

Biological soil crusts (biocrusts) as a model system in community, landscape and ecosystem ecology

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Abstract Model systems have had a profound influence on the development of ecological theory and general principles. Compared to alternatives, the most effective models share some combination of the following characteristics: simpler, smaller, faster, general, idiosyncratic or manipulable. We argue that biological soil crusts (biocrusts) have unique combinations of these features that should be more widely exploited in community, landscape and ecosystem ecology. In community ecology, biocrusts are elucidating the importance of biodiversity and spatial pattern for maintaining ecosystem multifunctionality due to their manipulability in experiments. Due to idiosyncrasies in their modes of facilitation and competition, biocrusts have led to new models on the interplay between environmental stress and biotic interactions and on the maintenance of biodiversity by competitive processes. Biocrusts are perhaps one of the best examples of micro-landscapes—real landscapes that are small in size. Although they exhibit varying patch

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heterogeneity, aggregation, connectivity and fragmentation, like macro-landscapes, they are also compatible with well-replicated experiments (unlike macro-landscapes). In ecosystem ecology, a number of studies are imposing small-scale, low cost manipulations of global change or state factors in biocrust micro-landscapes. The versatility of biocrusts to inform such disparate lines of inquiry suggests that they are an especially useful model system that can enable researchers to see ecological principles more clearly and quickly.

Keywords Biodiversity · Biological soil crusts · Ecosystem function · Global change · Landscape heterogeneity · Micro-landscape · Model system · Species interactions

Overview: historical importance of model systems in ecology

A brief glance at any ecology textbook will offer many examples of model systems being used to test and elucidate general principles. For example, the variation in beak size and shape in Galapagos finches was crucial to the development of Darwin's theory of natural selection (Weiner 1994). If Hutchinson (1959) had not observed three different species of water boatmen swimming in a fountain in a cave shrine, we may have waited much longer for the current concept of the realized ecological niche to emerge. Tilman's concept of resource competition and the definition of a best competitor for a given resource may grace every plant ecology textbook, but was initially developed and refined using easily distinguished freshwater diatoms (Tilman 1977). A final example is oceanic archipelagos, such as Hawaii, which were formed via volcanism and are composed of similar parent material of different ages. Peter Vitousek used Hawaii as a model to study how biogeochemistry changes as ecosystems age (Vitousek 2006). These examples demonstrate how model systems have been instrumental in the development of theory in biosciences in general and in ecology in particular.

What makes a good model system?

Vitousek (2002) states that model systems in ecology may be a gene, a species, a community, or an ecosystem that “displays a general process or property, in an understandable way”. Compared to alternative study systems, a model system ought to exhibit one or more of the following characteristics, the first five being derived from Vitousek (2002). Systems with several of these properties allow us to learn about nature in a maximally efficient way.

(1) It might be simpler, so that the property of interest is not obscured by other properties or processes. Soil nematode communities in the Antarctic dry valleys consist of only four species, thus they serve as a simple model to study intra-trophic species interactions among other processes (Hogg et al. 2006). We note that systems may sometimes be too simple which could limit generality (number 5, below).

(2) It might display more rapidly the process of general interest. Due to fast generation time, compelling arguments have been made for the use of microbial model systems in ecology (Jessup et al. 2004). As an example, McGrady-Steed et al. (1997) observed that microbial communities constructed with more species were more resistant to invasion by a new species.

(3) It might be smaller. Herbaceous plants are easier to observe and measure than, for example, trees. Therefore when addressing general processes and properties relevant to all

plants, the herbaceous plant would be the preferred model except in situations where the height and mass of the tree make it instructive (see below). Much of the seminal work on the relationship between plant biodiversity and production used herbaceous plants grown in combinations in small plots (e.g. Tilman and Downing 1994).

(4) It might be idiosyncratic or distinctive in a useful way that makes it instructive. For example, the coastal redwood is the tallest tree in the world, making it an excellent model to examine how hydraulic processes limit plant height (Koch et al. 2004).

(5) It should (usually) be generalizable. Vitousek (2002) considers ecological model systems to often be real and persistent examples of a larger set of systems. We tend to agree that to improve inference about other systems, a model should ideally (at least in most cases) have the property of generality. An important exception is when a model's idiosyncrasies or distinctions are what make it useful for study.

(6) It might be more amenable to experimentation. Perhaps because of his focus on large spatial scale and long temporal scale and taking advantage of “natural experiments”, Vitousek (2002) did not elaborate on characteristics that would make a model system easier for experimentation. Being simpler, faster, or smaller are all characteristics that might simplify or improve observations made in experiments, but in addition, a good model can be manipulated. The manipulation may come in the form of an altered resource, an added or removed species, imposed climate variation, etc.

Vitousek (2002) also was careful to distinguish true model ecosystems from two other types of study systems: the well-studied system and the artificial microcosm. All of these types can overlap, but have distinct characteristics. A well-studied system offers a wealth of information already gathered, saves the researcher the burden of learning basic properties of the system, and attracts new research to build on the old. However, unless some of the above six model system properties are displayed by the system, it does not necessarily allow us to learn about nature in a maximally efficient manner, and is therefore not always a model system. Construction of microcosms, with some properties of natural systems but omitting or holding others constant, is a useful means of reductionism and isolation of a process. These too can be model systems in our view, but the danger of these systems lies in simplifying them to the extent that the process of interest does not operate in the same manner as it would in a complex natural system, making results difficult to generalize.

We have collectively conducted several studies that can be considered to have exploited the model system characteristics of biocrusts to learn about ecological properties, principles, and processes. The purpose of this review is threefold: (1) To assert that biocrusts have many characteristics that fit the above Vitousekian concept of an ecological model system, and describe these key characteristics; (2) To review examples from our work, and that of others, which we believe highlights the utility of biocrusts for the study of ecological properties, principles and processes; and (3) To promote and encourage the use of this study system to further the study of ecology. All of these goals seek to inspire new ideas and new lines of research in both the biocrust and general ecological research communities.

Biocrusts as model systems

Model characteristics of biocrusts

Simple biocrusts?

The entire biocrust community, including primary producers, and multiple levels of consumers in the dependent food web, generally consists of hundreds of species (Bowker et al.

2010a, b). Thus, considering this a simple community is misleading. However within trophic levels, and within taxonomic groups within trophic levels, levels of diversity may be more tractable than in many communities. For example, in a given study area, biocrusts might have the potential to support around up to perhaps 40, but usually fewer bryophyte and lichen species. The true diversity of the cyanobacteria is currently being resolved; at this time, North American biocrusts support less than 20 generic or sub-generic taxa (Garcia-Pichel et al. 2013). This level of richness is comparable to, or less than, that of vascular plant communities in similar dryland environments.

Biocrusts: tortoise or hare?

One of the best known characteristic of biocrusts is their high vulnerability to disturbance and apparent slow recovery (reviewed in Belnap and Eldridge 2003). Biocrusts routinely exhibit rapid and stark responses to stressors, such as trampling (e.g. Belnap 1996) or changes in climatic conditions (e.g. Escolar et al. 2012; Reed et al. 2012). These responses include changes in species composition and abundance that result in altered carbon, nitrogen and hydrologic regimes. Under some conditions, recovery of biocrusts from disturbance might require centuries (Belnap and Warren 1998), although this process can be much faster (e.g. 10–20 years) in some semiarid areas (Lázaro et al. 2008). This property might discourage the study of certain ecological questions; for example, a community that changes on multi-decadal scales may not be the ideal model for repeatedly sampled succession studies.

However, biocrusts can be quite dynamic, growing and advancing in succession in fits and starts, and even changing abundance within the year (Belnap et al. 2006). Slow growth rates are not intrinsic to all biocrust organisms; rather, harsh environments constrain growth. Castillo-Monroy (unpublished data) observed that some transplanted lichens (e.g. *Squamarina lentigera*, *Diploschistes diacapsis*) grew twice their initial size (0.25 cm² fragment of lichen) in 2 years of sampling. In culture (see below) many biocrust species can grow quickly. For example, the moss *Syntrichia caninervis* in culture can gain an equivalent mass to 10 years in the field in only 2 months in a growth chamber (Xu et al. 2008).

Macroscopic, yet small

Biocrusts contain a mixture of micro- and macrobiota. Molecular techniques are required to fully characterize the microbial composition of the community (Steven et al. 2013), but the natural history and functional properties of most of these species are unknown. Despite the difficulties of studying these microbial components, the *macroscopic* components of biocrusts are of an ideal size to address ecological problems. Most lichens and bryophytes are large enough to be meaningfully enumerated in the field (e.g. percent cover), either with the naked eye or with the aid of a hand lens. Many can be identified under field conditions to the species level, and even the most difficult groups can be identified to the genus level (Rosentreter et al. 2007). The advantage of the small size of biocrust constituents is that natural variation can be meaningful at sub-hectare scales. In addition, many functional aspects of the different species are known (e.g. ability to fix nitrogen and carbon, stabilize soils). Therefore it is possible to encounter and measure fundamentally different community compositions with fundamentally different functional attributes within a square meter in the field. These attributes can, in turn, be related to environmental gradients or measurements of ecosystem processes (Bowker et al. 2006, 2011). It is also

possible to construct customized communities that are rich and complex in experimental units as small as petri dishes. At Cedar Creek, Minnesota, a famous experiment manipulated plant diversity, CO₂ concentrations and N-deposition rates to understand diversity–productivity relationships under climate change scenarios (Reich et al. 2001; Reich 2009). A similar experimental design could have been constructed and operated with a biocrust model system in a few tens of m² for a few thousands of dollars rather than the multiple hectares and millions of dollars required for the plant manipulations. This statement in no way disparages the great work that comes from experiments like those at Cedar Creek, but serves to ask how many groundbreaking experiments could have been conducted if biocrusts were the model system of choice.

Idiosyncratic biocrusts

There are times when a model is useful not because it behaves similarly to a larger set of systems, but because it behaves differently. A researcher may wish to exploit these unusual characteristics. For example, desert mosses exemplify extremely imbalanced sex ratios (Stark et al. 1998). If a researcher is interested in the adaptive outcomes of biased sex ratios, they present a useful model. Most research on inter-trophic species interactions has been conducted using vascular plant systems. As an alternative system for study of species interactions, biocrust species are intriguing because they exhibit a different set of facilitative and competitive mechanisms than vascular plant systems, or other alternatives such as corals. For example, biocrust lichens, unlike plants, do not “nurse” individuals of other species via canopy overlap (Bowker et al. 2013a), and also are much more likely to engage in parasitic interactions (Hawksworth 1982). Will our species interaction theories still hold if we test them in systems where different mechanisms operate? What new insights or hypotheses might this lead us to?

Manipulating biocrusts

Application of stressors such as surface disturbance or altered climate can easily and rapidly alter the composition and/or the relative cover of biocrust communities, as various biocrust components respond in different manners. The cyanobacterial, eukaryotic algal, and bryophyte components of biocrusts are readily cultured (Hu et al. 2002; Xu et al. 2008). Therefore, communities may be disassembled and reassembled in any configuration useful to the researcher. A researcher may maintain a library of species, or ecotypes of species for use in experimentation. These may be selected based upon their place of origin, genotype, phenotype, or for other reasons. Cultures can be used to create experimental biocrust communities with a variety of properties, useful in a variety of studies. Some examples might be a series of communities of varying species richness, different genotypes subjected to varying environmental conditions, or pairings of species in competition studies. Not all biocrust organisms are easily culturable *ex situ* (e.g. lichens; Stocker-Wörgötten 2001). Nonetheless, intact multi-species biocrusts can be easily moved to new settings that represent for example, novel climates (Darby et al. 2006), new soil types, or semi-greenhouse settings. Individual lichens thalli or pieces of thalli can also be moved to create new community organizational structures, facilitating the study of various types of relationships among biocrust components (Maestre et al. 2012a).

Biocrust models in community ecology

Model systems have been fundamental to the development of community ecology, though they are not always recognized as such. Historically, the study of vascular plant communities has dominated community ecology. To date, biocrusts have been used as useful models for the study of species interactions and to elucidate the roles of biodiversity in promoting ecosystem function.

Species interactions

Interactions among species have been proposed as an important determinant of community structure, constraining or enhancing the total number of species that can coexist and the particular species combinations that can exist (Brooker et al. 2008; Grime 1973). These interactions may include positive influences such as facilitation and negative interactions such as competition, parasitism, or allelopathy. Applying a null model approach to a crowded gypsiferous lichen community, Maestre et al. (2008) demonstrated that species were spatially segregated more than would be expected due to chance. Spatial segregation is a pattern that would be expected to arise due to interspecific competition; thus this finding can be taken as evidence that competition can structure biocrust lichen communities.

The stress gradient hypothesis proposes that as abiotic stress increases, the relative prevalence of positive species interactions increases compared to negative interactions (Bertness and Callaway 1994). This hypothesis is founded on the observation that plants growing under the canopies of other plants may be buffered from environmental extremes or be protected from herbivory, to the degree that the benefits afforded by this juxtaposition may outweigh the costs of competing for the same resource pools (Callaway 2007). The hypothesis has been well-supported in alpine plant communities limited by cold (Callaway et al. 2002). Some biocrust species may also benefit from nurse plant associations with vascular plants (Maestre 2003). Testing the stress gradient hypothesis among biocrust lichens and mosses is intriguing, as, unlike most desert or alpine vascular plants, these relatively two-dimensional organisms are primarily competing for space. Often when one species overtops another, there is no “nursing” due to canopy overlap; rather one species is displaced by the other. This is not to say that there is no 3-dimensional structure in the biocrust community (there is, especially when taller mosses and fruticose lichens are present), only that it appears to be less of a force shaping communities than in vascular plant communities. Thus, the fundamental observation which led to the stress gradient hypothesis largely does not apply in a biocrust system. This makes it an interesting system to determine if other mechanisms of species interaction change along stress gradients.

In a test of the stress gradient hypothesis along an aridity-based gradient in central and southern Spain, Bowker et al. (2013a) suggested that competition, rather than facilitation, structured biocrust moss and lichen communities. Species richness, which we would generally expect to be negatively affected by competition, was positively related to a competition index at low abiotic stress, and negatively related to a competition index at high abiotic stress. This observation led to a new hypothesis: stress acted as a filter that, when low, allowed a greater number of species from the regional species pool to enter the community (Fig. 1; Bowker et al. 2010a, b; Bowker and Maestre 2012). In this situation, it is less likely that there will be one single best competitor that can outcompete all other species. Rather, competition networks are more likely to be intransitive and competition can actually act as a biodiversity-conserving mechanism (Laird and Schamp 2006). This

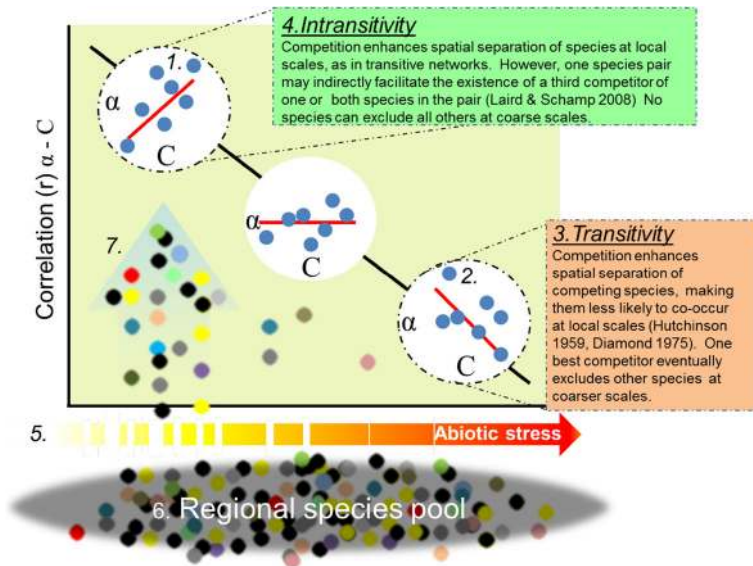


Fig. 1 Competition may switch from intransitive to transitive as abiotic stress increases: a general model based on observations within a biocrust model system (modified from Bowker et al. 2013a). *1* At low abiotic stress, species richness (α) positively correlates with local spatial segregation, a possible indicator of competition intensity (C). *2* At high abiotic stress, this relationship is negative. *3* A negative relationship between competition intensity and species richness is expected because the best competitor would be expected to exclude its competitors; the presence of an overall best competitor indicates a transitive competitive network. *4* The only known mechanism whereby competition could increase richness is in an intransitive competitive network. In this scenario there is no species that can outcompete all other under all scenarios. Some competition events allow the continued existence of additional species due to competitive release. *5* Abiotic stress can be viewed as a filter that determines which species form the regional species pool (*6*) can enter a community. It is a more porous filter at low stress. *7* More species are able to enter the community through the low-stress, porous end of the filter, because there are fewer species that can tolerate high-stress. As more species enter, the number of pairwise competitive interactions increases exponentially, making it increasingly unlikely that any one species can outcompete all others. Thus intransitivity is more likely to prevail under low abiotic stress and act as a richness conservation mechanism

model requires testing outside of the biocrust model system and manipulative experimentation, but could help explain some biodiversity hotspots in regions of low abiotic stress such as tropical rainforests (Connell 1978).

Biodiversity–ecosystem function relationship

Since the mid-1990s many studies, usually using vascular plant and microbial model systems, have demonstrated a positive, monotonic relationship between the richness of a community and its productivity (see Cardinale et al. 2012 for a review). Researchers have proposed that this relationship is either approximately linear, increasing with the addition of each species (the complementarity hypothesis), or asymptotic, ceasing to increase at some point of species addition (the redundancy hypothesis; Naeem et al. 2002). A previous review fully documented the utility of biocrusts as models in the study of biodiversity effects on ecosystem functioning (Bowker et al. 2013a), thus we will focus here on recent developments. Previous field research on biocrust communities has suggested that

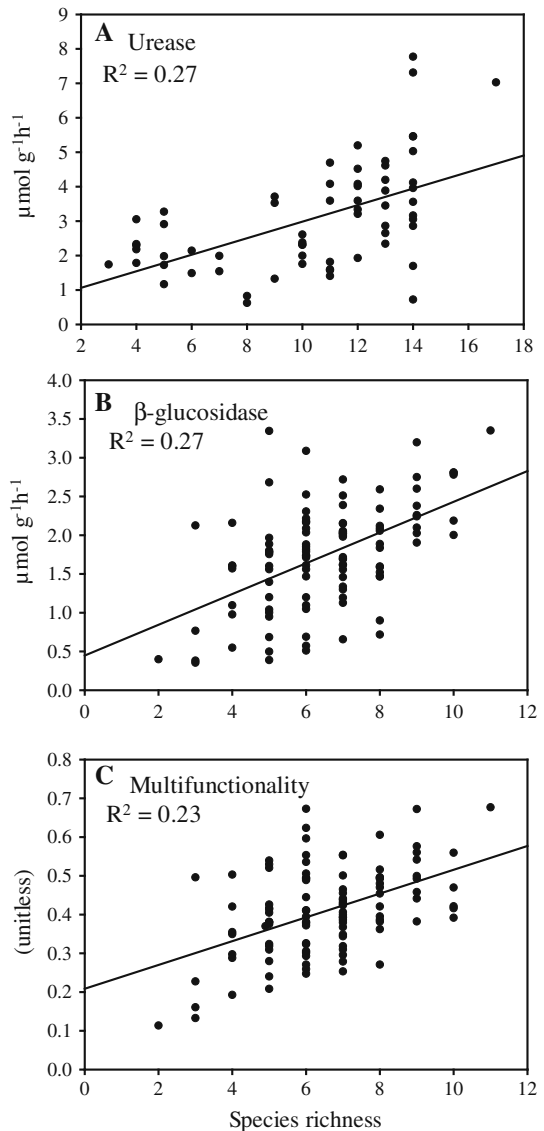
relationships between various ecosystems function indicators and biocrust richness are common, and usually positive and approximately linear (Bowker et al. 2013a), suggesting that biocrusts have species-specific unique contributions to ecosystem function (Bowker et al. 2011; Fig. 2). Finally, there is some evidence that the diversity of autotrophic biocrust components is more influential to ecosystem functions than diversity of associated bacteria in a field experiment (Castillo-Monroy et al. 2011). This is despite that microbial functional diversity is strongly influenced by lichen community structure (Castillo-Monroy et al. unpublished data).

The emerging view is that societies depend upon ecosystem multifunctionality (the simultaneous maintenance of multiple ecosystem functions), rather than any single ecosystem function such as productivity (Cardinale et al. 2012; Gamfeldt et al. 2008; Hector and Bagchi 2007; Zavaleta et al. 2010). Another of the most important questions in the biodiversity–ecosystem function discussion is which attributes of biodiversity most strongly promote ecosystem functions and services. Two recent studies using biocrust models and very different approaches have illustrated how multi-functionality is positively influenced not only by increasing richness in biocrusts, but also by changes in their composition or spatial pattern. Maestre et al. (2012a) experimentally constructed biocrusts with varying levels of richness, evenness, and spatial aggregation of cover, and different species compositions and measured several indicators of multiple ecosystem functions in the underlying soil (Fig. 3). They found that as species richness increased, more functional indicators were maintained at benchmark levels. Species richness and community composition consistently had the most influence on multifunctionality. Bowker et al. (2013a) evaluated how species richness, evenness, total cover, and the patch size distribution of biocrusts affect ecosystem multifunctionality in the field across a broad geographical area in Spain. The relative importance of these different community properties shifted depending on the ecosystem function being examined and the soil type. Species richness had a particularly positive influence on indicators of carbon cycling and was positively related to multifunctionality as well.

Biocrust models in landscape ecology

Landscape ecology focuses on the spatial arrangement of entities, such as patches of different landscape types, and the functional outcome of this spatial arrangement in determining movement of biota, energy, and materials among and within patches (Bastian 2001; Wu and Hobbs 2002). Traditionally, landscape ecology is large-scale, even though there is no inherent size of a landscape (Wiens and Milne 1989). There are several studies involving biocrusts in the landscape ecology literature. Read et al. (2008) demonstrated that size of multi-hectare habitat patches was a strong determinant of biocrust development. Multiple workers on different continents have studied the role of biocrusts as a defining characteristic of water runoff generating landscape patches in patterned landscapes (Australia: Bowker et al. 2013b; Israel: Kidron and Yair 1997; Niger: Malam Issa et al. 1999). Whereas these studies show that biocrusts can respond strongly to landscape patterns and properties, biocrusts may also define these same variables (Belnap et al. 2005). As studies show landscape functions can be strongly influenced by biocrust development, we believe that the study of biocrusts as micro-landscapes is both promising and underappreciated. It remains unknown under what conditions conclusions drawn from small-scale can be extrapolated to large ones or vice versa (Wiens and Milne 1989), but biocrusts can provide one way to examine these issues.

Fig. 2 Biocrust richness positively correlates with indicators of nitrogen cycling (a), carbon cycling (b) and greater ecosystem multifunctionality (c) (modified from Bowker et al. 2010a, b and Bowker et al. 2013a)



Portable micro-landscapes

The pinnacled biocrusts of the Colorado Plateau are a micro-landscape comprised by a series of micro-ridges dissected by micro-valleys (Fig. 4). The pinnacles generate distinct microclimates due to slope and aspect (Bowker et al. 2002), and the valleys may conduct water during heavy rains (Belnap 2006). Viewing distinct patterns in the biocrusts of semiarid woodlands of Australia is reminiscent of scenes of the land surface from the window of an airliner. In Fig. 5 we can view micro-landscapes with distinct productivity levels, community composition and biodiversity, and spatial heterogeneity that appear as



Fig. 3 Biocrusts can be manipulated and constructed in a variety of configurations (after Maestre et al. 2012a). **a** Intact lichen pieces collected from the field, cut into homogeneous 0.5 cm-side square fragments, **b** fragments of lichens added to the surface to achieve a 60 % coverage of each microcosm unit, **c** examples of microcosms with a clumped and random spatial pattern at the beginning of the experiment, **d** small spatial footprint of two multifactor replicated experiments

fundamentally different as desert shrublands, savannas, and forests. Distinct landscapes such as these can all be found within 100 m of one another.

We view biocrusts as complex micro-landscapes with the unusual and useful property of being portable. It is often difficult to execute experiments at a macro-landscape scale; however using multiple replicated biocrust micro-landscapes, we can generate and test hypotheses that may apply to landscapes of any spatial scale.

Spatial aggregation and heterogeneity

Landscapes can be considered systems of distinct patch types. The spatial patterning (aggregation, fragmentation, connectivity, and heterogeneity) of patches influences the flux of materials, energy, and organisms through the landscape (Milne 1992; Pickett and Cadenasso 1995). To date the most extensively studied properties of biocrust landscapes have been spatial aggregation and heterogeneity. The degree of spatial aggregation of biocrust patches in the field has a weak influence on nutrient cycling indicators compared to community properties such as species richness (Maestre et al. 2005). In an experimental test of similar hypotheses, Maestre et al. (2012a), generalized that richness was more important than spatial aggregation, but that random rather than clumped distributions of lichens promoted greater ecosystem functionality and microbial functional diversity (Castillo-Monroy unpublished data). The latter findings are supported by the well-accepted

notion that plant productivity in dryland ecosystems increases with heterogeneity (Noy-Meir 1975), thus showing the potential for using biocrusts to test commonly accepted paradigms. Bowker et al. (2013b) determined that spatial aggregation and the degree of heterogeneity in small plots had less influence on water infiltration than total biocrust cover or species composition. The above examples show how biocrust micro-landscape properties can influence the flux of energy or materials. Whether these spatial properties or related properties such as connectivity and fragmentation influence the movement or community structure of the biocrust-associated fauna is completely unexplored. Understanding this using a micro-landscape may help illuminate how connectivity and fragmentation influences faunal movements in macro-landscapes, a crucial topic within conservation biology (McRae et al. 2008).

Self-organizing spatial pattern

Researchers actively study spatial patterns of organisms generated by the growth of the organisms themselves, by abiotic factors such as frost-heaving, or biotic-abiotic interactions. For example, much research has been devoted to the origins of spotted, banded or labyrinthine patterning in semi-arid vegetation (see Rietkerk and van de Koppel 2008 and Tongway et al. 2001 for reviews). Likewise, fairy circles in semi-arid grasslands (Cramer and Barger 2013), and polygonal patterned ground in high latitude regions (Haugland and Beatty 2005) have long been objects of interest. Biocrusts are an exemplar of self-organized spatial pattern, and their study can help to advance our knowledge regarding the

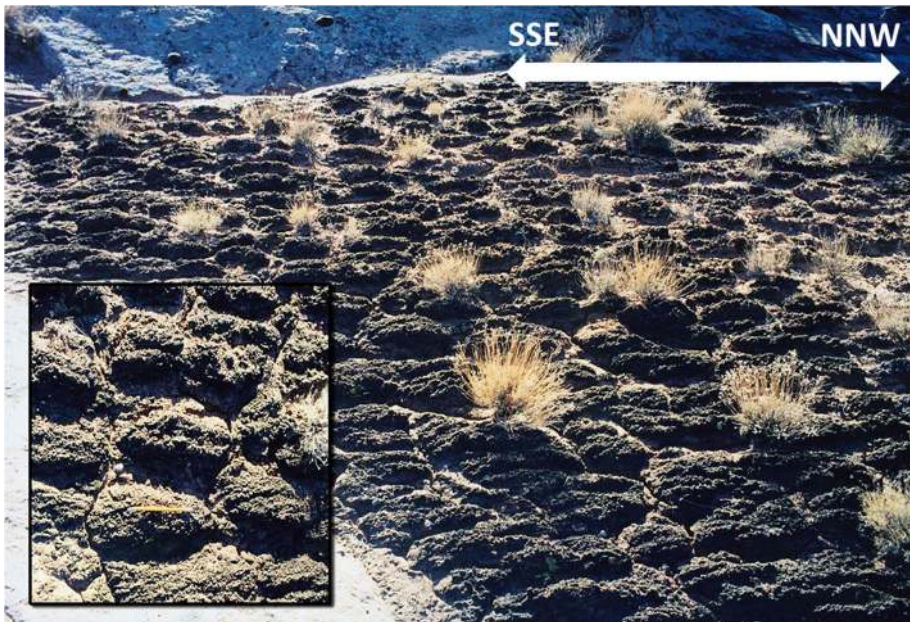


Fig. 4 Biocrust micro-landscapes of the Colorado Plateau display a distinctive parallel ridge and valley morphology. Vertical relief is commonly around 5 cm (up to 10 cm), and ridges (*pedicels*) tend to be elongated, extending along a NNW–SSE axis on average. These patterns generate distinct microenvironments differing in radiation input, heat load, and water retention dependent on directional aspect. Biocrust community composition may vary among aspects

origin and implications of different spatial patterns. On the Colorado Plateau, individual pinnacles in the biocrust micro-landscape are generally oriented along a NNW–SSE axis (Fig. 4; George et al. 2000). This gives rise to distinct microhabitats along the long ENE and WSW faces (Bowker et al. 2002), which in turn influence the biocrust community composition (Bowker et al. 2006; George et al. 2000). The origin of the pattern is not completely known. It may be due to differential deposition or erosion rates related to prevailing winds or it may be generated by the crust organisms themselves growing better on the most favorable surface (Davidson et al. 2002). The distinctiveness of this pattern appears to vary, perhaps based on environment, leaving many unanswered questions about this self-organized spatial pattern.

Patch-size distributions

Spatial patterns may also be induced by species interactions. Dryland vegetation is characteristically discontinuous, with patches of vascular plants separated by patches lacking

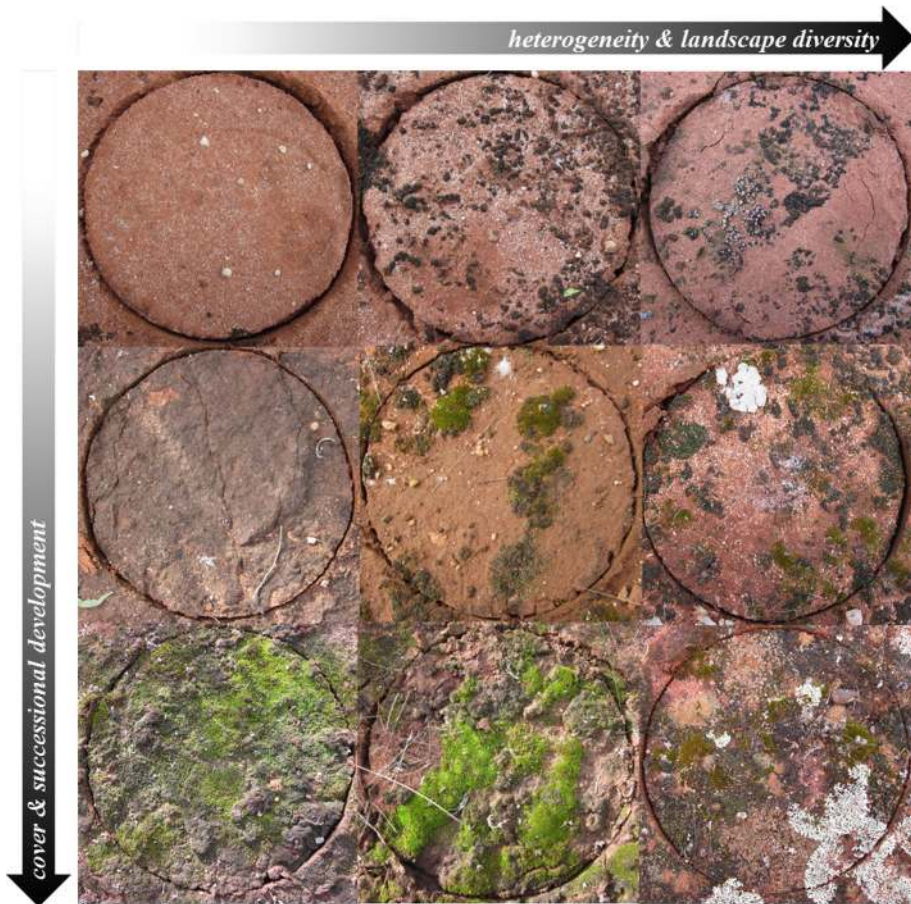


Fig. 5 “Aerial” views of multiple, highly distinct biocrust micro-landscapes in Australia (modified from Bowker et al. 2013b). Many combinations of productivity, successional development, heterogeneity and landscape diversity are possible in a small spatial extent

vascular plants (Valentin et al. 1999). The same applies to biocrusts at a smaller spatial scale (Fig. 5). Dryland vegetation patch-size often follows a power law distribution wherein the logarithm of vegetation patch size is linearly and negatively related to the logarithm of the number of patches (Kéfi et al. 2007; Scanlon et al. 2007; but see Maestre and Escudero 2009). This means that large patches occur in small numbers, but may be orders of magnitude larger than the smallest patches. Dynamic models suggest that this pattern occurs because of local facilitation under global competition (Kéfi et al. 2008). It is thought that because of climatic buffering and enhanced resources due to canopy overlap, benefactor plants may reduce the stress experienced by beneficiaries (Callaway 2007), leading to large multi-species patches which form the power law tail. Due to their useful idiosyncrasies, biocrusts helped generate a complementary hypothesis to this one (Bowker and Maestre 2012). Because biocrust lichens compete for space, they lack facilitative mechanisms due to canopy overlap (Bowker et al. 2013a). This raises the question of what sort of patch size distribution would be expected under these circumstances? A log-normal distribution was hypothesized for communities in which all or most community members were restrained in growth by competition (an intransitive scenario; Bowker and Maestre 2012). Further, one parameter of this distribution, μ , was demonstrated to be correlated with the intensity of intransitive competition (Bowker and Maestre 2012). From this work, it can be hypothesized that intransitive competition, similarly to facilitation, has a characteristic but different expression in the spatial patterning of dryland vegetation. Also, just as particular patch size distributions of vascular plants were correlated with more functional ecosystems (Kéfi et al. 2007), there is evidence that whether or not biocrust patches follow a log normal or power law distribution has an influence on ecosystem function (Bowker et al. 2013a; Fig. 6).

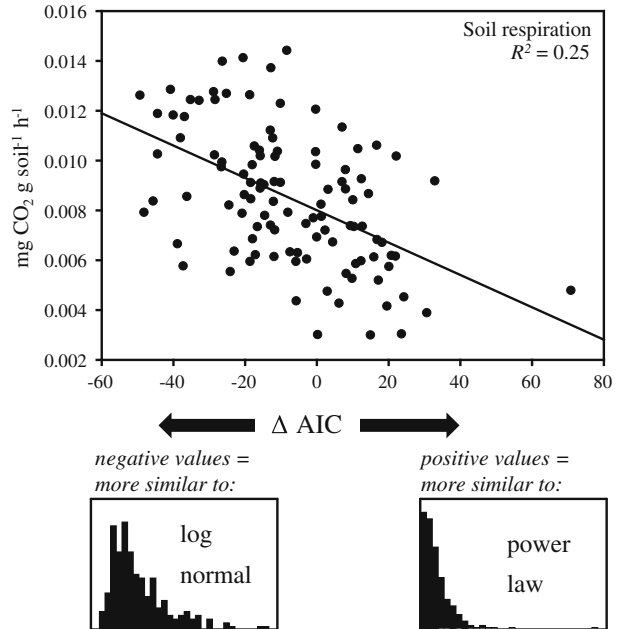
Biocrust models in ecosystem ecology

Ecosystem ecology is concerned with the nature and magnitude of fluxes of materials and energy from one pool to another (Odum 1969). Terrestrial ecosystem function can largely be broken into the influence of plants (e.g. primary production), the influence of soil organisms (e.g. decomposition and nutrient cycling), and their joint influence (e.g. capture and retention of soil and water). When the researcher wishes to track the fate of material or energy *within* an ecosystem (e.g. Carbon fluxes), a model system such as a forest provides a good scale to separately observe production, litterfall, and decomposition processes because there is a spatial segregation between the sites of these processes. On the other hand, if a researcher wishes to understand how whole autotroph-heterotroph systems affect and respond to their environment and how these dynamics change over time (e.g. during succession), biocrusts offer a useful alternative model. Biocrusts can be viewed as unusually multifunctional because, as a complex of diverse autotrophs and heterotrophs, they are a microcosm of the plant-soil system that can be easily manipulated (Bowker et al. 2013a). Thus they contribute to most of the functions commonly attributed to either plants or soil communities.

Understanding global change impacts

A major theme in ecosystem ecology and biogeochemistry research for the past two decades has been determining the impact of altered climate on primary production and other ecosystem processes (Vitousek 1994). Climate projections differ for different regions, but most localities can be expected to become warmer and some may experience

Fig. 6 The type of patch-size distribution in biocrusts can be correlated with ecosystem functions. In this example from Spanish gypsiferous soils (modified from Bowker et al. 2013a), biocrusts that followed a log normal distribution exhibited greater soil respiration rates than that which followed a power law distribution. ΔAIC difference in Akaike Information Criterion values for a power law and log normal distribution fit to patch size distribution in a sample



more or less rainfall, or altered seasonality or frequency of rainfall, compared with historical records (IPCC 2007). Many studies have been conducted to understand the ecological impacts of climate change in drylands (see Maestre et al. 2012b), but few of them have focused on biocrusts. Multiple methods have been applied to alter thermal regimes of biocrusts: (1) transplantation to a warmer and cooler environment (Darby et al. 2006), (2) use of infrared heating lamps (Reed et al. 2012; Zelikova et al. 2012), and (3) use of passive open-topped warming chambers (Escolar et al. 2012). These have often been combined with rainfall manipulations by either (1) reducing or excluding rainfall with shelters (Escolar et al. 2012), or (2) watering at different frequencies and amounts than average (Reed et al. 2012). Nitrogen deposition has been simulated with fertilization (Ustin et al. 2009) and CO_2 has been increased at FACE (Free Air Carbon Enrichment) sites (Coe et al. 2012, Wertin et al. 2012).

Thus far, results seem dependent on the locality of the study, and the major organisms in the biocrusts, and the warming regime. Working in Spain, where temperatures are expected to increase and total rainfall to decline, warming with passive shelters (high temperature increase in day, lesser at night) negatively impacted the diversity, growth and photosynthetic activity of lichen-dominated biocrusts, but reduced rainfall had less effect (Escolar et al. 2012; Maestre et al. 2013). In an experiment conducted on the Colorado Plateau, warming lamps (equal temperature increase day and night) had little effect on lichens or mosses, but increased frequency of small hydration events during the summer months led to dramatic moss mortality (Reed et al. 2012). These changes were closely followed by reductions in fungal and bacterial biomass, large changes in nitrogen cycling, and altered enzyme activities (Reed et al. 2012; Zelikova et al. 2012). Enrichment of CO_2 influenced biocrusts much less than recent precipitation patterns in the Mojave Desert (Wertin et al. 2012), but may enhance thermo-tolerance in mosses (Coe et al. 2012).

Whereas these same global change manipulation techniques can and are applied to vascular plant communities, in most circumstances only a few individuals of a few species are affected. When the same treatment is applied to a biocrust, an entire micro-landscape populated by many individuals of many species can be manipulated. To achieve a climate manipulation of many individuals of multiple plant species is feasible (Pangle et al. 2012; Reich 2009), but rare due to budget constraints. Applying these manipulations to biocrusts cannot serve as a model for responses specific to vascular plants, such as susceptibility to insect pathogens or cavitation under drought stress (Pangle et al. 2012). Rather, their value lies in understanding the general response of ecosystem processes to change in primary producer abundance and community composition induced by global change.

The downscaled critical zone?

The concept of a critical zone, “the 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” (NRC 2001) is becoming an important concept in ecology. In most ecosystems, high root biomass, deep soils, and high rainfall result in many ecosystem processes occurring at depth in the soil. In deserts, however, most rain events are <5 mm, resulting in many processes (e.g. weathering, C and nutrient cycles, decomposition) being concentrated at the soil surface where biocrusts dominate. In these downsized critical zones, biocrusts mediate almost all inputs and outputs of gases, water, heat, and light, as well as playing a crucial role in dust capture and soil stabilization (Belnap et al. 2003). Because biocrusts provide so many ecosystem services at local to regional scales, they are ideal for study as model ecosystems, both to examine the interaction of these many processes, as well as to better understand how the concept of the critical zone can be applied in different settings.

Manipulation of multiple state factors

One of the core foundational concepts of ecosystem ecology is stated by the Jenny–Dokuchaev–Chapin model (Chapin et al. 1996), which postulates that ecosystem processes are influenced by, but do not influence, five state factors: soil parent material, climate, potential biota, topography, and time. Under normal circumstances, manipulating these state factors in experiments presents major technical hurdles; some manipulations would be feasible but costly, and others cannot be practically done. However, the characteristics of biocrusts make them suitable for conducting experiments that independently manipulates four state factors. Biocrusts grow on soils derived from a variety of parent materials and intact biocrusts can and have been transplanted to common gardens side by side, such that parent material can be manipulated as an experimental factor while holding other state factors constant (Bowker unpublished data; Darby et al. 2006). Topography of the entire transplant can be manipulated by placement on constructed slopes (Csotonyi and Addicott 2004). Alternatively, in cases where biocrusts create considerable microtopography, such as the Colorado Plateau case, they may be rotated so as to preserve or reverse their orientation at the source site. This manipulation also serves to dissociate effects of initial biota from topographic effects on ecosystem processes. Finally, climate may be manipulated variously by water addition or precipitation reduction, and warming may be induced using the various techniques described above. This hypothetical experiment clearly illustrates the largely untapped value of biocrust models to serve as a platform to address ecosystem ecology questions that never before have been addressed experimentally.

Concluding thoughts: biocrusts in mainstream ecology

Biocrusts were only rarely studied and documented in the literature prior to the 1980s. Despite the youth of biocrust ecology, the amount of research on these communities has grown exponentially since that time, and is becoming increasingly internationally based. Part of this growth has been the increasing realization that, particularly in water-limited ecosystems, these previously unstudied communities play many critical roles in ecosystem function that are grossly disproportionate to their size (Belnap and Lange 2003). Until only very recently, the subject of biocrusts was viewed perhaps as a niche interest of at most local importance. Today we are seeing more and more high profile papers in the scientific literature on biocrusts (for example, a recent cover in the journal *Science*; Garcia-Pichel et al. 2013), a recurring conference solely devoted to biocrusts (as highlighted in this special issue), an avid interest in biocrusts from public land managers in countries like the USA and Australia, and large investment in research resources into the restoration of biocrusts in desertified regions around the world, notably China. As this trend unfolds and the importance of biocrusts to ecosystem functions and services and human wellbeing becomes more widely understood and accepted, we believe it is also timely to increase our contributions to ecological theory. No model system is ideal for every question, but we have reviewed a wide variety of ecological investigations in which biocrusts could play a major role. As we begin to use biocrusts in this new way, we will simultaneously advance ecology, and cement a place for biocrusts in mainstream ecological science. We believe that biocrusts deserve a place alongside freshwater diatoms, water boatmen, and oceanic archipelagos as highly valued instruments which have allowed us to see and learn more clearly and quickly about how the world surrounding us works, and how we can use this knowledge to preserve and restore it when degraded.

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