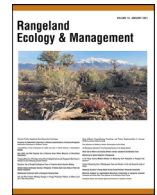




ELSEVIER

Contents lists available at ScienceDirect

Rangeland Ecology & Management

journal homepage: www.elsevier.com/locate/rama

Original Research

Biocrusts Indicators of Livestock Grazing Effects on Soil Stability in Sagebrush Steppe: A Case Study from a Long-Term Experiment in the Northern Great Basin ☆☆☆★

Stella M. Copeland^{1,*}, Lea A. Condon², Roger Rosentreter³, Jesse E.D. Miller⁴, Maya Kahn-Abrams¹¹ USDA-Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR, 97720, USA² Western Ecological Research Center, US Geological Survey, Reno, NV, 89512, USA³ Boise State University, Boise, ID, 83712, USA⁴ Stanford University, Stanford, CA, 94305, USA

ARTICLE INFO

Article history:

Received 1 December 2022

Revised 23 August 2023

Accepted 5 September 2023

Keywords:

lichen

morphogroup

moss

Tortula ruralis

ABSTRACT

Biocrusts are sensitive to changes in livestock grazing intensity in arid rangelands and may be useful indicators of ecosystem functions, particularly soil properties like soil stability, which may suggest the potential for soil erosion. We compared biocrust community composition and surface soil stability in a big sagebrush (*Artemisia tridentata*) steppe rangeland in the northwestern Great Basin in several paired sites, with or without long-term cattle grazing exclusion, and similar soils (mostly sandy loams), climate, and vegetation composition. We found that livestock grazing was associated with both lower surface soil stability and cover of several biocrust morphogroups, especially lichens, compared with sites with long-term livestock exclusion. Surface soil stability did not modify the effects of grazing on most biocrust components via interactive effects. Livestock grazing effects on total biocrust cover were partially mediated by changes in surface soil stability. Though lichens were more sensitive to grazing disturbance, our results suggest that moss (mostly *Tortula ruralis* in this site) might be a more readily observable indicator of grazing-related soil stability change in this area due to their relatively higher abundance compared with lichens (moss: mean, 8.5% cover, maximum, 96.1%, lichens: mean, 1.0% cover, maximum, 14.1%). These results highlight the potential for biocrust components as sensitive indicators of change in soil-related ecosystem functions in sagebrush steppe rangelands. However, further research is needed to identify relevant indicator groups across the wide range of biocrust community composition associated with site environmental characteristics, variable grazing systems, other rangeland health metrics, and other disturbance types such as wildfire.

Published by Elsevier Inc. on behalf of The Society for Range Management.

This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>)

* Current address: Maya Kahn-Abrams, University of Washington, Seattle, WA, 98195, USA.

☆☆ Stella M. Copeland and Maya Kahn-Abrams contributed equally.

* The EOARC is jointly funded by the USDA-ARS and Oregon State Agricultural Experiment Station, with additional support for this manuscript provided by the US Geological Survey Ecosystems Mission Area. USDA-ARS and Oregon State University are equal opportunity providers and employers. Mention of a proprietary product does not constitute a guarantee or warranty of the product by USDA-ARS, Oregon State University, or the authors and does not imply approval to the exclusion of other products. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US government.

* Correspondence: Stella M. Copeland, USDA–Agricultural Research Service, Eastern Oregon Agricultural Research Center, Burns, OR, 97720, USA.

<https://doi.org/10.1016/j.rama.2023.09.001>

1550-7424/Published by Elsevier Inc. on behalf of The Society for Range Management. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>)

Introduction

Biological soil crusts or “biocrusts,” communities of moss, lichens, and soil microorganisms on the soil surface, are prominent in dryland rangelands such as North American cold desert sagebrush steppe ecosystem (Condon and Pyke 2020). The sagebrush steppe ecosystem is currently under threat from invasive annual grasses and associated increases in fire frequency (Knick et al. 2003). Biocrust communities may be useful indicators for preventing rangeland degradation in this imperiled system due to their links to various ecosystem functions (Read et al. 2014; Mallen-Cooper et al. 2020), particularly soil stability and erosion control (Duniway et al. 2018; Fick et al. 2020).

Biocrusts are sensitive to physical disturbance, including livestock trampling (Belnap and Eldridge 2001), and responsive to

grazing intensity, even where differences in herbaceous plant communities are subtle or lacking (Ponzetti and McCune 2001; Root et al. 2020). Biocrust components, such as mosses versus lichens, and morphological and functional lichen groups vary widely in their responses to grazing disturbance (Condon and Pyke 2018; Root et al. 2020). This variation in disturbance response and/or ecosystem function within biocrust communities is associated with differences in colonization speed and sensitivity to altered soil properties (Eldridge and Rosentreter 1999; Read et al. 2014; Mallen-Cooper et al. 2020).

Change in biocrust communities may be a useful indicator of altered soil characteristics in rangelands due to their greater sensitivity to soil disturbance compared with vascular plants. However, useful biocrust indicators may also vary across sites because biocrust community structure varies with factors such as vascular plant community composition and soil properties (Root and McCune 2012; Condon and Pyke 2020). In particular, the long-term effects of livestock grazing on biocrust communities are poorly understood across the diversity and expanse of sagebrush steppe ecosystems (but see Condon et al. 2020), complicating efforts to understand how variables such as soil stability may mediate grazing effects.

In one site in the northern Great Basin, we examine the effects of moderate cattle grazing versus long-term (> 80 yr) grazing exclusion on biocrust communities in paired plots (pastures) in combination with soil stability, an indicator of rangeland health. We focus on differences in relatively easy-to-observe biocrust community components associated with disturbance response, such as mosses, lichens, and morphological and functional groups. Finally, we assess whether grazing indirectly affects biocrust communities via soil stability, suggesting biocrust changes could be a useful indicators of altered soil stability in this rangeland system.

Methods

Study site

This study was conducted in big sagebrush (*Artemisia tridentata* Nutt.) steppe at the 9 300-ha Northern Great Basin Experimental Range (NGBER) in eastern Oregon, United States (43°29'N, 119°43'W). Perennial native bunchgrasses that dominate herbaceous vegetation are primarily *Poa secunda* J. Presl, *Achnatherum thurberianum* (Piper) Barkworth, *Pseudoroegneria spicata* (Pursh) A. Löve, *Elymus elymoides* (Raf.) Swezey, and *Festuca idahoensis* Elmer. Western juniper (*Juniperus occidentalis* Hook.) trees are common at higher elevations.

NGBER is in a cold desert ecosystem (annual precipitation, 26.7 cm; monthly temperature, 7.6°C; range, -3.5 to 21.4°C) with most precipitation in the cool season (91% of total precipitation from September to May, September 2003 to August 2020, USCRN weather station at NGBER, Diamond et al. 2013). Study water year precipitation (September 2019–August 2020) was 82% of the long-term average. NGBER was heavily grazed by sheep for decades before 1936, when the research range was established along with 13 pairs of 2-ha livestock ungrazed (exclosure) and grazed areas, one per pasture, though pastures also varied in size (Appendix S1). Cattle replaced sheep in the late 1930s. Grazing intensity and timing varied throughout the 1950s. In recent decades, grazing intensity has been generally moderate and occurs from April to November with occasional rest years (Appendix S1). Recovery from a degraded state in the 1930s is suggested by increases in herbaceous vegetation in both the grazed and ungrazed areas over several decades (Copeland et al. 2021). This history mirrors broad management changes in the sagebrush steppe, with widespread overgrazing in the early 1900s replaced by moderate grazing (Holechek 1981). One pasture pair (#6) burned in 2014; there is no record of

other major disturbances (e.g., fire) affecting study areas since the experiment began.

Environmental characteristics are roughly similar between plot pairs but vary across pastures with an altitudinal range of 1 380–1 540 m, 0- to 15-degree slopes, and NNE-WNW aspects (Table S1, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)). Sandy loam is the predominant surface soil texture among plots (0–10 cm, Table S2, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)). Geological parent materials are Miocene age extrusive volcanics and derived from Quaternary alluvium and colluvium (Smith and Roe 2015).

Sampling

We estimated understory herbaceous (vascular) plant cover (nearest 1%, May–June) in 0.4 × 0.5 m frames 3 m apart along 7 parallel 30-m transects (15 m apart) in 12 of 13 pastures. In 1 pasture (#3), 5 transects (30 m) were sampled in each of 2 areas with different dominant big sagebrush subspecies (*wyomingensis* and *tridentata*), leading to 14 total pasture pair comparisons. We randomly selected 10 sampling frames across the 5–7 transects with 1–2 frames per transect for biocrust sampling (nearest 0.1%, August–September). Frame locations were replaced with the nearest location along the transect if they had > 25% cover of rocks, living sagebrush trunks, or bunchgrass bases, or contained ant hills, animal burrows or other soil disturbance, or fencing/debris (46/280 frames moved, mostly due to rocks [27] and sagebrush trunks [11]). These criteria likely led to slightly greater emphasis on soil ground cover and interspace areas in the dataset. Lack of suitable locations in two plots led < 10 total frames (pasture #1, ungrazed, N=8; #7, grazed, N=9).

We misted frames with a spray bottle to rehydrate biocrusts and improve visibility before sampling. We only recorded biocrusts growing on soil. We recorded moss cover by short (< 1 cm) or tall (≥ 1 cm) categories. All tall moss cover was *Tortula ruralis* (Hedw.) G. Gaertn., B. Mey. & Scherb. (synonym: *Syntrichia ruralis* [Hedw.] F. Weber & D. Mohr). We recorded lichen cover by morphogroup (crustose, fruticose, gelatinous, squamulose) and functional group (cyanolichen, chlorolichen, and nitrophile), a category assigned by dominant color, type of the photobiont, and high nitrogen tolerance (Appendix S2, Table S3, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)). We excluded foliose lichens due to their rarity (only two frames at one site). Gelatinous and cyanolichen groups completely overlapped in the final dataset.

Soil stability

We measured surface soil stability, a measure of erosion potential, with samples directly adjacent to each biocrust cover frame with a widely used protocol (adopted for rangeland health monitoring by federal land management across the western United States, Herrick et al. 2017). The method involves immersing soil fragments (2–3 mm thick, 6–8 mm diameter) in water and assigning a class from 1 to 6 (high stability values: 5–6) based on integrity with timed dipping tests.

Statistical analysis

We tested for relationships among grazing, soil stability, and biocrust with three complementary analyses in R version 4.2.1 (R Core Team 2022). First, we evaluated grazing effects on soil stability with paired *t*-tests (by pasture, *df* = 13). Second, we tested for the potential of soil stability (centered, for multicollinearity) to amplify or dampen grazing effects (via interactions) on total biocrust, biocrust component (moss, lichen, lichen functional groups, and biocrust morphogroups), and understory herbaceous plant cover using linear mixed models with a random effect for

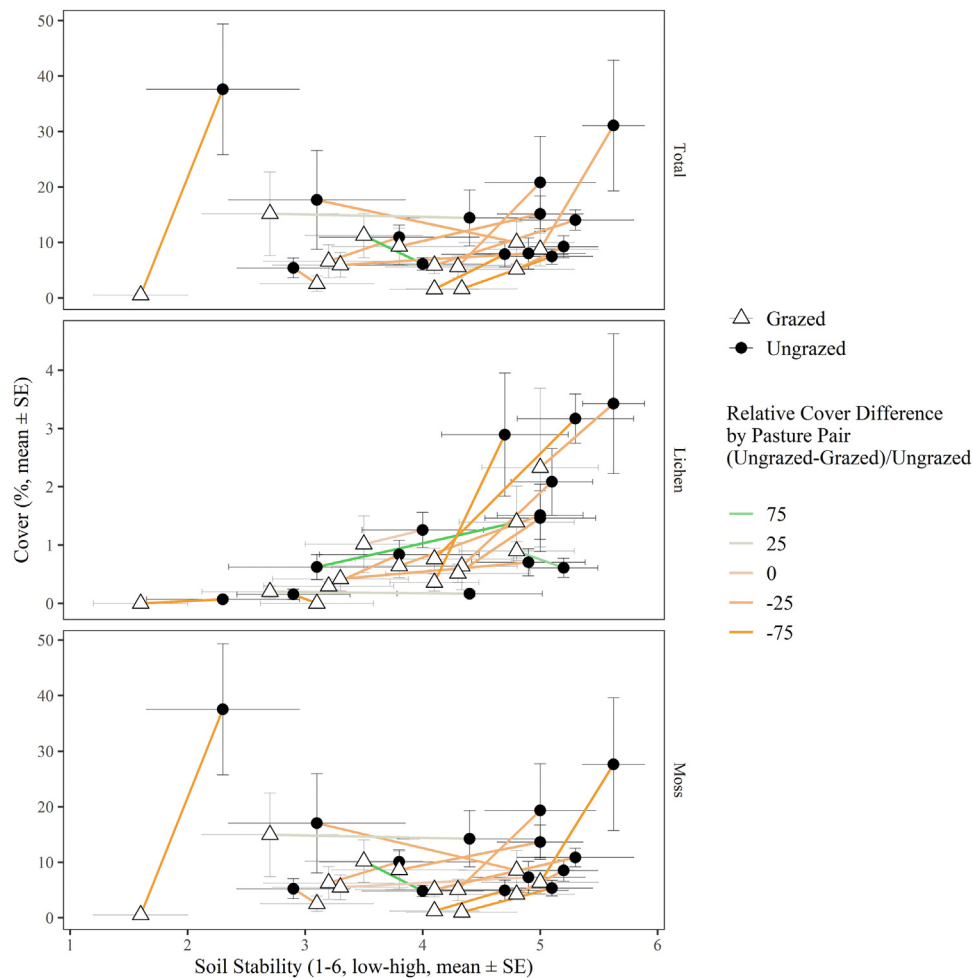


Figure 1. Lichen, moss, and total biocrust cover (% mean \pm SE) and soil stability (1–6, low to high, mean \pm standard of error) by livestock grazing treatment (open, grazed; closed, ungrazed). Pasture plot pairs are points connected by lines with color indicating the direction (negative, orange; positive, green) and magnitude (intensity) of the relative difference in cover.

Table 1

Statistics for final linear mixed models (random term for pasture pair) for livestock grazing versus exclusions, soil stability, and their interaction (R package lme4, Bates et al. 2015; R package car, type III Wald tests, Kenward-Roger degrees of freedom, Fox and Weisberg 2019). Cyanolichen and gelatinous groups are synonymous. Nonsignificant factors (n.s. in table, $P > 0.10$) were removed sequentially to arrive at final models (additional statistics in Table S4, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)).

Cover variable	Grazing		Soil stability		Interaction	
	F value	P value	F value	P value	F value	P value
Total biocrust	16.5	< 0.01	5.4	0.02	n.s.	n.s.
Lichen	9.0	< 0.01	11.1	< 0.01	n.s.	n.s.
Moss	14.2	< 0.01	3.9	0.05	n.s.	n.s.
Chlorolichen	4.4	0.04	7.7	0.01	n.s.	n.s.
Cyanolichen (gelatinous)	7.7	0.01	6.2	0.01	n.s.	n.s.
Nitrophile lichen	2.8	0.10	0.3	0.61	3.3	0.07
Crustose lichen	8.5	< 0.01	n.s.	n.s.	n.s.	n.s.
Fruticose lichen	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Squamulose lichen	8.3	< 0.01	7.1	0.01	n.s.	n.s.
Short moss	3.9	0.05	9.7	0.02	n.s.	n.s.
Tall moss	12.5	< 0.01	2.7	0.10	n.s.	n.s.
Herbaceous plant	7.8	0.01	7.1	0.01	4.5	0.03

pasture (intercept, lme4 package, Bates et al. 2015). Third, we quantified the degree to which grazing-induced differences in soil stability explain the effect of grazing on total biocrust cover with a mediation test (nonparametric bootstrap, $N=1000$, mediation package, Tingley et al. 2014). These latter two approaches are complementary because they evaluate the potential for soil stability to either alter grazing effects (via interactions) or mediate them (via an indirect effect).

Results

Livestock grazing was associated with lower soil stability ($t = -2.8$, $P = 0.02$, Fig. S1, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)). Grazing negatively affected total biocrust, lichen, moss, chlorolichen, and cyanolichen (gelatinous) functional group cover. Soil stability (centered, to avoid the effects of collinearity on the model outcomes) was positively associated with cover of these

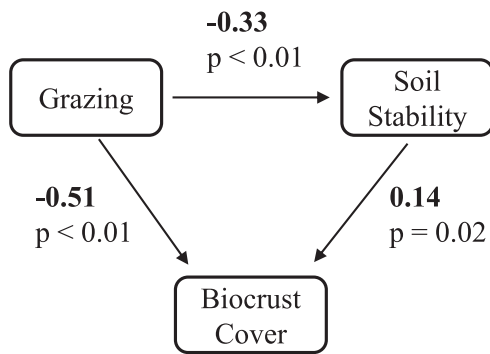


Figure 2. Diagram of mediation test relationships with *P* values and standardized coefficients (scaled and centered) from linear mixed models (Soil Stability ~ Grazing, Biocrust Cover ~ Soil Stability, and Biocrust Cover ~ Grazing + Soil Stability, *P* values based on type II tests). The average direct effect of grazing on biocrust cover was -7.4% (95% confidence interval [CI]: $-10.7, -4.1, P < 0.01$) while the average causal mediated effect was -0.8% (95% CI: -1.7 to -0.1).

same groups but did not modify the effects of grazing (no interaction, Figs. 1, S2–S6, Tables 1, S4, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)). Soil stability did alter the effects of grazing on nitrophile lichen cover (significant interaction), with lower cover in grazed areas with higher (but not lower) soil stability (interaction, see Tables 1, S4, Figs. S6). Among biocrust morphogroups, both grazing and lower soil stability were associated with lower squamulose lichen and short moss cover, grazing (but not soil stability) was associated with lower crustose lichen and tall moss (*T. ruralis*) cover, while neither predictor was associated with fruticose lichen cover (Tables 1, S4, Figs. S7–S8, available online at [10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001)). Soil stability modified the effect of grazing on herbaceous cover, with lower cover in areas with grazing and lower (but not higher) soil stability (interaction, Tables 1, S4, Fig. S9). Herbaceous cover was slightly positively associated with total biocrust cover (Pearson's product moment correlation = 0.1, $t = 1.8$, $df = 275$, $P = 0.08$). The effects of grazing on total biocrust cover were partially mediated by grazing-associated decreases in soil stability and explained 9% of the direct effect of grazing on biocrust cover (95% CI: 1–22%, $P = 0.02$, Fig. 2).

Discussion

Our results illustrate the magnitude and variation of differences in biocrust cover and surface soil stability associated with grazing versus long-term grazing exclusion in pastures with similar vegetation and soil characteristics. Soil stability was positively associated with biocrust cover but did not alter the negative effects of livestock grazing on most biocrust components (few interactive effects). However, grazing was also associated with lower soil stability, while soil stability partially mediated grazing effects on total biocrust cover. As a whole, these results suggest that some biocrust components may be useful indicators of grazing effects on soil stability. The observed differences in biocrust communities contrast with herbaceous plant recovery after historical overgrazing with both moderate grazing and removal in the same paired plots (Copeland et al. 2021). Similar patterns are observed in other western US rangelands, where herbaceous plant recovery after overgrazing and a shift to moderate grazing contrasts with persistently low soil stability and/or biocrust cover (multiple Nevada Great Basin sites, Condon et al. 2020; Colorado Plateau, salt desert site, Duniway et al. 2018).

We found that changes in some sensitive biocrust morphogroups are easier to observe than others in our study area, suggesting they may be useful for rangeland managers to identify changes in soil stability associated with grazing. While total lichen

and some lichen morphogroups were highly sensitive to both grazing and correlated with soil stability, shifts in lichen cover were difficult to detect due to their low abundance and associated magnitude of cover response ($< 1\%$ change with grazing, all groups). While less sensitive than lichens, tall moss (*Tortula ruralis*) cover may be a useful soil stability change indicator where it is common, as in this site, especially for rangeland managers unfamiliar with biocrusts, because it is relatively large and easy to observe even when dry and desiccated and cover changes were larger in magnitude than for lichen groups (with grazing, mean \pm SE: $-7.1\% \pm 2.9\%$). However, tall mosses are fire sensitive and therefore will not be useful soil stability indicators in recently burned areas (Condon and Gray 2020).

Our results are contingent upon our study site characteristics, such as moderate grazing intensity and primarily sandy loam soil texture. For example, nitrophilic lichens might increase with grazing (contrary to our results) if higher grazing intensity sufficiently increases nitrogen content. Our long-term grazing exclusion sites also had lower total biocrust, particularly lichen, cover compared with other Wyoming big sagebrush sites (1.3% mean cover in ungrazed sites vs. up to 50% in sites with similar vegetation elsewhere in the Great Basin, Condon and Pyke 2020). This relatively low abundance is likely due to specific combinations of soil chemistry and texture, climate, and vegetation type (Ponzetti and McCune 2001; Condon and Pyke 2020), though biocrust communities could also potentially still be recovering from historic overgrazing. Soil stability and biocrust cover were also highly variable across ungrazed plots in different pastures, as well as between grazed and ungrazed plot pairs (Figs. 1, S2), likely due to subtle differences in soil properties and vegetation, and grazing intensity associated with rockiness, slope, and/or water location. For instance, the large decreases in moss cover and soil stability with livestock grazing in Pasture 3 “Basin” illustrate the potential for soil texture and grazing practices to affect outcomes (Belnap and Eldridge 2001), as this plot pair had the highest sand content and higher grazing intensity, due to nearby water placement in recent years. Biocrust composition also varied across frames within plots, likely due to environmental variation at finer spatial scales, such as the presence of woody plant canopies, and might also vary over time in response to precipitation patterns (Belnap et al. 2006). While our results show that biocrust cover, soil stability, and livestock grazing are linked in this system, we did not manipulate biocrust or soil stability independently, meaning that we cannot absolutely separate grazing-related changes in soil stability from change in biocrusts.

Overall, our results suggest that changes in biocrust composition may be sensitive indicators of altered rangeland ecosystem functions, particularly soil properties like surface stability. Biocrust indicators could also highlight areas within rangeland landscapes where soil stability may be more or less resilient to livestock disturbance due to soil characteristics like texture. Alternatively, in areas where disturbance history is unclear, key biocrust components could suggest the degree and type of historic disturbance, such as intense grazing, fire, or their interaction (Condon and Pyke 2018; Duniway et al. 2018).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank Emma Campbell for collecting soil stability data; Jon Bates, Michelle Alden, Sam Wolfe, and Lily Strachan for assistance

collecting vascular plant data; and J. Bates for manuscript comments. We thank David Pyke for his mentorship and Peter Coates for his role in transitioning Lea Condon to the Western Ecological Research Center and for facilitating the publication of this manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:[10.1016/j.rama.2023.09.001](https://doi.org/10.1016/j.rama.2023.09.001).

References

- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67, 1–48.
- Belnap, J., Eldridge, D., 2001. Disturbance and recovery of biological soil crusts. In: Belnap, J., Lange, O.L. (Eds.), *Biological soil crusts: structure, function, and management*. Springer-Verlag Berlin Heidelberg, Berlin, Heidelberg, Germany, pp. 363–383.
- Belnap, J., Phillips, S.L., Troxler, T., 2006. Soil lichen and moss cover and species richness can be highly dynamic: the effects of invasion by the annual exotic grass *Bromus tectorum*, precipitation, and temperature on biological soil crusts in SE Utah. *Applied Soil Ecology* 32, 63–76.
- Condon, L.A., Gray, M.L., 2020. Not all fuel-reduction treatments degrade biocrusts: herbicides cause mostly neutral to positive effects on cover of biocrusts. *Land Degradation & Development* 31, 1727–1734.
- Condon, L.A., Pietrasiak, N., Rosentreter, R., Pyke, D.A., 2020. Passive restoration of vegetation and biological soil crusts following 80 years of exclusion from grazing across the Great Basin. *Restoration Ecology* 28, S75–S85.
- Condon, L.A., Pyke, D.A., 2018. Resiliency of biological soil crusts and vascular plants varies among morphogroups with disturbance intensity. *Plant and Soil* 433, 271–287.
- Condon, L.A., Pyke, D.A., 2020. Components and predictors of biological soil crusts vary at the regional vs. plant community scales. *Frontiers in Ecology and Evolution* 7, 1–10.
- Copeland, S.M., Davies, K.W., Boyd, C.S., Bates, J.D., 2021. Recovery of the herbaceous component of degraded sagebrush steppe is unimpeded by 75 years of moderate cattle grazing. *Ecosphere* 12, e03445.
- Diamond, H.J., Karl, T.R., Palecki, M.A., Baker, C.B., Bell, J.E., Leeper, R.D., Easterling, D.R., Lawrimore, J.H., Meyers, T.P., Helfert, M.R., Goodge, G., Thorne, P.W., 2013. U.S. Climate Reference Network after one decade of operations: status and assessment. *Bulletin of the American Meteorological Society* 94, 485–498.
- Duniway, M.C., Geiger, E.L., Minnick, T.J., Phillips, S.L., Belnap, J., 2018. Insights from long-term ungrazed and grazed watersheds in a salt desert Colorado Plateau ecosystem. *Rangeland Ecology & Management* 71, 492–505.
- Eldridge, D.J., Rosentreter, R., 1999. Morphological groups: a framework for monitoring microphytic crusts in arid landscapes. *Journal of Arid Environments* 41, 11–25.
- Fick, S.E., Belnap, J., Duniway, M.C., 2020. Grazing-induced changes to biological soil crust cover mediate hillslope erosion in long-term exclosure experiment. *Rangeland Ecology & Management* 73, 61–72.
- Fox, J., Weisberg, S., 2019. *An R companion to applied regression*, 3rd ed.. Sage Publications, Thousand Oaks, CA, USA, p. 608.
- Herrick, J.E., Van Zee, J.W., McCord, S.E., Courtright, E.M., Karl, J.W., Burkett, L.M., 2017. *Monitoring manual for grassland, shrubland, and savanna ecosystems. Volume 1: core methods*. USDA-ARS Jornada Experimental Range, Las Cruces, NM, USA, p. 76 p.
- Holechek, J.L., 1981. A brief history of range management in the United States. *Rangelands* 3, 16–18.
- Knick, S.T., Dobkin, D.S., Rotenberry, J.T., Schroeder, M.A., Vander Haegen, M.W., van Riper III, C., 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *The Condor* 105, 611–634.
- Mallen-Cooper, M., Bowker, M.A., Antoninka, A.J., Eldridge, D.J., 2020. A practical guide to measuring functional indicators and traits in biocrusts. *Restoration Ecology* 28, S56–S66.
- Ponzetti, J.M., McCune, B.P., 2001. Biotic soil crusts of Oregon's shrub steppe: community composition in relation to soil chemistry, climate, and livestock activity. *The Bryologist* 104, 212–225.
- R Core Team, 2022. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Read, C.F., Duncan, D.H., Vesk, P.A., Elith, J., Wan, S., 2014. Biocrust morphogroups provide an effective and rapid assessment tool for drylands. *The Journal of Applied Ecology* 51, 1740–1749.
- Root, H.T., McCune, B., 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., Miller, J.E.D., Rosentreter, R., 2020. Grazing disturbance promotes exotic annual grasses by degrading soil biocrust communities. *Ecological Applications* 30, e02016.
- Smith, R.L., Roe, W.P., 2015. *Oregon geologic data compilation (OGDC)—release 6*. Oregon Department of Geology and Mineral Industries, Newport, OR, USA.
- Tingley, D., Yamamoto, T., Hirose, K., Keele, L., Imai, K., 2014. mediation: R package for Causal Mediation Analysis. *Journal of Statistical Software* 59, 1–38.