University of Nevada, Reno

Biological Soil Crust Cover and Richness in Two Great Basin Vegetation Zones.

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in Geography

by

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Entitled

Biological Soil Crust Cover And Richness In Two Great Basin Vegetation Zones

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MASTER OF SCIENCE

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Abstract

Biological soil crusts are communities of bacteria, microfungi, algae, lichens, and/or bryophytes that colonize the surfaces of soils where other vegetation is sparse, aid in soil stabilization and aggregation, reduce erosion, and contribute to nutrient inputs in the soil. Although a significant body of work has emerged on soil crust function in arid and semiarid environments, there is still much to be learned about their geographical distributions within and across different vegetation communities. Sagebrush shrublands and pinyon-juniper woodlands are common plant communities in the Central Basin and Range ecoregion, but this region is under-studied with respect to biological crust composition and distribution.

I collected data on soil pH and the cover of plant functional groups, ground-cover, and biological soil crusts in sagebrush and pinyon-juniper zones in the Wassuk Range of western Nevada to determine what meter-scale habitat characteristicss are associated with soil crust cover and richness in these two plant communities. Crust cover was significantly different between the two woodland sites, but not significantly different between woodlands and shrublands. Crust richness was significantly higher in shrubland than woodlands. Regression models revealed that in the shrublands, soil crusts have a negative association with rock cover and hump-shaped relationship with shrub canopy. In the woodlands, soil crusts have a negative association with ground-cover of rocks and woody litter, but with wide variation in crust cover between different woodland sites.

Sagebrush and pinyon-juniper communities are facing many stressors and undergoing changes in structure. My results offer a possible starting point for assessing how the biological crusts in these habitats might respond to these changes based on their

current distributional controls. Future research should further explore the response of biological crusts to trajectories of change in the Central Basin and Range ecoregion, such as invasion of shrublands by exotic annual plants, and expansion, infilling, and die-back of trees in pinyon-juniper woodlands. Future work should incorporate multiple spatial scales and capture the array of soil parent materials found within the target region.

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1. INTRODUCTION

Biological soil crusts are communities of bacteria, microfungi, algae, lichens, and/or bryophytes that colonize the surfaces of soils where other vegetation is sparse (Belnap 2003). They are typically dominated by cyanobacteria, lichens, or mosses, and the dominant group often depends on regional and local climate conditions (Belnap 2003). Soil crust communities are best known from the world's arid and semiarid regions, including North America's hot and cool deserts, where they aid in soil stabilization and aggregation, reduce erosion, and contribute to carbon and nitrogen inputs in the soil (Belnap 2003). They also provide habitat and food resources for soil arthropods and increase subsurface biodiversity (Shepherd *et al.* 2002, Lalley *et al.* 2006, Li *et al.* 2011). For all of these reasons, the disturbance and loss of soil crusts can be a component of land degradation processes (Belnap 1995, Bowker *et al.* 2006), highlighting their importance in the management and conservation of rangelands (Bowker 2007, Bowker *et al.* 2008).

Although a significant body of work has emerged on soil crust ecology and function in arid and semiarid environments, there is still much to be learned about their geographical distributions within and across different vegetation communities. In the Great Basin, two of the most widespread vegetation communities are sagebrush shrublands and pinyon-juniper woodlands. These communities are common in the central basin and range ecoregion (Bryce *et al.* 2003), but this region is under-studied with respect to biological soil crust composition and distribution. Information about how soil crust communities differ between adjacent shrubland and woodland communities could provide a fresh perspective on how their ecological roles are distributed in Great Basin landscapes, and how structural and floristic changes might influence these communities.

2. BACKGROUND

a. Biogeography and distribution of biological crusts

Biological soil crusts fill a multitude of ecological roles related to nutrient cycling and modification of soil and hydrological processes, many of which are highly important to preventing soil degradation and desertification processes in their respective ecosystems (e.g. Loik *et al*. 2004; Belnap *et al.* 2005; Belnap 2006). Investigating the diversity and distribution of soil crust organisms is a critical step in the identification of reference conditions for a particular community, allowing for informed monitoring, restoration, and conservation goals (Bowker *et al.* 2006). Sites exhibiting an undisturbed reference state for soil crusts are uncommon in North America due to widespread grazing and other human alteration of rangelands, but information about environmental predictors of crust occurrence in disturbed areas can still be useful for creating meaningful management goals and predictive models of their potential distribution (Bowker *et al.* 2006). Knowledge of crust diversity and occurrence patterns is still incomplete for most regions, and overcoming this limitation will lend more strength to applications (Belnap & Lange 2001; Belnap *et al*. 2014).

The controlling factors in soil crust distribution at large scales are generally well recognized. Soil crust composition and distribution fall into broad regional divisions due to the influence of prevailing regional climate factors, particularly temperature and the amount and timing of precipitation, which correspond with different desert regions – the warm Chihuahuan and Sonoran deserts with mostly summer moisture, the warm Mojave desert with mostly winter moisture, the cool Colorado Plateau with both summer and winter moisture, and the cool Great Basin and Columbia Basin with mostly winter moisture (Rosentreter & Belnap 2001). A second controlling factor at larger scales is geologic parent material (Pietrasiak *et al.* 2011; Belnap *et al.* 2014), which is in part responsible for many of the soil properties that crusts are known to respond to, including texture, acidity, and calcium carbonate content (Pietrasiak *et al.* 2011; Rosentreter & Belnap 2001). At local scales (meters to kilometers), topography and vegetation structure affect soil crust composition and cover within the framework of the regional climate and geology (Ullmann & Büdel 2001). This is due to the influence of topography and vegetation on soil properties and microclimate (Rosentreter & Belnap 2001; Nagy & Grabherr 2009), both of which can affect the availability of water, the primary limiting factor for biological processes in arid and semiarid environments (Noy-Meir 1973; Wilcox & Breshears 1994). Vegetation also influences soil crust habitat via species-specific effects on soil chemistry and litter amounts (Binkley & Fisher 2013) and the structural heterogeneity associated with more diverse plant communities (Belnap *et al.* 2001a).

The factors described above appear in a variety of configurations across western North America, creating a diversity of locally and regionally adapted vegetation communities. Those factors that specifically determine soil-inhabiting lichen and moss distribution within regions are not well known (Belnap *et al.* 2014), and in some regions the crust flora have not been well documented (Belnap & Lange 2001**)**. Descriptive information is still needed on soil crust occurrence and community structure in several regions (Ponzetti & McCune 2001), particularly in the Central Basin and Range province of the Great Basin (henceforth Central Great Basin), a region occupied by much of the state of Nevada along with areas of eastern California and western Utah (Figure 1). The majority of published research on soil crusts of the North American deserts has come from the Colorado Plateau, Columbia Basin/Northern Great Basin, and Mojave Desert, and has largely been absent from central and western Nevada. Although ecoregional boundaries can be fluid and difficult to define, this target region differs from its neighbors in climate, topography, and vegetation, but is subject to similar land use practices and anthropogenic stressors. The Central Great Basin covers a large area that is generally higher in elevation than the Mojave Desert to the south, occupied by plant communities with different dominant plant species, and subject to cold winters with a moisture regime characterized more by winter snow than summer rain. Both of these regions exhibit extensive volcanic parent material, but granite is more common in the Mojave. In the Great Basin, granite is more abundant in the western portion of the region bordering the Sierra Nevada. The Northern Great Basin is similar to the Central Great Basin in topography, parent material, and general climate patterns (e.g. winter-dominated precipitation and presence within the western precipitation dipole zone (Wise 2010)), but exhibits lower potential evapotranspiration (PET), and the woodlands in the Northern Great Basin are dominated by juniper instead of pinyon pine. I chose to keep this region separate due to these characteristics, which it shares with the neighboring Columbia Plateau.

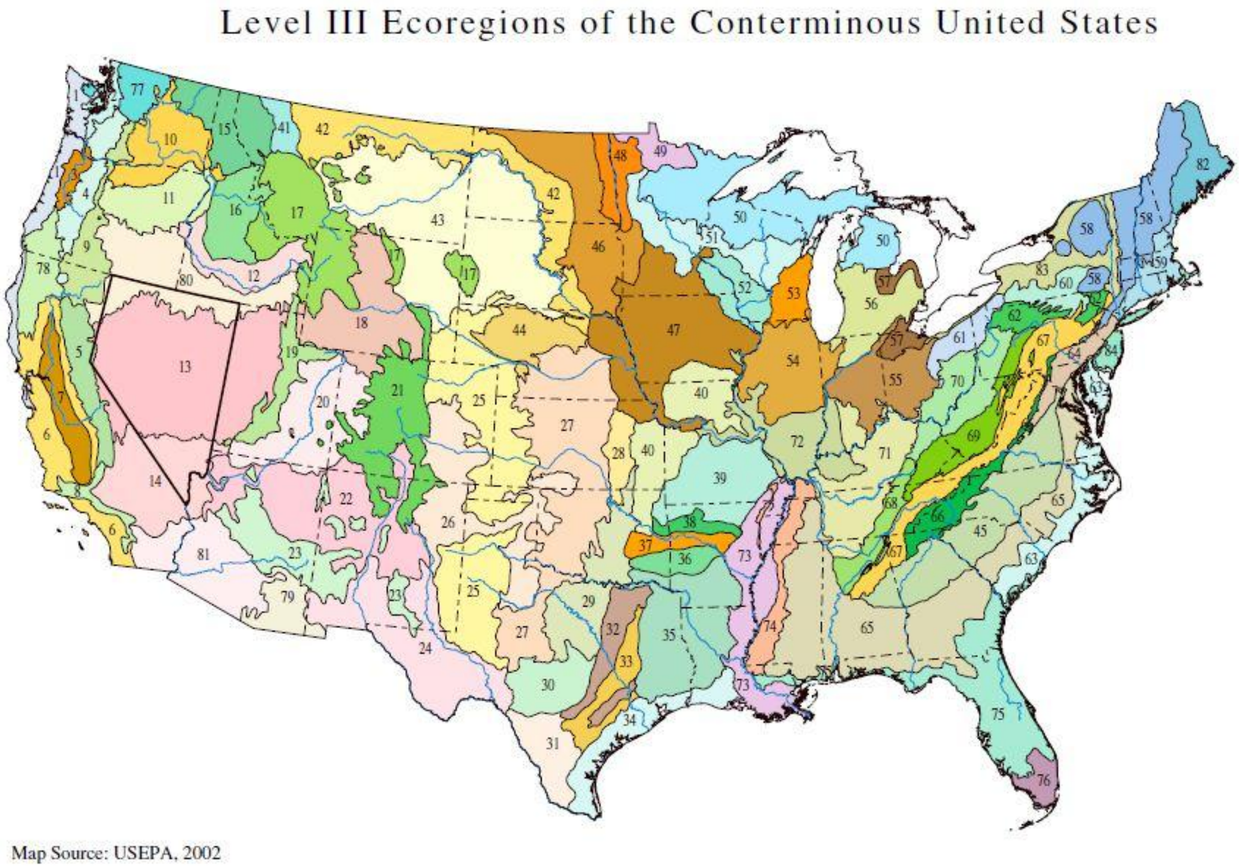

Figure 1. Ecoregions of United States. Central Basin & Range is denoted as #13. USEPA, 2002.

b. Crust diversity and function

The ecological functions of soil crusts can be specific to their morphological group or species. Macroscopic soil crust organisms can be divided into bryophytes and lichens; lichens can further be divided into groups based on their growth form – crustose (flat, two-dimensional), squamulose (scale-like), foliose (leaf-like), fruticose (branching or fruiting), and gelatinous (jelly-like). These morphological groups are accepted categories for many applications of soil crust monitoring and study (Eldridge &

Rosentreter 1999). Many of the physical and hydrological effects of crusts are a function of their external morphology – more three-dimensional growth forms create greater surface roughness, so that mosses and fruticose and squamulose lichens typically have the strongest influence on water infiltration and wind erosion (Eldridge & Rosentreter 1999), although cyanobacteria alone can increase soil water-holding capacity by absorbing significant volumes of water (Eldridge & Rosentreter 1999). Different morphological groups also vary in their resilience to disturbance (Eldridge & Rosentreter 1999, Read *et al.* 2008). In addition, ecological and ecophysiological differences occur between the mosses (Plantae: Bryophyta) and lichens (various families in Fungi: Ascomycota and Basidiomycota plus their associated algal and cyanobacterial taxa). For example, Read *et al.* (2008) found that statistically significant relationships between crust abundance and soil and vegetation characteristics changed when the aggregated crust data were divided into morphological groups. They did not expand their analysis to test this further for individual species effects, but have suggested that more studies should explicitly test how relationships vary across different levels of classification, so that an appropriate level of classification can be chosen for a particular research question or monitoring study.

Studies have shown that crust organisms show distinct species-specific responses to their environment, with varying preferences for pH, macro- and micro-nutrients, and vascular plant proximity (e.g. Ochoa-Hueso *et al.* 2011). Additionally, although physical and hydrological effects can be generalized to morphological group, crusts have species-specific effects upon their environment with regards to nutrient cycling and possibly competition with and facilitation of other species (Bowker *et al.* 2011, Pietrasiak *et al.*

2013). Thus, a greater diversity of crust species within a community can contribute to multifunctionality in a system (Bowker *et al.* 2010, Bowker *et al.* 2013).

c. Crusts in sagebrush and pinyon-juniper communities

Central Great Basin ecosystems where soil crusts occur include salt desert shrublands, sagebrush shrublands, and pinyon-juniper woodlands (Warren *et al.* 2015, Root & McCune 2012, Haubensak *et al.* 2009). These ecosystems face a number of stressors including drought, intensive land use (particularly grazing), and invasion by exotic annual plants such as cheatgrass, *Bromus tectorum* (Knapp 1996). Shrublands dominated by big sagebrush (*Artemisia tridentata*) are possibly the most characteristic vegetation type of the Great Basin, occurring across a wide range of valley and mountain landscapes in Nevada from 4,500 to 10,000 feet. (Nevada Division of Wildlife [NDOW], 2013). Healthy sagebrush steppe communities typically include a diversity of native bunchgrasses and herbs (NDOW, 2013). In some areas, biological soil crusts are also a component of this ecosystem in varying densities (Root *et al*. 2011).

Biological crusts are also recognized as a component of many pinyon-juniper woodlands (St. Clair *et al*. 1993;Wilcox & Breshears 1994; Ross *et al.* 2012), a widespread community that occurs most often in between desert zones and high elevation mountain zones in semiarid regions across western North America (Romme *et al*. 2009). In Nevada, they mostly occur on mountainsides and foothills between 5,000 and 8,000 feet but can be found as high as 10,000 feet (NDOW, 2013). This is typically a nitrogen-poor community (Law *et al*. 2012), and soil crusts can be important or even primary sources of plant-available nitrogen for these and other arid and semiarid systems when nitrogen-fixing crust species are present (Evans & Ehleringer 1994; Belnap 2002; Nowak *et al.* 1999). The protective effects of crust cover against soil erosion are also likely to be very valuable in such ecosystems, where nutrients can easily be lost along with topsoil, and soil regeneration times are typically very slow (Baker *et al*. 1994).

Some authors have incorporated soil crusts into research on ecohydrological patterns in the pinyon-juniper woodlands of New Mexico, to identify how patches of trees, crusts, and bare ground affect the transfer and reserve of water in the system (Wilcox & Breshears 1994; Madsen *et al*. 2008). These authors noted that the spatial arrangement of soil crusts at the patch scale may influence spatial patterns of hydrological processes in the woodland by minimizing the increased runoff and evaporative moisture loss typically seen in open inter-canopy spaces. Apart from two studies which had contrasting results with respect to soil crust and grass cover (Ladyman *et al.* 1993, Beymer & Klopatek 1992), the relationships between soil crusts and the vascular plant community in pinyon-juniper woodlands are not well known.

Across their range, many pinyon-juniper woodlands have experienced infilling leading to greater tree density in existing woodlands, as well as expansion of woodland edges into adjacent shrub-dominated communities (Romme *et al.*2009). The various proposed drivers of these changes have not yet been entirely disentangled (Romme *et al.* 2009), but the changes in vegetation structure, microclimate, and soil hydrological and chemical properties that may result from woodland expansion and infilling, as well as the various management techniques employed to address them, may cause changes in the distribution and function of soil crusts in these communities. Predicting these changes relies on having some baseline understanding of how soil crusts are associated with existing vegetation structure, soil, and ground-cover variables in woodlands and their adjacent shrublands.

d. Research objective

The purpose of this project is to characterize how the macroscopic elements of biological soil crusts (lichens and mosses) are distributed within adjacent sagebrush shrublands and pinyon-juniper woodlands of the Wassuk Range by investigating habitat characteristics. The specific questions addressed are:

1. What is the abundance (% cover) and species richness of soil crusts in sagebrush shrubland and pinyon-juniper woodland environments?
2. Do vegetation, groundcover, and soil pH influence soil crust cover and richness at the 1 m^2 scale, and do these relationships differ between shrublands and woodlands?

3. Study Area

The study was carried out in the Wassuk Range, a mountain range located in the Walker River Basin at the western edge of the Great Basin in Nevada (Figure 2). This mountain range was chosen for (1) exhibiting characteristic Great Basin vegetation zones: salt desert shrubland, sagebrush shrubland, pinyon-juniper woodland, montane conifer forest, subalpine conifer forest, and alpine; (2) the presence of sharp ecotonal boundaries between shrubland and woodland that would allow for sampling in adjacent communities without a strong difference in elevation or topographical position; (3)

granitic parent material, which has been identified as hospitable habitat for soil crust in a different region, the Mojave Desert (Pietresiak *et al*. 2011), and is common to the western edge of the Central Basin & Range region; (4) prior observational confirmation of soil crust communities being present in the region; and (5) accessibility with respect to the logistical limitations of this study. The ranges in Walker Basin are composed primarily of Mesozoic and Tertiary-aged igneous and sedimentary parent material, particularly late Mesozoic granitic rocks and mixed sedimentary and volcanic rocks, with scattered Tertiary extrusive volcanics (Ludington *et al.* 2005). Elevation ranges from about 1220 m at the base of the Wassuk's eastern foothills to 3444 m at the top of its highest peak, Mt. Grant. Average annual precipitation in the Wassuk ranges from 15-30 inches (WRCC 2014), with most precipitation for western Nevada historically tending to occur in the winter as snow (NOAA 1985).

Two sites in the Wassuk Range were selected for distinguishable adjacent shrubland and woodland communities and for accessibility (Figure 3). At both sites the geologic parent material is a combination of Cretaceous granodiorite and quartz monzonite, two rocks in the granitoid family (Stewart & Carlson 1978). Site 1 (Powell Mountain) is located on a broad footslope with a prevailing northwest aspect (Figure 4). Site 2 (Garfield Creek) is located on a mountain pass with a prevailing northwest aspect (Figure 5). Individual sampling zones were 10 ha in size and labeled PMW (Powell Mountain Woodland, 38°20'1.123"N, 118°43'38.09"W), PMS (Powell Mountain Shrubland, 38°20'22.875"N , 118°44'14.216"W), GCW (Garfield Creek Woodland, 38°26'13.528"N, 118°43'58.87"W), and GCS (Garfield Creek Shrubland, 38°26'22.875"N

, 118°43'31.155"W). Elevations at the sites range from 2190 to 2290 m.

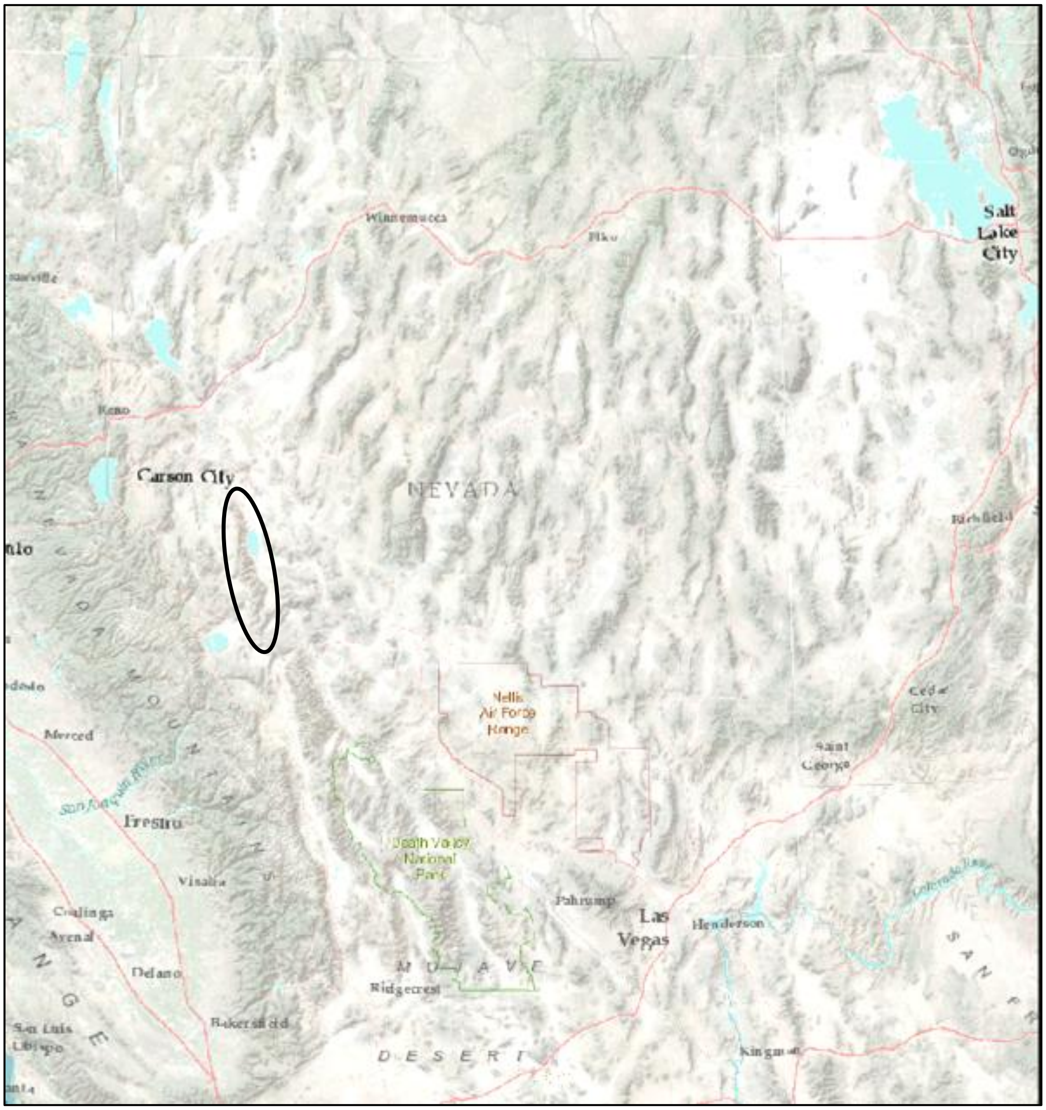

Figure 2. Location of the Wassuk Range in western Nevada.

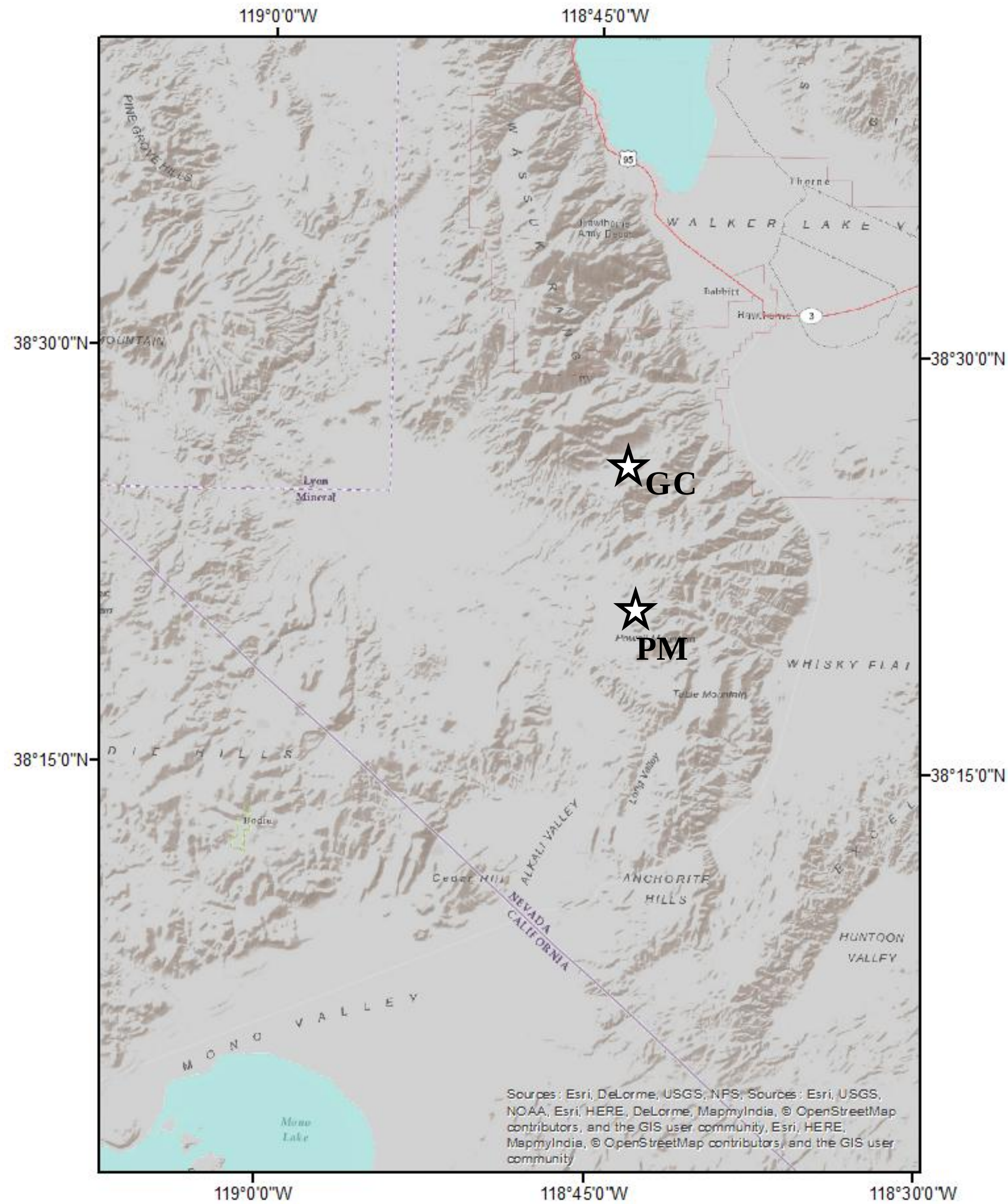

Figure 3. Location of study sites. GC: Garfield Creek. PM: Powell Mountain.

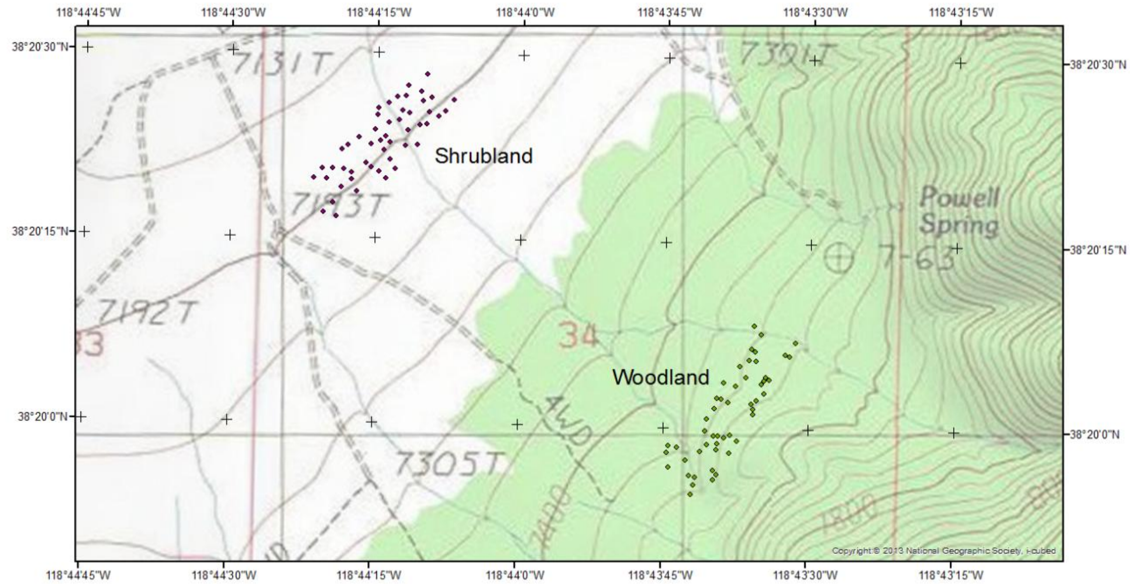

Figure 4. Location of shrubland (PMS) and woodland (PMW) plots at the Powell Mountain site.

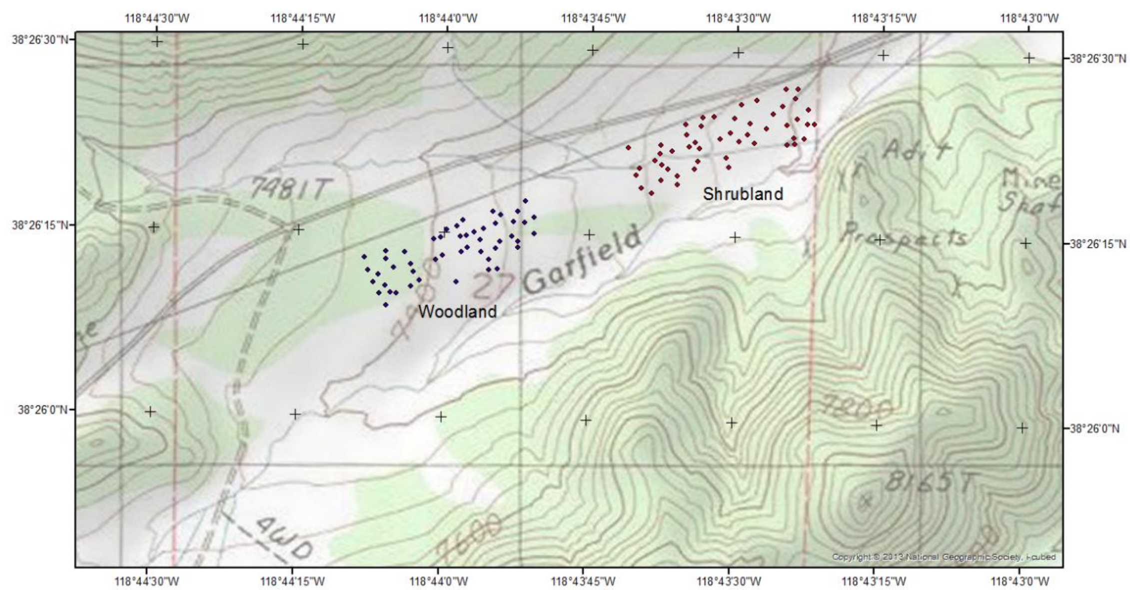

Figure 5. Location of the shrubland (GCS) and woodland (GCW) plots at the Garfield Creek site.

The vegetation communities of interest occurring within the study area include big sagebrush shrubland and pinyon-juniper woodland. The woodland at PMW is predominantly single-needle pinyon (*Pinus monophylla*), with only rarely Utah juniper

(*Juniperus osteosperma*). The shrub layer is dominated by big sagebrush (*Artemisia tridentata*) followed by antelope bitterbrush (*Purshia tridentata*) and yellow rabbitbrush (*Chrysothamnus viscidiflorus*) in similar proportions, and occasional ephedra (*Ephedra viridis*) and wax currant (*Ribes cereum*) in proximity to pinyon pines. Also relatively common are porcupine prickly-pear (*Opuntia polyacantha* var. *hystricina*), squirreltail (*Elymus elymoides*), needle-and-thread grass (*Hesperostipa comata*) and species of *Eriogonum* and *Lupinus*. The shrubland at PMS is dominated by shrubs *A. tridentata* and *C. viscidiflorus,* with lesser contributions from *Tetradymia sp.* Common grasses are *H. comata* and to a lesser degree *E. elymoides*. *Eriogonum sp.* is common as well. The woodland at GCW is entirely *P. monophylla* with no junipers. The shrub layer here is dominated by *Artemisia tridentata*, followed by *C. viscidiflorus* and *Tetradymia sp.* Also present are *H. comata* and *E. elymoides,* though they are less common. At the GCS shrubland, the shrub assemblage is richer. *A. tridentata* dominates, followed by common *C. viscidiflorus* and *Krascheninnikovia lanata*, with occasional *E. viridis, Ericameria nauseosa, Gutierrezia sarothrae*, and *Prunus andersonii*. *Eriogonum sp*. was common, along with grasses *H. comata*, *E. elymoides*, *Achnatherum hymenoides,* and occasional *Bromus tectorum*. *P. monophylla* is also sparsely present.

4. METHODS

a. Data collection

Within each sampling zone, 50 plots were randomly generated using ArcGIS, for a total of 200 plots. Plots were 1 x 1 m square, a scale identified as underutilized in soil crust studies (Garcia-Pichel & Belnap 2001). Plots were generated at a minimum distance of 15 m from each other, to avoid random dispersal of loose crust fragments into another plot by wind or animals(Heinken 1999). Plots were then located in the field using GPS, with the first location identified within 1 m corresponding to the southwest corner of the plot.

Within each 1 m^2 plot, I recorded the predominant microtopographic shape of the plot (concave, convex, flat, or a combination of the previous three) and ocular percent cover estimates of the following: total biological soil crust, grass, shrub stem, tree stem, shrub canopy, tree canopy, woody litter, fine litter, and surface rocks. Rocks were included from the coarse fraction of size class "very coarse gravel" or greater (>25 mm; Grabau 1913). Only the macroscopic crust types – mosses and lichens – were measured due to constraints on measuring and distinguishing microscopic crusts in the field (Eldridge & Rosentreter 1999, Briggs & Morgan 2008, Beymer & Klopatek 1992) and because lichen and moss crusts exert the strongest physical influences on their environments (Belnap *et al* 2014). A sample was taken from each crust found in each plot. Specimens were noted as being either moss or lichen, and then identified to species where I was able, or otherwise assigned to a "morpho-species" based on morphological characteristics. Species were counted and noted as being either moss or lichen.

One soil property, pH, was measured using a pH meter after removing 100 cm^3 of soil at 1 cm depth from the center of each plot. This volume was originally chosen with additional soil tests in mind (e.g. texture) which ultimately were not carried out in this study. If the plot center was inaccessible, soil was collected from as close to the center as possible. Because the anchoring structures of lichens and mosses (rhizines and rhizoids) do not extend very deep, properties of the top 1 cm of the soil have the greatest predictive power for terricolous lichen and moss crust distribution (Belnap *et al.* 2014).

b. Hypothesized relationships

Each measured variable was included in this study with multiple hypotheses about its relationship with crust cover and/or richness.

1. Shrub canopy:
    - Alternative hypothesis 1: associated with increased soil crust cover and richness via physical protection, moderated microclimate, and/or fertile soil microsite.
    - Alternative hypothesis 2: associated with decreased soil crust cover and richness via photosynthetic inhibition, competition, or litter burial.
2. Tree canopy:
    - Alternative hypothesis 1: associated with increased soil crust cover and richness via moderated microclimate.
    - Alternative hypothesis 2: associated with deceased soil crust cover and richness via photosynthetic inhibition, litter burial, or acidic soil conditions.
3. Shrub stem and tree stem:
    - Alternative hypothesis 1: associated with increased soil crust cover and richness via mechanisms listed for canopy cover.

- Alternative hypothesis 2: associated with decreased soil crust cover and richness via mechanisms listed for canopy cover or if the shrub or tree stem occupies otherwise colonizable area within the plot.

4. Woody and fine litter:
    - Alternative hypothesis: associated with decreased soil crust cover and richness via burial or acidic soil conditions.
5. Rocks (>25 mm):
    - Alternative hypothesis 1: associated with increased soil crust cover via water perching/water retention or protection from disturbance.
    - Alternative hypothesis 2: associated with decreased soil crust cover if rocks occupy otherwise colonizable area within the plot.
6. Soil pH:
    - Alternative hypotheses: show positive, negative, or nonlinear relationship with soil crust cover and richness depending on the length of the gradient and environmental preferences of the species present.
7. Microtopography:
    - Alternative hypothesis: concave or combination microtopography show a positive association with soil crust cover via water retention.

c. Data analysis

A series of t-tests and Levene's tests were used to determine whether measured variables had significantly different means and variances, respectively, between shrublands and woodlands. Tests were also run to determine if significant differences existed between sites within a particular vegetation type. Relationships were assessed with generalized linear regression models (GLM) in R (R Core Team 2013). Models were applied to three datasets: a woodland dataset covering both woodland sites, a shrubland dataset covering both shrubland sites, and a combined dataset that includes all sampling sites together. Both crust cover and crust species richness were modeled separately as the response against the suite of predictor variables listed in section 4a. After checking for collinearity with Spearman's correlations, the variable that was assumed to be the less explanatory of any pair of collinear variables was removed from further analysis. The response variable of crust cover was Poisson distributed and exhibited over-dispersion (variance greater than the mean), so a negative binomial model was implemented using the MASS package for R (Venables & Ripley 2002). This model applies a log link function, as in a Poisson GLM, with an additional parameter, theta, to account for over-dispersion (Venables & Ripley 2002). Species richness was also Poisson distributed but not overdispersed, so richness models were fit with a Poisson family GLM.

Final models for each dataset were selected using Akaike Information Criterion (AIC) scores for a set of models with progressively fewer variables until a lowest AIC was reached (Anderson *et al*. 2000), after which significant predictors were interpreted within each final model (Stephens *et al*. 2005). For each of the six final models, I assigned relative importance to each predictor variable by calculating the contribution of each to D^2, the reduction in the model's deviance when predictors are added to the null model (Guisan & Zimmermann 2000).

Spatial autocorrelation can result in inflated risk of Type 1 error (Legendre 1993). When Moran's I test for spatial autocorrelation was applied to each site, one site

(Garfield Creek Woodland) was identified as having nonrandom spatial distribution in the response. This site was removed from the woodland and combined datasets in a set of duplicate models to compare against those for the complete datasets. With GCW removed, p-values for significant variables (p<.05) changed but remained significant, so the nonrandom structure at GCW was deemed to not pose a risk for the false assignment of significance.

Finally, a series of t-tests was used to determine if mean values of each habitat variable differed between moss-present and lichen-present plots, with every plot assigned to a “moss” dataset, a “lichen” dataset, or both datasets if both functional groups were present.

5. RESULTS

a. Descriptive summary and differences in variables across sites

From the t-test results (Tables 3-13), shrublands displayed significantly higher mean crust richness, shrub canopy cover, shrub stem cover, grass cover, and pH, and significantly lower mean tree canopy, rock cover, fine litter, and woody litter than woodlands. Within the shrublands, the Garfield Creek site displayed significantly higher mean rock cover, fine litter, and woody litter than the Powell Mountain site. Within the woodlands, the Garfield Creek site displayed significantly higher mean pH and significantly lower crust cover, tree canopy cover, rock cover, fine litter, and woody litter. Variance for crust cover was significantly higher in Garfield Creek than Powell Mountain shrubland, and lower in Garfield Creek than Powell Mountain woodland. Variance for shrub canopy cover was significantly higher in shrublands than woodlands.

Variance for tree canopy cover was significantly lower in shrublands than woodlands, and lower in Garfield Creek than Powell Mountain woodland. Variance for shrub stem cover was significantly different higher in shrublands than woodlands. Variance for rock cover was significantly lower in shrublands than woodlands, higher in Garfield Creek than Powell Mountain shrubland, and lower in Garfield Creek than Powell Mountain woodland. Variance for fine litter cover was significantly lower in shrublands than woodlands, higher in Garfield Creek than Powell Mountain shrubland, and lower in Garfield Creek than Powell Mountain woodland. Variance for woody litter cover was significantly lower in shrublands than woodlands, higher in Garfield Creek than Powell Mountain shrubland, and lower in Garfield Creek than Powell Mountain woodland. Variance for grass cover was significantly higher in shrublands than woodlands. Variance for pH was significantly lower in shrublands than woodlands, higher in Garfield Creek than Powell Mountain shrubland, and lower in Garfield Creek than Powell Mountain woodland.

Shrubland Summary						
	Crust Cover (%)	Crust Richness	Shrub Canopy (%)	Tree Canopy (%)	Fine Litter (%)	Woody Litter (%)
Min	0.00	0.00	0.00	0.00	0.00	0.00
Mean	3.55	3.54	27.29	2.24	7.79	5.07
Max	32.00	12.00	96.00	100.00	86.00	34.00
St. Dev.	4.50	2.29	27.04	12.40	12.36	6.53
	Shrub Stem (%)	**Tree Trunk (%)**	**Grass (%)**	**Rocks (%)**	**pH**	**Microtopo. Class**
Min	0.00	0.00	0.00	0.00	5.33	Flat: 68
Mean	4.20	0.00	4.30	1.93	6.18	Concave: 2
Max	17.00	0.00	20.00	30.00	7.19	Convex: 8
St. Dev.	3.72	0.00	4.26	4.26	0.35	Combination: 22

Table 1. Minimum, mean, maximum, and standard deviation of all variables measured from 100 sagebrush shrubland plots, 1 m^2, Wassuk Range, 2015.

Woodland Summary						
	Crust Cover (%)	Crust Richness	Shrub Canopy (%)	Tree Canopy (%)	Fine Litter (%)	Woody Litter (%)
Min	0.00	0.00	0.00	0.00	0.00	0.00
Mean	2.96	2.04	6.11	21.91	27.35	9.91
Max	59.00	7.00	46.00	100.00	100.00	90.00
St. Dev.	7.56	2.06	8.82	33.53	31.70	14.52
	Shrub Stem (%)	**Tree Trunk (%)**	**Grass (%)**	**Rocks (%)**	**pH**	**Microtopo. Class**
Min	0.00	0.00	0.00	0.00	4.95	Flat: 74
Mean	1.77	1.18	1.92	6.85	6.01	Concave: 4
Max	30.00	100.00	15.00	80.00	6.71	Convex: 5
St. Dev.	3.63	10.01	3.13	15.30	0.43	Combination: 17

Table 2. Minimum, mean, maximum, and standard deviation of all variables measured from 100 sagebrush shrubland plots, 1 m^2, Wassuk Range, 2015.

Crust Cover				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	3.55 20.23	2.96 57.09	0.5	0.82
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	4.34 33.66	2.76 5.94	0.08	<.05
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	1.36 2.6	4.56 107.52	<.05	<.05

Table 3. Mean, variance, and results of t-tests and Levene's tests for crust cover (%) between community types (top row) and sites in each community (second and third rows).

Crust Richness				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	3.54 5.26	2.04 4.24	<.001	1
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	3.76 7.21	3.32 3.32	0.34	0.07
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	2.4 4.65	1.68 3.65	0.08	0.31

Table 4. Mean, variance, and results of t-tests and Levene's tests for crust richness between community types (top row) and sites in each community (second and third rows).

Shrub Canopy				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	27.29 730.96	6.11 77.84	<.001	<.001
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	26.02 546.02	28.56 927.52	0.64	0.24
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	7.1 93.77	5.12 61.5	0.26	0.36

Table 5. Mean, variance, and results of t-tests and Levene's tests for shrub canopy cover (%) between community types (top row) and sites in each community (second and third rows).

Tree Canopy				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	2.24 179.43	21.91 1123.9	<.001	<.001
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	4.48 352.3	0 0	0.1	0.1
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	8.86 526.33	34.96 1396.86	<.001	<.001

Table 6. Mean, variance, and results of t-tests and Levene's tests for tree canopy cover (%) between community types (top row) and sites in each community(second and third rows).

Shrub Stem				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	4.20 13.84	1.77 13.19	<.001	<.01
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	3.66 9.74	4.74 17.63	0.15	0.11
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	1.98 6.67	1.56 19.88	0.57	0.57

Table 7. Mean, variance, and results of t-tests and Levene's tests for shrub stem cover (%) between community types (top row) and sites in each community (second and third rows).

Tree Stem				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	0 0	1.18 100.17	0.24	0.24
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	0 0	0 0	NA	NA
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	0.08 0.2	2.28 199.72	0.28	0.27

Table 8. Mean, variance, and results of t-tests and Levene's tests for tree stem cover (%) between community types (top row) and sites in each community (second and third rows).

Rock Cover				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	1.93 18.17	6.85 234.09	<.01	<.01
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	3.06 30.47	0.8 3.63	<.01	<.05
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	1.12 4.72	12.58 401.23	<.001	<.001

Table 9. Mean, variance, and results of t-tests and Levene's tests for rock cover (%) between community types (top row) and sites in each community (second and third rows).

Fine Litter				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	7.79 152.81	27.35 1004.94	<.001	<.001
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	10.52 281.19	5.06 12.34	<.05	<.05
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	17.98 888.96	36.72 962.25	<.01	<.05

Table 10. Mean, variance, and results of t-tests and Levene's tests for fine litter cover (%) between community types (top row) and sites in each community (second and third rows).

Woody Litter				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	5.07 42.67	9.91 210.85	<.01	<.01
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	6.96 62.12	3.18 16.8	<.01	<.05
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	4.88 41.54	14.94 332.83	<.001	<.01

Table 11. Mean, variance, and results of t-tests and Levene's tests for woody litter cover (%) between community types (top row) and sites in each community (second and third rows).

Grass Cover				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	4.3 18.17	1.92 9.81	<.001	<.001
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	4.06 24.38	4.54 12.21	0.58	0.11
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	2.18 11.09	1.66 8.6	0.41	0.43

Table 12. Mean, variance, and results of t-tests and Levene's tests for grass cover (%) between community types (top row) and sites in each community (second and third rows).

pH				
	Shrublands	**Woodlands**	**t-test *p***	**Levene's test *p***
Mean Variance	6.18 0.12	6.01 0.18	<.01	0.05
	GC Shrub	**PM Shrub**	**t-test *p***	**Levene's test *p***
Mean Variance	6.24 0.2	6.12 0.04	0.08	<.001
	GC Wood	**PM Wood**	**t-test *p***	**Levene's test *p***
Mean Variance	6.21 0.08	5.81 0.21	<.001	<.001

Table 13. Mean, variance, and results of t-tests and Levene's tests for pH between community types (top row) and sites in each community (second and third rows).

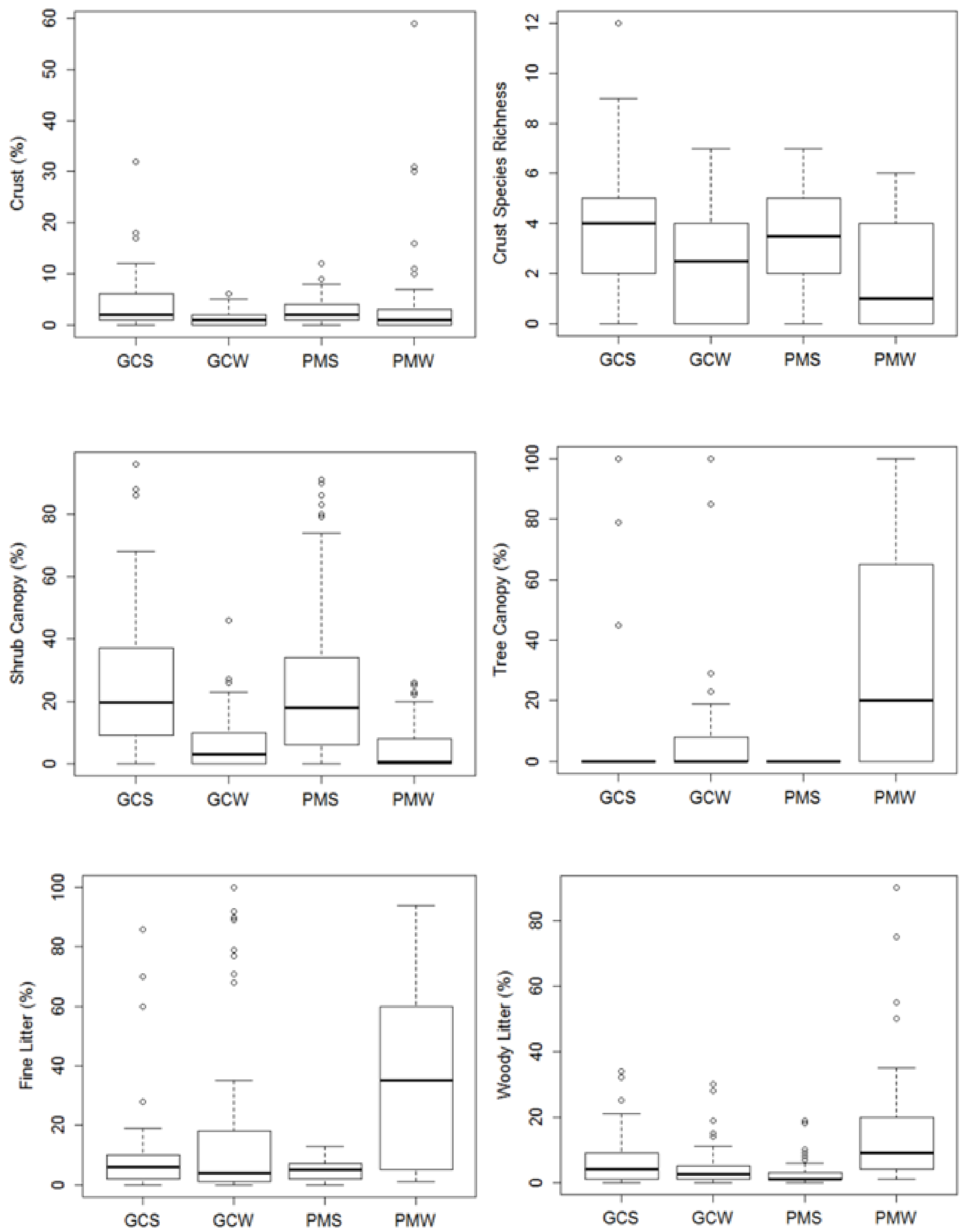

Figure 6. Boxplots showing distribution of variables: crust cover, crust species richness, shrub canopy, tree canopy, fine litter, and woody litter for each site.

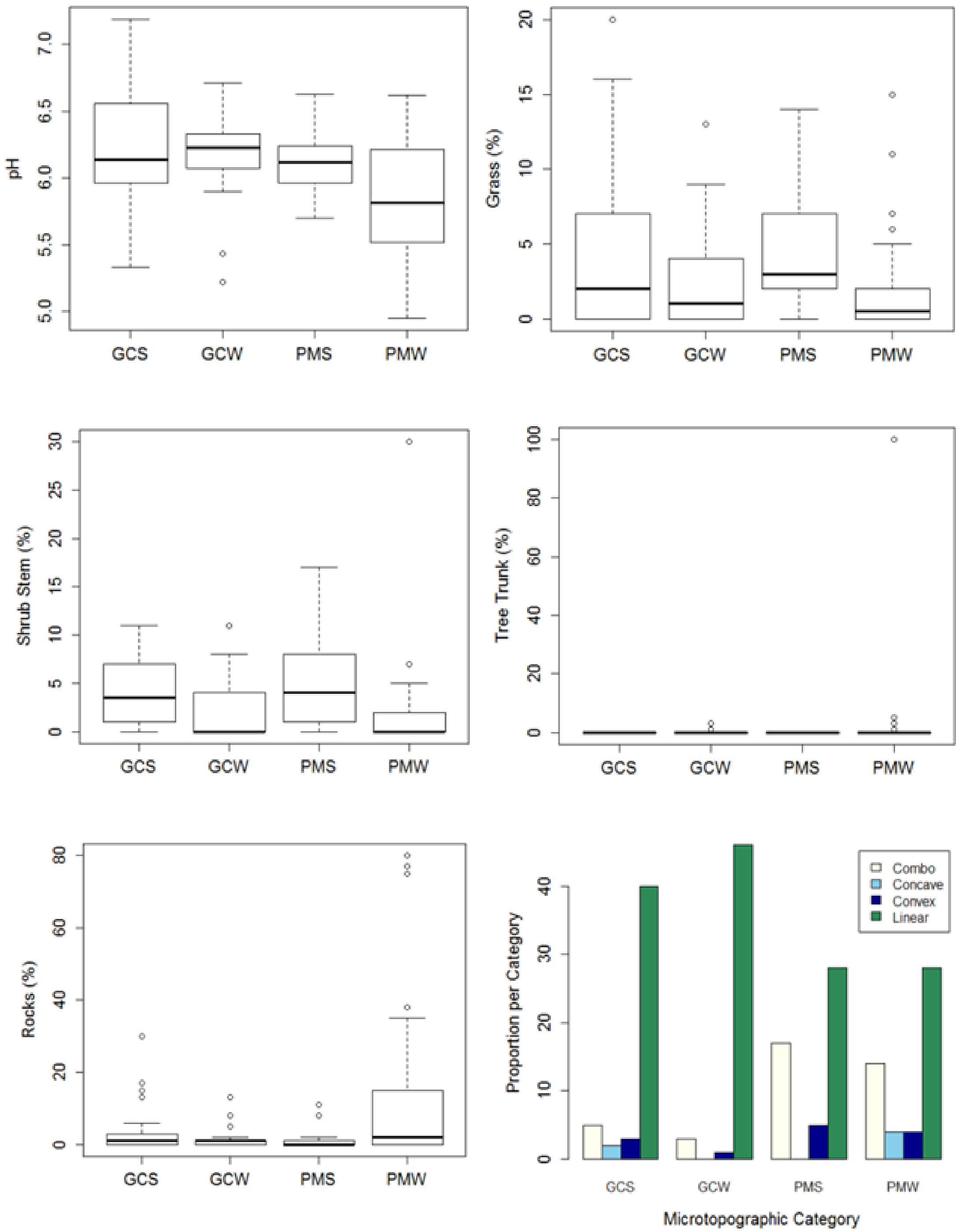

Figure 7. Boxplots showing distribution of variables: pH, grass cover, shrub stem cover, tree trunk cover, and rock cover for each site. Plot on bottom right shows frequency of each microtopographic category at each site.

b. Models: cover

At the shrubland sites, rock cover and shrub canopy cover had significant relationships with crust cover (p>.05), with shrub canopy displaying a quadratic (hump-shaped) relationship – crust cover was highest at intermediate cover of shrub canopy (Table 14). Rock cover showed a negative relationship with crust cover. Site was not significant, but its inclusion in the model produced a lower AIC and was therefore retained in the final model. Though not a statistically significant effect, there was less crust cover at the Powell Mountain Shrubland site. When proportion of reduced deviance was calculated for each predictor, shrub canopy was identified as the most important variable, followed by rock cover and site.

At the woodland sites, rock cover, woody litter cover, and site were significant predictors, and non-significant fine litter was included in the best final model (Table 15). Rock cover and woody litter both had significant negative relationships with crust cover, and fine litter had a non-significant negative relationship, while the Powell Mountain Woodland site showed a significant positive relationship. Here the site contributed the most to reduced deviance, followed by woody litter, rock cover, and fine litter.

When both shrubland and woodland plots were combined into a single dataset, shrub canopy, tree canopy, rock cover, woody litter, and site were significant (Table 16). Relationships that were present in the separate models showed the same directionality when combined – shrub canopy was quadratic, and rock cover and woody litter had negative relationships with crust cover. Tree canopy also had a significant negative relationship with crust cover only when the shrubland and woodland datasets were combined. Relative to Garfield Creek Shrubland, being in the Garfield Creek Woodland or Powell Mountain Shrubland had negative associations with crust cover, while being in the Powell Mountain woodland had a positive association. Site contributed the most to the reduction of deviance, followed by rock cover, shrub canopy, woody litter, and tree canopy.

Partial residuals plots (Figures 8-25) indicate direction and strength of the relationship with a particular predictor given the presence of the other variables in the model. Gray shading represents the confidence interval.

Shrubland: Crust Cover				
Variable	**Coefficient**	**Direction**	***p***	**Contributed D^2**
Intercept			**<.001**	
Shrub canopy	0.57	+	**<.001**	
Shrub canopy^2	-0.31	0	**<.01**	11.6%
Rocks	-0.25	-	**<.05**	3.46%
Site: PMS	-0.39	-	0.06	2.67%

Table 14. Results of shrubland cover model. *P*-values significant at α=.05 are in bold. Coefficients are scaled.

Woodland: Crust Cover				
Variable	**Coefficient**	**Direction**	***p***	**Contributed D^2**
Intercept			**<.001**	
Site: PMW	1.99	+	**<.001**	23.23%
Woody Litter	-0.97	-	**<.001**	12.27%
Rocks	-0.76	-	**<.001**	10.53%
Fine Litter	-0.33	-	0.06	2.40%

Table 15. Results of woodland cover model. *P*-values significant at α=.05 are in bold. Coefficients are scaled.

Combined: Crust Cover				
Variable	**Coefficient**	**Direction**	***p***	**Contributed D^2**
Intercept			**<.001**	
Site: GCW	-0.85	-	**<.001**	
Site: PMS	-0.50	-	**<.05**	
Site: PMW	1.16	+	**<.001**	20.91%
Rocks	-0.55	-	**<.001**	7.89%
Shrub canopy	0.66	+	**<.001**	
Shrub canopy^2	-0.22	0	**<.01**	4.63%
Woody Litter	-0.39	-	**<.01**	3.28%
Tree canopy	-0.35	-	**<.01**	3.19%

Table 16. Results of combined cover model. *P*-values significant at α=.05 are in bold. Coefficients are scaled.

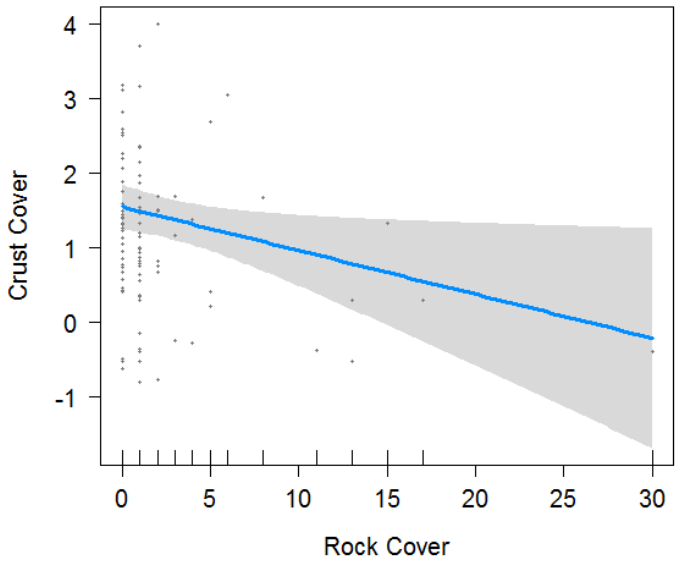

Figure 8. Partial residuals plot of rock cover against crust cover in the shrubland cover model. Crust cover is presented on a logarithmic scale.

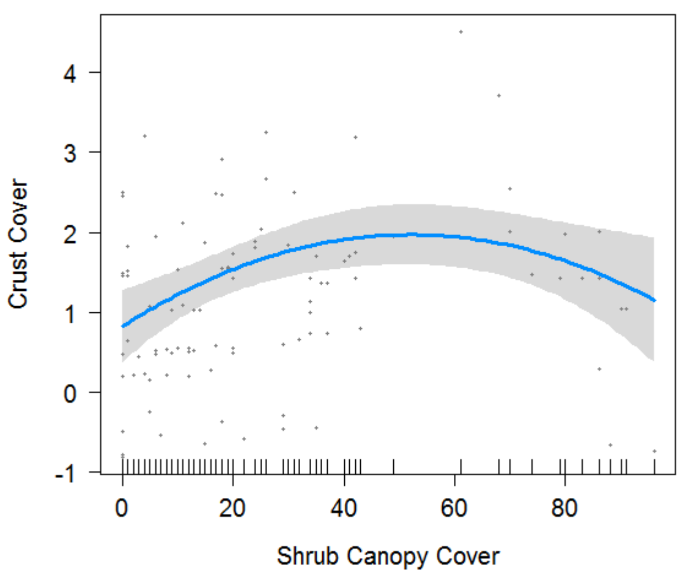

Figure 9. Partial residuals plot of shrub canopy cover against crust cover in the shrubland cover model. Crust cover is presented on a logarithmic scale.

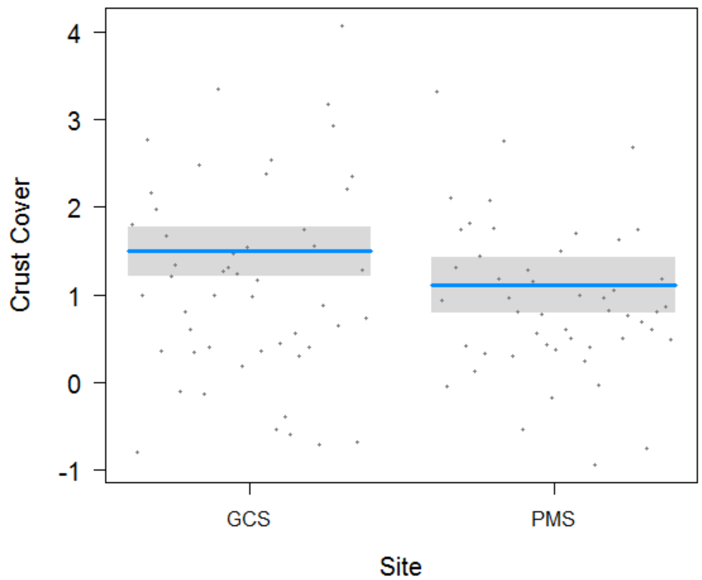

Figure 10. Partial residuals plot of sampling site against crust cover in the shrubland cover model. Crust cover is presented on a logarithmic scale.

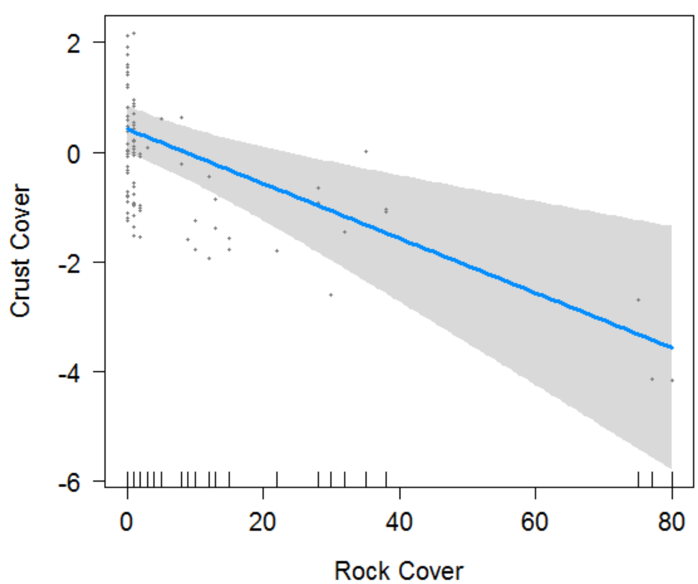

Figure 11. Partial residuals plot of rock cover against crust cover in the woodland cover model. Crust cover is presented on a logarithmic scale.

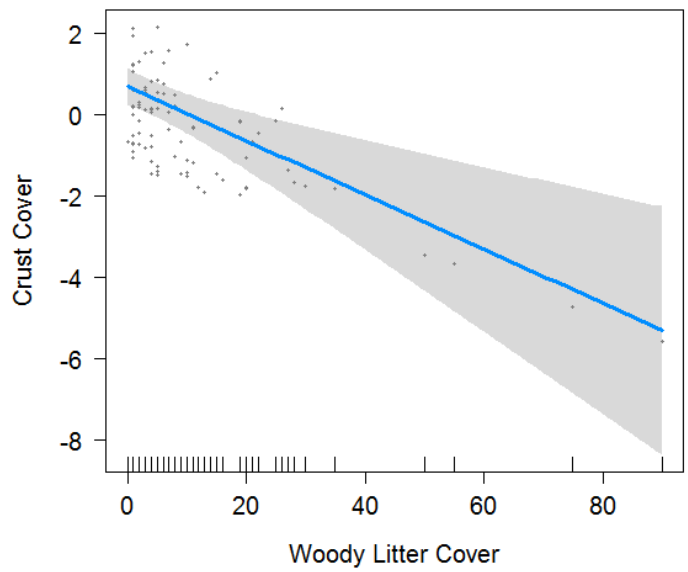

Figure 12. Partial residuals plot of woody litter cover against crust cover in the woodland cover model. Crust cover is presented on a logarithmic scale.

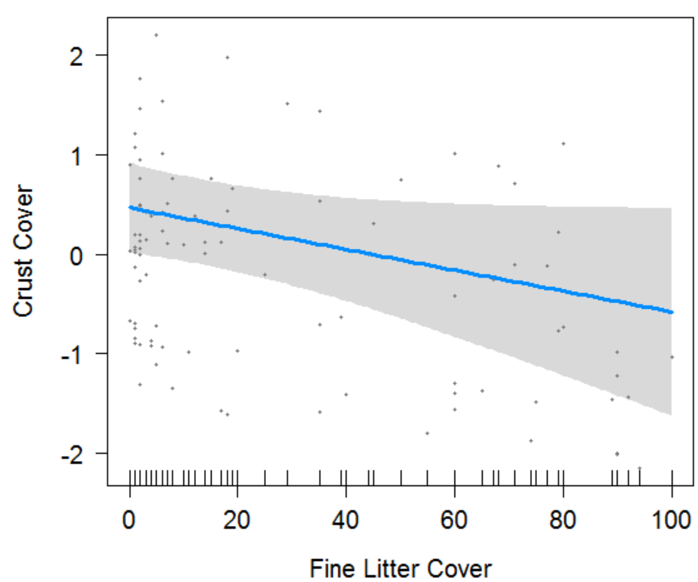

Figure 13. Partial residuals plot of fine litter cover against crust cover in the woodland cover model. Crust cover is presented on a logarithmic scale.

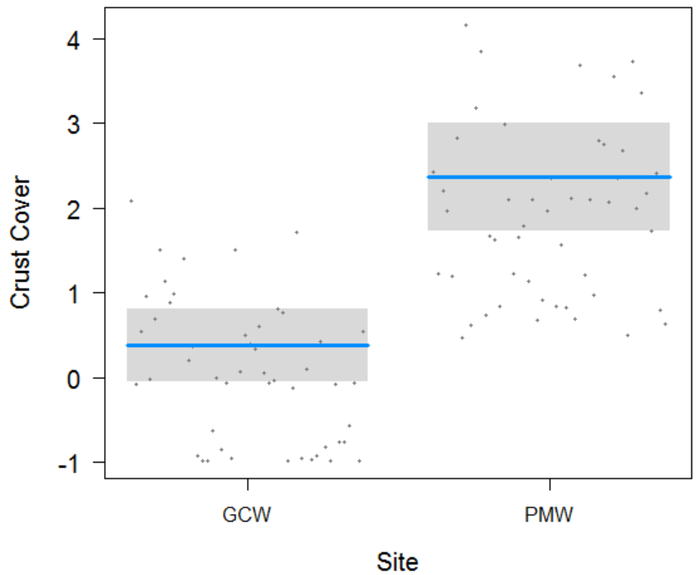

Figure 14. Partial residuals plot of sampling site against crust cover in the woodland cover model. Crust cover is presented on a logarithmic scale.

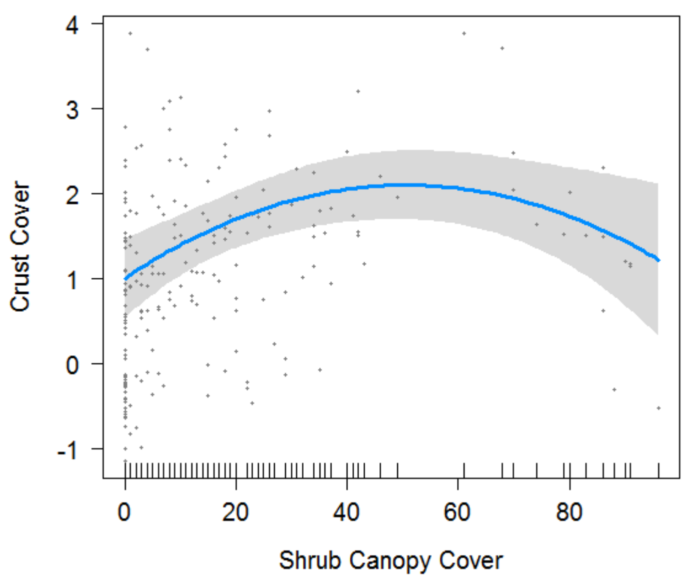

Figure 15. Partial residuals plot of shrub canopy cover against crust cover in the combined cover model. Crust cover is presented on a logarithmic scale.

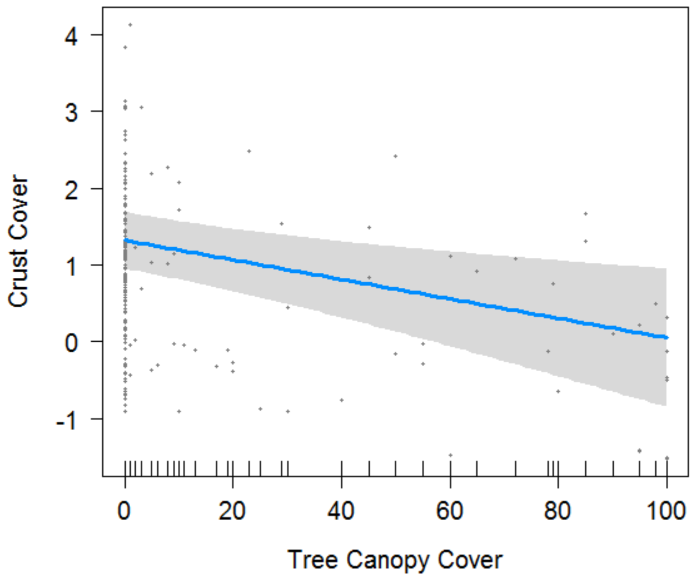

Figure 16. Partial residuals plot of tree canopy cover against crust cover in the combined cover model. Crust cover is presented on a logarithmic scale.

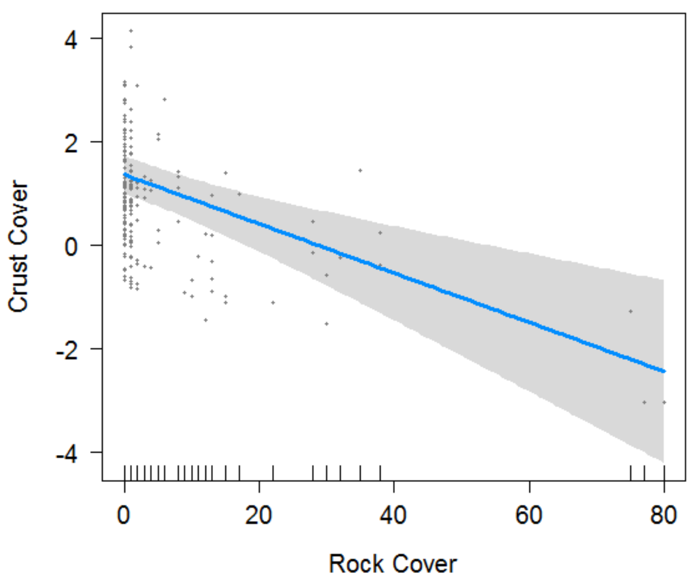

Figure 17. Partial residuals plot of rock cover against crust cover in the combined cover model. Crust cover is presented on a logarithmic scale.

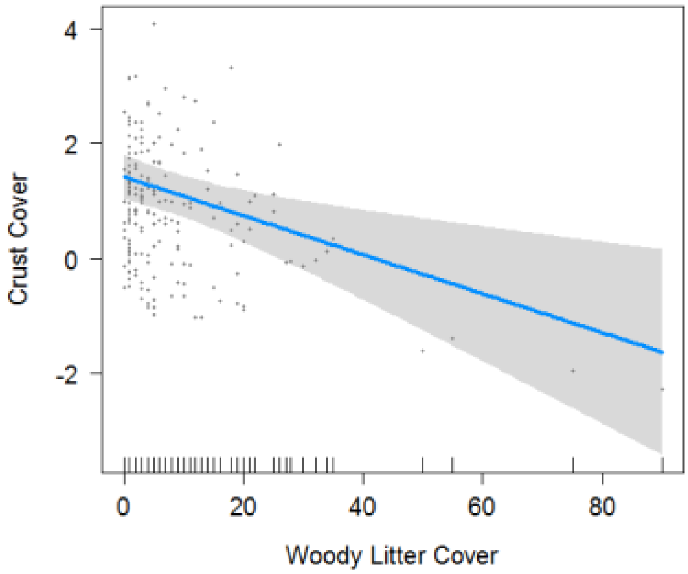

Figure 18. Partial residuals plot of woody litter cover against crust cover in the combined cover model. Crust cover is presented on a logarithmic scale.

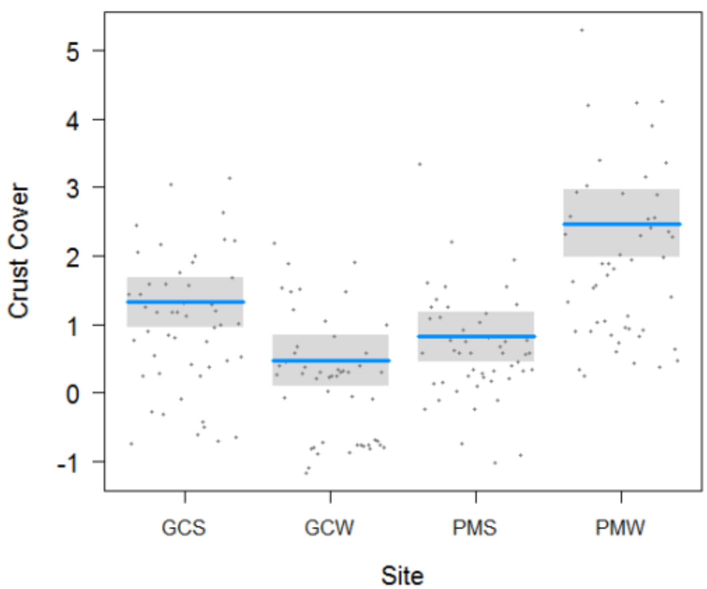

Figure 19. Partial residuals plot of sampling site against crust cover in the combined cover model. Crust cover is presented on a logarithmic scale.

c. Models: richness

At the shrubland sites, crust cover alone was significantly associated with high crust species richness (Table 17). At the woodland sites, tree canopy alone was significant (Table 18). When data were combined, crust cover was significant along with grass cover and shrub canopy cover, both of which were quadratic relationships (Table 19). The PMW site had a significant negative association with crust richness with respect to the default site, GCS. In this combined model, crust cover contributed the most to reduction of deviance, followed by site, grass cover, and shrub canopy.

Shrubland: Crust Richness				
Variable	**Coefficient**	**Direction**	***p***	**Contributed D^2**
Intercept			**<.001**	
Crust	0.26	+	**<.001**	26.71%

Table 17. Results of shrubland richness model. P-values significant at α=.05 are in bold. Coefficients are scaled.

Woodland: Crust Richness				
Variable	**Coefficient**	**Direction**	***p***	**Contributed D^2**
Intercept			**<.001**	
Tree canopy	-0.31	-	**<.001**	5.74%

Table 18. Results of woodland richness model. P-values significant at α=.05 are in bold. Coefficients are scaled.

Combined: Crust Richness				
Variable	**Coefficient**	**Direction**	***p***	**Contributed D^2**
Intercept			**<.001**	
Crust	0.27	+	**<.001**	13.35%
Site: GCW	-0.07	-	0.62	
Site: PMS	-0.04	-	0.74	
Site: PMW	-0.65	-	**<.001**	4.56%
Grass	0.29	+	**<.001**	
$Grass^2$	-0.09	-	**<.01**	3.47%
Shrub canopy	0.31	+	**<.001**	
Shrub $canopy^2$	-0.12	-	**<.01**	2.73%

Table 19. Results of combined richness model. P-values significant at α=.05 are in bold. Coefficients are scaled.

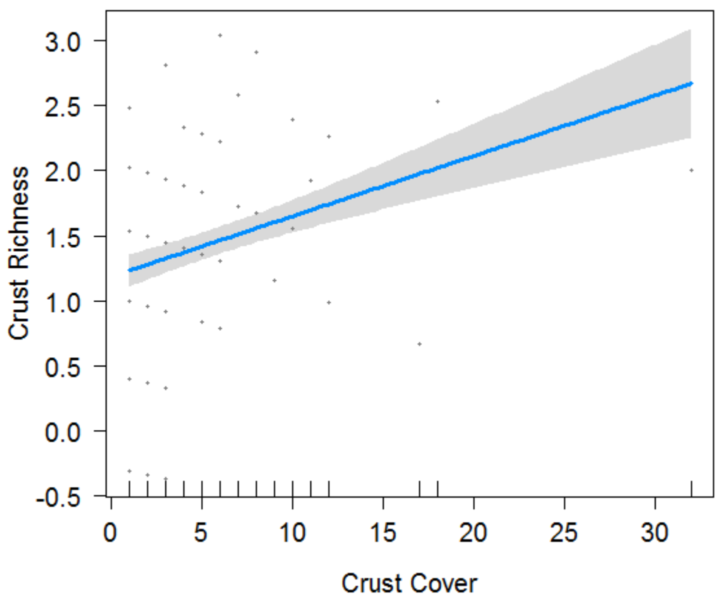

Figure 20. Partial residuals plot of crust cover against crust richness in the shrubland richness model. Crust richness is presented on a logarithmic scale.

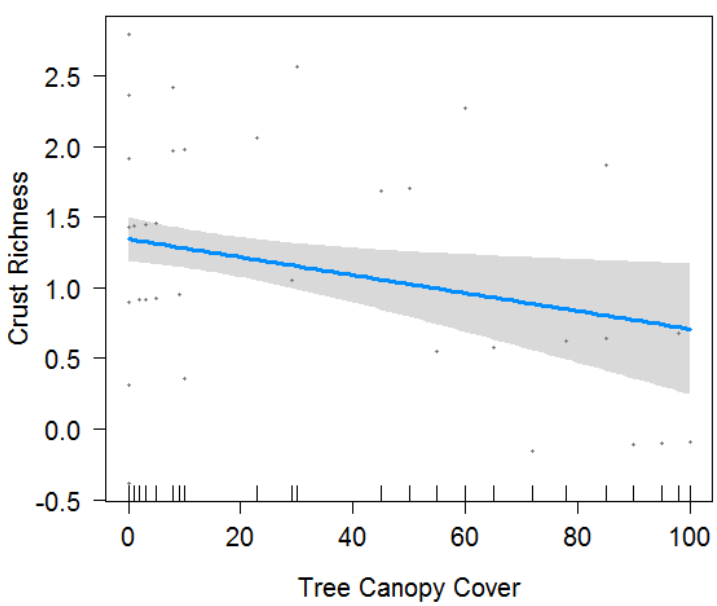

Figure 21. Partial residuals plot of tree canopy cover against crust richness in the woodland richness model. Crust richness is presented on a logarithmic scale.

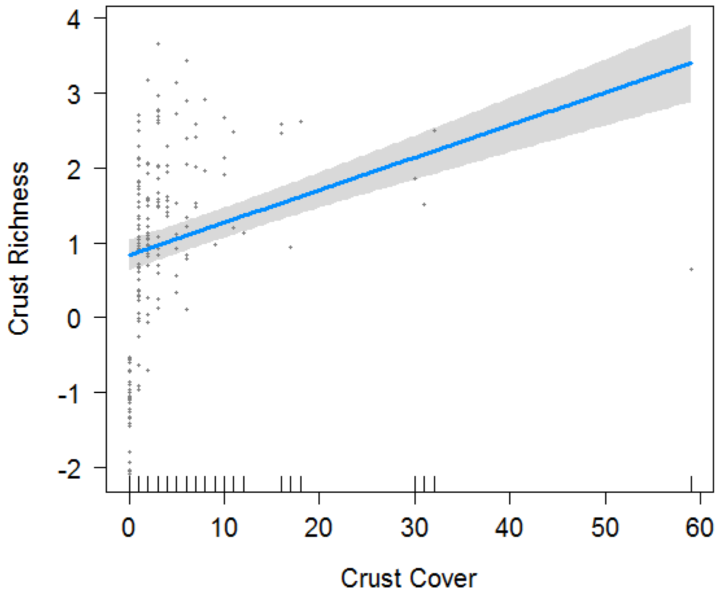

Figure 22. Partial residuals plot of crust cover against crust richness in the combined richness model. Crust richness is presented on a logarithmic scale.

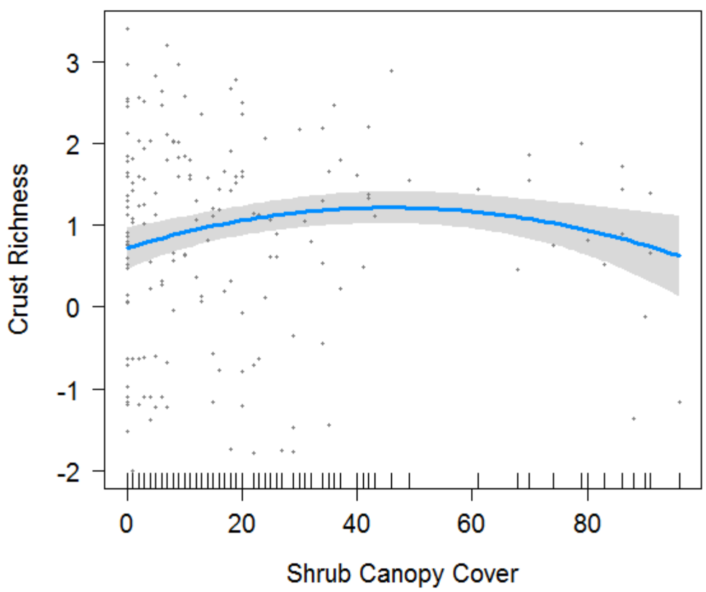

Figure 23. Partial residuals plot of shrub canopy cover against crust richness in the combined richness model. Crust richness is presented on a logarithmic scale.

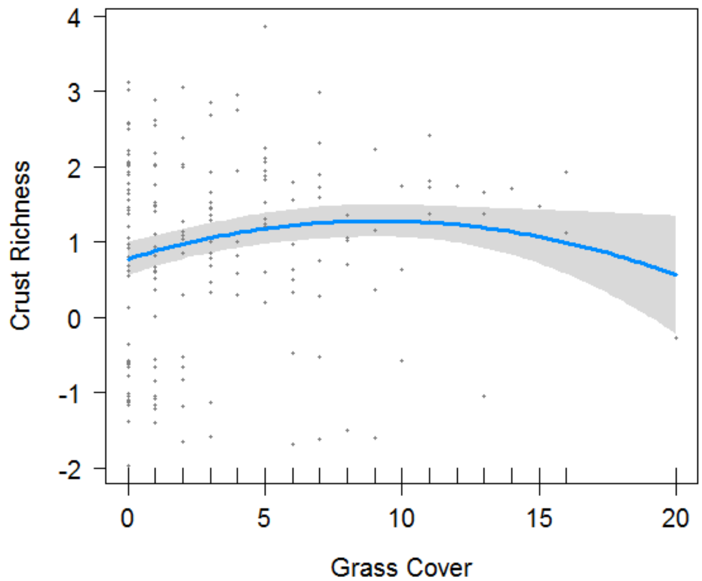

Figure 24. Partial residuals plot of grass cover against crust richness in the combined richness model. Crust richness is presented on a logarithmic scale.

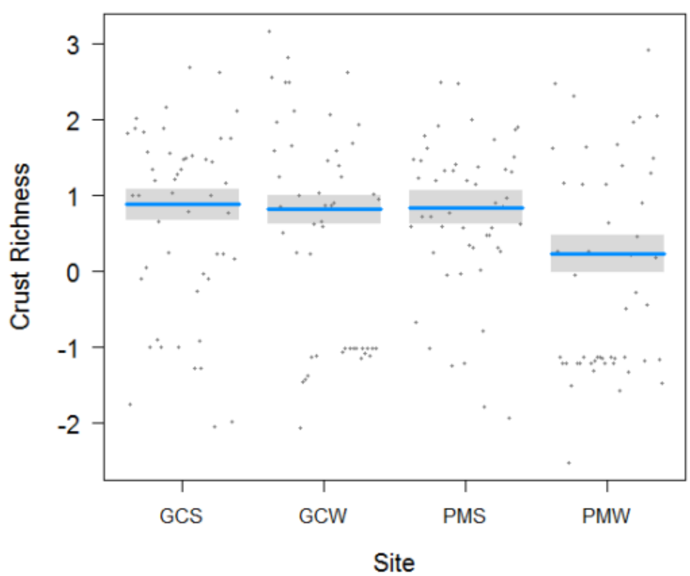

Figure 25. Partial residuals plot of sampling site against crust richness in the combined richness model. Crust richness is presented on a logarithmic scale.

d. Moss vs. lichen dominance

The results of the t-tests did not show significantly different mean values of the predictors for the presence of mosses and lichens, and chi-square tests did not show significantly differing effects of site and vegetation community on mosses versus lichens (Tables 20 and 21). Of the plots where any crust was present, the GCW site had the highest proportion of lichen presence (100% of plots with crust) and the lowest proportion of moss presence (62.5%) (Table 22). The PMW site had the lowest proportion of lichen presence (74.1%) and highest proportion of moss presence (96.3%). Both of the shrubland sites had relatively high proportions of both lichen and moss presence, with GCS having 90.2% lichen presence in crusted plots and 87.8% moss presence, while PMS had 91.3% lichen presence and 84.8% moss presence.

Variable	Moss mean	Lichen mean	t-test *p*
Shrub Canopy	21.54	19.52	0.51
Tree Canopy	9.63	6.45	0.27
Shrub Stem	3.82	3.56	0.63
Tree Stem	0.12	0.07	0.47
Fine Litter	15.15	12.92	0.42
Woody Litter	6.32	5.44	0.33
Grass	3.78	3.73	0.93
Rocks	3.82	3.62	0.87
pH	6.07	6.12	0.31

Table 20. Results of t-tests on the moss vs. lichen dataset. Mean values of each predictor variable in moss- vs. lichen-occupied plots. No results were significant.

Site		Vegetation Community	
χ^2:	0.79	χ^2:	0.02
p:	0.38	*p*:	0.89

Table 21. Results of chi-square tests on the moss vs. lichen dataset. No results were significant.

Site	% Lichen Present	% Moss Present
Garfield Creek Shrubland	90.2	87.8
Powell Mountain Shrubland	91.3	84.8
Garfield Creek Woodland	100	62.5
Powell Mountain Woodland	74.1	96.3

Table 22. Proportion of plots with lichen present and moss present at each site, calculated from only those plots that contained any soil crust.

6. DISCUSSION

a. Vascular plants: shrubs and grasses

My research found a unimodal (hump-shaped) response of crust cover to shrub canopy in the shrublands. Shrub canopy was identified as the most important variable in the shrubland model, but was less important (though still significant) in the combined model. T-tests did not reveal a different mean shrub canopy value for mosses vs. lichens. However, my moss and lichen measure is one of presence and absence rather than cover, so there may be differences in relative abundance between the two functional groups that were not identified in this study. The unimodal relationship over all suggests an intermediate cover of shrub canopy as being ideal for crust cover, perhaps as a tradeoff between litter accumulation and photosynthetic inhibition on the one hand which would negatively affect crust, and enhanced soil fertility, cooler microclimate, and protection from physical disturbances on the other (Noy-Meir 1973). The greater significance in the positive term of the quadratic (Tables 14 and 16) suggests a tolerance for shading that only declines at very high canopy cover.

The relationship between shrub cover and total crust cover is generally established as a positive one in the literature, but with differing effects between lichens and mosses. For example, moss and lichen cover is higher beneath shrub canopies than in interspaces in Wyoming sagebrush steppe (Muscha & Hild 2006), and Briggs and

Morgan (2008) report a positive relationship between crust cover and vascular plant cover in general (shrubs, herbs, and grasses combined) in Australian woodlands and grasslands. When mosses were separated from the total crust cover in that study, moss cover was not significantly related to plant cover, but the plant relationship with lichen cover was stronger than it was for the combined crust cover. In a study from semiarid Spain, moss and gelatinous lichen proportions are higher in crusts that are located in plots with shrubs present, while squamulose, crustose, and fruticose lichens have higher proportions in crusts that are in non-shrub plots (Maestre *et al.* 2009). In another Spanish study, total crust cover is positively related to shrub cover in an oak thicket, but lichen cover shows a negative relationship (Ochoa-Hueso *et al* 2011). In a study of eucalyptus woodlands in Australia, shrub cover is negatively related to cover of crustose lichens and positively related to squamulose lichens (Read *et al.* 2008). In the Mojave Desert, the optimal location for mosses is not right beneath shrub canopies but just at the edge of the dripline, where shade and soil nutrition are still enhanced by the shrub but litterfall does not accumulate on top of the crust (Smith & Stark 2014).

It is possible that the relationship between shrub canopy and crust is dependent on particular gradients of stress. In the Monte Desert in Argentina, Tabeni *et al* (2014) found that along a grazing gradient, crusts are positively associated with shrub cover at short distances from livestock settlements, but are independent of shrub cover at farther distances. In addition, crust cover is independent of grass and litter close to the settlements, but shows a negative association farther away. In this situation, the necessity for shrub cover protection from livestock and human disturbance may supersede a litter effect when located near the source of disturbance, but diminishes when crusts are located farther away. When protective cover becomes less critical, crust cover begins to show the negative relationship with litter while at the same time exhibiting what may be a shift to competitive interactions with grasses.

In my study there is no significant effect of grass cover on crust cover at any site, although there is a unimodal relationship with crust richness. Read *et al*. (2008) report a positive relationship between crust cover and perennial grass cover at low grass cover (0-5%), with crust cover increasing dramatically when grass cover was greater than 0%. They interpret this relationship as being a short-term result of recovery of both functional groups after grazing disturbance, rather than a sign of facilitation. Two studies from North American pinyon-juniper woodlands have conflicting results with respect to grass. In Beymer and Klopatek's (1992) study from Grand Canyon, Arizona, crust cover declines alongside declining cover of the dominant C-3 grass, muttongrass (*Poa fendleriana*), a relationship that follows a grazing gradient. In Ladyman's (1993) study from undisturbed (no recent grazing history) woodlands in New Mexico, grasses display a negative relationship with crust cover. In a study of crust cover in different successional stages from sagebrush shrub-steppe in Oregon (Dettweiler-Robinson *et al.* 2013), native bunchgrasses generally appear to have a positive relationship with cover of both moss and lichen, though this relationship is not statistically significant. The invasive annual grass *Bromus tectorum* has a negative effect on crust cover in their study, as has been demonstrated by others as well (e.g. Serpe *et al.* 2013, Belnap *et al.* 2006). Results from Ponzetti & McCune (2001) in Oregon sagebrush steppe report a positive relationship between crust cover and bunchgrass cover. Finally, in Baltic dry grasslands a negative relationship exists between total vascular plant cover and the species richness of both lichens and bryophytes (Löbel *et al.* 2006).

The high crust richness at intermediate grass cover in my study may be a result of both crust and grass preferring similar conditions, although this would need to be confirmed through further study. An effect of crust richness on soil fertility could also be a possibility, but soil nutrients were not measured. Ultimately, at highest grass cover values the crust species richness declines, perhaps due to either competitive exclusion or a lack of colonizable bare ground.

Relationships amongst vascular plant groups, bryophytes, and lichens are complex. Experiments designed to test effects of soil crust organisms on plant seedling emergence and performance, as well as field studies of facilitation vs. inhibition of vascular plants by cryptogams in various ecosystems, have yielded variable results that appear to be specific to the particular species of plants and morphological groups of crusts (e.g. Zhang & Belnap 2015, Mendoza-Aguilar *et al.* 2014, Doxford *et al.* 2013, Briggs & Morgan 2011, Deines *et al.* 2007, Serpe *et al.* 2006, Pendleton *et al.* 2004, Van Tooren 1988). Vascular plants, mosses, and lichens also have differing responses to various environmental gradients (e.g. Spitale *et al.* 2009, Grytnes *et al.* 2006), and can experience environmental stress at different times. For example, mosses and lichens are poikilohydric – they acquire water from ambient moisture in the atmosphere and soil, precluding the need for a root system (Vanderpoorten & Goffinet 2009, Noy-Meir 1973). This is an advantage in terms of colonization ability where soils are shallow (or there is no soil at all), but also limits them to growing and metabolizing only during wetter weather conditions, while during dry conditions vascular plants can still access water stored belowground. By necessity, the mosses have therefore evolved an impressive desiccation tolerance that allows them to resume metabolic activity almost instantly even after years of existing in a desiccated state (Vanderpoorten & Goffinet 2009).

Because plants and soil crusts vary in their ecophysiological responses to different stressors, the competitiveness of one functional group over another can depend on the particular combination of stressors at any site. In this study, the relationship between crust cover and shrub canopy in shrublands reveals that at my sites, soil crust communities are most successful where shrub cover is moderately dense.

b. Tree canopy and litter

In my study, a negative effect of woody litter on crust cover in the woodland dataset, a negative effect of tree canopy on crust cover in the combined dataset, and a negative relationship between tree canopy and crust richness support the trend that overall, higher canopy and accumulation of litter from trees tend to inhibit soil crusts in woodland environments. However, observations from soil crust literature repeatedly note that mosses appear to be more tolerant of these conditions than lichens. This trend is supported by mosses' adaptations to lower light environments that enable a high shade tolerance (Spitale *et al.* 2009, Marschall & Proctor 2004), allowing dryland species to take advantage of moist microhabitats in otherwise inhospitable conditions for poikilohydric organisms. Although below-canopy microsites would seem to be more hospitable to soil crust organisms in terms of soil temperature and moisture (Breshears *et al.* 1998, Royer *et al.* 2012), burial by litter probably counteracts these beneficial effects and explains the suppression of soil crusts overall in the litter zone. Notably, although tree canopy was a significant predictor in the combined model, it was not significant in the woodland model. Site, woody litter, and rock cover showed stronger relationships.

Read *et al.* (2008) observed a decrease in crust cover at >40% litter cover and at >20% tree cover in their Australian eucalyptus woodlands, and Briggs and Morgan (2008) found that not only does total crust cover decline with higher litter cover, this effect is even stronger when mosses are removed from the cover estimates. In North American pinyon-juniper woodlands, Beymer and Klopatek (1992) report an increase in tree cover where there is lower crust cover. Ladyman *et al.*(1993), in their study of recently undisturbed woodlands, examined crust cover responses to tree canopy and litter cover using several lines of differing lengths extending from selected trees. They found a significant negative relationship between total crust cover and tree canopy cover, as well as with coarse and fine litter. When divided into lichen and moss components, the trend was only apparent for lichens. Mosses, though still at low cover when underneath a tree canopy, reach their highest proportions in those lines that extended the shortest distance from the focal trees.

c. Rock cover

I found a negative effect of rock cover on crust cover in both the shrubland and woodland environments. This result contrasts with others such as Ladyman *et al.* (1993) where a positive association is present with pebbles. Embedded rocks can facilitate crusts by perching water at the soil surface and protecting the surface from disturbance (Belnap *et al.* 2001b). My study includes both large embedded rocks and small loose rocks in this category, with the former being especially pronounced at the Powell Mountain woodland. Observationally, plots in this zone with large embedded rocks in them leave less ground area available for crust colonization, but are located in areas that have a high cover of both large rocks and crust cover relative to the surrounding non-rocky areas. Although the rocks may indeed protect crust from physical disturbance at this site, such as erosion or wildlife traffic through less densely wooded spaces, their occupation of surface area overshadows this effect at the scale at which I was measuring. Small surface rocks in my plots are possibly associated with sandier soil texture in some areas, a condition that is unfavorable for crust establishment (Belnap *et al.* 2001b).

d. Soil pH

Although a unimodal pattern appeared in data exploration, which follows expectations based on the typical relationship seen for vascular plants on pH gradients, no significant effect of pH was found for crust cover or richness in any of the final models. Effects of pH in other crust studies are variable, including results where pH is not a significant predictor of cover (e.g. Belnap *et al.* 2014, Pietresiak *et al.* 2011, Briggs & Morgan 2008).

e. Microtopography

No significant effect of microtopography was found in any of the final models. When sites were examined individually during data exploration, crust cover appeared to be highest at PMW in plots designated “combination”, meaning more than one microtopographic category was present in a single plot. This potential relationship could be explored further in a more targeted research study.

f. Site

In the woodland cover model, the Powell Mountain woodland location has a significant positive effect on crust cover. The Garfield Creek woodland is noticeably lower in overall plant cover, with coarse sandy soil and small, stunted pinyon pines. The Powell Mountain woodland appears to be a more productive woodland than Garfield Creek with many large trees, a developed canopy, and finer soils. This woodland was also higher in elevation than at Garfield Creek. The elevation and the high canopy cover may have contributed to a cooler and less extreme soil microenvironment. In the combined richness model, Powell Mountain Woodland has a significant *negative* effect on crust species richness compared to the model's default location of Garfield Creek Shrubland. PMW had the highest proportion of moss presence, possibly because of other unmeasured habitat variables (such as microclimate or soil characteristics) or disturbance legacies. The positive effect of PMW location on crust cover and the negative effects of woody litter and tree canopy, which reach their highest values at this site, are not irreconcilable. Although crust cover is lower in canopy-associated microsites, the woodland overall benefits from the high canopy cover, which creates an overall cooler and moister climatic modification that extends to the intercanopy spaces where soil crusts are more likely to occur (Royer *et al.* 2012).

In both the woodland and combined models, the effect of site is the most important in terms of D^2. Unmeasured site-related factors such as disturbance, climate, or soil texture, may explain a great deal of the variation in crust cover from one site to another, and these factors should be taken into account in future studies with fewer time and cost limitations.

g. Summary and comparison to other regions

Mean crust cover is similar between woodland and shrubland datasets, but is more variable in the woodlands, with the effect of site being more important in the woodlands as well. In shrublands, the presence of moderately high shrub canopy cover in a plot is the most important variable favoring soil crust cover, followed by a negative influence of rock cover. In woodlands, canopy cover of any kind is not significant and instead the important predictors are site, woody litter cover, and rock cover. In these woodland environments, shrub and tree canopy may still influence soil crusts to some degree, but have less direct influence on crust occurrence than the occupation of colonizable space by ground-cover elements such as rocks and litter. A negative association with tree canopy in these woodlands may result more from accumulation of debris in the litter zone than from photosynthetic inhibition by shading, particularly given the success of mosses in low-light environments (Marschall & Proctor 2004). In shrublands, less debris is present overall, allowing the relationship with shrub canopy to be more apparent. It is important to note that this relationship does not mean that soil crusts were found exclusively underneath shrub canopies. They were also seen extending beyond the canopy edge or occupying the open space in between nearby shrubs. The absence of a significant relationship with shrub canopy in the woodland dataset (regardless of direction) was surprising, but the significantly lower presence of shrub-occupied plots at the woodland sites may have played into this result. From the models alone, it seems that soil crusts are more abundant near or below shrub canopies in the shrublands, while in the woodlands they are more abundant in tree interspaces.

The shrublands of my study area have on average 1.5 more crust morpho-species than woodlands, as well as higher maximum species richness. Crust cover is the only significant predictor of crust richness in shrublands, and tree canopy is the only significant predictor of crust richness in woodlands. Site effects and unimodal relationships with grass cover and shrub canopy only appear in the combined dataset, and may reflect a response to an unmeasured gradient such as disturbance or soil fertility.

My result of a hump-shaped relationship between shrub canopy cover and crust cover, with crust cover declining only at very high shrub canopy cover, seems to agree with the results found overall from other regions, where crust cover increased with shrub cover. Although I found no relationship between crust cover and grass cover, results from the Colorado Plateau are mixed (Ladyman *et al.* 1993, Beymer & Klopatek 1992) and Northern Great Basin studies found positive associations between crust cover and perennial grass cover and a negative relationship between crust cover and *Bromus tectorum* cover (Dettweiler-Robinson *et al.* 2013, Ponzetti & McCune 2001). Although the Northern and Central Basin and Range regions share many grass species, soil crust species and environmental stress gradients may differ enough to prevent extrapolation without further research.

The negative relationships found in my study between soil crusts and tree canopy (and/or its associated fine and woody litter accumulations) agrees with results from the Colorado Plateau (Ladyman 1993, Beymer & Klopatek 1992), though this association is stronger for lichens than for mosses (Ladyman 1993). However, my results for rock cover contrast with Ladyman's Colorado Plateau study (1993) in finding a negative relationship.

7. CONCLUSION AND RECOMMENDATIONS

My research attempts to address a gap in the documentation of soil crust occurrence in two major vegetation zones of the Central Great Basin region of Nevada, sagebrush shrublands and pinyon-juniper woodlands. In shrublands, soil crusts respond negatively to rock cover and positively to moderately dense shrub canopy. In woodlands, ground-cover of rocks and woody litter have a negative effect on soil crusts, but with wide variation in crust cover between different woodland sites. These two habitat types are experiencing ongoing structural change in this region. In particular, sagebrush shrublands are experiencing conversion to either annual grasslands in areas of cheatgrass invasion, or to early-stage woodlands in areas of pinyon-juniper woodland expansion (NDOW 2013). Pinyon-juniper woodlands are experiencing expansion and infill in some areas, and stress-induced diebacks in others (Romme *et al.* 2009). All of these changes may have important implications for the soil crusts in these places, influencing how much ecological functioning they contribute to their particular community.

Based on my results, we might expect that the reduction in shrub cover following annual grass invasion in *Artemisia* shrubland would also reduce crust cover. This expectation is based on the combination of my findings about the mostly positive association with shrub cover and the findings of others about the negative effects of *B. tectorum* invasion on soil crust. However, my study sites did not allow for analysis of soil crust cover in the presence of invasion. I found no invasive plants at Powell Mountain. Garfield Creek had areas nearer to the road that were heavily invaded by *Salsola*, but my sampling area was buffered from the road and did not have these plants. *Bromus tectorum* was present at Garfield Creek as well, but in low enough density that it did not appear in any of my plots. Earlier work with large vegetation datasets has suggested that the negative relationship seen between *B. tectorum* and crust cover may indicate the reverse effect as well, that an extensive crust cover inhibits establishment of this species (Peterson 2013), and some experimental tests have reached this conclusion as well, but with varying results depending on the type of soil crust (Serpe *et al.* 2008, Deines *et al.* 2007, Serpe *et al.* 2006). Collectively, there seems to be a trend in these experimental studies of decreasing grass success along a gradient from tall moss to short moss to lichen crust, but more work at local scales may be required in order to identify how hypotheses about crust effects on vascular plants manifest in the field.

Where shrublands are experiencing new recruitment of pinyon pine and juniper, effects of tree establishment may reflect the relationships seen in my woodland model, with subsequent losses of crust cover where litter accumulation is high. If infilling of trees in pinyon-juniper woodlands results in higher litter cover, the woodland may lose soil crust cover as well. The literature on soil crust effects on soil hydrology and erosion potential provide justification for maintaining soil crust in woodlands with an existing crust cover, and Loope and Gifford's (1972) study of soil crust effects on soil infiltration in a pinyon-juniper woodland in Utah found that areas chained for pinyon removal had significantly lower infiltration rates and higher potential for sediment production than areas with undisturbed soil crust. I would suggest that management activities designed to remove trees should consider whether the soil crust cover in the treatment area is extensive enough to warrant the selection of methods that minimize disturbance to the soil surface, especially given the high erosion potential and low potential herbaceous cover seen in some pinyon-juniper woodlands (Davenport *et al.* 1998) and the demonstrated role of soil crusts in reducing runoff and erosion. Additionally, locations where soil crust cover is low may still warrant careful consideration of impacts to soil crusts if they are within a region that is overall depauperate in soil crust, to provide source material for soil crust growth and recolonization over time.

Balancing management, conservation, and restoration goals requires an understanding of the outcomes of environmental change and management strategies on the subject of interest. Biological crusts are already being adopted in studies of the effects of various management techniques on ecological communities (e.g. Warren *et al.* 2015, Redmond *et al.* 2013). Further research should seek to (1) identify at a broader regional scale (specific mountain ranges and valleys) where in the Great Basin well-developed biological crusts occur, (2) determine habitat characteristics of soil crusts at multiple scales, and (3) monitor how biological soil crusts respond to structural change in Great Basin sagebrush and pinyon-juniper communities using repeat sampling over multiple years. Approaches for objectives (1) and (2) should include multiple parent materials in order to cover the geological variation of the Great Basin. My study sites were located on granitic parent material, which is common in the westernmost portion of Nevada, but future studies should include the carbonate sedimentary rocks of eastern Nevada and the volcanic rocks that characterize the majority of the region. Although granite favors crust development in the Mojave, crust development is significant on the Colorado Plateau's sedimentary materials, and personal observations in the Central Basin and Range suggest the fine silty products of weathered volcanic rock to be favorable for soil crusts as well. Mapping efforts related to objective (1) should also identify land use and disturbance history of sites, in particular sheep and cattle grazing, recreation, and fire. Scales utilized for objective (2) should include those that would capture vegetation structure (density of individual trees or shrubs per unit area) and larger landscape processes that could affect soil crust distribution (erosional and depositional environments associated with topography, slope positions, drainage networks, or specific geomorphological units). Comparison of my findings with results from other regions suggest similar relationships between soil crust cover and vegetation regardless of region, but studies specifically addressing the effect of overarching vegetation structure are sparse and this remains an important area of research and exploration.

Biological soil crust communities have already been identified as communities of conservation interest in the Colorado Plateau and Northern Great Basin/Columbia Basin regions (Bryce *et al.* 2012, Oregon Department of Fish and Wildlife 2006), and have been highlighted as a key component of sagebrush steppe ecosystems in general, meriting consideration of impacts during the planning of restoration activities (Pyke *et al.* 2015). Expanded research on crusts in Nevada’s Central Great Basin is necessary to determine the distribution of these communities in our own ecosystems.

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Appendix A: Soil crust morphospecies

Lichens	Morpho-species	Notes
	Aspicilia desertorum	Olive green squamulose. Present at PM sites. Possibly present at GC sites, where it could be Unidentified Lichen 3.
	Caloplaca tominii	Yellow, sorediate (powdery), present at PMS, GCS, GCW.
	Candelariella vitellina	Golden yellow, squamulose. Present at all sites.
	Cladonia pocillum	Pale to bright green squamulose, white on underside of squamules. Common in PMW, present at GCS.
	Placidium sp.	Brown leafy squamules. Present at GCS.
	Psora montana	Brown to green squamulose, black apothecia, sometimes pruinose. Common in PMW, not found in PMS or GCS.
	Thelenella muscorum	Drab white or green with black apothecia. Present at all sites.
	Unidentified lichen 1	White crustose with black apothecia. Found growing around sand and larger grains in open microsites. Common at GCW and GCS.
	Unidentified lichen 2	Present in 1 plot at PMW.
	Unidentified lichen 3	Pale green/gray squamulose. Found at PMS, GC sites.
	Unidentified lichen 4	White/beige. Disks blackish with white margins. Possibly *Lecanora sp.* or *Caloplaca sp.* Present at PMS, GCS, GCW.
	Unidentified lichen 5	Indistinct. Black apothecia. Present in 1 plot at PMS.
	Unidentified lichen 6	Black, indistinct. Possibly *Collema tenax*. Present in 2 plots at GCW, 1 plot at GCS.
	Unidentified lichen 7	Grayish squamulose. Possibly *Toninia sedifolia*. Present in 1 plot at GCW.
	Unidentified lichen 8	Black structures, indistinct. Present in 1 plot at GCW.
	Unidentified lichen 9	Disk is drab yellow with brown margins. Possibly *Caloplaca sp.* Present at GCW.
	Unidentified lichen 10	Present in 1 plot at GCW.
	Unidentified lichen 11	Present in 1 plot at GCS.
	Unidentified lichen 12	Blackish, present in 1 plot at GCS.
	Unidentified lichen 13	Gray, squamulose. Present in 1 plot at GCS.
	Unidentified lichen 14	Green. Disks yellow with green margins. Present in 1 plot at GCS.
	Unidentified lichen 15	Brown, squamulose. Present in 1 plot at GCS.
	Unidentified lichen 16	Black, squamulose. Present in 1 plot at PMW.

	Unidentified lichen 17	Green/brown round squamules. Present in 1 plot at PMW.
	Unidentified lichen 18	Gray/black squamulose. Present in 1 plot at GCS.
	Unidentified lichen 19	Round brown squamules. Possibly *Heteroplacidium congestum*. Common at PMS, GCS. Present at GCW.
Mosses		
	Bryum argenteum	Silvery green short moss, small leaves. Present at all sites.
	Syntrichia caninervis	Short twisting moss with large leaves, long awns. Common. Present at all sites.
	Syntrichia ruralis	Tall twisting moss with large leaves, long awns. Distinctly larger and longer than *S. caninervis*. Common. Present at all sites.
	Unidentified moss 1	Short moss, deeper green color than *B. argenteum*. Possibly *Didymedon vinealis*.
	Unidentified moss 2	Short twisting moss with tall spore capsules present. Possibly *Tortula inermis* or *S. ruralis*. Present at PMW.
	Unidentified moss 3	Short moss, deeper green color than *B. argenteum*, not identical to Unidentified moss 1. Present at GCS, GCW.
	Unidentified moss 4	Leaves long, twisting, rubbery, kelp-like. Present in 1 plot at PMW.
	Unidentified moss 5	Possibly *Pterygoneurum ovatum*. Present in 1 plot at PMW, 1 plot at GCS.

Table 23. Soil crust morpho-species found in this study's plots.

Appendix B: Photographs of study sites

Figure 26. Powell Mountain Woodland. Evidence of wood harvesting activity in foreground.

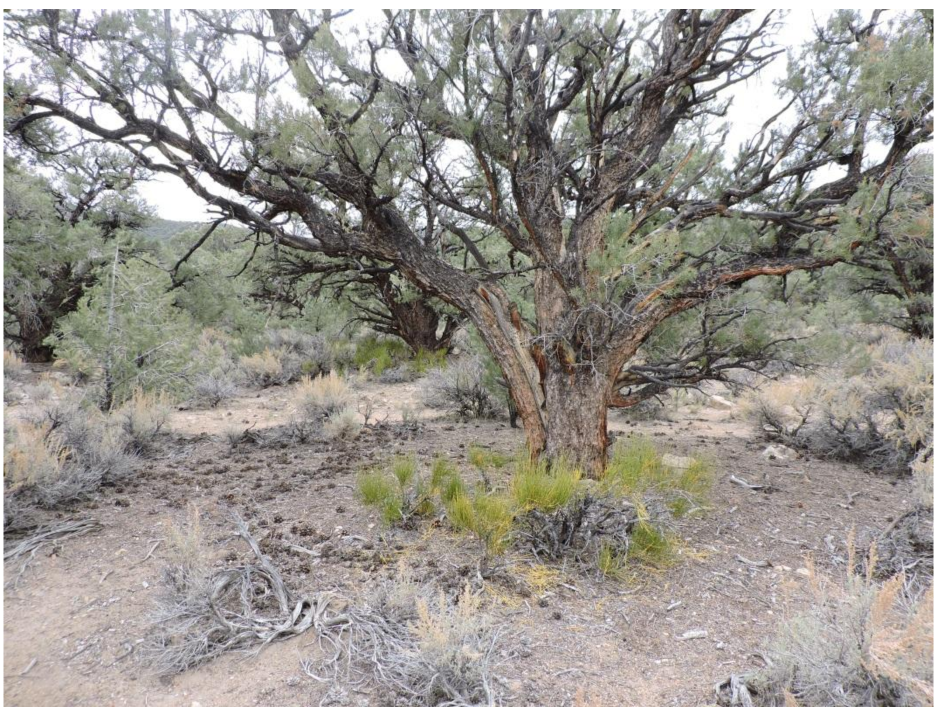

Figure 27. Powell Mountain Woodland.

Figure 28. Powell Mountain Woodland. A plot with soil crust.

Figure 29. Powell Mountain Woodland.

Figure 30. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 31. Soil crust in Powell Mountain Woodland. Sept. 2014.

Figure 32. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 33. Powell Mountain Woodland. A plot with high litter cover and no soil crust. Sept. 2014

Figure 34. Soil crust in Powell Mountain Woodland. Lichens *Psora montana* and *Cladonia pocillum* are present. Sept. 2014

Figure 35. Powell Mountain Woodland. A plot with soil crust. Sept. 2014

Figure 36. Soil crust in Powell Mountain Woodland. Sept. 2014

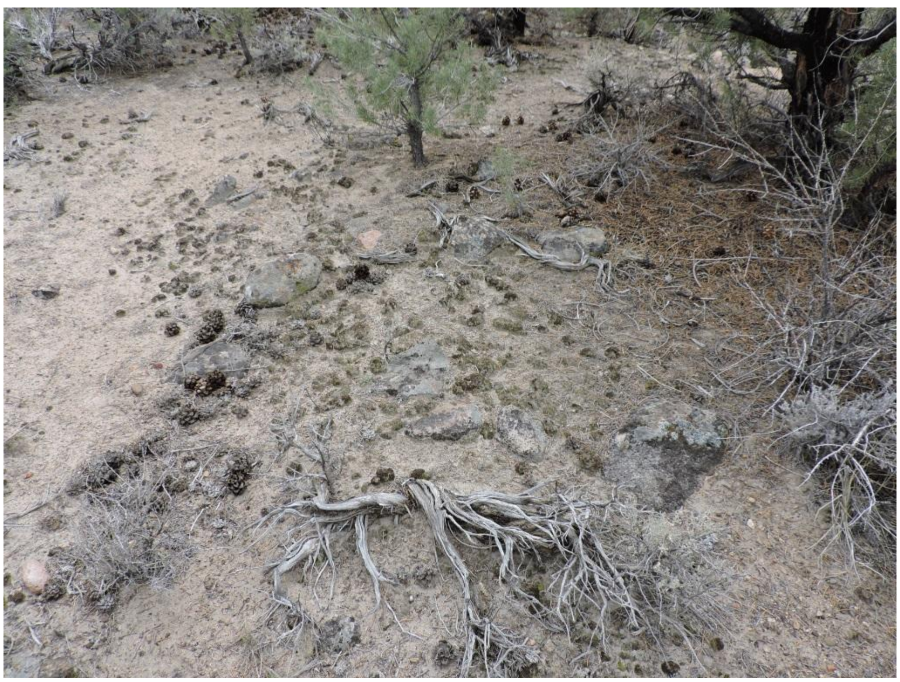

Figure 37. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 38. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 39. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 40. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 41. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 42. Soil crust in Powell Mountain Woodland. Sept. 2014

Figure 43. Soil crust in Powell Mountain Woodland. March 2015

Figure 44. Soil crust in Powell Mountain Woodland. March 2015

Figure 46. Powell Mountain Woodland. March 2015

Figure 45. Powell Mountain Woodland. March 2015

Figure 47.Powell Mountain Woodland. March 2015

Figure 48. Powell Mountain Woodland. March 2015

Figure 49. Powell Mountain Woodland. March 2015

Figure 50. Powell Mountain Woodland. Aug. 2015

Figure 51. Powell Mountain Woodland. Aug. 2015

Figure 52. Soil crust in Powell Mountain Woodland. The lichen *Candelariella vitellina* is present. Aug. 2015

Figure 53. Powell Mountain Shrubland. Aug. 2015

Figure 54. Powell Mountain Shrubland. Aug. 2015

Figure 55. Powell Mountain Shrubland. Aug. 2015

Figure 6. Powell Mountain Shrubland. Aug. 2015

Figure 57. Powell Mountain Shrubland. Aug. 2015

Figure 58. Powell Mountain Shrubland. Aug. 2015

Figure 59. Powell Mountain Shrubland. Aug. 2015

Figure 7. Powell Mountain Shrubland. Aug. 2015

Figure 61. Powell Mountain Shrubland. June 2015

Figure 62. Powell Mountain Shrubland. June 2015

Figure 63. Powell Mountain Shrubland. June 2015

Figure 64. Powell Mountain Shrubland. June 2015

Figure 65. Powell Mountain Shrubland. June 2015

Figure 66. Garfield Creek Woodland. Aug. 2015

Figure 67. Garfield Creek Woodland. Aug. 2015

Figure 68. Garfield Creek Woodland. Aug. 2015

Figure 69. Garfield Creek Woodland. Aug. 2015

Figure 70. Garfield Creek Woodland. Aug. 2015

Figure 71. Garfield Creek Woodland. Aug. 2015

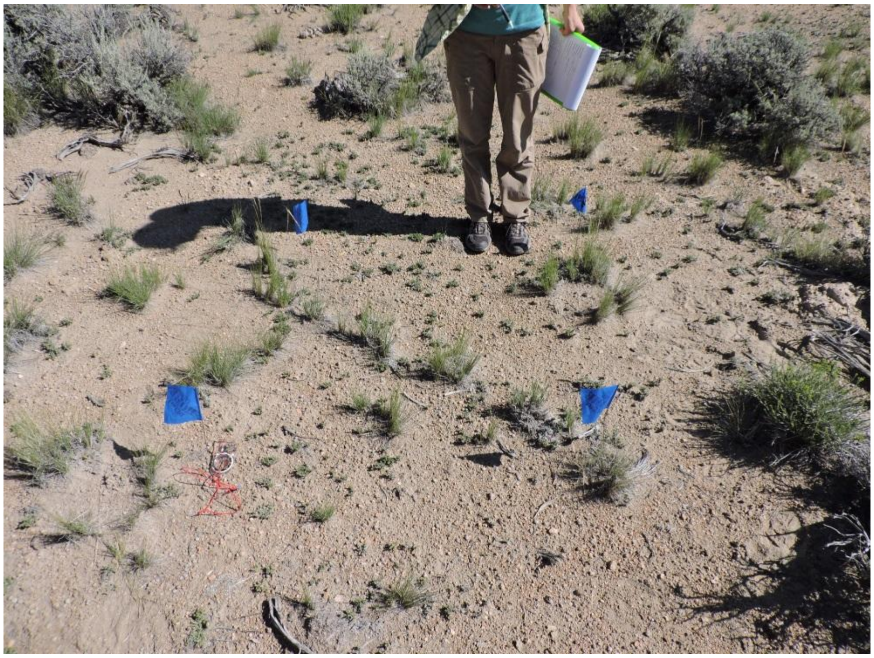

Figure 72. Garfield Creek Woodland. Aug. 2015

Figure 73. Garfield Creek Shrubland. Aug. 2015

Figure 74. Garfield Creek Shrubland. Aug. 2015

Figure 75. Garfield Creek Shrubland. Aug. 2015

Figure 76. Garfield Creek Shrubland. Aug. 2015

Figure 77. Garfield Creek Shrubland. Aug. 2015

Figure 78. Garfield Creek Shrubland. Aug. 2015

Figure 79. Garfield Creek Shrubland. Aug. 2015

Figure 80. Garfield Creek Shrubland. Aug. 2015

Figure 81. Garfield Creek Shrubland. Aug. 2015

Figure 82. Garfield Creek Shrubland. Aug. 2015

Figure 83. Garfield Creek Shrubland. Aug. 2015

Figure 84. Garfield Creek Shrubland. Aug. 2015

Figure 85. Garfield Creek Shrubland. Aug. 2015

Figure 86. Garfield Creek Shrubland. Aug. 2015

Figure 87. Garfield Creek Shrubland. Aug. 2015

Figure 88. Garfield Creek Shrubland. Aug. 2015

Figure 89. Garfield Creek Shrubland. Aug. 2015

Figure 90. Garfield Creek Shrubland. Aug. 2015

Figure 91. Garfield Creek Shrubland. Aug. 2015