Contributed Paper

Prioritizing Conservation Effort through the Use of Biological Soil Crusts as Ecosystem Function Indicators in an Arid Region

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Abstract: *Conservation prioritization usually focuses on conservation of rare species or biodiversity, rather than ecological processes. This is partially due to a lack of informative indicators of ecosystem function. Biological soil crusts (BSCs) trap and retain soil and water resources in arid ecosystems and function as major carbon and nitrogen fixers; thus, they may be informative indicators of ecosystem function. We created spatial models of multiple indicators of the diversity and function of BSCs (species richness, evenness, functional diversity, functional redundancy, number of rare species, number of habitat specialists, nitrogen and carbon fixation indices, soil stabilization, and surface roughening) for the 800,000-ha Grand Staircase-Escalante National Monument (Utah, U.S.A.). We then combined the indicators into a single BSC function map and a single BSC biodiversity map (2 alternative types of conservation value) with an unweighted averaging procedure and a weighted procedure derived from validations performance. We also modeled potential degradation with data from a rangeland assessment survey. To determine which areas on the landscape were the highest conservation priorities, we overlaid the function- and diversity-based conservation-value layers on the potential degradation layer. Different methods for ascribing conservation-value and conservation-priority layers all yielded strikingly similar results (r = 0.89–0.99), which suggests that in this case biodiversity and function can be conserved simultaneously. We believe BSCs can be used as indicators of ecosystem function in concert with other indicators (such as plant-community properties) and that such information can be used to prioritize conservation effort in drylands.*

Keywords: conservation planning, conservation prioritization, cryptogams, cyanobacteria, deserts, ecological indicators, ecosystem engineers, ecosystem function, ecosystem services, semiarid lands

Priorización del Esfuerzo de Conservación Mediante el Uso de Capas de Suelo Biológico como Indicadores del Funcionamiento del Ecosistema en una Región Árida

Resumen: *La priorización de la conservación usualmente se concentra en la conservación de especies raras o biodiversidad, en lugar de los procesos ecológicos. Esto se debe parcialmente a una carencia de indicadores informativos del funcionamiento del ecosistema. Las capas de suelo biológico (CSB) atrapan y retienen suelo y agua en los ecosistemas áridos y funcionan como fijadores de carbono y nitrógeno; por lo tanto, pueden ser indicadores informativos de la diversidad y funcionamiento de las CSB (riqueza de especies, uniformidad, diversidad funcional, redundancia funcional, número de especies raras, número de especialistas de hábitat, índices de fijación de nitrógeno y carbono, estabilización del suelo y aspereza superficial) de las 800,000*

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ha del Monumento Nacional Grand Staircase-Escalante (Utah, E. U. A.). Posteriormente combinamos los indicadores en un mapa funcional de CBS y un mapa de biodiversidad (con dos tipos alternativos de valor de conservación) con un procedimiento de media no ponderada y un procedimiento ponderado derivado del desempeño de las validaciones. También modelamos la degradación potencial con datos de la evaluación del terreno. Para determinar las áreas del paisaje que tenían la mayor prioridad de conservación, sobrepusimos las capas de conservación basadas en el funcionamiento y la biodiversidad con la capa de la degradación potencial. Todos los diferentes métodos para asignar capas de valor de conservación y de prioridad de conservación produjeron resultados sorprendentemente similares (r = 0.89–0.99), lo cual sugiere que, en este caso, la biodiversidad y el funcionamiento pueden ser conservados simultáneamente. Creemos que las CBS pueden ser utilizadas como indicadores del funcionamiento del ecosistema conjuntamente con otros indicadores (como las propiedades de las comunidades de plantas) y que tal información puede ser utilizada para priorizar los esfuerzos de conservación en tierras áridas.

Palabras Clave: cianobacterias, criptógamas, función del ecosistema, indicadores ecológicos, ingenieros del ecosistema, planificación de la conservación, priorización de la conservación, servicios del ecosistema, tierras semiáridas

Introduction

High rates of biodiversity loss and increasing human demands on natural systems challenge us to develop a conservation prioritization approach that addresses ecosystem functional properties as a complement to traditional species-centered approaches. Ecosystem functions may result directly or indirectly in ecosystem goods and services that benefit humans (Daily 1997). The goals of function-based approaches to conservation planning should include ensuring valuable ecosystem services to human societies and supporting the growth and reproduction of their component species of the ecosystem simultaneously. Nevertheless, ecosystem function has not been a primary focus of conservation because there is little understanding of how ecosystems work and no consensus on what ecosystem management means (Clark 1999; Goldstein 1999). Despite the inherent logic of function-based approaches, researchers tend to default to species-based approaches under the assumption that they provide appropriate indicators of ecosystem state. This is likely to remain the case until methodological approaches make it practical to observe and manage ecosystem functions at appropriate scales.

In many dryland areas, which comprise over one-third of Earth's terrestrial surface, communities of biological soil crusts (BSCs) are strong indicators of multiple ecosystem functions (Fig. 1), including N fixation (e.g., Evans & Ehleringer 1993), C fixation (e.g., Beymer & Klopatek 1991), soil building and retention (e.g., Reynolds et al. 2001), and modification of hydrological processes (Alexander & Calvo 1990). These crusts are soil-surface communities composed of cyanobacteria, lichens, and bryophytes and associated food webs. The spectral signature of BSC has been used as an index of C flux (Burgheimer et al. 2006), and BSC richness and evenness have been used as indicators of ecosystem-level resistance to erosion, infiltration, and nutrient cycling (Maestre et al. 2005).

Biological soil crusts have several additional attributes that make them good candidates as ecological indicators (Dale & Beyeler 2001). Some BSC parameters (e.g., cover by functional group, chlorophyll content) are easily measurable (Eldridge & Rosentreter 1999), and BSCs are often more vulnerable to degradation (Belnap 1995) than associated vascular plant or animal communities. In desert regions, they respond predictably to surface degradation (occasionally only minor impacts are observed [Muscha & Hild 2006], but the overwhelming majority of studies indicate strong negative impacts), usually require decades for full recovery, and can signify impending changes in ecosystem state (Belnap 1995). Thus, BSCs indicate function that is relatively easily lost. Information regarding the potential contribution of undisturbed BSC communities to various ecosystem functions is potentially useful in identifying areas in need of conservation efforts.

Our goal was to identify areas in a complex, approximately 800,000-ha landscape that were simultaneously high in conservation value of BSCs and highly at risk of degradation. We termed these areas "conservation priorities" (Sisk et al. 1994; Reid 1998). *Conservation value* of BSCs was defined in 3 ways: sites with relatively high BSC biodiversity, high functional significance of BSCs, or a combination of both. We based our GIS-assisted analyses on spatial models of 4 descriptors of ecosystem function that are largely attributable to BSCs (surface roughening, soil-surface stability, and soil-surface C and N fixation), 6 descriptors of biodiversity and compositional uniqueness of BSCs, and 1 descriptor of potential degradation. We propose that this is a practical way to more directly incorporate ecosystem function into conservation decision making and to efficiently distribute scarce conservation resources. If effective in our study area, the use of BSCs as indicators of ecosystem functions may prove transferable

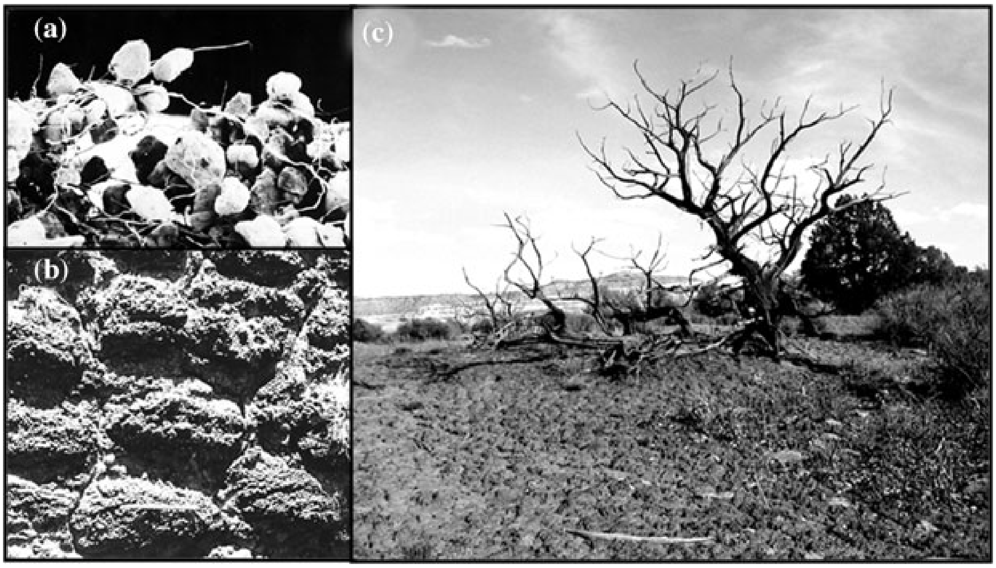

Figure 1. Biological soil crust (BSC) functions: (a) soil stabilization (scanning electron micrograph of soil cyanobacteria aggregating coarse sand), (b) surface roughness (BSCs preserve frost-heaved soil structure increasing surface roughness [view from above]), and (c) C and N fixation (BSCs are composed primarily of C fixers and may occupy greater area than vascular plants. Darker pigmented patches within the BSC (bottom right of [c]) are rich in N-fixing species. Photos courtesy of the U.S. Geological Survey.

to many arid and semiarid regions and provide a critically missing information source to complement the use of other functional indicators.

Methods

Field Sampling

Grand Staircase-Escalante National Monument, Utah (U.S.A.) (GSENM) is almost 800,000 ha, spans numerous abiotic gradients, and supports at least 19 major plant community types (Stohlgren et al. 2005; Supplementary Material). In this complex study area, BSCs are present in most habitats. Most of the response variables we used in our models were derived from 2 extensive data sets, one describing the potential (i.e., not degraded) condition of BSCs and one describing the existing levels of ecosystem degradation. The former data set consisted of 114 relatively undisturbed sampling sites in GSENM (Bowker et al. 2006) of approximately 1–2 ha, and the latter (hereafter referred to as "BLM unpublished" [BLM, Bureau of Land Management]) consisted of 468 sample sites (each approximately 0.5–1 ha) spanning the entire monument and was collected by the U.S. Bureau of Land Management (Table 1). Data from additional sources were used to partially derive some of the response variables and to serve as predictor variables (detailed later, Table 1). In the Bowker et al. (2006) data set, we used a step-point intercept method, totaling 300 points per site, along transects to calculate cover of BSCs by species. We estimated surface roughening in a parallel survey of approximately 60 points per site within the same transects. We sampled the least degraded (primarily due to livestock and off-road vehicles) sites we could locate, assuming these parameter values were at or near site potential and would therefore provide an estimate of a site's potential BSC development.

The BLM data set was compiled with the techniques proposed by Pellant et al. (2000) in a multiindicator range assessment of the GSENM in 2001–2004. In this study sample sites were stratified by pasture (management subunits of grazing allotments) and by the "ecological site" designation (an ecologically based land classification system USDA-NRCS 2005). This data set includes data from sites across GSENM that have experienced various degrees of degradation.

Estimation of Diversity and Functional Redundancy

To estimate taxonomic richness, we used the number of species observed per site in Bowker et al. (2006). To measure evenness, we computed Pielou's J (Magurran 1988) for each site. To estimate functional redundancy and number of functional groups present per site, we converted our species-level data with a scheme of BSC functional groupings determined from species' morphology and function (Eldridge & Rosentreter 1999): light cyanobacterial crusts, dark cyanobacterial crusts, N-fixing gelatinous lichens, nonN-fixing crustose lichens, N-fixing squamulose lichens, nonN-fixing squamulose lichens, N-fixing foliose lichens, nonN-fixing foliose lichens, fruticose lichens, macroscopic thalloid

Table 1. Data sources used as inputs for models of biological soil crust (BSC) function and biodiversity indicators and potential degradation.

Data source[a]	*Variables in data set*	*Variables derived from data set*
Bowker et al. 2006[b]	cover of BSC organisms by species surface roughness chlorophyll *a* content	descriptors of biodiversity and biological uniqueness descriptors of BSC function
BLM, unpublished[c]	rangeland health scores for site and soil stability, hydrologic function, biotic integrity	lowest of 3 summary scores
Belnap 2002	annual N fixation rates for various BSC types	annual N fixation
Lange 2003	C fixation rates for various BSC types	C fixation
K. Coe and J. Sparks, unpublished data	C fixation rates for mosses	C fixation
Bowker et al., unpublished data[d]	conversion from chlorophyll *a* to stability rating	soil stability
BLM-GSENM spatial database	maps of roads, range improvements, seedings, allotments, and pastures	distance from roads and range improvements
U.S. Geological Survey digital elevation model	elevation	topographic variability
PRISM climate model	average annual precipitation	
USDA-NRCS 2005	soil-map unit identification and description of rangeland productivity	

[a]*Abbreviations: BLM, Bureau of Land Management; GSENM, Grand Staircase-Escalante National Monument.*
[b]$n = 114$.
[c]$n = 468$.
[d]$n = 446$.

cyanobacteria, pleurocarpous mosses, tall acrocarpous mosses, and short acrocarpous mosses. In this grouping system, morphology (e.g., gelatinous, crustose, acrocarpous) allowed us to infer differences in hydrological, dust-trapping, and to some extent C fixation functions (Eldridge & Rosentreter 1999), and known N-fixing capability allowed for further group delineation. In the case of the cyanobacterial crusts, species-level identifications are impossible in the field; thus, "light" and "dark" crusts reflect different community types with different functional attributes (Belnap 2002). Both types are dominated by *Microcoleus*, but "dark" crusts represent more N-fixing taxa, greater biomass, a later successional stage, and greater concentration of several sunscreen and photosynthetic pigments (Bowker et al. 2002). To create a descriptor of functional diversity, we counted the number of these functional groups per site. To estimate functional redundancy, we calculated the average number of species per functional group in a site (Naeem 1998), excluding the light and dark cyanobacterial community types. Thus, we assumed cyanobacterial redundancy is similar because the possible number of cyanobacterial species within functional groups is similar (Garcia-Pichel et al. 2001). This is a reasonable assumption, but we cannot rule out over- or underestimation of redundancy.

Estimation of Number of Rare and Habitat-Specific Taxa and BSC Functions

As measures of biological uniqueness, we enumerated rare species and habitat-specific species for each site from Bowker et al. (2006; Table 1). We considered rare species those that occurred in <5% of our sampling sites, with no clear habitat-type affinity. There were 22 rare species. Habitat-specific species were defined as those that occur in only one soil type and in most samples were from that soil type. Seven habitat-specific taxa were associated with gypsiferous soils, 2 with limestone-derived soils, and 2 with noncalcareous sandy soils (Bowker & Belnap 2008).

We estimated indicators of 4 BSC functions: annual N fixation, C fixation, soil stability, and surface roughening. The estimation procedures for N fixation, C fixation, and soil stability are summarized briefly here and described in detail in Supplementary Material. All 3 of these estimates followed the same generalized procedure. First, we estimated the contribution of particular classes of BSC organisms (e.g., annual N fixation rates for 3 types of N-fixing BSCs: lichens and dark and light cyanobacterial crusts) to a particular function with additional data sources (Table 1). Second, we calculated the BSC contribution to a particular function across an entire site by multiplying the values generated in the first step by the proportional abundance of the corresponding organisms and adding all the resultant values.

During data collection (see Bowker et al. 2006; Table 1), we estimated the roughening of the soil-surface as an index of enhanced soil and water resource retention. On approximately every 5th step of our step-point transects, the maximal variation in soil roughening (i.e., the vertical distance between the highest and lowest point to the nearest cm) within a 25-cm^2 quadrat was estimated visually. This resulted in approximately 60 surface roughness measurements per site, which were averaged to obtain an overall roughness estimate for the site.

Estimation of Potential Degradation

In our study area, surface degradation is primarily attributable to long-term livestock grazing. As an index of existing degradation, we used the BLM unpublished data set (468 points; Table 1). The rangeland-health protocol assigns 5-level ordinal ratings on the basis of their perceived departure from desired or reference conditions of three key attributes per site (site and soil stability, hydrologic function, and biotic integrity [Pellant et al. 2000]). We used the lowest of the 3 values (i.e., furthest from reference conditions) as an index of potential degradation in at least 1 of the 3 attributes. Use of the lowest of the 3 attributes protected against overreliance on a single attribute, which could potentially reflect bias in the experience level of survey crews in assessing particular attributes. We used a statistical model to create a potential degradation surface from these points on the basis of several predictors (techniques described later). Results were then extrapolated to a map. In the degradation surface, areas that displayed a high degree of potential degradation likely consisted of a mosaic of areas disturbed in the past, and areas at risk of future surface degradation were "imperiled" (Sisk et al. 1994) because they shared important risk factors (e.g., easily traversed topography, proximity to cattle tanks) with currently degraded sites. If a site also had high value as estimated by either biodiversity or function indicators, the former might be considered a restoration priority, whereas the latter might be considered a conservation priority.

Statistical Modeling Techniques

The overall goal of our statistical modeling efforts was to produce maps of all 4 indicators of BSC function, 6 indicators of BSC biodiversity, and 1 indicator of potential degradation for use in the construction of prioritization maps. For the indicators of BSC function and biodiversity, we used the following spatial data as predictors (Table 1): 100 × 100-m digital elevation models (US Geological Survey), annual precipitation (PRISM, Spatial Climate Analysis Service, Oregon State University, Corvallis), and soil type (derived from USDA-NRCS 2005; Bowker et al. 2006; Bowker & Belnap 2007). We modeled our data from the 114 sites in the Bowker et al. (2006) data with classification and regression trees in the software Answer Tree (SPSS, Chicago, Illinois). This technique makes no data distribution assumptions and allows the prediction of a continuous response on the basis of any mixture of continuous or discrete predictors. Other methods, such as linear regression and logistic regression, do not share this combination of attributes (De'ath & Fabricius 2000). This method dichotomously splits data for a dependent variable on the basis of the values of predictor variables (e.g., a hypothetical split might suggest that the dependent variable "annual N fixation" is considerably different when annual precipitation is >20 cm compared with dyer conditions). At each split the greatest possible amount of variance is explained, and subsequent splits may be made resulting in a "tree." The end points of a tree (nodes) represent mutually exclusive combinations of independent variables (e.g., a hypothetical node might be composed of data points where precipitation was <20 cm, elevation was <2000 m, and soils were gypsiferous). A mean estimate of the dependent variable (e.g., annual N fixation) is calculated for each node from the data points that fall within that node. The trees were automatically pruned (pruning refers to the removal of nodes to prevent overfitting) with the standard-error rule (De'ath & Fabricius 2000).

For all models of BSC function or biodiversity, we used the validation protocol developed and described in Bowker et al. (2006). Briefly, this method involved the following steps: (1) random withdrawal of 14 data points from the data set, (2) construction of a model with the remaining data, (3) using the model to predict values for the 14 withheld data points, (4) comparison of the model predictions with the actual data values through linear regression and determination of R^2, and (5) 5 repetitions of step 4, averaging the R^2 values as a measure of validation performance. Finally, we created maps of our various model outputs as GIS layers with ArcMap (ESRI, Redlands, California). A map of a given model delineated the study area on the basis of the nodes generated by the tree and displayed the appropriate value of the modeled variable (e.g., annual N fixation).

In our model of potential degradation, we used the following predictors (Table 1): distance from roads; distance from ranching infrastructure (e.g., cattle tanks, corrals); grazing allotment and pasture (allotments are a portion of available rangelands leased by a particular rancher, and pastures are subdivisions within allotments. GSENM spatial database); rangeland productivity (USDA-NRCS 2005); and standard deviation of topographic relief (derived from digital elevation models). Because this potential degradation indicator is ordinal rather than continuous, we compared successful classification rates rather than regression fits of expected versus observed values. We withheld 95 data points to validate models and constructed models with 373 data points. We determined the successful classification rate, and defined a successful classification as a case in which the model correctly predicted the potential degradation value of a withheld data point. We compared successful classification rates of our model with those of 2 different types of null models: random (equal probability of classification in each of the 5 categories) and majority rule (each site classified as the most commonly occurring value in the data set) (De'ath & Fabricius 2000).

Prioritization Layers

We used 3 strategies to prepare conservation-priority layers (Fig. 2). In the first, we used measures of BSC

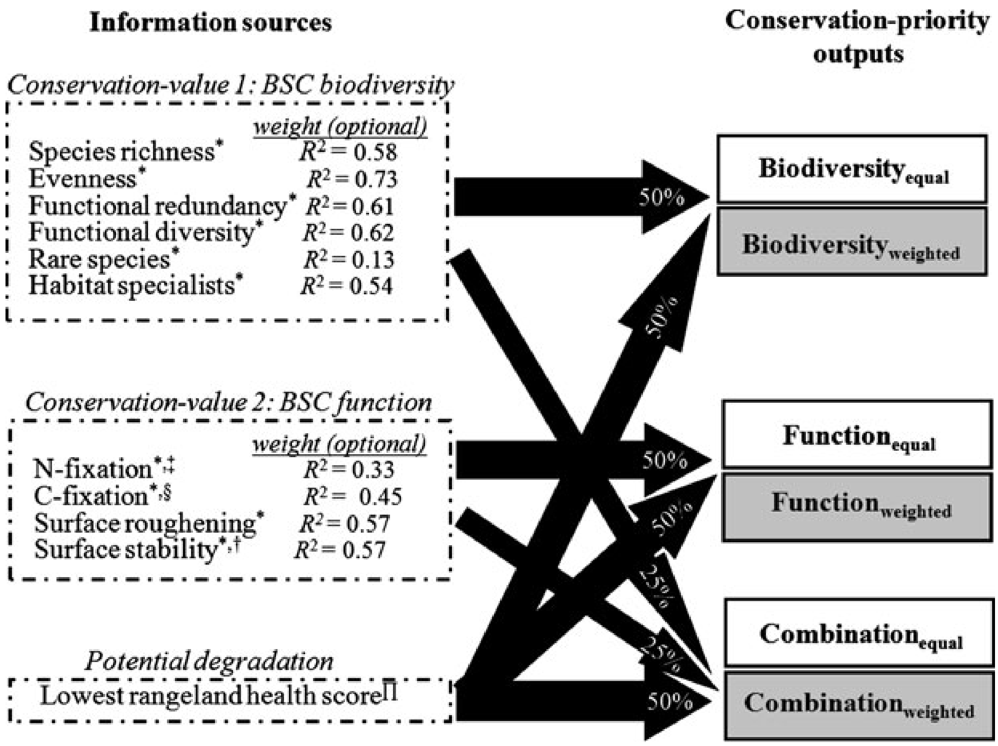

Figure 2. A flow diagram of the creation of 6 alternative conservation-priority layers derived from models of biological soil crust (BSC) biodiversity indicators, BSC function indicators, and potential degradation. Modeled indicators that correspond to potential degradation or 1 of 2 types of conservation value are in the dashed boxes: BSC biodiversity and BSC function. Data indicators are derived from (∗) percent cover, surface roughness, species counts, chlorophyll a *(data from ‡, Bowker et al. [2006]; §, Belnap [2002]; †, Lange [2003]) and calibration equations of chlorophyll* a *soil stability (Bowker et al., unpublished data) and (↑Π) Grand Staircase-Escalante National Monument (unpublished data). The* R^2 *describes validation performance and optional weighting of modeled indicators. Arrows and percentages indicate proportional influence of each information source on each output (equal, indicators are equally weighted; weighted, indicators are weighted by model performance [*R^2*]).*

biodiversity and biological uniqueness as indicators of conservation value, which is similar to more traditional methods (Myers et al. 2000; but see Karieva & Marvier 2003). In the second, we used estimates of specific BSC functions as indicators of conservation value. The final strategy incorporated information on both BSC diversity and function (henceforth referred to as combination).

Because biodiversity and function-related groupings of conservation-value information are composed of multiple indicators, we used 2 techniques to combine the indicators into a single information source (Fig. 2). The equal-weight technique consisted of rescaling all indicators to a common scale (from 0 to 1) and averaging them. Rescaling was accomplished by dividing all values in a data set by the largest value in the data set. This method allowed equal consideration of conceptually different aspects of conservation value, such as N and C fixation. The weighted-by-model-performance technique also involved rescaling all indicators to a common scale, but then we used a weighted average on the basis of that indicator's R^2 as a measure of our confidence in the data. This method may underrepresent unique conceptual information, but it reduces the influence of poorly performing models.

Every possible combination of strategy and weighting technique resulted in 6 alternate maps of conservation value: (1) biodiversity$_{equal}$, (2) function$_{equal}$, (3) combination$_{equal}$, (4) biodiversity$_{weighted}$, (5) function$_{weighted}$, and (6) combination$_{weighted}$ (*equal* refers to the equal-weight technique, *weighted* refers to the weighted-by-model-performance technique). In the case of the biodiversity-function combination strategy, we used the biodiversity strategy and the function strategy to develop conservation-value layers and then averaged the layers to incorporate information on both biodiversity and function. To create map outputs showing conservation priorities, we gave equal weight to information describing conservation value and potential degradation (similar to Sisk et al. 1994; Myers et al. 2000). Thus, each of the 6 conservation-value outputs was overlaid on our potential degradation layer, which was composed of a single indicator (Fig. 2). Areas that simultaneously had high potential degradation and conservation value were considered the highest conservation priorities.

To compare the stability of our prioritization outputs derived from these 3 different approaches to conservation value and 2 different weighting options, we calculated correlation coefficients for all pairings of our various conservation-value layers with the "stack stats" command of ArcGIS. This analysis was conducted prior to overlaying conservation-value data on potential degradation data, so use of common data did not create an upward bias in the correlation estimates.

Results

All models pertaining to elements of diversity performed well during evaluation when models were validated with withheld data. Expected and observed values corresponded most strongly in the model of evenness (Pielou's J; $R^2 = 0.73$). The other models explained over half of the variance in our validation data for functional diversity ($R^2 = 0.62$), redundancy ($R^2 = 0.61$), and richness ($R^2 = 0.58$). We had mixed success modeling indicators of compositional uniqueness. Our model of number of habitat-specific taxa present performed well ($R^2 = 0.54$); however, the number of rare species per site was poorly related to our predictors, which was not surprising given the difficulty of sampling rare species ($R^2 = 0.13$).

All models of BSC function performed at least moderately well. Our N fixation model accounted for one-third of the variance ($R^2 = 0.33$). Our models of whole-site stability and soil-surface roughening explained almost two-thirds of the variance (both $R^2 = 0.57$). Our model of C fixation rate explained almost half of the variance ($R^2 = 0.45$).

Our model of potential degradation classified 57% of our validation data points correctly into the 5 classes included in this broadly applied system. Where the model was incorrect, it classified validation points $\pm$ 1 class in 90% of cases and $\pm$ 2 classes in 100% of cases. This performance was clearly better than null models. The majority rule model resulted in 46% correct classifications, 84% were within 1 class of the observed value, 97% were within 2 classes, and 100 % were within 3 classes. The random model resulted in only 20% correctly classified sites on average.

Our determination of conservation priorities was quite stable and did not depend strongly on the type of conservation value used (function, biodiversity, or combination) or on the weighting of indicators (Fig. 3), although the type of conservation value used was relatively more influential than weighting. The correlation coefficients between biodiversity and corresponding function ranged from 0.89 to 0.93, whereas those between the 2 weighting options were all approximately 0.99.

Discussion

BSC Biodiversity as an Indicator of Ecosystem Functions and Services

Perhaps our most surprising result was that descriptors of biodiversity yielded similar maps of conservation value as descriptors of BSC function. This may suggest that in this system, BSC biodiversity promotes BSC function. This could be due partially to the fact that indicators of BSC function and diversity are not entirely independent of one another because they are derived from some of the same data. Nevertheless, it is unlikely that such high correlations (0.89–0.99) between functional and compositional outputs could be explained by this alone for 2 reasons. First, although partially derived from common data sources, function and biodiversity indicators were derived from different data: the function indicators were partially derived from abundance data, whereas biodiversity indicators were derived from species counts (except evenness, which relied on abundance data). Second, function indicators were all partially derived from additional data sources (Fig. 2). Literature on the relationship between biodiversity and ecosystem function has proliferated in the last decade, and at least 50 distinct models of this relationship have been advanced, with little consensus (Naeem et al. 2002, but see Hooper et al. 2005). The results of some studies indicate ecosystem functions saturate at relatively low species richness (Schwartz et al. 2000), whereas others suggest a more log-linear, positive relationship (Sphehn et al. 2000). The contention that the number of functional groups positively influences ecosystem functions is better supported (Tilman et al. 1997; Symstad 2000), but available data sets are strongly biased toward manipulative experiments of vascular-plant functional diversity in temperate grassland biomes (reviewed in Diaz & Cabido 2001).

Maestre et al. (2005) studied the causal influence of BSC richness, evenness, cover, and spatial patterning on several ecosystem functions performed by BSCs on gypsiferous soils of Spain. Their results contrast with ours in that they found a negative causal influence of BSC richness on soil C and N and respiration. They did, however, find that richness increased soil aggregate stability. Hu et al. (2002) found that aggregation (measured as threshold friction velocity) of artificial cyanobacterial BSCs was high in more species-rich BSCs, but was most strongly related to the presence of particular species. The conflicting results in Maestre et al. (2005) with our study may reflect differences in scale (30 cm^2 resolution in Maestre et al. [2005] compared with approximately 2 ha). The agreement of all 3 studies on the correlation between soil aggregation and BSC diversity suggests a scale-independent phenomenon.

It is possible that causal relationships are reversed, such that BSC functions promote diversity in BSC communities or that both BSC function and diversity are strongly

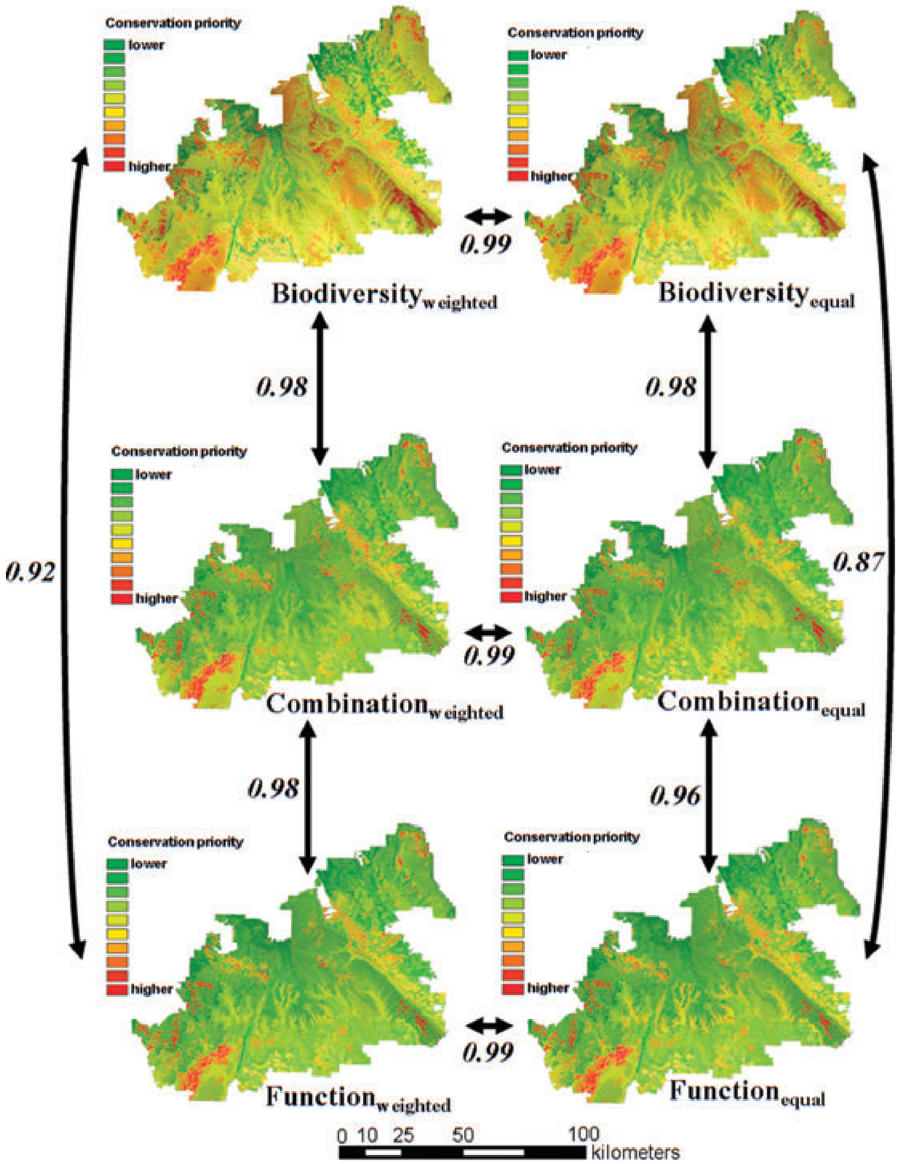

Figure 3. Maps showing conservation priority of Grand Staircase-Escalante National Monument on the basis of biological soil crust biodiversity and function indicators and their combination. Double-headed arrows denote a correlation, and the decimal value is a correlation coefficient (Pearson's r*). All maps converge on similar outputs, indicating that results are robust to alterations in conservation prioritization techniques (equal, indicators are equally weighted; weighted, indicators are weighted by model performance [*R^2*]).*

determined by a third variable, such as BSC abundance, which is in turn strongly determined by abiotic and biotic factors (Bowker et al. 2006). These different causal scenarios cannot be resolved in the current data set, but should be explored in greater detail in future work in this and other ecosystems. Regardless of the causal relationships, it appears that in this system, a composite layer of multiple descriptors of BSC biodiversity can suggest areas where BSCs are potentially important to ecosystem-level function.

A Flexible and Robust Approach to Conservation Planning

An ideal conservation-prioritization tool is flexible enough to accommodate different policy objectives, conservation goals, and management strategies, but stable enough so that results are reasonably consistent, despite the particular, often idiosyncratic conditions surrounding each application of the tool. For example, policy objectives may determine that biodiversity-based conservation value be favored over their function-based counterparts, or vice-versa, or that both be considered equally. Despite our use of 6 different permutations of our models for prioritizing areas according to BSCs, we obtained similar results in all cases, which suggests a robust and flexible approach to conservation planning.

Our approach is flexible in multiple ways: (1) users may alter which indicators are used and whether they indicate biodiversity, function, or both (2) weighting could derive from management goals instead of model performance, (3) additional indicators could be developed, such as hillslope-scale hydrology or dust-trapping functions of BSCs, and (4) functional organisms other than BSCs (e.g., vascular plants) could also be considered in the same analysis.

Our models gave equal weight to conservation value and potential degradation and combined these 2 concepts in an additive fashion. These assumptions could also be varied. Some workers suggest that the loss of ecosystem function in response to stress or disturbance is sigmoidal (Tongway & Hindley 1995); thus, if information pertaining to this response were available, an appropriate sigmoidal transformation of potential degradation might be favored.

Conservation priority is a difficult concept to validate because its determination depends on the suite of indicators used and management goals. When 2 very different techniques with different protocols tend to converge on similar answers they bolster one another. The BLM identified management priorities in areas that have been degraded because of drought and livestock grazing (USDI-BLM 2006). They based their selection of management priorities on field observations conducted by the Utah Division of Wildlife Resources for the conservation and restoration on habitat for mule deer (*Odocoileus hemionus*) and Sage Grouse (*Centrocercus* spp.) (USDI-BLM 2006). Identified sites exhibited low plant diversity, a high degree of dominance by sagebrush, sagebrush drought mortality, or soil erosion. Our conservation-priority maps rated the BLM priorities about 35% higher than the monument-wide average, which indicates the 2 methods converged on a similar conclusion.

Stohlgren et al. (2005) produced models of vascular plant endemism, uniqueness, and richness, and argued for a broader conception of hotspots that encompasses all these concepts. Our biodiversity-based conservation-value layers combined these concepts; however, BSC hotspots are poorly correlated with vascular plant hotspots (Stohlgren et al. 2005). It is common to find low spatial autocorrelation among hotspots for different groups of organisms (Reid 1998), and a comprehensive biodiversity-based conservation strategy would take into account hotspots for various groups or organisms rather than only vascular plants and BSCs.

We do not consider our results to be in conflict with Stohlgren et al. (2005) because our approach is fundamentally different. First, what Stohlgren et al. (2005) refer to as "conservation priority," we would define as conservation value: areas possessing high conservation value are high in biological diversity or uniqueness (at least in the focal group of organisms) or have a community composition that favors a high degree of ecosystem function. In contrast, we consider conservation priority has 2 components: conservation value, as defined earlier, and potential degradation. In other words, if a hypothetical site has high conservation value but essentially no probability of degradation, it cannot be a very high priority for conservation action.

The second distinction is that Stohlgren et al. (2005) focused only on endemism, uniqueness, and richness, rather than functions of the vascular plant community. Although we also examined indicators of endemism, uniqueness, and richness concepts for BSCs as one possible way of estimating conservation value, our main intent was to base an estimation of conservation value on the functional aspects of BSCs. We do not suggest BSCs are the only organisms with major functional implications. Rather, in our study region and many others like it, BSCs represent a portion of potential ecosystem functionality that is easily degraded compared with other highly functional organisms. Function-based approaches will likely differ in application in different regions, and in wetter areas BSCs may be less informative than other function indicators such as vascular plants.

Overall, our results suggest that use of BSCs for conservation prioritization is robust to differences in methods for characterizing conservation value across this large and heterogeneous study area. In the event that biodiversity-based and function-based indicators of conservation value are maximized in different areas, a hybrid conservation strategy that emphasizes both might be desired.

Potential of Biological Soil Crusts to Guide Function-Based Conservation Prioritization

Drylands account for about 40% of the terrestrial surface and are expanding due to desertification processes (Verón et al. 2006). Equally important, drylands are the home of about 1 billion people whose well-being depends on the resilience of often highly perturbed and fragile water-limited ecosystems (Arnalds 2000). For these reasons, there is a need to conserve ecosystem function in drylands. Conservation of function will tend also to conserve biodiversity and valuable ecosystem services including soil fertility and stability and water infiltration, which are particularly critical in arid and semiarid regions.

Other researchers have used indices of vegetation cover as indicators of the arid ecosystem's "leakiness," or ability to retain resources such as soil (Ludwig et al. 2006). These relatively simple indicators are informative and have the advantage of being quantifiable or measurable with remotely sensed data, unlike the BSC indicators we used here. Nevertheless, if retention of soil resources is a major component of ecosystem function in drylands and BSCs are a primary agent of soil-surface stabilization against erosive forces (Belnap & Gillette 1998), it may be appropriate to also focus attention on BSCs in many cases. In addition to retention of soil resources, BSCs account for a large "bundle" of discrete ecosystem functions in drylands and thus are ideal indicators of healthy ecosystem functioning (Tongway & Hindley 1995). The use of BSCs as indicators of dryland ecosystem function will become easier as remote-sensing tools are refined and diversified, perhaps closing the gap in the relative effort required for prioritization on the basis of vegetation and other biota. Currently, it is possible to remotely sense abundance and coarse composition of BSCs (Chen et al. 2005) and at least one function (C flux; Burgheimer et al. 2006). In the drylands of the world, conservation assessments on the basis of ecosystem function should seek to incorporate this information and use it in concert with functional information from other organisms.

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Supplementary Material

Information on soil, climate, and characteristics of plant communities (Appendix S1) and method details (Appendix S2) are available as part of the on-line article from http://www.blackwell-synergy.com/. The author is responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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