Prescribed Fire Decreases Lichen and Bryophyte Biomass and Alters Functional Group Composition in Pacific Northwest Prairies

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Abstract

The reintroduction of fire to Pacific Northwest prairies has been useful for removing non-native shrubs and supporting habitat for fire-adapted plant and animal species. However, very little is known about the influence of fire on prairie bryophyte and lichen communities. In this study, we investigated the effects of fire on ground-dwelling bryophytes and lichens by estimating standing biomass, cover, mat depth and functional group diversity in burned and unburned plots at five prairie sites located in the south Puget Sound bioregion of Washington State. After accounting for differences among sites, the bryophyte and lichen ground layer in burned plots had about 18% the biomass and about 60% the cover of unburned plots. All ground layer functional groups had lower average biomass in burned plots, except for ephemeral mosses, which had greater biomass. Forage lichens and nitrogen-fixing lichens were absent from all five burned plots. Of particular concern are the regionally rare, state-listed reindeer forage lichens (*Cladonia ciliata* var. *ciliata, Cladonia ciliata* var. *tenuis* and *Cladonia portentosa* ssp. *pacifica*), which occur at three of the five prairies we surveyed. Our results indicate that some lichen populations could be extirpated from these sites if they are not considered in prescribed burn management plans. We suggest some options that could maintain ground layer integrity while balancing other management objectives in the south Puget Sound prairies.

Keywords: prescribed fire, lichens, mosses, biomass, ground layer, prairies, Puget Sound

Introduction

The glacial outwash prairies of the Puget Sound bioregion of western Washington represent a critically endangered ecosystem with less than 2% of its historical area remaining. The open structure and composition of these glacially-formed prairies were maintained for centuries by Native American burning until the early 1800s when fire exclusion became standard practice (Boyd 1999). In addition to hosting a diverse vascular plant community (Dunwiddie et al. 2006, Dunwiddie et al. 2014), the south Puget Sound prairies are home to at least 65 ground-dwelling bryophytes (mosses, hornworts and liverworts) and lichens, including a number of rare lichen species restricted to this habitat (Smith et al. 2012, WNHP 2014, Calabria et al. 2015). However, ground layer mosses and lichens are seldom included in conservation and restoration programs. Prescribed burning is often the cornerstone tool used in restoring degraded prairie habitat because it effectively removes many non-native plants in favor of native, fire-adapted grasses and forbs, and prevents encroachment of surrounding coniferous forests (Stanley et al. 2011). Current management objectives for Puget Sound prairies include the reduction or removal of thick bryophyte layers to expose soil for native vascular plant germination (Hamman et al. 2011), although bryophytes may have facilitative or inhibitory effects on seed germination in grasslands (Ryser 1990, Jeschke and Kiehl 2008). The extent to which prescribed fire affects bryophyte and lichen ground layers of Puget Sound prairies is not well known.

Altered disturbance regimes, including over 100 years of fire exclusion, may explain why bryophytes and lichens are present in such great

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abundance in today's Puget Sound prairie remnants. Similar conclusions have been drawn for unburned Willamette Valley prairies where moss and lichen species more typical of mesic sites are abundant (Wilson 1998). Because these taxa are perceived as an artifact of fire suppression in Northwest prairies, little attention has been paid to understanding their ecological functions or the ecosystem services that they may be providing. Globally, ground-dwelling bryophytes and lichens contribute significantly to biogeochemical cycles by fixing nitrogen (N) and carbon (C) (Giddens 1982, Elbert et al. 2012, Lindo et al. 2013), in addition to reducing soil erosion (Schulten 1985), regulating soil temperature, influencing nutrient cycles and water cycles (Kasischke et al. 1995, van der Wal and Brooker 2004) and providing food, habitat and chemical defenses for vertebrates and invertebrates (Gersun 1982, Hesbacher et al. 1995, Cooper and Wookey 2001, Anderson 2006).

Previous studies have demonstrated negative immediate impacts of prescribed fire on ground-dwelling lichen communities in grassland and prairie ecosystems (Antos et al. 1983, Schulten 1985). Pre-fire lichen population size, fire intensity and fire frequency have been implicated as factors that influence post-fire lichen survival and recovery (Bowker et al. 2004, Johansson and Reich 2005). In boreal and tundra habitats, complete recovery of reindeer lichen mats may take anywhere from 30 to 120 years (Brodo et al. 2001, Holt et al. 2008). In a wet prairie ecosystem in the Willamette Valley of Oregon, Holt and Severns (2005) found a decreasing trend in lichen cover with increasing fire frequency and no recovery of reindeer lichens five years after a fall prescribed burn. A recent study at Mima Mounds prairie, in the south Puget Sound ecoregion of Washington, found that reindeer lichens occurred in areas that were burned 15–20 years ago, suggesting that reindeer lichens can recover at least partially following prescribed fires when healthy populations occur in close proximity to burned areas (Smith et al. 2012).

The main objective of this study was to investigate the effects of prescribed burning practices on prairie lichen and bryophyte communities and functions. We compared bryophyte and lichen cover, mat depth and functional group diversity in burned and unburned plots at five prairies in the south Puget Sound bioregion of Washington to quantify potential effects of burning. With this information, we estimated standing biomass and elemental content (carbon and nitrogen) for lichen and bryophyte functional groups in burned and unburned plots to test overall post-fire response.

Methods

Study Area

Our study was conducted at five Puget Sound prairies selected with three criteria: 1) similar habitat quality, defined by the ratio of native to non-native forbs and grass species; 2) available site management history; and 3) accessibility. The Puget Sound lowlands, where these prairies occur, receive an average of 118 cm of annual rainfall, concentrated in the fall and winter, and the average temperature is 11.4 °C (WRCC 2012). Our study sites included: Glacial Heritage Preserve (GH), Mima Mounds Natural Area Preserve (MM), Scatter Creek Wildlife Area (SC), West Rocky Prairie (WR), and one site located on Joint Base Lewis-McChord (JBLM), referred to as Training Area 15, or TA-15 (Table 1). All of these prairie sites occur on either Nisqually or Spanaway complex soil types, characteristic of prairies in this region. The gravelly sandy loam glacial outwash soils are excessively well-drained, supporting plant species adapted to seasonal drought and low nutrient availability, including native Roemer's fescue (*Festuca roemeri)* and common camas (*Camassia quamash)*. Lichens and mosses provide substantial ground cover in south Puget Sound prairies, particularly in areas of low management intensity. Restoration and management strategies over the past two decades have varied among sites (Table 1), but have typically included a combination of mowing, herbicide application, and prescribed burning to reduce exotic species. Exotic species include tall oatgrass (*Arrhenatherum elatius),* sweet vernal grass (*Anthoxanthum odoratum*), colonial bentgrass (*Agrostis capillaris*), oxeye daisy (*Leucanthemum vulgare*) and scotch broom (*Cytisus scoparius*). Post-fire treatments have included direct seeding and/or planting of native

TABLE 1. Summary of burn history and herbicide application for burned and unburned plots located at five south Puget Sound prairies. Fire history includes any burns conducted in the units we sampled between 1993 and 2013. Unburned sites have not been burned in at least 20 years. Abbreviations for seasons include FA = Fall (Sept–Oct) and SU = Summer (July–Aug). Herbicide treatments included Fusliade© or Poast© for grass-specific applications, Garlon© for broadleaf-specific applications, and Glyphosate© for broad-spectrum applications between 1993 and 2013. Frequency of herbicide applications varied between sites and most were "spot" treatments applied to target invasive species. All study areas were subject to scotch broom (*Cystisus scoparius*) removal using Garlon© herbicide, hand-pulling and/or mowing.

Site name	Fire history	Broad spectrum herbicide	Broad-leaf specific herbicide	Grass-specific herbicide
Glacial Heritage	FA06; SU09; SU11	Yes	Yes	Yes
	Unburned	No	Yes	Yes
JBLM TA-15	FA1998; SU10; SU12	No	Yes	No
	Unburned	No	Yes	Yes
Mima Mounds	FA1994; FA11	Yes	Yes	Yes
	Unburned	No	Yes	Yes
Scatter Creek	FA11	No	No	Yes
	Unburned	No	No	No
West Rocky	SU11	Yes	No	Yes
	Unburned	No	No	No

vascular plants. Many of the remaining Puget Sound prairie sites are also threatened by encroaching conifer forests dominated by Douglas-fir (*Pseudotsuga menziesii*).

Study Sites

Glacial Heritage Preserve (46.865861°N, 123.041178°W) is a 459 ha area managed by the Center for Natural Lands Management (CNLM) and owned by Thurston County. The federally endangered Taylor's checkerspot butterfly (*Euphydryas editha taylori*) and the federally threatened golden paintbrush (*Castilleja levisecta*), have both been reintroduced to this site within the past 10 years. Glacial Heritage prairie also hosts three state-listed lichens considered rare in Washington (WNHP 2014): *Cladonia novochlorophaea*, *C. ciliata* var. *tenuis* and *C. portentosa* ssp. *pacifica,* and one additional species, *C. concinna,* that has been recommended for state-listing as rare due to its limited distribution. These species have been previously reported from unburned (but not burned) areas at this site (Calabria et al. 2015).

Mima Mounds Natural Area Preserve (46.903076°N, 123.05028°W) was established in 1976 to protect rare examples of mima mound landforms and Puget prairie grasslands. Owned and managed by the Washington State Department of Natural Resources (DNR), the site hosts 257 ha of open, mounded grasslands and mature coniferous forest. The site also includes a small Garry oak (*Quercus garryana*) woodland and supports a variety of prairie-dependent butterflies and birds. In addition to endemic vascular plants and animals, robust populations of both mosses and lichens also occur; of special concern are state-listed and regionally rare reindeer lichens, *Cladonia ciliata* var. *ciliata*, *C. ciliata* var. *tenuis* and *C. portentosa* ssp. *pacifica* (Smith et al. 2012, Calabria et al. 2015).

West Rocky Prairie (46.891028°N, 123.873327°W) is a 323 ha wildlife area owned and managed by the Washington Department of Fish and Wildlife (WDFW). The site is situated on a large glacial outwash plain, which developed along the southern terminus of the Puget Lobe of the Vashon ice sheet. The site consists of short-grass prairie, oak woodland, wet prairie, forested wetlands, riparian forest, conifer-dominated forest, and mixed conifer/hardwood forest. The upland prairie at West Rocky has been invaded by several non-native grass, forb and shrub species. West Rocky prairie is home to the federally threatened Oregon spotted frog (*Rana pretiosa*) and golden paintbrush. Ground-dwelling mosses and lichens, including state-listed rare reindeer lichens, *Cladonia ciliata* var. *ciliata*, *C. ciliata* var. *tenuis*, *C. portentosa* ssp. *pacifica,* and *C. novochlorophaea*, are abundant in unburned areas (WNHP 2014, Calabria et al. 2015).

Scatter Creek Wildlife Area (46.831527ºN, 123.0226644ºW) is a 374 ha area owned and managed by WDFW, and is located on the historic Grand Mound Prairie 18 miles due south of Olympia, Washington. Scatter Creek hosts additional habitats surrounding the 264 ha of open prairie, including oak woodland, wet prairie and riparian habitat, mixed conifer with scattered oak woodland, and conifer forest. It also includes rare plant species such as dwarf checkerbloom (*Sidalcea malviflora* ssp. *virgata*), California compassplant (*Wyethia angustifolia*), Hall's aster (*Symphyotrichum hallii*) and smallflower trillium (*Trillium parviflorum*), as well as animal species of conservation concern including the mardon skipper butterfly (*Polites mardon*), Taylor's checkerspot butterfly, and the Mazama pocket gopher (*Thomomys mazama*). The rare reindeer lichens *Cladonia ciliata* var. *ciliata* and *C. ciliata* var. *tenuis* can be found scattered throughout this preserve.

Joint Base Lewis-McChord (JBLM) (46.862802ºN, 128.8474434ºW) hosts approximately 90% of the remaining prairie in the Puget Trough (Kronland and Martin 2015). While many prairies on JBLM have been invaded by scotch broom and other nonnatives, the upland prairies in the artillery impact areas host the most diverse and abundant native plants in the entire ecoregion. Four federally-listed species are found at JBLM, including the streaked horned lark (*Eremophila alpestris strigata*), Taylor's checkerspot butterfly, Mazama pocket gopher and the Oregon spotted frog. Managers at JBLM work with the U.S. Fish and Wildlife Service to conserve endangered habitat while maintaining open training lands. Our study site, referred to as Training Area 15 (TA-15), is located in the southwestern portion of the JBLM prairie complex. This relatively flat, open prairie consists of native grass- and forb-dominated areas as well as areas dominated by invasive pasture-grass with two riparian corridors (Muck Creek and South Creek) that converge in the middle of TA-15.

Burn History

Historical fire records pre-dating the 1980s are sparse for south Puget Sound prairie sites. We consulted with site managers to gather as much information as possible regarding recent burn history for each of the five prairies we surveyed. For the purposes of this study, sites with no known fire history within the last 20 years were designated as "unburned" reference sites, though these prairies were burned periodically (every 1–5 years) up through the mid-1800s by regional Native American tribes and some may have been burned in the early 1900s to clear areas for grazing (Boyd 1999, Storm and Shebitz 2006). Sites that experienced one to three fall-season burns within the last 10 years were considered "burned" (Table 1). All burned areas in our study were the result of intentionally managed prescribed fires, conducted during the dormant dry season (early August to early September).

Field Methods

We conducted all field sampling in March and April 2013. Within each burned and unburned area at each of the five prairie sites, we established one circular plot (68 m diameter, 0.378 ha area) based on a modified Ground Layer Indicator method (Smith et al. 2015). We used several criteria to select plot locations. First, we identified unburned areas that could hold a 68 m diameter circular plot. Then, we chose burned units of similar or greater size directly adjacent to the unburned area, with a buffer at least 30 m from the edge of the burn unit. If this was not possible, then the burned area was selected as near to the unburned plot as possible and with relatively similar topography, soil and vegetation types and management histories prior to burning. These parameters were determined using site management maps outlining polygons of burn treatments by year and by consultation with site managers. Plot centerpoints were selected randomly by tossing a microquad frame overhead near the center of the unit.

From a center stake within each plot, we established three 34 m transects radiating at 90, 210, and 330 degrees. We placed a 50 cm x 20 cm PVC quadrat frame lengthwise every three meters on the left side (facing outward from the centerpoint) of each transect, resulting in 33 microquads per plot. In each microquad, we visually estimated the percent cover of lichen and bryophyte functional groups using the cover classes 0–1%, 1–5%, 5–10% and 10% increments thereafter. Functional groups could overlap vertically, so total cover in microquads could exceed 100%. We recorded the depth of moss and lichen mats (thickness of both live and dead material) in the upper left and lower right hand corner of each microquad. We assigned functional group categories for each species according to Smith et al. (2015), with some modifications (Table 2).

Biomass, Carbon, and Nitrogen Estimates

We estimated standing biomass of bryophytes and lichens for burned and unburned plots using a bulk density calibration curve based on oven-dried moss and lichen samples (Smith et al. 2015). To calculate standing biomass, we multiplied bulk density estimates from the calibration curve by our field-measured volume (cover x mat depth) for each microquad, which we then averaged within and across sites, expressed in kg ha^{-1}. Carbon and nitrogen content were calculated using functional-group-specific percentages (Smith et al. 2015). Briefly, carbon was 44.38% of dry mass for all functional groups, and nitrogen ranged from 0.60–2.59% of dry mass, depending on functional group.

TABLE 2. Bryophyte and lichen functional groups occurring in south Puget Sound Prairies, WA including abbreviations, definitions, ecosystem functions and characteristic and common species. Functional group categories follow Smith et al. (2015), except ephemeral moss (EphMoss), which we designated as a new custom category for this study.

Abbreviation	Functional group	Definition	Ecosystem functions	Characteristic and common prairie taxa
FthrMoss	Feather mosses	Feather-like mosses with a prostrate growth form	Rainfall interception, soil cooling	*Brachythecium albicans, Kindbergia oregana, Niphotrichum elongatum, Rhytidiadelphus loreus*
TurfMoss	Turf mosses	Mosses with an upright or cushion-like growth form	Soil accrual, bare site colonization	*Gemmabryum caespiticium, Ceratodon purpureus, Dicranum scoparium, Polytrichum juniperinum,*
Livwrt	Liverworts	Non-moss bryophytes	Soil/detritus binding/ water infiltration	*Cephaloziella divaricata, Jungermannia rubra, Lophozia ventricosa*
EphMoss	Ephemeral mosses	Minute, short-lived mosses	Bare site colonization, disturbance indicator	*Funaria hygrometrica, Pleuridium subulatum*
ForagLich	Forage lichens	Fruticose macrolichens important for wildlife	Wildlife forage; habitat and nesting material	Branched *Cladonia (C. ciliata* var. *ciliata, C. ciliata* var. *tenuis, C. portentosa* subsp. *pacifica* f. *decolorans, C. rangiferina)*
NfixLich	N-fixing lichens	Macrolichens with N-fixing symbionts	N-fixation; decomposition of organic matter	*Peltigera* (*P. leucophlebia, P. neopolydactyla, P. ponojensis*)
OtherLich	Other lichens	Lichens that are not crusts, forage or N-fixing	Bare site colonization; soil trapping	Unbranched *Cladonia (C. albonigra, C. cervicornis, C. chlorophaea, C. cornuta, C. fimbriata, C. furcata, C. pyxidata, C. squamosa* var. *subsquamosa, C. verruculosa)*

Statistical Analysis

Ground layer attributes included biomass of mosses and lichens (both combined and separately), carbon content, nitrogen content, cover, and depth. Prior to analyses, we conducted a $\log_{10}(x+1)$-transformation on all attributes except cover to meet error distribution assumptions; we used arcsine square-root transformation on cover values. Inference on log-transformed data related to median, not mean, differences. We tested for burned vs. unburned differences in ground layer attributes using separate-means linear mixed models (random block effect = site; fixed effect = burn status; heterogeneous error variances among treatments) and orthogonal F-tests, which allow mean values to vary from site to site. We implemented these in package 'nlme' (Pinheiro et al. 2015) in R software version 3.1.2 (R Core Team 2015). Multiple comparisons for Table 3 (comparing mean values in burned vs unburned plots within each site) were simple linear models with R functions 'aov,' and 'TukeyHSD' in base R version 3.1.2 (R Core Team 2015).

To detect multivariate differences in functional group composition among burned and unburned sites, we performed blocked permutational multivariate analysis of variance (perMANOVA, Anderson 2001), implemented in R package 'vegan' (Oksanen et al. 2016). We used Bray-Curtis distances of $\log_{10}(x+1)$-transformed biomass values for each functional group per microquad, 9999 permutations, and restricted permutations within sites (blocks). We graphically interpreted functional group composition using nonmetric multidimensional scaling (NMS; Kruskal 1964) implemented in 'vegan' (Oksanen et al. 2016). We requested a 2-dimensional NMS solution with a maximum of 99 random starts and 500 iterations, Kruskal's (1964) stress formula 1, primary 'weak' treatment of ties, and final scores rotated to orthogonal principal axes. Variation explained was calculated as the Pearson correlation between ordination interpoint distances versus Bray-Curtis dissimilarities. We calculated weighted-average scores for functional groups in the ordination space.

Taxonomic Nomenclature

Bryophyte nomenclature follows Flora of North America (2007 and 2014). We used Missouri Botanical Garden's TROPICOS database (TROPI-

TABLE 3. Summary of averages ± standard deviations for bryophyte and lichen ground layer attributes at burned and unburned Puget prairie sites. Bold text indicates significance at 99.5% confidence level from an F-test of the burn coefficient in a simple linear model. Summaries for "each" site are based on 33 microquads per plot. Summaries for "all" sites are based on all 5 plots per burn status. See Methods section for site abbreviations.

Site Site	Burn status	Bryophyte+ lichen biomass (kg ha^{-1})	Bryophyte biomass (kg ha^{-1})	Lichen biomass (kg ha^{-1})	Carbon content (kg ha^{-1})	Nitrogen content (kg ha^{-1})	Cover (%)	Depth (cm)	Functional group richness
GH	Burned	4459 ± 3164	4459 ± 3206	**0 ± 0**	1980 ± 1405	45 ± 32	52 ± 20	**0.5 ± 1.0**	**2**
GH	Unburned	6177 ± 4046	5823 ± 4090	**352 ± 732**	2741 ± 1796	62 ± 40	60 ± 20	**2.0 ± 2.0**	**5**
JBLM	Burned	**338 ± 656**	**329 ± 657**	**10 ± 44**	**150 ± 291**	**3 ± 7**	**17 ± 17**	**0.2 ± 0.4**	4
JBLM	Unburned	**1766 ± 1810**	**1636 ± 1774**	**129 ± 311**	**783 ± 803**	**19 ± 20**	**42 ± 24**	**0.6 ± 0.7**	5
MM	Burned	**948 ± 1055**	**925 ± 1052**	**22 ± 86**	**420 ± 467**	**9 ± 10**	**29 ± 18**	**0.3 ± 0.5**	**5**
MM	Unburned	**8722 ± 4520**	**4279 ± 3690**	**4443 ± 4317**	**3871 ± 2006**	**71 ± 38**	**65 ± 22**	**2.5 ± 3.2**	**4**
SC	Burned	**1163 ± 1813**	**1163 ± 1837**	**0 ± 0**	**516 ± 805**	**13 ± 21**	**22 ± 14**	**0.5 ± 0.9**	**4**
SC	Unburned	**4195 ± 3426**	**3577 ± 2814**	**619 ± 1084**	**1862 ± 1520**	**48 ± 45**	**37 ± 27**	**1.9 ± 1.7**	**5**
WR	Burned	**1646 ± 2240**	**1646 ± 2270**	**1 ± 4**	**730 ± 994**	**16 ± 23**	**44 ± 27**	**0.4 ± 0.7**	**4**
WR	Unburned	**10461 ± 5955**	**5440 ± 4128**	**5020 ± 6895**	**4642 ± 2643**	**86 ± 41**	**68 ± 20**	**4.5 ± 3.4**	**6**
All sites	Burned	**1711 ± 1786**	**1705 ± 2461**	**7 ± 44**	**759 ± 792**	**17 ± 19**	**33 ± 19**	**0.4 ± 0.7**	**3.8**
All sites	Unburned	**6264 ± 3952**	**4151 ± 3694**	**2113 ± 4233**	**2780 ± 1754**	**57 ± 37**	**54 ± 23**	**2.3 ± 2.2**	**5.0**

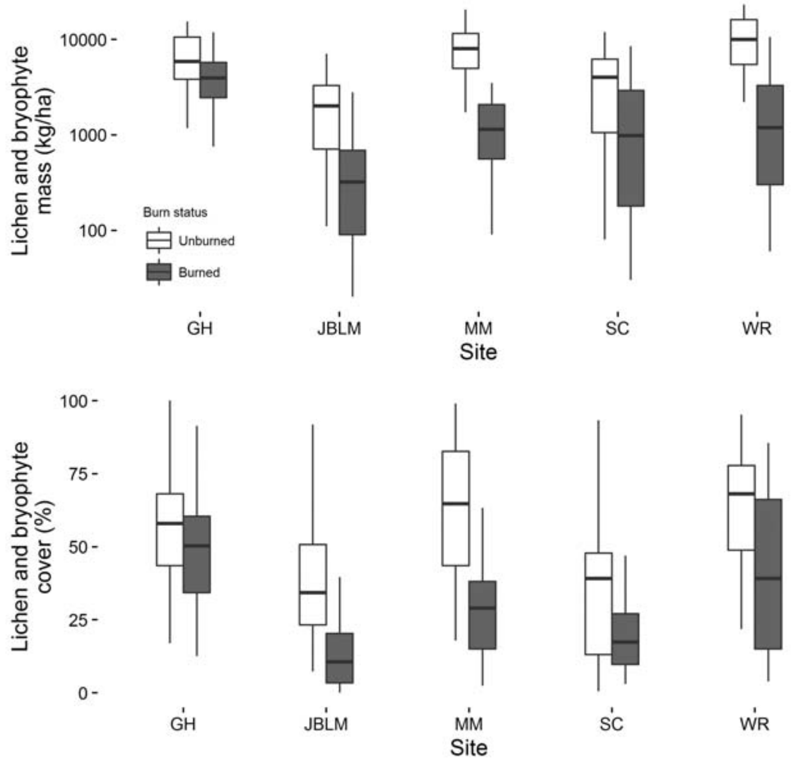

Figure 1. Boxplot distributions of biomass (*top row*) and cover (*bottom row*) of ground layer bryophytes and lichens at five Puget prairie sites, each with one burned and one unburned plot and 33 microquads per plot. Central bars are 50th percentile of microquad values (the median), boxes include the 25th thru 75th percentile of microquad values, whiskers include 1.5 times the interquartile range, outliers beyond 1.5 x IQR omitted for clarity.

COS 2016a, b, and c) for liverwort nomenclature not yet published in the Flora of North America. Lichen nomenclature follows Esslinger (2015).

Results

Bryophyte and lichen biomass differed significantly between burned and unburned areas. After accounting for differences among sites, median $\log_{10}$-biomass in the burned plots was 18.7% that of the unburned plots (95% CI: 8.1–43.0%; $F_{1, 2304} = 15.5$; $P < 0.0001$)(Figure 1). In other words, only about one-fifth the biomass of unburned sites (6264 ± 3952 kg ha^{-1}, mean ± SD) was found in burned sites (1711 ± 1786 kg ha^{-1}), or a decrease of about four-fifths. The ratio of bryophyte to lichen biomass shifted from 66:34 in unburned plots to 99:1 in burned plots (Table 3). All ground layer functional groups had lower biomass in the burned plots ($F_{6, 2292} = 47.7$, $P < 0.0001$ for burn x functional group interaction term), with the exception of ephemeral mosses which had greater biomass in burned plots (Figure 2).

After accounting for differences among sites, mean cover of ground layers in the burned plots was 20.8 percentage points lower than the unburned plots (95% CI: 11.8–29.8 percentage points; $F_{1, 2304} = 20.7$; $P < 0.0001$) (Figure 1), a decrease of about two-fifths. Lichens exhibited particularly severe decreases: in contrast to the unburned areas, where lichens comprised 26% of the total bryophyte and lichen ground layer cover, there were only trace amounts (0.03%) of lichens in

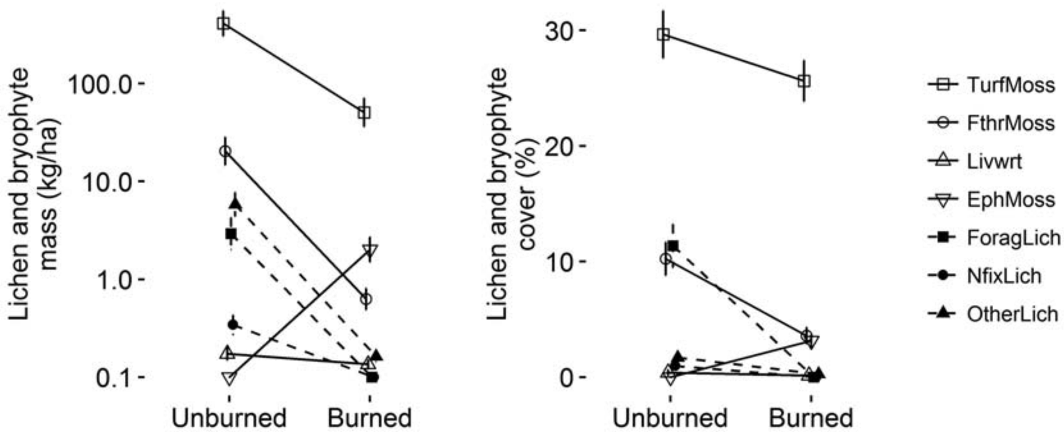

Figure 2. Biomass (*left*) and cover (*right*) of seven bryophyte and lichen functional groups recorded in burned vs unburned plots at five Puget Sound prairie sites (points = group means, bars = 99.5% CI). Bryophytes are open symbols with solid lines, lichens are filled symbols with dotted lines.

the burned plots. In total, terrestrial lichens and bryophytes contributed a mean ± SD of 57 ± 37 kg N ha^{-1} and 2780 ± 1754 kg C ha^{-1} to unburned plots and 17 ± 19 kg N ha^{-1} and 759 ± 792 kg C ha^{-1} to the burned plots (Table 3).

All functional groups had significantly lower cover in the burned plots ($F_{6, 2292} = 11.5, P < 0.0001$ for burn x functional group interaction term), with the exception of ephemeral mosses, which had greater cover (Figure 2). Functional group richness was also significantly lower in burned plots than in unburned plots (Table 3). Turf mosses contributed the greatest overall biomass and cover in both burned and unburned plots (Appendix 1). Mean biomass of turf mosses was 62.2% lower, while mean cover of turf mosses was 13.8% lower in burned plots than unburned plots. Forage lichens and nitrogen-fixing lichens were not observed in the burned plots (Appendix 1), but we observed trace amounts of these functional groups outside of our plots in some burned sites.

The final 2-dimensional NMS solution (Figure 3) had stress = 14.5%, explained 89.9% of the variation in functional group composition, and revealed clear differences in composition between burned and unburned plots. Ephemeral mosses and turf mosses characterized burned sites, while all other functional groups were almost entirely restricted to unburned sites. Functional group composition differed significantly among burned vs. unburned plots (blocked perMANOVA pseudo-F = 40.8, $P = 0.0001$), however burn status explained only 9.5% of the variation in functional group composition, while differences among sites explained 15.4% (Table 4).

Discussion

Fire Effects on Prairie Bryophyte and Lichen Biomass

This study provides the first standing biomass estimates for ground layer mosses and lichens in a western Washington prairie ecosystem, and identifies how fire management influences the functional group composition of ground layers. Bryophyte and lichen ground layer biomass for burned south Puget Sound prairies was approximately one-fifth that of unburned areas. Previous studies have demonstrated similar negative impacts of prescribed fire on ground-dwelling lichen communities in grassland and prairie ecosystems of the Midwestern US (Schulten 1985, Johansson and Reich 2005), the intermontane West (Antos et al. 1983), and the Willamette Valley of Oregon (Holt and Severns 2005). Our results also indicate a significant decrease in ground layer biomass due to prescribed burning practices in the south Puget Sound prairies. Such decreases may have lasting im-

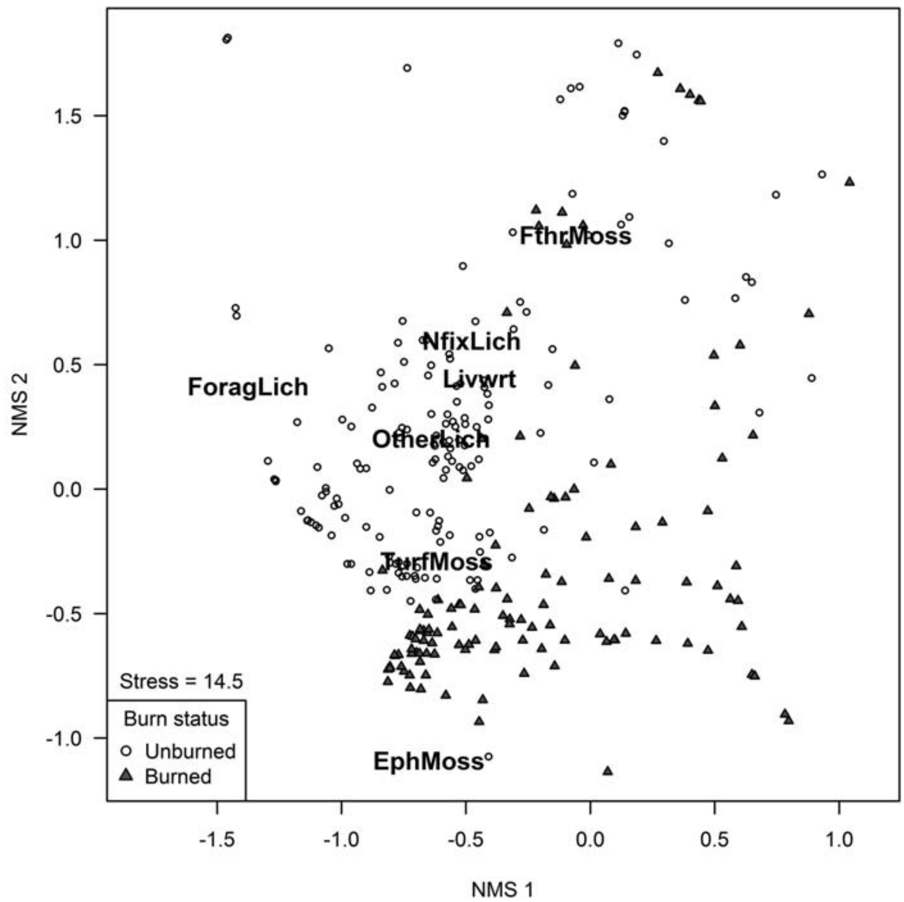

Figure 3. NMS ordination of burned and unburned microquads in functional group space. NMS was based on Bray-Curtis distances of $\log_{10}(x+1)$-transformed biomass values for each functional group per microquad. Each functional group name is the weighted average centroid for that group. The distance from each centroid to each plot roughly indicates how influential it is to that plot or set of plots. Ordination stress was 14.5%, and the configuration explained 89.9% of the variation in functional group composition.

TABLE 4. Results of blocked per MANOVA test of differences in functional group composition among sites and burn status groups, based on Bray-Curtis dissimilarities of $\log_{10}(x+1)$-transformed biomass data.

Coefficient	*df*	Sum of squared error	Mean squared error	Pseudo-*F*	R^2	*P*
Site	4	14.1	3.52	16.6	0.154	0.0001
Burn status	1	8.7	8.66	40.8	0.095	0.0001
Residuals	324	68.8	0.21	0.752		
Total	329	91.5	1			

pacts on ecosystem-level carbon sequestration, nutrient cycling capacity and water relations.

Differences in ground layer biomass between sites can likely be attributed to different site management histories, including varying fire regimes and overlapping management strategies such as direct seeding, herbicide application and mowing. For example, most JBLM prairies, including our TA-15 study site, have been burned regularly (at two- to five-year intervals) over the past four decades (Tveten and Fonda 1999), leading to the very low bryophyte and lichen cover we observed. Other site conditions such as proximity to forests and riparian areas and variation in soil types can contribute to differences in ground layer attributes. Future studies should examine pre- and post-burn plots and within-burn variability at additional sites to better understand prairie bryophyte and lichen recolonization rates and successional patterns after fire.

Fire Effects by Functional Group and Impacts on Rare Lichen Species

Some important ecosystem functions performed by lichens and bryophytes of the south Puget Sound prairies were generally absent in burned areas. Most notably, forage lichens and nitrogen-fixing lichens were absent from all burned plots. Forage lichen species of particular concern include regionally rare, state-listed reindeer lichens (*Cladonia ciliata* var. *ciliata, Cladonia ciliata* var. *tenuis* and *Cladonia portentosa* ssp. *pacifica*). These taxa occur at three of the five prairies we surveyed and are particularly sensitive to fire (Yahr 2000, Holt and Severns 2005, Calabria et al. 2015). Current management prescriptions for the south Puget Sound prairies include burning small management units (5–80 acres) on a rotation of three to five years (Hamman et al. 2011). At sites where forage lichen are broadly distributed, we recommend excluding fire from areas with high cover to create refugia; this should be sufficient to maintain populations of these lichens. Transplantation and sowing reindeer lichen fragments and/or whole thalli have been implemented with some success in northern-latitude caribou habitats (Roturier and Bergsten 2009). Similar experiments could be undertaken at prairie sites in the south Puget Sound where forage lichen populations have been negatively impacted by fire.

Shifts in bryophyte and lichen functional group composition due to prescribed burning practices could also impact nutrient cycling on the prairies through decreases in nitrogen-fixing species. Nitrogen-fixing lichens such as *Peltigera* spp. create soil microsites with higher biologically-available nitrogen (Knowles et al. 2006). Though not assessed in this study, feather moss–cyanobacterial associations result in substantial nitrogen inputs, since several feather mosses that occur in the south Puget Sound prairies (*Pleurozium schreberi, Rhytidiadelphus triquetrus*) associate with nitrogen-fixing cyanobacterial symbionts (DeLuca et al. 2002, Zackrisson et al. 2009, Lindo and Whiteley 2011). Future studies examining the overall abundance of nitrogen-fixing feather mosses in burned and unburned areas, as well as seasonal patterns of nitrogen-fixation rates for individual species, are needed to assess the effects of fire on prairie nitrogen cycles.

The "other lichen" functional group cover was lower in burned plots. Belonging to this functional group are the state-listed *Cladonia novochlorophaea* and *C. concinna*, which can both be easily overlooked in the field because of their small stature and morphological similarity to more commonly occurring species. The only collections of *C. novochlorophaea* from the western United States are from south Puget Sound prairies (Arnold 16 EVE; Hammer 1995 as *C. merochlorophaea* var. *novochlorophaea*; Hennings 1310, 1383, 1254 DUKE; Hynson 01 EVE; McCune 29914, OSC; Nelson 4249, herb. Nelson). Based on known collections (Charatz 05 EVE, Hammer 4379, FH, Rose 2015-95 EVE) and herbarium records (CNALH 2014), *Cladonia concinna* has only two localities in WA, one of which is our study site, Glacial Heritage Preserve. Therefore, these rare taxa may be at risk of local extirpation if strategic measures cannot mitigate their loss during prescribed burning. We suggest mapping known populations and creating fire exclusion areas to help foster recolonization by the dispersal of fragments and spores from existing populations. Additional surveys are also needed to estimate the distribution and abundance of these species at other sites.

On average, bryophytes covered a substantial portion of both burned (33%) and unburned (54%) plots in our study. Yet, bryophyte functional groups shifted dramatically with burning, as perennial feather mosses (*Rhytidiadelphus triquetrus, Kindbergia oregana*) and tall turf mosses (*Dicranum scoparium*, *Niphotrichum* *elongatum*) were found primarily in unburned plots, while early-colonizing and fire-adapted mosses characterized burned plots, including short and dense turf mosses (*Certatodon purpureus*, *Polytrichum juniperinum*), short-lived and ephemeral mosses (*Funaria hygrometrica, Pleuridium subulatum*) and leafy liverworts (*Cephaloziella divaricata*). Bryophyte mats sometimes inhibit germination and establishment of vascular plants due to allelopathy, alterations in moisture, light and temperature, or the physical barrier preventing seed-soil contact (van Tooren 1988, Morgan 2006, Serpe et al. 2006, Jeschke and Kiehl 2008). Less is known about how individual bryophyte species affect germination and survivorship of native (and non-native) vascular plant seedlings (Zamfir 2000, Serpe et al. 2006, Soudzilovskaia et al. 2011). Accordingly, shifts in bryophyte functional groups associated with burning should be further examined for potential impacts on plant germination and survival.

Prairie lichens and bryophytes play a large role in maintaining areas of "open" ground, which is an important habitat feature for the endangered Taylor's checkerspot butterfly (Schultz et al. 2011). "Open ground," as defined by regional biologists, is any type of ground cover (bare soil, litter, moss, lichen) less than two inches deep. This habitat component is important for butterflies, as it allows for warm, protected basking sites. In some unburned plots we observed an unbroken layer of short-statured, unbranched *Cladonia* and small turf mosses, species typical of biotic soil crusts in more arid ecosystems (Belnap et al. 2003). A review of the important habitat features for the Quino Checkerspot butterfly (*Euphydryas editha quino*) in southern California suggests that the presence of undisturbed cryptobiotic crust layers may promote higher cover of native annual host plants than in areas where the crust layer has been disrupted, and it may create "bare ground" features that support butterfly thermoregulation (Mattoni et al. 1997). Thus, protecting and maintaining areas with crust-like layers of unbranched *Cladonia* and small turf mosses may provide attractive basking sites for the native Taylor's checkerspot butterfly in south Puget Sound prairies.

Management Considerations

Prairie managers face many challenges when developing restoration and conservation targets for prairie plant and animal communities (Dunwiddie and Bakker 2011). They must consider a broad range of restoration strategies to manage a suite of habitats and rare species (both federally/state protected and unprotected), often with conflicting or opposing management needs. Bryophytes and lichens present a particular challenge for managers because they include many cryptic and taxonomically challenging taxa, little is known about their diversity and functional roles relative to vascular plants, and they are sensitive to commonly used restoration methods like prescribed fire (Ray et al. 2015). With few historical records on the presence and distribution of bryophytes and lichens across the south Puget Sound prairies, it is difficult to know the exact composition of the moss and lichen ground layer prior to historical fire exclusion. This presents a challenge to the development of conservation targets for prairie bryophyte and lichen communities. More information on the diversity, functionality and responses of these organisms to different fire regimes will guide their protection and management, while also allowing for continued burning to promote the rare and endemic, fire-adapted plant and animal communities of the south Puget Sound prairies.

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Appendix 1

Mean percent cover and standard deviation of bryophyte and lichen functional groups in burned (n = 5) and unburned (n = 5) plots at five glacial outwash prairies, Washington, United States. Bold text indicates significance at 99.5% confidence level from an F-test of the burn coefficient in a simple linear model. Functional group descriptions in Table 2.

Site	Burn Status	ForageLich	OtherLich	NfixLichen	FthrMoss	TurfMoss	EphMoss	Livwrt
Glacial	Burned	-	-	-	-	42.2 ± 17.7	**10.2 ± 10.8**	-
Heritage	Unburned	0.8 ± 4.4	**2.7 ± 5.0**	0.2 ± 0.7	6.6 ± 16.7	49.3 ± 24.7	-	-
West	Burned	-	-	-	0.1 ± 0.2	40.8 ± 26.6	**2.7 ± 4.1**	0.1 ± 0.5
Rocky	Unburned	**23.9 ± 31.8**	**2.1 ± 4.0**	0.1 ± 0.5	2.8 ± 8.2	38.3 ± 28.3	-	0.2 ± 0.7
Mima	Burned	-	0.6 ± 1.9	-	**0.2 ± 0.7**	25.6 ± 16.5	2.4 ± 7.9	0.1 ± 0.5
Mounds	Unburned	**32.1 ± 30.7**	0.3 ± 0.7	-	**7.9 ± 16.0**	24.8 ± 24.3	-	-
Scatter	Burned	-	-	-	**15.4 ± 15.4**	**5.9 ± 8.3**	0.1 ± 0.5	0.4 ± 1.2
Creek	Unburned	-	**1.5 ± 2.9**	**4.2 ± 7.5**	**5.9 ± 5.9**	**24.1 ± 18.8**	-	1.5 ± 6.2
JBLM	Burned	-	0.6 ± 2.6	-	**2.3 ± 3.8**	13.7 ± 13.7	0.3 ± 0.7	0.1 ± 0.5
	Unburned	-	1.7 ± 3.2	0.3 ± 1.3	**27.9 ± 26.2**	11.9 ± 18.9	-	0.2 ± 1.3

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