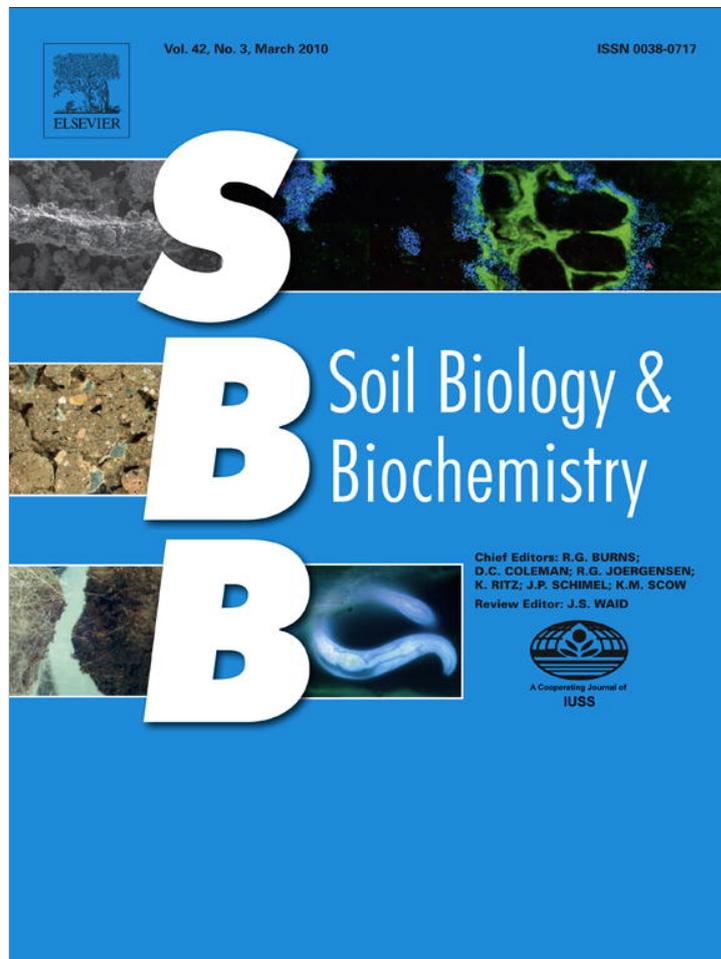


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Review

Biological crusts as a model system for examining the biodiversity–ecosystem function relationship in soils

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ABSTRACT

Despite that soils may be the greatest repository of biodiversity on Earth, and that most terrestrial ecosystem functions occur in the soil, research on the role of soil biodiversity in ecosystem function has lagged behind corresponding research on aboveground organisms. Soil organisms pose special problems to biodiversity–function research, including the fact that we usually do not know their identity nor what they do in soil ecosystems, cannot easily estimate their biodiversity, and cannot culture the majority of the organisms for use in manipulative experiments. We propose here that biological soil crusts (BSCs) of deserts and many other ecosystems may serve as a useful model system for diversity–function research because the species concept is relatively well-defined within BSC organisms, their functional attributes are relatively well-known, and estimation and manipulation of biodiversity in experiments are feasible, at least within some groups of BSC biota. In spite of these features, there is a pronounced lack of research on biodiversity–function using these organisms. At least two complementary approaches are possible: experiments using artificially-constructed BSCs, and observational studies which statistically control for the effects of other factors which are likely to covary with biodiversity. We applied the latter to four observational datasets collected at multiple spatial scales in Spain and the United States using structural equation models or path analysis using ecosystem function indicators relating to hydrology, trapping and retention of soil resources, and nutrient cycling. We found that, even when total BSC abundance and key environmental gradients are controlled for, direct and approximately linear relationships between species richness and/or evenness and indicators of ecosystem functioning were common. Such relationships appear to vary independently of region or spatial scale, but their strength seems to differ in every dataset. Functional group richness did not seem to adequately capture biodiversity–function relationships, suggesting that bryophyte and lichen components of BSC may exhibit low redundancy. More research employing the multi-trophic, multi-functional, and manipulable BSC system may enable more rapid understanding of the consequences of biodiversity loss in soils, and help enable a biodiversity–function theory that is pertinent to the numerous ecosystem services provided by soil organisms.

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1. Introduction

Of many topics in ecology, the message of the biodiversity crisis is one of the few that has permeated the popular culture. Human society is potentially affected by the consequences of biodiversity loss upon functioning of ecosystems and provision of ecosystem services. Beginning in the 1990s several studies were initiated concerning the effects of plant biodiversity upon productivity. Rather than creating a unified model, a variety of models of this relationship emerged and stimulated fundamental questions about

how exactly to study the effects of biodiversity on ecosystem function (henceforth referred to as biodiversity–function). Our relative lack of knowledge about biodiversity–function in soil ecosystems is exasperating, given that soils are possibly the greatest repository of biodiversity on the planet (Fitter et al., 2005). In the following review and reanalysis, we illustrate the utility of biological soil crusts (BSCs) as a model system for extending the breadth of biodiversity–function research, and delving into a better understanding of soil ecosystem function.

The numerous hypothetical relationships between biodiversity and ecosystem function follow three broad forms: the rivet hypothesis, the redundancy hypothesis, and the idiosyncratic hypothesis (Naem et al., 2002). The rivet or complementarity hypothesis suggests that each species has a unique role in an ecological system,

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and that the loss of species contributes toward the collapse of the system, therefore diminishing its function. The redundancy hypothesis proposes that organisms are functionally redundant, and to some degree the loss of some species may be compensated for others. Thus, although increasing richness may lead to increased function, such relationships are asymptotic and may saturate at fairly low levels of diversity, more quickly when there is high redundancy. The idiosyncratic hypothesis suggests biodiversity–function relationships that are not monotonic.

Many experimental studies have found some form of positive monotonic relationship between biodiversity and ecosystem function: those which do not asymptote or asymptote slowly are more similar to the rivet hypothesis, whereas those that asymptote quickly are interpreted as evidence for redundancy. The effects of species richness upon ecosystem functions have two primary mechanisms operating simultaneously, which have spurred much debate about interpretation of such findings (Tilman et al., 1997a,b; Wardle, 1999; Naeem et al., 2002). One mechanism is complementarity, wherein greater richness increases the probability of constructing species combinations with contrasting activity or limitations in space and/or time. The other mechanism has been termed “the sampling effect”, wherein one organism from the species pool contributes disproportionately to a particular function. As richness increases, the probability of the community containing this species, and therefore increasing the corresponding function, increases. The effects of species evenness or its contrary, dominance, upon biogeochemical function are less frequently studied. The effects of evenness–dominance seem to depend on functional traits of dominant species, for example, if the dominant is a highly productive species, there is likely to be a negative effect of evenness upon production (Mulder et al., 2004). The commonness of asymptotic relationships led some researchers to develop alternative concepts of diversity to species richness such as functional richness (number of functional groups), or even trait-based diversity schemes (Naeem and Wright, 2003; Statzner et al., 2007). These alternate conceptions of richness are attempts at quantifying the number of truly different organisms or traits that are present in an ecosystem with the expectation that the addition of new functional traits to an ecosystem is what enhances complementarity. Even as the concept of biodiversity seems to be evolving, recent advances have led to the development of the concept of multifunctionality of ecosystems (Hector and Bagchi, 2007; Gamfeldt et al., 2008). These authors argue that ecosystem functionality is a composite property of many functions, thus studies which are restricted to functional uni-dimensionality are biased toward observing redundancy. They argue that greater numbers of taxa are required to simultaneously provide multiple functions.

Perhaps because pioneer studies (Naeem et al., 1994; Tilman et al., 1996) on this dynamic topic focused upon plant communities, this body of literature is highly biased toward plants and their functions, particularly temperate grassland primary production (Díaz and Cabido, 2001). A notable extension of this research regarding soil biota suggests that arbuscular mycorrhizal fungi richness positively affects plant primary productivity and diversity in a way that is reminiscent of the rivet hypothesis (Van der Heijden et al., 1998). Given its importance, it is not surprising that so many studies have focused on production, but recently some have argued for a similar emphasis on decomposition, an ecosystem process that primarily occurs in the soil (Wall et al., 2005). Using experimental microcosms and fungal cultures, Setälä and MacLean (2004) found that decomposition rates were positively impacted by fungal diversity, but this relationship was asymptotic at low richness (~5 spp.) suggesting strong support for the redundancy hypothesis. Evidence of a large degree of redundancy and resiliency of function was also observed in a modeling-based study, in which

broad functional groups of soil organisms were removed from the soil ecosystem (Hunt and Wall, 2002), and in a reconstruction of a soil community wherein each treatment constituted the addition of a trophic level of soil fauna (Fitter et al., 2005). Andrén et al. (1995) found that the decomposition rate was uncorrelated to diversity of soil fauna, and Andrén and Balandreau (1999) also commented on the apparent redundancy of soil communities. Despite these interesting exceptions, for the most part, biodiversity–function research in soils has lagged more than a decade behind the plant-focused studies.

Wall et al. (2005) provides a list of tenets of soil ecology, some of which are also reasons why soil communities present special challenges to the extension of biodiversity–function research to soils. Perhaps most importantly: 1) soil biodiversity may be quite high, 2) soil systems are primarily microbial and not amenable to culture, thus easy identification is not possible, 3) the identity and functional capabilities of most species is not known. These characteristics would seem to strongly dissuade estimation of biodiversity, development of functional group or trait diversity indices, and selection and measurement of appropriate function indicators. It has been proposed that using natural soil ecosystems of low, and thus tractable, species diversity would be advantageous to understanding biodiversity–functional relationships in soils (Coleman and Whitman, 2005). In fact such model systems do exist in Antarctic soils, which may provide important insights about the biodiversity–ecosystem function relationship (Barrett et al., 2006). While we do not disagree that this would be advantageous, basing our knowledge primarily on such uniquely simple systems seems risky (Andrén and Balandreau, 1999), and we suggest that there may be a complementary model system that has been nearly completely overlooked thus far.

2. Review

2.1. Biological soil crusts as a model for biodiversity–function research

We propose that, unlike most soil biota, BSCs are a model system to study the linkage between diversity and function for five reasons: 1) They exhibit multiple trophic levels and functional complexity in small spatial extents, characteristic of soil ecosystems, 2) Unlike other types of soil communities, one of these functions is primary productivity, creating a natural complement to studies based upon vascular plants, 3) For the groups of organisms within the BSC that compose the greatest biomass, taxonomy is reasonably well-defined, diversity estimation is possible, and functional roles are at least partially understood, 4) Like plants and unlike most soil biota, some groups of BSC biota are readily visible, facilitating data collection, 5) A majority of the autotrophic components, and some heterotrophic components, of BSCs are culturable, or otherwise manipulable in experiments. As for many systems, the functional attributes of the fungal, bacterial and archaeal components remain poorly known, but we believe that enough is known of biodiversity and function in BSCs to enable a myriad of biodiversity–function studies. Given these characteristics it is surprising that this line of investigation has barely been approached using biological soil crusts as a study system. We expand upon the functional complexity of BSCs and review the sparse literature about biodiversity–function in BSCs below.

Biological soil crusts are a multi-trophic community of organisms which occur at the soil surface, particularly in drylands, but also to some degree in most ecosystems. By definition, they exist in close contact with mineral soil, and create a horizontal aggregate layer at the soil surface when well-developed (Belnap and Lange, 2003). They have an autotrophic component comprised one or more

of the following: mosses, lichens, liverworts, cyanobacteria, chlorophytes, diatoms, and other eukaryotic algae. In addition, they have a heterotrophic component of fungi, protists, bacteria and archaea. Furthermore, they serve as habitat for numerous micro- and macroscopic fauna of multiple trophic levels (Shepherd et al., 2002; Lalley et al., 2006; Darby et al., 2007). They are somewhat of an enigma, as they are clearly closely associated with and even completely immersed in soil, and are thus “soil organisms”, but in many ways they also behave like vascular plant communities. For this reason, BSCs are major or minor players in an unusually wide array of ecosystem functions, offering many possibilities for biodiversity–function research. The many functions of BSCs have been the subject of several extensive reviews (e.g. West, 1990; Evans and Johansen, 1999; Belnap, 2006) and a major topic of one book (Belnap and Lange, 2003), thus we recount the major ones only briefly here:

1. Carbon fixation: Cyanobacteria, eukaryotic algae, bryophytes and lichens are all primary producers providing an additional pathway other than vascular plants for C to enter the soil (Lange et al., 1992).
2. Nitrogen fixation: Nitrogen fixation is conducted in BSCs by lichens with cyanobacterial photobionts (e.g. *Collema*, *Heppia*), heterocystic cyanobacteria (e.g. *Nostoc*, *Scytonema*), and heterotrophic bacteria (Belnap, 2002; Billings et al., 2003).
3. Erosion resistance and sediment trapping: BSC organisms with filamentous structures (cyanobacterial trichomes, moss rhizoids, lichen rhizines), the many organisms which produce extracellular organic exudates (numerous examples, but particularly cyanobacterial polysaccharides), and organisms which physically shield the soil surface from erosive forces (bryophytes and lichens) reduce the amount of sediment lost to erosive forces (Bowker et al., 2008a; Chaudhary et al., 2009). Many of the same organisms and mechanisms also contribute to trapping of sediment and fertility transported from elsewhere (Reynolds et al., 2001).
4. Hydrological: By decreasing pore space on a microscopic scale, or increasing roughness on a macroscopic scale and slowing overland water flow, BSCs potentially exert a large influence on how much water infiltrates or is lost as runoff (Malam Issa et al., 1999; Maestre et al., 2002).
5. Nutrient cycling: BSCs are consumers of, and contributors (*via* the above mechanisms) to nutrient pools. In addition, numerous BSC activities involving alterations of chemistry or water status in the soil can alter nutrient availability and cycling rates (Harper and Belnap, 2001). BSCs also contain heterotrophic fungi, bacteria, archaea, and microfauna responsible for the decomposition of BSC organic matter.
6. Indirect effects on function *via* species interactions: BSCs interact, sometimes very closely, with other highly functional organisms such as vascular plants and their fungal symbionts (DeFalco et al., 2001; Escudero et al., 2007; Green et al., 2008), decomposer fungi and prokaryotes (Acea et al., 2001), and soil fauna (Darby et al., 2007). Thus, numerous indirect effects of BSC biodiversity on ecosystem functions are possible.

2.2. Biodiversity–ecosystem function in the biological soil crust literature

Surprisingly, little is known about the effects of BSC biodiversity on these biogeochemical functions for the simple reason that very few studies have examined this relationship. The reason why biodiversity–function relationships have not been studied frequently in the BSC research community is perhaps an accident of history. Biodiversity–function research is an intersection between

community and ecosystem ecology, and most BSC ecologists work within one of these disciplines. Further, most ecosystem ecologists tend to work at larger spatial scales than community ecologists.

In the field, correlations between BSC biodiversity and function have been reported in various locales and at varying spatial scales (Eldridge and Koen, 1998; Li et al., 2003; Bowker et al., 2008b). In Australia, Eldridge and Koen (1998) and Thompson et al. (2006) reported positive correlations between BSC species richness and a multi-indicator indices of soil stability ($r = 0.17–0.46$) and infiltration ($r = 0.26$), and nutrient cycling ($r = 0.34$). Though none were particularly strong correlations, some did appear to be independent of total BSC cover. When comparing sites along a chronosequence of stabilized dunes in China, researchers found strong correlations ($r > 0.85$ in all cases) between either algal–cyanobacterial or moss richness and HCO_3^- (related to C-exchange), and soil organic matter, though the study did not examine whether there was a direct link between richness and these functions or, more likely, an association due to dune age (Li et al., 2003). In addition to these examples there are numerous examples which compare function-related responses in “light” and “dark” cyanobacterial BSCs (Barger et al., 2006; Housman et al., 2006); the dark crusts do tend to be richer in cyanobacterial taxa, however these studies do not attempt to isolate effect of BSC diversity upon function from other differences between light and dark crusts. To date, only a single field based study has been conducted with a statistical design adequate to separate biodiversity (richness and evenness) effects from the most common covariates (e.g. total cover). This study found that biodiversity–function relationships differed by site, and by the functional attribute examined, in some cases were more important than total cover and in others not, and often times effects of richness or evenness on functions were negative (Maestre et al., 2005).

Published experimental results are currently lacking from studies designed to test biodiversity–function relationships in BSCs, though some studies are underway. Hu et al. (2002) compared erodibility of three monospecific synthetic cyanobacterial–algal BSCs, compared to a polyspecific combination of all four strains. Likewise, Acea et al. (2001) used a similar design of synthetic cyanobacterial crusts to study the response of heterotrophic microbial biomass. Both studies found that the more diverse polyculture was more highly functional in terms of erodibility or heterotrophic biomass than most monocultures, but differences may be primarily attributable to the presence of particular species (examples of the sampling effect *sensu* Wardle, 1999). Thus, in simple terms there is circumstantial evidence that BSC biodiversity influences various ecosystem functions in various places, but there are few definitive examples.

2.3. Technical considerations

In order to fully exploit the potential of BSCs as a model system for the study of biodiversity–function relationships in soils, we must first address some technical considerations: 1) How to measure BSC biodiversity? 2) How can we manipulate BSC biodiversity to study in experiments? 3) How can we study the BSC role in biodiversity–function relationships in uncontrolled observational studies?

2.3.1. Measuring BSC biodiversity

The full species richness of a BSC has never been determined at a single site, thus to gauge an estimate we must compare data from studies with disparate techniques. By a large margin, the BSC biomass is dominated by autotrophs, but the major reservoirs of diversity may be in the heterotrophic components. A typical small sample (<500 cm² of soil surface area) might contain 0–10 lichens, and 0–5 bryophyte species, according to our experience in arid and

semi-arid areas from Spain and the United States. Judging from data in the Sonoran and Colorado Plateau deserts (USA), total prokaryotic richness on a per sample basis, estimated using molecular techniques, is rather low, ranging from 10 to 32 strains, including only a handful of cyanobacteria (Nagy et al., 2005; Reddy and Garcia-Pichel, 2006). The number of cyanobacterial taxonomic units in lichen-dominated BSCs from SE Spain has been found to vary between 6 and 22, including both unicellular and filamentous genera (Maestre et al., 2006). In data from the Colorado Plateau and Israel, free-living fungi also display low richness ranging from 2 to 30 per sample (Grishkan et al., 2006; Bates et al., 2009). The fungal estimates do not include symbiotic fungi infecting bryophytes or lichens, which may comprise an unknown and potentially large number of taxa (States, 2003). Eukaryotic algal diversity can vary considerably from as low as a single species (Smith et al., 2004) in a coastal dune system, but simple morphology may hide considerable diversity in the deserts, which may have representatives of 6 of 10 chlorophyte classes (Cardon et al., 2008). Perhaps the greatest contributors to overall diversity are the soil fauna and protozoa (Bamforth, 2004; Neher et al., in press). In studies of the microarthropod and nematode taxa of the Colorado Plateau and Chihuahuan Deserts, >40 families and 3–21 genera might be encountered representing a potentially very large species pool (Darby et al., 2007; Neher et al., in press). Given this information it is not unreasonable to say that a BSC sample might contain hundreds of species.

Choosing an appropriate index of biodiversity is an old problem: it is most straightforward to measure taxonomic diversity, but what we truly desire is an index of functional diversity. There is a continuum of approaches along this spectrum, ranging from species richness and evenness, to functional group richness or evenness, to trait-based multivariate indices of functional diversity (e.g. Tilman et al., 1997a,b; Mason et al., 2006; Wright et al., 2006; Lavorel et al., 2008). At the current time, the first two are possible for at least for some groups of BSC organisms and are discussed below, whereas we hope to facilitate the development of the third. Unlike most soil communities, there is a well-defined species concept and the majority of species have been described in the moss and lichen component of BSCs, which in addition to a few large cyanobacteria are macroscopic and can be identified in the field, often to the species-level. Therefore, traditional metrics of biodiversity such as evenness and richness are easily estimated with mosses and lichens based upon percent cover or other abundance data. Cyanobacterial–algal abundance can be quantified fairly easily at the family or genus level (though some genera may not be truly monophyletic) by sampling micro-transects along slides with soil slurry, and therefore generic richness and evenness can be calculated for this group of biota. Confident species-level identification requires molecular techniques (Nagy et al., 2005; Maestre et al., 2006). Culture-based techniques are also valuable for identifications of BSC microorganisms, but may not easily represent abundances of different taxa in samples and are perhaps useful only for calculating richness rather than evenness.

Similar to other soil communities, the microscopic heterotrophic components of BSC conceal much hidden diversity that are revealed only with molecular techniques (Nagy et al., 2005; Maestre et al., 2006), or using labor intensive morphological methods which are usually only applied to familial or generic resolution (Darby et al., 2007; Neher et al., in press). Using molecular techniques, it is difficult to obtain quantitative abundance data for all of the heterotrophic microbes present. Further, and with the exception of some of the soil fauna (e.g. nematodes whose mouth morphology reveals what they eat), little is known of the ecology and function of these heterotrophic organisms. Therefore, only the broadest of functional classifications are possible.

Although less well-known than vascular plants, there is a reasonable amount of information available regarding the roles of many BSC organisms in ecosystems, making possible estimates of functional group richness and, in the foreseeable future, trait diversity (see below). Functional groups based upon the effects of activity of the species upon the ecosystem (Lavorel and Garnier, 2002), are of interest when evaluating biodiversity–function relationships. It was proposed that the morphology of BSC organisms is crucially important to inferring their activity and function, and thus could provide a shortcut to collection of monitoring data (Eldridge and Rosentreter, 2000). These authors proposed up to three tiers of classification of BSC organisms: morphological type, continuity or discontinuity of colony, and color. The first two strata deal with the way in which the organism is likely to interface with erosive forces, and its ability to redirect water, and therefore contribute to gain or loss of sediment and the infiltration-runoff balance. The color relates to surface albedo (Ustin et al., 2009), and therefore the ability to warm or cool underlying soil, and to chemistry, which especially in the case of lichens, can influence decomposition, nutrient cycling and the performance of other biota (Escudero et al., 2007; Cornelissen et al., 2007). The advantage of the Eldridge and Rosentreter (2000) scheme is that much can be inferred with minimal taxonomic knowledge. Bowker et al. (2008b) employed a modification of this scheme, which used two strata: morphological type, and nitrogen fixation ability. If species richness is known and all species can be assigned to a functional group, the number of species present within functional groups can be estimated as an index of species redundancy. Such redundancy has been proposed to be positively related to the resiliency of ecosystem function (Naeem, 1998), and provides another potentially useful metric. The functional group approach has been applied primarily to the macroscopic BSC components, bryophytes and lichens. Similar grouping systems for other biota are possible based upon feeding preferences, which can be ascribed to BSC nematode and microarthropod genera, although data are often incomplete (Darby et al., 2007; Neher et al., in press).

As more strata are added to any such functional grouping scheme, it begins to approximate a trait-based assessment of functional diversity, as proposed by Naeem and Wright (2003). The simplest quantifications of trait diversity count the total number of trait categories present in a sample. Most traits are actually quantitative, thus multivariate indices have been applied to estimate evenness or diversity of quantitative trait data (Mason et al., 2003; Botta-Dukát, 2005). Trait-based indices of functional diversity have not yet been applied to the BSC system, although there is a considerable amount of categorical data on response traits available, especially for lichens. Some authors have laid the groundwork for identification and quantification of key traits among bryophytes and lichens (Cornelissen et al., 2007). However, usable databases of such traits have yet to be compiled specifically for BSCs. Some of the traits proposed by Cornelissen et al. (2007) are relevant in BSCs, whereas others are primarily important in mesic to hydric environments rather than the drylands where BSCs are prevalent, some may be assessed or inferred more easily, and additional traits clearly need to be considered regarding hydrological and soil stabilization functions of BSCs. Using suggestions of Eldridge and Rosentreter (2000) and Cornelissen et al. (2007), we propose the beginnings of a system of effect traits for estimating trait diversity in BSCs (Table 1). The contents of the table are explained below.

Description of the morphology of lichen colonies can allow us to infer multiple functional properties such as permeability by water (Eldridge and Rosentreter, 2000). Continuity of the colony is also important, especially in crustose and squamulose growth forms. A quantitative permeability index would be a valuable functional trait. Regarding BSC-forming lichens, there are few data on tissue

Table 1

Informative effect traits of BSC-forming lichens (A.), mosses (B.), cyanobacteria and algae (C.) and corresponding ecosystem functions. In each section, column headers identify traits relevant for the group of organisms being considered. Subsequent text lists trait categories, or describes the range of quantitative traits. For each trait and its categories or range, one or more ecosystem functions is listed which may be affected by a given trait. Superscript letters indicate selected traits that are illustrated in a corresponding panel of Fig. 1. H = Hydrology, DT = dust trapping, ER = erosion resistance, CFIX = Carbon fixation, NFIX = Nitrogen fixation, D = decomposition, NUT = nutrient stocks, cycling or availability, UV = ultraviolet resistance, SA = surface albedo.

A. Lichens	Colony morphology	Density	Symbiosis type	Chem 1: norstictic acid	Chem. 2: pruina	Chem 3: metal uptake
Trait data	Gelatinous, crustose ^a , squamulose ^b , foliose ^c , fruticose ^d	Sparse ^b –continuous ^a	Chlorophyte, cyanobacterium, tripartite	Yes/no or strength of KOH reaction ^e	Absent–heavy ^f	Low pH activity (usnic acid), high pH activity (parietins), both low and high pH (rhizocarpic acid)
Functions	H, DT, ER	H, DT, ER	C FIX, NFIX	D, NUT	NUT	NUT
B. Bryophytes	Stem morphology	Height	Colony density	Leaf awns	Secondary metabolites	
Trait data	Erect (moss) ^g , prostrate (moss) ^h , thalloid (liverwort) ⁱ , leafy (liverwort)	<0.5 mm – several cm ^g	Scattered–loose cushions–tight cushions	Present ^j or absent	Oil bodies, terpenes	
Functions	H, DT, ER	H, DT, CFIX	H, DT, CFIX, ER	H	D, A, NUT	
C. Cyanobacteria –algae	Colony morphology	Polysaccharide production	Polysaccharide type	N-fixation	C-fixation	Pigmentation
Trait data	Unicellular, clustered, simple filaments, grouped filaments ^k , thalloid ^l	Low–very high (may greatly exceed live biomass)	Tubular sheath ^k , other shapes	None, consortial, heterocystic	Variable photosynthetic rates	Abundance of various sunscreens and carotenoids
Functions	DT, ER	DT, ER	DT, ER	NFIX	CFIX	UV, SA

concentrations of nutrients to infer photosynthetic properties, but direct measurement of maximal photosynthetic rates and chlorophyll *a* content (related to the former) are available, largely owing to the career of Otto Lange (see [Belnap and Lange, 2003](#) for a review). Further, considerable variation in photosynthetic rate can be explained simply by categorizing lichens into three groups based upon photobiont type: cyanobacterial, green algal, or both ([Palmqvist et al., 2002](#); [Belnap and Lange, 2003](#)). These are likely also useful classifications of lichen N-fixation capability, although more detailed data may eventually reveal differences based upon morphological groups. [Cornelissen et al. \(2007\)](#) emphasize the use of chemical attributes of cryptogams as functional traits. Because chemical information is used in lichen taxonomy, much is known and widely reported regarding the chemical constituents of these organisms. However, since only a few of the numerous secondary metabolites of lichens have been characterized functionally, we must be conservative with the use of these traits as they may not have particular importance to ecosystem function. At the moment we suggest the use of a few substances with at least some known functions. Examples include the antimicrobial activity of many substances including norstictic acid and usnic acid ([Tay et al., 2004](#)), and the weathering, nutrient acquisition, chelation, or sequestration activity of oxalic acid ([Lapeyrie et al., 1987](#)), usnic acid, rhizocarpic acids and other yellow anthraquinones ([Hauck et al., 2009](#)). Oxalic acid is a major weathering agent of soil and rock and its presence can be deduced from the appearance of oxalate pruina on dry lichen thalli. The yellow and green lichen pigments mobilize metals under complementary pH environments (low pH: usnic acid, high pH: anthraquinones, both high and low pH: rhizocarpic acid; [Hauck et al., 2009](#)). As more biogeochemical functions are ascribed to these lichen substances, many more potentially useful traits linked to nutrient availability and decomposition may emerge. The remaining traits addressed by [Cornelissen et al. \(2007\)](#), tissue dry mass, and others neglected by them (e.g. hydrological effects, sediment capture and erosion resistance), are likely reasonably well described by the soft traits used in the [Eldridge and Rosentreter \(2000\)](#) morphotyping system.

There is much less information available on BSC bryophyte traits. Reports of area-based photosynthetic rates are rare. We

know that bryophytes are rich in secondary metabolites such as terpenes and phenolics, which are likely to be allelopathic, affecting both herbivory and decomposition and therefore nutrient cycling ([Mues, 2000](#)). These traits are simply not reported in enough detail at this time to be useful in estimating trait diversity of BSC bryophytes with the exception of secondary metabolite-containing oil bodies in liverworts, a common character used in taxonomy ([Cornelissen et al., 2007](#)). Moss water relations are a key trait, because mosses can enhance the amount of water infiltrating the soil ([Liu et al., 2006](#)), or on the other hand can retain water at the surface out of reach of most vascular plant roots ([Orlovsky et al., 2004](#)). The presence of awns, visible hairs at the end of leaves, has been proposed to influence hydration status via frost and dew harvest, alteration of albedo, and boundary layer creation ([Giordano et al., 1993](#)). Perhaps the most important trait regarding water relations is area-based water storage capacity. Determination of this function will be dominated by morphological traits of the colony such as growth form (erect or prostrate), height of plants and density of colonies ([Eldridge and Rosentreter, 2000](#)). Finally, although many bryophytes can be colonized by arbuscular mycorrhizal fungi, there is virtually no information on colonization status for BSC species.

Applying functional traits to cyanobacterial and algal species will be especially difficult, because of the scale-dependency of these traits. More so than mosses and lichens, several important traits are properties of colonies or emergent properties of the aggregate BSC components, which may not be captured by individual species-scale traits (e.g. surface roughness). Colony type may be related to motility, which may affect the rapidity by which newly deposited sediment is entrained; filamentous growth forms grouped in a common sheath are known to be highly motile. Amount and form of polysaccharide excretions are likely to be important in dust capture and erosion resistance; more polysaccharides result in greater chemical microaggregation, whereas tubular polysaccharide sheaths may be important in macroaggregate formation ([Bowker et al., 2008a](#)). Amount and form of polysaccharides likely influence conductivity of soils and infiltration ([Belnap, 2006](#)). Key individual scale traits include N-fixation ability, which may be conducted by the cyanobacterium in heterocysts, or by bacteria living among cyanobacterial polysaccharides ([Steppe et al., 1996](#)).

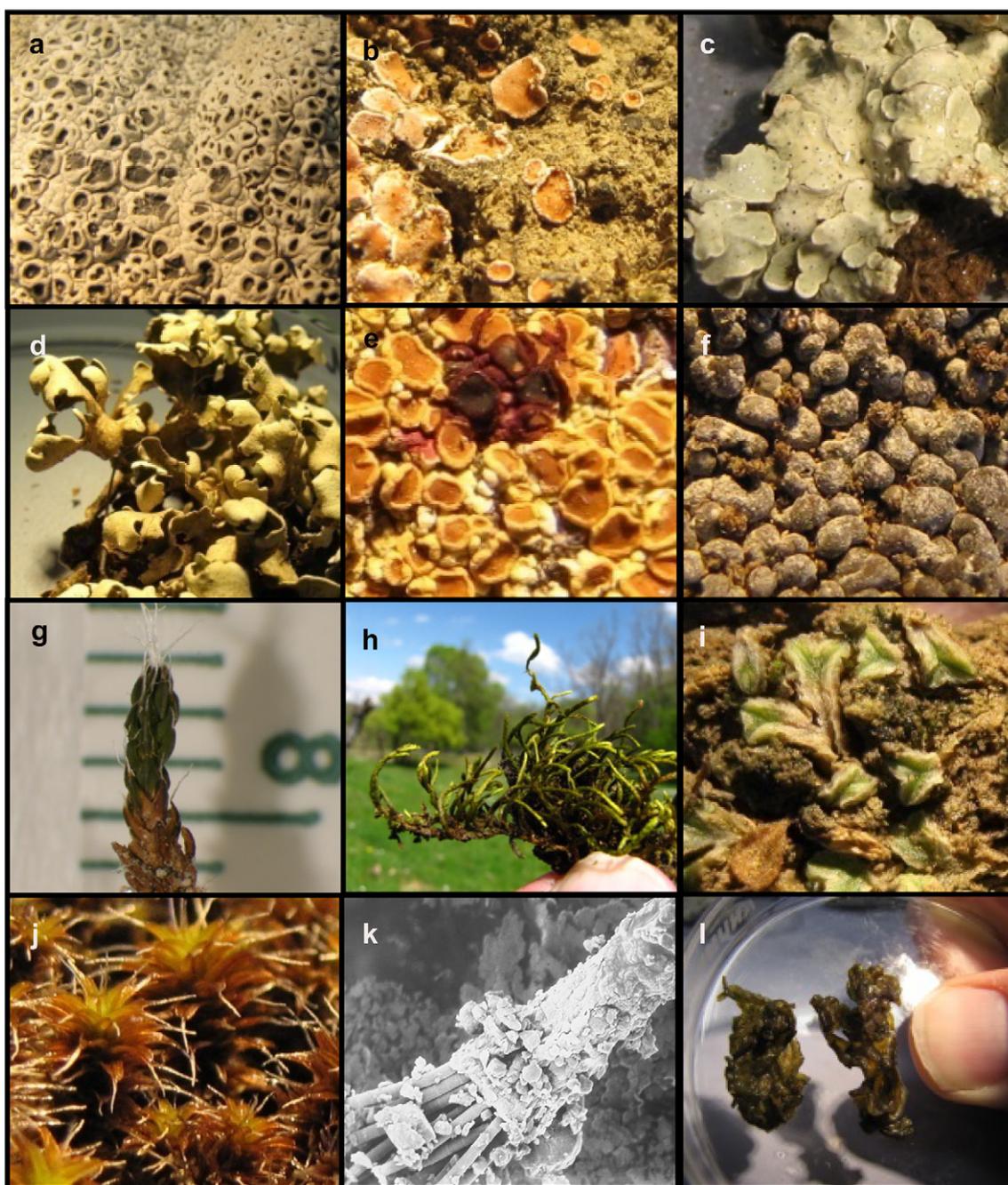


Fig. 1. Illustrations of selected effect traits in lichens, bryophytes and cyanobacteria of BSCs. a. *Diploschistes diacapsis*: a crustose lichen. This species also exhibits a high continuity. b. *Psora decipiens*: a squamulose lichen. c. *Squamarina lentigera*: a foliose lichen. d. *Cladonia convoluta*: a fruticose lichen. e. *Fulgensia subbracteata*: A crustose lichen, the red-purple reaction to KOH indicates presence of norstictic acid. f. *Tonia sedifolia*: A squamulose lichen, the white dusty crystals on surface are pruina indicating presence of oxalic acid. g. *Syntrichia caninervis*: An erect moss. Moss species have a characteristic range of stem height (photo: Lloyd Stark). h. *Brachythecium* sp.: A prostrate, branched moss. i. *Riccia* spp.: a thalloid liverwort, lacking stem-like and leaf-like structures. j. *Syntrichia ruralis*: Leaf tips terminate in a hair-like awn. k. *Microcoleus vaginatus*: a grouped filamentous cyanobacterium. Bundles of filaments are encapsulated in a tubular polysaccharide sheath (photo: Jayne Belnap). l. *Nostoc commune*: A macroscopic, thalloid cyanobacterial colony encapsulated in copious polysaccharides. Photos: Rebecca Mau, unless otherwise indicated.

Quantitative C-fixation rates for individual species are sparsely available, usually mixed species crusts are measured (Belnap and Lange, 2003; Maestre et al., 2006). Surface albedo is primarily governed by a number of sunscreen pigments, carotenoids, and density of photosynthetic pigments. Cyanobacterial species have been loosely grouped as “light” (e.g. *Microcoleus* spp.), or “dark” (e.g. *Nostoc* and *Scytonema*), based upon their disproportionate contributions to BSC darkness.

2.3.2. Manipulating BSC biodiversity in experiments

Since BSC biodiversity and functional diversity does appear to be tractable, albeit not yet fully known, the next logical technical hurdle is manipulation of biodiversity. Most experiments addressing the role of biodiversity in ecosystem function, have employed experimental plantations of vascular plants of varying levels of diversity in either random or realistic assemblages (Zavaleta and Hulvey, 2007). This approach need not be confined to the vascular

plant system. There are several examples of the creation of “custom crusts” using artificial BSCs of single or multiple species. There is no reason that such an approach cannot be extended to the creation of BSCs with varying levels of species richness, functional richness, cover, and evenness. There are two approaches: the inoculation method and the “mosaic” method.

Inoculated artificial crusts must begin with monospecific cultures of BSC organisms which are then added to a sterilized soil substrate and allowed to establish a BSC. Given the ease of culturing BSC cyanobacteria compared to many microbes (Hu et al., 2002), this process is perhaps best suited to the creation of cyanobacterial or eukaryotic algal crusts. However, some researchers have extended the approach to moss protonemata and fungi (McKenna Neuman and Maxwell, 1999, 2002; McKenna Neuman et al., 2005). It may be possible, albeit probably much more difficult, to apply the approach to lichen mycobionts, or synthetic lichens (Bäckor and Fahset, 2009). Acea et al. (2001) and Hu et al. (2002) each employed a comparison of several single-species artificial BSCs and an additional BSC composed of a mixture of these cyanobacterial or algal strains, although they were not specifically focused on studying diversity. To preserve experimental levels of richness, artificial BSCs must be maintained in axenic conditions, and this approach does not allow an easy manipulation of evenness.

BSC mosaics can be created by field-collecting small pieces of mosses or lichens from a moistened crust, and reassembling them on an uncrusted soil. It has long been known that such fragments can be translocated without incurring major damage to the organism (e.g. Scarlett, 1994; Bowler, 1999). Unlike inoculation-based experimental approaches, this approach allows manipulation of the spatial arrangement of the organisms, easier manipulation of evenness and, if desired, replication of realistic relative abundances (*sensu* Zavaleta and Hulvey, 2007). This approach is not as “clean” because in addition to the transplanted mosses and lichens, microscopic or otherwise cryptic prokaryotes, soil microfauna, and fungi are also transported. However, no species is an island, and the same problem is applicable to most of the studies of plant community biodiversity and ecosystem function which have formed the foundation of our current knowledge. Castillo et al. (2008) created mosaic BSCs compiled from 1 cm² samples of several lichen species which commonly co-occur in nearby field sites. The experiment employs mosaics with equal total cover, but with two levels of richness, two levels of evenness, and both a random and clumped spatial organization (Fig. 2).

2.3.3. Studying BSC biodiversity–function relationships in the field

Randomized experimental approaches are indeed the researcher's most powerful tool for drawing causal inference. However, all experiments create artifacts which can rarely be completely disentangled from the interpretation of results. The severity of this problem varies. For example, if artificial BSCs are studied, yet we are drawing inference about BSCs in general, we must assume that artificial and natural BSCs function similarly. Further, experiments may employ levels of richness, evenness or cover not realistic in the field, and randomized designs may yield entirely novel combinations of species (Zavaleta and Hulvey, 2007).

Analysis of field data provides the complementary approach to be undertaken when studying naturally occurring BSCs. The disadvantage of this approach is that various indices of BSC biodiversity intercorrelate with each other and with other community attributes such as total abundance. This means that simple bivariate comparisons of a biodiversity indicator and an ecosystem function indicator may be misleading. However, there are statistical methods which are compatible with such situations (Grace, 2006). Structural equation modeling (StEM) emerged as a synthesis of path analysis, factor analysis, and maximum likelihood techniques,

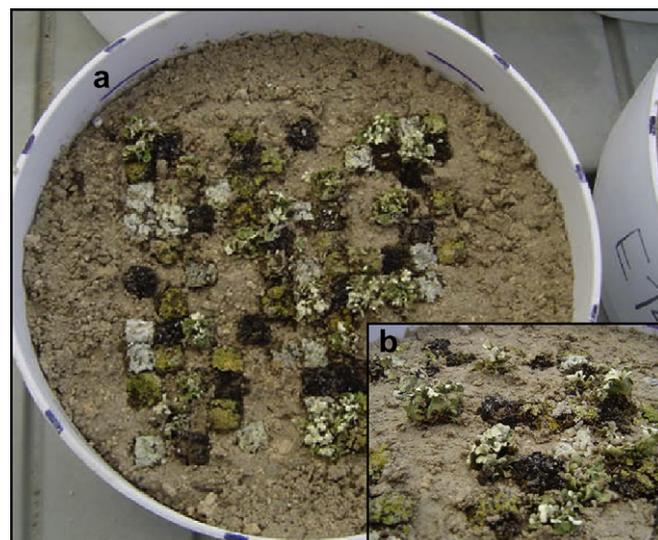


Fig. 2. An example of an artificial BSC mesocosm created using the “mosaic” technique (a). Lichen colonies are constructed using 1 cm² squares of field collected material (b). See Castillo et al. (2008) for details.

and has a long history of use as a causal inference tool. More recently, StEM has been conceived as an umbrella concept which encapsulates numerous methods such as ANOVA or regression, which can also be conducted in an StEM environment. One key difference between conducting these methods in the traditional way (e.g. multiple regression) compared to an StEM, is that StEM allows predictor variables to intercorrelate. Perhaps the most important capability of StEM is its ability to partition direct and indirect effects that one variable may have on another, and estimate the strength of these multiple effects. For example, an environmental variable is likely to modify ecosystem function directly, but may also exert an indirect effect by impacting biodiversity, which may in turn affect function. StEM, unlike regression or ANOVA, offers the ability to separate these multiple pathways of influence (Grace, 2006). Recently, Grace et al. (2007) applied an StEM meta-analysis approach to 12 datasets from various grassland communities, and found that a large degree of the correlation between production and diversity is explained by shared causal influences such as abiotic factors and disturbance regimes, and in the minority of cases where there were direct effects, production influenced diversity and not vice versa. Analogously, Antoninka et al. (2009) also applied an StEM approach to isolate the effects of microbial community composition on various ecosystem functions in prairie mesocosms from those of global change factors and plant community composition and biomass. Independently of the covariates, soil microbial community structure was shown to have the strongest effect upon organic carbon. These studies illustrate the need for and utility of complementary approaches to studying biodiversity–function relationships in BSCs: experiments may help identify and isolate a mechanistic force underlying a pattern, but field data from natural ecosystems with multiple covarying mechanisms allow us to gauge whether the mechanism is important in nature. It is not unreasonable that contrasting approaches would both yield correct but different results.

3. Reanalysis of existing data

3.1. Methods

Here we demonstrate a StEM and path analysis-based approach to analyzing biodiversity–function relationships on field data. We

reanalyze four datasets from the United States and Spain (Table 2) which contain data on taxonomic richness and evenness and overall abundance of BSC organisms, plot-level abiotic environmental variables, and indicators of ecosystems function. Original data collection methods for the various datasets is available in the original papers (Bowker et al., 2006a,b; Bowker and Belnap, 2007; Maestre et al., 2008), and is summarized in Appendix 1. The detailed structural equation modeling protocol and background on the method are also provided in Appendix 1.

In all cases we employ the same *a priori* model, which is the starting point of a structural equation modeling investigation (Fig. 3). The model summarizes the investigator's hypothesis set about the system being studied and takes into account past knowledge and prevailing theory. It may also distinguish between measurements and concepts. Our model has four conceptual variables (environment, abundance, diversity, and ecosystem function) which may be represented by various measured variables depending on availability for a given dataset. Arrows between variables represent hypothesized causal influences, which may be linked to one or more theoretical mechanisms. Most importantly, the possibility of a direct effect of biodiversity upon ecosystem function due to complementarity. Since these are natural communities rather than randomly assembled ones, complementarity rather than the sampling effect is assumed to underly any positive monotonic relationship between diversity and function. The lack of a positive monotonic relationship may be interpreted as supportive of the idiosyncratic hypothesis. The rivet and redundancy hypotheses are both positive monotonic relationships which can be distinguished by examining the shape of a scatterplot; a linear shape is consistent with the rivet hypothesis, and a rapidly saturating curve is consistent with the redundancy hypothesis. Our model also states that environment may influence diversity by controlling niche partitioning, and influence abundance and ecosystem functioning by controlling total energy and resource availability. In our model, there is a covariance specified between diversity and production, symbolized by a double-headed arrow. This indicates that while we acknowledge multiple mechanisms that contribute to correlation between these two concepts (complementarity may account for a positive effect of diversity upon abundance, whereas competition may account for a negative effect of abundance upon diversity), we do not attempt to discern the directionality of relationships. Rather our focus is the relative import of BSC diversity and total BSC abundance in determining several ecosystem function variables related to hydrology, nutrient cycling, and the trapping and retention of soil resources.

When constructing StEMs based upon the datasets, we used the single most influential edaphic or climatic variable as our environmental indicator. The biodiversity metrics used are based upon

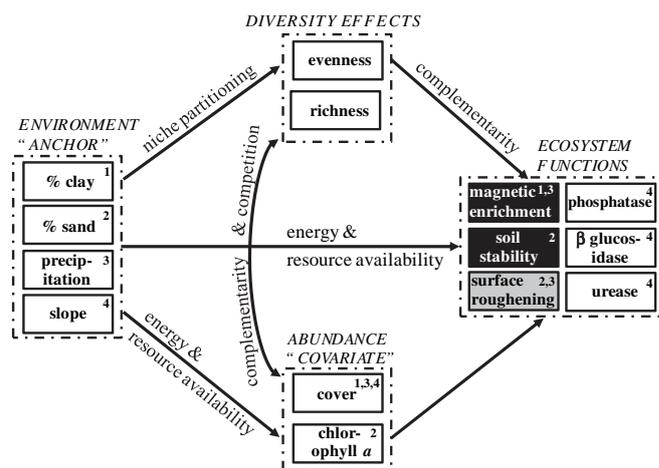


Fig. 3. *A priori* conceptual model of the effects of biodiversity and covarying factors upon ecosystem functions. Dashed boxes represent concepts which may be represented by one or more measured variables, depending upon the dataset being considered. Single-headed arrows represent a hypothesized causal relationship between two variables. Double-headed arrows indicate that two variables correlate, although a direction of influence is not specified. Hypothesized mechanisms appear directly adjacent to the arrows. Fill of ecosystem function boxes indicate the type of function: black = sediment trapping and retention, gray = sediment and water trapping, white = nutrient cycling. Numbers indicate which datasets in which a measured variable is used: 1 = Canyonlands, 2 = Northern Arizona, 3 = Grand Staircase-Escalante, 4 = Belmonte del Tajo.

mosses, lichens and thalloid cyanobacteria in the North American datasets, and on lichens in the Spanish datasets. Pielou's J statistic is used in all cases as a measure of evenness, and a richness variable is employed based upon either number of functional groups (Eldridge and Rosentreter, 2000; Bowker et al., 2008b) or number of species, depending on performance in the models. The indicator of BSC abundance was total cover of visible components or chlorophyll *a*, a pigment-based biomass index, depending on which is available and which is most closely related to other variables in the model. Ecosystem function indicators vary by dataset, but include the following: soil stability which is related to erosion resistance, surface roughening, which is related to infiltration and dust trapping, magnetic susceptibility or enrichment which are related to dust trapping (more detail is available in Appendix 1), and the activities of soil enzymes related to the phosphorus (phosphatase), carbon (β -glucosidase) and nitrogen (urease) cycling. We examined the bivariate relationships between the diversity and abundance variables to determine if they exhibited "conspicuous non-linearity" as commonly observed in studies of plants (Grace et al., 2007). We found that a linear model was adequate in every case,

Table 2
Properties of reanalyzed datasets and effects of BSC community properties on ecosystem functions. Spatial resolution denotes the size of each sampling unit. Effect statistics are path coefficients from StEM and path analyses. Original citations as follows: 1: Bowker et al. (2006a), 2: Bowker and Belnap (2008), 3: Bowker et al. (2006b), 4: Maestre et al. (2008).

Location	Spatial resolution	Function indicator	Effects of BSC community properties on function		
			Evenness	Richness	Abundance
Canyonlands, USA ¹	400 cm ²	Magnetic susceptibility	-0.59	0.49	-0.15
Northern Arizona, USA ²	~1.5 ha	Surface roughening	0	0.60	0.13
		Soil stability	-0.34	0.24	0.18
Grand Staircase-Escalante, USA ³	~1.5 ha	Magnetic enrichment	-0.15	-0.44	0
		Surface roughening	-0.21	0.31	0.54
Belmonte del Tajo, Spain ⁴	2500 cm ²	Phosphatase	0	0.11	0.23
		β -glucosamine	-0.17	0	0.41
		Urease	0.17	0.52	0.25

thus we modeled the covariance between cover or chlorophyll *a* and richness linearly. All unidirectional relationships are modeled linearly also.

3.2. Results

Due to the strong dependence of probability values upon sample size, and the strong difference in sample size among different datasets ($n = 16–96$), we primarily use path coefficients and partial correlation coefficients for comparisons among different datasets. Probability values are provided for reference in Figs. 4 and 5

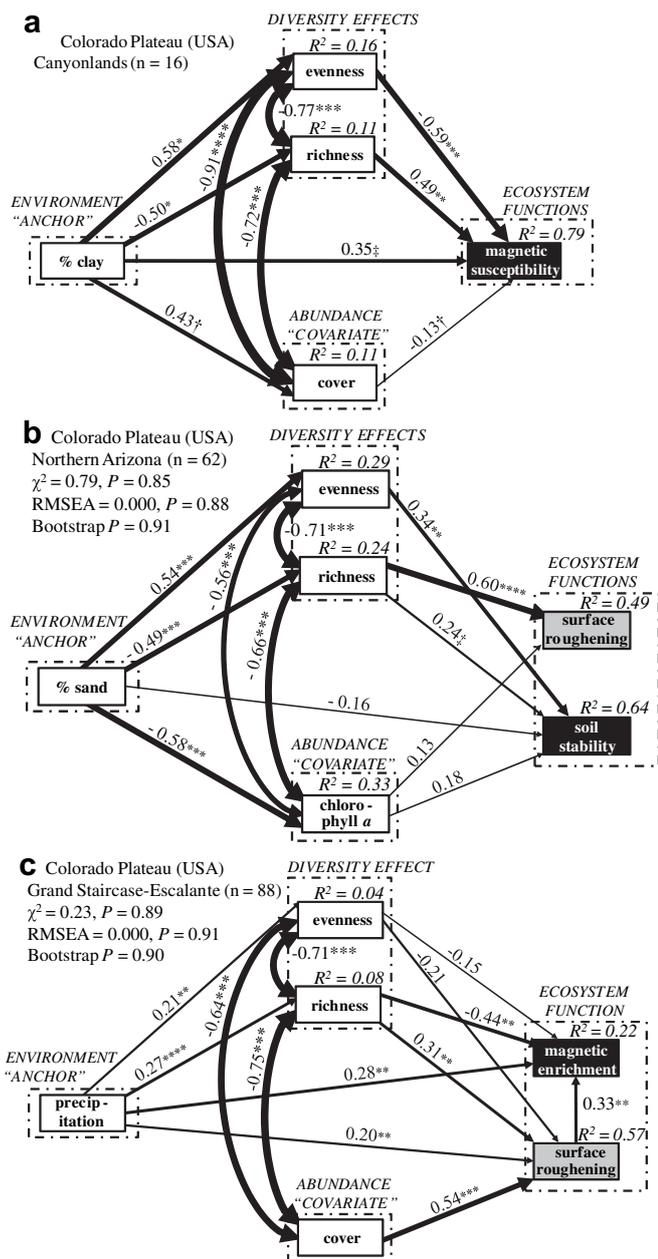


Fig. 4. Biodiversity effects upon ecosystem functions in the Colorado Plateau desert of the USA. Solid boxes represent measured variables, and dashed boxes represent the conceptual variables to which they correspond. Unidirectional arrows indicate a hypothetical causal relationship. Bidirectional arrows represent an undefined covariance. Arrow width is scaled to be proportional to path coefficients which appear adjacent to arrows. Corresponding probability values are indicated when <0.20 ($\ddagger P < 0.20$, $\ddagger P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $****P < 0.0001$). Statistics in upper left hand corners of panels b and c, indicate satisfactory overall goodness-of-fit.

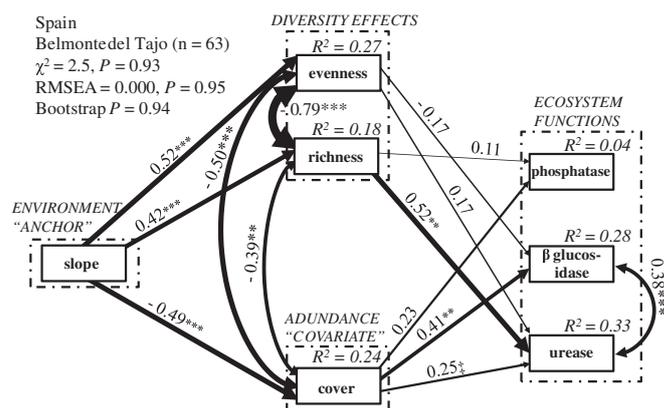


Fig. 5. Biodiversity effects upon ecosystem functions in the Belmonte del Tajo site in Central Spain. Solid boxes represent measured variables, and dashed boxes represent the conceptual variables to which they correspond. Unidirectional arrows indicate a hypothetical causal relationship. Bidirectional arrows represent an undefined covariance. Arrow width is scaled to be proportional to path coefficients which appear adjacent to arrows. Corresponding probability values are indicated when <0.20 ($\ddagger P < 0.20$, $\ddagger P < 0.10$, $*P < 0.05$, $**P < 0.01$, $***P < 0.001$, $****P < 0.0001$). Statistics in upper left hand corner indicate satisfactory overall goodness-of-fit.

when > 0.20 . Some STEM models required saturation to achieve model fit; in these cases no fit statistics are given.

3.2.1. Colorado Plateau (USA) results

In the Canyonlands dataset (Fig. 4a), we were able to explain 79% of the variance in centered magnetic susceptibility data. The strongest direct effect was a negative effect due to evenness ($r = -0.59$), however richness also exerted a relatively strong and positive effect ($r = 0.49$).

In the Northern Arizona dataset (Fig. 4b), we were able to explain 64% and 49% of the variation in soil aggregate stability and surface roughening, respectively. We found that much of this variance was ultimately attributable to the abiotic “anchor” variable, sand content, but the effects were largely indirect via BSC biodiversity and abundance. In the case of soil stabilization, the positive effect of evenness was the greatest direct effect upon stability ($r = 0.34$). In the case of surface roughening the greatest direct effect was that of species richness ($r = 0.60$).

In the Grand Staircase-Escalante dataset (Fig. 4c), we explained 57% and 22% of the variance in surface roughening and magnetic enrichment, respectively. The greatest direct effect upon surface roughening was due to cover ($r = 0.54$), however there was also a moderate effect of richness apparently independent of that of cover ($r = 0.31$). The greatest direct effect upon magnetic enrichment was the negative of richness ($r = -0.44$).

3.2.2. Belmonte del Tajo (Spain) results

In Belmonte del Tajo (Fig. 5), we found that there is much remaining unexplained variance for phosphatase ($R^2 = 0.04$), but we explained at least a quarter of the variance for β -glucosidase ($R^2 = 0.28$) and urease ($R^2 = 0.33$). The positive effect of richness upon urease ($r = 0.52$) was the strongest effect on any of the enzymes observed in the model. There were only minor effects of evenness in the model.

4. Conclusions

4.1. Initial generalizations and knowledge gaps

The overarching generalization we can draw from our work is that, even when total BSC abundance and the most influential

environmental variables are statistically controlled, there are effects of biodiversity upon ecosystem function more often than not providing evidence contrary to the idiosyncratic hypothesis. This generalization contrasts markedly with the results of Grace et al. (2007), who found that controls of plant biodiversity upon ecosystem function were generally negligible. Our goal here was not to definitively test biodiversity–function models in the BSC study system, but to provide an initial set of generalizations and contingencies which can be tested and revised in future research.

4.1.1. Richness–function relationships in BSCs support the rivet hypothesis

Although effects of BSC richness upon various functions were variable in strength, we saw no evidence that the shape of this relationship is a saturating curve; rather we saw approximately linear relationships (Fig. 6). This finding suggests that this relationship is predominantly consistent with the rivet hypothesis rather than the redundancy hypothesis (Naeem et al., 2002). Because these are natural communities rather than randomly-assembled artificial systems, they exhibit “realistic” variation in richness and evenness (Zavaleta and Hulvey, 2007). The sampling effect, whereby more diverse assemblages of species are more likely to contain a more highly functional species, is inflated in randomly-assembled experimental systems, but is unlikely to be strong in our data. This is because more diverse samples tend to include more rare species, whose presence cannot explain high functionality simply because they are present only in a few cases. Thus we propose that the patterns we observed are due to complementarity in mechanistic contributions to a particular function.

We might further hypothesize that the importance of complementarity in determining ecosystem functioning, and thus the linearity of the biodiversity–function relationship, will largely depend on the ecosystem function being studied. For example, on *a priori* grounds, we might expect a large role for complementarity when studying the BSC biodiversity effect upon soil stabilization because a large number of the species pool is involved to some degree and there are multiple mechanisms such as chemical bonding, physical enmeshment, and surface armoring. In contrast, N-fixation is conducted by relatively few species all using basically the same mechanism, thus complementarity might be less important and N-fixation maximized at low levels of richness.

4.1.2. Richness of BSC species, not functional groups, was most important to ecosystem function

In every case, functional group richness had a weaker relationship with function variables than species richness. Tilman et al. (1997a,b) suggested that if a habitat is colonized randomly, the strength of dependency of ecosystem function upon biodiversity would be expected to be greater if there is greater niche separation. Assignment of species to various functional group schemes is an attempt to ensure that there is niche separation between the accumulating entities. It is expected that the relationship of richness to a given function will saturate or asymptote more slowly, if functional group richness is considered rather than species richness. In our case, as stated above, the species richness–function relationship is not asymptotic in our data, it is already linear. Functional group richness is simply acting like a low-resolution surrogate for species richness. This suggests one of at least two things: that the trait diversity concept ought to be better defined and tested to replace functional grouping schemes, or that there is low functional redundancy among BSC-forming organisms. If the first is correct, better identification of functional traits is needed, and more measurements of such traits in various taxa are needed (as described in a previous section above) to use in place of

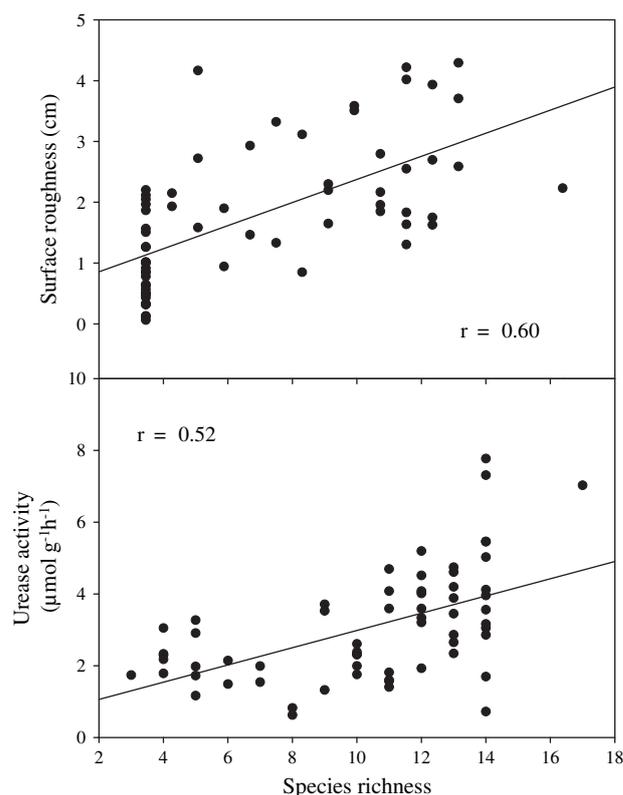


Fig. 6. In the two cases where diversity–function relationships are strongest (Top panel: Northern Arizona, Bottom panel: Belmonte del Tajo), bivariate relationships between ecosystem function indicators and species richness are approximately linear rather than saturating. This finding supports the complementarity hypothesis. r = path coefficients from corresponding StEM.

functional richness. The second would be true in the case of the intriguing possibility that chemical complexity is so great among BSC lichens and bryophytes, that each species with its unique array of secondary metabolites is effectively its own functional group.

4.1.3. Apparent BSC diversity effects upon function do not vary by scale

We examined two large scale studies and two small scale studies and did not find an obvious dependency of biodiversity effect size on ecosystem function measurements. Recent empirical and theoretical work has suggested that the relationship between biodiversity and productivity may be hump-shaped at local scales, but linear at regional scales (Chase and Leibold, 2002). Our small scales considered here are 5–6 orders of magnitude smaller than the large scale, but we observe approximately linear biodiversity–function relationships at either scale (Fig. 5). This finding implies that either functions other than productivity do not obey this dynamic, or that a “local scale” for BSC lichens and bryophytes is smaller than our finest resolution dataset. To definitively answer this question, more data spanning additional spatial scales are needed.

4.1.4. Apparent BSC diversity effects do not vary based upon region

Though our analysis cannot be considered comprehensive, we observed biodiversity effects in two continents, and three different locations within one North American desert. We found that it cannot be clearly concluded that one region or another tends to have stronger BSC biodiversity–function relationships. Rather we would propose that different regions differ primarily not in the

magnitude of biodiversity–function relationships, but rather in which functions are influenced by BSC biodiversity.

4.1.5. Species evenness may affect function

A few studies have shown important effects of evenness upon ecosystem functions (Wilsey and Potvin, 2000; Mulder et al., 2004; Maestre and Reynolds, 2006). We found that evenness can exert small to moderate effects on functional properties, and may account for some of the purported effects of richness. Perhaps most intriguing was the fact that evenness can be positively or negatively related to function, in fact negative relationships were common though most are weak. Evenness is the opposite of dominance, when a dominant is highly functional with regards to the particular function being considered we would expect to see a negative relationship with the function in question. Because the strongest effect of evenness was in a study focused upon moss and lichen BSCs (study 1), dominated by the moss *Syntrichia caninervis*, we might postulate that this widely spaced acrocarpous moss and others like it may be particularly effective at dust trapping. The opposite condition also holds, and in study 2, BSCs tended to be cyanobacterially-dominated, and greater evenness usually indicated greater moss and lichen cover. In this study, evenness was a positive predictor of dust trapping. Thus it is not unexpected that the evenness–function relationship would be variable and ungeneralizable. This is probably a case where the “mosaic” experimental method (Fig. 2), would be a useful tool to elucidate mechanisms underlying evenness–function relationships in the BSC study system. Generalization may be easier in field data when indices of multi-functionality (see below) are available.

4.1.6. Differential relationships among ecosystem functions highlight the need for an index of multi-functionality

Although we did find that approximately linear, non-saturating BSC biodiversity–function relationships occur, the effect size and even the sign of the relationship varied depending on the indicator of function being examined. Some authors have recently argued that considering only one ecosystem function at a time can be misleading, and that ecosystems exhibit multi-functionality (Hector and Bagchi, 2007). Modeling efforts have demonstrated that maintaining multiple functions at arbitrary minimum values requires a greater number of species than maintaining a single function (Gamfeldt et al., 2008). The development of a non-additive multi-functionality index, i.e. one in which high functionality of one type cannot compensate for low functionality of another type, may be very important in the study of biodiversity of multi-functional communities such as BSCs. Bowker et al. (2008a,b) applied an additive multi-functionality index in a GIS environment, but to date there have been no attempts to summarize the aggregate multi-functionality of BSC communities in a single, non-additive index.

4.2. The unique value of biological crusts to diversity-function research in soils

A complementary approach using experimental and observational approaches to examine diversity–function relationships in soil is possible using the multi-functional, multi-trophic, and manipulable system of biological soil crusts. We have shown evidence in field data, that biodiversity is linearly related to certain functions, which is consistent with a rivet hypothesis interpretation. This contrasts with temperate grasslands, the most frequent study system for biodiversity–function questions, where it seems diversity is a weak influence on productivity under field conditions (Grace et al., 2007). It also differs from studies that demonstrate that decomposition obeys a redundancy hypothesis-type dynamic, and thus suggest that soil ecosystems in general are highly

redundant. Using our biological crust study system, we have also expanded beyond the traditional focus of diversity–function research which has usually dwelt on productivity, and to a lesser extent decomposition and resistance to invasion. We have examined capture and retention of water and soil, and cycling of organic nutrients. Perhaps most importantly, we are able to do so with diversity data collected in the field using trained human eyes observing known and described species. In soil ecosystems this is extremely rare. While there is much to learn, we believe these attributes demonstrate that the BSC system has unique value in elucidating the role of biodiversity in soil functions.

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Appendix. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.soilbio.2009.10.025.

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