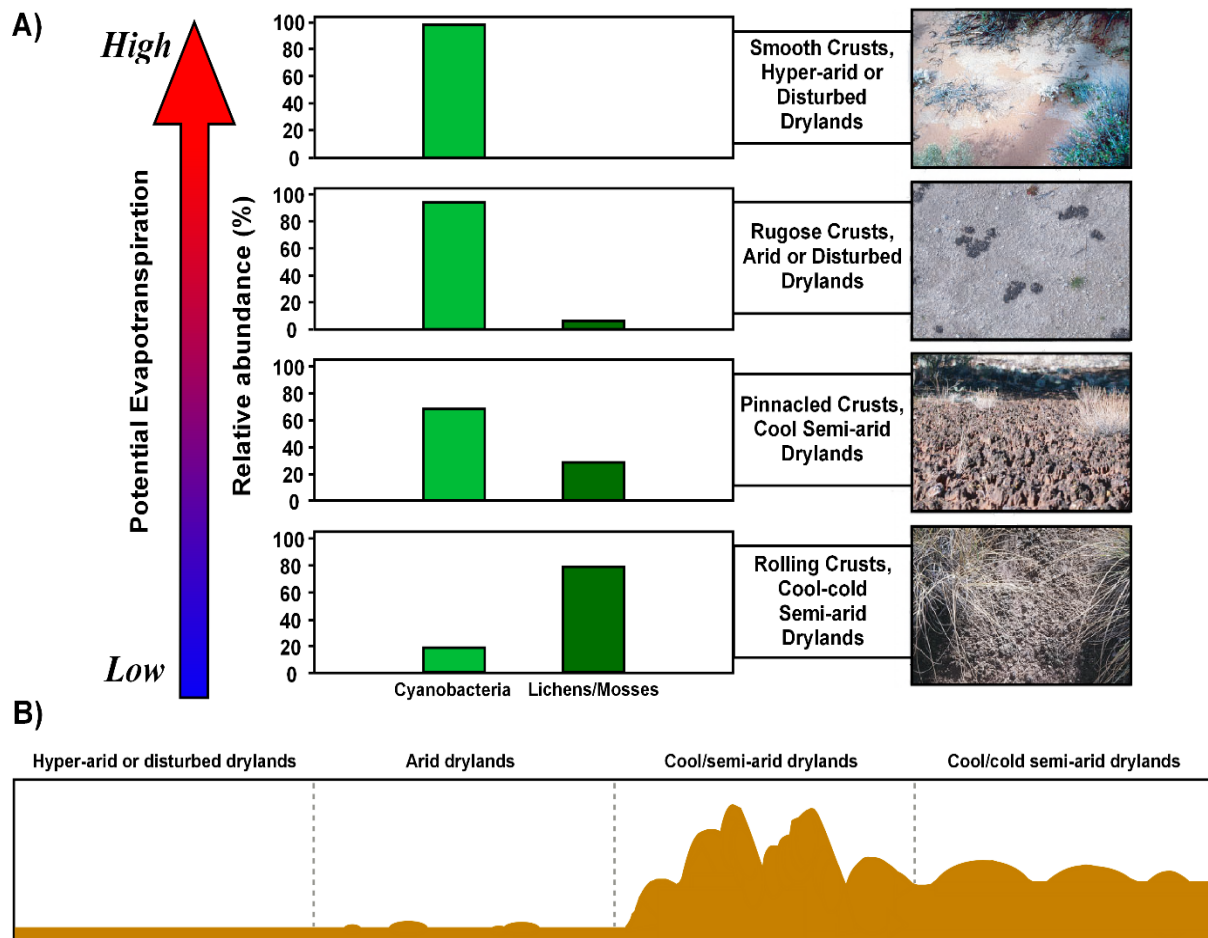


## **How will climate change impact Spanish dryland biological soil crust growth & diversity?**

### **Introduction**

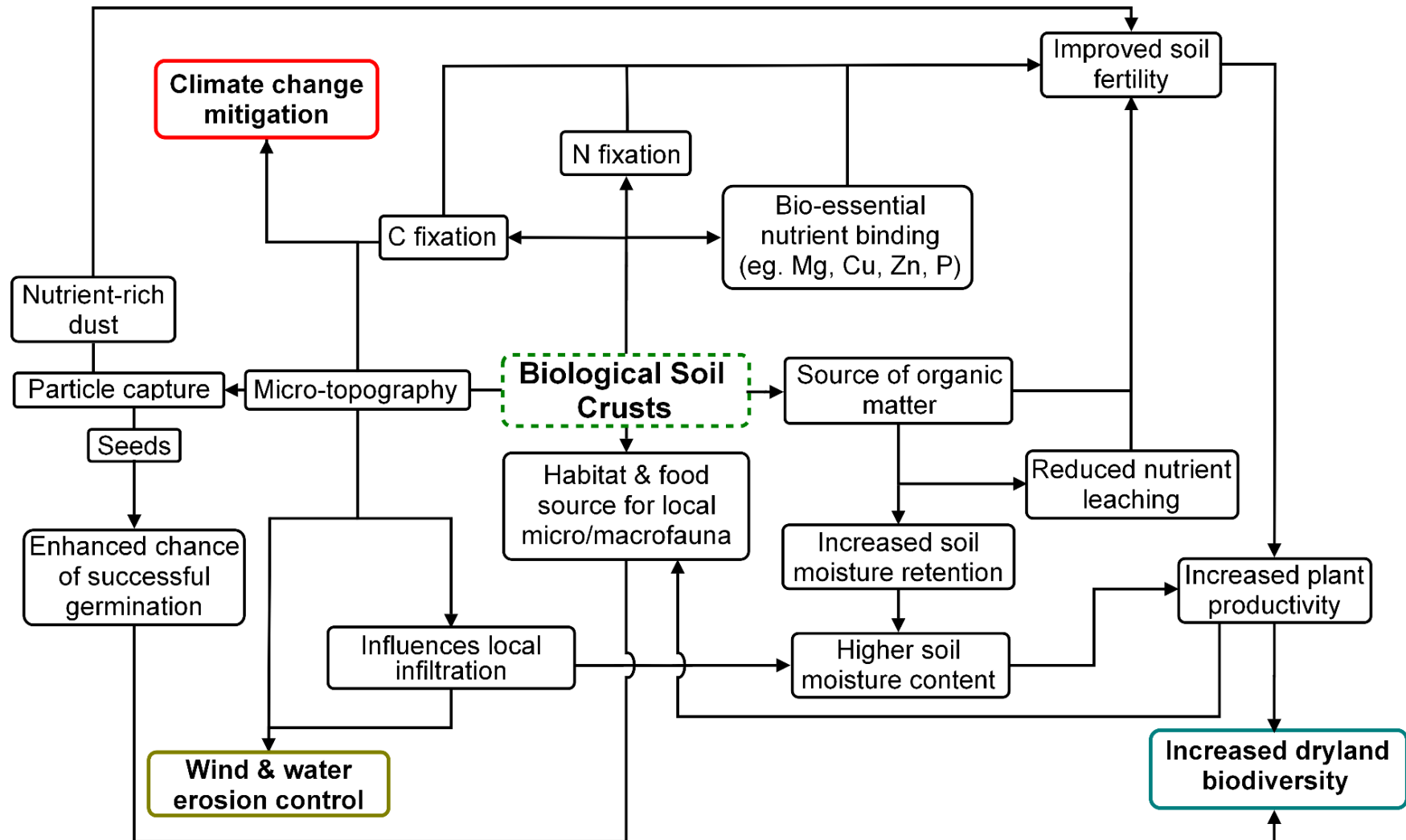
During the last century, changes in temperature and precipitation have impacted ecosystem structure and processes worldwide (Montoya & Raffaelli, 2010). These changes in climate have been attributed to the global migration of >2,000 species by 16.9 km/decade towards the poles (Chen *et al.*, 2011), and threaten one in six species with extinction (Urban, 2015). Fully understanding how biotic communities will respond to changes in temperature and precipitation, is crucial to improving current forecasts of the consequences of climate change (Zhou *et al.*, 2012), particularly in ecosystems where rainfall is already scarce and unpredictable such as drylands (Maestre *et al.*, 2012b; Huang *et al.*, 2016). Drylands cover ~40% of the Earth's surface and are home to over 38% of the human population (Reynolds *et al.*, 2007). However, there remain significant unknowns regarding dryland functioning in the context of future change, including the limited understanding of how biological soil crusts (BSCs) will respond to climate change (Belnap & Weber, 2013; Young *et al.*, 2016), as BSCs have only been a topic of research since the 1960s (eg. Friedmann *et al.*, 1967).

BSCs are the result of a close association between soil particles and cyanobacteria, eukaryotic algae, microfungi, lichens, and bryophytes which live within, or immediately on top of, the uppermost millimetres of the soil surface (Belnap *et al.*, 2003; Figure 1). Due to their poikilohydric nature, BSC organisms are uniquely adapted to limited moisture and low nutrient conditions and respond rapidly to pulsed environmental conditions, characteristic of dryland environments (Lange, 2003). For example, Feng *et al.* (2014) find cyanobacteria, lichen and moss crusts require negligible amounts of moisture to function ( $0.38 \pm 0.17$  mm,  $0.92 \pm 0.06$  mm, and  $2.10 \pm 0.02$  mm, respectively). Consequently, BSCs are the dominant functional vegetation unit in some of the harshest habitats in the world, comprising up to 70% of the living cover in dryland environments (Belnap & Lange, 2003). However, due to a soil pH of  $\geq 7$  and high potential evapotranspiration cyanobacteria, mosses and lichens are the dominant crust organisms in varying amounts (Belnap, 2006; Figure 1).



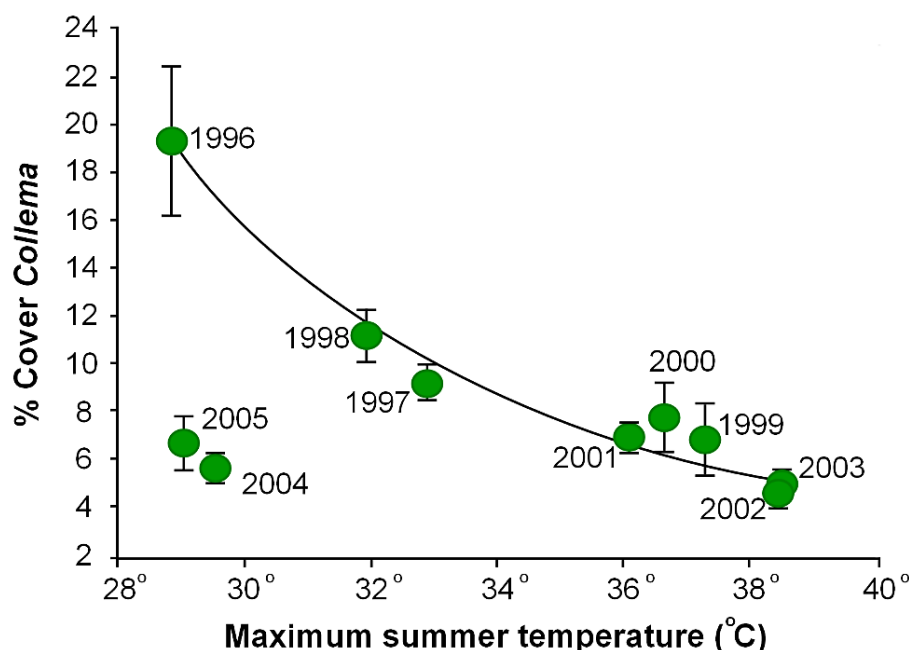
**Figure 1 | A)** Potential evapotranspiration and associated BSC community composition (with corresponding image of crusts on the right). **B)** Conceptual cross-sectional diagram of the four main soil crust types and their distinctive micro-topographies. Created in Serif (v. X6) using data and by adapting graphics in Belnap (2006).

BSCs are widely considered to be important ecosystem engineers, aggregating and stabilising soil surfaces, playing a dominant role in numerous ecosystem functions (Belnap & Lange, 2003; Figure 2). For example, recent reviews by Elbert *et al.* (2009; 2012) suggest annual global BSC net uptake of nitrogen (N) to be 45-49 Tg and 3.6-3.9 Pg for carbon (C), with ~1 Pg of this fixed by BSCs in arid and semi-arid regions. They may also buffer dryland ecosystems against the negative impacts of climate change (Delago-Baquerizo *et al.*, 2016; Figure 2). This is illustrated by Maestre *et al.* (2015) who find the micro-topography of semi-arid BSCs mitigate the warming-induced physiological stress on Gram-negative bacterial communities.



**Figure 2 |** Simplified conceptual model of BSC ecological roles and functions. Created in Serif (X6) using data from Elbert *et al.* (2009; 2012), Belnap (2006a), Harper & Belnap (2001), Williams *et al.* (2012), Hawkes (2004), Eldridge *et al.* (2000), Neher *et al.* (2009), Housman *et al.* (2006). See Belnap (2003) and Viles (2008) for full reviews.

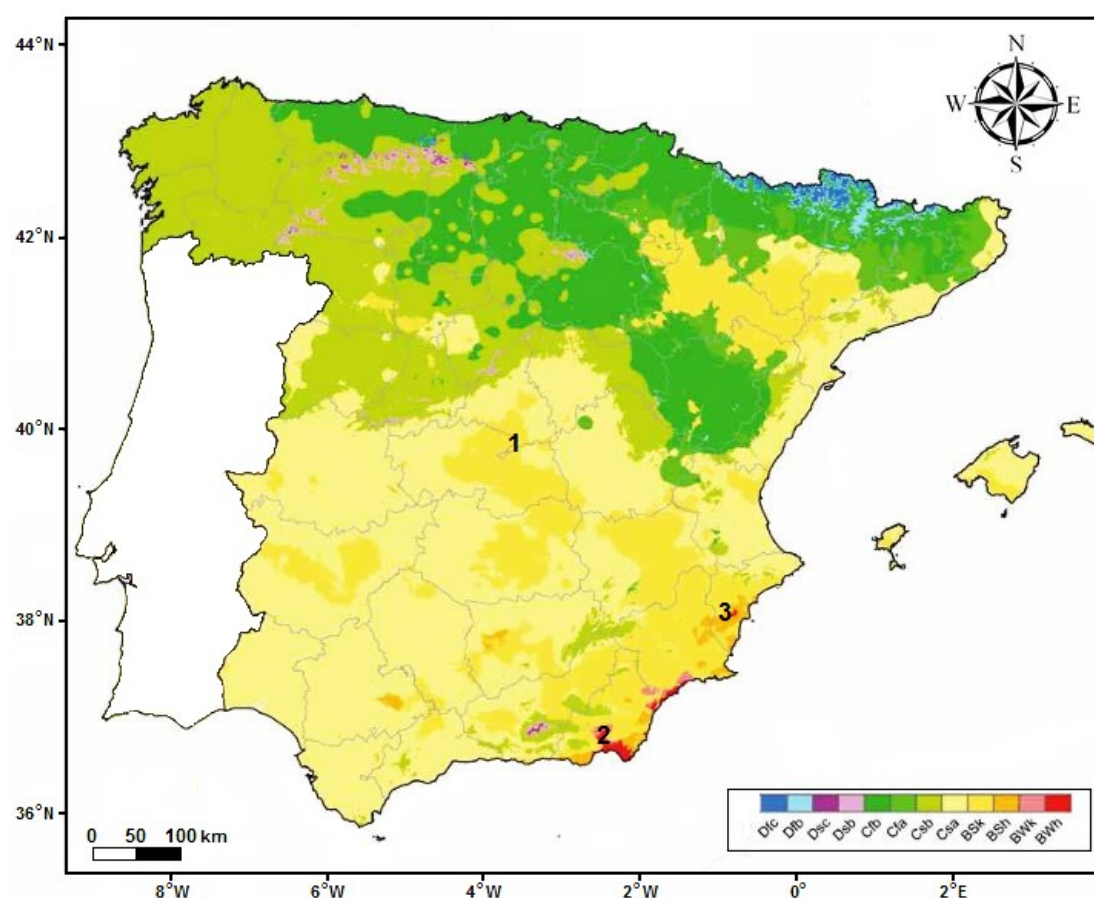
However, like all biota, their reliance on ambient environmental conditions to function also makes BSCs vulnerable to climate change (Maestre *et al.*, 2012a; Dettweiler-Robinson *et al.*, 2013). Climate change is expected to negatively impact soil crust lichens and mosses (Tuba *et al.*, 2011). This has been observed in the Succulent Karoo, Southern Africa, and on the Colorado Plateau, USA where warming and altered precipitation frequencies have negatively impacted the functioning and mortality of moss and lichen dominated BSCs (Zelikova *et al.*, 2012; see Figure 3). Additionally, reductions in BSC cyanobacteria have also been reported with change in precipitation patterns (Johnson *et al.*, 2012). Ferrenberg *et al.* (2015) and Steven *et al.* (2015) find climate change is as detrimental to BSC functioning and survival as chronic physical disturbances either by livestock/human trampling or off-road vehicles. Alterations in BSC community composition, due to environmental change, may considerably impact their ability to provide certain ecosystem services. For example, rougher surfaces trap dust more effectively, provide more habitat for soil invertebrates and increase soil moisture retention in comparison to flatter, cyanobacteria dominated crusts (Belnap, 2006; Viles, 2008; Figure 1).



**Figure 3 |** Decline of *Collema* lichen cover with increasing average maximum temperature of the previous June in the Canyonlands National Park, SE Utah ( $r^2 = 0.97$ ). Created using data from Belnap *et al.* (n.d) and Belnap *et al.* (2006b).

Increased temperature, and reductions in precipitation, have been observed across Spain since the 1960s (Gosling *et al.*, 2011). Furthermore, there is a high confidence that the drylands of the Iberian Peninsula are likely (>66% probability) to be severely

impacted by climate change (Field *et al.*, 2012; Kovats *et al.*, 2014). Despite this, few studies have elucidated the effects of changing ambient temperature and moisture on the BSCs of dryland Spain (see Maestre *et al.*, 2011; Figure 4), especially compared to the USA and Australia (Belnap & Weber, 2013). This has led to a limited understanding of their potential responses to climate change. This essay aims to: (i) outline the role temperature and moisture availability play in BSC growth; (ii) summarise the projected future climate change scenarios for Spain (up to 2100); and (iii) draw together this information to discuss the potential impacts these changes may have on Spanish dryland BSC growth and diversity.



**Figure 4** | Climate of Spain according to temperature and precipitation data from 1971-2000, using the Köppen-Geiger Climate Classification, ie. wetter continental climates (Group D: blue-dark green) to Mediterranean and to arid climates (Group B: light green-red). Adapted from AEMET (2011). Numbers denote general study areas on the interactions between climate and dryland BSCs (eg. Escolar *et al.*, 2012 = 1; de Guevara *et al.*, 2014 = 2; Maestre *et al.*, 2015 = 3).

### BSCs, Temperature & Moisture

Biological activity in deserts is primarily determined by the amount and availability of moisture (Noy-Meir, 1973). Similarly, low and unpredictable precipitation means desert BSCs are predominantly dry and inactive (Lange *et al.*, 1994). However, BSCs

do have an optimal level of hydration. High volumes of moisture increases diffusional resistance, decreasing CO<sub>2</sub> availability, whereas too little water inhibits basic cellular functioning (Grote *et al.*, 2010). Lange *et al.* (1997; 1998) observed that BSCs can obtain this moisture either directly from liquid water (eg. cyanobionts associated with lichens such as *Collema tenax*) or through dew and/or fog inputs (eg. phycobionts, associated with green algal lichens such as *Psora cerebriformis*).

Following adequate hydration, temperature plays a dominant role in the regulation of CO<sub>2</sub> exchange in BSCs. It is well known that photosynthesis is sensitive to inhibition by moderate heat stress (Berry & Björkman, 1980). Whilst photosynthesis has been observed in BSCs between 0-50°C, optimum temperatures for photosynthesis range from 10-28°C (Lange, 2003). This is largely attributed to alterations to key components of the Calvin cycle. As temperatures increases, the primary carboxylating enzyme Ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCo), increases affinity for O<sub>2</sub> and the activase aggregates and can no longer activate RuBisCo, thereby reducing carboxylation efficiency (Crafts-Brandner & Salvucci, 2000; Parry *et al.*, 2008).

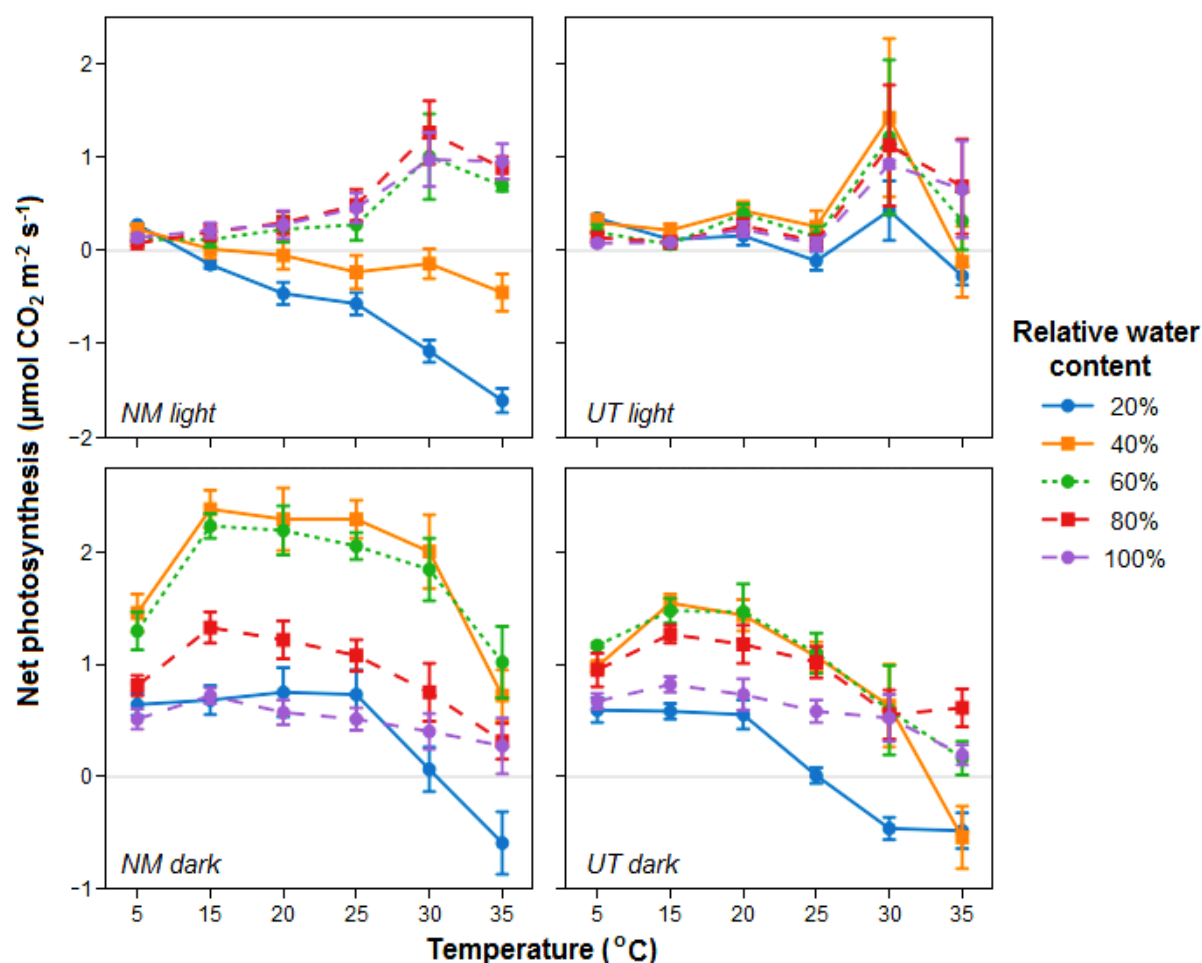
BSCs immediately lose some CO<sub>2</sub> after wetting through non-metabolic pathways (Farrar & Smith, 1976), such as osmotic shock and cell membrane leakage (Kieft *et al.*, 1987; Oliver *et al.*, 2000), followed by 'resaturation respiration' (Smith & Molesworth, 1973). This respiration is hypothesised to be associated with an increased energy demand to repair damages associated with desiccation. In general, desiccation events damage lipids, nucleic acids and proteins, attributed to excessive oxidative stress from the release of reactive oxygen species (ROS), such as hydroxyl radical and singlet oxygen, exacerbated by periods of intense light and UV irradiation (Holzinger & Karsten, 2013). For example, field experiments on the Colorado Plateau by Belnap *et al.* (2008) shows prolonged exposure to UV radiation leads to reductions in BSC quantum yield, chlorophyll *a*, UV-protective pigments, nitrogenase activity and exopolysaccharides.

Energy demand also increases as BSCs undertake in desiccation tolerance strategies which may include: (i) synthesising scytonemin, mycosporine-like amino acid, and carotenoid-xanthophyll UV-protective pigments to prevent ROS damage (Belnap *et al.*, 2008), (ii) the accumulation of compatible solutes including amino acids, various betaines and trehalose for osmoprotection (Kempf & Bremer, 1998), and (iii) in some

BSC organisms the production of exopolysaccharides that slow the speed of water loss (eg. observed in cyanobacteria by Rajeev *et al.*, 2013).

To reach net C gain, and therefore ensure long-term survival, growth and functioning, BSCs must remain hydrated long enough to overcome this initial C loss, repair and increase their resilience to next desiccation event (Belnap *et al.*, 2004). Consequently, Büdel *et al.* (2009) and Coe *et al.* (2012) suggest that rain frequency and the subsequent length of hydration period, largely determines BSC carbon balances and consequently survival, development and composition. This has been illustrated by Li *et al.* (2014) on *Bryum argenteum* from the Tengger Desert, China, where a lower desiccation time (one week in comparison to a year) increased the effective quantum yield of photosystem II (PSII) following rehydration, with one year treatments requiring a rehydration time >5 times longer to recover. Beyond enzymatic reactions, higher temperatures also influence rates of evapotranspiration and the overall hydration period (Grote *et al.*, 2010). For example, in BSC *Nostoc flagelliforme* assemblages, Zhao *et al.* (2008) observe that variations in the rate of photosynthetic recovery following desiccation are caused by different water absorption rates at higher temperatures.

Thus whilst higher temperatures may lead to an increase in photosynthetic activity, ultimately the duration of active photosynthesis will be significantly reduced because of more rapid rates of desiccation (Lange *et al.*, 2006). Observed in the field by Zedda *et al.* (2010; 2011) who find the richness and spatial coverage of lichen BSCs, across the BIOTA transect in Southern Africa, are positively correlated to lower temperatures and increased water availability. Studies by Feng *et al.* (2014) and Grote *et al.* (2010; Figure 5) find the optimum temperature and moisture content for maximum metabolic activity length and efficiency. These optimal environmental conditions are between 20 and 30°C for cyanobacteria dominated crusts and 15°C to 20°C in lichens and mosses, at an intermediate relative water content (40-60%).

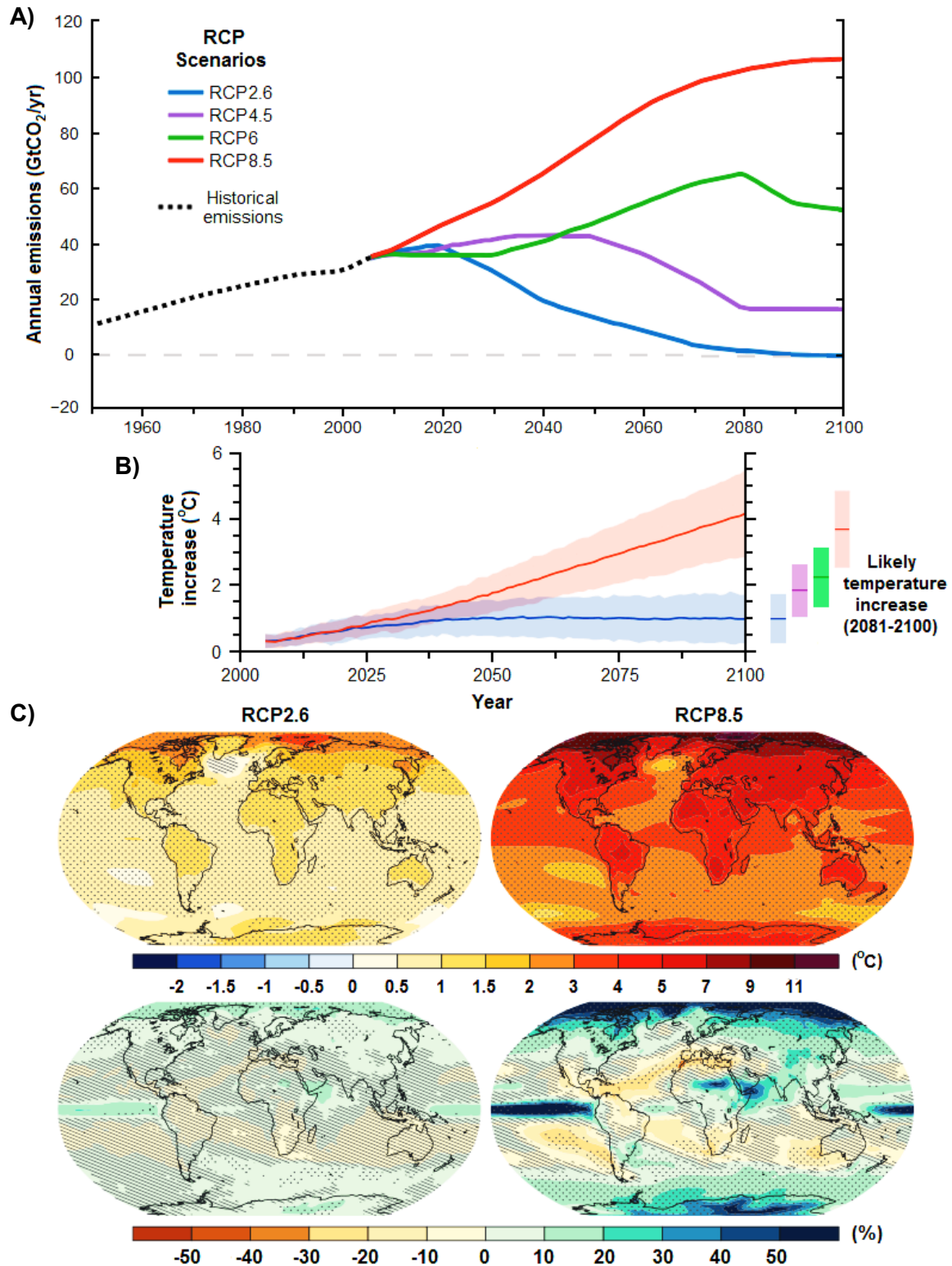


**Figure 5 |** Net photosynthetic rates ( $\pm$  standard error), as a function of temperature and percentage soil water content of light (early successional crust: cyanobacteria dominant) and dark (later successional crust: cyanobacteria/lichen and moss dominant) BSCs on the Colorado Plateau, Utah (UT) and at the Jornada Experimental Range, in the Chihuahuan Desert, New Mexico (NM), USA. Created in Plotly (v. 2.0) using data in Grote *et al.* (2010).

### Projected Climate Change Scenarios for Spain & Potential Impacts on BSCs

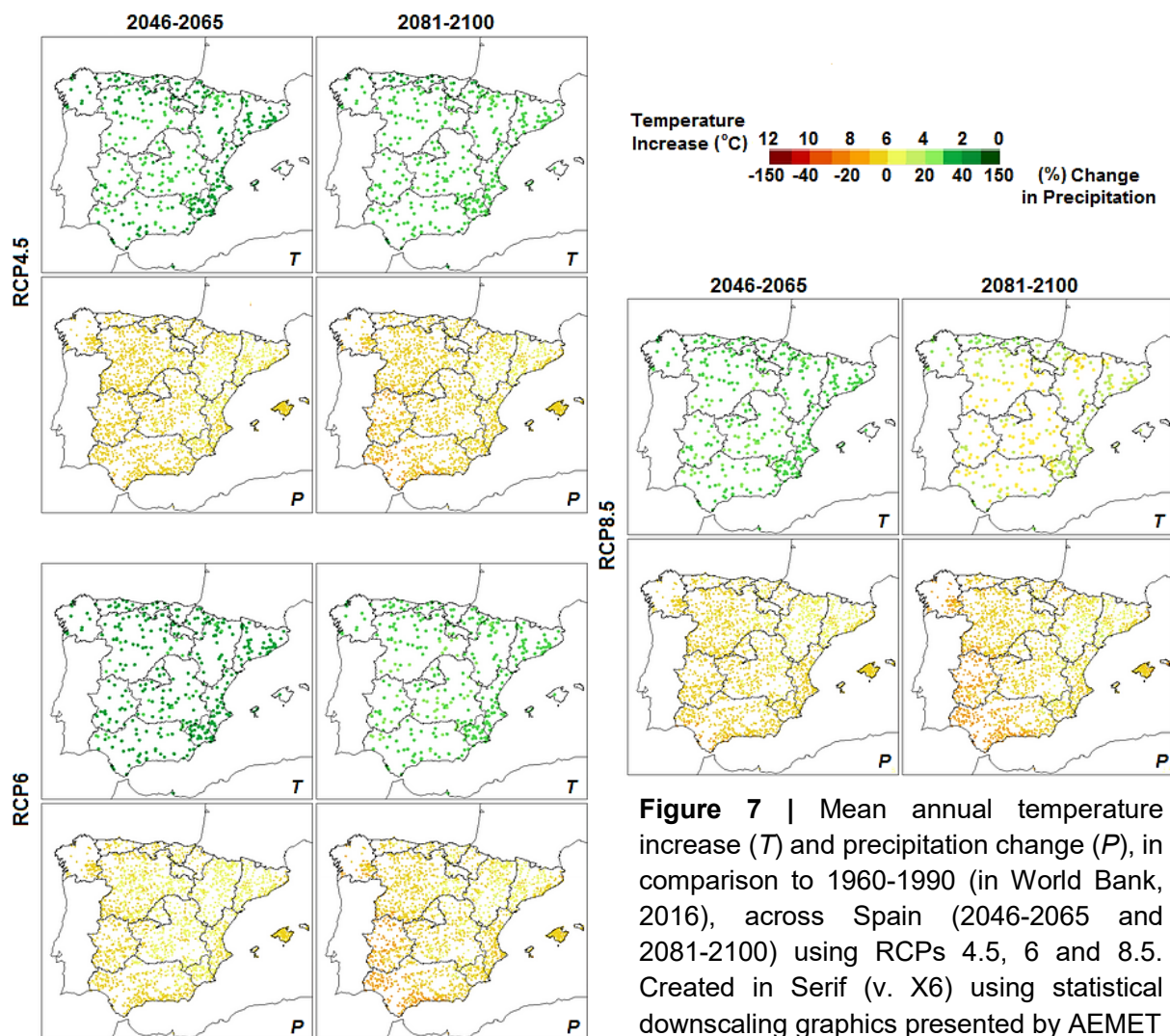
Currently, Spain is largely arid with an annual average precipitation of 200-500 mm across mid and south-eastern Spain between 1971 and 2000 (AEMET, 2011), with days exceeding 40°C most summers in southern Spain (de Castro *et al.*, 2005; AEMET, 2014). Representative concentration pathways (RCPs) have replaced the SRES emission scenarios of previous IPCC reports: the low (RCP2.6; van Vuuren *et al.*, 2011), medium-low (RCP4.5; Thomson *et al.*, 2011), medium-high (RCP6; Masui *et al.*, 2011), and high (RCP8.5; Riahi *et al.*, 2011) pathways are plausible trajectories of global greenhouse gas emissions based on potential ecological, physical and socioeconomic developments (see Moss *et al.*, 2010; Meinhausen *et al.*, 2011; Figure 6).





**Figure 6 | A)** Historical (1950-2005) and annual greenhouse gas emissions from RCPs (2005-2100). **B)** Global average surface temperature change between 2006-2100 (relative to 1986-2005) and *likely* (>66% probability) temperature increase range between 2081-2100. **C)** Global surface temperature rise and precipitation change projections (in 2081-2100 compared to 1986-2005) using the RCP 2.6 and RCP 8.5 pathways under 32 and 39 models, respectively (many these of these models and for RCPs 4.5 and 6 are available on the WorldClim (v 1.4) database). Created in Plotly (v. 2.0) and Serif PagePlus (v. X6) using data from van Vuuren *et al.* (2011), Thomson *et al.* (2011), Masui *et al.* (2011) and Stocker *et al.* (2013).

These RCPs have been utilised by the Agencia Estatal de Meteorología (AEMET) to model potential climate change scenarios across Spain (Figure 7). They find similar trends to the IPCC (C in Figure 6) and the downscaled EURO-CORDEX model for Europe (Jacob *et al.*, 2014): annual average surface temperature may rise by up to 7°C and precipitation may reduce by >30% in south-eastern Spain by 2081-2100 under RCP8.5, with increases in temperature of ~2-3°C and reductions in annual precipitation of 10% for all RCPs by 2065. However, AEMET do not include RCP2.6 in their projections as they consider that pathway to be “absolutely unrealistic” (AEMET, 2016, pers. comm., 23 March), by projecting comparatively negligible changes to present-day climatic conditions, with a ~0.5°C rise by 2081-2100 over the Mediterranean, as a result of radical, rapid mitigation activities to reduce greenhouse gas emissions by 50% over the next twenty years to stabilise present-day climatic conditions (van Vuuren *et al.*, 2011).







**Figure 7 |** Mean annual temperature increase (T) and precipitation change (P), in comparison to 1960-1990 (in World Bank, 2016), across Spain (2046-2065 and 2081-2100) using RCPs 4.5, 6 and 8.5. Created in Serif (v. X6) using statistical downscaling graphics presented by AEMET

(2016a). Each point represents observation areas included in AEMET's models.

Spanish BSCs will undoubtedly respond differently to the varied temperature and precipitation regimes of each RCP, with increased uncertainty in the possible range of each RCP (Table 1). This uncertainty is illustrated by studies on the Colorado Plateau, which suggest lichens and mosses can generally adapt to solely increased temperatures over a number of years (Zelikova *et al.*, 2012; Reed *et al.*, 2012). Johnson *et al.* (2012) suggest a 2°C rise, similar to those at RCP4.5 and 6 by 2065, may be insufficient to prompt a significant response from BSCs. In contrast, Escolar *et al.* (2012) find a 2.4°C increase reduced lichen coverage by 40-70% in the dryland BSCs of Aranjuez, Central Spain, with mosses displaying a slight increase (0.3-7%). This observation has recently been supported by Escolar *et al.* (2015) who find a 2-3°C warming increased soil respiration at Aranjuez, and Maestre *et al.* (2015) who report a 2°C rise over 53 months reduced BSC cover by 45% in Sax, SE Spain. The temperature increase associated with RCP8.5 over a long period exceeds thresholds for optimum photosynthetic activity (Lange, 2003; Figure 5), and will undoubtedly contribute to considerable reductions in BSC growth and diversity (Table 1).

**Table 1** | Summarised likely trends in Spanish BSC productivity and cover. Based on reported moisture and temperature thresholds, and the extent of projected climatic changes in temperature and precipitation, influencing activity and desiccation period frequency and length under each RCP (Figure 7; Figure 8; Table 2). Created in Serif (v. X6).

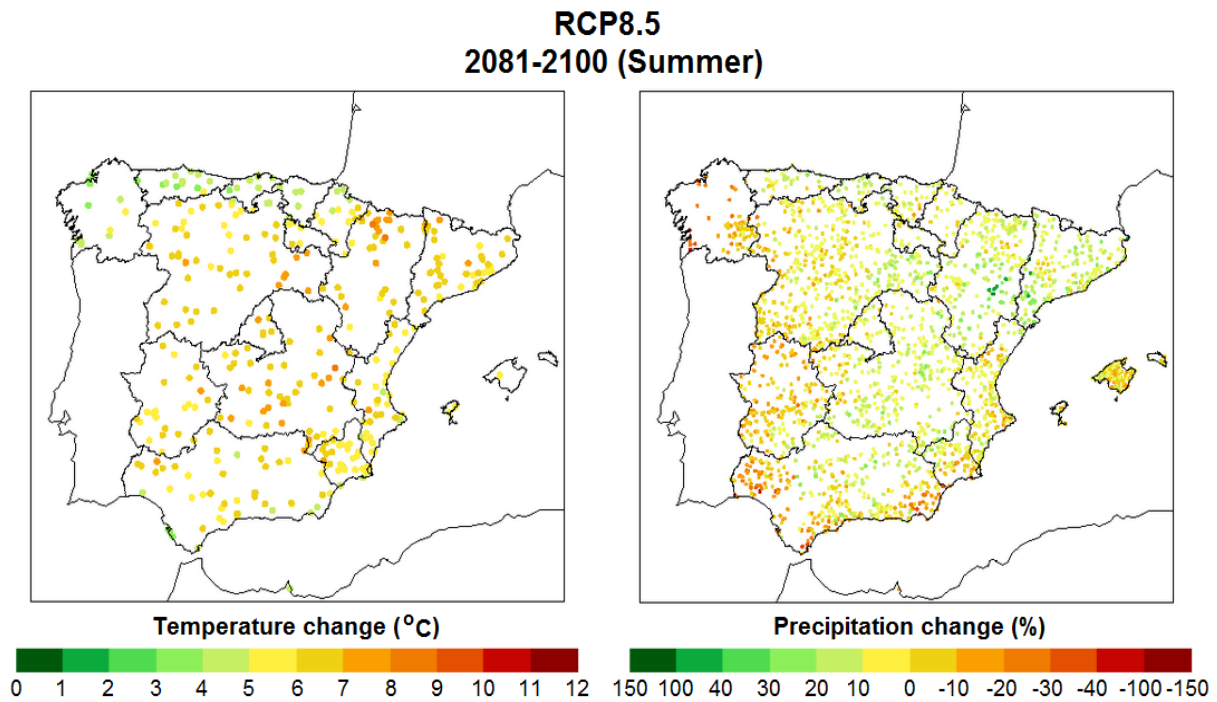
RCP	Lichens		Mosses		Cyanobacteria	
	2046-2065	2081-2100	2046-2065	2081-2100	2046-2065	2081-2100
2.6	—	—	—	—	—	—
4.5	↓	↓	—/↓	↓	↑	↑
6	↓	↓/↓	—/↓	↓/↓	↑	—/↓
8.5	↓	↓	↓	↓	↓/↓	↓/↓
<div>  Small increase            Small (hollow) and large (solid) decrease            Negligible change            Uncertainty in future trend, either outcome is possible         </div>						

Projected reductions in annual precipitation (Figure 7) will also negatively impact BSC growth and diversity. This is largely in response to prolonged unfavourable environmental conditions for metabolic activity (Figure 5) instigating continued negative C balances, and reducing the capacity to produce or repair chlorophyll a

and/or protective pigments (Belnap *et al.*, 2004). Indeed, a combined 2-3°C experimental warming and rainfall exclusion conducted by Maestre *et al.* (2013), in Sorbas, SE Spain and Aranjuez, finds a reduction in photosynthetic activity (~3.5 times lower) and in lichen and moss cover of >40% over 4 years. Seasonal temperatures and precipitation regimes (Table 2), as opposed to annual trends, under each RCP further elucidates the primary stresses and potential drivers of mortality in Spanish BSCs.

**Table 2 |** Mean changes in seasonal surface temperature and precipitation across the dryland regions of Spain in Figure 4, compared to average historical (1960-1990) environmental conditions presented in World Bank (2016). Temperature results are an average of the individual points of data presented in each seasonal graph by AEMET (2016a), with precipitation estimated as a range of the most common points in AEMET (2016a). Each season is defined as: Spring (March-May), Summer (June-August), Autumn (September-November) and Winter (December-February). See Figure 8 for an example of these seasonal graphs by AEMET (2016a).

Season		Temperature (°C)		Precipitation (mm)	
Historical	Spring	11.8		53.5	
	Summer	20.9		23.3	
	Autumn	14.7		58.5	
	Winter	7.1		66.4	
RCP		Temperature increase (°C)		Precipitation change (%)	
		2046-2065	2081-2100	2046-2065	2081-2100
4.5	Spring	1.92	2.77	-10 – +10	-10 – +10
	Summer	2.98	3.67	-10 – +10	-10 – +10
	Autumn	2.68	3.22	-20 – 0	-20 – 0
	Winter	2.00	2.58	-10 – 0	-10 – 0
6	Spring	2.01	2.97	-10 – 0	-20 – 0
	Summer	3.89	4.49	-10 – +10	-20 – -10
	Autumn	2.50	3.31	-10 – 0	-20 – 0
	Winter	1.89	2.36	0 – +10	-20 – 0
8.5	Spring	4.11	4.84	-10 – -20	-20 – 0
	Summer	4.07	6.61	-30 – +20	-40 – +30
	Autumn	3.78	6.05	-20 – 0	-40 – 0
	Winter	4.10	4.52	-10 – 0	-10 – -20



**Figure 8 |** Projected trends in summer temperature and precipitation under RCP8.5, used to calculate average seasonal temperature statistics and estimate seasonal rainfall change in Table 1. Created in Serif (v. X6) with graphics from AEMET (2016b) and AEMET (2016c).

Belnap *et al.* (2007) find scytonemin and canthoxanthin concentrations did not increase without 119 mm of precipitation over 6 months, with high concentrations of echinenone and  $\beta$ -carotene only maintained >98 mm, in BSCs of the Mojave Desert. Based on this data, Spanish BSC recovery periods will be seasonally restricted under some RCPs, or even for most/all of the year under climate change associated with higher CO<sub>2</sub> concentrations (Table 2). Furthermore, seasonal temperature increases may exacerbate this issue, by increasing evapotranspiration rates, resulting in wasted BSC activations. For example, Johnson *et al.* (2012) find a 2-3°C warming and an increased frequency of small (1.2 mm) rainfall events reduced BSC biomass (on average 78% less chlorophyll *a*) in Moab, Utah, as this water had evaporated within the ~30 minutes it took for the BSCs to become metabolically active. This is likely to occur in the summer under each RCP (Table 2), and even during the other seasons under some RCPs, exacerbating the reductions in precipitation (eg. RCP8.5; Table 2).

Nocturnal moistening by fog or dewfall heavily influences the photosynthetic activity and distribution patterns of lichen BSCs in Mediterranean drylands such as the Negev, Israel (Veste *et al.*, 2001), with some evidence of dew playing an important role in PSII activity in cyanobacterial crusts in the Hopq Desert, China (Rao *et al.*, 2009). Dewfall contributes greatly to the local moisture budget in SE Spain, although only  $0.17 \pm 0.10$



mm/night between 2007 and 2010, this represented a 94% contribution to the local water balance during dry periods, despite being shorter in comparison to winter and autumn dewfalls (Uclés *et al.*, 2014). The distribution and growth of *Teloschistes lacunosus* (del Prado & Sancho, 2007), in SE Spain are highly dependent on dewfalls, with *Diploschistes diacapsis* only active during these periods of prolonged dewfall (Pintado *et al.*, 2010). Similar results have been observed by Maestre *et al.* (2013) and de Guevara *et al.* (2014) in Central and SE Spain, where net CO<sub>2</sub> uptake in BSCs occurred predominantly during late autumn and winter, during these periods of increased moisture availability. Wilske *et al.* (2008) highlight that dew may also be important in initiating a 'pre-activated' state in BSCs during the transition from a long summer anabiosis towards the first rains later in the year. Maestre *et al.* (2013) find a 2-3°C warming substantially reduces the duration of suitable conditions for the formation and residence time of dewfall in Spain. Therefore increased temperatures will undoubtedly exacerbate the C deficit of Spanish BSCs by further reducing moisture availability, contributing to increased stress and mortality in BSC organisms (Table 1). For example, in South Africa, Maphangwa *et al.* (2012) find significant reductions in the quantum yield of BSC-forming lichens (up to 46%) with a 2.1-3.8°C warming and a 30.1-31.9% reduction in dew and fog inputs.

Overall, the decrease in length and frequency of recovery periods, associated with higher temperatures and reduced moisture availability, will likely lead to a reduction in BSC lichens and mosses. The most extreme environmental conditions may even instigate high stress or mortality in cyanobacteria, and thus a complete lack of BSC cover, under some RCPs (Table 1). For example, mosses may be more adaptable, compared to lichens, to the reduced precipitation and increases in temperature (Bjerke *et al.*, 2011). Therefore, climate change under RCP4.5 and RCP6 by 2065, may either negatively impact their growth, or their adaptability may be able to negate these unfavourable conditions, as previously highlighted by Escolar *et al.* (2012). However, this is unlikely to continue long-term (by 2100), as environmental conditions deteriorate (Table 1). Similarly, cyanobacteria can tolerate more extreme environmental conditions (Figure 5), especially as species such as *Microcoleus* use their filamentous sheaths to glide to the soil surface upon wetting, avoiding UV radiation and temperature damage during desiccation periods (Mazor *et al.*, 1996). Zelikova *et al.* (2012) find cyanobacteria dominate BSC assemblages as lichen and moss cover

reduces, leading to potential increases in cyanobacterial crusts under lower RCPs (Table 1). These unique coping mechanisms may also negate the impacts of climate change under RCP6 by 2100. However, under RCP8.5 these coping mechanisms may only mitigate the impacts of climate change, as even the optimum environmental thresholds for cyanobacteria are exceeded (Figure 5). This may lead to a complete lack of BSC cover, with widespread mortality amongst all BSC organisms (Table 1).

Additionally, the increased CO<sub>2</sub> concentrations driving these changes exacerbates the uncertainties involved in these estimations. Early experimental work by Tuba *et al.* (1998) on lichens and mosses, and more recently by Lane *et al.* (2013) on cyanobacteria, find increased ambient CO<sub>2</sub> concentrations may result in enhanced growth and functioning. However, in contrast, Wertin *et al.* (2012) find this is primarily mediated by ambient moisture availability, with a 10 year PCR survey of cyanobacteria small-subunit rRNA genes, by Steven *et al.* (2012), suggesting increased CO<sub>2</sub> may reduce cyanobacterial abundance and diversity.

## Conclusions

Despite some uncertainties in projected climate change scenarios and the potential impacts of these changes, it is clear that continued unprecedented greenhouse gas emissions, and associated changes in temperature and moisture availability, will drastically impact BSC growth and diversity (Table 1). Reductions in BSC assemblage diversity, and the length and duration of their metabolically active periods, will also impact local ecosystem processes. Either through alterations in BSC microtopography with cyanobacterial crusts dominating (Figure 1), to a complete lack of ecosystem services should BSC cover reduce to negligible amounts, or disappear entirely, which is a possibility under RCP8.5. Further research is essential across Spain, and globally, to fully elucidate the response of dryland BSCs, and their surrounding ecosystem, to projected changes in change.

## References

AEMET. (2011) 'Iberian Climate Atlas' [Report]. Madrid: Catálogo General de Publicaciones Oficiales.

AEMET. (2014) 'Resumen Annual Climatológico' [Report]. Madrid: Ministerio de Agricultura, Alimentación y Medio Ambiente.

AEMET. (2016a) Regionalización AR5-IPCC. Gráficos. Mapas de proyecciones [Online]. Available at: [http://www.aemet.es/en/serviciosclimaticos/cambio\\_climat/result\\_graficos?opc4=1&opc6=0](http://www.aemet.es/en/serviciosclimaticos/cambio_climat/result_graficos?opc4=1&opc6=0). Access Date: 21/03/2016.

AEMET. (2016b) Precipitación: Summer. Scenario of emissions (A1B) RCP 8.5 [Online]. Available at: [http://www.aemet.es/en/serviciosclimaticos/cambio\\_climat/result\\_graficos?opc4=1&w=0&opc1=Espan&opc2=P&opc3=Verano&opc5=rcp85&opc6=0&img=1](http://www.aemet.es/en/serviciosclimaticos/cambio_climat/result_graficos?opc4=1&w=0&opc1=Espan&opc2=P&opc3=Verano&opc5=rcp85&opc6=0&img=1). Access Date: 21/03/2016.

AEMET. (2016c) Temperatura máxima: Summer. Scenario of emissions (A1B) RCP 8.5 [Online]. Available at: [http://www.aemet.es/en/serviciosclimaticos/cambio\\_climat/result\\_graficos?opc=1&w=0&opc1=Espan&opc2=Tx&opc3=Verano&opc5=rcp85&opc6=0&img=1](http://www.aemet.es/en/serviciosclimaticos/cambio_climat/result_graficos?opc=1&w=0&opc1=Espan&opc2=Tx&opc3=Verano&opc5=rcp85&opc6=0&img=1). Access Date: 21/03/2016.

Belnap, J. (2003) The world at your feet: Desert biological soil crusts. *Frontiers in Ecology and the Environment*, **1** (4): 181-189.

Belnap, J. (2006) The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrological Processes*, **20** (5): 3159-3178.

Belnap, J., Phillips, S., Flint, S., Money, J. & Caldwell, M. (2008) Global change and biological soil crusts: effects of ultraviolet augmentation under altered precipitation regimes and nitrogen additions. *Global Change Biology*, **14** (3): 670-686.

Belnap, J., Phillips, S. & Smith, S. (2004) Response of desert biological soil crusts to alterations in precipitation frequency. *Oecologia*, **141**: 306-316.

Belnap, J., Phillips, S. & Smith, S. (2007) Dynamics of cover, UV-protective pigments, and quantum yield in biological soil crust communities of an undisturbed Mojave Desert shrubland. *Flora*, **202** (8): 674-686.

Belnap, J., Phillips, S., Troxler, T. & USGS. (2006b) Soil lichen and moss cover and species richness can be highly dynamic: The effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. *Applied Soil Ecology*, **32** (1): 63-76.

Belnap, J., Kuske, C. & Neher, D. (n.d) Climatic change in arid lands: effects on soil biota and ecosystem processes [Online]. Available at: <http://per.ornl.gov/Belnap.html>. Access date: 20/03/2016.

Belnap, J. & Lange, O. (2003) Biological soil crusts: Structure, function, and management. Berlin: Springer-Verlag.



- Belnap, J. & Weber, B. (2013) Biological soil crusts as an integral component of desert environments. *Ecological Processes*, **2**: 11.
- Berry, J. & Björkman, O. (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, **31**: 491-543.
- Bjerke J., Bokhorst S., Zielke M., Callaghan T., Bowles F. & Phoenix G. (2011) Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. *Journal of Ecology*, **99**: 1481-1488.
- Büdel, B., Darienko, T., Deutschweitz, K., Dojani, S., Friedl, T., Mohr, K., Salisch, M., Reisser, W. & Weber, B. (2009) Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. *Microbial Ecology*, **57** (2): 229-247.
- Chen, I-C., Hill, J., Ohlemuller, R., Roy, D. & Thomas, C. (2011) Rapid Range Shifts of Species Associated with High Levels of Climate Warming. *Science*, **333** (6045): 1024-1026.
- Coe, K., Belnap, J. & Sparks, J. (2012) Precipitation-driven carbon balance controls survivorship of desert biocrust mosses. *Ecology*, **93** (7): 1626-1636.
- Crafts-Brandner, S. & Salvucci, M. (2000) Rubisco activase constrains the photosynthetic potential of leaves at high temperature and CO<sub>2</sub>. *PNAS*, **97** (24): 13430-13435.
- de Castro, M., Martin-Vide, J. & Alonso, S. (2005) 'The climate of Spain: Past, present and scenarios for the 21<sup>st</sup> Century' [Report]. Madrid: Ministerio de Medio Ambiente.
- de Guevara, M., Lazaro, R., Quero, J., Ochoa, V., Gozalo, B., Berdugo, M., Ucles, O., Escolar, C. & Maestre, F. (2014) Simulated climate change reduced the capacity of lichen-dominated biocrusts to act as carbon sinks in two semi-arid Mediterranean ecosystems. *Biodiversity and Conservation*, **23** (7): 1787-1807.
- Delago-Baquerizo, M., Maestre, F., Eldridge, D., Bowker, M., Ochoa, V., Gozalo, B., Berdugo, M., Val, J. & Singh, B. (2016) Biocrust-forming mosses mitigate the negative impacts of increasing aridity on ecosystem multifunctionality in drylands. *New Phytologist*, **209** (4): 1540-1552.
- del Prado, R. & Sancho, L. (2007) Dew as a key factor for the distribution pattern of the lichen species *Teloschistes lacunosus* in the Tabernas Desert (Spain) *Flora*. 2007;202:417–428
- Dettweiler-Robinson, E., Ponzetti, J. & Bakker, J. (2013) Long-term changes in biological soil crust cover and composition. *Ecological Processes*, **2**: 5.
- Elbert, W., Weber, B., Büdel, B., Andreae, M. & Pöschl, U. (2009) Microbiotic crusts on soil, rock and plants: neglected major players in the global cycles of carbon and nitrogen?. *Biogeosciences Discussions*, **6**: 6983-7015.
- Elbert, W., Weber, B., Burrows, S., Steinkamp, J., Büdel, B., Andrae, B., Meinrat, O. & Pöschl, U. (2012). Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nature Geoscience*, **5**: 459-462.
- Escolar, C., Maestre, F. & Rey, A. (2015) Biocrusts modulate warming and rainfall exclusion effects on soil respiration in a semi-arid grassland. *Soil Biology & Biochemistry*, **80**: 9-17.

Escobar, C., Martinez, I., Bowker, M. & Maestre, F. (2012) Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: implications for ecosystem structure and functioning. *Philosophical Transactions B*, **367** (1606): 3087-3099.

Farrar, J. & Smith, D. (1976) Ecological physiology of the lichen *Hypogymnia physodes*. *New Phytologist*, **77** (1): 115-125.

Feng, W., Zhang, Y., Wu, B., Qin, S. & Lai, Z. (2014) Influence of Environmental Factors on Carbon Dioxide Exchange in Biological Soil Crusts in Desert Areas. *Arid Land Research and Management*, **28** (2): 186-196.

Ferrenberg, S., Reed, S. & Belnap, J. (2015) Climate change and physical disturbance cause similar community shifts in biological soil crusts. *PNAS*, **112** (39): 12116-12121.

Field, C., Barros, V., Stocker, T., Dahe, Q., Dokken, D., Ebi, K., Mastrandrea, M., Mach, K., Plattner, G-K., Allen, S., Tignor, M. & Midgley, P. (2012) 'Managing the risks of extreme events and disasters to advance climate change adaptation' [Report]. Cambridge: Cambridge University Press.

Friedmann, I., Lipkin, Y. & Ocampo-Paus, R. (1967) Desert algae of the Negev (Israel). *Phycologia*, **6** (4):185-195.

Gosling, S., Dunn, R., Carrol, F., Christidis, N., Fullwood, J., de Gusmao, D., Golding, N., Good, L., Hall, T., Kendon, L., Kennedy, J., Lewis, K., McCarthy, R., McSweeney, C., Morice, C., Parker, D., Perry, M., Stott, P., Willett, K., Allen, M., Arnell, N., Bernie, D., Betts, R., Bowerman, N., Brak, B., Caesar, J., Challinor, A., Dankers, R., Hewer, F., Huntingford, C., Jenkins, A., Klingman, N., Lewis, K., Lloyd-Hughes, B., Lowe, J., McCarthy, R., Miller, J., Nicholls, R., Noguer, M., Otto, F., van der Linden, P. & Warren, R. (2011) 'Climate: Observations, projections and impacts: Spain' [Report]. Met Office: Exeter.

Grote, E., Belnap, J., Housman, D. & Sparks, J. (2010) Carbon exchange in biological soil crust communities under differential temperatures and soil water contents: implications for global change. *Global Change Biology*, **16**: 2763-2774.

Harper, K. & Belnap, J. (2001) The influence of biological soil crusts on mineral uptake by associated vascular plants. *Journal of Arid Environments*, **47** (3): 347-357.

Hawkes, C. (2004) Effects of biological soil crusts on seed germination of four endangered herbs in a xeric Florida shrubland during drought. *Plant Ecology*, **170** (1): 121-134.

Holzinger, A. & Karsten, U. (2013) Desiccation stress and tolerance in green algae: consequences for ultrastructure, physiological, and molecular mechanisms. *Frontiers in Plant Science*, **4** (327): doi: 10.3389/fpls.2013.00327.

Housman, D., Powers, H., Collins, A. & Belnap, J. (2006) Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. *Journal of Arid Environments*, **66** (4): 620-634.

Huang, J., Yu, H., Guan, X., Wang, G. & Guo, R. (2016) Accelerated dryland expansion under climate change. *Nature Climate Change*, **6**: 166-171.

Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O., Bouwer, L., Braun, A., Colette, A., Deque, M., Georgievski, G., Georgeopoulou, E., Gobiet, A., Menut, L., Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., Kroner, N., Kotlarski, S., Kriegsmann, A., Martin, E., van Meijgaard, E., Moseley, C., Pfeifer, S., Preuschmann, S., Somot, S., Soussana, J-F., Teichmann, C., Valentini, R., Vautard, R., Weber, B. & Yiou, P. (2014) EURO-CORDEX: new high-resolution climate change projections for European impact research. *Regional Environmental Change*, **14** (2): 563-578.

Johnson, S., Kuske, C., Carney, T., Housman, D., Gallegos-Garves, L. & Belnap, J. (2012) Increased temperature and altered summer precipitation have differential effects on biological soil crusts in a dryland ecosystem. *Global Change Biology*, **18**: 2583-2593.

Kempf, B. & Bremer, E. (1998) Uptake and synthesis of compatible solutes as microbial stress responses to high-osmolality environments. *Archives of Microbiology*, **170**: 319-330.

Kieft, T., Soroker, E. & Firestone, M. (1987) Microbial biomass response to a rapid increase in water potential when dry soil is wetted. *Soil Biology and Biochemistry*, **19** (2): 119-126.

Kovats, R., Valentini, R., Bouwer, L., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M. & Soussana, J-F. (2014) 'Europe'. In: Barros, V., Field, C., Dokken, D., Mastrandrea, M., Mach, K., Bilir, T., Chatterjee, M., Ebi, K., Estrada, Y., Genova, R., Girma, B., Kissel, E., Levy, A., MacCracken, S., Mastrandrea, P. & White, L. (eds). 'Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects' [Report]. Cambridge: Cambridge University Press.

Lane, R., Menon, M., McQuaid, J., Adams, D., Thomas, A., Hoon, S. & Dougill, A. (2013) Laboratory analysis of the effects of elevated atmospheric carbon dioxide on respiration in biological soil crusts. *Journal of Arid Environments*, **98**: 52-59.

Lange, O. (2003) Photosynthesis of Soil-Crust Biota as Dependent on Environmental Factors. In: Belnap, J. & Lange, O. (eds.) Biological Soil Crusts: Structure, Function, and Management. Berlin: Springer.

Lange, O., Belnap, J. & Reichenberger, H. (1998) Photosynthesis of the cyanobacterial soil-crust lichen *Collema tenax* from arid lands in southern Utah, USA: role of water content on light and temperature responses of CO<sub>2</sub> exchange. **12** (2): 195-202.

Lange, O., Belnap, J., Reichenberger, H. & Meyer, A. (1997) Photosynthesis of green algal soil crust lichens from arid lands in southern Utah, USA: Role of water content on light and temperature responses of CO<sub>2</sub> exchange. *Flora*, **192**: 1-15.

Lange, O., Meyer, A., Zellner, H. & Heber, U. (1994) Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Functional Ecology*, **8**: 253-264.

Li, J., Li, X. & Zhang, P. (2014) Micro-morphology, ultrastructure and chemical composition changes of *Bryum argenteum* from a desert biological soil crust following one-year desiccation. *The Bryologist*, **117** (3): 232-240.

Maestre, F., Bowker, M., Cantón, Y., Castillo-Monroy, A., Cortina, J., Escolar, C., Escudero, A., Lázaro, R. & Martínez, I. (2011) Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. *Journal of Arid Environments*, **75** (12): 1282-1291.

Maestre, F., Escolar, C., Bardgett, R., Dungait, J., Gozalo, B. & Ochoa, V. (2015) Warming reduces the cover and diversity of biocrust-forming mosses and lichens, and increases the physiological stress of soil microbial communities in a semi-arid *Pinus halepensis* plantation. *Frontiers in Microbiology*, **6**: 865. doi: 10.3389/fmicb.2015.00865

Maestre, F., Escolar, C., de Guevara, M., Quero, J., Lazaro, R., Delago-Baquerizo, M., Ochoa, V., Berdugo, M., Gozalo, B. & Gallardo, A. (2013) Changes in biocrust cover drive carbon cycle responses to climate change in drylands. *Global Change Biology*, **19** (12): 3835-3847.

Maestre, F., Quero, J., Gotelli, N., Escudero, A., Ochoa, V., Delago-Baquerizo, M., Gracia-Goez, M., Bowker, M., Soliveres, S., Escolar, C., Garcia-Palacios, P., Berdugo, M., Valencia, E., Gozalo, B., Gallardo, A., Aguilera, L., Arredondo, T., Blones, J., Boeken, B., Bran, D., Conceicao, A., Cabrera, O., Chaieb, M., Derak, M., Eldridge, D., Espinosa, C., Florentino, A., Gaitan, J., Gatica, M., Ghiloufi, W., Gomez-Gonzalez, S., Gutierrez, J., Hernandez, R., Huang, X., Huber-Sannwald, E., Jankju, M., Miriti, M., Moneris, J., Mau, R., Morici, E., Naseri, K., Ospina, A., Polo, V., Prina, A., Pucheta, E., Ramirez-Collantes, D., Romao, R., Tighe, M., Torres-Diaz, Val, J., Veiga, J., Wang, D. & Zaady, E. (2012a) Plant species richness and ecosystem multifunctionality in global drylands. *Science*, **335** (6065): 214-217.

Maestre, F., Salguero- Gómez, R. & Quero, J. (2012b) It is getting hotter in here: determining and projecting the impacts of global environmental change on drylands. *Philosophical Transactions B*, **367** (1606): 3062-3075.

Maphangwa, K., Musil, C., Raitt, L. & Zedda, L. (2012) Experimental climate warming decreases photosynthetic efficiency of lichens in an arid South African ecosystem. *Oecologia*, **169**: 257-268.

Masui, T., Matsumoto, K., Hijioka, Y., Kinoshita, T., Nozawa, T., Ishiwatari, S., Kato, E., Shukla, P., Yamagata, Y. & Kainuma, M. (2011) An emission pathway for stabilization at 6 Wm<sup>-2</sup> radiative forcing. *Climatic Change*, **109**: 59-76.

Mazor, G., Kidron, G., Vonshank, A. & Abeliovich, A. (1996) The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. *FEMS Microbiology Ecology*, **21** (2): 121-130.

Meinhausen, M., Smith, S., Calvin, K., Daniel, J., Kainuma, M., Lamarque, J-F., Matsumoto, K., Montzka, S., Raper, S., Riahi, K., Thomson, A., Velders, G. & van Vuuren, D. (2011) The RCP greenhouse gas concentrations and their extensions from 1765 to 2300. *Climatic Change*, **109**: 213-241.

Montoya, J. & Raffaelli, D. (2010) Climate change, biotic interactions and ecosystem services. *Philosophical Transactions B*, **365** (1549): 2013-2018.

Moss, R., Edmonds, J., Hibbard, K., Manning, M., Rose, S., van Vuuren, D., Carter, T., Emori, S., Kainuma, M., Kram, T., Meehl, G., Mitchell, J., Nakicenovic, N., Riahi, K., Smith, S., Stouffer, R., Thomson, A., Weyant, J. & Wilbanks, T. (2010) The next generation of scenarios for climate change research and assessment. *Nature*, **463**: 747-756.

- Neher, D., Lewins, S., Weicht, T. & Darby, B. (2009) Microarthropod communities associated with biological soil crusts in the Colorado Plateau and Chihuahuan deserts. *Journal of Arid Environments*, **73** (6-7): 672-677.
- Noy-Meir, I. (1973) Desert Ecosystems: Environment and Producers. *Annual Review of Ecology and Systematics*, **4**: 25-51.
- Oliver, M., Velten, J. & Wood, A. (2000) Bryophytes as experimental models for the study of environmental stress tolerance: *Tortula ruralis* and desiccation-tolerance in mosses. *Plant Ecology*, **151**: 73-84.
- Parry, M., Keys, A., Madgwick, P., Carmo-Silva, A. & Andralojc, P. (2008) Rubisco regulation: a role for inhibitors. *Journal of Experimental Botany*, **59** (7): 1569-1580.
- Pintado, L., Sancho, J., Blanquer, T., Green, A. & Lázaro, R. (2010) Microclimatic factors and photosynthetic activity of crustose lichens from the semiarid southeast of Spain: long-term measurements for *Diploschistes diacapsis*. *Bibliotheca Lichenologica*, **105**: 211-224.
- Rao, B., Liu, Y., Wang, W., Hu, C., Li, D. & Lan, S. (2009) Influence of dew on biomass and photosystem II activity of cyanobacterial crusts in the Hopq Desert, northwest China. *Soil Biology and Biochemistry*, **41** (12): 2387-2393.
- Reed, S., Coe, K., Sparks, J., Housman, D., Zelikova, T. & Belnap, J. (2012) Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change*, **2**: 752-755.
- Rajeev, L., da Rocha, U., Klitgord, N., Luning, E., Fortney, J., Axen, S., Shih, P., Bouskill, N., Bowen, B., Kerfeld, C., Garcia-Pichel, F., Brodie, E., Northen, T. & Mukhopadhyay, A. (2013) Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust. *The ISME Journal*, **7** (11): 2178-2191.
- Reynolds, J., Smith, D., Lambin, E., Turner II, B., Mortimore, M., Batterbury, S., Downing, T., Dowlatabadi, H., Fernández, R., Herrick, J., Huber-Sannwald, E., Jiang, H., Leemans, R., Lynam, T., Maestre, F., Ayarza, M. & Walker, B. (2007) Global Desertification: Building a Science for Dryland Development. *Science*, **316**: 847-851.
- Riahi, K., Rao, S., Krey, V., Cho, C., Chirkov, V., Fischer, G., Kindermann, G., Nakicenovic, N. & Rafaj, P. (2011) RCP 8.5-A scenario of comparatively high greenhouse gas emissions. *Climatic Change*, **109**: 33-57.
- Smith, D. & Molesworth, S. (1973) Lichen physiology XIII: Effects of Rewetting Dry Lichens. *New Phytologist*, **72**: 525-533.
- Steven, B., Gallegos-Graves, L., Yeager, C., Belnap, J., Evans, R. & Kuske, C. (2012) Dryland biological soil crust cyanobacteria show unexpected decreases in abundance under long-term elevated CO<sub>2</sub>. *Environmental Microbiology*, **14** (12): 3247-3258.
- Steven, B., Kuske, C. & Reed, S. (2015) Climate Change and Physical Disturbance Manipulations Result in Distinct Biological Soil Crust Communities. *Applied and Environmental Microbiology*, **81** (21): 7448-7459.

- Stocker, T., Qin, D., Plattner, G-K., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P. (2013) 'Climate Change 2013 The Physical Science Basis' [Report]. Cambridge: Cambridge University Press.
- Thomson, A., Calvin, K., Smith, S., Kyle, G., Volke, A., Patel, P., Delago-Arias, S., Bond-Lamberty, B., Wise, M., Clarke, L. & Edmonds, J. (2011) RCP4.5: a pathway for stabilization of radiative forcing by 2100. *Climatic Change*, **109**: 77-94.
- Tuba, Z., Csintalan, Z., Szente, K., Nagy, Z. & Grace, J. (1998) Carbon gains by desiccation-tolerant plants at elevated CO<sub>2</sub>. *Functional Ecology*, **12** (1): 39-44.
- Tuba, Z., Slack, N. & Stark, L. (2011) Bryophyte Ecology and Climate Change. Cambridge: Cambridge University Press.
- Uclés, O., Villagarcía, L., Moro, M., Cantón, Y. & Domingo, F. (2010) Role of dewfall in the water balance of a semiarid coastal steppe ecosystem. *Hydrological Processes*, **28**: 2271-2280.
- Urban, M. (2015) Accelerating extinction risk from climate change. *Science*, **348** (6234): 571-573.
- van Vuuren, D., Stehfest, E., den Elzen, M., Kram, T., van Vliet, J., Deetman, S., Isaac, M., Goldewijk, K., Hof, A., Beltran, A., Oosenrijk, R. & van Ruijven, B. (2011) RCP2.6: exploring the possibility to keep global mean temperature increase below 2°C. *Climatic Change*, **109**: 95-116.
- Veste, M., Littmann, T., Friedrich, H. & Breckle, S-W. (2001) Microclimatic boundary conditions for activity of soil lichen crusts in sand dunes of the north-western Negev desert, Israel. *Flora*, **196**: 465-474.
- Viles, H. (2008) Understanding Dryland Landscape Dynamics: Do Biological Crusts Hold the Key?. *Geography Compass*, **2** (3): 899-919.
- Wertin, T., Phillips, S., Reed, S. & Belnap, J. (2012) Elevated CO<sub>2</sub> did not mitigate the effect of a short-term drought on biological soil crusts. *Biology and Fertility of Soils*, **48** (7): 797-805.
- Wilske, B., Burgheimer, J., Karnieli, A., Zaady, E., Andreae, M., Yakir, D. & Kesselmeier, J. (2008) The CO<sub>2</sub> exchange of biological soil crusts in a semiarid grass-shrubland at the northern transition zone of the Negev desert, Israel. *Biogeosciences*, **5**: 1411-1423.
- Williams, A., Buck, B. & Beyene, M. (2012) Biological Soil Crusts in the Mojave Desert, USA: Micromorphology and Pedogenesis. *Soil Science Society of America Journal*, **76** (5): 1685-1695.
- World Bank. (2016) Climate Change Knowledge Portal: Global Map > Europe > Spain [Online]. Available at: [http://sdwebx.worldbank.org/climateportal/index.cfm?page=country\\_historical\\_climate&ThisRegion=Europe&ThisCCCode=ESP](http://sdwebx.worldbank.org/climateportal/index.cfm?page=country_historical_climate&ThisRegion=Europe&ThisCCCode=ESP). Access Date: 21/03/2016.
- Young, K., Grover, H. & Bowker, M. (2016) Altering biocrusts for an altered climate. *New Phytologist*, **210** (1): 18-22.

Zedda, L., Gröngroft, A., Schultz, M. Petersen, A., Mills, A. & Rambold, G. (2011) Distribution patterns of soil lichens across the principal biomes of southern Africa. *Journal of Arid Environments*, **75** (2): 215-220.

Zedda, L., Gröngroft, A., Schultz, M. & Rambold, G. (2010) Patterns of Soil Lichen Diversity along the BIOTA Transect in Relation to Climate and Soil Features. In: Schmiedel, U. & Jürgens, N. (eds.) Biodiversity in southern Africa. Volume 2: Patterns and processes at regional scale. Göttingen & Windhoek: Klaus Hess Publishers.

Zelikova, T., Housman, D., Grote, E., Neher, D. & Belnap, J. (2012) Warming and increased precipitation frequency on the Colorado Plateau: implications for biological soil crusts and soil processes. *Plant Soil*, **355**: 265-282.

Zhao, X., Bi, Y., Chen, L., Hu, S. & Hu, Z. (2008) Responses of photosynthetic activity in the drought-tolerant cyanobacterium, *Nostoc flagelliforme* to rehydration at different temperature. *Journal of Arid Environments*, **72** (4): 370-377.

Zhou, J., Xue, K., Xie, J., Deng, Y., Wu, L., Cheng, X., Fei, S., Deng, S., He, Z., van Nostrand, J. & Luo, Y. (2012) Microbial mediation of carbon-cycle feedbacks to climate warming. *Nature Climate Change*, **2**: 106-110.