Ecological Applications, 30(1), 2020, e02016

Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities

Heather T. Root,[1,4] Jesse E. D. Miller,[2] and Roger Rosentreter[3]

[1]*Botany Department, Weber State University, Ogden, Utah 84401 USA*
[2]*Department of Biology, Stanford University, Stanford, California 94304 USA*
[3]*Biology Department, Boise State University, Boise, Idaho 83725 USA*

Citation: Root, H. T., J. E. D. Miller, and R. Rosentreter. 2020. Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities. Ecological Applications 30(1):e02016. 10.1002/eap.2016

Abstract. Exotic invasive plants threaten ecosystem integrity, and their success depends on a combination of abiotic factors, disturbances, and interactions with existing communities. In dryland ecosystems, soil biocrusts (communities of lichens, bryophytes, and microorganisms) can limit favorable microsites needed for invasive species establishment, but the relative importance of biocrusts for landscape-scale invasion patterns remains poorly understood. We examine effects of livestock grazing in habitats at high risk for invasion to test the hypothesis that disturbance indirectly favors exotic annual grasses by reducing biocrust cover. We present some of the first evidence that biocrusts increase site resistance to invasion at a landscape scale and mediate the effects of disturbance. Biocrust species richness, which is reduced by livestock grazing, also appears to promote native perennial grasses. Short mosses, as a functional group, appear to be particularly valuable for preventing invasion by exotic annual grasses. Our study suggests that maintaining biocrust communities with high cover, species richness, and cover of short mosses can increase resistance to invasion. These results highlight the potential of soil surface communities to mediate invasion dynamics and suggest promising avenues for restoration in dryland ecosystems.

Key words: biocrust; cheatgrass; disturbance ecology; diversity–ecosystem-function relationship; exotic annual grasses; livestock grazing; plant establishment; rangeland; resistance to invasion.

INTRODUCTION

Invasion by exotic plants threatens biodiversity (Heywood 1989) and can substantially affect ecosystem services and processes (Vitousek et al. 1996, Williamson 1999, Pimentel et al. 2000). However, drivers of invasion are difficult to generalize and likely include complex interactions among climate, disturbance regimes, traits of native plant communities, and dispersal pressure from potential invaders (Lonsdale 1999). When there is an increase in unused resources, plant communities are expected to be more susceptible to invasion (the fluctuating resource hypothesis; Davis et al. 2000). Because disturbance often results in reduction or loss of native plant communities, it can increase available resources and reduce competitive resistance to potential invaders (Chambers et al. 2007). Access to favorable microsites for establishment, such as sites without native competitors, may be a critical determinant of competitive success (Boeken 2018). Although numerous studies have examined how invasion is affected by characteristics of above-ground plants (Anderson and Inouye 2001, Chambers et al. 2014) and soil microbes (Levine et al. 2006), communities of organisms at the soil surface that modify establishment microsites may be a cryptic driver of invasion dynamics, particularly following disturbance.

Exotic annual grasses have had major impacts on ecosystem services in arid and semiarid ecosystems globally (D'Antonio and Vitousek 1992, Balch et al. 2013). In particular, these invasions are problematic because they degrade habitat quality for native plants and animals (Connelly et al. 2000, Condon and Pyke 2018) and increase wildfire frequency and size (Balch et al. 2013). Exotic annual grasses have occurred in western North America for over a century and have long been associated with intensive livestock grazing and wildfires (Stewart and Hull 1949). Many factors influence the resistance and resilience of sites to exotic annual grass invasion, including climate, soils, topography, established plant communities, and disturbance history (Chambers et al. 2014). Invasion by exotic annual grasses is strongly mediated by the native plant community (Anderson and Inouye 2001, Chambers et al. 2014) and some observational studies have suggested that invasion may be mediated by soil biocrusts (Peterson 2013, Reisner et al. 2013), diverse ground-dwelling communities of lichens, mosses, and free-living algae and bacteria.

Manuscript received 18 June 2019; revised 12 August 2019; accepted 11 September 2019. Corresponding Editor: Deborah A. Neher.

[4] E-mail: heatherroot@weber.edu

Biocrust cover is known to be generally inversely related to exotic annual grass cover, but the mechanisms linking biocrusts to exotic grasses remains incompletely understood. A negative relationship between exotic annual grasses and biocrusts may be caused by litter from the grasses suppressing biocrust development (Dettweiler-Robinson et al. 2013) or by biocrusts reducing germination and establishment of exotic annual grasses (Deines et al. 2007, Slate et al. 2018). Disentangling the relative importance of these processes remains an open question for both basic invasion ecology and applied range management questions. If biocrusts are inhibited by annual grass litter, intervention to reestablish biocrusts could improve resilience after invasion. If biocrusts increase site resistance and prevent invasion, however, a focus on maintaining the integrity of these communities could have long-term ecosystem benefits. Though field studies have suggested that disturbances can reduce biocrusts (Ponzetti and McCune 2001, Peterson 2013), and that biocrusts are negatively associated with exotic annual grasses (Peterson 2013, Reisner et al. 2013), the indirect causal pathway linking disturbance to invasion by exotic annual grasses via biocrusts has not been tested in a broad landscape-level field study.

The arid and semiarid ecosystems that cover approximately one-third of global terrestrial habitats (Schlesinger et al. 1990) typically support sparse vegetation with biocrusts occupying much of the open space between vascular plants (Belnap et al. 2016). Biocrust communities serve many ecosystem functions, such as decreasing erosion (Belnap and Büdel 2016) and contributing to nutrient cycling (Housman et al. 2006). Biocrust communities vary geographically in composition, often containing greater diversity than local vascular plant communities, and biocrusts have high landscape-scale species turnover that likely corresponds to functional trait variation (Root and McCune 2012, Rosentreter et al. 2016, Root et al. 2017). In general, biocrust communities are sensitive to disturbances by livestock grazing and wildfire (Ponzetti and McCune 2001, Ponzetti et al. 2007, Williams et al. 2008, Liu et al. 2009, Root et al. 2017). Following these disturbances, there is typically more bare soil (Reisner et al. 2013, Root et al. 2017), which could provide microsites for plant establishment. Though some studies have linked biocrust diversity with ecosystem functions (Bowker et al. 2010), the effects of different biocrust communities on resistance to invasion by exotic annual grasses are poorly known (Condon and Pyke 2018).

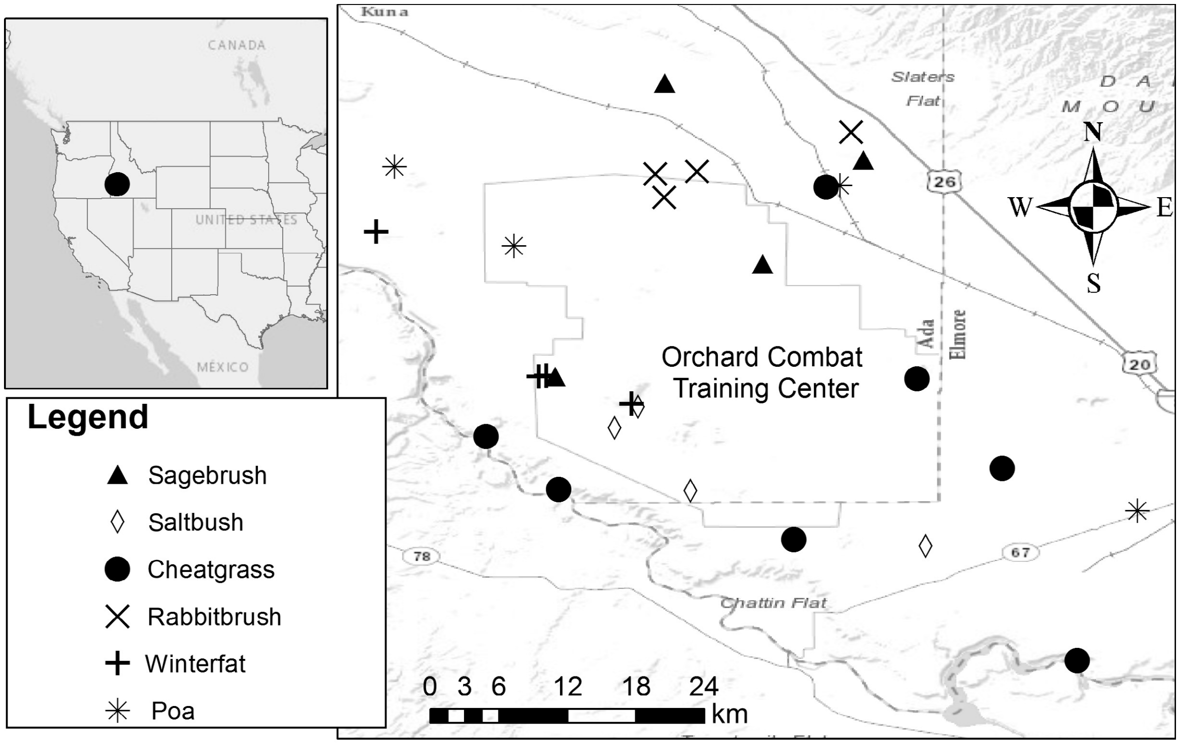
Biocrust communities may provide a critical physical barrier that modifies exotic seed establishment microsites (Serpe et al. 2008), despite being often overlooked because of their cryptic nature. Establishment microsites are central in determining outcomes of competition among plants, particularly for annual grasses in semiarid ecosystems (Boeken 2018, Condon and Pyke 2018). Intact biocrusts may play critical roles in restricting the establishment of exotic annual grasses, which often become dominant because of their speed and success in this early establishment stage (Stewart and Hull 1949). However, experimental studies examining the effects of biocrusts on seedling establishment have shown that biocrusts can either enhance or inhibit seedling establishment (Deines et al. 2007, Pando-Moreno et al. 2014, Slate et al. 2018). It is likely that the outcome of interactions between biocrust communities and establishment of plant seedlings depend on specific functional traits of each, such as continuity and thickness of the crust community as well as seed size and shape (Serpe et al. 2006, Slate et al. 2018). To effectively restore biocrust communities that maintain desirable ecosystem functions, an understanding of which functional groups are most effective at increasing site resistance is needed.

The exotic annual grass cheatgrass (*Bromus tectorum*) has high enough abundance to influence wildfire behavior (>15% cover) across 31% of the Intermountain West in North America (Bradley et al. 2018), and in this region over 40% of the native sagebrush (*Artemisia*) habitats are predicted to be at risk of displacement by cheatgrass in the next decades (Suring et al. 2005). Invasion by cheatgrass varies across the western United States with climate, elevation, and soil characteristics (Pechanec et al. 1937, Chambers et al. 2014). Habitats most susceptible to invasion include salt desert (dominated by species of *Atriplex*) and Wyoming big sagebrush (dominated by *Artemisia tridentata* ssp. *Wyomingensis*) such as those found in the Snake River Plain in southwestern Idaho (Chambers et al. 2014). We focus on these susceptible habitats to examine the effects of livestock grazing disturbance on biocrusts and exotic annual grasses. We capitalized on the presence of a military reservation with access restrictions to characterize undisturbed biocrust communities in a region that is otherwise widely disturbed. We focused on two main objectives: (1) test whether livestock grazing promotes exotic annual grasses directly or indirectly via effects on biocrust lichens and bryophytes and (2) explore whether biocrust lichen and bryophyte functional groups or species vary in how they respond to grazing disturbance or restrict exotic annual grasses.

Methods

Field sampling

We sampled 26 plots within and adjacent to the Idaho Army National Guard Orchard Combat Training Center south of Boise, Idaho on the Snake River Plain (Fig. 1) between 2014 and 2017. This steppe habitat is characterized by hot, dry summers and cold, moist winters with annual precipitation averaging 20–25 cm and elevation from 671 to 975 m. Soils are derived from volcanic ash and basalts. Disturbances include historic and current livestock grazing, roads, military training and recreational trails. In this study, we augmented previous sampling that had focused on biodiversity and community composition in five native-dominated habitats (described



Service Layer Credits: Esri, HERE, Garmin, © OpenStreetMap contributors, and the GIS user community
Sources: Esri, DeLorme, USGS, NPS

FIG. 1. Map of 26 plots in our study area in southwestern Idaho, USA symbolized by habitat type (these plant communities are described thoroughly in Rosentreter and Root [2019]).

in Rosentreter and Root 2019) with seven additional sites dominated by cheatgrass (*Bromus tectorum*). These sites were randomly selected with stratification to include a fairly even number of plots across grazing intensities and vegetation types. Low grazing intensity plots were randomly chosen within either protected exclosures or near perimeter fences that partially limit livestock movement. Selection criteria included: no roads through plots, no salt blocks or livestock watering troughs within 1/4 mile of plots (1 mile = 1.6 km), and no plow and seeded sites within plots.

To sample biocrust communities and vegetation, we used a modified version of the Forest Health Monitoring study plot protocol (McCune et al. 1997), with 30 min to 2 h examining each 34.7 m radius (0.4 ha) plot (McCune et al. 2009, Root and McCune 2012, Rosentreter and Root 2019). We assigned biocrust species abundance based on number of individuals or colonies: 0 (absent), 1 (≤5), 2 (5–10), and 3 (>10). We also recorded total percent cover of biocrust lichens and bryophytes, and vascular plant cover by species.

We collected samples of each biocrust lichen and bryophyte within the plot. We curated, identified, and assigned functional groups using standard methods (Brodo et al. 2001, McCune and Rosentreter 2007). A full list of biocrust species and their associated functional groups was reported in Rosentreter and Root (2019). Voucher specimens were deposited into the Snake River Plain herbarium at Boise State University (SRP) or with the Idaho Army National Guard. We combined vascular plants into functional groups using the USDA Plants Database (*available online*).[5] Exotic annual grasses were comprised mostly of *Bromus tectorum*, but also included *Eremopyrum triticeum* and *Taeniatherum caput-medusae*. Perennial grasses included several native species with *Poa secunda* being the most abundant. It also included the *Agropyron cristatum* complex, which is not native; however, this plant only occurred in trace amounts at two plots.

We scored grazing levels in each plot using three categories modified from Root and McCune (2012): Low grazing intensity plots had no fresh dung or heavily grazed plants. Medium intensity plots had only one or two fresh dung piles in the plot or some plants that had been partially eaten by livestock. High grazing intensity plots contained at least three fresh dung piles and abundant evidence of grazing on shrubs, forbs or grasses. In assessing evidence of grazing on vegetation, we evaluated whether there was evidence that plants had been eaten (for example, grass bases with grazed tops), but we did not use plant community composition to evaluate grazing intensity. Our data set included nine plots with

---

[5] https://plants.usda.gov

low, eight with medium, and nine with high intensity grazing.

Analysis

We used an analysis of variance (ANOVA) in the software R (v. 3.5.2; R Development Core Team 2018) to determine whether biocrust cover or richness was related to livestock grazing intensity. We performed pairwise comparisons using a Tukey correction for multiple tests. We used the same approach to determine whether exotic annual grasses or perennial grasses were related to livestock grazing intensity. Prior to analysis, we log-transformed exotic annual grass cover to better meet model assumptions.

To explore these direct and indirect relationships among grazing intensity, biocrust cover, and exotic annual grass cover, we used structural equation modeling (SEM). SEM is an analytic framework that models hypothesized networks of causation, making it ideal for analyzing the relative strength of direct and indirect relationships (Grace 2006, Miller et al. 2015). Multicollinearity among predictors can cause challenges in SEM because it can be difficult to isolate the effects of strongly correlated variables and their inclusion can inflate variance estimates (Grace 2006). To evaluate whether this was likely to be a problem in our data sets, we examined the correlation matrix among all variables (Appendix S1: Tables S1, S2). We then created a priori SEM meta-models with hypothesized pathways of causation (Appendix S1: Fig. S1, Table S3), including both direct effects of grazing on exotic annual grass cover, as well as indirect effects mediated by biocrust variables. After modeling all hypothesized paths, we reran the model excluding paths that were nonsignificant, following Grace's (2006) recommended process for refining SEMs. We evaluated model fit with the χ^2 statistic, for which high P values indicate adequate fit and low P values suggest lack of fit. We further evaluated fit using the directed separation (d-sep) statistic for each model, which is more conservative with smaller sample sizes, and is interpreted similarly to the χ^2 statistic (Shipley 2009). Prior to modeling, we examined histograms and scatterplots to visualize variable distributions, then log-transformed exotic annual grass and perennial grass cover to better meet model assumptions. Although grazing intensity was ordinal, we treated it as continuous following Grace's (2006) recommendation, and this choice seems to be supported by the approximately linear increase of biocrust richness with decreasing grazing intensity (see *Results*). All variables were *z*-scaled prior to analysis (Grace 2006), and SEMs were analyzed using the software R (v. 3.5.2 R Development Core Team 2018) in the package *piecewiseSEM* (v. 2.0.2; Lefcheck 2016). A potential path that was not in our a priori model could suggest that exotic annual grasses affect biocrust cover (marked by # in Fig. 2A and Appendix S1: Fig. S1). Such recursive paths cannot be specified in *piecewiseSEM*, so we evaluated the final model (Fig. 2A) in the package *lavaan* (v. 0.6-3; Rosseel 2012) with this recursive path. This allowed a post hoc test of whether the relationship between exotic annual grasses and biocrust cover was indeed better supported in the opposite direction than we had conceived it.

We used a second SEM to explore the effects of particular biocrust functional groups on total biocrust cover and exotic annual grass cover. We represented biocrust functional group abundance using relativized cover to minimize multicollinearity issues. This was calculated by summing abundance across all taxa in each functional group in each plot and dividing by total biocrust cover. Though there were nine functional groups represented in our data set (Rosentreter and Root 2019), we focused on the four most abundant groups: crustose lichens, gelatinous lichens, squamulose lichens (scale lichens), and short mosses (Fig. 3, components of each functional group described in detail in Rosentreter and Root [2019]). To better meet model assumptions, particularly linearity, we log-transformed squamulose and crustose lichen abundances. We modeled all hypothesized paths (Appendix S1: Fig. S1), including all covariances among functional groups, then reran the model without nonsignificant paths and covariances to assess fit (Grace 2006, Fig. 2B).

To explore how biocrust lichen and bryophyte communities varied among grazing intensities (objective 2), we used two species-level community analyses. We tested the multivariate differences in community composition among grazing intensities using multi-response permutation procedures with Sorensen distance (MRPP; Mielke and Berry 2007). The effect size for MRPP is expressed as *A*, the chance-corrected within-group agreement, which describes the within-group homogeneity and ranges from 0 to 1 (McCune et al. 2002). Indicator species analysis (Dufrêne and Legendre 1997) allowed us to test which species were most associated with low, medium, and high grazing intensity. Indicator values (IV) range from 0 to 100 with 100 being the strongest and indicating that a species is always found only in a particular grazing intensity.

RESULTS

Biocrust cover was negatively related to grazing intensity ($F_{2,23} = 17.77$, $P < 0.0001$, Fig. 4A). Plots experiencing the lowest grazing intensity supported 46% biocrust cover on average in comparison with only 7% soil crust in the high grazing intensity plots ($P < 0.001$). Medium intensity grazing plots were intermediate, supporting 25% cover ($P = 0.01$ for the comparison with low intensity and $P = 0.025$ for the comparison with high intensity).

Similarly, biocrust species richness was negatively related to grazing intensity ($F_{2,23} = 10.80$, $P = 0.0005$, Fig. 4B). Plots with the lowest grazing intensity had the highest biocrust diversity, supporting 30 species on

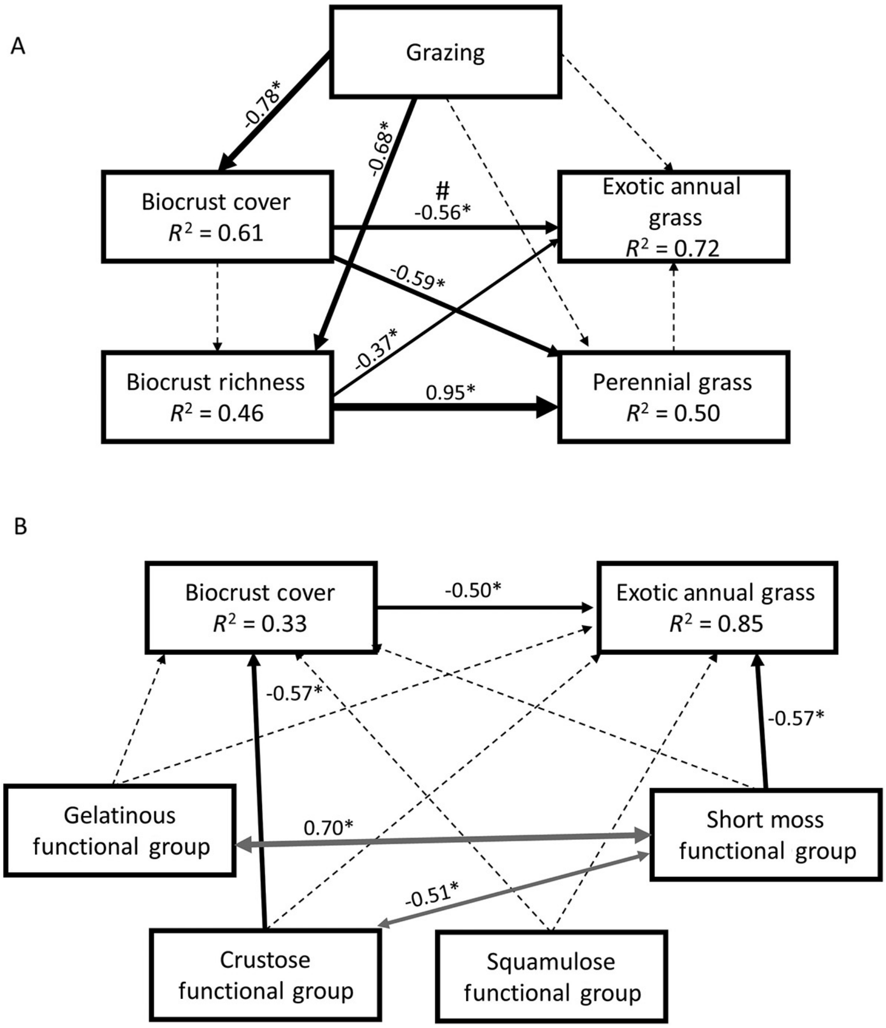


FIG. 2. Structural equation models (SEMs) testing the effects of grazing intensity on soil biocrust and vascular plant communities. These models are refined from a priori hypothesized models (Appendix S1: Fig. S1). Numbers indicate standardized path coefficients and arrow thickness is weighted by the strength of the path with their associated sign. Paths with $P < 0.05$ are labeled (*) and hypothesized paths that were not significant ($P > 0.1$) are shown as dashed black lines. (A) The first SEM examines the direct and indirect effects of grazing on exotic annual grass cover. A # marks a potential recursive path in which exotic annual grasses affect biocrust cover. (B) The second SEM examines the relative influence of individual biocrust functional groups and total soil crust cover on exotic annual grass cover. Gray double-headed arrows represent covariances.

average as compared with only 10 species on average in the high intensity grazing plots ($P = 0.0004$). Medium grazing intensity supported intermediate diversity with (on average) 24 biocrust species ($P = 0.29$ for the comparison with low intensity, $P = 0.014$ for the comparison with high intensity).

Exotic annual grasses were substantially more abundant in plots with higher grazing intensity ($F_{2,23} = 12.14$, $P = 0.0003$, Fig. 4C). Low grazing intensity plots had 1% cover of exotic annual grass compared with 58% in high intensity grazed plots ($P = 0.0002$). Medium intensity grazing did not significantly differ from low intensity (11% exotic annual grass cover, $P = 0.37$), but was significantly lower than the high intensity plots ($P = 0.005$). Perennial grasses did not significantly differ among grazing intensities ($F_{2,23} = 1.33$, $P = 0.28$, Fig. 4D). This may be due to removal of tall perennial grasses by historic grazing in winterfat and salt desert sites that are currently low or moderate grazing intensity as well as the shorter perennial grass, *Poa secunda,* not favoring sites with calcareous soils (Rosentreter and Root 2019).

SEMs indicated that grazing did not directly promote exotic annual grasses, but rather reduced biocrust cover and richness, which favored exotic annual grasses and disfavored perennial grasses (Fig. 2A). Biocrust cover negatively affected exotic annual grasses (with a path coefficient = −0.56, $P = 0.001$). This model exhibited good fit overall (P for χ^2 test = 0.76) and for

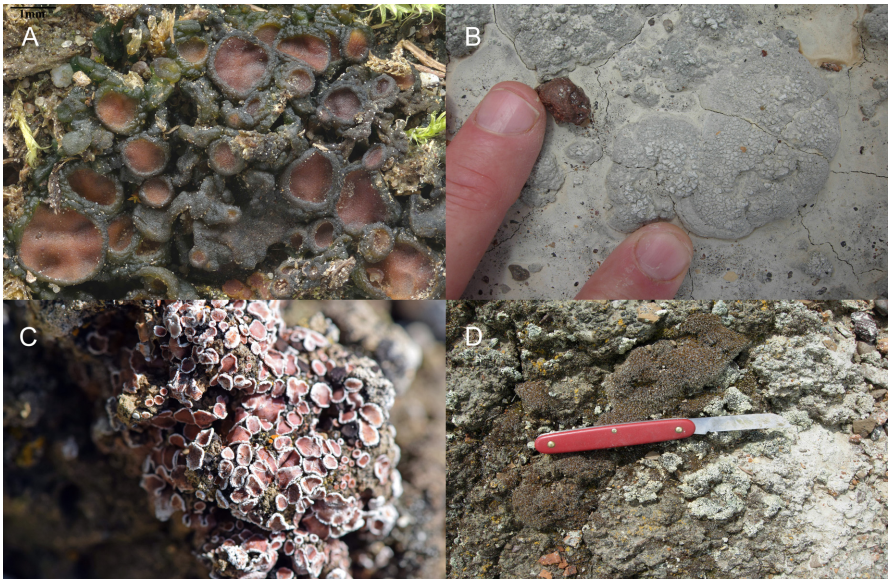


FIG. 3. Four functional groups of soil biocrusts investigated: (A) gelatinous lichen *Enchylium tenax* (A. DeBolt), (B) crustose lichen *Aspicilia* (R. Rosentreter), (C) squamulose lichen *Psora decipiens* (sometimes called scale lichens, E. K. Dodson), and (D) short moss *Syntrichia caninervis* (R. Rosentreter).

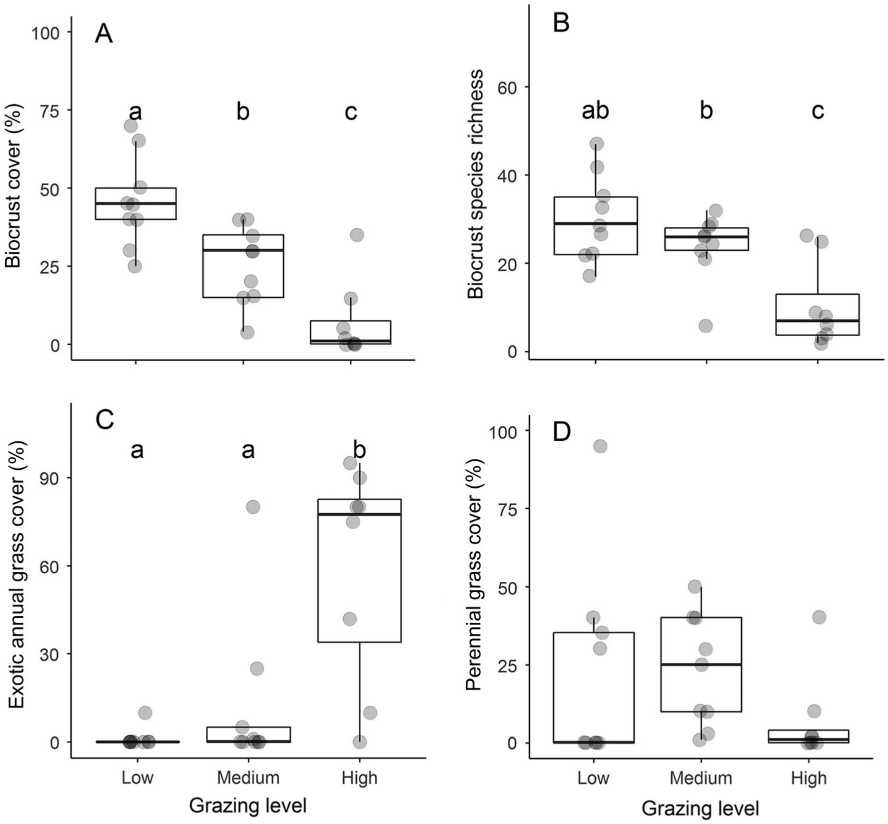


FIG. 4. Soil biocrust and vascular plants related to three levels of grazing intensity at 27 sites in Idaho, USA. Different lowercase letters indicate significantly different groups ($P < 0.05$). Box plot components are midline, median; box edges, 25th and 75th percentiles; and whiskers, 1.5 times the inter-quartile range.

each component (d-sep P all > 0.13). Covariances suggested that predictors were not so collinear as to preclude modeling (Appendix S1: Table S1). The correlation between grazing and biocrust cover (0.78) was borderline (Grace 2006) but was not of major concern because we expected this relationship and the two predictors did not co-occur in any of the final models. The post-hoc test for a reciprocal relationship between total biocrust cover and exotic annual grass cover (shown by the # in Fig. 2A and Appendix S1: Fig. S1) was not supported (path coefficient = 0.013, $P = 0.968$), supporting our hypothesis of biocrust cover conferring resistance to exotic annual grass invasion.

Short mosses had the strongest negative relationships with exotic annual grasses ($P < 0.0001$, Fig. 2B), suggesting that the loss of this functional group may precede exotic annual grass invasion. Total biocrust cover also had a negative relationship with exotic annual grasses ($P < 0.0001$). Crustose lichen abundance was negatively related to total biocrust cover, suggesting that this functional group is dominant when biocrust cover is poorly developed. There was no evidence that gelatinous, squamulose, or crustose lichens, as individual functional groups, were strongly related to total biocrust cover or affected exotic annual grasses directly. Crustose lichens negatively covaried with short mosses ($P = 0.008$) and gelatinous lichens positively covaried with short mosses ($P = 0.001$). As with the first SEM, model fit was good overall (P for χ^2 test = 0.15) and for each component (d-sep P all > 0.17); none of the correlations among variables was unacceptably high (Appendix S1: Table S2). This model explained 33% of the variance in biocrust cover and 85% of the variance in exotic annual grass cover.

Biocrust community composition differed among grazing intensities (MRPP $A = 0.085$, $P = 0.001$). Low and high intensity had the most different biocrust communities ($P = 0.0009$); low and medium intensity were not significantly different ($P = 0.16$), whereas medium and high intensity grazing also differed ($P = 0.018$). Indicator species of biocrust lichen and bryophytes were only found for the lowest grazing intensity. These included *Acarospora schleicheri* (IV = 45, $P = 0.033$), *Arthonia glebosa* (IV = 65, $P = 0.002$), *Aspicilia filiformis* (IV = 51, $P = 0.013$), *Aspicilia mansourii* (IV = 50, $P = 0.002$), *Enchylium tenax* (IV = 49, $P = 0.0002$), *Endocarpon loscosii* (IV = 53, $P = 0.006$), *Myriolecis flowersiana* (IV = 56, $P = 0.004$), *Placidium squamulosum* (IV = 46, $P = 0.031$), *Syntrichia ruralis* (IV = 48, $P = 0.004$), and *Chromatochlamys muscorum* (IV = 55, $P = 0.003$). No biocrust lichen or bryophyte species were associated most strongly with medium or high intensity grazing, suggesting that there are not species of lichens or bryophytes in the local species pool that are favored by livestock grazing.

Discussion

Our study highlights the importance of biocrust cover in maintaining site resistance to invasion by exotic annual grasses. Importantly, we show some of the first evidence that effects of biocrusts on plant germination and establishment documented by smaller-scale experimental studies (Serpe et al. 2006, 2008, Deines et al. 2007, Peterson 2013, Slate et al. 2018) appear to scale up to determine landscape-scale plant community dynamics. Specifically, since many invaders are successful because of their abundant, fast-establishing seeds (Williamson 1999), restricting their success at the seedling life stage is likely to be critical in maintaining native-dominated ecosystems. We also present some of the first quantitative evidence that different biocrust functional groups may have unique ecological roles in maintaining native plant communities. These findings are particularly important because biocrust communities, which are small in stature and difficult to identify, are rarely explicitly examined in studies of invasion ecology (Chambers et al. 2014, Bradley et al. 2018, Seipel et al. 2018, St Clair and Bishop 2019), despite previous evidence for a negative relationship between exotic annual grasses and biocrusts (Peterson 2013, Reisner et al. 2013). Since biocrusts are ubiquitous in arid and semiarid habitats (Belnap et al. 2016) that are at high risk of invasion by exotic annual grasses (Suring et al. 2005), these findings are potentially consequential for dry grassland ecosystems around the world.

The finding that biocrusts inhibit exotic plant invasion initially seems to contrast with evidence that exotic annual grasses suppress biocrusts with their litter (Hilty et al. 2004, Dettweiler-Robinson et al. 2013). Though we did not measure litter, the reciprocal pathway from exotic annual grasses to biocrust cover was not supported in our analyses. This apparent paradox may be due to different processes governing resistance to invasion as compared with resilience as sites recover from invasion (Chambers et al. 2014). Disturbances at uninvaded sites may reduce resistance by decreasing biocrust cover and facilitating annual grass invasion. After the initial invasion, annual grasses may be able to suppress remnant biocrusts, limiting resilience of the ecosystem to recover to a native-dominated community (Dettweiler-Robinson et al. 2013, Peterson 2013). Comparing these processes requires access to both relatively intact and degraded habitats; we were able to take advantage of areas that limit livestock grazing and contain well-developed biocrust communities. It is also possible that different types of disturbance such as wildfire or differing propagule pressure change the dynamic between exotic annual grasses and biocrusts. Because livestock grazing, wildfire, and exotic annual grasses co-occur throughout our study region, the effects of these ecosystem pressures can be difficult to untangle.

Our study is unique in evaluating the full diversity and community composition of biocrusts in the context of invasion at a landscape scale, and this allowed us to observe specific effects of short mosses on resistance to invasion and that particular biocrust species can be impacted by disturbance differently from others within the same functional group. Biocrusts form diverse and functionally complex communities and reducing this complexity to measures of total percent cover, as much previous research has, may obscure the varied roles biocrusts play in ecosystems (Read et al. 2008, Miller and Damschen 2017). For example, biocrust functional guilds may have unique effects on vascular plant seed germination and establishment. The thick crustose lichen *Diploschistes muscorum* can have a stronger negative effect on germination than a mixed-species biocrust (Deines et al. 2007) and short mosses can have more of an effect than tall mosses (Serpe et al. 2006). Short mosses were particularly important in preventing exotic annual grass invasion in our study; they may be valuable in providing a fairly thick continuous layer over the soil that prevents establishment (Condon and Pyke 2018). Other studies examining biocrust communities at landscape scales have found that their diversity and composition varies greatly (Root and McCune 2012, Rosentreter et al. 2016, Root et al. 2017), which is likely to create a patchwork of varying site resistance to invasion. Since biocrust diversity and the abundance of particular species were negatively affected by grazing intensity here, maintaining taxonomically and functionally diverse biocrust communities will likely require limiting disturbance (Ponzetti et al. 2007, Root et al. 2017).

Restoring a high overall cover and diversity of biocrust species, as well as the short moss functional group in particular, may enhance ecosystem resistance to invasion. Biocrust restoration is now viewed as a critical management practice in some arid and semiarid regions (Bowker 2007), and although there has been substantial progress in developing biocrust restoration practices, significant challenges remain (Doherty et al. 2015, Condon and Pyke 2016, Bowker et al. 2017). Recent developments in growing short mosses for restoration purposes (Bowker et al. 2017) seem especially promising in light of our study, because short mosses were particularly valuable in preventing cheatgrass invasion and can be among the first to colonized disturbed soils (Read et al. 2011). However, the limited ability to grow a diversity of lichens in bulk (Bowker et al. 2017) restricts active restoration of a full biocrust community. Our results highlight the value of developing cultivation methods for short mosses, and suggest that future restoration work will benefit by developing methods to cultivate more diverse biocrust communities and improve their establishment following applications in the field.

CONCLUSIONS

The role biocrusts play in invasion dynamics has been largely overlooked but may be a critical component of site resistance (Slate et al. 2018). While the cover of biocrusts as a whole is sometimes considered in invasion studies (Reisner et al. 2013), community composition and diversity of biocrusts is rarely considered, despite their role in providing resistance to invasion. In one of the first landscape-scale studies of the interplay between biocrusts and exotic annual grasses, we highlight the importance of biocrust diversity and the abundance short mosses in determining plant communities. These findings help prioritize management in places where site resistance can be maintained, and direct biocrust restoration efforts particularly with a focus on the functional groups that are most effective at promoting site resistance. Arid ecosystems face many pressures from invasive plants, development, disturbance, and changing precipitation regimes. As climate change has been shown to impact biocrust communities in ways similar to disturbance (Ferrenberg et al. 2015), determining how stressors on biocrusts will affect plant communities remains a question of critical importance.

ACKNOWLEDGMENTS

We would like to thank Bruce McCune, Othmar Bruess, and Rob Smith who graciously identified and verified several biocrust specimens. Ann DeBolt provided invaluable assistance and recommendations on the processing of the many plant specimens. We would also like to thank James Smith and the Snake River Plain Herbarium at Boise State University for storing most of the voucher collections associated with this project. We thank Matthew Bowker and one anonymous reviewer for constructive comments that substantially improved the manuscript.

LITERATURE CITED

Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. Ecological Monographs 71:531–556.

Balch, J. K., B. A. Bradley, C. M. D’Antonio, and J. Gómez-Dans. 2013. Introduced annual grass increases regional fire activity across the arid western USA (1980–2009). Global Change Biology 19:173–183.

Belnap, J., and B. Büdel. 2016. Biological soil crusts as soil stabilizers. Pages 305–320 *in* B. Weber, B. Büdel, and J. Belnap, editors. Biological soil crusts: An organizing principle in drylands. Springer, Cambridge, UK.

Belnap, J., B. Weber, and B. Büdel. 2016. Biological soil crusts as an organizing principle in drylands. Pages 3–13 *in* B. Weber, B. Büdel, and J. Belnap, editors. Biological soil crusts: An organizing principle in drylands. Springer, Cambridge, UK.

Boeken, B. R. 2018. Competition for microsites during recruitment in semiarid annual plant communities. Ecology 99:2801–2814.

Bowker, M. A. 2007. Biological soil crust rehabilitation in theory and practice: an underexploited opportunity. Restoration Ecology 15:13–23.

Bowker, M. A., F. T. Maestre, and C. Escolar. 2010. Biological crusts as a model system for examining the biodiversity–ecosystem function relationship in soils. Soil Biology and Biochemistry 42:405–417.

Bowker, M. A., A. J. Antoninka, and R. A. Durham. 2017. Applying community ecological theory to maximize productivity of cultivated biocrusts. Ecological Applications 27:1958–1969.

Bradley, B. A., C. A. Curtis, E. J. Fusco, J. T. Abatzoglou, J. K. Balch, S. Dadashi, and M. N. Tuanmu. 2018. Cheatgrass (*Bromus tectorum*) distribution in the intermountain Western

United States and its relationship to fire frequency, seasonality, and ignitions. Biological Invasions 20:1493–1506.

Brodo, I. M., S. D. Sharnoff, and S. Sharnoff. 2001. Lichens of North America. Yale University Press, New Haven, Connecticut.

Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invasible by *Bromus tectorum*? Ecological Monographs 77:117–145.

Chambers, J. C., B. A. Bradley, C. S. Brown, C. D'Antonio, M. J. Germino, J. B. Grace, J. B. Grace, S. P. Hardegree, R. F. Miller, and D. A. Pyke. 2014. Resilience to stress and disturbance, and resistance to *Bromus tectorum* L. invasion in cold desert shrublands of western North America. Ecosystems 17:360–375.

Condon, L. A., and D. A. Pyke. 2016. Filling the interspace—restoring arid land mosses: source populations, organic matter, and overwintering govern success. Ecology and Evolution 6:7623–7632.

Condon, L. A., and D. A. Pyke. 2018. Fire and grazing influence site resistance to Bromus tectorum through their effects on shrub, bunchgrass and biocrust communities in the Great Basin (USA). Ecosystems 21:1416–1431.

Connelly, J. W., M. A. Schroeder, A. R. Sands, and C. E. Braun. 2000. Guidelines to manage sage grouse populations and their habitats. Wildlife Society Bulletin 967–985.

D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annual Review of Ecology and Systematics 23:63–87.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology 88:528–534.

Deines, L., R. Rosentreter, D. J. Eldridge, and M. D. Serpe. 2007. Germination and seedling establishment of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 295:23–35.

Dettweiler-Robinson, E., J. D. Bakker, and J. B. Grace. 2013. Controls of biological soil crust cover and composition shift with succession in sagebrush shrub-steppe. Journal of Arid Environments 94:96–104.

Doherty, K. D., A. J. Antoninka, M. A. Bowker, S. V. Ayuso, and N. C. Johnson. 2015. A novel approach to cultivate biocrusts for restoration and experimentation. Ecological Restoration 33:13–16.

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

Ferrenberg, S., S. C. Reed, and J. Belnap. 2015. Climate change and physical disturbance cause similar community shifts in biological soil crusts. Proceedings of the National Academy of Sciences USA 112:12116–12121.

Grace, J. B. 2006. Structural equation modeling and natural systems. University Press, Cambridge, UK.

Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31–60 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley, Chichester, UK.

Hilty, J. H., D. J. Eldridge, R. Rosentreter, M. C. Wicklow-Howard, and M. Pellant. 2004. Recovery of biological soil crusts following wildfire in Idaho. Journal of Range Management 89–96.

Housman, D. C., H. H. Powers, A. D. Collins, and J. Belnap. 2006. Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. Journal of Arid Environments 66:620–634.

Lefcheck, J. S. 2016. piecewiseSEM: Piecewise structural equation modeling in R for ecology, evolution, and systematics. Methods in Ecology and Evolution 7:573–579.

Levine, J. M., E. Pachepsky, B. E. Kendall, S. G. Yelenik, and J. H. R. Lambers. 2006. Plant–soil feedbacks and invasive spread. Ecology Letters 9:1005–1014.

Liu, H., X. Han, L. Li, J. Huang, H. Liu, and X. Li. 2009. Grazing density effects on cover, species composition, and nitrogen fixation of biological soil crust in an inner Mongolia steppe. Rangeland Ecology and Management 62:321–327.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology 80:1522–1536.

McCune, B., and R. Rosentreter. 2007. Pages 1–105 *in* Biotic Soil Crust Lichens of the Columbia Basin. Monographs in North American Lichenology. Volume 1. Northwest Lichenologists, Corvallis, Oregon, USA.

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

McCune, B., J. B. Grace, and D. L. Urban. 2002. Analysis of ecological communities. MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B., E. A. Holt, P. N. Neitlich, T. Ahti, and R. Rosentreter. 2009. Macrolichen diversity in Noatak National Preserve, Alaska. North American Fungi 4:1–22.

Mielke, P. W., and K. J. Berry. 2007. Permutation methods: a distance function approach. Springer Science & Business Media, New York, NY.

Miller, J. E. D., and E. I. Damschen. 2017. Biological soil crust cover is negatively related to vascular plant richness in Ozark sandstone glades. Journal of the Torrey Botanical Society 144:170–178.

Miller, J. E., E. I. Damschen, S. P. Harrison, and J. B. Grace. 2015. Landscape structure affects specialists but not generalists in naturally fragmented grasslands. Ecology 96:3323–3331.

Pando-Moreno, M., V. Molina, E. Jurado, and J. Flores. 2014. Effect of biological soil crusts on the germination of three plant species under laboratory conditions. Botanical Sciences 92:273–279.

Pechanec, J. F., G. D. Pickford, and G. Stewart. 1937. Effects of the 1934 drought on native vegetation of the Upper Snake River Plans, Idaho. Ecology 18:490–505.

Peterson, E. B. 2013. Regional-scale relationship among biological soil crusts, invasive annual grasses, and disturbance. Ecological Processes 2:2.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–66.

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

Ponzetti, J. M., B. McCune, and D. A. Pyke. 2007. Biotic soil crusts in relation to topography, cheatgrass and fire in the Columbia Basin. Washington. Bryologist 110:706–722.

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Read, C. F., D. H. Duncan, P. A. Vesk, and J. Elith. 2008. Biological soil crust distribution is related to patterns of fragmentation and landuse in a dryland agricultural landscape of southern Australia. Landscape Ecology 23:1093–1105.

Read, C. F., D. H. Duncan, P. A. Vesk, and J. Elith. 2011. Surprisingly fast recovery of biological soil crusts following livestock removal in southern Australia. Journal of Vegetation Science 22:905–916.

Reisner, M. D., J. B. Grace, D. A. Pyke, and P. S. Doescher. 2013. Conditions favouring *Bromus tectorum* dominance of endangered sagebrush steppe ecosystems. Journal of Applied Ecology 50:1039–1049.

Root, H. T., and B. McCune. 2012. Regional patterns of biological soil crust lichen species composition related to vegetation, soils, and climate in Oregon, USA. Journal of Arid Environments 79:93–100.

Root, H. T., J. C. Brinda, and E. K. Dodson. 2017. Recovery of biological soil crust richness and cover 12–16 years after wildfires in Idaho, USA. Biogeosciences 14:3957–3969.

Rosentreter, R., and H. T. Root. 2019. Biological soil crust diversity and composition in southwest Idaho, USA. Bryologist 122:10–23.

Rosentreter, R., D. J. Eldridge, M. Westberg, L. Williams, and M. Grube. 2016. Structure, composition, and function of biocrust lichen communities. Pages 121–138 *in* B. Weber, B. Büdel, and J. Belnap, editors. Biological soil crusts: An organizing principle in drylands. Springer, Cambridge, UK.

Rosseel, Y. 2012. lavaan: an R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.

Seipel, T., L. J. Rew, K. T. Taylor, B. D. Maxwell, and E. A. Lehnhoff. 2018. Disturbance type influences plant community resilience and resistance to *Bromus tectorum* invasion in the sagebrush steppe. Applied Vegetation Science 21:385–394.

Serpe, M. D., J. M. Orm, T. Barkes, and R. Rosentreter. 2006. Germination and seed water status of four grasses on moss-dominated biological soil crusts from arid lands. Plant Ecology 185:163–178.

Serpe, M. D., S. J. Zimmerman, L. Deines, and R. Rosentreter. 2008. Seed water status and root tip characteristics of two annual grasses on lichen-dominated biological soil crusts. Plant and Soil 303:191–205.

Shipley, B. 2009. Confirmatory path analysis in a generalized multilevel context. Ecology 90:363–368.

Slate, M. L., R. M. Callaway, and D. E. Pearson. 2018. Life in interstitial space: Biocrusts inhibit exotic but not native plant establishment in semi-arid grasslands. Journal of Ecology 107:1317–1327.

St Clair, S. B., and T. B. Bishop. 2019. Loss of biotic resistance and high propagule pressure promote invasive grass-fire cycles. Journal of Ecology. https://doi.org/10.1111/1365-2745.13156

Stewart, G., and A. C. Hull. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. Ecology 30:58–74.

Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Pages 114–149 *in* M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. Habitat threats in the sagebrush ecosystems: methods of regional assessment and applications in the Great Basin. Alliance Communications Group, Lawrence, Kansas, USA.

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. American Scientist 84:468–478.

Williams, W. J., D. J. Eldridge, and B. M. Alchin. 2008. Grazing and drought reduce cyanobacterial soil crusts in an Australian Acacia woodland. Journal of Arid Environments 72:1064–1075.

Williamson, M. 1999. Invasions. Ecography 22:5–12.

Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2016/full

Data Availability

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.2s7g00v.