Microbial colonization and controls in dryland systems

Stephen B. Pointing[1,2] and Jayne Belnap[3]

Abstract | Drylands constitute the most extensive terrestrial biome, covering more than one-third of the Earth's continental surface. In these environments, stress limits animal and plant life, so life forms that can survive desiccation and then resume growth following subsequent wetting assume the foremost role in ecosystem processes. In this Review, we describe how these organisms assemble in unique soil- and rock-surface communities to form a thin veneer of mostly microbial biomass across hot and cold deserts. These communities mediate inputs and outputs of gases, nutrients and water from desert surfaces, as well as regulating weathering, soil stability, and hydrological and nutrient cycles. The magnitude of regional and global desert-related environmental impacts is affected by these surface communities; here, we also discuss the challenges for incorporating the consideration of these communities and their effects into the management of dryland resources.

Aridity has been a major feature of the Earth's surface for approximately 1.8 billion years[1], and drylands (here, we use arid, desert and dryland as interchangeable terms) account for the largest terrestrial biome[2,3], with more than 35% of the Earth's land mass being permanently or seasonally arid[2,4] (FIG. 1). Several approaches have been used to define deserts, variously based on climate, geomorphology, hydrology and vegetation[1]. A widely adopted criterion used by the United Nations Environmental Programme (UNEP) is the aridity index. This index reflects the moisture deficit in a system and is expressed as the ratio of precipitation to potential evapotranspiration (P/PET)[2]. These ratios are based on direct meteorological observations, and deserts are classed as regions for which P/PET <1 (REF. 2). For example, in the Mojave Desert, USA, potential evapotranspiration reaches 2,121 mm per year, which is 19-fold the amount of precipitation[5]. A further delineation based on mean annual temperature, dividing these drylands into hot (>18 °C) and cold (<18 °C) deserts, is also sometimes applied[3].

In deserts, small poikilohydric life forms (typically dominated microbially by cyanobacteria but also containing chlorophytes, fungi, heterotrophic bacteria, lichens and mosses) form a thin veneer of biological activity that occurs on or within the top few centimetres of most soil and rock surfaces. These communities, hereafter referred to as soil- and rock-surface communities (SRSCs), have often been regarded as curiosities of little ecological significance and, until recently, even their existence was unappreciated. However, recent studies have shown that species-rich SRSCs are more widespread than was earlier envisaged, occurring even in the most extreme climates[6–9]. Interestingly, despite there being clear differences between specific niches in terms of community assembly at higher taxonomic levels, general similarities exist for SRSCs in all the hot and cold deserts that have been examined worldwide[6,10]. These SRSCs are now understood to carry out crucial ecosystem functions in all biomes, but severe environmental constraints on higher plant and animal life serve to emphasize the importance of SRSCs in desert systems. The crucial role of SRSCs has recently been highlighted in the United Nations Convention on Combating Desertification (BOX 1).

In this Review, we illustrate the nature of microbial colonization in deserts and the adaptive strategies that are hypothesized to facilitate the survival of SRSCs in these environments. We further identify the central role of microbial interactions in desert ecosystem processes and highlight the fact that disturbance can result in catastrophic effects if this desert resource is not effectively managed.

Challenges to life in arid environments

The various types of SRSCs must be adapted to overcome stresses such as low moisture availability, low or high temperatures and ultraviolet (UV) irradiation. Water is essential to all cellular processes, and microbial life that is not adapted to moisture stress is generally unable to

Poikilohydric
Pertaining to an organism: relying solely on the environment for water. These organisms have therefore evolved mechanisms to tolerate desiccation.

Soil- and rock-surface communities
Communities containing the microorganisms, lichens and mosses that colonize surface soil and rocks.

[1]*School of Biological Sciences, The University of Hong Kong, Pokfulam Road, Hong Kong SAR, China.*
[2]*School of Applied Sciences, Auckland University of Technology, Private Bag 92006, Auckland 1142, New Zealand.*
[3]*US Geological Survey, Southwest Biological Science Center, 2290S Resource Boulevard, Moab, Utah 84532, USA.*
e-mails:
steve.pointing@aut.ac.nz;
jayne_belnap@usgs.gov
doi:10.1038/nrmicro2831

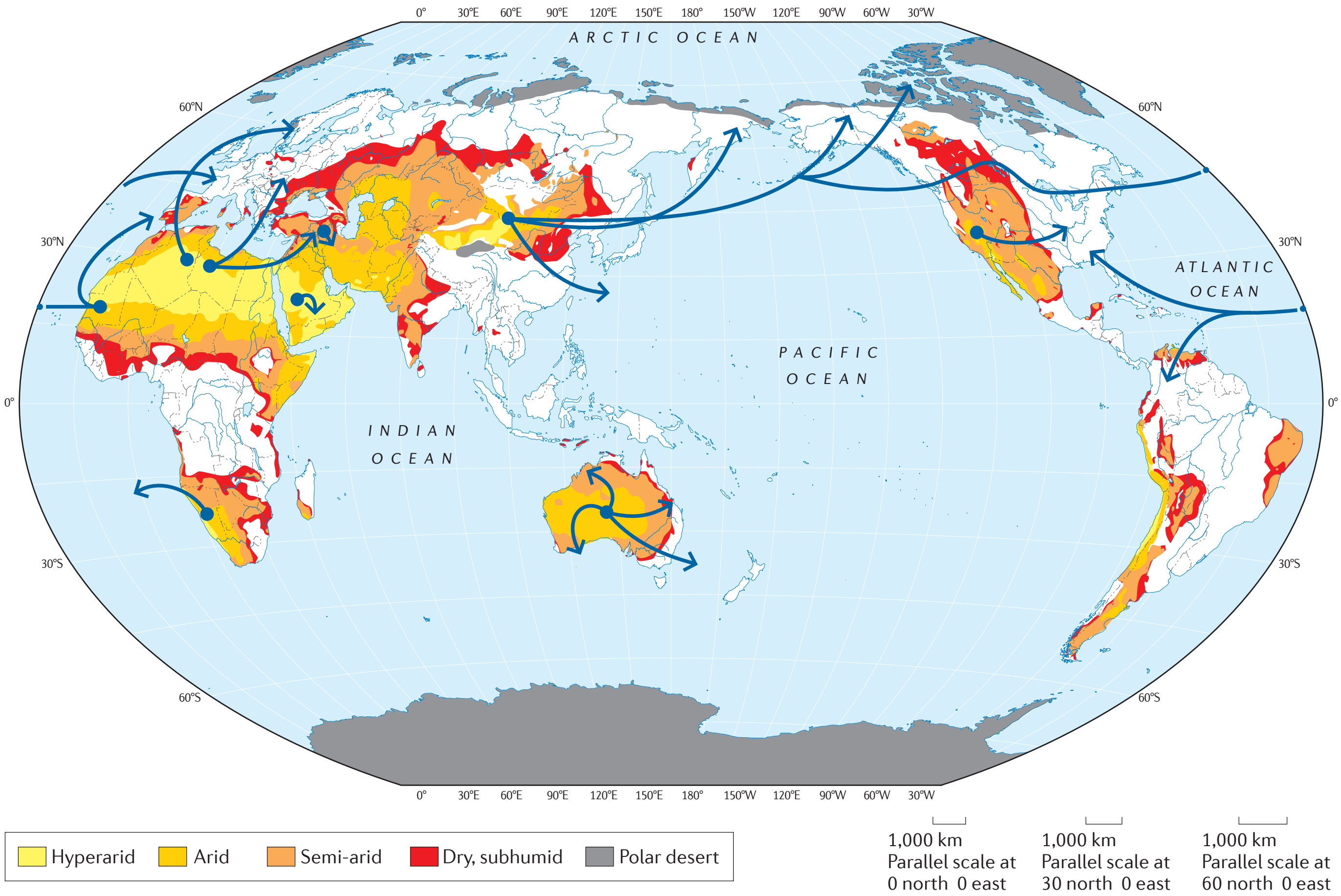


Figure 1 | **The global distribution of drylands.** The delineation of regions follows the aridity index (*AI*) of the United Nations Environment Program (UNEP)[2]. This index reflects the water deficit in these systems by expressing the ratio of precipitation to potential evapotranspiration. Four zones of aridity are identified on this basis: dry, subhumid regions (with an *AI* of 0.5 to <0.65), semi-arid regions (with an *AI* of 0.2 to <0.5), arid regions (with an *AI* of 0.05 to <0.2) and hyperarid regions (with an *AI* of <0.05). Arrows show the major intercontinental trajectories for desert dust. Polar deserts may also be hyperarid as a result of low liquid water availability, but these deserts are not considered in this Review.

tolerate long periods of desiccation or water containing solutes that reduce the water activity (a_W) to below 0.9. The bio-availability of water in deserts is primarily determined by precipitation and evaporation (FIG. 1), but is also influenced by the level of solutes in desert substrates. Surface deposits of halite (NaCl) and gypsum ($CaSO_4{\cdot}2H_2O$) may occur extensively in extreme deserts, resulting in osmotic challenge to SRSCs. Indeed, substrate a_W values of as low as 0.75 (equivalent to a saturated NaCl solution) have been reported to support growth of microbial biofilms in halite from the hyperarid core of the Atacama Desert in Chile[11]. It is also increasingly appreciated that non-rainfall water input may have a major role in shaping the colonization of hyperarid locations. The amount of fog- and dew-derived moisture in the Atacama Desert is up to three orders of magnitude greater than the amount of rainfall[7], and lithic biofilms at coastal sites in this desert survive almost exclusively on marine fog, as there is a near-complete absence of rainfall[12]. High relative humidity can also activate some green algal lichens, although cyanolichens require liquid moisture sources[13].

Importantly, climates that are not normally classified as arid may also support microniches that impose a high water stress in diurnal and/or seasonal cycles (for example, exposed soil and rock surfaces in temperate and subtropical areas). An appreciation of this fact means that we must substantially increase our estimates of the total geographical area containing organisms that face severe xeric stress on a regular basis, particularly for edaphic (soil and lithic) niches.

Thermal extremes and variations in diurnal and seasonal cycles also present major challenges in arid landscapes. Direct stresses are imposed by heat and cold shock and by freeze–thaw cycles, which are common in both hot and cold deserts[14]. Organisms in desert SRSCs can tolerate temperature extremes when dormant: temperatures in hot deserts are in excess of 60 °C[15,16], whereas in cold deserts, soil temperatures may drop to −24 °C, with daily freeze–thaw cycles[14]. Incident solar radiation also introduces stresses related to harmful UVA and UVB radiation, with irradiance being markedly higher in deserts than in other biomes owing to the low levels of atmospheric water vapour. For instance, measurements

Water activity
The vapour pressure of a liquid divided by that for pure water at the same temperature; pure water has a water activity of 1. This is a measure of how biologically available the water molecules are in a solution.

Xeric stress
The challenge that is imposed on a cell, population, community or ecosystem by water limitation.

Box 1 | **United Nations Convention to Combat Desertification**

Desertification — the degradation of land towards greater aridity — is increasing as a result of climatic variation and human activities. It is estimated to affect more than 1 billion people, in more than 100 countries, who depend on these regions for their livelihood and thus are placed at risk as desertification reduces plant productivity and water supplies. Of the world's 5.2 billion hectares of agriculturally used drylands, the United Nations Environment Programme (UNEP) estimates that 69% is degraded or undergoing desertification, costing an estimated US$42 billion per year. Given the large scope and serious implications of this problem, the United Nations (UN) formed the UN Convention to Combat Desertification (UNCCD), which was ratified in December 2006. Sixty countries have now ratified this convention, which is focused on conserving, rehabilitating and sustainably managing land and water resources in regions that are vulnerable to desertification.

Although desert regions are the most vulnerable areas, desertification is not completely restricted to drylands, because climate change and human use can create desert-like conditions in lands that were previously far more productive. Desertification also contributes to other environmental and social crises, such as mass migration of people and animals, species loss, climate change and the need for emergency assistance to human populations. Desertification affects both developed and underdeveloped nations; up to 66% of the African continent is threatened by aridity, and the US Bureau of Land Management considers almost 40% of land in the continental United States to be vulnerable to desertification.

The mobilization of desert dust as a result of disturbance on local scales can also have far-reaching regional consequences[91,92]. Local disturbance caused by agriculture, recreation and other activities results in a loss of soils that are fit for plant growth and an increased sediment loading in rivers. It is now increasingly realized that desert degradation can also be linked to regional problems, such as changes to hydrological regimens (as a result of increased snowmelt in montane regions)[94], to patterns of marine nitrogen fixation[95] and to public health in urban developments[29,96].

in North African deserts indicate that maxima at solar noon approach 1,000 W per m^2, which is approximately fivefold the maxima in temperate non-desert areas[17].

Community assembly under aridity

Given the carbon-limited nature of desert soils and rocks, it is not surprising that SRSCs are characterized by photoautotrophic organisms[6,10]. Carbon fixation by cyanobacteria, chlorophytes, lichens and mosses supports heterotrophic assemblages from all domains in all types of SRSC. In all SRSC types, biomass, cover and species richness increase as moisture availability becomes less limiting.

Biological soil crusts. Desert biological soil crusts (BSCs) are dominated by cyanobacteria (*Microcoleus* spp. in particular) and also include chlorophyte algae, heterotrophic bacteria, fungi, mosses (for example, *Bryum* spp. and *Tortula* spp.) and lichens (for example, those containing *Collema* spp.)[6]. BSCs cover most soil surfaces in deserts and can cover up to 70% of the total area[6] (FIG. 2a). Climate and species composition influence the morphology of BSCs. Rolling and pinnacled crusts, which have high percentages of lichen and moss cover, are found in less arid regions, where soils frost–heave in winter, and can be up to 15 cm high (FIG. 2b). Rugose and smooth cyanobacterial crusts are found in hotter deserts, where soils seldom freeze and thus are flat[18] (FIG. 2c).

Hypoliths. The ventral surfaces of translucent stones (for example, quartz and marble) support communities consisting of hypoliths. These communities occur in all deserts[12] but are of particular importance in the desert pavement that is typical of hyperarid areas, where they can be major sites of productivity and biomass[7,14]. Hypolithic biofilms are dominated by the cyanobacterial genus *Chroococcidiopsis* in all nonpolar deserts[19], but can also support substantial heterotrophic bacterial assemblages — notably, acidobacterial and proteobacterial populations — as well as lichens and mosses in colder deserts[20].

Epilithic colonists. Epiliths are observed in deserts of all aridity classes. Lichens and mosses commonly occur on rock surfaces[21] (FIG. 2d,e). These surfaces also support free-living microcolonies and biofilms in which cyanobacteria and fungi seem to be key components[22,23]. Desert varnishes (darkened rock surfaces) are commonly encountered, but their origin has long been controversial. Some researchers attribute their formation to metal oxides, whereas others associate them with biogenic mineral concentration and areas with periodic water flows[24] (FIG. 2f). Biogenic varnishes (that is, varnishes that are associated with microorganisms) consist mostly of actinobacteria and proteobacteria, although photosynthetic bacteria and fungal and archaeal signatures have also been recovered[25].

Endoliths in porous rocks. Perhaps the least appreciated components of desert SRSCs are endoliths. Rocks such as sandstone, limestone and weathered granite allow cryptoendoliths and chasmoendoliths (here, collectively termed endoliths) to colonize the pore spaces and the cracks and fissures, respectively, in rocks[26]. Such colonization typically occurs just a few millimetres below the surface and is associated with weathered rock layers (FIG. 2g,h). Similarly to hypolithic communities, endolithic assemblages in nonpolar deserts are dominated by the genus *Chroococcidiopsis* and other coccoid taxa, although differentially pigmented microbial layers (for example, black, green, pink and white layers) are often visible and consist of chlorophyte algae, lichens, heterotrophic bacteria and free-living fungi[9,27]. Interestingly, it is emerging that endolithic colonization might be ubiquitous among deserts of all aridity classes, reflecting the advantage that this refuge provides in terms of stress avoidance.

Bio-aerosols. Billions of tonnes of desert dust is transported annually over intercontinental distances (FIG. 1), and large seasonal pulses from African and Asian deserts are thought to have major effects on downwind ecosystems[28]. It is becoming increasingly appreciated that microorganisms — particularly spore-forming bacteria and mitosporic fungi, but also human and animal pathogens — are associated with this dust as bio-aerosols[29]. The extent to which these microorganisms are metabolically active or remain viable in such aerosols is uncertain, and the ability of taxa to establish a colony postdispersal is probably restricted by local factors; nonetheless, these organisms are likely to represent a major microbial reservoir that feeds the various desert microbial niches[19].

Biological soil crusts
Biological communities that inhabit soil surface layers to create a coherent structure.

Frost–heave
The movement of soil that is caused by freezing of subsurface moisture during freezing atmospheric conditions.

Hypoliths
Organisms that colonize the ventral surface (underside) of translucent stones and are usually in contact with the soil.

Epiliths
Organisms that colonize the exposed surface of rock or mineral substrates.

Biogenic mineral concentration
A localized increase in a mineral that is directly or indirectly due to biological activity.

Cryptoendoliths
Organisms that colonize the pore spaces of porous rocks or minerals.

Figure 2 | **Microbial colonization in arid landscapes.** **a** | A desert soil landscape illustrating soil crust development. **b** | A pinnacled biological soil crust (BSC). **c** | A smooth BSC. **d** | A lithic landscape. **e** | Epilithic colonization of a rock. **f** | A desert varnish. **g** | Endolithic colonization of a rock; the rock has been fractured to expose subsurface green and white colonization. **h** | A close-up of endolithic colonization, showing coloured bands of colonization (scale bar represents 2 mm).

Chasmoendoliths
Organisms that colonize existing cracks and fissures that have a connection to the surface in rock or mineral substrates.

Landscape-scale patterns in SRSCs

The major driver of SRSC occurrence and continuity at a regional scale is environmental stress, especially aridity (FIG. 3). In subhumid and semi-arid lands, SRSCs are often contiguous between edaphic niches (that is, SRSCs develop continuously and adjoin where substrates meet), whereas in arid deserts this continuous line gradually gives way to more patchy colonization (both intra- and inter-substrate gaps in colonization appear) and eventually to isolated islands of life under extreme

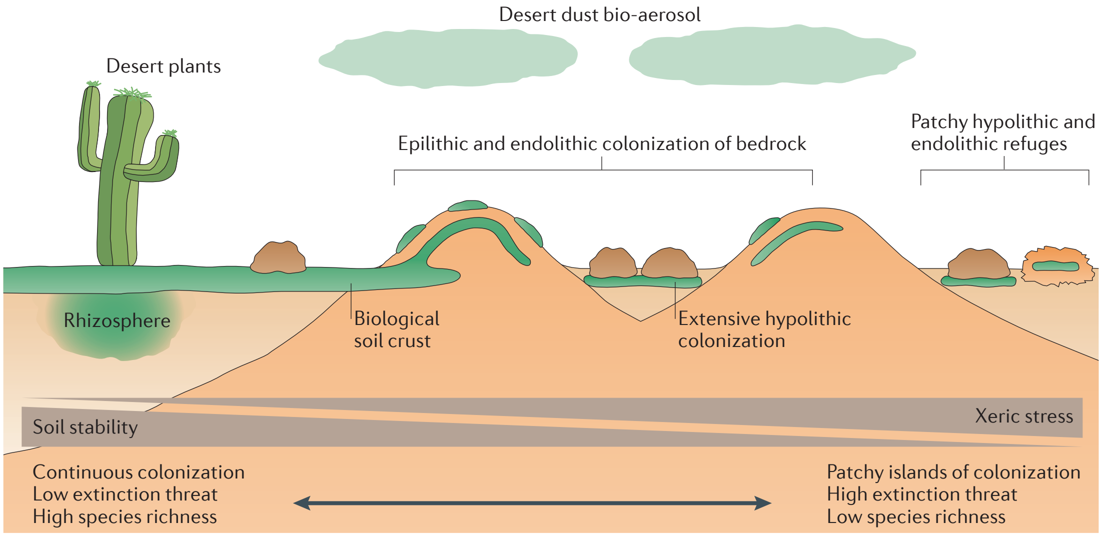


Figure 3 | **Microbial niches in arid landscapes.** Green shading denotes sites of microbial colonization and illustrates how contiguous colonization at intra- and inter-substrate levels in less arid regions (left) gives way to more patchy cover in more arid regions (right). Arrows illustrate the fact that soil stability and xeric stress are inversely related as a result of colonization patterns. Species richness and extinction threat also closely track aridity.

hyperaridity (FIG. 3). Species richness also declines with increasing aridity (for example, see REF. 30). In the most extreme hyperarid systems, microbial life retreats to isolated 'oases' that are formed as a result of biotic–abiotic relationships between the microorganisms and the available porous and deliquescent mineral substrates, permitting life in landscapes where extinction pressures would otherwise be too great. Such life is usually cryptic, surviving in sheltered niches either in or under rocks, halite, gypsum and other substrates as cryptoendoliths[11] (in) or as hypoliths[7] (under). Hypolithic colonization of translucent rocks is typically 100% in semi-arid regions[15,16], dropping to <50% in arid areas and finally to <1% in areas of extreme hyperaridity, where hypolithic oases occur as isolated patches[7,8,14]. The oasis concept applies both in terms of defining these isolated islands of productivity as a miniaturized reflection of their larger tree-lined oasis counterparts, and at a genetic level, such that they can be viewed as island reservoirs of highly specialized biological diversity[19]. It is interesting that these oases occur in the most arid locations investigated, including hyperarid areas that experience low precipitation and decades without rainfall, such as the Atacama Desert (~2 mm per year) and the Turpan Depression in China (~10 mm per year). Thus, it seems that there is no aridity-defined limit to terrestrial life on Earth[7,14].

In addition to aridity, the substrate geomorphology and mineralogy are strong drivers of the species composition and biomass of SRSCs. For example, at lower elevations in the Utah desert (USA), sandstone-derived soils support lichen- and moss-rich BSCs, whereas adjacent shrink–swell clay soils are relatively depauperate (although at high elevations on these same clay soils, the lichen and moss flora attains a similar richness to the flora of the sandstone-derived soils). Similarly, white sandstones in this region are preferentially colonized by lithic lichens and mosses compared to red sandstones (J.B., unpublished observations). The reasons for these patterns remain mostly uninvestigated. Slope orientation also affects SRSC biomass: in Northern Hemisphere deserts, north-facing slopes experience less solar stress than south-facing slopes, and so support more biomass and higher species numbers than south-facing slopes[21,31].

Dispersal of viable biomass also shapes the landscape distribution patterns of SRSCs. Localized dispersal is evident in soil and rock niches, where colonization spreads initially in patches before becoming contiguous under more favourable conditions. This may be enhanced by positive environmental feedbacks such as substrate modification (for example, bioweathering of the substrate to allow penetration of biomass) and secretion of extracellular polymeric substance (EPS), a highly hygroscopic substance that confers additional moisture retention and desiccation prevention properties to the entire community[32]. An interesting paradigm arises on larger scales, however. Despite the intercontinental transport of desert dust[28] that probably contains more cosmopolitan BSC-dwelling species, such as *Microcoleus vaginatus*, there is strong evidence for the existence of evolutionarily isolated lineages of hypolithic cyanobacteria between climatically similar hyperarid deserts worldwide[19]. Modelling indicates that dispersal limitation (caused by either a lack of transport or an inability to establish an invasive colony) may explain the stochastic demography of these photoautotrophs, although the distribution of heterotrophic taxa is more strongly correlated with environmental variables[10]. These findings suggest that a strong 'founder effect' contributes to cyanobacterial biogeography in deserts, in addition to allopatric and selective forces. Whether this is a feature of other desert communities or is particular to long-lived hypolithic biofilms in hyperarid terrains remains untested.

Bioweathering
Microorganism-mediated physical or chemical dissolution of mineral substrates.

Adaptation of SRSCs to stress

The often rapid changes in moisture availability and the stochastic nature of moisture input in arid systems, along with the high thermal and UV stress, necessitate an efficient metabolic stress response during growth, as well as the ability to transition between active and dormant states and to survive during long periods of inactivity. An extreme example of the challenges facing SRSCs can be seen in the hyperarid core of the Atacama Desert, where hypolithic SRSCs experience less than 75 hours a year when light, temperature and moisture availability allow photosynthesis to occur[7]. In semi-arid regions of Australia, photosynthetically favourable conditions may exist for only ~75 days per year[16]. Similarly, in the Utah desert, estimates made over a 2-year period found that carbon fixation can occur during only ~11% of daylight hours (J.B., unpublished observations). As a result, there are long periods of dormancy between periods of active growth, indicating that the individual cells that constitute SRSCs may be long-lived. Photographs and drawings show that some epilithic lichens survive for more than 100 years if undisturbed[33], and microbial desert varnishes on rock surfaces can survive for thousands of years[34]. Radiocarbon dating of Atacama Desert hypoliths revealed a positive correlation between aridity and the age of microbial communities, using radiocarbon residence time as a general proxy for residence time in open (living) systems. Surfaces at the driest site were estimated to have been continuously colonized for approximately 12,000 years, with estimated carbon turnover rates some fourfold faster than those of surrounding uncolonized soils[7], thus emphasizing the importance of these islands of life in desert carbon cycles.

Microbial stress responses that are elicited at the cellular level (for example, photoprotection[35], radiation repair[36], desiccation[37] and the response to thermal stress[38]) are reasonably well understood and have been extensively reviewed. Studies of model organisms have yielded important insights, but the response pathways that are elicited in members of SRSCs are far from clear, and this presents a major opportunity for future advances in our understanding of adaptation to dryland environments. Surface-dwelling organisms are directly exposed to high environmental stress levels. Most of these exposed organisms produce intracellular 'sunscreens' to mitigate the effects of UV radiation. These sunscreens include melanins, mycosporines and scytonemin[35], which have also been implicated in other stress responses[39]. Desiccation tolerance is mediated intracellularly by compatible solutes and osmoprotectants[37], in addition to the physical protection that is afforded by cell walls and other extracellular secretions[40] and by genome repair pathways[41]. Organisms colonizing subsurface 'refuge' niches experience less moisture, thermal and UV stress than surface-dwelling organsims[7,26], although the extent to which these subsurface organisms are less tolerant of environmental extremes than surface dwellers remains unknown.

Interestingly, cellular mechanisms that are used for tolerance and repair of desiccation damage, such as genome repair pathways and accumulation of osmoprotectants, are also elicited in response to radiation damage for certain desert bacterial genera such as *Deinococcus*[41] and *Chroococcidiopsis* [42]. Desert environments and their microbial colonists are ancient. Both the early Earth, with its lack of atmospheric ozone accumulation, and modern deserts, with their high incident UV levels, are environments in which there is (or was) substantial radiation and xeric stress[43], and it is possible that the need to combat this dual stress conferred an adaptive advantage during the evolution of desert microorganisms.

There are other commonalities among how desert SRSCs have adapted to environmental stressors, including several at the community assembly level. Endolithic and BSC communities often assume a layered structure that is typified by a heavily pigmented (photoprotective) fungal or cyanobacterial upper band protecting an underlying photoautotrophic layer with less UV tolerance[9,26]. This is an active process in cyanobacterium-dominated BSCs, in which the underlying photoautotrophs migrate to surface layers when soils are wet and retreat as substrates dry[44]. We view this 'microbial cabana' strategy (an upper protective layer of biomass or substrate shielding lower layers) as an emerging common theme for surface microbial communities in deserts and other stressful environments (for example, intertidal, hypersaline and geothermal locations) (BOX 2). Another common feature among all SRSCs is the extracellular secretion of EPS and gelatinous materials[9,14,45]. These secretions are thought to have key roles in increasing water retention around cells and slowing the drying process, thus alleviating desiccation damage to the community. Little is known about the synthesis, regulation or composition of these compounds and, given their likely importance to colonization, this is an area that warrants closer attention.

Dryland biogeological processes

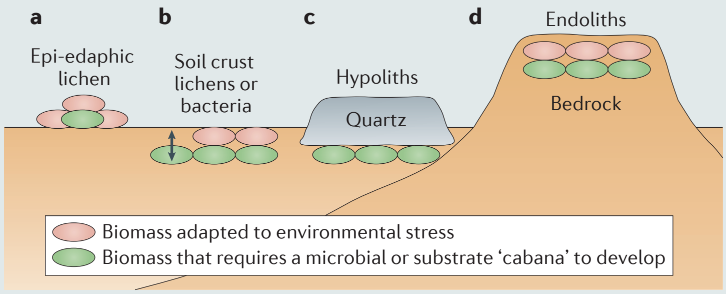
SRSCs contribute to the function of desert ecosystems in multiple ways that can have regional and global implications. These include enhancing the weathering of mineral rocks (and thus facilitating local soil formation), preventing water and wind erosion, and regulating local hydrological and nutrient cycles. In these ways, desert SRSCs contribute disproportionately more to the structure and function of desert communities than their visual appearance might suggest.

Rock weathering and soil stability. The weathering of exposed mineral surfaces by SRSCs is a major contributor to desert landscapes[46], as this process shapes the visual nature of this biome. Indeed, sandstone surfaces can be observed to undergo an 'exfoliation' (in which surface layers erode and flake off in a characteristic laminar manner) that is closely associated with SRSC presence (for example, see REF. 47). Bioweathering results from epilithic and endolithic activity (FIG. 4a). Epilithic bioweathering is more important in less stressful deserts, whereas endolithic weathering is more important in harsher environments[48] (FIG. 4b), and the degree of microbial colonization is highly correlated to weathering rates[49].

Box 2 | **The microbial 'cabana' as an adaptive strategy in drylands**

It is well known that cells exhibit stress tolerance mechanisms to cope with moisture, thermal and ultraviolet (UV) stress[35–38], but ecological studies are now revealing that adaptations at the level of community assembly are also critical to the colonization of harsh desert environments. Perhaps the most obvious visible feature of such colonization is a layered organization of biomass such that the more UV-sensitive photosynthetic cells are afforded protection either by biomass that possesses 'sunscreen' compounds, which attenuate incoming radiation via the production of melanins, mycosporines and scytonemin (reviewed in REF. 35), or by the overlying substrate itself during community assembly[7,9]. This is particularly prominent in soil- and rock-surface communities (SRSCs) that colonize rocky substrates as differentially pigmented bands of biomass. The production of sunscreens may be particularly important to desert SRSCs, as this passive protective mechanism remains functional (unlike active cellular repair mechanisms, for instance) even during the long periods of dormancy that are typically endured by poikilohydric life forms. Other biotic adaptations include secretion of a hygroscopic extracellular polymeric substance by some taxa to confer localized moisture retention for the whole community[9,32,45]. The colonization of a cryptic niche also holds advantages over exposed niches in terms of thermal and moisture buffering[7] as well as physical stability. The provision of this cabana-like microenvironment across different cryptic niches is visualized below.

In epi-edaphic lichens (see the figure, part **a**), the abundant mycobiont provides protection to phycobiont cells via production of UV sunscreens[104]. In soil crust lichens (see the figure, part **b**), the physical arrangement of hyphae in a dense cortex that overlays photosynthetic cells is common[105]. In cyanobacterium-dominated crusts (see the figure, part **b**), the structure is a little more amorphous, although lichens, cyanobacteria and fungi that produce UV-protective compounds, both intracellularly and in sheaths or cell walls, tend to be concentrated in the upper crust layer[6]. The more sensitive cyanobacterial taxa are located beneath and, in some cyanobacterium-dominated crusts, have been observed to display hydrotaxis towards surface layers under favourable conditions (see the figure, part **b**, arrow), retreating below the surface again when moisture stress increases[44]. In hypolithic communities (see the figure, part **c**), environmental buffering is provided by the overlying quartz substrate rather than by biological sunscreens, to the extent that near-complete filtering of UVA and UVB is achieved, as well as reduced thermal and moisture stress[7,20]. Endolithic colonization (see the figure, part **d**) usually exhibits a well-defined layering such that an upper layer of densely pigmented fungi and/or cyanobacteria occurs at a depth below the rock surface that also affords environmental buffering. This layer may also include biomineralized sunscreens (for example, micrite) in calcite and other desert precipitates that support endolithic colonization[106]. This dual protection allows endolithic colonization in even the most extreme locations.



Endo-edaphic
Pertaining to organisms that colonize the cracks or pore spaces within rocks or that live within (rather than on top of) the soil.

Epi-edaphic
Pertaining to organisms that colonize the exposed surface of rock or soil.

Accelerated weathering by SRSCs may be a passive by-product of metabolism or, as much evidence suggests, a result of organisms accessing limiting nutrients from the rock, especially nitrogen and phosphorus[23,50] (FIG. 4c). Rock weathering is accelerated by the physical penetration of SRSCs into mineral cleavages and along grain boundaries to an ~10 mm depth, and rock cracks are pushed apart with wetting–drying and heating–cooling cycles[23]. Secreted compounds also increase dissolution rates. These substances include EPS, which absorbs water and holds it against rocks for longer while also aiding the adherence of weathering-facilitating organisms to rock surfaces[45,51]; organic and inorganic acids, which reduce pH[50]; Ca^{2+} and OH^{-}, which increase pH[52]; and organic ligands that weaken oxygen–metal bonds or decrease solution saturation states[50].

Fungi seem to be better facilitators of weathering than bacteria, as they are able to dissolve minerals and mobilize metals faster and more efficiently at a higher pH and across a larger range of redox potentials than bacteria[53]. Invertebrates that graze on surface microorganisms also accelerate weathering by mechanically scraping rock surfaces[54]. Weathering rates, especially of silicates (representing 30% of all minerals and 90% of the Earth's crust[53]), are estimated to increase by up to 1,000-fold with the presence of microorganisms[55]. In one region, exfoliation owing to endolithic microorganisms was estimated to remove up to 2,400 kg per hectare per year[47]. By accelerating soil formation, bioweathering releases nutrients to surrounding soils, making these nutrients available for uptake by SRSCs and plants, and thus linking lithic and soil communities. Accelerated weathering ultimately increases the availability of dust to be released as aerosols and may also release epilithic and endolithic microbial cells for dispersal as bio-aerosols. This theory is untested but is strongly supported by observations that endolithic biosignatures are dispersed widely in soils of the Antarctic desert[56].

The role of BSCs in soil stabilization has been key in desert ecosystems throughout time. It is likely that these crusts were important for the evolution of terrestrial biomes on early Earth, as the newly formed soil that was derived from weathered rocks required microorganisms for stabilization in the face of high winds. These soils were, in turn, necessary for the evolution of land plants[51,55]. BSCs are still crucial today for soil stabilization, as soils are slow to form in deserts (<1 cm per 1,000 years) but are quickly lost[57]. The stabilizing influence of BSCs on contemporary soils varies with the species composition. Endo-edaphic filamentous microorganisms (cyanobacteria and fungi), which are ubiquitous to all crust types, provide most of the cohesion of the BSCs, as they penetrate throughout the uppermost soil layers[58]. The epi-edaphic lichens and mosses protect soils with their above-ground biomass and their anchoring structures, which are interspersed throughout the soil matrix. The dense aerial and subterranean microbial network that is formed in well-developed BSCs can eliminate soil erosion[18]. In hyperarid deserts, which are typically covered by desert pavements, hypolithic biomass (and associated EPS) may have a similar stabilizing role and may lead to islands of soil stability around colonized rocks[14,30].

Soil hydrology. Local hydrological cycles are influenced by BSCs, as BSCs affect most factors that determine water infiltration, including the permeability, absorptivity and roughness of the soil, the stability and texture of soil aggregates, and soil pore formation[59] (FIG. 5). The degree of influence of BSCs depends on the biomass, species composition and morphology of the crust community, as well as on climatic regimens and the characteristics

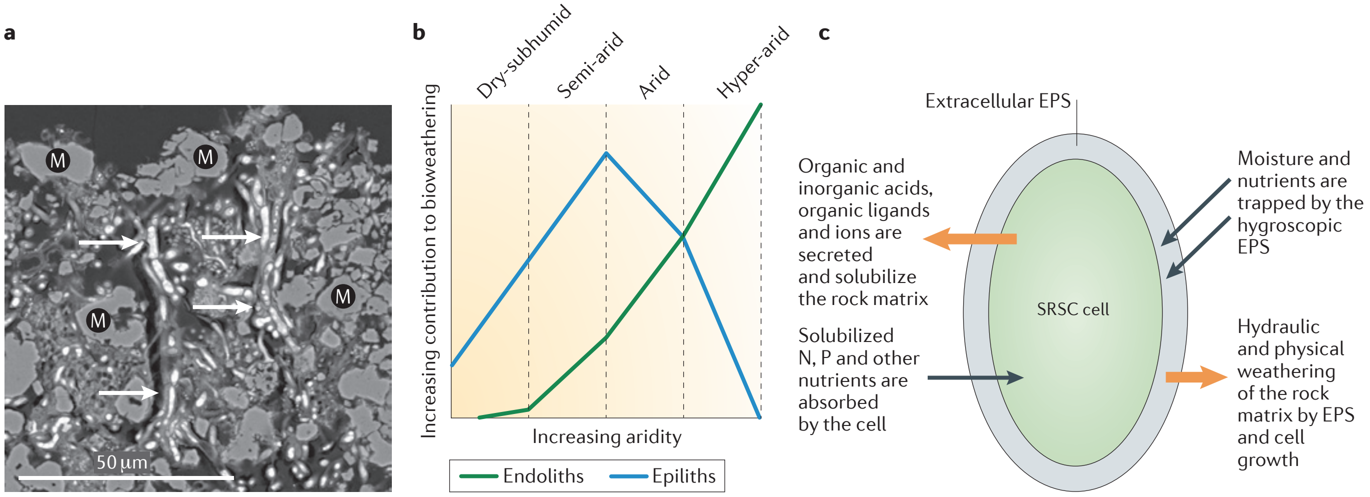


Figure 4 | **Bioweathering of mineral rocks by microorganisms.** **a** | Microbial colonization of pore spaces enhances rock weathering. In this electron micrograph of colonized rock, arrows indicate microbial colonization, and M denotes rock matrix. **b** | Colonization patterns suggest that in less arid regions, where epilithic cover is high, these epilithic communities are the main source of bioweathering. They assume reduced importance as aridity increases, and under these conditions endolithic refuge communities account for most bioweathering. **c** | As rocks become more exposed with increasing aridity, so too the role of physical erosion increases[48]. Bioweathering may be a physical process resulting from an increasing soil- and rock-surface community (SRSC) biomass and from extracellular polymeric substance (EPS) secretion by the SRSC. Alternatively, it can be an active metabolic process involving organic and inorganic acids, anion or cation accumulation, or secretion of organic ligands. Part **a** image courtesy of A. de los Rios-Murillo, Spanish National Research Council (CSIC), Spain.

of the underlying soil (some of which are modified by BSCs)[18]. Unfortunately, how these factors interact to influence local hydrological cycles is not sufficiently understood at present to allow us to generate a unifying framework that crosses all desert and vegetation types, and this remains a research challenge. In general, pinnacled and rolling BSCs, with rougher microtopography, slow water velocity and therefore increase infiltration around and between individual plants, creating a fairly homogeneous pattern of soil moisture. By contrast, the flatter smooth and rugose BSCs that are found in hot deserts or disturbed areas often increase run-off from plants and their interspaces to downslope obstructions. This creates a more heterogeneous infiltration pattern[60]. In regions where water is extremely limiting, vegetation often occurs in bands rather than being more evenly distributed[61]. Downslope bands depend on intact BSCs restricting infiltration further up the slope so that water reaches the lower regions; otherwise, the plants that are subsidized by this water can die[59]. BSCs, hypoliths and endoliths also collect and absorb dew, and the quantity collected correlates with EPS abundance[51]. The amount of moisture that is retained in soils and rocks is influenced by the biomass (including EPS amount) and morphology of the organisms in SRSCs, as these organisms increase evaporation by darkening soil surfaces but decrease it by blocking pores and retaining water. Moisture retention probably creates positive feedback for further colonization and weathering[51].

Nutrient availability. Desert SRSCs contribute directly to soil nutrient cycles (FIG. 5). Under optimal conditions of light, moisture and temperature, the photosynthetic rates of BSCs are similar to those of vascular plant leaves; therefore, when BSCs are wet, these crusts are equivalent, in terms of carbon fixation, to a layer of vascular leaves laid across the desert soil surface[13]. Although such conditions are limited in deserts, BSCs contribute substantial amounts of carbon to soils and, most importantly, to the carbon-poor interspaces between plants[13]. In a lichen soil crust from the Namib Desert (southern Africa), the rate of carbon fixation is estimated to be ~16 g carbon per m^2 per year[60]. Productivity varies between different types of BSC: well-developed lichen–moss BSCs have greater carbon fixation rates than less developed cyanobacterial BSCs[62]. Much of the carbon that is fixed by BSCs is released to underlying soils within minutes to a few days of fixation (FIG. 5), and the presence of BSCs over several years can increase the total amount of carbon in soil by up to 300%[63,64]. Endoliths can also have high photosynthetic rates. In the hot Negev desert of Israel, photosynthetic rates per unit surface area under optimal conditions are similar in endolithic lichens and BSCs from the same location[65]. However, other endolithic systems may be less productive; for example, a cryptoendolithic system from Tibetan drylands was shown to fix carbon at low rates (~2 g carbon per m^2 per year), but this is equivalent to rates of surrounding plants in this extreme location[9]. In contrast to BSCs, endolithic systems are likely to represent long-term slow-release sources of organic carbon to soils as a result of weathering-related release of biomass. Hypoliths may represent islands of high productivity in desert pavements, in which continuous BSCs are absent[15,16]. Contributions of carbon from various SRSC components all benefit the generally carbon-limited desert

Diazotrophy
The mechanism by which microorganisms fix atmospheric nitrogen into bio-available combined nitrogen.

heterotrophs (for example, see REF. 66). Stimulation of these organisms increases decomposition rates, resulting in increased soil fertility and availability of nutrients to plants, the growth of which can be limited by both water and nutrient availability in deserts[67] (FIG. 5).

Nitrogen is often regarded as a limiting nutrient in oligotrophic desert environments, and diazotrophy is a common feature of desert SRSCs (FIG. 5). In a cold North American desert, BSCs were estimated to fix up to 9 kg nitrogen per hectare per year, depending on species composition and climate factors[68]. Up to 70% of the nitrogen fixed by BSCs can be released immediately into underlying soils, becoming available to other biota[68,69] (FIG. 5). Soils underlying BSCs contain up to 200% more nitrogen than uncrusted soils[64,70,71]. Stable-isotope and other studies show that BSCs may be a dominant source of nitrogen for desert soils and plants[70], but the nature of this connection requires further investigation. Nitrogen losses seem to be controlled largely by fungi[72] and other organisms in BSCs[73], and although abiotic losses do occur[74], BSCs seem to be major drivers of nitrogen cycling in deserts. It has been suggested that the lack of diazotrophic taxa in endolithic systems indicates that nitrogen fixation is not an important process for these communities[26], and that *in situ* combined nitrogen levels (~1–8 g nitrogen per m^2) are sufficient to support these slow-growing communities[75].

Specific compounds that are secreted by BSCs and endoliths also increase nutrient availability. For example, respiratory products and phosphatases enhance the bio-availability of phosphorus[75]. Lichens secrete chelators that accelerate weathering, maintain metals in a bio-available form, and sequester essential trace metals at exceedingly low ambient concentrations[50]. Cyanobacteria in SRSCs may also secrete chelators, as such activity has been documented in marine plankton of the same genera that are found in SRSCs (for example, the genera *Anabaena*, *Lyngbya*, *Nostoc* and *Phormidium)*[76]. As chelators are water soluble, they may also affect soils at depth. In addition, cyanobacteria release organic nitrogen and riboflavin, which, together with siderochromes, can form complexes to keep copper, iron, nickle, phosphorus and zinc bio-available in soils[76–79]. Microbial EPS can also promote soil fertility. The lipid, protein and carbohydrate components create a mosaic of polyfunctional binding sites that keep excess heavy metals from the cell surface while concentrating growth-promoting nutrients on the sheath[78]. This is largely a passive binding process and therefore does not require organisms to be alive or active. Most adsorbed metals and nutrients stay on or in the extracellular sheath, thus avoiding leaching and potentially remaining bio-available to associated organisms[79]. The sticky EPS surface also helps retain nutrient-rich dust, which further increases soil fertility[57,80]. Dust inputs may also directly provide BSCs and epiliths with needed nutrients, as it is likely that the nutrients immediately surrounding these communities are depleted over time. Dust also infiltrates to the underside of rocks and could benefit hypoliths. However, despite dust having the potential to dramatically increase the nutrient availability to SRSCs, experimental evidence for this effect is lacking.

Other factors lead to a concentration of nutrients and carbon in the thin zone that is occupied by SRSCs. Soil faunal abundance and richness is higher in the well-developed BSCs in surface soils than at depth, resulting in higher decomposition rates and, hence, nutrients at the surface[81,82]. Dust deposition and the effects of SRSCs on nutrient availability, as discussed above, occur at the soil surface[80]. Because most desert rain events are typically for <5 mm of water[5], many rain events activate nutrient cycling in SRSCs but not in subsurface biota[83–84].

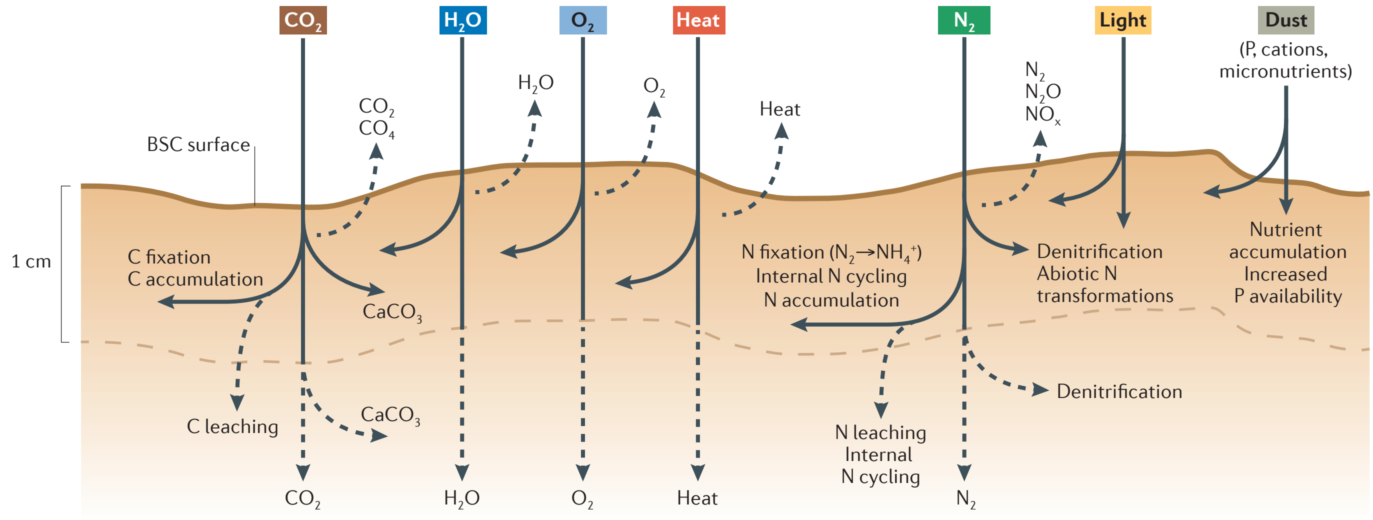


Figure 5 | **Biological soil crusts mediate the movement of materials and are responsible for energy entering and leaving the soil.** Biological soil crusts (BSCs) cover most desert soil surfaces. Gases, nutrients and water are held in the uppermost few centimetres of intact biocrusted soils. Light does not penetrate beyond this surface layer. Most of the biological activity (and therefore ecosystem processes) that is found in desert soils occurs in this top layer. Disturbance of soil crusts has severe negative impacts on these processes.

In addition, such light rain events limit the depth to which nutrients can leach[84]. The resultant concentration of nutrients at the soil surface may have favoured the development of direct linkages between SRSCs and nearby vascular plants, just as mycorrhizal associations were favoured between fungi and vascular plant roots at depth[85]. Indeed, one study used labelled substrates to demonstrate nitrogen transfer from root-free BSCs to plants and from plants to BSCs via a network dominated by dark septate fungi[86]. As these transfers occur at up to 100 cm per day, they clearly bypass transfer-retardant soils and perhaps even plant roots. They are also apparently controlled by fungal metabolism rather than plant or cyanobacterial demand. Flows of carbon in this experiment were found from plants to BSCs but not vice versa, indicating a possible subsidy of BSCs by plants under dry conditions. The relationship between mycorrhizal fungi (which are known to transfer carbon, phosphorus and water to plants[85]) and BSCs is not understood. Although mycorrhizal fungi are yet to be detected in BSCs, these crusts have been found to contain high levels of glomalin, which often indicate the presence of mycorrhizal associations (R. Rilling & J.B., unpublished observations). In addition, a strong positive correlation has been demonstrated between BSCs and the rate of mycorrhizal infections in plants[87]. Thus, direct transfer of water and nutrients between BSCs and plants may be occurring via dark septate fungi or even a linked network of dark septate and mycorrhizal fungi[88]. Fungi can also penetrate porous rock, transferring water and possibly nutrients from the rock to nearby plants[89]. However, despite the evidence showing that SRSCs enhance the nutrition and growth of vascular plants, only a few studies have provided insight into the mechanism behind this linkage. Thus, exploring and defining these connections presents another exciting new area for future research in these systems.

Local disturbance, regional impact

Disturbance effects. Desert SRSCs are threatened by human encroachment, environmental stochasticity (particularly drought) and predicted long-term climate change. An increasing percentage of the world's population lives in dryland areas, where agricultural production at local subsistence levels and large-scale farming are both causal agents of and threatened by desertification[90]. The disruption of BSCs and desert pavements is a major contributor in a positive feedback loop that enhances desertification (BOX 1), and impacts at local scales manifest as regional and global problems[91,92]. Dust storms reduce soil fertility at the source and result in highway fatalities and economic losses as they move across the landscape. For instance, dust production has increased dramatically during the past 150 years in the western United States owing to increased human activity[93]. Wind-blown soils resulting from BSC degradation is deposited on nearby snowpack, leading to accelerated melt rates, increased evapotranspiration from exposed soils and early plant germination. This reduces freshwater inputs to rivers, thus negatively affecting regional hydrological regimens[94]. Mobilization of desert dust also results in deposition of dust to ocean basins, where associated iron input has substantial effects on marine nitrogen fixation[95]. The fine particulate nature of desert dust also presents a direct threat to respiratory health, and we have increasing evidence to suggest that pathogens are transported in desert dust[29]. Urban bio-aerosols are substantially affected by desert dust events even across intercontinental distances[96].

Recovery and management options. Natural recovery rates for SRSCs are very slow. For BSCs, recovery rates are highest when soils are moist for longer (for example, at higher elevation, under shrub canopies and for fine-textured soils) and stable, and when inoculant occurs nearby. In disturbed soil crusts of a cold Colorado Plateau desert in the USA, the keystone taxon, *M. vaginatus*, was detectable at low levels following disturbance[97], but estimates for the recovery time of cyanobacterial soil crusts are 15–50 years, whereas soil lichens take decades to centuries to recover[98]. Hence, many species may not re-establish in typical management timeframes. At present, there is no information available about the natural recovery rates of disturbed endolithic or hypolithic communities. Growth and colonization rates for epilithic desert lichens have been studied worldwide for decades and found to be very low[33].

Assisted recovery has not been attempted for lithic communities in natural settings, although hypolithic colonization might be enhanced in desert pavements by the introduction of a colonizable substrate (for example, quartz pebbles), and these could also be inoculated with hypolithic taxa. Most research has focused on the regeneration of BSCs in dryland soils. Like natural recovery, assisted recovery is most successful where soils are stable and moist for longer and where inoculant is available. Crust material salvaged from one area and transplanted to another can speed recovery at the small-plot scale (for example, <20 hecatres (REF. 99)). Artificial cultivation and inoculation have been attempted for larger-scale rehabilitation, and although many such experiments have failed (for example, see REF. 100), there have been some successes (for example, see REFS 101,102). Studies show that although cultivation of large amounts of cyanobacteria for an inoculum is fairly straightforward, successful colonization in the harsh desert environment is a major hurdle. Successful efforts have generally pre-exposed the cyanobacteria to thermal, UV and moisture stress, and have physically stabilized target areas before application of the inoculum. Given our limited ability to rehabilitate BSCs, our best strategy for maintaining these communities is to reduce their disturbance. This will require industry, governments and the public to be educated as to the value of SRSCs in dryland ecosystems. Such a strategy is currently in use by the US National Parks Service in Utah, where the "Don't Bust the Crust" logo and associated educational materials have substantially raised awareness of the importance and fragility of BSCs (see links box).

Rethinking the 'critical zone' in deserts

The Earth's Critical Zone is defined as the "heterogeneous, near surface environment in which complex interactions involving rock, soil, water, air, and living organisms regulate the natural habitat and determine the availability of life-sustaining resources" (REF. 103). In most temperate and tropical ecosystems, tall plants and the large numbers of roots ramifying throughout deep soils result in a critical zone that is measured in many metres. Conversely, deserts have sparse, short vegetation, as well as soils that are shallow or non-existent and large amounts of rock surfaces. Therefore, we propose a different way of envisioning the critical zone in deserts: rather than encompassing many metres of life above and below the soil, and being mostly driven by processes that occur at depth, where most plant roots occur, the critical zone in deserts is, instead, just at, on or in the top few centimetres of rock or soil surfaces. This zone is characterized by the presence of SRSCs, not plant roots. This view is justified by the crucial nature of this surface layer in almost every ecosystem process that occurs in deserts, including weathering, carbon and nitrogen cycles, dust capture, ensuring the bio-availability of phosphorus and nutrients, decomposition, and modification of soil stability (most notably by reducing dust production). In addition, as SRSCs cover most soil and rock surfaces, these communities mediate almost all inputs and outputs (gases, nutrients and water) to and from strata above and below the surface. They may also facilitate direct delivery of carbon, nutrients and water from the soil interspace to nearby plants.

Critical zone
The physical location at which the major biogeological factors that affect a particular environment interact with each other.

Despite the ubiquity of SRSCs and their demonstrated control over desert ecosystem processes, there are still many unanswered questions regarding their biology, physiology and ecology. Future research should aim to open the 'black box' of SRSCs and unravel the structure–function relationships of these communities more clearly. For instance, we still do not know the mechanisms of stress responses at the cellular and community assembly levels, nor the contributions of these responses to successful colonization. This information could reveal novel pathways and inform us about the evolution of adaptive traits in organisms from SRSCs. Dispersal (including invasive colonization) of these organisms across local, regional and continental scales is also poorly understood but is undoubtedly a major factor in shaping the biogeography of SRSCs. To what extent is community assembly and functionality linked in different SRSCs? This question is currently being addressed using high-throughput omics-based interrogations, but field measurements of *in situ* responses over extended spatial and temporal scales and across regional and trophic boundaries are also essential to understand the functions of these communities. It will be intriguing to establish the extent to which biogeological processes and interactions with higher plants can be predicted by SRSC type, and whether a unifying theory can be developed to explain the role of all SRSCs. Such linkages may be crucial and also unique to dryland systems, given the nature of the critical zone in drylands.

Given the concerns about climate change, and given the environmental stochasticity that accompanies such change, it is timely that we attempt to more fully comprehend the role and responses of these desert surface communities during both the deterioration and remediation of desert landscapes. Furthermore, the extent of arid lands globally, the projected increase in aridity as a result of climate change, and the increasing level of human reliance on these ecosystems together mean that continued study of microbial life in arid environments is of the highest importance.

1. Thomas, D. S. G. in *Arid Zone Geomorphology: Process, Form and Change in Drylands* (ed. Thomas, D. S. G.) 3–16 (Wiley-Blackwell, 2011).
2. Barrow, C. J. *World Atlas of Desertification (United Nations Environment Program)* (Edward Arnold, 1992).
3. Peel, M. C., Finlayson, B. L. & McMahon, T. A. Updated world map of the Koppen-Geiger climate classification. *Hydrol. Earth Syst. Sci.* **11**, 1633–1644 (2007).
4. Millenium Ecosystem Assessment, 2005. *Ecosystems and Human Well-being: Desertification Synthesis* (World Resources Institute, 2005).
5. Laity, J. in *Deserts and Desert Environments* (Wiley-Blackwell, 2008).
6. Belnap, J., Budel, B. & Lange, O. L. in *Biological Soil Crusts: Structure, Function, and Management* (eds Belnap, J. & Lange, O. L.) 3–30 (Springer-Verlag, 2003).
An excellent introduction to the importance of desert surface communities, in a book that is recognized as the most comprehensive treatment of BSC ecology.
7. Warren-Rhodes, K. A. *et al.* Hypolithic bacteria, dry limit of photosynthesis and microbial ecology in the hyperarid Atacama Desert. *Microb. Ecol.* **52**, 389–398 (2006).
This study ascertains the dry limit for life in the most arid desert on Earth, as well as the positive correlation between aridity and the age of SRSCs.
8. Pointing, S. B., *et al.* Highly specialized microbial diversity in hyper-arid polar desert. *Proc. Natl Acad. Sci. USA* **106**, 19964–19969 (2009).
9. Wong, K. Y., *et al.* Endolithic microbial colonization of limestone in a high altitude arid environment. *Microb. Ecol.* **59**, 689–699 (2010).
10. Caruso, T., Chan, Y., Lacap, D. C., McKay, C. P. & Pointing, S. B. Stochastic and deterministic processes interact to determine global biogeography of arid soil bacteria. *ISME J.* **5**, 1406–1413 (2011).
11. Davila, A., *et al.* Facilitation of endolithic microbial survival in the hyperarid core of the Atacama Desert by mineral deliquescence. *J. Geophys. Res.* **113**, G01028 (2008).
12. Azúa-Bustos, A. *et al.* Hypolithic cyanobacteria supported mainly by fog in the coastal range of the Atacama Desert. *Microb. Ecol.* **61**, 568–581 (2011).
13. Lange, O. L. in *Biological Soil Crusts: Structure, Function, and Management* (eds Belnap, J. & Lange, O. L.) 217–240 (Springer-Verlag, 2003).
14. Warren-Rhodes, K. A., *et al.* Lithic cyanobacterial ecology across environmental gradients and spatial scales in China's hot and cold deserts. *FEMS Microbiol. Ecol.* **61**, 470–482 (2007).
15. Schlesinger, W. H., *et al.* Community composition and photosynthesis by photoautotophs under quartz pebbles, southern Mojave Desert. *Ecology* **84**, 3222–3231 (2003).
16. Tracy, C. R., *et al.* Microclimate and limits to photosynthesis in a diverse community of hypolithic cyanobacteria in northern Australia. *Environ. Microbiol.* **12**, 592–607 (2010).
17. Wendler, G. & Eaton, F. On the desertification of the Sahel Zone part 1: ground observations. *Clim. Change* **5**, 365–380 (1983).
18. Belnap, J. in *Biological Soil Crusts: Structure, Function, and Management* (eds Belnap, J. & Lange, O. L.) 177–192 (Springer-Verlag, 2003).
19. Bahl, J. *et al.* Ancient origins determine global biogeography of hot and cold desert cyanobacteria. *Nature Commun.* **2**, 163 (2011).
This article reveals the ubiquity of the cyanobacterial *Chroococcidiopsis* spp. in deserts worldwide and uncovers climate-related patterns in biogeography.
20. Wong, K. Y., *et al.* Hypolithic colonization of quartz pavement in the high altitude tundra of central Tibet. *Microb. Ecol.* **60**, 730–739 (2010).
21. Nash, T. H. I. I. I., White, S. L. & Marsh, J. E. Lichen and moss distribution and biomass in hot desert ecosystems. *Bryologist* **80**, 470–479 (1977).
22. Staley, J. T., Palmer, F. & Adams, J. B. Microcolonial fungi: common inhabitants on desert rocks? *Science* **215**, 1093–1095 (1982).
23. Gorbushina, A. A. Life on the rocks. *Environ. Microbiol.* **9**, 1613–1631 (2007).
24. Dorn, R. I. & Oberlander, T. M. Microbial origin of desert varnishes. *Science* **213**, 1245–1247 (1981).
25. Kuhlman, K. R., *et al.* Diversity of microorganisms within rock varnish in the Whipple Mountains, California. *Appl. Environ. Microbiol.* **72**, 1708–1715 (2006).
26. Friedmann, E. I. Endolithic microbial life in hot and cold deserts. *Orig. Life* **10**, 223–235 (1980).
A classic paper by one of the great pioneers of desert microbiology, identifying the nature of endolithic colonization in hot and cold deserts.
27. Buedel, B. & Wessels, D. C. J. Rock inhabiting blue-green algae cyanobacteria from hot arid regions. *Archiv. Hydrobiol.* **92**, 385–398 (1991).
28. Kellog, C. A. & Griffin, D. W. Aerobiology and the global transport of desert dust. *Trends Ecol. Evol.* **21**, 638–644 (2006).
29. Griffin, D. W. Atmospheric movement of microorganisms in clouds of desert dust and implications for human health. *Clin. Microbiol. Rev.* **20**, 459–477 (2007).
30. Pointing, S. B., Warren-Rhodes, K. A., Lacap, D. C., Rhodes, K. L. & McKay, C. P. Hypolithic community shifts occur as a result of liquid water availability along environmental gradients in China's hot and cold hyperarid deserts. *Environ. Microbiol.* **9**, 414–424 (2007).
31. Bowker, M. A., Belnap, J., Davidson, D. W. & Goldstein, H. P. Correlates of biological soil crust abundance across a continuum of spatial scales: support for a hierarchical conceptual model. *J. Ecol.* **43**, 152–163 (2006).
32. Liu, Y., *et al.* Control of lunar and martian dust—experimental insights from artificial and natural cyanobacterial and algal crusts in the desert of inner Mongolia, China. *Astrobiology* **8**, 75–86 (2008).

33. Lange, O. L. Twenty-three years of growth measurements on the crustose lichen *Caloplaca aurantia* in the central Negev Desert, Israel. *J. Bot.* **39**, 883–894 (1990).
34. Quade, J. Desert pavements and associated rock varnishes in the Mojave Desert: how old can they be? *Geology* **29**, 855–858 (2001).
35. Gao, Q. & Garcia-Pichel, F. Microbial ultraviolet sunscreens. *Nature Rev. Microbiol.* **9**, 791–802 (2011).
36. Daly, M. J. A new perspective on radiation resistance based on *Deinococcus radiodurans*. *Nature Rev. Microbiol.* **7**, 237–245 (2009).
37. Potts, M. Desiccation tolerance of prokaryotes. *Microbiol. Mol. Biol. Rev.* **58**, 755–805 (1994).
38. Yura, T., Kanemori, M. & Morita, M. T. in *Bacterial Stress Responses* (eds Storz, G. & Hengge-Aronis, R.) 3–18 (American Society for Microbiology Press, 2000).
39. Oren, A. & Gunde-Cimerman, N. Mycosporines and mycosporine-like amino acids: UV protectants or multipurpose secondary metabolites? *FEMS Microbiol. Lett.* **269**, 1–10 (2007).
40. Billi, D. & Potts, M. Life and death of dried prokaryotes. *Res. Microbiol.* **153**, 7–12 (2002).
41. Cox, M. M. & Battista, J. R. *Deinococcus radiodurans* — the consummate survivor. *Nature Rev. Microbiol.* **3**, 882–892 (2005).
42. Billi, D., Friedmann, I. E., Hofer, K. G., Grilli-Caiola, M. & Ocampo-Friedmann, R. Ionizing-radiation resistance in the desiccation-tolerant cyanobacterium *Chroococcidiopsis*. *Appl. Environ. Microbiol.* **66**, 1489–1492 (2000).
43. Cockell, C. S. & Horneck, G. The history of the UV radiation climate of the earth – theoretical and space-based observations. *Photochem. Photobiol.* **73**, 447–451 (2001).
44. Garcia-Pichel, F. & Pringault, O. Cyanobacteria track water in desert soils. *Nature* **413**, 380–381 (2001).
45. Mazor, G., Kidron, G. J., Vonshak, A. & Abelovich, A. The role of cyanobacterial exopolysaccharides in structuring desert microbial crusts. *FEMS Microbiol. Ecol.* **21**, 121–130 (1996).
46. Viles, H. in *Arid Zone Geomorphology: Process, Form and Change in Drylands* (ed. Thomas, D. S. G.) 131–180 (Wiley-Blackwell, 2011).
47. Buedel, B. *et al.* Reshaping of sandstone surfaces by cryptoendolithic cyanbacteria: bioalkination causes chemical weathering in arid landscapes. *Geobiology* **2**, 261–268 (2004).
48. Viles, H. Ecological perspectives on rock surface weathering: towards a conceptual model. *Geomorphology* **13**, 21–35 (1995).
49. Bennett, P. C., Rogers, J. R. & Choi, W. J. Silicates, silicate weathering, and microbial ecology. *Geomicrobiol. J.* **18**, 3–19 (2001).
50. Banfield, J. F., Barker, W. W., Weelch, S. A. & Taunton, A. Biological impacts of mineral dissolution: application of the lichen model to understanding mineral weathering in the rhizosphere. *Proc. Natl Acad. Sci. USA* **96**, 3404–3411 (1999).
51. Gorbushina, A. A. in *Fungi in Biogeochemical Cycles* (ed. Gadd, G. M.) 267–288 (Cambridge Univ. Press, 2006).
52. Garcia-Pichel, F., Ramirez-Reinat, E. & Gao, Q. Microbial excavation of solid carbonates powered by P-type ATPase-mediated transcellular Ca^{2+} transport. *Proc. Natl Acad. Sci. USA* **50**, 21749–21754 (2010).
53. Fomina, M., Burford, E. P. & Gadd, G. M. in *Fungi in Biogeochemical Cycles* (ed. Gadd, G. M.) 236–266 (Cambridge Univ. Press, 2006).
54. Danin, A. & Garty, J. Distribution of cyanobacteria and lichens on hillsides of the Negev Highlands and their impact on biogenic weathering. *Zeitschrift Geomorphol.* **27**, 423–444 (1983).
55. Schwartzmann, D. W. & Volk, T. Biotic enhancement of weathering and the habitability of Earth. *Nature* **340**, 457–460 (1989).
This report describes how SRSCs enhance weathering of mineral substrates by orders of magnitude.
56. Hopkins, D. W., *et al.* Isotopic evidence for the provenance and turnover of organic carbon by soil microorganisms in the Antarctic Dry Valleys. *Environ. Microbiol.* **11**, 597–608 (2008).
57. Dregne, H. E. *Desertification of Arid Lands: Advances in Desert and Arid Land Technology and Development* Vol. 3 (Harwood Academic, 1983).
58. Belnap, J. & Gardner, J. S. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. *Great Basin Nat.* **53**, 40–47 (1993).
59. Belnap, J. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrol. Process.* **20**, 3159–3178 (2006).
60. Lange, O. L., Meyer, A., Zellner, H. & Heber, U. Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Funct. Ecol.* **8**, 253–264 (1994).
61. Rietkirk, M., Dekker, S. C., de Ruiter, P. C. & van de Koppel, J. Self-organized patchiness and catastrophic shifts in ecosystems. *Science* **305**, 1926–1929 (2004).
62. Grote, E. E., Belnap, J., Housman, D. C. & Sparks, J. P. Carbon exchange in biological soil crust communities under differential temperatures and soil water contents: implications for global change. *Glob. Change Biol.* **16**, 2763–2774 (2010).
63. Rao, D. L. N. & Burns, R. G. Use of blue-green algae and bryophyte biomass as a source of nitrogen for oil-seed rape. *Biol. Fertil. Soils* **10**, 61–64 (1990).
64. Rogers, S. L. & Burns, R. G. Changes in aggregate stability, nutrient status, indigenous microbial populations, and seedling emergence, following inoculation of soil with *Nostoc muscorum*. *Biol. Fert. Soils* **18**, 209–215 (1994).
65. Lange, O. L., *et al.* Taxonomic composition and photosynthetic characteristics of the "biological crusts" covering sand dunes in the Western Negev Desert. *Funct. Ecol.* **6**, 519–527 (1992).
66. McLendon, T. & Redente, E. F. Effects of nitrogen limitation on species replacement dynamics during early secondary succession on a semi-arid sagebrush site. *Oecologia* **91**, 312–317 (1992).
67. Romney, E. M., Wallace, A. & Hunter, R. B. in *Nitrogen in Desert Ecosystems* (eds West, N. E. & Skujins, J. J.) (Dowden, Hutchison & Ross, 1978).
68. Belnap, J. in *Biological Soil Crusts: Structure, Function, and Management* (eds Belnap, J. & Lange, O. L.) 241–261 (Springer Verlag, 2003).
69. Johnson, S. L., Neuer, S. & Garcia-Pichel, F. Exports of nitrogenous compounds due to incomplete cycling within biological soil crusts of arid lands. *Environ. Microbiol.* **9**, 680–689 (2007).
70. Harper, K. T. & Belnap, J. The influence of biological soil crusts on mineral uptake by associated vascular plants. *J. Arid Environ.* **47**, 347–357 (2001).
71. Evans, R. D. & Ehleringer, J. R. A break in the nitrogen cycle in arid lands? Evidence from ^{15}N of soils. *Oecologia* **94**, 314–317 (1993).
72. Crenshaw, C., Lauber, C., Sinsabaugh, R. L. & Stavely, L. K. Fungal dominance of nitrogen transformation in semi-arid grassland. *Biogeochemistry* **87**, 17–27 (2008).
73. Johnson, S. L., Budinoff, C. R., Belnap, J. & Garcia-Pichel, F. Relevance of ammonium oxidation within biological soil crust communities. *Environ. Microbiol.* **7**, 1–12 (2004).
74. McCalley, C. K. & Sparks, J. P. Abiotic gas formation drives nitrogen loss from a desert ecosystem. *Science* **326**, 837–840 (2009).
75. Friedmann, I. E. & Kibler, A. P. Nitrogen economy of endolithic microbial communities in hot and cold deserts. *Microb. Ecol.* **6**, 95–108 (1980).
76. Lange, W. Chelating agents and blue-green algae. *Can. J. Microbiol.* **20**, 1311–1321 (1974).
77. Bose, P., Nagpal, U. S., Venkataraman, G. S. & Goyal, S. K. Solubilization of tricalcium phosphate by blue-green algae. *Curr. Sci.* **40**, 165–166 (1971).
78. Gadd, G. M. Biosorption. *Chem. Industry* **13**, 421–426 (1990).
79. Geesey, G. & Jang, L. in *Microbial Mineral Recovery* (eds Ehrlich, H. L. & Brierly, C. L.) 223–247 (McGraw-Hill, 1990).
80. Reynolds, R. L., Belnap, J., Reheis, M., Lamothe, P. & Luizers, F. Aoelian dust in Colorado Plateau soils: nutrient inputs and recent change in sources. *Proc. Natl Acad. Sci. USA* **98**, 7123–7127 (2001).
This work highlights the role of SRSCs in the capture and retention of desert dust.
81. Bowling, D. R., Grote, E. E. & Belnap, J. Rain pulse response of soil CO_2 exchange by biological soil crusts and grasslands of the semiarid Colorado Plateau, United States. *J. Geophys. Res.* **116**, G03028 (2011).
82. Austin, A. T. *et al.* Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* **141**, 221–235 (2004).
83. Belnap, J. in *Biological Soil Crusts: Structure, Function, and Management* (eds Belnap, J. & Lange, O. L.) 167–174 (Springer-Verlag, 2003).
84. Darby, B. J., Neher, D. A. & Belnap, J. Soil nematode communities are ecologically more mature beneath late- than early-successional stage biological soil crusts. *Appl. Soil Ecol.* **35**, 203–212 (2007).
85. Johnson, N. C., Wilson, G. W. T., Bowker, M. A., Wilson, J. A. & Miller, R. M. Resource limitation is a driver of local adaptation in mycorrhizal symbioses 2010. *Proc. Natl Acad. Sci. USA* **107**, 2093–2098 (2010).
86. Green, L. E., Porras-Alfaro, A. & Sinsabaugh, R. L. Translocation of nitrogen and carbon integrates biotic crust and grass production in desert grassland. *J. Ecol.* **96**, 1076–1085 (2008).
This article demonstrates the crucial role of SRSCs in carbon and nitrogen transfer to plant communities.
87. Harper, K. T. & Pendleton, R. L. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? *Great Basin Nat.* **53**, 59–72 (1993).
88. Porras-Alfaro, A. & Bayman, P. Hidden fungi, emergent properties: endophytes and microbiomes. *Annu. Rev. Phytopathol.* **49**, 291–315 (2011).
89. Egerton-Warburton, L. M., Graham, R. C. & Hubbert, K. R. Spatial variability in mycorrhizal hyphae and nutrient and water availability in a soil-weathered bedrock profile. *Plant Soil* **249**, 331–342 (2003).
90. Wiggs, G. F. S. in *Arid Zone Geomorphology: Process, Form and Change in Drylands* (ed. Thomas, D. S. G.) 583–598 (Wiley-Blackwell, 2011).
91. Middleton, N. J. in *Paleoclimatology and Paleometeorology: Modern and Past Patterns of Global Atmospheric Transport* (eds Leinen, M. & Sarnthein, M.) 97–132 (Springer-Verlag, 1989).
92. Field, J. P. *et al.* The ecology of dust. *Frontiers Ecol. Env.* **8**, 423–430 (2010).
93. Neff, J. C., Ballantyne, A. P. & Farmer, G. L. Increasing eolian dust deposition in the western United States linked to human activity. *Nature Geosci.* **1**, 189–195 (2008).
94. Painter, T. H., *et al.* Response of Colorado River runoff to dust radiative forcing in snow. *Proc. Natl Acad. Sci. USA* **107**, 17125–17130 (2010).
This report illustrates the fact that disturbance of desert SRSCs can lead to regional-scale disturbances in hydrology.
95. Sohm, J. A., Webb, E. A. & Capone, D. G. Emerging patterns of marine nitrogen fixation. *Nature Rev. Microbiol.* **9**, 499–508 (2011).
96. Jeon, E. M., *et al.* Impact of Asian dust events on airborne bacterial community assessed by molecular analysis. *Atmos. Environ.* **45**, 4313–4321 (2011).
97. Kuske, C. R., Yaeger, C. M., Johnson, S., Ticknor, O. L. & Belnap, J. Response and resilience of soil biocrust bacterial communities to chronic physical disturbance in arid shrublands. *ISME J.* **6**, 886–897 (2012).
98. Belnap, J. & Eldridge, D. in *Biological Soil Crusts: Structure, Function, and Management* (eds Belnap, J. & Lange, O. L.) 363–384 (Springer-Verlag, 2003).
99. Belnap, J. Recovery rates of cryptobiotic crusts: Inoculant use and assessment methods. *Great Basin Nat.* **53**, 89–95 (1993).
100. Buttars, S. A. *et al.* Pelletized cyanobacterial soil amendments: laboratory testing for survival, escapability, and nitrogen fixation. *Arid Soil Res. Rehabil.* **12**, 165–178 (1998).
101. Chen, L., *et al.* Man-made desert algal crusts as affected by environmental factors in Inner Mongolia, China. *J. Arid. Environ.* **67**, 521–527 (2006).
102. Wang, W., Liu, Y., Li, D., Hu, C. & Rao, B. Feasibility of cyanobacterial inoculation for biological soil crusts formation in desert area. *Soil Biol. Biochem.* **41**, 926–929 (2009).
103. US National Research Council. *Basic Research Opportunities in the Earth Sciences* (The National Academies Press, 2001).
104. Budel, B., Karsten, U. & Garcia-Pichel, F. Ultraviolet-absorbing scytonemin and mycosporine-like amino acid derivatives in exposed rock-inhabiting cyanobacterial lichens. *Oecologia* **112**, 165–172 (1997).
105. Rikkinen, J. What's behind the pretty colours? A study on the photobiology of lichens. *Bryobrothera* **4**, 1–239 (1995).
106. Garvie, L. A. J., Knauth, L. P., Bungartz, F., Klonowski, S. & Nash, T. H. 3rd. Life in extreme environments: survival strategy of the endolithic desert lichen *Verrucaria rubrocincta*. *Naturwissenscaften* **95**, 705–712 (2008).

Competing interests statement

The authors declare no competing financial interests.

FURTHER INFORMATION

Stephen B. Pointing's homepage: http://www.aut.ac.nz/study-at-aut/study-areas/sciences
Jayne Belnap's homepage: http://sbsc.wr.usgs.gov/about/contact/bio/belnap_jayne.aspx?id=211
Educational material about soil crusts and their conservation: http://www.soilcrust.org
UNCCD: http://www.unccd.int/

ALL LINKS ARE ACTIVE IN THE ONLINE PDF

ERRATUM

Microbial colonization and controls in dryland systems

Stephen B. Pointing & Jayne Belnap

Nature Reviews Microbiology **10**, 551–562 (2012)

In the original article, the wrong image was mistakenly introduced for Fig. 2h. The correct image has now been included. We apologize to the authors and to readers for this error and for any confusion caused.