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Recovery of biological soil crust richness and cover 12–16 years after wildfires in Idaho, USA

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Abstract. Changing fire regimes in western North America may impact biological soil crust (BSC) communities that influence many ecosystem functions, such as soil stability and C and N cycling. However, longer-term effects of wildfire on BSC abundance, species richness, functional groups, and ecosystem functions after wildfire (i.e., BSC resilience) are still poorly understood. We sampled BSC lichen and bryophyte communities at four sites in Idaho, USA, within foothill steppe communities that included wildfires from 12 to 16 years old. We established six plots outside each burn perimeter and compared them with six plots of varying severity within each fire perimeter at each site. BSC cover was most strongly negatively impacted by wildfire at sites that had well-developed BSC communities in adjacent unburned plots. BSC species richness was estimated to be 65 % greater in unburned plots compared with burned plots, and fire effects did not vary among sites. In contrast, there was no evidence that vascular plant functional groups or fire severity (as measured by satellite metrics differenced normalized burn ratio (dNBR) or relativized differenced normalized burn ratio (RdNBR)) significantly affected longer-term BSC responses. Three large-statured BSC functional groups that may be important in controlling wind and water erosion (squamulose lichens, vagrant lichens, and tall turf mosses) exhibited a significant decrease in abundance in burned areas relative to adjacent unburned areas. The decreases in BSC cover and richness along with decreased abundance of several functional groups suggest that wildfire can negatively impact ecosystem function in these semiarid ecosystems for at least 1 to 2 decades. This is a concern given that increased fire frequency is predicted for the region due to exotic grass invasion and climate change.

1 Introduction

Fire regimes are changing throughout western North America as a result of climate change, human management, and exotic invasive species (D'Antonio et al., 1992; Westerling et al., 2006; Millar et al., 2007). Changes in fire regimes may exceed ecosystem tolerances, resulting in a loss of resilience (Millar et al., 2007), particularly for species that are not well adapted to new disturbance regimes (Landres et al., 1999). Many sagebrush steppe ecosystems of the western USA have seen a fire surplus in recent decades, presumably due to increased human ignitions and introduced annual grasses (Parks et al., 2015). Estimates of fire return intervals in the Columbia Basin ecoregion vary, with expected return intervals of 425 years and observed intervals between 1984 and 2012 of 105 years (Parks et al., 2015). Furthermore, it is expected that wildfires will continue to increase in frequency and severity with climate change (Westerling et al., 2006; Millar et al., 2007) and exotic grass invasion (D'Antonio et al., 1992) in much of the western USA.

Biological soil crust (BSC) communities, comprised of a rich array of organisms, including algae, fungi, cyanobacteria, lichens, and bryophytes, serve as ecosystem engineers in many semiarid landscapes, stabilizing soil, cycling nutrients and increasing nutrient availability, increasing water infiltration, and influencing establishment of vascular plant species (Belnap and Gardner, 1993; Belnap, 1994, 2002; Belnap et al., 2001; Deines et al., 2007; Rosentreter et al., 2016). BSC functional groups may be related to ecosystem functions (Eldridge and Rosentreter, 1999; Rosentreter et al., 2016; Fig. A1 in Appendix A). For example, darker BSCs usually fix nitrogen (Belnap, 2002), and larger-statured

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functional groups increase surface roughness, which reduces soil erosion (Eldridge and Rosentreter, 1999; Belnap, 2001). The height of tall turf bryophytes and fruticose lichens helps them reduce wind erosion by serving as a barrier to saltation and creep (Eldridge, 1998). Squamulose lichens slow water flow and reduce water erosion (West, 1990). Cushion bryophytes can trap silts and clays (Danin and Gaynor, 1991). Thick lichen crusts such as *Diploschistes muscorum* are best at preventing *Bromus tectorum* L. germination (Deines et al., 2007; Rosentreter et al., 2016). Studies in Mediterranean ecosystems have suggested that BSC abundance and species richness have strong positive effects on ecosystem functions (Maestre et al., 2010). This suggests that if wildfire reduces BSC richness and cover or affects BSC community composition, we would expect changes in the ecosystem functions provided by these communities.

Several studies have documented immediate negative impacts of wildfire on BSC communities (Johansen, 1993, 2001; Hilty et al., 2004); however, resistance to wildfire has also been found (Bowker et al., 2004). In fact, BSCs may moderate the effects of wildfire if they promote less frequent or severe wildfire by reducing fuel load or preventing invasion by *Bromus tectorum* (Johansen, 2001). BSCs, particularly functional groups with taller growth forms, are also often quite sensitive to mechanical disturbance (Belnap and Eldridge, 2001; Weber et al., 2016).

Recovery rates of BSC communities may differ depending on whether disturbances are mechanical or caused by wildfire. Recovery following mechanical disturbance can vary with climate, soil texture, disturbance severity, and vascular plant community (Belnap and Eldridge, 2001; Belnap and Warren, 2002; Weber et al., 2016). Long-term trends in recovery following wildfire (or resilience; sensu Millar et al., 2007) are poorly understood. Recovery is likely to differ among pre-fire communities, which are patterned by soil texture, moisture availability, and vascular plant communities (Ponzetti and McCune, 2001; Bowker et al., 2006; Bowker and Belnap, 2008; Root and McCune, 2012). On fine spatial scales, the patchiness of mixed-severity fires can leave remnant populations that add to variability or act as sources of propagules for recovering areas nearby. Recovery of vascular plants after wildfire can also provide favorable microsites for BSC establishment (Hilty et al., 2004). Past studies suggest that algal and cyanobacterial communities recover most quickly, followed by bryophytes, then lichens (Weber et al., 2016); however, trajectories can be quite variable and different communities can recover in different ways (Read et al., 2016). Recovery times are estimated on the order of decades to centuries depending on fire severity and site conditions (Johansen, 2001), with some ecosystem functions recovering more quickly than others (Weber et al., 2016).

Our study focuses on four 12- to 16-year-old fires in Idaho, USA, a region that has seen more fires than expected between 1984 and 2012 based on climate data (Parks et al., 2015). Using plots inside and outside of the burn perimeters, we focused on three main questions to explore the effects on and recovery of BSC lichen and bryophyte communities following wildfire. (1) How do wildfires affect longer-term BSC cover and richness and is this affected by preexisting variation in BSC communities or vascular plant responses? (2) How does burn severity affect the impact and recovery following wildfire? (3) Are lichen and bryophyte functional groups differentially affected by wildfire?

2 Methods

2.1 Field sampling

We selected four study sites with mapped fire perimeters (mapped by Monitoring Trends in Burn Severity (MTBS), http://www.mtbs.gov; Eidenshink et al., 2007) in foothill steppe communities near the Salmon and Lemhi valleys in Idaho, USA (Fig. 1). Three of these sites were wildfires, whereas one, Table Mountain, was a prescribed burn. These habitats were dominated by grasses and shrubs, particularly species of *Artemisia*. Several species of *Artemisia* and hybrids were sampled on our plots, including *A. tridentata* ssp. *wyomingensis*, *A. tridentata* ssp. *vaseyana*, *A. nova*, *A. tripartita*, *A. arbuscula* group, and *A. frigida*; many of these are capable of resprouting or seeding following disturbance (Schultz, 2012). Sites were selected such that they were on public land, of similar age (12–16 years since fire), and within a relatively narrow elevation range (1565–2045 m, Table 1). After selecting sites, we opened burn perimeters in Google Earth and identified polygons of non-forested habitat within and adjacent to each fire. Because some of the fires were quite large, their upper elevations were forested; all our sites were lower to focus on sagebrush steppe habitat without live or dead trees within 50 m of plots. Within these polygons, we randomly selected 11 potential plots inside and outside the fire perimeter (using this tool: http://www.geomidpoint.com/random/). We visited six plots from our list inside and outside the fire perimeter in June through August 2015 for a total of 48 plots. In the field, plots were selected from the list of potential plots to maximize the comparability of habitats sampled (e.g., similar slope and aspect).

We used a GPS to locate plot centers and established circular plots with a 10 m radius. For each site, we downloaded the fire perimeter and two continuous measures of fire severity: the differenced normalized burn ratio (dNBR) and relativized differenced normalized burn ratio (RdNBR) from the MTBS website. Our plot size of 314 m^2 fits within a single MTBS pixel (900 m^2). Both dNBR and RdNBR varied substantially among our plots, allowing for a meaningful evaluation of the effect of fire severity (-32 to 381 for dNBR and -227 to 2629 for RdNBR), with smaller numbers indicating lower burn severity and negative numbers indicating increased greenness 1 year following the fire. At each plot, we measured slope and aspect and took 20 soil sam-

Table 1. Characteristics of sites sampled in Idaho, USA, in 2015. Includes fire ignition dates[a] and characteristics averaged across all plots, burned and unburned, at each site, including elevation, mean annual precipitation (30-year average from 1981 to 2010[b]), soil pH, and most common soil texture.

Site name	Ignition	Elevation (m)	Precipitation (mm)	pH	Soil texture
Texas	2 Aug 1999	1931	255	7.2	Sandy clay loam
Fenster Creek	14 Jul 2000	1983	343	6.5	Clay loam
Tobias	12 Jul 2003	1565	439	6.3	Clay loam
Table Mountain[c]	27 Apr 1999	2045	455	6.9	Sandy clay loam

[a] http://www.mtbs.gov/data/. [b] http://www.climatewna.com/. [c] This was the only prescribed fire in our study; the others were wildfires.

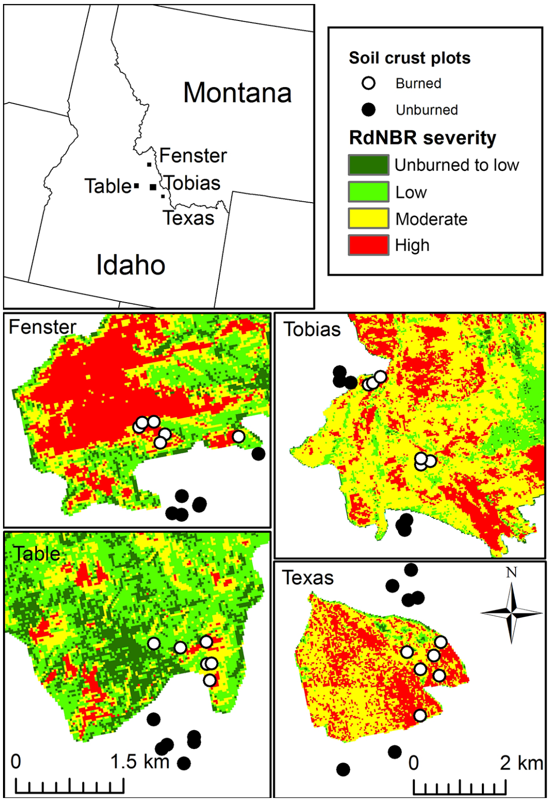

Figure 1. Study sites in Idaho, USA. Each of the four historic fires served as a site with six plots inside and six plots outside of the fire perimeter. Shading represents fire severity as measured by RdNBR following categorizations by Reilly et al. (2017).

ples distributed randomly throughout the plot with a small trowel that scraped the top 3–5 cm of soil. We mixed these soil samples in a plastic bag and took a subset to estimate texture by feel. In the lab, we measured soil pH with a 2 : 1 water : soil mix using a benchtop pH meter in a beaker with the sample kept suspended by a constantly spinning stir bar.

At each of the 48 plots, we established eight 1 m × 1 m square subplots for intensive vascular plant, lichen, and bryophyte cover sampling that we combined for analysis to maximize comparability with the scale of MTBS-mapped severity metrics. Subplots were laid out by running a measuring tape in each of the cardinal directions from the plot center and centering a plot frame on the tape at 3 to 4 m from plot center and again at 8 to 9 m from plot center. In each subplot, vascular plant cover was estimated to the nearest percent by functional group; functional groups with less than 1 % cover were recorded as 0.1 % cover. Vascular plant functional groups followed the USDA Plants (NRCS, 2015) database and included annual grasses, perennial graminoids (including *Carex*), forbs, and shrubs. We also recorded the cover of cow pies, other animal feces, litter, rock, and bare soil not covered by vascular plants, lichens, or bryophytes. Our estimates of bare soil included soil with microscopic algal or cyanobacterial soil crusts. We also estimated total percent cover of lichens and bryophytes. Heather T. Root recorded an estimated cover for each lichen species and presence of bryophyte species in each subplot and also collected vouchers for species not readily identifiable in the field. After sampling each subplot, we briefly surveyed the rest of the plot and recorded any lichen or bryophyte species that had not been captured by the subplots as having a trace abundance; these contribute to richness estimates for plots but not cover estimates.

Lichen and bryophyte samples were brought to the lab for identification using McCune and Rosentreter (2007), Flora of North America (2007, 2014), Doyle and Stotler (2006), and other primary literature. Voucher samples are stored at the Intermountain Herbarium at Utah State University (UTC) and Missouri Botanic Garden (MO). We used light microscopy and thin-layer chromatography as necessary for identification. Our nomenclature follows Esslinger (2016) for lichens and we combined some taxa that were not morphologically distinct in the field; these are listed on the same line in Appendix Table A1. We classified functional groups of lichens and bryophytes (Table A1 and Fig. A1 in Appendix A) broadly following the concepts in McCune and Rosentreter (2007) and Gimingham and Birse (1957).

2.2 Analysis

2.2.1 BSC lichen and bryophyte cover and richness

To test whether BSC lichen and bryophyte cover and richness were affected by fire, we used a linear mixed model and included the fixed effect of the burn as a treatment with two levels (burned or not) and the random effect of site using the package "lme4" (Bates et al., 2015) in the software R v3.3.2 (R Core Development Team, 2016) with the command "lme". We added fixed effects and their interactions corresponding to the average level of BSC cover or richness in unburned plots, with an error term representing the among-site variation ($n =$ four sites). We used a backwards stepwise approach to drop non-significant ($p > 0.05$) variables from the model. We visually checked residuals and log transformed as necessary to meet assumptions. To test the effects of fire severity, we used a similar approach but only included BSC cover and richness data from the 24 burned plots as the response variable and used a model with dNBR and RdNBR as continuous covariate predictors with a random effect of site. Similarly, we tested the relationship of BSC richness and cover with vascular plant functional group abundance. Because annual grasses were only common at one site and did not include enough plots to evaluate meaningfully, we could not test their relationship with BSC richness or cover.

2.2.2 Vascular plant functional groups and cow pies

We tested vascular plant functional group differences between burned and unburned plots using the same methods as above to describe how treatments differed in their vascular plant communities. We also tested whether burned and unburned plots differed in their abundance of cow pies to determine whether grazing pressure might confound our interpretation of wildfire effects.

2.2.3 BSC functional groups

We analyzed BSC functional groups by adding frequencies (out of the eight subplots per plot) across each species in each of 11 functional groups for each plot (Appendix Table A1). To test the effect of the burn treatments on functional groups (Fig. A1), we used a blocked permutational ANOVA (PERMANOVA; Anderson, 2001) with the site as the blocking variable. To determine whether specific functional groups were indicators of burned or unburned sites, we used blocked indicator species analysis (Root et al., 2010) in which burned vs. unburned plots served as the treatment and the four sites served as blocks. We report indicator values (IVs) and p values from this analysis. Indicator values range from 0 to 100 and represent a combination of the abundance times the frequency of the functional group in each treatment. High IVs suggest functional groups that are both abundant and frequent in a group, and p values are low if the IV for a particular group is higher than expected by chance.

To explore the relationship between functional groups and other variables, we performed unconstrained ordination with each dataset separately using nonmetric multidimensional scaling (Kruskal, 1964) using the slow and thorough autopilot settings and Sørensen (Bray–Curtis) distance in the software PC-Ord (v6, McCune and Mefford, 2011). We overlaid total BSC lichen and bryophyte cover and richness as well as vascular plant functional groups to interpret community composition. We also examined how functional groups were related to burn, site, soil pH, and climate covariates (30-year averages from 1981 to 2010 for each plot, www.ClimateWNA.com; Wang et al., 2012), including seasonal temperature, precipitation, and climatic moisture deficit (CMD). We considered these variables in the exploratory functional group analysis, but not for hypothesis testing because we designed our study to focus on fire effects rather than spanning the regional gradient of soil and climate with enough replication to ensure a robust test or ability to discriminate among those variables.

3 Results

3.1 BSC lichen and bryophyte cover and richness

We found 67 lichen taxa and 24 bryophyte taxa across our study sites (Appendix Table A1). Lichen and bryophyte communities differed considerably among sites and averaged 15.4, 17.6, 10.8, and 22.8 species per plot in the burned and unburned plots combined at the Fenster Creek, Tobias, Texas, and Table Mountain sites, respectively.

Because we did not sample immediately after the wildfires, our results combined the initial effect and recovery that has occurred since. The effect of fire on BSC lichen and bryophyte cover at sites depended on BSC lichen and bryophyte cover in adjacent unburned plots (interaction $p = 0.008$). At sites with greater average BSC lichen and bryophyte cover in the unburned plots, the wildfire had a greater negative effect on BSC lichen and bryophyte cover (Table 2, Fig. 2).

In contrast, the effect of fire on BSC lichen and bryophyte richness did not depend on BSC lichen and bryophyte richness in unburned plots (est. $= 0.44$, SE $= 0.39$, $p = 0.27$ for the interaction). There was weak evidence that BSC richness in unburned plots impacted BSC richness (Table 2, Fig. 2, $p = 0.057$). Unburned plots were estimated to have 65 % more species richness than burned plots (Table 2).

Fire severity, as measured by remotely sensed dNBR and RdNBR, was not a significant predictor of either BSC cover or richness (all $p > 0.60$). No vascular plant functional groups were significant in predicting BSC cover or richness (all $p > 0.30$), although there were not enough sites with annual grasses to test the relationship with that functional group.

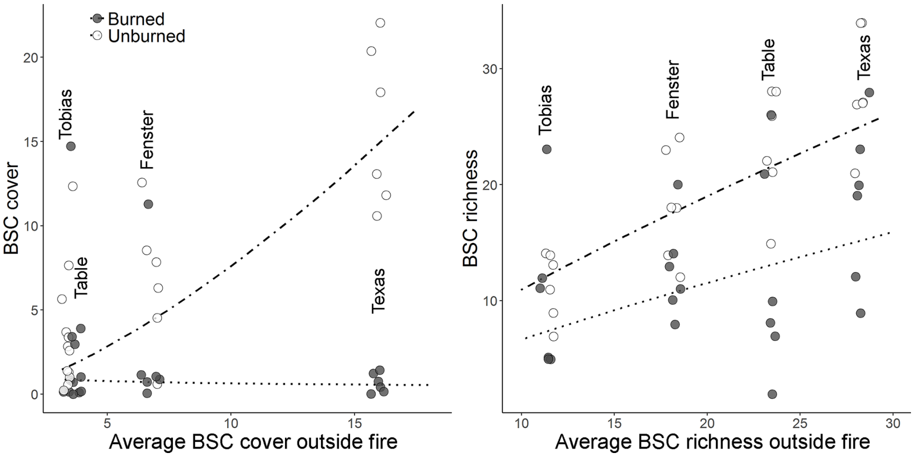

Figure 2. BSC cover and richness at four sites in Idaho, USA, in burned and unburned plots. The x axis represents the covariates average BSC cover and richness in unburned plots at each site, the fitted lines are regressions (details in Table 2), and the labels refer to site names.

Table 2. Model details for BSC cover and BSC richness at the four sites in Idaho, USA. Models have the random effect of site and allow variances to differ among treatments. The covariates are average BSC cover and richness in unburned plots at each site.

Response	Predictors	Est	SE	Df	p
ln(BSC cover + 0.1)	Int	0.342	0.898	42	0.71
	Unburned	−1.646	1.270	42	0.20
	ln(site level cover + 0.1)	−0.289	0.438	2	0.58
	Unburned × ln(site level cover + 0.1)	1.718	0.619	42	0.0083
ln(BSC richness + 0.1)	Int	0.082	0.597	43	0.89
	Unburned	0.500	0.134	43	0.0006
	ln(site level richness + 0.1)	0.796	0.199	2	0.057

3.2 Vascular plant functional groups, bare soil, and cow pies

Vascular plant communities differed substantially among sites, with some being dominated by shrubs and others by graminoids; however, there was little evidence that the vascular plant community was consistently affected by the wildfires (Fig. 3). Annual graminoids could not be tested across all sites because they were only common at the Fenster Creek site, where they did not significantly differ between burned and unburned plots ($p = 0.43$). Perennial graminoids and forbs did not differ between burned and unburned plots ($p = 0.28$, 0.85). In burned plots, fire severity was also not related to perennial graminoid or forb cover ($p = 0.15$, 0.33 for log(RdNBR)). In the field, it appeared that shrubs were slightly negatively affected by the burn at the Texas site and positively affected at the Fenster Creek site (Fig. 2). However, across the sites there was only marginal evidence of more shrubs in unburned plots ($p = 0.075$), and shrubs had an average of 14.7 % cover (SE = 3.0) in burned plots, with 6.6 % more cover in unburned plots (SE = 3.6). The increase in shrubs at some sites is likely due to resprouting species of *Artemisia* and other shrubs. In burned plots, there was no evidence that fire severity impacted shrub cover ($p = 0.16$ for log(RdNBR)). Burned plots had more bare soil than unburned plots; on average we estimated 23.7 % bare soil (SE = 3.7) on burned plots, with 4.5 % lower cover on unburned plots (SE = 1.9, $p = 0.024$; Fig. 2). Burned plots with higher burn severity had higher bare soil cover (slope estimate for log(RdNBR) = 0.265, $p = 0.020$).

There was evidence of livestock grazing at all sites, and cattle were able to move freely between burned and unburned habitat at each site with no obvious differences between grazing management observed in the field. Our test of cow pie cover supported this assumption with no significant difference between burned and unburned plots ($p = 0.86$). On average, burned plots had 0.80 % cow pie cover (SE = 0.23) and unburned plots had 0.06 % less cow pie cover (SE = 0.32).

3.3 BSC functional groups

The composition of functional groups significantly differed among sites (pseudo-$F = 4.29$, $p = 0.044$) and between burned and unburned plots (pseudo-$F = 2.56$, $p = 0.008$). Three functional groups were significant indicators for un-

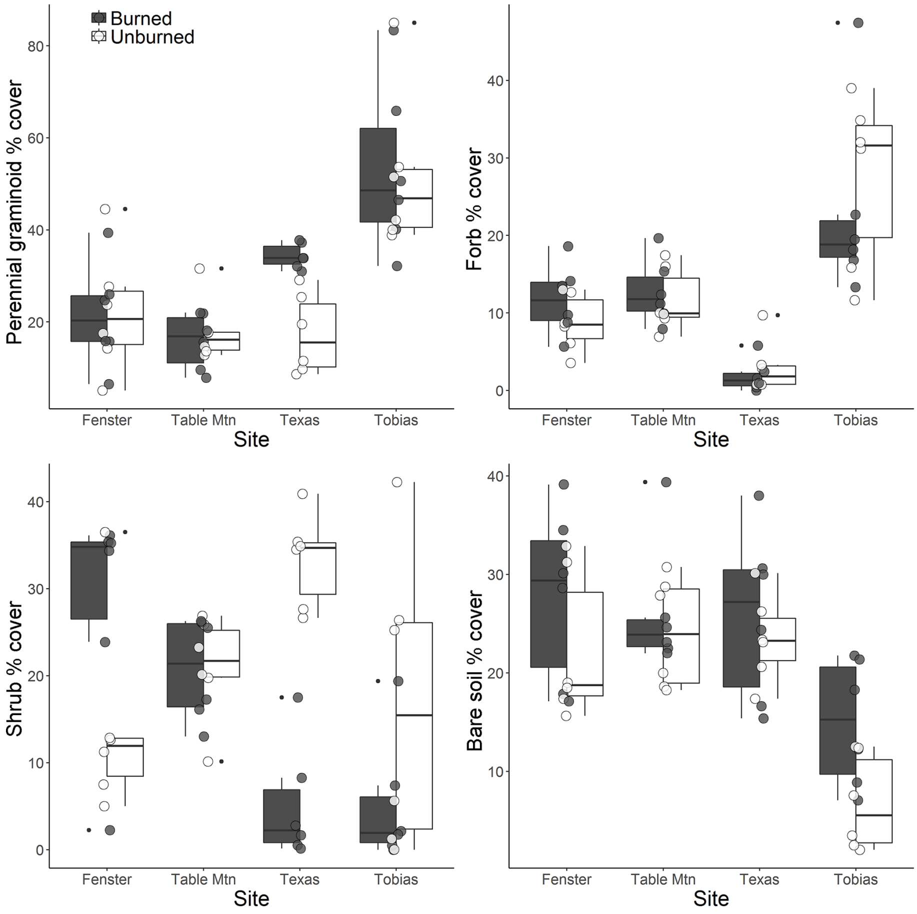

Figure 3. Vascular plant functional group cover at four sites in Idaho, USA, with symbols representing burned and unburned plots.

burned plots, including squamulose lichens (IV = 63.4, $p = 0.004$), vagrant lichens (IV = 16.4, $p = 0.031$), and tall turf mosses (IV = 59.7, $p = 0.006$). Vagrant lichens were likely significant despite their low IVs because of their strong association with unburned sites at the Texas site and absence at other sites. No functional groups were significant indicators for burned sites. No functional groups were strongly related to fire severity measured by dNBR or RdNBR ($p > 0.07$ for all).

Functional group abundance varied substantially among sites (Fig. 4). Mat-forming bryophytes were most common at the Fenster and Tobias sites with high minimum temperatures, more spring precipitation, lower autumn climatic moisture deficit, a low abundance of rocks, and a high abundance of forbs. Short turf mosses were less strongly associated with these same variables. Cushion mosses were not common in the dataset since they were only found at two plots at the Fenster site. Vagrant lichens were strongly associated with the Texas site, which had a high autumn climatic moisture deficit, a high cover of rocks, and cold minimum temperatures. Fruticose lichens showed a similar pattern, but less strongly, and were also common at the Table Mountain site. Crustose and squamulose lichens were most common at the Table Mountain and Texas sites, which were rocky and generally had the richest BSC communities. Foliose lichens and tall turf mosses were not strongly associated with particular variables or sites.

4 Discussion

Wildfire effects on BSC lichen and bryophyte cover and richness were still readily detectable 12–16 years after fire, suggesting that negative effects can persist for at least 1 to 2 decades or longer. Effects were more pronounced at sites with well-developed BSCs outside the burn that are likely similar to the pre-fire communities. This suggests that the initial impacts were more severe at those sites or that recovery to the pre-fire condition requires more time. Using soil and climate variables, places with high predicted BSC cover and richness in the absence of disturbance can be mapped (Bowker, 2007). Such mapping could help identify places where BSC communities are likely to be well-developed in the absence of disturbance and prioritize management activities that minimize wildfire risk.

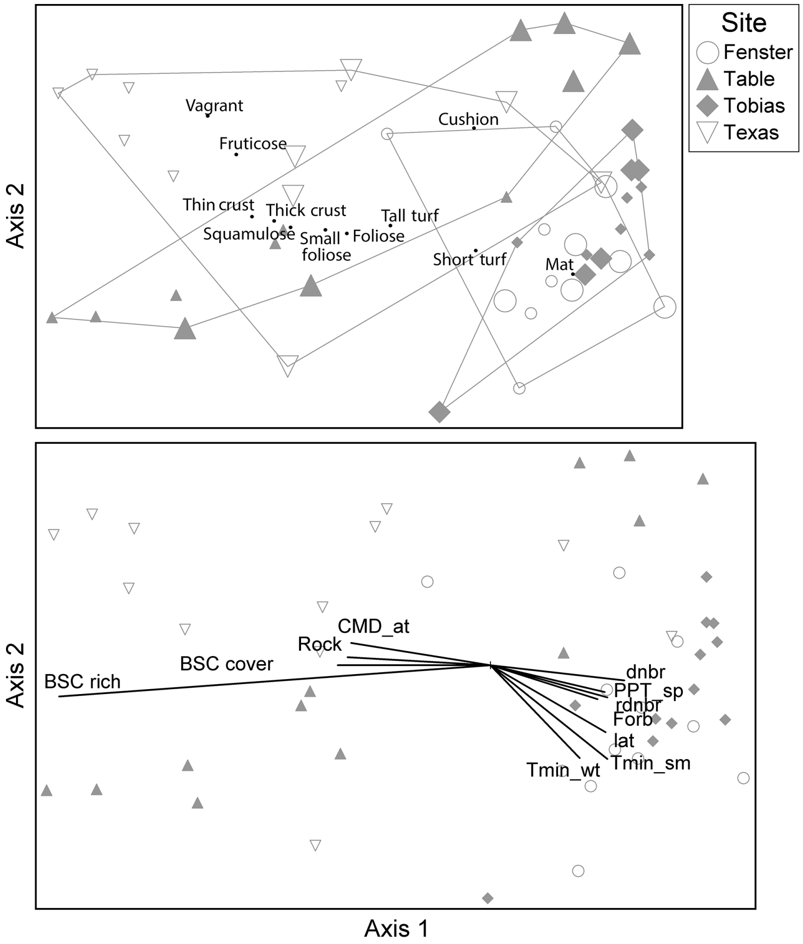

Figure 4. Ordination of BSC growth forms found at four sites in Idaho, USA. Each gray point represents a plot, with points closer to each other having a more similar composition of BSC growth forms. Plots from the same site have the same symbol. In the upper panel, plots are larger if they are within the fire perimeter and smaller if they are unburned; plots from the same site are connected into a polygon using gray lines. Small black circles represent the centroid of each BSC growth form on the ordination. In the lower panel, labeled vectors show relationships between variables and the ordination axes with $R^2 > 0.20$, including BSC richness and cover, rock and forb cover, latitude (lat), and fire severity metrics (dNBR and RdNBR). Climate variables include climatic moisture deficit in autumn (CMD_at), precipitation in spring (PPT_sp), and minimum temperature in summer and winter (Tmin_sm, Tmin_wt).

Our results are broadly consistent with other studies from the region that show some recovery of BSC lichen and bryophyte communities in that time period but suggest a longer timeframe for the recovery of a community similar to that outside the fire (Johansen et al., 1984; Hilty et al., 2004). Perhaps because our sites were not dominated by invasive annual grasses, our study did not suggest that sites with high BSC cover were less strongly affected by fire due to low fuel loads (Johansen, 2001). Alternatively, our sites have a climate that is cold and wet in the winter, and they support high cover of perennial graminoids and shrubs, which may mean fuels are not as strongly limiting for wildfires in our study region as they are in warmer and drier regions. Other studies have suggested that this combination of climate makes our study area, and many other regions of sagebrush steppe in the western USA, less suitable for one of the dominant annual invasive grasses, *Bromus tectorum* (Brummer et al., 2016).

While we found evidence that pre-fire BSC communities were important in predicting fire effects and recovery, we found no evidence that vascular plant cover affected BSC post-fire recovery, suggesting that the impacts of wildfire on crust communities were primarily a result of the wildfire itself. Vascular plant groups were similar inside and outside of the fires, despite strong differences in BSCs. This suggests that vascular plant functional groups (though not necessarily individual species) are likely to recover more quickly after wildfire than BSCs in these semiarid regions. This is contrary to studies that have suggested that seeding with perennial plant species can speed soil crust recovery (Hilty et al., 2004), perhaps because *Bromus tectorum* was not common at our study sites. In general, instead of increasing invasive annual grasses, where BSC cover was reduced in burned plots, bare soil increased; bare soil was also the only variable that we examined that was positively related to burn severity. The interaction between *B. tectorum* and wildfires has been the subject of several studies in the western USA (for example, Chambers et al., 2014), but less is known about similar sites without this exotic annual grass. Since our study suggests that these ecosystems may differ from the paradigm in areas dominated by *B. tectorum*, other sites not dominated by *B. tectorum*, which include a substantial area of the western USA (Brummer et al., 2016), may warrant further study.

Wildfire severity is of primary concern to ecologists and managers due to the potential for greater ecological effects in high severity fires. It is possible that severity metrics may not predict recovery as well as is often assumed in the literature. For example, some high-severity sites may recover more quickly than low-severity sites because of other environmental factors (Keely, 2009). We hypothesized that the effects of fire severity on the initial disturbance would have a lasting effect through to recovery and that differences in severity between fires in this study and others may account for differences among results in previous work (Bowker et al., 2004; Hilty et al., 2004). The effects of severity on BSCs had not been previously examined except by one study, which found minimal differences in BSC communities between unburned and low-severity burned sites (Johansen, 2001). We found that the two commonly used remotely sensed fire severity metrics (dNBR and RdNBR) were poor predictors of wildfire effects and recovery for BSC communities or vascular plant functional groups. While we suspected that dNBR, which measures the absolute change in the ratio of near-infrared to shortwave infrared wavelengths, would not perform well, we did expect that RdNBR, which is adjusted by the pre-fire values, would be well-suited to our study area (Dillon et al., 2011). Since BSCs vary in color depending on species composition, season, and moisture status, perhaps they are not well-detected using these metrics. The lack of correlation between severity and BSC cover in our study may also be due to scale mismatch; the scale that lichens and bryophytes respond to may be smaller than the scale measured by satellite metrics. This could also be true for vascular plants, which was a reason for combining data from eight subplots for analysis. An important management implication of our findings is that remotely sensed fire severity may not predict wildfire effects on BSC communities and thus will likely not predict all of the long-term ecological effects of wildfire in semiarid ecosystems.

We found much higher species richness than previous studies of post-fire BSC recovery. We detected 67 lichen and 24 bryophyte taxa at our study sites, whereas Hilty et al. (2004) found about half as many, Johansen (1984) found only five lichens and four bryophytes, and Bowker et al. (2004) found eight lichens and six bryophytes. Several of the taxa were observed in two or more of the studies, suggesting some overlap among communities. Differences in observed species richness may be methodological, due to attention to taxonomy or sampling design: we used larger plots and sampled at four sites with differing BSC communities. However, species richness observed in each study may also reflect differences in the development of pre-fire BSC communities. Fire effects differ depending on pre-fire communities, suggesting that it is important to document the undisturbed BSC community in order to understand effects. In particular, sites with poorly developed BSC communities prior to wildfire may be expected to show little response to this disturbance.

We observed significant long-term effects of wildfire on three functional groups: squamulose lichens, vagrant lichens, and tall turf mosses. These groups were all more abundant in unburned plots, while no functional groups were significantly more abundant in burned plots. Our findings are consistent with others in that tall turf mosses and lichens in general are often considered mid- to late-successional BSC functional groups (Weber et al., 2016). Recent work in ecosystems relieved of grazing pressure hypothesizes that loosely attached, open-structured BSC lichens and bryophytes (including vagrant lichens, foliose lichens, and tall turf mosses) are mid-successional, whereas later-successional species have higher structural density and are more closely attached to the soil (including short turf mosses, crustose and squamulose lichens; Read et al., 2016). However, responses to wildfire may be substantially different from grazing. While we found that some of these functional groups were more abundant in unburned plots, others, such as the crustose lichens and short turf mosses, were equally abundant in burned plots. Our results challenge the hypothesis that these functional groups are late-successional; this could be because they establish faster than previously thought or because they are more resistant to wildfire than to trampling. In general, we may expect loosely attached, open-structured species to burn more readily than those that are closely attached to soil because they may dry out more quickly or allow more air circulation during a fire.

The functional groups affected by wildfire in our study are generally large in stature and, in the cases of tall turf mosses and squamulose lichens, particularly valuable for soil stabilization (West, 1990; Eldridge, 1998; Rosentreter et al., 2016). We would therefore expect greater wind and water erosion in burned plots where there was lower abundance or absence of these functional groups. Small foliose lichens, and large foliose lichens, which included most of the nitrogen fixers, did not differ between our treatments, suggesting that at this point in recovery the functions of those groups are probably not strongly affected.

5 Conclusions

We found that the impacts of wildfire on BSC lichen and bryophyte communities last at least 1 to 2 decades and perhaps longer. BSC cover and richness were most strongly impacted by wildfire at sites with well-developed BSCs in unburned plots. There was no evidence of consistent effects of wildfire on vascular plant functional groups or that the vascular plant functional groups mediated BSC responses. Fire severity, as measured by the satellite metrics dNBR and RdNBR, did not predict BSC cover or richness or the abundance of plant functional groups. Three functional groups, squamulose lichens, vagrant lichens, and tall turf mosses, exhibited a long-term decrease in abundance that is likely to negatively impact the recovery of some ecosystem functions, for example, the reduction in soil erosion offered by taller soil crusts (Belnap, 2001).

Code availability. No unusual coding was used, and therefore R code for analysis is not included.

Data availability. The data are included as a Supplement.

Appendix A

Appendix A includes a table with BSC taxa sampled and a figure representing the functional groups.

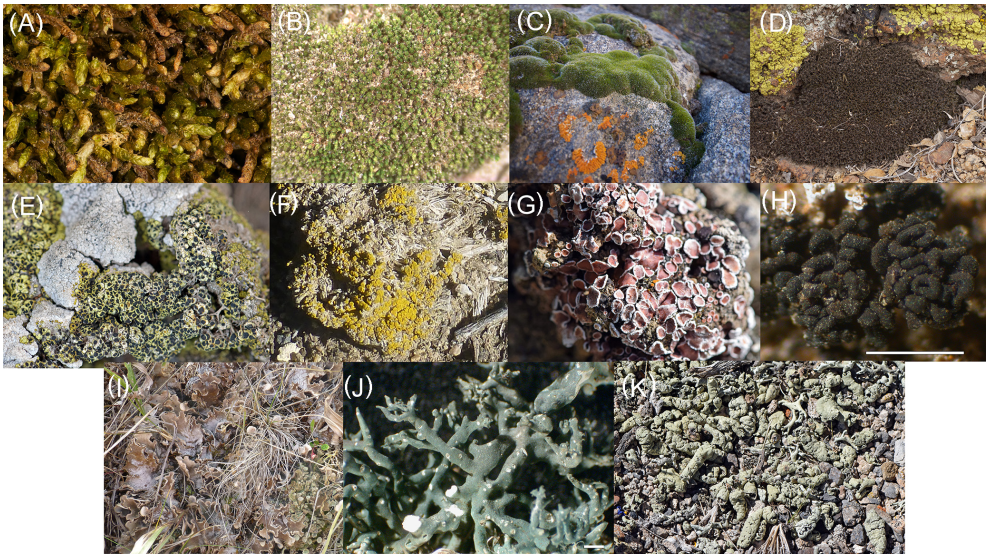

Figure A1. Photographs of functional groups; note that scale varies and most do not include scale bars. **(a)** Mat bryophyte *Eurhynchiastrum* (Photo: JB), **(b)** short turf bryophyte *Gemmabryum* (Photo: JB), **(c)** cushion bryophyte *Grimmia* (Photo: JB), **(d)** tall turf bryophyte *Syntrichia* (Photo: JB), **(e)** thick lichen crusts *Acarospora schleicheri* (yellow) and *Diploschistes muscorum* (white) (Photo: EKD), **(f)** thin lichen crust *Candelariella* (Photo HTR), **(g)** squamulose lichen *Psora decipiens* (Photo: EKD), **(h)** small foliose lichen *Enchylium tenax* (Photo: Bruce McCune, scale bar = 1 cm), **(i)** large foliose lichen *Peltigera* (Photo: HTR), **(j)** fruticose lichen *Circinaria hispida* (Photo: Bruce McCune, scale bar = 1 mm), and **(k)** vagrant lichens *Rhizoplaca* (rolled up) and *Xanthoparmelia* (Photo: EKD).

Table A1. Biological soil crust lichen and bryophyte species found in burned and unburned plots at the sites of four fires in Idaho, USA. Acronyms used in analysis and growth form designation for analysis. Sites with occurrences are abbreviated (TB: Table Mountain; TO: Tobias; TX: Texas; FN: Fenster).

Species	Acronym	Growth form	Sites with occurrences
Lichens			
Acarospora schleicheri	Acasch	Thick crustose	TX
Amandinea punctata	Buepun	Thin crustose	FN, TB, TO, TX
Arthonia glebosa	Artgle	Squamulose	TB, TX
Aspicilia filiformis complex	Aspfil	Fruticose	FN, TB, TX
Aspicilia reptans complex	Aspici	Thick crustose	FN, TB, TX
Bryoplaca jungermanniae	Caljun	Thin crustose	FN, TB, TO, TX
Buellia epigaea	Bueepi	Thick crustose	FN
Caloplaca atroalba	Calatr	Thin crustose	TB, TX
Caloplaca stillicidiorum	Calsti	Thin crustose	FN, TB, TO, TX
Candelariella aggregata	Canagg	Thin crustose	FN, TB, TO, TX
Candelariella rosulans	Canros	Thick crustose	TX
Circinaria hispida	Asphis	Fruticose	FN, TB, TX
Cladonia chlorophaea, *C. fimbriata*, *C. imbricarica*, *C. pocillum*, *C. pyxidata*	Cladon	Squamulose	FN, TB, TO, TX
Diploschistes muscorum	Dipmus	Thick crustose	FN, TB, TX
Enchylium tenax	Colten	Small foliose	FN, TB, TO, TX
Endocarpon loscosii	Endlos	Squamulose	TB, TX
Endocarpon pusillum	Endpus	Squamulose	FN, TX
Myriolecis crenulata	Leccre	Thin crustose	TX
Myriolecis flowersiana	Lecflo	Thin crustose	TX

Table A1. Continued.

Species	Acronym	Growth form	Sites with occurrences
Lichens			
Protoparmeliopsis garovaglii	Lecgar	Foliose	TX
Myriolecis hagenii	Lechag	Thin crustose	FN, TB, TX
Lecanora laxa	Leclax	Thin crustose	FN, TB
Lecanora sp. 4	Lecsp4	Thin crustose	TB, TX
Myriolecis zosterae	Leczos	Thin crustose	FN, TB, TX
Lecidea laboriosa	Leclab	Thin crustose	FN
Lecidella stigmataea	Lecsti	Thin crustose	TB, TX
Lecidella wulfenii	Lecwul	Thick crustose	FN, TB
Lepraria spp.	Leprar	Thick crustose	FN
Megaspora verrucosa	Megver	Thick crustose	TB, TX
Melanohalea exasperatula	Melexa	Foliose	FN, TX
Ochrolechia uppsaliensis	Ochupp	Thick crustose	FN
Parvoplaca tiroliensis	Caltir	Thin crustose	TB, TO
Peltigera canina	Pelcan	Foliose	TO
Peltigera didactyla	Peldid	Foliose	FN, TB, TO
Peltigera kristinssonii	Pelkri	Foliose	FN
Peltigera ponojensis	Pelpon	Foliose	FN, TB, TO
Phaeophyscia constipata	Phynar	Foliose	TX
Phaeorrhiza sareptana	Phasar	Squamulose	TB, TX
Physconia isidiigera, P. muscigena	Physcon	Foliose	TB, TX
Placidium sp.	Placid	Squamulose	FN, TB, TO, TX
Placynthiella icmalea	Plaicm	Thick crustose	TX
Placynthiella uliginosa	Plauli	Thick crustose	FN
Psora cerebriformis	Psocer	Squamulose	FN, TB, TX
Psora decipiens	Psodec	Squamulose	TX
Psora montana, P. globifera	Psomon	Squamulose	FN, TB, TO, TX
Psora tuckermanii	Psotuc	Squamulose	FN, TX
Rhizoplaca haydenii	Rhihay	Vagrant	TX
Rhizoplaca melanopthalma ssp. cerebriformis	Rhimel	Vagrant	TX
Rinodina terrestris	Rinter	Thin crustose	FN, TB, TO, TX
Scytinium lichenoides, *Scytinium tenuissimum*	Leptog	Small foliose	FN, TB, TO, TX
Tetramelas terricolus	Bueter	Thick crustose	FN, TO
Toninia sedifolia	Tonsed	Thick crustose	TX
Xanthocarpia lactea	Callac	Thin crustose	TX
Xanthocarpia tominii	Caltom	Thin crustose	FN, TX
Xanthomendoza fulva	Xanful	Foliose	TX
Xanthoparmelia wyomingica, *X. neochlorochroa*, *X. chlorochroa*, *X. camtschadalis*	Xantho	Vagrant	TX
Bryophytes			
Barbula convoluta	BBarcon	TurfShort	FN, TO,
Brachytheciastrum collinum	BBracol	Mat	FN, TO
Brachythecium albicans	BBraalb	Mat	FN, TO
Bryoerythrophyllum recurvirostrum	BBryrec	TurfShort	FN
Bryum argenteum	BBryarg	TurfShort	FN, TB, TO, TX
Cephaloziella divaricata	BCepdiv	Mat	FN
Ceratodon purpureus subsp. *conicus*	BCerpur	TurfShort	FN, TB, TO, TX
Clevea hyalina	BClehya	Mat	TO
Desmatodon leucostoma	BDesleu	TurfShort	TO
Encalypta rhaptocarpa var. *trachymitra*	BEncrhap	TurfShort	FN, TB, TO
Eurhynchiastrum pulchellum	BEurpul	Mat	FN, TO
Gemmabryum caespiticium	BGemcae	TurfShort	FN, TB, TO, TX
Grimmia calyptrata	BGrical	Cushion	FN
Grimmia ovalis	BGriova	Cushion	FN
Phascum cuspidatum	BPhacus	TurfShort	FN, TB, TO
Pohlia cruda	BPohcru	TurfShort	FN, TO
Polytrichum juniperinum	BPoljun	TurfTall	FN, TO
Pterygoneurum ovatum, P. subsessile	BPte	TurfShort	FN, TX
Syntrichia caninervis	BSyncan	TurfTall	TX
Syntrichia montana	BSynmon	TurfTall	TB
Syntrichia norvegica	BSynnor	TurfTall	TO
Syntrichia papillosissima	BSynpap	TurfTall	FN, TO
Syntrichia subpapillosissima	BSynsub	TurfTall	FN, TB, TO, TX

Information about the Supplement

The Supplement is an Excel spreadsheet with raw data requested that can be used to produce graphs.

The Supplement related to this article is available online at https://doi.org/10.5194/bg-14-3957-2017-supplement.

Author contributions. HTR took the lead on designing the study as well as conducting fieldwork and analysis and writing. JCB advised sampling design, identified bryophytes, performed bryophyte analysis, and contributed to writing and revising the paper. EKD assisted with the design of the study, fieldwork, analysis, and writing and revising the paper.

Competing interests. The authors declare that they have no conflict of interest.

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