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REVIEW ARTICLE

A practical guide to measuring functional indicators and traits in biocrusts

Max Mallen-Cooper[1,2,3], Matthew A. Bowker[4], Anita J. Antoninka[4], David J. Eldridge[1,2]

Biocrusts are multifunctional communities that are increasingly being used to restore degraded or damaged ecosystems. Concurrently, restoration science is shifting away from the use of purely structural metrics, such as relative abundance, to more functional approaches. Although biocrust restoration technology is advancing, there is a lack of readily available information on how to monitor biocrust functioning and set appropriate restoration goals. We therefore compiled a selection of 22 functional indicators that can be used to monitor biocrust functions, such as CO_2 exchange as an indicator of productivity or soil aggregate stability as a proxy for erosion resistance. We describe the functional importance of each indicator and the available protocols with which it may be measured. The majority of indicators can be measured as a functional trait of species by using patches of biocrust or cultures that contain only one species. Practitioners wishing to track the multifunctionality of an entire biocrust community would be advised to choose one indicator from each broad functional group (erosion resistance, nutrient accumulation, productivity, energy balance, hydrology), whereas a targeted approach would be more appropriate for projects with a key function of interest. Because predisturbance data are rarely available for biocrust functions, restoration goals can be based on a closely analogous site, literature values, or an expert elicitation process. Finally, we advocate for the establishment of a global trait database for biocrusts, which would reduce the damage resulting from repeated sampling, and provide a wealth of future research opportunities.

Key words: biocrust, ecosystem functioning, functional traits, monitoring, restoration

Implications for Practice

- Practitioners can monitor biocrust functions to provide an indication of how a restored biocrust is affecting the local ecosystem.
- Restoration goals can be defined by key ecosystem functions of interest (e.g. erosion).
- Reference sites are rarely available for biocrusts, so restoration goals can be based on "best on offer" analog sites, literature values, or expert elicitation.
- A commitment to establishing a global trait database for biocrust species will reduce the destructive sampling and stimulate future research.

Introduction

Ecological restoration is the assisted recovery of degraded, damaged, or destroyed ecosystems (Science for Ecological Restoration International Science & Policy Working Group 2004). Through the history of the science of restoration, ecosystem recovery has been based largely on structural elements (e.g. species composition and relative abundance). Progress over the last decade has been marked by advances in the fields of trait-environment response relationships, community assembly, and ecosystem functioning (Laughlin 2014; Ostertag et al. 2015; Miller et al. 2017). Biocrusts are soil-dwelling communities of lichens, bryophytes, algae, cyanobacteria, and other microbes that cover approximately 12% of the global land surface (Rodríguez-Caballero et al. 2018*a*). Biocrust restoration technology is currently maturing, but an emerging knowledge gap is how best to develop effective ways of detecting the extent to which restoration goals are met (Antoninka et al. 2016; Chiquoine et al. 2016). Methods to monitor the structure of biocrust communities are well-established, drawing on existing widely used techniques in plant ecology (e.g. percent cover estimation), microbial ecology (high throughput sequencing), and phycology (pigment assays). We now need a suite of complementary approaches to detect the functional consequences of restoring biocrusts. Here we provide a summary and guide to monitoring the functional recovery of restored biocrusts.

Biocrusts are highly multifunctional. In one sense, biocrusts could be likened to a vast leaf stretched over the soil surface. Similar to a leaf, photoautotrophic organisms within biocrusts

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[1]Centre for Ecosystem Science, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia
[2]Ecology and Evolution Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, Australia
[3]Address correspondence to M. Mallen-Cooper, email m.mallen-cooper@unsw.edu.au
[4]School of Forestry, Northern Arizona University, Flagstaff, AZ, U.S.A.

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fix carbon and in turn supply energy to themselves and to heterotrophic microbes and microfauna. In another sense, biocrusts have been referred to as the "living skin of the earth," which alludes to the capacity of the community to regulate the passage of essential resources such as water and nutrients into and out of the soil (Bowker et al. 2018). Biocrust organisms also interact with other biota, stabilize the soil, and regulate erosion (Maestre et al. 2011). Many of these functions provide benefits or services to humans, such as protecting the soil against erosion or enhancing soil fertility (Rodríguez-Caballero et al. 2018*b*). Consequently, there is no single indicator of all the functions of biocrusts.

Most functions are defined broadly and have many measurable components (functional indicators). For example, the effect of a lichen on soil stability could be quantified, in part, by the length of its rhizines (anchoring structures of lichens), assuming that longer rhizines stabilize soil to greater depths than shorter rhizines. Measurements of functional indicators can either be taken directly, on patches of habitat that may or may not contain biocrust, or indirectly, using a trait-based approach. Restoration, however, is performed at the scale of an ecosystem, so functioning must be monitored at the ecosystem scale. To do so, repeated direct functional measurements can simply be averaged to calculate an ecosystem-scale value of a particular function. In contrast, a trait-based approach generally involves measuring functional indicators at the species level (functional traits), either in individual organisms or monospecific populations. An ecosystem-scale value is then derived by summing the functional traits of the species present, weighted by their abundance (Garnier et al. 2004; see Appendix S1, Supporting Information). A benefit of the trait-based approach is that functionally important species can be prioritized (Montoya et al. 2012) and functional diversity can be compared across sites (Mallen-Cooper et al. 2018).

Although there are well-established functional indicators and traits for vascular plants (Pérez-Harguindeguy et al. 2013), the same does not exist for biocrusts. The functional traits of bryophytes and lichens, not limited to those found in biocrusts, were first reviewed by Cornelissen et al. (2007), who focused largely on nutrient cycling and tissue chemistry. Many of the important functions of biocrusts, however, relate to their close association with the soil environment, such as their effects on soil stability and hydrology. Biocrust-specific functional traits have been explored qualitatively (e.g. Bowker et al. 2011; Concostrina-Zubiri et al. 2014) and quantitatively in a handful of recent studies (e.g. Mallen-Cooper & Eldridge 2016; Concostrina-Zubiri et al. 2018). However, we lack a comprehensive handbook of biocrust functional indicators and traits with clear guidelines on how these could be measured and their importance. In this article, we aim to collate the current knowledge of functional measurements in biocrusts and provide an informative guide for practitioners and researchers.

Biocrust Functional Indicators

Here we present a list of functional indicators that can be used to assess biocrust functioning (Table 1). Additional indicators are discussed in Appendix S2. Our aim is to show that most of the following indicators can be measured directly on biocrust communities and indirectly as functional traits. As traits, these indicators would be considered functional "effect traits," because they quantify an *effect* of biocrust organisms on ecosystem functioning, but several could also be considered "response traits," which reflect how an organism responds to its environment (Díaz & Cabido 2001). Unlike vascular plant traits, many biocrust traits cannot be measured in individual organisms because the spatial resolution of measurement is larger than the typical body size of the organism, or because an effect is an emergent property of a population. Thus, traits are often measured in monospecific populations, which can be artificially created if necessary. Some indicators can only be measured in a subset of biocrust organisms. For example, "rooting" depth can only be measured in organisms with rhizoids (anchoring structures of bryophytes) or rhizines. Note that if biocrust organisms are difficult to identify to the level of species, they may be measured in groups of convenience such as genera or morphological groups (Eldridge & Rosentreter 1999).

The average time taken to measure a trait varies among traits and organisms. To indicate the different amounts of labor and expertise associated with each methodology, we provide a subjective scale of difficulty in Table 1, based on our collective personal experience.

Erosion Resistance

Maximal Rooting Depth. Maximal "rooting" depth is the length of the longest rhizoid or rhizine. Soil particles must be carefully removed using water or tweezers to reveal the intact rooting structures. This trait is effectively the depth of soil that can be physically stabilized by a biocrust organism. In highly depositional systems, where the stems of mosses can be partially submerged under sediment, the entire underground portion might be considered a "rooting" structure. This measurement was initially applied as a functional trait of species (Mallen-Cooper & Eldridge 2016); however, the same concept could be extended to mixed communities of lichens, bryophytes or cyanobacteria. In the case of communities dominated by filamentous cyanobacteria, maximal filament depth might be a natural extension of this method.

Soil Aggregate Stability. Biocrust organisms create soil aggregates by releasing glue-like exudates and physically wrapping soil particles together with rhizoids, rhizines, or filaments (Belnap & Büdel 2016). Soil aggregate stability quantifies the resistance of soil aggregates to disintegration after an erosive force is applied. Although there are more sensitive laboratory-based approaches such as wet sieving, simple low-cost field kits have been developed that enable researchers to directly assess stability in the field (Fig. 1A; Herrick et al. 2001). In general, multiple dry surface aggregates from directly under biocrusts are exposed to slaking and shear stress, and their resistance is rated on an ordinal scale. Well-developed lichen and bryophyte biocrusts typically attain the maximum

Table 1. The functional indicators of biocrusts and their various properties (A = algae, B = bryophytes, C = cyanobacteria, L = lichens). Difficulty was determined subjectively by the authors and is ranked on a scale of 1–5, with 5 representing the most difficult.

Functional Indicator	*Associated function(s)*	*Equipment*	*Destructive?*	*Taxa*	*Lab or in Situ?*	*Difficulty*	*Typical Units*	*References*
Absorptivity	Hydrology	Drying oven, mass balance	Yes	B, L	Lab	2	(g water)/(g sample)	Mallen-Cooper and Eldridge (2016)
Albedo	Energy balance	Albedometer, goniospectrometer	No	A, B, C, L	In situ	4	Unitless (ratio)	Rutherford et al. (2017)
Chlorophyll *a* content	Productivity	Many pieces of laboratory equipment	Yes	A, B, C, L	Lab	4	mg/(g soil)	Antoninka et al. (2016)
Chlorophyll fluorescence	Productivity	Fluorometer	No	A, B, C, L	Lab/in situ	3	Unitless (ratio)	Chiquoine et al. (2016)
CO_2 exchange	Productivity	Gas exchange system	No	A, B, C, L	Lab/in situ	5	$\mu mol\, m^{-2}\, s^{-1}$	Raggio et al. (2014)
Dry aggregation	Erosion resistance	Sieve, mass balance	Yes	A, B, C, L	Lab	2	%	Eldridge and Leys (2003)
Enzyme activities	Nutrient accumulation	Many pieces of laboratory equipment	Yes	A, B, C, L	Lab	5	$nmol\, g^{-1}\, hour^{-1}$	Mallen-Cooper and Eldridge (2016)
Height	Nutrient accumulation, erosion resistance, habitat complexity	Calipers	No	A, B, L	In situ	1	mm	Mallen-Cooper and Eldridge (2016)
Hydrophobicity	Hydrology	Pipette or hypodermic syringe	No	A, B, C, L	In situ	1	s	Kidron and Büdel (2014)
Infiltration	Hydrology	Infiltrometer or steel can	No	A, B, C, L	In situ	3	mm/hour	Li et al. (2005)
Level of development (LOD)	Energy balance, productivity	Reference photos	No	C	In situ	1	Unitless (ordinal scale)	Belnap et al. (2008)
Maximal rooting depth	Erosion resistance	Calipers	Yes	B, L	Lab/in situ	3	mm	Mallen-Cooper and Eldridge (2016)
N-fixation rate	Nutrient accumulation	Many pieces of laboratory equipment	Yes	A, B, C, L	Lab	5	$\mu mol\, cm^{-2}\, hour^{-1}$	Caputa et al. (2013)
Production of exopolysaccharides (EPS)	Productivity, nutrient accumulation, erosion resistance, hydrology	Many pieces of laboratory equipment	Yes	C	Lab	5	mg/(g soil)	Rossi et al. (2018)
Sediment capture	Nutrient accumulation, erosion resistance	Wind tunnel, mass balance	Yes	A, B, C, L	Lab	4	Unitless (proportion)	Mallen-Cooper and Eldridge (2016)
Soil aggregate stability	Erosion resistance	Soil stability kit or polythene pipe and pipette	Yes	A, B, C, L	In situ	3	Unitless (ordinal scale) or number of drops	Herrick et al. (2001); Cantón et al. (2009)
Soil nutrient pools	Nutrient accumulation, productivity	Many pieces of laboratory equipment	Yes	A, B, C, L	Lab	5	mg/(g soil)	Delgado-Baquerizo et al. (2015)
Soil penetration resistance	Erosion resistance	Penetrometer or air gun	Yes	A, B, C, L	In situ	2	kg/cm^2	Drahorad and Felix-Henningsen (2012); Li et al. (2010)
Soil shear strength	Erosion resistance	Shear vane	Yes	A, B, C, L	In situ	2	kg/cm^2	Schmidt et al. 2008
Spectral characteristics	Productivity	Hyperspectral camera or camera with infrared filter	No	A, B, C, L	In situ	2	Unitless	Lehnert et al. (2018); Fischer et al. (2012)
Surface roughness	Hydrology, erosion resistance, nutrient accumulation, habitat complexity	Fine tight-linked chain or profilemeter	No	A, B, C, L	In situ	1	Unitless (proportion)	Eldridge et al. 1997; Saleh 1993
Threshold friction velocity	Erosion resistance	Open-bottomed wind tunnel	No	A, B, C, L	In situ	3	cm/s	Li et al. 2010

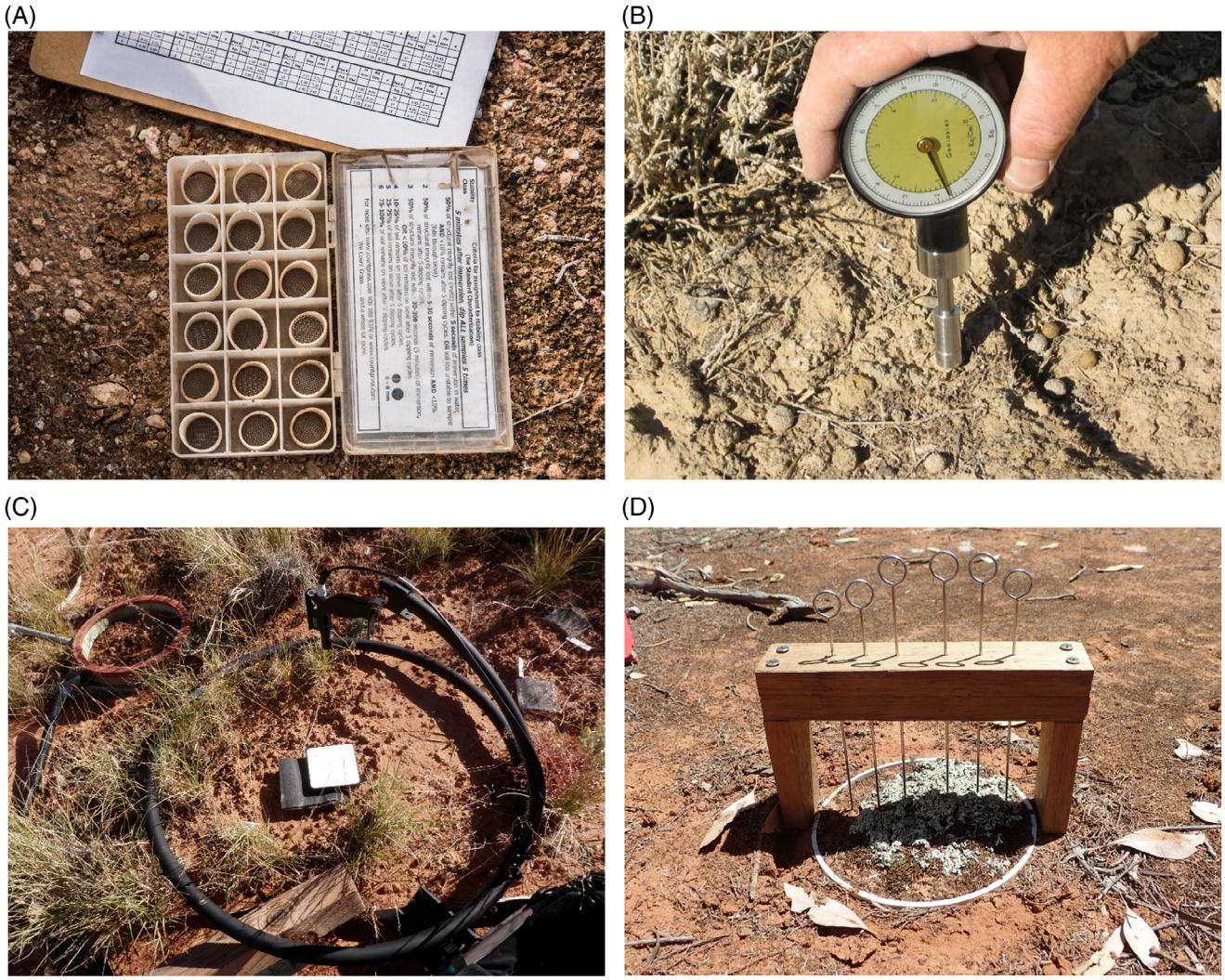

Figure 1. Photographs of instrumentation for measuring functional indicators: (A) a field kit for measuring aggregate stability, which is a functional indicator of erosion resistance (photographed by Stephen Dudrow); (B) a field penetrometer for measuring soil penetration resistance, another indicator of erosion resistance (photographed by David Eldridge); (C) a spectroradiometer–goniometer setup used to measure albedo, an indicator of energy balance (photographed by William A. Rutherford); (D) a profilemeter for measuring surface roughness, which is an indicator of hydrology, erosion resistance, nutrient accumulation, and habitat complexity (photographed by Max Mallen-Cooper).

value of 6, thus this technique is not useful as a functional trait of species. Another method for assessing aggregate stability, the drop test (Imeson & Vis 1984), assesses the number of drops of water required to disrupt an aggregate, and is highly correlated with water erosion rate (Cantón et al. 2009).

Soil Penetration Resistance. Soil penetration resistance is a component of soil stability. It is known to depend on bulk density and soil moisture content, both of which are moderated by biocrusts through their effects on aggregate formation and infiltration (Henderson et al. 1988; Garcia-Pichel et al. 2016). Penetration resistance also has a functional link to vascular plants, whose roots must establish through the soil matrix. When using a field penetrometer, penetration resistance is expressed as the amount of vertical pressure required to break through a surface (Fig. 1B; Li et al. 2010). This method is widely used because it is simple and inexpensive. Higher resolution measurements of penetration resistance can be obtained with an electronic micropenetrometer (Drahorad & Felix-Henningsen 2012).

Soil Shear Strength. Soil shear strength is a measure of the resistance of a soil surface to frictional forces created by wind and water (Zhang et al. 2018). Shear strength is generally measured on wet soils, but Zhang et al. (2018) argue that wind shear is the most likely to occur on dry soils, and thus tests should be done on dry soils. Shear strength can be modeled (Lagacherie & McBratney 2006), estimated in situ with a wind tunnel or shear vane (Li et al. 2010), or measured in the laboratory with various shear strength machines (Zhang et al. 2018). Possibly

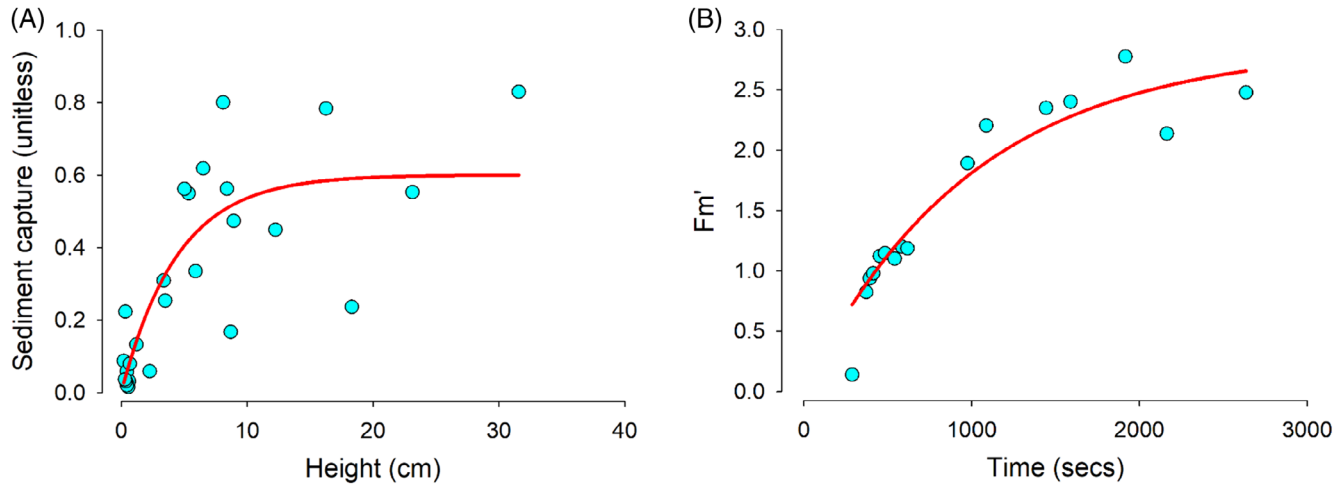

Figure 2. (A) The relationship between height and sediment capture in Australian biocrust species ($r^2 = 0.67$), sourced from Mallen-Cooper and Eldridge (2016), and (B) repeated measurements of maximal fluorescence (F_m' [arbitrary units]) on a patch of *Syntrichia caninervis*.

the simplest in situ method is to use a shear vane, a device that records the force required to break a soil surface (Fig. S1). In the literature, shear strength has been applied only to biocrust communities as a direct measure of erosion resistance (Schmidt et al. 2008) but might plausibly be developed further as a functional trait using a smaller vane. As with the penetrometer (above), determination of the vane or tip size needs to be made according to the type and thickness of the biocrust.

Nutrient Accumulation

N Fixation. Cyanolichens (lichens with a cyanobacterial symbiont), cyanobacteria, and other free-living diazotrophic bacteria in biocrusts fix atmospheric nitrogen (Pepe-Ranney et al. 2016). Biocrust-fixed nitrogen can be an important source of nutrients for vascular plants, particularly in resource-poor systems (Zhang et al. 2016). Two main methods are used to measure nitrogen fixation in biocrusts: acetylene reduction assays (ARA) and $^{15}N_2$ incubations. Acetylene assays are highly sensitive to ambient conditions and are an indirect (and possibly unreliable) measure of the nitrogen fixation rate, which greatly limits their value in assessing nitrogen cycling in biocrusts (Barger et al. 2016). We therefore recommend $^{15}N_2$ incubations, which are costlier but produce more robust results and directly measure the nitrogen fixation process.

Caputa et al. (2013) provide a detailed methodology for $^{15}N_2$ incubation. Samples of biocrust communities or specific species are typically standardized by area, which can be as small as a few square centimeters. For small or sparsely distributed species, multiple populations can be placed in the same chamber to attain the standardized area. Note that diazotrophic microbes living on macroscopic biocrust organisms will contribute to their rates of nitrogen fixation.

Enzyme Activities. The activities of cellular enzymes associated with nutrient cycles can be used as proxies for the contributions of biocrust organisms to these cycles (Mallen-Cooper & Eldridge 2016). Bell et al. (2013) developed a fluorometric method to estimate the activity of several enzymes associated with cellular function and microbial decomposition. This methodology was subsequently adapted for biocrusts (Fig. S2; Mallen-Cooper & Eldridge 2016).

Different research questions will require different modifications of the protocol. Standardized soil surface samples could be taken across an area of interest to directly measure enzyme activities in the developing biocrusts of a plot (see Bowker et al. 2013). As a trait, the enzyme activities of specific species can be estimated using axenic cultures or cleaned aboveground biomass. It is also possible to include the influence of a species on the microbial community by measuring samples that are highly dominated by the target species, including adherent soil and microbes.

Sediment Capture. Sediment capture assesses the capacity of biocrust organisms to intercept eroding soil particles and trap them in areas of low wind velocity created by biocrust structures. Sediment capture influences both erosion and nutrient deposition, because captured sediment is often rich in elements such as Mg and K (Reynolds et al. 2001). Mallen-Cooper and Eldridge (2016) provide a protocol for measuring sediment capture using a wind tunnel (Fig. S3).

Many variations on this protocol are possible and equally valid, using different sized sediment, wind exposure times, wind speeds, and wind angles. Those wanting to reduce labor time could consider measuring height instead (see below), which is strongly positively correlated with sediment capture (Fig. 2A; Mallen-Cooper & Eldridge 2016). This method can readily be applied to single species populations or mixed species communities. In systems with highly rugose or pinnacled biocrusts, where sediment capture is largely determined by indirect effects on roughness rather than the arrangement of aboveground biomass, a direct measurement of surface roughness is recommended.

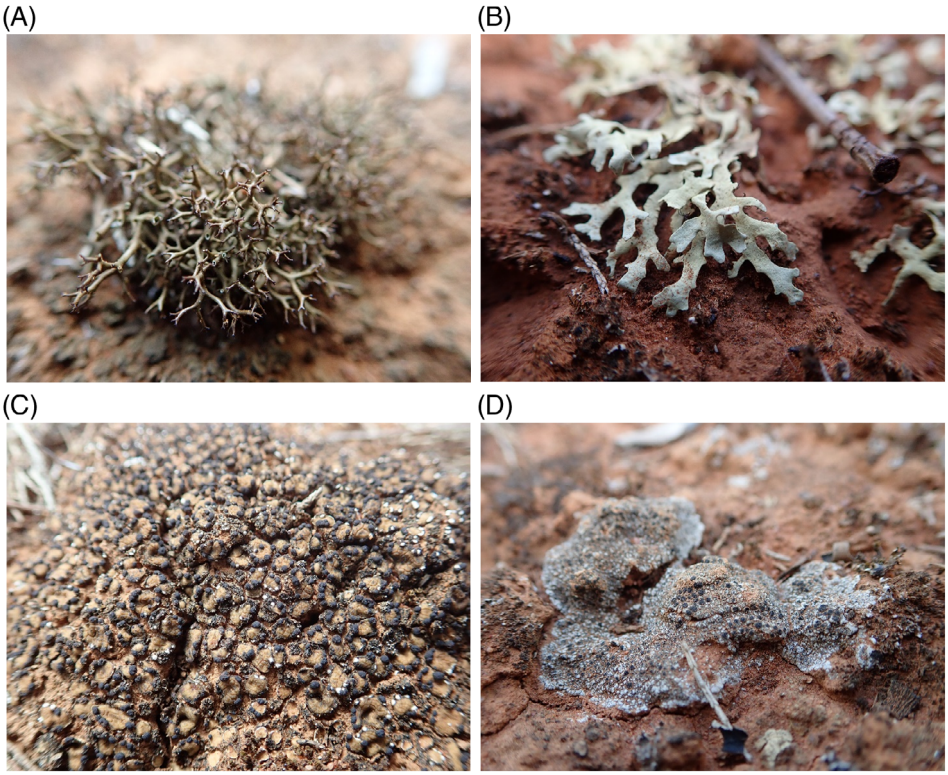

Figure 3. In order of decreasing structural complexity: fruticose lichen *Cladia aggregata* (A), foliose lichen *Xanthoparmelia* sp. (B), squamulose lichen *Psora decipiens* (C), and crustose lichen *Lecidea ochroleuca* (D).

Height. The height of a biocrust organism is the shortest distance between the uppermost living tissue (excluding reproductive structures such as sporophytes and podetia) and the mineral soil surface. This trait can therefore be measured in all biocrust organisms that project from, or rest upon, the soil (lichens, bryophytes, and some algae and cyanobacteria). Height is strongly positively correlated with sediment capture, and is thus functionally related to nutrient deposition and erosion resistance (Mallen-Cooper & Eldridge 2016). Height might also be a proxy for habitat complexity for invertebrates and microbes, as taller biocrust species tend to have the most complex structures (Fig. 3). Height is typically measured as a functional trait in individual organisms using digital calipers.

Productivity

CO_2 Exchange. A major role of bryophytes, algae, cyanobacteria, and lichens is fixing atmospheric CO_2. The exchange of CO_2 refers to the uptake of carbon through photosynthesis and the efflux of carbon through respiration. In biocrusts, CO_2 exchange is typically measured as net photosynthesis (NP), the net result of photosynthesis and respiration (Sancho et al. 2016). It is therefore a direct measure of net productivity. An estimate of carbon gain can be derived from the ratio of net photosynthesis to dark respiration (Raggio et al. 2018). Gas exchange systems used to measure CO_2 exchange in the field can be sophisticated automated setups (Bowling et al. 2011) or portable devices (Raggio et al. 2014). A challenge with automated setups is that biocrusts are only metabolically active for short periods of high humidity (Bowling et al. 2011). There is also a general issue with field measurements that CO_2 exchange includes efflux from soil respiration and abiotic processes (Sancho et al. 2016). This issue can be effectively resolved in a laboratory setting by removing excess soil from biocrust samples (Raggio et al. 2018). CO_2 exchange can be measured in a single species (e.g. Pintado et al. 2005) but would have to be standardized across a range of conditions to be a useful trait.

Chlorophyll Fluorescence. The photosynthetic capacity of a biocrust can be approximated by the fluorescence of chlorophyll *a*. Chlorophyll fluorometers apply a saturating flash of light and measure the reemitted light that was not used to drive photosynthesis. Using a combination of light- and dark-adapted measurements, one can derive the effective quantum yield of Photosystem II or the relative electron transport rate (Green et al. 1998). It is possible that a single measurement of light-adapted maximal fluorescence (F_m') could be used as a rapid estimate of chlorophyll activity, but this has yet to be explored empirically.

By varying the distance and field-of-view angle of the fluorometer, it is possible to measure fluorescence across a whole biocrust community or as a functional trait of just one species. Biocrusts require some time to activate cellular function upon hydration. On a single patch of *Syntrichia caninervis*, we found that it took approximately 30 minutes after wetting for F_m' to

reach a maximum value (Fig. 2B). A further complication is that mosses conditioned to rapid drying times (increased stress) tend to exhibit lower maximal fluorescence than those conditioned to slower drying (Stark et al. 2013). Fluorescence can therefore be considered both an effect trait and a response trait.

Production of Exopolysaccharides. Cyanobacteria produce several types of exopolysaccharides (EPS) that form a complex extracellular polymeric matrix (EPM) in the topsoil (Rossi et al. 2018). EPS are a substantial output of primary production in biocrusts and are known to enhance soil stability and trap nutrients before they can be leached (Belnap & Büdel 2016; Büdel et al. 2018; Swenson et al. 2018). When hydrated, EPS expand and clog micropores in the soil, resulting in a redistribution of runoff that competitively favors cyanobacteria (Mazor et al. 1996). Loosely bound EPS (LB-EPS), tightly bound EPS (TB-EPS), and the glycocalyx (G-EPS), which comprises the sheaths and capsules that surround cyanobacterial cells, can be extracted according to the methods of Rossi et al. (2018), and quantified with a phenol-sulfuric acid assay. Axenic cultures could theoretically be used to derive trait values for species, but EPS production is highly sensitive to environmental conditions (Moreno et al. 1998), and so it would be difficult to standardize measurements and those measurements are unlikely to represent cyanobacterial performance in field conditions.

Energy Balance

Albedo. Albedo, the ability of an object to reflect solar radiation, can be an important moderator of local microclimatic conditions and large-scale climate feedbacks (Belnap 1995; Hansen & Nazarenko 2004). Belnap (1995) reports that surface temperatures above dark biocrusts were 13°C higher than bare soil and 23°C higher than ambient temperatures. At a broader scale, biocrusts cover a sizeable portion of the Earth's terrestrial surface and shifts in species composition can substantially change the proportion of insolation that is reflected. When biocrusts on the Colorado Plateau, USA, were experimentally warmed and watered to simulate predicted changes in climate, a change in dominance from lichens and mosses to cyanobacteria resulted in a 33% increase in albedo (Rutherford et al. 2017).

As albedometers lack precision on small scales (180° field-of-view), spectroradiometer–goniometer setups are preferred for measuring the albedo of biocrusts (Fig. 1C; Hakala et al. 2014; Rutherford et al. 2017). The goniometer is typically a ring with a rotatable arm. With a spectroradiometer clipped to the arm, one can adjust the clip and arm for different zenith and azimuth angles respectively, and calculate a value of albedo that accounts for anisotropy (Rutherford et al. 2017). Rutherford et al. (2017) measured albedo in biocrust patches of 10-cm diameter but finer scale measurements, e.g. as a trait of individuals or monospecific populations, would be possible with smaller goniometer setups.

Level of Development. Level of biocrust development (LOD) was developed by Belnap et al. (2008) as a means of visually assessing the maturity of a biocrust community (Fig. S4). Generally, an observer places a small quadrat (25 cm × 25 cm) and records LOD from 0 to 6 based on a set of reference photographs. The original method is based strongly on the pigmentation of biocrusts, and thus this technique is a simple proxy for albedo. This method was also found to correlate well with chlorophyll *a*, EPS, and soil aggregate stability measurements, and thus can be used as a proxy for biocrust productivity and multifunctionality. Because this method was developed for the dark, pinnacled biocrusts of the Colorado Plateau, USA, the original visual categories would need to be recreated and recalibrated for different ecosystems. This method is especially useful because it is quick, information-rich, requires no special equipment or training, and is nondestructive. It is only applicable to mixed species communities and is therefore not measurable as a functional trait.

Hydrology

Absorptivity. Absorptivity is the capacity of biocrust organisms to trap moisture within, and on the surface of, their tissues (Mallen-Cooper & Eldridge 2016). Therefore, increasing absorptivity will result in less water available for run-off or to percolate through the soil. To measure absorptivity, a sample of biocrust is separated from the soil, submerged in water, removed from the water (allowing large drips to fall off), and weighed. After oven drying, the sample is reweighed and absorptivity calculated as the difference between wet and dry measurements per gram of dry biocrust (Mallen-Cooper & Eldridge 2016). Absorptivity can be measured as a functional trait by using a sample that contains only one species. For most biocrust species, exceeding the measurement error of a mass balance will require using multiple individuals per sample. Because soil would slake upon submerging, this methodology is limited to tissue samples.

Infiltration. Infiltration describes the process of water moving through the biocrust into soil pores. Biocrusts can influence infiltration via multiple mechanisms. These include providing entry points (e.g. micropores around rhizines or rhizoids) into the soil through which water can move, clogging soil pores by trapping fine particles, and simply providing a roughened surface that increases the hydraulic gradient and therefore enhances infiltration (Chamizo et al. 2016).

Infiltration measurements on biocrusts are generally performed in the field using an infiltrometer (Fig. S5; Li et al. 2005). Another technique available in the laboratory is the trickle irrigation method (Li et al. 2005). Up until now, these methods have been performed on mixed species communities, but it is feasible to measure infiltration as a trait using a microinfiltrometer (Tighe et al. 2012).

Surface Roughness. Surface roughness moderates the movement of water and eroding material through the landscape, and is a measure of niche space for invertebrates. In cold deserts, biocrusts mainly enhance roughness by stabilizing the soil directly beneath them, causing the less stable surrounding soil to be preferentially eroded and creating a pinnacled effect that is enhanced by frost heave (Belnap et al. 2001). In hot

desert systems, biocrusts enhance roughness largely through their aboveground biomass and the capturing of eroding sediment (Eldridge 1996; Williams et al. 2012).

Several methods are available to estimate surface roughness. A profilemeter, consisting of a frame with vertical pins, can be used to calculate roughness as the standard deviation of the heights of the pins (Fig. 1D; Eldridge et al. 1997). Roughness can also be assessed using digital models obtained from laser scanners or Structure from Motion photogrammetry, the latter of which might emerge as the preferred technique as it becomes more easily operated (Rodríguez-Caballero et al. 2012; Heindel et al. 2018). The chain method is a simple alternative whereby a tight-linked chain is draped over a patch of biocrust such that it matches the microtopography of the soil surface (Saleh 1993). An index of surface roughness (R) is calculated as:

$$R = 100\,(1 - L2/L1)$$

where L2 is the horizontal distance and L1 is the length of chain required to cover the same distance given surface roughness.

Discussion

Selecting Appropriate Functional Indicators

The key advantage of functional monitoring is that it enables us to track the impacts of a restoration project on an entire ecosystem. We have summarized a broad range of techniques that are available to assess biocrust functioning in the context of restoration. Most researchers, however, will not have the resources to measure all the functional indicators presented here in any one study. We generally advocate for monitoring a selection of functional indicators, but not to the exclusion of structural measures such as percentage cover, which are required for a trait-based approach and useful as a general measure of biocrust establishment success. Indeed, further research is needed into whether some functions could be used as early warning signs of establishment failure, such that the restoration trajectory might be altered.

We can envision two strategies for selecting complementary functional indicators. If one is interested in tracking the multifunctionality of the developing biocrust, we recommend the "one of each" strategy. This approach would avoid redundancy because the researcher would select one indicator per major function. Chiquoine et al. (2016) used this approach to assess different techniques for restoring biocrusts on disturbed roadsides in the United States. The authors monitored chlorophyll fluorescence, soil nutrient pools, and soil aggregate stability, reporting that inoculation with additional biocrust strongly assists the functional recovery of disturbed biocrusts. Similarly, Wang et al. (2009) chose to monitor soil penetration resistance, chlorophyll *a* content, and soil nutrient pools in recovering cyanobacterial biocrusts. In other situations, a targeted narrow-spectrum approach may be more useful. Applying this strategy would require identifying the primary reason why biocrusts are valuable for restoration goals in a given context, and selecting corresponding functional indicators. For example, Maestre et al. (2006) monitored both CO_2 exchange and chlorophyll *a* content, increasing the chances of detecting the specific way in which productivity was impacted by restoration treatment.

Setting Appropriate Functional Targets

How should we set functional targets for restored biocrust communities? We would not necessarily expect that the maximal value of an indicator is our goal. Indicators allow us to "take the pulse" of a recovering community, and we should expect there to be a normal healthy range in each indicator.

Predisturbance data on biocrust function are largely unavailable for use as a strict-sense reference. However, functional targets can be based on an estimate of potential function that is observable at an analog site, which should be as close to the restoration site in all relevant ecological dimensions, except degradation, as possible, e.g. "best on offer" (White & Walker 1997). The potential functional state would be assessed using the same indicators as monitored in the restoration area.

Biocrust recovery may be slow; therefore full recovery of function may not be a reasonable goal in all settings. Instead, pragmatic researchers may be satisfied to have set in motion a functional trajectory toward the chosen functional state. If no appropriate analog is available, values of potential function can be derived from literature. For example, Eldridge (1993) provides baseline values of soil aggregate stability and infiltration for well-developed biocrusts in eastern Australia. Another option is to undertake an expert elicitation process whereby experts use their collective wisdom to arrive at a potential assessment of former state. Spatial modeling approaches have also been advanced, which could estimate an entire surface of potential functional properties (Bowker et al. 2008).

Direct Versus Indirect Functional Monitoring

We have discussed how each indicator may be measured directly, on biocrust communities, and indirectly, using a trait-based approach, or both. Which is the better approach for the restoration ecologist? Direct monitoring of function is likely to require the least effort for any given project. By taking random community samples, time is not spent finding monospecific patches and identifying species, which requires a high level of expertise. On the other hand, many direct measurements are destructive and regular monitoring may result in considerable loss of restored biocrust.

Measuring functional traits requires substantial investment of resources, and as presented here, applies mainly to biocrust types characterized by high cover of macroscopic (lichens, mosses, and liverworts) rather than microscopic (e.g. cyanobacteria, algae) components. The initial measurement of most traits is also destructive, and measuring any function indirectly introduces a source of error. However, once the trait database is established, no further destruction is required. Using established mean trait values (for species, or genera, or morphofunctional groups), only abundance data is needed to infer functional patterns.

The Promise of a Global Trait Database

Functional trait data have immense value beyond a single restoration project. Creating such a database at a global scale for biocrusts is possibly less daunting than for other organisms (e.g. vascular plants), because many species, including ones that tend to be abundant, have broad multicontinental distributions (Bowker et al. 2017). Contributions from one research group to a trait database are likely to benefit other research groups, whose communities are likely to share some species.

Beyond restoration, a global trait database could be useful for other lines of investigation such as the impact of disturbance on biocrust function, or the testing of basic ecological theory. In vascular plant research, functional traits have led to remarkable advances in ecological theory (McGill et al. 2006). Rather than taxonomic diversity, which does not directly account for functional redundancy, we can now calculate functional diversity using a plethora of different indices (Schleuter et al. 2010). The versatility of trait-based approaches extends to agroecosystems, where they are being used to optimize ecosystem services (Wood et al. 2015). Overall, the biocrust research community would benefit greatly from following the lead of vascular plant ecologists and harnessing the power of trait-based ecology in restoration and beyond.

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Supporting Information

The following information may be found in the online version of this article:

Appendix S1. Calculating function from species' traits.
Appendix S2. Additional functional indicators.
Figure S1. A shear vane (torvane), consisting of a rotary knob and a disk with upraised ridges.
Figure S2. (A) Pipetting buffer into biocrust samples; (B) a microplate reader for measuring fluorescence; (C) biocrust species incubating in buffer and fluorescently tagged substrates.
Figure S3. Wind tunnel used to measure sediment capture, with roof (usually 10 cm above sample) removed to show internal setup.
Figure S4. Examples of level of development (LOD) classes 1 (A) and 5 (B).
Figure S5. A minidisk infiltrometer (www.metergroup.com) for measuring infiltration.

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