

Relative humidity predominantly determines long-term biocrust-forming lichen cover in drylands under climate change

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Funding information

Deutsche Forschungsgemeinschaft, Grant/Award Number: 408092731; Collaborative Research Centre 973; H2020 European Research Council, Grant/Award Number: 647038 (BIODESERT); Generalitat Valenciana, Grant/Award Number: CIDEGENT/2018/041; Ministerio de Economía y Competitividad, Grant/Award Number: CTM2015-64728-C21-R (CRYPTOCOVERT) and PRI-PIMBDV-2011-0874

Handling Editor: Shurong Zhou

Abstract

1. Manipulative experiments typically show a decrease in dryland biocrust cover and altered species composition under climate change. Biocrust-forming lichens, such as the globally distributed *Diploschistes diacapsis*, are particularly affected and show a decrease in cover with simulated climate change. However, the underlying mechanisms are not fully understood, and long-term interacting effects of different drivers are largely unknown due to the short-term nature of the experimental studies conducted so far.
2. We addressed this gap and successfully parameterised a process-based model for *D. diacapsis* to quantify how changing atmospheric CO₂, temperature, rainfall amount and relative humidity affect its photosynthetic activity and cover. We also mimicked a long-term manipulative climate change experiment to understand the mechanisms underlying observed patterns in the field.
3. The model reproduced observed experimental findings: warming reduced lichen cover, whereas less rainfall had no effect on lichen performance. This warming effect was caused by the associated decrease in relative humidity and non-rainfall water inputs, which are major water sources for biocrust-forming lichens. Warming alone, however, increased cover because higher temperatures promoted photosynthesis during early morning hours with high lichen activity. When combined, climate variables showed non-additive effects on lichen cover, and effects of increased CO₂ levelled off with decreasing levels of relative humidity.
4. *Synthesis*. Our results show that a decrease in relative humidity, rather than an increase in temperature, may be the key factor for the survival of the lichen *D. diacapsis* under climate change and that effects of increased CO₂ levels might be offset by a reduction in non-rainfall water inputs in the future. Because of a global trend towards warmer and drier air and the widespread global distribution of *D. diacapsis*, this will affect lichen-dominated dryland biocrust communities and their role in regulating ecosystem functions worldwide.

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KEYWORDS

biological soil crusts, climate change, dew, *Diploschistes diacapsis*, drylands, simulation model

1 | INTRODUCTION

Biocrusts, communities dominated by lichens, cyanobacteria and mosses living on the soil surface, are a major biotic community in global drylands (Weber et al., 2016). It is estimated that biocrusts cover around 12% of the land surface (Rodríguez-Caballero et al., 2018), providing important ecosystem functions across spatial scales. Locally, they prevent soil erosion (e.g. Bowker et al., 2008; Cantón et al., 2011), enhance soil fertility by fixing atmospheric nitrogen (Barger et al., 2013; Ferrenberg et al., 2018; Xiao & Veste, 2017) and impact vascular plant species performance depending on their species composition (Havrilla et al., 2019) by, for example, inhibiting the germination of exotic plant species (Slate et al., 2019). Globally, they contribute to the carbon cycle, directly by their own photosynthetic and respiratory activity (Porada et al., 2013; Rodríguez-Caballero et al., 2018) and indirectly by supporting carbon sequestration by vascular plants through nitrogen fixation (Weber et al., 2012). Due to their poikilohydric nature, biocrust constituents like lichens are highly adapted to high temperatures and limited water availability (Green et al., 2011). Through their opportunistic lifestyle and increased heat tolerance when dry, they avoid unfavourable conditions such as high light intensities and temperatures (Kappen & Valladares, 2007). Furthermore, lichens regain their metabolic activity at low water potentials, which leads to a fast recovery of CO₂ exchange even through water vapour uptake or liquid water input from dew (Kappen & Valladares, 2007; Proctor & Tuba, 2002). However, empirical upscaling shows that climate and land use change will decrease their suitable habitat by up to 40% in the next decades, with semi-arid regions being among the most affected (Rodríguez-Caballero et al., 2018). If biocrusts are lost, the ecosystem functions they provide will change as well, leading to reduced hydrological control and alterations in C and N cycling (García-Palacios et al., 2018; Lafuente et al., 2018; Reed et al., 2012).

Growing evidence shows that climate change will affect biocrust communities worldwide (Reed et al., 2019), albeit the effects might be highly area- and species-specific. Along natural aridity gradients, the composition and traits of lichen communities have also found to change in the Mediterranean drylands (Matos et al., 2015). Studies from the Colorado Plateau found that experimental warming and altered precipitation frequency led to a strong decline in moss cover and a shift towards cyanobacterial dominance (Ferrenberg et al., 2015; Reed et al., 2012; Zelikova et al., 2012). Experiments carried out in central and SE Spain showed how simulated warming led to a substantial reduction in biocrust-forming lichen cover and species richness (Ladrón de Guevara et al., 2018; Maestre et al., 2015). In contrast to the studies from the Colorado Plateau, the cover of mosses increased with warming in these experiments, but this did not suffice to compensate the drastic reduction in lichen cover observed (Escolar et al., 2012; Ladrón de Guevara et al., 2018). On a

physiological level, warming experiments have revealed that only some lichen species are able to adapt to warmer temperatures by increasing net photosynthesis, and thus balancing higher respiratory losses, but others are not (Colesie et al., 2018).

Despite the growing literature on this topic, studies on the response of biocrust communities to climate change are still rare compared to vascular plants (Reed et al., 2019). Considering the temporal and spatial scales at which climate change is operating, experiments and field studies have some major limitations. First, they are restricted to relatively small research areas and short time-scales: all experiments conducted to date have been running for 15 years or less (Dacal et al., 2020; Ferrenberg et al., 2015). Second, manipulative climate change treatments potentially introduce unintended side effects that can influence the results (Carlyle et al., 2011) and different manipulation methods can hamper the comparison between studies (Bokhorst et al., 2013; Klein et al., 2005; Ladrón de Guevara et al., 2018). Also, with experiments alone it is difficult to understand climate change impacts on individual physiological processes, and thus gaining a mechanistic understanding of how these impacts translate to the observed changes in growth, cover and composition at the community level.

Mechanistic simulation models are valuable complementary tools to empirical studies because they allow to make projections in time and space, which are difficult to make with experiments, and analyse the underlying physiological processes leading to the observed impacts of climate change on organisms (Pacifci et al., 2015). For vascular vegetation, the gap between empirical and modelling research has been approached in various studies investigating the effect of increasing atmospheric CO₂ and associated climatic changes using dynamic global vegetation models (DGVMs, e.g. Friend et al., 2014; Kolby Smith et al., 2016; Randerson et al., 2009). More locally, modelling studies have addressed topics such as the response of plant composition and traits to different rainfall regimes and aridity in dryland ecosystems (e.g. Henzler et al., 2018; Lohmann et al., 2018; Schwinning & Ehleringer, 2001). However, only few mechanistic modelling approaches focusing on biocrusts and non-vascular vegetation have been conducted so far (Kim & Or, 2017; Porada et al., 2013).

The use of mechanistic models offers great promise to advance our capacity to gain a mechanistic understanding and predict future changes in ground-dwelling lichens in drylands due to climate change. However, we are not aware of the existence of any species-specific physiological model of major biocrust constituents (such as lichens) that has been used to assess climate change effects on these key organisms in drylands. Here we used a mechanistic model developed to simulate a large number of artificial lichen and bryophyte strategies (LiBry; Porada et al., 2013, 2019) to assess the dynamics of the common biocrust-forming lichen *Diploschistes diacapsis* (Ach.) Lumbsch at two different sites

in Spain under simulated climate change. We chose this species because it is one of the most common biocrust-forming lichens on all continents except South America and Antarctica (Bowker et al., 2016) and because its physiology is relatively well studied in comparison to other species (e.g. Lange et al., 1997; Pintado et al., 2005, 2010; Raggio et al., 2014). Additionally, studies have shown a similar physiological responses of biocrusts dominated by this and other species to micro- and macro-environmental variables (Raggio et al., 2014, 2017), suggesting that results obtained for *D. diacapsis* might to some degree be generalisable. Empirical studies also show that this species is particularly affected by increased temperatures (Escolar et al., 2012; Ladrón de Guevara et al., 2018).

We parameterised and validated the LiBry model for the first time for a single species (*D. diacapsis*) and assessed the sensitivity of its metabolic activity and carbon balance (reflected in cover changes) towards changes in atmospheric CO₂ concentration, rainfall, temperature and relative air humidity. We used this model to (a) shed light on the long-term effects of climatic changes on *D. diacapsis*, and compare the effects of changing each of these climate drivers individually versus together on the physiological processes of activation and net primary productivity and the resulting cover and (b) determine the mechanisms leading to the observed decline in lichen cover under experimental warming in the field (Ladrón de Guevara et al., 2018). We also discuss the possibilities and current limitations of process-based models for assessing climate change impacts on biocrusts, as their use is being advocated for this aim specifically and for improving our understanding of biocrust ecology (Ferrenberg et al., 2017).

2 | MATERIALS AND METHODS

2.1 | Species and site description

We used *D. diacapsis*, a terricolous, crustose, greyish-white lichen with a 1–3 mm thick thallus (Figure S1) that is mostly found on calcareous substrate in exposed habitats (Lumbsch, 1988). This species has a global geographical distribution (Galun & Garty, 2001; Ghiloufi & Chaieb, 2018; Pant & Upreti, 1993; Rosentreter & Belnap, 2001), and is a model species representative of biocrusts in Spain (Pintado et al., 2005, 2010; Raggio et al., 2014) and worldwide (Bowker et al., 2016).

We simulated the physiological performance of *D. diacapsis* at two sites in South-eastern and central Spain, respectively: El Cautivo (37°0'N, 2°26'W, 200 m a.s.l.) and Aranjuez (40°2'N, 3°32'W, 590 m a.s.l.). Both sites are characterised by a semi-arid Mediterranean climate, with a higher mean annual temperature (MAT) and lower mean annual precipitation (MAP) in El Cautivo [closest weather station Tabernas MAT: 17.8°C (from 10.3°C in January to 27.0°C in August), MAP: 235 mm (from 2 mm in July to 29 mm in November)] than in Aranjuez [MAT: 14.5°C (from 5.7°C in January to 25.2°C in July), MAP: 410 mm (from 11 mm in July to 52 mm in May)]

(Agencia Estatal de Meteorología (AEMET), 2020b). The cover of vascular vegetation is <40% at both sites, and is mainly characterised by a mosaic of grasses, shrubs and annual plants. The interplant spaces are covered with bare soil or well-developed biocrusts dominated by lichens such as *D. diacapsis* (see Maestre et al., 2013 for a full species checklist). Detailed site descriptions of El Cautivo and Aranjuez are provided in Büdel et al. (2014) and Maestre et al. (2013), respectively.

2.2 | Model description

For the simulation of *D. diacapsis* we used LiBry, a mechanistic model that simulates lichens, bryophytes, terrestrial cyanobacteria and algae (Porada et al., 2013, 2019). A full description of the model can be found in Porada et al. (2019), so we only briefly describe it here. LiBry was developed to quantify the global carbon uptake of non-vascular vegetation driven by climate and environmental conditions. These processes are implemented similarly as in DGVMs (e.g. Cramer et al., 2001; Pavlick et al., 2013), but were adjusted for lichen- and bryophyte-specific properties, such as poikilohydry or the dependence of CO₂ diffusivity on the water content. LiBry is driven by hourly local climate input and environmental conditions determining the photosynthetic rate (based on Farquhar & Von Caemmerer, 1982) and thus gross primary productivity (GPP) and respiration (Q_{10} relationship). Both photosynthesis and respiration depend on the water saturation of the lichen. It increases through rainfall, snowmelt, dew and unsaturated air at relatively high relative humidity, and decreases through evaporation. Evaporation is calculated with a modified Penman–Monteith approach depending on the surface energy balance of the thallus (Monteith, 1981; Porada et al., 2013, 2018). In this modified approach, the surface resistance to water vapour transfer is zero because lichens and bryophytes cannot actively control water losses from the thallus. The aerodynamic resistance to heat transfer depends on the height of the surrounding vegetation, so the impacts of lichens and bryophytes on the roughness length are not considered. Simulated potential evaporation consists of two parts: one driven by net radiation and one driven by the atmospheric vapour pressure deficit. If the sum of these two parts is positive, water is lost by evaporation. If it is negative, dew forms on the thallus surface, which happens if either net radiation or vapour pressure deficit (or both) become negative. Net radiation becomes negative if the thallus emits more energy via long-wave radiation and ground heat flux to the surrounding soil than it receives via downwelling long- and short-wave radiation. The vapour pressure deficit becomes negative if relative humidity exceeds 100%, which did not occur in the measurements from our study site. Moreover, water uptake from unsaturated air is possible in the model if the saturation vapour pressure at the surface is reduced due to negative water potential inside the thallus, which occurs at low water saturation. The model does not explicitly simulate near surface air moisture; therefore, the potential maximum amount of dew condensation was limited to 60 mm/year (evenly distributed to 365 nights) to avoid simulating an infinite reservoir of moisture. This maximum

value was chosen based on measurements of annual dew from El Cautivo, which lay between 35 and 57 mm/year (Uclés et al., 2014).

Water saturation is a proxy for lichen activity, which linearly increases between the minimum saturation necessary for metabolic activation (sat_{\min}) and the saturation at maximum activity (sat_{\max}). Net primary productivity (NPP) is based on the difference between GPP and respiration and is reduced by a species-specific constant turnover rate before being translated to the actual growth rate using the specific thallus area. The growth rate is positive when photosynthetic carbon gains exceed the sum of respiratory and turnover losses, and is negative when either the turnover rate is higher than NPP or when respiratory carbon losses exceed photosynthetic carbon gains (i.e. negative NPP). In the dormant dry state (i.e. no activity), the NPP and respiration are zero and only the turnover rate leads to a slightly negative net growth.

Monthly values for thallus expansion and retreat are calculated based on the actual growth rate. Expansion occurs when the growth rate is positive; thallus cover increases are then limited by the available ground area for growth and reduced by a dispersal efficiency of 85% (Porada et al., 2016). Retreat occurs when the growth rate is negative. The total cover change in each month consists of the sum of thallus expansion and retreat reduced by a constant mortality due to disturbances (e.g. perturbation by rabbits; Eldridge et al., 2010).

In past applications, LiBry simulated the processes described above for different physiological strategies (Porada et al., 2013, 2018). Each strategy is defined by a unique combination of parameter values for 15 physiological traits and thus represents one (theoretical or actual) species. LiBry has been applied to assess the contribution of lichens and bryophytes to global cycles of biogeochemistry and hydrology (Porada et al., 2013, 2014, 2018) and to predict biocrust cover at local and global scales (Porada et al., 2019). However, it has never been applied to analyse species-specific responses at local scales as we are doing here.

2.3 | Model parameterisation

Most physiological model parameters could be derived from a study on the differences in functional ecology of a sun and shade population of *D. diacapsis* close to El Cautivo (Pintado et al., 2005). These include water storage capacity, water saturation at maximum activity, thallus height, optimum temperature for photosynthesis, Q_{10} value of respiration and reference maintenance respiration at 10°C. We used the mean value of these parameters obtained from sun and shade populations. Lichen albedo was calculated from a reflectance curve of a light-coloured lichen dominated biocrusts with a high proportion of *D. diacapsis* (Chamizo et al., 2012).

No direct measurements were available for seven of the parameters necessary to calculate the photosynthetic activity of *D. diacapsis*: molar carboxylation and oxygenation rate of Rubisco ($V_{C,\max}$, $V_{O,\max}$), enzyme activation energy of Michaelis–Menten Constants K_C and K_O , and of $V_{C,\max}$ and J_{\max} (electron transport capacity) and thallus CO_2 diffusivity. These parameters were calibrated using

data on the relationship between net photosynthesis (NP) and light intensity at different temperatures and the dependence of NP on thallus water saturation (Pintado et al., 2005). For doing so, the relevant model functions to calculate NP depending on the light and temperature conditions, and the water content of the thallus, were isolated from LiBry. Calibration was done by visually assessing the differences between measured and modelled values for different value combinations of the calibration parameters within their global possibility range (Porada et al., 2013). The parameter combination that best fit the light curves at different temperatures and the water curve were taken as input parameters to the model (Figure 1, light curves for all temperatures are shown in Figure S2).

For the parameters thallus porosity and turnover rate, no values could be deduced from the available literature. Porosity was therefore assumed to be within a range of 0.3–0.4. Porosities lower than 0.3 led to specific thallus areas lower than 3.6 m² thallus kg⁻¹ C, which led to an unrealistic 100% mortality rate of *D. diacapsis* in El Cautivo. Porosities higher than 0.4 led to high specific thallus areas (>4.3 m² thallus kg⁻¹ C), which are unrealistic considering the structure of *D. diacapsis*. The constant turnover rate (how much of the lichen biomass is lost per time step) is unknown. Therefore, we assumed it to be 0.03 year⁻¹ which is at the lower end of the global value range reported by Porada et al. (2013) because of low turnover rates expected in semi-arid environments.

In LiBry, the negative thallus water potential ($\Psi_{\text{H}_2\text{O}}$) increases with thallus water content and reaches zero at a specific water content $x_{\phi\theta,\text{sat}}$ at which all water is stored extracellularly. $\Psi_{\text{H}_2\text{O}}$ influences how well the lichen can uptake water from the moisture in the air, which can contribute to metabolic activation. We could not find any data on $\Psi_{\text{H}_2\text{O},\text{min}}$, $x_{\phi\theta,\text{sat}}$, and the shape parameter $x_{\Psi_{\text{H}_2\text{O}}}$ of the saturation-dependent water potential curve for *D. diacapsis*. We therefore chose these values such that the obtained water potential curves are within the range observed for dryland lichens (Pintado & Sancho, 2002; Scheidegger et al., 1995; Figure S3).

A more detailed description of the values of species parameters and the respective references are provided in Table S1. The two traits porosity and thallus saturation at which $\Psi_{\text{H}_2\text{O}}$ becomes negative ($x_{\phi\theta,\text{sat}}$) remained unknown. To include the uncertainty in these two parameters in our simulations, all model runs were conducted with a total of 22 strategies. Each strategy represents *D. diacapsis* with all trait values fixed as described in Table S1, but with two different values for the unknown trait porosity (values of 0.3 and 0.4) and 11 values for $x_{\phi\theta,\text{sat}}$ (values from 0.05 to 1). This approach is identical to that usually used with LiBry when it is not applied in a species-specific context (Porada et al., 2013).

2.4 | Modelling hydrophobicity of *D. diacapsis*

The thallus structure of *D. diacapsis* is characterised by a relatively impervious upper cortex, so it has a hydrophobic behaviour when dry (Souza-Egipsy et al., 2002). This property can affect the lichen thallus itself (Pintado et al., 2005) and its impacts on infiltration

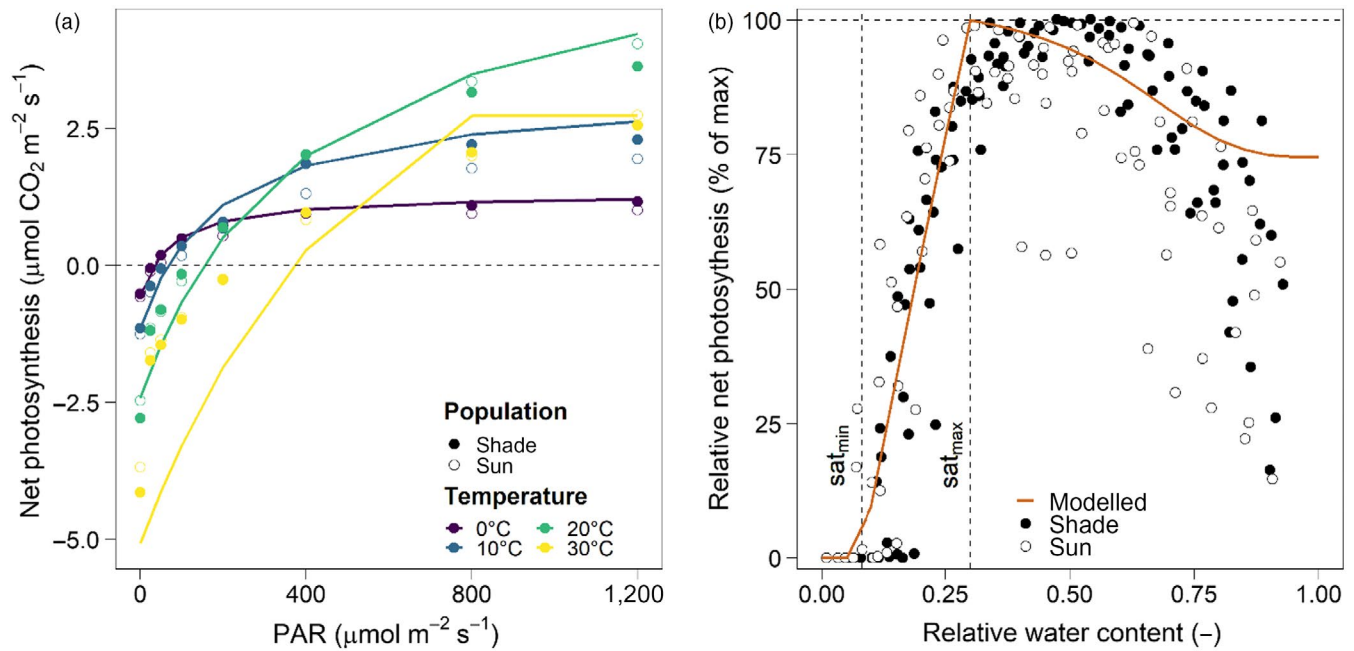


FIGURE 1 Calibration results for photosynthesis (data from Pintado et al., 2005). (a) Light curves of net photosynthesis (NP) at different temperatures and optimal water content; points represent measured values of the sun and shade population. Lines represent the modelled light curves for the best fitting value combination of calibrated parameters. (b) Water curve of relative NP at 15°C and 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ light; points represent measured data for shade and sun populations. Dashed lines indicate the saturation needed for an onset of photosynthesis (sat_{\min}), and the saturation at which maximal photosynthesis is reached (sat_{\max})

(Cantón et al., 2002). We therefore extended the original LiBry model and included a simple formulation of hydrophobicity by introducing the hydrophobicity factor f_{hyd} , which reduces all water uptake by the lichen if the thallus is dry (i.e. if the thallus water content is below a critical saturation Θ_{crit} until which hydrophobicity occurs). The hydrophobicity factor f_{hyd} is calculated from two likely species-specific parameters: the critical saturation Θ_{crit} , and $p_{\text{min,hyd}}$ which is the minimum value for f_{hyd} at a water content Θ of zero:

$$f_{\text{hyd}} = \begin{cases} p_{\text{min,hyd}} * e^{\frac{-1}{\Theta_{\text{crit}}} * \ln(p_{\text{min,hyd}} * \theta)}, & \text{if } \theta \leq \theta_{\text{crit}} \\ 1, & \text{else} \end{cases}$$

The hydrophobicity factor f_{hyd} increases exponentially, taking values from $p_{\text{min,hyd}}$ for $\Theta = 0$ to 1 for $\Theta = \Theta_{\text{crit}}$ (Figure S4). Modelled water uptake is then multiplied by f_{hyd} . Because of the reduced water uptake, and consequently reduced activity at low thallus moisture contents, related with hydrophobicity, photosynthetic and respiratory activity are also reduced. This effect is removed as soon as the moisture content of the thallus is sufficient to show no hydrophobic behaviour anymore. This mechanism ultimately also affects the carbon balance of the lichen, which is reflected in the cover. In other words, the stronger the hydrophobicity, the lower the resulting cover. The parameters Θ_{crit} and $p_{\text{min,hyd}}$ are unknown, and we could not find any indication in the literature as to how their values should be chosen. However, modelled lichen activity was sensitive to both parameters. We thus tested different value combinations and visually assessed the fit of modelled and measured lichen activity (Figure S5). We selected the value combination of

$\Theta_{\text{crit}} = 0.03$ and $p_{\text{min,hyd}} = 0.1$ for all further analyses. Including this simple representation of hydrophobicity greatly improved the model fit of lichen activity to measured data from El Cautivo (Figure S5), indicating that hydrophobicity represents an important mechanism that should be considered when modelling biocrust-forming lichens. Additional simulation results for the model without hydrophobicity and for a different value combination show quantitative but no qualitative differences, that is, general model assessments are robust, despite the parameter uncertainty (Figure S6).

2.5 | Climate forcing data

The model is driven by hourly climate data (long-wave radiation, short-wave radiation, snow cover, rainfall, relative air humidity, air temperature and wind speed). For both simulation sites (El Cautivo and Aranjuez), we obtained on-site climate data of all necessary variables except long-wave radiation, which was taken from the WATCH dataset (Weedon et al., 2011; see Porada et al., 2019 for a detailed description of data preparation).

For El Cautivo, we used data from 2013 with a temporal resolution of 10 min, which were aggregated to hourly values (Büdel et al., 2014). Data gaps of more than four consecutive hours were filled with the values of the corresponding hours from the day before. Data gaps of <4 hr were linearly interpolated using the last and the next available data point. For the Aranjuez site, we used climate data from an in situ meteorological station (2009–2016). This dataset contained larger periods of missing data, which were filled with

data from the nearby Aranjuez weather station of the Spanish meteorological service (AEMET), located 3.7 km away. If these data were not available, missing values were taken from 2012, a year without missing values. Due to the unreliable on-site wind measurements, wind data were taken from AEMET, and only larger gaps in the data were filled with field station measurements.

2.6 | Model validation

To validate the model results under current climatic conditions, we used chlorophyll fluorescence as an estimate of lichen metabolic activity and surface temperature field data of *D. diacapsis* from El Cautivo (Büdel et al., 2014; Raggio et al., 2017). These data were collected in 2013 and had a temporal resolution of 30 min. We compared daily and monthly activity and surface temperature patterns of simulated mean values in the steady state with measured chlorophyll fluorescence and temperature data.

2.7 | Simulation experiments

After model calibration and validation, we conducted two simulation experiments. The first one (hereafter Experiment 1) in El Cautivo, where we assessed the sensitivity of lichen physiological processes and cover towards systematic changes in single and combined climate variables. The second experiment (hereafter Experiment 2) mimicked and extended an ongoing climate change experiment in Aranjuez (Dacal et al., 2020; Maestre et al., 2013) to determine the mechanisms leading to the observed changes in biocrust cover and to see how well the model can be transferred to other sites despite the intra-specific physiological variability of *D. diacapsis* (Lange et al., 1997; Pintado et al., 2005).

For Experiment 1, the initial lichen cover was set to 10%, and simulations were run for 900 years until a steady state in cover (i.e. cover between years is not changing anymore and thallus expansion and retreat balance each other) was reached. The chosen initial cover value did not influence the steady state cover but only the simulation time that is needed to reach the steady state. We first run the model under current climatic conditions with an atmospheric CO₂ concentration of 395 ppm (values observed in 2013, Tans & Keeling, 2020). To test the sensitivity of *D. diacapsis* to altered climate conditions, we afterwards simulated two different climate change scenarios according to the Representative Concentration Pathway (RCP) 4.5 and 6.0 scenarios (Moss et al., 2010). For both scenarios, we altered climatic drivers (rainfall, temperature, air humidity) in isolation and combined, in each setting with the given concentration of atmospheric CO₂ (RCP 4.5:650 ppm, RCP 6.0:850 ppm; Moss et al., 2010). The changes in climate variables were applied to hourly values so that the annual variability in the time series remained the same. For the RCP 4.5 and 6.0 scenarios, we increased temperature by 3 and 5°C, respectively, which corresponds to the projections of annual change in maximum temperature for Southern Spain in 2100

(Agencia Estatal de Meteorología (AEMET), 2020a; IPCC, 2014). To disentangle the isolated effect of a temperature increase, we scaled relative humidity down so that the actual saturation vapour pressure of the air remained the same across all temperature scenarios. Rainfall was decreased by 30% for both scenarios (Agencia Estatal de Meteorología (AEMET), 2020a; IPCC, 2014).

Linear trend analyses showed that relative humidity in Southern Spain decreased between 0.7% and 2.5% per decade between 1973 and 2002 (Moratíel et al., 2010). We decreased relative humidity by both 10% and 25% in each RCP scenario to represent two possible reductions in relative humidity over the next 100 years. In both RCP scenarios, we tested both interactions of all three variables. Additionally, we changed the same climate variables without increasing atmospheric CO₂ in a control scenario.

For Experiment 2, the model was run with the exact same parameterisation of *D. diacapsis* as for El Cautivo but driven by local climate resembling the ongoing climate manipulation experiment in Aranjuez (Escolar et al., 2012; Ladrón de Guevara et al., 2018). This full factorial experiment includes lichen-dominated biocrust plots under control and climate change treatments which are warming (on average +2.7°C), rainfall exclusion (interception of 33% of rainfall) and a combination of both warming and rainfall exclusion (Figure S7). Micro-climatic measurements showed that the warming treatments decreased relative air humidity (on average by 11.5% in 2016). For a detailed description of the experiment, see Escolar et al. (2012).

We first generated new time series of temperature, humidity and rainfall mimicking the manipulation experiment in Aranjuez. For doing so, we used the biocrust surface temperature and near surface relative humidity measured within the experimental plots to calculate the relative difference of these two variables between control and warming treatments for each hour of the years 2016–2018. We applied the mean relative differences to the climate time series of Aranjuez to generate new time series of air temperature and relative humidity based on the observed differences between the treatments. For the months June, July and August, no measurements were available; therefore, we linearly interpolated hourly differences between May and September. To generate a time series with reduced rainfall, we reduced hourly rainfall values by 33%. With this new climate data, we conducted five simulation experiments: (a) control treatment without manipulations, (b) rainfall exclusion, (c) warming alone treatment with an increase in temperature (d) warming treatment with an increase in temperature and a decrease in air humidity and (e) a combination treatment of (b) and (d). We ran the model for 900 years with an initial lichen cover equal to the mean initial cover value (68%) of all experimental plots. We then compared the changes in *D. diacapsis* cover driven by the treatments with the respective experimental results for biocrust-forming lichens. Since the modelled dynamics are slower than the observed ones, we compared the measured response over 10 years of climate manipulation with the steady-state response in the model.

Since the model is deterministic, no replicates were simulated. In all scenarios of the two modelling experiments, we simulated

an undisturbed environment without competition with vascular or non-vascular plants, meaning that *D. diacapsis* grows on bare ground and could potentially cover the full area. Although biocrusts are vulnerable to anthropogenic and natural disturbances that can lead to changes in their cover and biomass (reviewed in Zaady et al., 2016), we excluded them from our simulations due to a lack of quantitative estimates of their frequency and resulting cover reduction.

3 | RESULTS

3.1 | Model validation

In a steady state under current conditions, *D. diacapsis* was metabolically active 16% of the time during the year. In general, the model corresponded reasonably well with observed daily patterns of *D. diacapsis* activity in El Cautivo [Figure 2, root mean square error (RMSE) between 0.02 (June and July) and 0.26 (October)]. Activity peaks occurred during the early morning hours, whereas activity during the day was very low. Most active hours occurred in autumn and winter (from September until January) and only a few were observed in the summer months (May until August). In September and October, the magnitude of the early morning activity peak was overestimated

by the model, although the timing of the peak corresponded well to the measured data.

Average monthly thallus surface temperature was predicted very accurately, whereas maximum and minimum temperatures, respectively, were underestimated and slightly overestimated by the model (Figure S8). The surface temperature peak in the warmer months was shifted by around 2 hr and underestimated in magnitude by the model (Figure S9). However, during the most active hours of the day, the temperature validation was very satisfactory.

Simulated dew occurred during 78% of the nights and amounts to 30% of the time in a year. It was characterised by relatively small but constant watering events resulting in a total dew input of 24.8 mm/year, which was mainly accumulated during the nights between September and April and was particularly high in September and October (Figure S10). Rainfall events occurred in 1.3% of the hours and generally delivered larger water amounts in a short period. Rain and dew impacted the thallus water saturation differently, as shown exemplarily for 3 days in Figure 3a,b. In most cases, rainfall led to an immediate increase in lichen water saturation to values exceeding the threshold saturation of 0.3 for maximum activity (sat_{max}). In contrast, dew led to a more gradual increase in thallus saturation; a dew event must be sufficiently long and intense for the saturation to exceed the levels necessary for activation (sat_{min}).

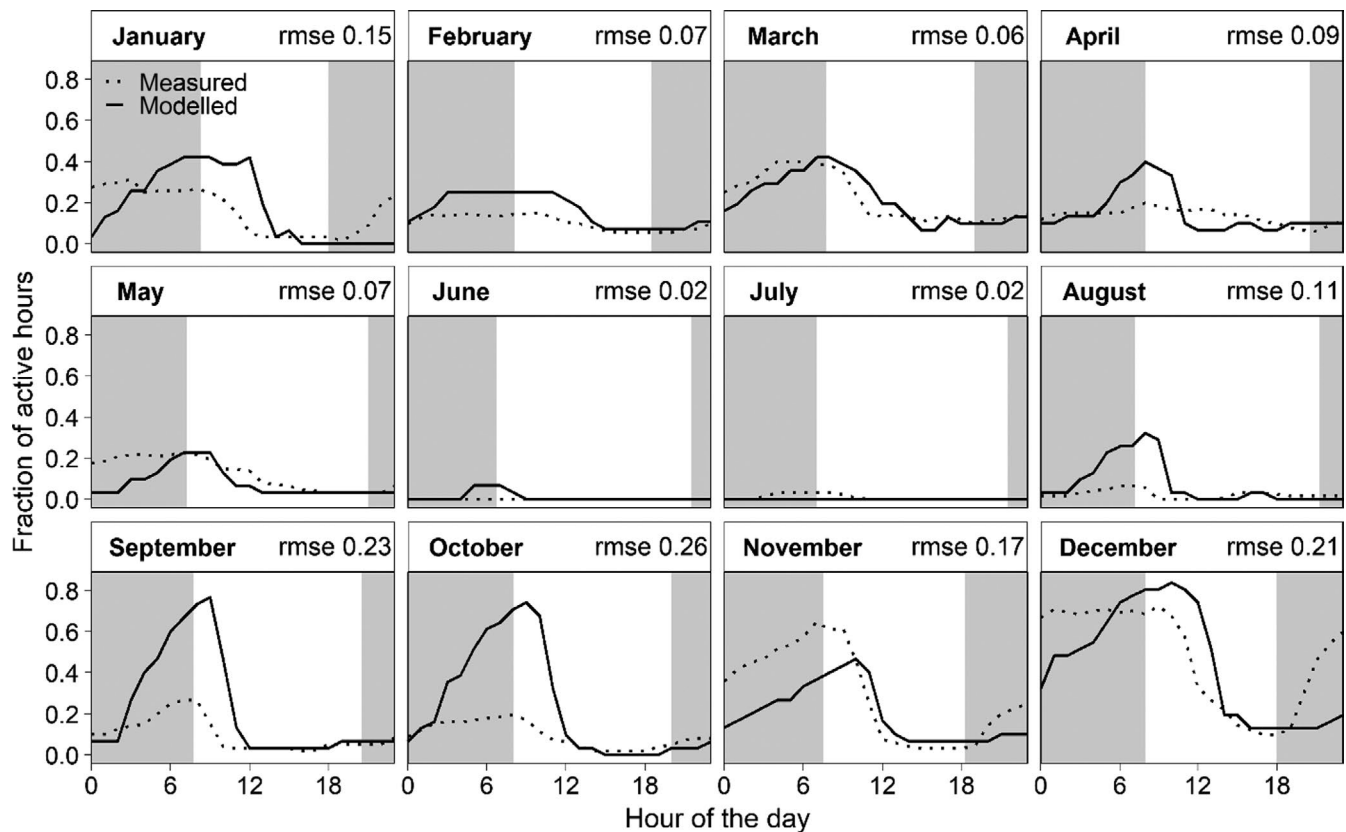


FIGURE 2 Daily fraction of active hours in each month. Modelled and measured values represent the mean of a binary representation of photosynthetic yield (yield/no yield; two samples) at the El Cautivo field site and binary values of activity represented by saturation status, respectively. Grey and white plot areas indicate night- and daytime, respectively

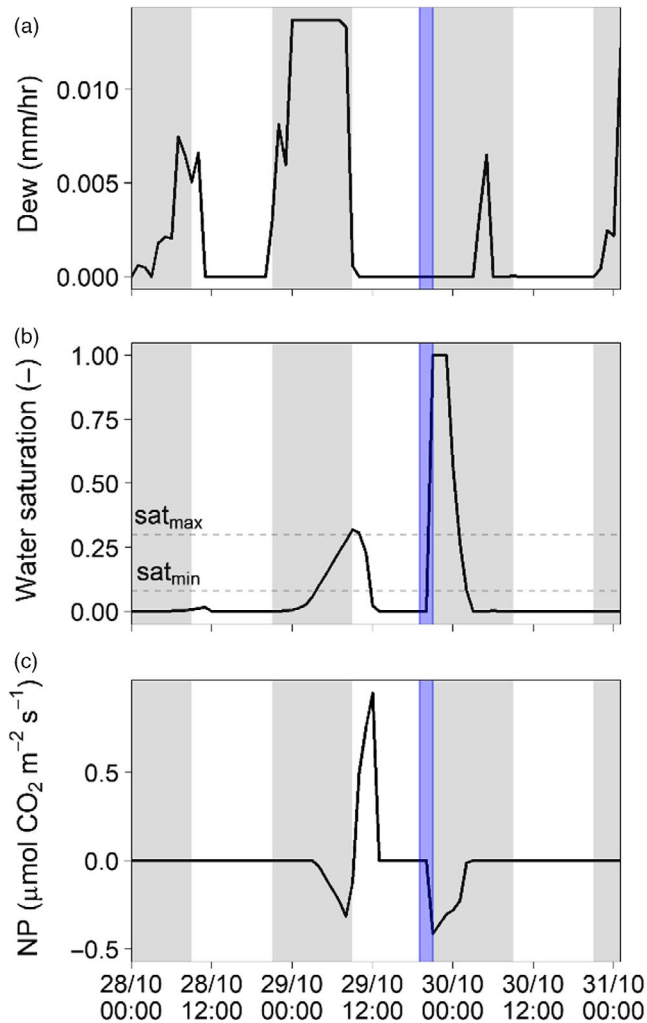


FIGURE 3 Modelled water saturation and net photosynthesis (NP) in response to dew formation and rainfall. (a) Simulated dew formation, (b) water saturation with indication of saturation values of onset of photosynthesis (sat_{min}) and maximal photosynthesis (sat_{max}), and (c) NP in hourly resolution for a period of two days in October 2013. Grey and white plot areas indicate night- and daytime, respectively. The blue plot area marks a large precipitation event with a total amount of rainfall of 18.8 mm and a duration of 3 hr

3.2 | Experiment 1: Sensitivity of lichen physiological processes and cover towards changes in climate

The modelled steady state cover of *D. diacapsis* after 900 simulation years under current climatic conditions was 37%. We found that, in the model, changing climatic variables had varying and interacting effects on the steady-state cover (Figure 4). We observed a consistent positive effect of increased CO_2 levels for all climate scenarios. Under current climatic conditions (control scenario), the net carbon gain was higher in the scenarios with increased CO_2 despite the same annual activity time of 16% (annual NPP under current CO_2 : 8, RCP 4.5: 9.5, RCP 6.0: 10 $g\ C\ m^{-2}\ s^{-1}$), leading to a cover increase by 30% and 32% for the RCP 4.5 and the RCP 6.0 scenario, respectively (Figure 4). The cover difference between the control and RCP 4.5 scenarios was larger

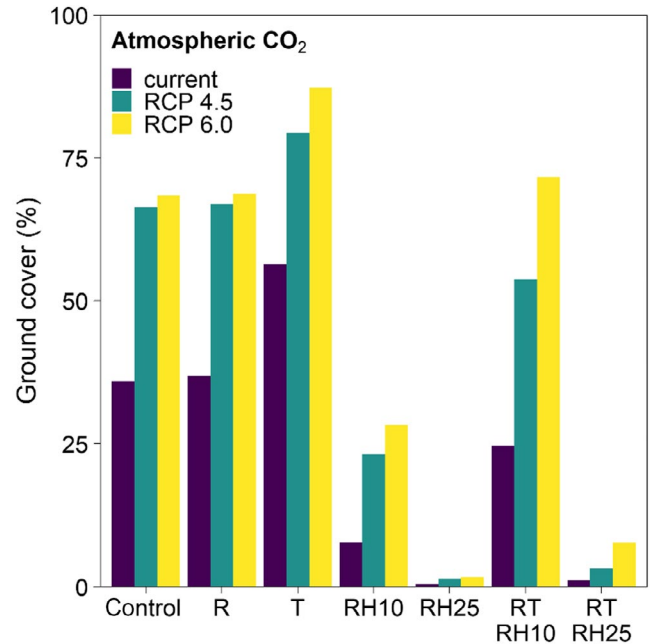


FIGURE 4 Steady-state cover of *Diploschistes diacapsis* for different atmospheric CO_2 (current = 395 ppm, RCP 4.5 = 650 ppm, RCP 6.0 = 850 ppm) and climate scenarios. Control = no changes in rainfall, temperature and relative humidity, R = rainfall reduction by 30%, T = temperature increase by 3°C for current and RCP 4.5 scenario and 5°C for RCP 6.0, RH10 = reduction of relative humidity by 10%, RH25 = reduction of relative humidity by 25%, RTRH10 = combination of R, T and RH10 scenario, RTRH25 = combination of R, T and RH25 scenario

than the differences between RCP 4.5 and 6.0 scenarios, indicating a saturation type response of the effect of increased CO_2 levels. This was particularly visible under current climate and decreased rainfall.

Increasing temperature by 3 or 5°C had a positive effect on modelled steady-state cover (Figure 4). The activity between the three temperature scenarios was similar (annual active time fraction = 18%, 18% and 19% for current, RCP 4.5 and RCP 6.0 scenarios) because moisture availability was the same in all of them. A reduction in rainfall did not show an effect on lichen cover in any climate change scenario and climate variable combination.

A decrease in relative humidity by 10% and 25% led to a substantial decrease in lichen cover to values below those of the control scenario in both RCP scenarios considered (Figure 4). At a 25% reduction of relative humidity, lichen cover was reduced to values from 1% to 8% depending on atmospheric CO_2 resulting from a reduction in dew input (decrease by 31%–36% relative to control) and associated activity time (decrease by 63%–69% relative to control; Table S2).

The climate sensitivity results indicate an interaction between the effects of the single climate variables because the cover change of the combined scenarios differed from the additive changes of the respective single variables. Generally, cover decline was lower for the combined scenario with 10% lower relative humidity (17% for RCP 4.5 and 24% for RCP 6.0) and higher for the one with a 25% lower relative humidity (11% for RCP 4.5 and 13% for RCP 6.0) compared to what would have been expected from adding the single effects.

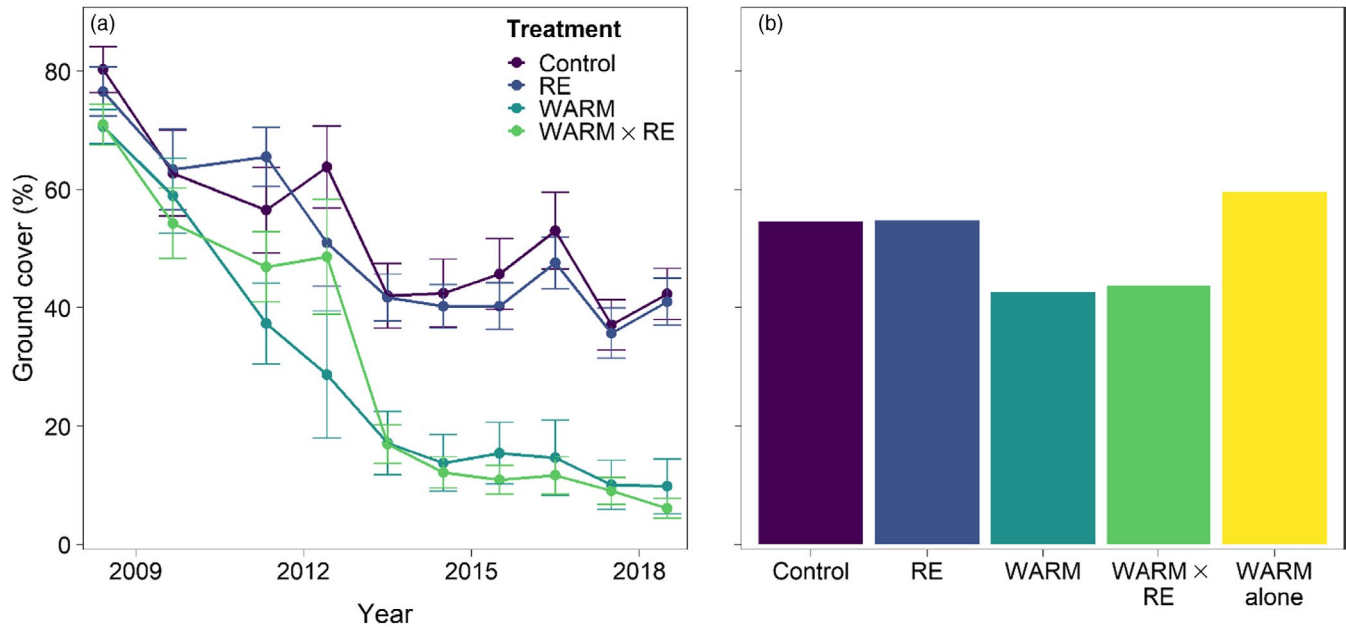


FIGURE 5 Changes in the cover of *Diploschistes diacapsis* as a result of climatic conditions in the Aranjuez experiment and in the model. (a) Measured cover change of biocrust lichens (including *D. diacapsis*), (b) modelled cover in steady state. RE (rainfall exclusion) refers to a 30% reduction in rainfall, WARM (warming) to an increase in temperature by 2.7°C and the associated indirect reduction in relative humidity, WARM × RE is the combination of the scenarios RE and WARM (associated with reduced relative humidity) and WARM alone refers to the simulated scenario where the effect of an increased temperature by 2.7°C was tested without the associated reduction in relative humidity

3.3 | Experiment 2: Revealing the mechanisms leading to observed cover decline under climate change

Steady-state cover of the control scenario in Aranjuez was higher than in El Cautivo (Figure 5b). However, the observed effects of warming and rainfall reduction on the cover of *D. diacapsis* were qualitatively comparable between these sites. In the steady state, we found no effect of rainfall exclusion on lichen cover (55% cover for both control and rainfall exclusion treatments). The warming alone treatment had a slight positive effect on steady-state cover (59%) but the associated changes in relative humidity as observed in the field experiment led to a decrease in lichen steady-state cover (warming scenario: 43%, combination of warming and rainfall exclusion: 44%). The qualitative effects of climate change treatments on modelled cover were similar to the observed effects (Figure 5a), but modelled effects were not as strong as those observed in the field.

4 | DISCUSSION

4.1 | LiBry reproduces physiological behaviour and cover of *D. diacapsis*

Overall, the validation results were satisfactory; LiBry predicted mean daily activity reasonably well for all months except September and October and daily lichen surface temperature for the midday peak temperatures from April to October. During these hours, however, the lichen was mostly inactive and this difference between

measured and modelled temperature should not influence modelled lichen cover.

An explanation for the dampened diurnal temperature response in the model could be the relatively simple approach for calculating soil heat transfer, which accounts for the temperature gradient between soil and thallus and the soil parameters of heat capacity and thermal conductivity. A decrease in the thermal conductivity would increase the amplitude of the diurnal temperature response of the thallus surface. Also, the approach for calculating the aerodynamic resistance to heat transfer (adapted by Allen et al., 1998; Porada et al., 2013), which depends on surface roughness and wind speed, might have led to an overestimated cooling of the thallus surface in the early morning hours and therefore a higher dew input. This dew input could partly explain the overestimation of activity that we see during some periods of the year.

Periods of activity over- and underestimation by the model can be explained by two different mechanisms. First, the underestimation of activity during some periods (especially November until January) could be explained by different mechanisms of rainfall activation in the model and in the field. In the field, rainfall is an important source of hydration, leading to extensive moist periods in the winter months (Raggio et al., 2014). Rainfall water can be stored within the thallus, on its surface, or as soil moisture (Berdugo et al., 2014). This temporal storage can indirectly lead to longer activation periods through rainfall and are not represented in the model, where excess water is lost from the system. Second, the overestimation of activity could be explained by the thallus saturation model. The high activity in September and October can thus be explained by the relatively high dew input in these months

(Figure S10). One potential reason for this is that dew is estimated correctly by the model, but the dew amount taken up by the thallus is higher in the model compared to the field (either due to evaporation or underestimated hydrophobicity). Alternatively, the model may have overestimated dew inputs, and thus lichen activity. However, dew production in the model agrees with measured values from a nearby area (Cabo de Gata-Níjar national park), where dew occurs in 78% of the nights (Uclés et al., 2014). The estimated total amounts differ between that study (35–57 mm/year from 2007 to 2010) and our model (25 mm/year). Apart from the inter-annual and spatial variability in dewfall, these discrepancies might result from different reference surface areas. Model results reflect dew formation on the thallus surface, whereas the field study reflects a range of surface covers, including plants and stones that have higher relative contributions to dew formation compared to biocrusts (Uclés et al., 2016).

The analysis of physiological processes in hourly resolution (Figure 3) showed that the diurnal response of modelled lichen hydration and NP is similar to the responses observed in the field. Dew activation during the night was the main hydration source in the model, leading to 89% of the lichen's active time, whereas rainfall alone only accounted for 6% of active time. In 5% of the time, there was an overlap when both watering events occurring simultaneously. The activity window caused by simulated dew is typically longer than that caused by rain. This finding is not fully supported by field observations that showed the longest activation periods from rain events followed by cloudy days in the same research area (Green et al., 2018; Raggio et al., 2014). However, this does not contradict the well-known reliance of biocrust-forming lichens on dew in the study area, which allows for frequent net carbon gains independent of rainfall and interrupts long desiccation periods that negatively impact their physiological performance (Green et al., 2011; Pintado et al., 2010; del Prado & Sancho, 2007; Raggio et al., 2014).

Modelled steady-state cover under current conditions (37%) corresponds to the total biocrust cover in the Tabernas region (40%–45%), but it is higher than the measured proportion of chlorolichens (15%; Büdel et al., 2014). This discrepancy is not surprising, since the model did not include competition for space with vascular plants and other lichens and bryophytes, which is intense in these communities (Maestre et al., 2008). Against this background, the modelled steady-state cover seems to be within a reasonable range for this ecosystem, and falls within what has been observed in the field (Lázaro et al., 2008).

4.2 | Relative humidity drives climate change responses of *D. diacapsis*

Changes in single climate variables are unrealistic under climate change conditions and research generally suggests that the effect of different climate change drivers is interactive rather than additive (e.g. Rillig et al., 2019; Sala et al., 2000). However, isolating and testing the effects of single variables using a simulation model can

help to disentangle the overall effects of climate change on lichen cover and activity and determine how the single variables interact, something not always possible to do with field experiments. Overall, the modelled response of *D. diacapsis* to changes in single climate variables was in good agreement with laboratory and field measurements.

Carbon exchange studies with biocrust-forming lichens (including *D. diacapsis*) show increasing photosynthetic rates with CO₂ partial pressure, albeit the effect size varies between species and depends on the thallus water content (Lange, 2002; Lange et al., 1997, 1999). However, it must be considered that modelled carbon uptake and growth are not nutrient limited because nitrogen and phosphorus cycles are not included in the model. In reality, the positive effect of increased CO₂ levels will probably be counteracted by limited nutrient availability (Goll et al., 2012). If the crust is active (i.e. no water limitation), modelled photosynthesis is generally light- and temperature-limited, which partly explains the small cover difference observed between the RCP 4.5 and 6.0 scenarios.

Increased temperatures resulted in a higher NP of *D. diacapsis* in the model. This lichen is mainly active in the early morning hours, when conditions for photosynthesis are suboptimal (low radiation and temperature; Figure S11) and resemble the climate of more temperate environments (Pintado et al., 2010). Under these conditions, NP can benefit from higher temperatures given enough moisture from overnight dew.

Although both rainfall and non-rainfall water inputs (NRWI) are important sources of hydration for biocrust-forming lichens (Raggio et al., 2014, 2017), our modelling results show no effect of a decrease in overall precipitation but a very large effect of decreases in relative humidity. The lack of effects of rainfall reduction on lichen cover can be explained by the fact that, albeit reduced, rainfall events are still large enough to saturate the lichen. Studies investigating how different sources of hydration shape activity patterns of biocrusts across Europe found similar evidence (Colesie et al., 2016; Raggio et al., 2017). When testing the relationship between monthly activity and monthly rainfall amount across different sites, the effect rainfall on activity showed a saturation type response (Raggio et al., 2017). Similarly, in that study, the maximum net photosynthesis of lichen-dominated biocrusts from the Alps was independent of rainfall duration and showed similar photosynthesis rates following activation by rainfall events of one or several days (Colesie et al., 2016). Accordingly, other studies have shown that the timing, size and frequency of individual rainfall pulses, rather than average rainfall amount, affect biocrust performance and cover (Baldauf et al., 2018; Belnap et al., 2004; Zelikova et al., 2012).

Our results correspond to field results from Aranjuez showing a much larger influence of reductions of NRWI driven by experimental warming than of rainfall on the photosynthetic performance of biocrust-forming lichens (Ladrón de Guevara et al., 2014). They underline the importance of NRWI for *D. diacapsis* (Pintado et al., 2010) because a reduction in relative humidity drastically reduces dew input, and thus leads to a reduction in activity time and lichen cover.

Activity was reduced most in the morning hours (Figure S12), when the lichen usually gains carbon leading to a reduced NPP (Figure S13) and consequently cover.

Activation by dew events during the night and early morning usually leads to activity events under suboptimal radiation and temperature conditions (Colesie et al., 2016; Raggio et al., 2014). Dew nights are often followed by sunny and clear days, which leads to a reduced activity time compared with cloudy conditions after rain events (Raggio et al., 2014). Our model results show a similar pattern, with higher median carbon fixation for large precipitation events. However, precipitation is scarce and the smaller activity pulses by dew sum up to substantial carbon gains over the year.

We found an interaction rather than an additive effect when changing all climate variables at the same time. Generally, our results suggest that an increase in atmospheric CO₂ could mitigate some of the negative effects of reduced water availability, and that this effect is larger at higher temperatures. However, the net benefits of mitigation at higher atmospheric CO₂ become smaller if relative humidity decreases (a trend being already observed in Spain in Moratiel et al., 2010). Additionally, there is a general trend towards warmer and dryer soils that can further reduce water availability and increase drought stress for biocrusts (Soong et al., 2020). Field studies on this subject are still very rare, but a study conducted in the Mojave desert suggests that higher atmospheric CO₂ cannot mitigate the negative effects of drought on biocrust cover (Wertin et al., 2012). Our results highlight the key role of relative humidity, although its importance for biocrust activity has been discussed in empirical studies (Pintado et al., 2010; Raggio et al., 2017), the use of a model allowed us for the first time to quantitatively and qualitatively compare its effect to those of other climate drivers.

General trends for relative humidity under climate change are still under debate and seem to be regionally variable. Some studies suggest that globally, the averaged land relative humidity trends are insignificant (Dai, 2006; Willett et al., 2008); however, regionally variable tendencies of decreasing or increasing relative humidity have been observed widely over the last decades (e.g. Moratiel et al., 2010; Simmons et al., 2010; Vicente-Serrano et al., 2018). For Spain, specifically, long-term climate data consistently show a negative trend in land relative humidity with particularly large decreases in spring and summer (Espadafor et al., 2011; Vicente-Serrano et al., 2014, 2018). Model projections also predicted a drop in relative humidity by 2070–2099 in Southern Europe with a response amplitude depending on the strength of the climate forcing (Ruosteenoja & Räisänen, 2013). Despite variable results, global observational data from the last decade show a decreasing trend in relative humidity over terrestrial areas in large parts of the world (Simmons et al., 2010; Vicente-Serrano et al., 2018). These areas include almost all regions where biocrust coverage is present (Rodríguez-Caballero et al., 2018) and since *D. diacapsis* is among the most frequent biocrust species in all continents except South America and Antarctica (Bowker et al., 2016), many of these regions also include *D. diacapsis*.

Additionally, universal and significant relationships between biocrust activity and climate variables were found across European habitats irrespective of particular species composition (Raggio et al., 2017). These responses are in line with findings in El Cautivo, where biocrusts differing in their dominant species resembled each other with regard to activity and carbon exchange patterns (Raggio et al., 2014). Therefore, the observed and simulated trend in *D. diacapsis* cover decline at our study sites is likely to be representative of other lichen-dominated biocrusts. For global vegetation, this association has already been shown with satellite-based models, which suggest that a positive effect of higher CO₂ levels is offset by the increase in vapour pressure deficit (i.e. reduction in relative humidity) leading to an overall decrease in the NDVI (normalised difference vegetation index), leaf area index and estimated gross primary productivity (Yuan et al., 2019).

4.3 | Modelling results mimic observed responses in the field

Application of the model to the climate change experiment in Aranjuez showed qualitatively similar effects as the systematic climate sensitivity analysis in El Cautivo, whereas quantitative cover estimates are higher in the model compared to the field experiment. We found no effect of rainfall exclusion, and a negative effect of both warming and a combination of warming and rainfall exclusion on lichen cover. Warming alone, without the associated reduction in relative humidity, had a slightly positive effect.

Overall, the higher quantitative cover estimates in the model can partly be explained by the lack of disturbance in our study design. Anthropogenic and natural disturbances can lead to changes in biocrust community structure, cover, biomass and species richness (see review by Zaady et al., 2016). Physical disturbance such as trampling can have similar effects on biocrusts as climate change (Ferrenberg et al., 2015), therefore potentially exacerbating its negative effects. Once disturbed, biocrusts generally have slow recovery rates especially under dry conditions (Weber et al., 2016). In Aranjuez, natural disturbances such as perturbation by rabbits can reduce biocrust cover (Eldridge et al., 2010) and the experimental setup might have introduced disturbances such as a reduction in water availability by run-on. These effects are not included in the model.

Qualitatively, model results are in line with field observations, which showed no significant effect of decreased rainfall, but a strong negative response of the lichen to increased temperatures. Between 2008 and 2011, *D. diacapsis* cover declined by around 8% in the warmed plots and by roughly 5% in the plots with both, warming and rainfall exclusion (Escolar et al., 2012). Total biocrust lichen and *D. diacapsis* cover continued to decline until the total cover difference between warmed and non-warmed plots was about 40% in 2016 (Ladrón de Guevara et al., 2018). The modelled steady-state cover differences between warmed and non-warmed treatments (difference of ca. 10% cover) correspond well to the reported

values for the first period of the experiment (Escolar et al., 2012). However, the model did not reproduce the drastic further decline in lichen cover over the next years. This is not surprising as Ladrón de Guevara et al. (2018) stated that the rapid loss of lichen cover could partly be explained by the easy detachment of the lichen thalli from the soil surface and the consecutive loss of thallus parts through wind. This process is not represented in the model; thus, it was to be expected that modelled cover losses are less drastic than the observed losses. Additionally, the physiological trait values of *D. diacapsis* are variable between different locations and even between plots of different exposure within one site (Lange et al., 1997; Pintado et al., 2005). Therefore, the population in Aranjuez might differ in some physiological parameters from the population in El Cautivo, which could further explain differences between model and experiment.

Escolar et al. (2012) hypothesised that the decline in cover under warming could be promoted by an associated increase in respiratory carbon losses, which could not be compensated by photosynthetic activity. However, they found a significantly higher Fv/Fm ratio of *D. diacapsis* under warming, indicating a higher efficiency of photosystem II, and therefore raise doubts about this hypothesis. If photosynthetic carbon losses were large enough to impair the carbon balance, they would likely have led to a lower Fv/Fm ratio as this is an indicator of the photosystem II efficiency and of the general health and stress state of the lichen (e.g. Demmig-Adams et al., 1990; Gauslaa & Solhaug, 1996; Pirintsos et al., 2011). With our model, we showed that increasing temperatures alone led to an increase rather than a decline in lichen cover, which is consistent with their observation of a higher photosynthetic efficiency under warming. The indirect effects of warming on relative humidity and therefore NRWI were responsible for the cover decline in the model. Therefore, we hypothesise that they were also responsible for the cover decline observed in the field experiment (Ladrón de Guevara et al., 2018).

5 | CONCLUSIONS

Our modelling results provide the first forecasts of long-term climate change effects on a dominant biocrust-forming lichen. They highlight the importance of relative humidity as a driver of the physiological responses of *D. diacapsis* to climate change, and indicate that increasing CO₂ concentrations could mitigate the effects of decreasing water availability to a certain degree. Negative effects of drier air rather than higher temperatures might be the key factor in determining dryland lichen survival and cover under future conditions. Global climate trends suggest that this mechanism is of relevance for many lichen-dominated dryland biocrust communities that rely on dew deposition as a major water source. Our study showed that the LiBry model can project local and species-specific changes in *D. diacapsis* abundance under climate change. Since *D. diacapsis* is a relatively well-studied species with some knowledge on its trait-variability and has a wide global distribution, a follow-up

study could improve our understanding of the future distribution of *D. diacapsis*-dominated biocrusts worldwide using data from global climate projections. These findings might even be partly transferable to other biocrust communities, as the physiological response of some biocrusts to micro- and macro-environmental variables can be very similar across biocrusts of different species compositions. Our results highlight the value of process-based modelling to disentangle the effects and interactions of major climate change drivers acting simultaneously and in isolation, something that it is difficult to do in the field, and provide guidelines for future climate change experiments with biocrusts. They should explicitly consider the indirect effects of increased temperature on relative humidity and non-rainfall water inputs, especially in areas where these are important sources of biocrust hydration. We showed that a detailed understanding of the underlying processes by complementing experimental work with modelling is necessary to explain non-additive effects of altered climate drivers on biocrust performance. This will hold even more in more complex studies focusing on whole biocrust communities. We therefore advocate for an integration of the strength of experimental approaches, field studies and modelling to gain a detailed view on how lichens and biocrusts might respond to future climate change from all possible angles.

ACKNOWLEDGEMENTS

This research was supported by the Collaborative Research Centre 973 (www.sfb973.de) of the German Research Foundation (DFG) and by the European Research Council (grant agreement no. 647038 (BIODESERT)). P. Porada appreciates funding by Deutsche Forschungsgemeinschaft (DFG, German Research Foundation)—408092731. F.T. Maestre acknowledges support from Generalitat Valenciana (CIDEGENT/2018/041) and the Alexander Von Humboldt Foundation. J. Raggio acknowledges the ERA-Net BiodivERSa program as Soil Crust InterNational (SCIN) and The Spanish Ministerio de Economía y Competitividad (MINECO) project numbers PRI-PIMBDV-2011-0874 and CRYPTOCOVER, CTM2015-64728-C21-R. We thank Cristina Escolar, Victoria Ochoa, Beatriz Gozalo, Sergio Asensio, Roberto Lázaro, David Sánchez-Pescador, Mónica Ladrón de Guevara and Patricia Alonso for their help with the setting up, maintenance and monitoring of the field experiments over the years. We thank Bettina Weber and Burkhard Büdel for providing the meteorological data for El Cautivo which was collected within the Soil Crust InterNational (SCIN) project. We thank the high-performance computing service of the Freie Universität Berlin (ZEDAT) for providing the resources for running the simulation experiments. Open Access funding enabled and organized by Projekt DEAL. WOA Institution: Freie Universität Berlin Blended DEAL: Projekt DEAL.

AUTHORS' CONTRIBUTIONS

S.B., P.P., B.T. and F.T.M. planned and designed the research; S.B. conducted the modelling experiments; J.R. and F.T.M. provided the field data; S.B. and P.P. did the data analysis, all authors contributed to data interpretation; S.B. wrote the manuscript and all authors revised it.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13563>.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study, all modelling results and R-Scripts to reproduce the findings and the model source code are openly available in 'figshare' at <https://doi.org/10.6084/m9.figshare.12274979.v5> (Baldauf, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Baldauf S, Porada P, Raggio J, Maestre FT, Tietjen B. Relative humidity predominantly determines long-term biocrust-forming lichen cover in drylands under climate change. *J Ecol*. 2021;109:1370–1385. <https://doi.org/10.1111/1365-2745.13563>