Fire History and Woody Encroachment Influence Saxicolous Macrolichen Community Composition on Dolomite Outcrops in Dry Bluff Prairies of the Minnesota Driftless Area

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Abstract–Driftless Area bluff prairies are remnant dry grassland systems often containing abundant bedrock outcroppings. Bluff prairies frequently experienced fire before settlement and prescribed fire is an important tool used by contemporary managers to limit the spread of woody species in prairies. The frequency of occurrence of macrolichen taxa was investigated on dolomite rocks in southeastern Minnesota bluff prairies of differing fire histories and amounts of woody encroachment near Winona, Minnesota. Dolomite boulders or outcrops in prairie vegetation were surveyed randomly with a 1-m^2 plot and all saxicolous macrolichen taxa were recorded, as well as the fire history and estimated class of woody encroachment. Differences in plot richness among treatments were assessed for all taxa, and differences in plot richness between treatments were tested for three of the most frequently occurring taxa. There was a significant decrease in taxa richness per plot with increased numbers of burns. Plots with little or no woody encroachment had significantly lower richness per plot than those with high woody encroachment.

Introduction

Dry prairies occurring typically on steep bluff slopes with a southern or western aspect, locally referred to as goat prairies, are remnant grassland communities in the Driftless Area of the Upper Midwest, USA (Minnesota DNR 2005). Remnant bluff prairies are dry, exposed sites that have persisted through post-settlement fire suppression and land use change, and were once more widespread and contiguous with other fire-dependent communities, especially oak savannas (Curtis 1959, Thompson 1979). Bluff prairies in southeastern Minnesota are characterized by thin soils formed in loess and residuum with abundant rock fragments from the underlying bedrock and frequent bedrock outcrops (Minnesota DNR 2005). In these systems edaphic factors including exposure, slope, and soil texture play an important role in limiting woody invasion (Thompson 1979).

The effects of fire and woody encroachment on prairie plant communities have been studied extensively. Along with grazing, recurrent fire is a major disturbance process in prairies that affects species composition, community structure, and plant biomass production (Brockway et al. 2002, Dix and Butler 1954, Knapp et al. 1999). Weather conditions (temperature, humidity, wind velocity, year-to-year variation), topography, and seasonal timing, frequency, and intensity of burns are important factors in the effect of fire on prairies (Ewing and Engle 1988, Gibson and Hulbert 1987, Novak et al. 2021). Encroachment of woody plants into prairies follows either mismanaged grazing, complete lack of grazing, the cessation of frequent fire, or any combination of these factors (Briggs et al. 2002, Capozzelli et al. 2020). In general, woody encroachment in North American prairies and savannas decreases vascular plant species diversity and alters community composition (Abella et al. 2020, Ratajczak et al. 2012), while also impacting carbon dynamics (Scharenbroch et al. 2010).

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Lichens are diverse symbiotic organisms that contribute essential functions to ecosystems worldwide (Allen et al. 2019). Lichens grow very slowly compared to plants, generally within the range of 0.5–4 mm annually, and they exhibit a range of general growth forms with many intermediate types that defy easy classification (Brodo et al. 2001). Since lichens are highly diverse, they occur in diverse environmental conditions in a wide variety of microhabitats. Some species tolerate infrequent moisture whereas others need high humidity and frequent wetting to survive, and this variability in moisture requirements is very important in the distribution of lichens (Wetmore and Bennett 1997). Many important ecosystem functions are provided by lichens, such as mechanical and chemical weathering of rock surfaces, primary colonization, soil formation, nitrogen fixation, photosynthesis, as well as carbon fixation, denitrification, regulation of water flow, and water quality regulation (Zedda and Rambold 2015).

Relatively little is known about the effects of fire or woody encroachment on lichens in North American grasslands. In an ungrazed Montana grassland, terricolous lichens were almost completely eliminated by a hot wildfire and showed little signs of re-establishment a year later (Antos et al. 1983). In Puget Sound prairies in Western Washington state, mean terricolous lichen coverage was severely reduced (from 26% to 0.03%) by prescribed fires (Calabria et al. 2016). In a Minnesota old field grassland, soil-dwelling lichens were greatly reduced by fire in both the short and long term but survived lower intensity fire proportionally to their pre-fire population size (Johansson and Reich 2005). In an Iowa sand prairie, soil-dwelling lichens were reduced to 32.4% of their original cover by end of one season after fire and 10.7% by the end of the second season after fire (Schulten 1985). Previous studies have focused on the effects of fire on soil lichens, but no research has investigated the effects of fire on saxicolous lichens in upper Midwest prairies. As lichens are poikilohydric organisms, lacking mechanisms for regulating uptake and loss of water, lichen growth is dependent upon local microclimatic conditions (Canters et al. 1991, Hauck et al. 2007, Pearson and Lawrence 1965, Palmqvist and Sundberg 2000, Renhorn et al. 1997). Variations in light, moisture, and inclination of slope have previously been reported as important for community composition of limestone outcrop lichen communities in the Driftless Area (Foote 1966). It is assumed that with woody encroachment in a prairie there will be more shade coverage and higher humidity in microsites (Siegert and Levia 2011). Availability to light and moisture are important factors for lichen growth (Palmqvist and Sundberg 2000).

The objective of this study was to assess how the saxicolous macrolichen community composition was affected by fire history and woody encroachment. To address this objective, wecont assessed two hypotheses: Taxa richness at a given plot (plot richness) in the macrolichen community will decrease as number of burns at that plot increases; and Plot richness will be greater at plots with high woody encroachment than plots with low woody encroachment. In cases where individual lichens could not be reliably identified to species across all study sites, they were recorded as their genus; we collectively refer to species and generic groupings in this study as taxa. While we expect fire and woody encroachment to broadly influence the saxicolous microlichen communities, since lichens are a diverse group of organisms, we expect these factors to affect the frequency of individual lichen taxa differently.

Study Area

This study was carried out at sites in Winona County within 6.5 km of Winona, Minnesota in the Driftless Area (Fig. 1). In Minnesota, the Driftless Area is a plateau of rock strata that formed in the Paleozoic Era that is dissected by rivers and streams, and is character-

ized by steep-sided bluffs. The entire region of the Driftless Area in Wisconsin, Minnesota, Iowa, and Illinois was not glaciated during the last glacial maximum and retains a rugged topography distinct from the surrounding area (Knox 2019).

The areas of study sites ranged from approximately 0.4 to 9.8 ha (Table 1). The geological setting of the study sites is characterized by Prairie du Chien Group dolomite outcroppings on the upper portions of bluffs above Jordan sandstone exposures and scattered dolomite boulders of the Prairie du Chien Group mostly on the lower portions of the slopes (Setterholm 2014). Of eight sites, seven are actively managed to restore and maintain tallgrass prairie and oak savanna communities. They have been cleared of woody encroachment within nine years of the time of this study (Table 1). One site was not actively managed and not cleared at the time of study. Burned sites were done so by prescribed fire within six years of the time of this study, except one area burned by accidental fire in 2023 on Pleasant Bluff. All sites were bluff prairies with vegetation characterized by tallgrass prairie grasses, forbs, and occasionally trees of *Quercus macrocarpa* Michx. (Bur Oak), *Carya ovata* (P. Mill.) K. Koch (Shagbark Hickory), *Prunus serotina* Ehrh. (Black Cherry), and *Juniperus virginiana* L. (Eastern Redcedar). The most common species encroaching upon these sites was *Rhamnus cathartica* L. (European Buckthorn). Other encroaching species include European *Lonicera* spp. (honeysuckles), *Rhus* spp. (sumacs), *Populus tremuloides* Michx. (Quaking Aspen), and Eastern Redcedar. All sites were isolated prairie communities surrounded by oak savanna,

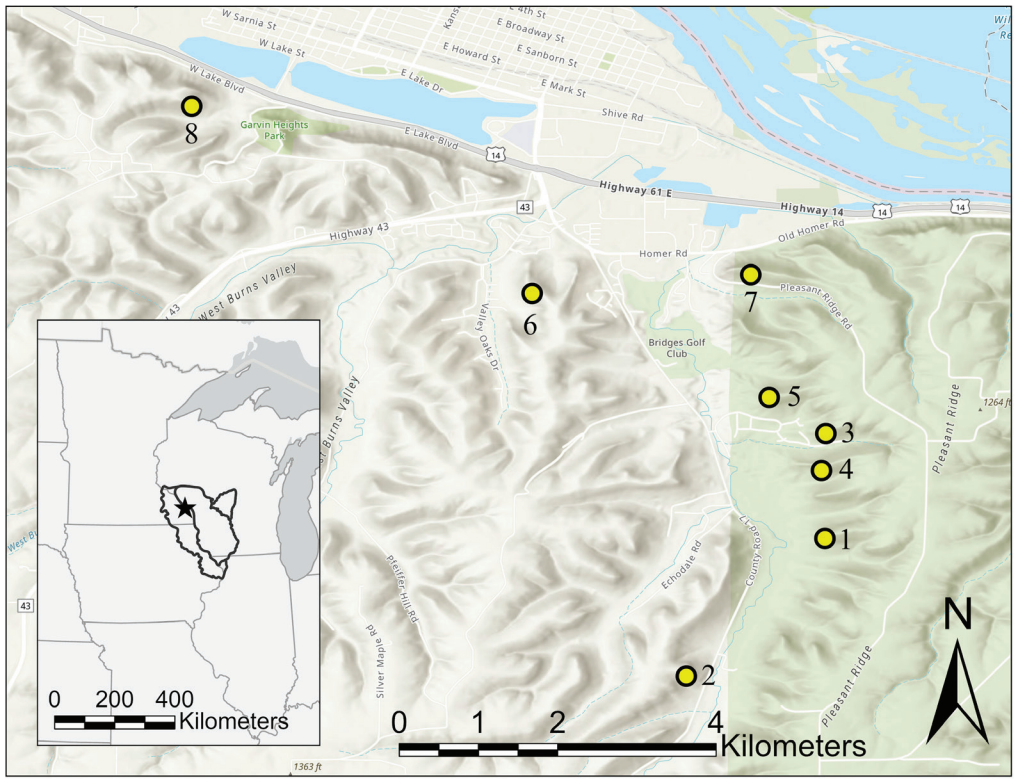

Figure 1. Map of study sites (indicated by yellow dots) near Winona, Minnesota, and location of Winona within the Driftless Area of the Upper Midwest, USA (indicated by a star). Sites and their corresponding numbers included Busch Bluff (1), Ericksen Bluff (2), Lallaman Bluff (3), McGuire Bluff (4), Miller Bluff (5), Old Baldy Bluff (6), Pleasant Bluff (7), and Woodlawn Bluff (8)

juniper-dominated woodland, or deciduous forest. Cut material in six of the seven managed sites had previously been concentrated into large piles and burned during the next winter following clearing. Miller Bluff was the only cleared site with unburned piles. Burn scars from such piles were not surveyed under the assumption that the fire intensity was extreme. Finer woody debris that was not piled was left in place and consumed by prescribed fire.

Materials and Methods

Field surveys

Surveying was completed between August 21 and October 5, 2023, and totaled 172 plots in eight sites: 52 plots with zero burns, 51 plots with 1 burn, and 69 plots with ≥2 burns. These sites included Busch Bluff, Ericksen Bluff, Lallaman Bluff, McGuire Bluff, Miller Bluff, Old Baldy Bluff, Pleasant Bluff, and Woodlawn Bluff. Sites were selected with known fire histories of the following three categories: unburned for at least 30 years or more, burned once, or burned two or more times.

Sites were surveyed by random 1-m^2 quadrat sampling, and sampling effort was scaled with the area of habitat at each site. Plots were randomly placed in targeted habitat recognized by level of woody encroachment and presence of herbaceous prairie vegetation in study sites. Quadrats were placed across large outcrops and immovable boulders at the eight study sites. Such habitat was assumed to have been exposed and available to macrolichens for a long period of time, rather than small fallen rocks or small outcrops more recently exposed by erosion. The term "macrolichen" traditionally refers to fruticose and foliose lichens. Although *Lecanora valesiaca* (Müll. Arg.) Stizenb., *L. muralis* (Schreb.) Rabenh., and *Squamulea galactophylla* (Tuck.) Arup, Søchting and Frödén are commonly classified as crustose microlichens, for this study we are including them with macrolichens given their size, relatively thick thalli, and lobed margins. All macrolichen taxa growing directly on rock within a 1-m^2

Table 1. Study sites and approximate study areas (ha), greatest number of burns at each site, management activities, and number of plots sampled of each fire history. The two largest sites, Old Baldy Bluff and Pleasant Bluff, had multiple burn units with different fire histories.

Site	Study Area (ha)	Greatest Number of Burns	Management	Number of Plots Sampled
Busch Bluff	0.6	1	Cleared (2021), burned (2023)	7 (1 burn)
Ericksen Bluff	0.4	≥2	Cleared (2015), burned (2017 onward)	6 (≥2 burns)
Lallaman Bluff	1.3	≥2	Cleared (2017 onward), burned (2021 onward)	11 (≥2 burns)
McGuire Bluff	0.7	1	Cleared (2021), burned (2023)	8 (1 burn)
Miller Bluff	0.8	0	Cleared (2022 onward)	7 (0 burns)
Old Baldy Bluff	4.0	1	Cleared (2021 onward), half burned (2023)	24 (0 burns), 31 (1 burn)
Pleasant Bluff	9.8	≥2	Cleared (2017 onward), burned (2017 onward)	1 (0 burns), 5 (1 burn), 52 (≥2 burns)
Woodlawn Bluff	1.2	0	Not managed	20 (0 burns)

plot were recorded (Fig. 2). Only living lichens were recorded, (i.e., they turned green when sprayed with water, indicating the presence of living algae and photosynthetic capacity). Material insufficient to be identified to species with a hand lens and spot tests was recorded as its genus, or in two cases to multi-generic taxa (*Placidium/Clavascidium*).

The degree of woody encroachment of each plot was evaluated in the field qualitatively and recorded in two categories: low woody encroachment or high woody encroachment. The class of woody encroachment for each plot was estimated by examining the number of stumps of various sizes inside the plot and within 1 meter of the plot. Plots were classified as having high woody encroachment if a plot contained more than 10 1–2-cm diameter stumps or a 10-cm diameter stump or larger, or if the area located within 1 meter surrounding the plot in all directions had several 10-cm diameter or larger stumps. All plots sampled contained herbaceous prairie vegetation or were surrounded by herbaceous prairie vegetation if the outcrop completely filled the plot. Areas of very high woody encroachment, approaching a closed tree canopy or extremely high density of shrubs were excluded. Plots within or adjacent to an obvious fire scar from a large pile of burned material were likewise not surveyed, under the assumption that fire intensity was extreme in such areas.

Statistical analyses

Plot richness was calculated to quantify the lichen community of each plot. Plot richness was defined as the number of unique taxa within a plot. To test the effects of burn history and woody encroachment on lichen community composition, comparative analyses were used with burn history categories (0, 1, and ≥2) and woody encroachment categories (high and low) as independent variables and plot richness as the dependent variable. The effects of burn history and woody encroachment on plot richness were assessed via two-factor ANOVA with burn history and woody encroachment categories fitted as main effects. Differences in plot richness between treatment groups were tested via Tukey's multiple range test.

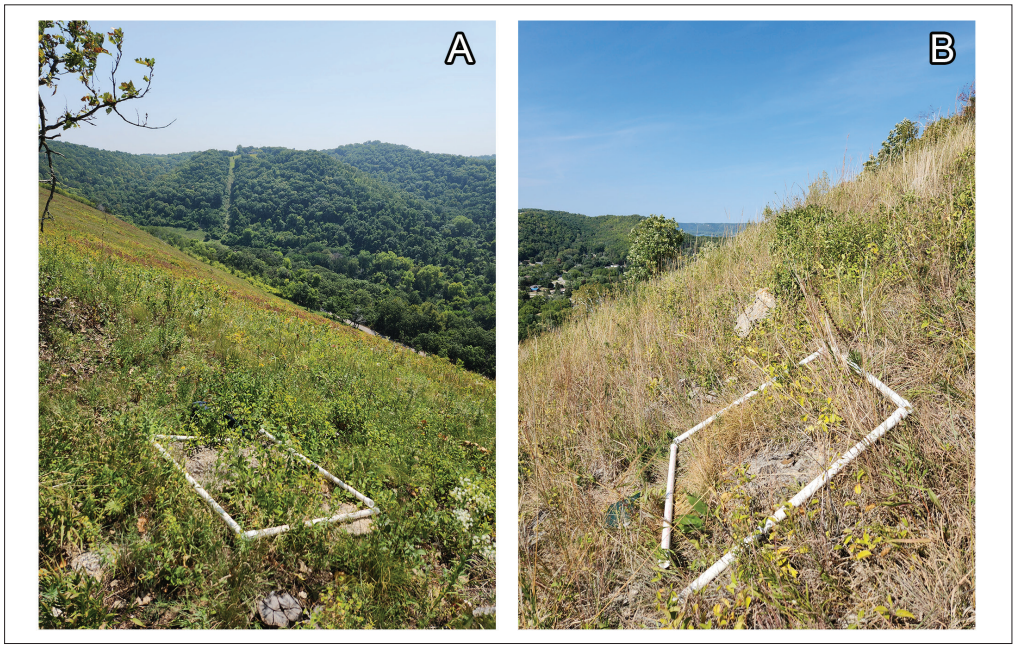

Figure 2. Survey plots on Pleasant Bluff on August 22, 2023 (A) and on Old Baldy Bluff on September 14, 2023 (B). Photos by Connor J. Johanson.

The effects of burn history and woody encroachment on individual taxa also were assessed. To test these effects, logit function generalized linear models (GLMs) were fit with burn history and woody encroachment categories as independent variables and frequency of occurrence for the target taxon as the dependent variable. Differences in frequency of occurrence between treatment groups were tested via pairwise chi-squared tests with Bonferroni adjustment. Highly pruinose specimens of *Lecanora muralis*, which require thin layer chromatography (TLC) to positively discern from *L. valesiaca*, are reported from the Great Plains. As TLC was not performed for identification, we have grouped *L. valesiaca* and *L. muralis* in our analyses and refer to them as the *Lecanora* spp. *Dermatocarpon dolomiticum* Amtoft, *Lecanora* spp., and *Phaeophyscia* spp. (Neck.) Moberg were selected for taxon-specific analysis. Statistical significance for analyses were determined with $\alpha = 0.05$. Analyses and graphing were conducted in R (R Core Team 2023) and RStudio (RStudio Team 2023) using the packages "car" (Fox and Weisberg 2019), "tidyverse" (Wickham et al. 2019), "plotrix" (Lemon 2006), "rcompanion" (Mangiafaco 2023), and "ggeffects" (Lüdecke 2018).

Results

In total, 14 taxa of saxicolous macrolichens were identified and recorded in the 172 plots surveyed across eight sites in southeastern Minnesota. Supplemental Fig. 1 (available online at https://www.dropbox.com/scl/fi/ob12fhlqcymlsncck88hb/supp_fig1.pdf?rlkey=u21wpggzfeb9k0o52714rlqx5&st=8gegg4zc&dl=0). Nineteen species were identified on outcrops or boulders across all study sites (Table 2). Taxon richness in a single plot ranged from zero to nine taxa per plot. Seven of the nineteen species identified are primarily corticolous and likely require a woody source of spores and/or vegetative propagules to establish on rocks nearby (Table 3). Two commonly saxicolous species identified in our plots, *Phaeophyscia adiastola* and *Physconia leucoleiptes,* require shade to grow on rock. The most common taxa, found in more than 50% of all plots, were *Dermatocarpon dolomiticum* Amtoft and *Lecanora* spp. All other taxa occurred in less than 30% of all plots. Macrolichens were absent from 17% of all plots; all but one of such plots were burned two or more times. Among treatments, both number of burns and class of woody encroachment separately affected plot richness. Specifically, plots with greater numbers of burns had significantly lower richness ($P < 0.001$), while plots with high woody encroachment had significantly higher richness than plots with low woody encroachment ($P < 0.001$; Fig. 3).

Table 2. Total number of plots across all study sites in each category of greatest number of burns and class of woody encroachment.

Burns	Woody Encroachment	Plots
0	Low	26
0	High	26
1	Low	32
1	High	19
≥2	Low	31
≥2	High	38

Table 3. Study taxa (bolded) and identified species present on dolomite at each study site are marked with an X. Primarily corticolous species are indicated with an asterisk. Numbers 1–8 correspond to sites Busch Bluff (1), Ericksen Bluff (2), Lallaman Bluff (3), McGuire Bluff (4), Miller Bluff (5), Old Baldy Bluff (6), Pleasant Bluff (7), and Woodlawn Bluff (8).

	1	2	3	4	5	6	7	8
CANDELARIACEAE								
Candelaria concolor*	X			X	X	X	X	X
COLLEMATACEAE								
Lathagrium fuscovirens	X					X	X	
Scytinium lichenoides			X					
Thyrea confusa					X			
LECANORACEAE								
***Lecanora* spp.**	X		X	X	X	X	X	X
L. muralis	X			X	X	X	X	X
L. valesiaca	X		X	X	X	X	X	X
TELOSCHISTACEAE								
Squamulea galactophylla			X	X		X	X	
***Rusavskia* spp.**	X	X	X	X	X	X	X	X
R. elegans	X	X		X	X	X	X	X
R. sorediata						X	X	
***Xanthomendoza* spp.**	X			X	X	X	X	X
*X. fallax**					X	X		
*X. ulophyllodes**	X			X	X		X	X
*X. weberi**						X	X	
PHYSCIACEAE								
***Phaeophyscia* spp.**	X			X	X	X	X	X
P. adiastola						X		
*P. hirsuta**	X					X	X	
***Physciella* spp.**	X				X	X	X	X
*P. chloantha**	X					X		
*P. melanchra**								X
***Physconia* sp.**					X	X		
Physconia leucoleiptes					X	X		
PSORACEAE								
Psora pseudorussellii	X		X	X		X	X	X
VERRUCARIACEAE								
Dermatocarpon dolomiticum	X	X	X	X	X	X	X	X
***Placidium/Clavascidium* spp.**	X		X	X	X	X	X	X

The most common species in this study was *Dermatocarpon dolomiticum*, present on 72% of all plots. This is the first record of *D. dolomiticum* in Minnesota following its description by Amtoft et al. (2008) as a new species distinct from *Dermatocarpon miniatum* (L.) W. Mann. Species-specific analysis of *D. dolomiticum* indicated that its frequency of occurrence was significantly lower in plots with greater number of burns ($P < 0.001$; Fig. 4). Class of woody encroachment was not found to have a significant effect on *D. dolomiticum* frequency of occurrence ($P = 0.056$). We observed that *D. dolomiticum* thalli appear to reduce drastically in size with greater numbers of burns (Fig. 5). In sites burned once, burned thalli often had curled edges and some were blackened. In sites burned two or more times, the curled margins of many damaged thalli had broken or burned off. Most thalli in sites burned two or more times were reduced to the central parts of the thalli around the umbilicus attached to the substrate; many were bleached white and no longer turned green when sprayed with water and were assumed to no longer be photosynthetically active.

Lecanora spp. was the second most common taxon in this study, present on 65% of all plots. *Lecanora* spp. frequency was significantly lower (as determined by logistic regression) in plots with greater number of burns ($P = 0.013$; Fig. 6), but there was no significant difference between plots of low and high woody encroachment ($P = 0.083$). Pairwise chi-squared with Bonferroni adjustment failed to detect significant differences between treatment groups. In plots with low woody encroachment that were unburned, burned once, or burned two or more times, the frequency of *Lecanora* spp. was 0.85, 0.63, and 0.48, respectively (Table 4). In plots with high woody encroachment that were unburned, burned once, or burned two or more times, the frequency of *Lecanora* spp. was 0.54, 0.68, and 0.42, respectively.

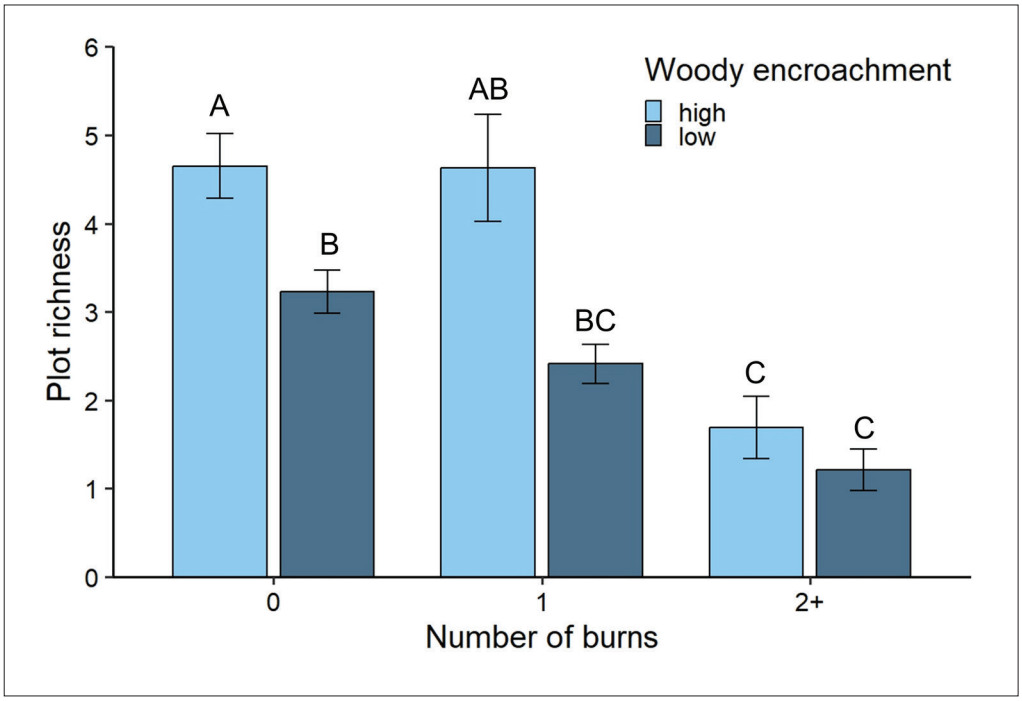

Figure 3. Mean plot richness (mean number of taxa per plot) categorized by number of burns and class of woody encroachment. P-values indicate significance of main effects on plot richness as determined by two-way ANOVA: $P < 0.001$ for woody encroachment; $P < 0.001$ for number of burns. Significant pairwise comparisons as determined by Tukey's range test are indicated by letter display. Error bars ±1 SE.

The frequency of *Phaeophyscia* spp. in plots burned two or more times was significantly less than in unburned plots ($P < 0.001$; Fig. 7). Similarly, the frequency of *Phaeophyscia* spp. in plots of low woody encroachment was significantly less than in plots of high woody encroachment ($P < 0.001$). In plots with low woody encroachment that were unburned, burned once, or burned two or more times, the mean frequency of *Phaeophyscia* spp. was 0.04, 0.09, and 0, respectively (Table 4). In plots with high woody encroachment that were unburned, burned once, or burned two or more times, the mean frequency of *Phaeophyscia* spp. was 0.58, 0.53, and 0.11, respectively.

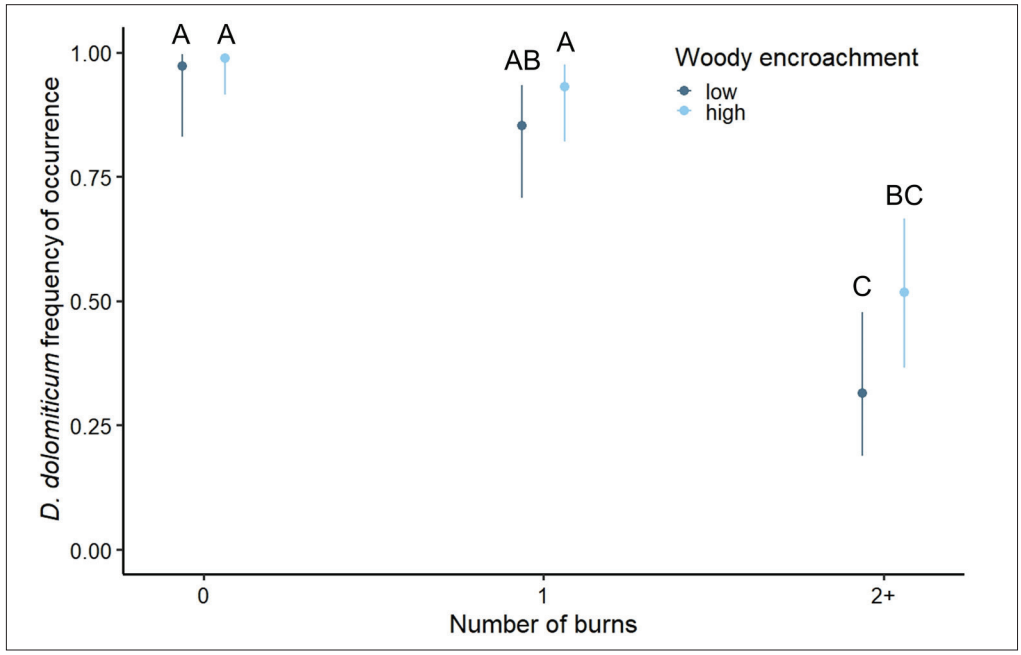

Figure 4. *Dermatocarpon dolomiticum* frequency of occurrence across all plots categorized by number of burns and class of woody encroachment. P-values indicate significance of effects on plot richness as determined by logistic regression: $P < 0.001$ for number of burns; $P = 0.056$ (not significant) for woody encroachment. Significant pairwise comparisons as determined by pairwise chi-square test (P-values adjusted using Bonferroni method) are indicated by letter display. Error bars±1 SE.

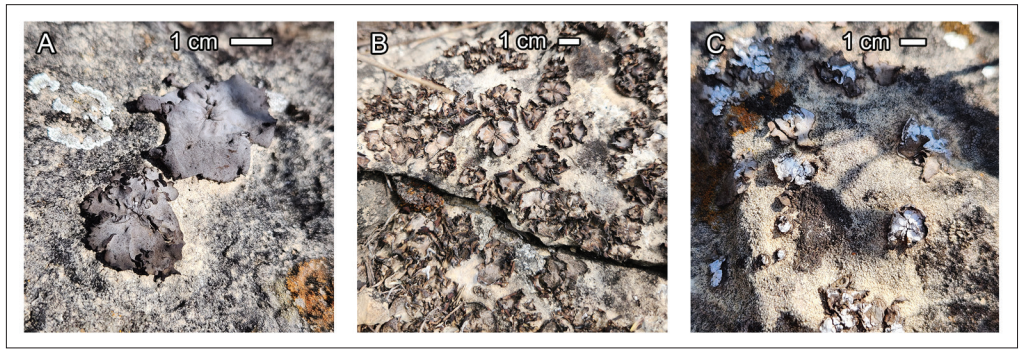

Figure 5. *Dermatocarpon dolomiticum* thalli on dolomite outcrops in bluff prairie study sites of differing fire histories. Thalli in a prairie not burned within the last 30 years of the time of this study (A). Thalli in a prairie burned once in 2023 (B). Thalli in a prairie burned twice (2021 and 2022; C). Photos by Connor J. Johanson.

Discussion

The results of this study show a significant decline in plot richness as number of burns increased, thus supporting our first hypothesis. Additionally, our data show significantly greater plot richness in plots with high woody encroachment than in plots with low woody encroachment, which supports our second hypothesis. While these effects were broadly applicable to saxicolous macrolichen communities, they affected individual taxa within those communities independently. *Dermatocarpon dolomiticum* was selected for species-specific analysis because it was the most frequently encountered species in this study and appeared to be strongly damaged by fire, from observations made while surveying. *Lecanora valesiaca* was analyzed because it has a growth form that lies closer to the substrate, compared to foliose species, and it appeared to maintain similar mean frequencies across all burn categories. *Phaeophyscia* spp. was chosen for taxon-specific analysis because *Phaeophyscia* species exhibited greater mean frequency in plots with high woody encroachment but were mostly absent from plots burned two or more times regardless of class of woody encroachment.

Lichen species are highly microhabitat-sensitive, with numerous variables potentially affecting each species differently on each individual rock. At the eight sites we studied factors which may be important to saxicolous lichen diversity but for which we could not control include: bluff aspect (south-facing vs. west-facing slope), bluff slope steepness, intensity and extent of controlled burns (amount of fuel, wind speed, and direction), year of most recent burn, year each site was cleared, plot position on the slope (top, middle, or bottom), total area of exposed rock within each plot, maximum height of exposed rock at each plot, angle of tilt of the face of each rock, and presence of irregularities, cracks, and seepage tracks on rock surfaces.

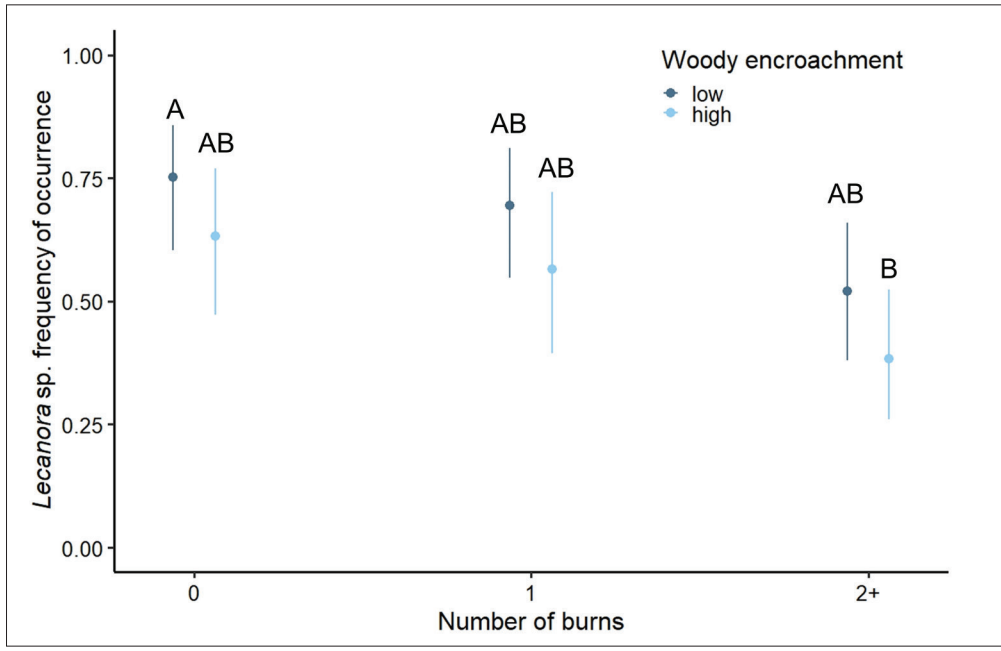

Figure 6. *Lecanora* spp. frequency of occurrence across all plots categorized by number of burns and class of woody encroachment. P-values (as determined by logistic regression) for effect on plot richness achieved significance for burn frequency (P = 0.013) but not for woody encroachment (P = 0.083). Significant pairwise comparisons as determined by pairwise chi-square test (P-values adjusted using Bonferroni method) are indicated by letter display. Error bars ±1 SE.

Fire effects

This study found lower lichen richness in plots with increasing numbers of burns. For three individual taxa, plots with greater numbers of burns had significantly lower frequency of occurrence. Frequencies of occurrence for *Dermatocarpon dolomiticum*, *Lecanora* spp., and *Phaeophyscia* spp. were significantly lower in plots with higher number of burns and were observed to be lowest in plots burned twice or more. Interestingly, crustose saxicolous microlichens were present in all plots, even when macrolichens were absent. These observations are consistent with a similar anecdotal observation of relatively high survival of saxicolous crustose lichens in a burned Montana grassland (Antos et al. 1983). It is worth noting that some outcrops in recent burn scars did not have crustose microlichens, which were present in every plot surveyed in this study, even when macrolichens were not present.

The effects of fires on saxicolous lichen communities in grasslands have rarely been studied. In native Brazilian grasslands an accumulation of vegetation on a site that had not burned in 15 years created fire intensity that significantly decreased saxicolous lichen cover and taxa richness compared with a control parcel managed by grazing and annual burning (Koch et al. 2015). In dry mediterranean grasslands frequent fires drastically reduced the biodiversity of saxicolous lichens on calcareous outcrops (Giordani et al. 2016). No prior studies have been conducted on the effects of fire on saxicolous lichens in the Upper Midwest of the USA.

Wildfire intensity has an important effect on corticolous lichen communities in forests (Miller et al. 2018, Johansson et al. 2006). Terricolous lichens, unlike many vascular plants, do not have extensive perennating parts below ground that would survive a fire (Schulten 1985). Grassland soil lichens are known to be very vulnerable to fire (Antos et al. 1983,

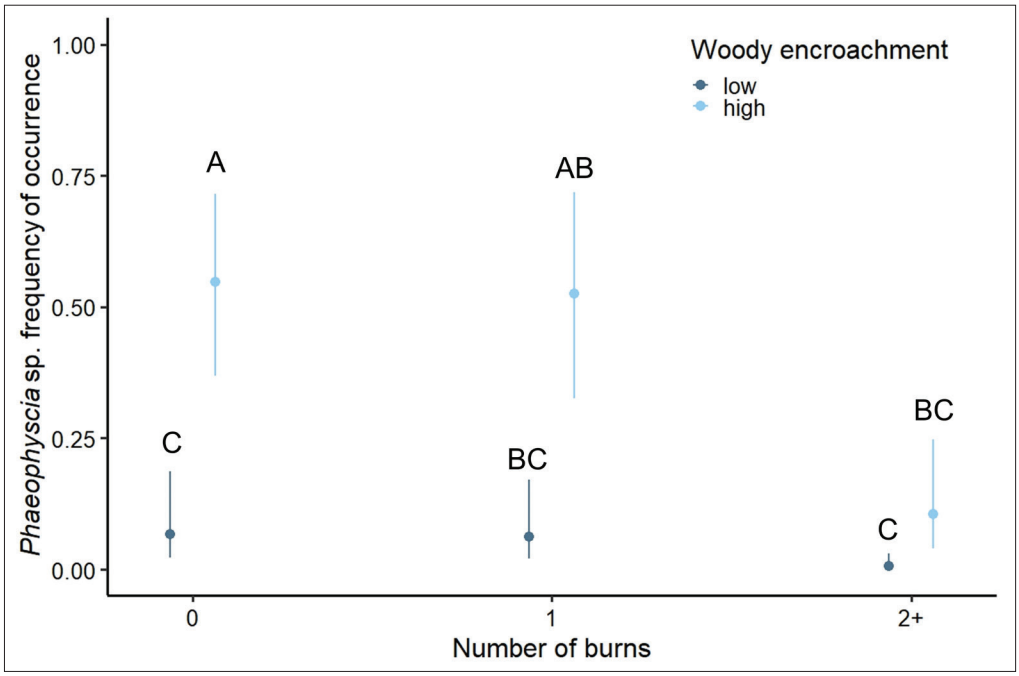

Figure 7. *Phaeophyscia* spp. frequency of occurrence across all plots categorized by number of burns and class of woody encroachment. P-values indicate significance of effects on plot richness as determined by logistic regression: $P < 0.001$ for number of burns; $P < 0.001$ for woody encroachment. Treatment groups that share a letter are not significantly different as determined by pairwise chi-squared with Bonferroni adjustment. Error bars±1 SE.

Schulten 1985) and slow to recolonize burned areas (Johansen et al. 1984). In burned areas of Allison Savanna in Anoka County, MN, Wetmore (1981) reported that most soil lichens were largely eliminated by fires and only sterile *Cladonia* squamules were present. Johansson and Reich (2005) reported that soil lichens in prairies survived a low-intensity fire proportionally to their pre-fire population size, but experienced high mortality rates above a certain fire-intensity threshold. Holt and Severns (2005) found that burning reduced terricolous lichen diversity and abundance in wet prairies in Western Oregon; the persistence of fire-damaged thalli, protective microhabitats, and post-fire propagule dispersal were important in the recovery of wet prairie lichen communities subjected to prescribed fire. More research is needed on saxicolous lichen communities to determine the effects of differing fire intensities, how long recolonization takes after such fires, and what protective microhabitats might be important for lichen survival.

Woody encroachment effects

This study found that lichen plot richness was higher under high woody encroachment than under low woody encroachment. Foote (1966) studied the lichen and bryophyte community of limestone outcrops in the Wisconsin portion of the Driftless Area and concluded that outcrops without visible water runoff that were in shade for half or more of the daylight supported the most species. Our results were consistent in that higher lichen richness was observed under high woody encroachment in the present study within the western Driftless Area.

In the present study there appeared to be a group of taxa associated with high woody encroachment that were mostly absent from prairie dolomite outcrops in sites burned two or more times: *Candelaria concolor* (Dicks.) Trevis, *Phaeophyscia* spp., *Physciella* spp., *Physconia* spp., and *Xanthomendoza* spp. All these taxa very commonly grow on the bark of trees and shrubs in the surrounding forested landscape and can reproduce vegetatively via soredia (propagules containing fungal hyphae and algal cells) which support colonization of new locations (Johansson et al. 2006). Woody encroachment expands shaded and moist habitat for these species and contributes to the sources of vegetative propagules that colonize the rocks below. These primarily corticolous lichen species do not persist on rocks in cleared prairies burned twice or more.

Management implications

Although prairie management necessitates the use of frequent fire, especially in early stages of restoration and management of woody encroachment, fire intensity should be considered when burning areas of significant saxicolous macrolichen habitat. We observed that plots at the top of Pleasant Bluff burned two or more times still had macrolichens present in them that appeared to have suffered only minor damage. In contrast, many plots on the lower slope of the same site were devoid of macrolichens. A possible explanation for this distribution may be due to reduced fire intensity on the top of the site from the practice of

Table 4. Frequency of occurrence in all study plots by number of burns (0, 1, ≥2) and class of woody encroachment (low, high) for *Dermatocarpon dolomiticum*, *Lecanora* spp., and *Phaeophyscia* spp.

Taxon Frequency	0, Low	0, High	1, Low	1, High	≥2, Low	≥2 High
Dermatocarpon dolomiticum	0.91	1	0.86	1	0.39	0.42
Lecanora spp.	0.85	0.54	0.63	0.68	0.48	0.42
Phaeophyscia spp.	0.04	0.58	0.09	0.47	0	0.11

"back-burning". Prescribed burning of bluff prairies usually starts with the burning of the uppermost part of the slope, letting the fire burn slowly downhill; "backing" into the wind. When this burned area has expanded sufficiently, the unit is usually lit on fire down the sides. Often, the same back-burning approach is applied on a downwind side. Finally, fire is ignited along the bottom edge, whereupon the fire rapidly moves uphill and with any prevailing wind. The back-burned areas are an effective firebreak for this rapid uphill burning (G. Ericksen, LandSpirit Design Landscaping Inc., Winona, MN, 2024 pers. comm.). Managers may reduce fire intensity around outcrops by backburning directly around them. This may be too time-consuming for many sites; possible practices may include walking through the burn unit with a drip torch and lighting points of fire wherever they may encounter a large outcrop, or simply lighting a series of continuous lines through the unit perpendicular to the slope to slow down the uphill speed of the fire and possibly reduce fire intensity. Additionally, carefully managed grazing may reduce fuels in prairies to sufficiently reduce fire intensity (Briggs et al. 2002, Knapp et al. 1999).

Conclusions

Fire history and woody encroachment affect saxicolous macrolichen communities on dolomite, prairie outcrops, and boulders in southeastern Minnesota bluff prairies. Our data is limited, and further research is needed to discern the specific effects of fire and woody encroachment on saxicolous macrolichen communities. Low intensity fire is likely important in the survival of macrolichens in fire-adapted grassland systems. Although we do not present any fire intensity data here, our results indicate that plot richness (number of taxa per plot) on dolomite outcrops and boulders significantly decreased with greater number of burns. Managers are recommended to reduce fire intensity around areas of significant saxicolous lichen habitat when managing bluff prairies.

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