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Biological soil crust communities 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) is 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. In contrast, there was no evidence that vascular plant functional groups or fire severity (as measured by satellite metrics dNBR or RdNBR) significantly affected longer-term BSC responses. Three BSC functional groups (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 semi-arid ecosystems for at least one to two 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). 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 semi-arid landscapes; stablizing soil, cycling nutrients and increasing nutrient availability, increasing water infiltration, and influencing establishment of vascular plant species (Belnap and Gardner, 1993; Belnap, 1994; Belnap et al., 2001; Belnap, 2002; Deines et al., 2007; Rosentreter et al., 2016). Species and functional group composition of BSC communities can have strong impacts on their ecosystem functions. Cyanobacteria and cyanobacterial lichens are the primary nitrogen-fixers (Belnap, 2002). Thick lichen crusts are best at preventing *Bromus tectorum* L. germination (Deines et al., 2007; Rosentreter et al., 2016). Taller soil crusts contribute more to soil surface roughness and reduce soil erosion (Belnap, 2001). Studies in Mediterranean soil crust 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.

BSCs are often quite sensitive to disturbance; several studies have examined recovery rates of different BSC communities following mechanical disturbance and found that recovery can vary with climate, soil texture and disturbance severity (Belnap and Eldridge, 2001; Weber et al., 2016). BSC recovery after mechanical disturbance also depends on the vascular plant community and is generally more rapid in microsites under shrubs (Belnap and Warren, 2002). Generally, functional groups with taller growth forms are more susceptible to mechanical disturbance and take longer to recover (Belnap and Eldridge, 2001; Weber et al., 2016).

Fire often has a negative impact on BSC abundance and richness, but effects are variable and long-term trends (or resilience sensu Millar et al., 2007) are poorly understood. Several studies have documented negative impacts of wildfire on BSC communities (Johansen, 1993; Johansen, 2001; Hilty et al., 2004), however, resistance to wildfire has also been found (Bowker et al., 2004). Recovery is likely to differ with 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). At fine spatial scales, the patchiness of mixed severity fires can leave remnant populations within burns 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). Sites with high BSC cover may experience less frequent or severe wildfire if the crust does not support high fuel loads or has prevented widespread invasion by *Bromus tectorum* (Johansen, 2001). Despite this variability, past studies suggest that algal and cyanbacterial communities recover most quickly, followed by bryophytes, then lichens (Weber et al., 2016); however, trajectories can be quite variable (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 12-16 year-old fires in Idaho, USA, a region that that has seen more fires than expected between 1984-2012 based on expectations from 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 pre-existing variation in BSC communities or vascular plant responses? (2) How does burn severity affect the impact of 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 MTBS, http://www.mtbs.gov, Eidenshink et al., 2007) in foothill steppe communities near the Salmon and Lemhi Valleys in Idaho, USA (Fig. 1). These habitats were dominated by grasses and shrubs, particularly species of *Artemisia.* 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. Within these polygons, we randomly selected 11 potential plots inside and outside the fire perimeter. We visited 6 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). At each plot, we measured slope and aspect, and took 20 soil samples distributed haphazardly 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 x 1 m square subplots for intensive vascular plant, lichen, and bryophyte cover sampling. Subplots were laid out by running 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 by functional group to the nearest percent, with functional groups having less than 1% cover 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 cover of cowpies, other animal feces, litter, rock and bare soil not covered by vascular plants, lichens, or bryophytes. Our estimates of bare soil included soil with algal or cyanobacterial microscopic soil crusts. We also estimated total percent cover of lichens and bryophytes. HTR 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 (2010), *Flora of North America* (2007 and 2014), Doyle and Stotler (2006), and other primary literature. Voucher samples are stored at UTC and MO herbaria. 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 1) broadly following the concepts in McCune and Rosentreter (2010) 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 generalized 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. 2013) in the software R v. 3.3.2 (R Development Core 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 = 4 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 between 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 cowpies

We tested vascular plant functional group differences between burned and unburned plots to describe how treatments differed in their vascular plant communities using the same methods as above. We also tested whether burned and unburned plots differed in their abundance of cowpies to compare evidence of grazing pressure.

2.2.3 BSC functional groups

We analysed BSC functional groups by adding frequencies (out of the 8 subplots/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, we used a blocked permutational ANOVA (PerMANOVA, Anderson, 2001) with 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) where burned vs. unburned plots served as the treatment and the four sites served as blocks. We report indicator values (*IV*) 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 *IV*s 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 (NMS, Kruskal, 1964) using the slow and thorough autopilot settings and Sorensen (Bray-Curtis) distance in the software PC-Ord (v. 6, McCune & 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 community analysis, but not 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.

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, *s.e.* = 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 $p > 0.6$). 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.

3.2 Vascular plant functional groups, bare soil, and cowpies

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 (*s.e.* = 3.0) in burned plots with 6.6% more cover in unburned plots (*s.e.* = 3.6). 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 (*s.e.* = 3.7) on burned plots with 4.5% lower cover on unburned plots (*s.e.* = 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, but no suggestion in the field that grazing pressure differed between burned and unburned areas. Our test of cowpie cover supported this assumption with no significant difference in between burned and unburned plots (*p* = 0.86). On average, burned plots had 0.80% cowpie cover (*s.e.* = 0.23) and unburned plots had 0.06% less cowpie cover (*s.e.* = 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 unburned 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 Indicator Values because of their strong association with unburned sites at the Texas site and absence at other sites.

Functional group abundance varied substantially among sites (Fig. 4). Mat-forming bryophytes were most common at Fenster and Tobias sites with high minimum temperatures, more spring precipitation, lower autumn climatic moisture deficit, a low abundance of rocks, and high abundance of forbs. Short turf mosses were less strongly associated with these same variables. Cushion mosses were not common in the dataset, found only at two plots at the Fenster site. Vagrant lichens were strongly associated with the Texas site, which had a high autumn climatic moisture deficit, 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 Table Mountain and the 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 one to two decades or longer. 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). In our study, the strongest effects of wildfire were observed at sites where BSC cover was high in adjacent unburned plots, likely representing more well-developed pre-fire BSC communities. This is contrary to the idea that sites with high BSC cover are not likely to be strongly affected by fire due to low fuel loads (Johansen, 2001), perhaps because our sites were not dominated by invasive annual grasses. Alternatively, our sites have a climate that is cold and wet in the winter, and support high cover of perennial graminoids and shrubs, suggesting that fuels are not strongly limiting for wildfires. 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.

While we found evidence that pre-fire BSC communities were important in predicting fire effects, 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 recovery more quickly after wildfire than BSCs in these semi-arid 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 *B. tectorum*-dominated areas, other sites without *B. tectorum* 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. Differences in severity between fires in this study and previous studies may account for previous findings of little change in BSC communities following wildfire (Bowker et al., 2004) in contrast to the lasting effects documented in this study. However, we found that the two commonly used remotely-sensed fire severity metrics (dNBR and RdNBR) were poor predictors of wildfire effects on 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 colour 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 scale mismatch; the scale that lichens and bryophytes respond to may be smaller than the scale measured by satellite metrics. Another study found minimal differences in BSC communities between unburned and low severity burned sites (Johansen, 2001); however, we do not know of studies examining severity effects on BSC communities across a broad gradient. An important management implication of our finding 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 semi-arid ecosystems.

We found much higher species richness than previous studies of post-fire BSC recovery. We detected 67 lichen and 24 bryophyte taxa in our study sites, whereas Hilty et al. (2004) found about half as many, Johansen (1984) found only 5 lichens and 4 bryophytes, and Bowker et al. (2004) found 8 lichens and 6 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 these 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 rested from 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. Because the functional groups affected by fire in our study are generally large in stature and, in the cases of tall turf mosses and squamulose lichens, particularly valuable for soil stabilization (Rosentreter et al., 2016), we expect some loss of associated ecosystem functions for decades or longer following wildfires.

5. Conclusions

We found that the impacts of wildfire on BSC lichen and bryophyte communities last at least one to two 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 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

Upon acceptance, we will make our data available through Data Dryad. Currently the data necessary to produce graphs are included as a supplement as requested in the Instructions for Authors.

Appendices and Supplementary data

Appendix 1 includes a table with BSC taxa sampled.
Supplement 1 is an Excel spreadsheet with raw data requested that can be used to produce graphs.

Author contribution

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

Competing interests

The authors declare that they have no conflict of interest.

Special issue statement

Biological soil crusts and their role in biogeochemical processes and cycling.

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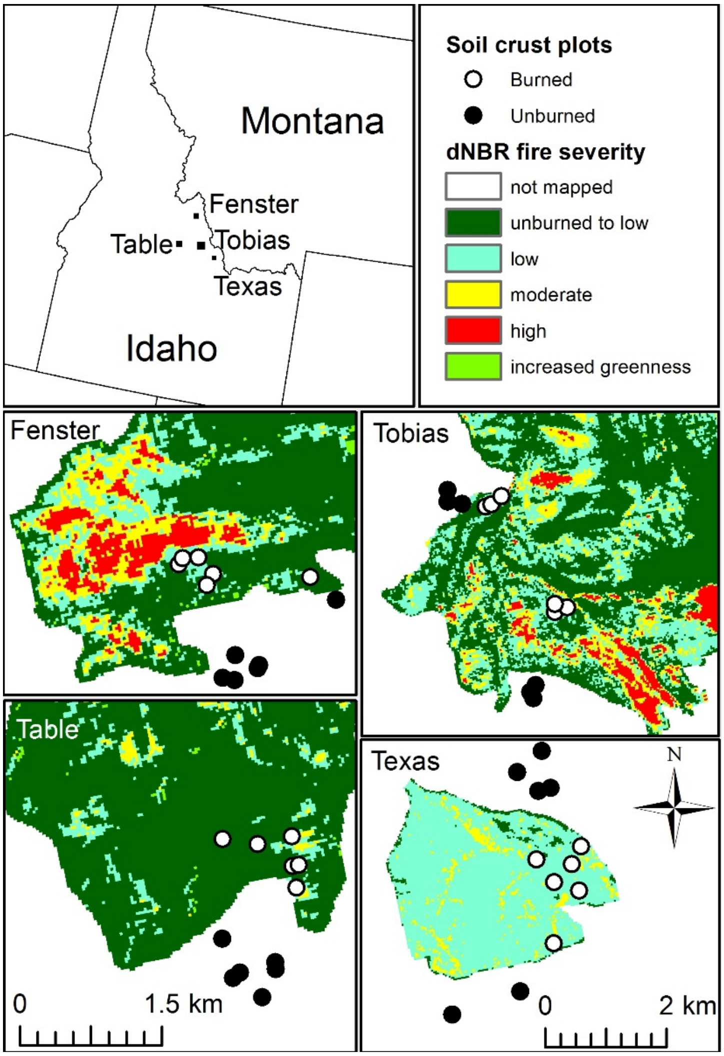

Figure 1: Study sites in Idaho, USA. Each of the four historic fires served as a site with six plots inside and six plots outside of the fire 5 perimeter. Shading represents fire severity as measured by dNBR.

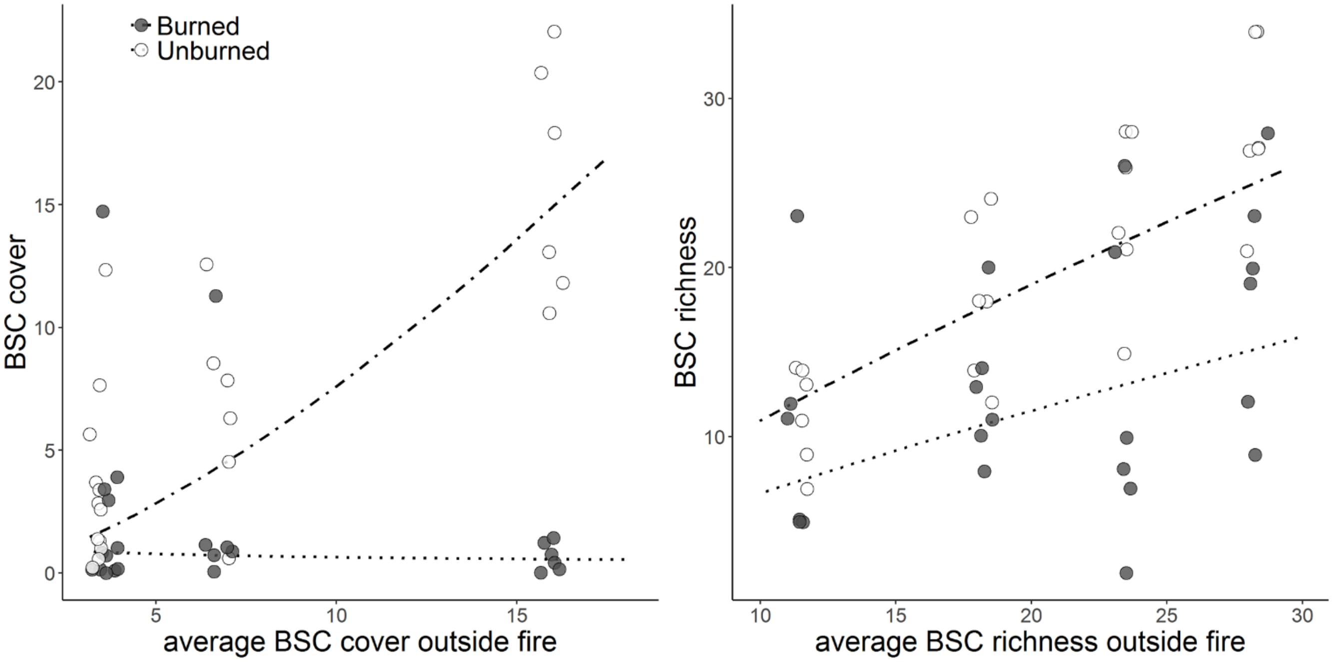

Figure 2: BSC cover and richness at four sites in Idaho, USA in burned and unburned plots. The x-axis represents the covariates average BSC cover and richness in unburned plots at each site, and the fitted lines are regressions (details in Table 2).

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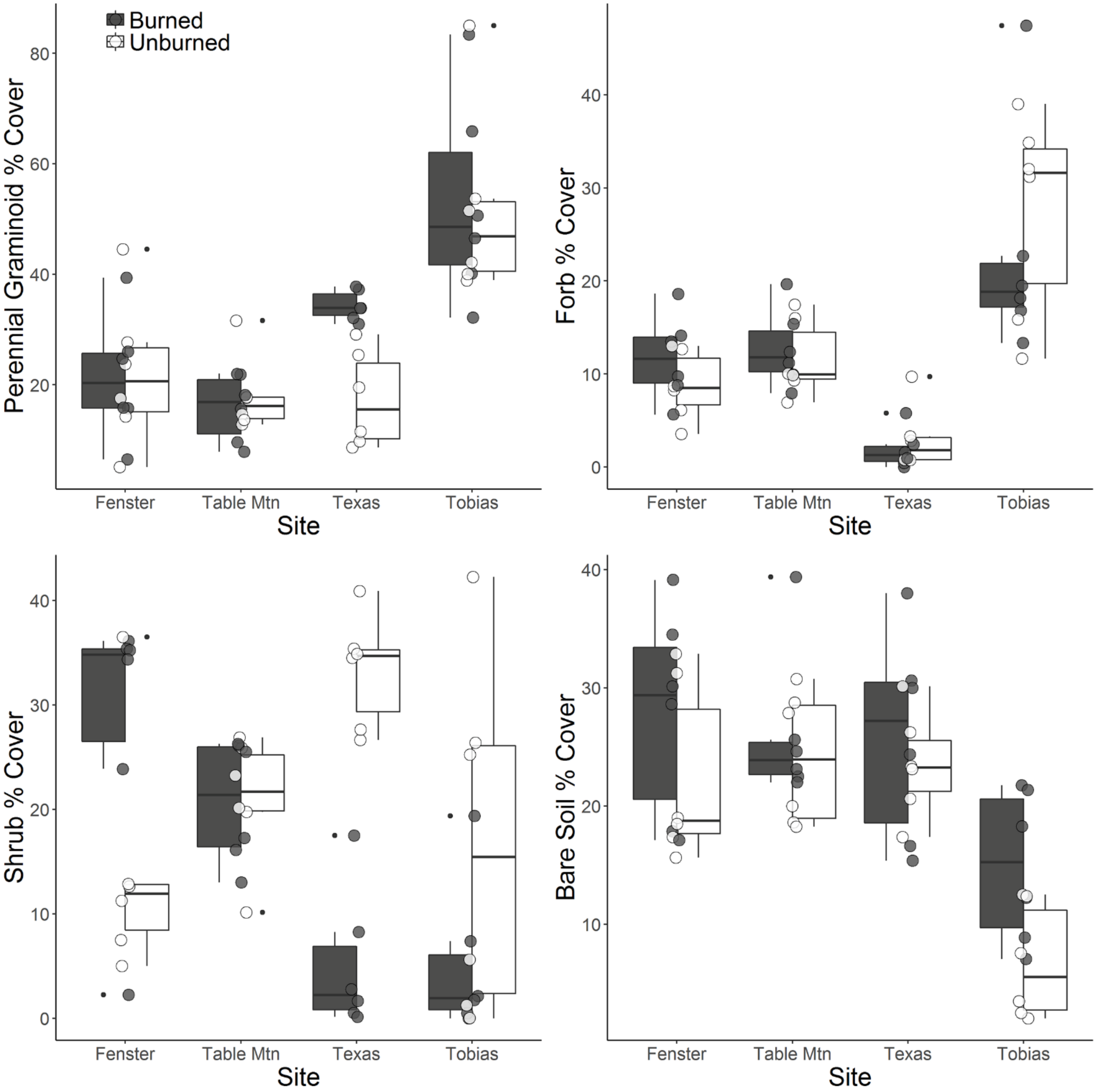

Figure 3: Vascular plants functional group cover at four sites in Idaho, USA with symbols representing burned and unburned plots.

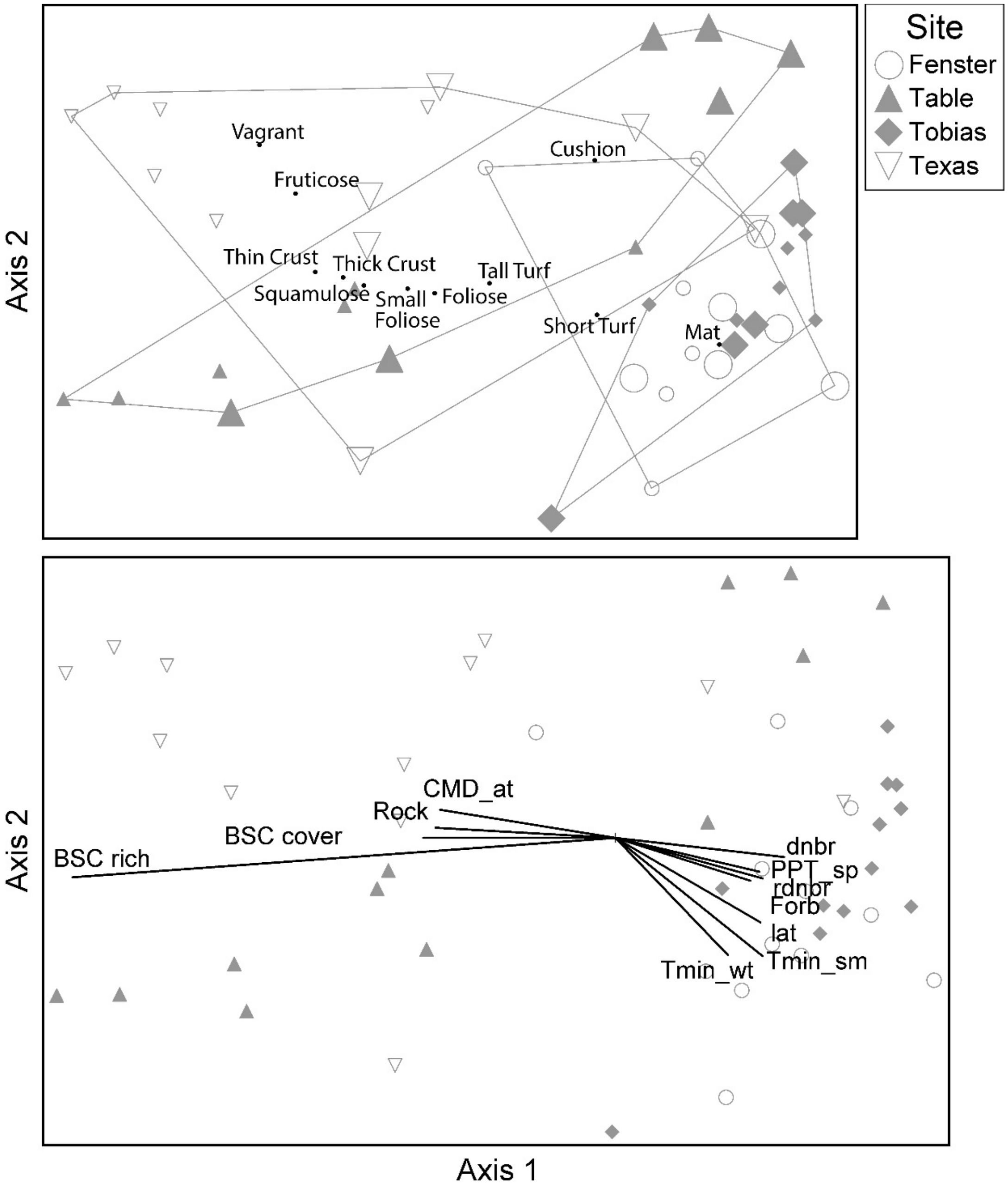

Figure 4: Ordination of BSC growth forms found at four sites in Idaho, USA. Each gray point represents a plot, with points closer to each other having a more similar composition of BSC growth forms. Plots from the same site have the same symbol. In the upper panel, plots are larger if they are within the fire perimeter and smaller if they are unburned; plots from the same site are connected into a polygon using 5 gray lines. Small black circles represent the centroid of each BSC growth form on the ordination. In the lower panel, labelled 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 the autumn (CMD_at), precipitation in spring (PPT_sp), and minimum temperature in summer and winter (Tmin_sm, Tmin_wt).

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Table 1: Characteristics of sites sampled in Idaho, USA in 2015. Includes fire ignition dates[1] and characteristics averaged across all plots, burned and unburned, at each site, including elevation, mean annual precipitation (30-year average from 1981 to 2010[2]), soil pH and most common soil texture.

Site name	Ignition	Elevation (m)	Precipitation (mm)	pH	Soil texture
Texas	Aug 2 1999	1931	255	7.2	Sandy clay loam
Fenster Creek	Jul 14 2000	1983	343	6.5	Clay loam
Tobias	Jul 12 2003	1565	439	6.3	Clay loam
Table Mountain[3]	Apr 27 1999	2045	455	6.9	Sandy clay loam

[1] http://www.mtbs.gov/data/

[2] http://www.climatewna.com/

[3] This was the only prescribed fire in our study; the others were wildfires.

Table 2: Model details for BSC cover and BSC richness at the sites of four sites in Idaho, USA. Models have a 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

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Appendix

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.

Species	Acronym	Growth Form
Lichens		
Acarospora schleicheri	Acasch	Thick crustose
Amandinea punctata	Buepun	Thin crustose
Arthonia glebosa	Artgle	Squamulose
Aspicilia filiformis complex	Aspfil	Fruticose
Aspicilia reptans complex	Aspici	Thick crustose
Bryoplaca jungermanii	Caljun	Thin crustose
Buellia epigaea	Bueepi	Thick crustose
Caloplaca atroalba	Calatr	Thin crustose
Caloplaca stillicidiorum	Calsti	Thin crustose
Candelariella aggregata	Canagg	Thin crustose
Candelariella rosulans	Canros	Thick crustose
Circinaria hispida	Asphis	Fruticose
Cladonia chlorophaea, C. fimbriata, C. imbricarica, C. pocillum, C. pyxidata	Cladon	Squamulose
Diploschistes muscorum	Dipmus	Thick crustose
Enchylium tenax	Colten	Small foliose
Endocarpon loscosii	Endlos	Squamulose
Endocarpon pusillum	Endpus	Squamulose
Myriolecis crenulata	Leccre	Thin crustose
Myriolecis flowersiana	Lecflo	Thin crustose
Protoparmeliopsis garovaglii	Lecgar	Foliose
Myriolecis hagenii	Lechag	Thin crustose
Lecanora laxa	Leclax	Thin crustose
Lecanora sp. 4	Lecsp4	Thin crustose
Myriolecis zosterae	Leczos	Thin crustose
Lecidea laboriosa	Leclab	Thin crustose
Lecidella stigmataea	Lecsti	Thin crustose
Lecidella wulfenii	Lecwul	Thick crustose
Lepraria spp.	Leprar	Thick crustose
Megaspora verrucosa	Megver	Thick crustose
Melanohalea exasperatula	Melexa	Foliose
Ochrolechia uppsaliensis	Ochupp	Thick crustose
Parvoplaca tiroliensis	Caltir	Thin crustose

Peltigera canina	Pelcan	Foliose
Peltigera didactyla	Peldid	Foliose
Peltigera kristinssonii	Pelkri	Foliose
Peltigera ponojensis	Pelpon	Foliose
Phaeophyscia constipata	Phynar	Foliose
Phaeorrhiza sareptana	Phasar	Squamulose
Physconia isidiigera, P. muscigena	Physcon	Foliose
Placidium sp.	Placid	Squamulose
Placynthiella icmalea	Plaicm	Thick crustose
Placynthiella uliginosa	Plauli	Thick crustose
Psora cerebriformis	Psocer	Squamulose
Psora decipiens	Psodec	Squamulose
Psora montana, P. globifera	Psomon	Squamulose
Psora tuckermanii	Psotuc	Squamulose
Rhizoplaca haydenii	Rhihay	Vagrant
Rhizoplaca melanopthalma ssp. cerebriformis	Rhimel	Vagrant
Rinodina terrestris	Rinter	Thin crustose
Scytinium lichenoides, Scytinium tenuissimum	Leptog	Small foliose
Tetramelas terricolus	Bueter	Thick crustose
Toninia sedifolia	Tonsed	Thick crustose
Xanthocarpia lactea	Callac	Thin crustose
Xanthocarpia tominii	Caltom	Thin crustose
Xanthomendoza fulva	Xanful	Foliose
Xanthoparmelia wyomingica, X. neochlorochroa, X. chlorochroa, X. camtschadalis	Xantho	Vagrant
Bryophytes		
Barbula convoluta	BBarcon	TurfShort
Brachytheciastrum collinum	BBracol	Mat
Brachythecium albicans	BBraalb	Mat
Bryoerythrophyllum recurvirostrum	BBryrec	TurfShort
Bryum argenteum	BBryarg	TurfShort
Cephaloziella divaricata	BCepdiv	Mat
Ceratodon purpureus subsp. *conicus*	BCerpur	TurfShort
Clevea hyalina	BClehya	Mat
Desmatodon leucostoma	BDesleu	TurfShort
Encalypta rhaptocarpa var. *trachymitra*	BEncrhap	TurfShort
Eurhynchiastrum pulchellum	BEurpul	Mat
Gemmabryum caespiticium	BGemcae	TurfShort
Grimmia calyptrata	BGrical	Cushion
Grimmia ovalis	BGriova	Cushion
Phascum cuspidatum	BPhacus	TurfShort

Pohlia cruda	BPohcru	TurfShort
Polytrichum juniperinum	BPoljun	TurfTall
Pterygoneurum ovatum, P. subsessile	BPte	TurfShort
Syntrichia caninervis	BSyncan	TurfTall
Syntrichia montana	BSynmon	TurfTall
Syntrichia norvegica	BSynnor	TurfTall
Syntrichia papillosissima	BSynpap	TurfTall
Syntrichia subpapillosissima	BSynsub	TurfTall