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Passive Restoration of Vegetation and Biological Soil Crusts Following 80 years of Exclusion from Grazing Across the Great Basin

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RESEARCH ARTICLE

Passive restoration of vegetation and biological soil crusts following 80 years of exclusion from grazing across the Great Basin

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Restoration targets for biological soil crusts are largely unknown. We surveyed seven 80-year-old grazing exclosures across northern Nevada for biocrusts to quantify reference conditions at relatively undisturbed sites. Exclosures were associated with the following plant communities: Wyoming big sagebrush, black sagebrush, and areas co-dominated by winterfat and Wyoming big sagebrush. Cover of biocrusts and shrubs were generally higher than other plant groups at these sites, regardless of being inside or outside of the exclosures, suggesting these groups make up most of the native flora across the region. Important in forming soil structure, cyanobacteria of the order Oscillatoriales were less abundant and diverse in black sagebrush communities. Grazing had a negative effect on the abundance of Oscillatoriales but not the number of algal taxa, including cyanobacteria. Abundance of light algal crusts were not influenced by plant community or grazing. Dark algal crusts were generally less abundant on grazed sites. Influences of plant community and grazing were most apparent when accounting for reproductive rates of lichens and mosses based on establishment mechanisms. Abundance of shrubs, perennial grasses, Oscillatoriales, fast reproducing biocrusts and the number of algal and cyanobacterial taxa, varied by plant community, suggesting that restoration should be plant community specific. We demonstrate the affinity of rapidly reproducing biocrusts for winterfat-Wyoming big sagebrush co-dominated plant communities, regardless of grazing pressure. Across sites, the effects of grazing were most evident on the abundance of Oscillatoriales and slowly reproducing biocrusts following 80 years of cessation from grazing.

Key words: algae, biocrusts, black sagebrush, cyanobacteria, livestock grazing, winterfat, Wyoming big sagebrush

Implications for Practice

- Restoration targets for biocrusts, like vascular plants, should be plant community specific.
- Inventories of biocrusts should be conducted before restoration as many species, particularly biocrusts that are fast reproducers, may not need to be reintroduced and restoration may not be necessary.
- Both the abundance of Oscillatoriales (order containing cyanobacteria that create soil structure) and biocrust species with slow rates of reproduction demonstrated passive recovery following 80 years of cessation from grazing, suggesting that passive recovery is a viable option over this time frame and that these species may be indicative of relatively undisturbed sites.

Introduction

Globally, biological soil crusts (biocrusts: lichens, mosses, fungi, prokaryotic bacteria, and eukaryotic algae) contribute to ecosystem functions such as the prevention of soil erosion, nutrient, and hydrologic cycling (Evans & Ehleringer 1993; Belnap & Gillette 1998; Belnap & Lange 2003; Cantón et al. 2004; Bowker et al. 2011). Specifically, biocrust components provide many complementary ecosystem functions. Lichens alter

water retention and infiltration, enhance soil stability, fix nitrogen, and sequester carbon (Eldridge et al. 2010; Chamizo et al. 2012; Elbert et al. 2012). Mosses facilitate water infiltration, trap mobile soil surface particles, and directly contribute organic matter to soils (Danin & Gaynor 1991; Melick & Seppelt 1992; Zhang et al. 2009). Cyanobacteria, other bacteria, and eukaryotic algae contribute to the stabilization of soils and contribute to carbon and nitrogen cycling (Garcia-Pichel & Wojciechowski 2009; Büdel et al. 2016).

Author contributions: LAC, DAP conceived the study and wrote the manuscript; LAC analyzed the data; NP contributed to the methods used and data collection on algae, including cyanobacteria; RR assigned reproductive rates of species.

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In semiarid and arid regions biocrust often cover up to 70% of the undisturbed landscape (Belnap & Lange 2003). Additionally, the primary land use in semiarid and arid regions is livestock grazing (West 1983). In the sagebrush steppe of North America, overgrazing leads to the dominance of annual invasive grasses such as cheatgrass, *Bromus tectorum* L. However, high cover of biocrusts in conjunction with vegetation cover is associated with low cover of cheatgrass (Reisner et al. 2013; Condon & Pyke 2018a, 2018b). Following disturbance, cheatgrass fills the interspaces between perennial plants, resulting in an increase in the frequency and extent of fire (Germino et al. 2015). Despite the important association between biocrusts and low cover of cheatgrass, little is known about what biocrusts look like in the absence of anthropogenic disturbance across the region.

The practice of restoration ecology is not a science unless it is grounded in observational and experimental studies (Bradshaw 1983). Scientifically based restoration targets require reference sites; sites that share potential community compositions with the target restoration site under intact ecosystem processes (White & Walker 1997). Both restoration sites and associated reference sites are experiencing change through time and similar current conditions. This concept should not be confused with trying to restore to historical conditions. Without reference sites, restoration efforts do not have ecologically meaningful targets. These targets are challenging in the sagebrush steppe of the Great Basin given historical overgrazing across the region (Leopold 1924). In response to overgrazing, the Taylor Grazing Act was implemented in 1934 “[t]o stop injury to the public grazing lands by preventing overgrazing and soil deterioration, to provide for their orderly use, improvement, and development, to stabilize the livestock industry dependent upon the public range, and for other purposes” (48 Stat 1269, “Act of June 28, 1934” codified at 43 U.S.C. 315 et seq). Associated with the Act, 28 livestock exclosures were constructed across the state of Nevada. Exclosure locations were cooperatively selected by the U.S. Forest Service Intermountain Forest and Range Experiment Station, the University of Nevada Agricultural Experiment Station, and the Taylor Grazing Service on areas considered to be severely overgrazed (Holmgren 1976; Burnside 1988). Although some exclosures are in areas that have since become private land or have been damaged, the remaining sites are potential reference sites that have not been grazed or burned in the last 80 years. Additionally, these exclosures present an opportunity to observe the effects of passive restoration on biocrusts. We define passive restoration as the removal of a disturbance with the intent of seeing a community return to its native components through natural successional and climatic processes. Rest from disturbances such as grazing may be a viable restoration alternative in some scenarios if a threshold of species change has not been reached (Suding & Hobbs 2009; Pyke 2011).

In other ecosystems, such as the Namib Desert (southwest coast of Africa), southeast Australia, the Monte Desert (Argentina), the Mojave Desert (U.S.A.), and oak woodlands in Portugal, the passive recovery of biocrusts has been noted following the cessation of disturbance, but these studies have all been on the timescale of 4–50 years following disturbance

(Lalley & Viles 2008; Pietrasiak et al. 2011; Read et al. 2011; Gómez et al. 2012; Concostrina-Zubiri et al. 2016). The Taylor Grazing Act exclosures have been in place for 80 years and represent the first study that we know of within this time frame. Although our study is in the cold desert of the Great Basin, many of the growth forms and genera of biocrust species found in the Great Basin also occur in arid and semiarid systems globally (Bowker et al. 2016). An evaluation of these exclosures may provide insight into recovery patterns of biocrusts that we would expect to find globally following the removal of disturbance such as grazing. These exclosures were surveyed with the purpose of addressing four questions: (1) Is there a difference in the abundance of biocrust components, specifically light algal, dark algal, moss and lichen crusts as well as vascular plant groups: annual forbs, perennial forbs, cheatgrass, perennial grasses and shrubs following 80 years of exclusion from grazing?; (2) Does the recovery of biocrusts from grazing vary by reproductive rate of species?; (3) Is the abundance of cyanobacteria in the order Oscillatoriales and species richness of algae in the soil different following 80 years of cessation from grazing?; (4) Does the identity of the associated plant community affect the presence or recovery of any of the above-mentioned groups?

The first question gives us an opportunity to assess the abundance of vascular plants and biocrust components across the region, elucidating restoration targets (the goals of restoration) with passive recovery in mind. We differentiate light and dark algal crusts because this can easily be done in the field. Light algal crusts are dominated by members of the cyanobacterial order Oscillatoriales. Species of the order Oscillatoriales such as *Microcoleus vaginatus*, *Microcoleus steenstrupii*, *Kastovskya adunca*, *Phormidium* spp., and *Symplocastrum* spp. are known to produce copious amounts of sticky exopolysaccharides and are recognized as key species in biocrust formation and establishment. Species that dominate dark algal crusts are often the photobionts in cyanolichens, such as *Nostoc* spp. and *Scytonema* spp., darkening the soil surface due to their sun screen pigmentation. These species fix greater amounts of nitrogen compared to other groups (Pietrasiak et al. 2013). The second question gives us insight into restoration targets that are related to the reproductive rates of biocrust species. The third question allows us to assess if the potential of Oscillatoriales and algae to recover following disturbance is limited by being present onsite. We use the terms “algae” or “algae, including cyanobacteria” to refer to both cyanobacteria and eukaryotic algae unless specified. The fourth question gives us insight into potential targets for biocrust and vascular plant restoration amongst varying environmental gradients. The influence of plant community is examined with each of the preceding questions. Restoration of plant communities has historically balanced what is present onsite with what should be onsite, weighing what can most reliably be achieved with active versus passive restoration over an acceptable time frame. We expect that the compilation of findings from our research questions will provide the first documented attempt at creating a restoration framework for biocrusts considering both biocrust and vegetation components as well as biocrusts as related to reproductive speed.

Table 1. Ecological site descriptions and environmental information on each of the grazing exclosures.

Exclosure	Elevation (m)	Average Freeze-Free Period (days)	Ecological Site Description	30-Year Averages
Baker 38°56'42.70" N 114°03'10.18" W	1,617	100–120	Loam 8–10 P.Z., R028AY015NV <i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> / <i>Achnatherum hymenoides</i> - <i>Hesperostipa comata</i>	33.11°C max temp –8.92°C min temp 221 mm precipitation
Conner Station 39°01'57.08" N 114°33'11.25" W	1,846	100–140	Shallow Calcareous Loam 8–10 P.Z., R028AY013NV <i>Artemisia nova</i> / <i>Achnatherum hymenoides</i> - <i>Hesperostipa comata</i>	31.12°C max temp –9.85°C min temp 257 mm precipitation
Dinner Station 41°08'16.39" N 115°50'52.69" W	1,789	100–120	Loamy 8–10 P.Z., R025XY019NV <i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> / <i>Achnatherum thurberianum</i> / <i>Pseudoroegneria spicata</i>	29.42°C max temp –11.07°C min temp 300 mm precipitation
Newark Valley 1 39°24'49.18" N 115°35'25.84" W	1,909	100–120	Shallow Calcareous Loam 8–10 P.Z., R028BY011NV <i>Artemisia nova</i> / <i>Achnatherum hymenoides</i> - <i>Hesperostipa comata</i>	30.57°C max temp –10.38°C min temp 237 mm precipitation
Newark Valley 2 39°25'36.08" N 115°38'15.92" W	1,850	90–150	Silty 8–10 P.Z., R028BY013NV <i>Krascheninnikovia lanata</i> / <i>Achnatherum hymenoides</i> - <i>Elymus elymoides</i>	30.89°C max temp –10.48°C min temp 230 mm precipitation
Paradise Valley 1 41°22'26.50" N 117°33'51.57" W	1,339	90–120	Loamy 8–10 P.Z., R024XY005NV <i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> / <i>Achnatherum thurberianum</i>	32.7°C max temp –7.6°C min temp 242 mm precipitation
Paradise Valley 2 41°33'44.89" N 117°32'45.25" W	1,472	90–110	Loamy 8–10 P.Z., R024XY005NV <i>Artemisia tridentata</i> ssp. <i>wyomingensis</i> / <i>Achnatherum thurberianum</i>	31.26°C max temp –7.88°C min temp 321 mm precipitation

Methods

Sixteen of the original 28 exclosures within the Nevada portion of the Great Basin were relocated and surveyed by Courtois et al. (2004). These same 16 exclosures were visited in the summer of 2016 and notes were made as to the status of the exclosures and if their fence lines were intact. Seven exclosures were noted as having intact fences and these were revisited in May of 2018 (Table 1). Most exclosures cover an area of 1.6 ha (100 m × 160 m). In most exclosures, the area immediately surrounding the ladder into each exclosure appeared trampled. This was the only area in each surveyed exclosure where trampling appeared to be of concern. We started each transect at the edge of the trampled area and extended the transect in the direction of the opposing exclosure corner. Transects outside of each exclosure continued in the same direction as the transect inside of the exclosure. Fifteen, 0.25-m × 0.25-m quadrats were surveyed both inside and outside of each exclosure. Quadrats were placed 10 m apart along a transect. Within a quadrat, 40 point-vertex intercept readings were used to measure cover of all vascular plant, lichen and moss species as well as light and dark algal crusts. Species of biocrusts were identified using McCune and Rosentreter (2007). Cover was summarized for each component by location: inside or outside of each exclosure. Soils were collected from each quadrat using a core set to a 1 cm depth and pooled by location (inside or outside) per exclosure for algal enumeration.

Separate from the abundance data collected in the field survey, algal enumeration was performed with a second assessment using the moistened soil method (MSM, Johansen et al. 2001). Replicates consisted of 9 g of soil placed in 5 cm diameter petri dishes and three replicates were used per location (inside

or outside) per exclosure. Soil in petri dishes was wetted to glistening and kept under an illumination schedule of 16 hours of light followed by 8 hours of darkness. Illumination ranged from 35–44 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Given the variation in light, dishes were blocked within this range. Replicates were randomly assigned positions within each of three blocks. At 1, 2, and 7 days after wetting, petri dishes were examined under a dissecting microscope. Hardware cloth with a 6-mm mesh size was shaped to fit over each petri dish and used to quantify cover of algae that intersected each of 36 vertices at predetermined marks the hardware cloth. In general, cyanobacteria of the order Oscillatoriales are the first algae (including cyanobacteria) to colonize the soil surface in the petri dishes, appearing at the surface after 24 hours. Algae of other orders and phyla often require more incubation time. After 7 days heterocytous cyanobacteria and eukaryotic algal colonies can therefore be detected, which warrants this time point.

Data on grazing intensity follow methods in Condon and Pyke (2018a). Examining grazing intensity can be more informative than presence or absence of grazing because allotments differ in size, number of animal unit months (AUMs), and pattern of use. AUMs that are actively being grazed on an allotment as well as those that have been suspended from an allotment were obtained from the Rangeland Administration System (RAS 2018). AUMs are an estimate of the amount of forage needed to sustain a standard animal unit (for example, a 454-kg cow with a suckling calf for 1 month) (Ruyle & Ogen 1993). This can be translated into the grazing capacity of a site as well as possible overgrazing of a site as RAS reports the number of suspended AUMs, which is the number of AUMs removed from use that are not likely to be replaced because vegetation and

soil management objectives are not being met (Ruyle & Ogen 1993). We use ratios as presented in Condon and Pyke (2018a) of active AUMs over permitted AUMs and suspended AUMs over permitted AUMs to represent grazing intensity and possible overgrazing. We also use a piosphere approach creating a proxy for declining grazing intensity with increasing distance from water (Andrew & Lange 1986). We repeated the methods used in Condon and Pyke (2018a), mapping distance to the closest water source in ESRI ArcMap 10.2 with a combination of 1-m resolution imagery from the National Agriculture Imagery Program and the National Hydrography Dataset (accessed 10 February, 2016; <http://nhd.usgs.gov>, ESRI 2013).

Species vary in their ability to reproduce via fragmentation or asexual propagules, such as pycnidia, soredia, and isidia versus sexual structures such as spores (Rosentreter unpublished data). Working under the assumption that smaller, more numerous propagules would result in faster rates of reproduction, reproductive rates were assigned to frequently encountered species in the region (Table S1). These assignments allow for the testing of ability of species to recover passively with more knowledge about how they establish compared with broad classifications based on morphological groups.

Analyses

Before determining the influence of passive restoration on cover of vascular plants and biocrusts, we wanted to establish the degree to which community composition differed amongst locations and determine which locations had similar plant communities. Plant community identities were defined using cluster analysis with Ward's method as the group linkage method on each combination of enclosure and location, whether the survey location was inside or outside of the respective enclosure. This approach uses both cover data of vascular plants as well as biocrusts. Identified groups were tested for statistical differences with multi-response permutation procedure. Euclidean distance was used as the distance measure in both analyses.

To characterize the driving factors that separated these groups, including grazing, we used non-metric multidimensional scaling ordinations with Sorenson distance measure. We did not transform the data. We used a random starting configuration with 250 runs of real data. Ordinations were overlaid with elevation, climatic variables: 30-year average precipitation, maximum temperature and minimum temperature, maximum number of frost-free days, minimum number of frost-free days and disturbance variables related to grazing intensity: distance from water, and ratios of active and suspended animal unit months (AUMs) over permitted AUMs. Climate data were taken from PRISM (2010).

We tested for the influence of grazing exclusion and plant community identity on vascular plant groups, individual components of biocrusts (grouped by light algal crusts, dark algal crusts, moss, and lichen), the abundance of algal propagules, including cyanobacteria (from MSM, day 7), and number of taxa in the soil, as well as species of biocrusts categorized by reproductive rate (fast, medium, slow). Analysis of variance

(ANOVA) was performed on separate linear models of each category listed: each vascular plant group, biocrust component, abundance of algal propagules, and each reproductive speed. Models were checked for assumptions of normality and symmetry. Linear models and associated ANOVA tables were performed in R version 3.4.0 and R Studio version 1.0.143 (R Core Team 2017). Multivariate analyses were performed in PC-ORD version 7. F statistics with p values of 0.1 or less are discussed.

Results

Pruning the dendrogram with 60% information remaining resulted in three groups: Baker, Newark Valley 2; Conner, Newark Valley 1; and Dinner Station, Paradise Valley 1 and Paradise Valley 2. We arrived at the same groups with 60% information remaining regardless of whether we included both vascular plants and biocrusts or just biocrusts. All groups were determined to be statistically different from one another (A -statistic = 0.40, p value < 0.001) and differed in dominant plant species that define communities. The Baker-Newark Valley 2 group is co-dominated by Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and winterfat (*Krascheninnikovia lanata* [Pursh] A. Meeuse & Smit). The Conner Station, Newark Valley 1 group is dominated by black sagebrush (*Artemisia nova* A. Nelson) with calcareous soils. The Dinner Station, Paradise Valley 1 and 2 group is dominated by Wyoming big sagebrush and are on similar ecological sites, but Dinner Station is in the adjacent Major Land Resource Area (MLRA 25 Owyhee High Plateau) from the Paradise Valley exclosures (MLRA 24 Humboldt Area). Burnside (1988) reports that the outside of the Paradise Valley exclosures had been sprayed and seeded to crested wheatgrass in the past.

Non-metric multidimensional scaling ordination resulted in a 2D solution with a final stress of 7.90 and a final instability of 0.00 after 37 iterations. Along Axis 1, groups separated by abundance of Oscillatoriales in the soil, minimum temperature, and rabbit dung, and opposed elevation, gravel, minimum number of frost-free days (Fig. 1, Table S2). The influence of elevation ($R = 0.729$, $R^2 = 0.531$) and gravel ($R = 0.807$, $R^2 = 0.652$) were notably strong. The abundance of Oscillatoriales was strongly associated with community structure along both Axis 1 ($R = -0.704$, $R^2 = 0.495$) and Axis 2 ($R = -0.544$, $R^2 = 0.296$, Fig. 1, Table S2). Axis 1 explained 63.4% of the variance and Axis 2 explained 25.9% of the variance for a total of 89.3% variance explained by the ordination.

The influence of plant community and grazing demonstrated different and sometimes interacting effects on the abundance of biocrust and vascular plant components. ANOVA on a linear model of cover of light algal crust did not demonstrate effects of grazing or plant community (Table S3). ANOVA on a linear model of cover of dark algal crust demonstrated an interaction between grazing and plant community ($F_{2,9} = 3.48$, $p = 0.08$, Table S3). Cover of dark algal crusts alternated between higher and lower cover, inside and outside of the Wyoming big sagebrush exclosures (Fig. 2) driving the weak interaction. An effect

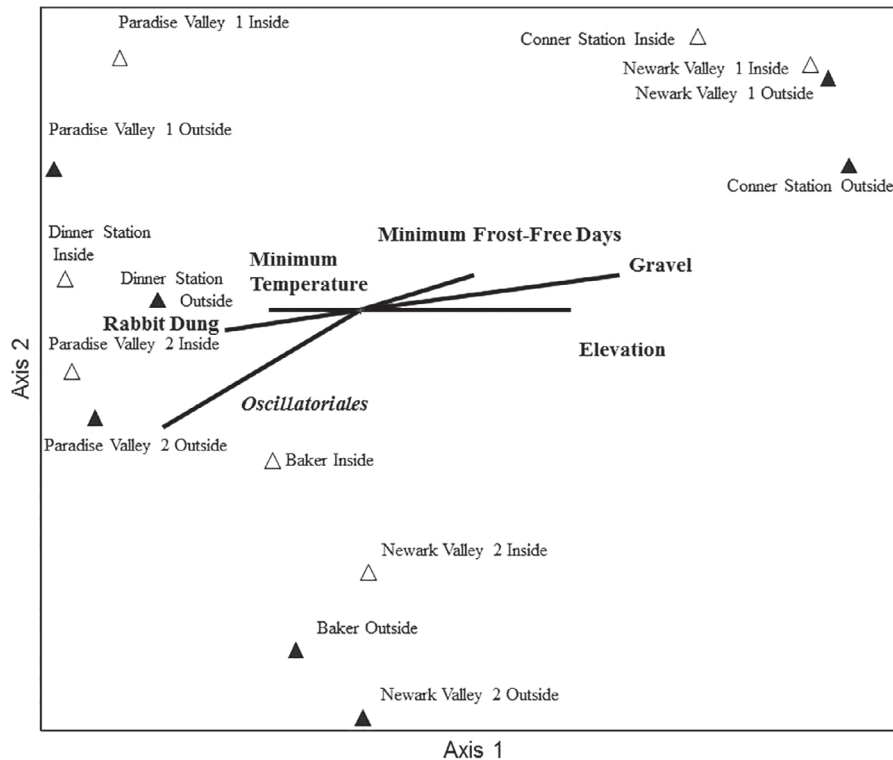


Figure 1. Non-metric multidimensional scaling ordination of enclosure-locations in species space. Both vascular plant and biocrust species are included. Results from cluster analysis assigned sites to the following groups: black sage (Conner Station, Newark Valley 1), winterfat-Wyoming big sagebrush (Baker, Newark Valley 2), and Wyoming big sagebrush (Paradise Valley 1, 2, and Dinner Station).

of plant community was found on the abundance of moss ($F_{2,9} = 3.37$, $p = 0.09$, Table S3). The effect of grazing on lichen cover trended towards negative (Fig. 2). When taking reproductive speed into account, grazing influenced the cover of slow reproducers ($F_{1,9} = 3.54$, $p = 0.10$, Fig. 3, Table S4) and plant community influenced the cover of fast reproducers ($F_{2,9} = 7.57$, $p = 0.01$, Fig. 3, Table S4). Plant community was associated with differences in cover of shrubs ($F_{2,9} = 3.22$, $p = 0.09$, Table S3), perennial grasses ($F_{2,9} = 4.33$, $p = 0.05$, Table S3), and cheatgrass ($F_{2,9} = 14.72$, $p = 0.001$, Table S3), but not other vascular plant groups. Abundance of cheatgrass was also influenced by grazing ($F_{1,9} = 22.308$, $p = 0.002$, Table S3) as well as an interaction between plant community and grazing ($F_{2,9} = 18.538$, $p = 0.001$, Table S3).

Abundance of Oscillatoriales in the soil as determined by MSM varied by site (Fig. 4). Grazing effects on abundance of Oscillatoriales were negative ($F_{1,9} = 3.75$, $p = 0.09$, Table S3, Fig. 3), and abundance of Oscillatoriales varied by plant community ($F_{2,9} = 13.66$, $p < 0.001$, Table S3). Sites belonging to the black sagebrush plant community group (Conner Station and Newark Valley) demonstrated a lower abundance of Oscillatoriales although these soils did have some presence of Oscillatoriales by day 7 of the MSM (Fig. 4) and were lower in cover compared to all other enclosures surveyed (Fig. 1). Species richness of algae, including cyanobacteria, followed similar patterns as the number of taxa varied by plant community and were lowest in the black sagebrush plant community

sites (Fig. 4, $F_{2,9} = 10.49$, $p = 0.01$, Tables S4 & S5). Functional groups have been assigned to identified algal taxa based on morphologies but algae have not been analyzed according to functional groups in this study because many of these functions have yet been tested empirically (Table S5, Fig. 5, Ettl & Gartner 1995; Komárek & Anagnostidis 1998, 2005; Rosentreter et al. 2007).

Discussion

We demonstrate that the composition and abundance of biocrusts vary with plant community across the Great Basin, indicating that restoration targets should be plant community specific. The effects of grazing were most apparent on the abundance of Oscillatoriales, cheatgrass, and biocrusts as grouped by reproductive rate. Slow reproducers, biocrust species that are largely dependent on spores for reproduction, were less abundant in actively grazed areas in plant communities dominated by Wyoming big sagebrush or co-dominated by winterfat and Wyoming big sagebrush. Although a significant interaction was not found between plant community and grazing on the abundance of slow reproducers, slightly greater abundance of slow reproducers in grazed black sagebrush sites likely weakened the relationship between grazing and slow reproducers. Fast reproducers, biocrust species that reproduce via asexual structures or with lots of spores, were more abundant

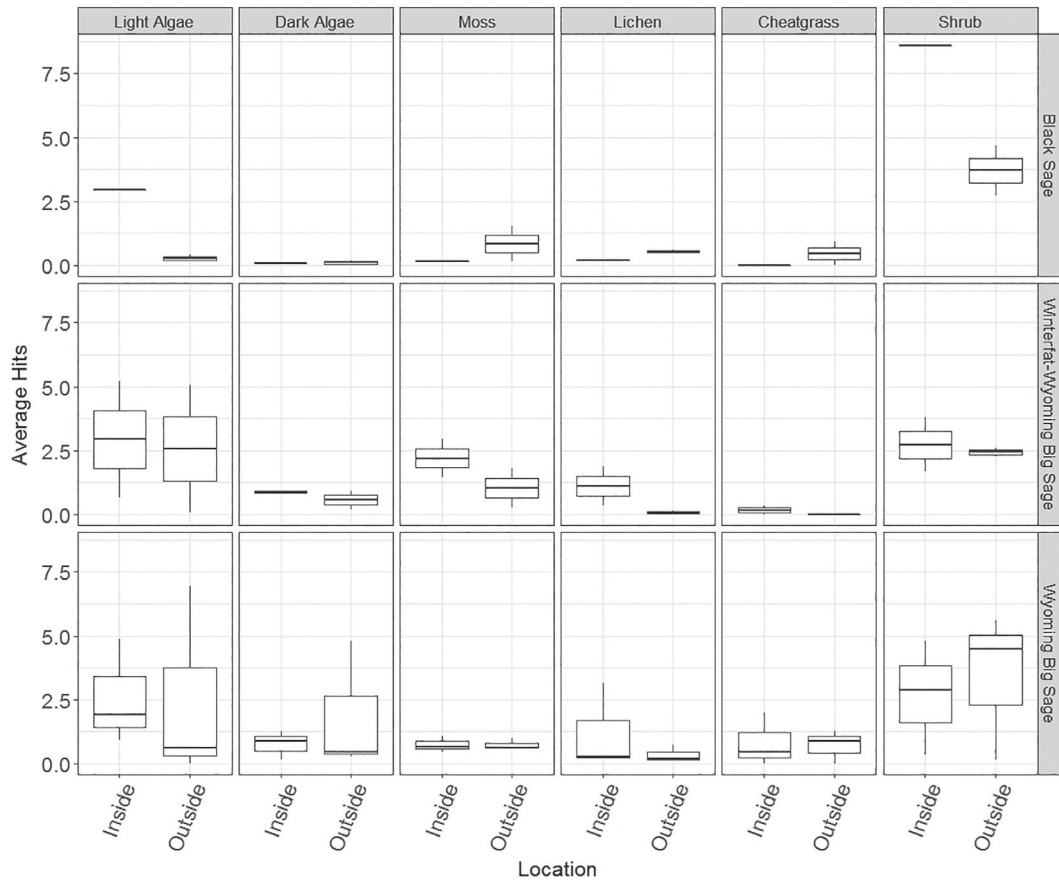


Figure 2. Boxplots of point intercept hits of vegetation and biocrust components by plant community groups.

in winterfat-Wyoming big sagebrush co-dominated plant communities. Effects of grazing on Oscillatoriales as determined by MSM were associated with abundance and not on the number of taxa, suggesting that propagules of algae, including cyanobacteria, are in the soil and have the potential to recover under the right conditions.

Although cyanobacteria from the order Oscillatoriales are reported to occur globally, “everything is not everywhere” and habitat characteristics are likely influencing the presence of some species (Ribeiro et al. 2018). Dust movements between continents make it likely that there is genetic flow amongst these organisms at global scales (Kellogg & Griffin 2006). However, we saw lower numbers of algal taxa, including cyanobacteria from sites that are dominated by black sagebrush and are high in carbonates, suggesting that algae are not naturally abundant in all plant communities. Some environments such as desert pavements naturally have low diversity of biocrusts (Pietrasiek et al. 2014), indicating that restoration targets for biocrust communities should be specific to the plant community and site conditions of the target restoration site.

Although few differences in vegetation cover between inside and outside of the exclosures were apparent in the previous survey of these sites (Courtois et al. 2004), we demonstrate differences in the abundance of Oscillatoriales and slowly

reproducing biocrust species following the removal of grazing pressure. With the exception of cheatgrass, which was sometimes found to be more abundant outside of exclosures, differences that were seen in vegetation cover were associated with differences in plant communities and not the presence or absence of grazing. Similar observations have been made in the sagebrush steppe of eastern Oregon where differences in the cover of vascular plants following the cessation of grazing were not observed but the cover and composition of biocrusts differed (Ponzetti & McCune 2001). In western Colorado, reference conditions in the sagebrush steppe, specifically black sagebrush and Wyoming big sagebrush plant communities, were associated with high cover of biocrusts (Shinneman et al. 2008). Our data corroborate that relatively higher cover of some biocrust components are indicative of low levels of disturbance in the sagebrush steppe (Condon & Pyke 2018b), and that in arid and semiarid systems in general, species composition is affected by grazing (Hodgins & Rogers 1997).

We were surprised to see mostly moderate relationships between biocrust components, plant communities, and grazing. Condon and Pyke (2018b) intentionally covered disturbance gradients related to fire and grazing. In this study, we examined 80-year-old grazing exclosures that were judged to be the most intact seven of the original 28 exclosures and remaining 16 exclosures in Nevada (U.S.A.). It is possible that

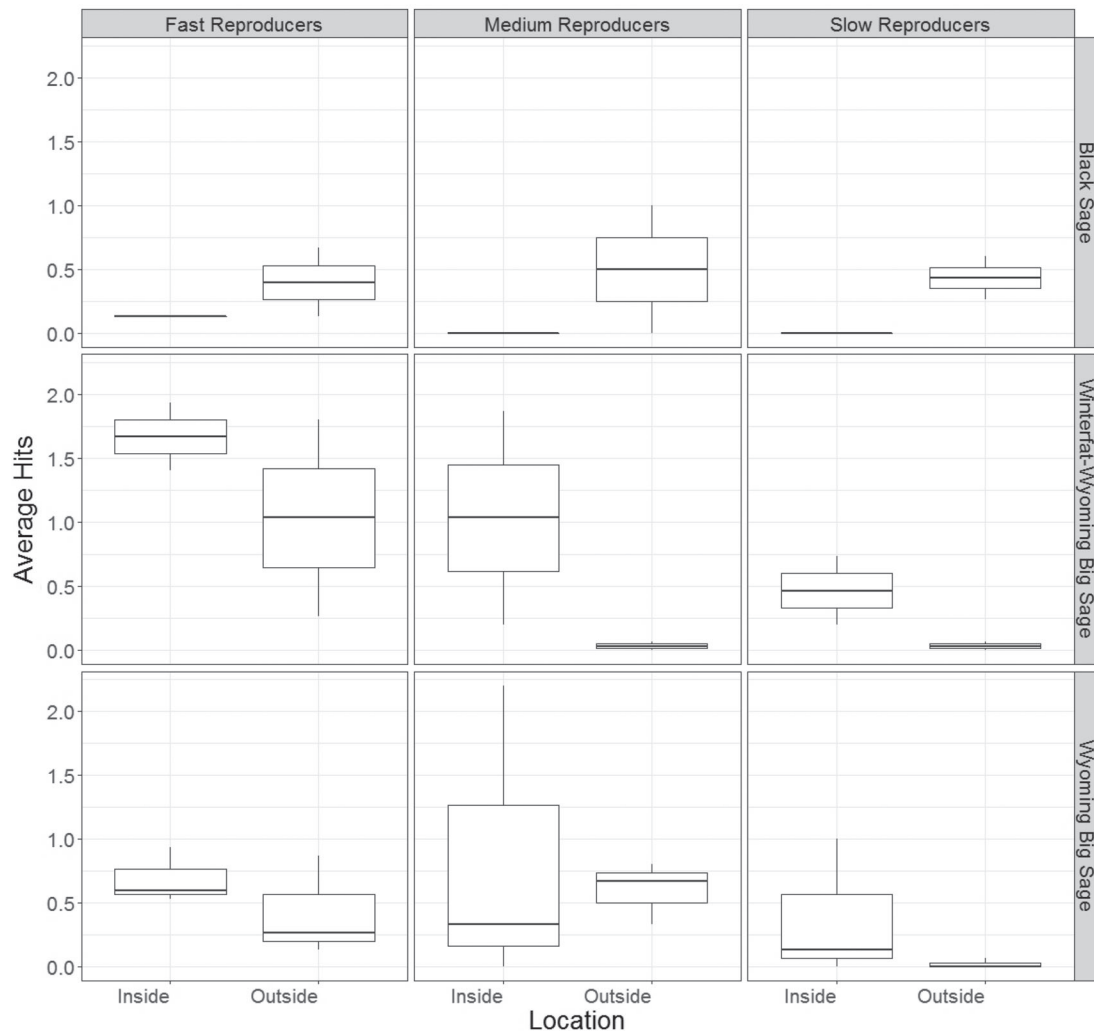


Figure 3. Boxplots of point intercept hits of biocrust categorized by reproductive speed and grouped by plant community.

these seven exclosures were intact because they received less traffic over the last 80 years compared with the other exclosures. If that is the case, this study addresses the low end of the disturbance spectrum, where we detected differences in the composition of biocrusts related to reproductive speed but only weak differences with components. Over this period of low to no disturbance (inside and outside of the exclosures), vegetation cover was fairly low with the exception of shrub cover. In Wyoming big sagebrush communities, perennial grasses increase with some disturbance and many have been shown to remain at the same density or decrease over a period of 13 years (Nafus et al. 2015; Condon & Pyke 2018b). Low vegetation cover with intact biocrusts can be indicative of low levels of disturbance.

Passive recovery of biocrusts, particularly of algae, including cyanobacteria and other crust species with fast rates of reproduction, has the potential to be a viable option in some areas, over short time frames (Miller et al. 2017; Warren et al. 2018). The occurrence of these species was more associated with identified plant communities compared to the presence of grazing.

Following the removal of heavy disturbance in Wyoming big sagebrush communities, we should expect to see increases in the abundance of fast reproducing biocrust species. Given the limited number of species representing each reproductive rate in this observational study (4–10 species, Table S1), future work aimed at specifically relating the number of propagules that a species produces with the ability of that species to quickly establish after disturbance should be further examined. If passive recovery of mosses in semiarid environments is the goal, a time frame of approximately 20 years has been shown to be realistic in eucalyptus and bull oak woodlands in southeastern Australia and Mediterranean oak woodlands respectively (Read et al. 2011; Concostrina-Zubiri et al. 2016). However, if sites are devoid of propagules due to intensive disturbance or if higher cover of biocrusts over a shorter period of time is a management goal, active restoration may be warranted. Active restoration on sterile soils in a field setting has led to regular increases in moss cover of 30% annually (Condon & Pyke 2016) and the

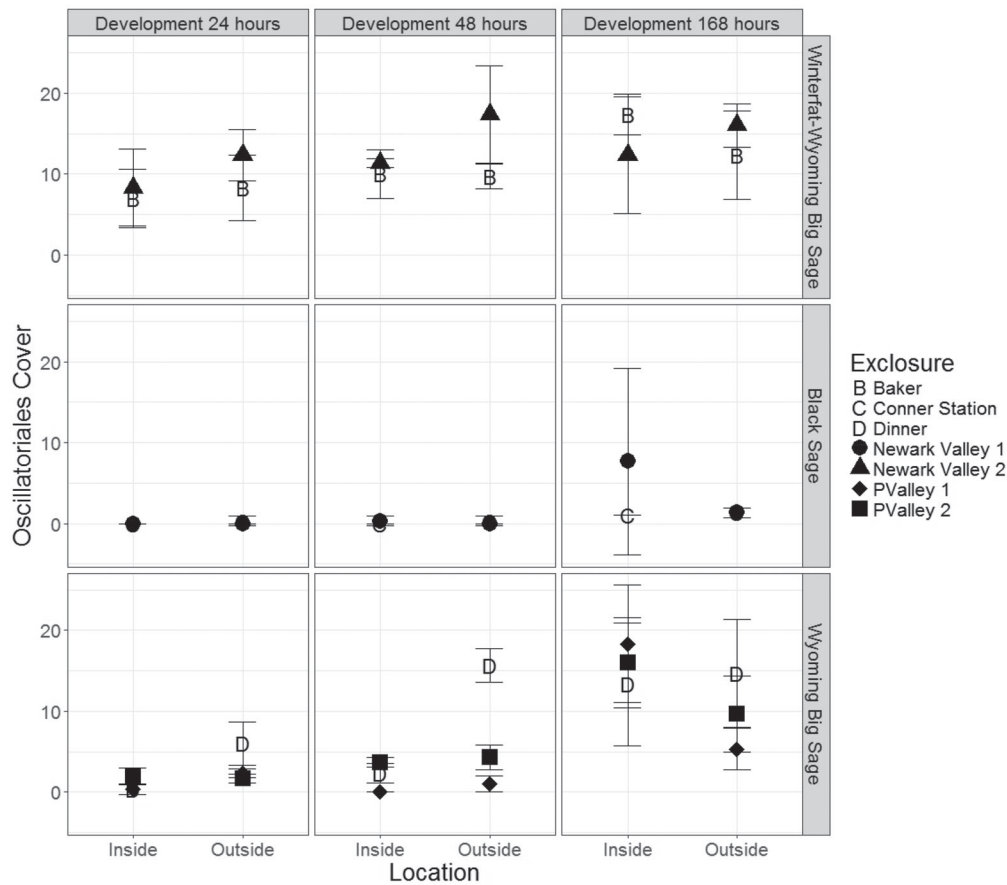


Figure 4. Oscillatoriales cover as determined by the moistened soil method (MSM) following wetting at 24, 48, and 168 hours. PValley refers to the Paradise Valley sites.

use of tackifiers shows potential for facilitating moss establishment and growth in hydromulch applications (Blankenship et al. 2019).

Previous work has demonstrated a positive influence of both wetter climates (Belnap & Lange 2003; Lalley & Viles 2008) and finer textured soils (Belnap & Eldridge 2003) on the recovery of biocrust. Our study consists of sites that all generally experience 8–10 inches of precipitation a year (203–254 mm) and are predominately loamy soils. Under these conditions, sites clustered into three distinct plant communities. The one site that was described as having silty soils (Newark Valley 2) was co-dominated by Wyoming big sagebrush and winterfat. This vegetation type consistently showed higher abundance and cover of algae and higher cover of biocrust components regardless of assigned reproductive rates. Interpreting precipitation as constant, as it relates to ecological site descriptions, we see a positive influence of fine textured soils on the recovery of biocrusts as inferred by plant community composition.

The practice of restoration pairs disturbed sites that are to be restored with undisturbed or minimally disturbed reference sites to define the species and ecosystem processes for reintroduction (Bradshaw 1983). In the case of biocrusts, biodiversity and

function tend to overlap (Bowker et al. 2008). Although we use these exclosures across northern Nevada as potential reference sites, these sites only provide two to three locations per plant community. The plant communities that are addressed in this study are indicative of the elevation ranges present in this region (West & Young 2000). Most other plant communities in the region are either higher in elevation, riparian, or on the edge of the region such as those mixing with the Mojave Desert. There are noticeable differences in the recovery of each site, signifying that all restorations are to some extent unique (Stuble et al. 2017). We know that the history of use at each site varied and the exclosure locations were likely selected to document “recovery” from grazing and not because they were pristine (Holmgren 1976). Our knowledge of disturbance history of these sites prior to the exclosures being constructed is minimal and it is possible that the sites varied in disturbance intensity prior to the construction of the exclosures, which would obviously influence trajectories of recovery. These exclosures have been in place for 80 years, which is a long period of time to have experienced the removal of disturbance but given past linear approximations of the recovery of biocrusts, this time scale could be considered short (Belnap & Eldridge 2003), possibly explaining why we saw low cover of biocrusts with slow to medium speed of

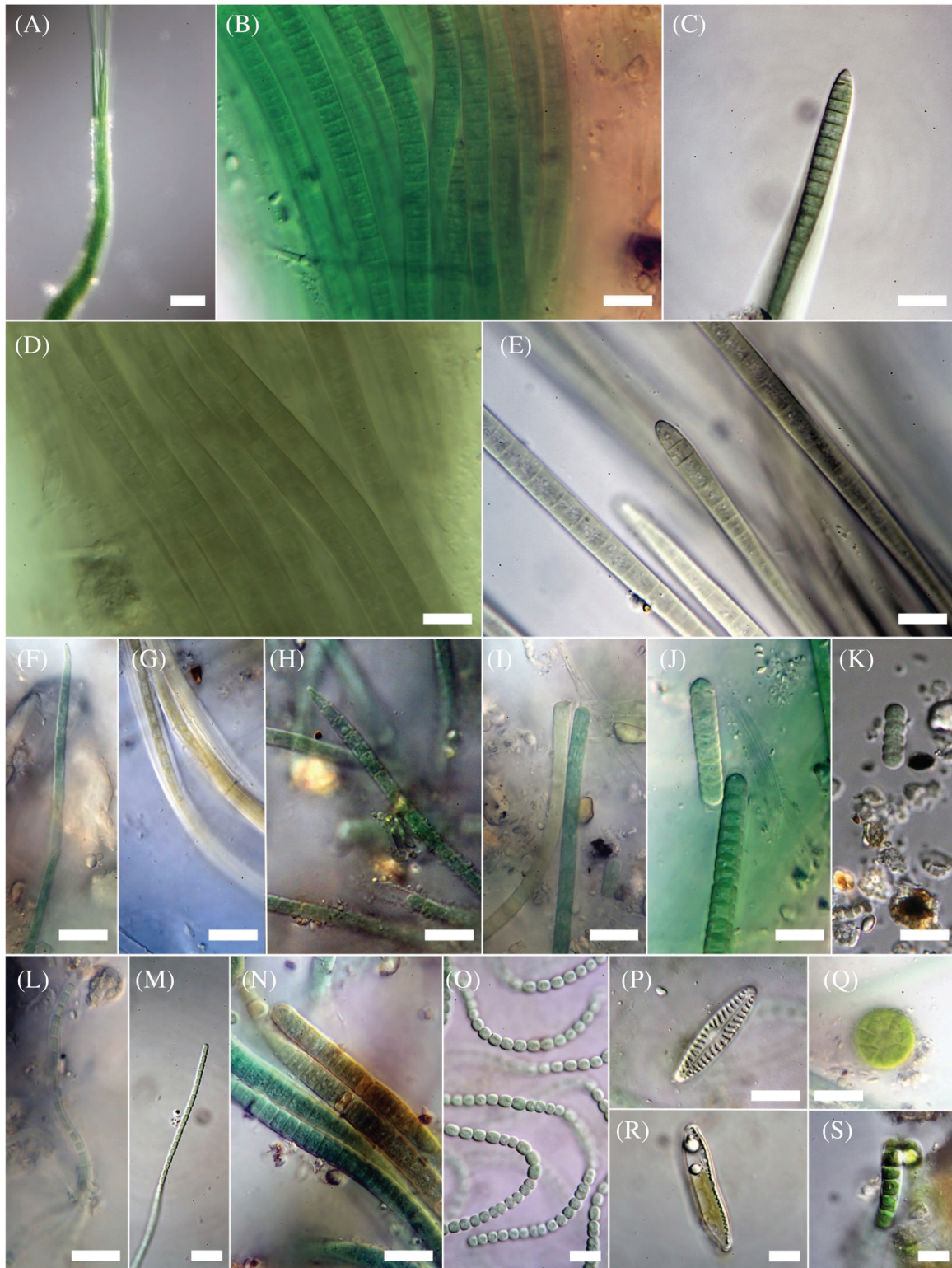


Figure 5. Microscopy images of selected algal taxa observed in the soil plates after performing the modified moistened soil method: (A–C) *Microcoleus vaginatus*—variety: bluegreen; (D–E) *M. vaginatus*—variety: brownish-bluegreen; (F) *M. cf. vaginatus* with bend tip; (G) *Symplocastrum* sp.; (H) *Microcoleus steenstrupii*; (I) *Microcoleus* sp.; (J) *Phormidium* sp.; (K) *Hormoscilla* sp.; (L) unknown *Synechococcales* cyanobacterial sp.; (M) unknown *Leptolyngbyaceae* cyanobacterial sp.; (N) *Hassallia* sp., (O) *Nostoc* sp., (P) *Pinnularia* sp.; (Q) *Bracteacoccus* sp.; (R) *Hantzschia* cf. *amphioxys*; (S) *Klebsormidium* sp. Scale bar in (A) represents 100 μm and scale bars shown in (B–S) represent 10 μm . Identification were made using Ettl & Gartner 1995; Komarek & Anagnostidis 1998, 2005.

reproduction. We hope to call attention to the need to document biocrusts in the region and the need to identify and protect areas with intact communities given their potential use as reference sites.

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Supporting Information

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

Table S1. Common species of lichens and mosses and their associated reproductive rate based on establishment mechanisms.

Table S2. Correlations of predictor variables with non-metric multidimensional scaling ordination axes for all enclosure-locations.

Table S3. Analysis of variance table testing for differences in cover of biocrust components amongst plant communities and in the absence of grazing.

Table S4. Analysis of variance table testing for difference in cover of biocrusts as classified by reproductive speed. Assigned reproductive speeds are reported in Table S1.

Table S5. Taxon (species and varieties) of cyanobacteria encountered. Identifications are based on morphology.

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