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Review Paper

Biological soil crusts of the Succulent Karoo: a review[§]

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The Succulent Karoo is characterised by a dense coverage of biological soil crusts (biocrusts) belonging to different types and successional stages. Whereas the Soebatsfontein region hosts cyanobacteria-dominated and minor amounts of lichen- and bryophyte-dominated biocrusts, the Knersvlakte comprises a rich cover of hypolithic crusts growing on the sides and undersides of quartz pebbles. Apart from dominating photosynthesizers used to classify biocrusts, each crust type hosts a rich and specific fungal and bacterial community and also diverse protists. In a remote-sensing mapping approach, soil-inhabiting biocrusts of the Soebatsfontein region covered ~27% of the surface area, whereas in the Knersvlakte soil-inhabiting biocrusts covered ~16% and hypolithic biocrusts ~42% of the region. Combining these data with biomass contents, results suggested that the Knersvlakte, despite somewhat harsher environmental conditions, harboured about 65% more biocrust biomass per surface area. In physiological measurements we observed that biocrusts emit the reactive nitrogen compounds nitric oxide and nitrous acid, showing water pulse-dependent emission patterns. In addition, CO_2 gas fixation showed characteristic type-specific patterns depending on climatic conditions. Long-term microclimate measurements along a gradient revealed that forecasted climate and land-use change may be detrimental for biocrusts with potentially adverse effects on soil stability and overall fertility of the Succulent Karoo.

Keywords: biodiversity, climate change, CO_2 gas exchange, reactive nitrogen compounds, remote sensing

Introduction

Biological soil crusts (biocrusts) form a regular soil surface community covering about 12% (~18×10^6 km²) of the global terrestrial surface area mainly in dryland regions all over the world (Rodríguez-Caballero et al. 2018a). They are composed of varying proportions of photosynthesizing cyanobacteria, lichens and bryophytes, which grow together with heterotrophic fungi, bacteria and archaea as well as microfauna such as protozoa, nematodes and microarthropods (Büdel et al. 2016; Darby and Neher 2016; Maier et al. 2016; Rosentreter et al. 2016; Seppelt et al. 2016). Biocrusts form encrustations covering the uppermost millimetres of the soil, thus effectively stabilising surface soils (Bowker et al. 2008). They have been shown to fix carbon (C) and nitrogen (N), thus bringing nutrients into the mostly impoverished soils and influence water cycling and plant growth in drylands (Zhang et al. 2015; Barger et al. 2016; Chamizo et al. 2016; Sancho et al. 2016; Whitney et al. 2017; Rodríguez-Caballero et al. 2018b).

In a long-term biodiversity mapping approach of southern Africa conducted within the project BIOTA South (financed by the German Ministry of Education and Research; BMBF), we studied the occurrence and composition of biocrusts along a >2 000 km transect running from north-eastern Namibia to south-western South Africa, i.e. the Cape of Good Hope (Büdel et al. 2010). Along that transect, 28 biodiversity observatories were investigated with regard to the presence and species composition of biocrusts, and in all six major biomes along the transect biocrusts were found (Büdel et al. 2009, 2010; Haarmeyer et al. 2010; Mager and Hui 2012). During that study, a total of 120 species of cryptogams comprising 58 cyanobacteria, 29 green algae, one heterokont alga, 12 cyanolichens, 14 chlorolichens, two genera of liverworts and two genera of mosses were identified (Büdel et al. 2009). In the course of the project, two observatories within the Succulent Karoo proved to be of particular interest, i.e. Soebatsfontein (no. S22; 30°11′11.40″ S, 17°32′36.14″ E, elevation 392 m above sea level [asl]) and Goedehoop (no. S26; 31°16′36.78″ S, 18°35′29.48″ E, elevation 245 m asl; Haarmeyer et al. 2010) in the Knersvlakte, and thus these and the adjacent regions were studied in more detail in subsequent follow-up studies (Figure 1).

Study areas

The observatory at Soebatsfontein is located ~50 km south-west of Springbok about 30 km from the west coast

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[§] This article is from the 'Karoo Special Issue: Trajectories of Change in the Anthropocene'.
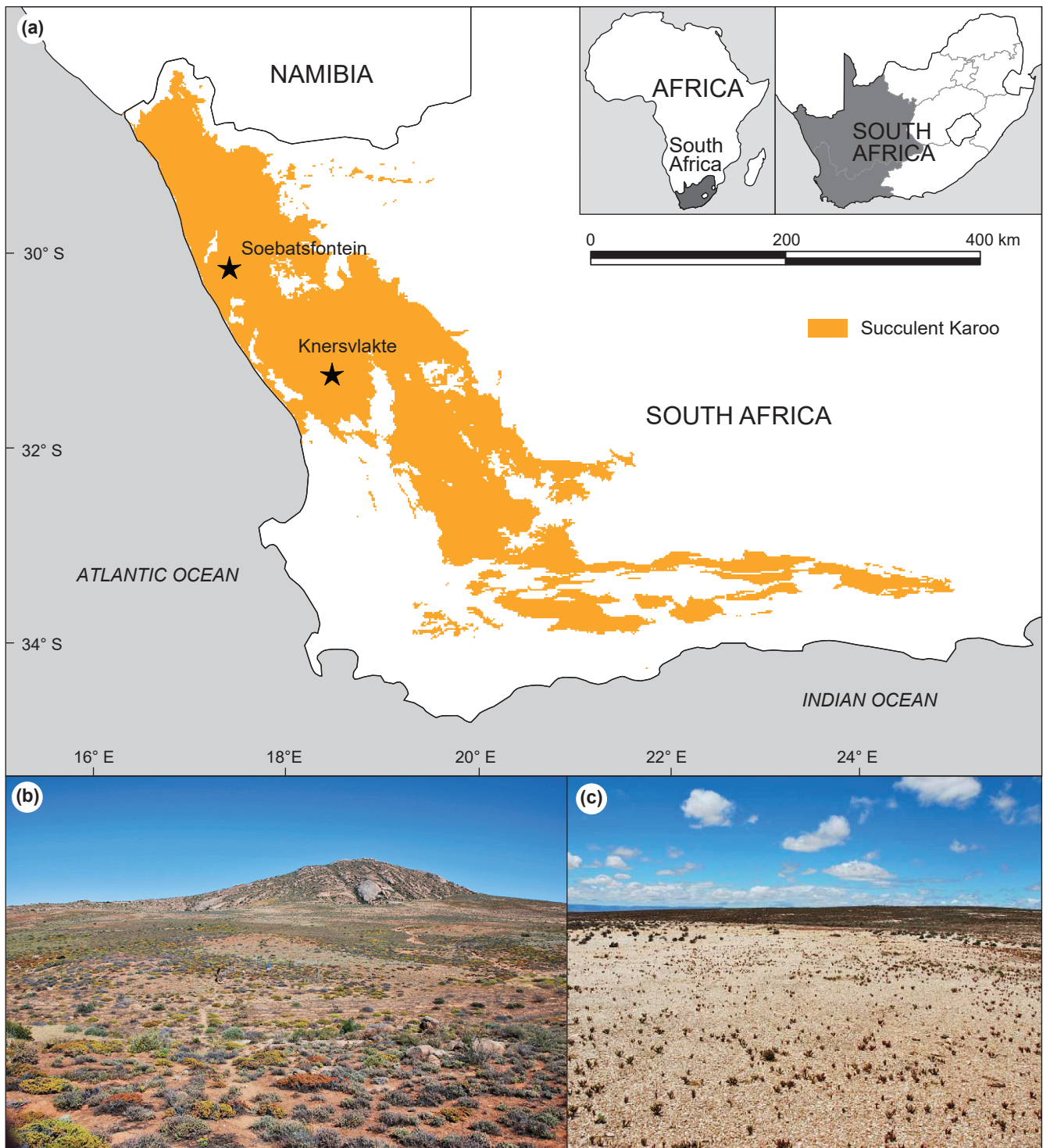
Figure 1: Spatial delimitation of Succulent Karoo and the two study areas (a), and overview of the landscape at Soebatsfontein (b) and in the Knersvlakte (c)

of South Africa (Figure 1). The climate is characterised by arid conditions (aridity index: 0.09) and moderate seasonality with mean annual precipitation of 131 mm mainly falling during the winter months. The mean annual air temperature is 19.4 °C ranging from 3.5 °C during winter to 42.5 °C on hot summer days. The region is characterised by gently undulating hills and broad valleys with some gneiss

outcrops forming local inselbergs (Haarmeyer et al. 2010). A characteristic morphological feature within the region are heuweltjies, i.e. fossil termite mounds with a diameter of up to 32 m, which can be easily recognised in high-resolution remote sensing imagery (Figure 2a), forming fertile islands with altered soil properties causing the vegetation to differ from that on the surrounding matrix soils (Kunz et al.
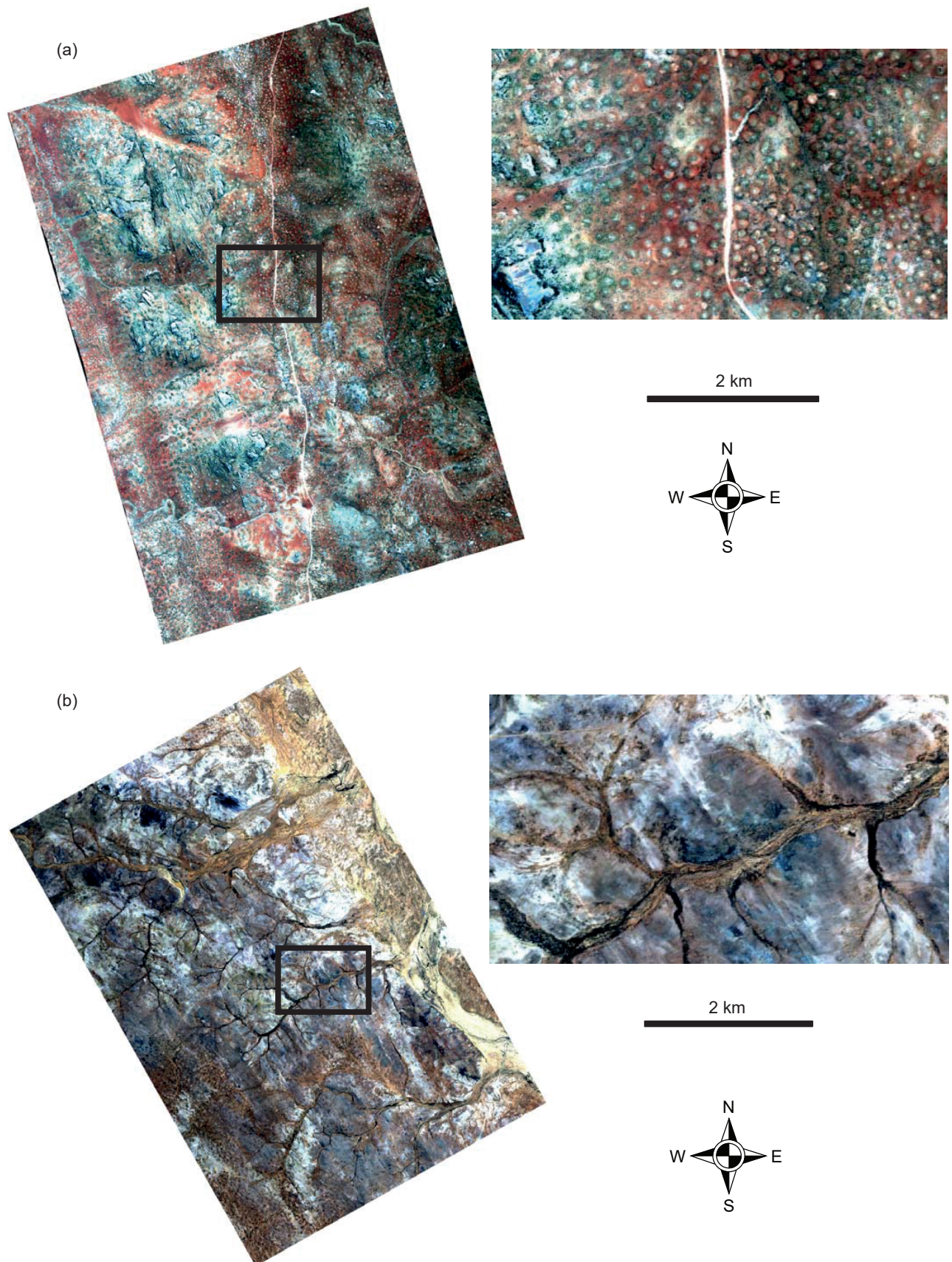
Figure 2: Research site at Soebatsfontein (a) and in the Knersvlakte (b). RGB composites of CASI 2 images; in both images, the central marked area has been enlarged and is shown on the righthand side

2012). The dominating soil groups within the region are Leptosols, Durisols and Cambisols. While Durisols occur on heuweltjies, Cambisols are mainly found in lower valleys between them, where deeper substrates occur. Leptosols mainly occur in areas with shallow bedrock. The vegetation is dominated by leaf-succulent dwarf shrubs, and after sufficient rainfall a rich variety of annuals and geophytes can be observed. The plant families dominating within the area are Aizoaceae and Asteraceae (Haarmeyer et al. 2010).

The observatory of Goedehoop, also known under the name Flaminkvlakte, is located within the Knersvlakte, about 40 km north of Vanrhynsdorp, east of the N7 National Road (Figure 1; Haarmeyer et al. 2010). The climate is arid (aridity index: 0.08) and rainfall shows moderate seasonality with 124 mm of annual precipitation mainly falling during the winter months and peaking in May. The mean annual air temperature is 19.9 °C, reaching minima of 3.5 °C and maxima of 46 °C. The region is characterised by gently undulating plains with intruding quartz veins and a river valley with multiple small tributaries (Figure 2b). Whereas uncovered soils and vascular vegetation occur along the tributaries, the area in-between is characterised by a dense cover of quartz gravel, causing the region to be named Knersvlakte (Figure 2b). The soils within the region comprise Cambisols, Leptosols, Fluvisols and Solonchak. While Solonchaks are typical for salt-enriched quartz fields, Cambisols occur on less saline substrates and are characterised by an intense red colour and loamy texture. Fluvisols occur in dry rivers with frequent occurrence of the shrub *Galenia africana*, whereas Leptosols are found over shallow bedrock or larger quartz outcrops. The vegetation is dominated by leaf-succulent dwarf shrubs comprising two distinct vegetation types; outside the quartz fields, taller shrubs, mainly belonging to the families Aizoaceae, Chenopodiaceae and Asteraceae, are found, whereas the quartz fields are typically inhabited by a rich variety of compact dwarf succulent Aizoaceae (Haarmeyer et al. 2010). One hundred and fifty-five plant taxa (species and subspecies) are restricted to the quartz fields with the majority of them being local or regional endemics (Schmiedel 2002).

Biocrust types

Our studies in the Succulent Karoo demonstrated that biocrusts are complex communities that can be classified according to the dominating photoautotrophic organism (Büdel et al. 2009). These biocrust types differed between the two study sites. At Soebatsfontein, cyanobacteria-dominated biocrusts prevailed. After local disturbance, light cyanobacteria-dominated biocrusts were the first to form thin layers of patchy darker colouration on previously bare soils (Figure 3). Under favourable climatic conditions without disturbance these started to transform into well-established dark cyanobacteria-dominated biocrusts, recognised by their uniformly dark-coloured surface, already within the first wet season after disturbance (Figure 3d; Dojani et al. 2011). Frequently, this biocrust type was accompanied by cyanobacterial lichens, i.e. lichens with cyanobacteria as the photobiont, thus forming cyanolichen-dominated biocrusts. These successional stages of cyanobacteria-dominated

biocrusts were necessary predecessors for chloro-lichen- and bryophyte-dominated biocrusts to develop (Figure 3e and f). Thus, only if soil conditions remained stable and water availability was sufficient, bryophyte-dominated biocrusts could develop within two years after disturbance (Dojani et al. 2011). Within this group the two types of liverwort- and moss-dominated biocrusts can be distinguished, and both of them, as well as chloro-lichen-dominated biocrusts, occurred at Soebatsfontein covering ~2%–4% of the surface area (Figure 3). The two bryophyte-dominated biocrusts colonised somewhat different microhabitats, as liverwort-dominated crusts grew in unshaded open spots if enough water was available, whereas moss-dominated biocrusts mainly occurred under shrubs and thus in shaded habitats (Weber et al. 2012). An additional, but rather rare, biocrust type comprised cyanobacteria growing on the lower part and the sides of translucent quartz pebbles, forming so-called hypolithic biocrusts. This biocrust type occurred independently of succession wherever quartz pebbles and favourable climatic conditions occurred (Figure 3h). Hypolithic biocrusts are exposed to lower light intensities, decreased temperature amplitudes and higher moisture contents compared to the surrounding soil conditions (Schmiedel and Jürgens 2004; Weber et al. 2013).

At Goedehoop, most of these biocrust types could also be found in areas with comparable water availability, but in differing composition. Here, hypolithic biocrusts formed the most prominent biocrust type, as ~44% of the area was covered by quartz pebbles with 69% of them being colonised by a hypolithic crust (Weber et al. 2013). Soils adjacent to the dry rivers hosted light and dark cyanobacteria-dominated as well as cyanobacterial lichen-dominated biocrusts. In stable biocrust regions some chlorolichen-dominated biocrusts also occurred, whereas bryophyte-dominated biocrusts were not or only rarely observed.

The successional sequence described above, starting with cyanobacteria- and leading towards lichen- and bryophyte-dominated biocrusts, has been described from a variety of dryland regions, for example the Tengger Desert in China (Hu and Liu 2003), the Negev Desert in Israel (Kidron et al. 2008), the Tabernas Badlands in Spain (Lázaro et al. 2008) and the Colorado Plateau in the USA (Belnap et al. 2013). Hypolithic crusts have been described to occur widely within deserts, such as the Atacama Desert of Chile (Warren-Rhodes et al. 2006), the Mojave Desert of the USA (Schlesinger et al. 2003), the Negev Desert in Israel (Berner and Evenari 1978), the Taklimakan Desert (Warren-Rhodes et al. 2007), Australia's Northern Territory (Tracy et al. 2010) and Antarctica (Chan et al. 2013), as long as translucent (mostly quartz) stones were present and sufficiently embedded in the soil (Pointing 2016). Hypolithic crusts were observed to even occur under hyper-arid conditions that were too dry for any other crust type to develop (Warren-Rhodes et al. 2006).

Biodiversity of biocrusts

Biocrusts comprise photoautotrophic organisms accompanied by heterotrophic decomposers and inhabited/grazed by microfauna. Although the different organism groups inhabiting

Figure 3: Different types of biocrusts occurring in the Succulent Karoo. During succession, starting out with bare soil (a), light cyanobacteria- (b), dark cyanobacteria- (c) and dark cyanobacteria-dominated biocrusts with cyanolichens (d) often form in a subsequent manner. From the latter two types chlorolichen- (e), moss- (f) or liverwort-dominated biocrusts (g) may form. Hypolithic biocrusts (h) rely on translucent quartz pebbles and form independently of succession

biocrusts of the Succulent Karoo have been investigated in varying detail, their overall diversity is quite impressive.

Photoautotrophs

In general, the photoautotrophic organisms in biocrusts belong to the groups cyanobacteria, algae, lichens (cyano- and chlorolichens) and bryophytes (liverworts and mosses; Belnap et al. 2016) and all of them also occur in the Succulent Karoo. The cyanobacterial diversity of Succulent Karoo biocrusts has been studied in detail by Dojani et al. (2014), who used both morphological and genetic techniques (a so-called biphasic approach) to determine the species composition and diversity. They identified 33 species from 12 genera at Soebatsfontein, while 24 species belonging to 13 genera were identified in the Knersvlakte by means of morphological identification techniques. By means of genetic determination based on 16S rRNA gene sequences, 59 operational taxonomic units (OTUs) were identified in biocrusts of Soebatsfontein, while 25 OTUs were determined in Knersvlakte samples (based on a 95% similarity level). At Soebatsfontein and in the Knersvlakte, 17 and 14 taxa were identified by means of both (morphological and molecular) techniques, respectively. The genera *Leptolyngbya*, *Microcoleus*, *Phormidium*, *Pseudanabaena* and *Scytonema* showed high species diversity at both sites (Dojani et al. 2014). There were some differences in species composition between both sites, which may be linked to differing moisture conditions,

as observed in studies in the Negev dunefields (Kidron et al. 2010), but varying sampling intensity at both Succulent Karoo sites may also be relevant here (Dojani et al. 2014).

Lichens within biocrusts of the Succulent Karoo have not been a particular study focus, but during the BIOTA South studies, 12 cyanolichen and 14 chlorolichen species were identified in biocrusts along the transect (Büdel et al. 2009), with taxa such as *Psora* spp. and *Toninia* spp. being frequently observed in the Soebatsfontein region. Lichens colonising different habitats along the BIOTA South transect were investigated by Zedda and Rambold (published in Haarmeyer et al. 2010), who listed 23 soil-inhabiting lichen taxa for Soebatsfontein and 32 for the Knersvlakte, the majority of them probably serving as biocrust compounds.

Unfortunately, bryophytes of biocrusts in southern Africa have not been studied in greater detail, yet. Presently, only two genera of liverworts and three genera of bryophytes have been found along the BIOTA South transect (Büdel et al. 2009). In the Soebatsfontein region, mosses occurred quite regularly under shrubs, provided mesoclimatic conditions were favourable (see section on global change below), and here *Ceratodon purpureus* was a dominant species (Weber et al. 2012). Occasionally, liverworts of the genus *Riccia* were observed in unshaded areas with sufficient water availability.

In addition, quite a number of different algae, i.e. 29 green algae and one heterokont alga, were discovered in observatories along the BIOTA transect (Büdel et al. 2009, 2010),

and in the Succulent Karoo 19 different taxa were found. Generally, algae did not dominate but grew in lower organism numbers within biocrusts (T Friedl, University of Göttingen, pers. comm., 2006) and were therefore not appropriate for the delineation of biocrust types.

In general, the biodiversity of photoautotropic organisms in biocrusts has been reported to be large, with ~320 species of cyanobacteria, ~350 species of eukaryotic algae, ~550 lichen and ~320 bryophyte species being reported on a global scale (Büdel et al. 2016; Rosentreter et al. 2016; Seppelt et al. 2016). The cyanobacterial genera prominent within biocrusts of the Succulent Karoo are well-known biocrust taxa that also fulfill key functional roles, for example stabilisation of the soil and nutrient input (Büdel et al. 2016). In addition, many lichens, in particular frequently occurring species, such as *Psora* spp., *Toninia* spp. and *Diploschistes* spp., have been described to occur in multiple biocrust habitats under varying macroclimatic conditions (Büdel et al. 2014; Leavitt et al. 2018).

Heterotrophic decomposers
The heterotrophic decomposers within different biocrust types as compared with bare soil have recently been investigated for the Soebatsfontein region (Maier et al. 2018). Quantitative real-time PCR estimates revealed that 16S and 18S rRNA gene copy numbers of bacteria and fungi increased from bare soil to dark cyanobacteria-, chlorolichen-, and moss-dominated biocrusts with the relevance of fungi increasing along a successional gradient (Figure 4a). In addition, the alpha diversity of bacteria and archaea within biocrusts increased along succession with median species numbers (i.e. number of OTUs) ranging between 8 178 for bare soil and 11 011 for moss-dominated biocrusts at a sequencing depth of 48 009 reads per sample. Using the same procedure, a Shannon index ranging between 9.7 for bare soil and 11.0 for moss-dominated biocrusts was calculated, which is in the same range as the bacterial diversity within temperate grassland and forest soils (Figure 4b; Kaiser et al. 2016; Maier et al. 2018). Bacteria and archaea belonged to 13 bacterial and one archaeal phyla. Whereas Bacteriodetes, Cyanobacteria and Alphaproteobacteria had the highest relative abundance in bare soil, additional phyla, such as the Acidobacteria, Chloroflexi, Planctomycetes and Verrucomicrobia, were also relevant in biocrusts (Figure 4c). The bacterial/archaeal community composition on the phylum level appeared fairly similar for the different types of biocrusts, whereas there were clear differences between communities on the family level. The relative abundance of OTUs related to the family Phormidiaceae were increased in cyanobacteria-dominated biocrusts, whereas Chitinophagaceae were more abundant in chlorolichen- and moss-dominated biocrusts compared with bare soil. Flavobacteriaceae, Flammeovirgaceae, Rhodobacteraceae and Trueperaceae were found more frequently in bare soil compared with biocrusts (Figure 4d).

Similar results have been obtained on the Colorado Plateau, where gene copy numbers and diversity values increased with successional stage (Garcia-Pichel et al. 2003). An investigation of the microbial diversity within biocrusts of the Kalahari Desert obtained significantly lower Shannon indices (~3–5). This difference is probably due to the use of different sequencing platforms, primers and average number of sequences per sample (1 004 vs 48 009). However, observed phyla were similar with Acidobacteria, Actinobacteria, Bacteriodetes, Chloroflexi, Cyanobacteria and Proteobacteria being abundant (Elliott et al. 2014). In addition, in lichen-dominated biocrusts of the Tabernas Badlands, phyla were similar with Actinobacteria, Proteobacteria and Bacteriodetes being most abundant (Maier et al. 2014). In a study investigating the microbial community in different biocrust types and bare soil of the Tengger Desert, observed species numbers were lower but also increasing along biocrust successional stages. Some phyla showed similar patterns, such as Acidobacteria and Chloroflexi, being more abundant in biocrusts compared with bare soil, whereas others, such as Actinobacteria and Alphaproteobacteria, showed different patterns, while Verrucomicrobia were absent (Liu et al. 2017). A change in the bacterial composition along the successional stages was also observed in biocrusts of the Gurbantunggut Desert (Zhang et al. 2016). Bacterial communities in cold desert biocrusts of south-western Idaho, USA, comprised overall similar bacterial phyla, but Actinobacteria had a much higher abundance of ~40%, whereas Acidobacteria and Verrucomicrobia were less abundant (Blay et al. 2017).

Microfauna
In an initial exploratory study the protists within cyanobacteria-, chlorolichen-, and moss-dominated biocrusts from the Soebatsfontein region were investigated (Dumack et al. 2016). During the study, 21 000–27 000 cultivable individuals belonging to the groups of amoebae, flagellates and ciliates were determined per gram dry weight of crust material. In total, 23 different morphotypes were identified with gliding bodonids, Spumella-like chrysomonads, heteroloboseans and glissomonads being particularly abundant. Protist abundance was highly variable between samples and thus diversity and abundance did not differ significantly between biocrust types. As high diversity numbers and biocrust type-specific diversity patterns of microfauna have been observed in biocrusts occurring in other parts of the world (e.g. south-western USA: Darby et al. 2007), we expect a much higher and crust type-specific diversity of microfauna to occur within the Succulent Karoo.

Biocrust classification and mapping

Biocrust coverage within the Soebatsfontein and Knersvlakte region was mapped by means of a newly developed hyperspectral remote-sensing technique, which proved to be also transferable to other regions of the world (Weber et al. 2008; Rodríguez-Caballero et al. 2017a, 2017b). This technique utilises the method of continuum removal (Clark and Roush 1984) to analyse the spectral traits of biocrusts allowing for discrimination between biocrusts and bare soil (Weber et al. 2008; Rodríguez-Caballero et al. 2017a, 2017b). At Soebatsfontein, ~27% of a 2 837 ha site was classified as biocrusts, whereas in the Knersvlakte only ~16% of the area was classified as biocrusts, while ~42% of the area covering 2 351 ha was classified as quartz pebbles potentially hosting hypolithic
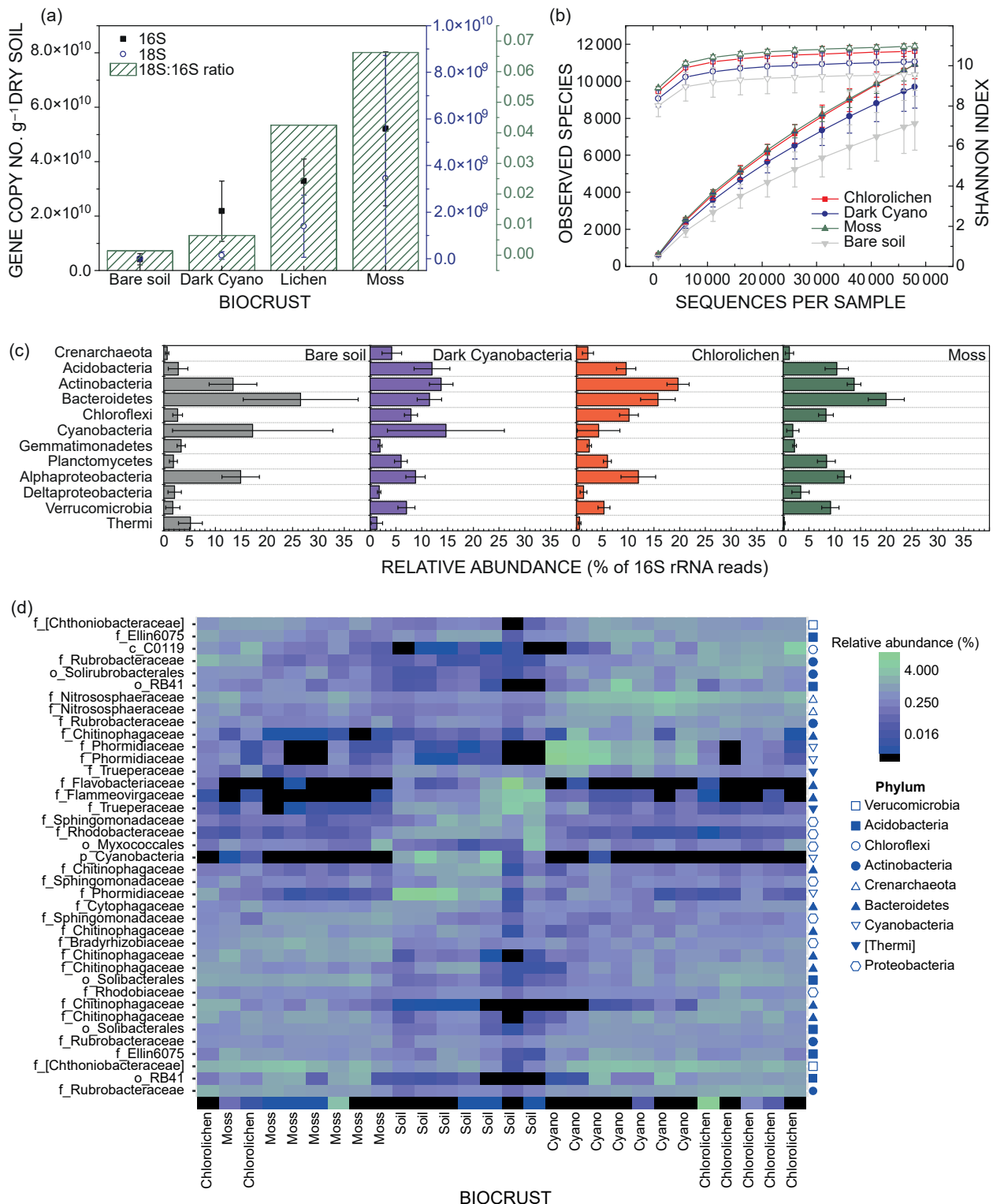
Figure 4: Fungal and bacterial abundance and diversity in bare soil and in heterotrophic fraction of dark cyanobacteria-, chlorolichen-, and moss-dominated biocrusts of the Soebatsfontein region. (a) Quantitative real-time PCR estimates of fungal and bacterial abundance and its ratio in bare soil and biocrust types. (b) Alpha diversity measures calculated from Illumina 16S rRNA gene sequencing data of bacteria in bare soil and biocrust types, shown as number of observed species (number of operational taxonomic units; filled symbols) and Shannon index (open symbols) depending on sequencing depth. (c) Relative abundance, shown as percentage of 16S rRNA reads, of bacterial and archaeal phyla in bare soil and biocrust types. (d) Relative abundance of bacterial and archaeal families in bare soil and biocrust types, shown as heatmap using ordination method-based ordering of the rows and columns (ordination method: NMDS; ecological distance method: Bray–Curtis). The most abundant taxa across all samples are shown. Note that apparent clusters at the far right/left or top/bottom of the heatmap may actually belong to the same one. For further details and methods see Maier et al. (2018)
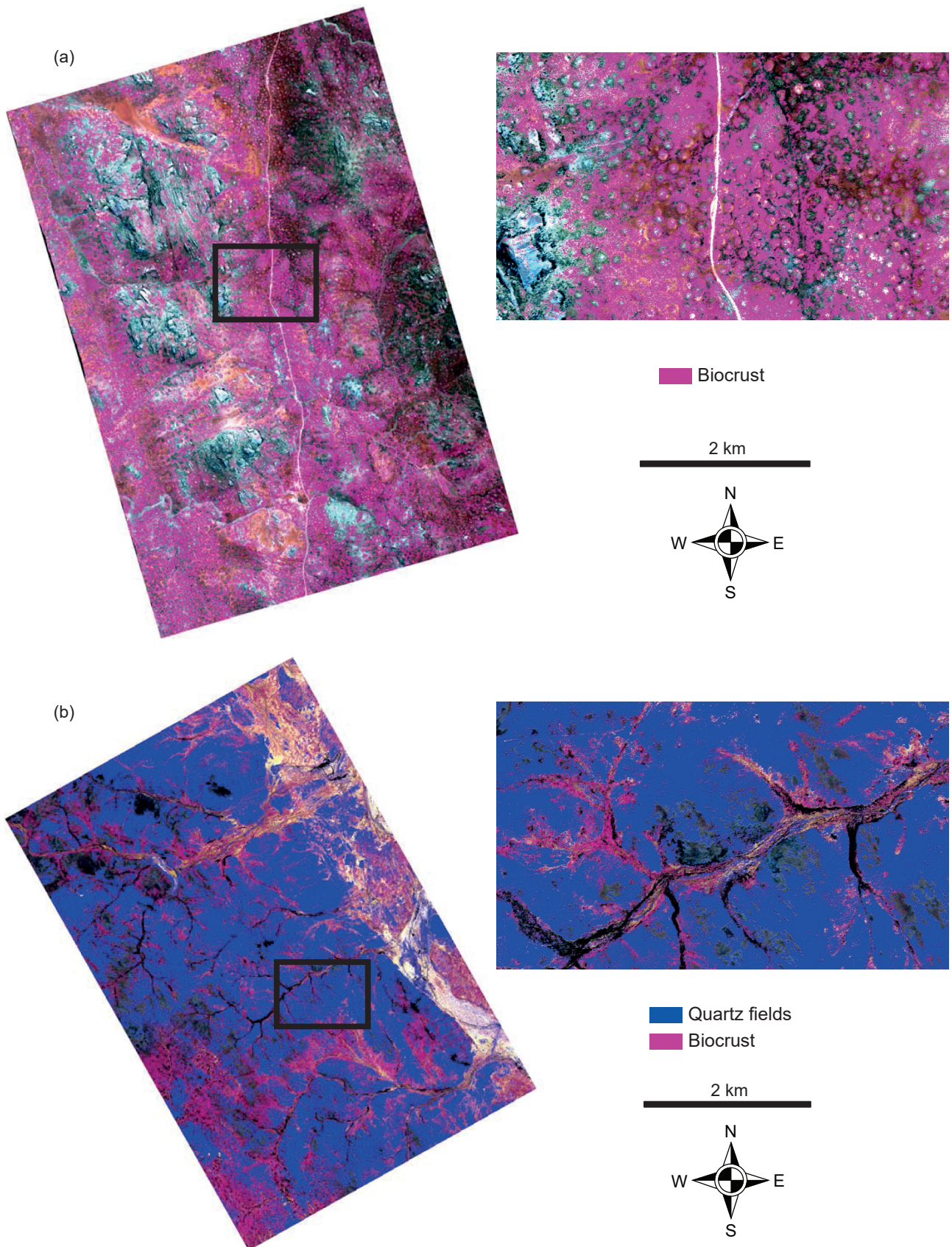
Figure 5: Research site at Soebatsfontein (a) and in the Knersvlakte (b) shown as RGB composites from CASI 2 images with biocrust and quartz field classification. In both images, the central marked area has been enlarged and is shown on the righthand side

biocrusts (Figure 5). In the next step, the biomass of the photoautotrophic compounds of biocrusts, expressed as the chlorophyll content, were analysed for soil-inhabiting and hypolithic crusts (Table 1) and thus the overall habitat biomass of biocrusts could be determined. Chlorophyll contents per surface area were somewhat higher for soil-inhabiting biocrusts of Soebatsfontein compared with soil-inhabiting and hypolithic crusts in the Knersvlakte, the latter two being very similar. Nevertheless, as the overall cover value of biocrusts was higher in the Knersvlakte compared with those at Soebatsfontein (58 vs 27%), mean habitat biomass values were also higher (i.e. 78 vs 47 mg m^{-2}, respectively). These higher biomass values were attained despite the somewhat harsher environmental conditions, but facilitated by the additional and widely available hypolithic habitat with favourable microclimatic conditions (Schmiedel and Jürgens 2004; Weber et al. 2013; Rodríguez-Caballero et al. 2017a).

The biomass values recorded for soil-inhabiting and hypolithic crusts are in a similar range as those previously reported for cyanobacteria- and cyanolichen-dominated biocrusts from Inner Mongolia, the Negev Desert in Israel, and the south-western USA (Kidron et al. 2012; Lan et al. 2012; Green and Proctor 2016). In other studies, quartz fields have been described as a stable habitat for cyanobacteria, algae, lichens and mosses, and the communities have been observed as ecologically relevant primary producers (Schlesinger et al. 2003; Warren-Rhodes et al. 2006; Temina and Kidron 2015; Pointing 2016).

Nitrogen- and carbon-cycling within biocrusts of the Succulent Karoo

Biocrusts have been shown to play a relevant role in regional and even global N cycling, as cyanobacteria and also other bacteria within the biocrusts fix atmospheric N (Elbert et al. 2012; Pepe-Ranney et al. 2015; Barger et al. 2016). After fixation, the N could be used for biomass formation (Veluci et al. 2006), but N compounds could also be released into the surrounding environment, being leached into deeper soil strata (Thiet et al. 2005), or redistributed by wind and water erosion (Eldridge and Rosentreter 1999; Barger et al. 2006). In a study conducted using biocrust and bare soil samples from the Soebatsfontein region, we investigated if and to what extent reactive N compounds, such as nitric oxide (NO), nitrous acid (HONO), and nitrogen

dioxide (NO$_2$), are released during wetting and drying cycles (Weber et al. 2015). For this experiment, the samples were watered to full water holding capacity (WHC) and the release of reactive compounds at 25 °C (room temperature) was measured during drying. Whereas no measurable amounts of NO$_2$ were emitted by any of the samples, clear emission patterns were recorded for NO and HONO. The highest emissions were recorded for dark cyanobacteria-dominated biocrusts, which emitted maximum amounts of ~173 ± 18 ng m^{-2} s^{-1} of HONO-N and ~208 ± 15 ng m^{-2} s^{-1} of NO-N at relatively low water contents ranging between 20% and 25% WHC (Figure 6). In addition, light cyanobacteria-dominated biocrusts emitted NO and HONO, but at lower concentrations and over a wider moisture range between 20% and 40% WHC. Chlorolichen- and moss-dominated biocrusts showed even lower maxima over a wider range of water contents, while emissions from bare soil were negligible. If such precipitation-linked emissions occur in drylands on a global scale, they may account for 1.7 Tg y^{-1} (1.1 Tg y^{-1} of NO-N and 0.6 Tg y^{-1} of HONO-N) of reactive N emissions, corresponding to ~20% of global NO emissions from soils under natural vegetation (Stocker et al. 2013; Weber et al. 2015). In a later study investigating the NO and HONO emissions in Cyprus, values were clearly lower for biocrusts and highest for bare soil samples. In this study, emissions correlated with nitrite and nitrate contents, which has not been observed for the South African samples (Meusel et al. 2018).

As described above, biocrusts are composed of photo-autotrophic producers, heterotrophic decomposers (i.e. bacteria, fungi and archaea) and microfaunal consumers. Thus, their overall CO$_2$ gas exchange during active daytime periods is mostly the sum of photoautotrophic photosynthesis and heterotrophic respiration processes, whereas during night-time all organism groups respire in an active physiological state. For the Soebatsfontein region, the three main types of cyanobacteria-dominated biocrusts with cyanolichens (cyanobacteria/cyanolichen-dominated), chlorolichen-dominated and moss-dominated biocrusts have been thoroughly analysed by means of CO$_2$ gas exchange chamber measurements. Data were assessed under controlled laboratory conditions to investigate the physio-logical response to varying water-, light-, and temperature conditions, and in the field to confirm that laboratory measurements conformed to the response under natural conditions (Weber et al. 2012; Tamm et al. 2018). Whereas

Table 1: Determination of habitat biomass of biocrusts, based on biocrust biomass and biocrust cover values. Biocrust biomass per surface area is shown as chlorophyll (chl) *a* and chl *a*+*b* contents, biocrust cover values are given as absolute values within remote sensing imagery and as fractional cover values. Habitat biocrust biomass values were calculated by multiplying biomass values per surface area with surface area. Whereas in Soebatsfontein biocrusts mainly occur on soil, the Knersvlakte comprises both soil-inhabiting and hypolithic crusts

| | | Soebatsfontein | Knersvlakte | |
		Biocrusts	Soil-inhabiting biocrusts	Hypolithic crusts
Biocrust biomass	Chl *a* content (mg m²)	120.8 ± 38.2	86.1 ± 37.8	87.5 ± 37.9
	Chl *a*+*b* content (mg m²)	177.9 ± 49.2	133.7 ± 59.9	135.2 ± 48.7
Biocrust habitat coverage	Area (ha) and fractional coverage (%)	766 (27%)	378 (16%)	986 (42%)
Habitat biocrust biomass	Total Chl *a* content (kg)	925	325	862
	Total Chl *a*+*b* content (kg)	1 356	505	1 333
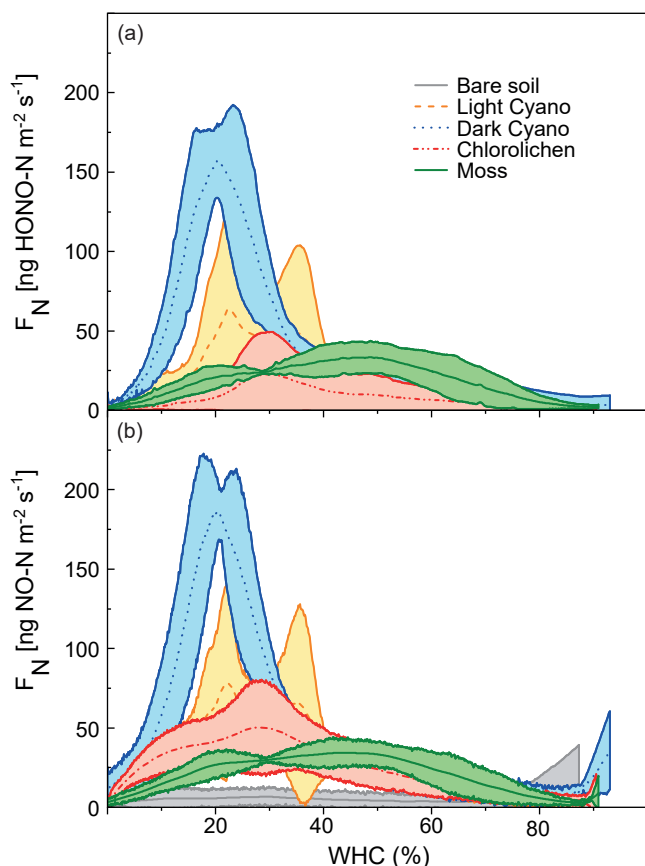
Figure 6: Characteristic emission patterns of nitrous acid (HONO-N) (a) and nitric oxide (NO-N) (b) from bare soil, light cyanobacteria-, dark cyanobacteria-, chlorolichen-, and moss-dominated biocrusts collected in the Soebatsfontein region during wetting and drying cycles. Data are shown as emissions (in ng m^{-2} s^{-1} of HONO-N or NO-N, respectively) at varying water contents defined as percentage of water holding capacity (WHC). The 100% WHC corresponds to 5.14 ± 1.52, 6.81 ± 0.13, 7.41 ± 1.84, 7.83 ± 0.40, and 9.68 ± 0.96 mm precipitation equivalent in bare soil, light cyanobacteria-, dark cyanobacteria-, chlorolichen-, and moss-dominated biocrusts, respectively. For further details and methods see Weber et al. (2015)

their general response patterns were similar, as they had a temperature and water optimum and attained saturation at high light intensities, they also showed crust type-specific physiological characteristics (Figure 7). With regard to water, cyanobacteria/cyanolichen-dominated biocrusts attained their optimum at the lowest water content (0.52–0.78 mm H$_2$O), followed by chlorolichen- (0.75–1.15 mm H$_2$O) and moss-dominated biocrusts (1.76–2.38 mm H$_2$O). In contrast, the water compensation point, i.e. the lowest water content at which positive net photosynthesis (NP) rates are attained, did not differ between biocrust types. Cyanobacteria/cyanolichen-dominated biocrusts needed the highest light intensities before saturation was attained, followed by chlorolichen-dominated with medium and moss-dominated biocrusts with lowest saturating light intensities. Regarding temperature, cyanobacteria/cyanolichen-dominated biocrusts had the highest optimum at 37 °C, followed by chlorolichen- and moss-dominated biocrusts (both 22 °C).

Thus, our data revealed that cyanobacteria/cyanolichen-dominated biocrusts are well-adapted to unshaded high-temperature environments and lower amounts of rainfall. Chlorolichen-dominated biocrusts need somewhat more favourable environmental conditions, i.e. larger amounts of water and lower temperatures during active periods. Moss-dominated biocrusts make the highest demands, as they need relatively large amounts of water and lower light and temperature conditions to attain optimum conditions for photosynthesis. The highest NP rates under optimal conditions were attained by chlorolichen-dominated biocrusts (3.9 ± 0.1 μmol m^{-2} s^{-1}), whereas cyanobacteria/cyanolichen- and moss-dominated biocrusts had substantially lower maximum rates (2.7 ± 0.4 and 2.8 ± 0.5 μmol m^{-2} s^{-1}, respectively); for additional information and figures, see Weber et al. 2012 and Tamm et al. 2018).

The described overall CO$_2$ gas exchange patterns were also observed for biocrusts from other regions. Investigating biocrusts of the Namib Desert, Lange et al. (1992) obtained optimum curves for biocrust response to varying water contents and saturation curves for their response to increasing light intensities. They measured maximum NP rates between 0.72 and 1.12 μmol m^{-2} s^{-1}, thus being somewhat lower than the rates observed by our study. For cyanolichen-dominated biocrusts from the Sonoran Desert with *Peltula richardsii* and *P. patellata* as dominating organisms, somewhat lower maximum NP values were obtained (Büdel et al. 2013), whereas *Collema tenax* biocrusts from the south-western USA attained substantially higher maximum NP rates (i.e. 5.3 ± 0.9 μmol m^{-2} s^{-1}; Lange et al. 1998). For mosses, maximum NP values were observed to be within a medium range, as DeLucia et al. (2003) obtained values up to 1.9 μmol m^{-2} s^{-1} for soil-inhabiting rainforest bryophytes, whereas Williams and Flanagan (1996) measured higher maxima of ~7 μmol m^{-2} s^{-1} for isolated *Sphagnum* and 2 μmol m^{-2} s^{-1} for isolated *Pleurozium* moss tufts. The response of biocrusts to high water contents depends on internal diffusion barriers and on the dominant biocrust organism. Whereas NP rates of the cyanobacterial lichen *Collema tenax* were suppressed at high water contents, lichens such as *Cladonia convoluta* showed no reduced rates at high water contents (Lange et al. 1998; Lange and Green 2003; Green and Proctor 2016).

Effects of global change

In September 2008, four microclimate stations were installed in the Soebatsfontein region to assess the microclimatic conditions and the variability between the sites over the course of a whole year at 5-minute intervals (Weber et al. 2016). Our measurements revealed that mesoclimatic conditions at the sites showed clear differences, despite the fact that they were maximally 9.3 km apart from each other. Sites 1 and 2, which were located somewhat further away from the coast, had a lower amount of annual precipitation, a lower number of rainy days, and higher mean annual temperatures (Figure 8a). At site 4, the mean annual temperature was only slightly lower but the annual precipitation substantially higher. Site 3 had the lowest mean annual temperatures and annual precipitation amounts comparable
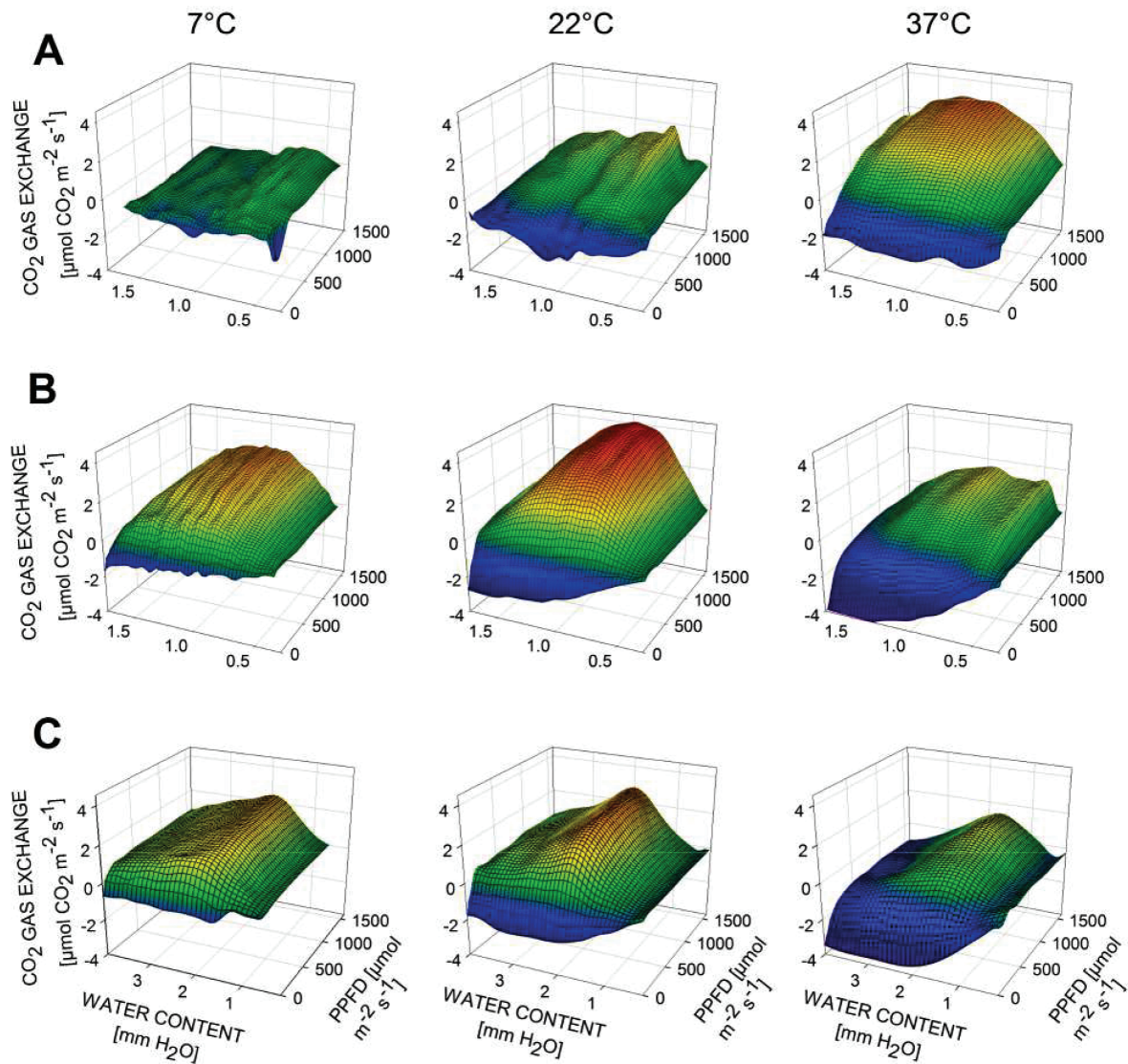
Figure 7: CO_2 gas exchange of dark cyanobacteria-dominated biocrust with cyanolichens (a), chlorolichen-dominated biocrust (b) and moss-dominated biocrust (c) at varying temperatures, i.e. 7, 22 and 37 °C. Measurements were conducted at varying photon flux density (PPFD) and water content at 380 ppm CO_2. For further details and methods see Tamm et al. (2018)

to site 4. These clear mesoclimatic differences were reflected in overall biocrust cover and compositional data. Total biocrust cover increased from sites 1 to 4 and was significantly higher at sites 3 and 4 compared with sites 1, and in addition chlorolichen- and moss-dominated biocrusts occurred more frequently at sites 3 and 4, whereas at sites 1 and 2 they were only rarely found (Figure 8).

The warmer and drier conditions at sites 1 and 2 compared with sites 3 and 4 are analogous to an increase in daily temperature and a reduction in total precipitation forecast for the region by the International Panel for Climate Change until the year 2100 (Stocker et al. 2013; Figure 8b and c). Thus, our data indicate that the cover of well-developed, i.e. chlorolichen- and moss-dominated, biocrusts, which also have higher biomass contents compared with initial biocrusts, may decrease over the next decades, which is in line with the described physiological

preferences analysed during CO_2 gas exchange measurements. According to these results, overall biocrust cover may also decline.

These results are in line with experimental global change studies, where increased temperatures had detrimental effects on biocrust cover, and altered precipitation regimes caused a complete loss of moss-dominated biocrust within a single growing season (Reed et al. 2012; Maestre et al. 2013). Analyses of a long-term field study revealed that both altered climate and physical disturbance had similar detrimental effects on the biocrust community structure (Ferrenberg et al. 2015). A recently published global analysis combining measurement and modelling approaches suggested that overall biocrust cover may decrease by ~25%–40% within the next 65 years due to both climate change and land-use intensification to similar extents (Rodríguez-Caballero et al. 2018a).
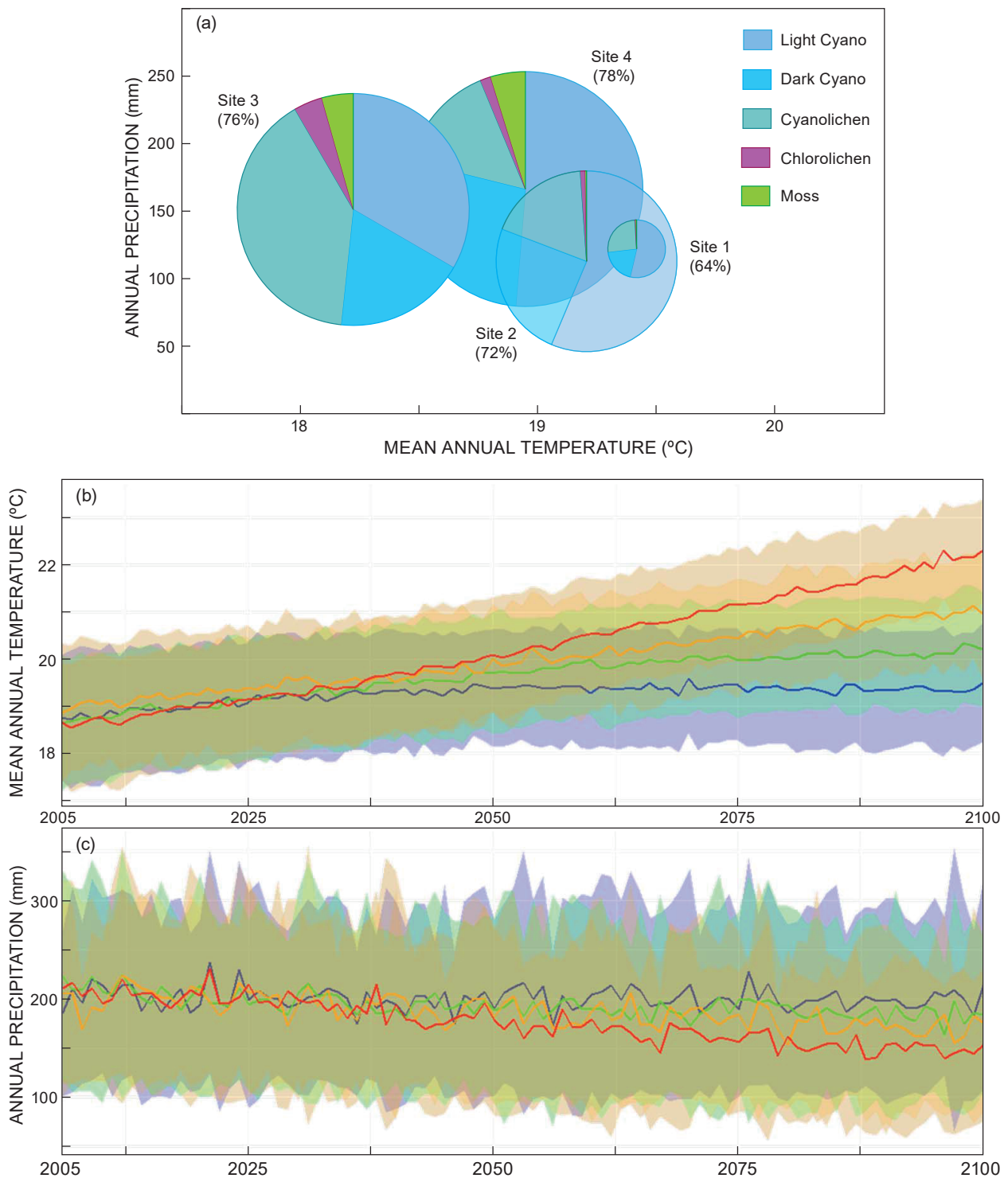
Figure 8: Average biocrust coverage (represented by piechart size), composition, precipitation, and temperature at the four different study sites along an aridity gradient (a), historical and predicted future mean annual temperature (b) and precipitation (c) for the years 2005 to 2100 according to four different scenarios: RCP2.6 (blue), RCP4.5 (green), RCP6.0 (orange), and RCP8.5 (red; b). Climatic data were obtained from KNMI Climate Explorer using the ensemble data set within the CMIP5 (IPCC AR5 Atlas subset)

Conclusion

The Succulent Karoo is characterised by a high cover of biocrusts, composed of various biocrust types that increase along a successional pathway in overall biodiversity, biomass and C-fixation potential (Figure 9). These biocrust types are not equally distributed throughout the region, as well-developed chlorolichen- and moss-dominated biocrusts require cooler temperatures and sufficient amounts of precipitation, but also stable soil conditions. Thus, with increasing
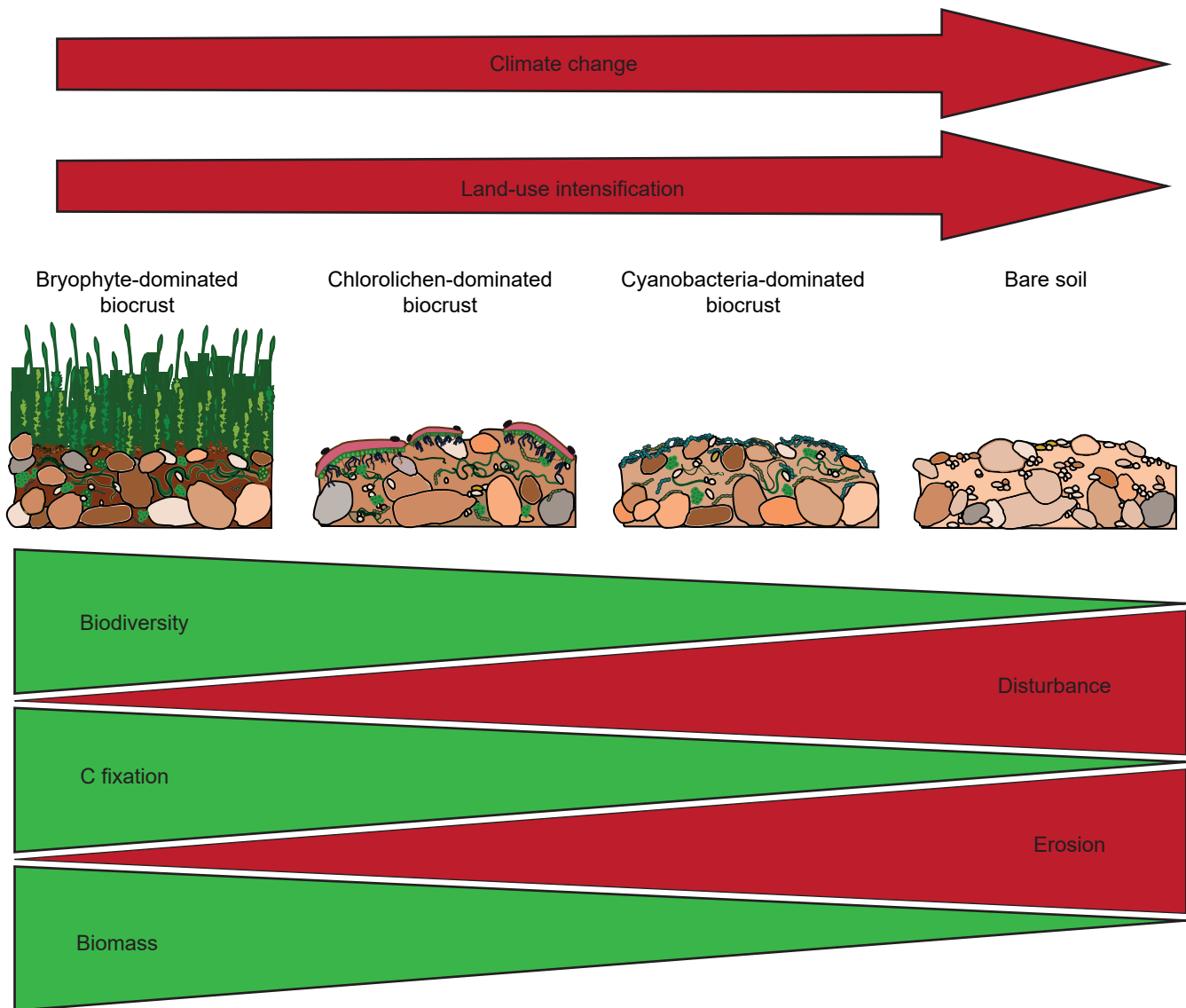
Figure 9: Regional climate change and land-use intensification predicted for the Succulent Karoo are expected to cause a decrease in the coverage of well-developed biocrusts as well as an overall decrease in biocrust coverage. This will involve decreasing biodiversity, C-fixation rates and biomass contents as well as increasing disturbance and erosion

temperatures, decreasing precipitation and increasing land-use intensity, overall biocrust cover as well as the cover of well-developed biocrusts are expected to decline, therefore exposing the region to higher overall erosion rates and an increased risk of desertification (Figure 9).

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