Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin, Washington

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Abstract. We studied lichen and bryophyte soil crust communities in a large public grazing allotment within a sagebrush steppe ecosystem in which the biotic soil crusts are largely intact. The allotment had been rested from grazing for 12 years, but experienced an extensive series of wildfires. In the 350, 4×0.5 m plots, stratified by topographic position, we found 60 species or species groups that can be distinguished in the field with a hand lens, averaging 11.5 species groups per plot. Lichen and bryophyte soil crust communities differed among topographic positions. Draws were the most disturbed, apparently from water erosion in a narrow channel and mass wasting from the steepened sides. Presumably because of this disturbance, draws had the lowest average species richness of all the topographic strata we examined. Biotic crust species richness and cover were inversely related to cover of the invasive annual, cheatgrass (*Bromus tectorum*), and positively related to cover of native bunchgrasses. Integrity of the biotic crust was more strongly related to cheatgrass than to fire. In general, we observed good recovery of crusts following fire, but only in those areas dominated by perennial bunchgrasses. We interpret the resilience of the biotic crust, in this case, to the low abundance of cheatgrass, low amounts of soil disturbance and high moss cover. These fires have not resulted in an explosion of the cheatgrass population, perhaps because of the historically low levels of livestock grazing.

Keywords. Biotic soil crusts, soil lichens, soil bryophytes, microbiotic crusts, Columbia Basin, Washington, community composition, cheatgrass, fire.

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Biotic soil crusts are a diverse layer of organisms living at the soil surface in arid and semi-arid ecosystems worldwide. They may include lichens, bryophytes, algae, cyanobacteria, fungi and soil microfauna. Biotic crusts contribute to nutrient cycling, soil stability and hydrologic functions. Terricolous lichens and bryophytes reduce soil erosion by providing soil surface cover, trapping and binding soil particles, and creating rough surface microtopographies (Danin & Ganor 1991; Danin et al. 1998; Eldridge & Kinnell 1997; Mücher et al. 1988; Williams et al. 1995a, 1995b). Soil algae, cyanobacteria and fungal hyphae increase soil aggregate stability by physically binding soil particles with polysaccharide exudates (Bailey et al. 1973; Belnap & Gardner 1993; Campbell et al. 1989), and crusts composed of free-living and lichenized cyanobacteria contribute fixed atmospheric nitrogen to arid and semi-arid ecosystems (Belnap et al. 1994; Evans & Ehleringer 1993; Jeffries et al. 1992). Collectively, biotic crusts increase availability of nitrogen and other minerals for vascular plants, and increase soil carbon and organic matter content (Belnap & Harper 1995; Harper & Pendleton 1993; Snyder & Wullstein 1973). However, biotic crusts are also sensitive to physical disturbances, including fragmentation and burial from livestock trampling, fire and various forms of human recreation (Anderson et al. 1982; Belnap & Eldridge 2001; Beymer & Klopatek 1992; Cole 1990; Hodgins & Rogers 1997).

The distribution and composition of crust communities are influenced by the amount and timing of precipitation, temperatures, soil texture, soil chemistry and vascular plant structure (Rosentreter & Belnap 2001). However, few biotic crust communities have been characterized for the major North American arid and semi-arid regions. In particular, we are aware of only a few published reports for the Columbia Basin (Johansen et al. 1993; Link et al. 2000; McCune & Rosentreter 2007; Ponzetti & McCune 2001). In this study, we examined soil-dwelling lichen and moss community composition in a low-elevation area of the Columbia Basin.

Intensive studies of biotic crust structure and function can give the impression that their results apply broadly across a given landscape. However, casual observation suggests important variation in response to small-scale environmental differences. So we wanted to examine landscape-level patterns of variation in community composition. We explored variation in crust community composition with regard to topographic position, soils, vegetation, and historical disturbances.

Methods

Study area. The Horse Heaven Hills is a large anticlinal uplift of Columbia River Basalt forming an escarpment running approximately east-west, with a steep, broken, northern exposure, and a gently sloping southern exposure (Rasmussen 1971; **Fig. 1**). We studied the eastern portion of this escarpment, just south of Benton City, in the Columbia Basin of south-central Washington (46°14′N, 119°30′W; **Fig. 1**). Our study area included 2279 ha of public land administered by the United States Department of the Interior, Bureau of Land Management (BLM), 16 ha of private land and 113 ha of public land administered by the Washington Department of Natural Resources. Elevations range from 198 m on the northern toe-slopes to 624 m at the crest of Chandler Butte. Soils are in the Kiona-Ritzville association, silt loam throughout, very deep to shallow over basalt rubble or bedrock, and formed from silty, wind-deposited material and basalt residuum (Rasmussen 1971). Rocky, thin soils along the top of the ridge grade into deep soils on lower slopes and benches.

The area is hot and dry in the summer; winters are damp and cool. Average maximum temperatures range from 30°C in July to 4°C in January. Average minimum temperatures range from 12°C in July to −4°C in January (Western Regional Climate Center 1999). Average annual precipitation is 199 mm, with annual extremes ranging from 88 to 342 mm (data from Prosser, WA, 1961–1990; Rasmussen 1971). Over two-thirds of the precipitation occurs during the fall and winter (October–March). Considerable fog and cloudiness occur in winter, with heavy fog expected on 5–10 nights per month (Rasmussen 1971). We frequently observed thick daytime fog in the study area in the late fall. Less than 10% of the annual precipitation occurs during the summer months of July–September (Western Regional Climate Center 1999).

Vegetation in the study area is dominated by bluebunch wheatgrass-Sandberg's bluegrass (*Pseudor-*

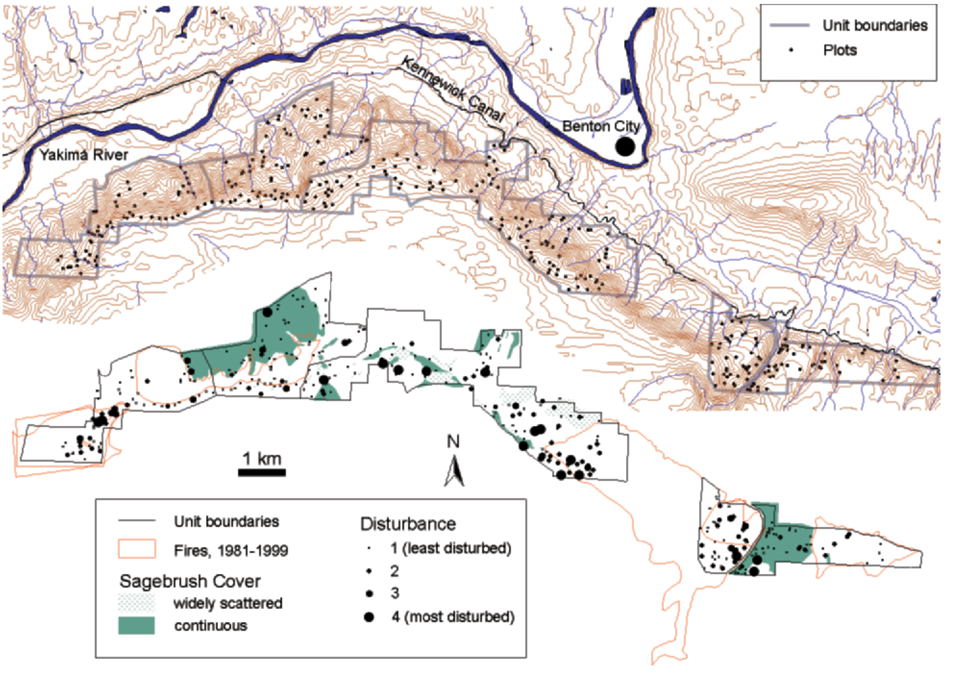

Figure 1. Horse Heaven Hills, southern Washington. **Upper.** Topography and plot locations. The study area is managed by the Bureau of Land Management in four units. **Lower.** Known wildfires from 1981–1999, sagebrush (*Artemisia tridentata*) distribution based on low-elevation aerial photos and field reconnaissance, and levels of disturbance of the biotic crust.

oegneria spicata-Poa secunda) perennial grasslands, with significant remnant stands of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*). Cusick's bluegrass (*Poa cusickii*) is frequent and abundant on north slopes. The ridges are dominated by lithosols with bluebunch wheatgrass-Sandberg's bluegrass and rock buckwheat (*Eriogonum sphaerocephalum*)-Sandberg's bluegrass communities (Daubenmire 1970). Cheatgrass (*Bromus tectorum*) is abundant along roads, the numerous deeply-incised, dry draws and the deeper soils of the ridgetop saddles. There are occasional patches of calcareous soil with scattered surface caliche fragments and infrequent occurrences of spiny hopsage (*Grayia spinosa*) and winterfat (*Krascheninnikovia lanata*), indicators of moderately alkaline soils. Nomenclature for vascular plants follows the PLANTS database (USDA 2005).

Historically, most of the study area was grazed by cattle, but livestock use was discontinued in 1986, 12 years before our data collection. The grazing history of the western portion of the area is unknown; this area was not included in a federal grazing lease until 1979. Generally, grazing occurred during the winter months, from November or December through March or April. Water availability probably limited livestock distribution on the site; the main water source is a canal running along much of the northern, lower slopes (**Fig. 1**). Many portions of Horse Heaven Hills have burned in recent decades. According to BLM records, at least eight fires of various sizes have burned parts of the study area since 1981.

Sampling. We sampled the entire landscape with non-permanent plots. Additionally, we used permanent plots arranged as paired grazed/ungrazed comparisons at exclosures, because at the time, we anticipated that grazing would be re-initiated at the site. As of this writing, grazing has not resumed at the site, but the permanent plots have been included in our landscape-level data and used to assess data quality.

We collected the same set of measurements in both the permanent and non-permanent plots. Plot placement and measurements were designed to be rapid (target: 1 plot per hour by an experienced observer, not counting travel time between plots), repeatable (target: 90% agreement between trained

Table 1. Landscape strata and diversity statistics for biotic crust variables. N = number of plots, % = area as a percentage, alpha = the average number of species per plot for a given stratum, gamma = the total number of species, and beta = gamma/alpha. Overall alpha is a weighted average based on the percentage of each stratum on the landscape.

	area			diversity		
Stratum	**ha**	**%**	**N**	**alpha**	**gamma**	**beta**
Ridges	188.6	8.3	51	13.3	45	3.4
Warm slopes	334.4	14.7	63	13.1	41	3.1
Warm draws	19.7	0.9	46	8.7	44	5.1
Cool slopes	1061.2	46.6	60	11.1	48	4.3
Cool draws	219.3	9.6	50	8.4	42	5.0
Toe-slopes & benches	450.7	19.8	80	12.4	46	3.7
Talus	4.8	0.2	0	0	0	0
Overall	2278.8	100	350	11.53	60	5.3

observers, 95% agreement between repeated observations by the same observer). We distinguished between species to the maximum extent that a trained observer can do so in the field.

Sampling was stratified by topographic position, such that each stratum was sampled with approximately equal effort (**Table 1**). We required a minimum of 15 plots per stratum. We visually stratified the study area from USGS 7.5' topographic maps and refined our results with field reconnaissance. The strata were digitized with ArcInfo 7.1.2. We differentiated "cool" and "warm" draws and slopes based on azimuth. "Warm" slopes and draws were defined to have azimuths 135–315° E of N, primarily south and west aspects, while "cool" slopes and draws had azimuths 315–135° E of N, primarily north and east aspects. These map-based criteria were field-checked at each sample point.

We placed plots by walking transect lines based on pre-selected routes or compass bearings within a selected sample area. The driving force in selecting sampling areas was our requirement for approximately equal numbers of plots in each stratum. Plots were placed at every 300 paces in open terrain, or by randomly chosen numbers of paces in the draws. Plots in draws were paired, so that both sides of the draw slopes were sampled; these pairs were placed either 25 or 50 paces from each other, depending on the size of the draw. Although this system is not a truly randomized method of sampling, we avoided most visual bias by selecting sample locations and routes from topographic maps rather than in the field. However, 48 permanent plots were pre-selected by the presence of small fenced grazing exclosures, located and installed by BLM personnel; these were all on benches or lower, gentle slopes. Plots were sampled September–November 1998, and April–June 1999.

Plot measurements. Sample units were 4×0.5 m rectangular plots. The long axis of the plot was oriented along the slope contour. Within each plot, we recorded percent cover of biotic crust species or species groups in classes on an approximately logarithmic scale: 0, 1 = 0–1%, 2 = 1–10%, 3 = 10–50%, 4 = 50–100%. We scored individual species whenever possible with a hand lens. Otherwise, we used species groups, sometimes combining morphologically similar yet phylogenetically distant species (**Table 2**). Only two observers were used and they were calibrated against each other. We used quality assurance procedures similar to those used for lichen indicators in the Forest Health Monitoring program (McCune et al. 1997). Repeatability of plot measurements was calculated and reported, as described below. Nomenclature follows Esslinger and Egan (1995) for lichens, Anderson et al. (1990) for mosses and Stotler and Crandall-Stotler (1977) for liverworts, except where otherwise noted.

At each plot we recorded topographic position, elevation, latitude and longitude (with GPS and/or by map), slope (degrees), aspect (degrees E of N), total biotic crust cover, rock cover, cover of bare soil and cover of dominant vascular plant species (for those with greater than 5% cover). The following additional variables were calculated after data collection: species richness (total number of biotic crust species in each plot), sum of cover classes, plot scores on a disturbance gradient as indicated by ordination scores, potential annual direct incident radiation and heat load.

Aspect, slope and latitude were used to estimate potential annual direct incident radiation (PDIR) and heat load for each plot (McCune & Keon 2002). PDIR estimates solar radiation reaching a plot for a given combination of aspect, slope and latitude, not considering cloud cover and topographic shading.

Table 2. Biotic soil crust variables and their member taxa.

Variable Name	Members
LICHENS	
Acarospora schleicheri	*Acarospora schleicheri*
Arthonia glebosa	*Arthonia glebosa*
Aspicilia spp., crustose	*Aspicilia* spp., including *A.* cf. *terrestrialis* and *A. reptans*
Aspicilia filiformis	*Aspicilia filiformis*
Black Crust	A complex mixture including *Collema* spp., *Placynthiella icmalea*, *P. uliginosa*, *P. oligotropha*, free-living cyanobacteria, and small bits of *Massalongia carnosa* and *Leptogium* spp.
Brown Crust	Predominantly *Placynthiella* spp.
Brown squamules	*Acarospora obpallens*, *A. terricola*, *Endocarpon* cf. *subnitescens*
Buellia papillata group	Predominantly *Buellia papillata* and *B. geophila*, with occasional *B. terricola*, *Aspicilia* sp. and *Lecidea* sp.
Buellia punctata group	*Buellia punctata*, *Lecidella stigmatea*, *Arthonia glebosa* with reduced thallus
Caloplaca jungermanniae group	*Caloplaca jungermanniae*, *C. lactea* and *C. tiroliensis*
Caloplaca stillicidiorum	*Caloplaca stillicidiorum*
Caloplaca tominii	*Caloplaca tominii*
Caloplaca lactea	*Caloplaca lactea*
Caloplaca unknown no. 2	unidentified *Caloplaca* sp.
Candelaria concolor	*Candelaria concolor*
Candelariella terrigena	*Candelariella terrigena s.l.*
Cladonia fimbriata	*Cladonia fimbriata*
Cladonia pocillum	*Cladonia pocillum*, *C. chlorophaea*, *C. pyxidata*
Cladonia verruculosa	*Cladonia verruculosa*
Cladonia unknown	*Cladonia imbricarica*, *C. pulvinella* and *C.* squamules
Collema tenax group	*Collema tenax* group spp., *C. coccophorum*
Diploschistes muscorum	*Diploschistes muscorum*
Endocarpon/Placidium group	*Endocarpon loscosii*, *E. pusillum*, *Placidium imbecillum*, *P. pilosellum*, *P. squamulosum* var. *argentinum*
Evernia prunastri	*Evernia prunastri* (found one time on moss over soil)
Fuscopannaria cyanolepra	*Fuscopannaria cyanolepra*
Lecanora muralis group	*Lecanora garovaglii*, *L. muralis*
Lecanora zosterae group	*Lecanora hagenii*, *L. zosterae*, *L. laxa*, *L. albellula*, *L. crenulata*, *L. dispersa*, *L. flowersiana*, *Rinodina mucronatula*
Lecidea sp.	*Lecidea fuscoatra s. str.* on soil
Lepraria sp.	*Lepraria neglecta* group (non *L. neglecta s. str.*)
Leptochidium albociliatum	*Leptochidium albociliatum*
Leptogium spp.	*Leptogium intermedium*, *L. lichenoides*, *L. tenuissimum s. lat.*, *Polychidium muscicola*
Massalongia carnosa	*Massalongia carnosa*
Megaspora verrucosa	*Megaspora verrucosa*
Neofuscelia spp.	*Neofuscelia loxodes*, *N. subhosseana*, *N. verruculifera* on soil
Peltigera didactyla	*Peltigera didactyla*
Peltigera rufescens group	*Peltigera rufescens*, *P. ponojensis*
Peritheciate white crust	Unknown white crust parasitized by *Muellerella pygmaea*
Phaeorrhiza sareptana	*Phaeorrhiza sareptana*, *P. nimbosa*
Physconia spp.	*Physconia isidiigera*, *P. enteroxantha*, *P. perisidiosa*
Polychidium muscicola	*Polychidium muscicola*
Psora cerebriformis	*Psora cerebriformis*
Psora decipiens	*Psora decipiens*
Psora globifera group	*Psora globifera*, *P. montana*
Rhizocarpon malenconianum	*Rhizocarpon malenconianum*

Table 2. Continued.

Variable Name	Members
Texosporium sancti-jacobi	*Texosporium sancti-jacobi*
Toninia sedifolia	*Toninia sedifolia*
Trapeliopsis bisorediata	*Trapeliopsis bisorediata* (McCune et al. 2002), *T. granulosa*
Trapeliopsis steppica	*Trapeliopsis steppica* (McCune et al. 2002)
Trapeliopsis glaucopholis	*Trapeliopsis glaucopholis* (Printzen & McCune 2004)
Unknown Lichen	various unidentifiable lichens
White Crust	unidentifiable white crustose lichens
Xanthoria spp.	*Xanthoria* spp.
BRYOPHYTES	
Brachythecium albicans	*Brachythecium albicans*
Bryum argenteum	*Bryum argenteum*
Cephaloziella divaricata	*Cephaloziella divaricata*
Encalypta rhaptocarpa	*Encalypta rhaptocarpa*
Homalothecium aeneum	*Homalothecium aeneum*
Pterygoneurum ovatum	*Pterygoneurum ovatum*
Short Mosses	*Aloina bifrons*, *Bryoerythrophyllum columbianum*, *Bryum* spp., *Ceratadon purpureus*, *Didymodon* spp., *Trichostomopsis australasiae*
Tortula ruralis	*Tortula ruralis*

Heat load is an index that rescales PDIR to be symmetrical about the northeast-southwest axis, with a minimum at 45° and a maximum at 225°.

We also calculated diversity statistics for biotic soil crusts: average species richness per stratum (alpha), the total number of species found per stratum (gamma) and beta, a measure of community heterogeneity (gamma/alpha) per stratum. Looking at the whole landscape, we calculated a weighted landscape-level richness based on the percentage of each stratum found on the landscape.

GIS-derived data. We derived site data associated with each plot location from Geographic Information System (GIS) map layers, including topographic, soil, geologic, fire history and sagebrush cover layers. Software for these analyses included the Environmental Systems Research Institute's ArcInfo 7.1.2 and ArcView 3.2.

Elevation, aspect and slope variables were based on a Digital Elevation Model (USGS 1999). We also calculated "flow accumulation," "curvature" and "hillshade" in conjunction with this topographic layer. "Hillshade" calculates a relative shade value for each pixel by combining shade based on sun illumination angle, and shadow from surrounding pixels. We calculated two hillshade scenarios. The first, "shade at solstice," approximates peak radiation for the site, with a solar altitude of 67.5° and azimuth of 180°. The second, "shade from the SW," approximates peak heat load, with a solar altitude of 33.5° and azimuth of 225°. "Flow accumulation" approximates the accumulated water flowing down slope by calculating the number of pixels that drain into each pixel. "Curvature" calculates the curvature of the surface in the center of each pixel. We also derived planiform curvature and profile curvature from this function.

We utilized a pre-existing geologic map layer (Harris 1998), and created a soil map layer by digitizing Benton County soil survey maps for the immediate research area (Rasmussen 1971). We digitized a fire history map based on BLM fire records for 1981–1996, and from our own field reconnaissance after a 1998 fire at the site. We digitized a sagebrush cover map layer based on a combination of low-elevation oblique aerial photos, historical conventional air photos and field reconnaissance. Oblique air photos were taken June 23, 1999 at 0730–0830 with 35 mm film and a 50 mm lens. Conventional aerial photographs from the years 1962, 1986, 1991 and 1998 were available through the Washington Department of Natural Resources, Olympia, and the

Benton County Department of Public Works, Prosser, Washington.

Analysis. We explored patterns in biotic crust community composition with nonmetric multidimensional scaling (NMS; Kruskal 1964; McCune & Mefford 1999). Using Sørensen's distance measure, we employed the "autopilot" mode with the "slow and thorough" setting to find the best solution (McCune & Mefford 1999). NMS is an iterative ordination method that seeks to minimize "stress" (i.e., maximize fit) between distances in the original distance matrix and distances in the reduced ordination space. The use of ranked Sørensen distances makes it particularly good for community data (McCune & Grace 2002).

Relationships between abundance of individual species and the strongest ordination axis were represented with nonparametric regression using kernel smoothers (Hastie et al. 2001; McCune & Mefford 2004). This is a more flexible approach than the usual linear correlations in that it accommodates nonlinear relationships of species and environment to ordination axes. Smoothing parameters for nonparametric regression were optimized for each species, using a local mean and Gaussian weighting function. Fit was expressed with a cross-validated R^2 ($\times R^2$) obtained with a "leave one out" method: each data point is excluded from the basis for the estimate of the response at that point. Otherwise, $\times R^2$ is calculated the same as the usual R^2, as one minus the ratio of the residual sum of squares to the total sum of squares. Although local linear models often had slightly better fit than local mean models, we chose to use the latter. Local mean models produce a response surface that at the ends of gradients is slightly biased toward the central tendency (Hastie et al. 2001). This bias is usually viewed as a problem, but we intentionally chose this model form for its more conservative behavior toward the edges of the predictor space, and its impossibility of producing an estimate of the response variable that falls outside the observed range in the response variable.

We tested for multivariate differences between groups (topographic and disturbance) with multi-response permutation procedures (MRPP) in PC-ORD using Sørensen distances. MRPP is a nonparametric technique that tests for multivariate differences between predefined groups (McCune & Grace 2002; Mielke & Berry 2001). The resulting A statistic, the chance-corrected within-group agreement, expresses degree of departure from random expectation ($A = 0$), with $A = 1$ resulting for perfect separation of groups (all plots identical within each group). The p-value represents the likelihood of obtaining differences between groups as large or larger than the observed difference, solely by chance.

Indicator Species Analysis (Dufrêne & Legendre 1997; McCune & Mefford 1999) evaluates individual species differences among groups. Indicator values combine relative abundance and frequency of occurrence in each group. A species receives the maximum indicator value of 100% when it occurs in only one group and within all sample units of that group. A randomization test evaluates significance of the maximum indicator value for each species.

Repeat measurement error. Sampling of biotic soil crust communities are one of the most challenging lichen and bryophyte sampling tasks that we know of, because of the small size, inconspicuous coloration and intricate intermixing of taxa. We therefore deemed it important to evaluate and report sampling error. We evaluated two kinds of repeat-measurement error for key response variables. Between-observer error was based on the differences between two observers reading the same plots on the same date. Between-date error was based on the differences between dates for one observer, using permanent plots.

Our estimates of repeat-measurement error could not be broken down into components of accuracy and bias, because true values were not known. Here, repeat measurement error is expressed in two ways: the signal-to-noise ratio, and percent agreement between observations. The signal-to-noise ratio for a given response variable is based on the landscape-level range in the response variable and the estimate of error. The signal is the range in the response over all sample units. The noise (s_{diff}) is the root mean squared error between observers (or between dates), so:

$$Signal\text{-}to\text{-}noise\ ratio = range/s_{diff}$$

The percent agreement between observations was calculated as follows:

$$\% \; agreement = \frac{100(range - s_{diff})}{range}$$

Seven non-permanent between-observer plots were read consecutively by Ponzetti and McCune. Twelve permanent between-date plots were read by Ponzetti in May and again in October 1999.

Results

Distribution and abundance of biotic crusts. A total of 60 terricolous biotic crust species and species groups occurred in the 350 plots (**Table 2**). Of these 60 variables, 35 are individual lichen or bryophyte species; the other 25 variables are small groups of species that we could not consistently distinguish in the field with a 14× hand lens. These morphological groups are composed of two or more species with superficially similar growth forms and coloration; the member species may be in the same genus, or entirely unrelated. We collected over 350 specimens to voucher our field identifications and to determine the members of our morphological groups. For simplicity, we refer to all 60 of the biotic crust variables as "species."

The average species richness of the 350 plots (alpha) was 11.4 species, and landscape-level (weighted) alpha was nearly the same, with 11.5 species (**Table 1**). Numbers of species per plot ranged from zero to 21, but only four of the 350 plots entirely lacked soil lichens and bryophytes. Among the six landscape strata, alpha diversity was highest in the ridge and warm slope strata and lowest in the warm draws and cool draws. Gamma diversity was similar among the strata, ranging from 41 species in plots on warm slopes to 48 species in plots on cool slopes. Beta diversity, a measure of community heterogeneity, was highest for cool draws and warm draws, and lowest for ridges and warm slopes.

For community analysis, we reduced the number of biotic crust variables to 51 by excluding those species occurring in fewer than three plots. The resulting 51 species by 350 plot matrix yielded an NMS ordination with three axes, explaining a total of 84.2% of the variation in the data. After rotation to align Axis 1 with the strongest environmental gradient, axis 1 represented 62% of the variation in the data, with Axes 2 and 3 being much weaker (11% and 12% of the variation, respectively; **Fig. 2**).

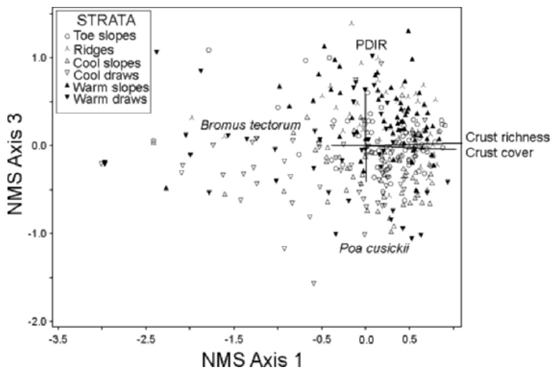

Figure 2. NMS ordination of plots in biotic crust species space, axes 1 and 3. Plot symbols represent sampling strata. Vectors represent the strongest linear relationships of site variables and vascular plant species to the ordination; the longer the vector, the stronger that variable is correlated with an axis. Crust richness = biotic crust species richness, Crust cover = total biotic crust cover, and PDIR = potential annual direct incident radiation.

Axis 1 can be summarized as a gradient of biotic crust integrity. Plots with high integrity (defined as a well-developed biotic crust, with high total cover and high diversity) are on the right end of the axis. The site variables with the strongest positive relationships with Axis 1 are total crust cover ($\times R^2 = 0.68$; **Fig. 3**) and crust species richness ($\times R^2 = 0.78$; **Fig. 3**); others include bluebunch wheatgrass and Sandberg's bluegrass ($\times R^2 = 0.17$ and 0.18, respectively; **Fig. 3**). The following crust variables all had strong relationships with this axis, all peaking on the right half of the axis: *Acarospora schleicheri*, *Buellia punctata* group, *Cladonia pocillum* group, crustose *Aspicilia* spp., *Diploschistes muscorum*, *Leptochidium albociliatum*, *Leptogium* spp., *Massalongia carnosa*, *Megaspora verrucosa*, "short mosses" and *Tortula ruralis* (**Fig. 4**). In contrast, no crust variables monotonically decreased along this axis, and none of the crust species was more abundant on disturbed sites. Cheatgrass ($\times R^2 = 0.23$; **Figs. 2, 3**) was the only vascular plant strongly peaking on the low end of this axis; the site variable "bare soil" had a peak in the center of this axis ($\times R^2 = 0.14$; **Fig. 3**).

Our fire variables, including years since fire, were only weakly related to axis 1. Fitting a response surface of axis 1 scores (crust integrity) to years since fire and cover of cheatgrass (**Fig. 5**), shows that crust integrity is much more strongly related to cheatgrass

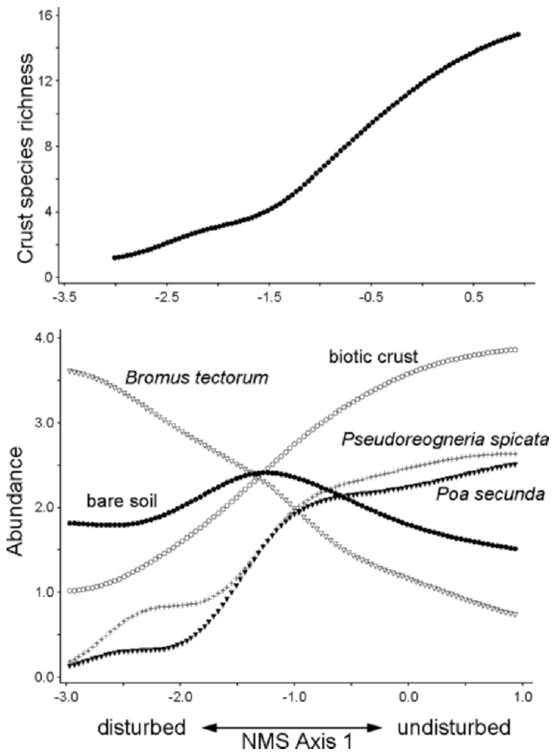

Figure 3. Nonparametric regression curves of biotic crust species richness, cover class of bare soil and biotic crust, and abundance of selected vascular plants, all in relationship to the first ordination axis, interpreted as a disturbance gradient.

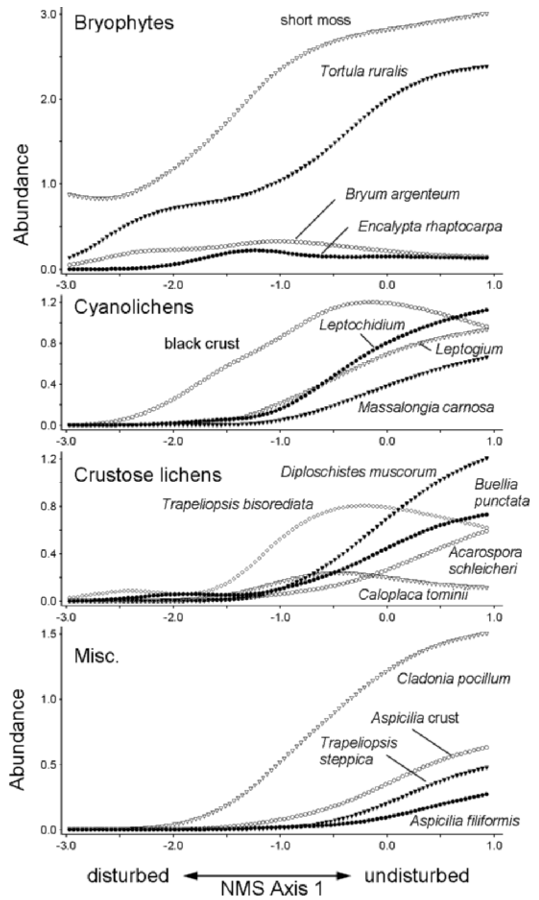

Figure 4. Nonparametric regression curves of biotic crust species relationships to the first ordination axis, interpreted as a disturbance gradient. Curves are shown for the most abundant species, grouped by life forms.

than it is to fire history. For example, plots in the upper left of the response surface (**Fig. 5**) have been recently burned, but have fairly high scores for crust integrity. Plots toward the lower right of the response surface are in cheatgrass-dominated patches in areas that have not burned recently—these have poor development of the biotic crust. Areas in the foreground had insufficient data to reliably estimate the response surface—these are recently burned areas with high cheatgrass cover. Based on observations in other areas, however, these too should have low crust cover and diversity.

Axis 2 represents a soil chemistry gradient that we refer to as "caliche exposure." Caliche was occasionally exposed on steep, eroding slopes and draws, as well as near rimrock. Species that were positively associated with this axis are known calciphiles: *Collema tenax* group, *Caloplaca tominii*, *C. jungermanniae* group, the morphological group Black Crust, and the *Endocarpon/Placidium* group. A

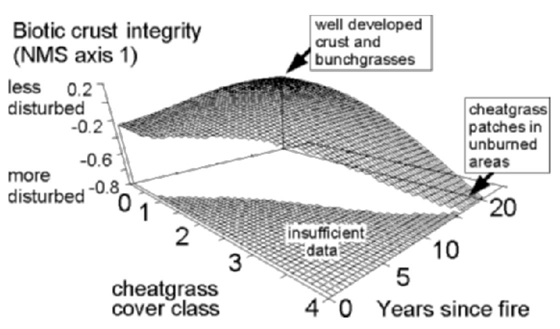

Figure 5. Nonparametric regression of NMS axis 1, representing a gradient of biotic crust disturbance, against cover of cheatgrass (*Bromus tectorum*) and years since fire ($\times R^2 = 0.34$). Areas not burned in the preceding 20 years were lumped into the 20-year age class, because of lack of fire data before that date. Integrity of the biotic crust was more strongly related to *Bromus tectorum* than fire.

number of crust species that are known to associate with non-calcareous substrates (Ponzetti & McCune 2001; Rosentreter & Belnap 2001) were negatively correlated with Axis 2, including *Diploschistes muscorum*, *Megaspora verrucosa*, *Leptochidium albociliatum* and *Acarospora schleicheri*.

Axis 3 showed monotonically increasing relationships to site variables derived from solar radiation. The strongest relationship was with potential direct incident radiation (PDIR; $\times R^2 = 0.41$), followed by heat load index ($\times R^2 = 0.25$), the GIS-derived "shade at solstice" ($\times R^2 = 0.25$) and "shade from the SW" ($\times R^2 = 0.09$). A number of crust species are weakly associated with increased solar radiation, including *Caloplaca tominii*, *Candelariella terrigena*, crustose *Aspicilia* spp., and the *Endocarpon*/*Placidium* group. Variables decreasing along Axis 3 (i.e., more abundant on shadier sites) include Cusick's bluegrass ($\times R^2 = 0.35$), and the cryptogams *Brachythecium albicans*, *Cephaloziella divaricata*, *Cladonia fimbriata*, *Lepraria* sp. and *Fuscopannaria cyanolepra*.

We categorized plot positions on Axis 1, the crust integrity axis. We refer to these categories as "disturbance classes" because crust integrity was clearly related to previous soil disturbance, based on field observations and negative relationships of crust richness and cover to cheatgrass and bare soil. We created these classes by dividing the range of scores on Axis 1 into four equal partitions. Class 1 is the least disturbed, with the highest scores on the crust integrity axis, while Class 4 is the most disturbed group, with the lowest scores on the crust integrity axis. According to Indicator Species Analysis, a total of 20 biotic crust variables differed among disturbance classes ($p < 0.05$; **Table 3**). Of these 20 indicators, ten are strong indicators of Class 1, and six are strong indicators of both Class 1 and Class 2. The lichen *Collema tenax* is a strong indicator of Class 2, and the moss *Pterygoneurum ovatum* is a strong indicator of Class 3. There are no strong indicators of the most disturbed class, Class 4; rather, the absence of many species distinguishes it. *Tortula ruralis* and "short mosses" (**Table 2**) are abundant and frequent in all four groups, but are considerably less abundant and less frequent in Class 4 (**Table 3**).

Biotic crust communities differed with respect to landscape strata (MRPP, $A = 0.073$, $p << 0.001$). Partial spatial separation among strata in the ordination supports this conclusion (**Fig. 2**). More than half of the biotic crust variables indicate one or more strata, according to Indicator Species Analysis (**Table 4**). For example, *Acarospora schleicheri* is most frequent on toe-slopes and benches, but is quite sparse on warm draws and cool slopes; these differences are stronger than expected by chance.

Biotic soil crusts are extensive throughout the study area, often covering most of the available space between the vascular plants. Exceptions where soil crusts are notably limited include talus slopes and scree slopes with little soil substrate, steep slopes with active soil erosion (typically in draws), very dense stands of cheatgrass, fresh mounds of soil formed by digging rodents, roads and fire lines. Well-developed biotic crusts are frequent in all units, at all topographic positions, and in areas of differing fire histories.

Repeatability of biotic crust sampling. Repeat measurement error for between-observer and between-date comparisons mostly met target values (**Table 5**). Signal-to-noise ratios varied by type of comparison and variable compared. Individual cover class estimates had the highest signal-to-noise ratio for both types of comparisons. The lowest signal-to-noise ratio was for crust species richness between dates; richness estimates were more consistent between observers on the same date than with the same observer on different dates. However, observations of total crust cover were more consistent with the same observer on different dates than between observers. Percent agreement values largely mirrored signal-to-noise ratios.

Discussion

Landscape strata. The composition of biotic soil crusts clearly differed by landscape strata, as shown by diversity statistics, MRPP, Indicator Species Analysis and ordination results. Biotic soil crusts are, therefore, not uniform on the landscape. For example, the NMS ordination (**Fig. 2**) places plots in draws lower on the crust integrity axis (Axis 1) relative to the majority of the plots. Draws at Horse Heaven Hills tend to have lower crust richness and cover than other landscape features.

Disturbance. At Horse Heaven Hills crust integrity is inversely related to soil disturbance. All

Table 3. Frequency (%) and mean cover class of biotic crust species by disturbance classes. Disturbance classes are based on partitioning the biotic crust integrity axis of the ordination. Species in **bold** differed among disturbance classes according to Indicator Species Analysis ($p < 0.05$). Note that the mean cover classes cannot be back-transformed to percent cover; the use of cover classes directly in the statistics allows minor species to express themselves.

	Disturbance class							
	1 (least)		2		3		4 (most)	
Species or species group	Mean	Freq	Mean	Freq	Mean	Freq	Mean	Freq
Acarospora schleicheri	**0.46**	**44.4**	**0.23**	**22.5**	**0.06**	**5.7**	**0.00**	**0.0**
Arthonia glebosa	0.20	20.1	0.23	22.5	0.09	8.6	0.00	0.0
Aspicilia spp., crustose	0.51	45.0	0.46	40.3	0.12	11.5	0.00	0.0
Aspicilia filiformis	0.20	20.1	0.14	13.9	0.03	2.9	0.00	0.0
Black Crust	**0.89**	**67.5**	**1.23**	**85.3**	**0.60**	**42.9**	**0.08**	**7.7**
Brown Crust	0.01	0.6	0.01	0.8	0.06	5.7	0.00	0.0
Brown Squamules	0.05	5.3	0.10	10.1	0.09	8.6	0.00	0.0
Brachythecium albicans	0.14	8.3	0.01	0.8	0.03	2.9	0.00	0.0
Bryum argenteum	0.08	8.3	0.33	32.6	0.40	40.0	0.24	23.2
Buellia papillata group	0.03	3.5	0.00	0.0	0.00	0.0	0.00	0.0
***Buellia punctata* group**	**0.61**	**60.4**	**0.38**	**38.0**	**0.14**	**14.3**	**0.08**	**7.7**
Caloplaca jungermanniae group	0.02	2.4	0.09	8.5	0.09	8.6	0.00	0.0
Caloplaca lactea	0.01	0.6	0.02	2.3	0.00	0.0	0.00	0.0
Caloplaca stillicidiorum	0.08	8.3	0.07	7.0	0.00	0.0	0.00	0.0
Caloplaca tominii	0.05	4.7	0.27	27.1	0.26	25.7	0.00	0.0
Candelaria concolor	0.02	2.4	0.02	1.6	0.03	2.9	0.00	0.0
Candelariella terrigena	0.15	14.8	0.38	38.0	0.26	25.7	0.16	15.4
Cephaloziella divaricata	**0.43**	**37.9**	**0.05**	**5.4**	**0.00**	**0.0**	**0.00**	**0.0**
Cladonia fimbriata	**0.35**	**27.2**	**0.03**	**3.1**	**0.00**	**0.0**	**0.00**	**0.0**
Cladonia pocillum	**1.78**	**97.0**	**1.09**	**89.9**	**0.29**	**28.6**	**0.00**	**0.0**
***Collema tenax* group**	**0.07**	**5.9**	**0.32**	**27.9**	**0.14**	**14.3**	**0.08**	**7.7**
Diploschistes muscorum	**1.18**	**85.8**	**0.36**	**33.3**	**0.03**	**2.9**	**0.00**	**0.0**
Encalypta rhaptocarpa	0.19	18.9	0.12	11.6	0.09	8.6	0.00	0.0
Endocarpon/Placidium group	0.17	16.6	0.36	34.9	0.17	17.1	0.00	0.0
Fuscopannaria cyanolepra	**0.23**	**20.1**	**0.05**	**4.6**	**0.00**	**0.0**	**0.00**	**0.0**
Homalothecium aeneum	0.06	3.0	0.00	0.0	0.00	0.0	0.00	0.0
***Lecanora muralis* group**	**0.38**	**36.1**	**0.25**	**24.0**	**0.09**	**8.6**	**0.00**	**0.0**
Lecanora zosterae group	0.07	7.1	0.16	15.5	0.03	2.9	0.00	0.0
Lepraria spp. group	0.15	14.8	0.04	3.9	0.03	2.9	0.00	0.0
Leptochidium albociliatum	**0.97**	**88.8**	**0.65**	**62.0**	**0.06**	**5.7**	**0.00**	**0.0**
***Leptogium* spp.**	**0.85**	**83.4**	**0.53**	**52.7**	**0.06**	**5.7**	**0.00**	**0.0**
Massalongia carnosa	**0.65**	**60.4**	**0.15**	**14.7**	**0.00**	**0.0**	**0.00**	**0.0**
Megaspora verrucosa	**0.60**	**56.2**	**0.23**	**20.9**	**0.00**	**0.0**	**0.00**	**0.0**
Neofuscelia spp.	0.02	1.8	0.00	0.0	0.00	0.0	0.00	0.0
Peltigera didactyla	0.03	3.0	0.02	1.6	0.00	0.0	0.00	0.0
Peltigera rufescens group	0.02	1.8	0.00	0.0	0.00	0.0	0.00	0.0
Peritheciate white crust	0.05	4.7	0.04	3.9	0.03	2.9	0.00	0.0
Phaeorrhiza sareptana	0.02	2.4	0.05	3.9	0.00	0.0	0.00	0.0
Physconia spp.	0.14	13.6	0.13	13.2	0.06	5.7	0.08	7.7
Psora cerebriformis	0.03	3.5	0.04	3.9	0.00	0.0	0.00	0.0
Psora globifera group	0.33	33.1	0.30	30.2	0.00	0.0	0.00	0.0
Pterygoneurum ovatum	**0.01**	**1.2**	**0.09**	**8.5**	**0.23**	**22.8**	**0.08**	**7.7**
Rhizocarpon malenconianum	**0.17**	**17.2**	**0.02**	**2.3**	**0.00**	**0.0**	**0.00**	**0.0**

Table 3. Continued.

Species or species group	**Disturbance class**							
	1 (least)		**2**		**3**		**4 (most)**	
	Mean	**Freq**	**Mean**	**Freq**	**Mean**	**Freq**	**Mean**	**Freq**
Short Mosses	**3.08**	**100.0**	**2.88**	**100.0**	**2.03**	**100.0**	**0.85**	**84.6**
Toninia sedifolia	0.01	0.6	0.04	3.1	0.00	0.0	0.00	0.0
Tortula ruralis	**2.62**	**98.8**	**1.62**	**89.2**	**0.74**	**65.7**	**0.37**	**38.6**
Trapeliopsis bisorediata	**0.66**	**62.7**	**0.78**	**65.9**	**0.32**	**31.4**	**0.00**	**0.0**
Trapeliopsis steppica	**0.51**	**37.3**	**0.09**	**8.5**	**0.00**	**0.0**	**0.00**	**0.0**
Trapeliopsis glaucopholis	0.15	11.2	0.06	3.9	0.00	0.0	0.00	0.0
Unknown Lichen	0.06	5.9	0.02	1.6	0.06	5.7	0.00	0.0
White Crust	0.05	4.7	0.05	4.6	0.20	20.0	0.08	7.7

topographic positions and soil types observed here have the potential for nearly 100% biotic crust cover in the spaces between the vascular plants. The biotic crust appears to be limited only by disturbance to the soil surface and foliar cover by vascular plants. The spaces between vascular plants allow excellent development of the biotic crust throughout Horse Heaven Hills, except in the scattered areas with recent disturbance of the soil surface or with high abundance of annual weeds.

The crust integrity axis (**Fig. 2**: Axis 1) is by far the strongest gradient detectable in this data set. Plots near the high end of this gradient have high crust cover and richness; plots low on the axis have low crust cover and richness. Most of the significant soil crust indicator species are indicators of the least disturbed plots. No crust indicator species were found for the most disturbed plots, Class 4.

Biotic crust integrity and cover of cheatgrass are inversely related. The high amounts of diffuse litter produced by dense stands of cheatgrass may inhibit biotic soil crusts by increasing competition for light and moisture (Eldridge 1996; Kaltenecker 1997). In addition, our data indicate that cover of the dominant bunchgrasses, bluebunch wheatgrass (*Pseudoroegneria spicata*) and Sandberg's bluegrass (*Poa secunda*), is positively related to biotic crust cover at this site (**Fig. 3**). These bunchgrasses typically maintain interspaces with few other vascular plants thus providing an open soil surface for biotic crust species to establish and survive.

The primary large-scale historical disturbances have been fire and livestock grazing and its associated hoof disturbance. More localized disturbances include infrequent water erosion and mass wasting in the draws and soil disturbance by burrowing small mammals. Burrows are frequent, occurring in most areas except rocky sites with very thin soils. Direct human disturbance is mostly found around roads, trails, off-road vehicle tracks and the soil disturbance along fire lines.

Much of the study area has burned in the last few decades. Fire has greatly reduced the abundance of sagebrush and increased the dominance of bluebunch wheatgrass. Areas recently burned clearly correspond with absence of sagebrush, a fire-sensitive species (**Fig. 1**), except for their skeletal remains. For example, in Webber Canyon, the west-facing slope, unburned in recent decades, is dominated by sagebrush, while the east slope, burned at least twice recently, is dominated by bluebunch wheatgrass.

Remarkably, the biotic crust has recovered well on most of the burned areas (**Fig. 5**). Our data revealed only weak relationships between the crust integrity axis and fire-related variables such as sagebrush cover, number of fires and number of years since fire. We interpret the resilience of the biotic crust, in this case, to the low abundance of cheatgrass, low amounts of soil disturbance and high moss cover. These fires have not resulted in an explosion of the cheatgrass population, perhaps because of the historically low levels of livestock grazing. In this case,

Table 4. Frequency (%) of biotic crust variables by landscape strata. Frequencies are the percentage of plots in a given stratum containing a given species. Species in **bold** differed among strata according to Indicator Species Analysis, based on a randomization test on the highest indicator value for each species.

	Stratum						Whole landscape	
Variable	Ridges	Warm slopes	Warm draws	Cool slopes	Cool draws	Toe-slopes & benches	Mean	Freq.
Acarospora schleicheri	**33**	**49**	**2**	**4**	**20**	**56**	**0.32**	**31**
Arthonia glebosa	**20**	**44**	**9**	**4**	**12**	**20**	**0.19**	**19**
***Aspicilia* spp., crustose**	**59**	**72**	**13**	**6**	**19**	**48**	**0.44**	**38**
Aspicilia filiformis	**31**	**36**	**0**	**2**	**7**	**13**	**0.15**	**15**
Black Crust	61	74	54	62	78	78	0.96	69
Brown Crust	2	3	0	0	0	1	0.01	1
Brown squamules	**6**	**25**	**4**	**2**	**2**	**4**	**0.07**	**7**
Brachythecium albicans	**0**	**0**	**13**	**8**	**7**	**3**	**0.07**	**5**
Bryum argenteum	**26**	**39**	**28**	**18**	**9**	**11**	**0.21**	**21**
Buellia papillata group	2	0	0	0	5	3	0.02	2
***Buellia punctata* group**	**74**	**61**	**17**	**14**	**51**	**47**	**0.46**	**45**
Caloplaca jungermanniae group	12	8	9	0	2	3	0.05	5
Caloplaca lactea	**0**	**2**	**7**	**0**	**0**	**0**	**0.01**	**1**
Caloplaca stillicidiorum	**29**	**2**	**2**	**4**	**7**	**0**	**0.07**	**7**
Caloplaca tominii	**29**	**23**	**20**	**10**	**3**	**9**	**0.15**	**15**
Candelaria concolor	0	0	2	4	2	4	0.02	2
Candelariella terrigena	**53**	**46**	**22**	**10**	**9**	**13**	**0.25**	**25**
Cephaloziella divaricata	12	13	22	16	25	30	0.23	21
Cladonia fimbriata	**2**	**3**	**17**	**28**	**36**	**5**	**0.19**	**14**
Cladonia pocillum	**88**	**85**	**65**	**66**	**93**	**95**	**1.30**	**84**
***Collema tenax* group**	**26**	**21**	**35**	**12**	**2**	**4**	**0.17**	**15**
Diploschistes muscorum	**55**	**61**	**26**	**32**	**61**	**76**	**0.71**	**55**
Encalypta rhaptocarpa	**6**	**7**	**13**	**40**	**19**	**8**	**0.15**	**14**
Endocarpon/Placidium group	35	29	35	12	12	18	0.23	23
Fuscopannaria cyanolepra	**2**	**2**	**13**	**22**	**27**	**6**	**0.13**	**12**
Homalothecium aeneum	0	0	4	4	2	0	0.03	1
***Lecanora muralis* group**	**53**	**39**	**17**	**2**	**19**	**30**	**0.29**	**27**
Lecanora zosterae group	20	7	15	8	12	1	0.10	10
***Lepraria* spp. group**	**2**	**0**	**20**	**16**	**20**	**1**	**0.09**	**9**
Leptochidium albociliatum	**78**	**77**	**48**	**38**	**66**	**82**	**0.72**	**67**
***Leptogium* spp.**	**69**	**62**	**37**	**42**	**61**	**81**	**0.62**	**61**
Massalongia carnosa	**18**	**33**	**24**	**22**	**46**	**54**	**0.37**	**35**
Megaspora verrucosa	**55**	**31**	**4**	**14**	**42**	**52**	**0.38**	**35**
Neofuscelia spp.	4	0	0	0	0	1	0.01	1
Peltigera didactyla	**0**	**0**	**2**	**2**	**9**	**0**	**0.02**	**2**
Peltigera rufescens group	0	0	2	0	3	0	0.01	1
Peritheciate white crust	6	8	2	0	0	6	0.04	4
Phaeorrhiza sareptana	**16**	**0**	**0**	**0**	**0**	**1**	**0.03**	**3**
***Physconia* spp.**	**12**	**10**	**7**	**26**	**17**	**6**	**0.12**	**12**
Psora cerebriformis	**14**	**3**	**2**	**0**	**0**	**1**	**0.03**	**3**
***Psora globifera* group**	**53**	**41**	**13**	**2**	**10**	**38**	**0.28**	**27**
Pterygoneurum ovatum	**8**	**10**	**15**	**10**	**0**	**0**	**0.06**	**6**
Rhizocarpon malenconianum	**4**	**8**	**0**	**0**	**12**	**23**	**0.09**	**9**
Short Mosses	100	100	100	100	98	99	2.82	99
Toninia sedifolia	4	0	4	2	0	0	0.02	1

Table 4. Continued.

	Stratum						Whole landscape	
Variable	Ridges	Warm slopes	Warm draws	Cool slopes	Cool draws	Toe-slopes & benches	Mean	Freq.
Tortula ruralis	**100**	**90**	**76**	**86**	**97**	**87**	**1.97**	**90**
Trapeliopsis bisorediata	**37**	**77**	**41**	**54**	**68**	**63**	**0.65**	**58**
Trapeliopsis steppica	**8**	**31**	**2**	**6**	**15**	**48**	**0.28**	**21**
Trapeliopsis glaucopholis	**0**	**11**	**0**	**0**	**2**	**20**	**0.10**	**7**
Unknown Lichen	2	7	2	10	2	3	0.04	4
White Crust	6	7	7	10	7	4	0.06	6

the physical disturbance from fire-line plowing is more damaging to the crusts than the fires themselves.

The extensive 1998 fire at the west end of the study area resulted in only partial mortality of the biotic crust, based on observations the following year. At a fine scale, crust cover remains high and appears to be a mosaic of dead, partially burned and live patches of crust. Frequently, we observed top-killed mosses regenerating at the gametophyte bases. One year after the fire, survival was high enough that we anticipate a rapid recovery of the biotic crust in areas with little soil disturbance (for example, away from the soil disturbance along fire control lines).

GIS-derived site variables. Most of the GIS-derived site variables were not useful in interpreting crust community ordination results. This may be a problem of scale. While the field-derived variables were measured in the exact location of each plot, the GIS-derived variables could not account for small differences on the landscape. Biotic soil crusts can vary quite markedly depending on local slopes, depressions, soil surface features and vascular vegetation, on scales of less than 1 m. We found that differences among our plots often reflected this microhabitat variation on the landscape, but our GIS resolution generally was not sensitive to the variation we observed in our plots. The strongest relationship between a community ordination axis and a GIS variable was “shade at solstice” with axis 3 ($\times R^2 = 0.25$). We anticipate that future GIS-based analysis of biotic soil crusts would be more useful with larger plot sizes.

Repeatability. Repeat measurement errors differed among the response variables. In comparing measurements between observers, we achieved our target of 90% agreement for three of the five variables being tested. For measurements between dates, we achieved our target of 95% agreement for only one of the variables being tested. Most of the variables were near or better than 90% agreement, with the exceptions of species richness between dates (78% agreement) and total crust cover between observers (83% agreement).

Table 5. Repeat-measurement error for key community response variables. The value *s* is the standard deviation of the difference between repeat measurements. Signal:Noise is the ratio of the range in response over all sample units to the mean squared error between observers (or dates).

	Between observers (same dates)			Between dates (same observer)		
Variable	*s*	Signal: Noise	% Agreement	*s*	Signal: Noise	% Agreement
Biotic crust species richness	1.38	11.0	91	2.16	4.5	78
Total crust cover class	0.81	6.0	83	0.54	13.8	93
Sum of cover classes	1.68	9.3	89	1.75	8.5	88
Score on Axis 1 (integrity)	0.52	13.5	93	0.50	14.7	93
Individual cover class estimates	0.36	30.0	97	0.40	25.2	96

Agreement in total crust cover estimates between observers could be improved by increasing calibration efforts between observers. Error in richness estimates may be difficult to reduce. Species richness of biotic soil crusts is dependent upon the ability of the observer to notice minute lichens and mosses, many of which are considerably smaller than 1 cm^2. With subjects so small, subtle changes in the angle of the sun, cloud cover, humidity and time since the last rain or fog can introduce variation in species detection, even with the same skilled observer. In addition, the error we documented here may be a product of slight differences in the placement of plots, or seasonal changes in plots. In the fall, litter accumulation from dormant grasses and vascular plants is more likely to obscure visibility of the smaller and less abundant species. Finally, the repeat measurement error between dates is confounded by any actual changes in the plots over time.

One way to increase the consistency of species richness estimates over time would be to use broader morphological groups (Eldridge & Rosentreter 1999). Grouping similar species together will minimize the effects of missing very small species. However, the resulting richness measurement will be further from a true picture of species richness, and valuable diversity information will be lost. Note in **Fig. 4** the variation within a life form group in relationship to crust integrity.

Scope. Species' responses to grazing and fire are surely some of the most widely and intensively studied problems in semi-arid ecosystems throughout the world. Yet we have barely begun to understand their effects on the development and destruction of biotic crust communities. We have no illusions that our results will apply to the huge variation in semi-arid landscapes throughout western North America. We do believe, however, that the basic antagonism of weedy annual grasses, stimulated by disturbance, and the integrity of the soil crust, is likely to be seen many other places in the West. The drivers for that antagonism are likely to vary, both within a landscape and regionally. For example, in contrast to our study area, fire greatly stimulates cheatgrass on sites in the Great Basin, resulting in dramatic reductions in perennial grasses and biotic crusts (Young & Evans 1978).

We found that within our study area, the plot-level variables (e.g., soil disturbance, direct incident radiation, heat load, topographic position) were more important to understanding patterns in biotic crust composition than larger-scale patterns, such as fire history and broad soil differences. Clearly, fire history and soils are important to biotic crust composition across sites, but within our study area, cheatgrass and site variation by topographic position yielded the most dramatic patterns.

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Literature Cited

Anderson, D. C., K. T. Harper & S. R. Rushforth. 1982. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. Journal of Range Management 35: 355–359.

Anderson, L. E., H. A. Crum & W. R. Buck. 1990. List of the mosses of North America north of Mexico. The Bryologist 93: 448–499.

Bailey, D., A. P. Mazurak & J. R. Rosowski. 1973. Aggregation of soil particles by algae. Journal of Phycology 9: 99–101.

Belnap, J. & D. Eldridge. 2001. Disturbance and recovery of biological soil crusts. *In* J. Belnap & O.L. Lange (eds.), Biological soil crusts: structure, function and management. Ecological Studies 150: 363–383.

—— & J. S. Gardner. 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53: 40–47.

—— & K. T. Harper. 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Research and Rehabilitation 9: 107–115.

——, —— & S. D. Warren. 1994. Surface disturbance of cryptobiotic soil crusts: nitrogenase activity, chlorophyll content, and chlorophyll degradation. Arid Soil Research and Rehabilitation 8: 1–8.

Beymer, R. J. & J. M. Klopatek. 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Park. American Midland Naturalist 127: 139–148.

Campbell, S. E., J. Seeler & S. Golubic. 1989. Desert crust formation and soil stabilization. Arid Soil Research and Rehabilitation 3: 217–228.

Cole, D. S. 1990. Trampling disturbance and recovery of cryptogamic soil crusts in Grand Canyon National Park. Great Basin Naturalist 50: 321–325.

Danin, A. & E. Ganor. 1991. Trapping of airborne dust by mosses in the Negev Desert, Israel. Earth Surface Processes and Landforms 16: 153–162.

——, D. Inka, A. Sandler & R. Amit. 1998. Desert crust morphology and its relations to microbiotic succession at Mt. Sedom, Israel. Journal of Arid Environments 38: 161–174.

Daubenmire, R. 1970. Steppe vegetation of Washington. Washington Agricultural Experiment Station Technical Bulletin 62: 1–131.

Dufrêne, M. & P. Legendre. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67: 345–366.

Eldridge, D. J. 1996. Distribution and floristics of terricolous lichens in soil crusts in arid and semi-arid New South Wales, Australia. Australian Journal of Botany 44: 581–599.

—— & P. I. A. Kinnell. 1997. Assessment of erosion rates from microphyte-dominated calcareous soils under rain-impacted flow. Australian Journal of Soil Research 35: 475–489.

—— & R. Rosentreter. 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. Journal of Arid Environments 41: 11–25.

Esslinger, T. L. & R. S. Egan. 1995. A sixth checklist of the lichen-forming, lichenicolous, and allied fungi of the continental United States and Canada. The Bryologist 98: 467–549.

Evans, R. D. & J. R. Ehleringer. 1993. A break in the nitrogen cycle in arid lands? Evidence from δ^{15}N of soils. Oecologia 94: 314–317.

Harper, K. T. & R. L. Pendleton. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? Great Basin Naturalist 53: 59–72.

Harris, C. F. T. 1998. Digital Geologic Mapping Project. Washington Department of Natural Resources, Division of Geology and Earth Resources. Open-file Report.

Hastie, T., R. Tibshirani & J. Friedman. 2001. The Elements of Statistical Learning. Springer, New York.

Hodgins, I. W. & R. W. Rogers. 1997. Correlations of stocking with the cryptogamic soil crusts of a semi-arid rangeland in southwest Queensland. Australian Journal of Ecology 22: 425–431.

Jeffries, D. L., J. M. Klopatek, S. O. Link & H. Bolton Jr. 1992. Acetylene reduction by cryptogamic crusts from a blackbrush community as related to resaturation and dehydration. Soil Biology and Biochemistry 24: 1101–1105.

Johansen, J. R., J. Ashley & W. R. Rayburn. 1993. Effects of rangefire on soil algal crusts in semiarid shrub-steppe of the lower Columbia Basin and their subsequent recovery. Great Basin Naturalist 53: 73–88.

Kaltenecker, J. 1997. The Recovery of Microbiotic Crusts Following Post-Fire Rehabilitation on Rangelands of the Western Snake River Plain. M.S. Thesis, Boise State University, Boise, ID, U.S.A.

Kruskal, J. B. 1964. Nonmetric multidimensional scaling: a numerical method. Psychometrika 29: 115–129.

Link, S. O., B. D. Ryan, J. L. Downs, L. L. Caldwell, J. A. Soll, M. A. Hawke & J. Ponzetti. 2000. Lichens and mosses on shrub-steppe soils in southeastern Washington. Northwest Science 74: 50–56.

McCune, B., F. Camacho & J. Ponzetti. 2002. Three new species of *Trapeliopsis* on soil in western North America. The Bryologist 105: 78–85.

——, J. Dey, J. Peck, D. Cassell, K. Heiman, S. Will-Wolf & P. Neitlich. 1997. Repeatability of community data: species richness versus gradient scores in large-scale lichen studies. The Bryologist 100: 40–46.

—— & J. B. Grace. 2002. Analysis of Ecological Communities. MjM Software, Gleneden Beach, OR, USA.

—— & D. Keon. 2002. Equations for potential annual direct incident radiation and heat load. Journal of Vegetation Science 13: 603–606.

—— & M. J. Mefford. 1999. PC-ORD: Multivariate analysis of ecological data. Version 4.02. MjM Software, Gleneden Beach, OR, U.S.A.

—— & ——. 2004. HyperNiche. Nonparametric Multiplicative Habitat Modeling. Version 1.0. MjM Software, Gleneden Beach, OR, U.S.A.

——— & R. Rosentreter. 2007. Biotic soil crust lichens of the Columbia Basin. Monographs in North American Lichenology 1: 1–105.

Mielke, P. W. Jr. & K. J. Berry. 2001. Permutation Methods: A Distance Function Approach. Springer, New York.

Mücher, H. J., C. J. Chartres, D. J. Tongway & R. S. B. Greene. 1988. Micromorphology and significance of the surface crusts of soils in rangelands near Cobar, Australia. Geoderma 42: 227–244.

Ponzetti, J. M. & B. McCune. 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. The Bryologist 104: 212–225.

Printzen, C. & B. McCune. 2004. *Trapeliopsis*. Pages 538–541. *In* T. H. Nash III, B. D. Ryan, C. Gries & F. Bungartz (eds.), Lichen Flora of the Greater Sonoran Desert Region, Vol. 2. Lichens Unlimited, Tempe, AZ.

Rasmussen, J. J. 1971. Soil Survey of Benton County Area. Washington Agricultural Experiment Station and U.S.D.A. Soil Conservation Service. U.S. Government Printing Office, Washington, D.C.

Rosentreter, R. & J. Belnap. 2001. Biological soil crusts of North America. *In* J. Belnap & O.L. Lange (eds.), Biological soil crusts: structure, function and management. Ecological Studies 150: 31–50.

Snyder, J. M. & L. H. Wullstein. 1973. The role of desert cryptogams in N-fixation. American Midland Naturalist 90: 257–265.

Stotler, R. & B. Crandall-Stotler. 1977. A checklist of the liverworts and hornworts of North America. The Bryologist 80: 405–428.

USDA. 2005. The PLANTS Database, Ver. 3.5. Baton Rouge, Louisiana 70874-4490: U. S. Department of Agriculture, National Plant Data Center. http://plants.usda.gov

USGS. 1999. U.S. GeoData 7.5 Minute Digital Elevation Model. U. S. Geological Survey, EROS Data Center. http://edc.usgs.gov/

Western Regional Climate Center. 1999. Prosser 4 NE, Washington: Period of Record Monthly Climate Summary. http://www.wrcc.dri.edu/cgi-bin/cliRECtM.pl?wabent

Williams, J. D., J. P. Dobrowolski & N. E. West. 1995a. Microphytic crust influence on interrill erosion and infiltration capacity. Transactions of the American Society of Agricultural Engineers 38: 139–146.

———, —— & D. A. Gillette. 1995b. Microphytic crust influence on wind erosion. Transactions of the American Society of Agricultural Engineers 38: 131–137.

Young, J. A. & R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. Journal of Range Management 31: 283–289.

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