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Lea A. Condon
*U.S. Geological Survey*

Douglas J. Shinneman
*U.S. Geological Survey*

Roger Rosentreter
*Boise State University*

Peter S. Coates
*U.S. Geological Survey*

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**Lea A. Condon**[1] | **Douglas J. Shinneman**[2] | **Roger Rosentreter**[3] | **Peter S. Coates**[4]

[1]U.S. Geological Survey, Western Ecological Research Center, Reno, Nevada, USA

[2]U.S. Geological Survey, Forest and Rangeland Ecosystem Science Center, Boise, Idaho, USA

[3]Department of Biology, Boise State University, Boise, Idaho, USA

[4]U.S. Geological Survey, Western Ecological Research Center, Dixon, California, USA

**Correspondence**
Lea A. Condon
Email: lcondon@usgs.gov

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For decades, large portions of the semi-arid sagebrush ecosystem have been experiencing increased frequency and extent of wildfire, even though small, infrequent fire is a natural disturbance in this ecosystem (Baker, 2006). Increased wildfire is threatening the existence of sagebrush ecosystems and the wildlife species that depend upon them (Baker, 2006; Coates et al., 2016). Increased wildfire in sagebrush ecosystems is often driven by invasive annual grasses, especially cheatgrass, *Bromus tectorum* (L.). Invasion can initiate a trajectory toward a "grass-fire cycle", in which cheatgrass increases fine fuel loadings that promote fire, and native plant species do not recover quickly after fire, leading frequently burned sites to transition to monocultures of cheatgrass (Brooks et al., 2004). Although cheatgrass has been extensively studied in the sagebrush steppe, less attention has been given to the organisms that would have filled the interspaces that cheatgrass replaces, namely, biological soil crusts ("biocrusts"). Semi-arid environments are characterized by sparse cover of vascular plants and substantial cover of biocrusts (Belnap & Lange, 2001). Biocrusts contain organisms that live on the soil surface and include lichens, mosses, and light algal crusts (including cyanobacteria). Although biocrusts were included in some of the first descriptions of the vegetation in the region (Flowers, 1934), biocrusts are rarely included in contemporary studies of sagebrush ecosystems. Comprehensive community studies have concluded consistent negative relationships between abundance of biocrusts and annual invasive grasses, specifically cheatgrass (Condon & Pyke, 2018a,b; Daubenmire, 1970). We postulate that biocrusts, and particularly lichens, facilitate a pattern of small, infrequent, low intensity fire given their association with reduced fine fuels (cheatgrass).

Observations of the response of biocrusts to fire as a sole disturbance are rare. For example, grazing by livestock is the primary land use in sagebrush ecosystems and biocrusts are lost to the compound disturbances of grazing and fire (Condon & Pyke, 2018a). Researchers face great challenges in identifying sites for study where fire is not coupled with grazing, perhaps because cattle preferentially use burned areas (Clark et al., 2014). Conversations in the literature speak to the difficulty in separating the effects of these disturbances on biocrusts (O'Connor & Germino, 2020; Root et al., 2020).

We surveyed a wildfire in October of 2021 outside of Boise, Idaho, that burned 15–20 acres of intact biocrusts the previous month (personal communications Rosentreter, October 20, 2021; Condon & Coates, 2022). This small fire occurred on private land and was not named. The area had not experienced grazing by livestock since 1984 and prior to the fire, it was free of other anthropogenic disturbances. Herbivores found onsite, which may cause ground disturbance, include Paiute ground squirrel (*Urocitellus mollis*), cottontail rabbit (*Sylvilagus leporid*), black-tailed jackrabbit (*Lepus californicus*), and American badger (*Taxidea taxus*) (personal communications Mason, October 20, 2021). The dominant shrub onsite is *Artemisia tridentata* ssp. *wyomingensis* Beetle and Young, and the occurrence of shrubs was patchy. We sampled 20, randomly placed, 0.25 $m^2$ quadrats within the burn perimeter to estimate the susceptibility of biocrusts by morphogroup to fire (sensu Eldridge & Rosentreter, 1999). Percent char (organic material visibly browned/blackened by fire) was estimated ocularly within each quadrat as a representation of fire intensity. Quadrats were physically tossed into the burned area but tossed again if they fell upon areas with vehicle tracks from fire-fighting efforts. We avoided areas where burning shrubs sterilized the soil, which was a rare condition. Biocrusts and vascular plants were surveyed via point-vertex intercept at 40 points per quadrat. Vascular plants were split into categories of annual forbs and

**FIGURE 1** Intact biocrusts within the burn perimeter. (a) Overview of the burned area. (b) Close-up of the soil surface with a glove for scale. (c) Close-up for the soil surface with a mallet for scale. White patches are crustose lichens. The green and reddish-brown patches are mosses. Patches with the most char are primarily the perennial grass, Sandberg's bluegrass (*Poa secunda* J. Presl.) and some of the mosses. Perennial grasses were already resprouting at the time of the photograph (October 20, 2021). All photographs by L.A. Condon.

perennial grasses. Other functional groups of vascular plants were not detected within the fire perimeter at the time of sampling, although cheatgrass occurs onsite. Pictures from the site show intact biocrusts and no evidence that the lichens had burned (Figure 1). Char was restricted to mosses and perennial grasses, primarily Sandberg's bluegrass (*Poa secunda* J. Presl.), a shallow-rooted native that is typically dormant by early summer. Sandberg's bluegrass was already showing evidence of resprouting at the time of our survey (Figure 1).

Surveyed quadrats were representative of the burned area and were divided into categories of fire intensity: low (5% percent char or less, 13 quadrats), moderate (12%–20% percent char, 4 quadrats), and high (95%–98% percent char, 3 quadrats). From our char estimates, we believe that most of the fire burned at low intensity. We did not have any quadrats with char values between 21% and 94%. Across the site, light algal crusts, vascular plants, lichens, and mosses were observed with increasing abundance (cover), in that order (Figure 2). Considering lichens specifically, crustose lichens were found in the greatest abundance followed by cup lichens (Figure 2). Crustose lichens are completely appressed to the soil surface and provide continuous cover. Cup lichens have thalli of scales (squamules) and are frequently found with mosses. Abundance of morphogroups was analyzed with non-metric multidimensional scaling ordination using a Sørenson distance measure. Final stress for the ordination was low, 7.06 for a three-dimensional solution (Figure 3). The ordination was rotated to align with our explanatory variable of interest, percent char, which was used to represent fire intensity. We do not interpret Axis 2 because it did not include any additional information that is not included in our discussion of Axis 1 or 3. Char was significantly correlated with Axis 1 ($r = 0.468$, $r^2 = 0.219$) and directly opposed cover of crustose lichens ($r = -0.832$, $r^2 = 0.692$). Axis 3 was significantly correlated with tall mosses ($r = 0.770$, $r^2 = 0.592$) and perennial grasses ($r = 0.513$, $r^2 = 0.263$). On this axis, cover of these groups directly opposed cover of more ruderal groups: short mosses ($r = -0.777$, $r^2 = 0.604$) and light algal crusts (LAC, $r = -0.636$, $r^2 = 0.404$). Cover of bare ground was also significantly negatively correlated with this axis (Bare ground, $r = -0.460$, $r^2 = 0.212$). While Axis 1 appeared to represent a gradient of fire intensity, Axis 3 represented a gradient of biocrust succession from more ruderal groups to later successional groups as one moves up the axis. These ruderal groups are described in greater detail in Rosentreter (2020) and may be the result of small-scale ground disturbances caused by squirrels or badgers.

We observed that the lichen components of biocrusts, particularly crustose lichens (at this site *Diplochistes muscorum* (Scop.) R. Sant), were largely unaffected by fire alone, corroborating other work in the region. Warren et al. (2015) found that the overall impact of fire on biocrusts in an early seral juniper woodland was minimal, even though trees were killed by fire and cover of mosses was reduced. Mosses, specifically tall mosses are often susceptible to fire in the sagebrush steppe (Condon & Gray, 2020; Condon & Pyke 2018a,b), and early successional, short mosses can be stimulated by fire and other disturbances (Condon & Pyke, 2018b). Although the cover of lichens appeared to be lower in the quadrats with the highest fire intensity (Figure 2c), this is likely due to quadrats with relatively high cover of lichens not having enough char to be classified as burning at high intensity (Figure 2a–c). This suggests there was little lichen cover in the high-intensity quadrats before fire, unlike the quadrats with high moss cover, which did show char on the mosses. This further suggests that where lichens are abundant, fire severity may be lower relative to sites with higher moss or grass cover, as fire intensity and residence time are reduced (sensu Brooks, 2008, Figure 3). These findings highlight the need to identify and conserve biocrusts where they are intact, especially where reducing the impacts of fire is of interest.

In the Great Basin, USA, understanding the responses of biocrusts to fire, especially by morphogroup, is timely. Increasing loss of sagebrush habitat from fire throughout the region has led to a plan by the Bureau of Land Management to construct an extensive network of fuel breaks, with over 17,000 km of linear fuel breaks planned for the Great Basin region (BLM, 2020). Suggestions for preserving intact sagebrush habitats and sagebrush obligate wildlife species include prioritizing fire suppression efforts (Baker, 2006). This highlights the question of how to best configure and implement fuel breaks in a way that minimizes negative impacts on habitat, including the potential to facilitate cheatgrass invasion, while maximizing their capacity to reduce fire spread (Shinneman et al., 2019). Some fuel reduction treatments have been shown to minimize damage to biocrusts, which is useful given known negative relationships between biocrusts and cheatgrass (Condon & Gray, 2020; Condon & Pyke, 2018a). The information presented here suggests that sites with higher lichen cover could help reduce fire intensity, making fuel breaks more effective under certain conditions. Moreover, other research has shown that similar environments with higher pre-fire cover of biocrusts were more likely to have lower post-fire cover of cheatgrass (Shinneman & Baker, 2009), another desirable attribute to enhance fuel break functionality.

We demonstrate that fire had differing effects on morphogroups of biocrusts, as crustose lichens were observed to be free of char. Mosses demonstrated char, suggesting that they may have experienced a reduction in

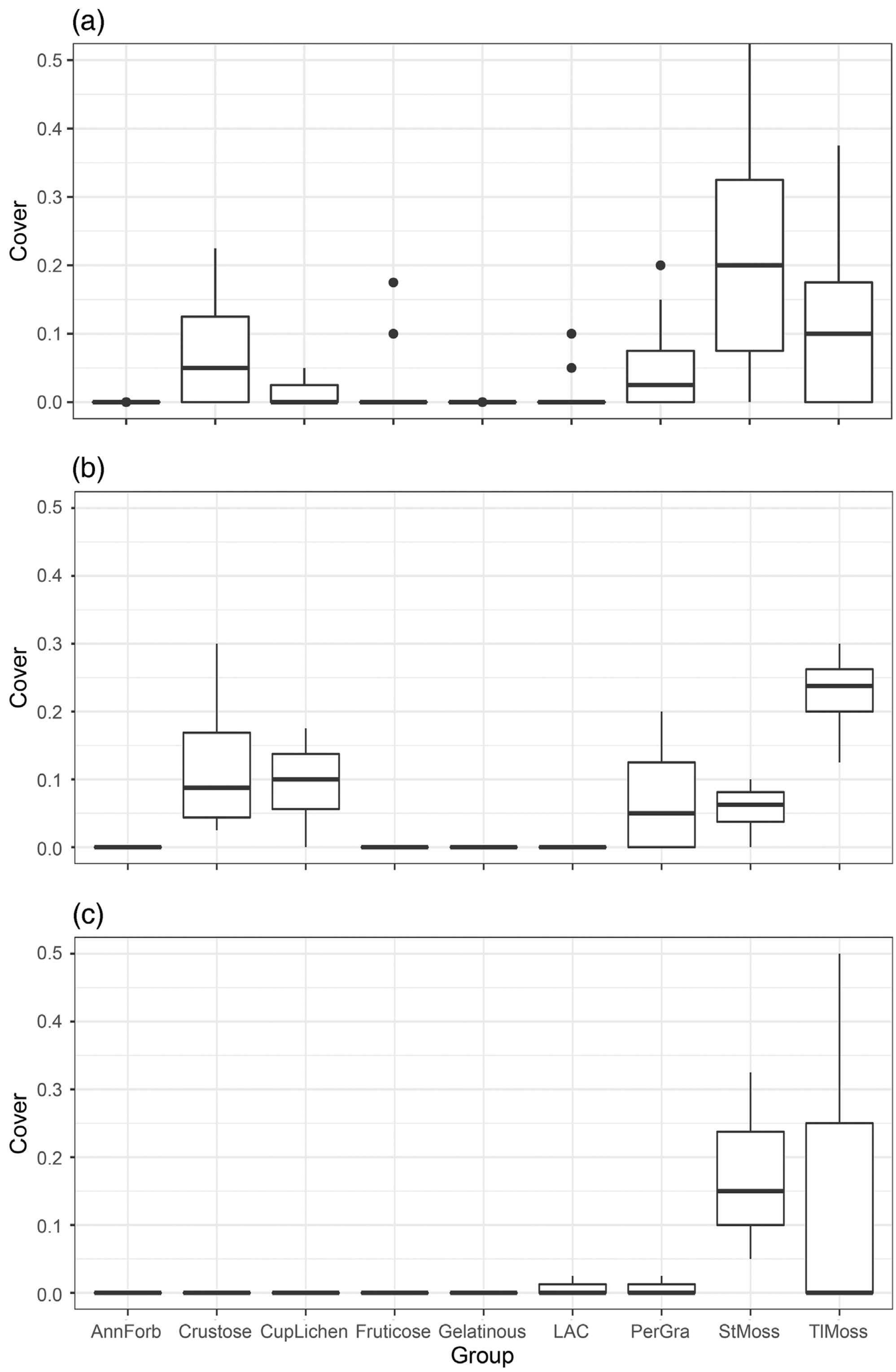


**FIGURE 2** Boxplots show median values, 1st and 3rd quartiles and whiskers extending out to the largest values within 1.5 times the distance between the 1st and 3rd quartiles. (a) low intensity fire (5% percent char or less, 13 quadrats) (b) moderate intensity fire (12%–20% percent char, 4 quadrats) (c) high intensity fire (95%–98% percent char, 3 quadrats). Lichens include the following groups: Crustose, Cup Lichen, Fruticose and Gelatinous. Mosses include StMoss (short moss) and TlMoss (tall moss). Other abbreviations are as follows: AnnForb (annual forb), LAC (light algal crust), and PerGra (perennial grass).

cover, but they were not lost from the site, following fire. This finding could benefit studies on the restoration of biocrusts, because biocrusts may not need to be reintroduced to a site following fire. Studies related to the physiology of morphogroups and their susceptibility to fire would add to our understanding of this phenomena.

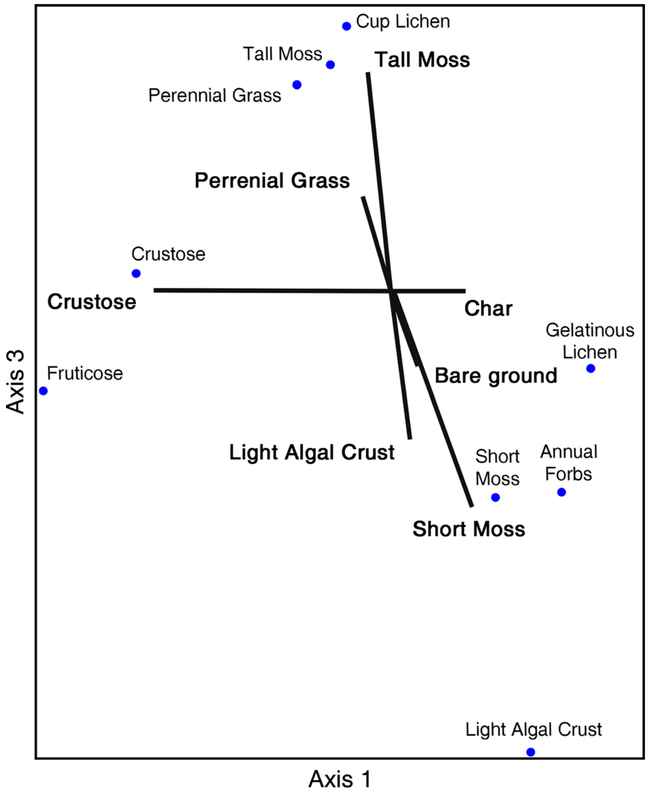


**FIGURE 3** Non-metric multidimensional scaling ordination of the abundance of biocrust morphogroups after fire. Increment $R^2$ for Axis 1 = 0.266, Axis 2 = 0.068, and Axis 3 = 0.601, for a cumulative $R^2$ of 0.935. Blue dots represent the centroids of biocrust morphogroups.

Studies on the effects of fire on biocrusts could benefit from the inclusion of disturbance history and plant community identity, as the composition of biocrusts differs amongst plant communities (Condon & Pyke, 2020c). Although it has been asserted that biocrusts are highly susceptible to wildfire in a recent meta-analysis (Palmer et al., 2020), the current study (where fire is the sole disturbance, albeit some inferred disturbance by small rodents) and those cited here examining compound disturbances with fire, suggest that disturbances that are compounding with fire have a greater effect on cover of morphogroups compared with fire alone. The study presented here demonstrates the complex nature of this topic, necessitating more research. Such research would be timely considering the potential benefits to land management efforts to minimize the spread of wildfire and reduce the loss of sagebrush habitat and dependent wildlife (Coates et al., 2016).

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

Data (Condon & Coates, 2022) are available in the USGS ScienceBase Data Catalog: https://doi.org/10.5066/P943JB43.

## ORCID

*Lea A. Condon* https://orcid.org/0000-0002-9357-3881
*Douglas J. Shinneman* https://orcid.org/0000-0002-4909-5181
*Peter S. Coates* https://orcid.org/0000-0003-2672-9994

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