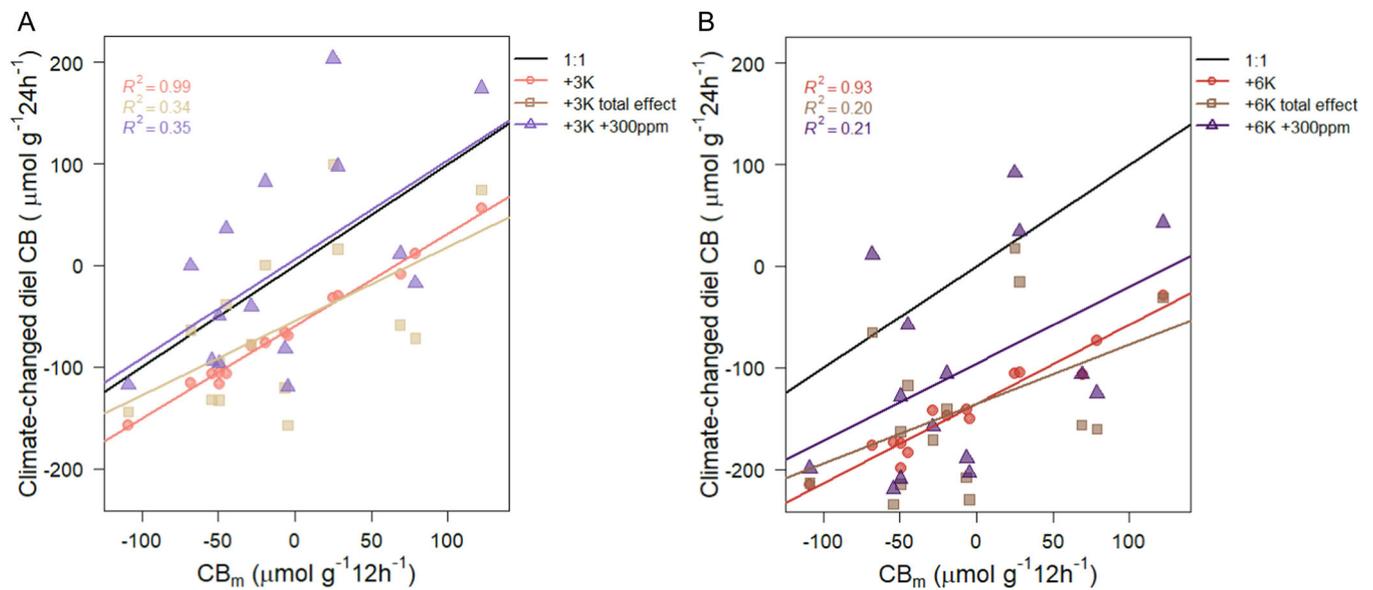


FIGURE 8 Diel carbon balances of the lichen *Crocodia aurata* modelled under different climate-change scenarios (y -axis) compared to the diel balances modelled with the original climatic conditions (x -axis). The black line represents the 1:1 line, i.e., no change due to climatic warming. The colored points and lines represent different warming scenarios and warming effects: Temperature increased by 3 K (A) and 6 K (B) with just effects on metabolic rates (red), effects on both metabolic rates and drying speed (brown) and an additional increase in $[\text{CO}_2]$ of 300 ppm (purple). $N = 15$ days (17 September to 1 October 1993).

interactive effects of temperature and light as well as $[\text{CO}_2]$ and light on CO_2 exchange, not yet implemented in the model, may increase the importance not only of these single-factor curves but also on data on the nature and magnitude of the interactions between these factors (e.g., Lange, 2002). In addition, we need to keep in mind that in principle this elasticity analysis is only valid for the microclimatic conditions in our validation data set. Under more extreme temperature conditions (e.g., in tropical-lowland or polar conditions), temperature responses, for example, may well become more critical to the accurate estimation of carbon balances.

The elasticity analysis also shows what measurement errors and other sources of variation have the strongest impact on calculated carbon balances. Measurement errors occur when determining response curves and when measuring diel courses and can be due either to sample handling or instrument limitations (Peek et al., 2002). Differences can also be due to intraspecific variation (Smith and Griffiths, 1998; Smith et al., 1998), which can have genetic (random variation or adaptation) or direct environmental causes (local or seasonal acclimation, hydration history, stress responses). Knowing the extent of this variation for the studied species or group of species will help to evaluate the accuracy and precision of the model output and to calculate ranges of possible outcomes rather than a single value. In the *C. aurata* data set, we did not have a measure of variation for the input, but it is clear from the model output that the A_{max} in the light-response curve was lower than the A_{max} observed in the diel courses. A repetition of the light-response-curve measurements would probably include these high values in some of the curves. It

may be argued that the highest measured light-response curve should be used to calculate the input parameters, since this curve is least affected by photosynthesis-reducing factors such as a suboptimal water content. However, variation in measured A may also be due to instrument limitations or intraspecific variation, causing variation in both directions. If these are the suspected cause of variation in the response curves, the mean of the curves should provide the best parameters, or a range of parameters may be modelled to produce a range of likely outcomes.

Not to be confused with measurement errors and random (in the sense of unexplained) variation between measurements, the effects of which should be averaged out, any expected seasonal variation in ecophysiological responses should be explicitly taken into account (Hickleton and Oechel, 1976; Lange and Green, 2005; Colesie et al., 2018). To obtain more accurate outputs for the annual balances outside the tropics, we suggest using two or more sets of response curves measured in different seasons to include the potentially important impacts of seasonal acclimation of CO_2 -exchange rates (Ma et al., 2022).

Of the parameters used, the light compensation point (c_l), with the water-content curve parameters a_{wc} and c_{wc} were most critical. These three parameters have a strong effect on the model outcome and also vary greatly between measurements. The light-compensation point is especially important for species living in shady habitats, such as the tropical forest understorey. However, even in the upper canopy of a tropical forest, it is highly relevant, because photosynthetic activity is often restricted to the early morning hours, when light levels are still low, with inactivity due to drying preventing the use of high light levels around midday (Zotz and Winter, 1994).

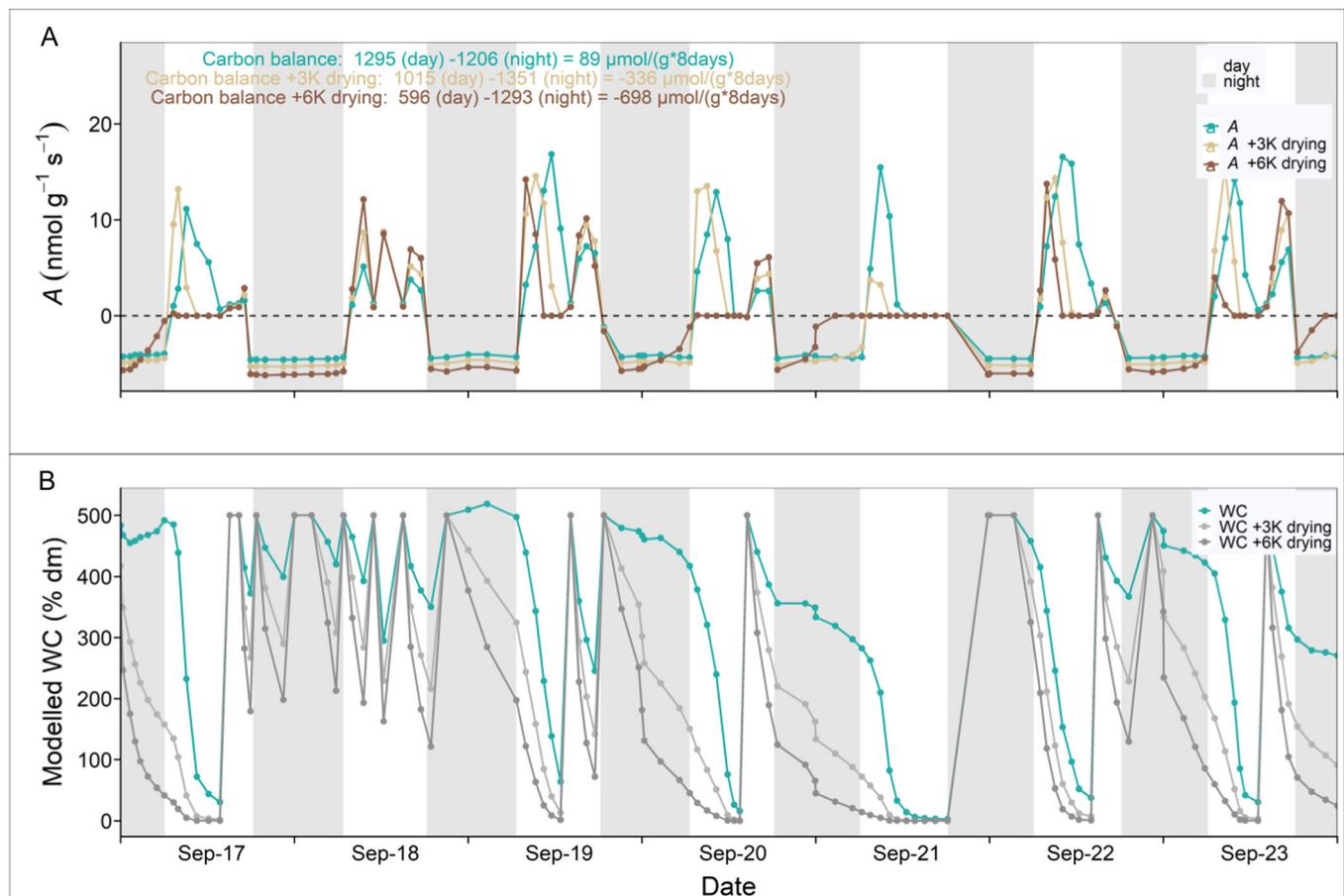


FIGURE 9 Model experiment 2. (A) Modelled CO₂-exchange rates of the lichen *Crocodia aurata* comparing patterns modelled with measured microclimatic data (turquoise line) and with temperature increased by 3 K (light brown line) and 6 K (dark brown line). Unlike Figure 7, temperature increases affected both the carbon-dynamics module and the water-dynamics module, so that the full effect of warming included the effects of drying too, as shown in the water-content dynamics shown in (B). Grey areas represent the nights. The plot shows the first week (17 to 23 September 1993) of 15 days of microclimatic data. The last 8 days are shown in Appendix S3, Figure S4.

Because dark respiration tends to be high relative to photosynthesis in published bryophyte light-response curves, the light compensation point tends to be rather high, posing a serious problem for attaining a positive carbon balance if these values are realistic, in particular in tropical species (Wagner et al., 2014a). A careful determination of this parameter is therefore a clear priority when measuring CO₂-exchange characteristics in bryophytes. Water-content-response curves are, in general, less commonly reported in the literature than light-response curves, but, as shown here, they are essential for predicting and understanding diel courses of CO₂ exchange in bryophytes and lichens. The critical parameters of the water-content-response curve describe the width and position of the optimal water-content peak, the depression in photosynthetic rates at high water contents, and the lower water content at which photosynthesis ceases. Together with the drying speed, the described photosynthetic response determines the time available for photosynthesis after wetting. Therefore, these curves as well as hydration dynamics strongly affect the carbon balance. For this reason, and while the optimal water content needs to be known to obtain valid light-response

curves, water-content-response curves should always be determined when measuring CO₂ exchange in bryophytes and lichens.

Our search for validation data sets exposed the lack of information on water-content fluctuations for bryophytes and lichens in situ (see also Ma et al., 2022) and on water uptake and drying speeds in controlled conditions. Both vary strongly among life-forms and species, as well as within species depending on thallus size and shape (e.g., Gauslaa and Solhaug, 1998; Merinero et al., 2014), and are highly relevant for their carbon balance and for their distribution among habitats (Wang and Bader, 2018), but very little quantitative information is available. Fluctuations in situ, in particular, are rarely measured, reflecting the lack of a reliable field method to monitor water contents in bryophytes and lichens. Studies using chlorophyll fluorescence can document activity and thereby distinguish wet and dry states but cannot quantify the water content (Green et al., 1998). Studies based on impedance measurements (i.e., increases in electrical conductivity in wet thalli) have been executed with variable success (e.g., Coxson, 1991a; Weber et al., 2016; Leo et al., 2019; Löbs et al., 2020) and

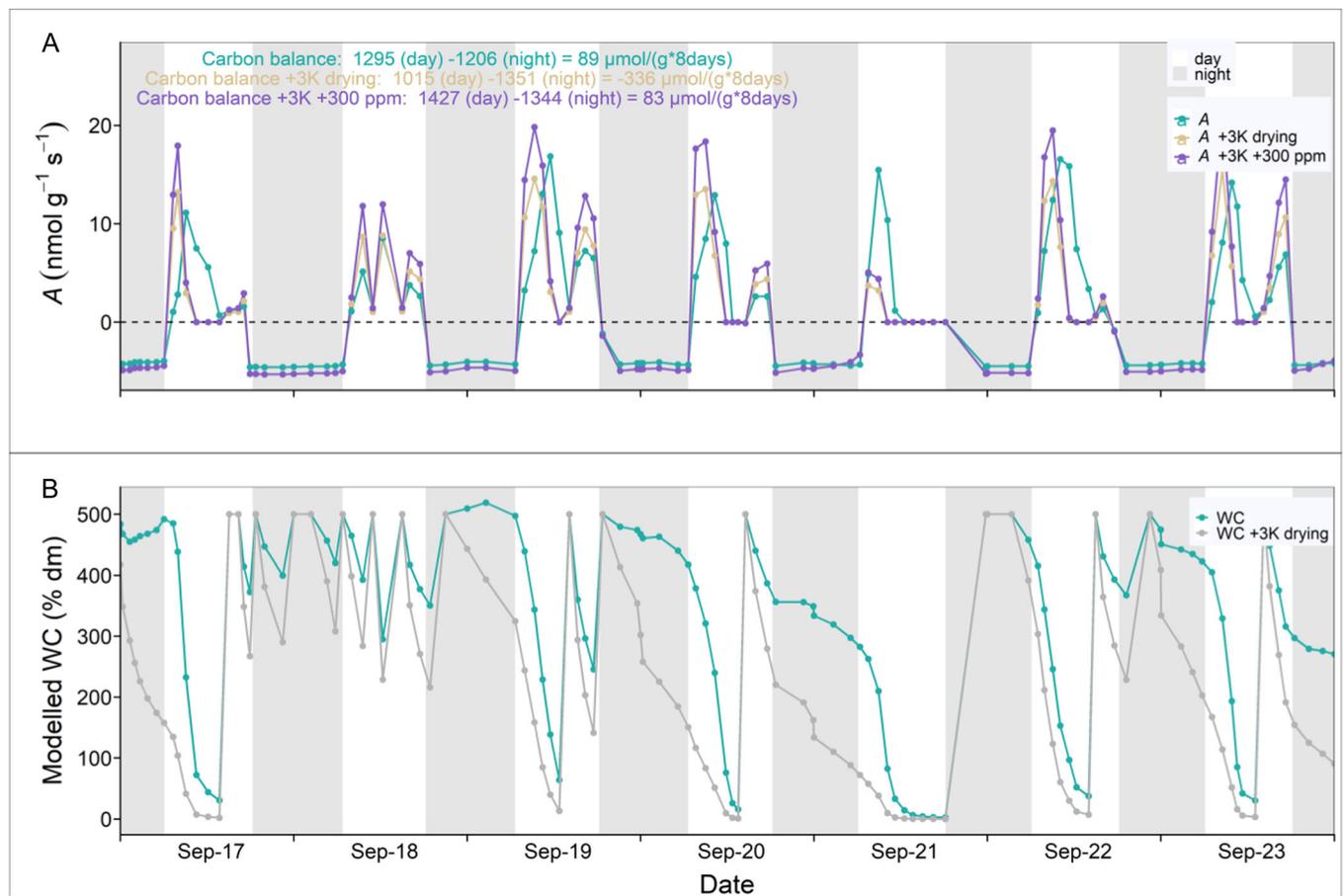


FIGURE 10 Model experiment 3. Effect of increased temperature (+3 K) and $[\text{CO}_2]$ (+300 ppm) on modelled CO_2 -exchange rates of the lichen *Crocodia aurata*. Temperature increase was set to affect both the metabolic rates (via the temperature-response curves) and the drying speed (B; the +3 K caused the same water-content dynamics with and without the +300 ppm CO_2). Grey areas represent the nights. The plot shows the first week (17 to 23 September 1993) of 15 days of microclimatic data. The last 8 days are shown in Appendix S3 (Figure S5) and these same graphs for a +6 K warming are shown in Appendix S3 (Figure S6).

require a well-defined and constant matrix in the millimeter range between the electrodes, which can be provided only by large and sturdy species. In terrestrial carpets of *Sphagnum* and *Polytrichum*, water content has even been monitored using soil moisture probes, although it seems unlikely that these would accurately measure the full range of possible water contents in the mosses (Street et al., 2012). Methods based on recording changes in mass are promising for larger samples with no interference from a substrate (e.g., Maphangwa et al., 2012; Ah-Peng et al., 2017), which unfortunately restricts the applicability of this method to certain life-forms and habitats (e.g., it could work well with pendant epiphytes or fruticose lichens). Spectral reflectance (e.g., the normalized difference vegetation index [NDVI] or even standard RGB images) may provide a proxy for hydration in some lichens, in particular foliose or crustose cyanolichens (e.g., Bednaríková et al., 2023), and the possibilities for exploiting this possibility deserve further research. Noting the importance of hydration data for understanding bryophyte and lichen CO_2 -exchange patterns and habitat preferences, we hope that method development will continue, providing more data to validate and

complement modelled patterns in water-content fluctuations. Additionally, to allow a more refined modelling of hydration in dependence of moss/lichen morphology and microclimatic conditions, more research is needed into both wetting and drying mechanisms in bryophytes and lichens (e.g., Gauslaa and Solhaug, 1998; Rice et al., 2001; Rice and Schneider, 2004; Phinney et al., 2018).

Fine-resolution data, both temporally and spatially, are needed to understand interactions between climate and physiology in general, and especially when studying bryophytes and lichens. For these organisms, data from available global climate databases like Chelsa (Karger et al., 2017; Karger et al., 2020) and WorldClim (Fick and Hijmans, 2017) does not include the most important sources of variation: microclimatic gradients and short-term climatic fluctuations. Even though data from these sources are considered high-resolution data for some purposes, for small organisms like mosses and lichens, a resolution of ~ 1 km is far too coarse. Many studies have shown that bryophytes and lichens are tightly tied to their microhabitats, even species with large geographic ranges requiring specific microhabitats within those ranges. Excellent examples are tropical epiphytic

bryophytes, many of which prefer a particular part of the tree, so that vertical microclimatic gradients in the forest canopy have a stronger effect on species composition than landscape characteristics or geographical distances of up to hundreds of kilometers (Mota de Oliveira et al., 2009, 2015; Silva and Pôrto, 2013; Berdugo-Moreno et al., 2022).

More in situ microclimatic measurements from various microhabitats, or the development of physical models to derive microclimate from macroclimate (Maclean et al., 2019, 2021), would thus be very useful for carbon-balance modelling of poikilohydric organisms. Therefore, we should keep in mind that when measurements less frequent than ca once per 1.5 h are used, the chance of large errors in the annual carbon budget strongly increases (Bader et al., 2010), since important fluctuations in environmental conditions and thallus water status can occur within such a time period, as seen clearly in the narrow peaks in the diel courses of CO₂ exchange in our validation data set. For obtaining accurate diel budgets, an even higher frequency in the climatic input data is needed. For field measurements, Bader et al. (2010) recommend a frequency of one measurement every 30 min, as a compromise between disturbing the sample and having a high enough temporal resolution for reliable carbon-balance estimations. However, this reasoning does not apply to modelling, and a higher temporal resolution in the climatic input data, e.g., records every 5 or 10 min, is preferable.

Climate-change responses

The dominant role of water content for diel carbon balances was obvious when including climatic warming in the model. When higher temperature affected only the CO₂-exchange rates, based on the temperature response curves of photosynthesis and respiration, carbon gain was invariably reduced. However, when also including the effect on water content dynamics, the warming effect became less predictable and was even positive on some days due to changes in the length and timing of activity times; drying can cause inactivity at night, leading to a positive effect on the carbon balance, while inactivity during the day tends to reduce diel carbon gains. In addition, wet–dry cycles can affect the carbon balance through recovery respiration after rewetting and through carbohydrate leaching. Recovery respiration, in particular, arguably explains counterintuitive, negative effects of increased precipitation frequencies in experiments with dryland soil crusts (Reed et al., 2012). These aspects are not yet implemented in PoiCarb but are a possible future extension. To further explore the importance of hydration patterns and variation due to climate change, future experiments with the model may include modifications of the precipitation patterns, including fog and dew, using real or hypothetical climate projections (see also Baldauf et al., 2021).

Climate warming effects could be compensated by increased atmospheric CO₂ concentrations. In the model,

a 300-ppm increase in [CO₂] largely made up for the negative effect of increased temperature. This compensatory effect may imply some good news for the future of poikilohydric organisms. However, this simple model experiment is not yet sufficient to drawing such strong conclusions, especially considering that we lack data on atmospheric [CO₂] in the lichen microhabitat. If [CO₂] is already elevated due to local respiration (e.g. from decomposition processes), a further increase in [CO₂] in the free atmosphere may have little effect on the [CO₂] experienced by the lichen, and photosynthesis may already operate at or close to the saturation level indicated by the CO₂-response curve. Both factors would reduce the CO₂ fertilization effect. Additional reasons for caution are results from experimental and modelling studies in which ameliorative effects of increased atmospheric [CO₂] did not compensate for reduced carbon gain due to other climatic changes (Smith et al., 2018; Baldauf et al., 2021; Meyer et al., 2023).

In addition, for both warming and CO₂ effects, projections into the future need to consider the potential of species to acclimatize or adapt to changing conditions, e.g., by changing the environmental responses of their CO₂ exchange (Wagner et al., 2014a). For vascular plants, a partial acclimation of CO₂ exchange to experimental warming and CO₂ fertilization is commonly observed (e.g., Larigauderie and Körner, 1995; Tjoelker et al., 1999; Ainsworth and Long, 2005; Warren et al., 2015). For bryophytes, a potential for temperature acclimation is suggested by seasonal changes in the optimal temperature for photosynthesis or in respiration rates, as found for some high-latitude mosses and lichens (Hicklenton and Oechel, 1976; Lange and Green, 2005; Colesie et al., 2018). Another indication is the general match of optimum temperatures for photosynthesis with ambient temperature across species from different climate zones, although this match is not very tight and may be due to adaptation rather than acclimation (Wagner et al., 2014b). Much is thus still unclear concerning bryophyte and lichen acclimation to climate change, so that model predictions of future carbon balances need to be interpreted with caution. Our modelling exercise was meant to demonstrate a potential use of the PoiCarb model, not to be a full-fledged climate-change experiment. The latter would need to include predictions of changes in the moisture availability, which probably has a stronger effect than changes in temperature. Additionally, due to interactions with other ecosystem components, predicting long-term climate-change effects on bryophyte performance in real ecosystems requires models that include but go beyond the ecophysiology of individuals (Mitchell et al., 2002; Serk et al., 2021).

Further model development

Changes in thallus water contents are highly critical to the carbon balance of poikilohydric organisms. Hence, the

water-dynamics module deserves particular attention in the further development of PoiCarb. Although the dependence on VPD allows a reasonable estimation of drying speed in still and shady conditions, e.g., in forest understoreys, wind and direct radiation are additional climatic factors that can strongly affect drying (e.g., Uchida et al., 2002; Rice et al., 2011), which should be included to allow a wider application of the model. Moreover, additional inputs of water in the form of dew or fog can be very relevant for lichens and bryophytes, both in deserts (Lange et al., 2006; Lehnert et al., 2018; Jung et al., 2019) and in cloud forests (Stam et al., 2020). Including this type of water input in the model is already possible. The larger challenge is to obtain data on fog and dew occurrence in different climate zones and microhabitats.

Yet another water source, which can activate photosynthesis in some green-algal lichens, but not in cyanolichens or bryophytes, is high air humidity (Green et al., 2011). Our example lichen, *C. aurata*, is a green-algal lichen (and a cephalolichen, i.e., with internal cephalopodia containing *Nostoc* cyanobacteria as secondary photobiont), and reactivation by high air humidity (low VPD) may be possible. Whether such reactivation was possible for this species could not be reconstructed based on the available data, since rainstorms caused strong wetting every day in the late afternoon, as described in the original publication (Lange et al., 2004). However, for ecosystems where high humidity occurs without a concurrent liquid water supply, it would be useful to include rehydration by moist air in the model as an option for those species that can reactivate carbon exchange at the resulting thallus water content. The hydration and activation by different water sources are highly species-specific, depending on thallus structure (Phinney et al., 2018; Ås Hovind et al., 2020) and photobiont identity (Phinney et al., 2019), so that specific parameters are needed to incorporate this process accurately in the model. Currently, high air humidity prevents drying, but in the model, it does not cause rehydration. If data are available, such a rehydration option can be added easily. Conveniently, air-humidity data are standard in micro- and macroclimatic studies, and information on moisture dynamics and photosynthetic activation (though often based on chlorophyll fluorescence rather than on gas exchange) is available for at least some lichen species (e.g., Phinney et al., 2018, 2019; Ås Hovind et al., 2020).

Finally, as discussed above, future expansions of the model could consist in the inclusion of carbohydrate losses by leaching after rewetting of the dry lichens or bryophytes (Dudley and Lechowicz, 1987; Coxson, 1991b; Coxson et al., 1992) as well as restoration respiration after rewetting (Smith and Molesworth, 1973). Other physiological processes, like a depression of photosynthesis due to photo-inhibition or feedback from high sugar concentrations, or night-time recovery and growth processes (implying positive effects of night-time hydration beyond the negative effects of carbon losses due to respiration; Bidussi et al., 2013), would also be interesting additions, and

modelling them may help to interpret and guide the still scarce experimental studies.

CONCLUSIONS

We developed a relatively simple model, which yields useful temporal simulations of CO₂-exchange patterns of poikilohydric organisms, as a tool to understand how microclimatic factors limit species distributions and for testing hypotheses and different scenarios of climate-change impacts at the level of ecophysiological responses. Putting more emphasis on the model's water-dynamics module, ideally validated with field data of water-content fluctuations, would allow additional improvements to the carbon balance estimations.

There have been numerous efforts to model carbon gain of mosses and lichens in the past, all of which struggled with the complexity of the metabolic activity patterns in these poikilohydric organisms. Our approach is an important step forward, with a focus first on the most essential elements that determine CO₂-exchange patterns, allowing an evaluation of weather influences on long-term carbon balances. The model can be further developed to include other important processes such as carbohydrate leaching and recovery respiration, to approach the full complexity of moss and lichen carbon relations. Combining an elasticity analysis with a literature review of the ranges of values found for the different parameters allowed us to identify the most critical parameters that affect estimates of carbon balances, guiding efforts in data collection to improve the predictive power of the model.

Although we primarily aimed to improve our understanding of the functioning of poikilohydric organisms, our modelling approach could be combined with detailed predictions of future climate patterns to provide guidelines for conservation efforts. For example, if we knew the current microclimatic preferences of certain moss or lichen species, we could identify and protect potential microhabitats that will have the same microclimate in the future (microrefugia) or propose other conservation measures based on ecophysiological insights from the model. The predicted negative impacts of global change on this group of organisms (Zotz and Bader, 2009) makes further efforts in model development, supported by experimental studies of bryophyte and lichen ecophysiology, particularly urgent.

AUTHOR CONTRIBUTIONS

M.Y.B. and G.Z. conceived the project and the model, N.N. implemented the model and did all analyses, N.N. led the writing of the manuscript with the supervision of M.Y.B. All authors revised the final manuscript and agreed to its publication.

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DATA AVAILABILITY STATEMENT

The data set we used to validate the model and to run the climate change simulations (extracted from Lange et al., 2004) and the model code are archived in the Dryad repository (<https://doi.org/10.5061/dryad.v15dv422v>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Equations used for the CO₂-response curve and the water-content dark-respiration curve.

Appendix S2. Table of a range of parameters data.

Appendix S3. Figures S1–S8. Graphs for the last 8 of 15 days of measurements and model experiment with +6 K and +300 ppm.

Appendix S4. Table with a summary of parameter values.

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