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RESEARCH ARTICLE

LICHEN COMMUNITY RESPONSE TO PRESCRIBED BURNING AND THINNING IN SOUTHERN PINE FORESTS OF THE MID-ATLANTIC COASTAL PLAIN, USA

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ABSTRACT

The effects of prescribed burning and thinning on lichen communities is a poorly understood aspect of biodiversity conservation, despite the widespread use of these practices to achieve conservation-oriented land management goals. To address this knowledge gap we documented apparent changes in the diversity and abundance of lichens following 0 to 2 growing-season burns preceded by 0 to 1 commercial thinnings within nine southern pine dominated stands on the Delmarva Peninsula of Maryland, USA. Corticolous lichens growing on the stems and within the canopies of pines and co-occurring hardwoods were identified to species and fractional coverage was estimated; growth forms and reproductive modes were also determined. A total of 93 lichen taxa were recorded on the 19 tree species (4 pines, 15 hardwoods) represented in this study. Burning emerged as a strong driver of reductions in lichen diversity (*P* = 0.002), whereas thinning in the absence of burning did not (*P* = 0.279). In general, we found that lichens growing on tree bases and lower bole sections were more strongly impacted by burning, both in terms of

RESUMEN

Los efectos de quemas prescriptas y raleos sobre comunidades de líquenes es un aspecto poco comprendido de la conservación de la biodiversidad, a pesar del extenso uso de esas prácticas para lograr metas de manejo orientadas a la conservación. Para llenar este vacío en el conocimiento, documentamos los cambios aparentes en la diversidad y abundancia de líquenes de 0 a 2 temporadas de crecimiento después de las quemas y precedidas de 0 a 1 raleo comercial, dentro de nueve rodales dominados por pinos del sur en la península de Delmarva en Maryland, EEUU. Los líquenes cortícolas creciendo en tallos y dentro del dosel arbóreo de pinos y latifoliadas circundantes, fueron identificados a nivel de especie y se estimó la fracción de su cobertura; las formas de crecimiento y modos reproductivos fueron también determinados. Un total de 93 taxones de líquenes sobre 19 especies de árboles (4 pinos y 15 latifoliadas) fueron registrados en este estudio. Las quemas emergieron como fuertes conductoras en la reducción de la diversidad de líquenes (*P* = 0.002), mientras que los raleos en ausencia de quemas no tuvieron ningún efecto (*P* = 0.279). En general, encontramos que los líquenes que crecen en la base de los árboles y en las porciones bajas del tronco fueron más impactados por las quemas, tanto en diversidad como en cobertudiversity and cover, than those residing in the canopy. The apparent refugia represented by the canopy was qualified by the limited overlap in lichen species composition observed among the various sampling heights. This work calls attention to an understudied component of biodiversity that appears to be sensitive to fire management; however, we suggest that these results need to be interpreted in the context of altered disturbance regimes and the trajectory of community assembly resulting from long-term fire exclusion.

ra, que aquellos ubicados en el dosel. El aparente refugio representado por el dosel fue estimado por la limitada superposición en la composición de especies de líquenes observados entre las distintas alturas de muestreo. Este estudio llama la atención sobre un aspecto poco estudiado de la biodiversidad que aparenta ser sensible al manejo del fuego; desde luego, sugerimos que estos resultados deben interpretarse en el contexto de regímenes de disturbios alterados y la trayectoria del ensamble de la comunidad resultante de la exclusión del fuego por largos períodos de tiempo.

Keywords: biodiversity, disturbance regime, lichens, prescribed burning, restoration, southern pines, thinning, woodlands

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INTRODUCTION

Terrestrial biodiversity has been substantially diminished by anthropogenic factors including land-use change, altered disturbance regimes, and, increasingly, as a result of global climate change (IPCC 2013). Contributing to these trends, substantial areas of mixed-species upland forest in the Mid-Atlantic Coastal Plain region of the US have been displaced by agriculture and development or converted to intensively managed pine plantations (Auch 2000). Contemporary approaches to land management that seek to re-establish missing elements of ecosystem composition, structure, and function in order to enhance biodiversity and resilience typically embrace approaches grounded on historic disturbance regimes (Kohm and Franklin 1997, Seymour *et al.* 2002, Egan 2005, Mitchell *et al.* 2006, Wiens *et al.* 2012).

Wildland fires, both natural and human caused, have shaped forest communities and influenced plant specialization for millennia in eastern North America (Whitney 1994, Delcourt and Delcourt 1997, Frost 1998, Platt 1999, Ryan *et al.* 2013). However, European settlement altered extant fire regimes, culminating in government agency policies that greatly reduced the number and area of wildland fires throughout the twentieth century (Pyne 1982, 2010). As a result, historic woodland and savanna systems in eastern North America have largely been transformed into closed-canopy forests through the recruitment of shade-tolerant, fire-sensitive vegetation (Anderson 1991, Wolf 2004, Bond *et al.* 2005, Nowacki and Abrams 2008). It is now widely accepted that many ecosystems in eastern North America depend on periodic burning to maintain plant communities and associated habitats for native wildlife. Prescribed burns are increasingly used in an effort to reverse the detrimental impacts that fire exclusion has had on these fire-adapted ecosystems (Platt 1999, Brooks *et al.* 2004, Agee and Skinner 2005, Ryan *et al.* 2013).

Similar to fire exclusion, forest management and, more specifically, practices commonly associated with intensive southern pine silviculture (e.g., site preparation, herbicide release, fertilization, and maintenance of high stocking) are also widely considered to have negative impacts on biodiversity. While not without merit, this view can be overly simplistic, and approaches have been suggested to mitigate some of the negative impacts of these practices (Andreu *et al.* 2008, Hartmann *et al.* 2010). Coxson and Stevenson (2005) reported on the short-term impacts of partial harvesting practices on canopy lichens in mixed conifer forests of British Columbia, Canada, concluding that, while species exhibiting pendulous growth forms were susceptible to wind damage, the other groups that they studied appeared relatively unaltered by the treatments.

In contrast to the extensive body of literature describing the response of vascular plants to prescribed burning, similar resources are not currently available for lichens (see FEIS 2015). Lichens are symbiotic organisms comprised primarily of a fungus and an alga that form a single unit in which the fungus tends to dominate (Brodo *et al.* 2001). They are recognized as keystone members of terrestrial ecosystems, performing diverse services contributing to nitrogen fixation, animal forage, soil stabilization, and moisture retention, and hosting diverse and unique communities of bacteria, fungi, and other microorganisms (Brodo *et al.* 2001, Arnold *et al.* 2009, Hodkinson and Lutzoni 2009, Gauslaa 2014). Despite their importance, many aspects of lichens, from taxonomy to basic biology, remain understudied (Brodo *et al.* 2001, Lendemer and Allen 2014). Similarly, lichens have demonstrated utility as indicator species for environmental pollution and degradation (Nash 1975, Showman 1981, Muir and McCune 1988, Wolseley 1995, McCune *et al.* 1997), yet their responses to disturbances and how disturbance regimes shape the composition and structure of lichen communities has yet to be studied in many ecosystems.

The majority of studies documenting the relationship between lichens and disturbance regimes suggest that lichens are highly impacted by burning, both in terms of diversity and abundance, across a range of habitats (Klein 1982, Antos *et al.* 1983, Mistry 1998, Reinhart and Menges 2004, Johansson and Reich 2005). Reduced lichen cover may persist in burned areas due to slow growth and colonization rates, and as the result of unprotected organelles in ground-layer lichens (Antos *et al.* 1983, Holt and Severns 2005). Nonetheless, a study of reindeer lichens (*Cladonia* spp. P. Browne) in grasslands of Minnesota, USA, suggests that recovery is largely a factor of fire intensity and frequency, whereby lichens subjected to low intensity fires are quicker to recover compared to those exposed to higher intensity burns (Johansson and Reich 2005). Many of the studies detailing lichen community response to fire in North America have focused on soil lichens within grassland habitats of the West (Bowker *et al.* 2004, Holt and Severns 2005, Johansson and Reich 2005), and therefore provide limited insight to the response of corticolous lichen communities in forest and woodland settings.

Because prescribed burning and tree density reduction (i.e., thinning) represent the most widely used management techniques being employed to restore and promote resiliency within overly dense, fire-excluded forests, we sought to better understand the impacts of these practices on affiliated lichen communities. Here we present the results of an observational study describing the short-term effects of these treatments on corticolous lichens within southern pine forests of the Mid-Atlantic Coastal Plain. The study was undertaken in the broader context of a large-scale inventory of lichens on protected lands throughout the region, which revealed unexpectedly high levels of diversity, including on the Delmarva Peninsula (Lendemer and Allen 2014). Discussions undertaken with land managers and agency officials during the larger project revealed that, although these practices were being used to achieve conservation benefits in this region, the possible impacts of these management actions on lichen communities were not being considered and were largely unknown.

METHODS

Study Area

This study took place on Nassawango Creek Preserve located in Wicomico and Worcester counties, on the Eastern Shore of Maryland, USA (38° 16’ 09.5” N 75° 28’ 15.2” W; Figure 1). The ~4050 ha property is owned and managed by The Nature Conservancy and was acquired for the purpose of biodiversity and watershed protection beginning in the late 1970s. Floodplain forests dominated by bald cypress (*Taxodium distichum* [L.] Rich.), black gum (*Nyssa sylvatica* Marshall), and red maple (*Acer rubrum* L.) predominate across much of the Preserve. Excessively drained and nutrient-poor upland sites known as inland dunes (Denny and Owens 1979) account for roughly 10% of the land base and, by contrast, host a variety of fire-adapted woodland species. Under historic or pre-European settlement conditions, the inland dunes are thought to have been vegetated by drought-tolerant tree species including oaks (white oak [*Quercus alba* L.], black oak [*Q. velutina* L.], blackjack oak [*Q. marilandica* Münchh.], post oak [*Q. stellata* Wangenh.]), sand hickory (*Carya pallida* [Ashe] Engl. & Graebn.), and southern pines (loblolly pine [*Pinus taeda* L.], shortleaf pine [*P. echinata* Mill.], Virginia pine [*P. virginiana* Mill.]). Understory vegetation on the dunes is typically characterized by a diversity of pyrogenic herbaceous, grass, and shrub species, at least when a sufficient canopy openness is maintained (Harrison 2011, NatureServe 2011).

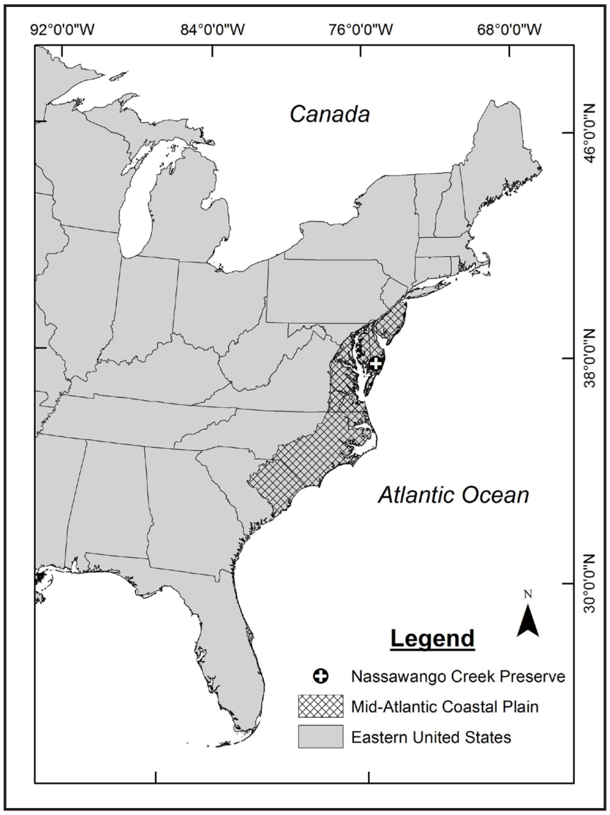

Figure 1. Map of the Mid-Atlantic Coastal Plain showing the location of the study area on the lower Eastern Shore of the Delmarva Peninsula, Maryland, USA

The region has a complex and lengthy land-use history, wherein extensive areas of wetland forests were drained and converted to productive agriculture and plantation forestry. Despite the lower productivity of plantations grown on the inland dunes, the fact that this ground remains operable by heavy equipment throughout the year makes it a valuable asset to the forest industry during periods of wet weather. As a result, loblolly pine is often the dominant tree species encountered on these sites and within adjacent upland ecotones, where this study took place. Restoration practices, including the re-introduction of fire, reduction of tree stem density, and enrichment planting with site-adapted species, are being implemented to enhance the biodiversity and habitat values of degraded inland dunes and affiliated uplands across the property.

An observational study design was used to characterize differences in lichen community response to restoration management practices while controlling, to the extent possible, for edaphic setting, stage of stand development, and tree composition. Study plots were established in middle-aged (20 yr to 40 yr) pine stands that were previously (1) thinned but not burned (*n* = 3 stands; code = 10), (2) thinned once and burned once (*n* = 2 stands; code = 11), (3) thinned once and burned twice (*n* = 2 stands; code = 12), or (4) an unaltered reference (*n* = 2 stands; code = 00). Thinning to reduce canopy density was accomplished with conventional logging equipment and always occurred at least one year prior to burning. Pine tree basal areas on the thinned plots were reduced to between 16.1 m^2 ha^{-1} and 18.4 m^2 ha^{-1} by commercial thinning treatments carried out between 2007 and 2012. Prescribed burns were conducted during the early growing season (March through May). Descriptions of the treatments are presented in Table 1.

Sample Selection

Corticolous lichens were sampled from trees growing on plots drawn from a nominal 2 ha systematic grid used for forest inventory on the property. The sample trees were selected as follows: within a search radius of 15.2 m from the plot center and in a randomly selected quadrat (i.e., NE, SE, SW, NW), we chose the closest tree of each species within two diameter-based size classes (2.54 cm dbh to 11.2 cm dbh, and >11.2 cm dbh). One representative of each tree species was sought within each size class on each plot. Species present at lower densities were searched for within the remaining quadrats until the entire plot area was used (730 m^2).

Lichens were inventoried on each of the selected trees within established sampling heights based on three height categories: (1) base (forest floor to 0.3 m up the stem), (2) bole (0.3 m to 2.4 m, or up to the lowest live branch within the tree canopy), and (3) canopy (defined as the lowest live branch, excluding epicormic sprouts). Measurement of lichens on the base and bole sections of the stem were accomplished from the ground, whereas canopy samples were either collected from the ground with a pole saw or required climbing equipment to excise the selected branch. Lichen thalli were identified and recorded in the field within each sampling interval. Voucher specimens for each species identified on a plot were collected. Vouchers were later examined

Table 1. Selected attributes of the study plots including the timing of commercial thinning and prescribed burns (Treatment: 00 = control; 10 = thinned, not burned; 11 = thinned, burned once; 12 = thinned, burned twice). Means and standard deviations for basal area (BA) and average stand diameter (Dq), and the relative abundance of pines to hardwoods (Pine BA, %). na = not applicable.

Treatment	Stand name	Plot (*n*)	Thinning	Prescribed burn	BA (m^2 ha^{-1})	Pine BA (%)	Dq (cm)
00	Ace	2	na	na	26.5 ± 11.4	55	21.7 ± 1.3
00	Laws	4	na	na	39.7 ± 8.3	81	22.8 ± 3.2
10	Ches/Som	2	2011	na	16.1 ± 13.0	72	23.5 ± 1.6
10	SCI-P2	3	2005	na	23.0 ± 4.0	87	21.7 ± 1.5
10	WIC-5	4	2013	na	16.7 ± 8.3	95	28.5 ± 5.3
11	WIC-2	4	2007	May 2011	27.6 ± 13.9	96	26.6 ± 4.5
11	WOR-1	2	2006	April 2011	16.1 ± 6.5	~100	26.9 ± 3.6
12	WOR-4	4	2005	April 2009, April 2013	19.0 ± 8.3	~100	27.9 ± 2.3
12	WOR-7	2	2007	April 2011, May 2013	13.8 ± 6.5	~100	22.5 ± 0.5

in the lab using compound and dissecting microscopes, chemical spot test, and thin layer chromatography when appropriate. All vouchers were deposited in the New York Botanical Garden, Bronx, New York, USA. In addition to abundance (counts for a given species within a sampling height), cover was also visually estimated in the field for each lichen taxon recorded. Cover was placed into five groups as follows: 1 (1% to 5%), 2 (6% to 25%), 3 (26% to 50%), 4 (51% to 75%), and 5 (76% to 100%). An estimate of total lichen cover for each sampling interval was also made independent of those for the individual taxa. For the purposes of assessing growth form and reproductive mode, a table of all species found during the study was produced and these characters were scored for all taxa using existing references and standard literature. This resulted in the assignment of a growth form (i.e., crustose, foliose, fruticose) and reproductive mode (asexual vs. sexual) to each taxon.

Statistical Analyses

Estimates of lichen diversity and cover obtained from the individual trees ($n = 177$) were treated as sub-samples, and values for the experimental unit, represented by plots ($n = 27$) for correlation and stands ($n = 9$) for Anova, were arrived at by either summing (for diversity measures) or averaging (for cover) over the sub-samples. Dependent variables were calculated for each plot or stand and sampling height (Base = BAS, Bole = BOL, Canopy = CAN) as follows: (1) lichen diversity (taxa) was determined as the number of unique taxa observed across all trees, (2) lichen cover (cover) as the average of the fractional cover estimate for each sampling height, (3) lichen morphology (growth form) as the proportion of lichens within three categories (crustose, foliose, and foliose) across treatments, and (4) lichen reproductive strategy (reproductive mode) as the proportion of lichens exhibiting either sexual or asexual reproductive structures (indeterminate samples were discarded from the analysis) across treatments.

Sørensen similarity values (Sørensen 1948) were used to compare lichen taxa among sampling heights, (i.e., BAS and BOL, BOL and CAN, and BAS and CAN). Values were calculated using EstimateS for Windows v9.10 (Colwell 2013) by tree species group (hardwoods = HW, pines = PI) for each treatment category. More formal analysis was not possible with this dataset due to a preponderance of missing values on the burned plots, which resulted in a highly unbalanced dataset. A combination of factors contributed to this occurrence, but it was largely attributable to lichens having been eliminated from the BAS sampling height of trees in the burn treatments. The zero values in this analysis correspond to situations in which lichens were present within both heights that were being compared, but no taxa were common to both.

We took an analysis of variance approach to assessing how lichen communities were impacted by the treatments. Models of the following general form were used to evaluate the contribution of independent variables:

$$\begin{array}{l} \textit{taxa} \text{ or } \textit{cover} \text{ or } \textit{growth form} \text{ or} \\ \textit{reproductive mode} = \textit{treat} + \textit{cov}, \end{array} \tag{1}$$

where the lichen variables were determined in total or at the different sampling heights, *treat* is a class variable describing the combination of fire and thinning treatments ($n = 4$, coded 00, 10, 11, 12), and *cov* is a quantitative covariate representing the number of hardwood species sampled in each stand. This variable was included in an attempt to account for known differences in the morphology and chemistry of tree bark between pines and hardwoods as they relate to lichen occupancy (Culberson 1955, Schmitt and Slack 1990). Owing to the small sample size available for this analysis, a limited number of contrasts were chosen *a priori* for evaluation with *post hoc* significance tests. Specifically, we compared the burned and unburned (00 + 10 = 11 + 12), and the thinned and unthinned (00 = 10) treatments. The GLM procedure in SYSTAT 12 (SYSTAT Software, San Jose, California, USA) was used to carry out all statistical tests.

Quantification of Fire Severity

Methods developed by the Monitoring Trends in Burn Severity program (MTBS; http://www.mtbs.gov/index.html) were used to obtain plot-level estimates of fire impacts on the vegetation (e.g., Picotte and Robertson 2011). Paired Landsat scenes collected approximately one year before and as soon as possible following the prescribed burns provided the basis for this assessment. The value of the fire severity variable (differenced normalized burn ratio, dNBR) determined at each plot location was paired with lichen taxa and cover variables. For this analysis, the lichen taxa variable was given by the cumulative number of lichen species recorded on each plot by tree species group (PI and HW), and lichen cover as the average of the base, bole, and canopy sampling heights. The highest value of the dNBR variable recorded for each plot was used to describe fire severity on the twice-burned plots ($\mathrm{dNBR}_{\mathrm{MAX}}$). Simple correlation analysis was used to assess the strength of the relationship between fire severity and the lichen variables.

RESULTS

Considering the availability of different substrates for corticolous lichens, hardwood tree species were notably more common on the unburned than burned plots (Table 2), and large-sized hardwoods were limited to the reference plots. Of the common hardwood species, only sweetgum (*Liquidambar styraciflua* L.), southern red oak (*Quercus falcata* Michx.), and sassafras (*Sassafras albidum* [Nutt.] Nees) were substantially represented on both the burned and unburned plots. Furthermore, the hardwood species on the burned plots were typically found in subordinate crown positions to the pines, within the midstory layer, presumably as a result of past cultural treatments (i.e., broadcast herbicide release to favor the pines). A number of more mesic and generalist species, including red maple, American holly (*Ilex opaca* Aiton), and water oak (*Q. nigra* L.), were also well represented on the unburned plots. Pines, and most notably loblolly pine, were a dominant feature across all the study plots (Table 2). On average, tree basal areas (BA, $\mathrm{m}^2\ \mathrm{ha}^{-1}$) were highest in the reference areas and lowest in stands that had been thinned and burned twice, although these values varied considerably among plots within a treatment (Table 1).

A grand total of 93 lichen species were found growing on trees sampled in this study. Among these, 76 were found on trees in the reference areas (T = 00), 83 in the thinned and unburned plots (T = 10), 35 in the thinned and once-burned plots (T = 11), and 8 in the thinned and twice-burned plots (T = 12). Trends in tree species diversity paralleled those for the lichens, with 16 tree species represented in the reference, 13 in the thinned, 5 in the thinned and burned, and 3 in the thinned and twice-burned stands. Viewed across all plots and treatments, the relationship between the number of tree species and lichen diversity was strong for the hardwoods ($r = 0.862$, $P < 0.001$) but not for pines ($r = 0.143$, $P = 0.477$). In contrast, no significant correlations were found when comparisons were restricted to plots within the burned and unburned treatments, although the relationship was marginal for the unburned hardwood category (Figure 2).

While fewer in total number, the lichen species found on the pines exhibited substantial overlap with those found on the hardwoods (Table 3). For example, three quarters (75 % ± 10 % mean and SD) of the lichen taxa growing on the pines were also found on the hardwoods in all but the twice-burned plots. The higher

Table 2. List of tree species on which lichens were sampled, by species group (HW = hardwood, PI = pine) and treatment (00 = control; 10 = thinned, not burned; 11 = thinned, burned once; 12 = thinned, burned twice). Values indicate tree frequency (the proportion of plots on which each tree species was present) by treatment and for the study. Taxa refers to the total number of lichen species found on each tree species.

		Treatment					
Tree species	**Species group**	**00**	**10**	**11**	**12**	**Total**	**Taxa**
Pinus echinata	PI	0.17	0.00	0.00	0.00	0.04	6
Pinus serotina Michx.	PI	0.33	0.00	0.17	0.00	0.11	10
Pinus taeda	PI	0.83	1.00	1.00	1.00	0.96	40
Pinus virginiana	PI	0.33	0.11	0.00	0.00	0.11	17
Acer rubrum	HW	1.00	0.89	0.00	0.00	0.52	56
Carya pallida	HW	0.33	0.00	0.00	0.00	0.07	29
Cornus florida L.	HW	0.33	0.00	0.00	0.00	0.07	21
Diospyros virginiana L.	HW	0.00	0.11	0.00	0.00	0.04	20
Ilex opaca	HW	0.83	0.89	0.00	0.00	0.48	27
Liquidambar styraciflua	HW	0.83	0.89	1.00	0.00	0.70	59
Magnolia virginiana L.	HW	0.17	0.00	0.00	0.00	0.04	9
Nyssa sylvatica	HW	0.50	0.22	0.17	0.00	0.22	36
Quercus alba	HW	0.33	0.11	0.00	0.00	0.11	28
Quercus falcata	HW	0.17	0.67	0.5	0.00	0.37	46
Quercus nigra	HW	0.67	0.22	0.00	0.00	0.22	35
Quercus rubra L.	HW	0.00	0.11	0.00	0.17	0.07	19
Quercus stellata	HW	0.17	0.11	0.00	0.00	0.07	29
Sassafras albidum	HW	0.50	0.89	0.17	0.17	0.48	45

diversity of lichens found on the hardwood trees corresponded to more taxa in common among sampling heights than for the pines (Figure 3, top panels). Similarity values were comparable for the BAS and BOL interval of hardwoods (0.51 ± 0.01) and pines (0.59 ± 0.09) on the unburned plots, and appeared to remain stable for the hardwoods, yet declined for the pines on the burned plots, although reduced sample size due to missing values on the burned plots makes this comparison less clear cut (Figure 3, bottom panels). Similarity values for the BOL and CAN interval were generally lower than those determined for the more proximate BAS and BOL interval, and, when averaged across treatments, values for the hardwoods (0.45 ± 0.18) were more than double those for the pines (0.18 ± 0.01). The lowest similarity values were obtained for the most distant BAS and CAN interval.

The Anova model assessing overall lichen diversity suggested a highly significant treatment effect and, further, that the covariate representing the number of hardwood tree species was also important to consider (Figure 4, top panel). The subsequent contrasts revealed that burning substantially reduced the overall diversity of lichens in stands subject to one or two fires, where, on average, 36.0 ± 5.2 (least squares mean and SE) more taxa were represented in the unburned (T = 00 and T = 10) than burned (T = 11 and T = 12); no effect of

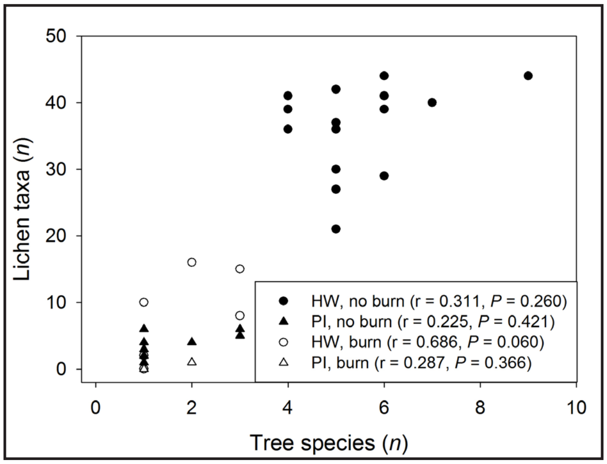

Figure 2. Relationship between the number of tree species and lichen species found growing on hardwood (HW) and pine (PI) tree species for burned and unburned plots. Pearson correlation coefficients and *P*-values.

thinning in the absence of burning was indicated (Figure 4). Models evaluating treatment effects on lichen diversity within the base and bole sampling heights yielded significant results, whereas no difference was apparent among samples taken from the canopy (Figure 5, top panel). The number of lichen taxa found on the boles of trees in the unburned stands averaged 39.3 ± 6.1 more than in the burned stands.

In contrast to the findings for lichen diversity, analysis of overall cover did not yield a significant result, despite that the ratio of cover in the unburned to burned stands approaches 3:1 (Figure 4, bottom panel). Findings for the discrete base and bole sampling heights were more intuitive, in both cases suggesting that cover was substantially lower in the burned plots, by 0.28 ± 0.08 and 0.36 ± 0.9, respectively (Figure 5, bottom panel). Consistent with the findings from the sampling height analysis of the diversity variable, lichen cover within the canopy was apparently unaltered by burning or thinning.

We were unable to demonstrate differences in either the proportion of lichens exhibiting different growth forms (Figure 6, top panel) or reproductive modes (Figure 6, bottom panel) in response to the treatments. Lichens exhibiting a crustose growth form were most common across stands 0.72 ± 0.14 (mean and SD), and appeared to maintain a similar proportion of that total across treatments. While not supported by the results of any formal statistical tests, there did appear to be a tendency for the proportion of lichens with a foliose growth form to decline, and reciprocally for those with a fruticose growth form to increase, or more likely to simply persist within the burned stands (Figure 6, top panel). Similarly, while the statistics do not support any shift in the reproductive mode exhibited by the lichens persisting in treated stands, we did note an apparent downward trend in the occurrence of lichens exhibiting a sexual reproductive mode (Figure 6, bottom panel).

Assessment of the relationship between plot-level fire severity ($dNBR_{MAX}$) and lichen variables was restricted to observations made

Table 3. The number of lichen species found within each sampling height and in total by species group (HW = hardwood, PI = pine) and treatment (00 = control; 10 = thinned, not burned; 11 = thinned, burned once; 12 = thinned, burned twice). "Both" indicates the number of lichen taxa in common across the tree species groups, and na = not applicable.

	Base			Bole			Canopy			Total		
Treatment	**HW**	**PI**	**Both**	**HW**	**PI**	**Both**	**HW**	**PI**	**Both**	**HW**	**PI**	**Both**
00	34	7	7	57	16	10	42	17	14	71	27	21
10	39	20	12	62	14	12	38	16	12	76	31	26
11	8	3	2	2	16	4	1	58	4	3	0	49
1	2 1	0	n	a 4	0	n	a 1	5	1	4	5	1

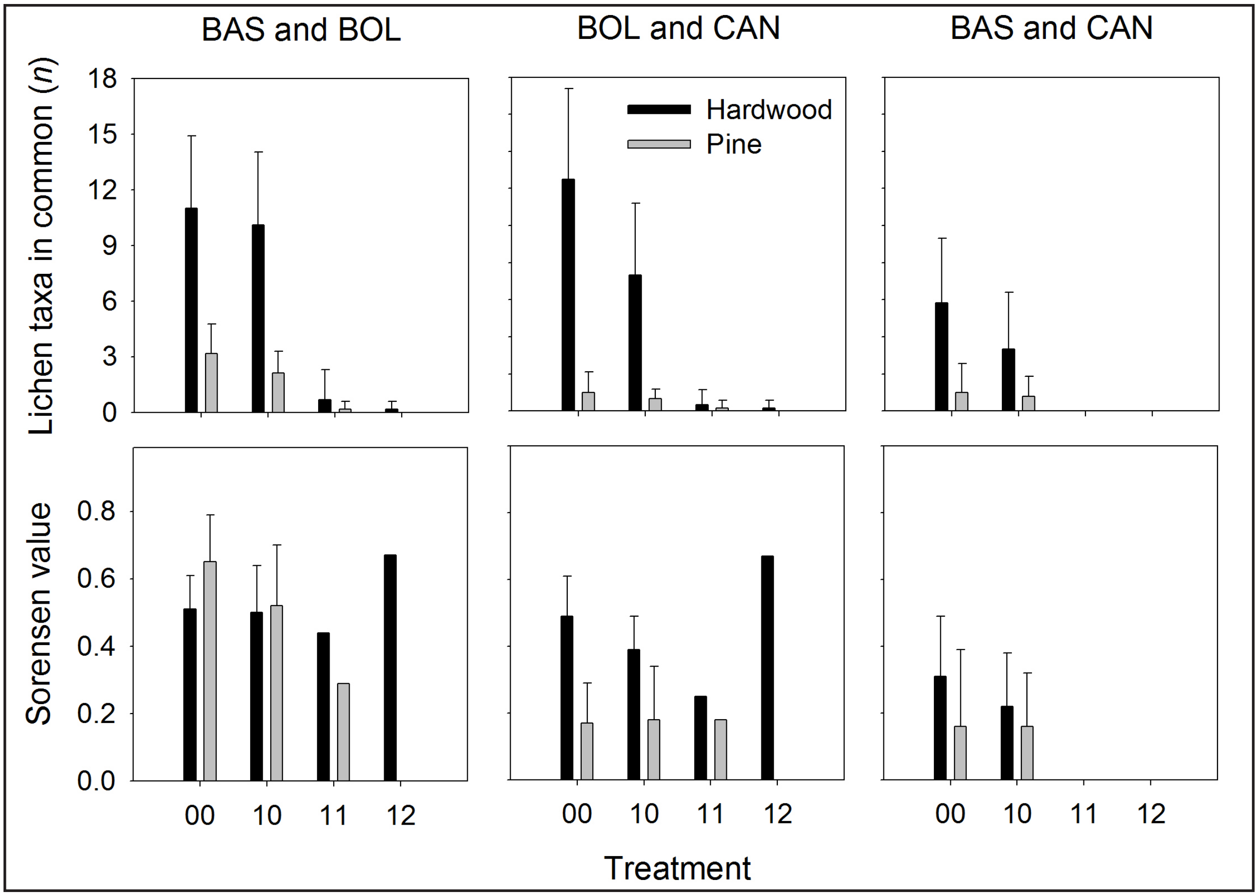

Figure 3. Similarity of lichen species found growing on hardwood and pine species at different sampling heights for the various treatments (00 = control; 10 = thinned once, not burned; 11 = thinned once, burned once; 12 = thinned once, burned twice). Means and standard deviations for the total number of species in common (top panels) and corresponding Sorensen similarity coefficient (bottom panels).

on pine trees because hardwoods were not well represented in the burned stands, particularly those that had been subjected to two fires. The range of dNBR values determined across the burn blocks (range = −235 to 621) was considerably wider than for dNBR_{MAX} recorded on the study plots (range = 175 to 466), and fell well within the range of possible values indicated for the methodology (approx. −600 to 1200). Similarly, the average dNBR values determined across all burn blocks (168 ± 140, mean and SD) was both lower and more variable than the dNBR_{MAX} values (317 ± 84) included in the analysis. Plots that were burned twice tended to have higher $\text{dNBR}_{\text{MAX},}$ values, but there was some overlap within the central part of the distribution (Figure 7). A significant negative correlation was observed between fire severity and the number of lichen taxa found on pine trees; however, no relationship was detected for lichen cover. One of the plots had a substantially higher average cover value than the others (dNBR_{MAX} = 367, cover = 0.20), an observation that was attributable to high lichen cover within the crown (0.60), as opposed to the more exposed base or bole sections of the stem.

DISCUSSION

We acknowledge that findings from this research are tempered by the observational study design and that the variability in the timeframe over which the treatments were applied result-

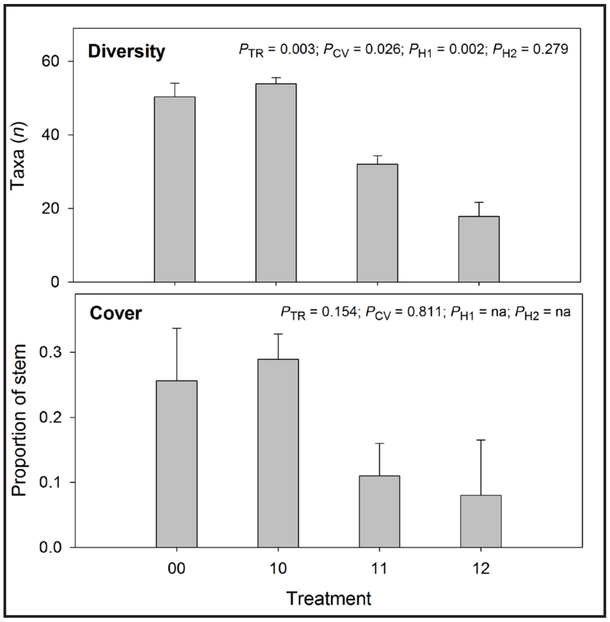

Figure 4. Overall trends in lichen diversity and cover for the different treatments (00 = control; 10 = thinned once, not burned; 11 = thinned once, burned once; 12 = thinned once, burned twice). Statistics from the GLM are presented, where P_{TR}, P_{CV}, P_{H1}, and P_{H2} are *P*-values associated with tests for the effects of the treatment, covariate, and contrasts associated with burning (00 + 10 = 11 + 12) and thinning (00 = 10), respectively.

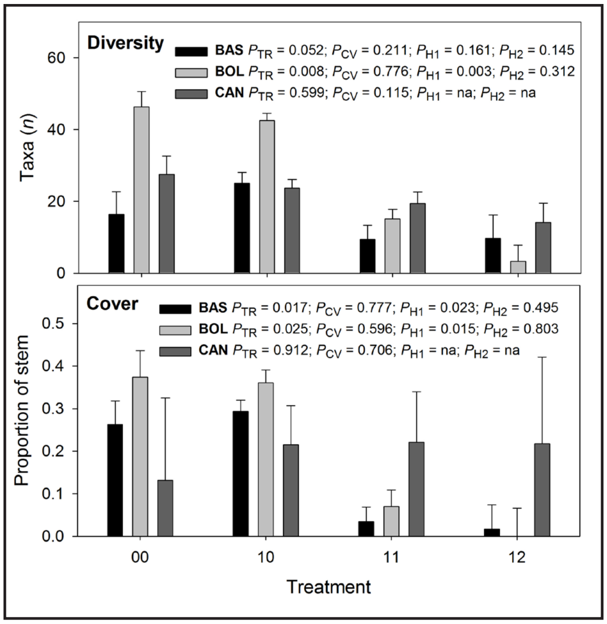

Figure 5. Trends in lichen diversity and cover by sampling height for the different treatments (00 = control; 10 = thinned once, not burned; 11 = thinned once, burned once; 12 = thinned once, burned twice). Three discrete heights were analyzed: BAS, BOL, and CAN. Summary statistics from the GLM are presented, where P_{TR}, P_{CV}, P_{H1}, and P_{H2} are *P*-values associated with tests for the effects of the treatment, covariate, and contrasts associated with burning (00 + 10 = 11 + 12) and thinning (00 = 10), respectively.

ed in different recovery periods when the lichen samples were collected. Also, hardwood trees in the treated stands tended to be younger and smaller than the pines, with correspondingly higher vulnerability to fire-induced mortality. However, available evidence suggests that the variable lag times between treatments and observations represented here are not likely to have been sufficient for lichen taxa to become reestablished or expand substantially following these types of disturbances (Jandt and Meyers 2000, Coxson and Marsh 2001).

The treatments documented in this study, prescribed burning and thinning, were undertaken to restore aspects of structure and composition that had been diminished through species conversion and long-term fire exclusion (Andreu *et al.* 2008, Nowacki and Abrams 2008, Ryan *et al.* 2013). Historic vegetation assemblages on these sites straddle the designations of Coastal Plain Oak–Loblolly Pine Forest and Inland Sand Dune and Ridge Woodland community types in Maryland (Harrison 2011), and these community types are known to harbor fire tolerant or pyrogenic vegetation supporting the use of prescribed burning as a management tool for restoration. Similarly, fire exclusion has led to tree densification with negative consequences for associated understory vegetation and wildlife (Taft 2009). We viewed the retention of off-site pines, noting that shortleaf pine would probably be more abundant than loblolly on the inland dune sites, as desirable, at least over the short term, because the highly flammable needle litter represents an important source of fuel that facilitates burning (*sensu* Kirkman *et al.* 2007).

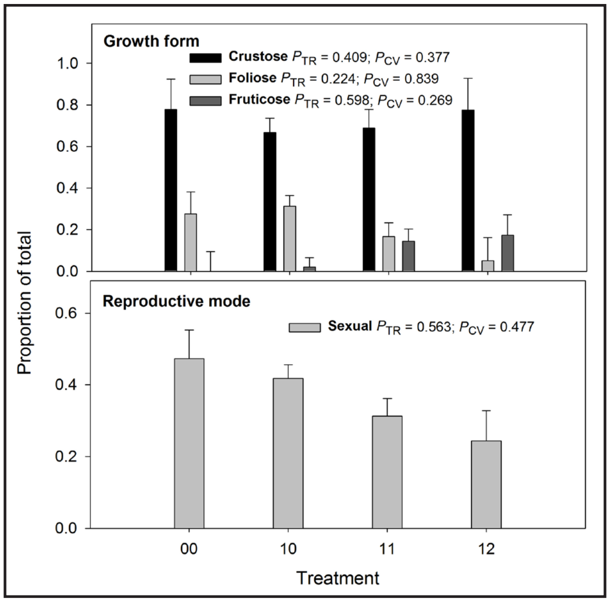

Figure 6. Trends in the proportion of lichen growth forms and reproductive modes determined across treatments (00 = control; 10 = thinned once, not burned; 11 = thinned once, burned once; 12 = thinned once, burned twice). Summary statistics from the GLM are presented, where P_{TR}, P_{CV}, P_{H1}, and P_{H2} are P-values associated with tests for the effects of the treatment, covariate, and contrasts associated with burning (00 + 10 = 11 + 12) and thinning (00 = 10), respectively.

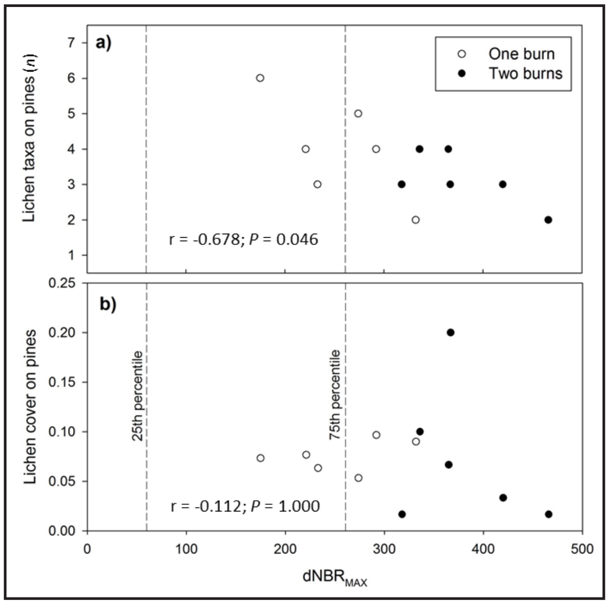

Figure 7. For pine trees only, the relationship between fire severity (dNBR) and a) the total number of lichen taxa, and b) lichen cover on plots subjected to one or two prescribed burns. Pearson correlation coefficient (r) and P-values. Dashed vertical lines represent the 25th and 75th percentiles of the dNBR values recorded across the burn blocks in 2009, 2011, and 2013 when prescribed burns were carried out.

In combination, these practices have resulted in substantial increases in understory plant diversity and structural heterogeneity of the forest canopy (The Nature Conservancy's Nassawango Creek Preserve, Wicomico and Worcester counties, Maryland, USA, unpublished data), yet relatively little is known about associated impacts on understudied groups such as lichens (Lendemer and Allen 2014), which collectively comprise an overwhelming proportion of earth's biodiversity (Hawksworth 1991, Whitman *et al.* 1998, Mora *et al.* 2011). Lichens also often function as indicator and keystone organisms in many ecosystems, providing vital services for other members of the community (Brodo *et al.* 2001, Gianinazzi *et al.* 2010). Thus, the general lack of data documenting how management practices impact these groups represents a risk because they are being carried out and evaluated without considering one of the most diverse and important components of the ecosystem.

Our findings suggest that corticolous lichen communities similar to those present in the unburned stands reported on in this study have the potential to be substantially altered by the reintroduction of fire. Most notable was the apparent reduction in the diversity of lichen taxa found in burned stands (Figure 4, top panel). An explanation for this result may be traced, at least in part, to the reduced number and smaller stature of the otherwise generally higher lichen diversity supporting hardwood species present on the burned plots (Tables 1 and 2). Moreover, the canopy samples collected from the hardwoods on burned plots tended to be in closer proximity to the forest floor than for the larger pines, suggesting that exposure of canopy lichens to damage by the fires was also higher. We speculate that if more large, fire-tolerant hardwoods had been present in the burned stands, their canopies would have acted as more of a refugium for the lichen diversity, similar to that of pines. However, the extent to which the canopy layer represents a refugium from fire damage is tempered by the compositional dissimilarity among lichens encountered at the various sampling heights, with possible implications for post-fire colonization of the lower bole sections.

While the average number of lichen taxa found on pines was substantially lower than on the unburned hardwoods, those values remained fairly stable following the fires (Figure 2). Taken together, these findings support the idea that hardwoods harbor more diverse lichen communities than pines (Schmitt and Slack 1990), but this may be countered by a correspondingly higher vulnerability to damage by fire. A surprising result was that total lichen cover was not identified as significantly related to the treatments (Figure 4, bottom panel). We attribute this counterintuitive finding to two primary issues: first is the small sample size available for the Anova (n = 9 stands) in conjunction with the relatively high variability in the cover variable among stands, and secondly that important differences were revealed for the base and bole sampling heights when they were analyzed independent of the null response of lichen cover in the canopy (Figure 5, bottom panel).

Thin-barked hardwoods are highly vulnerable to damage by fires independent of their size, a factor that has been used to infer the encroachment of fire-sensitive species across the landscape (e.g., Kirwan and Shugart 2000, Nowacki and Abrams 2008). Therefore, any lichen diversity associated with fire-susceptible hardwood species (e.g., red maple, American holly, American beech) should be assessed in the context of the broader restoration objectives for these natural areas by recognizing that mesophication of the tree community resulting from long-term fire exclusion may also have given rise to uncharacteristic lichen communities. Whether such reductions in lichen diversity will be offset by other species that become established on site-adapted hardwood trees is an open question requiring further study.

Abiotic factors such as humidity and solar insulation may represent stronger selective pressures on lichens than tree species, pushing lichen taxa to be more generalist in terms of their use of substrates (Gauslaa 2014). Some lichen species are known to depend on specific humidity levels for survival (Kantvilas and Minchin 1989), a condition that is altered by the removal of canopy trees as in a thinning. However, in this study, thinning in the absence of fire did not appear to result in meaningful changes in lichen diversity or cover. We speculate that this finding may be due to the relatively short and variable intervals following thinning (a period spanning over seven years between 2007 and 2013) when the samples were collected, in relation to rates of colonization by lichens. Alternatively, the lichen communities encountered in this study may be relatively insensitive to the magnitude of microclimatic changes brought about by the thinning treatments. Wind damage to pendulous lichens along the edges of harvest gaps was reported by Coxson and Stevenson (2005), but short-term impacts to lichens with other growth forms were somewhat ambiguous.

Previous research has documented differences in lichen communities based on the height gradient within trees, suggesting a level of discrimination among the base, bole, and canopy (Lesica *et al.* 1991, Peck and McCune 1997, Campbell and Coxson 2001, Cleavitt *et al.* 2009). While our findings generally support this observation, we also observed some notable similarities among the lichens on the bases and boles of hardwoods and pines, particularly on the unburned plots (Figure 3). Burning tended to eliminate lichens from the tree base, effectively disallowing the calculation of similarity values for that sampling height in the burned plots, but values determined on the unburned plots were consistent with the hypothesis that lichen composition would become more different with increasing vertical separation in trees.

Evidence from other studies suggests that all lichen morphologies (i.e., crustose, foliose, fruticose) are highly vulnerable to fires (Romangni and Gries 1997, Wolseley and Aguirre-Hudson 1997, Johansson *et al.* 2012). While our findings do not provide any solid evidence contradicting this assertion, we did note an interesting trend in the data suggesting that lichens with a fruticose growth form may be better suited than foliose lichens to persist in fire adapted systems (Figure 6, top panel), but this contention will require further study. Crustose lichens were the dominant growth form in both the unburned and burned plots, where their relative abundance was unchanged. Lichens exhibiting the crustose growth form have relatively lower surface area exposed to fire compared to those with foliose and fruticose morphologies, providing a possible explanation for the neutral response of crustose lichens to fire observed here. In the case of fruticose lichens, we speculate they may have an advantage related to either the rapidity with which they can colonize new habitats, or to their ability to occupy microhabitats on the bark surface that are less exposed to fire.

Changes in the proportion of lichens with different reproductive modes following disturbance also has implications for colonization and persistence under a re-established burning regime. Previous research has indicated lichen soredia, which are small vegetative reproductive structures composed of fungal hyphae and algae (Brodo *et al.* 2001), are an effective dispersal mechanism for colonizing recently burned habitats (Eversman and Horton 2004). Over half of the lichens collected in this study primarily reproduce asexually through the dispersal of soredia or other specialized vegetative propagules. In contrast, the colonization of canopy branches by sexual species present in adjacent forest blocks might be expected considering the increased dispersal abilities of small fungal diaspores, such as ascospores, compared to relatively much larger asexual diaspores (Löbel *et al.* 2009, Wagner *et al.* 2006, Werth *et al.* 2006, Johansson *et al.* 2012, Lendemer *et al.* 2014). Our findings related to possible changes in the reproductive mode favored by lichens following thinning and burning were ambiguous (Figure 6, bottom panel), yet trended with the idea that a vegetative dispersal mechanism might dominate, at least over the short term.

It is reasonable to assert that the variability of fire effects on vegetation may not be adequately captured by a simple count of the number of times a stand has been burned. To address that possible limitation, the once- and twice-burned class variable used to represent the treatment in the Anova models was further explored using the dNBR approach to quantifying fire severity (http://www.mtbs.gov/index.html; e.g., Picotte and Robertson 2011) (Figure 7). While these results generally supported our use of the simpler class variable approach (i.e., lower values of dNBR were consistently associated with the once-burned plots and higher values with those that were burned twice), a considerable range of dNBR values was also represented within each burn treatment. The study plots were located at higher and drier than average landscape positions within the respective burn blocks, and were consistently associated with higher dNBR values. Anecdotal evidence suggests that the second fires in these areas burned hotter than the first as the result of abundant dead fuels generated by the initial burn, helping to explain why the burn count variable performed adequately in the context of this study. Findings for the pine trees based on this analysis are entirely consistent with the overall results presented in Figure 4, in which a stronger negative relationship is indicated for lichen diversity than for cover.

MANAGEMENT IMPLICATIONS

While burning appears to have reduced the abundance and diversity of lichens previously found growing in the study area, we suggest that this outcome should be interpreted in light of restoration goals and in the context of an altered disturbance regime brought about by fire exclusion. From this perspective, it makes sense that the phenomenon of mesophication (Nowacki and Abrams 2008) would also extend to organisms for which component trees act as hosts. Available references suggest that a relatively frequent and low-intensity fire regime was characteristic of the coastal plain landscape where this study took place (Frost 1998, Guyette *et al.* 2012).

It is fairly well established that lichens are highly vulnerable to damage by fire, yet, through various avoidance and dispersal type mechanisms, they are still able to maintain a presence within fire-adapted systems (Longán *et al.* 1999, Eversman and Horton 2004, Johansson 2008). The initial fires in these areas burned under conditions that led to more intense fire behavior than desired over the long term (e.g., as a result of heavy fuel loads following thinning and timing in the early growing season), and may have led to greater impacts to the lichen communities. If so, these factors could be mitigated by initially reintroducing fires under conditions that would give rise to less active fire behavior while reducing fuel loads. Other studies have documented detrimental effects of forest densification on lichens, of the type that occurs in the absence of fires (Bond *et al.* 2005, Root *et al.* 2010), although this could conceivably be addressed through thinning.

Over time, repeated burning can be expected to act as a filter selecting for fire-tolerant tree species that will in turn provide stable substrates for similarly adapted lichens to colonize (Bartos and Mueggler 1981, Espelta *et al*. 2003). The mature pine component of these stands is arguably already functioning in this way, whereas fire adapted hardwood species and associated lichen diversity still need to be recruited into these areas. For example, dry-site and fire-adapted oak species (e.g., post oak and black oak) are being sought as future overstory components in these areas, but recruitment in the context of a moderately frequent fire regime presents a challenge (see Arthur *et al.* 2012). Possible approaches to overcoming these limitations include: (1) waiting to re-introduce fire until repeated thinning of the pine canopy has released oaks already present in the understory or midstory and enabled them to grow to sizes (attain a bark thickness) that will be able to resist damage from subsequent understory fires, (2) using ignition techniques or other protection measures (e.g., raking; Williams *et al.* 2006) to guard selected areas and trees from fire damage within a burn block, and (3) periodically allowing for extended fire-free intervals so that new cohorts can attain sizes that will confer resistance to damage as in (1).

Recognizing and incorporating biodiversity concerns into forest and restoration management activities benefits from taking a multidisciplinary approach. This observational study of the impacts of thinning and fire on lichen communities within pine-dominated forests of the Mid-Atlantic Coastal Plain calls attention to a previously overlooked component of biodiversity—one that appears to be responsive to these types of treatments. Additional study will be required to determine whether a new equilibrium is established between the lichens and fire-adapted tree community on these sites where burning was reinstituted to benefit other more conspicuous aspects of biodiversity.

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