Chapter 10
Controls on Distribution Patterns of Biological Soil Crusts at Micro- to Global Scales

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10.1 Introduction

Like all biological phenomena, biological soil crusts (biocrusts) are spatially variable. Considerable research has been devoted to determining what drivers generate this heterogeneity. The earliest investigations, to our knowledge, are

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those of Rod Rogers in Australia in the early 1970s (Rogers 1972, 1973). He developed a continental scale conceptual model depicting biocrust type and abundance as a function of amount and seasonality of rainfall (Rogers 1973). In the 1990s, additional work in Australia further delineated the types of biocrusts occupying a system of landscape types (Eldridge and Tozer 1997). In the early 2000s, Belnap and Lange (2003) synthesized in several chapters what was known about the composition and characteristics of biocrusts within different continents and regions, and two chapters addressed the specific drivers of biocrust distribution at multiple scales and their quantitative relationships with biocrusts or particular biocrust components (Garcia-Pichel and Belnap 2003; Ullmann and Büdel 2003). At the time the latter two chapters were written, the amount of literature to be reviewed was sparse, and the collective knowledge was that there were a few key soil properties (alkalinity, calcareousness, gypsum concentration, texture) and climate-related factors (continentality, annual precipitation, thermal regime) known to commonly influence biocrust abundance or composition (Eldridge and Tozer 1997; Rogers 1972). Also in Belnap and Lange (2003), Büdel (2003) provided the first global study of the biogeography of biocrust genera. As our science has progressed, literature on this topic has accumulated, and the geographic scope of our regional knowledge of biocrust distributions has expanded in North America (e.g., Bowker et al. 2005; Ponzetti and McCune 2001; Rivera-Aguilar et al. 2006; Root et al. 2011), Asia (e.g., Rosentreter et al. 2014; Tirkey and Adhikary 2005; Zhang et al. 2007; Zhang et al. 2011), Africa (e.g., Büdel et al. 2009; Lalley et al. 2006; Zedda et al. 2011), the Middle East (e.g., Abed et al 2010, 2013), and Europe (e.g., Concostrina-Zubiri et al. 2013; Martínez et al. 2006). Our synthesis presented here does not encompass the distribution of hypoliths (see Chap. 11 by Pointing).

10.1.1 Nomenclature for Scale

Because biocrust distribution patterns may differ based on the spatial scale of observation (Bowker et al. 2006a; Concostrina-Zubiri et al. 2013), we adopt the following nomenclature to denote scale. Microscopic and submillimeter scales (Garcia-Pichel and Belnap 2003) are discussed in another chapter (see Chap. 13 by Garcia-Pichel et al.) and are thus omitted here.

Global scale—Pertaining to variability across all habitats in the world (e.g., Büdel 2003)

Intracontinental scale—Pertaining to variability across a continent or major land mass [e.g., Australia (Eldridge 2003), North America (Rivera-Aguilar et al. 2006)]

Ecoregional scale—Pertaining to variability across an ecologically defined (based on environmental conditions, major vegetation associations, etc.) portion of a major land mass [e.g., Gurbantunggut Desert (Zhang et al. 2007)]

Local scale—Pertaining to variability within a collection of nearby sites [e.g., a local altitudinal-climatic gradient (Hernandez and Knudsen 2012) or a comparison among soil types (Bowker et al. 2006a)]

Intra-site scale—Pertaining to variability within a "typical" (as defined by most literature) sample unit which may range from multiple 10s of m^2 to 1 ha (Bowker et al. 2005, 2006b; Büdel et al. 2009; Concostrina-Zubiri et al. 2013; Eldridge and Tozer 1997), such as distance gradients from shrub canopies (Thomas and Dougill 2007) or small-scale soil gradients (Martínez et al. 2006)

Microscale—Pertaining to variability within a few square meters or less [e.g., soil chemistry or texture gradients within interspaces (Bowker et al. 2006a) or micro-aspect effects (George et al. 2000)]

10.2 Determinants of Biocrust Distribution at Different Spatial Scales

The forces underlying the distribution of biocrusts in space can be described as biogeographic, climatic, edaphic, topographic, and biotic (Fig. 10.1). These forces are distinct but partially dependent upon one another. The influence of these forces abruptly shifts from primarily biogeographic at the largest scales, to primarily climatic at intermediate scales, to primarily edaphic, topographic, and biotic at smaller scales. Biogeographic influences are those that act on the dispersal capabilities of the biocrust organisms themselves. For example, distance or degree of isolation is a barrier for biocrust propagule (e.g., spores, cells, thalli) dispersal over long distances (Marshall and Chalmers 1997). We may hypothesize that land masses that are isolated from one another by large distances or lacking connection via major wind patterns will tend to support less similar biocrusts; the temporal duration of this isolation will also act to promote distinction.

Biocrust variation within the dryland biome is primarily climatic. Climatic forces change among geographic areas, with latitude and altitude shaping thermal regimes and rain shadows and continentality further shaping the amount, type, and timing of precipitation received. For example, several different, yet contiguous, dryland regions are present in western North America and are distinguished by climate (e.g., Chihuahuan desert, hot/arid to semiarid, dominated by summer rainfall; Great Basin, cool/semiarid, dominated by winter rain/snow).

At ecoregional and smaller scales, biocrust variation is dictated increasingly by edaphic, topographic, and biotic forces. The physical and chemical properties of soils are determined by the parent materials and the degree of weathering that these parent materials have undergone. Most ecoregions are a mosaic of different soils, and substantial heterogeneity exists within a given soil, even at the very smallest scales. At smaller scales, topographic influences generate deviations from larger-scale climate patterns. The erosional-depositional setting generates geomorphological features that can be important across ecoregional to microscales. Biotic forces,
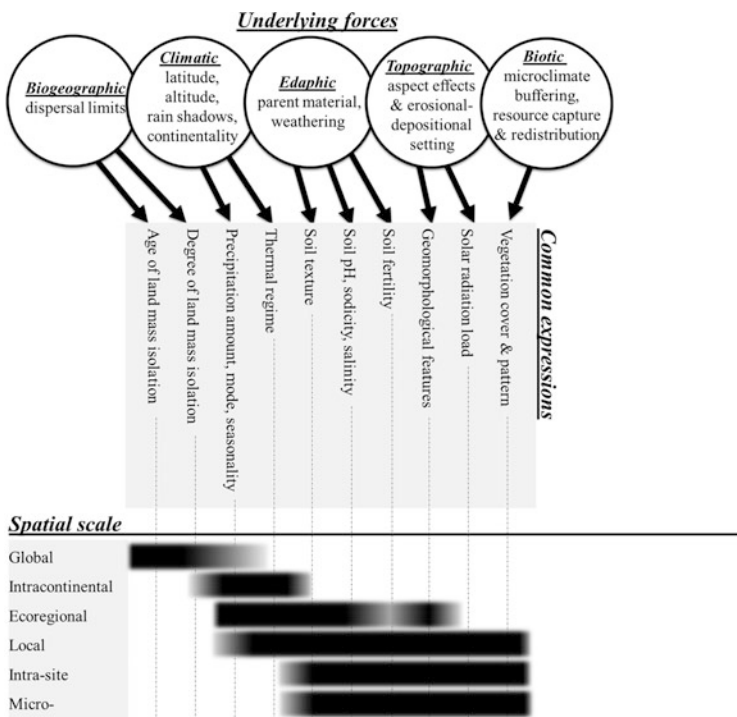
Fig. 10.1 Scale dependency of forces underlying biocrust distribution

especially the type and arrangement of vascular plants, are additional modifiers by providing shade and capturing or redirecting the flow of resources (e.g., water, nutrients, litter, and/or soil) at local or smaller scales.

10.2.1 Biogeographic Factors

Since the first description in the late eighteenth century by Pallas (1776), the presence of biocrusts has been reported in hot and cold deserts around the world, as well as having some presence in other biomes. However, little is known about the main determinants of their composition, distribution, and abundance at the biogeographic scale (Steven et al. 2013). Despite this situation, some intracontinental studies suggest biogeographic patterning of biocrusts. In a 2000 km transect in southern Africa, the six different dryland ecosystems surveyed had distinct biocrusts (Büdel et al. 2009). Similarly, arid to subhumid regions supporting biocrusts differ strongly in community composition within North America (Rivera-Aguilar et al. 2006).

Table 10.1 Number of species in biocrusts reported for different organism groups on different continents worldwide

	Europe	N. America + Greenland	S. America	Africa	Australia	Asia	Antarctica	Global
Cyanobacteria	98	53	40	83	58	82	66	320
Eukaryotic algae	137	86	1	76	3	179	44	353
Mosses + liverworts	90	45	22	22	131	28	14	320
Lichens	212	226	4	77	72	126	42	551
Total	537	410	67	258	264	415	166	1544

Compiled from: Büdel et al. (2009), Dojani et al. (2014), Haarmeyer et al. (2010), Zhao et al. (2008), Belnap and Lange (2003), Pichrtova et al. (2013), Eldridge and Tozer (1997), Rogers (2006), McCune and Rosentreter (2007), De los Rios et al. (2011), Nagy et al. (2005), Pushkareva and Elster (2013), Pócs (2009), Frey et al. (1990), Fritsch (1916), Hu et al. (2003), Eldridge (1996), Eldridge and Koen (1998), Pointing et al. (2009), Stewart et al. (2011), Dettweiler-Robinson et al. (2013b), Tirkey and Adhikary (2005), Phillipson (1935), Flechtner et al. (2008), Flechtner et al. (1998), Flechtner (2007), Hawkes and Flechtner (2002), Lewis and Flechtner (2002), Montoya et al. (1998), Novichkova-Ivanova (1972), Novichkova-Ivanova (1980), Azúa-Bustos et al. (2009), Azúa-Bustos et al. (2011), Forest and Weston (1966), Williams and Büdel (2012)

A meta-analysis of species composition and richness of biocrusts compiled from the literature revealed a total of 1544 cyanobacteria, algae, bryophyte, and lichen species worldwide. When compared on a biogeographic scale, lichen species numerically dominate the European and North American floras, whereas bryophyte and liverwort species prevail in Australian biocrusts (Table 10.1). Europe and Asia stand out as having the highest species numbers of cyanobacteria and eukaryotic algae (Table 10.1). These patterns may indicate a geographic imbalance of biocrust species diversity data and/or possibly of taxonomic expertise.

We conducted a floristic similarity analysis using the Sörensen coefficient (Qs) that weights matches in taxon composition of biocrusts between two samples. As a consequence of the uneven species richness data from continents and sub-continents, this analysis can only be regarded as a first approach to the real conditions.

Cyanobacteria are the most ancient group of biocrust organisms, appearing up to 2.6 billion years ago on land, and as might be expected, they are also the most homogenous when compared among land masses. Even for the most isolated continent, Antarctica, the similarity with all other continents is >10 % (Fig. 10.2a). This pattern may reflect either a common community prior to the breakup of Pangaea or possibly a very effective intercontinental dispersal via the atmosphere. With the exception of South America, lichens are quite well investigated in terms of diversity. The high similarity coefficient between Europe and North America (Fig. 10.2c) might be explained by the long connection between these continents in geological history, but may also be an artifact of more extensive sampling in these regions and therefore a greater degree of detection of the species present. Bryophytes and eukaryotic algae have not been investigated as thoroughly as lichens, and species numbers are much lower, making reliable comparisons possible only for restricted geographic regions (Fig. 10.2b, c). One clear pattern that emerges is the distinctness of the bryophyte flora of Australia from other land masses, possibly reflecting its long-term isolation. While cyanobacteria occur in biocrusts across the globe, eukaryotic algae are more common on continents with a higher proportion of temperate regions (Tables 10.2 and 10.3).

From this preliminary diversity analysis of biocrusts, we can conclude that biocrusts contribute considerably to the biodiversity of the ecosystems to which they belong (also see Chap. 1 by Belnap et al.), despite the species assessment of biocrusts being far from sufficiently known. As most of the data presented here are based on classical determinations and only a few on molecular studies, we would like to emphasize that it is of great importance to relate operational taxonomic units generated by molecular data to described taxa. Only with those analyses can we thoroughly test biogeographic hypotheses.

Fig. 10.2 Sörensen floristic similarity coefficient (Qs) at the species level between continents for (**a**) cyanobacteria, (**b**) eukaryotic algae, (**c**) bryophytes including liverworts, and (**d**) lichens. Values below a Qs of 10 % are not shown; species numbers are given in *red* numbers at each continent; Qs in *black* numbers at each connecting line between continents; *bold lines* indicate Qs values of 30–39 %; *semi-bold lines* between 20 and 29 %, and *thin lines* between 10 and 19 %
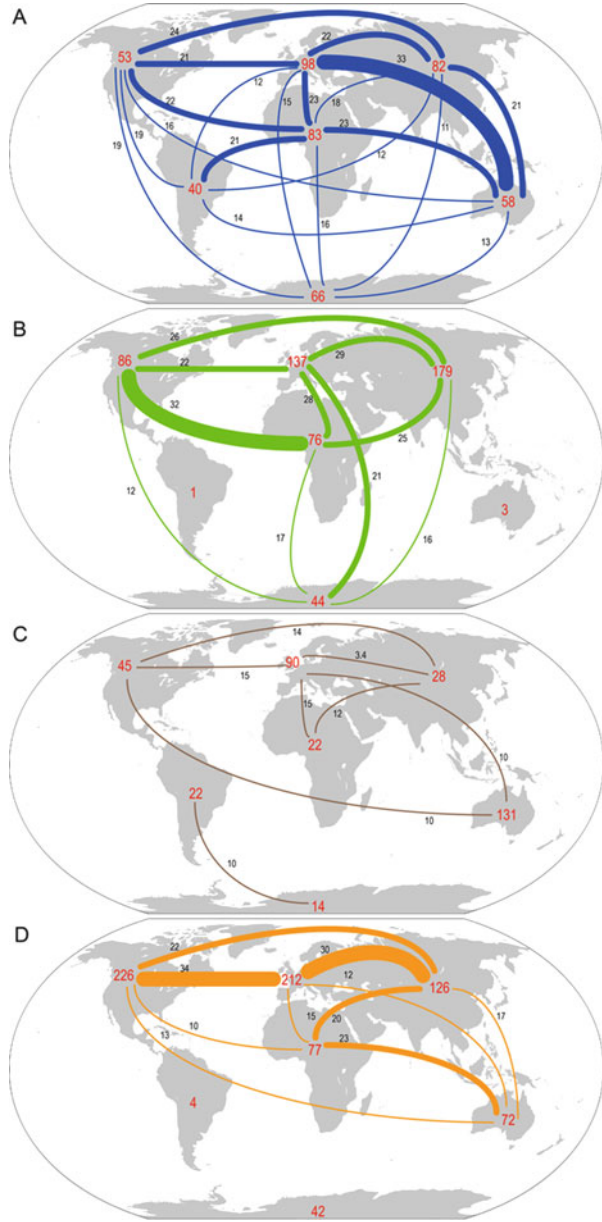
Table 10.2 Distribution of algae with a 43 % frequency (three out of seven continents)

	Europe	N-America + Greenland	S-America	Africa	Australia	Asia	Antarctica
Bracteacoccus minor (g)	■	■				■	
Pinnularia borealis (d)	■	■	insuf-			■	
Klebsormidium montanum (g)	■		ficiently			■	■
Stichococcus bacillaris (g)	■					■	■
Hantzschia amphioxys (d)	■		investi-			■	■
Desmococcus olivaceus (g)		■	gated			■	■
Klebsormidium flaccidum (g)	■	■		■			
Klebsormidium crenulatum (g)	■			■	■		

d = diatom, g = green alga

10.2.2 Moisture Availability

That moisture influences biocrust distribution at multiple scales has been amply demonstrated on multiple continents (Belnap and Lange 2003). In general, where space between plants is large, biocrust abundance and level of development increase with moisture availability (Bowker et al. 2006a; Büdel et al. 2009; Kidron et al. 2010). However, as vascular plant and plant litter cover becomes more continuous, there is less available habitat for biocrusts (Bowker et al. 2005) and less light reaching the soil surface (Belnap et al. 2003). In the most hyperarid regions (Aridity Index < 0.05; Pointing and Belnap 2012; e.g., Atacama, Sahara, Negev, Colorado deserts), biocrusts contain only a low biomass of microbial components (e.g., endedaphic cyanobacteria, bacteria, and fungi). Arid zones often support primarily cyanobacterial biocrusts with subdominant mosses and lichens (Kidron et al. 2010; Pietrasiak et al. 2011a). As aridity further decreases, cyanolichens become more prevalent, followed by chlorolichens (Galun et al. 1982). Mosses and liverworts are generally only found in wetter microhabitats (e.g., under shrubs, on polar exposures), due to their higher moisture requirements than lichens and cyanobacteria. In cooler semiarid deserts and grasslands (e.g., Colorado Plateau, Columbia Basin, and Great Basin, USA; Gurbantunggut Desert, China), soil moisture is much more abundant, and the cover and biomass of biocrusts, especially bryophytes and lichens, increase until they often fully cover soil surfaces (Ponzetti and McCune 2001; Marsh et al. 2006; Zhao et al. 2014).

Table 10.3 Most frequent species

	Aus-tralia	Africa	S-America	Antarc-tica	Asia	N-America + Greenland	Europe
Nostoc commune (c)							
Microcoleus vaginatus (c)							
Coleofasciculus chtonoplastes (c)							
Trichocoleus sociatus (c)							
Chlorella vulgaris (g)							
Bryum argenteum (b)							
Schizothrix calcicola (c)							
Nostoc microscopicum (c)							
Diploschistes diacapsis (l)							
Diploschistes muscorum (l)							
Heppia despreauxii (l)							
Placidium lacinulatum (l)							
Placidium squamulosum (l)							
Psora decipiens (l)							
Toninia sedifolia (l)							
Fulgensia fulgens (l)							
Tolypothrix byssoidea (c)							
Collema tenax (l)							
Klebsormidium flaccidum (g)							
Peltula patellata (l)							
Collema coccophorum (l)							
Heppia lutosa (l)							
Bryum caespititium (b)							
Placidium pilosellum (l)							
Microcoleus paludosus (c)							
Nostoc muscorum (c)							
Ceratodon purpureus (b)							
Calothrix parietina (c)							
Nostoc punctiforme (c)							
Aphanothece saxicola (c)							
Stigonema ocellatum (c)							
Chroococcidiopsis spp. (c)							

c = cyanobacterium, g = eukaryotic alga, b = bryophyte or liverwort, l = lichen, black = in all areas (100 %), dark gray = 6 of 7 continents/subcontinents (86 %), gray = 5 of 7 continents/subcontinents (71 %), light gray = 4 of 7 continents/subcontinents (57 %)

10.2.3 Moisture Mode, Seasonality, and Temperature Effects

In addition to the total amount of precipitation received, the timing, frequency, and size of precipitation events are critical in determining the species composition of biocrusts. Summer monsoonal events can be large but are often short and intense, with little water infiltrating into the soils. Soil temperatures after summer events can rise quickly, and rapid evaporation rates result in short activity times for biocrusts. Small rain events, especially combined with the high temperatures of summer, also
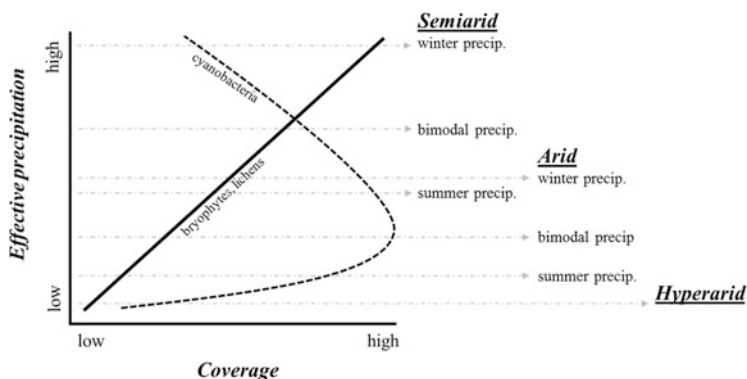
Fig. 10.3 Conceptual model depicting the general interplay of amount and timing of precipitation and its influence on community composition in biocrusts. The model applies to cool to hot semiarid and drier zones, excluding polar and alpine regions, fog deserts, and unique or unusual edaphic environments such as gypsiferous soil

result in short activity times. When wetted, all biocrust organisms respire carbon, but the replacement rate of this carbon is species specific; thus, only some species are able to handle short wetting times (e.g., Lange 2003). Other species will die: experimentally repeated frequent small rain events resulted in moss mortality within only a few months on the Colorado Plateau, USA (Reed et al. 2012). Garcia-Pichel et al. (2013) recently showed that the cyanobacterium *Microcoleus vaginatus* dominates cool desert soils dominated by winter precipitation, whereas *Microcoleus steenstrupii* dominates hot arid to semiarid deserts with summer precipitation. Thus frequency of rain events may also influence biocrust composition at a given locality.

The lichen composition of biocrusts has been observed to also vary where rainfall timing is different (i.e., winter versus summer dominated) in North America (Rosentreter and Belnap 2003), Africa (Büdel et al. 2009), Australia (Eldridge 2003), and Asia (Mongolia to Uzbekistan; Belnap pers obs). Figure 10.3 illustrates in a general sense how amount and seasonality of precipitation codetermine absolute and relative abundance of different groups of biocrust species in these drylands.

The type of precipitation is also important in determining the composition of biocrusts. Cyanobacteria, and therefore also cyanolichens, require liquid water for photosynthesis, whereas green algae and chlorolichens can also utilize water vapor (Lange 2003). Thus, in deserts where most moisture is derived from fog and dew (e.g., Namib, Atacama, central Negev), the lichen flora is dominated by chlorolichens, and cyanolichens are generally absent. In addition, fog and dew are more effectively captured by species with a three-dimensional growth form (e.g., foliose lichens) compared to those appressed (e.g., crustose lichens) to the surface.

10.2.4   Soil Properties

Biocrust cover, richness, and composition are strongly influenced by differences in soil properties at ecoregional to microscales. The extent to which the biocrusts themselves have an effect on underlying soil properties by forming a stable, nutrient-rich, near-surface layer is described elsewhere (see Chap. 1 by Belnap et al., Chap. 13 by Garcia-Pichel et al., and Chap. 23 by Weber et al.).

At ecoregional and local scales, parent material influences substrate quality and degree of weathering, directly affecting soil water-holding capacity (Noy-Meir 1973) and thus indirectly controlling the distribution and composition of biocrusts. Biocrust organisms have been shown to vary in abundance and richness among soils derived from different parent material (e.g., sandstone and shale bedrock-derived soils on the Colorado Plateau in the western USA, Bowker et al. 2006a; on igneous, sedimentary, and metamorphic bedrock-derived soils in the Mojave Desert, Belnap et al. 2014) or in soils subjected to different levels of weathering (e.g., fluvisols, regosols, and calcisols in the Tehuacan Desert, Mexico; Rivera-Aguilar et al. 2006). For example, filamentous cyanobacteria can flourish in sandy, poorly aggregated soils, which are less likely to support highly developed lichen and moss communities (Root and McCune 2012), whereas mosses and lichens are more likely to reach their strongest development on calcareous or gypsiferous soils (Bowker et al. 2006b; Bowker and Belnap 2008; Martínez et al. 2006).

Globally, the most significant soil properties influencing the ecoregional-scale cover and richness of biocrusts in dryland environments are soil texture, pH, and to a lesser extent, soil calcareousness (e.g., Rogers 1972; Eldridge and Tozer 1997; Ponzetti and McCune 2001; Eldridge 1996; Lalley et al. 2006; Lobel et al. 2006; Bowker and Belnap 2008; Root et al. 2011; Ochoa-Hueso et al. 2011). At smaller local, intra-site, or microscales, however, biocrust distribution and cover are tightly coupled to a relatively narrow range of soil physical and chemical properties, often in idiosyncratic ways. Biocrusts are likely to respond to small gradients in nutrients, such that small-scale changes in microrelief, temperature, and/or soil characteristics such as texture, salinity, structure, porosity, and oxidation can potentially play an important part in determining patterns of fine-scale distribution (Bowker et al. 2006a).

The concentrations of macro- (C, N, P, Ca, K, Mg) and micro- (Cu, Fe, Mn, Zn) nutrients are also important in influencing biocrust distribution and composition. Lichens are often associated with high levels of soil N, C, and P (e.g., Read et al. 2008) or K (Martínez et al. 2006), but the extent to which these nutrients are the drivers or the result of a well-developed crust is unknown. Lichen and moss biocrusts have been shown to be positively correlated with Mn, Zn, K, and Mg, but can also be negatively correlated with P across a range of spatial scales (Bowker et al. 2005; Bowker et al. 2006a). Similarly, Fe, Mg, and Ca have been shown to be positively associated with lichen cover, while Mn and sometimes Zn have been negatively associated with lichen diversity (Ochoa-Hueso et al. 2011). Other minerals such as Cd, Li, Cu, Mo, and Sr are known to negatively affect either

abundance or diversity of algae (Starks and Shubert 1979). Read et al. (2011) identified the Th/K ratio as a chemical signature that can be a remotely sensed proxy for soil texture and thus predict biocrust distribution (see Chap. 12 by Weber and Hill).

10.2.5   Solar Radiation Load

Most biocrust organisms exhibit the photosynthetic characteristics of "sun" plants (reviewed in Lange 2003). Despite this, the production, abundance, and diversity of biocrusts are often negatively correlated with high radiation at local and smaller scales. This is because high-light habitats are also drier due to shorter residence time of moisture and receive detrimental ultraviolet radiation loads. Polar-facing aspects receive lower radiation loads, resulting in greater biocrust abundance at the local or subhectare scale, on both hillslopes (Nash et al. 1977) and dune slopes (Veste et al. 2001), although not all authors have observed this effect (Dettweiler-Robinson et al. 2013b). Radiation load may also be reduced by shade-providing vascular plant canopies or rocks, favoring greater biocrust abundance at intra-site scales (Bowker et al. 2006a; Li et al. 2010; Maestre 2003), although in the case of plant canopies, burial by litter or dew interception by the plant canopy may counterbalance this positive effect (Hernstadt and Kidron 2005; Thompson et al. 2005). Protruding rocks provide favorable microhabitats and the capture of resources (e.g., nutrient-rich dust and water, spores, biocrust fragments) which, in turn, facilitates biocrust development, especially moss and lichen propagation (Pietrasiak et al. 2011b, 2014; Williams et al. 2012, 2013). Even at microscales, different faces of 10 cm biocrust pinnacles (Bowker et al. 2006a; George et al. 2000) or depressions such as hoof prints (Csotonyi and Addicott 2004) may generate different micro-aspects supporting differing levels of biocrust cover or different communities.

10.2.6   Vegetation Cover and Spatial Patterns

At intra-site- and microscales, biocrust communities often differ among habitats when comparing beneath plant canopies and plant interspaces. The influence of plant canopies on soil stability, fertility, and moisture is complex. Plants create shade, increase or decrease dew and moisture inputs to soils depending on their architecture, and collect wind- and waterborne sediments and plant materials at their base, increasing soil fertility. Furthermore, plants facilitate or discourage animal digging and trampling. Often, biocrust absolute cover and richness are greater in microsites with a sparse cover of vascular plants (e.g., Eldridge et al. 2002, 2005; Pintado et al. 2005; Langhans et al. 2010; Zaady et al. 2013) and litter (e.g., Briggs and Morgan 2008; Serpe et al. 2013; Zhang et al. 2013).

However, enhanced biocrust cover and/or richness in habitats nearby or under plant canopies is also reported (Maestre 2003; Bowker et al. 2005; Li et al. 2010) because vascular plants buffer environmental stress by generating distinct microhabitats. Different effects of plants on biocrusts can be mediated by differences in soil type (Eldridge et al. 2005), vegetation community type, plant successional stage (Dettweiler-Robinson et al. 2013a), or intensity of grazing (Root and McCune 2012). For example, when erosion or grazing impacts are high, biocrusts may refuge near shrubs (Zhao et al. 2010, 2011). Effects of plants will also vary according to the distributional pattern of vascular plants (Maestre and Cortina 2002) or the composition of the biocrust community. For example, positive plant-biocrust correlations in space are common for bryophytes, but not necessarily for other biocrust organisms (Pharo and Beattie 1997).

Banded and other patterned landscapes have distinctive distributional patterns of plants and biocrusts. Banded landscapes are usually found on gentle uniform slopes in arid and semiarid climate around the world (Malam Issa et al 1999). Biocrusts play a substantial role in the flow of water, seed, and sediment to the downslope run-on zones that are usually dominated by perennial vegetation (Tongway and Ludwig 1994; Malam Issa et al 1999; Belnap et al. 2005). These source-sink relationships, which operate across at mostly local and intra-site scales, arise largely through the redistribution of water, which exerts tight controls on landscape function, productivity, and diversity (Ludwig et al. 1997). Sources and sinks may sometimes support fundamentally different biocrust communities. For example, sinks tend to be dominated by biocrust morphological types that trap resources (e.g., tall mosses, fruticose lichens), while those in the runoff zones tend to be resource-shedding types (e.g., squamulose and crustose lichens or cyanobacteria; Dunkerley and Brown 1995).

10.2.7 Geomorphological Features

The distribution of dryland biocrusts is shaped by both eolian (Li et al. 2010; Veste et al. 2001) and alluvial geomorphologies (Briggs and Morgan 2008) at ecoregional, local, and intra-site scales. For example, the distribution of biocrusts on the dune fields of the Negev Desert in Israel has been described in detail by several authors [reviewed in Veste et al. (2001)]. Dune crests lack biocrusts, while lower slopes are stabilized by biocrusts and interdune spaces are characterized by higher vegetative cover and biocrusts. Aspect effects may be expressed on dune slopes with mosses becoming more common on north slopes. Zhang et al. (2007) and Li et al. (2010) describe a similar segregation of different organisms on dune crests, hollows, leeward, and windward slopes in the deserts of China. At ecoregional or local scales, different depositional-erosional processes can lead to distinct alluvial geomorphological surfaces, such as outwash slopes, sand plains, or riverine plains, which support distinctive vegetation and biocrust communities (Briggs and Morgan 2008; Eldridge 1996). Similar effects can be observed at

intra-site scales. For example, in the badland clay domes of Tuscany, Italy, biocrust cover increases from the eroded slope to the edge of the eroding surface, but eventually decreases in portions of domes with greater plant cover (Loppi et al. 2004). More recently, a detailed understanding of the ecoregional influence of alluvial geomorphology on biocrusts has been developed for the Mojave Desert (Sect. 10.3).

10.3   The Emerging Understanding of Ecoregional Biocrust Distribution in Three Case Studies

Studies of the controls on biocrust distribution at the ecoregional scale are becoming less descriptive, more predictive, and more often being expressed in the form of maps or conceptual models than in the past. Three case studies including the Sahel region of Africa and both the Colorado Plateau and Mojave Deserts of North America allow some generalizations to be made. First, they support the generalization in Fig. 10.1 that, at ecoregional scales, biocrust distribution is controlled by climatic gradients and edaphic gradients, both of which may be dictated by geomorphological gradients. Second, the specific climatic, edaphic, or geomorphic driver that is most informative differs by ecoregion. Third, heterogeneity in biocrust distribution patterns is largely driven by the degree of edaphic heterogeneity. In an area with a low degree of edaphic complexity (e.g., the Sahel Region), biocrust distribution will be primarily based on (usually) gradual climate gradients. In an edaphically complex region with young soils (e.g., the Colorado Plateau), distinctions among parent materials may be among the best predictors of biocrust distribution. Finally, in edaphically complex regions with older, more weathered soils and complex ancient and modern alluvial features (e.g., the Mojave Desert), geomorphological age may emerge as the most informative parameter.

10.3.1   Case Study: Ecoregional Patterns in the Sahel (Africa)

The Sahel is normally defined as the north to south zone that corresponds to the 200–600 mm mean annual precipitation gradient. It is located between the Sahara in the North and the Sudanian zone in the south and between the Atlantic Ocean in the west and the Red Sea in the east. Previous studies demonstrated that biocrusts (mostly cyanobacterial) are present over a large proportion of the Sahel, mostly in the form of filamentous cyanobacteria (Malam Issa et al. 1999; Valentin et al. 2004). Later, a north-south transect to document biocrusts along a latitudinal rainfall gradient concluded that biocrust fractional soil cover was strongly positively correlated with average annual rainfall, with very little biocrust cover where
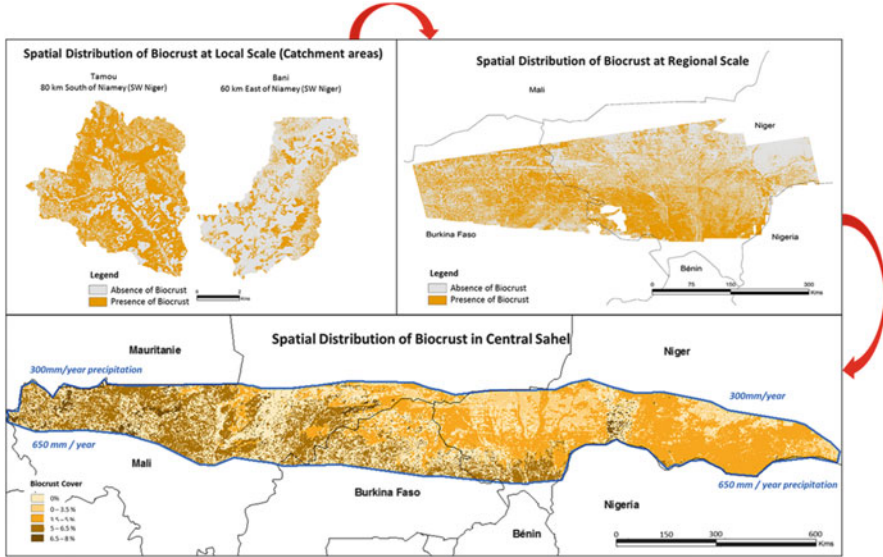
Fig. 10.4 Upscaling of biocrust spatial distribution maps from local scale to ecoregional (central Sahel) based on satellite-derived variables, the ESA GlobCover dataset, and a logistic regression predictive model

precipitation was <350 mm (Malam Issa et al. 2010). A geomorphological gradient was also quite important because it dictated both human use and edaphic properties. Soil cover of biocrusts was observed in the two main representative geomorphological units: ferricrete-capped (erosion-resistant sediment layer cemented by iron oxides) plateau soils with tiger bush vegetation and vegetated sand dune deposits that have lain fallow for up to 10 years.

More extensive data from western Niger and Burkina Faso were used to produce a map of the spatial extent and distribution of biocrusts over the central portion of the Sahel region, based on a logistic regression model that combined annual average rainfall, land use, vegetation cover, and soil types with field data on biocrust fractional soil cover and satellite imagery (Beaugendre et al. 2012; Fig. 10.4). The model was later upscaled for the entire central Sahel (Bontemps et al. 2013). As the region is characterized by two main types of geomorphic surface, a large proportion of the variability in the region is explained by a simple total precipitation gradient.

10.3.2 Case Study: Ecoregional Patterns on the Colorado Plateau (USA)

In contrast to the Sahel, other ecoregions are made up of widely different parent materials and can be expected to exhibit very heterogeneous mosaics of higher and lower quality biocrust habitat. The Colorado Plateau ecoregion is one such area. It is typified by many young soil types and much exposed parent material that ranges from marine limestones and shales to eolian sandstones. A recent ecoregional-scale modeling effort produced a map and statistical model of potential biocrust distribution of the Colorado Plateau (Bryce et al. 2012). The model was based upon an integrated dataset of 593 samples from around the Colorado Plateau and its Northern, Southern, and Eastern ecotones assembled from several sources (summarized in Bryce et al. 2012). All sites were in low-disturbance condition at the time of sampling, and biocrust cover was assumed to be at or near its potential. The models used 16 predictors aimed at capturing key climatic (based on longer-term 1971–2000 averages), edaphic, and topographic influences.

At the ecoregional scale, out of all 16 predictors, the proportional summer precipitation was the single most informative predictor (Fig. 10.5). A threshold was identified, whereby if greater than ~ one third of rainfall was received in summer, late successional biocrust cover was only about 2 %, whereas sites receiving a lower proportion of precipitation in summer had anywhere from 6 to 44 % cover, depending on other predictors. The low cover of late successional elements is believed to result from the inability of lichens and mosses to withstand the frequent short wetting events associated with summer precipitation (see discussion above in Sect. 10.2.3; Reed et al. 2012). This result indicates that the seasonality of precipitation can be as influential, or more so, than total precipitation where
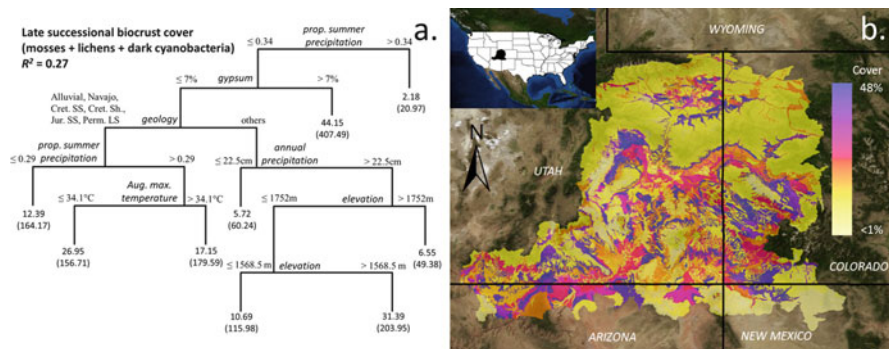

Fig. 10.5 Potential biocrust distribution in the Colorado Plateau ecoregion. (**a**) A regression tree model indicates that the most informative predictor of late successional biocrust cover is proportional summer precipitation. (**b**) A map of potential late successional biocrust abundance based on an ensemble of regression tree models. The palest *yellow shades* particularly common in the southeastern part of the extent receive mostly summer precipitation and thus have low biocrust potential

these gradients exist. The next two most informative predictors, percent gypsum and parent material, indicate the tremendous influence that different soil types can have on biocrusts. As the distribution of parent materials on the Colorado Plateau is highly heterogeneous, the map of biocrust abundance and development is a patchwork of biocrust types, with abrupt transitions from very high to very low cover. These characteristics contrast strongly with the more gradual transitions within the Sahel.

10.3.3 Case Study: Ecoregional Patterns in the Mojave Desert (USA)

The Mojave Desert displays typical intermontane basin geomorphology based on a long history of alluvial processes (Peterson 1981). Episodes of erosion, sediment movement, and deposition alternated with periods of stability throughout the Holocene (up to 11,700 years old) and Pleistocene (11,700–2,500,000 years old) eras, creating a mosaic of differently aged soil surfaces that we see today (Miller et al. 2009). It is a more complex geomorphological system than the Sahel, has a greater mixing of soil parent materials than the Colorado Plateau, and is a system where age of surfaces is expected to dictate soil properties and habitat quality.

These geomorphic surfaces are associated with suites of unique environmental factors important to biocrust establishment and propagation, such as surface stability, topography, rock cover, soil texture, and hydrological dynamics. Biocrust cover is greatest on moderately young to intermediate aged (20–7000 years old) surfaces, whereas coverage is negligible on very young (<20 year; e.g., active washes, recent sediment deposits) and very old surfaces covered with well-developed desert pavements (i.e., surfaces of interlocking rock fragments that are at least thousands of years old; Pietrasiak et al. 2014; Williams et al. 2013; Belnap et al. 2014).

Moreover, diversity and dominance of biocrust community types varies with geomorphology. Cyanobacterial crusts are most abundant on moderately active sand sheets of Holocene age, suggesting that motile filamentous cyanobacteria can withstand some sand deposition and burial (Williams et al. 2013; Fig. 10.6). In contrast, moss and lichen biocrusts are more prevalent on stable surfaces and are associated with fine-grained substrates that occur between embedded surface rocks (Pietrasiak et al. 2014; Williams et al. 2013; Belnap et al. 2014; Fig. 10.5). These conditions are commonly met in soils of early to late Holocene age, with the highest diversity of biocrust types found on moderately young (0.5–1 kyr) surfaces (Pietrasiak et al. 2014). Though perhaps less influential than surface age, parent material also influences biocrust type in the Mojave. Soils derived from grussy granites and those containing mixed rock and fine sand show the highest biocrust cover, with cover then decreasing from igneous to limestone to metamorphic-derived soils (Pietrasiak et al. 2011a; Belnap et al. 2014; Williams et al. 2013).
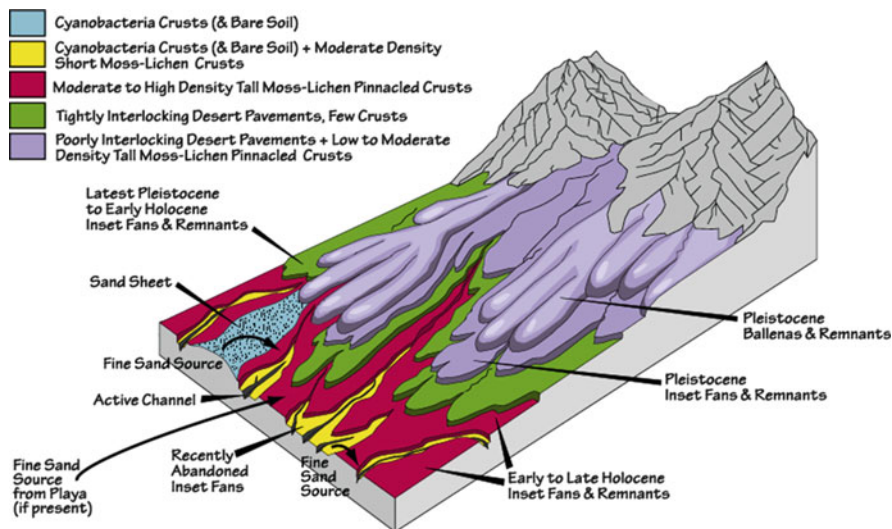
Fig. 10.6 Geomorphic surface type and age predicts interspace cover by biocrusts and desert pavements; reproduced with permission from Williams et al. (2013), courtesy of Elsevier. Fine sand sources include sand sheets, active channels, and alluvial flats or playas (not shown)

10.4   Conclusions: Gaps in Our Knowledge and the Way Forward

Although knowledge has accumulated significantly in the past decade on the distribution patterns of biocrusts and factors controlling the distribution of specific taxa, the state of our collective knowledge is heterogeneous at best. Our missing knowledge can be categorized as geographic gaps and taxonomic gaps.

Most studies on biocrusts have occurred in Australia, China, Europe, Israel, and North America. It has only been in the last few years that surveys have included major portions of Africa and the Indian subcontinent (Büdel et al. 2009; Rosentreter et al. 2014). There remain significant geographic gaps, where few, if any, surveys have been conducted. The biggest gaps currently include central Asia, South America, and the Middle East/Arabian Peninsula (excluding Israel). Data on species composition of biocrusts in South America are especially rare and would benefit from a major research effort in the future. Even within relatively well-studied land masses, there are areas that have received little attention. This is likely a result of uneven distribution of research funding, infrastructure, and the availability of researchers.

Taxonomic gaps arise primarily because few researchers are simultaneously competent in the taxonomy, identification, or molecular characterization of all of the diverse groups of biota encompassing biocrusts and thus do not report on all of them in detail sufficient to build an understanding of their distribution patterns. We

may, for example, have a detailed understanding of lichen distribution, but know little about cyanobacterial distribution, within a given region. A related problem is taxonomic inconsistency, which restrains our ability to compare results from one place to another. In addition, molecular tools are not available to all researchers, making identification of the microbial components of the biocrusts difficult to impossible.

How can we move beyond some of these gaps? The most effective way to fill our information gaps is with more scientific effort. As most of the taxonomists that work on biocrusts are reaching retirement age, this will require training of young scientists in the taxonomy of the different biocrust organisms. To accomplish this, we urge universities to maintain strong programs in taxonomy of these organisms. Also, we should continue to make easily used identification resources such as field guides available to and targeted to the public (rather than taxonomic specialists; e.g., Rosentreter et al. 2007) and transition into web-based resources and smartphone apps.

With additional survey efforts, we can begin filling our data gaps. This information would then allow for intra- and intercontinental comparisons, giving us the ability for truly global-scale studies. The effort required for a global study is clearly too great for any single research group. A promising development has been networked studies, which are becoming increasingly common in a variety of fields. Within the biocrust research community, one such network completed a variety of similarly designed research in multiple arid regions of Africa (Büdel et al. 2009), and another network (Soil Crust InterNational) is currently maintaining a linked set of sites in Europe (Büdel et al. 2014). We envision a multidisciplinary network of international researchers simultaneously sampling biocrusts along key environmental gradients in multiple deserts of the world. The important gradients will differ among ecoregions, but a set of common sampling methods, pooled taxonomic expertise, and pooled analytical capabilities (e.g., soil measurements, GIS, and statistical analysis) will facilitate comparisons among regions.

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