

AN ABSTRACT OF THE DISSERTATION OF

Lea A. Condon for the degree of Doctor of Philosophy in Botany and Plant Pathology presented on May 4, 2016.

Title: Biological Soil Crusts of the Great Basin: An Examination of their Distribution, Recovery from Disturbance and Restoration

Abstract approved:

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We are at risk of losing the sagebrush steppe in the floristic Great Basin to the invasion of *Bromus tectorum* L., cheatgrass. The floristic Great Basin includes the Central Basin and Range, the Northern Basin and Range, and the Snake River Plain. The Great Basin receives most of its precipitation as winter snow and experiences hot and dry summers. Early accounts of invasion by cheatgrass associated it with farming and grazing practices. The non-farmed areas in the region are still actively grazed and referred to as rangelands. On invaded sites, cheatgrass changes the flammability of fuels on invaded landscapes, across the Great Basin, from coarser fuels that are widely spaced to fine fuels that are continuous, filling interspaces between perennial plants. The fuel load created by cheatgrass regenerates annually. This has resulted in a change in the fire regime of the Great Basin from infrequent, small fires to more frequent large fires.

In arid lands globally, soil interspaces between perennial plants are typically filled by biological soil crusts (biocrusts). This is also true for ecoregions in and surrounding the Great Basin. Biocrusts are known to influence many ecosystem processes that cheatgrass influences, specifically nutrient cycling and availability of soil moisture.

However, little work has been done on biocrusts of the Great Basin and to my knowledge, no one had restored biocrusts within the Great Basin. I attempt to fill some of this knowledge “interspace” by relating biocrust presence to disturbances and cheatgrass invasion and to demonstrate the potential for biocrust restoration within this region.

Previous work in eastern Oregon demonstrated relationships between declines in biocrusts and increases in cheatgrass with increasing grazing intensity, soil temperature, and decreasing soil moisture. Grazing intensity influences the cover of biocrusts as well as the abundance and composition of native bunchgrasses. Native bunchgrasses influence the interspace gap size between perennial herbaceous vegetation which is directly associated with the cover of cheatgrass. In a region where grazing records may be incomplete and may exist in various forms of data, having a simple indicator of grazing impacts would be useful. It is also crucial that we have an understanding of what leads to loss of site resistance to cheatgrass. This previous work suggested that cover of biocrusts, in addition to bunchgrass composition, were associated with increased site resistance to cheatgrass.

In Chapter 2, I used current grazing records from a range of suspected grazing intensities, to examine the ability of both biocrusts and perennial vegetation to maintain site resistance to cheatgrass after fire. I examined the ability of mosses and lichens to maintain site resistance separately given that these are two very different kinds of organisms. Mosses are non-vascular plants and early colonizers of sites in primary succession. Lichens have a symbiotic relationship between a fungus and a photosynthesizing partner, a cyanobacteria, an algae or both. Using structural equation models, I corroborated that perennial vegetation and lichens are associated with increased site resistance to cheatgrass and that mosses are associated with and may facilitate both lichens and perennial herbaceous vegetation. Also in Chapter 2, I identified that burned sites were associated with increased grazing pressure by

livestock as shown by increases in cow dung density and increases in gap size between perennial herbaceous vegetation.

The Great Basin is managed for cover of perennial vegetation but it could also be managed for morphogroups of biocrusts. Considering morphogroups of biocrusts, which were shown in the Chapter 2 to be important for site resilience and resistance, I wanted to determine if there were site characteristics associated with biocrust distribution and recovery from disturbance, across the Great Basin. Outside of the Great Basin on the Columbia Plateau, others had found that mosses were still present on disturbed sites whereas lichens were often lost. In addition, biocrust species were more associated with soil properties than with grazing by livestock. Given that grazing by livestock and fire are common disturbances across the region, I wanted to know if the same relationships between biocrusts, soil properties and disturbance were true in the Great Basin. I found that cover of the lichen component of biocrusts was higher on sites that were both ungrazed and unburned. Factors related to disturbance characteristics were correlated with the recovery of biocrusts, even after accounting for time since fire. Factors related to disturbance, a composite of grazing and fire, were more important for structuring the cover and composition of morphogroups as opposed to environmental conditions. Lichens were the most sensitive morphogroup, compared to tall mosses, followed by short mosses which were favored by some disturbance but reduced in cover immediately after fire. Perennial grasses were also favored by some disturbance and perennial forbs did not show an obvious relationship with a disturbance gradient. Chapter 3 highlights that grazing by livestock and fire are common disturbances across the region so much so that the effects of one on the abundances of morphogroups could not be separated from the other.

Given the observed contributions of biocrusts to site resilience and resistance, I wanted to know if we could restore biocrusts in the field. Others have grown mosses in a lab setting but this was the first study to restore mosses in the Great Basin. I

tested the influence of factors that are commonly used in the field of restoration for facilitating plant establishment. I tested the influence of season of inoculation (fall versus spring), the addition of organic matter (in the form of jute net), irrigation (in the spring season) and the climatic setting of moss the collection sites (for moss propagation), in comparison to the experiment site (warm, dry versus cool, moist) on moss growth. I used two moss species: a ruderal (*Bryum argenteum*) and a later successional species (*Syntrichia ruralis*). Moss cover increased when the climatic setting of the collection site matched the experiment site. Mosses were facilitated by the addition of the organic jute netting, putting on most of their growth in winter. Although there is still a great deal of work to be done developing moss material for restoration and working out inoculation rates of moss fragments, similar to seeding rates, land managers have another tool to consider when rehabilitating sites after disturbance.

Managing the Great Basin for biocrusts in the presence of grazing and fire will not only increase site resistance to cheatgrass but it will add to the conservation of ecosystem functions related to nutrient cycling, hydrologic cycling and soil erosion. Site resistance will be improved with increased periods of rest from grazing following fire. The lichen component of biocrusts is a more sensitive indicator of disturbance when compared with mosses or perennial vegetation but we are currently actively managing for perennial vegetation and not biocrusts. The moss component of biocrusts can be successfully restored in the Great Basin, without irrigation. This dissertation shows that land managers should consider a suite of organisms, in addition to perennial plants to achieve management goals and maintain site resistance to cheatgrass.

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Biological Soil Crusts of the Great Basin: An Examination of their
Distribution, Recovery from Disturbance and Restoration

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Lea A. Condon

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Lea A. Condon, Author

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available to offer support and guidance not only related to my dissertation but on topics related to someone trying to figure out how to be a scientist after graduate school. Dave has always provided me with the right thing, at the right time, and without pressure. Mahalo.

When I read the acknowledgements sections in dissertations I always notice the word *support*. In those trying times when doing something new or pushing your limits, there is a need for support. Without it, life is too stressful and it is hard to make progress. I hope that this dissertation is an example of how great things can happen when you are surrounded by supportive people. I would like to thank the Live Well Yoga Teacher Training Cohort of 2015 for numerous discussions on support and providing a warm and welcoming environment.

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CONTRIBUTION OF AUTHORS

Dr. David Pyke assisted with funding, study design, data interpretation and editing of all manuscripts.

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DEDICATION

I would like to dedicate this work to my parents Jim and Marsha Condon who have shown me what persistence is and what can be gained from it.

**Biological Soil Crusts of the Great Basin: An Examination of their
Distribution, Recovery from Disturbance and Restoration**

Chapter 1 General Introduction

The sagebrush steppe ecosystem is one of the most imperiled ecosystems in North America (Noss et al. 1995). Numerous disturbances impact this ecosystem: off highway vehicle traffic (Tull and Brussard 2007), mining (Morris and Rowe 2014), agriculture (Vander Haegen 2007), pinyon-juniper expansion (Miller and Wigand 1994), and climate change (Redmond 2010). The additional disturbances of fire and inappropriate grazing by livestock are primarily responsible for the extirpation of many native plant communities and the conversion of the region into monocultures of non-native annual grasses (Pickford 1932) with 25 million acres estimated as being at risk (Pellant and Hall 1994). The establishment of these annual invasive species into interspaces between perennial plants has changed the historically patchy fuel structure in the region into a continuous layer of fine fuels (Brooks et al. 2004). Fire is a natural disturbance in the Great Basin, with sites historically burning every few decades in cool moist environments to burning once in nearly a hundred years in warm and dry environments (Miller et al. 2011), but fire now occurs across the region at increased frequencies and extents (Whisenant 1990). Losses of sagebrush steppe threaten the existence of sagebrush obligate species such as the sage grouse (Patterson 1952) and the pygmy rabbit (Shipley et al. 2006).

Restoration Efforts in Sagebrush Steppe

Despite efforts to restore sagebrush steppe include seeding, reducing fuels, applying herbicides on invasive species and amending soil (Mazzola et al. 2010, Knutson et al. 2014, Pyke et al. 2014), the sagebrush steppe in many areas continues to undergo a transformation to weedy monocultures. Ecologists often look at undisturbed sites to understand natural processes and community composition. Given the number and extent of disturbances across the region, this is a challenging task. European settlers in the region were ranchers and so much our knowledge of the Great Basin follows the

introduction of this disturbance. Information on the historical vegetation consists of general cultural (journals, photographs, maps, etc.) and biological evidence (pollen records, dendrochronology, packrat middens) (Egan and Howell 2001) and is typically limited to vascular plant communities.

Biological Soil Crusts and their Ecosystem Functions

In arid lands globally, biological soil crusts (biocrusts) occupy interspaces amongst perennial plants (Belnap and Lange 2001). Biocrusts refer to a community of lichens, mosses, cyanobacteria, fungi, etc. that live on the soil surface. They are prominent ecosystem components in the Columbia River Basin and Colorado Plateau, which border the Great Basin to the north and south respectively. Biocrusts are particularly sensitive to grazing by livestock (Ponzetti and McCune 2001) and it is estimated that more than 99% of the historical range of sagebrush steppe has been subjected to livestock grazing (West 1999). The extensive range of grazing by livestock might account for the relative lack in abundance of biocrusts in the Great Basin compared to neighboring ecoregions.

Biocrusts maintain critical ecosystem functions related to nutrient cycling (Evans & Ehleringer 1993), the distribution of water from precipitation events (Chamizo et al. 2012), and erosion control (Mazor et al. 1996). When found growing with biocrusts, vascular plants may have higher nutrient contents and greater growth (Harper and Belnap 2001; Pendleton et al. 2003), likely due to the fact that they can share fungal partners (Green et al. 2008). Restoring biocrusts may aid the restoration of native plants with which they evolved, as evidenced by nutrient translocation between the two (Green et al. 2008). Ecosystem functions carried out by biocrusts vary with the identity of individual biocrust components. For example, water infiltration rates are higher where mosses are

present as opposed to lichen and algal dominated crusts (Brotherson and Rushforth 1983). Mosses are poikilohydric, using available moisture immediately (Proctor et al. 2007) and increasing localized infiltration of precipitation (Chamizo et al. 2012).

The presence of biocrusts is likely to help in the maintenance of hydrologic and nutrient cycles that are altered by non-native annual graminoids. Cheatgrass has been successful across the Great Basin because it is a winter annual and uses soil moisture before native perennial vegetation (Melgoza et al. 1990). It also takes advantage of pulses in nitrogen (Monaco et al. 2003), which occur following fire (Neary et al. 1999). Sites with higher cover of biocrusts are likely to have more cycling of water and nutrients, which will favor native perennial vegetation at the expense of cheatgrass.

Management of Sagebrush Steppe

Seventy percent of land in the Great Basin is public and the Bureau of Land Management is responsible for the management of the largest area, 78 million acres (Torregrosa and Devoe 2008). Federal multiple use mandates require that agencies managing these areas provide for grazing, mining, and OHV use. In Nevada, 69% of BLM-administered land is under grazing allotments (Torregrosa and Devoe 2008). The region has been managed for domestic livestock without taking into account the biocrusts that would have been present or that still remain in the interspaces amongst vegetation. The soil has also seen a cascade of disturbances. To favor understory vegetation, ship anchor chains are sometimes dragged across the soil surface in an effort to reduce cover of pinyon and juniper trees (Bristow et al. 2014). Seeding efforts can consist of an aerial application but are often done by seed drills so that seeds are buried beneath the soil surface (Knutson et al. 2014). There has been minimal work done on the effects of these common surface soil

disturbances on biocrusts. Given the ecosystem functions provided by biocrusts, it is necessary that we gain a better understanding of where they exist across the ecoregion and how they interact with the plant communities that we are trying to restore, especially in the face of common disturbances such as fire and grazing.

Specific Objectives

Much of the current work being done in the Great Basin following fire focuses on understanding site resistance to invasion and site resilience from disturbance (Chambers et al. 2014). Condon et al. (2011) demonstrated the role of perennial vegetation in maintaining site resistance to cheatgrass following fire and Reisner et al. (2013) demonstrated that both perennial vegetation and biocrusts maintain site resistance in the presence of livestock grazing. This dissertation builds upon these prior studies and goes further by including the influence of fire and by sampling sites across the Great Basin. Chapter 2 compares effects fire and grazing on the ability of perennial vegetation and biocrusts to maintain site resistance as these disturbances generally overlap across the region. Biocrusts refer to the whole community of soil surface organisms and within each component (lichens, mosses, etc.) there are species with different morphologies and functional roles. Chapter 3 looks at the abundance of biocrusts grouped by morphology along gradients of disturbance and environmental factors thought to be related to the distribution of biocrusts. Even though biocrusts provide critical ecosystem functions and were likely more prominent in the Great Basin before the introduction of domestic livestock, there have been few efforts to restore them (Bowker 2007). Restoration of biocrusts has been minimally successful (Belnap 1993; Gross 2009). Chapter 4 presents a field experiment that successfully reintroduces the moss component of biocrusts in the

Great Basin and demonstrates the need for source materials to be collected from sites that are climatically similar to the sites being restored.

Scientists know that many ecosystem within the Great Basin are imperiled, as evidenced by changes in the fauna, which depend upon the dramatically-changing flora. However, scientists have overlooked biocrust communities that would have naturally filled interspaces amongst native plant species. This dissertation aims to fill some of our knowledge gaps regarding biocrusts in the Great Basin.

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Chapter 2 Site resistance as maintained by perennial vegetation and biocrusts is reduced by fire and interactions with grazing

Summary

1. Biological soil crusts (biocrusts) contribute to site resistance of plant invasions in rangelands. Even though the fire regime of the Great Basin is changing, the ability of the lichen and moss components of biocrusts to maintain site resistance has not been studied following fire in the region.

2. In a survey across the Great Basin, we recorded cover of lichens and mosses on areas burned between 12 and 23 years. Sampling of fires was balanced by average precipitation for each of three water years following the fire, fire severity, time since fire, season of ignition, total acres burned and grazing intensity as represented by cow dung frequency.

3. Overall, fire led to decreased site resistance, as measured by cover of *Bromus tectorum*, which was more pronounced on fires of greater extent. Some of the losses of site resistance were offset by increases in perennial herbaceous cover following fire and the recovery of perennial herbaceous cover and mosses with time. Indicators of grazing effects were more pronounced on burned sites, leading to further losses in site resistance. Shrub cover had a positive relationship with cover of lichens and mosses. Moss cover had a positive relationship with cover of perennial herbaceous vegetation and lichens. Site resistance to invasion by *B. tectorum* was associated with increases in cover of shrubs, lichens, and perennial vegetation.

4. Synthesis and applications: Lichen cover and perennial herbaceous cover add to site resistance to *B. tectorum* following fire on rangelands of the Great Basin. Independent of fire, grazing impacts resulted in reduced site resistance via increases in the gap size between perennial plants, indicating that management of grazing prior to fire influences site resistance before and after fire. Fire reduced near-term site resistance and the

interactive effects between fire and grazing added to further reductions in site resistance. This interaction indicates that site resistance would likely be facilitated by periods of rest from grazing following fire until such time that cattle no longer show a preference for grazing inside of the fire perimeter.

Introduction

Steppe communities worldwide experience two coarse scale disturbances: fire and grazing (Belnap & Lange 2001). Fire and grazing are known to affect the abundance and composition of plant species and biological soil crusts (biocrusts), specifically lichens, mosses, and cyanobacteria on the soil surface, in rangelands of Australia (Williams, Eldridge & Alchin 2008, O'Bryan et al. 2009), and western United States (Colorado Plateau Kleiner & Harper 1972; Great Basin Anderson et al. 1982; Johansen et al. 1984; St. Clair, Johansen & Rushforth 1993). Effects of grazing on biocrusts have been documented in fire prone rangelands of South Africa, Argentina, and Mexico (Dojani et al. 2011; Gómez et al. 2012; Concostrina-Zubiri et al. 2014), although limited attention has been given to the combined impacts of fire and grazing in rangeland systems (Mack & Thompson 1982). Effects of fire and grazing are confounded throughout much of the Great Basin. Cattle graze selectively on areas with light to moderate burn severity over unburned areas (Clark et al. 2014). To date, no one has looked at these disturbances simultaneously on the maintenance of native plant and biocrust communities across the region. In the Great Basin, site resistance to the annual exotic grass, cheatgrass, *Bromus tectorum* (L.), is influenced by perennial vegetation (Condon, Weisberg & Chambers 2011) and biocrusts (Reisner et al. 2013). We define site resistance as it is used by D'Antonio et al. (2009) in an ecological sense to mean the “ability of a community to

withstand encroachment by nonnative species”. Both biocrusts and invasive annual grasses may occupy interspaces between perennial herbaceous vegetation, but often not simultaneously (Reisner, Doescher & Pyke 2015). At the microsite scale, the interaction between biocrusts and disturbance may have significant repercussions for the maintenance of native plant communities.

In steppe communities of the Great Basin, livestock grazing has accompanied the establishment of *B. tectorum* (Pyke et al. 2016). In the presence of *B. tectorum*, fire frequency increases, dramatically altering the fire regime (Miller et al. 2013). The time between fires, especially in arid areas, may become less than the time for some native species to reach maturity and produce seed resulting in the extirpation of some native species from invaded sites (D’Antonio & Vitousek 1992). Site conversion to *B. tectorum* monocultures is widespread, making the Great Basin one of the most threatened ecosystems in North America (Noss, LaRoe III & Scott 1995). The Greater Sage-grouse, *Centrocercus urophasianus* (Bonaparte), a sagebrush obligate bird that depends upon the continuity of sagebrush plants for food and nesting success (Wisdom et al. 2011), is in peril as a result of loss of habitat to increased fire (U.S. Fish and Wildlife Service 2010). Understanding the interactions between factors maintaining site resistance to *B. tectorum* and disturbance is crucial to the survival of sagebrush obligates and sagebrush ecosystems.

Repeated disturbance by fire and grazing do not allow for a linear model of plant succession in the Great Basin. A more appropriate model may be that of windows of

opportunity, a concept frequently applied in riparian and coastal systems (Balke et al. 2014). This concept postulates that disturbances need to be appropriately timed to allow for plant establishment to occur. For example, if grazing on a site has resulted in large gaps between perennial plants and a fire burns through, *B. tectorum* might be more likely to establish. In comparison, if grazing on a site has been light or infrequent, and perennials plants are growing in the interspaces, *B. tectorum* might be less likely to establish. Perennial vegetation and biocrusts might be responding to a characteristic of one of these disturbances, grazing or fire, more so than the other. This indicates that if management could alter that disturbance characteristic in some way, site resistance to *B. tectorum* might increase. Mosses and lichens respond differently to disturbance (Johansen 1984; Aquilar et al. 2009), justifying an examination of their responses to disturbances separately, as opposed to grouping them more generally as biocrusts.

Due to the large number of potential interacting relationships, we present our hypotheses as a conceptual model (Figure 2-1). A structural equation model (SEM) can account for correlations that might mask relationships of interest (Grace 2006). SEM also allows for the development of new hypotheses, by corroborating both what we know and what we do not know about a set of relationships. Hypothesized pathways are justified in Table 2-1. Pathways are presented as linear relationships given the relatively short time frame sampled (time since fire of 12-23 years) and limited environmental conditions. If longer gradients were covered, we would expect some of these hypothesized relationships to be non-monotonic such as pathway 4c in Table 2-1. Shrubs are likely to physically protect lichens at some sites, but increases in shrub cover past a certain threshold might lead to

reductions in shade intolerant lichens. In general, we hypothesized that single fires in recent history would lead to temporary declines in site resistance, as measured by cover of *B. tectorum*, but that increases in grazing intensity by livestock either before or after the fire would lead to continued losses of site resistance to *B. tectorum*. The landscapes that we are working within experience repeated grazing that has been ongoing for at least the last 100 years, with the exception of a period of rest following fire.

Methods

We hypothesized different relationships between effects of fire and grazing on the recovery of lichens, mosses, shrubs and perennial herbaceous vegetation (the combination of perennial grasses and forbs). Surveys inside and outside of livestock exclosures demonstrated differences in biocrust abundance in Utah (Kleiner & Harper 1972) and community composition in the Columbia Basin (Ponzetti & McCune 2001), indicating that some biocrusts are sensitive to grazing. Additionally, biocrusts survive fire, in the Palouse prairie of the Columbia Basin (Bowker et al. 2004). We represent fire by characteristics used to define fire regimes: frequency, severity, extent, and season of fire (Sugihara, Van Wagtendonk & Fites-Kaufman 2006). However, the frequency, severity and extent of livestock grazing are difficult to quantify because monitoring data are often of different data types across sites (Veblen et al. 2014) making for incomplete datasets. Distance to water (Ganskopp 2001) and cow pie counts are used to quantify actual use by livestock, as usage is generally not uniform across a given allotment (Reisner et al. 2013). Reisner et al. (2013) also used gap size between perennial vegetation as a more direct indicator of effects of grazing on cover of *B. tectorum* with *B. tectorum* cover increasing with increasing gap size. Public records, such as the Rangeland

Administration System (RAS; <http://www.blm.gov/ras/>, accessed 15 September 2015), provides information related to grazing allotment size, numbers of active (currently allowed use) and permitted (estimated grazing capacity) Animal Unit Months (AUMs). In addition, RAS reports the number of suspended AUMs, which is a long-term suspension that is often dictated by monitoring data indicating that grazing utilization is not meeting desired objectives. Long-term suspensions may not be lifted as opposed to temporary suspensions that are issued in response to drought or fire, (Ruyle & Ogden 1993). For each allotment, we obtained animal unit months (AUMs) that were active or suspended (long-term) and relativized them by the number permitted due to the difference in size of allotments. BLM grazing records immediately before and after each fire were not accessible for all sites and so we used records that were available as of 15 September 2015 from the RAS. According to BLM staff (Lynnda Jackson, personal communication, 9 September 2015). AUMs do not change much making these records an acceptable substitute for pre and post fire livestock use. Common federal practice, at the time of these fires has been that livestock grazing is halted for a minimum of two growing seasons following fire and then reinstated (Clark et al. 2014), although some federal agencies require plant establishment or recovery objectives, based on vegetation and soil stabilization, be met before grazing may resume (Bureau of Land Management 2007).

Study Area

The study area consists of big sagebrush (*Artemisia tridentata* subspecies) ecosystems within eastern Oregon, southwestern Idaho, northern Nevada, and western Utah. The region spans a gradient of increasing productivity from south to north and from lower to

higher elevations. Based on the EPA Level III Ecoregions of the United States, this includes the Central Basin and Range, the Northern Basin and Range, and Snake River Plain, being bordered by the Mojave Basin and Range to the south and the Eastern Cascades, Blue Mountains, Idaho Batholith, and Middle Rockies ecoregions to the north (EPA Level III Ecoregions, accessed 14 April 2016).

Study Sites

Fires occurred on land managed by the Bureau of Land Management and were previously surveyed by Knutson et al. (2014) in 2010 and 2011 (Figure 2-2). These fires occurred across a range of Major Land Resource Areas (USDA NRCS 2006), but were restricted to having loamy soils and burned once since 1970. Fifteen fires, a subset from Knutson et al. (2014) were visited in our study. This subset covered a range of predictor variables including average precipitation for each of three water years following the fire, fire severity, time since fire, season of ignition, total acres burned and grazing intensity as represented by cow dung frequency (Table 2-2). Three burned and three unburned plots per fire were randomly located in the Knutson et al (2014) study and resampled in this study for detailed moss and lichen data. There were two exceptions to this where one fire had a total of six unburned plots and three burned plots and another fire had a total of six unburned plots and six burned plots for a total of 99 plots.

Field Methods

In 2012 and 2013, we visited the 15 sites, each within a single grazing allotment. A minimum of three burned and three unburned plots on a site, consisted of three, 50-m

transects beginning 5 m from a central point and separated by 120° (Herrick et al. 2005). Cover of all biocrusts and plant species were estimated visually (to the nearest 1 %) within 0.25-m² square quadrats at 10-m intervals along each transect for a total of 15 quadrats per plot. Biocrust and plant species data were lumped into life forms for analyses: lichens, mosses, perennial herbaceous vegetation, shrubs, with *B. tectorum* being assessed separately.

Data from Knutson et al. (2014) included the distance between perennial plants (gaps) collected via the same transects described above. Shrub cover and cow dung frequency were measured by Knutson et al. (2014) with 6-m x 50-m belt transects on burned plots and 2-m x 50-m belts on unburned plots. We use the standard deviation of the average gap size between perennial plants as an index of cattle grazing impact on invasion by *B. tectorum* because the standard deviation of the average gap size showed a stronger correlation with *B. tectorum* cover than just the average gap size. Reisner et al. (2013) demonstrated that grazing intensity, as represented by distance from water, affects native perennial bunchgrass abundance and composition, which subsequently influences the size of the gaps between perennials and the cover of *B. tectorum*. Distance to water, including spring seeps, wells, and associated water troughs, was used as an after-the-fact proxy for grazing intensity and measured in ArcMap 10.2 using a combination of 1-m resolution images from the National Agriculture Imagery Program and the National Hydrography Dataset (accessed 10 February 2016; <http://nhd.usgs.gov>).

Soils were collected within each quadrat with three randomly placed, 5-cm diameter by 1-cm deep soil cores. The presence of soil carbonates were assessed with an effervescence test, using 1 M HCl dropped onto roughly a gram of the sieved 2mm soil fraction from each plot as described in Karunaratne et al. (2014). When the combination of soil and HCl resulted in an audible effervescence sound (violent effervescence), soils were recorded as having carbonates.

Data Analysis

Structural equation modeling (SEM) using observed variables with AMOS v. 23.0.0 was used to separate direct and indirect effects of fire and grazing and the potential interactions between biocrusts and vegetation (Figure 2-1). Unlike many SEM applications, this method does not use a measurement model (relating latent variables to indicators) or a structural model (relating latent variables to one another) because all variables are measured directly. SEM requires the development of an a-priori conceptual model that delineates hypothesized causal and correlational relationships amongst measured variables (Grace 2006). Casual relationships should be interpreted as statistical dependencies and do not demonstrate causation. Pathways from the conceptual model were added sequentially, beginning with those thought to be most closely associated with cover of *B. tectorum*, followed pathways associated with grazing and ending with pathways associated with fire. Pathways related to grazing were tested before fire because most of our sites were grazed first with fire being a secondary disturbance. In an effort to achieve parsimony, pathways were only kept in the model if the associated p-value was less than 0.1. Model fit was evaluated with both a chi-squared test and a root

mean squared error of approximation (RMSEA). A RMSEA takes into account the sample size and the number of pathways evaluated. A RMSEA that includes zero and an insignificant chi-squared test indicates that the model fits the data well. Only half of the surveyed sites were burned and most, fourteen out of fifteen sites, experienced some level of grazing immediately before the fire. All variables included in the hypothetical model were z-transformed, so that the mean was subtracted from each value and the resulting difference was divided by the standard deviation of the variable with the exception of the “burned” variable, which was binary (burned or not burned) and so not standardized. The summed effects of compound pathways related to disturbance characteristics (the interaction of burning and grazing, burning alone, time since fire, total area burned, proportion of suspended AUMs, and cow dung frequency) were calculated by multiplying all partial path coefficients along complete pathways. These pathways originated with the mentioned disturbance characteristics and terminated on our representation of site resistance: cover of *B. tectorum* and mediated site resistance: lichens, perennial herbaceous vegetation and shrubs. Where there were multiple pathways originating from these disturbances and terminating on factors representing site resistance and mediated site resistance, related pathways are summed to calculate total effects.

We visually examined relationships between variables of interest as we constructed our a-priori conceptual model. Fire was represented by whether or not a plot burned, time since fire, and the total area burned. Season of ignition, as represented by the Julian date of ignition (Table 2-2), did not show a relationship with biocrust or perennial vegetation recovery and so it was not included in our a-priori model. Additionally, fire severity as

calculated by MTBS (Monitoring Trends in Burn Severity, <http://mtbs.gov>) is an estimation of shrub cover lost due to fire. This factor was included in our subset selection of surveyed sites. However, in our conceptual model, we included fire severity as a direct relationship between whether a plot burned and shrub cover as opposed to MTBS derived fire severity because the former relationship was stronger. Other hypothesized pathways were as described above.

Results

The model only including significant pathways from the conceptual model fit the data well (RMSEA 0.000, $X^2 = 45.5$, $p = 0.330$, $df = 42$, Figure 2-3). Pathway coefficients are partial correlations, taking into account all of the other pathways in the model when calculating the relative strength of relationships between variables. The model confirmed that both perennial herbaceous species and the lichen component of biocrusts are associated with site resistance to invasion by *B. tectorum*. Increased cover of mosses indirectly affected the maintenance of site resistance as sites with increased moss cover also demonstrated increased cover of perennial vegetation and lichens, which in turn related to decreased cover of *B. tectorum*. Increased shrub cover was negatively associated with cover of *B. tectorum* via direct and indirect pathways by being associated with greater cover of lichens and mosses (Figure 2-3).

Fire-related variables (burned plots, time since fire, and total acres burned) demonstrated mixed effects on ability of native flora to maintain site resistance. Cover of perennial vegetation and mosses increased with time since fire, but lichen cover decreased (Figure

2-3). Overall, time since fire led to increased site resistance when all associated pathways were considered (Figure 2-4). Total acres burned resulted in decreased cover of perennial vegetation and shrubs (Figure 2-3, Figure 2-4), which in total, led to increased cover of *B. tectorum* (Figure 2-3, Figure 2-4). Whether a site burned or not demonstrated complex relationships; fire favored perennial herbaceous vegetation but directly led to reduced lichen and shrub cover. Shrub cover lost to fire was indirectly associated with reduced cover of mosses and lichens (Figure 2-3, Figure 2-4). Sites that burned were more likely to show increased grazing pressure as represented by increased cow dung frequency and gaps in perennial vegetation, resulting in additional increases in cover of *B. tectorum* (Figure 2-3, Figure 2-4). There was no direct relationship between the cover of *B. tectorum* and whether a site burned or not (Figure 2-3). The presence of fire led to both increases and decreases in site resistance to *B. tectorum*, mediated through perennial vegetation and biocrusts respectively.

All variables related to increases in livestock grazing intensity in the final model led to reductions in site resistance. Decreased distance from water (increased grazing intensity) was associated with increased cow dung frequency and increased cow dung frequency was associated with increased gaps between perennial herbs. Decreases in perennial herb cover were related to increases in gaps (Figure 2-3) and increased gaps between perennial herbs directly related to decreased site resistance to *B. tectorum* (Figure 2-3). The ratio of the number of suspended AUMs to the number of permitted AUMs for a given allotment had a strong negative influence on perennial herb and shrub cover that ultimately had positive indirect effects on the cover of *B. tectorum* (Figure 2-3). The ratio of active

AUMs did not have a significant role in the final model. Cow dung frequency was not directly related to perennial herb cover.

Discussion

We are the first to date to simultaneously test the influences of both fire and grazing intensity on the maintenance of site resistance to *B. tectorum* mediated by perennial herbaceous vegetation and two components of biocrusts: mosses and lichens, across the Great Basin ecoregion. We found that increased grazing intensity, as related to an increase in the standard deviation of gap size between perennials, led to continued reductions in site resistance as measured by cover of *B. tectorum*, even after accounting for the potential overuse of vegetation by livestock that was implied by the proportion of suspended over permitted AUMs. Even though fire did lead to reductions in site resistance, not all fire-related effects reduced site resistance, as fire itself favored perennial vegetation and some recovery of site resistance was observed with time since fire of 12-23 years. Wright et al. (1979) states that grasslands scattered with sagebrush were likely maintained by fire, which corroborates our finding of a positive effect of fire on herbaceous cover. Although one study has observed a positive effect of grazing on the vitality of perennial herbs following small prescribed fires in one general location in Oregon (Davies et al. 2016), across the Great Basin ecoregion, we demonstrate a net negative effect of grazing on site resistance to *B. tectorum*.

The association between mosses and the maintenance of site resistance was complex.

Plots with increased cover of mosses were associated with increased cover of perennial

vegetation and lichens, although, as a group, mosses were not directly associated with cover of *B. tectorum*. Lichen establishment was observed within a moss restoration experiment on soils that had been autoclaved and inoculated with moss fragments (Condon per. obs.), suggesting that mosses facilitate some lichen establishment. Mosses have also been shown experimentally to facilitate perennial vegetation, specifically grasses (St. Clair et al. 1984). However, we were surprised to not observe a significant pathway between mosses and cover of *B. tectorum*. Moss species range in their ability to resist establishment by *B. tectorum*. Serpe et al. (2006) found that the early successional moss, *Bryum argenteum*, reduced final germination of *B. tectorum* by half when compared to bare soil as opposed to the tall, later successional moss, *Syntrichia ruralis*, which did not reduce final germination percentages of *B. tectorum* but increased the seed water content of both *B. tectorum* and native perennial grasses. Rates of water infiltration and nitrogen fixation affect the germination and establishment of *B. tectorum* (Chambers et al. 2007) and vary with moss development (Chamizo et al. 2012; Arróniz-Crespo et al. 2014). Relationships between mosses and other organisms are likely complex and should be explored further particularly in regards to species roles and development. Although we did not observe a direct relationship between mosses and site resistance, the increased presence of moss we found to be associated with increased cover of perennial vegetation and lichens, which directly and positively influenced site resistance.

Lichens and perennial vegetation were instrumental in maintaining site resistance to *B. tectorum* (Figure 2-3). Lichens provide a physical barrier, reducing the germination and rooting depth of plants (Serpe et al. 2008; Mendoza-Aguilar, Cortina & Pando-Moreno

2014). However, lichens are particularly sensitive to trampling (Kleiner & Harper 1972; Anderson et al. 1982), making them early indicators of soil surface disturbance. It is likely that lichens not only physically maintaining sites resistance but functionally as well. Green, Porras-Alfaro & Sinsabaugh (2008) observed the translocation of nitrogen and carbon between biocrusts and patches of plants, indicating that they are functionally integrated. The authors also found substantial overlap in fungal community composition between plant roots and biocrusts, reaffirming this integration. Regardless of the mechanism, lichen cover is associated with site resistance.

Fire in the Great Basin reduces cover of mosses (Johansen et al. 1984) and lichens (Hilty et al. 2004; Ponzetti et al. 2007). We expected that the native flora would be temporarily affected by fire but recover. We found this to be true of perennial vegetation and mosses but not lichens. Fire favored perennial herbaceous vegetation, which increased further with time since fire. Increases in perennial vegetation cover contribute not only to increased site resistance but also to increased cover of *A. tridentata* (Condon et al. 2011), which is likely to have positive, cascading effects on sage-grouse (Wisdom et al. 2011). However, we did not see lichens increase with time since fire and in fact, our model demonstrated a partial negative correlation between lichen cover and time since fire of 12-23 years, prompting the development of revised hypotheses in regards to lichens and fire in recently burned and actively grazed rangelands of the Great Basin. The partial negative correlation between time since fire and lichen cover may indicate that lichen recovery following fire may take longer than 23 years, the age of our oldest fire. It may take centuries for some lichens to recover following disturbance Johansen (2001).

Additionally, a Pearson's correlation of 0.01 between lichen cover and time since fire suggests that another factor might be influencing the partial correlation that we observed between lichen cover and time since fire. Other disturbances may be inhibiting the recovery of lichens following fire (Muschka & Hild 2006), such as a pulse of invasion by *B. tectorum* following fire. Increased cover of *B. tectorum* is related to decreased cover of lichens (Ponzetti et al. 2007), relating to a decrease in lichen cover with time since fire in the short term. To gain a better understanding of lichen recovery from fire, we need to be looking at previously undisturbed or lightly disturbed sites that are maintained in this state long enough to begin to document lichen recovery from fire.

Even though our study is representative of the majority of the sagebrush steppe of the Great Basin, which experiences both grazing and fire, a thorough understanding of lichen recovery, and overall site recovery from fire may only be possible when looking at sites that have not been grazed. Zhang, Eldridge & Delgado-Baquerizo (2015) found that even with the positive effects of a diverse plant community and biocrusts on ecosystem function, the negative effects of grazing pressure were not offset with time in Australian rangelands. The time that it takes for these systems to fully recover from grazing may be longer than the time it takes for lichens to recover from disturbance.

Our survey of perennial vegetation and biocrust recovery following fire on rangelands of the Great Basin highlights the needs for a greater understanding of three major topics in order to more fully understand site resistance as mediated by perennial vegetation and biocrusts. We observed an interaction between fire and increased grazing pressure but we

do not know how long this effect lasts or if these sites are at risk for overgrazing if favored by cattle. We need a better understanding of what drives the recovery of the lichen component of biocrusts from fire, especially given that they contribute to site resistance to invasion by *B. tectorum*. We also need a better understanding of the role of mosses in facilitating perennial vegetation and lichen cover.

We corroborate the findings of Reisner et al. (2013) that biocrusts contribute to the site resistance to *B. tectorum*, expanding the range of this trend beyond eastern Oregon to the extent of the northern Great Basin. Additionally, we demonstrate that as a group, lichen cover is instrumental as a proxy for site resistance and that increased moss cover is related to increased cover of both perennial herbaceous vegetation and lichens, both of which are directly associated with reduced cover of *B. tectorum*. A holistic approach to understanding ecosystem function that includes biocrusts is necessary to understanding and maintaining functioning ecosystems. Future work on the recovery of arid land systems from disturbance should include not only the plant community response but the response of biocrusts as well.

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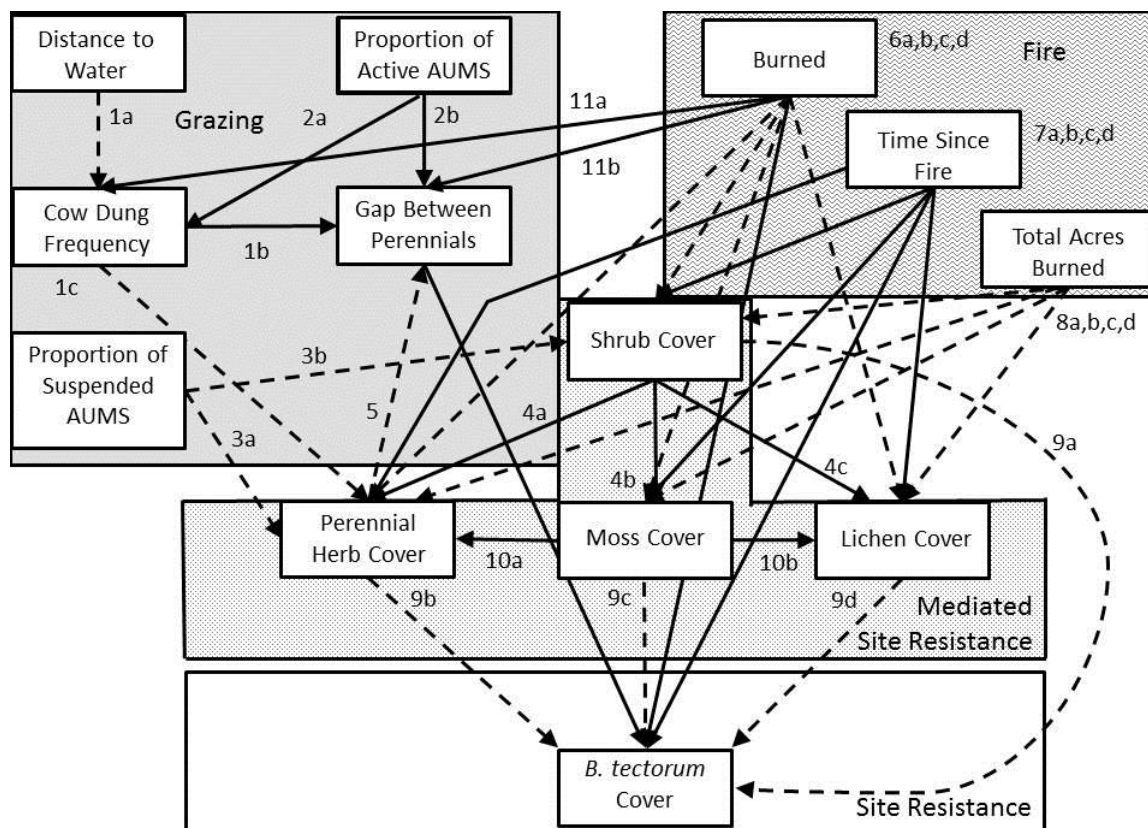


Figure 2-1. Hypothesized observed variable model examining the role of perennial vegetation cover (herb and shrub) and biocrusts (lichen and moss) in maintaining site resistance to invasions by *Bromus tectorum*. Small boxes represent observed variables, which are measured directly. Large boxes delineate variables into groups related to the disturbances of grazing and fire, factors thought to mediate site resistance to *B. tectorum* and site resistance, represented by cover of *B. tectorum*. Arrows represent direct effects of one factor on another. Dashed pathways represent negative relationships and solid pathways represent positive relationships. Labels on pathways correspond to justifications for their inclusion in the model presented in Table 2-1.

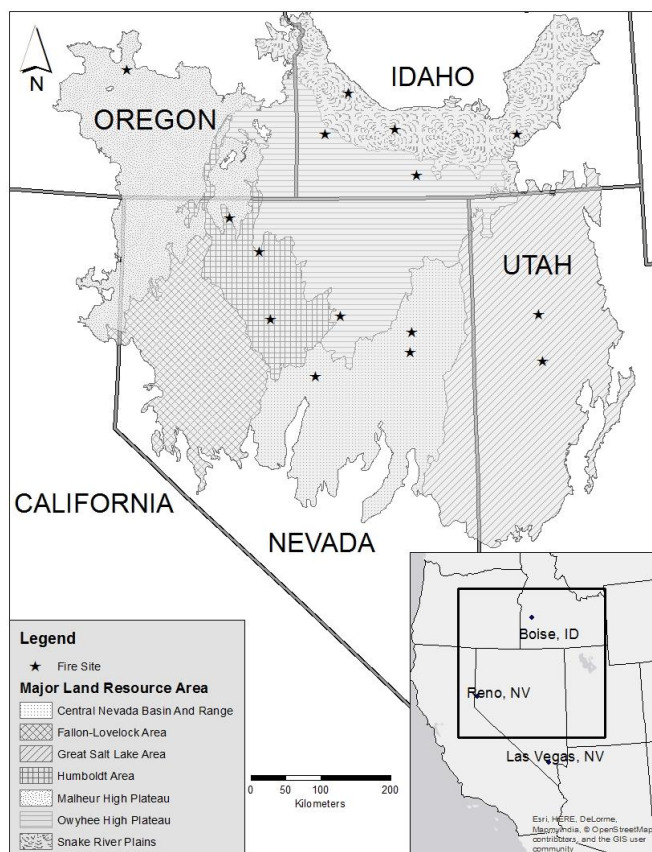


Figure 2-2. The locations of the fifteen fires surveyed across the Great Basin, USA.

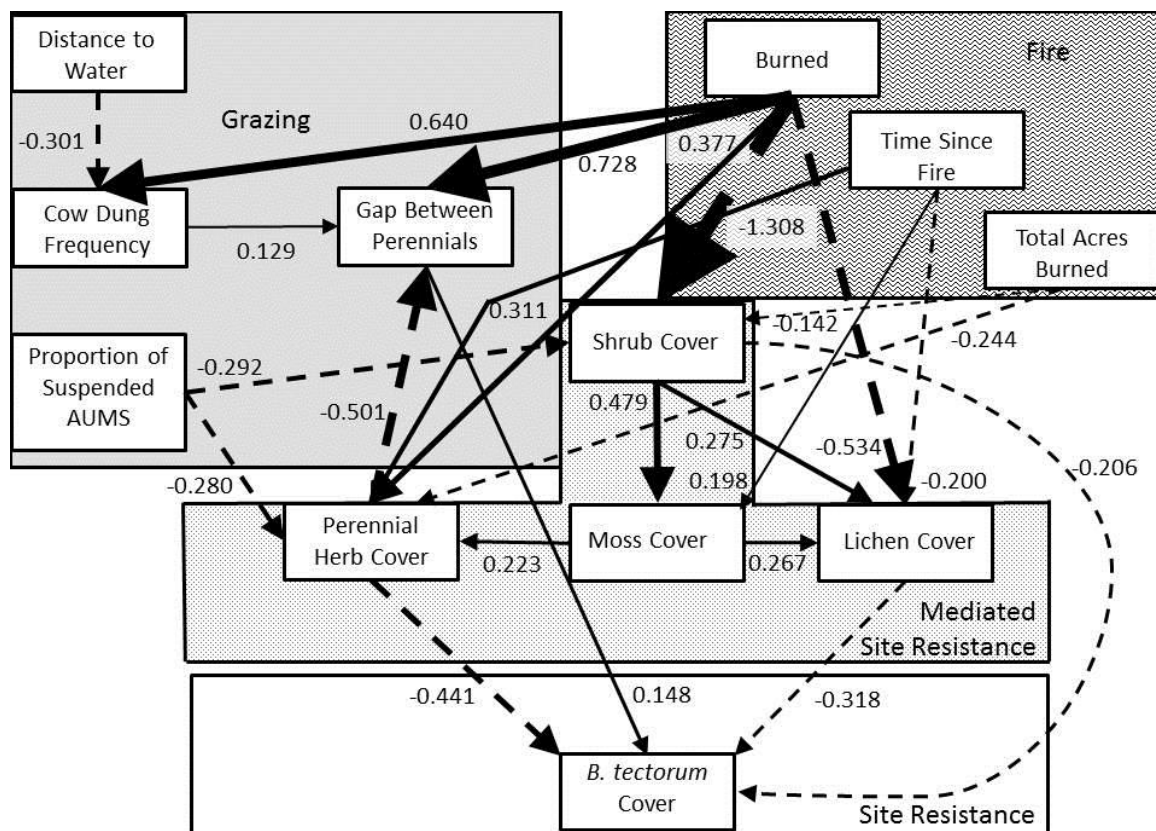
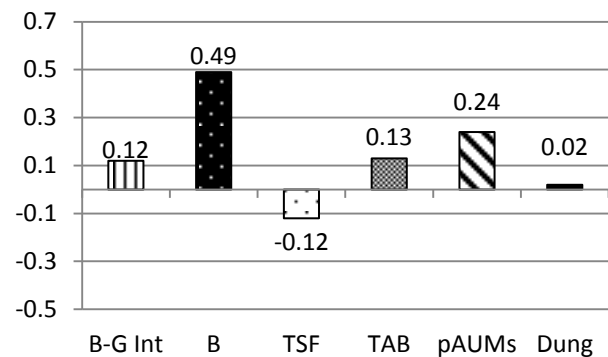
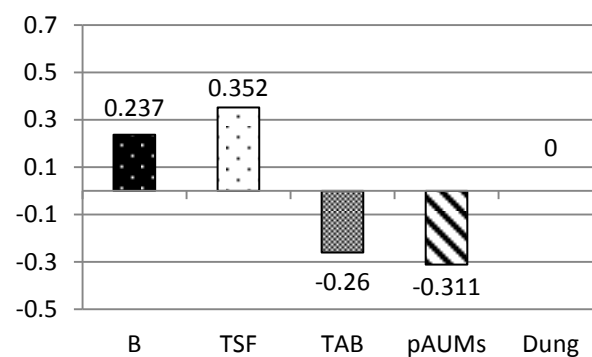


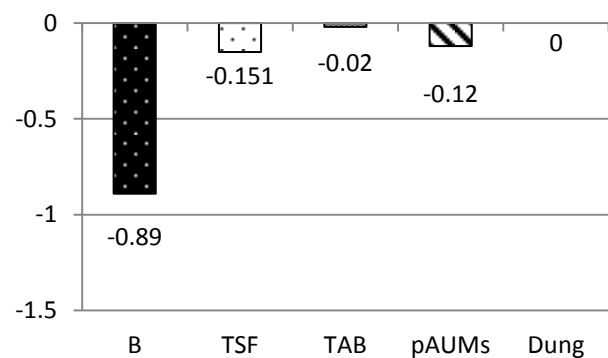
Figure 2-3. Structural Equation model diagram of the most parsimonious model examining the role of perennial vegetation cover (herb and shrub) and biocrusts (lichen and moss) in maintaining site resistance to invasion by *Bromus tectorum*. Dashed lines represent negative partial correlations and solid lines represent positive partial correlations. The widths of the arrows represent the magnitude of the relationships. Errors between cow dung frequency and moss cover as well as moss cover and *B. tectorum* are correlated and not shown.

(a) *Bromus tectorum* cover

(b) Perennial herbaceous vegetation cover



(c) Lichen cover



(d) Shrub cover

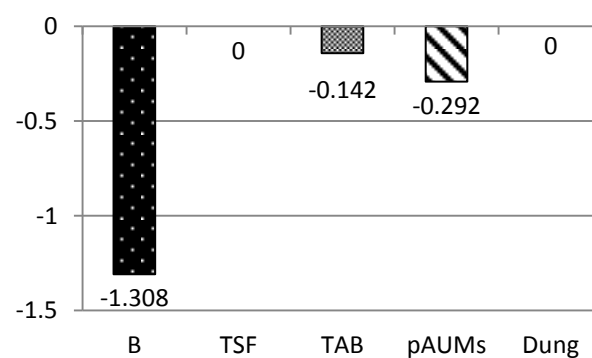


Figure 2-4. Sum of the measured effects on (a) *Bromus tectorum* (b) perennial herbaceous vegetation (c) lichen and (d) shrub cover. Abbreviations for significant factors are as follows: B- Burned, B-G Int- Burned Area-Grazing Interaction, TSF- Time Since Fire, TAB- Total Area Burned, pAUMs- proportion of suspended AUMs. Y-axis is unit-less.

Table 2-1. Hypothesized pathways used to form our conceptual model of the roles biocrusts and perennial herbaceous vegetation in mediating fire and grazing impacts on site resistance to cheatgrass, *B. tectorum*. AUMs- animal unit months, used to charge ranchers for land use.

Pathway	Justification
Grazing Impacts	
1a,b,c	Cow dung frequency decreases with increasing distance from water (a) and increases in dung frequency relate to increases in the gap size between perennials (b) and decreases perennial herb cover (c) (Reisner et al. 2013).
2a,b	Increases in grazing intensity relates to increases in dung frequency (a) and increases in gap size between perennial herbs (b) (Reisner et al. 2013) which we tested indirectly by using the proportion of active AUMs.
3a,b	Increases in grazing intensity relates to decreases in cover of perennial herbs (a) and shrubs (b) in the interspaces (Owens & Norton 1992; Reisner, Doescher & Pyke 2015) which we tested indirectly by using the proportion of suspended AUMs, the number of AUMs that the BLM saw fit to suspend over the long-term.
4a,b,c	Shrubs physically protect perennial herbs (a), mosses (b) and lichens (c) from grazing impacts (Belnap & Eldridge 2001; Reisner, Doescher & Pyke 2015).
5	Increases in perennial herb cover relates to decreases in gap size between perennial herbs (Reisner et al. 2013).
Fire Impacts	
6a,b,c,d	Fire (burned) relates to decreases in the cover of shrubs (a), perennial herbs (b), mosses (c) and lichens (d) (Johansen et al. 1984; Pyke et al. 2015).
7a,b,c,d	Shrubs (a), perennial herbs (b), mosses (c) and lichens (d) recover with time since fire.
8a,b,c,d	Fire extent (total area burned) relates to decreases in the cover of shrubs (a), perennial herbs (b), mosses (c) and lichens (d), taking longer to disperse propagules into burns of increasing size from unburned areas (Johansen et al. 1984; Condon & Weisberg 2016).
9a,b,c,d	Shrubs (a) (Reisner, Doescher & Pyke 2015), perennial herbs (b) (Condon, Weisberg & Chambers 2011), mosses (c) (Serpe et al. 2006) and lichens (d) (Serpe et al. 2008) mediate site resistance measured by their correlation with reduced cover of <i>B. tectorum</i> .
Biotic Interactions for Mediated Site Resistance	
10a,b	Biocrusts directly affect the establishment, survival, nutrient status and water relation of vascular plants (Prasse & Bornkamm 2000; DeFalco et al. 2001; Harper & Belnap 2001). Some mosses are early colonizers (Zobel & Antos 1997) and we expect that mosses as a group may facilitate perennial herb and lichen cover.
Interaction between Fire and Grazing	
11a,b	Fire and grazing impacts interact, as cattle are more likely to use burned sites (Clark et al. 2014). The presence of fire relates to an increase in the gap size between perennial herbs (a) and an increase in dung frequency (b).

Table 2-2. Variables* considered in site selection and in the quantification of fire and grazing intensity from Knutson et al. 2014. Sites were selected to represent the range of values. Additional variables were used in analysis. Average values and standard deviations are shown. Abbreviations: AUMs- animal unit months, dNBR- differenced Normalized Burn Ratio, MTBS- Monitoring Trends and Burn Severity database, p- plots, WY- Water Year. Headings are variables (and sources of information).

Description	Units	Mean (S.D.)	Range
<u>Average Precipitation*</u> (PRISM 2010)			
Average precipitation is given for each of the three water years following the fire as modeled by PRISM.	mm	WY 1- 256 (54) WY 2- 274 (74) WY 3- 300 (101)	WY 1- 179-373 WY 2- 168-437 WY 3- 155-556
<u>Fire Severity*</u> (MTBS 2012)			
Fire severity was estimated with dNBR. Sites were selected to cover a range of fire severities. Plots were classified according to their dominant fire severity.	N/A	N/A	Unburned- 51 p Low Severity- 29 p Moderate Severity- 16 p High Severity- 3 p
<u>Season of Ignition*</u> (MTBS 2012)			
Julian date of ignition	N/A	222 <i>August 10</i> (24.5)	160-259 (<i>June 9 – Sept 16</i>)
<u>Time Since Fire*</u> (Pilliod & Welty 2013)			
The number of years between the fire and the 2012-13 sampling date.	Years	16 (3.8)	12-23 (1990-2001)
<u>Total Area Burned*</u> (Pilliod & Welty 2013)			
The area inside the fire perimeter measured in ArcMap.	Hectares	6013.9 (10269.3)	540.7-42920.6
<u>Average and Standard Deviation in the Gap Between Perennial Plants</u> (Field measured, Knutson et al. 2014)			
Standard deviation of the average (avg) gap between perennial plants along the 50-m transects at each plot.	Cm	Avg gap-230.1 (553.7) SD of avg gap- 199.5 (297.8)	Average- 36.3-5000 SD- 0-1962
<u>Cow Dung Frequency*</u> (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx))			
Cow dung per meter squared counted in shrub belt transects.	#/m ²	5 (5)	0-25
<u>Distance from Water</u> (derived from GIS with http://nhd.usgs.gov and 1-m resolution NAIP imagery)			
Mapped and measured with NAIP & National Hydrography Dataset.	Meters	1915.1 (1294.2)	144.3-5802.8
<u>Active AUMs</u> (Rangeland Administration System http://www.blm.gov/ras/)			
Active AUMs as of 15 September 2015	AUMs	5320.7 (4555.9)	0-13,326
<u>Suspended AUMs</u> (Rangeland Administration System http://www.blm.gov/ras/)			
Suspended AUMs as of 15 September 2015	AUMs	1297.6 (2269.6)	0-7473
<u>Permitted AUMS</u>			
Permitted AUMs as of 15 September 2015 (estimated capacity)	AUMs	6618.2 (5858.8)	0-15174

**Chapter 3 Morphological group abundance of biological soil crusts and
perennial herbaceous vegetation in response to fire across the northern
Great Basin**

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Abstract

Biological soil crusts play key roles in ecosystem processes that are altered by fires and invasions of *Bromus tectorum*. However, few have looked at recovery of biological soil crusts following fire and we are the first to do so across the Great Basin. We surveyed for the cover of plant and biological soil crust (biocrust) morphogroups in paired burned and unburned plots on fires across the Great Basin. Fires were selected based on factors such as livestock grazing (cow dung density), time since fire, fire severity, fire size, and precipitation in each of the three water years following fire. The abundance of biocrust morphogroups was related to a gradient of disturbance, represented by the combined effects of grazing and fire. Biocrust morphogroups of lichens, tall mosses and short mosses demonstrated decreasing sensitivities to disturbance with short mosses actually preferring some level of disturbance. Perennial grasses were associated with some disturbance, while perennial forbs lacked a clear relationship with disturbance. These findings suggest that biocrusts are lost from disturbance before perennial herbaceous plants and that lichens are a sensitive indicator of disturbance.

Introduction

Fire regimes in sagebrush steppe ecosystems of the Great Basin eco-region are changing from infrequent, small fires to more frequent large fires (Whisenant 1990; Miller et al. 2013). By “Great Basin”, we are referring to the Central Basin and Range, the Northern Basin and Range, and Snake River Plain, (EPA Level III Ecoregions, https://archive.epa.gov/wed/ecoregions/web/html/level_iii_iv-2.html, accessed 14 April

2016). This change in fire regime is due primarily to invasive annual grasses, predominantly cheatgrass (*Bromus tectorum* L.). *Bromus tectorum* fills interspaces between native plants, resulting in continuous fuel loads that regenerate yearly (Klemmedson and Smith 1964). Repeated fires at short intervals have extirpated big sagebrush (*Artemisia tridentata* Nutt.) and other native plant species from large parts of the Great Basin (Whisenant 1990). In undisturbed semi-arid systems, biological soil crusts (biocrusts), referring to lichens, mosses and cyanobacteria that grow on the soil surface, are common in interspaces between native plants (Belnap and Lange 2001). Site resistance to invasion by *B. tectorum* is increased by biocrusts (Reisner et al. 2013), including after fire (Condon Chapt #2).

In semiarid ecosystems, the combination of fire and exotic annual grasses has led to ecosystem changes beyond altered fire regimes. Ecosystem changes include increased soil erosion (Field et al. 2011), changes in soil nutrients (Witwicki et al. 2013; Norton et al. 2004) and changes to the pattern of water infiltration (Adams et al. 1970). Biocrusts are known to reduce soil erosion (Eldridge and Greene 1994; Belnap and Gillette 1998), contribute to nutrient cycling (Evans and Ehleringer 1993), increase water infiltration when dominated by mosses (Bowker et al. 2011; Chamizo et al. 2012), and concentrate water runoff and reduce evaporation when dominated by lichens (Brotherson and Rushforth 1983; Cantón et al. 2004). Understanding how sagebrush steppe ecosystems recover from fire requires understanding both vascular plants and biocrusts components.

Given that biocrusts are a communities of organisms, it is simplistic to assume that all biocrusts will recover from fire in the same way. Eldridge and Rosentreter (1999) relate morphological groups of biocrusts to ecological functioning and disturbance of a site. We examined the ability of both biocrusts and perennial vegetation of different morphological groups to recover from fire. We specifically examined: short mosses, tall mosses, and lichens (as used by Hilty et al. 2004), as well as perennial forbs, perennial grasses and annual grasses (*Bromus arvensis* L., *Bromus diandrus* Roth, *Bromus hordeaceus* L., *Bromus tectorum* L., *Vulpia bromoides* (L.) Gray and *Vulpia octoflora* (Walter) Rydb., with *B. tectorum* being the most abundant across the region). Lichen morphology included gelatinous, crustose and squamulose lichens from McCune and Rosentreter (2007).

Biocrusts are influenced by the amount and timing of precipitation, temperature, soil chemistry and texture (Belnap et al. 2001; Bowker and Belnap 2008). We also included grazing impacts because the predominant land use across the majority of the sagebrush steppe of the Great Basin is grazing by livestock. Studies of biocrusts in the Columbia Plateau (EPA Level III Ecoregions, https://archive.epa.gov/wed/ecoregions/web/html/level_iii_iv-2.html, accessed 14 April 2016), north of the Great Basin, corroborate that community composition of biocrusts is influenced by soil and climatic gradients (Ponzetti and McCune 2001), but there is an absence of such studies across the Great Basin. The recovery of biocrusts from fire has been studied at single sites, mostly on the periphery of the Great Basin (Johansen et al. 1984; Dettweiler-Robinson et al. 2013; Bowker et al. 2004). Working at the regional

scale, we examined the occurrence of biocrusts across the Great Basin and specifically address the questions: (Q1) Are there common factors that sites with high cover of biocrusts share across the Great Basin? (Q2) What drives (via correlation) the recovery of morphological groups of both plants and biocrusts in these eco-regions following fire? We looked specifically at time since fire, fire severity, grazing impacts from cattle, soil properties, and precipitation, being particularly interested in time since fire. (Q3) Do the drivers of recovery change if we control for time since fire? (Q4) Do we see a difference in the resiliency of morphological groups: short mosses, tall mosses, lichens, perennial grasses, perennial forbs and annual grasses to the disturbances of fire and grazing? Are there other factors that are structuring the cover of morphogroups?

We expected recovery patterns of morphogroups to follow what has been observed in other regions. Globally, biocrusts are prominent in warm, dry ecosystems with less cover of vascular plants and greater cover of bare ground (Belnap and Lange 2001). Across the Great Basin ecoregions, we expected to see relationships between morphogroups and heat load index (a unit-less index derived from latitude, slope and aspect, McCune and Keon 2002), as well as precipitation, with biocrusts being dominated by mosses to the north and lichens to the south (Belnap et al. 2001). We also expected that cover of perennial grasses and perennial forbs would be more likely to co-occur with mosses, preferring more productive sites in regards to soil moisture and temperature (Miller et al. 2011). Many biocrust species are also indicators of calcium carbonate and high soil pH, being more prominent on sites with these soils (McCune and Rosentreter 2007). Gelatinous lichens are nitrogen fixers (Harper and Belnap 2001), correlating their abundance with

low soil nitrogen concentration. We expected that soils with increased coarse fragments would inherently be protected from disturbance because of less susceptibility to erosion, relative to fires without coarse fragments. Fires with coarse fragments were expected to have higher cover of biocrusts. Disturbance related to grazing, represented by cow dung density and gap size between perennial plants (Reisner et al. 2013), was expected to result in reduced cover of perennial grasses, perennial forbs and biocrusts but increased cover of *B. tectorum*. Crustose and squamulose lichens are fragile and likely more sensitive to trampling than other morphogroups (Aquilar et al. 2009). Disturbance related to fire, as represented by time since fire and fire severity, was also expected to result in reduced cover of biocrusts (Johansen 2001) but short-term increases in cover of perennial grasses and perennial forbs (Keeley 1981). We expected fire to favor *B. tectorum*. Fire results in short term increases in resource availability following fire (Davies et al. 2007), which favors *B. tectorum* (Beckstead and Augspurger 2004). We expected short mosses to establish earlier than other biocrusts following fire given that short mosses establish and grow rapidly (Hilty et al. 2004).

Methods

Study Sites

The study area consists of wildfires within the sagebrush steppe of eastern Oregon, southwestern Idaho, northern Nevada, and western Utah on land managed by the Bureau of Land Management. Fires were previously selected and surveyed by Knutson et al. (2014) in 2010 and 2011 to cover the range of Major Land Resource Areas in the Great Basin (USDA NRCS 2006; Figure 3-1) but were restricted to loamy soils that only

burned once since 1970. Paired burned and unburned plots were surveyed at each fire as a space for time substitution for pre-burn conditions. The region spans a gradient of increasing productivity from south to north and from lower to higher elevations. We selected a subset of fires from the previous study on 87 fires, attempting to balance sampling across each of the following factors: precipitation for each of three water years following the fire, fire severity, time since fire (12 to 23 years), and grazing impact represented only as cow dung density (Table 3-1). A total of 15 fires were selected and 99 plots were surveyed in the summers of 2012 and 2013. Only one fire was known to be ungrazed. Six burned and six unburned plots were randomly surveyed at this fire. Otherwise, three burned and three unburned plots per fire were randomly selected and revisited from Knutson et al. (2014) with one additional exception that had a total of six unburned plots, which we also surveyed.

Plant, Biocrust and Soil Sampling

Plots consisted of three, 50-m transects radiating from a central point and separated by 120° (Herrick et al. 2005). Biocrusts were surveyed ocularly within 15, 25-cm² quadrats located at 10-m intervals along each transect. Cover of all biocrusts and plant species encountered in a plot were recorded and grouped into cover by morphogroups of plants (perennial forbs, perennial grasses and annual grasses) and biocrusts (short mosses, tall mosses, gelatinous lichens, squamulose lichens, and crustose lichens).

Soils were collected within each quadrat with three randomly placed, 5-cm diameter by 1-cm deep soil cores. Soils were kept in brown paper bags and kept at ambient conditions

within the Forest and Rangeland Ecosystem Science Center in Corvallis, Oregon, USA. Soil chemistry measures included pH, carbonates, NH_4^+ and NO_3^- on the 2-mm sieved soil fraction. Soil solution pH, 2 parts water to 1 part soil by mass was assayed using a Fisher brand Accu-flow pH meter and combination probe. The presence of soil carbonates were assessed with an effervescence test, using 1 M HCl dropped onto roughly a gram of the sieved 2mm soil fraction from each plot as described in Karunaratne et al. (2014). When the combination of soil and HCl resulted in an audible effervescence sound (violent effervescence), soils were recorded as having carbonates. Extractable NH_4^+ and NO_3^- were extracted from 7 g of soil for 1 hour with 35 mL of 0.5 M K_2SO_4 and filtered through Whatman 42 filters. Solutions were analyzed colorimetrically using a Lachat RFA 5000A autoanalyzer (Lachat methods #12-107-06-2-E and #12-107-04-1-H).

Data Analysis

To determine if there are common factors that would allow biocrusts to have higher cover on some fires across the Great Basin (Q1), 99 plots were grouped using hierarchical agglomerative cluster analysis with Ward's linkage method and Euclidean distance. The validity of groups was assessed with Multi-Response Permutation Procedure (MRPP), using Sørensen distance measure so as to be comparable with Non-Metric Multidimensional Scaling ordinations (NMS). MRPP uses an A-statistic to relate homogeneity within groups to random expectation with values near zero being closer to what is expected by chance and values near one indicating that test units within groups are similar (McCune and Grace 2002).

We expected lichens, short mosses and tall mosses would recover with time since fire (Q2) and we examined the recovery of these morphogroups with boxplots of the difference between burned and unburned cover for all plots, grouped by the number of years between the fire and our survey of biocrusts. Recovery of all 99 plots was further examined with NMS (Q2) and joint plots of relationships with measures of fire and grazing disturbance as well as environmental conditions related to topography, soil properties, soil texture, temperature (heat load index), and precipitation. To determine if factors associated with recovery changed when we held time since fire constant, both burned and unburned plots surveyed 13-14 years after fire (36 plots, 5 fires) were assessed again with NMS (Q3). The resiliency of morphological groups: short mosses, tall mosses, lichens, perennial grasses, perennial forbs and annual grasses, to the disturbances of fire and grazing were visually assessed along NMS axes most representative of disturbance and other identified drivers (Q4). Abundances of morphogroups along gradients (NMS axes) are reported as species scores from NMS. Multivariate analyses were performed in PC-Ord version 7. Boxplots were calculated in R version 3.0.2.

Results

Agglomerative cluster analysis of morphogroups of biocrusts and vegetation identified three groups of plots with 60% information remaining (Figure 3-2). Identified groups were dominated by one of the following three morphogroups: lichens, mosses / perennial grasses and perennial forbs. Groups were determined to be statistically different from one another with a MRPP derived A-statistic of 0.25. Visual examination of the plots

identified as having greater cover of lichens indicated that these plots were both unburned and ungrazed. Plots with greater cover of mosses / perennial grasses were often unburned and grazed but sometimes burned and grazed. Plots that were more defined by perennial herbs were often, but not always, burned and grazed.

Time since fire ranged from 12 to 23 years. Over that period of time, the difference in median cover of lichens between burned and unburned plots remained below zero indicating that the lichen component of biocrusts had not recovered to pre-fire levels (Figure 3-3a). The opposite trend was seen with short mosses, as burned plots had higher short moss cover relative to unburned plots, with the oldest fires having the greatest increases (Figure 3-3b). Immediately after fire, short moss cover in burned plots did decline below the short moss cover in the unburned plots. Tall moss cover generally increased with time since fire, although at 23 years after fire, the oldest fires were still in the process of recovering to pre-burn cover values of tall mosses (Figure 3-3c).

Groups from the agglomerative cluster analysis were overlaid on a NMS ordination of plots in morphogroup space to identify factors related to the separation of these groups. Final stress for the ordination was 11.64 with a 2-D solution. Axis 1 was rotated to align with the cover of *B. tectorum* to aid in interpretation and the ordination had a cumulative $R^2 = 0.925$ (Axis 1 $R^2 = 0.777$, Axis 2 $R^2 = 0.148$). Biotic variables including the cover of lichens, tall mosses, and shrubs were all negatively correlated with Axis 1, in opposition with *B. tectorum*, which was positively correlated with Axis 1 (Figure 3-4, Table 3-2). Disturbance variables related to both fire (difference in woody biomass and MTBS fire

severity) and grazing (gap between perennial plants) were all positively correlated with Axis 1 (Figure 3-4, Table 3-2). However, cow dung density was only weakly correlated with this Axis 1 even though there is a known relationship between dung density and the gap size between perennial herbaceous vegetation (Condon Chapt #2). Post-fire herbaceous biomass was also correlated with Axis 1. Given that the vector associated with herbaceous biomass aligned well with MTBS fire severity and perennial herbaceous cover was observed to increase fire in Chapter 2, it was grouped with the variables associated with fire. The joint plots of gap between perennial plants and cover of *B. tectorum* overlap in Figure 3-4, after rotating the ordination by cover of *B. tectorum*. Environmental variables (soil chemistry, soil texture, precipitation, etc.) were not correlated significantly with the occurrence of morphogroups in our ordination. Axis 2 is associated with increased cover of bare ground and increases along this axis were associated with increases in cover of lichens.

Plots from fires that burned in 1999 or 2000 were ordinated using NMS. We used data from only these two years to control for time since fire and determine if other factors were driving abundance and recovery of morphogroups following fire. Because no new relationships were seen in comparison with Figure 3-4, I chose not to show the ordination. The NMS ordination has a final stress of 6.9 and a 2-D solution was recommended. Axis 1 was rotated to align with the cover of *B. tectorum* to aid in interpretation. This ordination had a cumulative $R^2 = 0.963$ (Axis 1 $R^2 = 0.914$, Axis 2 $R^2 = 0.050$). Correlations between disturbance variables and Axis 1 were stronger in this ordination (difference in woody biomass $R^2 = 0.554$, post-fire herbaceous biomass $R^2 =$

0.392, and MTBS fire severity $R^2 = 0.368$ and grazing, gap between perennial plants $R^2 = 0.341$).

The abundance of morphological groups: short mosses, tall mosses, lichens (gelatinous, squamulose and crustose), perennial grasses, perennial forbs, and annual grasses were plotted against NMS axes representing disturbance (Axis 1, Figure 3-5) and increases in the cover of bare ground (Axis 2, Figure 3-6). The abundances of all morphogroups of lichens declined steeply with increasing disturbance (Figure 3-5b) and there was a more gradual decline in the abundance of tall mosses with increasing disturbance (Figure 3-5a). The cover of short mosses was low with low levels of disturbance, increasing with some disturbance but never gaining dominance (Figure 3-5a). Perennial grasses also increased in abundance with some disturbance and perennial forbs did not show a relationship with disturbance (Figure 3-5a). Axis 1 of the NMS ordination had been rotated to align with cover of *B. tectorum*, which is known to increase in cover with increasing disturbance. Annual grass cover as a group was shown to increase along this gradient (Figure 3-5a). All morphogroups of lichens became more abundant on plots with greater cover of bare ground and this was in opposition to increases in the cover of annual grasses (Figure 3-6b). Tall mosses gained higher cover earlier than lichens, increasing with increased cover of bare ground, but ultimately achieved lower maximum cover than lichens (Figure 3-6). Short mosses increased with increasing amounts of bare ground but peaked in abundance just before perennial grasses (Figure 3-6a). Perennial grasses achieved higher cover earlier than other morphogroups but were replaced by tall mosses and lichens on

the plots with more bare ground (Figure 3-6). Perennial forbs ultimately lacked a strong relationship with bare ground cover (Figure 3-6b).

Discussion

We demonstrated that disturbance is related to the cover of biocrust morphogroups across the Great Basin and that biocrusts are sensitive indicators of disturbance, when compared with perennial forbs and grasses. Biocrusts, particularly lichens, were most abundant on plots that were both ungrazed and unburned, represented by the convex hull that sat apart from the other groups and opposed gradients of grazing impacts (gaps between perennial plants) and the fire severity (difference in woody biomass between unburned and burned plots) (Table 3-2, Figure 3-4). The magnitude of the effect of disturbance is clear when looking at plots from fire X075, which was ungrazed prior to burning. Unburned plots from X075 had high cover of lichens. However, burned plots from X075 were no longer dominated by lichens, indicating that plots with high cover of lichens prior to fire can become more similar to other disturbed plots after fire.

We detected mixed responses of biocrusts to increasing time since fire. Over the range of years since fire included in our study, 12 to 23 years, we observed increased cover of short mosses and reduced cover of lichens and tall mosses following fire that was still present even at our oldest fire, 23 years after burning. These plots are still recovering from fire. However, the effects of fire and grazing are not addressed separately in this study as both were correlated with Axis 1 of our NMS ordination (Table 3-2, Figure 3-4). Much of the variability surrounding biocrust recovery given time since fire is likely due to the composition of morphogroups being structured by not just fire severity but also grazing impacts (Table 3-2, Figure 3-4). Throughout the Great Basin, both of these disturbances are common (Reisner et al. 2013; Knutson et al. 2014; Pyke et al. 2015) and

overlapping. Although we would have a better understanding of the amount of time it takes morphological groups of biocrusts to recover from fire if we could focus on areas that were only experiencing fire and not the secondary disturbances, our study is representative of the conditions found over much of the Great Basin.

Morphological groups of biocrusts and vegetation varied with increasing disturbance and secondarily by the amount of bare ground cover on a plot (Table 3-2, Figure 3-4). Short mosses and perennial forbs had slightly higher cover on disturbed plots but also appeared to be generalists (Figure 3-3, Figure 3-4, Figure 3-5) with short mosses increasing with increasing cover of bare ground but never gaining dominance (Figure 3-6). Short mosses tend to be ruderal species that quickly colonize burned areas of all fire intensities (Warcup 1981) even though individual moss species may be more or less prevalent given fire intensities or amounts of time since fire (Esposito et al. 1999; Smith et al. 2013). Mosses lay the groundwork for the succession of biocrusts and plant communities (Read et al. 2011). Perennial forbs are also generally stimulated by fire (Keeley et al. 1981). Given the wide range of perennial forbs encountered (Knutson et al. 2014), no individual species or group of species appeared to dominate across the region.

Perennial grasses were stimulated by some disturbance, but showed decreases in cover at the highest levels of disturbance, in our case, the combination of grazing and fire impacts (Figure 3-5). Cover of tall mosses gradually declined with increasing disturbance but did not show significant declines until cover of perennial grasses started to decline as well.

Tall mosses tolerate some disturbance but are greatly reduced in cover on heavily

disturbed sites (Ponzetti et al. 2007). Both perennial grasses and tall mosses were favored by increases in cover of bare ground, not changing much in cover over the portion of the gradient dominated by annual grasses. *B. tectorum* competes with perennial grasses primarily at the germination stage because it germinates under cold winter temperatures before perennial grass seeds germinate (Aquirre and Johnson 1991) and exhibits greater root elongation under low temperatures (Harris 1967), possibly explaining why we do not see a change in cover of perennial grasses over this portion of the gradient. Perhaps established perennial grasses were able to maintain cover but no new individuals were recruited. Almost two-thirds through the gradient of increasing bare ground cover, from left to right, cover of annual grasses begins to decline and cover of tall mosses continues to increase, with perennial grasses peaking in cover. Although higher elevation, cooler, wetter sites are inherently more resistant to invasion by *B. tectorum*, a mixture of two things might be happening on the opposite end of this gradient where cover of bare ground is high. Conditions might be stressful for vascular plants in regards to aridity, where even though *B. tectorum* is still present, its cover is reduced (Chambers et al. 2007) or lichens are hindering the establishment of *B. tectorum* (Deines et al. 2007). Lichens were highly sensitive to disturbance and dramatically decreased in cover along this gradient but increased in cover along the gradient of increasing cover of bare ground. Lichens are both sensitive to disturbance (Johansen et al. 1984; Belnap et al. 2001) and are favored under conditions that tend to be stressful for vascular plants (Bowker et al. 2011).

Morphological groups of lichens did not demonstrate a clear difference in response to gradients of increasing disturbance or cover of bare ground across the sagebrush steppe of the Great Basin, but instead tended to respond as an intertwining unit. Although the range of time since fire that we analyzed was enough to see some recovery of tall mosses, it was likely not enough to see the recovery of various morphological groups of lichens. Lichens are sensitive to trampling to the extent that Belnap et al. (2006) observed that many biocrust species found on ungrazed sites were not found on sites that had been previously grazed at either intermittent or continuous frequencies. The low amount of cover of lichens that we observed might have been due to most of our sites being actively grazed. In protected areas in the Palouse Prairie, Bowker et al. (2004) observed that there was no difference in the species composition of mosses and lichens following fire, indicating that grazing might be structuring the abundance of lichens more so than fire.

This study examines the determinants of biocrust and perennial vegetation morphogroup abundance two scales: fine scale relations to soil properties and the fire scale in relation to grazing impact and fire intensity. Maestre et al. (2005) demonstrated that the richness and evenness of biological soil crust species, directly and negatively relates to total N content in surface soils, implying that nitrogen inputs are related to the abundance of particular species. Ponzetti and McCune (2001) found that gradients of soil pH and electrical conductivity, more so than grazing impacts were a stronger driver behind the occurrence of biocrusts species. It is possible that we did not detect the influence of soil properties because we examined the abundance of morphogroups and not species. Species may be responding individually to soil properties and not responding as

morphogroups. This corroborates Bowker et al. (2011) that found many functional attributes were not predictable from existing grouping systems based on morphology. We surveyed fires across the Great Basin, stratified by MRLA and precipitation in water years following fire. Although a climate gradient was not evident in our analysis, we did find a relationship between bare ground cover and the abundance of morphogroups. Perhaps this captures the influence of climate but allows for site-specific differences that would influence bare ground cover such as soils and topography (Gardiner and Miller 2004). Alternatively, the influence of disturbance may be overriding the response of morphogroups to soil properties. Although plot scale differences in disturbance were the primary driver that we observed in relation to the abundance of morphogroups, we might have been able to pick up other gradients if species identity was examined.

The relationship between cover of *B. tectorum* and biocrusts is complex and inconsistent in the existing literature. Similar to work done by Dettweiler-Robinson et al. (2013) and Ponzetti et al. (2007) in the Columbia Basin, we observed a strong negative relationship between the cover of *Bromus tectorum* and biocrusts across the Great Basin. Although Dettweiler-Robinson et al. (2013) notes that increasing cover of *B. tectorum* leads to reductions in biocrusts there is evidence that biocrusts maintain site resistance to *B. tectorum* (Reisner et al. 2013; Condon et al. Chapter #2). Many of the interactions between biocrusts and vascular plants are likely morphogroup, if not species specific (Escudero et al. 2007). Lichen-dominated crusts, compared with bare soil, resulted in a one-third reduction in germination of both *B. tectorum* and *Vulpia microstachys* (Nutt.) Munro. (Deines et al. 2007), because lichen dominated biocrusts provide a physical

barrier to establishment of annual grasses. Lichens might also be maintaining site resistance via antibiotic effects and fungal networks. Castillo-Monroy et al. (2011) examined the apparent antibiotic effects of some lichen species upon soil bacteria. *Bromus tectorum* is favored by soil microbial communities that are dominated by bacteria as opposed to fungi (Owen et al. 2013). The fungal partner of many lichens is also often found in the rhizosphere of perennial plants (Green et al. 2008). Given the unique ecological functions of individual lichen species, it is also possible that lichen species are maintaining site resistance in concert with one another. Site resistance maintained by the presence of biocrusts might also depend more upon the preservation of intact crusts as opposed to their recovery. Ponzetti et al. (2007) demonstrated that integrity of biocrust had a stronger relationship with *B. tectorum* than fire. Given the scarcity of evidence related to the full recovery of lichen components following human disturbances (Johansen et al. 1984; Lalley and Viles 2008), sites with intact biocrusts are prime places for further research within the Great Basin.

Sites that have not experienced anthropogenic disturbance within the Great Basin are rare. There were pockets within some fires that might have been previously ungrazed (Condon personal observation) but there are no available data to support these observations. Future work involving biocrusts and disturbance should include reference sites that are known to be free of disturbance (or have high likelihoods of being free of disturbance) to thoroughly explore the difference between the two. A comparison between disturbed and undisturbed sites is often done in the field of restoration ecology (Hobbs et al. 2014) similar to control sites in field experiments. If we hope to gain a

thorough understanding of the biocrusts of the Great Basin, we need to prioritize the study of paired disturbed and undisturbed sites.

Given disturbances of grazing and fire in the sagebrush steppe of the Great Basin, we are seeing reductions in the cover of biocrust morphogroups, particularly lichens, across the Great Basin. If we are losing morphogroups, then we are clearly losing species and their associated ecosystem functions. The species identity of many lichens is still being worked out with chemical and genetic analyses, making an effort to include crust identity at the species level, challenging. However, this is clearly needed in the Great Basin.

If we are managing these landscapes for ecosystem function, functional diversity should be a metric of interest for determining the net functional attributes of this ecosystem (Tilman et al. 1997). Biocrusts provide ecosystem functions and exert a strong impact on associated communities such as vascular plants (Green et al. 2008) as well as soil bacteria and fungi (Bates and Garcia-Pichel 2009). If post-fire site evaluations were to include biocrusts, we would have a better sense of the ecological functioning of a site, managing not just for plant communities but nutrient cycling, hydrologic cycling and erosion potential as well.

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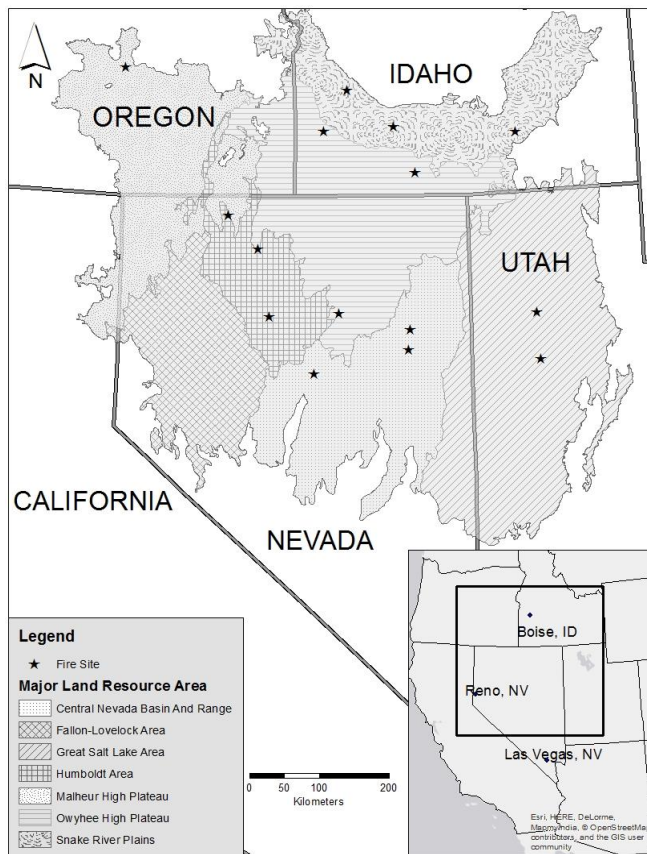


Figure 3-1. The locations of the fifteen fires surveyed across the Great Basin, USA.

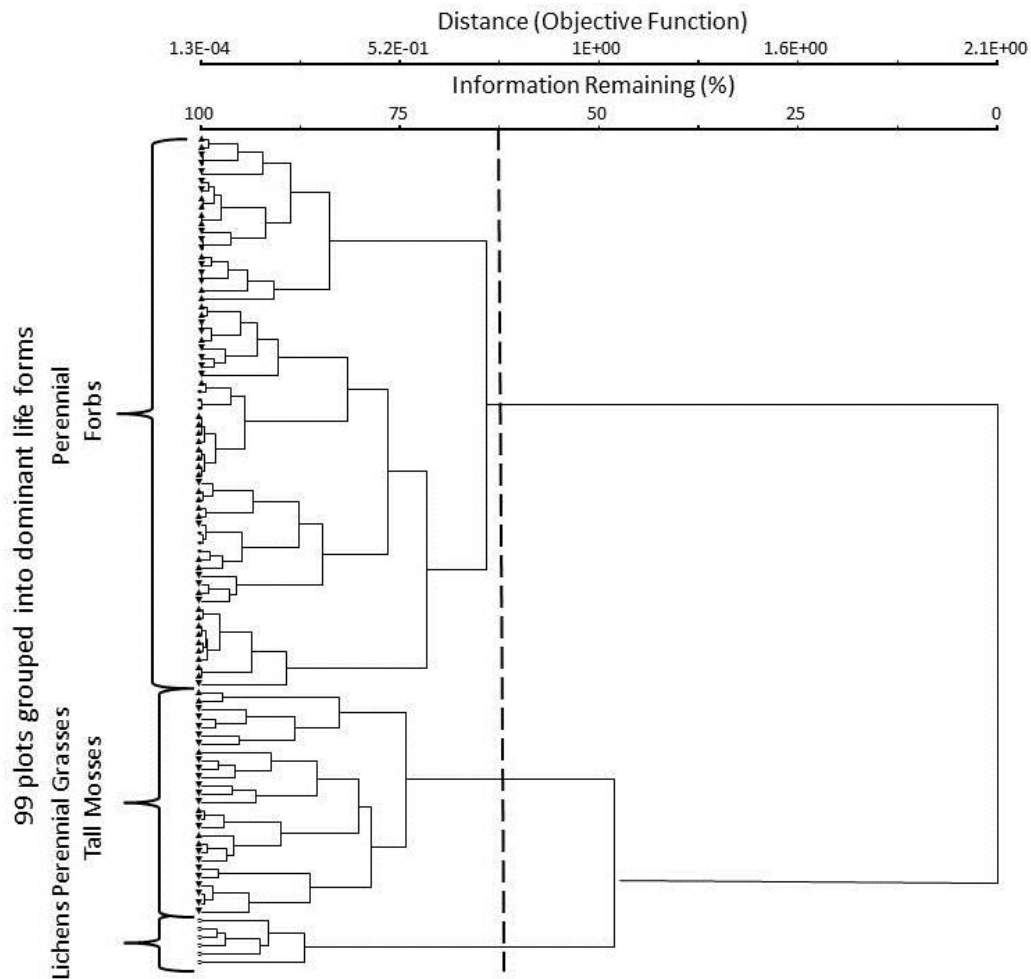


Figure 3-2. Dendrogram of cluster analysis with plots grouped by dominant life forms. Dashed line indicates grouping with 60% information remaining. Distance measure was Euclidean distance with Ward's linkage function. Identified groups clustered with increasing distance amongst group members as determined by MRPP: higher cover of lichens (0.13), perennial grasses and tall mosses (0.27), and perennial forbs (0.41). Symbols represent the grazing and burn status of plots: ▲ -burned and grazed, ▼ -unburned and grazed, ● -burned and ungrazed, ○ -unburned and ungrazed.

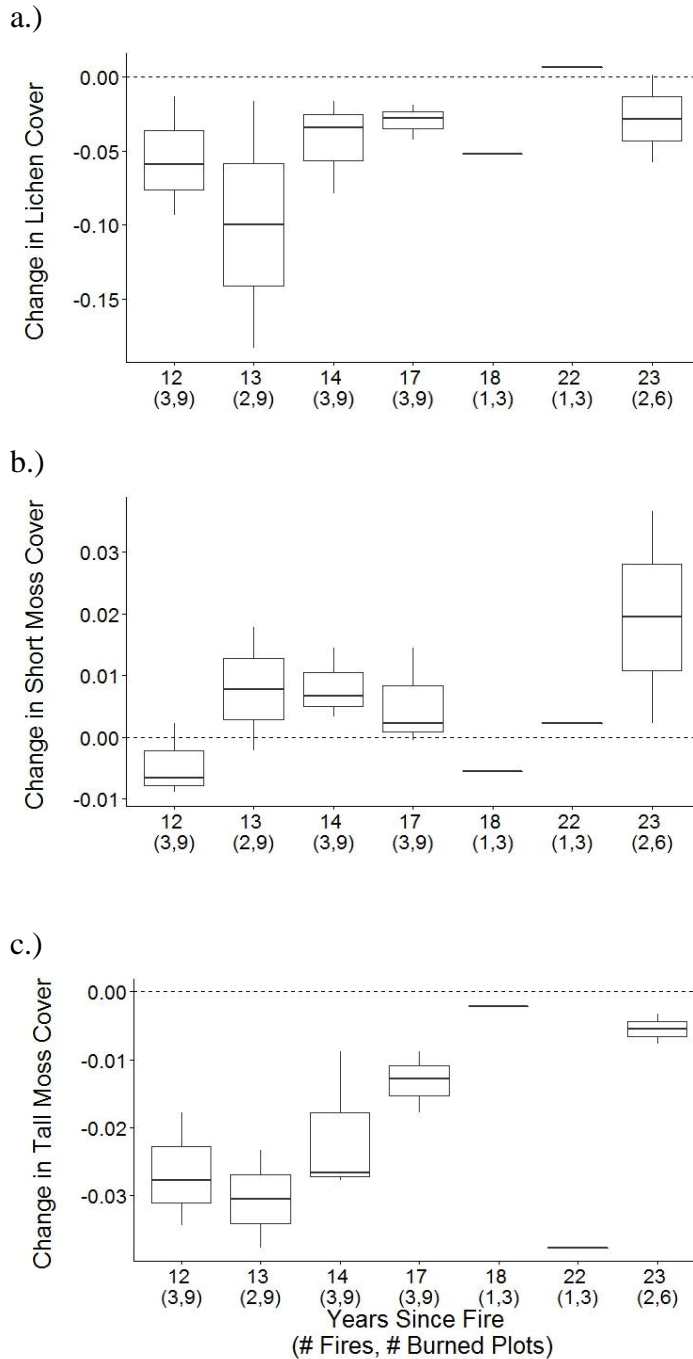


Figure 3-3. Boxplots of the median difference in cover of a.) lichens b.) short mosses c.) tall mosses between burned and unburned sites by years since fire. Lower and upper edges of a box are the 1st and 3rd quartiles. Whiskers extend to the lower and upper data values within 1.5 of the interquartile range. Number of unburned plots matches the number of burned plots with the exception of three additional unburned plots at one fire, 17 years since fire. Negative numbers indicate that cover values are lower than unburned plots. Positive numbers indicate higher cover when compared with unburned plots.

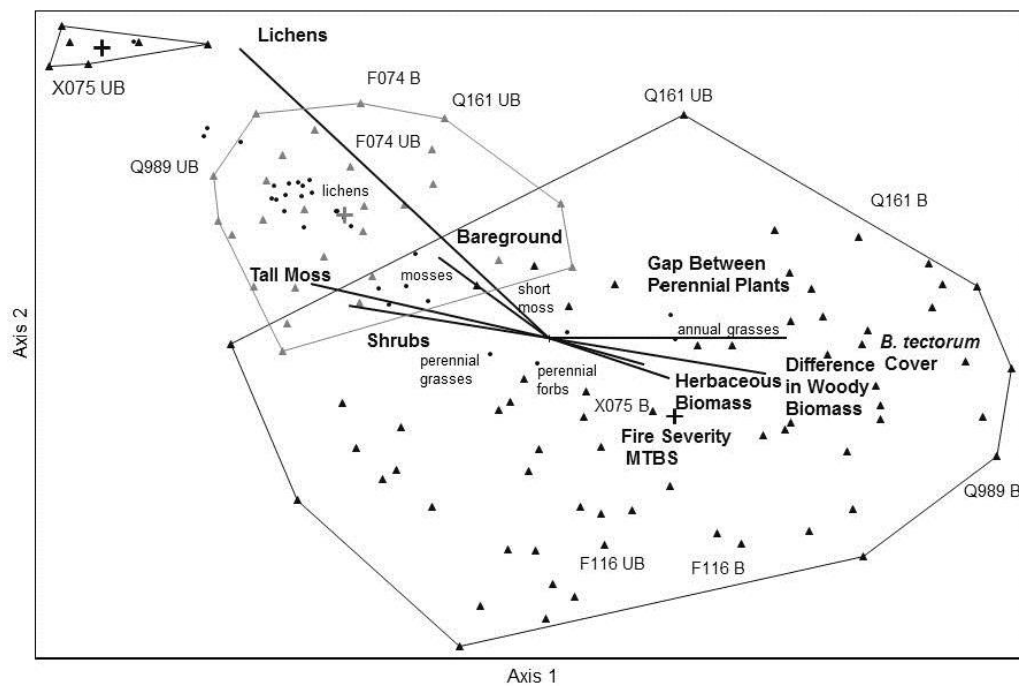


Figure 3-4. Non-metric multidimensional scaling ordination of plots in morphogroup space for all sites. Triangles are plots. Dots are morphogroups. The ordination was rotated to align with cover of *B. tectorum*, which is perfectly superimposed on the gap between perennial plants. Radiating lines show the relative strength in correlation of variables with at least one axis, in excess of 0.2. Disturbance variables include grazing impacts as represented by the gap between perennial plants and fire severity represented by the difference in woody cover between unburned and burned plots as well as MTBS (Monitoring Trends in Burned Severity). Cover of lichens and mosses are overlaid as variables. Plots are shaded to match convex hulls, representing groups identified by the cluster analysis. Alphanumeric codes represent site labels of select plots: B- burned and UB- unburned.

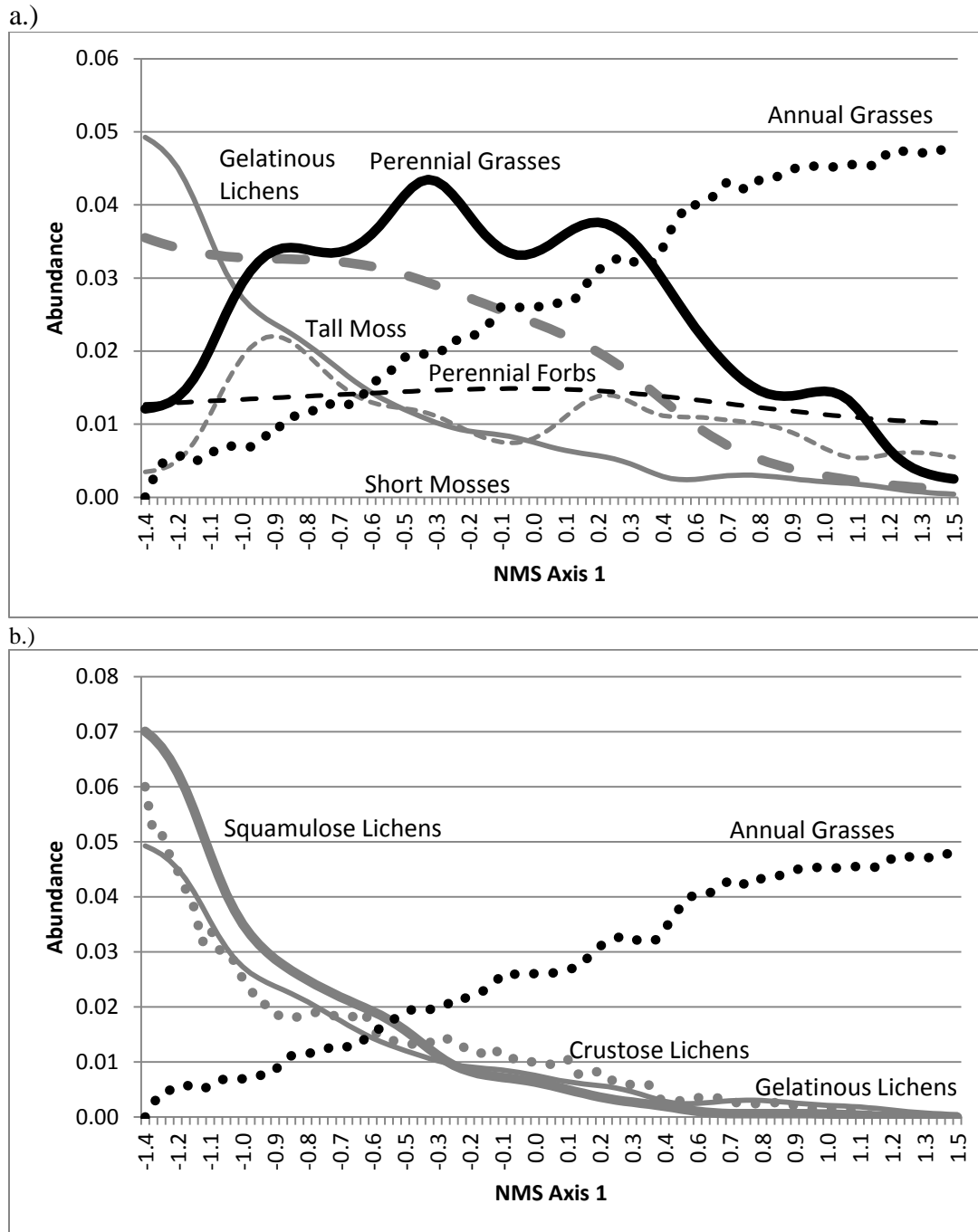


Figure 3-5. Abundances of morphogroups on all plots in relation to non-metric multidimensional scaling ordination Axis 1, representing disturbance (difference in woody biomass and gap between perennial plants). X-axis represents a gradient of increasing disturbance, Axis 1 from the NMS ordination. Y-axis represents abundances of morphogroups in relation to one another from the NMS ordination. a.) Abundances of vascular plants are in black and biocrusts are in gray. b.) Abundances of squamulose lichens are in thick gray, gelatinous lichens are in thin gray, crustose lichens are gray dots and annual grasses are black dots.

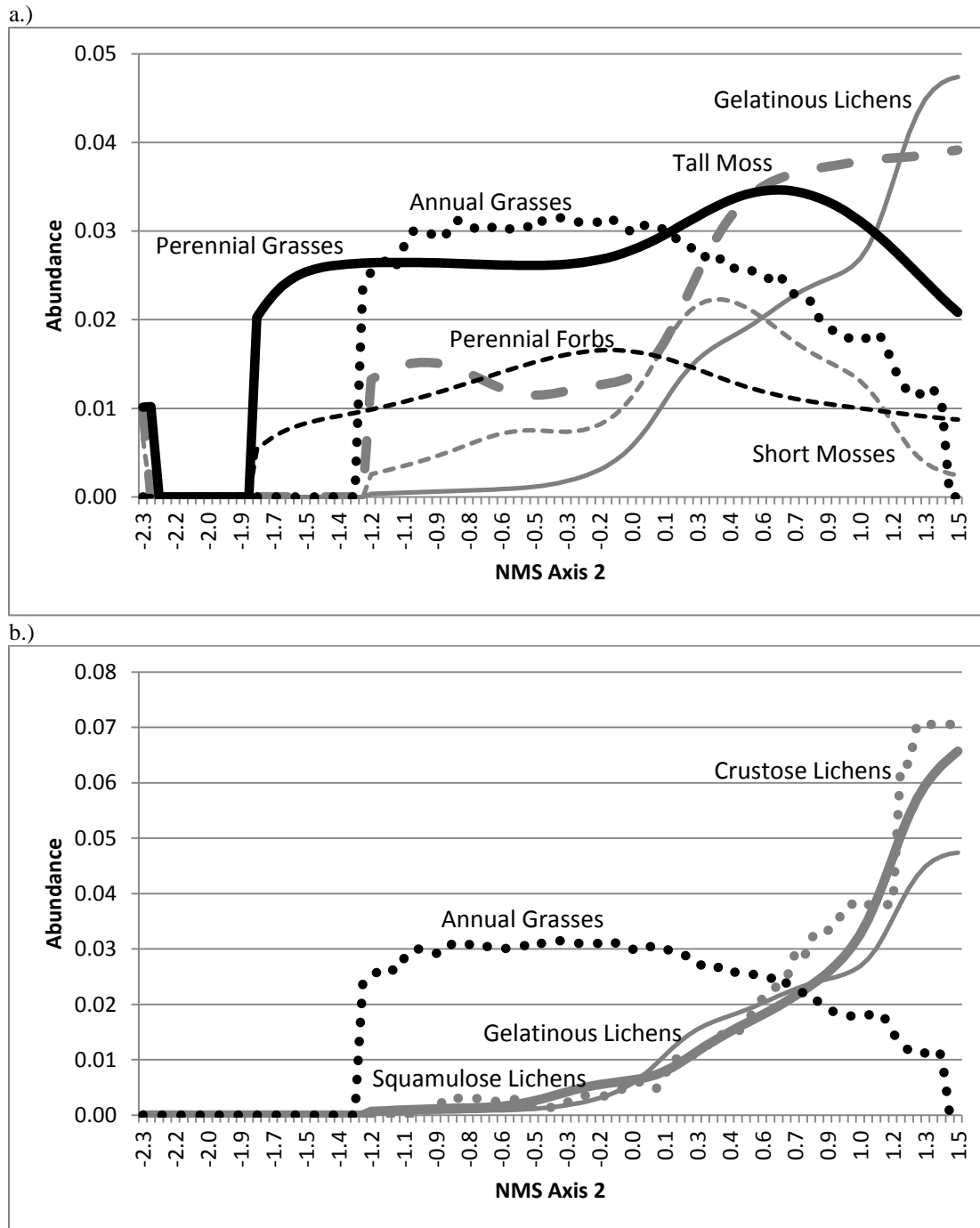


Figure 3-6. Abundances of morphogroups in relation to non-metric multidimensional scaling ordination Axis 2, representing inherently bare sites. X-axis represents a gradient of bare ground, Axis 2 from the NMS ordination of all plots. Y-axis represents abundances of morphogroups in relation to one another from the NMS ordination. a.) Abundances of vascular plants are in black and biocrusts are in gray. b.) Abundances of squamulose lichens are in thick gray, gelatinous lichens are in thin gray, crustose lichens are gray dots and annual grasses are black dots.

Table 3-1. Variables* considered in site selection from Knutson et al. 2014. Selected sites represented the range of values. Additional variables were used in analysis. Average values and standard deviations are shown. Abbreviations: dNBR- differenced Normalized Burn Ratio, MTBS- Monitoring Trends and Burn Severity database, p- plots, WY- Water Year following the fire. Headings are *variables* (and sources of information).

Description	Units	Mean (S.D.)	Range
<u>Precipitation*</u> (PRISM 2010)			
Precipitation is given for each of the three water years following the fire as modeled by PRISM.	Mm	WY 1- 256 (54) WY 2- 274 (74) WY 3- 300 (101)	WY 1- 179-373 WY 2- 168-437 WY 3- 155-556
<u>Fire Severity*</u> (MTBS 2012)			
Fire severity was estimated with dNBR. Sites were selected to cover a range of fire severities. Plots were classified according to their dominant fire severity.	N/A	N/A	Unburned- 51 p Low Severity- 29 p Moderate Severity- 16 p High Severity- 3 p
<u>Fire Severity Woody Consumed</u> (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx))			
Using line-point intercept at 1-m intervals, the total of all shrub hits was used to calculate average unburned shrub cover of a site. Shrub cover for each site was subtracted from the unburned average and divided by this number to get a proportion of what burned.	Proportion	0.41 (0.04)	0-1
<u>Post-Fire Herbaceous Biomass</u> (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx))			
This is above-ground biomass only, and includes both live plant material plus standing dead plant material.	g/m ²	100.8 (9.6)	0.5-542.7
<u>Time Since Fire*</u> (Pilliod & Welty 2013)			
The number of years between the fire and the 2012-13 sampling date.	Years	16 (3.8)	12-23 (1990-2001)
<u>Total Area Burned*</u> (Pilliod & Welty 2013)			
The area inside the fire perimeter measured in ArcMap.	Ha	6013.9 (10269.3) 14860.6 (25376.1)	540.7-42920.6 1336-106059
<u>Standard Deviation in the Gap Between Perennial Plants</u> (Field measured, Knutson et al. 2014)			
Standard deviation of the average (avg) gap between perennial plants along the 50-m transects at each plot.	Cm	Avg gap-230.1 (553.7) SD Avg gap- 199.5 (297.8)	Average- 36.3-5000 SD- 0-1962
<u>Cow Dung Density*</u> (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx))			
Cow dung per meter squared counted in shrub belt transects.	#/m ²	5 (5)	0-25
<u>Bare ground Cover</u> (unpublished data, archived at USGS SAGEMAP (http://sagemap.wr.usgs.gov/ESR_Chrono.aspx))			
Using line-point intercept at 1-m intervals, bare ground is defined as no top canopy hits followed by an intercept of soil.	%	11.5 (1.1)	0-51.3

Table 3-2. Correlations of predictor variables with non-metric multidimensional scaling ordination axes for all fire sites. Values in bold are R^2 values that are greater than or equal to 0.2. Variables associated with these values are interpreted as explaining community structure.

	All Plots (Cumulative $R^2 = 0.925$)					
	Axis 1			Axis 2		
Variable	R	R^2	Tau	R	R^2	Tau
<i>Biotic</i>						
<i>Bromus tectorum</i> cover	0.707	0.500	0.524	-0.026	0.001	-0.020
Cyanobacteria	-0.356	0.127	-0.308	0.381	0.145	0.303
Lichen	-0.797	0.635	-0.694	0.788	0.621	0.562
Mosses (Short)	-0.207	0.043	-0.154	0.154	0.024	0.127
Mosses (Tall)	-0.707	0.493	-0.545	0.353	0.125	0.218
Perennial Forbs	-0.044	0.002	-0.047	-0.137	0.019	-0.069
Perennial Grasses	-0.306	0.094	-0.262	-0.122	0.015	-0.099
Shrub Cover	-0.643	0.414	-0.512	0.273	0.075	0.150
<i>Disturbance-Fire</i>						
Difference in Woody Biomass	0.673	0.453	0.514	-0.286	0.082	-0.147
Fire Severity (MTBS)	0.500	0.250	0.415	-0.297	0.088	-0.249
Post-fire Herbaceous Biomass	0.448	0.201	0.432	-0.238	0.057	-0.208
<i>Disturbance-Grazing</i>						
Cow dung density	0.126	0.016	0.040	0.070	0.005	0.039
Gap Between Perennial Plants	0.525	0.276	0.438	0.000	0.000	0.007
<i>Environment</i>						
Bare ground Cover	-0.423	0.179	-0.299	0.491	0.241	0.302
Calcium carbonate	0.050	0.002	0.084	0.262	0.069	0.167
Coarse Fragment (%)	-0.140	0.020	-0.079	-0.203	0.041	-0.118
Heat Load Index	0.115	0.013	0.104	0.038	0.001	0.052
NH ₃	-0.078	0.006	-0.068	-0.250	0.062	-0.054
NO ₃	0.082	0.007	0.054	-0.089	0.008	-0.025
pH	-0.006	0.000	-0.006	0.236	0.056	0.124
Water Year 1	0.161	0.026	0.118	-0.144	0.021	-0.095
Water Year 2	0.120	0.014	0.089	-0.277	0.077	-0.184
Water Year 3	-0.084	0.007	-0.027	-0.170	0.029	-0.058

**Chapter 4 Restoring resilience and resistance in arid environments via
mosses: source populations, organic matter and overwintering govern
success**

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Summary

1. Biological soil crusts are crucial components to arid land ecology and contribute to ecosystem resilience and resistance to plant invasions. Knowledge of their restoration potential is desirable given ongoing changes to fire regimes and grazing pressures.
2. In a common garden, we examined establishment and growth of two moss species common to the Great Basin, USA: *Bryum argenteum*, and *Syntrichia ruralis* from two distinct environmental settings (warm dry vs. cool moist). Moss fragments were introduced into a warm dry setting, on bare soil in spring and fall both with and without a jute net and irrigation. Moss cover was monitored in three spring seasons.
3. Both moss species increased in cover over the winter. When *Bryum* received irrigation that was out of sync with natural precipitation patterns, moss cover increased and then crashed, taking two seasons to recover to the same values as mosses that were not irrigated. *Syntrichia* did not respond to the irrigation treatment. The addition of jute net increased moss cover under all conditions, except *Syntrichia* following fall introduction, which required a second winter to increase cover. Mosses, from both species, consistently achieved higher cover from warm dry populations than cool moist. The warm dry population of *Bryum* combined with jute achieved on average 60% cover compared to *Bryum* from the cool moist population that achieved only 28% cover by the end of the study. Differences were less pronounced for *Syntrichia* where moss from the warm dry population with jute achieved on average 51% cover compared to *Syntrichia* from the cool moist population that achieved 43% cover by the end of the study. Findings suggest that although mosses are cosmopolitan in regards to spore dispersal, they are not plastic in regards to environmental stresses at a regional scale. When establishing arid land

bryophytes, it is necessary to allow them to overwinter before assessing their affinity for a given site.

4. *Synthesis and applications:* Arid land mosses show potential for rapid restoration of cover with minimal effort relative to vascular plant restoration. Restoration of arid land mosses may provide a quicker method for protecting soils from erosion while occupying sites before invasive plants.

Introduction

Worldwide, biological soil crusts (BSCs) are important ecosystem components. BSCs reduce aeolian soil erosion (Belnap & Gillette 1998), influence water infiltration (Chamizo *et al.* 2012), and nutrient cycling (Pendleton *et al.* 2003). BSCs thrive in environments that are stressful to vascular plants (Bowker, Soliveres & Maestre 2010) because they are poikilohydric, making use of moisture as it becomes available (Proctor & Tuba 2002). As undisturbed Mediterranean and arid environments become increasingly stressful to vascular plants along gradients of increasing aridity, the prominence of BSCs increases in Mexico (Aquilar *et al.* 2009), Australia (Read *et al.* 2011), Spain (Bowker, Soliveres & Maestre 2010), China (Su *et al.* 2009) and the southwestern United States (Bowker & Belnap 2008). BSCs were likely more prominent on some arid lands before livestock were introduced (Aquilar *et al.* 2009; Read *et al.* 2011; Reisner *et al.* 2013), suffering reductions in cover and species richness due to trampling (Anderson, Harper & Rushforth 1982). Although BSCs are common and important worldwide, they are rarely considered in the restoration literature (Bowker 2007).

Ecologists aim to maintain site resistance and resilience to ruderal plant species, which is conserved by BSCs (Reisner *et al.* 2013). Ruderal *Bromus* species commonly invade disturbed arid environments (Pyke 2011). BSCs reduce the establishment of *Bromus* species (Zaady *et al.* 2003) and increase time to germination (Serpe *et al.* 2006). Mosses increase site resistance to invasion by some annuals (Li *et al.* 2005) and increase resilience by facilitating establishment of perennial grasses (St. Clair *et al.* 1984) and *Artemisia* species (Su *et al.* 2009).

Given that mosses are poikilohydric, season of introduction might influence the success of moss restoration. Winter precipitation is the main moisture input in Mediterranean systems like the Great Basin (Dobrowoski, Caldwell & Richards 1990). Additions of organic matter might favor mosses as increased water holding capacity of litter leads to greater growth of bryophytes (Rincon 1988). In the Great Basin, litter is often dominated by sagebrush leaves as grazing animals consume grasses (West *et al.* 1984). Mosses are more prevalent under shrubs, as shrubs protect mosses from trampling (West 1990) and their litter, plus shade provide higher soil moisture (Bowker *et al.* 2000).

When restoring vascular plant species it is important to select site-appropriate ecotypes but we do not know if the same is true for bryophytes. The distribution of a single vascular plant species over a range in climate is known to enhance development of ecotypes (Clausen, Keck & Hiesey 1948), which often vary in their ability to thrive under environmental conditions. A precipitation gradient ranging from 200-460 millimeters

exists over the Great Basin sagebrush steppe on sites surveyed by Knutson *et al.* (2014) (30-year average, PRISM 2010), as the region is wetter in the northeast and more arid towards the southwest (USDA NRCS 2006). Although a single moss species can occur over wide gradients, foreign genetic material can join any existing moss population because bryophytes produce several hundred thousand spores per sporangium, with potential to be distributed globally (Frahm 2008).

Our study is the first to date to examine the potential existence of moss ecotypes based on collections from widely different environmental settings and the restoration capability of common arid land mosses by utilizing factors thought to increase soil moisture. We pose the following questions regarding restoration of mosses common to the Great Basin,

Bryum argenteum and *Syntrichia ruralis*:

- (1) Do treatments of jute net (organic matter) application, irrigation or the combination of the two, increase cover of these mosses?
- (2) Does season of introduction effect moss cover? Does a jute net influence this effect?
- (3) What time of a typical year is moss growth greatest?
- (4) Does the source of mosses effect moss cover relative to amelioration treatments?

Materials and methods

Study Species and Site Descriptions

The study was conducted using *Bryum argenteum* Hedw., a cosmopolitan, (Pisa *et al.* 2013) and ruderal species (De Las Heras, Herranz & Martinez 1993; Esposito, Mazzoleni & Strumia 1999) and *Syntrichia ruralis* (Hedw.) F. Weber & D. Mohr, a later

successional species (Esposito, Mazzoleni & Strumia 1999). *Bryum argenteum*, is generally between 0.5-1 mm tall with bulb-shaped shoots. *Syntrichia ruralis* is generally 2-20 mm tall and leaves are twisted around stems when dry. Both species were collected from two environmentally distinct locations to address the effect of presumed ecotypes on rate of establishment and growth. We did not replicate within locations. The two collection sites are separated by 235 km: the Morley Nelson Snake River Birds of Prey National Conservation Area (BoP) south of Boise, Idaho and the Steens Mountain Cooperative Management and Protection Area (Steens) south of Burns, Oregon, both managed by the Bureau of Land Management (Table 4-1). According to Chambers *et al.* 2014, BoP is likely to demonstrate low site resilience and low resistance to invasion by *B. tectorum* given its mesic soil temperature and aridic soil moisture regime in contrast to the Steens, which is likely to demonstrate moderately high site resilience and moderate resistance with its frigid soil temperature and xeric soil moisture regimes.

The recipient site, where the experiment was located, is on private land one mile north of Madras, Oregon, USA (Table 4-1). The recipient site, like BoP, was predicted to demonstrate low site resilience and low resistance to invasion by *B. tectorum* due to mesic soil temperature and aridic soil moisture regimes (Chambers *et al.* 2014). During the 2013-2014 water year this site received 178 mm of precipitation (89 mm between 1 Oct. and 1 March) and in the 2014-2015 water year it received 185 mm of precipitation (122 mm between 1 Oct. and 1 March). Average precipitation over the period of record beginning in 1909 is 242.4 mm (WRCC 2014). Over the period of study, maximum temperature was 38°C on 27, 28 June and 3 July 2014 and minimum was -31°C on 9

December 2013. At the time of field application, maximum temperature was 23.6°C on 5 May 2013 and 8.94°C on 16 November 2013. Mean humidity on those days was 41% and 63%, respectively.

Soils were collected under the moss, no deeper than 10 cm, and used in the experiment because arid land mosses might show preferences for soil types (Bowker & Belnap 2008). Using the procedure outlined in Thien (1979), surface soils from both BoP and Steens were determined to have a loamy texture. Soils were autoclaved to eliminate moss propagules and kept sterile until use. Flats (12.7 cm x 17.8 cm x 5.1 cm deep) were initially filled halfway with soil from recipient site and the remaining 2.54 cm was filled with soil paired with associated moss populations.

In March and April of 2013, mosses were collected from each site and dried to ambient humidity within the Forest and Rangeland Ecosystem Science Center in Corvallis, Oregon, USA. Moss fragments selected for use were apical leaves that remained green at the time of desiccation because green fragments recolonize more rapidly than older moss (Barker *et al.* 2005). Mosses were rubbed through a 2-mm sieve to create fragments for even application of inoculants, stored and transported in paper bags.

Experimental Design

Both moss species were collected at BoP and Steens. We refer to each species in association with its collection location (species-location, from here after source population). We used a factorial design to examine potential effects of source population

(*Bryum*-ST, *Bryum*-BoP, *Syntrichia*- ST, and *Syntrichia*-BoP), jute net (yes or no), season of introduction (spring and fall), and irrigation in the spring season only (yes or no) on the average cover of these mosses. Moss material was pooled by location, so we did not have replication of each location and could not statistically test for the effect of collection location on average moss cover. We scored ocular estimates of cover to the nearest 1% with a 12.7 cm x 17.8 cm gridded frame with 25.4 mm x 25.4 mm grids. .

The experiment was conducted between April of 2013 and May of 2015. Treatment replicates were flats, buried so the top of flat was flush with the native soil surface. Flats were randomly located within four, 1.8 m x 1.8 m x 0.6 m-caged blocks to discourage wildlife damage. Cages were made from a frame of welded aluminum 2.5-cm x 2.5-cm square stakes, 60 cm tall, with the sides draped in green plastic fencing attached with zip ties (1.9-cm x 1.9-cm mesh). Hog fence (7.6 cm x 20.3 cm) was welded to the top of the frame to exclude deer. Hardware cloth (0.6 cm x 0.6 cm) was used along the base of each cage and to a height of 10.2 cm to exclude small mammals. This minimized the use of galvanized metal, which contains zinc, a common ingredient in moss control herbicides. Flats were arranged adjacent to one another and with roughly 5 cm between the outer flats and the sides of the cage. A section was left open in the center of the block for accessibility.

Moss fragments (1 g) were hydrated with approximately 60 ml of water for twenty minutes in the field immediately prior to being spread over the surface of a flat to yield an application rate equivalent to 43.5 g of moss per m². This ensured that moss fragments

were actively photosynthesizing at the time of application (Proctor & Smirnov 2000), likely resulting in a net carbon balance and minimizing stress to individual fragments. The water brought the soil to approximately field capacity. Twelve replicates of each treatment resulted in a total of 384 flats. Some flats were lost to disturbance but no treatment had fewer than 11 flats. Season of moss introduction was tested with a spring (5 May 2013) and a fall (16 November 2013) application. An irrigation treatment consisted of watering flats with tap water to field capacity weekly during the first spring (May-June), after which ambient precipitation was the only source of water. Jute net was applied over mosses to increase water retention on the soil surface and the boundary layer experienced by the moss. Our scope of inference is limited to the four previously mentioned source populations grown outdoors in Madras, Oregon USA between April 2013 and May 2015.

Data Analysis

Data were analyzed with linear mixed models to allow for an unbalanced design and repeated measures of each flat fit by maximum likelihood. This approach does not allow for the calculation of traditional ANOVA tables. F-values are used to report significance for variables of interest. Research questions were addressed as three separate experiments: the treatment experiment, the seasonal experiment and the overwintering experiment with separate additive models being fit for each. We fit full models, including three- and four-way interactions where appropriate, because we were interested in quantifiable additive differences in percent moss cover given treatments and significant interactions amongst treatments. For example, we wanted to quantify expected increases

in mean percent cover of inoculating moss with jute net compared to inoculating moss without treatment. This translates into a difference in mean percent cover between treatments.

The treatment experiment model assessed the mean effect of each treatment combination on average moss cover, evaluating all main effects and interactions of four levels of source population, two levels of spring irrigation, and two levels of jute net. This model only included data from mosses inoculated in the spring of 2013. Using the difference in mean effects on cover, each treatment combination was compared to moss without treatment but from the same source population. The seasonal experiment model tested the effect of season of introduction and the presence of jute net on average moss cover using data from both seasons of introduction between 7 April 2014 and 3 May 2015. Mean effects on cover of moss introduced in the fall were subtracted from moss inoculated in spring both with and without jute net. The overwintering experiment model evaluated the mean effect of overwintering once and twice on average moss cover for each treatment combination, using data from one May sampling date in each of three years (26 May 2013, 25 May 2014, and 3 May 2015). Differences in mean effects of earlier years were subtracted from those of later years.

A random effect of flat, identified by replicate number for each source population was used as flats were measured repeatedly through time. Moss cover did not vary by cage and so cage was not accounted for in the models. Residuals met assumptions of normality and symmetry within years, so models were weighted by year. This was done by using a

compound symmetry correlation structure to allow for heterogeneity of variance by year. Average cover of moss was the response variable. Confidence intervals were Bonferonni adjusted for multiple comparisons.

Results

Using each flat as the experimental unit, interactions in all three models were statistically significant indicating that the observed change in moss cover, due to any one of the included factors, varied with the value of the other factors. These included a three-way interaction in the treatment experiment between source population, jute net, and irrigation ($F_{3,176}=5.0$, $P=0.002$), a three-way interaction in the seasonal experiment between source population, jute net, and season of introduction ($F_{3,182}=2.6$, $P=0.054$), and a four way interaction in the overwintering experiment between source population, irrigation, jute net, and year ($F_{6,352}=4.7$, $P=0.0001$).

Treatment Experiment: Source Population, Jute Net and Irrigation

Source populations reached different amounts of cover, at different rates, when introduced in the spring (Fig. 1). *Bryum*-BoP achieved twice as much cover as *Bryum*-ST (34.5% vs 14.6% cover without irrigation and 52.8% vs 22.8% with irrigation) (Fig. 1). The same trend in source population was seen with *Syntrichia* -BoP compared to *Syntrichia* -ST (24.2% vs 18.8% cover without irrigation and 26.8% vs 20.4% with irrigation). The highest amounts of moss cover were observed for *Bryum* -BoP when grown with jute net and for *Syntrichia* -BoP when grown with the combination of jute net and irrigation (60.4% and 59.6% respectively, Fig. 1). Irrigation initially had a

significant positive effect on cover of *Bryum* -BoP regardless of the presence of the jute net. However, when *Bryum* -BoP and *Bryum* -ST received jute net and irrigation concurrently, the combination resulted in a die-back of *Bryum* -BoP and *Bryum* -ST in the first year that recovered in later years (Fig. 1a,c). Irrigation did not result in increased growth or die-back of *Syntrichia* (Fig. 1b,d).

Jute net additions increased moss cover for all source populations (Fig. 3). The combination of jute net and irrigation also resulted in increases in mean moss cover for all source populations (Fig. 3). By the end of the experiment, this was apparent for *Syntrichia* -BoP and *Syntrichia* -ST (Fig. 1f) but not for *Bryum*-BoP and *Bryum* -ST that had to recover from die-backs, which reduced average cover (Fig. 1c,e). Irrigation had short-term, negative effects on *Bryum* -BoP and *Bryum* -ST moss cover and less apparent effects on *Syntrichia* -BoP and *Syntrichia* -ST moss cover. Source population had mixed long-term effects on moss cover.

Seasonal Experiment: Source Population, Season of Introduction and Jute Net

Following both seasons of introduction, *Bryum* -BoP achieved greater cover than *Bryum* -ST and *Syntrichia* -BoP achieved greater cover than *Syntrichia* -ST (Fig. 2). A fall introduction resulted in a visible, but not statistically significant increase in cover of *Syntrichia* -ST and *Syntrichia* -BoP over a spring introduction, although the same was not true for *Bryum* -BoP or *Bryum* -ST (Figs 2 & 4). In the third spring, the greatest average cover of *Bryum* -BoP was achieved with a spring introduction and jute net (60.4%, Figs 2) and for *Syntrichia* -BoP, the greatest average cover was achieved with a fall

introduction and jute net although cover achieved following a spring introduction with jute net was not much different (51.3% vs 49.5%, Fig. 2).

A three-way interaction between jute net, season of introduction and source population was significant as *Syntrichia* -BoP and *Syntrichia* -ST achieved greater cover earlier without jute net following a fall introduction but achieved greater cover earlier with jute net following a spring introduction (Fig. 2). All spring introductions showed increased cover with jute (Figs 2 & 4). When inoculated in the fall, the effect of jute net with a fall introduction was minimal, as the addition of jute led to minimal increases for *Bryum* -BoP or *Bryum* -ST and decreases in cover for *Syntrichia* -ST and *Syntrichia* -BoP (Figs 2 & 4). By the end of the experiment, cover values of *Bryum* -BoP, *Bryum* -ST, and *Syntrichia* -BoP with jute net started to converge regardless of season of introduction, making season of introduction a short term effect.

Overwintering Experiment

We refer to overwintering as the ability of moss to put on substantial growth in the winter as opposed to the spring growing season of most plants in the region.

Overwintering generally had a positive effect on moss cover that was visually more dramatic than any treatment effect (Fig. 1). This was apparent when looking at moss cover between the sampling dates of 8 June 2013 and 2 April 2014 and then again between 26 May 2014 and 3 May 2015. Source population, irrigation, jute net and year resulted in a significant four-way interaction. Moss growth in the winter months (overwintering) is represented by the difference in mean moss cover amongst years.

Most single year comparisons and all differences between 2013 and 2015 were significant at a $P < 0.05$, with the exception of *Bryum*-ST without treatment (See Appendix 1 in Supporting Information, Table S1). Winter moss growth resulted in long-term positive effects on moss cover for all source populations. This analysis also corroborates the long-term positive effect of jute net on moss cover seen in the treatment experiment (See Appendix 1, Table S1).

Discussion

Although others have grown arid land mosses in greenhouses (Serpe *et al.* 2006, Doherty *et al.* 2015), we are the first to rapidly grow arid land mosses in the field and specifically the Great Basin Floristic Province as defined in Lentz (2000). With the application of irrigation and jute net, these mosses can rapidly increase in cover. Irrigation had short-term effects on moss cover, but long-term positive increases resulted from the application of jute net and following winter. In the first two years of the study, the more ruderal species, *Bryum*, achieved higher cover over the later successional species, *Syntrichia*. By the third spring, both species with treatments, achieved approximately 60% cover (Fig. 1), which is greater than cover achieved by vascular plants in arid land restoration efforts, over the same period (Knutson *et al.* 2014).

Quantity of moss fragments used likely influenced the amount of cover achieved over this period as with seeding rates for vascular plants (Aicher, Larios & Suding 2011) and should be further explored. Populations of both species collected from the warm dry location, BoP, reached higher cover than populations from the cool moist location,

Steens. The superior performance of mosses from BoP and the similarity in climatic conditions between BoP and Madras, suggest that mosses used for restoration should be gathered from sites that are climatically similar to restoration sites, as is practiced for plant communities (Knapp & Dyer 1998). We did not replicate collection sites so this result should be further evaluated with a broader set of sites. Although edaphic properties might influence the restoration potential of mosses, we intentionally controlled for those here.

Addition of jute net had long-term effects of increasing cover of all source populations. It is likely that organic matter enhanced the boundary layer (Kimmerer 2003) and therefore the length of available moisture experienced by the moss, although these effects cannot be separated from possibility that the jute net also held the moss in place, possibly decreasing soil surface temperature and exposure (Graf & Rochefort 2010). The presence of jute net might mimic the soil properties present in intermediate successional stages of mosses, specifically humus rich soils (Esposito, Mazzoleni & Strumia 1999). Long-term effects of applying jute net on all source populations tested (Fig. 1, Table 1) warrants its inclusion with the reintroduction of mosses.

Season of introduction had short-term positive effects on moss cover when mosses were introduced in spring with jute net (Figs 1, 2, & 4). Regardless of the season of introduction, mosses from all source populations significantly increased in cover during winter months (Fig. 1), making mosses ideal candidates for restoration efforts in either

season. This is not surprising given that mosses are immune to most freezing events as the formation of ice causes mosses to desiccate before freezing (Malek & Bewley 1978).

Effects of irrigation on moss cover were mixed and short-term. Our efforts to irrigate mosses in the spring had little to no effect on *Syntrichia* and led to spikes in cover of *Bryum* followed by die-backs, necessitating two seasons for mosses to recover to pre-die-back levels. These findings corroborate Reed *et al.* (2012) who observed die-backs in mosses following increases in small summer precipitation events. Rapid drying events for mosses result in negative net-carbon gain (Alpert 2000) through the breakdown of thylakoid membranes and chlorophyll a (Schonbeck & Bewley 1981). A single rapid drying event can result in 60% tissue death and 90% following two successive events (Stark, Brinda & McLetchie 2011). Mosses that survive rapid drying events demonstrate reduced vitality, net photosynthesis, and de-greening of tissues (Schoenbeck & Bewley 1981). For a moss in the Great Basin, spring irrigation may result in a rapid drying event. On May 5th at the experiment site, the spring introduction date, the temperature was warm at 23.6°C and the mean daily humidity was 41%. Irrigation treatments followed this date and continued until June 8th. Our study shows that irrigation, under warm conditions, should be avoided in moss restoration efforts.

Generally, community resilience is increased by the presence of biological soil crusts, as vascular plants growing with BSCs have higher concentrations of essential plant nutrients (Harper & Belnap 2001) and higher seed production (DeFalco *et al.* 2001). Mosses may increase community resistance to climate change as mosses buffer soil temperatures

(Gornall *et al.* 2009), facilitate the germination of some vascular plants (Su *et al.* 2009) and seedling survivorship (St. Clair *et al.* 1984), possibly due to increased water infiltration maintained by mosses (Chamizo *et al.* 2012).

Worldwide, mosses are present in the earliest stages of primary succession as demonstrated by the presence of moss on the tephra surface deposited by the eruption of Mount Saint Helens (Zobel & Antos 1997). Mosses can grow rapidly on unstable (Esposito, Mazzoleni & Strumia 1999) or sandy (Bowker & Belnap 2008) substrates, increasing soil stability and protecting against raindrop splash erosion (Williams, Dobrowolski & West 1995a). This indicates that mosses may be an appropriate restoration material in heavily disturbed areas, especially given that moss establishment is a positive feedback on newly exposed terrain (Bowden 1991), influencing soil properties (De Las Heras, Herranz & Martinez 1993) and adding carbon and nitrogen as mosses are often associated with cyanobacteria (Arroniz-Crespo *et al.* 2014).

Future work should include the restoration or conservation of additional biological soil crust species to maintain additional ecosystem functions (Bowker, Maestre & Escolar 2010). Use of slurries has also been shown to be effective for growing cyanobacteria (Maestre *et al.* 2006). The affinity of arid land mosses for wetter environments is shared with gelatinous, nitrogen fixing lichens such as *Collema* sp., (Davidson *et al.* 2002), suggesting that similar restoration treatments may also favor these lichens. The methods proposed here could be used to facilitate not only arid land mosses but also cyanobacteria and early successional lichens.

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Table 4-1. Moss collection sites and the recipient site. PZ- precipitation zone.

	Recipient (Madras, Oregon) 44°43'36.54"N, 121°04'00.10"W	Birds of Prey, Idaho 43°10'53.86"N, 116°03'43.76"W	Steens, Oregon 42°47'18.10"N, 118°39'46.40"W
Elevation	836 m	931 m	1430 m
Topographic Setting	lava plains	lava plateaus	intermontane plateaus
Average Freeze Free Period (USDA 2006)	125 days	127 days	60 days
Average Maximum Summer Temperature (USDA 2006)	28.7°C	33.1 °C	27.9°C
Average Minimum Winter Temperature (USDA 2006)	-4.8°C	-2.9°C	-4.3°C
Average annual precipitation (WRCC 2014)	242.8mm	200.4mm	451.1mm
Soils (Soil Survey Staff 2015)	mesic, Aridic Haploxerolls	mesic, Durinodic Haplocalcids and shallow, Typic Argidurids	frigid, Lithic Argixerolls and frigid, Lithic Xeric Haplargids
Ecological Site Type (Soil Survey Staff 2015)	Loamy 8-10 PZ (203-254 mm), R023XY216OR	Calcareous Loam 7-10 PZ (178-254 mm) , R011XY010ID	Clay Pan 12-16 PZ (305-406 mm), R023XY216OR
Dominant Vegetation for Ecological Site Type (Soil Survey Staff 2015)	<i>Artemisia tridentata</i> spp. <i>wyomingensis</i> (Condon per obs.) Not Listed	R011XY010ID: <i>Atriplex confertifolia</i> , <i>Picrothamnus desertorum</i> & <i>Artemisia tridentata</i> spp. <i>wyomingensis</i>	R023XY216OR: <i>Artemisia arbuscula</i> , annuals & <i>Poa secunda</i>

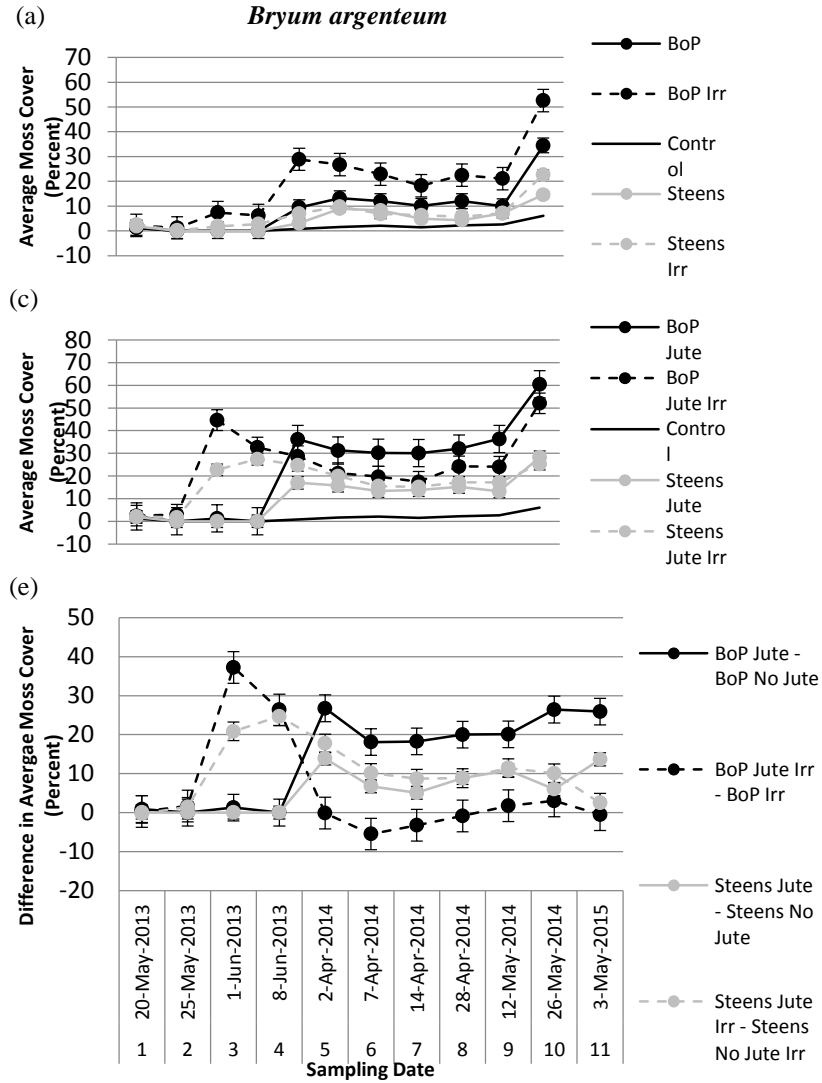


Figure 4-1. Average moss cover (percent) from Treatment Experiment on spring introductions, by sampling date, over the course of the study. Graphs in the first column (a,c, and e) are of *Bryum argenteum* and graphs in the second column (b,d, and f) are of *Syntrichia ruralis*. Graphs in the first row (a,b) show the effect of spring introduction with and without irrigation. Graphs in the second row (c,d) show the effect of jute net with and without irrigation. Graphs in the third row (e,f) show a difference in moss cover with and without jute net between otherwise similar treatment. Abbreviations are as follows: BoP- Birds of Prey, Idaho population, Steens, Oregon population, Jute- jute net, and Irr- irrigation. Weeks 1 and 5 did not include all possible replicates but cover is averaged amongst all flats surveyed in that week. Weeks 1 and 5 were not used in the analysis because they were not complete datasets. Week 2 was not used because of a large number of zeros which broke assumptions of normality and symmetrical variance

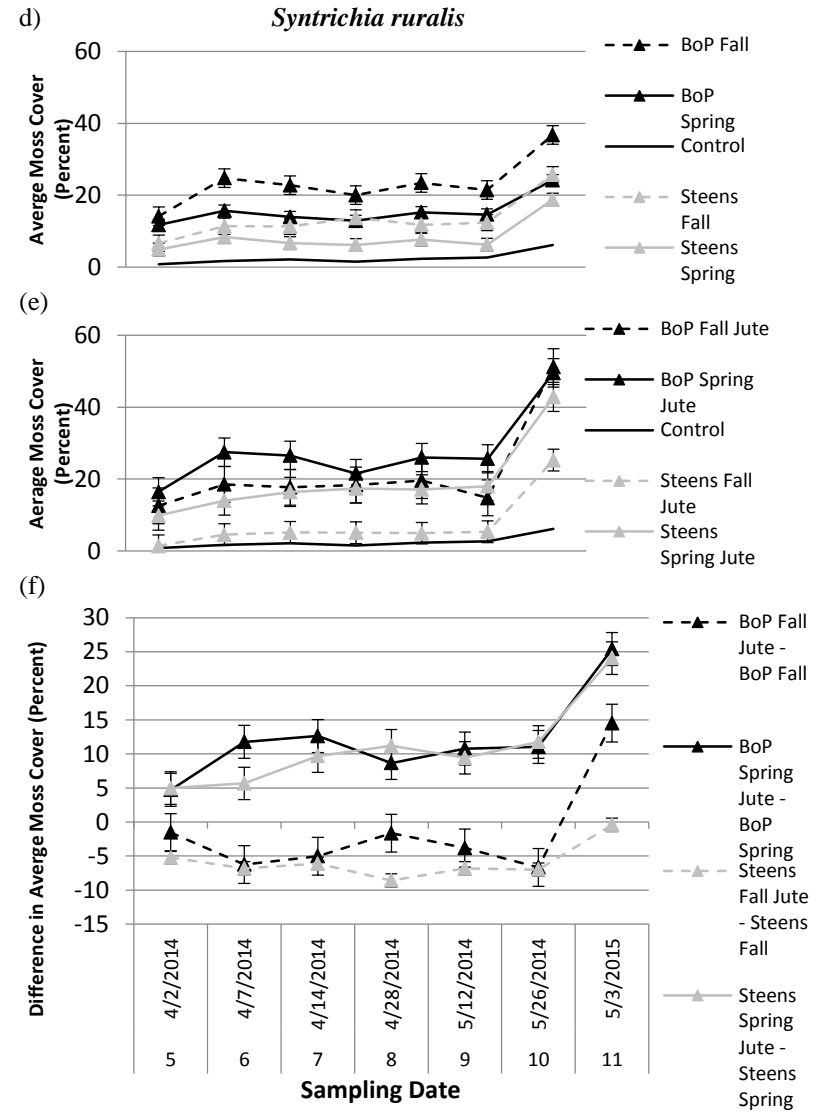
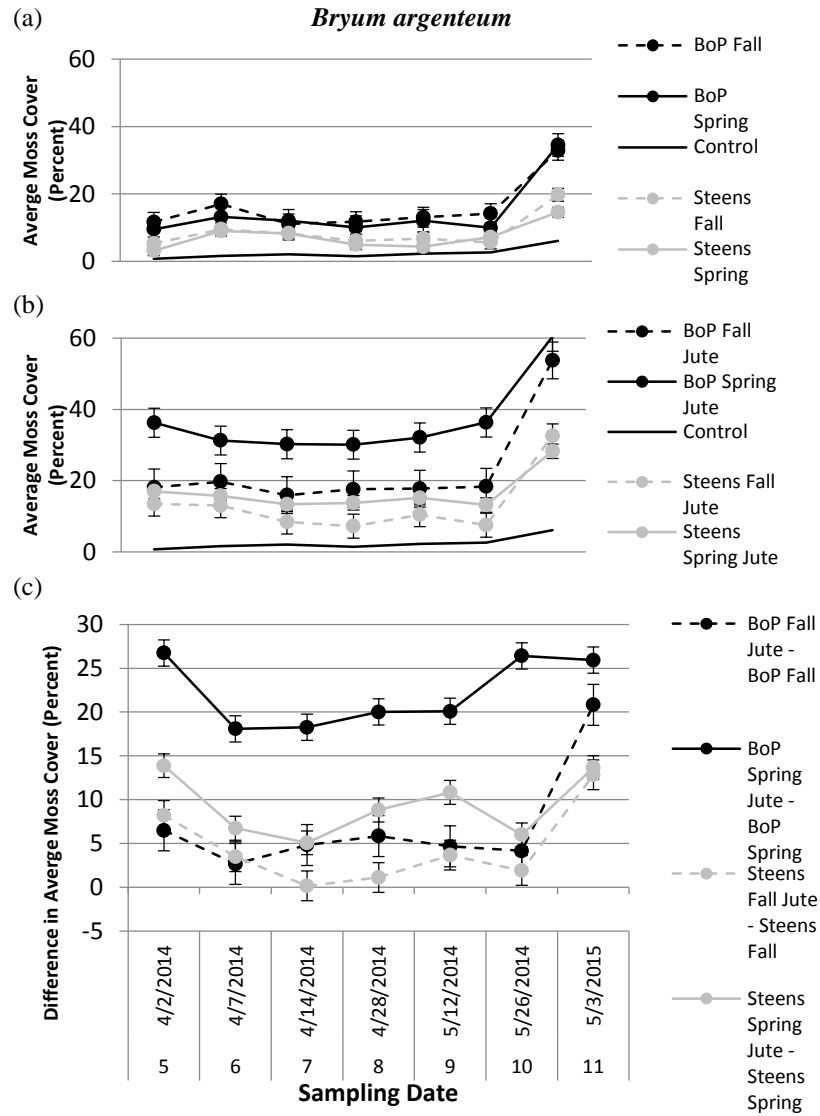


Figure 4-2. Average moss cover (percent) from Season Experiment on spring and fall introductions by sampling date, over the course of the study. Graphs A-C show *Bryum* cover and graphs D-F show *Syntrichia* cover: a) & d) moss cover from both seasons of introduction, b) & e) moss cover with jute net treatment from both seasons of introduction, c) & f) difference graph of moss cover with and without jute net from the same season of introduction in cover of seasonal treatments with and without jute net. Abbreviations follow Fig. 1. Week 5 was not used in analysis because it did not include all possible replicates but cover shown above is averaged amongst all flats surveyed in that week.

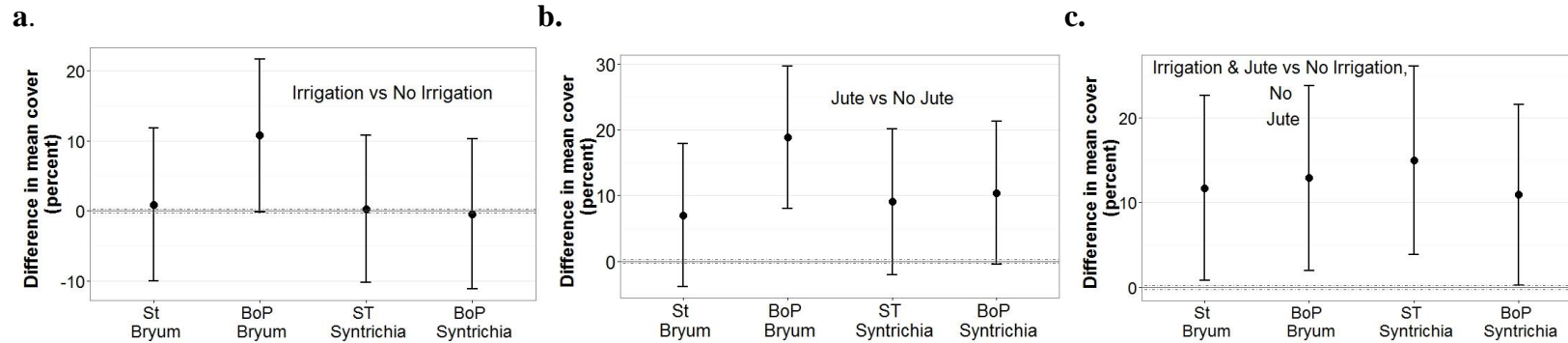


Figure 4-3. Differences in mean cover between mosses inoculated in the spring with a given treatment minus cover of those without treatments. Treatments considered include irrigation, jute net and the interaction between the two. Error bars represent 99% CI. The following include the difference in mean cover value, (the lower CI, the upper CI) and the associated P . a.) Irrigation vs No Irrigation: ST-*Bryum*: 0.9 (-10.0, 11.8), $P = 0.781$, BoP-*Bryum*: 10.8 (-0.1, 21.6), $P = 0.001$, ST-*Syntrichia*: 0.3 (-10.2, 10.8), $P = 0.926$, BoP-*Syntrichia*: -0.4 (-11.1, 10.2), $P = 0.896$. b.) Jute vs No Jute: ST-*Bryum*: 7.0 (-3.9, 17.9), $P = 0.032$, BoP-*Bryum*: 18.9 (8.0, 29.7), $P = <0.001$, ST-*Syntrichia*: 9.1 (-2.1, 20.2), $P = 0.007$, BoP-*Syntrichia*: 10.4 (-0.5, 21.3), $P = 0.002$. c.) Irrigation and Jute vs No Irrigation, No Jute: ST-*Bryum*: 11.7 (0.8, 22.6), $P = <0.001$, BoP-*Bryum*: 12.9 (2.0, 23.7), $P = <0.001$, ST-*Syntrichia*: 15.0 (3.9, 26.1), $P = <0.001$, BoP-*Syntrichia*: 10.9 (0.3, 21.6), $P = <0.001$.

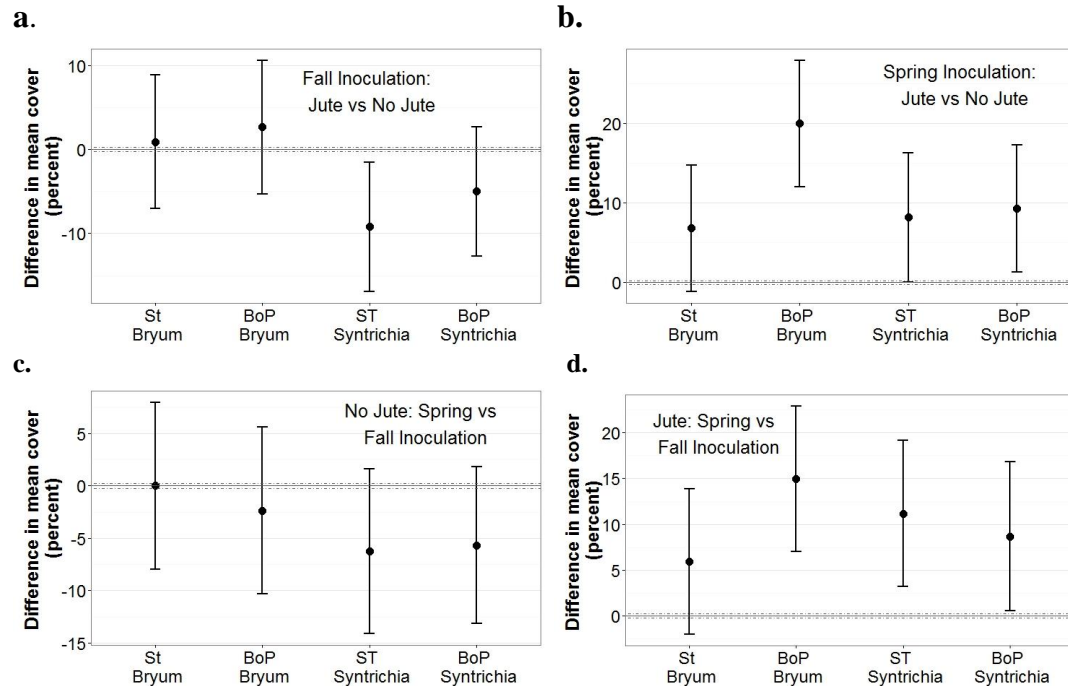


Figure 4-4. Differences in mean cover between mosses inoculated in the spring minus those inoculated in the fall, with and without jute. Error bars represent 99% CI. The following include the difference in mean cover value, (the lower CI, the upper CI) and the associated *P*. a.) Fall Introduction: Jute vs No Jute: ST-Bryum: 0.9 (-7.1, 8.8), *P* = 0.70, BoP-Bryum: 2.6 (-5.3, 10.6), *P* = 0.27, ST-Syntrichia: -9.2 (-16.9, -1.5), *P* = <0.001, BoP-Syntrichia: -5.0 (-12.6, 2.7), *P* = 0.03. b.) Spring Introduction: Jute vs No Jute: ST-Bryum: 6.8 (-1.1, 14.8), *P* = 0.005, BoP-Bryum: 20.0 (12.0, 28.0), *P* = <0.001, ST-Syntrichia: 8.2 (0.04, 16.3), *P* = <0.001, BoP-Syntrichia: 9.3 (1.3, 17.3), *P* = <0.001. c.) No Jute: Spring vs Fall Introduction: ST-Bryum: -0.1 (-8.0, 8.0), *P* = 0.99, BoP-Bryum: -2.4 (-10.3, 5.6), *P* = 0.32, ST-Syntrichia: -6.3 (-14.1, 1.6), *P* = 0.008, BoP-Syntrichia: -5.7 (-13.1, 1.8), *P* = 0.01. d.) Jute: Spring vs Fall Introduction: ST-Bryum: 5.9 (-2.0, 13.9), *P* = 0.01, BoP-Bryum: 14.9 (7.0, 22.9), *P* = <0.001, ST-Syntrichia: 11.1 (3.1, 19.1), *P* = <0.001, BoP-Syntrichia: 8.7 (0.5, 16.8), *P* = <0.001.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Differences in mean (percent) cover (dCover) between years (overwintering periods) of mosses.

Table S1. Differences in mean (percent) cover (dCover) between years (overwintering periods) of mosses inoculated in the spring from a given treatment combination. * Indicates that there is a significant difference for this listed treatment and source population for the years compared at a $P < 0.05$ and a 99% CI that does not cross zero.

Treatment	Years Being Compared	dCover (99.9% CI)	<i>P</i> (df = 352)	dCover (99.9% CI)	<i>P</i> (df = 352)	dCover (99.9% CI)	<i>P</i> (df = 352)	dCover (99.9% CI)	<i>P</i> (df = 352)
		<i>Bryum argenteum</i> from Birds of Prey		<i>Bryum argenteum</i> from Steens		<i>Syntrichia ruralis</i> from Birds of Prey		<i>Syntrichia ruralis</i> from Steens	
No Treatment	2015 vs 2014	24.6* (10.3 to 38.8)	<0.001	7.4 (-6.8 to 21.7)	0.08	9.5 (-4.1 to 23.2)	0.02	12.5 (-1.7 to 26.7)	0.004
	2014 vs 2013	9.9* (1.8 to 18.1)	<0.001	7.2 (-1.0 to 15.3)	<0.004	14.6* (6.8 to 22.4)	<0.001	6.3 (-1.9 to 14.2)	0.011
	2015 vs 2013	34.5* (17.2 to 51.8)	<0.001	14.6 (-2.7 to 31.9)	<0.005	24.2* (7.5 to 40.8)	<0.001	18.8* (1.5 to 36.0)	0.0004
Irrigation	2015 vs 2014	31.5* (17.3 to 45.7)	<0.001	15.7* (1.4 to 29.9)	<0.001	11.9 (-2.3 to 26.2)	<0.006	11.8 (-1.4 to 25.0)	0.003
	2014 vs 2013	19.5* (11.4 to 27.7)	<0.001	6.8 (-1.3 to 15.0)	<0.006	14.8* (6.7 to 23.0)	<0.001	8.6* (1.1 to 16.2)	<0.001
	2015 vs 2013	51.0* (33.8 to 68.4)	<0.001	22.5* (5.2 to 39.8)	<0.001	26.8* (9.5 to 44.0)	<0.001	20.4* (4.4 to 36.4)	<0.001
Jute net	2015 vs 2014	24.1* (9.8 to 38.3)	<0.001	15.1* (0.9 to 29.3)	<0.001	23.9* (9.0 to 38.8)	<0.001	22.5* (7.7 to 37.4)	<0.001
	2014 vs 2013	36.3* (28.2 to 44.5)	<0.001	13.2* (5.0 to 21.3)	<0.001	25.6* (17.1 to 34.1)	<0.001	18.0* (9.5 to 26.5)	<0.001
	2015 vs 2013	60.4* (43.1 to 77.7)	<0.001	28.3* (11.0 to 45.5)	<0.001	49.5* (31.5 to 67.6)	<0.001	40.5* (22.5 to 58.6)	<0.001
Irrigation x Jute net	2015 vs 2014	28.0* (13.5 to 42.5)	<0.001	8.1 (-6.2 to 22.3)	0.06	32.4* (18.2 to 46.7)	<0.001	24.6* (9.8 to 39.5)	<0.001
	2014 vs 2013	20.8* (12.2 to 29.3)	<0.001	15.2* (7.0 to 23.3)	<0.001	27.2* (19.0 to 35.3)	<0.001	24.2* (15.7 to 32.7)	<0.001
	2015 vs 2013	48.8* (31.4 to 66.0)	<0.001	23.3* (6.0 to 40.5)	<0.001	59.6* (42.3 to 76.9)	<0.001	48.8* (30.8 to 66.9)	<0.001

Chapter 5 General Conclusions

Throughout portions of the Great Basin, fire regimes have changed to become characterized by fires of greater extent and frequency (Miller et al. 2013). This is due to a change in the continuity of fuels, primarily by the invasion of annual exotic grasses, such as cheatgrass, into the interspaces between perennial plants (Miller et al. 2011; Pyke 2011). In more arid and less productive sites of the Great Basin, these interspaces were likely filled with biological soil crusts (biocrusts) that increased site resistance to invasion by cheatgrass (Reisner et al. 2013; Condon Chapt #2). This leads to the conclusion, that to understand changing fire regimes of the Great Basin, we need to understand not just how the vascular vegetation recovers from fire, but how biocrusts recover from fire. With that in mind, I have attempted to partially fill the biocrust knowledge “interspace” for the Great Basin. My major objectives were to determine 1) if the role of biocrusts in maintaining site resistance to invasion by cheatgrass was maintained after fire, 2) where are we more likely to find biocrusts across the Great Basin, and 3) if we could restore the moss component of biocrusts.

Results from Chapter 2 indicate that both perennial vegetation and lichens contribute to site resistance across the Great Basin, with both non-woody life forms (perennial herbaceous vegetation and lichens) being facilitated by mosses over the time frame of my study. Globally, biocrusts are prominent in the interspaces between vegetation (Belnap and Lange 2001). In my survey across the Great Basin, lichens and mosses were more prominent with increasing shrub cover. The presence of shrub cover indicates that these sites were unburned for at least the last several decades because it takes shrubs several

decades to re-establish after fire (Ziegenhagen and Miller 2009). The association between shrubs and biocrusts might indicate that decades are required for both to establish after fire or that there are community associations between some species. Alternatively, in rangelands outside of the Great Basin, a close association of biocrusts and shrub cover is an indication of over-grazing (Berkeley et al. 2005; Tabeni et al. 2014; Eldridge et al. 2015). Future studies will benefit our understanding of these relationships by trying to understand the spatial associations of biocrusts in the Great Basin.

In Chapter 2, I identified an interaction between the presence of fire and grazing impacts. These disturbances are often studied individually (Mack and Thompson 1982). However, I showed there are synergistic effects between the two, with impacts and evidence of cattle grazing being greater on burned sites. Burned sites in our study were given a minimum of two years of rest from grazing. Depending on management goals, two years may not be a long enough rest from grazing following fire, particularly if we are concerned about increased grazing effects following fire. If we are managing for biocrusts, the benefit of a longer rest from grazing following fire should be examined.

The sensitivity of biocrusts and particularly lichens to disturbance was demonstrated in Chapter 3. Community analyses of sites included not just biocrusts, but perennial forbs and grasses, since the latter two are what are currently being managed in the region. In this chapter, grazing and fire effects were combined to create a single gradient of disturbance. Along this gradient we see all morphological classes of lichens (gelatinous,

squamulose, and crustose lichens) declining quickly with increasing disturbance. Tall mosses were more resilient compared with lichens, but still declined with increasing disturbance and short mosses appeared to be more generalists. Work by Ponzetti and McCune (2001) corroborates that lichens are more sensitive to disturbance than mosses in the Columbia Basin, north of the Great Basin. I detected increased cover of perennial grasses with some disturbance and perennial forbs were present at low levels along the disturbance gradient. In the Columbia Basin, Belnap et al. (2001) reports observing succession of biocrusts with lichens such as *Cladonia* sp. establishing in moss. *Cladonia* sp. can be overgrown by *Diplochistes* sp., followed by *Acarospora* sp. Lichens are likely indicative of later successional status in the Great Basin. To gain further understanding of their successional patterns and responses to gradients outside of disturbance, we will have to look at sites with known protections from disturbance.

In Chapter 4, I present the results of an experiment designed to restore two arid land mosses on bare soil, a ruderal species *Bryum argenteum* and a later successional species *Syntrichia ruralis*. Increases in *Bryum* cover were achieved in weeks. However, both species greatly increased in cover with the addition of an organic jute net and particularly over the winter. I observed that mosses put on most of their growth during the winter. This is prior to the germination of common vascular plant species in the region such as sagebrush, *A. tridentata*, which typically germinates by April (Wijayratne and Pyke 2012), while cheatgrass is still small. I demonstrated that arid land mosses can easily be

incorporated into restoration plans, without the need for irrigation and that there are likely population differences, indicating that mosses need to be matched to restoration sites.

Future Directions

We refer to the sagebrush steppe of the Great Basin as rangelands, as they have been managed as rangelands with an emphasis on perennial grasses for forage. However, perennial grasses do not grow in isolation from the rest of the ecosystem. There is a growing body of work looking at interactions between plants in these communities (Leger et al. 2014), including their soils and climate (Chambers et al. 2014a, b).

Biological soil crusts are players in this greater community of organisms, interacting with vascular plants (Green et al. 2008). There is a lot of work to be done looking at the interactions of biocrust components, both morphological groups and species, with native and non-native plants. If we are worried about the maintenance of native plant communities then we also need to be worried about the interactions between biocrusts and the maintenance of soils, specifically in regards to runoff and erosion and to soil temperature and moisture as is already been done in other regions (Gornall et al. 2009; Xiao et al. 2015).

This dissertation points to several areas of research on biocrusts that would be of particular benefit in the Great Basin over the next decade: climate change scenarios, the distribution and site potential of biocrusts, the potential of biocrusts to form ecotypes, and the restoration of biocrusts. The further development of our knowledge on these subjects is likely to have global implications. As demonstrated in Chapter 4, the moss component

of biocrusts can be successfully restored in the Great Basin with minimal effort.

However, restoration of biocrusts will continue to be a test of our understanding of the ecology of these communities. For example, some climate change scenarios predict an increase in the amount of winter precipitation and temperatures (IPCC 2007). In our restoration experiment, we demonstrated that the moss component of biocrusts do most of their growing over the winter. This change in winter conditions might have consequences for the cover of mosses across the region. Moss growth in the Great Basin should be examined under climate change scenarios.

Fire seasons are expected to increase in duration under climate change scenarios (Weiss et al. 2009). The Great Basin is already experiencing increases in fire frequency (Miller et al. 2013), which might become even more frequent with an extended fire season. The interplay between vascular plants and biocrusts in the Great Basin is likely to have effects on fuel structure, particularly if the presence of both reduces invasion by *Bromus tectorum* as demonstrated in Chapter 2. In a region where a changing fire regime is resulting in the transition of native plant communities into weed dominated landscapes, understanding the potential role and mechanisms of how biocrusts maintain natural fuel structures may be critical to the conservation of native communities.

Biocrusts are a community of organisms. Biocrust communities need to be defined and incorporated into wider syntheses of knowledge such as Ecological Site Descriptions. Such efforts will lay the groundwork for understanding the potential for biocrusts species

across landscapes. With this kind of baseline, we can further examine limitations on the growth and development of biocrusts, the contributions of biocrusts to ecosystem function, and their response to disturbance.

The incorporation of biocrusts into restoration and revegetation plans is only at the beginning stages. Currently, we can easily and quickly achieve a fair amount of cover, of a few species. However, restoration practitioners will likely need mixes of desirable species. Mosses are commonly associated with cyanobacteria that fix nitrogen. Although mosses increase water infiltration, the extent of the resulting increases in soil moisture is unknown, as is their possible interaction with the growth and establishment of vascular plants. The restoration of vascular plants may be strongly influenced by the restoration of biocrusts.

Furthering our understanding of biocrusts in regards to climate change, distribution and site potential of biocrusts, the potential of biocrusts to form ecotypes and restoration will increase our understanding of ecosystem process within the Great Basin sagebrush. These findings will affect how sagebrush dominated landscapes are managed with possible implications for rangelands worldwide.

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