The world at your feet: desert biological soil crusts

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Desert soil surfaces are generally covered with biological soil crusts, composed of a group of organisms dominated by cyanobacteria, lichens, and mosses. Despite their unassuming appearance, these tiny organisms are surprisingly important to many processes in past and present desert ecosystems. Cyanobacteria similar to those seen today have been found as 1.2 billion-year-old terrestrial fossils, and they probably stabilized soils then as they do now. Biological crusts are vital in creating and maintaining fertility in otherwise infertile desert soils. They fix both carbon and nitrogen, much of which is leaked to the surrounding soils. They also capture nutrient-rich dust, and can stimulate plant growth. These organisms are able to tolerate extreme temperatures, drought, and solar radiation, despite having relatively little wet time for metabolic activity. Under most circumstances, they are extremely vulnerable to climate change and disturbances such as off-road vehicles and grazing livestock. Recovery times are generally measured in decades or centuries.

Most people imagine the desert as a lifeless place, covered with rocks and sand, but this is not true. Deserts are exploding with life, although much of it is barely visible to the untrained eye. Despite their barren appearance, rocks and sand are often covered with a thin film of cyanobacteria, microfungi, lichens, and/or mosses that can occur on the surface or within the rock (endolithic) and on or just below the sand. The organisms living on and just beneath the soil surface are collectively known as biological soil crusts (Figure 1).

This incredibly diverse group has been called many things since it was first named in the 1950s, including cryptogamic, cryptobiotic, microphytic, microfloral, organogenic, and microbiotic soil crusts (Harper and Marble 1988). These communities often dominate the living ground cover in hot, cool, and cold arid and semi-arid regions. They also occur in temperate regions where plant cover is reduced, either temporarily (eg tree falls) or permanently (eg pine barrens). Despite their widespread occurrence, the major influence biological crusts have on terrestrial ecosystems has only been recognized in the past two decades (Belnap and Lange 2001).

Cyanobacteria form the matrix of biological soil crusts. They first appear in the fossil record as marine stromatolites over 3 billion years ago (Walter *et al.* 1976). These large floating mats have been credited with oxygenating the atmosphere and forming the basis of the marine food web. The earliest terrestrial cyanobacteria are found in 1.2 billion-year-old rocks (Horodyski and Knauth 1994). Just as soil crusts do today, cyanobacteria probably accelerated the weathering of exposed bedrock and conferred stability on the newly formed soils as they spread across the land, thus aiding the evolution and spread of vascular plants and other terrestrial life forms (Schwartzman and Volk 1989).

■ Ins and outs of soil crusts

The term "biological soil crust" refers to the cohesiveness of the soil surface created by soil crust organisms. Most of this cohesion is due to large filamentous cyanobacteria, most notably the ubiquitous genus *Microcoleus* (Figure 2a), which is common around the world. When moistened, *Microcoleus* filaments extend towards the soil surface, and retract as the soil dries. This frequent movement results in copious sheath material being left in the uppermost soil layers, linking otherwise loose particles together to form larger soil aggregates (Figure 2b). It is easy to see this aggregation: hold a piece of desert soil aloft and look for small dangling soil clumps attached to cyanobacterial sheaths (Figure 3). Physical soil crusts, which result from raindrop or trampling impacts, often coexist with biological crusts, and also contribute to soil cohesion. Unlike biological crusts, physical crusts reduce water infiltration, often inhibit plant establishment, and

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In a nutshell:

- Biological soil crusts are composed of soil cyanobacteria, lichens, and mosses, and are found in environments with sparse plant cover
- These crusts are essential in providing stability and fertility to desert soils
- The component organisms are easily damaged by soil surface disturbance, and are very slow to recover
- Protecting biological soil crusts should be a top management priority in desert regions, or we will lose the important ecosystem services they provide

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Figure 1. *(a-c) Soil crusts cover the large interspaces between vascular plants. (d) Close-up showing crust mounds that greatly roughen soil surfaces, enhancing retention of water, organic matter, dust, and seeds.*

do not always protect the soil surface from erosion, because they dissolve when wet.

Hundreds of species of cyanobacteria and eucaryotic green algae are associated with biological soil crusts (Evans and Johansen 1999). Since these photosynthetic organisms require light, most biomass is concentrated in the upper soil layers (Figure 4, top). At the soil levels where they occur, they alter pH as well as oxygen, ammonium, and nitrate concentrations. Most of the cyanobacteria and green algae in biological crusts are small in size relative to *Microcoleus*, and are of secondary importance in forming the crust matrix. These smaller species (eg *Nostoc*, *Scytonema*, *Chroococcidiopsis*) have limited mobility, and therefore manufacture large amounts of pigments to protect themselves from excess radiation on the surface. *Microcoleus* has almost no protective pigmentation, and lives tucked beneath the pigmented species, at a depth where ultraviolet radiation is reduced, but photosynthetically active radiation is still adequate (Figure 4, bottom). Without the radiation "umbrella" offered by the pigmented species, *Microcoleus* experiences high summer mortality (Bowker *et al.* 2002). This type of microbial stratification is common in both terrestrial and aquatic habitats (Bowker *et al.* 2002).

The external morphology of biological soil crusts is determined by climate and species composition, and this morphology influences how materials such as dust, water, and seeds move across the surface (Figure 5). Smooth crusts, dominated by cyanobacteria, are found in hyperarid regions without frost heaving, and where potential evapotranspiration (PET) is too high (due to excessively low rainfall and/or high air temperatures) to support lichens or mosses. As PET decreases, moss and lichen cover increases. Rugose crusts, with a microtopography of up to 3 cm, are found in hot deserts (high PET) where there is no frost heaving and very low lichen–moss cover. Pinnacled crusts, with a microtopography of up to 15 cm, occur in cool deserts (moderate PET) where lichen cover is <40% and soils freeze in winter. Rolling crusts are found in cool and cold deserts (low PET) where soils freeze, but the cohesion of the high lichen–moss cover restricts pinnacling to about 5 cm.

The taxa of soil crusts are similar around the world, despite their occurrence in areas with a wide range of climates and vegetation types. Many genera and species occur on almost all continents, including *Microcoleus vaginatus*, *Psora decipiens*, *Collema tenax*, *Collema coccophorum*, and *Catapyrenium squamulosum*. Non-related taxa exhibit comparable structures and functions, implying that soil surface conditions have produced convergent evolutionary trends within these taxa (Belnap *et al.* 2001a).

Figure 2. *Scanning electron micrographs of biological soil crusts: (left)* Microcoleus vaginatus *in desert soils, x 700. (right)* Microcoleus vaginatus *sheaths, winding through sand grains, x 90.*

■ In the frying pan

The desert soil surface is one of the most extreme environments on earth. The combination of incoming solar rays and those reflected from the soil surface creates a zone of high radiation. Soil surface temperatures can range from –20°C to over 70°C. Rainfall is infrequent and sparse. The ability of crust organisms to tolerate extreme dehydration is a key to survival. Dry-weight water content can drop to 5% or less, terminating all metabolic processes (Bewley and Krochko 1982). This allows these organisms to withstand extended periods of high heat, strong light, and no water.

Other adaptations also help soil crust organisms to survive on the soil surface. Many species have ways to prolong their activity periods. For instance, many lichens can photosynthesize at high and low temperatures, have large water-holding capacities, and require little moisture to begin metabolism (Lange 2001). Mosses have special structures to store and conduct water, light hairs, and revolute (curled-under) leaf margins to reduce water loss through transpiration (Frey and Kürschner 1991). Pigments are used by many crust species to reflect and/or absorb excessive radiation. Pigmented tissue can keep 50–93% of incoming radiation from reaching the interior of these organisms. If excessive radiation enters the cell, intracellular carotenoids and xanthophylls are there to absorb it (Castenholz and Garcia-Pichel 2000). Unpigmented species can use pigmented species as protection, as discussed above. In addition, mosses, lichens, and liverworts can "roll up" while drying, thereby protecting their sensitive photosynthetic tissue from radiation (Büdel and Wessels 1986; Frey and Kürschner 1991).

■ Multiple roles

Biological crusts have many roles in the formation, stability, and fertility of soils. Relatively undisturbed crusts have more biomass and are better able to perform the functions discussed below, than crusts kept at an early successional stage by disturbance. Despite current levels of information on biological crusts, there is much we don't know, and there are many possible ecosystem services that have never been investigated.

Dust trapping

The increased surface roughness and sticky polysaccharide sheaths associated with biological soil crusts increase the capture of nutrient-rich dust. This dust can augment the levels of most plant-essential nutrients, including nitrogen, phosphorus, and potassium, up to fourfold (Reynolds *et al.* 2001). This increases both the fertility and water-holding capacity of soils (Verrecchia *et al.* 1995). The greater surface roughness found in well-developed crusts captures more dust than disturbed (flattened) surfaces.
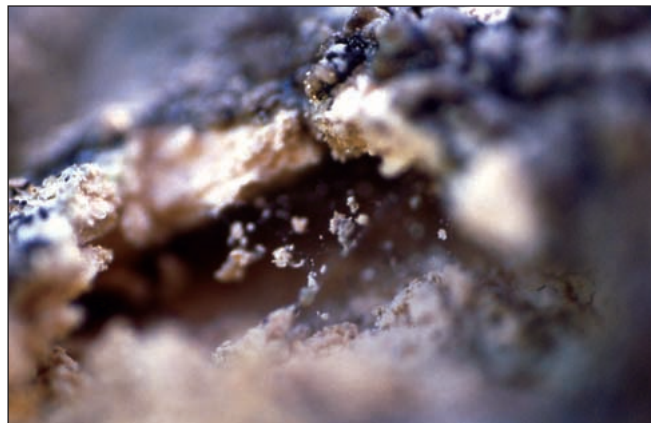

Figure 3. *Close-up view of a soil surface, sliced vertically. The soil aggregates are formed by web-like cyanobacterial fibers, which also hold the aggregates in place.*
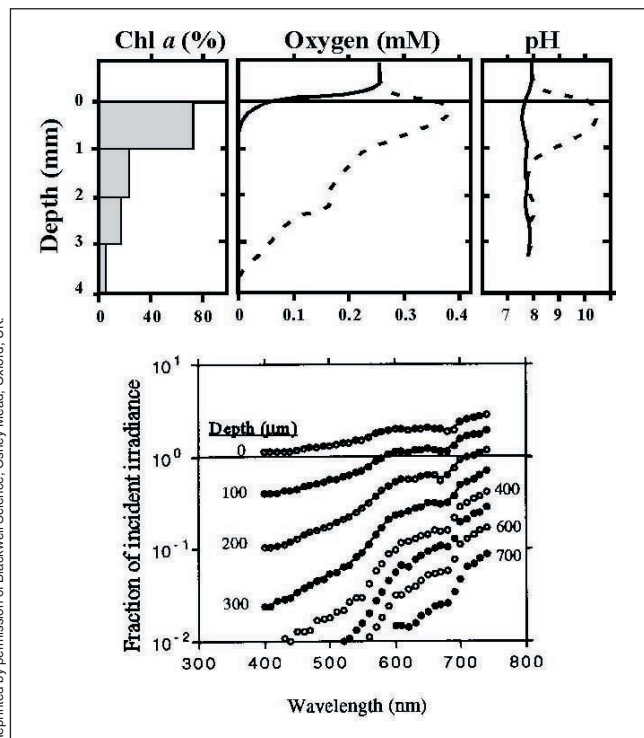
Figure 4. (top) Micro-profiles of cyanobacterial biomass (indicated by chlorophyll a), oxygen production, and pH. Solid lines indicate samples in darkness, dotted lines indicate light (500 umol/m²/s). (bottom) Spectral attenuation of visible radiation as it passes through soil. Notice how the quantity of shorter (UV) wavelengths drops off much more quickly than do longer, photosynthetically active wavelengths, and how light trapping at the surface increases radiation above incident radiation levels.

Weathering

Soil crust organisms in the US, Venezuela, and South Africa increase substrate alkalinity from about pH 8 to about pH10.5 (Garcia-Pichel and Belnap 2001). Crusts also hold water longer, enhancing mineral dissolution and freeze–thaw action. Combined, these factors can accelerate bedrock weathering rates up to 100 times (Schwartzman and Volk 1989). The greater biomass associated with well-developed crusts would be expected to have higher rates than the reduced biomass of disturbed crusts.

Soil physical structure

Polysaccharides extruded by crust organisms bind soil particles together into aggregates critical to soil functioning (Figure 2). Aggregate surfaces are where most soil biota and nutrient transformations occur, and aggregates increase soil aeration, infiltration (Herrick and Wander 1998), and resistance to soil erosion (McKenna-Neuman et al. 1996). Because all crust organisms secrete polysaccharides, crusts with greater biomass (relatively undisturbed crusts) foster more soil aggregation than those with lower biomass (disturbed crusts).

Soil stabilization

Soils in arid regions are slow to form and are highly erodable (Dregne 1983). Biological soil crusts protect desert surfaces from wind and water erosion. Whereas well-developed biological crusts containing lichens and mosses protect these surfaces almost completely from wind and water erosion, disturbed (cyanobacterial) crusts allow up to 35 times more sediment loss in high winds or overland flow (Belnap and Eldridge 2001).

Soil–water relations

The effect of biological soil crusts on water infiltration and soil moisture depends on climate, soil texture, soil structure, and the flora and morphology of the crusts. Because organisms in smooth and rugose crusts reduce the size and number of pores where water can enter the soil, and there is little soil surface roughness to increase water residence time, water infiltration is generally decreased. This can be offset somewhat by water stored by the crust organisms, depending on the amount of rainfall. The resultant runoff in these high PET regions is critical in supporting the often heterogeneously distributed or banded downslope plants. Experimental disruption of the biological crust in these regions, allowing greater localized infiltration, can lead to the death of downslope plants (Eldridge et al. 2000). In contrast, pinnacled and rolling crusts found in regions with lower PET have greatly roughened surfaces that slow water enough to increase infiltration. (Again, the crust organisms themselves absorb and store water.) Highly localized infiltration supports a higher cover of the more homogeneously distributed vegetation found in cooler deserts.

Carbon and nitrogen inputs

Biological soil crusts are an important source of fixed nitrogen and carbon in deserts where vascular plant cover is limited (Beymer and Klopatek 1991; Belnap 2001a). Most inputs occur during the cooler fall, winter, and spring. Carbon inputs range from 0.4–2.3 g/m²/year for cyanobacterial crusts to 12–37 g/m²/year for lichen crusts (Evans and Lange 2001). Both free-living and lichenized cyanobacteria also contribute fixed nitrogen. Many deserts have only a few nitrogen-fixing plants and atmospheric inputs are low (Peterjohn and Schlesinger 1990; Wullstein 1989). As lichen crusts can fix up to 10 kg/ha/year (cyanobacterial crust can fix up to1 kg/ha/year) (Belnap 2002), their input can be the dominant source of new nitrogen for desert soils (Evans and Ehleringer 1993). Much of the carbon and nitrogen fixed by crusts is released upon wetting, so rainfall events contribute both water and nutrient pulses to desert soils. The carbon and nitrogen released by the soil crusts is used by nearby vascular plants, fungi, actinomycetes, and bacteria (Belnap 2001b).
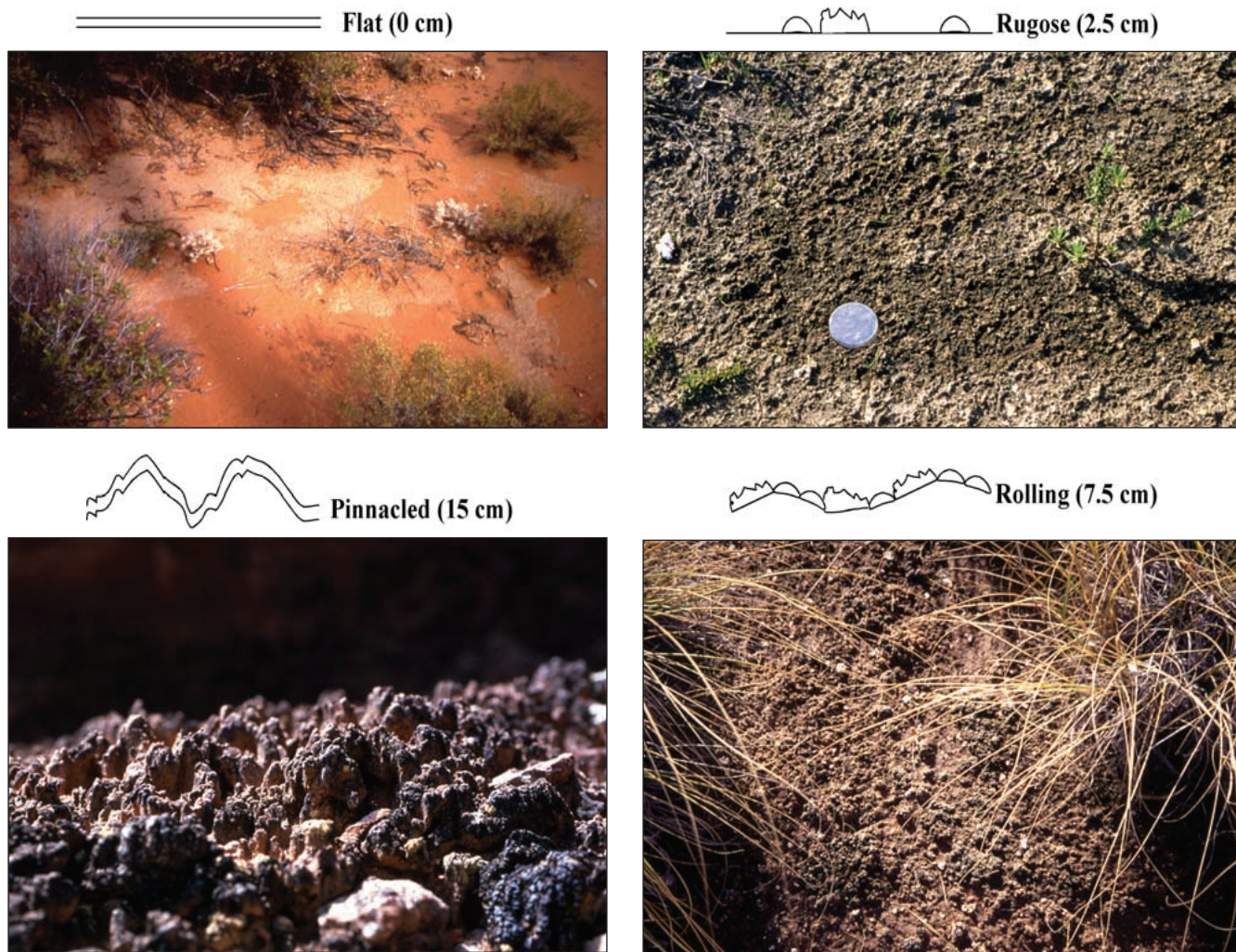
Figure 5. External morphologies of biological crusts, as determined by climate and species composition.

Albedo (reflective power)

Lichen–moss crusts reflect only half the light of uncrusted or cyanobacterially crusted surfaces, decreasing surface energy flux by approximately 40 Joules/sec/m² and increasing surface temperatures by 10–14°C (Belnap 1995). Surface temperatures regulate many ecosystem functions, including rates of nitrogen and carbon fixation, microbial activity, plant nutrient uptake and growth, soil water evaporation, and seed germination (Belnap 2003). Timing of these events is often critical for desert plants, and relatively small alterations can reduce species fitness and seedling establishment, eventually affecting community structure (Bush and Van Auken 1991). Many ants, arthropods, and small mammals partition their environment on the basis of foraging times and burrowing depths, both controlled by surface temperature (Crawford 1991).

Vascular plants and soil fertility

In deserts, vascular plant cover increases crust cover at lower elevations, probably because of the shade found under the plant canopy. At higher elevations, vascular plants and plant litter occupy most of the soil surface, reducing colonization opportunities for crust organisms.

Crust morphology can influence plant establishment patterns. Smooth and rugose crusts increase the tendency of seeds and organic matter to skid from the space between plants on to the next obstacle, be it rock or plant, whereas pinnacled and rolling crusts increase the retention of seeds and organic materials (Belnap *et al.* 2001b). Although a few laboratory studies have shown that soil crusts in hot deserts may reduce native plant germination, this has not been corroborated under field conditions. In contrast, multiple field studies show that germination and survival of native plants is either higher or unaffected in biologically crusted, as compared with uncrusted, areas. Several studies in both Australia and the US indicate that soil crusts can slow the germination of exotic annual grasses (Belnap *et al.* 2001b).

Once established, vascular plants growing in crusted soils generally have greater biomass and higher nutrient concentrations than plants growing in uncrusted soils. There are many ways in which biological crusts can influence soil fertility and plant nutrient concentrations: (1) contributing carbon and nitrogen to the soils; (2)

exuding sticky, negatively charged polysaccharides which bind and prevent leaching loss of positively charged nutrients essential to plants; (3) secreting ring-shaped chemical compounds called chelators that keep nutrients available for plants, despite high soil pH; (4) increasing soil temperatures and nutrient uptake rates; (5) increasing dust capture and soil stabilization, thereby improving soil fertility and water-holding capacity; and (6) increasing soil aggregation. In addition, soil food webs under biological crusts are more diverse and food web groups are more abundant than under cyanobacterial crusts, so decomposition rates and nutrient availability are generally higher (Belnap 2001b). Because lichen–moss crusts have greater diversity, biomass, and soil surface roughness than cyanobacterial crusts, the influence of the factors listed above are greater when soils support a lichen–moss cover rather than a cyanobacterial cover.

■ Resistance and resilience to disturbance

Many types of disturbances threaten the integrity of biological soil crusts, including climate change, increasing human use, and invasion by exotic annual grasses and the subsequent increase in fire risk. Most of these disturbances produce a similar result: the total crust cover is reduced, disturbance-intolerant lichens and mosses are replaced with more disturbance-tolerant cyanobacteria, soil surface temperatures are reduced, and soil surfaces are flattened. The reduction of crust cover and loss of lichens and mosses lead to a loss of soil stability and reduced soil fertility as less polysaccharide material is extruded, less carbon and nitrogen is fixed, less dust and other surface materials are captured, fewer chelators and growth factors are secreted, nutrient uptake rates are lowered, and soil food web organisms decrease in number and diversity. Flattened soil surfaces change the way crusts affect local hydrologic regimes and vascular plant establishment. In other words, the contribution of biological soil crusts to the surrounding ecosystem is greatly compromised.

Land use

As tough as soil crust organisms are in the face of natural stresses (heat, radiation, drought), they are no match for animal hooves, human feet, tank treads, or off-road vehicle tires. The compressional and shear forces these activities generate essentially pulverize soil crusts, especially when they are dry (as they most often are). This leaves pieces of crust free to blow or wash away. If buried, they die, since they need light to photosynthesize. Relative to other disturbance types, direct human impact has probably been most responsible for the simplification and/or destruction of biological soil crusts, and human activities remain the dominant cause of crust loss. Human use of deserts, in terms of recreation, energy development, live-stock grazing, habitation, and military exercises, is expanding rapidly (Brooks and Pokshishevsky 1986). Although no firm quantitative estimates are available, the fragility of soil crusts, combined with the extensive expansion of human activities over the past century, has undoubtedly led to a historically unprecedented loss of lichen–moss cover, and associated ecosystem services, over vast swaths of the western US. Given the inability of soil crusts to withstand the forces generated by such activities, and in view of their slow recovery rates in most deserts, the decreases we currently observe in crust cover and diversity are likely to be relatively permanent. Although the situation is less well known in other countries, the increase in human use of "marginal" lands has become apparent, as the size and frequency of global dust storms have increased dramatically over time (Pimm 2001).

Exotic annual grasses and fire

Invasion by annual grasses also results in the loss of crust cover and biodiversity, as annuals occupy plant interspaces once dominated by soil crusts, and the rich perennial diversity of the crusts is replaced by a few cyanobacterial and annual moss species. In the absence of fire, the increase in rodent numbers and their burrows is probably responsible for this compositional shift. However, the presence of annual grasses also increases the size and frequency of wildfires. Crust organisms will die if burned. In the past, fires generally skipped from shrub to shrub, bypassing the soil crusts between them. However, the presence of annuals in the interspaces means that fires now often scorch large areas, including the soil crusts between plants. Short fire cycles prevent colonization by perennial lichens and mosses, leaving soils dominated by cyanobacteria and annual mosses. Given the millions of hectares of western rangelands that are now dominated by exotic annual grasses (mostly in areas with lower PET), and the hundreds of thousands of hectares that are annually being converted, irreversibly, to annual grass, we stand to lose large amounts of well-developed lichen–moss crusts throughout much of the cooler western US deserts.

Atmospheric changes

Soil crusts are metabolically active only when wet, and their rates of physiological functioning are highly responsive to temperature. Because climate models predict higher temperatures, greater summer precipitation, and drier-than-normal winters for the western US (Cayan 1996), soil crust structure and function will undoubtedly be affected. Soils will dry faster at higher temperatures. In moderate and high PET deserts, soil crusts often already experience carbon deficits in the summer (Jeffries et al. 1993). Increased rates of soil drying will mean greater summertime carbon deficits, as crust organisms will be even more likely to dry before respiratory losses are compensated for by photosynthetic gain. Less winter rain will

also mean less carbon gain, which translates into less nitrogen fixation, as this process requires photosynthetic products. With reduced access to adequate carbon and nitrogen, crusts will be less able to avoid or repair radiation damage (Belnap *et al.* unpublished). This will probably result in increased mortality or even alteration of distribution patterns. Current lichen and moss distribution patterns support this scenario: in the US, Australia, and central Asia, lichen diversity decreases sharply as air temperature and summer rainfall increase (Belnap *et al.* 2001a). Increased ultraviolet (UV) radiation as a result of ozone thinning is expected to be reversed by 2050, due to reductions in chlorofluorocarbon (CFC) production. However, volcanic eruptions, airplane exhaust, and/or the renewed manufacture of CFCs may slow this recovery (UNEP/WMO 2002). All crust species are sensitive to UV, because it increases mortality and disrupts photosynthesis, growth, motility, photomovements (movements induced by light), nitrogen fixation and uptake, and cell differentiation (Castenholz and Garcia-Pichel 2000). The limited activity time of organisms that require rehydration can heighten their susceptibility to UV damage. For example, while soil crusts experience some level of UV radiation for approximately 4400 hours per year near Moab, UT, soils can experience less than 100 daylight hours of wetness per year, greatly limiting their ability to acquire the carbon necessary to repair and produce new tissue (Belnap *et al.* unpublished). Predicted temperature increases are likely to exacerbate this situation, as activity times will be limited even further.

Elevated atmospheric CO_2 levels may increase crust primary production. Soil lichen photosynthesis is CO_2-limited, as rates at ambient CO_2 levels are 70–80% of maximum (Lange *et al.* 1999). In contrast, higher plants show substantial down-regulation after long-term exposure to elevated CO_2 (Moore *et al.* 1999). We have no comparable data on soil crusts. Cyanobacteria already possess intracellular CO_2 concentration mechanisms, however, and are therefore less likely to experience altered photosynthetic rates than are free-living and lichenized green algae. As a result, more CO_2 may differentially favor green algae and green algal lichens over cyanobacteria and cyanolichens. On the other hand, the greatest impact of elevated CO_2 on soil crusts will probably be an increase in the cover and altered species composition of higher plant communities. Large increases in net primary productivity are predicted to occur in arid ecosystems as a result of enhanced water availability (Melillo *et al.* 1993). Elevated CO_2 may also shift the competitive balance among higher plants, favoring invasive annual grasses such as cheatgrass (*Bromus tectorum*) (Smith *et al.* 1987), resulting in reduced crust cover and diversity, as is seen today in *Bromus*-dominated communities.

■ Recovery rates

Total recovery of soil crusts from disturbance can be fairly quick (20 years) in regions with low PET, but extremely
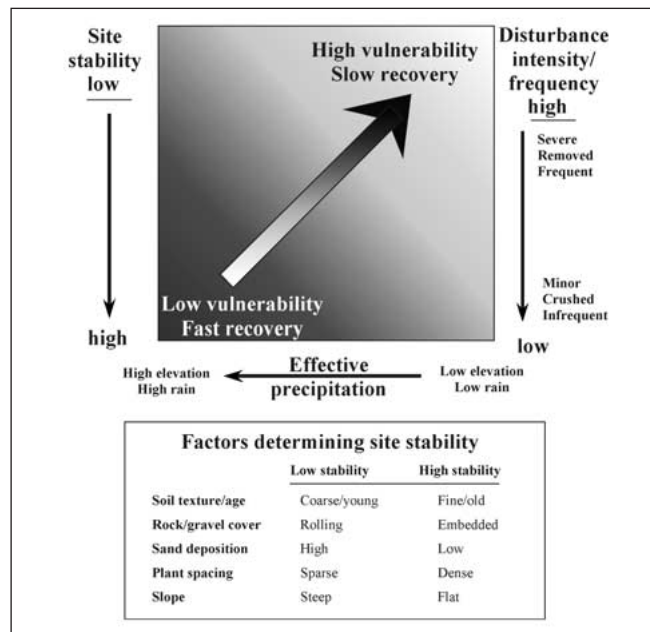
Figure 6. *A simplified model depicting large-scale factors that influence recovery rates in biological soil crusts. Many other factors, such as microhabitat, the size and shape of disturbance, and the condition of adjoining crusts, also influence recovery rates.*

slow (≥1000 years) in deserts with high PET. Recovery rates depend on the characteristics of the soil, site, climate, and disturbance (Figure 6), the availability of inoculant, and how recovery is defined (Belnap and Eldridge 2001; Figure 7). Coarse soils with low stability, fertility, and water-holding capacity recover more slowly than fine-textured soils. Stable areas, with low slopes, low wind deposition of sand, and/or embedded rocks, are quicker to recover than less stable sites with steep slopes, high sand deposition, and/or unstable rocks. Because crust organisms are only metabolically active when wet, microhabitats such as shrub canopies and regions with lower PET, including higher elevations and cool deserts, recover more quickly than places with higher PET, such as plant interspaces, low elevations, and/or hot deserts. When disturbance is severe or frequent enough to remove crust material, recovery is slower than if organisms are crushed but left in place.

In all deserts, cyanobacteria are often blown in after disturbance. The large, highly mobile filamentous cyanobacteria such as *Microcoleus* can tolerate some burial, and so are generally the first colonizers of unstable soils (Figure 7). Once soils are stabilized by the larger cyanobacteria, the less mobile, smaller cyanobacteria appear. In regions where PET is low enough to support lichens and mosses, the non-mobile, early successional lichen and moss species appear next, often led by the cyanolichen genera *Collema*. This species appears able to reproduce through spores, as colonization often occurs far from intact lichens. As PET decreases further, mid- and late-successional desert lichens, most with green algal phycobionts (the photosynthetic partner), colonize next. These species
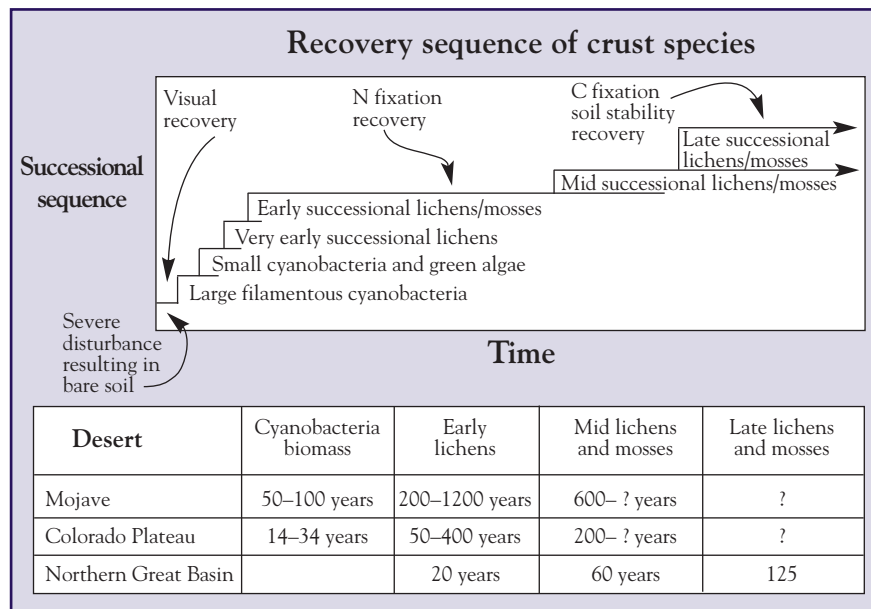
Recovery sequence of crust species

Figure 7. *The successional sequence of biological crust organisms when colonizing a severely disturbed area. Depending on the potential evapotranspiration at a site, the successional sequence may stop at cyanobacteria or a few early successional lichen–moss species (low elevation hyper-arid deserts) or early successional lichens and mosses with a few mid-successional species (low elevation hot deserts). Estimated years to recovery in the different deserts are based on flat sites with coarse soils and disturbance severe enough to remove all material. They are based on linear recovery rates, which probably overestimate recovery times.*

Desert	Cyanobacteria biomass	Early lichens	Mid lichens and mosses	Late lichens and mosses
Mojave	50–100 years	200–1200 years	600– ? years	?
Colorado Plateau	14–34 years	50–400 years	200– ? years	?
Northern Great Basin		20 years	60 years	125

seem to rely less on spores for dispersal and more on pieces of nearby lichens washing or rolling in from the disturbance edge. This may be because the high pH of most desert soils greatly limits green algal abundance, making it difficult for germinating fungal spores to find a green algal partner. Recolonization of these later-successional species can therefore be very slow, especially if the disturbed areas are large. Visual recovery (generally based on surface roughness) is much quicker to recover than species composition, biomass, soil stability, or full physiological functioning (Belnap and Eldridge 2001; Figure 7). Because most reported estimates of recovery time have been based on visual assessments, many underestimate the time to full recovery.

Intact crust material salvaged from one area and reapplied to another has long been used to speed up recovery at the small (<10 acres) plot scale (Belnap 1993). Although commercial production of cyanobacterial inoculants has been attempted (Buttars *et al.* 1994), field applications have not yet been successful. Using inoculants for even moderately large disturbances is not feasible now, or in the near future. Even with such cyanobacterial inoculants, only a few lichen species have been successfully grown in the laboratory, and the feasibility of ever producing lichen inoculant is very low. Recovery will therefore still take decades or centuries, and many desert areas will lack fully functioning biological soil crusts for many years after disturbance.

■ The outlook for soil crusts

Biological soil crusts provide many of the basic needs for plants and animals found in the desert environment. Unfortunately, human activities are often incompatible with the presence of soil crusts. The cyanobacteria fibers that confer such tensile strength to these crusts are no match for the many stresses placed on them by human activity. Exotic annual grasses and increased fire often follow surface disturbance, further simplifying species composition and flattening the crusts. Increased air temperatures and summer precipitation are likely to further reduce the activity times critical for maintaining and repairing damaged tissue. Compromised crusts contribute less to soil fertility and are less able to offer protection from wind or water erosion. Unlike vascular plant cover, biological crust cover is not reduced during droughts, and unlike physical soil crusts, they are present under all soil moisture conditions. Consequently, biological crusts offer many ecosystem services over time and under adverse conditions. The condition of biological soil crusts should be considered a top management priority in desert regions, because once this resource is gone, it is often gone for more than a human lifetime. It may seem odd to curtail our activities for something so inconspicuous, but it is the only way to protect this microworld that does so much for us.

■ Acknowledgements

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