The impact of climate change on biological soil crusts in drylands

Drivers, mechanisms and feedbacks with landscape hydrology

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Selina Baldauf

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1st reviewer: **Prof. Dr. Britta Tietjen** (Freie Universität Berlin)

2nd reviewer: **Prof. Dr. Matthias Rillig** (Freie Universität Berlin)

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Own contribution: I contributed to the planning and design the research. I conducted the modelling experiments and contributed to analysing the data. I analysed the data, prepared figures and tables, authored the first draft of the paper and reviewed it based on co-authors' suggestions.

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[1] Theoretical Ecology, Institute of Biology, Freie Universität Berlin, Berlin, Germany

[2] Departamento de Biología y Geología, Física y Química Inorgánica, Escuela Superior de Ciencias Experimentales y Tecnología, Universidad Rey Juan Carlos, Móstoles, Spain

[3] Berlin-Brandenburg Institute of Advanced Biodiversity Science, Berlin, Germany

[4] Institute of Plant Science and Microbiology, University of Hamburg, Hamburg, Germany

[5] Departamento de Farmacología, Farmacognosia y Botánica, Facultad de Farmacia, Universidad Complutense de Madrid, Madrid, Spain

[6] Instituto Multidisciplinar para el Estudio del Medio "Ramon Margalef", Universidad de Alicante, Alicante, Spain

[7] Departamento de Ecología, Universidad de Alicante, Alicante, Spain

[8] Agronomy Department, University of Almeria, Almeria, Spain

[9] Centro de Investigación de Colecciones Científicas de La Universidad de Almería (CECOUAL), Almería, Spain

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Summary

Biocrusts are communities of organisms such as lichens, bryophytes, and cyanobacteria that live on and within the first few millimetres of the soil. They are particularly abundant in drylands where they stabilise the soil, increase nutrient availability and redistribute the scarce rainfall from crusted parts of the landscapes towards vegetated areas. Through stabilising ecohydrological feedbacks between biocrusts and vascular vegetation, a heterogeneous landscape can emerge and be sustained. The stability of such landscapes is dependent on an intact cover of biocrusts. However, biocrusts are threatened by climate change which can alter their species composition and reduce their overall cover. Such changes can reduce soil stability, increase runoff connectivity and soil erosion which can ultimately lead to ecosystem degradation. How different climate change factors affect biocrusts and what this means for landscape hydrology is still not fully understood.

In this thesis, I used empirical and process-based modelling approaches to assess the impact of different climate change factors on biocrusts and the landscapes they inhabit.

After a general introduction to the topic in chapter 1, I conducted a rainfall-manipulation experiment in early spring and compared the effects of altered precipitation frequency on the short-term photosynthesis and respiration of a lichen-dominated biocrust (chapter 2). In contrast to other studies conducted in summer, I found that a higher frequency with smaller individual pulses was beneficial in terms of net photosynthesis because it allowed for a longer and more constant activity time of the biocrust. Seasonality and the environmental conditions were important mediating factors for the effect of precipitation patterns on carbon exchange, therefore results from previous experiments conducted in summer do not necessarily apply to other seasons.

Climate change not only affects precipitation patterns but also changes other climate variables. Therefore, in chapter 3, I looked at the effects of additional climate change factors and their interactions on short-term biocrust activity and assessed how they translate to long-term cover. I used a process-based non-vascular vegetation model to simulate the same lichen species as in chapter 2 in two locations in Spain. I found that the single climate change factors had positive (increased temperature and atmospheric CO_2), negative (decreased relative humidity) or neutral (decreased rainfall) effects on the lichen. However, in combination, the factors interacted and led to a long-term decline in cover. The main driver behind this decline was a decrease in relative humidity which could not be compensated by an increase in atmospheric CO_2 because it led to a strong decrease in the availability of dew. With this study, I could explain the probable mechanisms behind observed cover losses in field experiments and quantify potential effects of climate change on a common biocrust lichen. My results are likely to represent a larger trend in drylands under climate change, as the investigated lichen species is ubiquitous and distributed globally.

In chapter 4, I assessed the effects of such potential biocrust changes on landscape hydrology and water availability. For this, I extended a process-based ecohydrological model by including a dynamic biocrust layer. I simulated the effect of biocrusts on water redistribution and soil moisture availability on a hillslope in south-west Spain. I found that biocrusts have a positive effect on landscape-scale soil moisture distribution because runoff from the crusted upper

hillslope infiltrated in the vegetated lower parts of the hillslope. A shift towards less lichen and more early successional biocrusts, as is predicted under climate change and also suggested by the previous chapters, reduced water redistribution and plant-available water. This indicates that under climate change, changes to the stabilising ecohydrological feedbacks between crusted and vegetated areas are to be expected with uncertain effects for dryland landscapes.

In this thesis, I focused on the effects of different climate change factors on the short-term carbon exchange of biocrusts, how this translates to long-term changes in cover and the consequences this will have on the landscape scale. By integrating biocrusts into process-based models, my results provided a more mechanistic understanding of these effects. Using such novel tools and integrating them with empirical experiments will help to further promote our understanding of biocrusts under climate change and how we can better protect them in the future.

Zusammenfassung

Biologische Bodenkrusten sind Gemeinschaften von Organismen wie Flechten, Moose und Cyanobakterien, die auf und in den obersten Millimetern des Bodens leben. Sie sind besonders in Trockengebieten verbreitet, wo sie den Boden stabilisieren und die Nährstoffverfügbarkeit erhöhen. Weiterhin tragen sie dazu bei, dass sich die knappen Niederschläge von den offenen, mit Bodenkrusten bedeckten Teilen der Landschaft in Richtung der mit Vegetation bedeckten Gebiete umverteilen. Durch diese stabilisierende ökohydrologische Rückkopplung zwischen biologischen Bodenkrusten und Vegetation kann eine heterogene Landschaft entstehen und erhalten werden. Eine intakte Bedeckung mit biologischen Bodenkrusten ist deshalb entscheidend für die Stabilität solcher Landschaften. Der Klimawandel kann Auswirkungen auf die Artenzusammensetzung der biologischen Bodenkrusten haben und ihre Gesamtbedeckung verringern. Diese Veränderungen können die Bodenstabilität verringern, die Konnektivität des Oberflächenabfluss erhöhen und die Bodenerosion verstärken, was letztlich zu einer Degradierung der Ökosysteme führen kann. Wie sich die verschiedenen Faktoren des Klimawandels auf biologische Bodenkrusten auswirken und was dies für die Hydrologie in Trockengebieten bedeutet, ist jedoch noch nicht vollständig geklärt.

In der vorliegenden Arbeit wurden empirische Ansätze und prozessbasierte Modellierung verwendet, um die Auswirkungen verschiedener Klimawandelfaktoren auf biologische Bodenkrusten und die Landschaften in denen sie vorkommen zu bewerten. Nach einer generellen Einführung in das Thema (Kapitel 1) wurde in Kapitel 2 ein Niederschlagsmanipulationsexperiment im Frühling durchgeführt. Ziel war es, die Auswirkungen veränderter Niederschlagsmuster auf die kurzfristige Photosynthese und Atmung einer von Flechten dominierten Bodenkruste zu vergleichen. Im Gegensatz zu anderen Studien, die im Sommer durchgeführt wurden, ergab das Experiment im Frühling einen positiven Effekt einer höheren Frequenz mit kleineren Einzelpulsen für die Netto-Photosynthese, da dies eine längere und konstante Aktivierung der Bodenkruste ermöglichte. Dabei waren Saisonalität und Umweltbedingungen wichtige Einflussfaktoren für die Auswirkungen der Niederschlagsmuster auf den Kohlenstoffaustausch. Daher lassen sich die Ergebnisse früherer, im Sommer durchgeführter Experimente nicht ohne Weiteres auf andere Jahreszeiten übertragen.

Außerdem beeinflusst der Klimawandel nicht nur die Niederschlagsmuster, sondern auch andere Klimafaktoren. Daher wurden in Kapitel 3 weitere Faktoren des Klimawandels und ihre Interaktionen auf die kurzfristige Aktivität von Bodenkrusten und die Auswirkungen auf ihre langfristige Bedeckung untersucht. Um die gleiche Flechtenart wie in Kapitel 2 an zwei Standorten in Spanien zu simulieren, wurde ein prozessbasiertes Vegetationsmodell für nicht-vaskuläre Pflanzen verwendet. Die Ergebnisse zeigten, dass die Faktoren des Klimawandels einzeln betrachtet positive (erhöhte Temperatur und CO_2 Gehalt der Luft), negative (verringerte relative Luftfeuchtigkeit) oder neutrale (verringerter Niederschlag) Auswirkungen auf die Bodenkrusten hatten. In Kombination interagierten die Faktoren jedoch und führten zu einem langfristigen Rückgang der Flechtenbedeckung. Die Hauptursache für diesen Rückgang war eine Abnahme der relativen Luftfeuchtigkeit, die durch den Anstieg des CO2-Gehalts nicht kompensiert werden konnte und zu einer starken Abnahme der Kondensation von Tau führte. Mit dieser Studie konnten in Feldexperimenten beobachtete Bedeckungsabnahmen

mechanistisch erklärt und die potenziellen Auswirkungen des Klimawandels auf eine häufige Flechtenart in Bodenkrusten quantifiziert werden. Diese Ergebnisse sind wahrscheinlich repräsentativ für einen generellen Trend in Trockengebieten unter Klimawandelbedingungen, da die untersuchte Flechtenart häufig vorkommt und weltweit verbreitet ist.

In Kapitel 4 wurden die Auswirkungen dieser potenziellen Bodenkrusten-Veränderungen auf hydrologische Prozesse und die Wasserverfügbarkeit in der Landschaft untersucht. Zu diesem Zweck wurde ein prozessbasiertes ökohydrologisches Modell um eine dynamische Bodenkrustenschicht erweitert und die Auswirkungen von Bodenkrusten auf die Wasserumverteilung und die Verfügbarkeit von Bodenfeuchte an einem Hang im Südwesten Spaniens simuliert. Das Resultat war, dass sich Bodenkrusten positiv auf die Bodenfeuchte in der Landschaft auswirken, da der Oberflächenabfluss aus dem mit Krusten bedeckten, oberen Hangbereich im bewachsenen unteren Teil des Hangs infiltriert. Eine Verschiebung hin zu weniger Flechten und mehr Bodenkrusten der frühen Sukzessionsphase, wie sie im Zuge des Klimawandels vorhergesagt wird und auch in den vorangegangenen Kapiteln angedeutet wurde, reduzierte die Wasserumverteilung und das pflanzenverfügbare Wasser. Dies deutet darauf hin, dass im Zuge des Klimawandels Veränderungen der ökohydrologischen Rückkopplungen, welche die Landschaft stabilisieren, zu erwarten sind.

In dieser Arbeit habe ich mich auf die Auswirkungen verschiedener Faktoren des Klimawandels auf den kurzfristigen Kohlenstoffaustausch von biologischen Bodenkrusten konzentriert. Ich habe untersucht, wie sich dies auf langfristige Veränderungen der Bedeckung auswirkt und welche Folgen dies auf der Landschaftsebene haben wird. Die Integration von Bodenkrusten in prozessbasierte Modelle ermöglichte hierbei ein verbessertes mechanistisches Verständnis dieser Auswirkungen. Die Verwendung von Modellen und ihre Verknüpfung mit empirischen Experimenten wird dazu beitragen, das Verständnis von biologischen Bodenkrusten unter Klimawandelbedingungen weiter zu vertiefen und sie in Zukunft besser besser schützen zu können.

Part I

General Introduction

1 General Introduction

Biological soil crusts (biocrusts hereafter) are communities of cyanobacteria, lichens, bryophytes and other organisms that live in close association with the upper millimetres of the soil (Belnap et al., 2001, 2016). They cover around 12% of the earth's terrestrial surface (Rodríguez-Caballero et al., 2018a), inhabit almost all ecosystems and can be found on all continents including Antarctica, but they are particularly abundant in drylands where vascular vegetation is sparse (Belnap et al., 2001; Bowker et al., 2016; Rodríguez-Caballero et al., 2018a). Biocrusts are important for the functioning of dryland ecosystems and the societies that inhabit them (Rodríguez-Caballero et al., 2018b) because they influence landscape hydrology (Chamizo et al., 2016a, 2013b; Eldridge et al., 2020), reduce soil erosion (Cantón et al., 2014; Gao et al., 2020) and increase soil fertility (Ferrenberg et al., 2018; Xiao and Veste, 2017). Biocrusts are vulnerable to climatic changes and anthropogenic disturbances (Delgado-Baquerizo et al., 2014; Ferrenberg et al., 2015; Ladrón de Guevara et al., 2014) and their total cover is predicted to decline between 25 and 40% until the year 2070 (Rodríguez-Caballero et al., 2018a). This projected change in cover and species composition of biocrusts will have far-reaching consequences for the ecosystems they live in. A robust mechanistic understanding of these changes and feedback responses they have with other ecosystem components and processes is therefore important to support ecosystem restoration efforts. In recent years, the number of studies on biocrusts has increased exponentially, but studies on the effects of climate change on biocrusts are still few compared to those on vascular plants. Also, new methods such as mechanistic modelling are rarely used (Reed et al., 2019). Mechanistic modelling can provide important insights into the processes behind observed phenomena and help to assess potential future scenarios for biocrust development under climate change and its effect on the landscape. In this thesis, I aim to contribute to filling this knowledge gap by assessing climate change effects on biocrusts and dryland landscapes using experimental approaches and process-based models.

1.1 Biocrust communities in drylands

Drylands are characterised by harsh habitats with variable and low water availability, where temperature and radiation can become very high (Green et al., 2018). They are often specified by sparse and patchy vegetation cover and biocrusts dominate the otherwise bare inter-plant spaces. In this position, biocrusts mediate all inputs and outputs to and from the soil they cover which makes them an "organizing principle" in drylands and essential to ecosystem functioning (Weber et al., 2016b).

1.1.1 Distribution and species composition

The species composition and total cover of biocrusts is context dependent and driven by biogeographic, climatic, edaphic, topographic and biotic forces acting on different spatial scales (Bowker et al., 2016).

On a global and regional scale, present and past climate, especially temperature and water availability and variability determine biocrust cover and species composition (Bowker et al., 2016; Colesie et al., 2016a; Eldridge and Delgado-Baquerizo, 2019). Lichen and bryophyte cover increases linearly with precipitation amount, resulting in high cover values in semiarid regions; cyanobacteria on the other hand, are most abundant in hyperarid or arid environments with less precipitation(Bowker et al., 2016). On a regional to local scale, soil properties and particularly soil texture influence the biocrust species composition (Bowker and Belnap, 2008; Bowker et al., 2016; Li et al., 2010). Cyanobacteria tend to be more dominant on sandy soils, whereas lichen cover increases with higher silt content of the soil (Belnap et al., 2001; Bowker et al., 2016; Colesie et al., 2016a). On a microscale (~ 100 cm2), the community composition can be affected by microtopography which controls local water availability and light intensity (Bowker et al., 2006). For example, north-oriented locations with lower radiation and higher moisture availability can support a higher cover of lichens and mosses compared to the warmer south-facing areas with high radiation and evaporative water losses (Bowker et al., 2006). This differentiation by topography between sunnier and shadier areas can also be observed on larger scales with biocrusts being more common on shadier and less steep hillslopes (Lázaro et al., 2022).

The spatial variation in species composition due to the above-mentioned abiotic conditions is accompanied by a temporal variation because biocrusts dynamically change and, if undisturbed, follow successional stages. According to a widely adopted framework of biocrust succession, cyanobacteria and cyanolichens first colonise and stabilise the soil and fix atmospheric nitrogen (Belnap and Eldridge, 2003; Eldridge and Greene, 1994). This creates a stable and nutrient enriched habitat for the following succession of phycolichens and mosses (Belnap and Eldridge, 2003). This succession model is characteristic of dry environments with unstable soils; under more favourable conditions, facilitation through soil stabilisation and nutrient enrichment through early successional species might not play such an important role (Read et al., 2016).The species composition and the corresponding phenotypical and physiological properties of the biocrust determines which ecological role they play and how they structure other components of the ecosystem on both a local and a landscape scale (Belnap et al., 2016)

1.1.2 Ecosystem functions

On a local scale, biocrusts alter the properties of the soil surface and the top millimetres of the soil such as porosity and texture (Felde et al., 2014). Through these changes, they affect water fluxes from and into the soil, mainly infiltration and evaporation (Chamizo et al., 2016a, 2012a). In most cases, biocrusts reduce infiltration e.g. due to pore clogging (Colica et al., 2014; Mager and Thomas, 2011; Malam Issa et al., 2009) but this effect depends on soil type, environmental conditions and species composition (Eldridge et al., 2020). For example, a study on sandy loam soil on the Colorado plateau showed higher infiltration rates with increasing developmental stage of the crust and infiltration is higher if the antecedent soil beneath the crust is lower (Belnap et al., 2013). The effect of biocrusts on soil evaporation is ambiguous and context dependent (Chamizo et al., 2013b; Guan and Liu, 2019; Zhang et al., 2008). Some studies report a reduction of evaporation through biocrusts because they constitute a barrier against water losses from the soil (Cantón et al., 2020; Chamizo et al., 2016b). But, dark coloured biocrusts with low albedo can also significantly increase soil and surface temperature compared to bare soil surfaces and as a consequence also evaporation rates (Chamizo et al., 2016a; Kidron et al., 2022).

On a landscape scale, biocrusts help to create and maintain a differentiated landscape that is characterised by a source-sink relationship between runoff-generating areas and areas of higher infiltration capacity that capture this runoff and use it to sustain vascular vegetation cover (Ludwig et al., 2005; Puigdefábregas, 2005; Puigdefábregas et al., 1999). In such differentiated landscapes, biocrusts occupy the bare interplant-spaces where they form zones of high nutrient deposition, transformation and availability and, through reduced infiltration and increased runoff, facilitate water and nutrient redistribution towards vascular plants (Belnap et al., 2016; Zhang et al., 2016). Through their tight association with the soil, biocrusts stabilise the soil surface and promote soil aggregation (Belnap and Büdel, 2016; Mugnai et al., 2018; Sepehr et al., 2019), thus protecting the soils from erosion by wind or water (Bowker and Belnap, 2008; Cantón et al., 2014; Elliott et al., 2019). This tight ecohydrological coupling of crusted and vegetated areas is crucial in maintaining vascular plant productivity and stability of dryland ecosystems (Rodríguez-Caballero et al., 2018c; Turnbull et al., 2012).

In addition to these local- and landscape-scale hydrological and ecohydrological effects, biocrusts also significantly contribute to the biogeochemical cycle of the ecosystem (Elbert et al., 2012; Porada et al., 2014; Weber et al., 2015). Biocrusts fix atmospheric carbon and nitrogen and it is estimated that they account for roughly 15% of global net primary productivity and more than half of the nitrogen fixation by photoautotrophic surface communities (Elbert et al., 2012; Rodríguez-Caballero et al., 2018a). This makes them not only important for local ecosystems but gives them a global relevance. Potential effects of climate change on biocrusts and their ability to support ecosystem functioning might therefore have far-reaching consequences on the local, regional and global level.

1.2 Climate change effects on biocrusts

Biocrusts are much more vulnerable to climatic changes than vascular plants and it is estimated that their global cover will decline by ca. 25-40% by 2070, depending on the realised emission pathway (Rodríguez-Caballero et al., 2018a). Climate change will drastically change conditions in drylands with higher aridity and more drought events (Guan et al., 2019b; Huang et al., 2017; Schlaepfer et al., 2017) as well as decreased overall precipitation amounts and a shift towards less frequent but more extreme rainfall (Lionello and Scarascia, 2018; Tramblay et al., 2020; Vicente-Serrano et al., 2014b; Vogel et al., 2021). In this context, it is important to gain a better mechanistic understanding of how different biocrusts in different environmental contexts respond to climate change, in order to support dryland restoration efforts and conservation strategies for the future. In the following, I highlight several aspects and potential mechanisms of climate change effects on biocrusts.

Rising temperatures affect the biocrust community composition and functioning and have been associated with a shift from late-successional, lichen- and moss-dominated biocrusts to early-successional, cyanobacteria-dominated crusts as well as an overall loss in cover (Ferrenberg et al., 2015; Finger-Higgens et al., 2022; Ladrón de Guevara et al., 2014). Biocrust lichens are especially affected and dramatic cover declines have been reported from both long-term climate manipulation experiments (Escolar et al., 2012; Ladrón de Guevara et al., 2018, 2014) and observations (Finger-Higgens et al., 2022). Several explanations for the negative effect of warming are plausible, they are however difficult to disentangle because of the close correlation of temperature with other climate variables (Finger-Higgens et al., 2022). First, values exceeding the threshold of optimum temperature for photosynthesis for a given species can lead to lower photosynthesis rates and a domination of respiration leading to net carbon loss (Grote et al., 2010; Lange, 2001). Additionally, higher temperatures reduce water availability e.g. by reducing relative humidity and dew condensation, which some lichen species use for their metabolic activity (Chamizo et al., 2021; Dai, 2006; Uclés et al., 2014).

In addition and in comination with higher temperature, changes in rainfall amount, timing and frequency affect dryland biocrust communities. The effect of overall precipitation is ambiguous and studies report substantial drought-induced losses of biocrust cover (Wertin et al., 2012), while others show no effect of reduced rainfall on biocrust cover (Escolar et al., 2012; Ladrón de Guevara et al., 2014). However, studies are difficult to compare and reason for discrepancies can be a difference in the absolute rainfall amounts between the studies but also the size and frequency of individual wetting events. For example, an increase in the frequency of small precipitation events during the warm summer months can lead to a dramatic decline in moss cover in some areas despite the overall higher water input (Ferrenberg et al., 2015; Reed et al., 2012). Frequent but short activation periods through small rainfall pulses at high temperatures can lead to an overall negative carbon balance because the rewetting of dry crusts is accompanied with a burst of CO_2 that is only compensated if the active time is long enough for photosynthesis to balance the loss (Lange, 2001; Reed et al., 2012).

Theoretically, higher atmospheric CO_2 could compensate for some of these climate change induced carbon losses (Reed et al., 2016). A positive effect of increased CO_2 levels on biocrusts can however only be expected if the overall climate does not become much drier (Reed et al., 2016) because the effect of CO_2 on biocrust carbon exchange is highly controlled by water content (Lange, 2002; Lange et al., 1999). However, this is not likely to happen, given the climate projections that indicate a much drier future (Guan et al., 2019b; Huang et al., 2017; Schlaepfer et al., 2017). Also, Free Air CO_2 Enrichment (FACE) experiments already showed that elevated CO_2 levels could not compensate for drought-induced biocrust losses (Wertin et al., 2012).

The alteration of dryland biocrusts caused by changes in temperature, rainfall characteristics and atmospheric CO_2 will not only affect the biocrust itself but the whole ecosystem because of feedback loops and interactions that link biocrusts and ecosystem functions and processes. For example, a poor biocrust cover makes the soil vulnerable to detachment and erosion especially in areas with low vascular vegetation cover and steep hillslopes (Bu et al., 2015; Cantón et al., 2020; Faist et al., 2017). With sediment loss, nutrients are also removed from the system which negatively affects the vascular plant community and ecosystem productivity (Cantón et al., 2014; Chamizo et al., 2017). This can in turn reduce the ability of vegetated areas to capture runoff, thus further exacerbating droughts, soil erosion and land degradation (Imeson and Prinsen, 2004). In addition, a shift towards earlier successional biocrust stages with a higher cover of dark cyanobacteria can reduce surface albedo and increase soil and surface temperatures thus leading to higher evaporative water losses (Kidron et al., 2022; Reed et al., 2019).

In summary, the body of evidence clearly shows that climate change alters biocrust species composition and cover which has potentially large effects on the landscape and ecosystem functioning. The interactions between the different climate change factors and how they affect individual biocrusts species and the community as a whole are complex and not fully understood. This makes it hard to disentangle effects and understand underlying mechanisms of climate change induced biocrusts changes. Once biocrust cover and richness is lost, restoration and regrowth is difficult considering the long recovery especially of late-successional biocrusts (Belnap and Eldridge, 2003). Therefore, it is important to gain a mechanistic understanding of biocrust response to these climatic changes and what this means for dryland ecosystems worldwide.

1.3 Biocrusts and simulation models

Process-based models are useful tools to help us understand the mechanisms behind climate change driven biocrust changes and to model scenarios of how changes in biocrusts can affect the ecosystem as a whole. However, biocrusts are rarely considered in hydrological, vegetation and earth system models. To date, only few models have been developed that specifically account for biocrusts (Reed et al., 2019) although empiricists call for an integration of their results into models (e.g. Hui et al. (2021); Rodríguez-Caballero et al. (2015)). Modelling studies that include biocrusts, often do so in a simplified way, for example by adjusting soil infiltration in a soil erosion model at the presence of biocrusts (Li et al., 2002; Rodríguez-Caballero et al., 2015) or by reducing soil evaporation by a constant factor in an ecohydrological model (Tietjen et al., 2009). Models with dynamic and process-based biocrusts are scarce but there exist some models that offer the potential to assess climate change effects on biocrusts and dryland landscapes (see Table A.1.1 for details on existing biocrust models).

The existing ecohydrological biocrust models include either a soil-water (Whitney et al., 2017) or both a soil-water and a vegetation module (Chen et al., 2019, 2018; Jia et al., 2019) and they simulate processes such as water infiltration into biocrusts or evaporation from the biocrust layers. These models have been used, for example, to assess the impact of biocrusts on restoration efforts of degraded drylands (Chen et al., 2019, 2018) or to investigate how the dominant vegetation type might shift depending on rainfall amount and biocrust cover (Jia et al., 2019). Ecohydrological models have also been used to assess the effect of biocrusts of different levels of development on the soil water balance (Whitney et al., 2017). Another model that has been applied to biocrust organisms mimics dynamic global vegetation models (DGVMs) but is adapted to simulate the water and metabolic processes of non-vascular organisms (Porada et al., 2013). It has been used for example to quantify regional and global carbon uptake by lichens and bryophytes (Porada et al., 2013) and their contribution to the biogeochemical cycle (Porada et al., 2014). Other biocrust models include a small scale biophysical and chemical model to simulate early stage microbial communities and their response to gradients in their physical and chemical environment (Kim and Or, 2017) and a simple model to assess vegetation-crust patterns in a theoretical landscape, depending on the rainfall amount (Kinast et al., 2016).

Process-based models with dynamic biocrusts offer the possibility to complement short-term experiments and observational studies with long-term simulations and scenario analyses. The growing body of knowledge and process understanding stemming from empirical studies can thereby support the development, parameterisation and validation of biocrust models while in turn, modelling results can be used to develop theories and design experiments to test them. However, until now, only few biocrust models have been developed and broadly applied. Especially modelling studies with a focus on climate change and spatially-explicit models that can assess landscape patterns of ecohydrological processes are missing. However, they are needed to predict future scenarios of biocrust cover and functioning (e.g. biocrust metabolic activity and cover under climate change) or to quantify the contributions of biocrusts to ecosystem functioning (e.g. landscape hydrology, water redistribution and plant-available water).

1.4 Aims and structure of the thesis

The aim of this thesis is to contribute to a mechanistic understanding of climate change effects on biocrusts, and to assess how these changes affect dryland hydrology and ecosystem functioning. In particular, I aim to

1. understand the effects of different climate change factors (rainfall frequency and amount, temperature, atmospheric CO_2 and relative air humidity) on biocrust activity, carbon exchange and cover (Chapter 2 and 3),
2. understand how the environmental context and interactions between climate change factors modulate these effects (Chapter 2 and 3),
3. quantify the effect of biocrusts on landscape-scale water availability (Chapter 4), and
4. assess how potential future biocrust changes could affect water distribution and availability in the landscape (Chapter 4).

To investigate this, I use both short-term experimental and long-term process-based modelling approaches, focusing first on the biocrust scale and then zooming out to the landscape scale (Figure 1.1). The thesis focuses on biocrusts in Spain, and the models are combined with results from field and experimental data from the region to parameterise and validate them for site- and species-specific contexts.

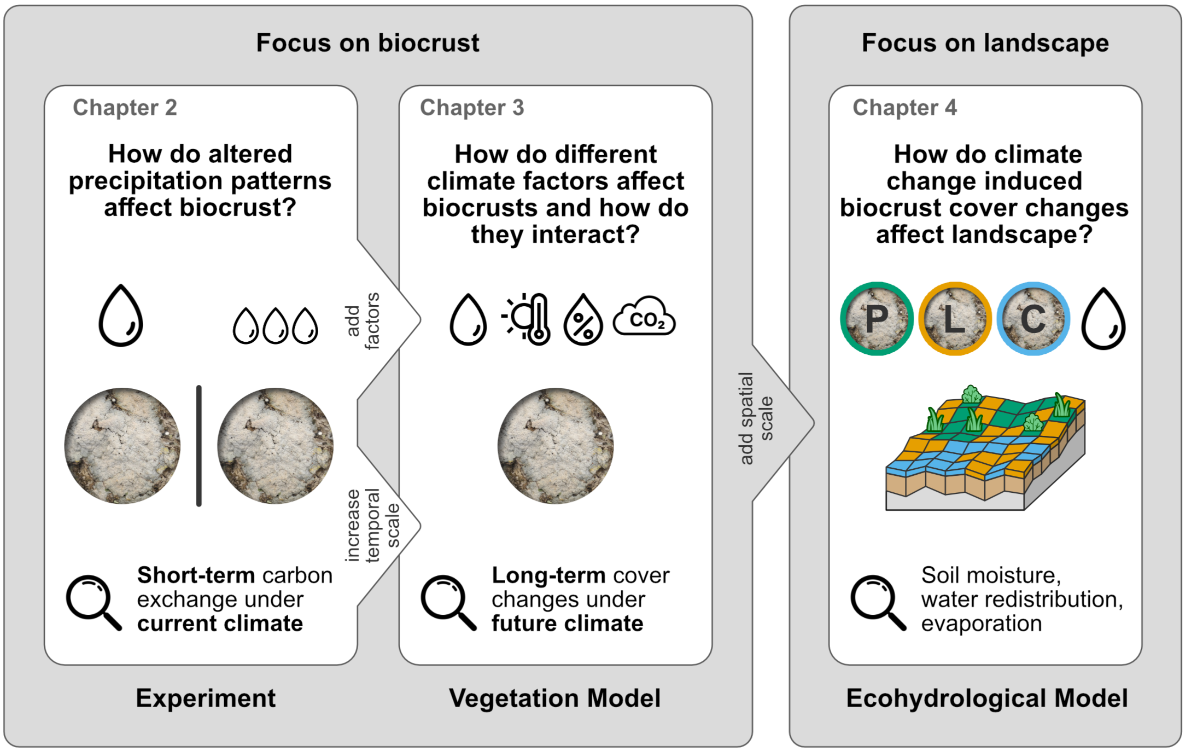

Figure 1.1: Overview of methods and links between the three study questions presented in chapters 2–4. In each of the chapters, different variables were manipulated. The manipulated variables are depicted below the research question: Rainfall frequency in chapter 2; overall rainfall, temperature, relative humidity and atmospheric CO_2 in chapter 3; crust cover types (physical, lichen, cyanobacteria) and overall rainfall in chapter 4. On the bottom, the main analysed output variables are listed for each chapter. In chapters 2 and 3, the focus was on the biocrust and in chapter 4 on a landscape covered with biocrusts. To answer the research questions, I conducted a rainfall manipulation experiment (chapter 2), used a non-vascular vegetation model (chapter 3) and an ecohydrological model (chapter 4).

In **Chapter 2**, I assessed how changes in rainfall patterns affect the short-term carbon exchange of lichen-dominated biocrusts (mainly *Diploschistes diacapsis*) from central Spain (published in *PeerJ* as Baldauf et al. (2018)). For this, I conducted a rainfall manipulation experiment that tested the effect of two precipitation patterns on crust photosynthesis and respiration. Both patterns provided the same overall amount of water, but one with more frequent and smaller individual pulses, and the other with less frequent but larger individual pulses. I measured and compared the CO_2 gas exchange of the biocrusts subjected to the different rainfall patterns and assessed how the environmental conditions (soil temperature, soil moisture and radiation) interacted with them.

In **Chapter 3**, I complemented this experiment by assessing the effect of additional climate change factors on the common biocrust lichen *D. diacapsis* that was was dominant in the biocrust from chapter 2 (published in *Journal of Ecology* as Baldauf et al. (2021)). For this, I used a process-based simulation model of non-vascular vegetation and parameterised it with field data from Spanish drylands. I investigated the effect of different climate change factors (increased temperature and atmospheric CO_2, decreased rainfall and relative humidity) and their interactions on metabolic activity and the potential future cover of *D. diacapsis*.

Additionally, I mimicked a long-term climate-manipulation experiment in which significant cover losses of lichens have been observed. The process-based modelling approach thereby allowed me to investigate the effects of climate change on the biocrust lichen but also to understand the underlying physiological mechanisms that might have led to observed cover losses under warming.

In **Chapter 4**, I shifted the focus from the crust itself to the effects of biocrusts on the landscape. I incorporated the knowledge from the previous chapters on the potential impact of climate change on biocrusts and assessed how this might affect the landscapes they inhabit. I did this by extending an ecohydrological simulation model to include a dynamic layer of biocrusts. I parameterised and calibrated the model to a dryland hillslope in south-east Spain and assessed the contribution of uphill biocrust cover on landscape water redistribution and availability for the downhill vegetation. I tested in how far biocrusts might be able to sustain soil moisture for vegetation in drought years. Then, I assessed how a shift in the biocrust community (e.g. from lichen-dominated to cyanobacteria-dominated or physical crust) could affect landscape-scale soil moisture and therefore plant-available water.

Finally, in **Chapter 5**, I discussed the theoretical and practical implications of the results and conclusions from chapters 2–4 in the context of the scientific literature on the topic. In particular I discussed the following questions: (1) Which climate change factors affect biocrusts most and how do they interact and depend on environmental context? (2) What do the results from this thesis mean for global biocrust communities and dryland hydrology? (3) What did I learn from integrating different modelling approaches and empirical data and experiments? (4) What are the next steps moving forward with this research?

Part II

Study questions of the thesis

2 Soil moisture dynamics under two rainfall frequency treatments drive early spring CO_2 gas exchange of lichen-dominated biocrusts in central Spain

This chapter has been published as: Baldauf, S., Ladrón de Guevara, M., Maestre, F. T., and Tietjen, B. (2018). Soil moisture dynamics under two rainfall frequency treatments drive early spring CO_2 gas exchange of lichen-dominated biocrusts in central Spain. *PeerJ*, 6:e5904. https://doi.org/10.7717/peerj.5904

Background. Biocrusts, communities dominated by mosses, lichens, cyanobacteria and other microorganisms, largely affect the carbon cycle of drylands. As poikilohydric organisms, their activity time is often limited to short hydration events. The photosynthetic and respiratory response of biocrusts to hydration events is not only determined by the overall amount of available water, but also by the frequency and size of individual rainfall pulses.
Methods. We experimentally assessed the carbon exchange of a biocrust community dominated by the lichen *Diploschistes diacapsis* in central Spain. We compared the effect of two simulated precipitation patterns providing the same overall amount of water, but with different pulse sizes and frequency (high frequency: 5 mm/day vs. low frequency: 15 mm/3 days), on net/gross photosynthesis and dark respiration.
Results. Radiation and soil temperature, together with the watering treatment, affected the rates of net and gross photosynthesis, as well as dark respiration. On average, the low frequency treatment showed a $46 \pm 3\%$ (mean ± 1 SE) lower rate of net photosynthesis, a $13 \pm 7\%$ lower rate of dark respiration and a $24 \pm 8\%$ lower rate of gross photosynthesis. However, on the days when samples of both treatments were watered, no differences between their carbon fluxes were observed. The carbon flux response of *D. diacapsis* was modulated by the environmental conditions and was particularly dependent on the antecedent soil moisture.
Discussion. In line with other studies, we found a synergetic effect of individual pulse size, frequency, environmental conditions and antecedent moisture on the carbon exchange fluxes of biocrusts. However, most studies on this subject were conducted in summer and they obtained results different from ours, so we conclude that there is a need for long-term experiments of manipulated precipitation impacts on the carbon exchange of biocrusts. This will enable a more complete assessment of the impacts of climate change-induced alterations in precipitation patterns on biocrust communities.

2.1 Introduction

Biocrusts are communities dominated by cyanobacteria, algae, fungi, lichens and bryophytes living on the soil surface. They are a major feature in drylands worldwide, with an estimated cover of around 12% of the terrestrial surface (Rodríguez-Caballero et al., 2018a), and act as a boundary layer between the soil and the atmosphere (Belnap et al., 2001, 2016). Biocrust constituents, such as lichens and mosses, are poikilohydric organisms, which are dormant when desiccated and, unlike vascular plants, cannot actively control their water balance. Their activity time is thus limited to hydration events with water inputs from the atmosphere in the form of rain, fog, dew or water vapor (Darrouzet-Nardi et al., 2015; Lange, 2001). Despite their restricted activity time, biocrusts play an important role in the carbon cycle of drylands through their photosynthetic and respiratory activity (Elbert et al., 2012; Sancho et al., 2016). The duration of moisture availability thereby controls the ratio of respiratory losses to photosynthetic gains (Belnap et al., 2004; Jeffries et al., 1993). Therefore, larger rainfall events are generally associated with higher carbon gains, whereas small rain events can result in a carbon deficit, because the initial respiratory losses cannot be compensated by subsequent photosynthesis (Coe et al., 2012; Reed et al., 2012; Su et al., 2012).

In addition to the importance of individual event size, rainfall frequency is a key factor in determining the duration of moisture availability at the soil surface (D'Odorico and Porporato, 2004), which affects the activity of biocrust constituents (Raggio et al., 2017). As an example, a laboratory study with the common biocrust moss *Syntrichia caninervis* showed that a higher frequency of sufficiently large rainfall events is beneficial in terms of photosynthesis (Coe et al., 2012). These authors found that a shift in the interval between two wetting events from one day to five days led to a decrease in the mean carbon balance by nearly 90%, and became negative at an interval of ten days. Furthermore, the effect of watering patterns on the carbon flux response depends on the season considered, as it plays an important role in determining the event size that is necessary to reach the compensation point for net photosynthesis (Büdel et al., 2009; Lange, 2001). Precipitation patterns can be beneficial in winter and lead to carbon losses in summer due to higher temperatures and different physiological responses to rainfall events of the same size (Coe et al., 2012).

A spring to fall rainfall manipulation experiment on the Colorado Plateau (southwestern United States) showed that a 50% above-average precipitation frequency negatively impacts quantum yield, chlorophyll α, and protective pigment concentration in lichen- and cyanobacterial biocrusts, especially if applied for a longer period (Belnap et al., 2004). In another study located in the same area, an increase in the frequency of small summer rainfall events led to a negative carbon balance and rapid mortality of *S. caninervis* (Reed et al., 2012; Zelikova et al., 2012). The additional small rainfall events caused C starvation due to non-sufficient hydration of the moss (Reed et al., 2012). In the same experiment, soil cyanobacterial biomass and abundance also declined significantly following the second summer of altered precipitation patterns although the treatment increased overall moisture availability compared to control conditions (Johnson et al., 2012). In the long term, an increase in the summer precipitation frequency has been found to drive a shift in species composition from lichen- and moss-dominated to cyanobacteria-dominated biocrusts (Ferrenberg et al., 2015; Zelikova et al., 2012).

Precipitation and water availability are the major driver of biocrust activity (Wertin et al., 2012) and hence, changes in precipitation patterns, such as those projected for climate change in drylands worldwide (IPCC, 2014), will directly and indirectly influence the ability of biocrusts to fix and store carbon (Belnap et al., 2004). However, we still know little about the impact of changes in precipitation on the carbon uptake across biocrust communities in different dryland regions and across seasons. In order to contribute to filling this knowledge gap, we have conducted a short-term manipulative experiment in early spring to assess the effect of rainfall patterns on photosynthesis and respiration of *Diploschistes diacapsis*, a lichen that generally is dominant in the biocrust communities in central Spain (Maestre et al., 2011). We compared the carbon exchange fluxes in response to two rainfall patterns that provided the same overall water amount; in one of the treatments, single rainfall events were smaller, but more frequent; while in the other one, single rainfall events were larger, but less frequent. By doing so, we seek to understand which rainfall pattern could be more beneficial for carbon fixation by biocrusts, and to set the direction for follow-up long-term experiments in the field.

2.2 Materials and Methods

2.2.1 Sample collection and experimental design

In March 2017, we collected twelve undisturbed soil cores (diameter: 10 cm, height: 7 cm) with a high crust cover (between 80 and 100%) of *D. diacapsis* at the rural estate El Espartal, in the Southeast Regional Park of Madrid, central Spain (40°11′N 3°36′W, 574 m a.s.l.). The bioclimate of El Espartal is upper semiarid meso-Mediterranean, with a mean annual temperature of 14.5 °C and a mean annual precipitation of around 389 mm in the period from 1971–2000 (Cano Sánchez, 2006). The mean precipitation in March and April is 36 and 52 mm, respectively. However, the historical minimum and maximum monthly precipitation (1981–2010) are 1 and 196 mm in March and 11 and 162 mm in April with maximum daily precipitation amounts of 29 mm in March and 45 mm in April (Agencia Estatal de Meteorología, 2012). The soils of the area are classified as Gypsic Regosols (Ortíz-Bernard et al., 1997) and Calcic Gypsisol (Monturiol Rodriguez and Alcala del Olmo, 1990). Perennial plant coverage is lower than 40% and the site hosts a well-developed biocrust community dominated by lichens, such as *D. diacapsis*, *Squamarina lentigera*, *Fulgensia subbracteata* and *Buellia zoharyi* (see Figure A.2.1).

After collection, we covered the bottom of the soil cores with a fine-meshed fabric to avoid soil loss and then took them to the lab, where they were watered to full saturation with low mineralised water and drained for 24 h to determine the weight at saturation water content. The undisturbed cores were placed on a structure that allowed water to drain from the cores under a transparent roof at the Climate Change Outdoor Laboratory, located at the facilities of Rey Juan Carlos University (Móstoles, Spain: 40°20′N, 3°52′W, 650 m a.s.l., see Figure A.2.2). Rainfall was excluded by the roof, whereas temperature and radiation remained similar to those at ambient conditions. Five days after placing the cores under the roof, we started to apply a daily water pulse of 5 mm to six of the samples (high frequency treatment), and a 15 mm pulse at a three-day interval to the other six samples (low frequency treatment). In total, all samples received a water amount of 60 mm during 12 days (from March 21st 2017 until April 1st 2017). Although *D. diacapsis* can already activate the photosynthetic system at smaller rainfall pulses (Lange et al., 1997; Pintado et al., 2005), the watering patterns were chosen such that they were sufficient to provide enough water to both stimulate a pulse of lichen activity and wet the soil beneath the sample. Also, we wanted to ensure that the pulses exceed the threshold for ecologically effective precipitation, which has been reported to be five mm in a semiarid steppe ecosystem (Hao et al., 2013).

2.2.2 Measurements

One of the six samples from each treatment was used to monitor soil temperature at 3 cm depth with a temperature sensor (UP Umweltanalytische Produkte GmbH, Cottbus, Germany). In the other five soil cores, we conducted gas exchange measurements using a Li-6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA). Measurements were taken every day after the water application and started earliest at 9:30 AM. The mean time between water application and the first measurement of the samples was 77 min (SD = 13 min). In each sample, light and dark measurements were paired. First, the net CO_2 flux was measured by placing a transparent chamber on the sample (hereafter referred to as net photosynthesis), waiting for equilibrium to be reached between the chamber (see Ladrón de Guevara et al. (2015)) for a detailed description of the chamber) and the sample prior to measurement. For each measurement under light conditions, we recorded photosynthetically active radiation (PAR) with a Field Scout Quantum Light Meter (Spectrum Technologies, Plainfield, IL, USA). Next, measurements were conducted in the dark using the same technique as before, but this time placing an opaque cloth around the chamber to exclude light (hereafter referred to as dark respiration). Similar to the net photosynthesis measurements, we waited for the gas exchange to stabilise before taking the measurements, a process which took ca. 3-5 min. We assume, that after this time of dark-acclimation and stabilisation, there is no longer a dynamic evolution of gas exchange due to a decrease in reminiscent photosynthesis (compare Smith and Griffiths (1996); Smith and Griffiths (1998)). Between each measurement, the infrared gas analyzers were standardised using the “match” procedure of the measuring device. With these constraints, the paired measurements were taken at the closest time possible to avoid a shift in the environmental conditions between them. The difference between the paired light and dark measurements was calculated, and will be referred to as gross photosynthesis hereafter. As the underlying soil was not removed from the crusts, the measurements comprise the fluxes from both biocrusts and underlying soil. With this, we follow an ecological approach, taking into account the contribution of the whole soil profile and avoiding any mechanical disturbance to the lichen (e.g. by thallus clipping) that could affect its functioning.

Paired measurements were taken alternatingly between the samples receiving a high and low frequency watering treatment to minimise the differences in environmental variables between the measurements. In total, three paired measurements were taken daily for every sample with a mean interval of 88 min between measurements. The last measurements were taken with a mean time of 4.5 h after the watering of that day (for detailed information on the mean times since the last watering see Table A.2.1). On the 23rd of March, only one paired measurement was made for each sample due to snow and heavy wind being registered. Further measurements on that day were cancelled to avoid damage to the measuring device. After daily gas exchange measurements, the sample weights were determined to calculate the volumetric soil moisture. An average of on-site bulk density measurements of $1.03\,\mathrm{g\,cm^{-3}}$ was used for all calculations.

The occurrence of dew could potentially influence the photosynthetic activity in our microcosms. Therefore, we estimated dewpoint temperature according to Lawrence (2005). For the calculation, we used the relative air humidity and temperature recorded by the Li-6400 device and compared it to the lichen surface temperature which was recorded by the device as well (see Figure A.2.3 for relative humidity, dewpoint and lichen surface temperature during the measurements). Relative humidity did not exceed 76% and the dewpoint never was reached. Hence, we assume that dew did not confound the response of the microcosms to the applied watering treatments.

2.2.3 Data analysis

We applied linear mixed effect models to evaluate the effect of the high and low watering frequency treatment and the environmental conditions on dark respiration, net and gross photosynthesis. We used the R statistical software (R Core Team, 2018) with the "nlme" package (Pinheiro et al., 2018) to conduct these analyses. Due to a high correlation between PAR, air and soil temperature (T_{soil}), we used PAR as a covariate in the models of net and gross photosynthesis, and T_{soil} in the model of respiration. Because of problems with the measuring device, soil temperature data on the first day were only available for the low frequency treatment from 11 to 12 AM. We used the average of these temperatures to fill the day's measurement gaps because soil temperature did not differ substantially between treatments. The watering treatment, PAR or T_{soil} and their interaction were included as fixed factors in the models. We followed a protocol for model selection based on the AIC and maximum likelihood ratio tests to compare between models (Zuur et al., 2009). We considered the sample identification as a random intercept to account for the repeated measures, and we used a continuous autocorrelation structure of order 1 (CAR1 correlation structure) to correct the temporal autocorrelation within each sample. We monitored the AIC to choose the best-fitting model and checked model assumptions using QQ-plots of the residuals and a plot of the standardised residuals vs fitted values. Due to the heteroscedasticity of the residuals, we allowed each day to have a different variance structure. Next, we sequentially excluded the fixed factors from the full model starting with the interaction and compared the models using a maximum likelihood ratio test. In this way, we selected a final model that only contained terms significant at the 5% level. The final model was refitted with restricted maximum likelihood estimators.

We performed Wilcoxon rank sum tests to compare the soil moisture of the two treatments on day 0, 1, and 2 since the last watering of the low frequency treatment. Because data were not normally distributed, paired Wilcoxon rank sum tests were used to compare CO_2 fluxes of dark respiration, net and gross photosynthesis between the two treatments overall and on the different days since the last watering. This data analysis was also performed using R statistical software (R Core Team, 2018).

2.3 Results

2.3.1 Environmental conditions during the experiment

The temporal dynamics of the measured environmental variables (PAR, soil and air temperature and soil moisture) were highly variable during the experiment (see Figure 2.1 and Figure 2.2). PAR values ranged from 50 to 2000 µmol m^{-2} s^{-1}, and exceeded the light compensation point of *D. diacapsis* of around 100 µmol m^{-2} s^{-1} (Lange, 2001) for all but five measurements. Ambient air and soil temperatures ranged from 6 to 31 °C and from 3 to 25 °C, respectively. These wide ranges reflect the variable climatic conditions during the experimental phase, with PAR, air and soil temperature decreasing after March 21st and increasing towards the end of the experimental phase. Soil temperature was slightly lowered in the high frequency treatment samples ($W = 1156, p < 0.001$). The difference in soil temperature was markedly higher during the last 4 days of the experiment (mean difference of 1 °C) compared to the period before (mean difference of 0.3 °C).

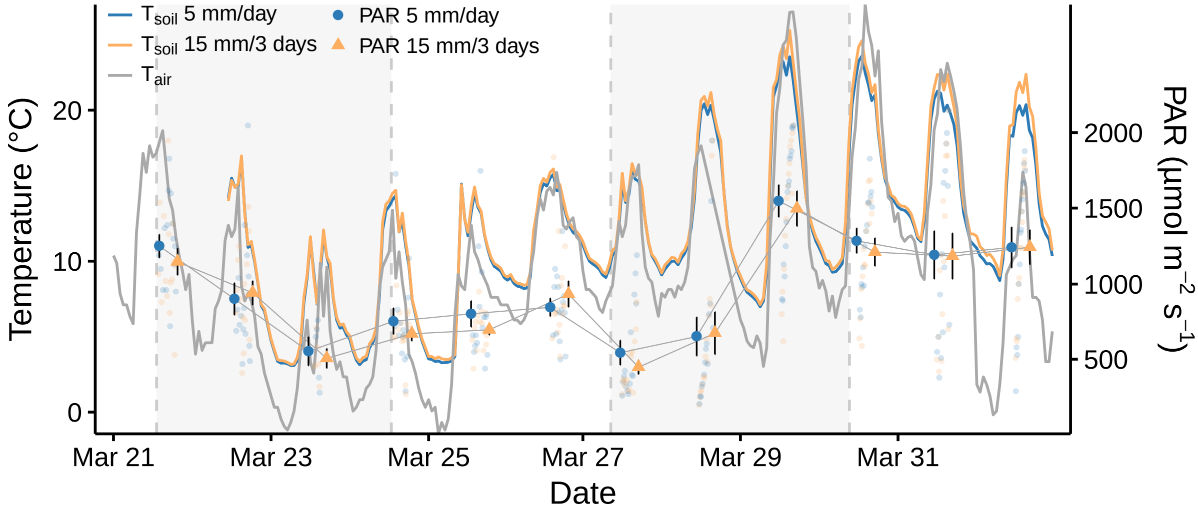

Figure 2.1: Time progression of PAR, soil and air temperature during the experiment. Points and error bars represent the mean ± 1 SE ($n = 15$ for each data point in PAR), the smaller, transparent points are the individual PAR measurements. The dashed, grey vertical lines indicate the days on which samples of both treatments were watered and the grey background visually separates the measuring time into four periods of three days.

Soil moisture dynamics generally reflected the applied watering patterns. The samples of the low frequency treatment showed a decrease in soil moisture following the days after the 15 mm pulse. The soil moisture of the high frequency treatment increased during the first days because temperature and therefore evaporation were low and thus moisture accumulated in the samples. When air temperature exceeded 20 °C, evaporation was high enough for soil moisture to decrease. On the days when the samples of both treatments were watered, soil

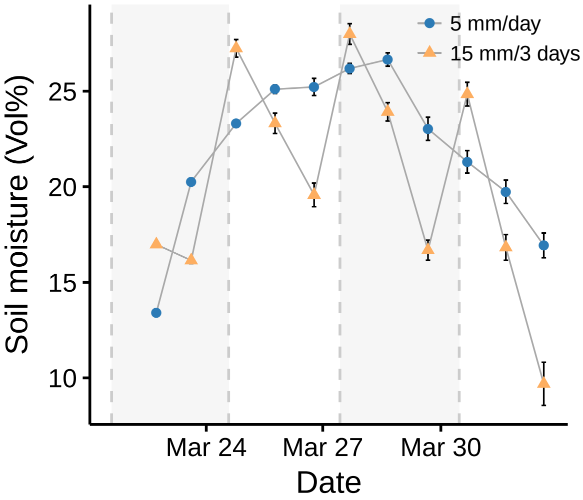

Figure 2.2: Soil moisture dynamics during the experiment. Points and error bars represent the mean ± 1 SE ($n = 5$ for each data point). The dashed, grey vertical lines indicate the days on which samples of both treatments were watered and the grey background visually separates the measuring time into four periods of three days.

moisture was 13% higher for the low watering frequency samples, which received 15 mm ($W = 195, p < 0.001$). On the following day there was no significant difference in soil moisture between the treatments (W=246, p=0.221), and on the second day after watering, soil moisture was 27% lower for the low watering frequency samples ($W = 354, p < 0.001$). An overall comparison of soil moisture for the entire experimental period did not indicate moisture differences between the treatments ($W = 1262, p = 0.135$). However, cumulative moisture was higher in the high frequency treatment for all four periods of three days (see Table A.2.2 for details).

2.3.2 Watering effects on CO_2 fluxes

Similar to the environmental conditions, the CO_2 flux measurements showed a high variability. On the first day of the experiment, we observed a negative net photosynthesis associated with high respiration rates in all samples measured (see Figure 2.3 A). On the second day, net photosynthesis increased and stayed above or close to zero for the remaining experiment. The flux difference between treatments became more pronounced from the 29th of March until the end of the experiment. During these days, temperature and radiation were higher and the largest flux differences were associated with the largest differences in soil moisture between treatments.

Overall, we observed a net CO_2 uptake (i.e. positive net photosynthesis) with mean net fluxes of 0.35 ± 0.05 (mean ± 1 SE) and $0.56 \pm 0.06\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$ for the low and the high frequency treatment, respectively. When comparing the mean CO_2 fluxes of the two frequency treatments, all fluxes were significantly lower in the low frequency treatment, with $13 \pm 7\%$ (mean ± 1 SE) lower dark respiration ($W = 4046, p < 0.001$), $46 \pm 3\%$ lower net photosynthesis ($W = 9818, p < 0.001$) and $24 \pm 8\%$ lower gross photosynthesis ($W = 17602, p < 0.001$) (see Figure 2.3 B).

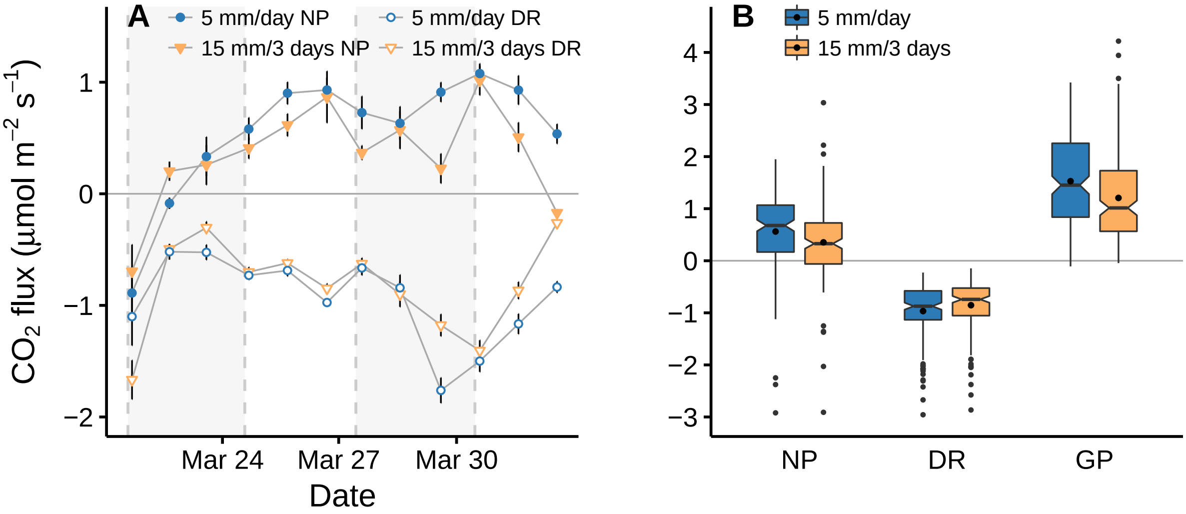

Figure 2.3: Time progression (A) and overall comparison (B) of carbon flux measurements for the low and high frequency watering treatment. Points and error bars (A) represent mean ± 1 SE ($n = 15$ for each data point) for net photosynthesis (closed symbols) and dark respiration (open symbols). The boxplots (B) of net photosynthesis (NP), dark respiration (DR) and gross photosynthesis (GP) include a black dot indicating the group mean ($n = 170$ in each group). The non-overlapping notches represent the 95% confidence interval of the median and suggest differences between treatments over the experimental period.

The relative difference between treatments changed with the days since the last watering of the low frequency treatment (see Table 2.1 and Figure A.2.4). On days when both treatments were watered, no significant flux differences between them were found (see Figure 2.4 A–C, net photosynthesis: $W = 1032, p = 0.391$; dark respiration: $W = 980, p = 0.635$; gross photosynthesis: $W = 931, p = 0.909$). In the low frequency treatment, the CO_2 fluxes for dark respiration, net and gross photosynthesis decreased on the days following water application. For dark respiration the difference between the two treatments was significant on the first and second day after watering ($W = 587, p = 0.016$). Net and gross photosynthesis were more variable among samples, therefore means only differed significantly on the second day following water application (net photosynthesis:$W = 1034, p < 0.001$, gross photosynthesis: $W = 1118, p < 0.001$).

Table 2.1: Median and 95% confidence interval of the median (in brackets) of the pairwise relative differences (%) between the two treatments by days since the last watering of the low frequency treatment.

Days since last watering of low frequency treatment	Net photosynthesis	Dark respiration	Gross photosynthesis
0	6 (-30.68)	1 (-4.8)	-2 (-14.20)
1	15 (-44.64)	**7*** (-2.14)	5 (-3.27)
2	**136***** (-92.182)	**38***** (27.52)	**71***** (55.91)

Note: Significant differences resulting from a Wilcoxon rank sum test are marked in bold ($^{*}p < 0.05$,$^{***}p < 0.001$).

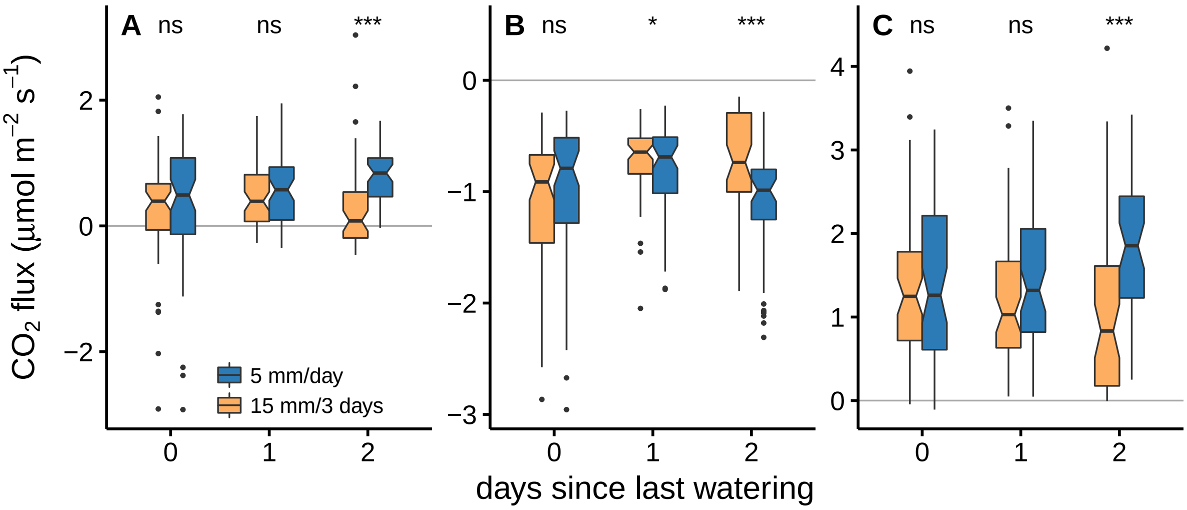

Figure 2.4: Comparison of net photosynthesis (A), dark respiration (B) and gross photosynthesis (C) between the two treatments on the different days since the last watering of the low frequency treatment. Measurements are displayed separately for each of the three low frequency interval days and compared to the corresponding values of the daily watered high frequency treatment. The asterisks indicate significant differences between the two treatments, calculated with a paired Wilcoxon rank sum test ($p < 0.05*, p < 0.001 * **$, ns = not significant, $n = 60$ for 0 and 1 days since the last watering and $n = 50$ for 2 days since the last watering). Note the significant difference in dark respiration on day 1 since the last watering despite largely overlapping notches, which arises due to the paired nature of the test. An unpaired test did not show significant differences in this case.

The linear mixed model analysis (see Table A.2.3 for results of final model) showed a significant influence of both the watering treatment and the environmental conditions on the measured carbon fluxes. We found a significant watering treatment:PAR interaction and a watering treatment:T_{soil} interaction on net photosynthesis and on dark respiration, respectively (saturated model vs. model without interaction: $df = 17$, $L - ratio = 6.96$, $p = 0.008$ for net photosynthesis and $df = 17$, $L - ratio = 7.85$, $p = 0.005$ for dark respiration). Therefore, we could not exclude the single effects from the model. In contrast, the interaction between these variables was not found to be significant for gross photosynthesis (saturated model vs. model without interaction: $df = 17$, $L - ratio = 2.65$, $p = 0.104$). The additive fixed terms PAR and the watering treatment both significantly affected the model (additive model vs. model without PAR: $df = 16$, $L - ratio = 147.7$, $p < 0.001$, additive model vs. model without the watering treatment: $df = 16$, $L - ratio = 4.2$, $p = 0.040$).

2.4 Discussion

The carbon balance of biocrust communities depends on the patterns of moisture availability, which are likely to be altered by climate change. Therefore, it is important to assess how different biocrust communities respond to an alteration in the rainfall event size and frequency and how regional and seasonal differences can influence this response. In this study, we assessed how two different precipitation frequency patterns providing the same overall amount of water (i.e. 5 mm/day vs. 15 mm/3 days) affected photosynthesis and respiration of biocrusts dominated by *D. diacapsis* in central Spain. We observed that radiation and soil temperature, together with the watering treatment, affected the rates of net and gross photosynthesis, as well as dark respiration.

During most of the experimental period, temperature was below the optimum of 22–24 °C for NP reported from *D. diacapsis* in Spain (Pintado et al., 2005). We observed the highest carbon flux rates on the days when temperatures exceeded 20 °C. However, the rates of 4–5 $\mu mol\,m^{-2}\,s^{-1}$ that are reported at optimum temperature (Pintado et al., 2005) were not reached in our experiment, where the maximum rates of net photosynthesis and dark respiration were ca. 3 $\mu mol\,m^{-2}\,s^{-1}$. A major contribution to the difference of our measurements to the maximum net photosynthesis at optimum conditions reported in the literature is possibly the hydration status of the lichens, because PAR values exceed NP compensation point of *D. diacapsis* at this temperature (Pintado et al., 2005).

In addition to the different water availability in the treatments, the lowered soil temperature in the high frequency samples (0.3–1 °C difference) possibly contributed to the observed differences between the treatments due to the exponential sensitivity of respiration to temperature. A difference of 1 °C in temperature can lead to a difference of around 5–8% in additive respiration of bare soil and *D. diacapsis* at the temperatures relevant to our study (Lange et al. (1997); Pintado et al. (2005); Castillo-Monroy et al. (2011), see Figure A.2.5). However, these temperature differences can only explain a small part of the observed total changes in dark respiration and net photosynthesis. Thus, we conclude that the main driver of the differences is water availability but that soil temperature differences also contributed to the observed patterns.

2.4.1 Individual pulse sizes

We did not find differences in the mean photosynthetic and respiratory response between the two pulse sizes evaluated (5 mm and 15 mm) on days when they were both applied. However, on the first day of the experiment, when soils and lichens were dry prior to watering, respiration and net photosynthesis were higher in the samples receiving the larger pulse. The lichen *D. diacapsis* can achieve its maximum net photosynthesis rate at thallus water contents of around 0.5–0.75 mm precipitation equivalent (Lange, 2001; Pintado et al., 2005). There are studies showing an effect of suprasaturation at a relative water content of around 50% of the maximum water holding capacity (Pintado et al., 2005) and others that do not show a depression of photosynthesis at suprasaturation (Lange, 2001). Following these studies, we can assume that in our experiment both pulses were large enough for moisture within the lichen to exceed this threshold. However, it is unclear whether suprasaturation limited photosynthesis. An indication for a suprasaturation effect could be the fact that the larger watering pulse did not lead to a higher NP response, as we would have expected. Generally, larger rainfall events lead to longer periods of moist conditions and therefore, more carbon can be fixed (Coe et al., 2012; Reed et al., 2012). Su et al. (2012) reported higher net carbon fluxes and respiration rates from cyanobacterial-lichen crusted soils in the Gurbantunggut Desert after applying a single rainfall pulse of 15 mm compared to a 5 mm pulse applied on dry soil. On the first days of our study, the 15 mm pulse led to higher net photosynthesis despite the higher respiration compared to the 5 mm pulse. The rewetting of dry biocrust communities and the underlying soil can lead to large immediate carbon losses caused by physical processes, and increased respiration due to cell reparation processes (Farrar, 1973; Lange, 2001; Smith and Molesworth, 1973). This explains the high respiration rates on the first day despite soil moisture being lower than in the following days. The beneficial effect of the 15 mm watering pulse was not sustained throughout the experiment, despite the soil moisture level after the water application being always higher for this pulse size. This indicates that not only the moisture content itself, but also the condition of a sample prior to moistening plays a role in the carbon exchange response of biocrusts. Applying the larger pulse on previously wetted soil was not beneficial in comparison to a smaller pulse that was already large enough to sufficiently wet the sample to trigger photosynthetic activity.

2.4.2 Inter-pulse frequency

When looking at the simulated rainfall patterns, we found that smaller, more frequent watering pulses were beneficial in terms of net photosynthesis. The observed differences between treatments increased with differences in soil moisture, and were higher during the last days of the experiment (when temperature and radiation increased). Our findings suggest a synergetic effect between the individual watering pulse size, the frequency of its occurrence and other environmental factors such as antecedent moisture, temperature and radiation. Apart from the size and frequency of rainfall events, temperature is an important control for moisture availability in drylands (Tietjen et al., 2017) and evaporative losses increase with it. Consequently, the response of biocrusts to altered precipitation frequencies is seasonally different because the water amount necessary to exceed the photosynthetic net compensation point differs between summer and winter (Büdel et al., 2009; Lange, 2001). There is evidence that, apart from the indirect effect of temperature on water availability, desiccation tolerance is also a seasonally dynamic physiological property in lichens and mosses (Green et al., 2011). For example, the carbon balance of the biocrust moss *S. caninervis* was higher for the same watering event when collected in winter compared to summer despite identical laboratory conditions (Coe et al., 2012).

The interacting effect of season and temperature with alterations in rainfall patterns on the performance of biocrust constituents is a common observation in many studies. The correlation between rainfall frequency and biocrust growth was found to be positive for winter rain and negative for summer rain areas in a study across southern African sites (Büdel et al., 2009). In the southwestern United States, the carbon balance of *S. caninervis* in response to rainfall frequency and amount was modulated by season and events leading to a positive carbon balance in winter could result in carbon losses in summer (Coe et al., 2012). Other studies from the same area reported a negative effect of an increased summer precipitation frequency on different variables related to the photosynthetic performance of cyanobacterial- and lichen-dominated soil crusts (Belnap et al., 2004; Johnson et al., 2012; Zelikova et al., 2012).

To our knowledge, there are no rainfall manipulation studies assessing the response of *D. diacapsis*-dominated biocrusts to different rainfall frequencies. Most of the studies evaluating how alterations in the precipitation frequency affect physiology and functioning of biocrust constituents have been conducted in summer, and therefore reported a negative impact of a higher frequency of small pulses. We conducted this study in early spring, with rather cold nights and maximum temperatures around 30 °C. These moderate temperatures enabled a constant activation of lichen photosynthesis during daily measurements. The rainfall patterns applied in this study provided a total water amount of 60 mm, which is well above the monthly saturation rainfall of 40 mm that is reported for maximum biocrust activity across Europe (Raggio et al., 2017). In combination, this led to a positive net photosynthesis and crust activity during the experiment. Field measurements with lichen-dominated biocrusts in Spain show that periods of net carbon fixation occur during the winter months, and are commonly restricted to a few hours in the morning or the late afternoon; in summer and during midday, net photosynthesis is mostly negative (Ladrón de Guevara et al., 2014; Maestre et al., 2013; Raggio et al., 2014). In summer, potential evaporation rates are high and both biocrusts and the underlying soil dry out relatively quickly upon rewetting. For an identical experiment conducted in the summer time, we would therefore expect results that are more similar to those reported from the summer studies mentioned above. However, since most rainfall events in central Spain occur during the spring and autumn/winter period (Lafuente et al., 2018), the impact of different rainfall patterns should also be studied during these phases of high biocrust activity.

2.5 Conclusion

In accordance with other studies, we showed that precipitation frequency plays an important role for the carbon balance of lichen-dominated biocrusts in central Spain. Previous studies revealed a large variability in the carbon exchange response of different biocrust constituents and communities to rainfall. To our knowledge, no studies so far have assessed the responses of *D. diacapsis*-dominated biocrusts to altered early spring precipitation frequency. In contrast to what has been found in previous studies at high summer temperatures and conducted with other biocrust-forming lichens and mosses, our results indicate that at moderate temperatures, a higher rainfall frequency is beneficial given the same overall water amount over a short period. This clearly shows that the gas exchange response to different rainfall frequencies is modulated by radiation and temperature conditions leading to seasonal differences. We therefore call for detailed cross-site and cross-season comparisons of the impacts of altered rainfall patterns on the carbon fluxes of biocrust-dominated soils.

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

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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 CO_2, 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 CO_2 levelled off with decreasing levels of relative humidity.
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 CO_2 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.

3.1 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., 2016b). It is estimated that biocrusts cover around 12% of the land surface (Rodríguez-Caballero et al., 2018a), 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 and 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., 2018a) and indirectly by supporting carbon sequestration by vascular plants through nitrogen fixation (Elbert 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 and Valladares, 2007). Furthermore, lichens regain their metabolic activity at low water potentials, which leads to a fast recovery of CO_2 exchange even through water vapour uptake or liquid water input from dew (Kappen and Valladares, 2007; Proctor and 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., 2018a). 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 (Pacifici 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 CO_2 and associated climatic changes using dynamic global vegetation models (DGVMs, e.g. Friend et al. (2013); 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. (2017); Schwinning and Ehleringer (2001)). However, only few mechanistic modelling approaches focusing on biocrusts and non-vascular vegetation have been conducted so far (Kim and 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); Porada et al. (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. (2010); Pintado et al. (2005); 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., 2017, 2014), suggesting that results obtained for *D. diacapsis* might to some degree be generalizable. 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 CO_2 concentration, rainfall, temperature, and relative air humidity. We used this model to: i) 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 vs. together on the physiological processes of activation and net primary productivity and the resulting cover, and ii) 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).

3.2 Materials and Methods

3.2.1 Species and site description

We used *D. diacapsis*, a terricolous, crustose, greyish-white lichen with a 1 to 3 mm thick thallus (Figure A.3.1) that is mostly found on calcareous substrate in exposed habitats (Lumbsch, 1988). This species has a global geographic distribution (Galun and Garty, 2001; Ghiloufi and Chaieb, 2018; Pant and Upreti, 1993; Rosentreter and Belnap, 2001), and is a model species representative of biocrusts in Spain (Pintado et al., 2010, 2005; 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 less than 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.

3.2.2 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., 2019, 2013). A full description of the model can be found in Porada et al. (2013); 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 CO_2 diffusivity on the water content. LiBry is driven by hourly local climate input and environmental conditions determining the photosynthetic rate (based on Farquhar and 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., 2018, 2013). 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 $60\,\mathrm{mm\,yr^{-1}}$ (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 $57\,\mathrm{mm\,yr^{-1}}$ (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., 2018, 2013). 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., 2018, 2013, 2014) and to predict biocrust cover at a local and global scale (Porada et al., 2019). However, it has never been applied to analyse species-specific responses at local scales as we are doing here.

3.2.3 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., 2011).

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 3.1, light curves for all temperatures are shown in Figure A.3.2).

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 and 0.4. Porosities lower than 0.3 led to specific thallus areas lower than $3.6\,\mathrm{m}^2$ 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 ($> 4.3\,\mathrm{m}^2$ 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 $0.03\,\mathrm{yr}^{-1}$ 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 (Ψ_{H_2O}) increases with thallus water content and reaches zero at a specific water content $x_{\Phi\Theta,sat}$, at which all water is stored extracellularly. Ψ_{H_2O} 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 $\Psi_{H_2O,min}$, $x_{\Phi\Theta,sat}$, and the

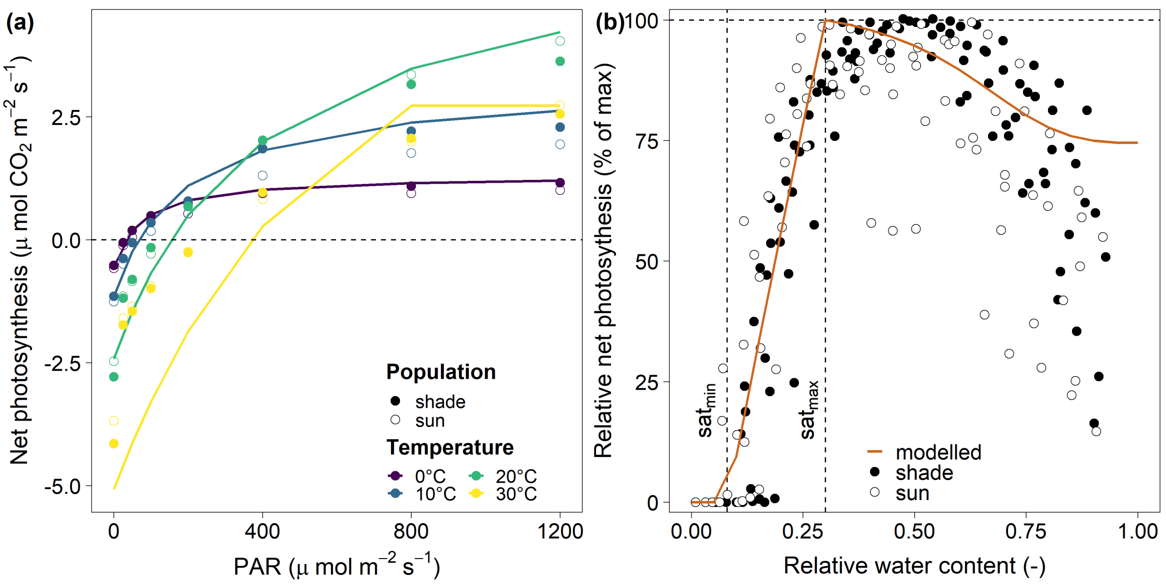

Figure 3.1: Calibration results for photosynthesis (data from Pintado et al. (2005)). a): light curves of net photosynthesis (NP) at different temperatures and optimal water content; points represent measured values of the sun and shade population. Lines represent the modelled light curves for the best fitting value combination of calibrated parameters. b): water curve of relative NP at 15 °C and 400 µmol m^{-2} 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}).

shape parameter $x_{\Psi H_2O}$ 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 and Sancho, 2002; Scheidegger et al., 1995) (Figure A.3.3).

A more detailed description of the values of species parameters and the respective references is provided in Table A.3.1. The two traits porosity and thallus saturation at which Ψ_{H_2O} becomes negative ($x_{\Phi\Theta,sat}$) 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 A.3.1, but with two different values for the unknown trait porosity (values of 0.3 and 0.4) and eleven values for $x_{\Phi\Theta,sat}$ (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).

3.2.4 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 (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 $p_{min,hyd}$ which is the minimum value for f_{hyd} at a water content Θ of zero:

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

The hydrophobicity factor f_{hyd} increases exponentially, taking values from $p_{min,hyd}$ for $\Theta = 0$ to 1 for $\Theta = \Theta_{crit}$ (Figure A.3.4). 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 $p_{min,hyd}$ 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 A.3.5). We selected the value combination of $\Theta_{crit} = 0.03$ and $p_{min,hyd} = 0.1$ 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 A.3.5), 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, i.e. general model assessments are robust, despite the parameter uncertainty (Figure A.3.6).

3.2.5 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.

3.2.6 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.

3.2.7 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 CO_2 concentration of 395 ppm (values observed in 2013 (Tans and 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 CO_2 (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 °C 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 (Moratiel 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 CO_2 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 A.3.7). Microclimatic 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: (i) control treatment without manipulations, (ii) rainfall exclusion, (iii) warming alone treatment with an increase in temperature (iv) warming treatment with an increase in temperature and a decrease in air humidity, and (v) a combination treatment of (ii) and (iv). 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.

3.3 Results

3.3.1 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 3.2, 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 where 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.

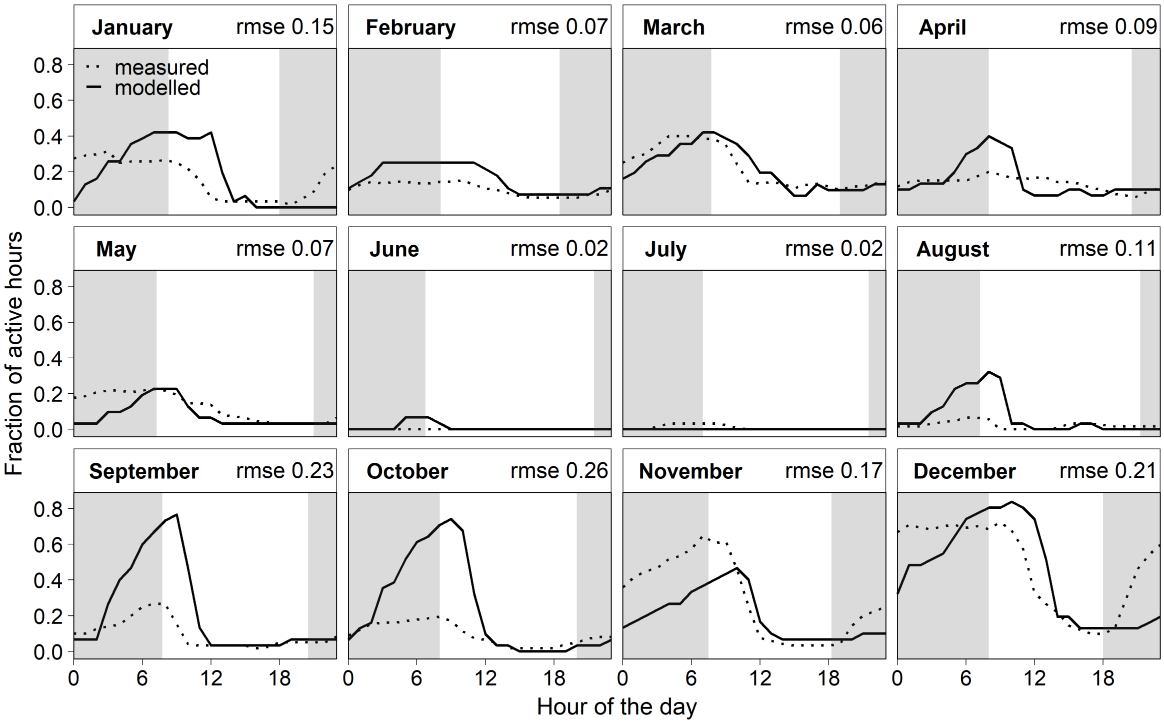

Figure 3.2: Daily fraction of active hours in each month. Modelled and measured values represent the mean of a binary representation of photosynthetic yield (yield/no yield; two samples) at the El Cautivo field site and binary values of activity represented by saturation status, respectively. Grey and white plot areas indicate night- and daytime, respectively.

Average monthly thallus surface temperature was predicted very accurately, whereas maximum and minimum temperatures, respectively, were underestimated and slightly overestimated by the model (Figure A.3.8). The surface temperature peak in the warmer months was shifted by around two hours and underestimated in magnitude by the model (Figure A.3.9). 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 $\mathrm{mm\,yr^{-1}}$, which was mainly accumulated during the nights between September and April and was particularly high in September and October (Figure A.3.10).

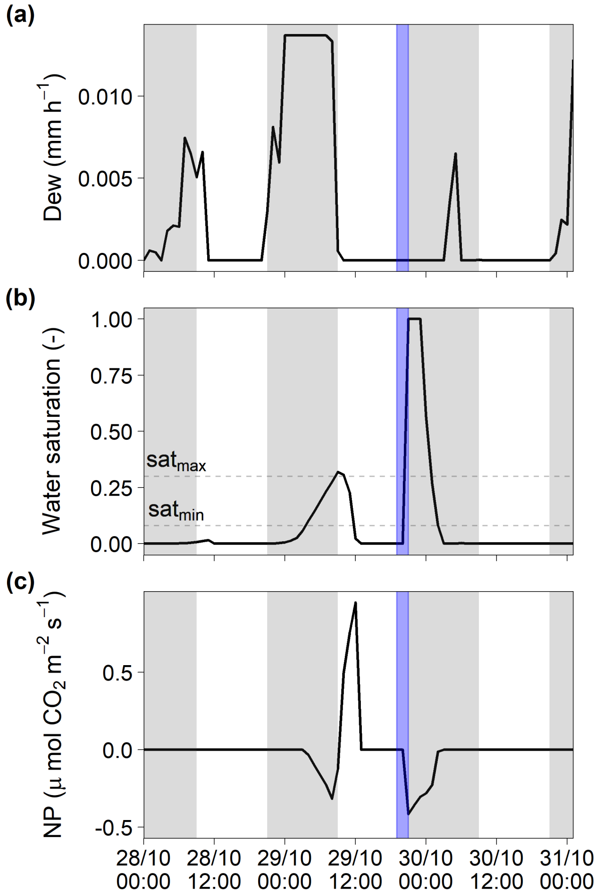

Figure 3.3: Modelled water saturation and net photosynthesis (NP) in response to dew formation and rainfall. a): simulated dew formation, b): water saturation with indication of saturation values of onset of photosynthesis (sat$_{min}$) and maximal photosynthesis (sat$_{max}$), and c): NP in hourly resolution 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 h.

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 three days in Figure 3.3 a, 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$_{min}$).

3.3.2 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 3.4). 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: $10\,\mathrm{g\,C}/\mathrm{m}^2/\mathrm{s}$), leading to a cover increase by 30% and 32% for the RCP 4.5 and the RCP 6.0 scenario, respectively (Figure 3.4). The cover difference between the control and RCP 4.5 scenarios was larger 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 °C or 5 °C had a positive effect on modelled steady-state cover (Figure 3.4). 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 3.4). 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 to 36% relative to control) and associated activity time (decrease by 63 to 69% relative to control) (see Table A.3.2).

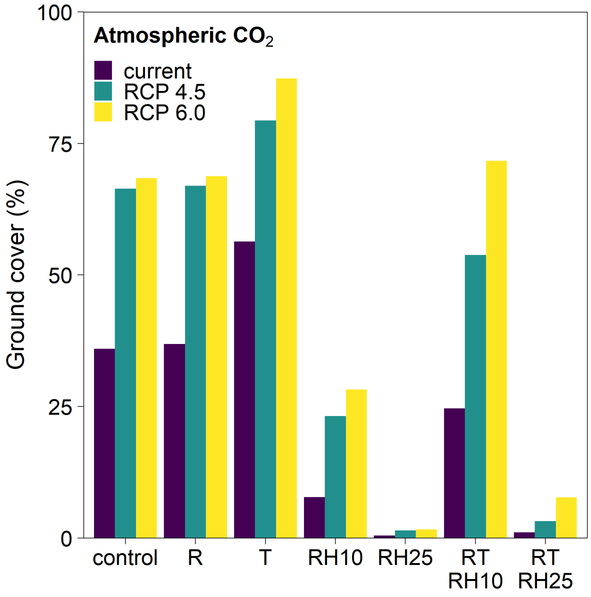

Figure 3.4: Steady-state cover of *Diploschistes diacapsis* for different atmospheric CO_2 (current = 395 ppm, RCP 4.5 = 650 ppm, RCP 6.0 = 850 ppm) and climate scenarios. Control = no changes in rainfall, temperature and relative humidity, R = rainfall reduction by 30%, T = temperature increase by 3 °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.

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.

3.3.3 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 3.5 b). 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 3.5 a), but modelled effects were not as strong as those observed in the field.

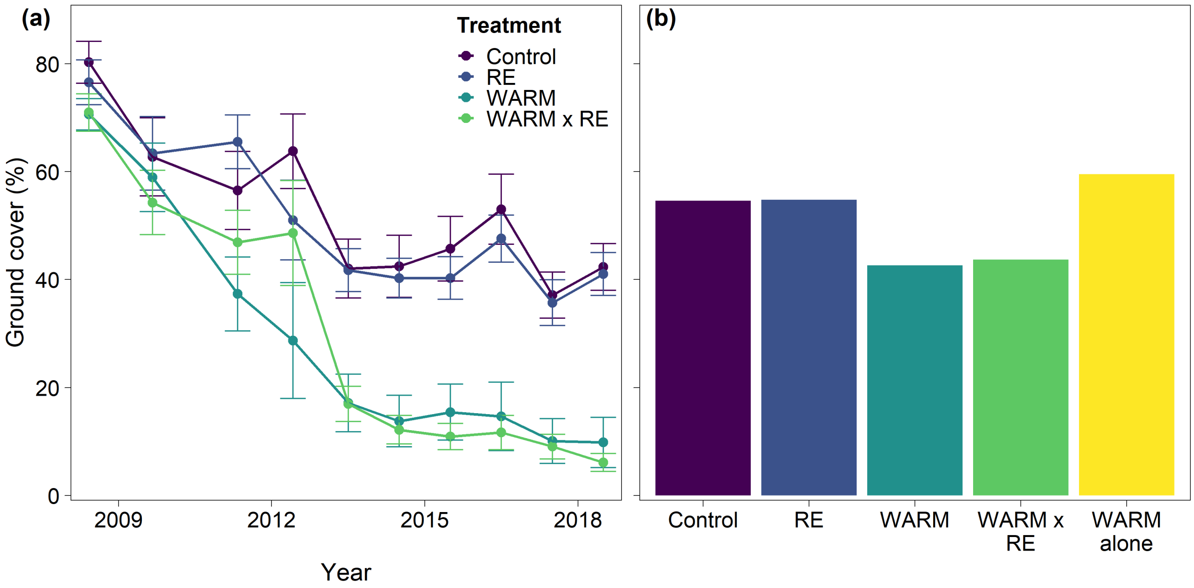

Figure 3.5: Changes in the cover of *Diploschistes diacapsis* as a result of climatic conditions in the Aranjuez experiment and in the model. a): measured cover change of biocrust lichens (including *D. diacapsis*), b): modelled cover in steady state. RE (Rainfall exclusion) refers to a 30% reduction in rainfall, WARM (warming) to an increase in temperature by 2.7 °C and the associated indirect reduction in relative humidity, WARM x 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.

3.4 Discussion

3.4.1 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 of 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 A.3.10). 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 $\mathrm{mm\,yr^{-1}}$ from 2007 to 2010) and our model (25 $\mathrm{mm\,yr^{-1}}$). 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 3.3) 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 (Del Prado and Sancho, 2007; Green et al., 2011; Pintado et al., 2010; 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).

3.4.2 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 CO_2 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 CO_2 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 A.3.11) 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., 2017, 2014), 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., 2016b; 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., 2016b). 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 NWRI 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 A.3.12), when the lichen usually gains carbon leading to a reduced NPP (Figure A.3.13) 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., 2016b; Raggio et al., 2014). Dew nights are often followed by sunny and clear days, which leads to a reduced activity time compared to 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 CO_2 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 CO_2 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 CO_2 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., 2013, 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 and 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., 2018a) 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 CO_2 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).

3.4.3 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, while 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., 2016a). 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 and 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).

3.5 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 CO_2 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-variably and has a wide global distribution, a follow-up study could improve our understanding of the future distribution of *D. diacapsis*-dominated biocrusts worldwide by 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.

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4 Soil crusts influence water redistribution and enhance water availability for plants

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Introduction. In sparsely vegetated drylands, the bare interplant spaces are often colonised by biological soil crusts, communities dominated by cyanobacteria, lichens and mosses. Living at the interface between soil and atmosphere, these communities affect landscape ecohydrology by altering soil infiltration and evaporation as well as water redistribution through surface runoff which provides important resources for vascular vegetation. Biocrusts are thus important ecosystem engineers that structure the landscapes they inhabit. Despite their importance, they have rarely been included in ecohydrological models to investigate their effect on dryland landscapes.

Methods. We extended a spatially explicit, process-based ecohydrological dryland model and included a layer of biological soil crusts. The model was parameterised and calibrated for a dryland hillslope in South East Spain. With the model, we investigated the effect of the biocrust community on landscape-scale soil moisture distribution, plant-available water and the hydrological processes behind it. We also assessed if biocrust can buffer some of the negative effects of drought years on soil moisture. Finally, we compared the effect of physical crusts, cyanobacteria- and lichen-dominated biocrusts on hydrology and soil moisture to evaluate possible paths forward if biocrust communities change as a result of climate change.

Results. Our model was able to reproduce the typical runon-runoff patterns observed in the landscape and the spatial differentiation of plant-available water matched the observed distribution of vascular vegetation in the landscape. We could show that compared to a simulation without biocrusts, the model with biocrusts led to higher water availability for the vegetated areas of the landscape and that this positive effect in part also held for dry years. Compared to bare soil and physical crusts, biocrusts protected the soil from evaporation thus preserving the soil moisture despite lower infiltration rates while at the same time redistributing water towards downhill vegetated areas.

Conclusion. Biocrust cover is vital for water redistribution and plant-available water but potential changes of biocrust composition and cover can reduce their function as water sources for sustaining dryland vegetation. The process-based model used in this study is a promising tool to further quantify and assess long-term scenarios of climate change and how it affects the ecohydrological feedbacks that shape and stabilise dryland landscapes.

4.1 Introduction

Semiarid landscapes are often characterised by patterned or patchy vegetation cover and close ecohydrological interactions between vegetated areas and bare interplant spaces. Unvegetated areas of the landscape yield runoff, which can infiltrate in vegetated areas and support vascular plant productivity (Ludwig et al., 2005; Thiery et al., 1995). In such landscapes, the interplant space is often covered by a continuous layer of biological soil crusts (biocrusts), communities of poikilohydric organisms such as lichens, cyanobacteria and mosses (Weber et al., 2016b). Biocrusts grow on and within the first few centimetres of the soil surface and act as a boundary layer between the soil and the atmosphere (Belnap and Büdel, 2016; Belnap et al., 2001). In this position, biocrusts mediate all water inputs and outputs from the soil and alter soil infiltration (Chamizo et al., 2012a; Guan and Liu, 2021; Xiao et al., 2019), evaporation (Chamizo et al., 2016b; Kidron et al., 2022; Kidron and Tal, 2012) and the generation and distribution of surface runoff (Cantón et al., 2011; Chamizo et al., 2012b; Guan and Cao, 2019; Kidron, 2021). The effect of biocrusts on evaporation is still unclear and can change during the evaporation stages (Guan and Liu, 2019) with studies reporting both a reduction (Cantón et al., 2020; Chamizo et al., 2016b; Kakeh et al., 2021) and an increase (Kidron et al., 2022; Kidron and Tal, 2012) in evaporation in biocrust covered compared to bare soil. At the same time, biocrusts generally reduce infiltration (Eldridge et al., 2020), especially for high intensity rainfall events (Chamizo et al., 2016b) which, together with other factors such as hydrophobicity of some lichens species (Kidron et al., 1999; Pintado et al., 2005; Souza-Egipsy et al., 2002), can increase runoff, especially for high-intensity rainfall (Rodríguez-Caballero et al., 2013).

Local interactions between biocrusts and hydrological processes have a cascading effect on the landscape-scale redistribution of rainfall water. In this way, biocrusts shape water fluxes in the landscape and drive the interaction between uphill runoff-dominated source and downhill runon-dominated sink zones (Belnap et al., 2005; Eldridge et al., 2021; Ludwig et al., 2005; Noy-Meir, 1973). For this reason, biocrusts have been regarded as an “organizing principle” (Belnap et al., 2016) in drylands, because they support the formation of islands of fertility (Belnap et al., 2016), where runon infiltrates and vascular plants can grow and benefit from the increased water and nutrient input (Belnap and Büdel, 2016; Rodríguez-Caballero et al., 2018c).

The exact mechanisms of how biocrusts mediate hydrological processes are complex, and the sign and size of the effect is often context dependent (Chamizo et al., 2016a; Eldridge et al., 2020). Patches covered by biocrusts can modify hydrological processes in opposite ways: Either they can either retain water by increasing infiltration and reducing evaporation and runoff, or they can yield water by increasing runoff and reducing infiltration (Chamizo et al., 2016b). The specific impact of a biocrust covered patch depends on various direct and indirect factors that moderate the crust’s response to rainfall events and their effect on hydrological processes (Chamizo et al., 2016a). One important direct factor is the species composition of the crust. For example, higher moss cover and an advanced crust developmental stage can increase soil infiltration and reduce runoff from the crust due to increased surface roughness and macroporosity (Belnap et al., 2013; Miralles-Mellado et al., 2011). In contrast, some lichen species have hydrophobic surfaces which reduce their capacity to take up water, therefore reducing infiltration and increasing surface runoff (Cantón et al., 2002; Souza-Egipsy et al., 2002). These direct factors can interact with indirect factors such as precipitation magnitude and intensity. For example, biocrusts can decrease runoff during low intensity rainfall events, but this effect can disappear for more intense and high magnitude events that saturate the soil and the biocrust layer (Chamizo et al., 2013b, 2012b; Rodríguez-Caballero et al., 2014). Moreover, environmental conditions such as the soil type (Chamizo et al., 2013b; Warren, 2003) play an important role in governing the effect of crusts on hydrology. Biological soil crusts on sandy soils tend to decrease infiltration compared to uncrusted soils, whereas on more clay or loam soils, effects are less clear or opposite (Eldridge et al., 2020; Warren, 2003). Spatial scale is also important to consider, because the connectivity between retentive (e.g. vascular vegetation) and conductive (e.g. biocrusts or bare soil) elements ultimately determines landscape-scale runoff (Ludwig et al., 2005). Although the effect of biocrusts on hydrological processes is context dependent, a general emerging pattern in drylands worldwide seems to be that biocrusts increase runoff and decrease infiltration, while at the same time they increase soil moisture of the most active top soil layers and reduce soil erosion (Eldridge et al., 2020).

In the light of these effects, an intact network of biocrust areas is vital for dryland ecosystem functioning. This becomes especially important considering that climate change reduces the overall water availability in drylands (Cramer et al., 2018; Huang et al., 2017) and changes individual rainfall characteristics towards less frequent but more extreme events in many regions (IPCC, 2021; Toreti and Naveau, 2015; Toreti et al., 2013). An intact network of biocrust patches can help to buffer drought years and provide vital water and nutrient input for vascular vegetation growth (Antoninka et al., 2020; Rodríguez-Caballero et al., 2018c). At the same time, it can reduce or even prevent land degradation by erosion following intense and high magnitude rainfall events (Belnap et al., 2016; Chamizo et al., 2017). Biocrusts are thus vitally important for dryland ecosystems to mitigate the impacts of climate change. However, climate change and other disturbances affect the biocrusts themselves, reducing their species richness (Ladrón de Guevara et al., 2018), functional diversity (Mallen-Cooper et al., 2018), and ultimately reducing their overall cover (Baldauf et al., 2021; Finger-Higgens et al., 2022). This threatens the complex interactions and feedbacks between biocrust and vegetated patches in drylands which help to sustain the landscape's productivity.

Most studies on the interaction between biocrusts and hydrology have been field studies conducted on spatial scales below $10\,\mathrm{m}^2$, and many of these studies focus on scales below $0.05\,\mathrm{m}^2$ (Eldridge et al., 2020). Small scale effects cannot be necessarily extrapolated and quantified on the landscape scale (Chamizo et al., 2016a), as important processes such as the runoff-runon network on the hillslope are not captured (Rodríguez-Caballero et al., 2014). To address this gap and to improve predictions, previous studies called for including biocrusts into ecohydrological and hydrological models (Hui et al., 2021; Rodríguez-Caballero et al., 2015). Ecohydrological models have long been used to study the interactions between local and landscape-scale hydrological processes and their effect on vegetation in drylands (e.g. Franz et al. (2010); Tietjen (2016); Tietjen et al. (2010)). However, until today there are only few ecohydrological or hydrological models that explicitly account for biocrusts (Chen et al., 2019, 2018; Jia et al., 2019; Rodríguez-Caballero et al., 2015; Whitney et al., 2017). Those that exist either focus on the time scale of single rainfall events rather than on longer time scales (Rodríguez-Caballero et al., 2015) or are not spatially explicit and can therefore only capture point scale processes (Chen et al., 2019, 2018; Jia et al., 2019; Whitney et al., 2017). Spatially explicit ecohydrological simulation models have a large potential to complement experimental and observational studies to assess landscape-scale patterns and long term effects of biocrusts on landscape ecohydrology.

In this study, we aim to understand the effect of different biocrusts on landscape-scale soil moisture as a result of the redistribution of water via runoff, soil evaporation and infiltration. To achieve this aim, we extended the spatially explicit, process-based ecohydrological simulation model EcoHyD (Tietjen et al., 2010, 2009) by including biocrusts and their impacts on hydrological processes. We calibrated and validated the model with field measurements from south-eastern Spain and evaluated the impact of different biocrust types and rainfall amount on water redistribution from biocrust patches to vegetated areas. In particular we are interested in the following questions:

- What are the main processes shaping spatio-temporal soil moisture patterns and plant-available water in the landscape under current conditions? We hypothesise that the water redistribution from uphill crusts plays a major role for soil moisture in lower areas, particularly during the wet winter months when runoff is high. During the dry summer, we expect only small effects.
- What is the quantitative contribution of biocrusts to landscape-scale soil moisture distribution in wet and dry years and which are the major processes involved? We hypothesise that soil moisture is generally higher in the presence of biocrusts as they enhance the water retention capacity, which is particularly important in dry years.
- To what extent will landscape-scale hydrological processes and soil moisture be affected if biocrusts shift from lichen-dominated to cyanobacteria-dominated or physical crusts under climate change? We hypothesise that with declining lichen cover, less water will be redistributed and more water will be lost through evaporation.

4.2 Materials and Methods

4.2.1 Site description

The El Cautivo site is located in the badlands of the Tabernas desert in south-east Spain (37°0′N, 2°26′W, 200 m a.s.l.). The climate is semi-arid Mediterranean [mean annual temperature Tabernas weather station: 17.8 °C (from 10.3 °C in January to 27.0 °C in August), mean annual precipitation: 235 mm (monthly means ranging from from 2 mm in July to 29 mm in November)] (Agencia Estatal de Meteorología (AEMET), 2020b). In this study, we concentrated on one south-east-facing hillslope characterised by sparse vegetation cover, dominated by annual and perennial grasses and dwarf shrubs (Figure 4.1 a,b). The vegetation distribution is mainly controlled by the topography: biocrusts and physical crusts cover the steep upper parts of the

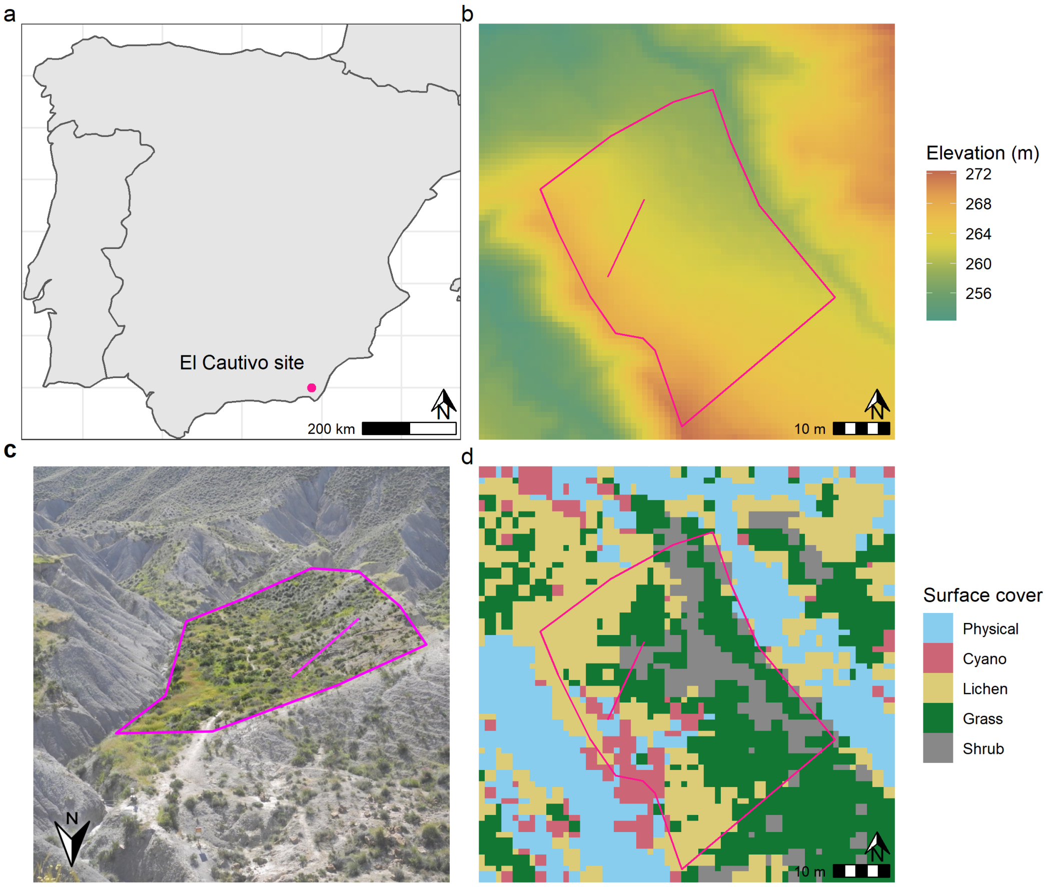

Figure 4.1: Study site location and hillslope in the Tabernas badlands. a) Location of the study site in south-east Spain. b) Elevation map of the region (1 m resolution). b) Photo of the study site. The pink polygon roughly encloses the hillslope investigated in this study (picture: Selina Baldauf, 03/2017). Please note that the orientation in this image is different from the maps (see north arrow). c) Vegetation and crust cover map from hyperspectral imaging conducted in 2010. The pink polygons in b) and d) enclose the hillslope simulated in this study. The pink line in b–d shows the transect for which modelling results are analysed in detail.

hillslope, whereas vascular vegetation, i.e. perennial grasses and shrubs, covers the lower and less steep parts of the hillslope (Figure 4.1 c) (Cantón et al., 2004a). A detailed site description of El Cautivo is provided in (Rodríguez-Caballero et al., 2013).

4.2.2 Field data

We used field data from the study site to parameterise the model and scenarios. In the following, we describe the field data we obtained and how it was pre-processed before using it in the model.

Climate data

We used climate data for the hydrological year 2009–2010 (October 2009–September 2010) from an on-site weather station. Temperature and rainfall data were aggregated from 30 min (rain) and 10 min (temperature) to 1 h intervals by calculating the mean temperature and the sum of rainfall. We filled one missing temperature value by linear approximation between the two nearest measurements. In the rainfall time series, 504 values were missing. We replaced the missing values with 0 because a linear approximation would have increased annual rainfall by 76 mm. The hydrological year 2009–2010 is already wet in comparison to average years (MAP of Tabernas 235 mm) and we wanted to avoid artificially inflating the total rainfall of this year. We reordered the time series to start in June, because the EcoHyd model starts simulations in the dry season in June. The final climate time series used as input to the model had a mean annual temperature of 19.5 °C and an annual rainfall sum of 375 mm (Figure A.4.4).

Soil moisture data

We obtained hourly soil moisture data in two depths (3 cm and 10 cm) for the same period as the climate data and reordered the time series accordingly (Chamizo et al., 2016b). The data was collected under three different surface cover types: incipient cyanobacteria crust (in the further analyses this is referred to as physical crust), cyanobacteria crust and lichen crust, respectively. The incipient cyanobacteria crust is characterised by a low to very low biomass density of cyanobacteria and is very thin and light-coloured. It represents the first successional stage of biocrust formation in this area and as such is still very similar to physical crust. As cyanobacterial biomass increases, the cyanobacteria crust forms which shows higher biomass density and a darker colour. The lichen crust is dominated by light-coloured lichens mainly *Squamarina lentigera* and *Diploschistes diacapsis*.

Landscape data

We used a digital elevation map of the region with a 1 m resolution (Figure 4.1 b). To parameterise vegetation cover, we used a surface cover map obtained by classification of a hyperspectral image taken in 2010. The resolution of the surface cover map was increased from 1.5 m to 1 m, using a nearest neighbour interpolation method. The resulting landscape data consisted of 74 x 74 grid cells of 1 m resolution (ca. 5500 m^2). For the analysis of the results, we only used the part of the landscape that represented the hillslope (see Figure 4.1 b–d). The surface cover of the hillslope consisted of five cover classes: Shrubs (20% of hillslope cells), perennial grasses (40% of hillslope cells), lichen crust (39.5% of hillslope cells), cyanobacteria crust (6.5% of hillslope cells) and physical crusts (4% of hillslope cells).

4.2.3 Model description

We used the process-based ecohydrological dryland model EcoHyD (Tietjen et al., 2010, 2009) and included biocrusts and their effect on hydrological processes. EcoHyD is spatially explicit and divides the landscape into squared grid cells of variable size. The model consists of a hydrological (Tietjen et al., 2009) and a vegetation (Lohmann et al., 2012; Tietjen et al., 2010) sub-model. Biological soil crust processes were implemented based on the processes of the one-dimensional ecohydrological biocrust model by Whitney et al. (2017). In the following, we give a brief summary of the model. A more detailed process description with all the changes that were made to the original model can be found in Section A.4.1.

The hydrological sub-model of EcoHyD calculates the water dynamics of two soil layers in each grid cell on an hourly time step. This sub-model was extended to include biocrusts as a layer on top of the first soil layer. The crust layer modulates all water input and output to and from the soil. Rainfall is first transformed into surface water and can then infiltrate into the biocrust layer, depending on its porosity and current moisture. If the crust type that covers the cell is hydrophobic, infiltration is reduced by a hydrophobicity factor which depends on the crust type and its current moisture content. The remaining surface water after crust infiltration (i.e. when the crust is saturated) leaks through the biocrust into the upper soil layer where it infiltrates following a Green and Ampt approach (Green and Ampt, 1911). As soon as the upper soil layer is saturated (i.e. its water content reaches field capacity), water drains from the upper into the lower soil layer. If the lower soil layer is saturated, water drains into deeper layers that are not explicitly simulated. The remaining surface water is redistributed within the landscape via surface runoff. Each cell passes runoff to its lowest neighbouring cell. The amount of runoff from a cell depends on the amount of surface water, the slope and the surface roughness of the cell. Vascular vegetation linearly reduces runoff by a factor between 1 (for 0% vegetation cover) and 0.5 (for 100% vegetation cover) (Tietjen et al., 2009). Biocrust increase runoff by a factor of 3.6 because measurements at the research site showed that runoff from crusted soil on average is 3.6 times higher than on non-crusted soils (Cantón et al., 2001, 2002). Crust evaporation and soil evapotranspiration are evaluated once at the end of each day based on the mean, minimum and maximum temperature of that day. Water from the crust can evaporate if the moisture is above a crust specific hygroscopic point. Soil evapotranspiration depends on the vegetation cover of the cell as well as the crust specific evaporation reduction factor. Vegetation cover was constant throughout the simulation, therefore all processes in the vegetation sub-model except for transpiration were switched off in this study. Shrub and grass coverage were set at the beginning of the simulation according to observed coverages.

4.2.4 Model parameterisation

The model requires soil, crust and vegetation parameters as input, as well as maps with the elevation and the surface cover of each grid cell (separate for grass, shrub and soil crust type) and an hourly time series of temperature and rainfall (Figure A.4.4). Climate and elevation input were prepared as described above. The surface cover map from 2010 was used to assign perennial grass cover, shrub cover and crust cover to each grid cell of the model. Cells covered by vascular vegetation were assigned a cover value of 80% of the respective vegetation type, cells covered by crusts were assigned 100% crust cover. For simplicity, we assumed that grasses and shrubs did not occur in the same cell. All vegetated cells were additionally covered by 100% cyanobacteria crusts leaving no bare ground on the hillslope, except for the physical soil crusts.

The relevant vegetation parameters in this study were parameters on the shading effect on evaporation and the relationship between aboveground cover and belowground root fractions, impacting water losses by transpiration. Since we did not have measured values from Tabernas for these parameters, we used the same values as in (Tietjen et al., 2010). Wherever possible, we used literature data on crust and soil characteristics to parameterise the model. However,

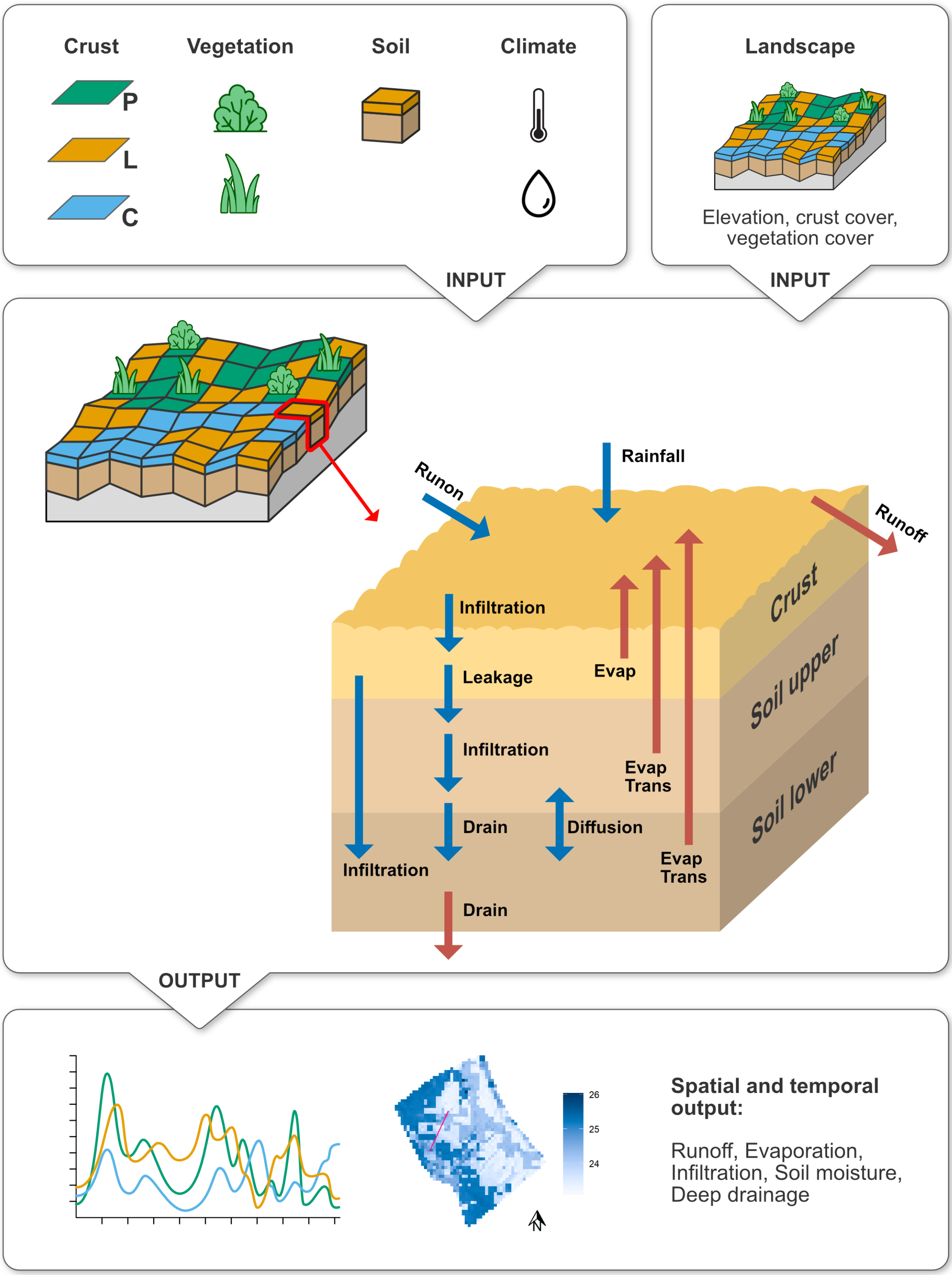

Figure 4.2: Model concept of the EcoHyD model with biocrust layer. The first row shows the model input parameters for crust (physical, lichen, cyanobacteria), vegetation (shrub, perennial grass), soil and climate (temperature, rainfall) variables. The landscape (top-right) is paramterised by values for elevation, crust and vegetation cover in each grid cell. In the middle, the all model processes in one grid cell are shown for the 3 layers. Blue arrows represent processes that provide water input into a cell, red arrows represent water output. On the bottom, the model output that is analysed is shown: temporal output of the different hydrological processes for each of the crust cover types and spatial output of the processes foreach grid cell.

as many crust and soil specific parameters remained unknown or were variable between studies, we conducted a sensitivity analysis to determine the parameters that had the highest influence on the fit of measured to modelled soil moisture. Afterwards, we calibrated these parameters to best match observed patterns of soil moisture.

The sensitivity analysis was conducted using a modified version of the Morris method of elementary effects (Campolongo et al., 2007) as implemented in the morris function of the R package sensitivity (Iooss et al., 2021). The target function of the sensitivity was the fit (root mean square error (RMSE)) of modelled to measured soil moisture data. The sensitivity analysis was conducted using two wet winter months of the climate time series (December 2009–January 2010) for ten crust and four soil parameters (see Table A.4.1 for details on parameters and tested value ranges). This period covered the start of the wet season with a large increase in soil moisture, as well as some weeks of the wet season with generally high soil moisture (Figure A.4.4). We used parameter value ranges that were realistic from the literature research (see Table A.4.1 for references). As the soil moisture measurements were conducted in a flat part of the hill, we conducted the sensitivity analysis on a flat hillslope. The most sensitive parameters (both in terms of direct and interactive effect) were the four crust-related parameters crust thickness, crust porosity, crust saturated hydraulic conductivity and crust evaporation factor as well as all four parameters soil saturated hydraulic conductivity, field capacity, suction at the wetting front and wilting point (see. Figure A.4.5).

These parameters were calibrated for the three different crust types (physical, cyanobacteria, lichen), using the soil moisture data from El Cautivo. We calibrated the parameters within the same value range as used for the sensitivity analysis (Table A.4.1). Calibration was performed with a genetic differential evolution algorithm procedure using the “DEoptiom” R package (Ardia et al., 2011; Mullen et al., 2011). The target of the calibration function was the RMSE of simulated and measured soil moisture in the two soil layers. We chose a calibration period of 2 months (December 2009–January 2010). Crust parameters were calibrated for the three crust types and soil parameters were calibrated to be the same underneath all crust types. The calibration results are shown together with the parameterisation in Tables A.4.2, A.4.3, A.4.4. The calibrated model was able to reproduce the soil moisture dynamics in the two soil layers that were measured in the field reasonably well (overall RMSE upper layer: 3.2-3.4%, lower layer 3.1-3.6%, Figure A.4.6). Crust parameters that were not calibrated were taken from Whitney et al. (2017). In their modelling study, they report calibrated parameter values for different crust roughness index classes. Generally, crust roughness increases with the developmental stage (Caster et al., 2021), therefore we used the parameter values of the first (lowest) roughness class for the physical crust, the second for the cyanobacteria and third for the lichen crust. The hydrophobicity function was parameterised using results from water drop penetration tests (WDPT), conducted on different crust samples from El Cautivo. We used quadratic fits of water drop penetration time depending on crust moisture for physical, cyanobacteria and lichen crusts. The results of the WDPT showed a large difference between cyanobacteria, incipient cyanobacteria and lichen crust (Figure A.4.7). In a dry lichen crust, the water could take up to 300 min to be absorbed whereas the time in the other crust types was below 2 min. Considering the model time step of 1 h, we therefore included hydrophobicity only for the lichen crust (hydrophobicity parameters see Table A.4.2).

4.2.5 Simulation experiment

We ran several simulation experiments to answer our research questions. First, we established a baseline scenario in which we simulated the El Cautivo site under current conditions (scenario “El Cautivo”). For this baseline scenario, we used the data and parameterisation as described above. We looked at the hydrological processes of water redistribution, evapotranspiration, deep drainage and runoff in each grid cell to evaluate how water is distributed in the landscape and how uphill areas covered by biocrusts affect downhill soil moisture. Here, we additionally looked at deep drainage as an estimate for plant-available water in the soil layers that exceed the thin soil layer that we simulated explicitly. To analyse these processes in detail and in different months, we looked at the spatial distribution patterns of these processes in the whole landscape but also in a selected hillslope transect that contained both uphill biocrusts and downhill vegetation (see Figure 4.1 b,d).

Second, we removed all crust cover from the landscape and ran the model with bare soil, as it is originally represented in EcoHyD (scenario “no crust”). We then compared the soil moisture distribution in the landscape between the “El Cautivo” scenario with and the “no crust” scenario to get a quantitative estimate of the crust contribution and effect on soil moisture. To look at the processes behind this estimate in detail, we compared water redistribution, evapotranspiration, deep drainage and soil moisture in the selected hillslope transect between the two scenarios.

Third, we ran both the baseline “El Cautivo” and the “no crust” scenario with a 50% reduced rainfall time series (every rainfall event -50%, scenarios “El Cautivo dry” and “no crust dry”) and compared the soil moisture distribution between the two scenarios. We evaluated if biocrusts could sustain a higher soil moisture in years with less rainfall compared to uncrusted soil.

Finally, we compared the effect of the three different crusts types (physical, cyanobacteria, lichen) on hydrological process and soil moisture. For this, we conducted three simulations, in which the landscape was covered by only one of the three crust types, respectively. Vascular vegetation in this scenario was described as above and was the same in all three scenarios. We compared landscape mean values of infiltration, evapotranspiration, runoff, deep drainage and soil moisture between the landscapes covered by the different crust types. With this scenario we wanted to get an estimate of how landscape hydrology and plant-available water might change if the biocrust cover shifted from lichen towards cyanobacteria and physical crusts in the future due to climate or land-use change.

4.3 Results

4.3.1 Soil moisture patterns and plant-available water under current conditions

In general, the baseline scenario shows a clear differentiation of the hillslope by surface cover in terms of soil moisture and hydrological processes in the wet winter season (Figure 4.3 shows

January, see Figures A.4.8, A.4.9, A.4.10 for other months). Runoff is highest in the crusted uphill areas where the slope is steep and runoff concentration in channels can be observed. Runoff decreases as soon as it reaches the vegetated part of the hillslope and it is lowest in the flat areas of the lower hillslope. The runoff from the crusted hillslope area provides additional water input especially in the middle part of the hillslope that is mainly covered by perennial grasses and some shrubs. These are the areas with a positive water gain (calculated for each cell as the difference between runon and runoff), i.e. a net water input through runoff. In contrast, the crusted upper parts of the hillslope are characterised by a net water loss through runoff (negative water gain). The vegetation in these zones benefits from the additional water input through higher deep drainage that provides water to the deeper soil zones. Generally, deep drainage is higher under vegetation, indicating an increased water availability for vegetation below the first 20 cm of the upper soil two layers. At the same time, evapotranspiration from both layers is also higher under vegetation particularly under perennial grasses.

The summary of these hydrological processes leads to differences in soil moisture that can be observed underneath different surface covers. Soil moisture in the upper layer is relatively similar in all parts of the hillslope with slightly drier soils under areas covered by physical crusts. In the lower soil layer, however, a clear difference between crusted and vegetated areas of the hillslope can be observed: soil moisture is highest below lichen biocrusts in the upper part of the hillslope and lowest under perennial grass vegetation in the downhill parts while areas with physical soil crusts are in between. These differences can be relatively well explained by the differences in evapotranspiration.

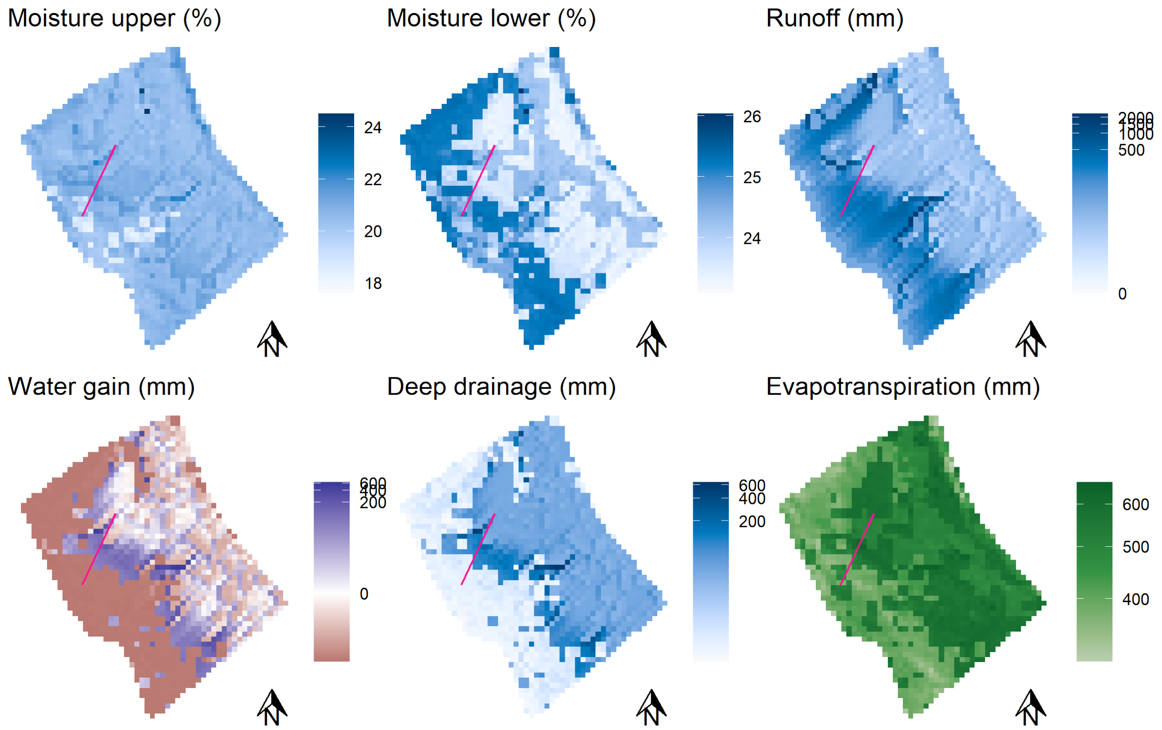

Figure 4.3: Mean monthly soil moisture and monthly sum of hydrological processes for each grid cell on the El Cautivo hillslope in January. The pink line shows the hillslope transect that was selected for further detailed spatio-temporal analysis. It crosses a crusted section at the top (SW) and a vegetated section further down the hillslope (see also Figure 4.1).

A detailed analysis of the processes in a selected hillslope transect that crosses different surface cover areas shows a similar spatial differentiation of hydrological processes and soil moisture over the course of a year (see Figure 4.4). At the beginning of the wet season which starts with the first rainfall in December, soil moisture in both layers rapidly starts to increase in all parts of the transect. The rewetting-pulse in December is strongest for the upper vegetated cells in the lower soil layer. In this area, water gains are particularly high, as runoff from the upper crusted metres of the transect infiltrates. In general, water redistribution is only visible in the wet season from December until March and is particularly strong in January and February. Then, water is redistributed from the upper, crusted cells into the vegetation cell of the whole transect. In the next months (February and March) water redistribution can only be observed for the upper vegetated metres of the transect and the lower part does not receive additional water anymore. This pattern of water redistribution is directly reflected in deep drainage. Cells with positive water gain show higher levels of deep drainage, indicating that the additional water input infiltrates into lower layers where it is available for vegetation growth. While in December and January, the whole vegetated transect benefits from high levels of deep drainage, in February and March, only the upper metres of the vegetated cells benefit. Evapotranspiration is highest in the wet season because in the summer months, there is almost no water available. Evapotranspiration increases in the wet season with increasing temperature until March, when it is highest. In April, soil moisture sharply declines together with evapotranspiration and the dry season begins. Soil drying is much faster in the upper than in the lower soil layer and is also faster in the vegetated lower part of the transect compared to the crusted upper part.

4.3.2 Quantification of crust effects under current and dry conditions

In the wet season, soil moisture in the upper layer is generally higher in the scenario with crusts (“El Cautivo” scenario) than without crusts (“no crust” scenario), except for December where this pattern is reversed (Figure 4.5). In the lower soil layer the pattern is similar, but soil moisture in the upper transect part is lower in the “El Cautivo” compared to the “no crust” scenario. This is also reflected in the results for deep drainage which is consistently lower in the upper part of the transect in the scenario with biocrusts. Interestingly, the differences in soil moisture already shift from positive to negative in August and September for the upper and the lower layer, respectively. Still, the overall soil moisture differences are very low (max -3% in December) in these months because the moisture is already at or close to the wilting point in summer. Evapotranspiration is consistently lower in the “El Cautivo” scenario compared to “no crusts”. The highest differences can be observed in March, when overall evapotranspiration is maximal (Figure 4.4). The differences in water gain between the scenarios are well reflected in the deep drainage with values being almost the same. This suggests that water that reaches a cell through redistribution, normally drains to the deeper soil layers where it is available for vegetation. Consequently, if water gain is reduced (or increased) also deep drainage is reduced (or increased). The temporal patterns of water gains are less clear. In December, water gains are higher in the upper part of the transect if there are crusts, which leads to less water gains in the first vegetated cells of the hillslope. In January, this pattern starts to reverse and the

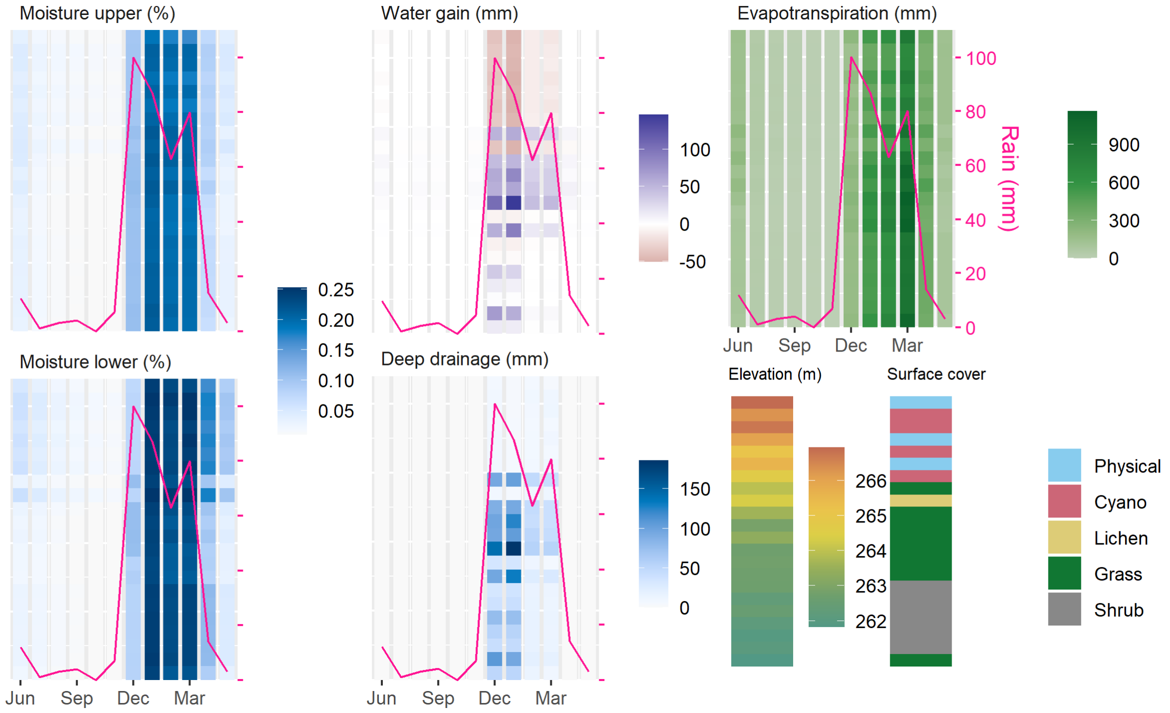

Figure 4.4: Spatio-temporal development of soil moisture, water gain, deep drainage and evapotranspiration in the cells of the selected hillslope transect. The figures show monthly mean moisture and monthly sum of the hydrological processes for each of the cells in the transect over the course of one year (x-axis). The last panel shows the elevation and surface cover of the transect cells that are displayed along the y-axis of the spatio-temporal plots.

upper transect parts of the hillslope redistribute more water if they are covered in biocrusts which leads to higher positive water gains in the vegetated cells in this scenario.

The overall soil moisture distribution in all grid cells shows that soil moisture in the upper layer is consistently higher in the scenario with crusts compared to the scenario without crusts in the wet season (Figure 4.6, see Figure A.4.11 for all months). Similar to the transect results (Figure 4.4), the month of December is an exception because in December, soil moisture is higher in the scenario without crust. In the lower layer, the soil moisture distributions are less distinct and overlap between the “El Cautivo” and the “no crust” scenarios. However, there is a tendency for higher soil moisture in the scenario with crusts except in December. In the dry scenarios with 50% less rainfall, soil moisture clearly declined, except for January, when mean moisture was similar for the dry and the default scenario. In the dry scenario, the differences between the “El Cautivo” and the “no crust” scenario are less clear. While soil moisture in December is still higher in the scenario without crusts in both soil layers, soil moisture in the upper layer tends to be higher in the scenario with crusts. In the lower layer, however, soil moistures becomes very variable in the landscape in February and March and the distributions completely overlap between the scenarios with and without crusts.

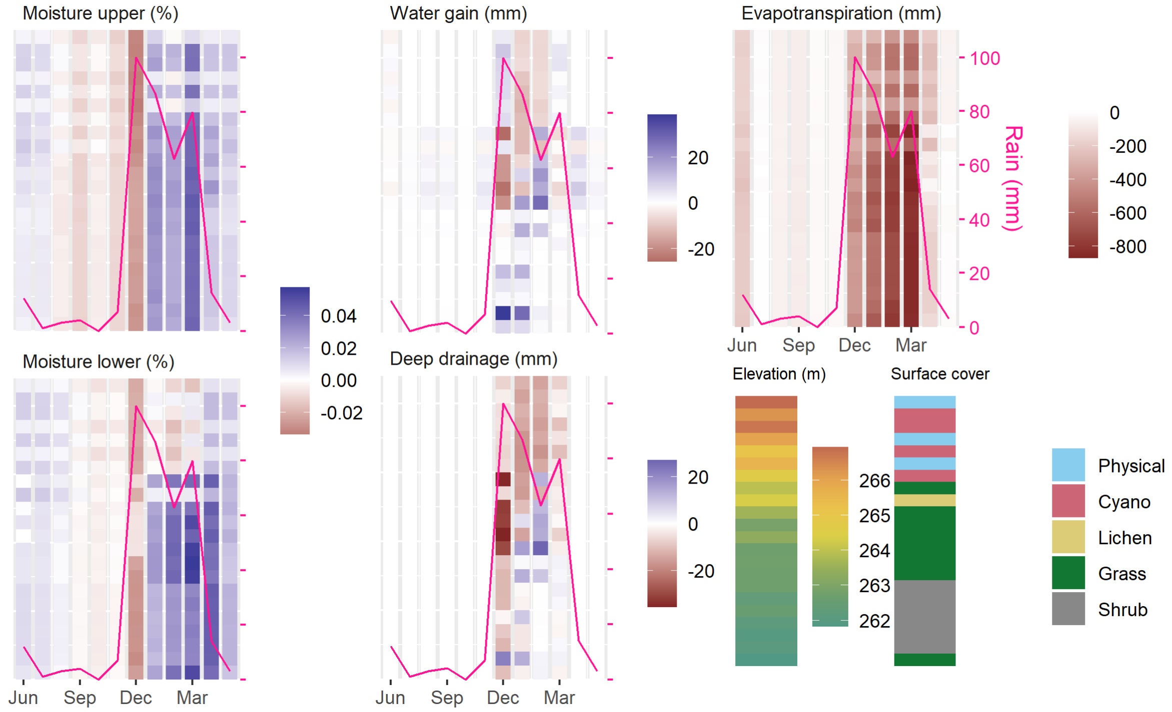

Figure 4.5: Spatio-temporal development of the absolute differences between the “El Cautivo” scenario with biocrusts and the “no crust” scenario without biocrusts. The plot shows soil moisture, water gain, deep drainage and evapotranspiration differences in the cells of the selected hillslope transect. Differences are calculated by subtracting mean monthly soil moisture or monthly sums of hydrological processes of the scenario without crusts from the baseline scenario with crusts. Therefore, red colours indicate cells in which the value is lower in the “El Cautivo” baseline scenario and blue colours show cells in which the values are higher in the “El Cautivo” scenario compared to the “no crust” scenario. The last panel shows the elevation and surface cover of the transect cells that are displayed along the y-axis of the spatio-temporal plots.

4.3.3 Effect of different crust types on soil moisture and hydrological processes

Substantial differences in soil moisture between the three different crust types (physical, cyanobacteria, lichen) can only be observed in the wet winter season and mostly in the upper soil layer (Figure 4.7 a,b). In these months, soil moisture below cyanobacteria and lichen crust is higher than under the physical crust. This trend can also be observed in the lower soil layer where moisture is generally high in January, and in February and March is higher under lichen and cyanobacteria crusts (Figure 4.7 b). Infiltration into the upper soil is similar for all crusts and follows the course of rainfall (Figure 4.7 c). Deep drainage differs under the three crust types: It is lowest under the physical crust and highest under the lichen crust (Figure 4.7 d). Also, there are some rainfall events in March, when deep drainage was only observed under lichen and cyanobacteria crust but not under physical crust. Physically crusted grid cells loose more water through evaporation than cells covered with lichen or cyanobacteria crust (Figure 4.7 e). Runoff is highest in December and January when soil moisture in the upper layer is close to saturation and rainfall is high (Figure 4.7 f). Runoff is similar between the three crust types but slightly higher on lichen crusts. There are some small rainfall events in February and March that only trigger runoff on lichen crust. In these times, soil moisture

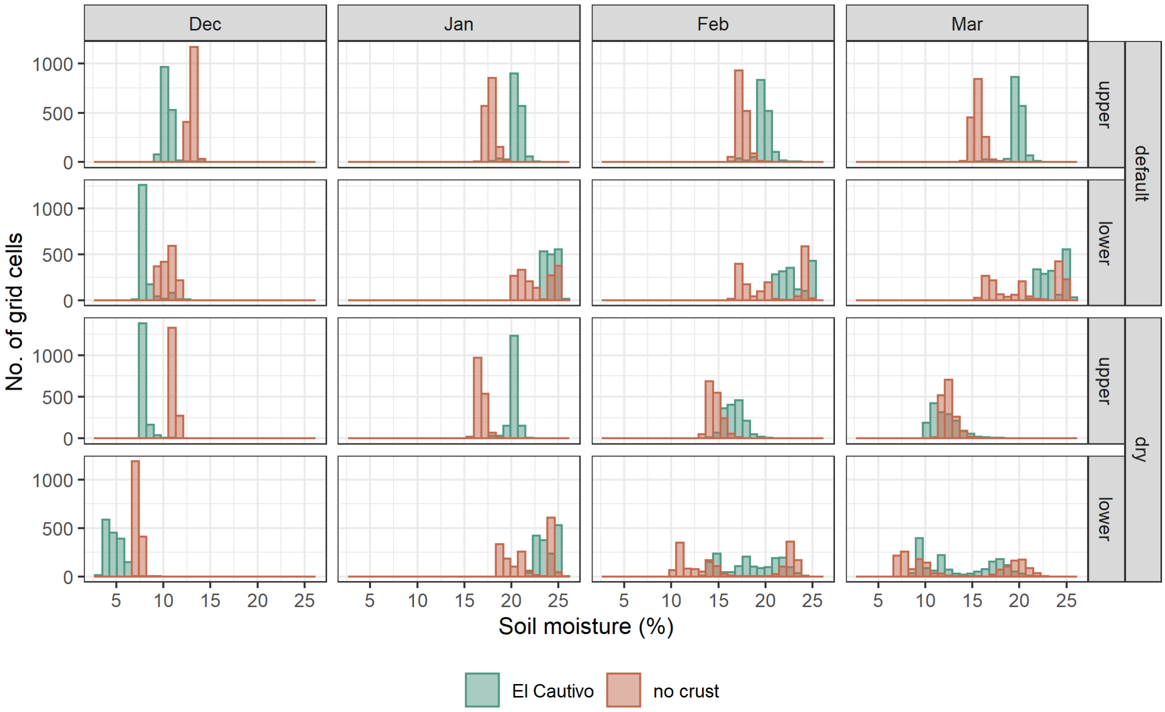

Figure 4.6: Distribution of mean monthly soil moisture in the upper and lower layer of all grid cells of the hillslope between the baseline "El Cautivo" scenario with and the "no crust" scenario without biocrust cover. The first two rows show the distribution under current climate conditions (default) and the last two rows show the distribution for the scenario with 50% reduced rainfall.

and therefore also crust moisture was low and due to the lichen's hydrophobicity, runoff was produced where the water could infiltrate into the other crusts.

4.4 Discussion

4.4.1 Soil moisture patterns and plant-available water under current conditions

The spatial patterns of soil moisture and hydrological processes that emerge from the model underline the interaction between topography, surface cover and rainfall. The results show a clear water redistribution from the steep uphill and crusted areas towards lower parts of the hillslope. The zone that benefits from this additional water input is limited to the first metres of vegetation where the additional runon can infiltrate and drain into lower layers. Soil moisture in the upper and lower layer are mainly governed by seasonal patterns of rainfall and evapotranspiration and less by water redistribution. The simulated distribution of soil moisture in the upper layer is relatively homogeneous especially in the wet winter months, whereas the moisture in the lower layer shows a clear differentiation by surface cover. In our simulations, the upper soil layer is rather thin (6 cm) and therefore saturated almost instantly from large precipitation events in winter regardless of the differences in infiltration capacities between surface cover. In the lower soil layer, however, infiltration was slower and evaporation or evapotranspiration led to lower soil moisture under vegetated and physically crusted grid

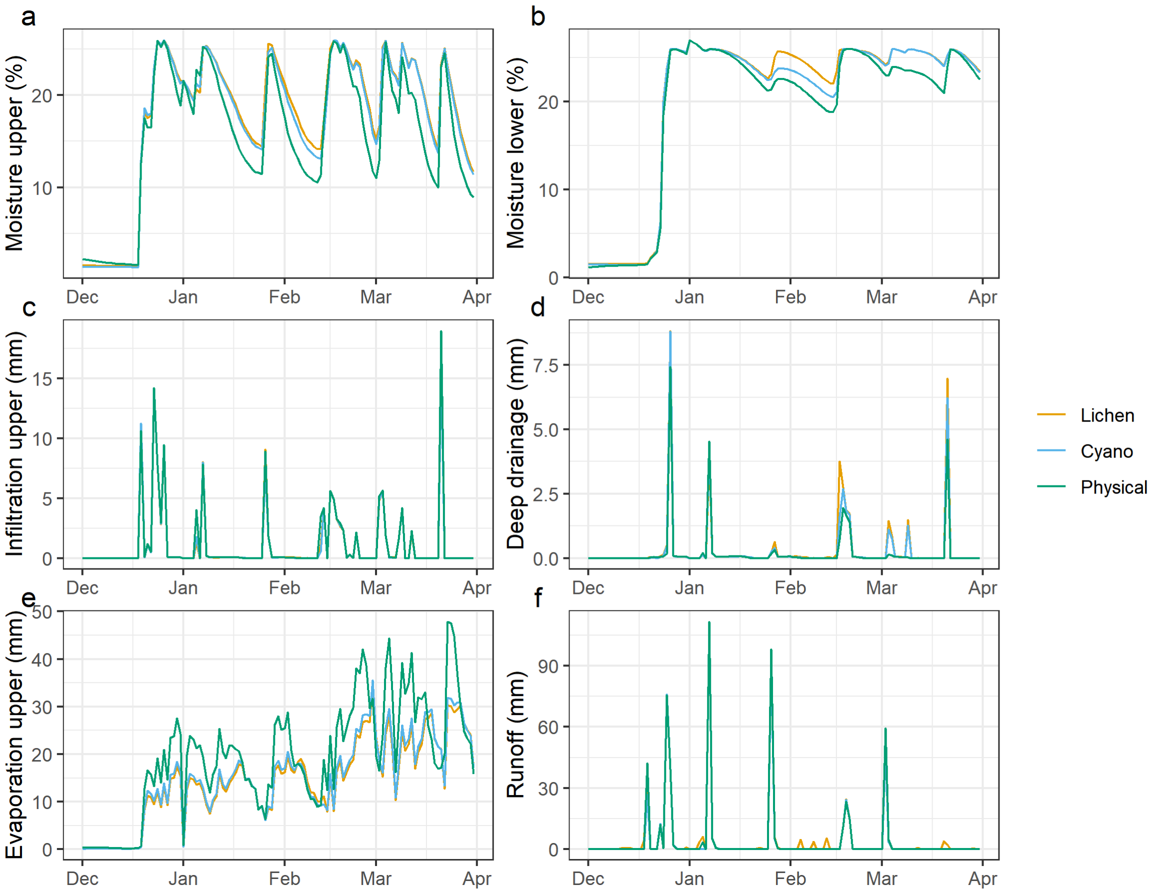

Figure 4.7: Simulated daily mean soil moisture (a, b) and sum of hydrological processes (c–f) in the wet season from January until March. In the three scenarios the hillslope was covered with either physical, cyanobacteria or lichen crust. Please note that means were only calculated for grid cells that were not covered by vascular vegetation in order to get a comparison between the three crust types.

cells compared to biocrusts. This is in line with field observations at the study site that found higher soil moisture under lichen crusts compared to vegetated or physically crusted areas (Cantón et al., 2004a). Since measurements showed lower infiltration (Chamizo et al., 2013b) and higher runoff (Cantón et al., 2002) from lichen crusts, this difference in soil moisture may be explained by a reduction in evaporation under lichens (Cantón et al., 2004b; Chamizo et al., 2013b). The importance of evaporation differences is reflected by the high sensitivity of the evaporation factor in the model and the calibration which resulted in a lower evaporation below lichen crusts, compared to cyanobacteria and physical crusts. In general, the effect of biocrusts on evaporation is however still debated and studies report both positive and negative effects (Kidron et al., 2022). For example, a microlysimeter experiment with soil cores from the same area as our study site, found only small differences in evaporation between crusted and non-crusted soils with slightly higher evaporation below lichen crusts (Chamizo et al., 2013a). Hence, it is possible that the calibrated evaporation factor in the model captured multiple crust effects on soil moisture and not only the effect on evaporation itself. However, there are still few direct measurements of evaporation under biocrusts with contradictory results which makes it difficult to reliably parameterise the evaporation factor directly from data.

The simulated spatial pattern of water redistribution is mirrored in the observed vegetation distribution at the El Cautivo site: The middle hillslope areas that receive additional runon from biocrusts, are primarily colonised by perennial grasses and shrubs (Cantón et al., 2004a). These plants, for example the grass *Macrochloa tenacissima* (L.) Knuth (*Stipa tenacissima* L.), benefit from the additional runon because it allows for higher photosynthetic performance, carbon uptake rates and water-use efficiency (Rodríguez-Caballero et al., 2018c). Our model results suggest that this additional water input is particularly important towards the end of the wet season in March and April when rainfall has already declined and only the runon zones still receive enough water for deep drainage. The lower and flatter parts of the hillslope that do not receive additional runon are predominantly colonised by annual plants such as *Stipa capensis*, *Plantago ovata* and *Bromus rubens* (Cantón et al., 2004a). In these positions they are more vulnerable to drought events occurring within a season because they lack the extensive rooting system of perennial plants to tap on deeper water sources (Hamilton et al., 1999; Ruppert et al., 2015). However, in general annual plants evade these dry periods with dormancy which gives them an advantage over perennial plants in particularly dry sites. Therefore, as aridity increases, as is the case for the bottom of the El Cautivo hillslope, perennial vegetation abundance decreases while annual plants increase (Nunes et al., 2017).

4.4.2 Quantification of crust effects under current conditions

In the wet season, soil moisture in both layers is generally higher if the hillslope is covered with biocrusts compared to bare soil as in the original EcoHyD model. However, the differences are more pronounced in the upper layer compared to the lower one. In the lower soil layer, moisture tends to be higher in the vegetated but lower in the non-vegetated cells if they are covered with biocrusts compared to bare soil. An exception to this pattern is the month of December, where overall hillslope moisture was higher in the bare soil scenario. In the dry season, the differences are small because soils are generally close to the wilting point. In the upper soil layer, the protection from evaporation under crusts (see discussion above) seems to be the main process driving higher soil moisture under crusts compared to bare soil. In the lower soil layer, however, soil moisture retention by reduced evaporation is contrasted with lower infiltration rates under biocrusts compared to bare soil. In the vegetated cells this is balanced by the vegetation increasing infiltration through preferential flow paths along the roots which increased soil moisture under vegetation (Tietjen et al., 2009). A possible reason for the reversal of the pattern in December is that in this month soils were very dry before the first major precipitation event (see also Figure A.4.4). This resulted in high hydrophobicity and therefore reduced infiltration into the soils covered with lichen crust, while more water infiltrated into the non-crusted soils. This higher infiltration capacity appears to significantly outweigh the benefits of lower evaporation in crusted soil and therefore led to overall higher moisture in non-crusted soils in December. Higher infiltration rates in non-crusted soils or soils after biocrust removal have also been reported in field studies (Guan and Liu, 2021; Xiao et al., 2019), particularly on dry soils (Chamizo et al., 2012a). However, here it has to be noted that the non-crusted scenario from this study is only theoretical and not realistic for the study site. In El Cautivo, physical crusts form quickly on bare soil and therefore non-crusted soils do not exist unless the crust was recently disturbed (Chamizo et al., 2012a).

4.4.3 Implications of climate change and possible effects on landscape hydrology

The overall soil moisture distribution for the scenario with 50% lower rainfall is less distinct between the crusted and non-crusted landscape. There is still higher soil moisture in the upper layer if the landscape is crusted but this difference becomes smaller over the months in the wet season. In the lower layer, the distributions overlap and soil moisture variability is high in February and March. This result was contrary to our hypothesis that biocrusts have a positive effect on soil moisture particularly in years with below-average rainfall. The reason for this mismatch between hypothesis and result was that in the two scenarios (crusted vs. non-crusted hillslope) the higher infiltration capacity in non-crusted soils became more important compared to the protection from evaporation in the crusted soils as the conditions became drier. But, as already described above, the non-crusted scenario is not realistic and adding the dynamic formation of physical crusts on bare soil to the model would likely yield results more similar to the ones expected.

The hydrology differed between hillslopes covered with each of three crust types (physical, cyanobacteria and lichen). While infiltration into the upper soil layer was similar between all types during most times, evaporation was higher under physical crusts which led to lower soil moisture under them in both layers. Deep drainage was higher under biocrusts, especially lichens. Runoff was similar from all crust types but lichen crusts yielded small runoff amounts when other crusts infiltrated all rainfall water. Although these differences in hydrology between the crust types were relatively small on a daily or monthly time scale, the effects still accumulated and translated to the landscape scale which was expressed in the higher soil moisture in vegetated patches if the hillslope is covered with biocrusts compared to physical crusts (Figure A.4.12). This effect might be even stronger in reality because of possible lateral subsurface flow from the steep and crusted parts of the hillslope, a process which is not represented in our model. At our study site, soils under lichen biocrusts in the upper part of the hillslope are shallow (0-2 cm of AC horizon followed by 2-30 cm C horizon, see Cantón et al. (2002)) which means that the simulated additional drainage under lichen (and also cyanobacteria) crusts could at least in part redistribute via subsurface flow towards downhill vegetated areas (Moore et al., 2015).

Under climate change, the biocrust species composition in El Cautivo might shift towards more early-successional, cyanobacteria crusts, because the main lichens from the region, e.g. *Diploschistes diacpasis*, suffer from rising temperatures (Baldauf et al., 2021; Escolar et al., 2012; Ladrón de Guevara et al., 2018). Such a shift in species composition can be accompanied by an overall decrease in biocrust cover (Ladrón de Guevara et al., 2018). This can create new open spaces of bare soil that are usually quickly replaced with physical crusts at our study site (Chamizo et al., 2013b). In the following, these spaces can also be re-colonised by biocrusts provided that soils are stable and no major erosion events occur during the recovery period (Lázaro et al., 2008; Zhao et al., 2016). However, recovery can be slowed down or even reversed if rainfall is not sufficient or if high intensity rainfall destroys parts of the crust (Cantón et al., 2020; Thomas and Dougill, 2007).

Our study site is covered with 40% biocrusts, 30% of which are lichens, therefore potential shifts in crust composition and cover affect the ecohydrological processes and interactions between biocrusts and vegetated patches in the landscape. The model results suggest that a shift towards physical crusts will lead to an overall lower soil moisture and less plant-available water for perennial grasses and shrubs because of a reduction in deep drainage and water redistribution towards these areas. This can negatively affect perennial grass productivity and their capacity to effectively capture water (Li et al., 2008; Rodríguez-Caballero et al., 2018c) and act as a sink area for runoff (Ludwig et al., 2005; Puigdefábregas, 2005) thus increasing the potential for runoff flow connectivity (Rodríguez-Caballero et al., 2014). Such a disturbance of the source-sink interactions is especially problematic in the context of reduced biocrust development. Therefore, erosion rates are higher for crusts of lower development so a shift towards light cyanobacteria crusts with low biomass can lead to higher sediment loss through erosion compared to lichen crusts (Belnap et al., 2013; Cantón et al., 2001, 2011). This is especially problematic for large rainfall events that fall on dry soils (Belnap and Büdel, 2016; Belnap et al., 2013; Rodríguez-Caballero et al., 2012), conditions that will become more frequent under climate change and increasing aridity in drylands across the globe (Huang et al., 2017). Ultimately, if soils are destabilised by this process, and recovery of biocrusts is not possible, a breakdown of the ecohydrological balance in dryland landscapes can be a result (Turnbull et al., 2012).

4.4.4 Using EcoHyD to model the effects of biocrusts on drylands

In this study, we used for the first time a spatially explicit ecohydrological model (EcoHyD) to evaluate landscape-scale effects of water redistribution on a hillslope covered by biocrusts. The EcoHyD model has already been successfully applied to drylands in the Middle East (Tietjen et al., 2009), Southern Africa (Guo et al., 2016; Lohmann et al., 2012; Tietjen et al., 2010) and China (Geissler et al., 2019). The extended EcoHyD model reproduced the soil moisture dynamics in two layers under physical, cyanobacteria and lichen crusts in south-east Spain and produced realistic dynamics of hillslope soil moisture variability and water redistribution. It has to be noted here, that in this study, we calibrated the model for the hydrological year 2009–2010 which was particularly wet with 63% more rainfall than the long-term average precipitation (374 mm vs. 235 mm average from 1967–1997, Lázaro et al. (2001)). Therefore, in the next step, it will be interesting to see if the calibrated parameters are robust and independent of the calibrated year and its rainfall.

Moving forward, the model can be used to assess long-term hydrological dynamics and interactions between vegetated sink and crusted source areas in drylands. However, to study long-term dynamics using the model, both biocrust and vegetation dynamics should be taken into consideration. In our study, this step was not necessary because we only simulated one single year and therefore did not expect much change with respect to biocrust and vegetation cover in the simulation time span. However, for long-term studies both these dynamics become important because from them arise the stabilising feedbacks that help to maintain the heterogeneous landscape (Puigdefábregas, 2005; Turnbull et al., 2012). In a next step this should be included in the model as well. With such an extended model, feedback mechanisms between biocrust community change, runon-runoff dynamics and vegetation changes could be investigated as well as thresholds, e.g. with regard to aridity or biocrust disturbance for irreversible damage to the ecohydrological balance could be explored.

4.5 Conclusion

In this study, we successfully included biocrusts in a process-based ecohydrological model and simulated the landscape-scale processes of water redistribution and soil moisture for the first time in a spatially-explicit way. We found that areas covered with biocrusts effectively redistribute rainfall in the landscape leading to a differentiation in the soil water balance. This redistribution created a zone of higher water gain which was colonised by perennial vegetation in the landscape. The process-based model used in this study is a tool with which we can assess, quantify and upscale these observed processes and compare them in different scenarios of landscape configuration. The model is well tested in other dryland areas where biocrusts are common. This opens the possibility to explore biocrust effects on landscape hydrology in these drylands as well. In a next step, the inclusion of dynamic vegetation, biocrusts and soil properties can allow us to investigate feedback and buffer mechanisms between source areas covered by biocrusts and sink areas covered by vascular vegetation. With this tool we can address questions regarding the resilience of dryland systems under climate change.

Part III

General Discussion

5 General Discussion

In the previous chapters, I explored the effects of different climate change factors on biocrusts and their implications on the landscape hydrology. I used both experimental and modelling approaches that assessed aspects of this topic on different temporal and spatial scales.

First, I conducted a rainfall manipulation experiment that compared the effect of two precipitation patterns that provided the same overall amount of rainfall, but with different individual pulse sizes and frequencies on the short-term gas exchange of a lichen-dominated biocrust (mainly *D. diacapsis*). The effect of the individual pulse size and frequency on the CO_2 gas exchange was modulated by the environmental conditions (radiation, temperature, antecedent soil moisture). I discovered that the higher frequency pattern was beneficial for net photosynthesis because it allowed for a longer and more constant activity time of the lichen. This result was in contrast to other studies conducted in summer that found a negative effect of a high frequency of small watering events. The results highlight the interactions between biocrust, environmental conditions and soil with regard to the carbon balance. The study supports the need for long-term assessments that investigate the effect of different rainfall patterns on biocrusts and the soil underneath in different seasons.

Second, I parameterised and validated the process-based non-vascular vegetation model LiBry for the same lichen species (*D. diacapsis*). With this model, I tested how short-term changes in biocrust activity and carbon exchange due to multiple climate change factors translate into long-term cover changes. I found that biocrust cover could drastically decline under future climate, mainly because of a reduction of dew as a hydration source caused by reduced relative humidity. This decline in cover could not be compensated by the positive effects of higher temperature and atmospheric carbon content. Surprisingly, an overall reduction in rainfall had no effect on long-term lichen cover. With this study, I could explain mechanisms behind observed cover losses in a field experiment and quantify potential effects of climate change on the common biocrust lichen *D. diacapsis*. This is especially important considering rising temperatures, a trend towards drier air in drylands and the ubiquitous nature and global distribution of this lichen species.

Finally, I modelled the effects of these potential biocrust changes on dryland landscape hydrology and what this means for plant water availability using the process-based ecohydrological model EcoHyD with a dynamic biocrust layer. The results showed the important effect of crusts on soil moisture and water redistribution on the simulated hillslope under both a default and a drought scenario. Increased runoff from the crusted upper hillslope infiltrated in the first metres of the vegetated lower part of the hillslope thus providing additional water in these areas. At the same time, biocrusts reduced soil evaporation and thus protected non-vegetated areas from excessive soil water loss. The simulated pattern of water redistribution corresponded well to the observed vegetation pattern in the field where areas of high water gain are inhabited by perennial grasses and shrubs whereas areas without additional water gain are dominated by annual vegetation. I found that a potential shift from lichen towards cyanobacteria or physically crusted soils can have negative consequences for the hydrology on a local, but also on a landscape scale.

In the next sections, I discuss the theoretical and practical implications of the findings from chapters 2–4. First, I discuss the meaning of my results for the future of biocrusts and the landscapes they inhabit. In particular, I explain the interactions of climate change factors and the dependency on environmental context. Second, I discuss what these results mean for biocrust community composition in general and how these changes might affect dryland ecohydrology. Third, I analyse and discuss the methodological approaches taken in this thesis. I discuss advantages, limitations and potential synergies between the different approaches and explore potential ways to move forward with it.

5.1 Climate change effects on biocrusts in drylands

Under climate change, the Mediterranean region warms at a faster pace than the global average (Cramer et al., 2018) and higher temperatures already led to a decline in relative humidity (Vicente-Serrano et al., 2014a, 2018). Additionally, lower overall rainfall amount but more individual extreme rainfall events are predicted for the future, which together with warming increases the risks for meteorological droughts and heat waves (Lionello and Scarascia, 2018; Tramblay et al., 2020; Vicente-Serrano et al., 2014c; Vogel et al., 2021). Investigating the effects of these different climate change factors on the biocrust community and how this affects the ecohydrological balance in drylands is therefore important. In the following, I discuss the findings of this thesis and what we can learn from them with regard to climate change effects on biocrust communities and the landscapes they inhabit.

5.1.1 Effects of selected climate change factors

I found both short-term (chapter 2) and long-term (chapter 3) effects of climate change factors on biocrust activity, carbon exchange and ultimately cover. Overall, my results suggest that climate change negatively affects lichen-dominated biocrusts. I found positive effects of increased atmospheric CO_2 and temperature in chapter 3 that were outweighed by the negative effects of lower water availability (relative humidity and rainfall frequency) found in chapter 2 and 3. In general, this result was expected because many other empirical studies report a negative effect of simulated climate change on biocrusts (e.g. Escolar et al. (2012); Ferrenberg et al. (2015); Li et al. (2021); Wertin et al. (2012); Zelikova et al. (2012)). However, many of these studies report negative effects of increased temperatures, so my findings that higher temperatures are beneficial were initially surprising. I found a positive effect of air temperature on the cover of *D. diacapsis* (chapter 3) and on net photosynthesis rates (chapter 2). The main reason for this is that in both studies the lichens were mostly active under suboptimal conditions with regard to temperature (Lange et al., 1997; Pintado et al., 2005). However, it has to be noted that this positive effect of higher temperature was conditional on the sufficient water availability in both studies, through relative humidity and dew (chapter 3) or the large enough water pulses that kept the lichen crust and the underlying soil wet throughout the experimental period (chapter 2). Depending on the moisture level, higher temperatures also increase soil microbial activity and thus heterotrophic respiration and carbon release from the soil therefore affecting the net ecosystem balance (Cavicchioli et al., 2019; Chamizo et al., 2022).

This thesis clearly showed the importance of timing of hydration for the short-term activity and photosynthesis and the long-term cover of lichen biocrusts. In chapter 2, the frequent but smaller pulses allowed for a longer active time despite the same overall water amount and in chapter 3, a reduction of hydration at the critical time for photosynthesis (i.e. dew in the early morning hours) dramatically reduced lichen cover. At the same time, my results showed no effect of reduced overall rainfall on *D. diacapsis* cover (chapter 3). This was corroborated by the findings of long term climate manipulation experiments in the same region (Escolar et al., 2012; Ladrón de Guevara et al., 2014). These results taken together suggest that the timing of hydration could be even more important than the hydration event size itself, provided that rainfall does not fall below a certain threshold (Raggio et al., 2017).

5.1.2 Interactions between climate change factors and environmental conditions

In chapter 2 and 3, I looked at the effect of five different climate change factors under two different settings: a soil core covered with a lichen biocrust community dominated by *D. diacapsis* under ambient conditions and an isolated thallus of *D. diacpasis* under different simulated climate conditions without soil. The climate change factors that were mainly investigated in other field studies on biocrusts are warming, often in combination with reduced overall precipitation (Escolar et al., 2012; Guan et al., 2019a; Ladrón de Guevara et al., 2014; Li et al., 2021) or altered precipitation patterns (Darrouzet-Nardi et al., 2018; Johnson et al., 2012; Reed et al., 2012; Zelikova et al., 2012), mostly in the form of additional small rainfall pulses in the summer months. I also looked at additional factors, such as relative humidity or increased atmospheric CO_2 (chapter 3) which were seldom included in empirical climate change studies because they are much more difficult to manipulate in the field. However, looking at only one or two factors of climate change may limit the understanding that can be gained from such studies. Factors may interact and some impacts may only result from the simultaneous action of multiple factors of climate change (Rillig et al., 2019). Furthermore, I found that the environmental conditions are tightly coupled to the effect of climate change on biocrusts (chapter 2 and 3). In the following, I will discuss these interaction aspects and how they are shown in the results of this thesis. For the sake of clarity, I will discuss them separately although some of the aspects overlap or are linked through feedback mechanisms.

First, climate change factors and other environmental conditions interact and influence each other which is why they are not always clearly separable in climate change studies. In chapter 3, I found that higher temperatures, which are directly related to lower relative humidity in my study area (Vicente-Serrano et al., 2013, 2018) reduced the water availability in the form of dew which ultimately affected lichen activity. Another example of this type of interaction was found in chapter 2, where rainfall increased soil moisture which in turn reduced soil temperature. This interaction is relevant because soil moisture and temperature are the main factors influencing soil microbial activity and respiration and ultimately determine if biocrust photosynthesis can balance the respiratory losses and lead to a positive overall carbon balance (Bowling et al., 2011; Chamizo et al., 2022; Miralles et al., 2018).

Second, environmental conditions mediate the impact of climate change factors on the carbon exchange of biocrusts. This was shown in chapter 2, where the effect of rainfall pulse size and frequency on carbon exchange interacted with soil temperature, radiation and antecedent soil moisture. The significance of environmental conditions was also reflected in the seasonality of the effect: Whereas in winter a higher frequency was beneficial (chapter 2), in summer a similar treatment might lead to carbon losses because frequent but short activation periods lead to a negative carbon balance (Johnson et al., 2012; Reed et al., 2012; Zelikova et al., 2012). I also found an interaction between antecedent soil moisture content and net carbon exchange in chapter 2, which is another reason for the benefit of a higher rainfall frequency in winter. If there is a longer dry period between rainfall events of lower frequency, soils can dry in between. Dry soils are associated with high infiltration rates and therefore a steep increase in soil moisture after a rainfall event (see chapter 4 at the beginning of the wet season, Belnap et al. (2013)). In chapter 2, I found that this rapidly activated both the biocrust and the soil microbial community and led to high initial respiratory carbon losses. This phenomenon has also been found in other studies (Borken and Matzner, 2009; Bowling et al., 2011; Miralles et al., 2018), e.g. because the organisms need to repair damaged tissues (Lange, 2001). However, if rain falls on already wetted soil and crust, the biocrust could immediately start photosynthesis and soil respiration is already balanced. Dry soil conditions will become more likely in the future as climate projections predict higher temperatures and a lower precipitation frequency with larger event sizes for Mediterranean drylands (IPCC, 2021; Schlaepfer et al., 2017; Toreti and Naveau, 2015; Toreti et al., 2013).

Third, there are interactions between the effects of different climate change factors on biocrust cover. This was shown in chapter 3 where I did not find an additive effect of the different factors, but rather an interaction. For example, the positive effect of increased atmospheric CO_2 on biocrust cover was dampened if relative humidity decreased as well. In part, these interactions can also be explained by the saturation type response of many climate change factors with regard to biocrust activity and carbon exchange which depends on the species composition and their optimum temperature, water content, and atmospheric CO_2 for photosynthesis (Lange, 2001, 2002; Lange et al., 1997; Pintado et al., 2005). For example, the species *D. diacapsis*, investigated in chapters 2 and 3, has an optimum temperature for photosynthesis of ca. 25 °C (Pintado et al., 2005) and an optimum water content of ca. 0.3 until the tradeoff between water content and CO_2 diffusivity into the thallus becomes negative (so-called supersaturation effect that limits photosynthesis at very high water contents, see Lange et al. (1997); Pintado et al. (2005)).

In summary, my results show that climate change effects on biocrusts underlie complex interactions between the different climate factors. This has also been hypothesised for climate change effects on biodiversity in general and particularly for biodiversity in Mediterranean ecosystems (Sala et al., 2000). It is therefore to be expected that the species composition of the biocrust will also change in the course of climate change.

5.1.3 Significance for global soil crust communities

The results of this thesis, in combination with previous findings of other studies, outline two possible consequences of climate change that are likely to occur together: A shift in biocrust species composition, because some species are more vulnerable than others, and a change in biocrust cover overall, if the decline in cover of one species cannot be compensated by another one. In this context, the results of this thesis suggest a negative overall effect of climate change on lichen-dominated biocrusts in Spain (chapter 2 and 3) which is in line with research from the same study region (Escolar et al., 2012; Ladrón de Guevara et al., 2018, 2014). Worldwide, a shift in species composition with climate change is also observed, but the direction is less clear. Some studies suggest a general shift towards more early-successional biocrusts (Ferrenberg et al., 2015; Finger-Higgens et al., 2022) characterised by reduced functional diversity (Mallen-Cooper et al., 2018) and species richness (Ladrón de Guevara et al., 2018; Roncero-Ramos et al., 2020). However, the results are different depending on the region and type of study. Some studies suggest a positive effect of warming and/or rainfall reduction on biocrust mosses but a dramatic decline of lichens (chapter 3, Finger-Higgens et al. (2022); Ladrón de Guevara et al. (2018)), while others report negative effects on mosses and little or no effects on lichens (Ferrenberg et al., 2015; Li et al., 2021). This ambivalence of results is also reflected in the projection of overall biocrust cover changes under climate change: While correlative approaches suggests an overall decrease in global biocrust cover, there is a large variability with positive cover changes for some regions and negative changes for others (Rodríguez-Caballero et al., 2018a). It would be interesting to apply the model from chapter 3 to some of the regions where regression analysis suggests biocrust changes in the future (Rodríguez-Caballero et al., 2018a) and test if the process-based model confirms these results and if the mechanisms behind positive and negative cover changes are similar in different drylands.

5.1.4 Effects on the landscape

In chapters 2 and 3, I showed that lichen biocrusts are affected by climate change and that their cover can decline by up to 80% of the current cover values depending on the emission scenarios. Field studies corroborate these findings and suggest a shift in the biocrust community towards more early-successional cyanobacteria crusts, but also a general loss of biocrost cover, which might be replaced with physical crusts (Chamizo et al., 2012a; Ferrenberg et al., 2015; Ladrón de Guevara et al., 2018, 2014). In chapter 4, I found that such a shift reduced landscape-scale soil moisture and plant-available water due to less water redistribution and higher evaporation rates because the crust types differed in their effect on hydrological processes (Eldridge et al., 2020). Less water redistribution can negatively affect vegetation performance and ultimately result in a reduction of ecosystem productivity with important implications for landscape ecohydrology (Rodríguez-Caballero et al., 2018c). A reduced capacity of vegetation to capture runoff and a higher connectivity between open physically crusted areas increases the water amount that leaves the system (Cantón et al., 2011; Puigdefábregas et al., 1999; Rodríguez-Caballero et al., 2014), especially during high-intensity rains that are predicted to become more frequent in the future (Lionello and Scarascia, 2018; Tramblay et al., 2020; Vicente-Serrano et al., 2013). With lower crust development, erosion will also increase during these events (Belnap and Büdel, 2016; Belnap et al., 2013; Cantón et al., 2001, 2011) which can lead to soil degradation through the loss of nutrients and water storage capacity (Cantón et al., 2018). This exacerbates the negative effects on both biocrusts and vascular vegetation and creates a feedback loop that can ultimately lead to the breakdown of the ecohydrological equilibrium that sustains the patterned landscape if biocrusts cannot recover (Turnbull et al., 2012).

5.2 Modelling biocrusts in the context of climate change

Biocrusts have gained increasing attention in recent decades, but there are still very few modelling approaches compared to vascular vegetation (see chapter 1 and Reed et al. (2019)). One reason for this is that until now a detailed mechanistic and general understanding of the modelled systems was lacking which is necessary to create robust process-based models (Cuddington et al., 2013). Many aspects of biocrusts and how they affect the landscapes they inhabit still remain unclear and studies often yield context dependent or even contradicting results. However, the general and process-based understanding steadily increases and meta studies help to reveal general patterns (Chamizo et al., 2016b; Eldridge et al., 2020; Kidron et al., 2022). In this context, I discuss the lessons learned from the modelling approaches used in this thesis. I analyse advantages and limitations of my approaches, how they can be integrated with experimental results like the ones presented in chapter 2, and outline some potential next steps that may arise from the modelling work done in this thesis.

5.2.1 Perspectives on my approach

Advantages of process-based models

In addition to the insights into climate change effects on biocrusts and dryland landscapes (see above), this study highlights some benefits of using process-based models in ecology, three of which I will discuss in the following.

First, once a model is parameterised, it is relatively easy to run simulation experiments with a full factorial combination of different treatments and include treatments and factors that are difficult or even impossible to manipulate in a real world experiment. In chapter 4, I manipulated landscape-scale biocrust cover, which is impossible to do in field experiments. In chapter 3, I addressed five climate change factors at different factor levels in all combinations. Also, I manipulated climate change factors such as increased atmospheric CO_2 and relative humidity (chapter 3) which are difficult to manipulate in reality. These factors require expensive facilities such as free air CO_2 enrichment facilities (FACE) (Norby et al., 2016; Norby and Zak, 2011), free air humidity manipulation facilities (FAHM) (Godbold et al., 2014; Hansen et al., 2013; Truu et al., 2017) or growth chambers (e.g. Talbott et al. (2003)). So far, only one FACE site was used to investigate biological soil crusts (Wertin et al., 2012) and the effect of increased relative humidity has not been tested yet for biocrusts. While the effort needed to conduct a full-factorial climate change experiment with such difficult to manipulate factors increases exponentially, in simulation experiments, most of this additional effort is taken over by computers. The number of treatment combinations and the types of scenarios that can be run is primarily limited by the available computational power and the time it takes to run one simulation.

Second, process-based models allow us to disentangle the mechanisms behind observed phenomena because they are based on a mechanistic understanding of the ecosystem and its processes (Cuddington et al., 2013; Evans et al., 2016). They make it possible to isolate and analyse specific ecosystem processes or interactions in great detail which are normally too entangled to be separated. For example, in chapter 3 I found that the observed negative effect of increased temperature on biocrusts found in an experimental study (Escolar et al., 2012; Ladrón de Guevara et al., 2014)is most likely not related to the temperature directly, but to the reduction in relative humidity and therefore early morning activity time. Similarly, in chapter 4, I could separate and quantify the contributions of evaporation, runon, runoff and infiltration to soil moisture.

Third, process-based models can be used for spatio-temporal upscaling to predict and quantify the effects of environmental change on ecosystems (Cuddington et al., 2013; Evans, 2012). In this regard, they can complement experimental studies by incorporating the knowledge gained from them and applying it to larger temporal (e.g. changes in long-term biocrust cover due to short-term changes in activity, chapter 3) or spatial (e.g. landscape-scale water redistribution and soil moisture availability, chapter 4) scales. This is important because naturally experimental time scales are limited and the longest climate change observations and experiments on biocrusts range from 15-53 years (Dacal et al., 2020; Ferrenberg et al., 2015; Finger-Higgens et al., 2022). Although spatial scales are theoretically less limited than temporal ones, the logistic and time effort of assessing e.g. landscape-scale soil moisture, evaporation and runoff is still immense. Therefore, most hydrological studies on biocrusts focussed on small spatial scales (Eldridge et al., 2020) which often cannot adequately address water redistribution and hydrological connectivity in the larger landscape (Rodríguez-Caballero et al., 2014). In these areas, where experiments reach their limits, the modelling approaches used in chapters 3 and 4 contributed to a better mechanistic understanding of climate change effects on biocrusts on larger spatial and temporal scales. This understanding can now also be applied to future empirical climate change studies. For example, relative humidity changes can be measured in climate-change experiments with manipulated temperatures. In the data analysis, both temperature and relative humidity could then be taken into consideration as potential drivers of biocrust response to the treatment.

Limitations of process-based models

Naturally, process-based models are not without their limitations and model predictions should always be considered together with their corresponding uncertainty (Cabral et al., 2017). For the modelling work of this thesis, I collaborated with empiricists and used literature to obtain the data needed for the parameterisation of biocrusts, climate and landscapes. Although I simulated a relatively well studied biocrust species (*D. diacapsis*) in a landscape with a long history of biocrust research (Cantón et al., 2001; Solé-Benet et al., 1997), many parameters were still not available and had to be determined using a sensitivity analysis and calibration approach in both chapters 3 and 4. This is a common issue for such process-based models because as they become more complex, more data are needed to parameterise, calibrate and validate them. If these data are not available, model uncertainty can increase exponentially (Cabral et al., 2017; Cuddington et al., 2013). Physiological and hydrology-related data of biocrust species are difficult to obtain, because there is no global trait database as there is for plants (Mallen-Cooper et al., 2020). Also, it is unclear to what extent inter-specific variability in biocrust species can affect physiological end ecosystem processes (Pintado et al., 2005). Recent efforts began to synthesise effects of different biocrusts on hydrology (Chamizo et al., 2016a; Eldridge et al., 2020), but there is still a lack of detailed cross-species and cross-site data that raises the question of how to parameterise complex and dynamic biocrust models in the future.

Another important limitation of models is that they can only be applied to contexts in which the relationships and processes they describe are valid. The application of an existing model to new conditions might involve model adjustments to keep relationships valid. The models used in this study are tested for a range of regions and ecosystems (e.g. Lohmann et al. (2012); Porada et al. (2016, 2019, 2013); Tietjen et al. (2010, 2009)) which makes them suitable to simulate biocrust landscapes in other regions as well. However, if for example the EcoHyD model from chapter 4 is used to simulate biocrust landscapes in central China, the model functions need to be adapted from a water- to a temperature-limited vegetation period (e.g. Geissler et al. (2019)). Experiments and field studies are needed to determine the validity of any mechanisms and relationships across contexts in models.

5.3 Outlook

In the future, efforts should be made to close the gap between empirical biocrust research and process-based modelling approaches. With my work I have created a basis for this task. In particular, because the models I have used are suitable for addressing questions about biocrusts with regard to climate change in an integrated approach. In the following, I propose a way to couple the models used in chapter 3 and 4 to address more long-term landscape developments under climate change. Afterwards, I briefly outline two directions in which my research could continue.

5.3.1 Coupled biocrust-ecohydrological model

With the models used in this study, I assessed two aspects of the same ecosystem and region in south-east Spain, each with their own focus and limitations. Both models represent biocrusts in a dynamic way and complement each other in their functionality. The non-vascular vegetation model LiBry in chapter 3 simulates physiological processes and dynamic growth of biocrust species. In contrast, biocrust cover and composition are static in the version of the ecohydrological model EcoHyD in chapter 4 and therefore cannot respond to changes in water availability and climate. EcoHyD is spatially explicit which allows for a differentiation of the distribution and composition of biocrusts in the landscape according to variables such as slope (Lázaro et al., 2022; Rodríguez-Caballero et al., 2019), moisture availability (Bowker et al., 2016) or vascular vegetation distribution (Zhang et al., 2016), which is not possible in the spatially non-explicit LiBry model.

The models separately are therefore suitable to assess questions of climate change on biocrust growth (LiBry) and the effect of a static but spatially differentiated biocrust cover on landscape hydrology (EcoHyD). A next step forward to increase applicability would be to integrate the two models and assess these questions in a coupled way. Both models can simulate similar environmental contexts (e.g. drylands in south east Spain), have the same temporal resolution (1 hour) and extent (from years to centuries) and the biocrusts implemented in both models share many parameters (e.g. saturation water content, thickness, porosity and hydrophobicity). In a coupled biocrust-ecohydrological model, each grid cell would have a dynamic cover of biocrust with a specific composition and cover which influences the hydrology of the cell (e.g. infiltration into the soil, runoff, hydrophobicity, protection from soil evaporation). In turn, biocrust growth and composition depends on the water availability in the cell (rainfall, runon, runoff and infiltration and, if the biocrust species can access it, soil moisture). The interfaces between the two models have to be clearly defined: What are the hydrological properties of the species simulated by the physiological model part? How does vascular vegetation affect biocrust growth and can crusts compete with vascular plants for cover? An advantage of combining the two modes would be that feedback mechanisms between biocrust growth, type and hydrology could be included (Eldridge et al., 2021). For example, the variable water distribution in the landscape would affect biocrust growth and spatial heterogeneity of biocrusts would in turn affect the landscape and water redistribution. In models with vascular vegetation, such dynamic feedbacks between vegetation and hydrology are already established (e.g. Beaulieu et al. (2016); Gerten et al. (2004); Oleson et al. (2008); Tietjen et al. (2010)) but they are still not implemented for biocrusts. However, they are needed for simulating dynamic changes of dryland ecohydrology under climate change on a long time scale.

5.3.2 Future directions of coupled empirical and process-based modelling in biocrust research

In this thesis, I contributed to both modelling and empirical aspects of biocrust research by combining a short-term experiment with long-term simulation modelling driven by empirical data. Moving forward, I advocate for a tight coupling of process-based modelling of biocrusts and empirical studies to increase the understanding of biocrusts and their effect on the landscape in a changing climate. Such a coupled framework has been proposed before in the context of ecosystem restoration and its value lies in the synergies that can arise by integrating the strengths of both approaches (Fiedler et al., 2018). Empirical biocrust research can support modelling by developing hypotheses and research questions to be tested and addressed by models. Additionally, they can provide data and expert knowledge for parameterisation, calibration and validation (Fiedler et al., 2018; Grimm et al., 2014; Schmolke et al., 2010). In turn, process-based models can help to uncover context dependencies and mechanisms behind empirical results. Models can also be used as tools to identify variables to be measured or factor levels that are interesting to manipulate. In this way, models can support empiricists in the design of experiments or field campaigns. Two examples of how such a coupled empirical-modelling approach might be used in the context of the effects of rainfall frequency on biocrusts or biocrust restoration are outlined in the following.

First, based on the findings from chapter 2, a coupled empirical and modelling approach could further explore the mechanisms behind the effects of altered rainfall frequency on short-term carbon exchange and their consequences on long-term biocrusts growth. There are several interesting open research questions to be explored: Is there a threshold ratio of rainfall pulse size to frequency at which the net carbon balance becomes negative? If yes, does this threshold differ between biocrust types? What is the effect of environmental context and seasonality? Are the answers to these questions the same across different dryland regions? These questions can be tackled with a combination of rainfall manipulation experiments and physiological modelling using the adapted LiBry model from chapter 3. Modellers can identify trait or species-specific parameter values that are needed to parameterise the model for the biocrust communities of interest. These parameters can then be measured by empiricists. Together, modellers and empiricists can develop simulation experiments that look at rainfall frequencies on biocrusts. These simulation experiments can comprise a range of scenarios and explore different patterns of rainfall (individual pulse size and frequency but also duration and overall amount) under various environmental conditions in a full factorial way. From the results, the environmental conditions (e.g. season) and the rainfall patterns that are most interesting to assess experimentally, can be selected. The results from these experiments can then be compared to the model predictions. Ideally, through iteration, this approach leads to a better mechanistic understanding of the context-dependent effects of rainfall patterns on biocrusts. Once this understanding is established, the model can be used to simulate long-term consequences of altered precipitation frequency on biocrust cover in different regions.

Second, the coupled biocrust-ecohydrological model proposed above can be used to support ecosystem restoration efforts with biocrusts especially if integrated with empirical research. Biocrusts are being increasingly recognised as promising organisms to restore dryland ecosystems and their functions (Antoninka et al., 2020). With the advancement of related biotechnology, biocrust species (often cyanobacteria) can be actively selected and cultivated or salvaged from a field source to inoculate the soil of degraded landscapes (Chamizo et al., 2018; Faist et al., 2020; Raul Roman et al., 2018; Slate et al., 2020). However, restoration time frames are often years or even decades (Chen et al., 2018; Zhou et al., 2020) and the success of biocrust establishment depends on the climatic conditions and soil properties (Antoninka et al., 2020; Faist et al., 2020). To date, much of the biocrust restoration efforts have been conducted on small spatial scales, but larger areas are needed to gain ecological relevance (Antoninka et al., 2020). In the planning efforts of such large-scale restoration projects, a long-term assessment of potential environmental and management scenarios is important to maximise restoration outcomes (Cuddington et al., 2013). This becomes especially important in the context of climate change and the long time scales of restoration projects. Here, models can be used to assess the long-term success probability of potential restoration strategies under different climate trajectories. The proposed coupled biocrust-ecohydrological model from this thesis is useful in this context because it can assess biocrust development in terms of carbon fixation and long-term cover and biomass accumulation. Because of the spatially explicit nature of the model, water availability and variability in the landscape can be taken into account as well. Using such a model together with empirical research and experiments can support decision makers to select efficient restoration strategies and maximise restoration outcomes.

5.4 Conclusion

Biocrusts are vital for the functioning of dryland ecosystems, yet they are vulnerable to climate change. In this thesis, I provide insights from short-term experimental and long-term process-based modelling approaches to improve the mechanistic understanding of the effects of climate change factors on biocrusts and how this affects dryland ecohydrology. I showed that climate change negatively affects the carbon exchange, activity and cover of lichen-dominated biocrusts in a Mediterranean dryland with consequences for water redistribution and availability in the landscape. These results likely represent a larger trend for drylands with biocrusts because of the ubiquitous nature of the crusts investigated in this study and studies from other regions reporting similar findings. In this context, the process-based modelling tools could help to uncover context dependencies and explain mechanisms behind observed phenomena. With the novel integration of biocrusts into simulation models, I contributed to a more mechanistic understanding of climate change effects in drylands and I propose to couple the models used in this thesis to dynamically assess physiological and ecohydrological processes under different scenarios of climate change and potential other disturbances. Moving forward, combining empirical and process-based simulation modelling will contribute to an even better understanding of biocrust-rich drylands and help their restoration and protection efforts.

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A | Appendix

A.1 General Introduction

Table A.1.1: Overview of existing process-based biocrust models (continued on next page)

Model reference	**Type**	**Description**	**Main output variables**	**Spatial scale**	**Temporal scale/ resolution**	**Examples of research questions adressed with the model**
Porada et al. (2013)	Non-vascular vegetation	A process-based vegetation model, similar to dynamic global vegetation models (DGVMs) but designed for non-vascular organisms such as lichens and mosses.	Carbon exchange and uptake, cover, biomass	Not spatially explicit	Years/1 h	Quantify global carbon uptake by lichens and bryophytes (Porada et al., 2013) and their effect on global biogeochemical cycles (Porada et al., 2014). Effect of climate change on biocrust lichen (Baldauf et al., 2021).
Whitney et al. (2017)	Ecohydrological	Modified soil-water balance model to simulate the hydrological processes of a biocrust and a subsoil layer. Biocrusts are static and simulated similar to the subsoil layer and parameterised for different levels of development.	Soil moisture	Not spatially explicit	Years/1 d	Quantify the effect of different crust levels of development on subsoil hydrology and run off
Chen et al. (2018)	Ecohydrological	Soil-water balance and vegetation model with simulation of a biocrust layer on top of soil layers that modifies water flows. Crusts layer grows in thickness over time.	Soil moisture in different layers, vegetation cover	Not spatially explicit	Years/1 d	How do biocrusts affect soil-water content and hydrological processes and how is this affected by changes in rainfall regime?

Chen et al. (2019); Jia et al. (2019)	Ecohydrological	Combination of a soil-water balance model and a vegetation growth model. The vegetation growth model includes grasses, shrubs and biocrusts as life forms which grow depending on the soil water content. Based on model structure by Chen et al. (2018).	Soil moisture in different layers, vegetation cover	Not spatially explicit	Years/1 d	How does the dominance of vascular plants and biocrusts change with rainfall amount and frequency (Jia et al., 2019)? What is the effect of different biocrust types on vegetation dynamics after restoration (Chen et al., 2019)?
Kinast et al. (2016)	Mathematical	Simple model that couples vegetation and crust biomass as well as soil and surface water availability to assess vegetation patterns along a rainfall gradient.	Spatial profiles of biocrust and vegetation biomass, soil and surface water	Spatially explicit but theoretical units	Theoretical time steps	What are vegetation-crust states along a precipitation gradient and which stable vegetation patterns develop?
Kim and Or (2017)	Biophysical and -chemical	Individual-based model for early-successional biocrusts and the main biophysical and chemical processes involved. Simulation of within-crust hydrological processes and trophic interactions within the microbial community consisting of aerobic heterotrophs, anaerobic heterotrophs, photoautotrophs and cheomautotrophs.	Spatial distribution of microbial processes, diurnal cycles of gas exchange (CO_2, NH_3, N_2O)	10 mm	Days/unclear	How does the stratification of the microbial community within soil crust work? How does the chmical environment shape microbial cyles of gas exchange, hydration, and carbon and nitrogen cycling?

A.2 Soil moisture dynamics under two rainfall frequency treatments drive early spring CO_2 gas exchange of lichen-dominated biocrusts in central Spain

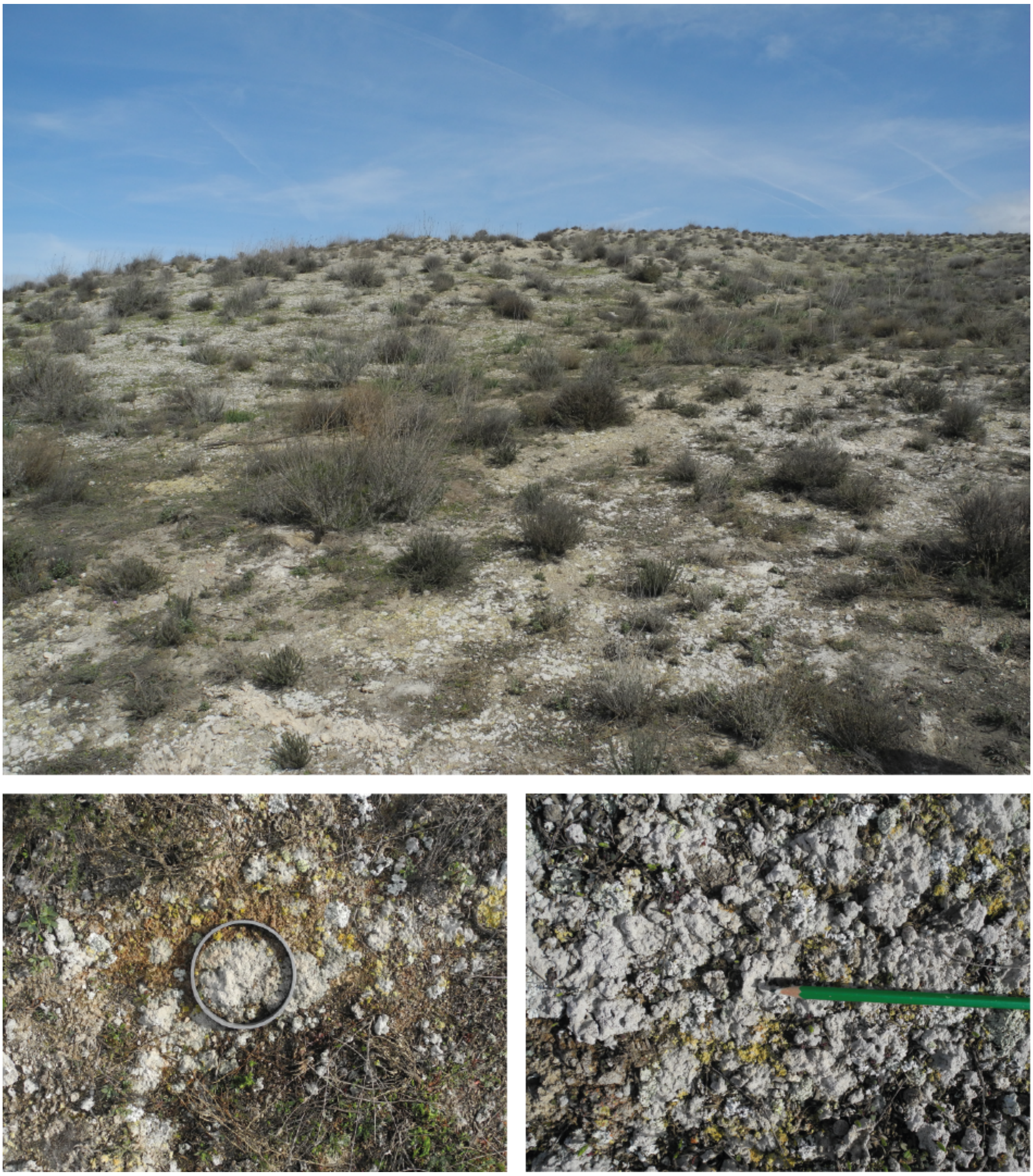

Figure A.2.1: Picture of the hillslope (top) at El Espartal, central Spain (40°11′N, 3°36′W, 574 m a.s.l.), where the soil cores (bottom left) for the experiment were collected. The lichen-dominated biocrusts cover a substantial part of the interplant space and are characterized by a high cover of *Diploschistes diacapsis* (bottom right) (Photo credit: Selina Baldauf).

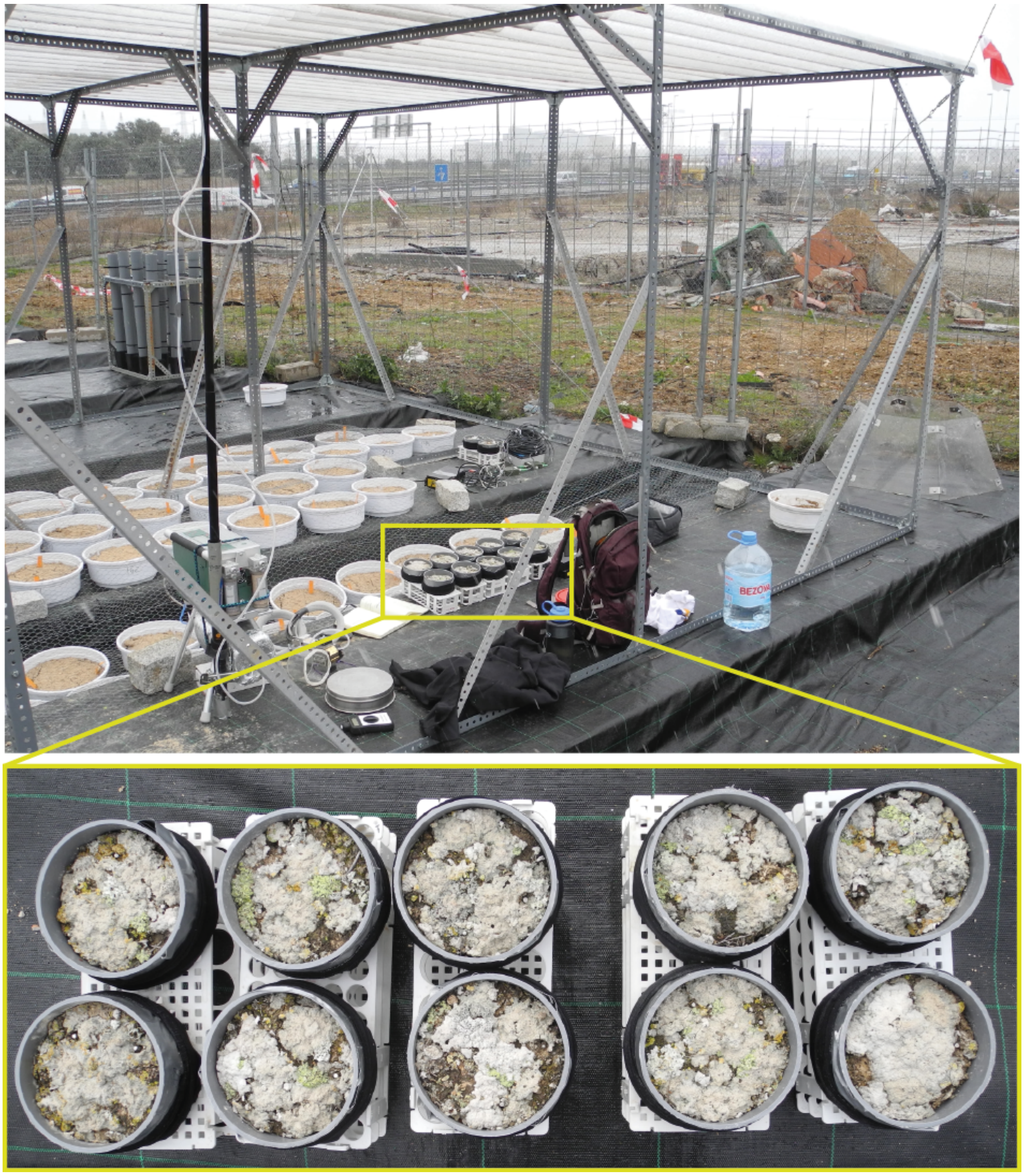

Figure A.2.2: Experimental setup with the soil cores at the Climate Change Outdoor Laboratory of the Rey Juan Carlos University in Móstoles (Photo credit: Selina Baldauf).

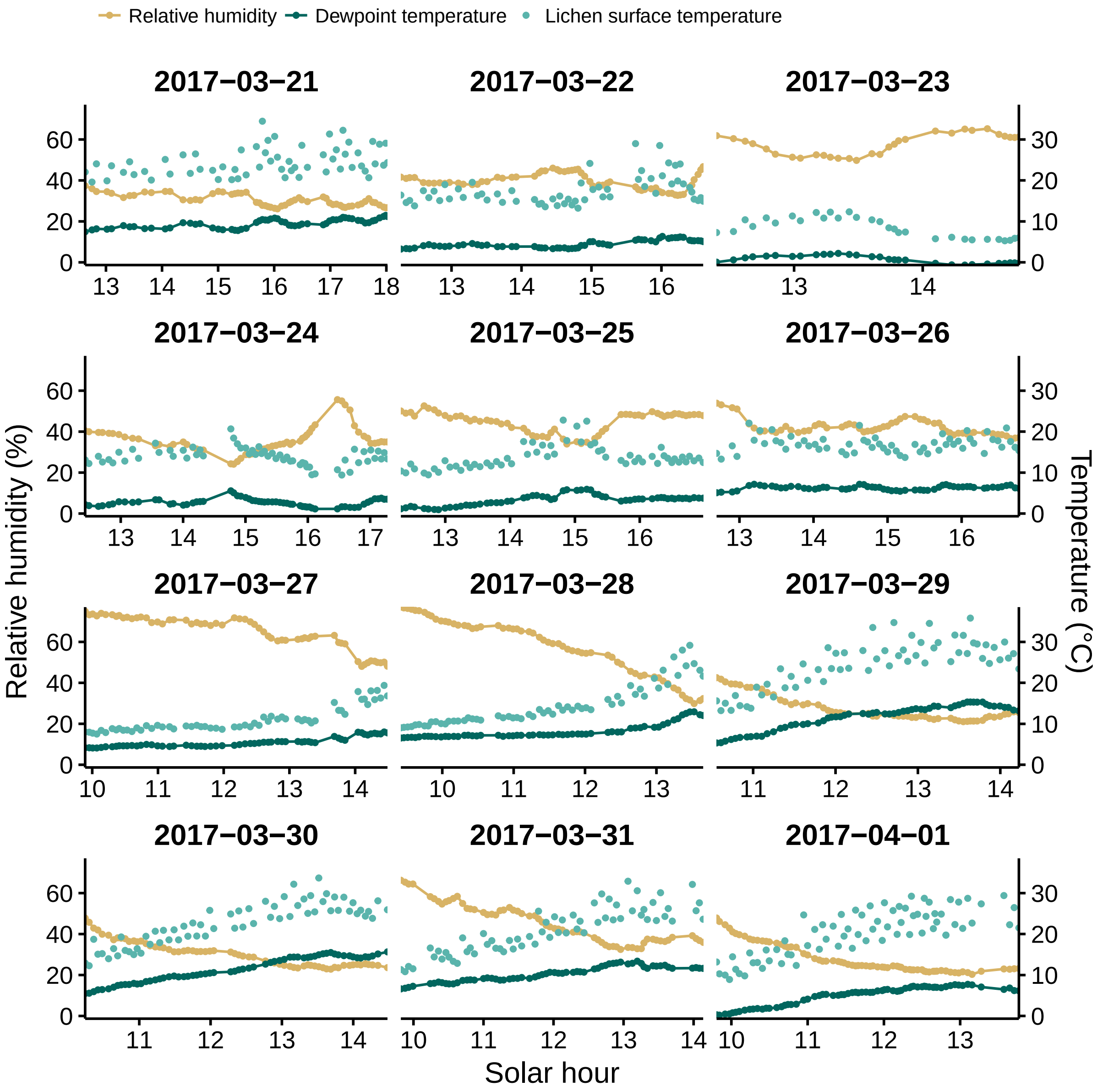

Figure A.2.3: Relative air humidity (%) and lichen surface temperature as recorded with the Li-6400 device and calculated dewpoint temperature. During the measurements the lichen surface temperature was always higher than the dewpoint temperature, i.e. no dew occurred during the measuring.

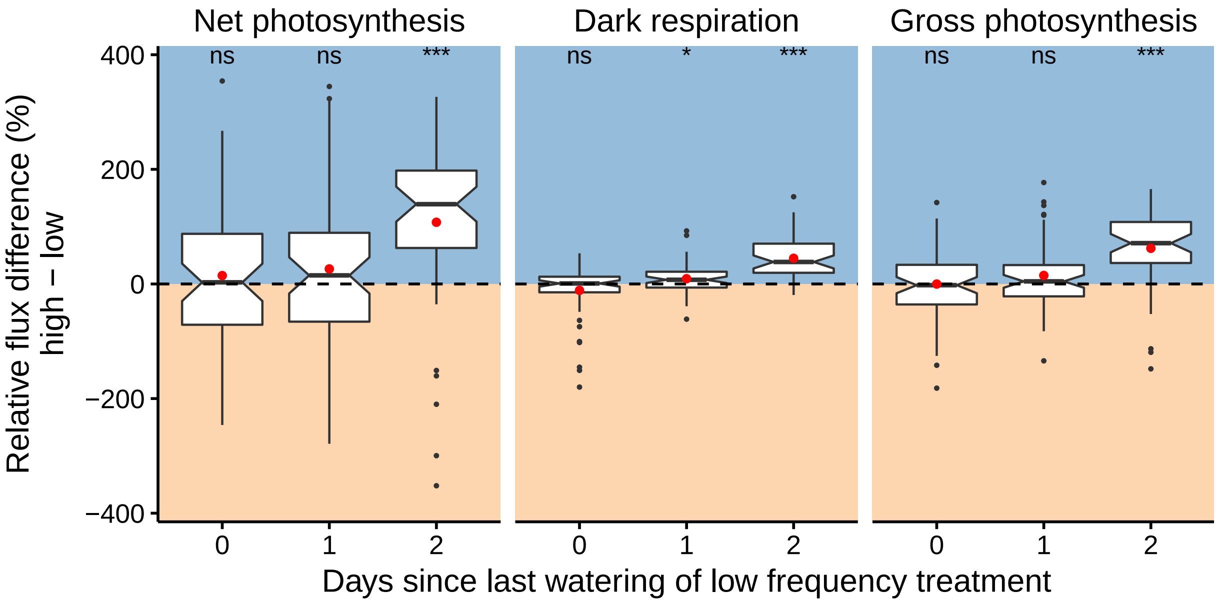

Figure A.2.4: Boxplots with relative differences (%) of net photosynthesis, dark respiration and gross photosynthesis between the high and the low frequency treatment on the different days since the last watering. The blue area indicates that the high frequency flux was higher and the orange area indicates that the low frequency flux was higher. The red dots represent the mean. The asterisks show significant differences between the two treatments, calculated with a paired Wilcoxon rank sum test ($p < 0.05^*$, $p < 0.001^{***}$, ns = not significant, $n = 60$ for 0 and 1 days since the last watering and $n = 50$ for 2 days since the last watering).

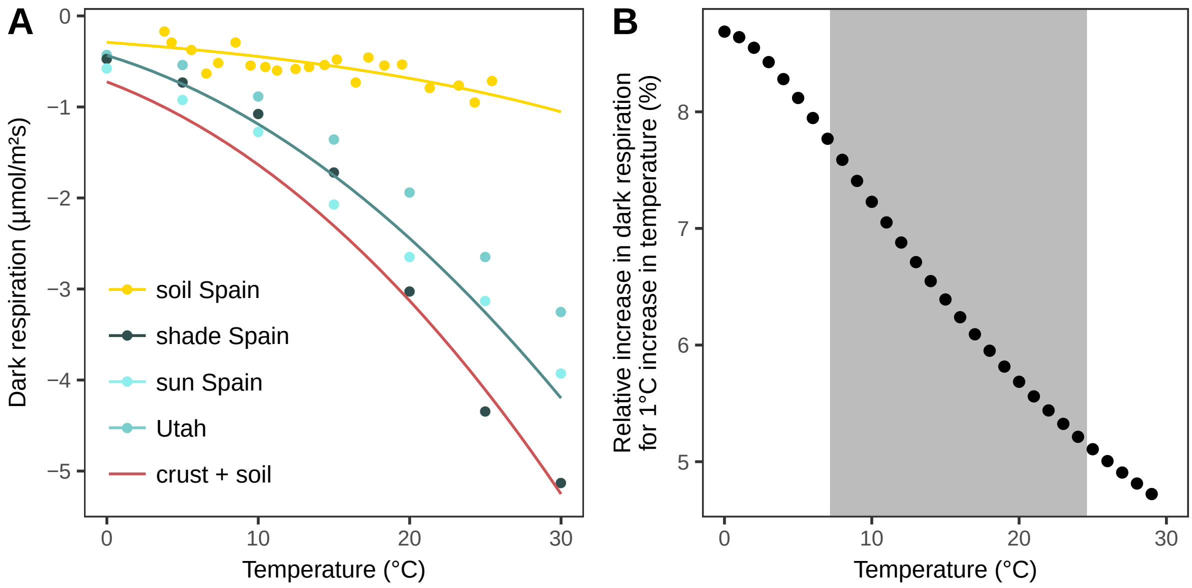

Figure A.2.5: Effect of soil temperature differences on additive dark respiration of soil and *D. diacapsis*. A) Temperature dependency of respiration. Crust data is from a population in Utah (Lange et al., 1997) and a sun and shade population in Spain (Pintado et al., 2005), both measured at optimal water content. Bare soil respiration data is from a study conducted in Aranjuez (central Spain) with soil similar to the soil used in this study at soil moistures above 25%. The blue and yellow lines are fits for crust and soil respiration, the red line is the additive respiration of soil and crust. B) Relative increase in crust and soil dark respiration for a 1 °C increase in temperature as calculated from the red line in 2 A. The grey box indicates the soil temperature relevant to our study in which relative increases in dark respiration of ca. 5–8% are expected.

Table A.2.1: Mean measurement times since the last watering (h) of the respective samples for the three daily measurements.

daily measurement no	watering treatment	days since last watering	mean time since last watering (h)
1	5 mm/day	0	1.5
2			3.1
3			4.5
1	15 mm/3 days	0	1.3
2			3.0
3			4.5
1	15 mm/3 days	1	24.8
2			26.3
3			27.8
1	15 mm/3 days	2	49.2
2			50.9
3			52.0

Table A.2.2: Cumulative soil moisture obtained by summarising the moisture values for 0, 1 and 2 days since the last watering of the low frequency treatment. Note that on March 21st, no moisture measurement was available, therefore, the cumulative moisture is lower than in the other periods.

Period	cumulative moisture 5 mm/day (%)	cumulative moisture 15 mm/3 days (%)
March 21st – March 23rd	33.7	33.1
March 24th – March 26th	73.6	70.1
March 27th – March 29th	75.9	68.6
March 30th – April 1st	58.0	51.4

Table A.2.3: Results of the final linear mixed model. Effects of the watering treatments and photosynthetically active radiation (PAR) or soil temperature (T_{soil}) on net photosynthesis, dark respiration and gross photosynthesis. Significant values are highlighted in bold.

Response	Source	Chisq	Df	Pr(>Chisq)
Net photosynthesis ~	watering treatment	0.09	1	0.767
	PAR	82.02	1	<**0.001**
	watering treatment:PAR	8.44	1	**0.004**
Dark respiration ~	watering treatment	4.05	1	**0.044**
	T_{soil}	322.41	1	<**0.001**
	watering treatment:T_{soil}	9.93	1	**0.002**
Gross photosynthesis ~	watering treatment	4.87	1	**0.027**
	PAR	358.10	1	<**0.001**

A.3 Relative humidity predominantly determines long-term biocrust-forming lichen cover in drylands under climate change

Figure A.3.1: *Diploschistes diacapsis*-dominated biocrust from Aranjuez (Photo by Fernando T. Maestre).

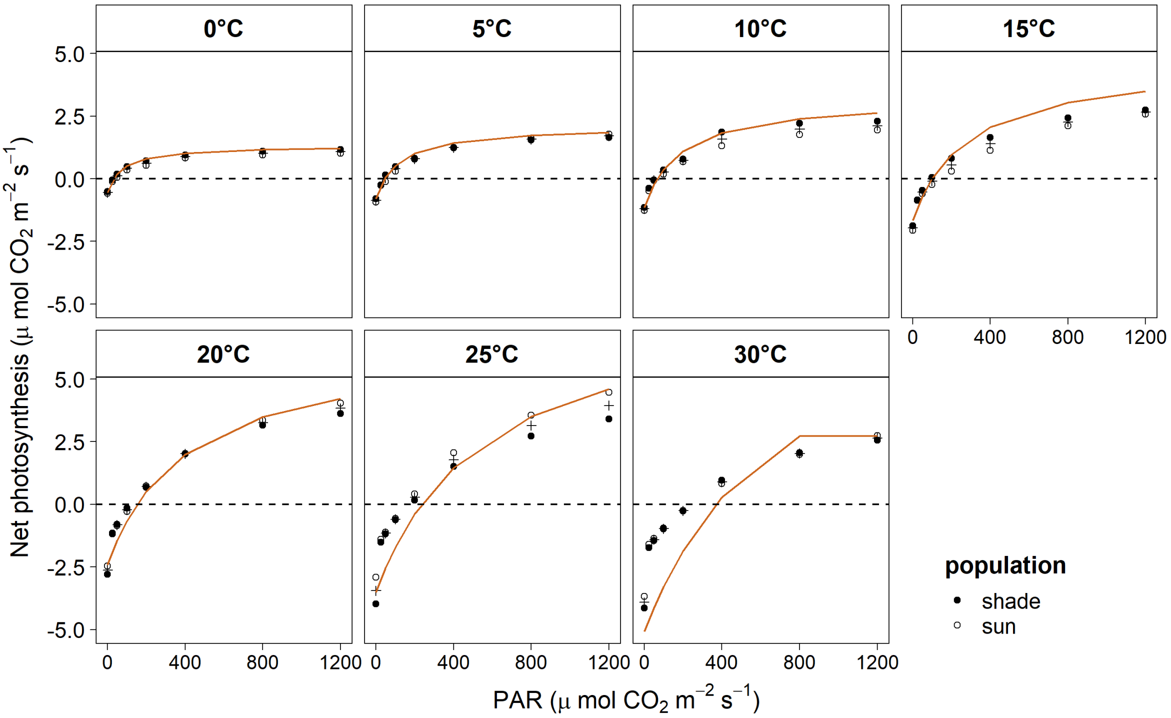

Figure A.3.2: Calibration results for photosynthesis: Modelled and measured light curves of net photosynthesis at different temperatures. Points represent measured data of sun and shade populations of *Diploschistes diacapsis* (data from Pintado et al. (2005)), the cross represents the mean of sun and shade populations and lines are modelled values.

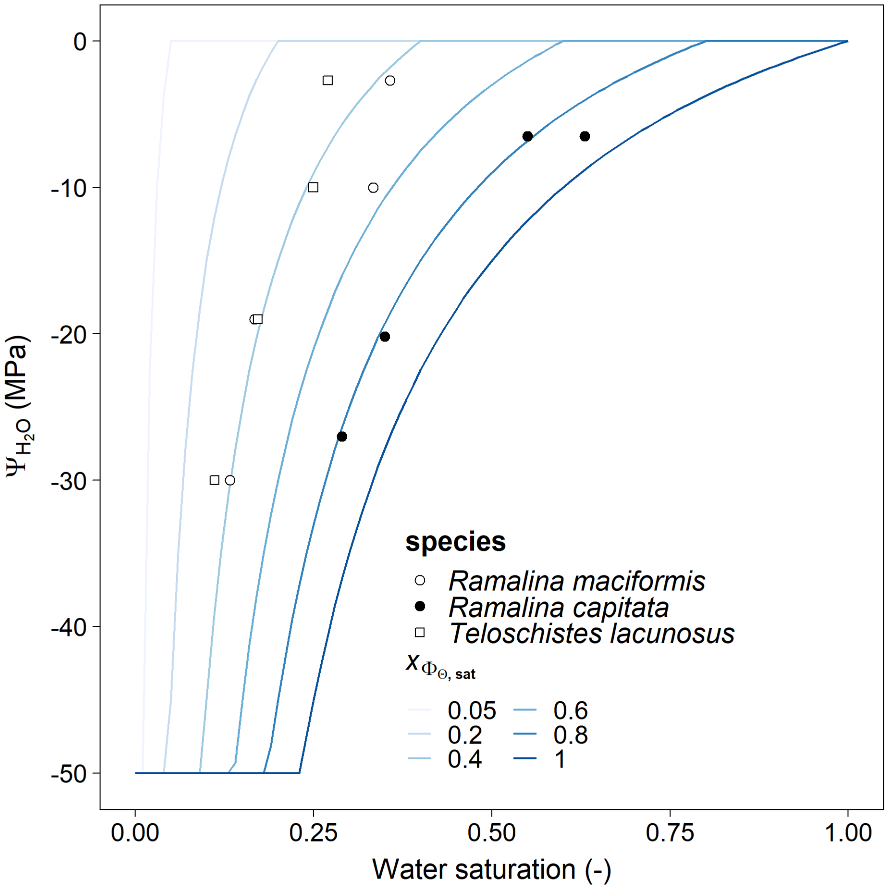

Figure A.3.3: Water potential Ψ_{H_2O} as function of changing thallus water saturation Θ. Points represent measured relationships of the three different dryland lichen species, lines show the relationship for different values of the threshold saturation $x_{\Phi\Theta,sat}$. *Ramalina capitata* data from central Spain (Pintado and Sancho, 2002), and *Ramalina maciformis* and *Teloschistes lacunosus* from the Negev desert (Scheidegger et al., 1995).

Table A.3.1: Literature and calibrated values for parameters of *Diploschistes diacapsis* used in the simulation (continued on next page).

Parameter	Value	Unit	Reference	Details
albedo	0.298	-	Chamizo et al. (2012a)	Average reflectance of short-wave radiation (square root of sum of squares of the reflectance of light-coloured lichen-dominated biocrusts at every wavelength between 300 and 1100 nm)
thallus height	1.4	mm	Pintado et al. (2005)	Mean thallus height (sun and shade population) of *D. diacapsis*
thallus porosity	0.3–0.4	-	-	Chosen such that resulting specific thallus area is between 3.6 and 4.2 m^2 thallus kg^{-1} C
water storage capacity	0.58	% of dry weight	Pintado et al. (2005)	Mean water storage capacity (sun and shade population) of *D. diacapsis*
saturation at maximum activity	0.3	-	Pintado et al. (2005)	Deduced from the relation between net photosynthesis and thallus water saturation (Figure 3.1 b)
saturation at which water potential becomes negative	0.05–1	-	-	Unknown, range of possible values was used (Figure A.3.3)
optimum temperature for photosynthesis	25	°C	Pintado et al. (2005)	Maximum of temperature dependent gross photosynthesis; mean of sun and shade population
Q_{10} value of respiration	2.1	-	Pintado et al. (2005)	Mean of all Q_{10} values calculated from the relationship between temperature and dark respiration with $Q_{10} = \frac{R_1 * \frac{10}{T_1 - T_2}}{R_2}$ with R_1 and R_2 being the dark respiration rates at temperature T_1 and T_2 respectively

reference maintenance respiration	3.5	µmol m^{-2} s^{-1}	Pintado et al. (2005)	Calculated from dark respiration at 10 °C (R_{spec}), temperature (T_{surf}, here 10 °C), optimum temperature for photosynthesis (T_{opt}) and the Q_{10} value: $R_{main} = \frac{R_{spec}}{Q_{10}{*}^{\frac{T_{surf}-T_{opt}}{10}}}$
$V_{C,max}$	2.1	s^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
$V_{O,max}$	0.3	s^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
thallus CO_2 diffusivity	0.01	mol m^{-2} s^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
enzyme activation energy K_C	80000	J mol^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
enzyme activation energy K_O	55000	J mol^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
activation energy V_m	10000	J mol^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
activation energy J_m	60000	J mol^{-1}	Pintado et al. (2005)	Calibration using light curve (Fig. A.3.2)
$x_{\Phi\Theta,sat}$threshold saturation for water potential	0.05–1	-	Pintado and Sancho (2002); Scheidegger et al. (1995)	Values were chosen such that the obtained curves are within a range of relationships observed for the dryland lichens *Ramalina capitata* in Central Spain and *Ramalina maciformis* and *Teloschistes lacunosus* from the Negev desert in Israel (see Fig. A.3.2)
$x_{\Psi H_2O}$ shape parameter for the water content dependent water potential curve	15	-	Pintado and Sancho (2002); Scheidegger et al. (1995)	Values were chosen such that the obtained curves are within a range of relationships observed for the dryland lichens *Ramalina capitata* in Central Spain and *Ramalina maciformis* and *Teloschistes lacunosus* from the Negev desert in Israel (see Fig. A.3.2)

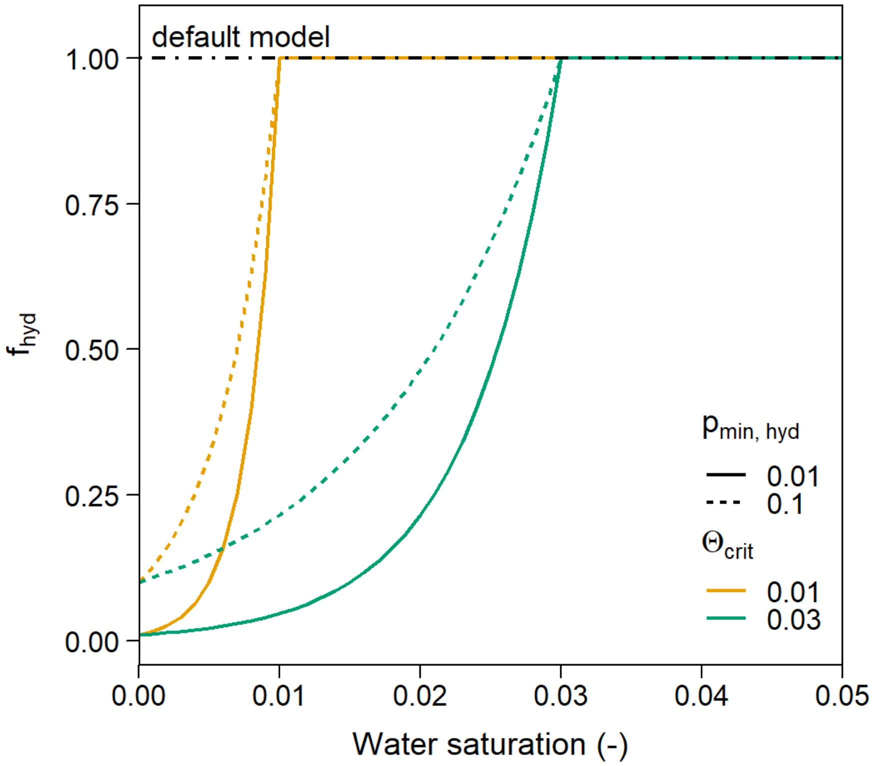

Figure A.3.4: Exponential increase of f_{hyd} for different parameterisations of $p_{min,hyd}$ and Θ_{crit}. The default model without hydrophobicity corresponds to a value of 1 for f_{hyd} independent of the current thallus water saturation Θ.

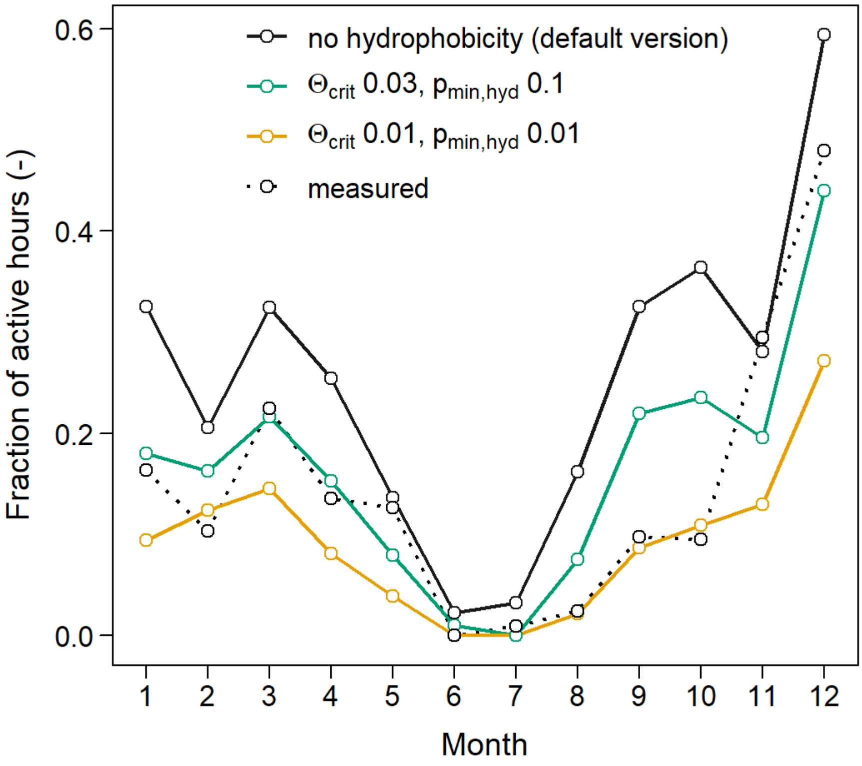

Figure A.3.5: Calibration of the hydrophobicity parameters against mean monthly active time of *Diploschistes diacapsis*. For different parameterisations of the hydrophobicity function, the simulated proportion of active time (continuous line) is compared with measured activity (dotted line).

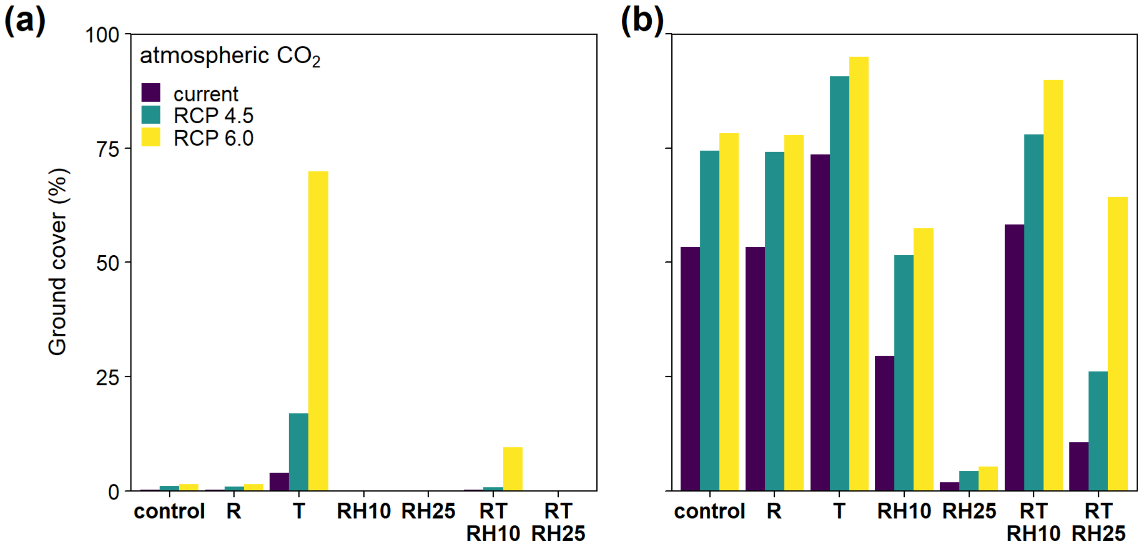

Figure A.3.6: Lichen cover for different climate scenarios and hydrophobicity parameterisations. a): Hydrophobicity parameterized with $\Theta_{crit} = 0.01$ and $p_{min,hyd} = 0.01$, b): Default model without hydrophobicity. Note that for (a) the simulation was only run for 200 instead of 900 years because for this parameterisation of hydrophobicity, the species has a 100% mortality rate after 200 years. Bars represent cover values for different atmospheric CO_2 concentrations (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).

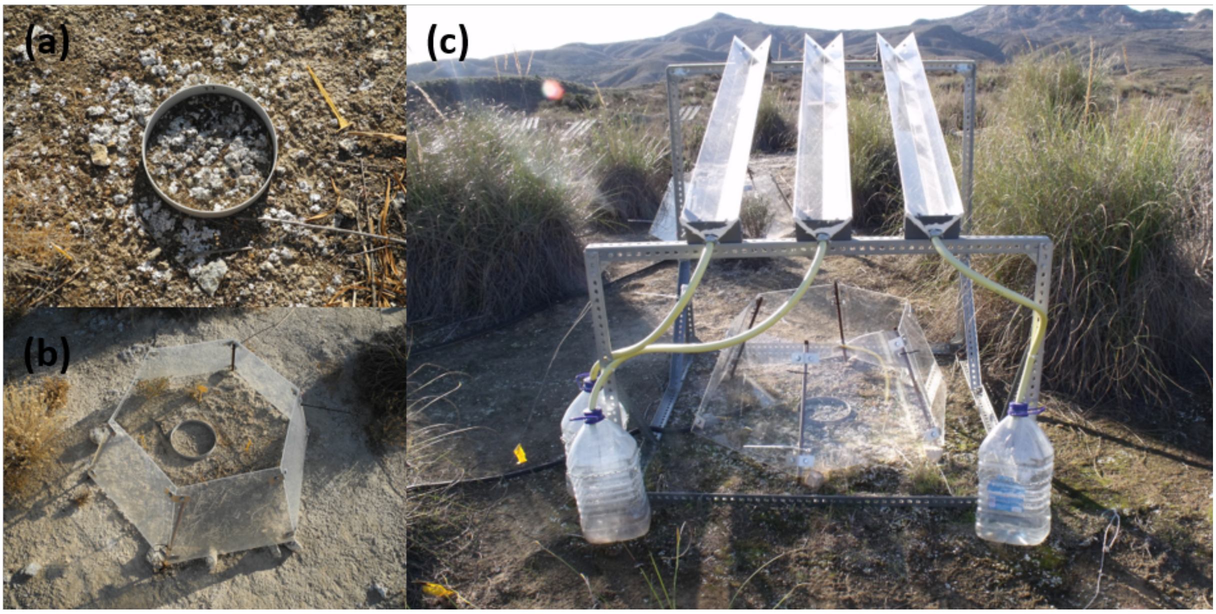

Figure A.3.7: Experimental setup of the manipulative climate change experiment in Aranjuez. a): control treatment, b): warming treatment with the open top chamber, c): combination scenario with a combination of warming and rainfall exclusion with a rainfall shelter. Note: the treatment where only rainfall is reduced by a rainfall shelter is not shown here (Photos (a) and (b) by Selina Baldauf, Photo (c) by Fernando T. Maestre).

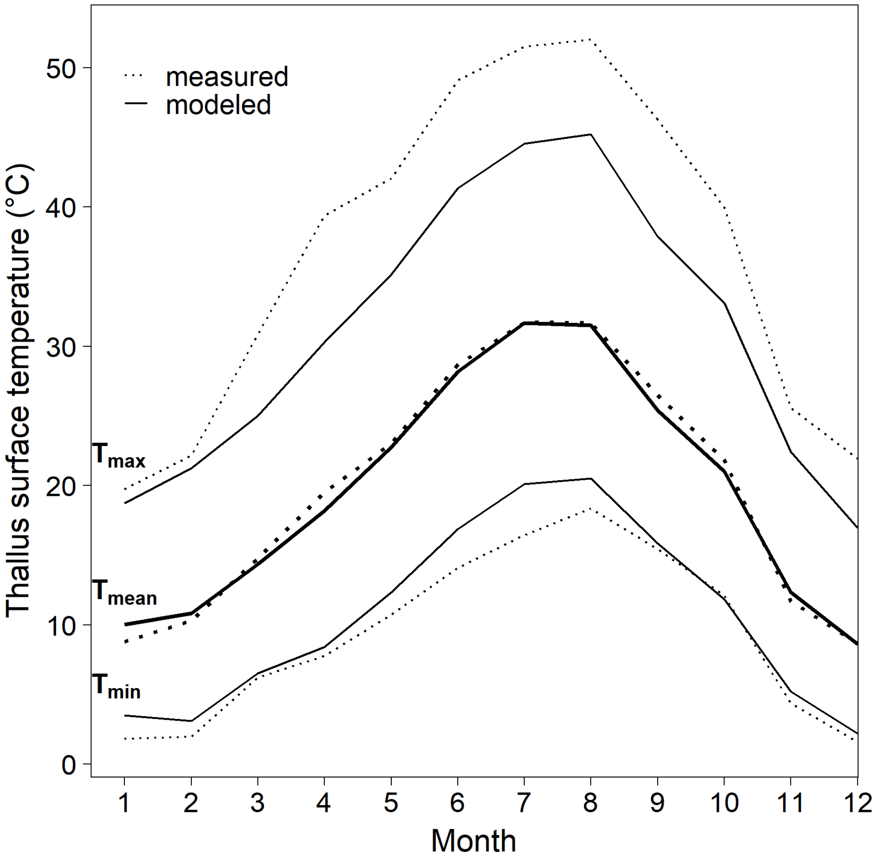

Figure A.3.8: Measured and modelled mean, minimum and maximum monthly *Diploschistes diacapsis* thallus surface temperature in El Cautivo.

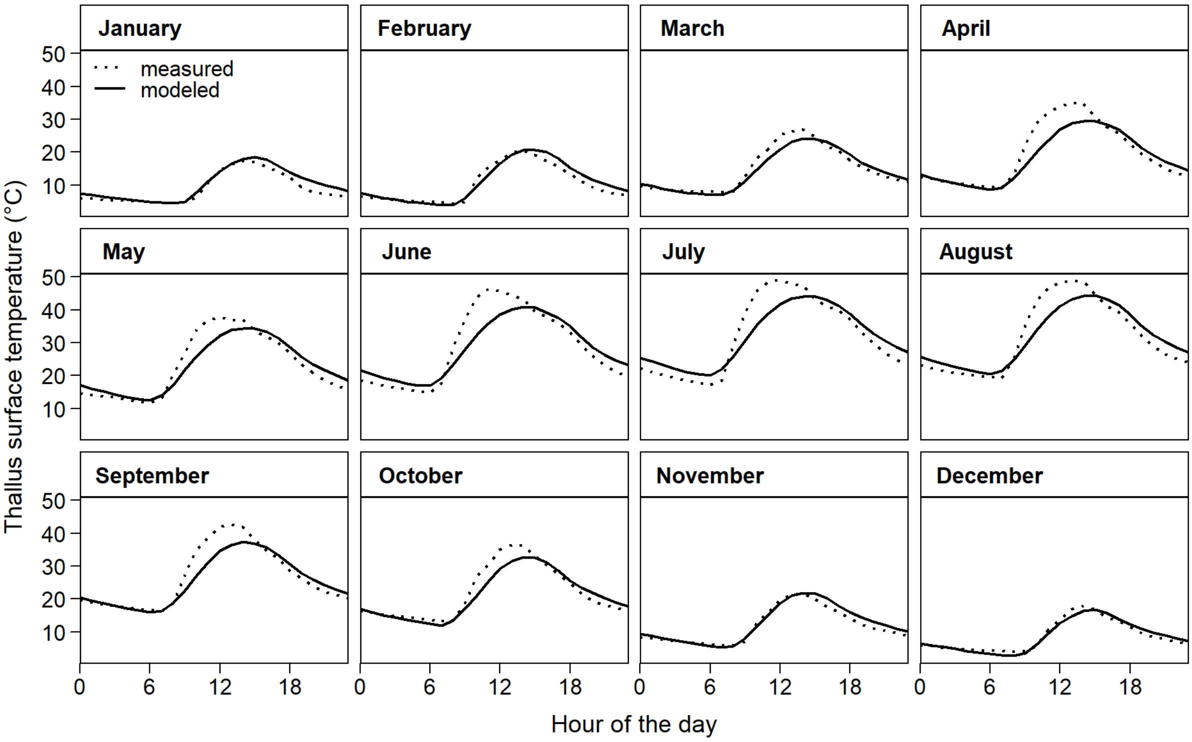

Figure A.3.9: Measured and modelled hourly means of *Diploschistes diacapsis* thallus surface temperature in El Cautivo.

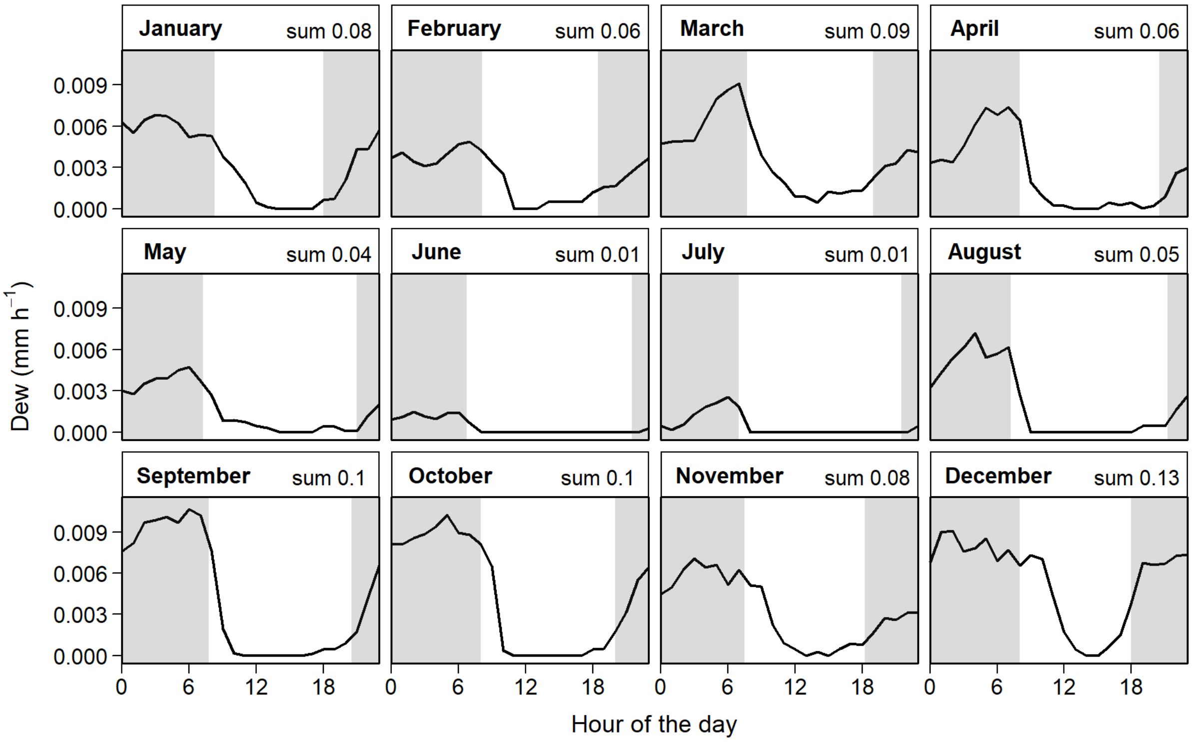

Figure A.3.10: Modelled mean hourly dew rates and mean sums per day for the El Cautivo site. The grey areas in the plots indicate times before sunrise and after sunset.

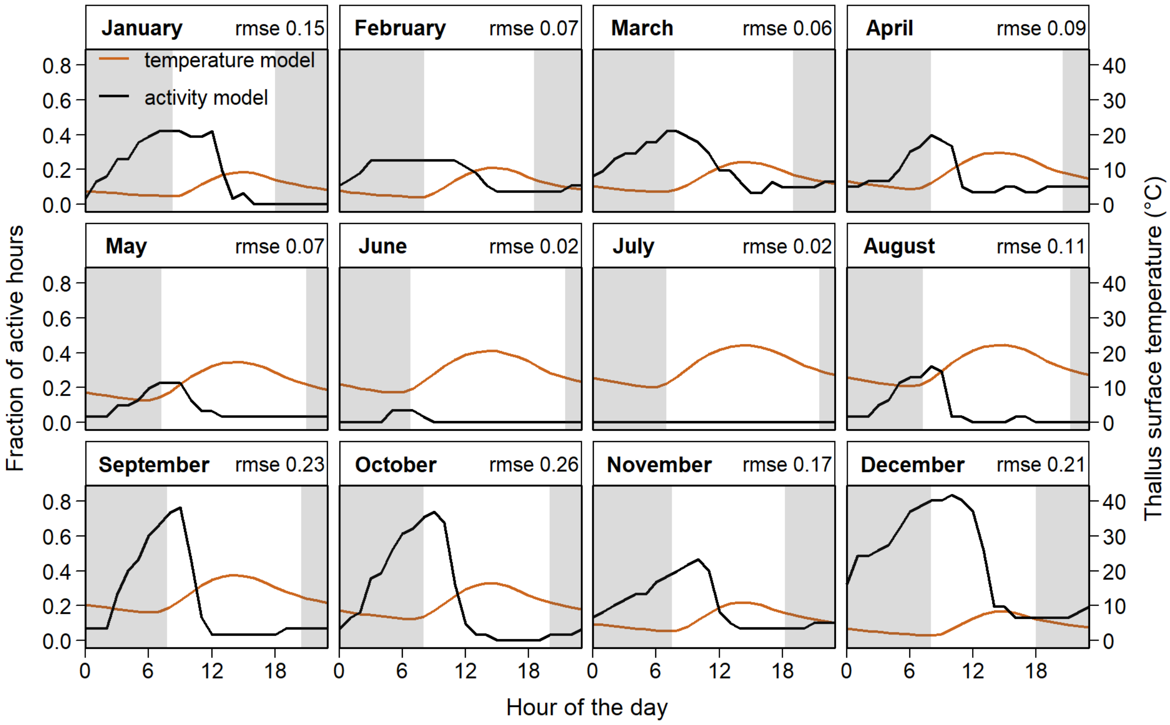

Figure A.3.11: Modelled diurnal fraction of active hours in each month and modelled thallus surface temperature. The grey areas in the plots indicate times before sunrise and after sunset.

Table A.3.2: Comparison of nights with dew input (%), total lichen active time fraction (%) and steady state cover (%) for the different climate change scenarios used.

Atmospheric CO_2	**Scenario**[1]	**Dew nights (%)**	**Active time (%)**	**Steady state cover (%)**
current	control	78	16	36
RCP 4.5	control	78	16	66
RCP 6.0	control	78	16	68
current	R	78	16	37
RCP 4.5	R	78	16	67
RCP 6.0	R	78	16	69
current	T	81	37	62
RCP 4.5	T	79	18	79
RCP 6.0	T	80	19	87
current	RH10	67	11	8
RCP 4.5	RH10	67	11	23
RCP 6.0	RH10	67	11	28
current	RH25	47	4	0
RCP 4.5	RH25	47	4	1
RCP 6.0	RH25	47	4	2
current	RTRH10	73	25	31
RCP 4.5	RTRH10	70	12	54
RCP 6.0	RTRH10	72	13	72
current	RTRH25	55	11	1
RCP 4.5	RTRH25	50	5	3
RCP 6.0	RTRH25	54	6	8

[1] 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.

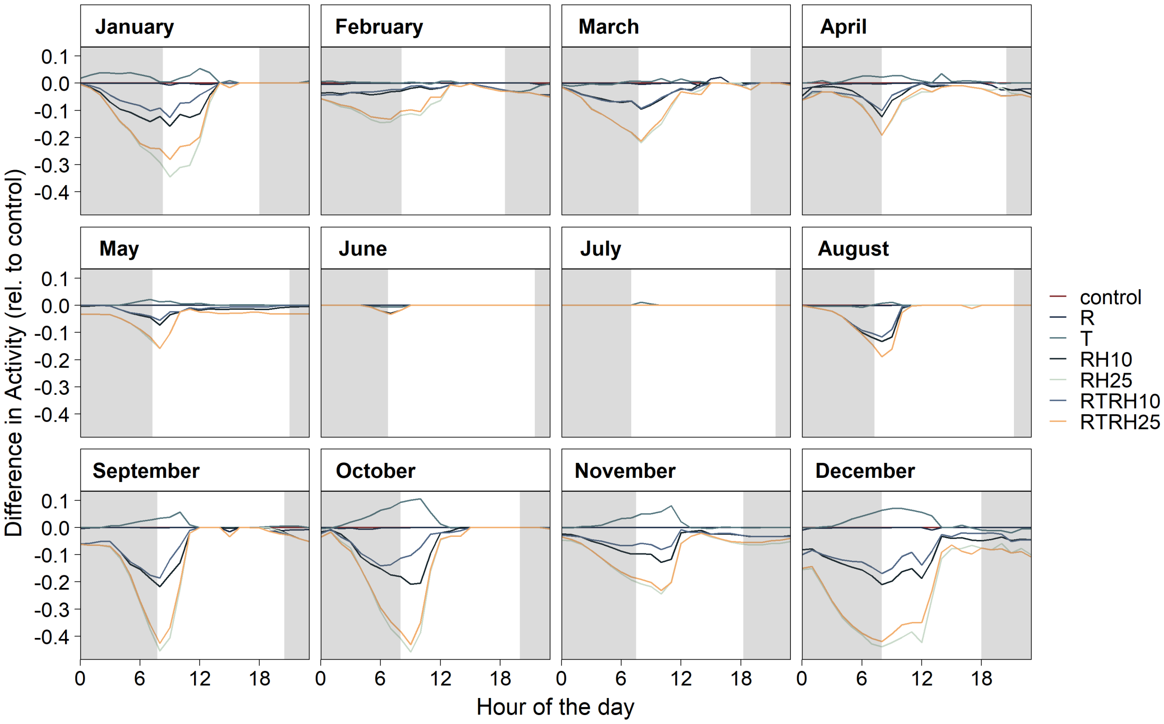

Figure A.3.12: Difference of modelled activity relative to the control treatment in Experiment 1. The grey areas in the plots indicate times before sunrise and after sunset. Lines represent different climate scenarios under current atmospheric CO_2 concentrations (395 ppm) (control = no changes in rainfall, 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).

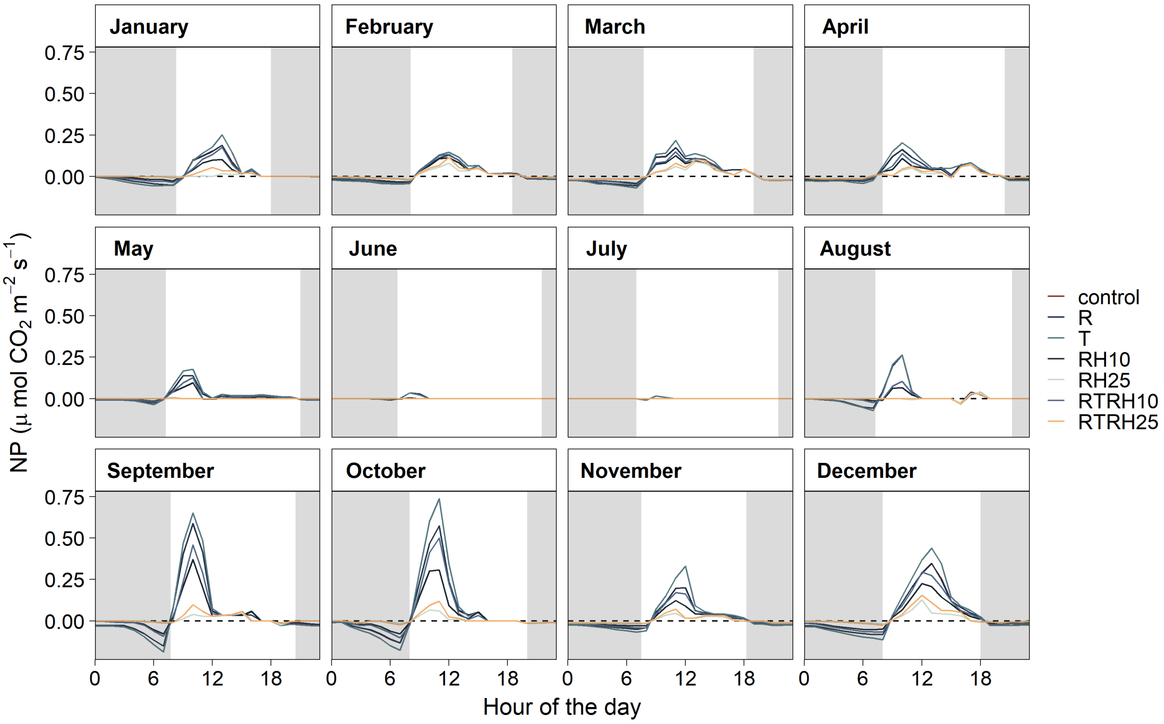

Figure A.3.13: Modelled mean hourly net photosynthesis for the different climate change scenarios in Experiment 1. The grey areas in the plots indicate times before sunrise and after sunset. Lines represent different climate scenarios under current atmospheric CO_2 concentrations (395 ppm) (control = 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).

A.4 Soil crusts influence water redistribution and enhance water availability for plants

A.4.1 Model description

In this study, we used the process-based ecohydrological dryland model EcoHyD and implemented a layer of biological soil crusts on top of the upper soil layer.

The main model description of EcoHyD can be found in previous publications (hydrological submodel: Tietjen et al. (2009), vegetation sub-model: Lohmann et al. (2012); Tietjen et al. (2010)). Biocrusts were implemented based on the model by Whitney et al. (2017).

Biocrusts were realised as a layer on top of the first soil layer that mediates all water flows between the soil and the atmosphere. Figure A.4.1 shows a flowchart of the main model processes and the order in which they are calculated.

Hourly hydrological processes

Rainfall First, rainfall is converted into surface water ($water_{L0}$).

Crust infiltration Surface water can infiltrate into the biocrust until it is saturated. The potential biocrust infiltration (I_c, in $\mathrm{mm\,h^{-1}}$) depends on the thickness of the crust layer (Z_c), the crust porosity (n_c) and the current crust moisture (s_c):

$$I_c = \min\left(water_{L0}, Z_c * n_c * (1 - s_c)\right) \qquad (\mathrm{mm\,h^{-1}})$$

I_c is multiplied with a hydrophobicity factor f_{hyd} to account for water repellency of some biocrusts at low water contents. f_{hyd} depends on two crust-specific parameters: The minimum value of the factor for a crust moisture of zero (h_{min}) and the critical crust water content θ_{crit}, at which the hydrophobicity factor becomes 1. Hydrophobicity increases exponentially between a crust moisture of 0 and θ_{crit} (Figure A.4.2):

$$f_{hyd} = h_{min} * e^{\left(\frac{-1}{\theta_{crit}} * log(h_{min}) * s_c\right)} \qquad (-)$$

The potential crust infiltration is multiplied with the hydrophobicity factor to determine the actual infiltration into the crust:

$$I_c = I_c * f_{hyd} \qquad (\mathrm{mm\,h^{-1}})$$

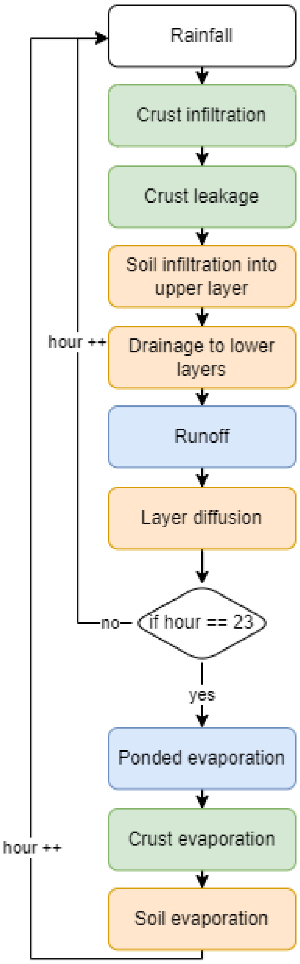

Figure A.4.1: Flowchart of model processes. Crust processes are shown in green, soil processes in orange and surface processes in blue.

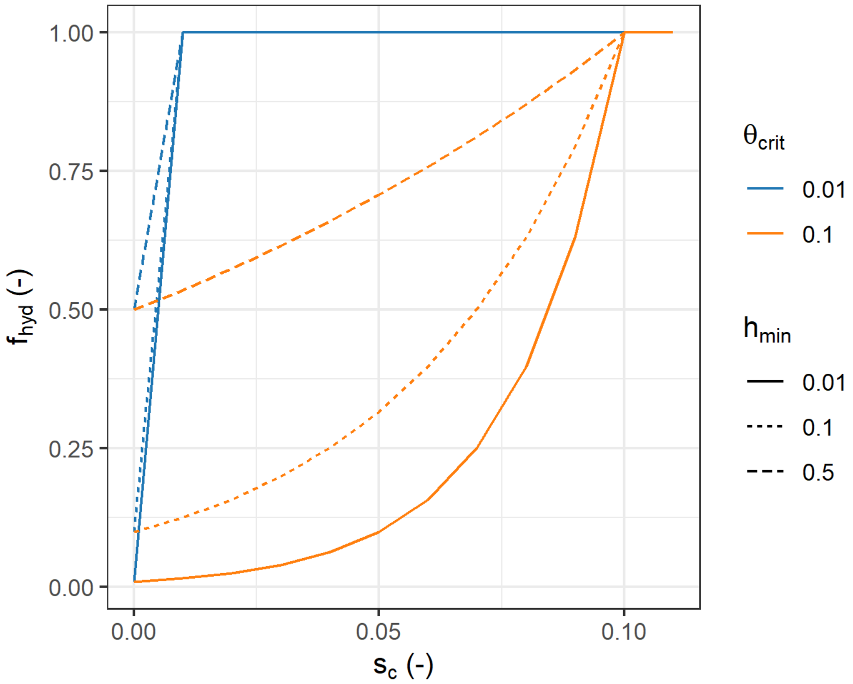

Figure A.4.2: Hydrophobicity factor f_{hyd} for different values of h_{min} and θ_{crit}

Crust leakage If the crust moisture exceeds the field capacity of the crust layer, surface water leaks into the upper soil layer.

The amount of water that leaks through the biocrust layer into the upper soil layer depends on the saturated hydraulic conductivity of the crust ($K_{s,c}$), the pore size distribution (β_c) and the field capacity ($s_{fc,c}$) of the biocrust layer:

$$L_c = K_{s,c}\left(\frac{e^{\beta_c(s_c - s_{fc,c})} - 1}{\beta_c(1 - s_{fc,c}) - 1}\right) \quad (\mathrm{mm\,h^{-1}})$$

If fully saturated, leakage is maximal and limited by the saturated hydraulic conductivity of the crust. The pore size distribution β_c is calculated from the pore distribution parameter b_c:

$$\beta_c = 2 * b_c + 4 \quad (-)$$

Soil infiltration upper layer The water that leaks through the biocrust can infiltrate into the upper soil layer according to the Green and Ampt approach (Green and Ampt, 1911), where a wetting front proceeds through the soil. Above the wetting front, the soil is saturated, below it is not. See Tietjen et al. (2009) for further information on the soil infiltration in EcoHyD.

If not all the leaked water could infiltrate into the soil in this time step, ponding occurs. The ponded water is added back to the surface water $water_{L0}$.

Drainage to lower layers If after soil infiltration, the soil moisture in the upper layer exceeds its field capacity, the excess water drains into the lower soil layer. If moisture in the lower soil layer also exceeds field capacity after drainage from the upper soil layer, excess water drains from the lower soil layer.

Runoff The remaining surface water is available for runoff. Runoff is calculated following a Manning-Strickler approach (Dingman, 1994; Tietjen et al., 2009):

$$QD = water_{L0}^{\frac{2}{3}} * \sqrt{sl} * (1 - \frac{c_g + c_s}{2}) * c_f \quad (\mathrm{mm\,h^{-1}})$$

with

- $water_{L0}$: surface water mm
- sl: downward slope of the cell (lowest neighboring cell) (-)
- c_g and c_s: vegetation cover of grasses and shrubs (-)
- c_f: factor for biocrust cover (-)

c_f was taken to be 3.6 in this study because measurements at the research site showed that runoff from crusted soil on average is 3.6 times higher than on non-crusted soils (Cantón et al., 2001, 2002)

Diffusion Diffusion balances differences in soil moisture between the upper and the lower soil layer. Diffusion follows Darcy's law, adopted for soil moisture (see Tietjen et al. (2009)) and depends on the difference in soil moisture between layers, the geometric mean of saturated and unsaturated hydraulic conductivity, and a dimensionless diffusion constant (Tietjen et al., 2009).

Daily hydrological processes

Evaporation of the surface water and the crust layer and evapotranspiration from the soil layers is calculated once at the end of every day.

First, the potential evapotranspiration demand of the given day is calculated (ET_{pot}). Potential evapotranspiration is calculated based on Hargreaves (1974). It depends on the daily mean ($\overline{T}$), minimum (T_{min}) and maximum (T_{max}) temperature and the extraterrestrial radiation (R_{ext}) on that day (estimated from the latitude of the site and the Julian day (J)).

$$ET_{pot} = 0.0023 * (\overline{T} + 17.8) * (T_{max} - T_{min})^{0.5} * R_{ext} \quad (\mathrm{mm\,d^{-1}})$$

with

$$R_{ext} = 15.392 * d_r * (\omega_s * \sin\phi * \sin\delta * \sin\omega_s) \quad (-)$$

with

- $d_r = 1 + 0.033 * \cos(\frac{2\pi}{365} * J)$: distance between earth and sun
- $\omega_s = \arccos(-\tan\phi * \tan\delta)$: sunset hour angle
- $\phi = \frac{lat*\pi}{180}$: latitude of site in radian
- $\delta = 0.4093 * \sin(\frac{2\pi}{365} * J - 1.405)$: solar declination in radian.

ET_{pot} is then sequentially met by evaporation of ponded surface water (free evaporation of all surface water), crust evaporation and soil evapotranspiration.

Crust evaporation Water can only evaporate from the biocrust if biocrust moisture is above the hygroscopic point ($s_{h,c}$ $(-)$), otherwise it is bound to the crust layer (Whitney et al., 2017). Evaporation from the biocrust layer is represented as a fraction k_c of the potential evaporation which is a parameter depending on the level of development of the crust.

$$E_c(s_c) = \begin{cases} 0 & s_c \leq s_{h,c} \\ k_c * PET & s_c > s_{h,c} \end{cases} \qquad (\mathrm{mm\,d^{-1}})$$

with

- $s_{h,c}$: hygroscopic point of biocrust layer (-)
- k_c: weighting term to limit biocrust evaporation (-)

If the evaporation of the biocrust exceeds the remaining evporative demand, the remaining demand is met and the rest of the water remains within the biocrust layer. Otherwise, the remaining evaporative demand is reduced by the amount of water evaporated from the biocrust layer.

Soil evapotranspiration Soil evaporation adopts a conceptual HBV model, similar to other ecohydrological models. If soil moisture is above the wilting point, evaporation is maximal and depends only on the vegetation cover and a factor that reduces evaporation due to soil crusting. Between the residual water content (s_{res}) and the wilting point (WP), soil evaporation increases exponentially (Figure A.4.3).

$$E_s = \begin{cases} min(ET_{pot} * \cos incl * vegfunction * f_c, (s - s_{res}) * Z_s) & s > WP \\ max(0, min(ET_{pot} * (s/WP)^2 * vegfunction * f_c, (s - s_{res}) * Z_s)) & s <= WP \end{cases} \qquad (\mathrm{mm\,d^{-1}})$$

with

- ET_{pot}: potential evaporation (here: remaining evaporative demand after ponded and crust evaporation) $(\mathrm{mm\,d^{-1}})$

- $incl$: inclination of the current cell (-)
- $vegfunction$
  - in layer 1: $vegfunction = c_{vegET_1} - c_{vegET_2} * (cover_g + cover_a + cover_s)$ (-)
    - c_{vegET_1} & c_{vegET_1}: Coefficients determining the influence of vegetation cover on evapotranspiration due to shading effects (-)
  - in layer 2: $P_{totroot_g} + P_{totroot_s}$ (-)
    - $P_{totroot} = f_{root} * cover$ with f_{root} being a parameter determining the conversion of surface cover of a pft to the root fraction in the specific layer (-)
    - Total roots calculated for both perennial grasses $P_{totroot_g}$ and shrubs $P_{totroot_s}$ (-)
- f_c: factor reducing soil evaporation due to presence of crusts (depends on crust type) (-)
- s: soil moisture (-)
- s_{res}: residual soil moisture (-)
- Z_s: depth of soil layer (m)
- WP: wilting point (-)

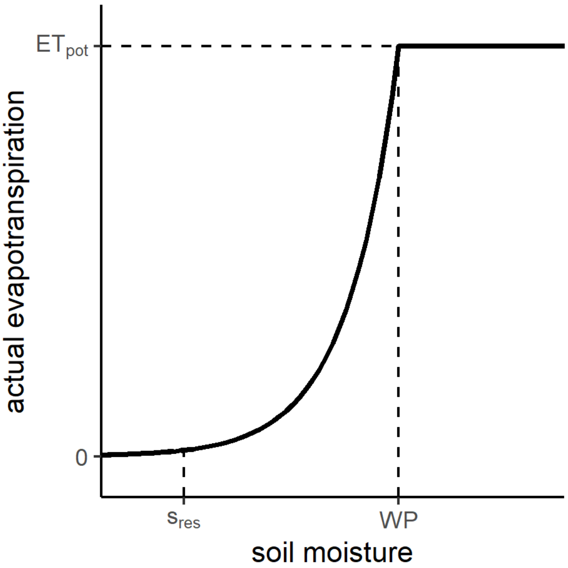

Figure A.4.3: Conceptual overview of actual evapotranspiration E_s depending on soil moisture. The actual evapotranspiration increases exponentially between the residual water content s_{res} and the wilting point WP. Figure from Tietjen et al. (2009)

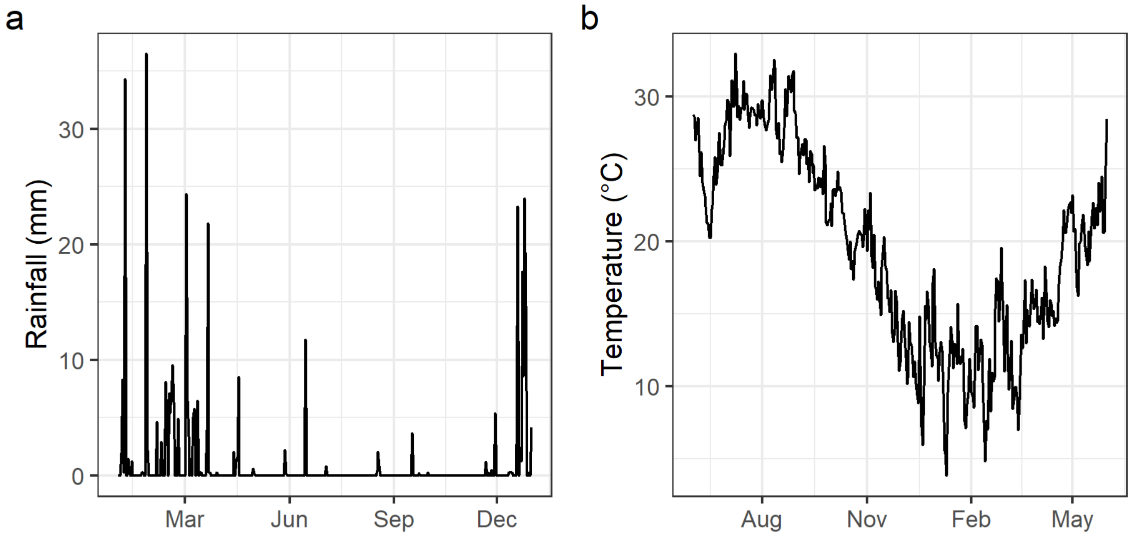

Figure A.4.4: a) Time series of daily rainfall sums, b) Time series of daily mean temperatures. Time series was reordered from the hydrological year October 2009–September 2010 and used as model input.

Table A.4.1: Parameters and the value ranges used in the sensitivity analysis and calibration.

Parameter	Symbol	Unit	Lower bound	Upper bound	References	Note	Calibration
Crust parameters							
Porosity	n_c	-	0.3 (0.3, 0.3, 0.3)	0.5 (0.5, 0.5, 0.5)	Whitney et al. (2017)	No measurements available, used values within range reported in literature	yes
Thickness	Z_c	mm	1 (1, 1, 5)	20 (10, 15, 20)	Chamizo et al. (2013b)	No measurements available, used range reported in litature	yes
Saturated hydraulic conductivity	Ks_c	mm/h	2.7 (9.5, 9.5, 2.7)	25.9 (20.9, 25.9, 15.1)	Chamizo et al. (2012a)	Range of mean ± standard deviation of Ks reported under the different biocrust types	yes
Evaporation reduction factor	f_c	-	0.1 (0.1, 0.1, 0.1)	1 (1, 1, 1)	-	-	yes
Minimum hydrophobicity factor	h_{min}	-	0.01	1	-	Only calibrated for lichen crust	yes
Pore distribution parameter	b	-	2	3.5	Whitney et al. (2017)	-	no
Crust field capacity	$s_{fc,c}$	-	0.2	0.8	Chamizo et al. (2012b); Whitney et al. (2017)	-	no
Hygroscopic point	$s_{h,c}$	-	0.08	0.44	Whitney et al. (2017)	-	no
Soil parameters							
Suction at the wetting front	sf	mm	133	201	Tietjen et al. (2009)	No measurement available, but standard value for silty loam is 166.8 in EcoHyD. Here we took this value and tested sensitivity within a range of ±20%	no
Saturated hydraulic conductivity	Ks_s	mm/h	5	20	Chamizo et al. (2012b)	Range of mean ± standard deviation	yes
Wilting point	WP	-	0.08	0.18	Cantón et al. (2002); Chamizo et al. (2012b); Tietjen et al. (2009)	Range taken from reported values in literature and the standard value for silty loam in EcoHyD	yes
Field capacity	$s_{fc,s}$	-	0.25	0.31	Cantón et al. (2002); Chamizo et al. (2012b); Tietjen et al. (2009)	Range taken from reported values in literature and limited by the maximum soil moisture observed in the data	yes

Note: The three upper and lower bound values in parantheses refer to the upper and lower bound of physical, cyanobacteria and lichen crust, respectively.

Table A.4.2: Parameter values used for the different biocrust types

Parameter	Symbol	Unit	Physical	Cyano	Lichen	Reference
Porosity	n_c	-	0.5	0.5	0.38	Calibration
Thickness	Z_c	mm	10	16.6	17.2	Calibration
Saturated hydraulic conductivity	Ks_c	mm/h	17.9	17	8.9	Calibration
Evaporation reduction factor	f_c	-	0.6	0.4	0.38	Calibration
Minimum hydrophobicity factor	h_{min}	-	-	-	0.47	Calibration
Pore distribution parameter	b	-	3.1	2.8	2.5	Whitney et al. (2017)
Crust field capacity	$s_{fc,c}$	-	0.27	0.28	0.47	Whitney et al. (2017)
Hygroscopic point	$s_{h,c}$	-	0.08	0.09	0.12	Whitney et al. (2017)

Table A.4.3: Parameter values used for the soil.

Parameter	Symbol	Unit	Value	Reference
Suction at the wetting front	sf	mm	166	Tietjen et al. (2009)
Saturated hydraulic conductivity	Ks_s	mm/h	6.9	Calibration
Wilting point	WP	-	0.18	Calibration
Field capacity	$s_{fc,s}$	-	0.26	Calibration
Saturation water content	$s_{s,max}$	-	0.26	Same as Field capacity
Depth upper layer	$Z_{s,1}$	mm	60	From data (soil moisture measurements)
Depth lower layer	$Z_{s,2}$	mm	80	From data (soil moisture measurements)
Residual water content	$s_{s,res}$	-	0.01	From data (soil moisture measurements)
Diffusion constant	c_{diff}	-	0.05	Tietjen et al. (2009)

Table A.4.4: Parameter values used for the vegetation parameters.

Parameter	Symbol	Unit	Value	Reference
Vegetation regression factor 1	c_{vegET_1}	-	1.2	Tietjen et al. (2009)
Vegetation regression factor 1	c_{vegET_2}	-	0.2	Tietjen et al. (2009)
Conversion of surface cover to roots grass	$f_{root,g}$	-	0.37	Tietjen et al. (2009)
Conversion of surface cover to roots shrub	$f_{root,s}$	-	0.64	Tietjen et al. (2009)

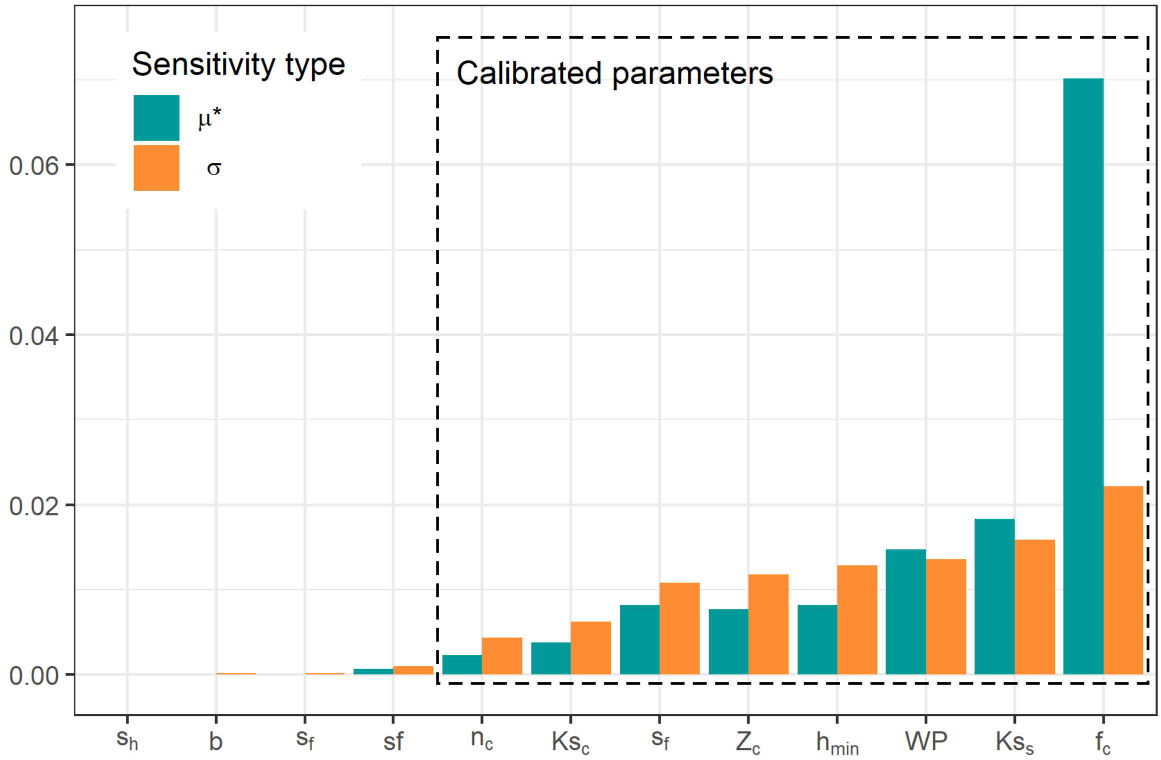

Figure A.4.5: Results of Morris screening for the target function of the calibration (RMSE of observed and modelled soil moisture in 3 and 10 cm depth). Soil parameters are written in blue font and crust parameters in red font. The parameters in the black rectangle on the right are used for calibration. μ^* represents the overall influence of a factor (mean of distribution) and σ shows the non-linear/interactive effects of a factor (standard deviation of the distribution).

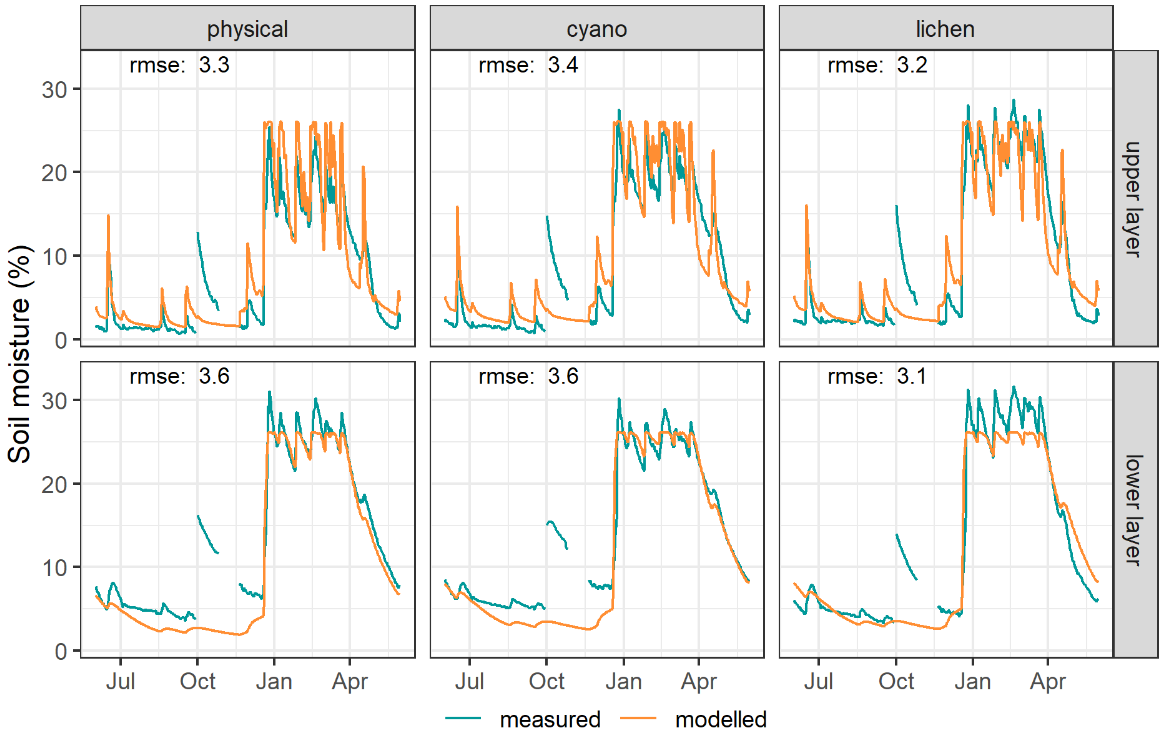

Figure A.4.6: Calibration results for the 3 biocrust types

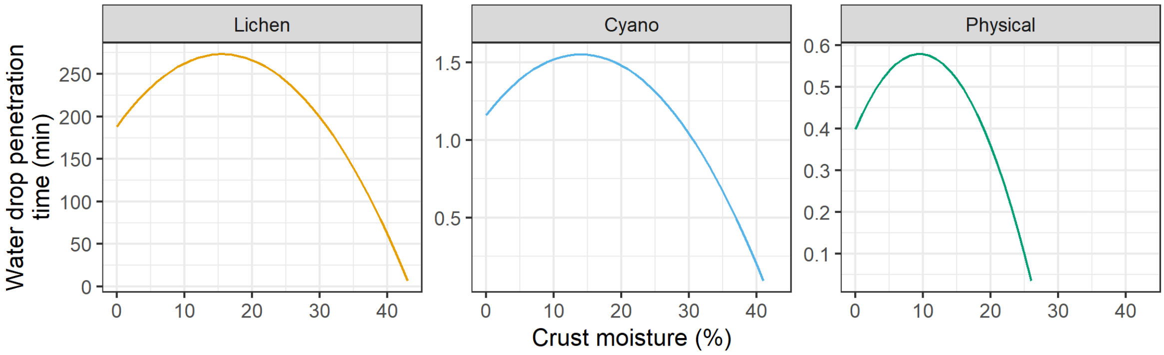

Figure A.4.7: Quadratic fit of water drop penetration time measured in the laboratory for the different crust types.

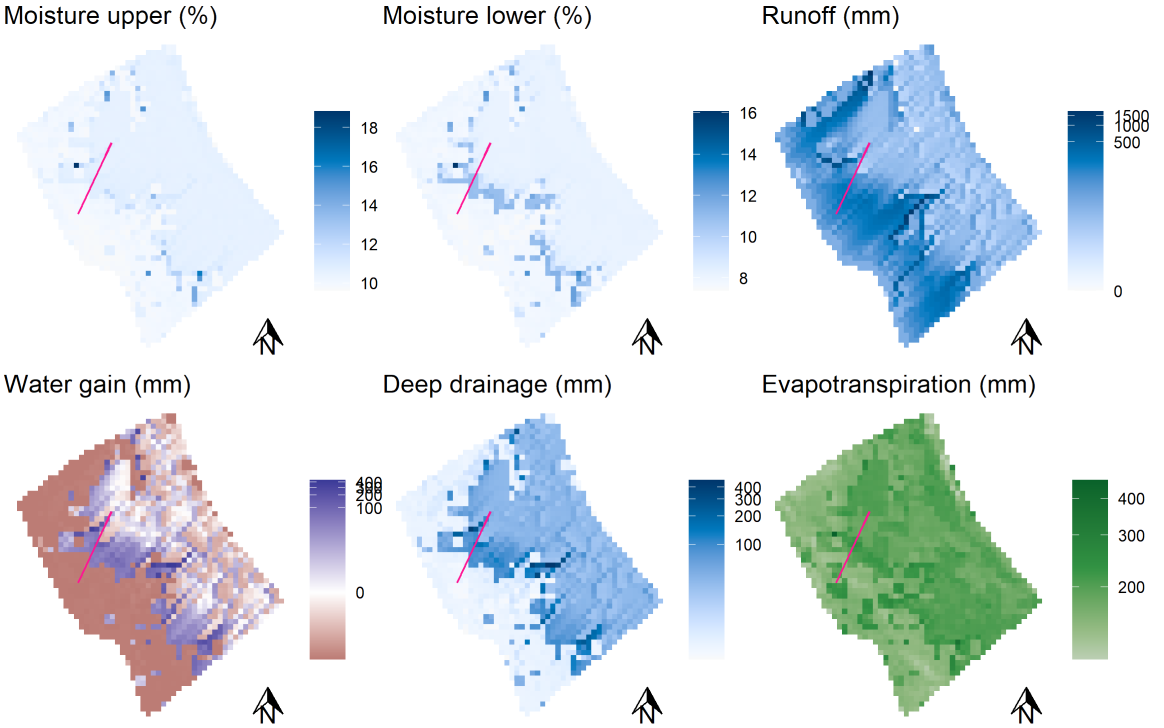

Figure A.4.8: Mean monthly soil moisture and monthly sum of hydrological processes for each grid cell on the El Cautivo hillslope in December. The pink line shows the hillslope transect that was selected for further detailed spatio-temporal analysis. It crosses a crusted section at the top (SW) and a vegetated section further down the hillslope (see also Figure 4.1).

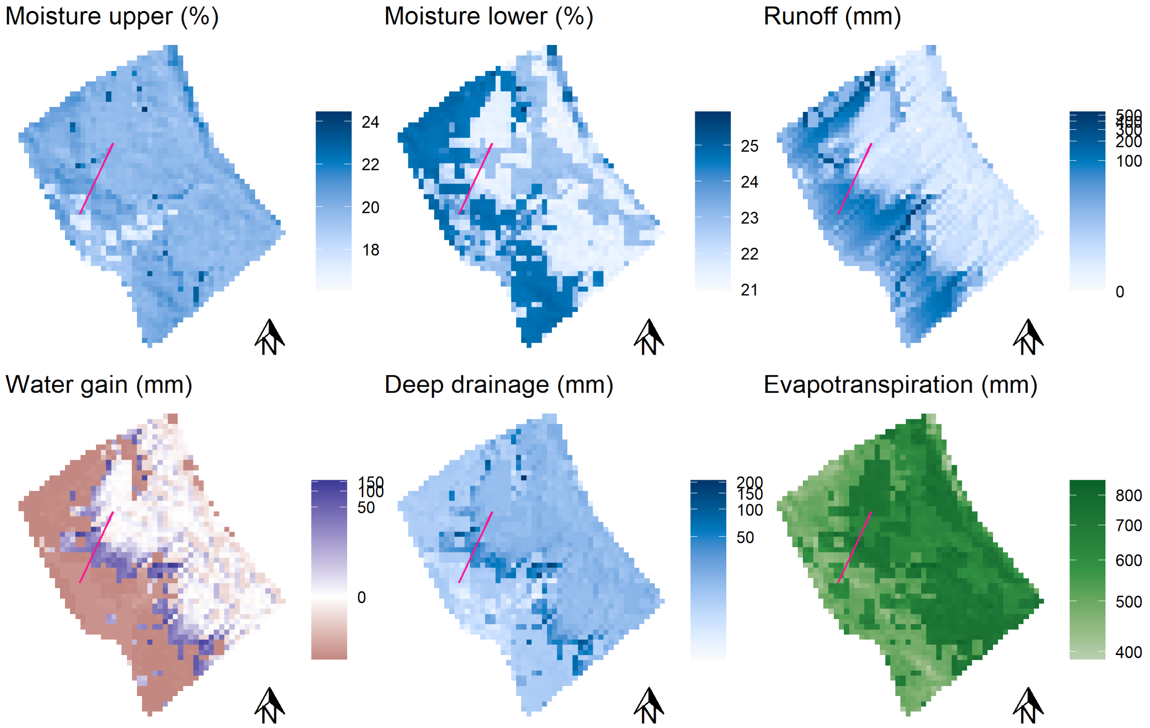

Figure A.4.9: Mean monthly soil moisture and monthly sum of hydrological processes for each grid cell on the El Cautivo hillslope in February. The pink line shows the hillslope transect that was selected for further detailed spatio-temporal analysis. It crosses a crusted section at the top (SW) and a vegetated section further down the hillslope (see also Figure 4.1).

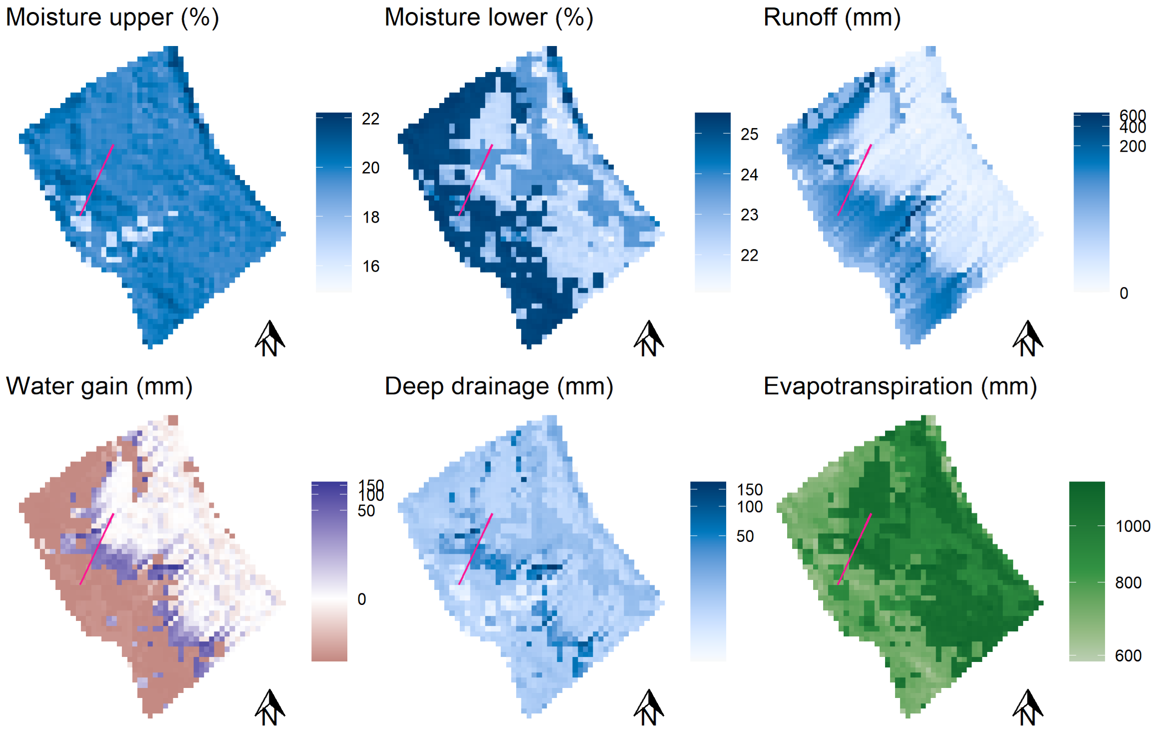

Figure A.4.10: Mean monthly soil moisture and monthly sum of hydrological processes for each grid cell on the El Cautivo hillslope in March. The pink line shows the hillslope transect that was selected for further detailed spatio-temporal analysis. It crosses a crusted section at the top (SW) and a vegetated section further down the hillslope (see also Figure 4.1).

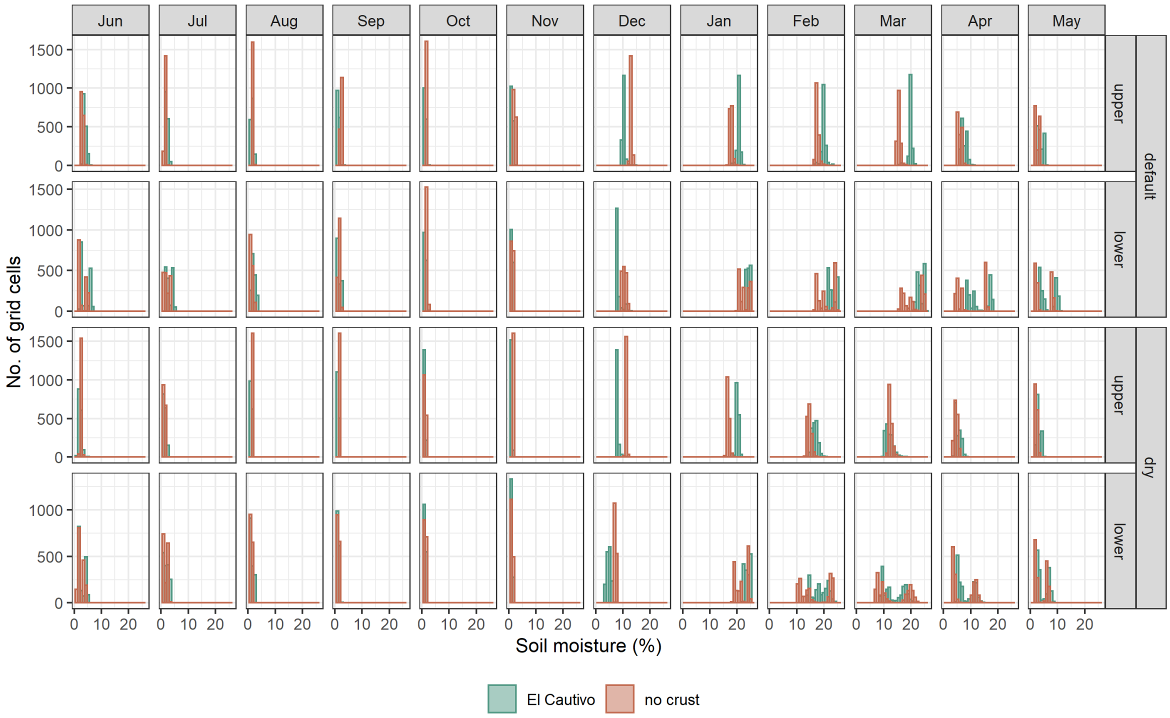

Figure A.4.11: Distribution of mean monthly soil moisture in the upper and lower layer of all grid cells of the hillslope between the baseline "El Cautivo" scenario with and the "no crust" scenario without biocrust cover. The first two rows show the distribution under current climate conditions (default) and the last two rows show the distribution for the scenario with 50% reduced rainfall.

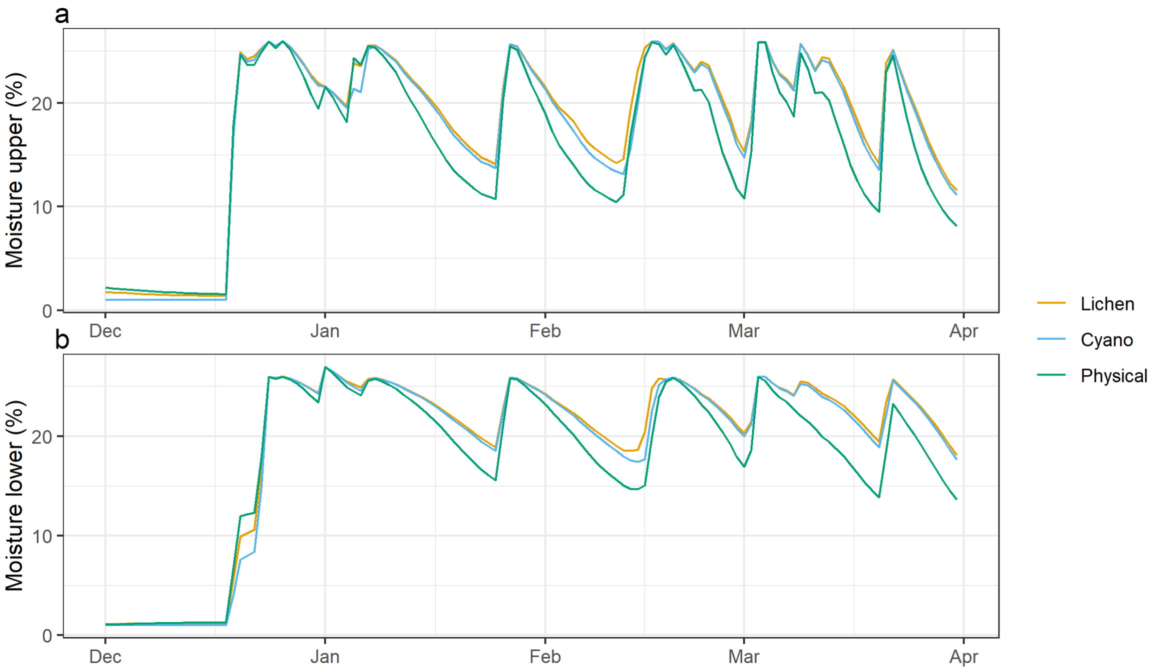

Figure A.4.12: Simulated daily mean soil moisture in the upper a) and lower b) layer under vegetated cells in the wet season from January until March. In the three scenarios the hillslope was covered with either physical, cyanobacteria or lichen crust.

Curriculum Vitae

Due to data privacy, the CV is not included in the electronic version of the thesis.

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Selbständigkeitserklärung

Hierdurch versichere ich, dass ich meine Dissertation selbstständig verfasst und keine anderen als die von mir angegeben Quellen und Hilfsmittel verwendet habe. Die Dissertation ist in keinem früheren Promotionsverfahren angenommen oder abgelehnt worden.

Berlin, den 31.05.2022

Selina Baldauf