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Effects of climate change and land use intensification on regional biological soil crust cover and composition in southern Africa

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Abstract

Biological soil crusts (biocrusts) form a regular and relevant feature in drylands, as they stabilize the soil, fix nutrients, and influence water cycling. However, biocrust forming organisms have been shown to be dramatically vulnerable to climate and land use change occurring in these regions.

In this study, we used Normalized Difference Vegetation Index (NDVI) data of biocrust-dominated pixels ($NDVI_{biocrust}$) obtained from hyperspectral and LANDSAT-7 data to analyse biocrust development over time and to forecast future $NDVI_{biocrust}$ development under different climate change and livestock density scenarios in Southern Africa. We validated these results by analysing the occurrence and composition of biocrusts along a mesoclimatic gradient within the study region.

Our results show that $NDVI_{biocrust}$, which reached maximum values of 0.2 and 0.4 in drier and wetter years, respectively, mainly depended on water availability. A predicted decrease in rainfall events according to all future climate scenarios combined with increased temperatures suggested a pronounced decrease in $NDVI_{biocrust}$ by the end of the 21st century caused by reduced biocrust coverage. Livestock trampling had similar effects and exacerbated the negative impacts of climate change on biocrust coverage and composition. Data assessed in the field concurred with these results, as reduced biocrust cover and a shift from well-developed to early stages of biocrust development were observed along a gradient of decreasing precipitation and increasing temperatures and livestock density.

Our study demonstrates the suitability of multi-temporal series of historical satellite images combined with high-resolution mapping data and Earth system models to identify climate change patterns and their effects on biocrust and vegetation patterns at regional scales.

1. Introduction

Earth's drylands (mainly dominated by sensitive forests, steppes and deserts) occupy nearly half of the Earth´s terrestrial surface, and their coverage is expected to increase by the end of the century (Feng and Fu, 2013). Global climate models predict more frequent long-lasting droughts and increased warming within these ecosystems (Wang et al., 2016). This, as well as land use intensification has the potential to produce abrupt changes in multiple ecosystem attributes, thus affecting ecosystem functions, global Earth system functioning and human livelihood (Maestre et al., 2016; Berdugo et al., 2020).

One of the most representative biotic components of dryland regions around the world are biological soil crusts (abbreviated as biocrusts), which are complex communities of photosynthetic organisms, such as cyanobacteria, algae, lichens, and bryophytes, growing together with heterotrophic bacteria, fungi, and archaea within the uppermost millimeters of the soil (Weber et al., 2016). These diminutive communities are estimated to cover ~12 % of the terrestrial soils (Rodriguez-Caballero et al., 2018a), influencing energy (Couradeau et al., 2016; Rutherford et al., 2017), water (Chamizo et al., 2016, Eldridge et al., 2020), C and N fluxes between the soil and atmosphere (Elbert et al., 2012; Porada et al., 2013, 2014, 2017; Weber et al., 2015; Lenhart et al., 2015). Moreover, they affect biogeochemical cycling within the soil (Delgado-Baquerizo et al., 2013; Maestre et al., 2013), with important effects on soil fertility (Chamizo et al.,

2012a), local hydrology (Chamizo et al., 2016; Eldridge et al., 2020), and soil resistance to erosive forces (Belnap et al., 2014). Thus, they provide stable environments and additional resources for vascular vegetation (Luzuriaga et al., 2012; Rodriguez-Caballero et al., 2018b; Havrilla et al., 2019) and the soil fauna (Bamforth, 2008).

Although biocrusts are adapted to aridity, surviving extreme environmental conditions (Pointing and Belnap, 2012), biocrust forming organisms have been shown to be dramatically vulnerable to subtle changes of climatic parameters (Reed et al., 2012; Maestre et al., 2013; Darrouzet-Nardi et al., 2015). According to global change scenarios, their global coverage is expected to decrease dramatically by the end of this century (Rodriguez-Caballero et al., 2018a). Besides this overall reduction in biocrust coverage, climate manipulation experiments also showed that warming, and changes in precipitation patterns (i.e. an increase in the frequency of small water pulses during warm periods) will cause changes in cyanobacteria composition and a reduction of lichen or bryophyte coverage (Maphangwa et al., 2012; Reed et al., 2012; Escolar et al., 2012; Garcia-Pichel et al., 2013; Maestre et al., 2013; Ladrón de Guevara et al., 2014 and 2018), with important implications for ecosystem functioning (Escolar et al., 2012; Maphangwa et al., 2012; Delgado-Baquerizo et al., 2013; Couradeau et al., 2016; Rutherford at al., 2017). Disturbance derived from land use intensification (e.g., trampling) has also been demonstrated to be a relevant threat for biocrusts. In fact, it has similar negative effects as climate change on their coverage and composition (Ferrenberg et al., 2015), causing an increase of soil erosion (Chamizo et al., 2012) and modifications of water (Chamizo et al., 2016) and nutrient (Belnap 1996) cycling in the soil. Thus, both climate change and disturbance caused by land use intensification have major effects on the composition, survival, and distribution of biocrusts. However, especially field experiments on climate change have been limited to very few sites (e.g.,

Mojave Desert, Colorado Plateau, Iberian Peninsula), that only represent a small fraction of the whole range of ecosystems and climatic conditions under which biocrusts occur. These experimental studies are time-consuming, expensive, and often involve interfering side effects. Passive open-top chambers not only cause a warming inside the chambers, but also cut down the impact of dew and fog (Maphangwa et al., 2012), and warming lamps only heat the uppermost soil region with a downward gradient (Kimball 2005). Such negative side-effects of field experiments can be avoided by combining experimental results with direct observations in the field or by applying remote sensing technologies (Palmer et al., 2002).

Space-for-time (SFT) substitutions, where spatial climatic and disturbance gradients are used to investigate the response of biocrusts to anticipated future conditions, form one of these options. This method has been frequently applied to analyse plant succession and to model climate change effects on biodiversity and species richness (Blois et al., 2013). In a recent study, it provided valuable data on the long-term effects of temperature and precipitation on the composition and coverage of biocrust communities (Garcia-Pichel et al., 2013). Another methodology is the use of historical and open access high temporal resolution satellite images combined with coverage and composition data along climatic gradients. Such multi-temporal series of satellite images could provide crucial information on biocrust dynamics and response to environmental factors, such as temperature, precipitation, and disturbance (Karnieli et al., 1996; Karnieli 2003; Burgheimer et al., 2006; Rodriguez-Caballero et al., 2015; Panigada et al., 2019).

The main objective of this paper is to investigate the long-term response of biocrusts to warming, livestock trampling, and changes in precipitation amount and frequency

predicted for the Succulent Karoo. The study region is located within an arid winter rainfall biome of southern Africa (Mucina et al. 2006; Figure 1) that comprises a great diversity and unique flora of succulent plants (Mucina et al., 2006; Schmiedel and Jürgens 1999). It also harbours a variety of different biocrust types that are considered as a critical component of the ecosystem (Büdel et al., 2009). To achieve the objective, we apply a multidisciplinary approach, in which we first utilize climate data and satellite imagery, covering a time-span of 10 years, to analyse the seasonal response of biocrusts to climate fluctuations, identified as variations in the Normalized Difference Vegetation Index (NDVI) values in biocrust-dominated pixels ($NDVI_{biocrust}$). We then apply three different climate change scenarios (RCP 2.6, 4.5, and 8.5) in two general circulation models to predict changes in biocrust development and cover, expressed as $NDVI_{biocrust}$ under future climatic conditions and different livestock densities until 2100. Finally, we validate our results by investigating biocrust cover, composition, and NDVI values along a climatic and disturbance gradient, which reflects precipitation and temperature changes expected for this region under different livestock pressure.

We hypothesize that i) NDVI will reflect the rapid response of biocrusts to variations in climatic factors, and ii) as a consequence, the $NDVI_{biocrust}$ will be reduced in the future due to a predicted increase in aridity according to the IPCC predictions for the region (Weber et al., 2018). We further suggest that iii) the reduced $NDVI_{biocrust}$ will be the result of changes in both biocrust coverage and composition.

2. Material and methods

This study was conducted in a semi-arid ecosystem in the Succulent Karoo, South Africa, near the BIOTA biodiversity observatory Soebatsfontein S22 (Supplementary

Fig. S1). More detailed information on the study site is provided in section 1 of the supplementary material and in Schmiedel et al., (2016).

To obtain information on the seasonal patterns of $NDVI_{biocrust}$, we used an already existing biocrust map of the study area obtained from a hyperspectral Compact Airborne Spectrographic Imager (CASI 2) (see Weber et al. 2008, for further details). This biocrust distribution map with a spatial resolution of 1 m was used to identify all pixels in LANDSAT ETM+ 7 images (hereafter Landsat images; spatial res. 30 m) with a biocrust coverage above 80 % (i.e., with more than 80 % of the 1 m-pixels herein classified as biocrusts). Ninety-three biocrust-dominated pixels were identified in the Landsat images. A series of 44 Landsat images covering the biocrust map region, which had been acquired during the period between 2001 and 2010 (see Supplementary Table 2 for a detailed description of all images), were obtained from Earth Explorer (https://earthexplorer.usgs.gov/). All Landsat images were converted into reflectance data using gain and offset values, and image gaps, caused by mirror failure on March 31, 2003, were masked before subsequent analyses. The final images were checked for clouds, and scenes with cloud presence in the study region were excluded from the analyses. Subsequently, we estimated the Normalized Difference Vegetation Index (NDVI; Rouse et al., 1973) within the 93 biocrust-dominated pixels (hereafter "$NDVI_{biocrust}$"). We used the $NDVI_{biocrust}$ as a proxy of biocrust dynamics, because it has been demonstrated to be directly related to the chlorophyll concentration of different biocrusts types over a wide range of soil conditions (Roman et al., 2019), thus being a good index to monitor biocrust biomass, development, cover, and physiological conditions (Karnieli, 2003; Burgheimer et al., 2006; Fischer et al., 2012; Rodriguez-Caballero et al., 2015; Young and Reed, 2017; Panigada et al., 2019). Image

preprocessing and calculations were performed in ENVI 4.7 software (ITT VIS, Boulder, CO, USA); see section 2.1 in the supplement for more detailed information.

Then, we investigated the parameters potentially influencing the $NDVI_{biocrust}$. Specifically, we analysed if and to what extent the $NDVI_{biocrust}$ is influenced by the soil water content (SWC, as a proxy for the short-term response of biocrusts to water availability), water deficit (WD; as a proxy for the response of biocrusts to long periods of limited water availability), solar radiation, and by the grazing intensity (detailed information on the calculation of these parameters is provided in section 2.2 of the supplement). Subsequently, we analysed the influence of the environmental factors and land use intensity on $NDVI_{biocrust}$ values by fitting General Linear Mixed Models (LMMs) with repeated measures using the "lme4" package (Bates et al., 2015) in R (R Core Team 2013). For that, pixel "ID" was considered as a fixed factor, and incoming solar radiation, WD and SWC on the image acquisition day, recent land use intensity, as well as the interaction between land use intensity and the other variables were considered as independent continuous predictors.

In a next step, we combined the LMM with a climate prediction obtained from the two different Earth system models (ESM) to forecast future trends in daily $NDVI_{biocrust}$ values for the biocrust-dominated pixels within the Succulent Karoo for the period between 2010 and 2100 under different management scenarios. For this, we assumed two different livestock density levels: i) sustainable management with 50 % of the recommended livestock density and ii) overgrazing with 200 % of the recommended livestock density. We focussed on three different Representative Concentration Pathways (RCPs) defined in the Fifth Assessment Report of the Intergovernmental Panel on Climate Change (IPCC 2014), i.e., RCP2.6, 4.5, and 8.5 (more details are given in section 2.3 of the supplement).

Finally, we analyzed the environmental factors to identify potential monotonic temporal trends and predicted the mean annual $NDVI_{biocrust}$ and maximum annual NDVI values of biocrust-dominated areas for the whole period using the Mann–Kendall trend test and Kendall's tau statistics (Hirsch and Slack, 1984) using the "trend" package (Pohlert 2015) in R. The confidence level for the test was set to 0.05, and slopes with a p-value <0.05 were considered significant.

To validate our predictions, we conducted a space-for-time (SFT) study along a regional climate and disturbance gradient, reflecting long-term effects of changes in temperature, precipitation, and livestock density (Supplementary Figure S1) on biocrust coverage and composition (see section 2.4 of the supplement for further details). For that, biocrust coverage and composition was determined in four 100 m x 100 m field sites within the same macroclimatic and pedological region with a maximum distance of 12 km between the sites and subjected to different livestock densities. The mesoclimate at the four sites has been characterized by continuous measurements over a whole year as described in section 2.4.2 in the supplement. Basic soil parameters (i.e., pH, total carbon and nitrogen content and soil texture) have also been also determined (see section 2.4.3 of the supplement for a detailed description). Additionally, the spectral response of bare soils and soils covered by the different biocrust communities was measured in the field under dry conditions. We used field spectra to model the mean $NDVI_{biocrust}$ value per study site as a linear mixture of the different components weighted by their relative coverage within the pixel (Hill et al., 1999; Rodriguez-Caballero et al., 2014; Panigada et al. 2019; for details, see section 2.4.4 in supplement).

To compare the community composition between the study sites and to investigate potential long-term effects of climate factors (mean daily air temperature, total annual precipitation, number of rainfall events, and mean annual photosynthetic active

radiation [PAR]), land use intensity, and soil properties (pH, particle size, C, N content) on biocrust composition and distribution, we performed a Non-Metric Multidimensional Scaling (NMDS) as described in section 2.4.5 of the supplement.

3. Results

3.1 Analysis of biocrust NDVI response to water pulses under different levels of disturbance

During the period from 2001 to 2010, biocrust-dominated areas within the Succulent Karoo had a mean daily NDVI value of 0.19, that varied strongly between seasons and years (Figure 2). About 74 % of the variation in $NDVI_{biocrust}$ could be explained by WD, SWC and incoming solar radiation (Supplementary Table S3). Water deficit, which is strongly influenced by temperature and precipitation, was the factor that exerted the largest effect on daily NDVI values, controlling its annual seasonality (Figure 2, Supplementary Table S3). As general pattern, we observed that daily $NDVI_{biocrust}$ values were very low during the dry periods of the year (with daily values about 0.10), when WD was high, and increased during the rainy season, with maximum daily NDVI values reaching 0.44 during periods with low WD (Figure 2). At the end of the year, when WD increased again, $NDVI_{biocrust}$ decreased to similar values as those observed before the rainy season (Figure 2). SWC had the opposite effect on NDVI, as NDVI increased with increasing SWC. For solar radiation, the maxima were reached when the NDVI declined strongly again and the NDVI maximum was reached when the solar radiation was strongly rising. However, the effects of SWC and solar radiation were less important than those of WD (Supplementary Table S3), as SWC only controlled the small $NDVI_{biocrust}$ peaks that occurred after rainfalls (Figure 2).

The magnitude of $NDVI_{biocrust}$ response to changes in WD, SWC, and solar radiation was also affected by the livestock density, as demonstrated by a significant interaction

between these factors (Supplementary Table S3). Thus, although minimum annual $NDVI_{biocrust}$ values were similar in all biocrust-dominated pixels, the increase of $NDVI_{biocrust}$ during the rainy season of wet years was less pronounced in pixels under intense land use pressure compared to pixels from camps characterized by low livestock density, reaching maximum NDVI values of ~0.38 and ~0.44, respectively (Figure 2).

3.2 Predicted changes in temperature, precipitation, and biocrust response

Based on MIROC and ECHAM models we obtained results on the RCPs 2.6, 4.5, and 8.5, indicating an increase in temperature by ~0.002 - 0.046 degrees per year for the Succulent Karoo during the next ~80 years (Supplementary Figure S3). Annual precipitation and the number of rainfall events are expected to be reduced under most of the different climate change scenarios and Earth system models (Supplementary Figure S3c, d). These changes are expected to be especially relevant during the wet season (April to September), as shown in both models and by all RCPs (Supplementary Figure S4).

Under these conditions of climate change, SWC values are expected to decrease while WD will be more pronounced (Supplementary Figure S5), causing a decrease of mean biocrust NDVI, maximum biocrust NDVI as well as minimum biocrust NDVI values by the end of the century (Figure 3). The largest changes are expected for maximum annual peaks of biocrust NDVI, showing a significant negative trend according to the Mann-Kendall test ($p<0.05$; Supplementary Figure S6). According to our calculations, the predicted altered climatic conditions will cause an average reduction of $NDVI_{biocrust}$ of ~25 % of their current value by the end of the century (Figure 3). These effects are consistent in all RCPs and model simulations, although the decreases in $NDVI_{biocrust}$ are most dramatic in the most severe scenario (RCP8.5) and under the highest livestock density (Figure 3).

3.3 Space-for-time study

3.3.1 Biocrust occurrence and distribution

Biocrusts occurred at all four sites with overall cover values being significantly higher at sites 3 and 4 compared to site 1 and 2 (Figure 4). Light cyanobacteria-dominated biocrusts reached high cover values at sites 1, 2 and 4 and significantly lower values at site 3. Dark cyanobacteria-dominated biocrusts covered significantly larger areas at site 4 as compared to site 1. The sum of dark cyanobacteria- and cyanolichen-dominated biocrusts was higher at site 3 when compared to sites 1 and 2, whereas site 4 showed intermediate values. Cyanolichen-dominated biocrusts had significantly higher cover values at site 3 compared to all other sites, and chlorolichen-dominated biocrusts reached higher cover values at site 3 compared to site 1 (Figure 4b). Mean cover values of bryophyte-dominated biocrusts tended to be higher at sites 3 and 4, but due to large standard deviations, the differences were not significant.

Differences in biocrust coverage and composition caused significant differences in NDVI values derived from composite dry field spectra between all sites (Figure 4). The highest values were found for site 3 (0.19) and site 4 (0.18), coinciding with the highest coverage of well-developed biocrust communities, and progressively decreased to study sites 2 and 1 (Figure 4).

3.3.2 Mesoclimatic conditions and soil properties

Our mesoclimate measurements over one full year revealed a north-south gradient of increasing temperature and decreasing precipitation for the four study sites located within the same macroclimatic region (Figure 4c). As shown in Figure 5, sites 1 and 2 showed higher mean monthly temperatures (with mean annual values, MAT: 19.4 and 19.1 °C, respectively) as compared to sites 3 and 4 (18.2 and 18.9 °C, respectively), which are located south to southwest of the first two sites (Supplementary Figure S.1).

This temperature increase corresponds to the warming predicted by the most conservative scenario (RCP2.6) for the next 95 or 478 years according to the MIROC and ECHAM models, respectively (Supplementary Figure S3). Mesoclimate measurements for the observation period of 12 months also revealed a decrease in total precipitation and in the number of precipitation events from site 3 and 4 to site 1 and 2 . This difference is within the same range as the climate predictions of rainfall decrease by the MIROC and ECHAM models according to RCP2.6 for the next 123 or 216 years, respectively. Harsher climatic predictions are obtained by the other two scenarios, especially for RCP8.5, which predicts an increase in temperature and a decrease in precipitation as observed along our sampling gradient within less than 50 years for both models (Supplementary Table S4).

A detailed analysis of the seasonal variation (Figure 5) showed that the four different study sites are characterized by similar air temperature patterns with high values from October to April (southern hemisphere summer) and lower temperatures between May and September (southern hemisphere winter). Mean monthly temperatures were always between 1 and 1.5 degrees higher at site 1 compared to site 3, whereas temperatures of site 4 were closer to those of site 3 during summer and nearly identical to these of site 1 during the winter months (Figure 5a). Monthly means of daily maxima also showed a clear pattern throughout the year with the highest values at site 1, followed by site 2, 4, and 3 (Figure 5a), whereas for monthly means of daily minima, the pattern was less clear. Precipitation showed an opposite pattern, with most rainfall events between May and September and almost no rain between November and January (Figure 5b). During most of the wet season (March-September), precipitation amounts were higher at sites 3 and 4 compared to sites 1 and 2 and only in February, at the end of the dry season, precipitation amounts were higher at sites 1 and 2. Also, the number of precipitation

events differed between sites with a higher number of events from June to September (site 3) and in September (site 4).

3.3.3 Land use intensity

Land use intensity showed a similar gradient, with sites 3 and 4 being characterized by a low livestock density (25 and 23 % of their recommended stoking density) whereas sites 2 and 3 are characterized by medium grazing pressure (Supplementary Figure S1). Differences in soil properties were less clear, as all sites were dominated by the same soil type (Supplementary Figure S1) and we only found slight differences in some soil properties between sites. The organic C and total N contents of site 3 were significantly higher compared to most (C) or some of the measurements (N) at the other sites, which showed no significant differences between them (Figure 6). In addition, soil texture was similar at study sites 1, 2 and 4 (sandy loam), whereas site 3 showed significantly lower sand contents and higher proportions of clay (Supplementary Table S5).

3.3.4 Effect of climatic conditions and livestock density on biocrust occurrence and distribution

Differences in biocrust coverage and composition were mainly driven by differences in livestock density, precipitation, and temperature along the observed disturbance and mesoclimate gradient. As shown in Figure 7, an NMDS ordination of all field plots illustrates a climate and livestock density (disturbance) gradient along axis 1, with the main constituents of the biocrust and the NDVI aligning along this axis. Light cyanobacteria-dominated biocrusts characterize one end with the highest values of temperature, PAR, and livestock density. Well-developed chlorolichen- and bryophyte-dominated biocrusts occur at the opposite end of the axis with low values of livestock density, higher C, N and clay contents, the highest numbers of precipitation events, and highest overall precipitation amounts.

An effect of temperature and precipitation on biocrust composition was also elucidated by linear regression analysis between these and the coverage of the different biocrust constituents. The coverage of light cyanobacteria-dominated biocrusts showed a strong positive correlation with daily temperature and PAR and a strong negative one with the number of precipitation events and the amount of rain (Supplementary Figure S7). The coverage values of dark cyanobacteria-dominated biocrust were more affected by incoming solar radiation, but not very much by temperature and precipitation (Supplementary Figure S8). Cyanolichen-dominated biocrust coverage increased with decreasing temperature and PAR amounts and increasing numbers of precipitation events, whereas the precipitation amount played only a minor role (Supplementary Figure S9). The coverage of chlorolichen- and bryophyte-dominated biocrusts correlated positively with the precipitation amount and the number of precipitation events, but showed a strong negative correlation with temperature (Supplementary Figure S10 and S11).

4. Discussion

This study shows that water deficit is the environmental factor most relevant for the occurrence and composition of biocrusts, which is reflected by both satellite ($NDVI_{biocrust}$) and field mapping data. Predicted increasing temperatures and decreasing rainfall amounts and numbers suggest a decrease in biocrust coverage and diversity during the next decades, which is aggravated by high livestock density.

Biocrusts NDVI dynamics

Currently, biocrusts cover more than 25 % of the soil surface in the Succulent Karoo with cyanobacteria-dominated biocrusts forming the main crust type in areas where environmental conditions limit the establishment of more developed communities (Weber et al., 2018). Under good environmental conditions, light cyanobacteria- are

quickly replaced by dark cyanobacteria-dominated biocrusts and at a later stage also the more developed lichen- and bryophyte-dominated biocrusts are formed (Büdel et al., 2009). This development affects the soil surface reflectance, as the different biocrust types have a specific spectral signature that clearly differs from the underlying soil (Weber et al., 2008; Rodriguez-Caballero et al., 2017a). With increasing biocrust development and chlorophyll content, the spectral absorption in the red region of the spectrum also increases (see Hill et al., 1999; Weber et al., 2008; Chamizo et al., 2012b; Young and Reed, 2017; Weber and Hill, 2016 among many others). This results in an increase of the values of the most widely used vegetation indices, such as the NDVI (Rodriguez-Caballero et al., 2015; Roman et al., 2019). In the current study we calculated $NDVI_{biocrust}$, which appeared to be driven by land use intensity and by environmental factors that controlled frequency and duration of water pulses and droughts, such as temperature, precipitation, and solar radiation (Supplementary table S3).

As expected, during most of the year, when the soil was dry, biocrust-dominated areas within the Succulent Karoo reached minimum $NDVI_{biocrust}$ values around 0.1, increasing quite rapidly after the first wetting events (Figure 2). This fast response of biocrusts has previously been described to result both from the nearly instantaneous darkening of biocrusts upon water pulses and from metabolic activity and quick regrowth after wetting (Karnieli et al., 1996; Weber et al., 2008; Rodriguez-Caballero et al., 2015; Panigada et al., 2019). Under favorable environmental conditions with high soil moisture contents over prolonged time-spans, $NDVI_{biocrust}$ reached the highest values and the largest differences between areas under different livestock density, suggesting that biocrust growth and net C gain were strongly affected by the disturbance regime. During dry years, as e.g., in 2004 and 2005, $NDVI_{biocrust}$ values remained low,

indicating only a minor growth or even a carbon deficit, which may slow down biocrust succession and reduce overall biomass in a similar way as disturbance does (Dojani et al., 2011, Figure 2). Given the spatial heterogeneity of dryland regions, we might expect some plants within these pixels, whose response might slightly overlap with biocrust greening. However, it can be reasonably assumed that this signal is very low compared to the biocrust signal, as biocrusts represent at least 80 % of the total cover. Indeed, as shown in supplementary Table S1, the response of these pixels to the different environmental factors analyzed in this study differs significantly from the vegetation response.

Biocrust response to climate change and land use intensity

The modelling results on future climatic conditions obtained from three different RCPs in two different models suggest a decrease in annual rainfall, mainly winter rainfall, coupled with increased mean annual temperature and aridity during the next decades (Supplementary Figure S3 and S4). These climatic changes as well as high livestock densities will result in a decrease of the mean and maximum annual NDVI values of biocrust-dominated areas (Figure 3), most probably due to a decrease of the overall biocrust coverage and a shift from well-developed to early stages of biocrust communities, mainly dominated by cyanobacteria. . This is in line with the results of previous climate and disturbance manipulation studies within South Africa (Maphanwa et al., 2012) and in other desert regions around the world (Reed et al., 2012; Maestre et al., 2013; Ferrenberg et al., 2015; Ladrón de Guevara et al., 2014). Most of these studies described changes from well-developed biocrusts to earlier stages of development (Reed et al., 2015). Livestock has previously been demonstrated to affect biocrust communities both directly by trampling and indirectly thorough the alteration of

vascular plants and by the addition of nutrients into the soil (Mallen-Cooper et al., 2018). As a result, the magnitude of the negative impact of climate change on biocrusts will increase under high livestock density scenarios (Figure 3).

Changes in biocrust composition and coverage along a disturbance and mesoclimate gradient

Expected regional changes upon climate change and land use intensification are analogous to changes in biocrust coverage and composition observed along our SFT disturbance and mesoclimate gradient. As shown in Figure 4, biocrusts were not evenly distributed along the study sites, but overall biocrust coverage was significantly higher at sites 3 and 4 as compared to sites 1 and 2. Dark cyanobacteria-dominated biocrusts occurred more frequently at site 4 compared to site 1, and cyanolichen- and chlorolichen-dominated biocrusts were mapped more frequently at site 3 compared to all other sites and site 1, respectively. These differences in biocrust coverage and composition between sites and the lower NDVI at site 1 compared to site 3 (Supplementary Figure S2) may well be caused by differences in the observed climatic properties and livestock density.

As shown in Figure 5, the annual precipitation was higher at site 3 and 4, while temperature was lower during the observation period of 12 months. This likely caused sites 3 and 4 to be wet over longer time spans. As all photoautotrophic organisms within biocrusts are poikilohydric, meaning that their activity is governed by water, our data suggest that at sites 3 and 4 biocrust organisms remained wet and photosynthetically active over longer time spans. Higher water availability and the low livestock density at these sites likely explain the higher overall biocrust cover values, and the higher cover values of cyanolichen- and chlorolichen-dominated biocrusts at site 3, as lichens are

very sensitive to disturbance and need to be photosynthetically active over longer time spans throughout the year to sustain their larger biomass (Figure 4, 7; Belnap et al., 2004 and 2006; Maestre et al., 2013; Ladrón de Guevara et al., 2014).

It has been shown, that short hydration periods can be detrimental for bryophytes if the time-span of positive net photosynthesis is too short to compensate for C losses invested into maintenance and repair functions (Belnap et al., 2004; Reed et al., 2012). Thus, not only the overall amount of annual rainfall, but also the quantity and timing of individual rainfall events are relevant in determining biocrust response to climate change. As the mesoclimatic dataset covers only one year and one microclimate station per site, these data need to be interpreted with caution. Nevertheless, it seems reasonable to assume that they describe an overall pattern mainly determined by landscape topography and distance to the coast, which previously has been described along larger spatial scales in the region (Büdel et al., 2009).

Although temperature and precipitation followed the overall gradient, site 3 had elevated nutrient and organic carbon, lower sand and higher clay contents than the other sites. This may be caused by the fact that site 3 is located at a SW inclined slope oriented towards the Atlantic coast, which may cause larger inputs of dew and fog, supporting the growth of well-developed lichen- and bryophyte-dominated biocrusts (Ladron de Guevara et al. 2014; McHugh et al. 2015).

Ecological implications of biocrust response to climate change and disturbance

In a similar way as shown for the Succulent Karoo (Büdel et al., 2009), biocrusts have been described as one of the most important biotic components within many other dryland ecosystems (Weber et al., 2016; Rodriguez-Caballero et al., 2018). A reduction in overall biocrust coverage is expected to negatively affect C and N uptake and input

into the ecosystem (Zhao et al., 2010; Ladron de Guevara et al., 2014; Sancho et al., 2016). This, together with the expected increase in CO_2 release as a consequence of the decomposition of dead biomass (Maestre et al., 2013), and the reduction of photosynthetic efficiency of well-developed lichens (Maphanwa et al., 2012) will likely promote a depletion of already low soil C and N pools (Haarmeyer et al., 2010). Besides these direct biogeochemical effects, biocrust cover loss and changes in community composition towards earlier successional stages will reduce soil stability (Chamizo et al., 2012b; Belnap et al., 2014) and modify soil surface albedo (Couradeau et al., 2017; Rutherford et al., 2017), with potential effects on water erosion, dust emission, and the solar radiation budget. Thus, further analyses are needed in order to conduct an upscaling of already existing experimental data to regional and ecosystem scales.

Here, we present a new replicable methodology to analyze the biocrust response upon climate change and disturbance that complements ongoing manipulative experiments. Although our measurements cannot be used to identify the mechanisms underlying the observed changes in biocrusts coverage and composition and they neglect the potential acclimation of some biocrust forming organisms, they can be used as an initial approximation in areas without information and to upscale existing local results from manipulative experiments to the entire region or ecosystem.

Conclusions

Our results demonstrate that the combination of multi-temporal series of historical satellite images and Earth system models is well suited to identify climate change patterns and effects on biocrust cover and composition at regional scales. Doing this, we found that biocrust distribution within southwestern African drylands is governed by the interplay of climatic factors that determine whether biocrusts are active, the duration of

activity periods and droughts, and by land use intensity. This is also corroborated by field data, showing that well-developed lichen- and bryophyte-dominated biocrusts preferably occurred at the wetter and cooler sites of low livestock density, whereas their coverage declined as conditions became warmer and drier and land use increased, which also affected local NDVI biocrust values.

Climate change scenarios predict a decrease in amount and frequency of precipitation and an increase in temperature and aridity in southwestern African deserts, similar to these observed along our SFT substitution study. These changes may result in a reduction of $NDVI_{biocrust}$ values that is caused by a decrease in total biocrust coverage and a shift in biocrust communities towards early cyanobacteria-doiminated crusts. This pattern can be exacerbated by increased land use intensity, and it should be considered when designing future land use in the region. Overall, our study shows that the combined effect of climate change and land use intensification will affect biocrust cover and composition, which may have strong negative impacts on biogeochemical cycles, water availability, soil stability and the solar radiation budget with potential feedbacks to future climate.

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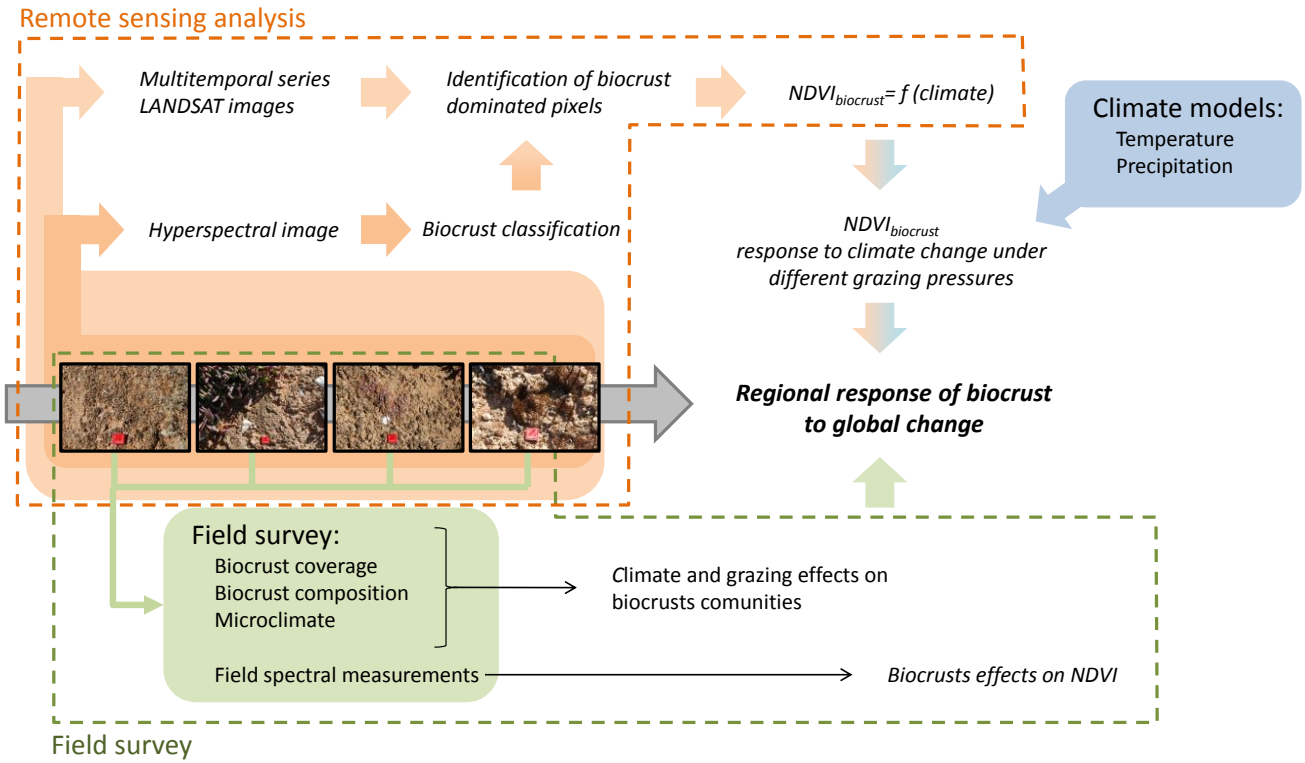

Figure 1: Flow chart describing the experimental approach to understand the effect of climatic factors and land use intensification on biocrust coverage and composition within the South African Karoo. We combine climate data and satellite imagery to analyze the seasonal biocrust response to climate fluctuations, identified as variation in the Normalized Difference Vegetation Index values in biocrust-dominated pixels ($NDVI_{biocrust}$). Then we apply three different climate change scenarios (RCP 2.6, 4.5, and 8.5) in two general circulation models to predict the changes of biocrust development and cover under future climatic conditions and different livestock densities until the year 2100. Finally, we validate our results by investigating biocrust cover and composition along a climatic and disturbance gradient.

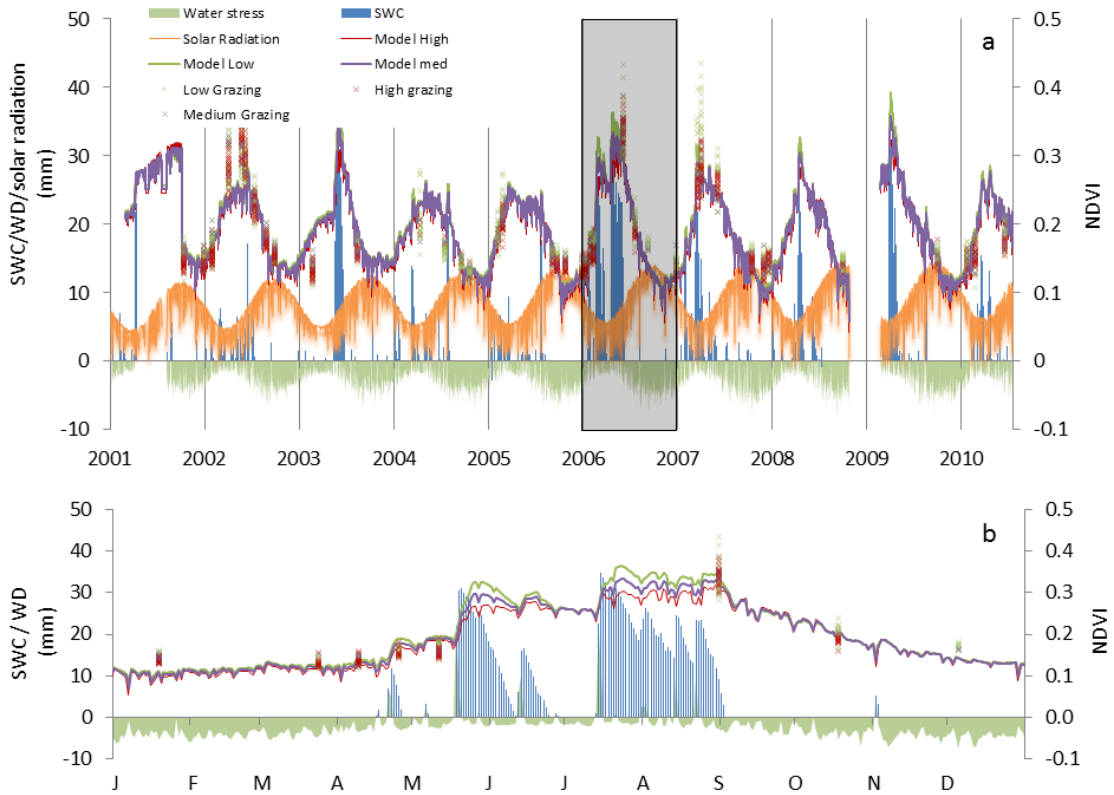

Figure 2: Seasonal patterns of Normalized Difference Vegetation Index values of biocrust dominated pixels ($NDVI_{biocrust}$; shown as crosses), and modelled $NDVI_{biocrust}$ using a general linear model (lines) under low (green) medium (purple) and high (red) grazing pressure, as well as soil water content (SWC), water deficit (WD) and solar radiation for the period 2001-2010 (a) and detailed variation of the modelled biocrust NDVI and SWC and WD during the year 2006 (b).

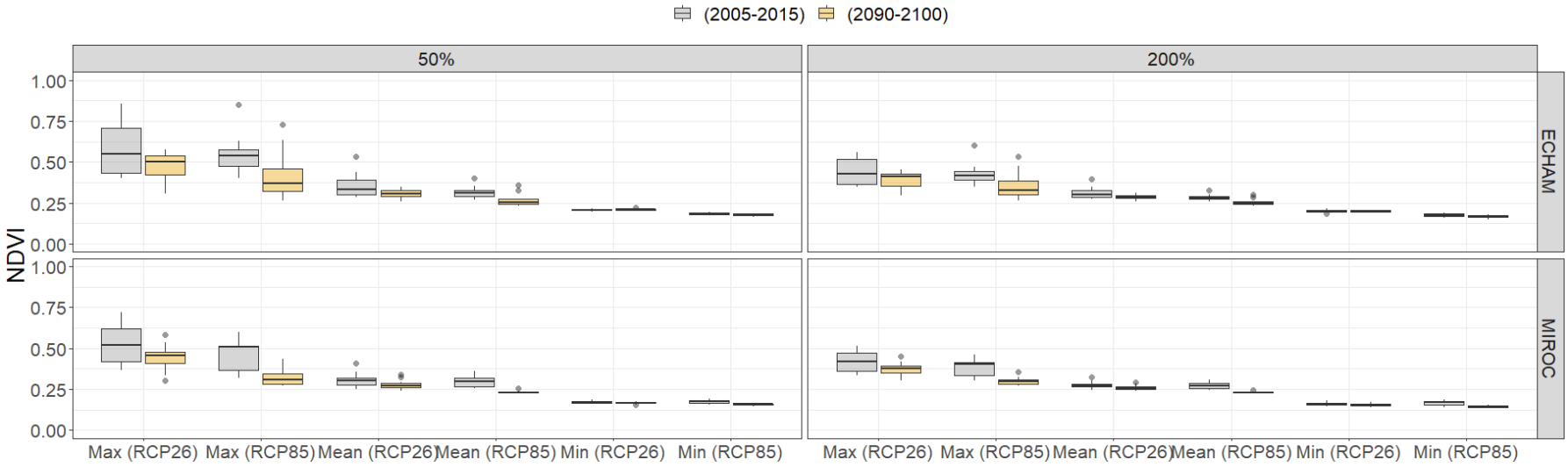

Figure 3: Comparison between predictions of mean, maximum and minimum annual NDVI for the period 2005-2015 (grey) and 2090-2100 (yellow) according to RCP2.6 and RCP8.5 for ECHAM and MIROC climate predictions at 200% (left) and 50% of livestock density (right). Box-plots show median (line) ± 25-75% intervals (box) and maximum and minimum values (whiskers) of NDVI values of biocrust dominated pixels. Outliers are marked by dots. Complete annual time series are shown in Supplementary figure S6

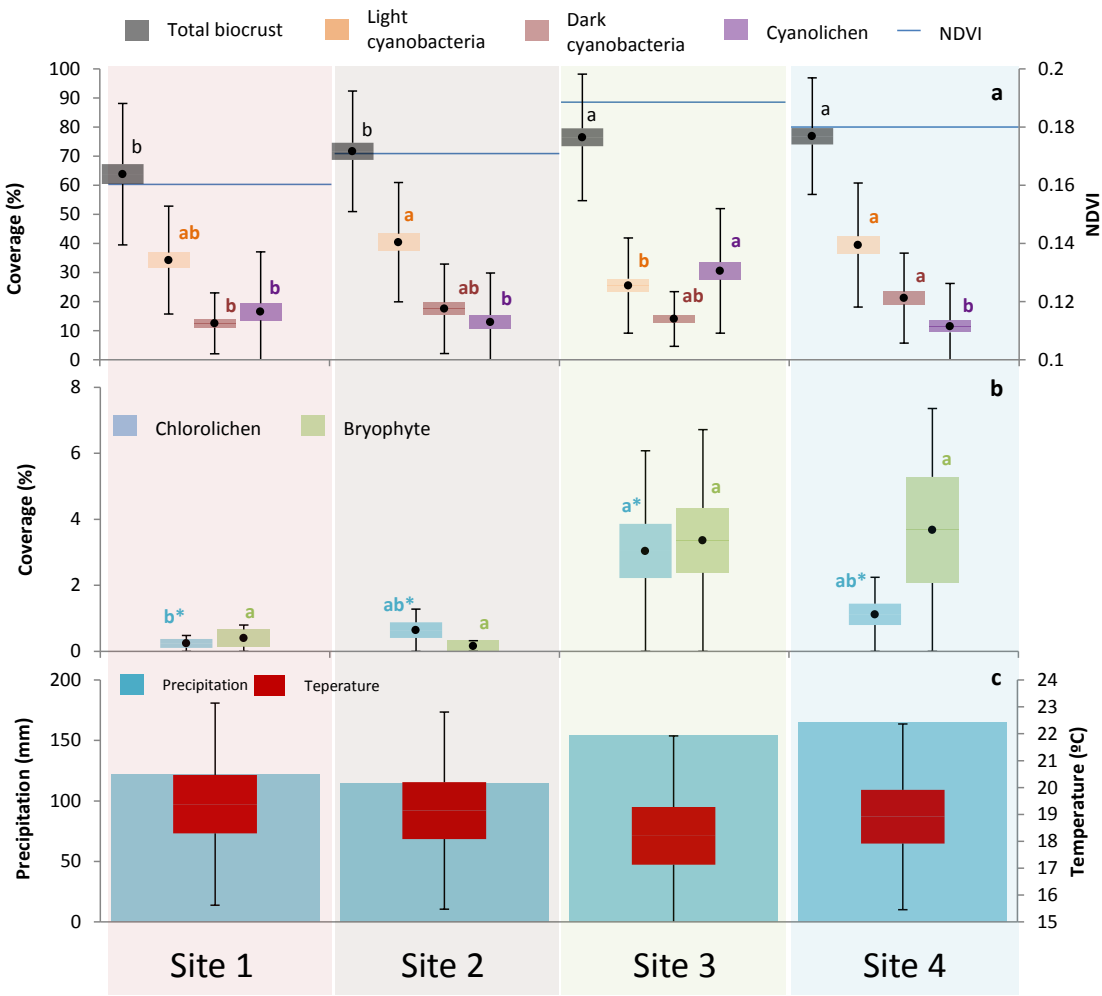

Figure 4: Biological soil crust coverage, composition, and NDVI values calculated from field spectra at the four study sites. NDVI of each study site shown as line and Box plots showing mean (dot) ± standard error (box) and standard deviation (whiskers) of mean biocrust, light cyanobacteria-, dark cyanobacteria-, and cyanolichen-dominated biocrust coverage (a), as well as chlorolichen- and bryophyte-dominated biocrust coverage (b). Mean annual precipitation (blue bars) and box plots showing mean (dot) ± standard error (box) and standard deviation (whiskers) of monthly temperature (red) at the four different study sites- Different letters indicate significant differences of each factor at $p < 0.05$ between sites and * indicates significant differences at $p < 0.01$.

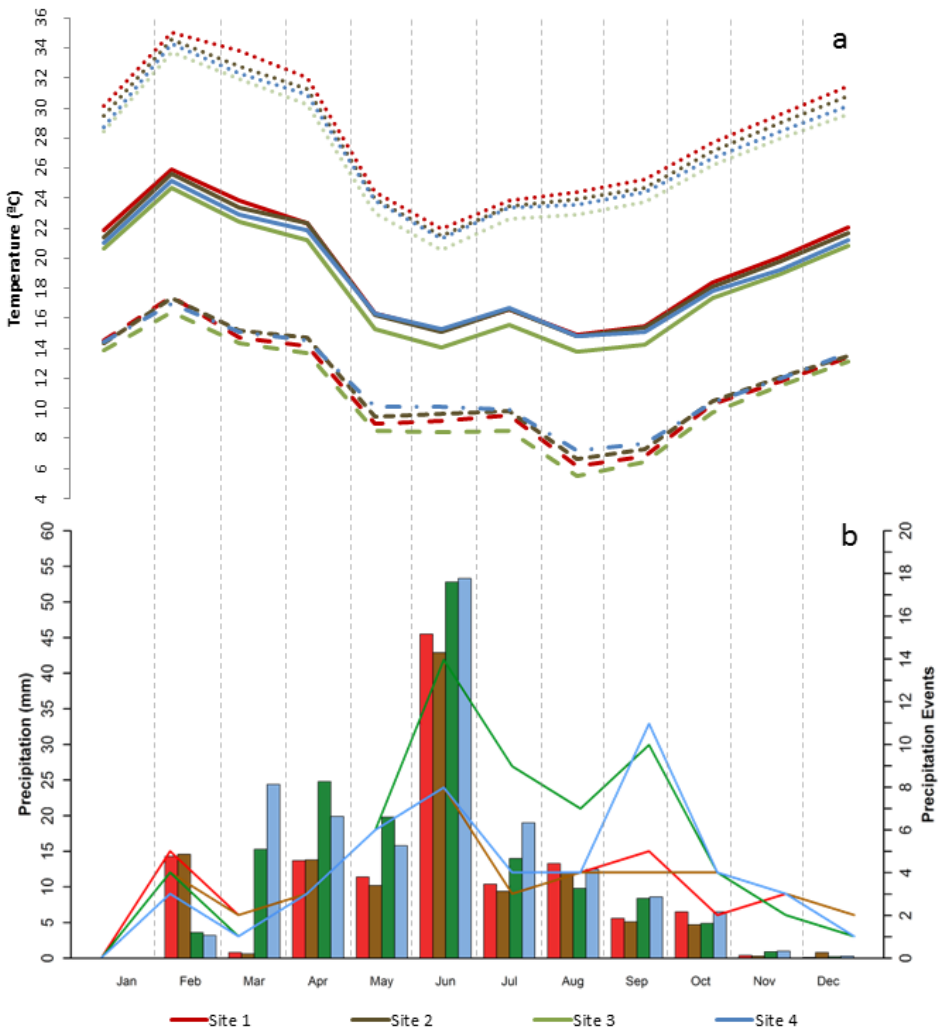

Figure 5: Monthly mean values of daily mean (solid line), maximum (dotted line), and minimum temperatures (dashed line) (a), as well as monthly precipitation amount (bars) and number of precipitation events (lines) at the four different study sites (b).

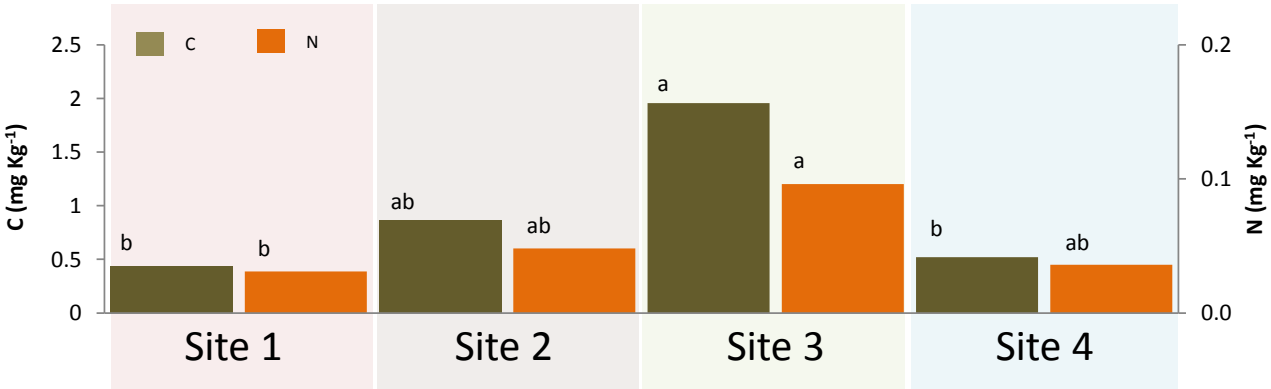

Figure 6: Soil C and N content at 7-9cm depth (b) at the four different study sites. Different letters indicate significant differences of each factor at $p < 0.05$ between sites.

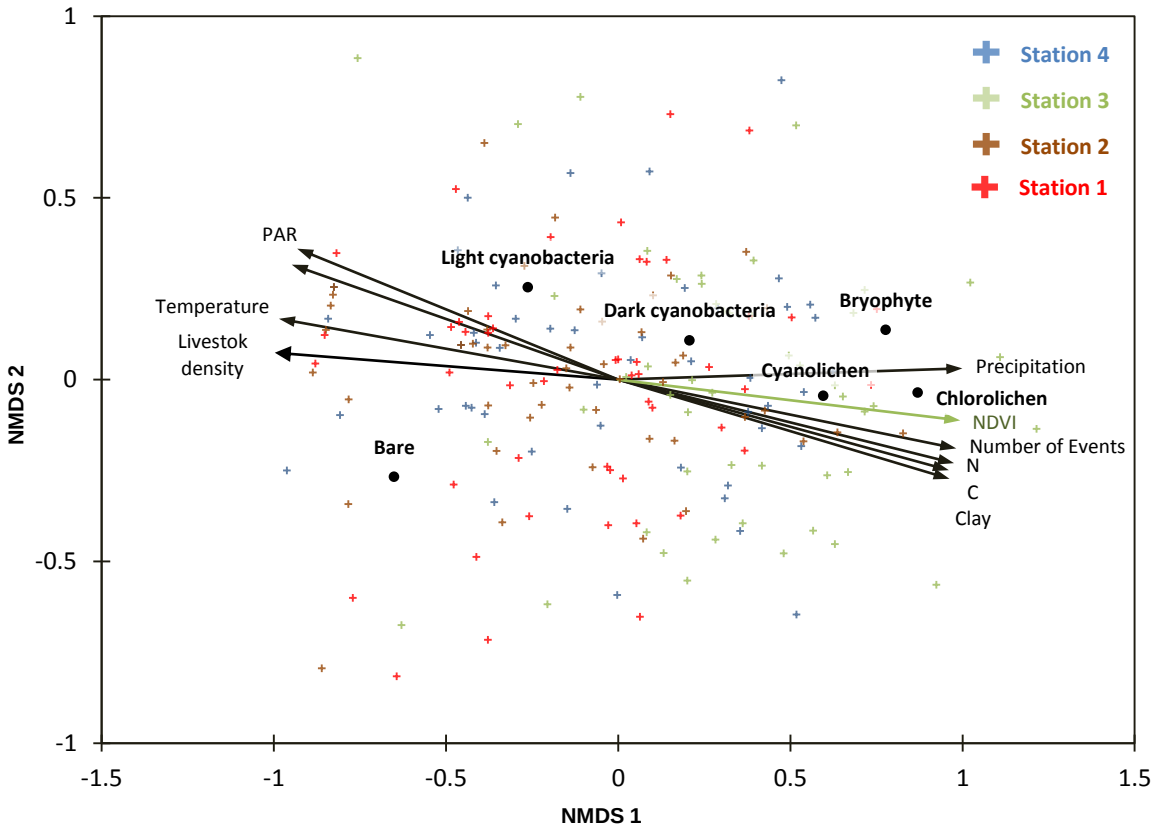

Figure 7: Non-Metric Multidimensional Scaling (NMDS) plot of Bray–Curtis similarities of different biocrust types (light cyanobacteria-, dark cyanobacteria-, cyanolichen-, chlorolichen-, and bryophyte-dominated biocrusts) along the four study sites in the Succulent Karoo, South Africa. Arrows indicate the direction of increase along a gradient of the corresponding variable (normalized difference vegetation index (NDVI; green) and temperature, photosynthetically active radiation (PAR), mean annual precipitation (Precipitation), number of precipitation events (Events), and livestock density. Length is proportional to the correlation between the predictor variable and the ordination. Crosses represent different plots and colors indicate different mesoclimate stations.