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Prescribed burn frequency, vegetation cover, and management legacies influence soil fertility: Implications for restoration of imperiled pine barrens habitat

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ABSTRACT

In fire-dependent ecosystems, the absence of fire can contribute to a positive feedback in which increased vegetation cover leads to increased accumulation of soil organic matter and nutrient stocks. These changes in turn can influence competitive shifts among plant communities, resulting in increased woody plant establishment, canopy closure, and ultimately leading toward mesophication. Poor soil conditions may be especially important for maintaining the open structure characteristic of pine barrens ecosystems, which are imperiled due to loss of key ecosystem processes such as fire and land conversion to cropland or pine plantations. Our objectives were to determine how soil characteristics are related to recent prescribed fire management, and how soils vary along gradients of current and historic vegetation cover in a barrens-forest mosaic in northern Wisconsin, USA. We sought to understand whether management with prescribed fire shifts soils toward barrens-type soil conditions, and whether soil conditions typify barrens habitat relative to shrub and forest habitat We analyzed organic (i.e. forest floor) and mineral soil horizons collected along gradients of recent prescribed burn history and current (barrens, pine woodlands, brush, and closed-canopy forest) and historic vegetation cover types (barrens, pine plantations, deciduous forests) to investigate the influence of each on specific components of soil fertility. Using a model selection approach, we found forest floor soil properties were most frequently associated with differences in current vegetation cover; for instance, pine woodland sites had greater organic matter stocks than barrens sites, and cation stocks were generally greater at brush sites than barrens and pine woodland sites. Some soil properties, including pH, however, appeared to be driven by prescribed burn frequency. Using ordination techniques to characterize multidimensional characterizations of soils, we identified a soil legacy effect related to historic vegetation cover and land management; native barrens sites had soil characteristics intermediate to restored barrens of pine woodland and deciduous forest origin. Our findings suggest restoration of pine plantations to barrens could benefit from fire activities that enhance consumption of the forest floor, while restoration of deciduous forest and brush habitats will likely be more related to the effective control of hardwood regeneration, after which soil conditions may return to a more archetypical barrens state.

1. Introduction

Fire is a widespread, keystone disturbance that influences the global distribution of plant communities both directly (i.e. by consuming plant biomass) and indirectly (e.g. by changing microenvironment and soil properties). Plant species or communities may be classified along a spectrum of fire-tolerance to fire-intolerance, and those that are fire-adapted have specific traits related to avoidance, tolerance, or regeneration (Lavorel and Garnier, 2002). For example, traits associated with fire-adapted species include heat-tolerant seeds or fire-stimulated seed germination (Paula and Pausas, 2008; Wiggers et al., 2017), thick bark (Pausas, 2015), or vigorous re-sprouting capability (Clarke et al., 2013). In contrast, fire intolerant species lack these traits but may have other traits, such as shade tolerance or rapid growth, with potential to

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outcompete fire-adapted species under mesic, fertile soil conditions (Parker, 1987; Varner et al., 2016).

Soil conditions also influence plant community composition, and fire can alter soil chemical, physical, and biological properties (Neary et al., 2005). Fire alters nutrient cycling by volatilizing, combusting, and mineralizing soil nutrients bound in organic matter, and fire-soil relationships show ecosystem-dependent patterns. For instance, unburned conifer and deciduous forest soils have greater total C and N stocks than burned forest soils in the U.S. Great Lakes region (Miesel et al., 2012), whereas low-intensity surface fires are associated with increased soil pH and nutrient availability in some grasslands (Úbeda et al., 2005). Fire frequency, intensity, and severity also matter. For instance, one study comparing single, low-intensity lightning-ignited spot fires in mixed conifer forest (*Pinus ponderosa* Lawson and *Pseudotsuga menziesii* Mirb.) to adjacent unburned forest found that O and A horizon soil chemical properties did not differ between burned and unburned areas (Hatten et al., 2005). Repeated low severity prescribed fires, however, resulted in increased organic horizon (0–10 cm) pH and nutrients (Ca, Mg, K, Na, NO_3, total N, and organic C) in an oak (*Quercus* spp.) forest subjected to annual to biennial burns for a 20–year period, suggesting that when fire intensity is low, many burns may be needed to alter soil properties (Scharenbroch et al., 2012). In contrast, high severity burns are generally related to soil organic matter loss and enrichment in aromatic organic compounds and base cations, especially in soil O horizons (Bodi et al., 2014; Kolka et al., 2014, 2017; Merino et al., 2018; Miesel et al., 2015).

Just as the presence of fire influences soils and plants, so may fire exclusion. Fire exclusion may result in changes to the structure and composition of plant communities and lead to fuel accumulation outside its natural range of variation (Drobyshev et al., 2008; Frelich, 1995). Furthermore, extended fire-free intervals can allow fire-intolerant species to invade open-canopy habitats and outcompete fire-tolerant species, potentially resulting in conversion from open-canopy habitat to closed-canopy forest (Corace et al., 2012; Nyamai et al., 2014). For instance, fire exclusion policy that followed extensive late 19th century logging activity has resulted in forest densification throughout the Great Lakes region (Radeloff et al., 1999). Pine barrens, a type of coniferous savanna occurring on infertile (i.e., "barren") soil, were once widespread throughout the Great Lakes region but are now considered globally imperiled, having experienced a 99% reduction in their pre-settlement extent (Wisconsin DNR, 2015). Remnant pine barrens of the Great Lakes region are thought to represent vegetation characteristic of this region for the past 100 years, and potentially since the last Ice Age (Curtis, 1959; Fassett, 1944; Hamerstrom Jr., 1963). Soil conditions underlying extant pine barrens may, therefore, reflect the conditions that limit tree growth and favor native plant communities.

Fire exclusion, woody encroachment, and altered soil conditions in pine barrens illustrate the early stages of mesophication, an ecological phenomenon in which decreased ecosystem flammability results from fire suppression, canopy closure, and an increase in mesophytic tree species (Dickinson et al., 2016; Nowacki and Abrams, 2008). During mesophication, novel mesophytic communities create positive feedbacks with soils that support the persistence of shade-tolerant and fire-sensitive plant species, at the expense of fire-tolerant species. These characteristic feedbacks may result in a stable state shift from semi-open savannas and woodlands to closed forest as belowground changes in soil nutrient and water availability occur. In pine barrens, for example, soils are nutrient limited and N accumulation through plant inputs has the potential to drive barrens toward mesophication. However, data to support the assumption that nutrient limitation is associated with barrens persistence are extremely limited (e.g. Pregitzer and Saunders, 1999), and therefore the immediate and long-term effects of fire or fire exclusion on barrens soils are unknown.

Past land use and management history may also have persistent legacies affecting belowground processes (Perring et al., 2016). Pine plantation establishment was widespread on historic barrens of the region, in part because they were comparatively easy to plow, creating furrows in the sandy soils to enhance water availability to pine seedlings. These furrows remain evident to this day, but it is unclear how this widespread historic land use practice affects current belowground processes. Afforestation efforts more generally are known to modify belowground storage and distribution of C and N from open grassland systems (Li et al., 2012). Deciduous tree species can further invade the understory of established plantations, and these understory saplings are often released by the opening of the canopy during woodland and barrens restoration treatments. Vegetative reproduction is particularly vigorous for young deciduous species of most genera (Del Tredici, 2001), such that the hardwood brush stage is among the most challenging transitional stage to restore to a barrens condition (Buckman, 1964). Given that the development of the forest floor (i.e., O horizons) is a key component of the mesophication process, the legacy of that forest floor may persist well past the structural restoration of barrens systems (i.e., the immediate and repeated removal of aboveground stems via mechanical cutting and burning). Likewise, conifer and deciduous forests differ systematically with respect to belowground C and nutrients (Vesterdal et al., 2013). These more general patterns suggest that past vegetation states may interact with current management activities to affect the ability of prescribed fire to reverse the belowground mesophication processes necessary for successful barrens restoration.

The objectives of this study were to determine how soil characteristics are related to recent prescribed fire management and how soils vary along gradients of current and historic vegetation cover in a barrens-forest mosaic in northern Wisconsin, USA. We sought to understand whether soil conditions (i.e. nutrient-depleted soils) typify barrens habitat relative to shrub and forest habitat, and whether prescribed fire management shifts soil conditions towards barrens-type soil conditions. Our specific study questions were: (1) how do individual components of soil fertility (i.e. nutrient stocks) relate to vegetation cover and recent burn history, (2) how do overall soil conditions differ among vegetation cover types and/or along gradients of burn frequencies, and (3) how do past vegetation states, including the historic practice of soil furrowing with pine plantation establishment, create soil legacies that may either impede or enhance barrens restoration? We addressed these questions by comparing soils of long unburned ($\geq$60 years) sites to soils of managed sites that have experienced between one and nine prescribed burns since the 1960s, crossed with historic vegetation factors that include past plantation establishment, and we hypothesized that sites in later successional stages (i.e. brush-encroached and deciduous forest) would exhibit increased nutrient stocks relative to earlier successional stages (i.e. barren and woodland sites). Addressing this crucial knowledge gap will provide essential baseline data to help land managers optimize pine barrens restoration.

2. Material and methods

2.1. Study area

The Moquah Barrens (latitude 46.6235° N, longitude 91.2123° W) is a ~5100 ha area located in the Northwest Sands ecological landscape of Wisconsin, USA (Fig. 1). This region has flat to gently rolling topography and a relatively short growing season (121 days), with a mean annual temperature of 5.2 °C and mean annual precipitation of 800 mm (Wisconsin DNR, 2015). The ecological landscape is classified as pine barrens and northern dry forest (Wisconsin DNR, 2015). Soils are well-drained to excessively-drained Spodosols (primarily Entic Hapolorthods [Sultz, Vilas, and Rubicon series] and sparse Alfic Haplorthods [Rubicon series]) of glacial outwash origin, up to 180 m deep. The Moquah Barrens landscape is managed by the Chequamegon-Nicolet National Forest, and management activities include timber harvest, invasive species control (i.e. herbicide application), mechanical brush-cutting, and prescribed burning, which together are designed to restore the

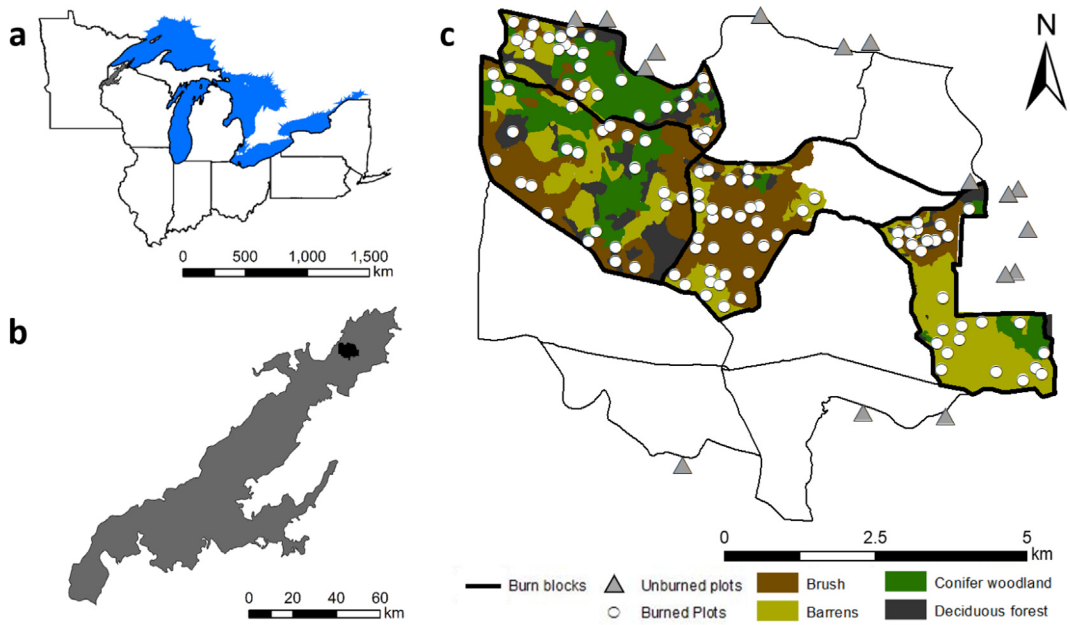

Fig. 1. Map of the study area showing (A) the Lake States region of the United States, (B) the "Northwest Sands" region of Wisconsin, consisting of sandy glacial outwash soils, and (C) the Moquah Barrens area including burned and unburned study sites spanning a range of vegetation cover. Vegetation cover is indicated by color for the four burn blocks (dark borders) included in this study.

plant community composition and structure that typify pine barrens.

2.2. Vegetation classifications

Our study includes 127 sites spanning a spectrum of vegetation structure and composition, which we categorized into four vegetation cover types: barrens, brush (i.e., shrub-dominated), pine woodlands, and deciduous forest (Fig. 2), using the cover type definitions used by the Chequamegon-Nicolet National Forest to guide restoration treatments. The current vegetation classification was crossed with historic vegetation condition during initial site selection, whereas fire history was determined post-site selection (see below). The term 'barrens' was used to encompass structural and compositional stages ranging from open-canopy, treeless patches to savannas with scattered large trees or shrub-dominated patches. Barrens were defined as having < 50 trees acre^{-1} (*Pinus banksiana* Lamb., *P. strobus* L., *P. resinosa* Aiton.) and oaks (*Quercus ellipsoidalis* E.J. Hill*, Q. rubra* L.) and < 30% shrub/sapling cover (*Salix humilis* Marshall, *Prunus serotina* Ehrh., *Corylus cornuta* Marshall, *C. Americana* Walter). Barrens support a characteristic ground cover of blueberry (*Vaccinium* spp.), sweet fern (*Comptonia peregrina* [L.] J.M. Coult.), sand cherry (*Prunus pumila* L. var *pumila*), and native grasses, sedges, and forbs. Brush sites had ≥ 50% cover of shrubs with DBH < 11.4 cm. The most common shrub/sapling species at brush sites were oak (*Q. ellipsoidalis, Q. rubra*), cherry (*P. serotina*), hazel (*C. cornuta*, *C. Americana*), red maple (*Acer rubrum*), serviceberry (*Amelachier* spp.), Aspen (Populus tremuloides Michx., P grandidentata Michx.) and willow (*S. humilis*). Pine woodlands consist of recently (within 10 years of sampling) thinned large diameter (> 11.4 cm DBH) *P. resinosa* and *P. banksiana* plantations to create semi-open conditions (basal area target 7–14 m^2 ha^{-1}). Deciduous forest sites had a closed

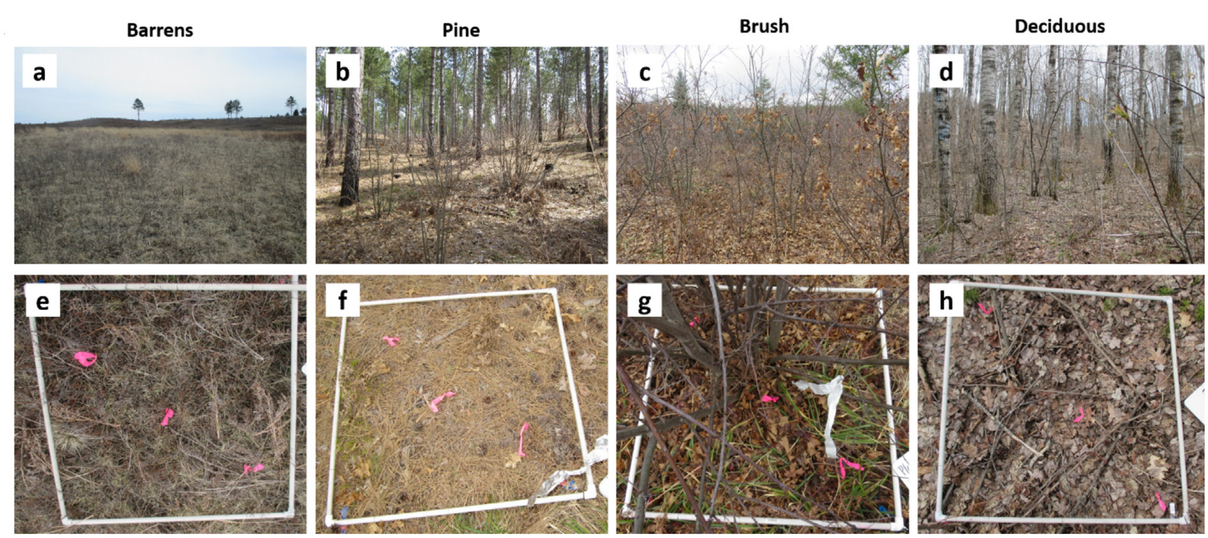

Fig. 2. Photographs showing the aboveground vegetation cover (a-d) and corresponding soil surface (e-h) at barrens, pine, brush, and deciduous sites, respectively. White quadrat frames in images e-h are 1-m^2, and all photos were taken during the dormant season in mid-May. See text for description of the dominant tree and herb species present for each cover type.

canopy with tree basal area > 14 $m^2 ha^{-1}$, and dominant tree species included aspen (*Populus tremuloides* Michx., *P. grandidentata* Michx.), and oaks (*Q. ellipsoidalis* and *Q. rubra*).

Historic vegetation cover data was obtained from a 1951 timber survey (US Department of Agriculture Forest Service, 1954). The timber survey classified regions by plant community types including grassland (i.e. barrens), aspen-paper birch, scrub oak, red pine, and jack pine communities. Pine-dominated sites denoted whether communities were natural or the result of planting, which typically involved furrowing during plantation establishment. In some cases, pine plantation establishment occurred just after the survey, in the early 1960s, based on USDA Forest Service records. For consistency with the current vegetation cover classifications, we simplified the USDA classifications into three historic vegetation cover categories: barrens, pine, and deciduous. Almost all pine historic vegetation cover plots were of pine plantation origin, generally established using furrowing practices.

2.3. Fire history

Tree ring data indicate that from ~1660 to 1925, the historic mean fire return interval for Moquah Barrens was approximately 9–15 years and has since increased to > 40 years (Guyette et al., 2016). Prescribed fire management was introduced to Moquah in the late 1960s, during which time burns were managed in small 50–100 ha units. Prescribed burns are conducted during the dormant season, typically in mid to late May. Our study included four management units, each comprising 200–800 ha, plus unburned areas immediately adjacent to the management area (Fig. 1). Within the Moquah Barrens, our study plots had a recent burn history of 0–9 prescribed burns since 1970. We classified burned plots as low (1–3), moderate (4–6), or high (7–9) burn frequency. At the time of soil sampling, one burn block was last burned in 2014, two were last burned in 2013, and one block consisted of subunits last burned in 2003 and subunits that had not been burned for ≥ 60 years. Thus, burn frequency classes were distributed unevenly among vegetation cover types (see Table 1).

2.4. Field sampling

We sampled pre-fire forest floor (organic layer; i.e. litter, duff, and O horizon) and upper mineral soils (0–5 cm and 5–10 cm depth increments) during the summer of 2015 and late spring of 2016, within 1-m^2 quadrats near the center of each established study plot. We first collected the forest floor from within 30 cm diameter sampling ring. After removing the forest floor, we collected two 10 cm deep mineral soil cores into plastic PVC tubes using a 5 cm radius soil bulk density hammer (AMS, Inc., American Falls, Idaho, USA). We then capped the tubes and transported them to the laboratory.

2.5. Laboratory analysis

Forest floor samples were air-dried to constant mass, weighed, and ground to pass a 1 mm screen before analysis for NO_3^-, NH_4^+, P, K, Ca, Mg, pH, and organic matter (OM) at the Michigan State University Plant and Soil Nutrient Lab. Nitrate-N and ammonium-N were extracted from 5 g of soil in 50 ml of 1 N KCl and analyzed using a LaChat 8500 flow injection analyzer, and total inorganic N (TIN) was calculated as the sum of nitrate (NO_3^-)and ammonium (NH_4^+). Phosphorous was extracted by the Olsen method (Olsen et al., 1954) and measured using a Brinkman PC 950 probe. K, Ca, and Mg were extracted in ammonium acetate and measured by flame photometry (K, Ca) or colorimetric analysis (Mg). Sample pH was determined for a slurry of 5 g of soil in 5 ml of deionized water using a Labfit pH analyzer. Organic matter was calculated as loss on ignition by ashing 5 g of soil at 360 °C for two hours. Forest floor subsamples were pulverized to a fine powder and analyzed for total C and N with a Costech dry combustion elemental analyzer (Costech Analytical Technologies Inc., Valencia, California, USA).

Each mineral soil sample was subdivided into the upper 0–5 cm and lower 5–10 cm portions. They were air-dried to constant mass, and sieved to 2 mm. We calculated mineral soil bulk density as dry mass per volume (g cm^{-3}). We analyzed mineral soils for total C and N, NO_3^-, NH_4^+, P, K, Ca, Mg, pH, and OM using the procedures described above.

2.6. Statistical analyses

Statistical analyses were conducted in R v3.5.0 (R Core Team, 2018). We used a model comparison approach to identify the best predictors of individual soil variables within each horizon. Briefly, we used Akaike's Information Criterion (AIC) to compare models that included current vegetation cover (CV), historic vegetation cover (HV), fire frequency (FF), and combinations of these (CV + HV, CV + FF, HV + FF, CV + HV + FF, CV * FF, and HV * FF) resulting in the comparison of 9 different models. In the case of equivalent models (i.e. $\Delta AIC \leq 2$), we selected the most parsimonious model (Burnham and Anderson, 2004). Following model selection, we used Tukey's tests for post-hoc multiple comparisons of vegetation cover types and burn frequency categories, with statistically different groups identified at the $p < 0.05$ level.

We used non-metric multidimensional scaling (NMDS) to evaluate overall soil chemical environment and to relate separation in soil fertility space to differences in vegetation cover and burn frequency. Each soil variable included in the ordination (pH, Ca, Mg, K, P, N, and OM) was log- transformed to normalize values and avoid inflating the influence of extreme values. Next, we ordinated the normalized values into a Euclidean distance matrix; to investigate whether effects were constrained to upper horizons or extended into the mineral soil, we performed a separate ordination for each soil horizon (forest floor, 0–5 cm mineral soil, and 5–10 cm mineral soil). Next, we compared

Table 1
Distribution of the 127 study sites across fire frequency and current vegetation classes at the Moquah Barrens, Wisconsin, USA. "Decid" denotes deciduous forest. Early prescribed burn activity (1960s–1990s) occurred predominantly in barrens and brush habitat, resulting in a bias toward these cover types in our moderate and high fire frequency classes.

Current Vegetation	Burn frequency class											
	Unburned			Low			Moderate			High		
	Historic Vegetation			Historic Vegetation			Historic Vegetation			Historic Vegetation		
	Barrens	Pine	Decid	Barrens	Pine	Decid	Barrens	Pine	Decid	Barrens	Pine	Decid
Barrens	4	2	–	3	8	2	3	4	5	2	2	9
Pine	–	11	–	–	8	–	–	–	–	–	–	–
Brush	–	2	5	–	18	10	–	2	13	–	2	–
Decid	–	1	5	–	–	5	–	–	1	–	–	–

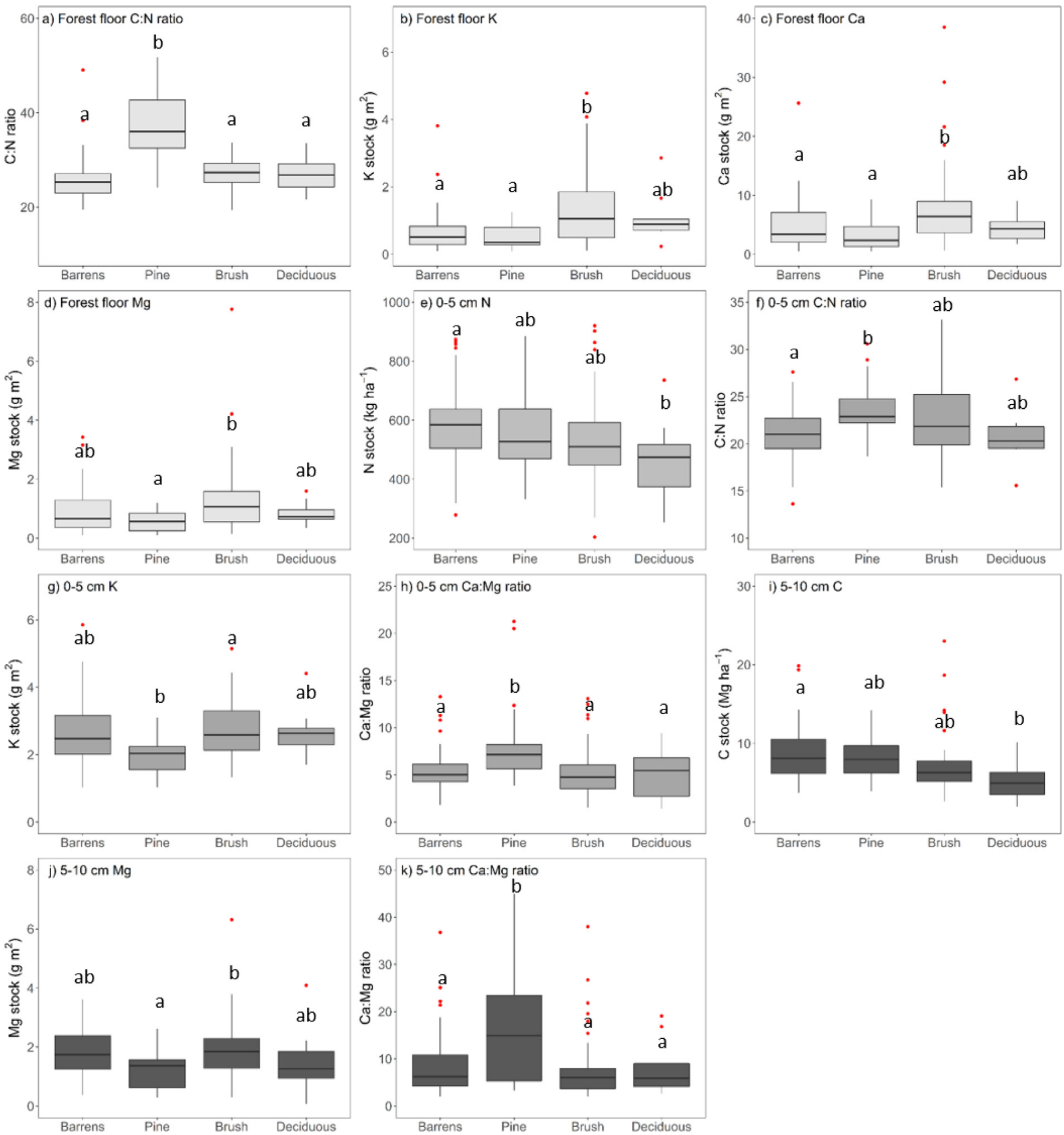

Fig. 3. Current vegetation cover best explained variation in 11 soil properties, among the three distinct horizons. Boxes with different letters indicate significantly different groups ($p < 0.05$) according to Tukey's posthoc tests. Light gray indicate forest floor samples (a-d), medium gray indicates 0–5 cm mineral soils (e-h), and dark gray indicates 5–10 cm mineral soils (j-l).

stress values for each ordination with two dimensions versus three dimensions (i.e. $k = 2$ and $k = 3$) and selected the number of dimensions that resulted in the lowest stress value. Similarly, we used NMDS to evaluate differences between soils of native and restored barrens, distinguishing between those that were historically pine plantations or deciduous forest. NMDS plots were created using the vegan package in R (Oksanen et al., 2011) and analyzed using the 'Adonis' function in vegan to conduct permutatational multivariate analysis of variance (PERMANOVAs) to determine differences among current and historic vegetation cover groups and burn frequency groups. We used post-hoc correlations to identify the soil variables that explained variation in the first two NMDS axes, and $\alpha = 0.05$ to determine statistical significance for all analyses.

3. Results

3.1. Forest floor nutrients

Current vegetation cover, historic vegetation cover, and fire frequency were included in 4, 3, and 3 significant forest floor models, respectively (Figs. 3 a–d, 4a–c, and 5 a-c). Forest floor C stocks were more than two-fold greater at sites with historic pine cover (13.2 ± 1.2 Mg ha^{-1}C) than sites with historic barrens cover (6.3 ± 1.6 Mg ha^{-1}C), and forest floor organic matter displayed a similar pattern (Fig. 4a-b). Although neither forest floor total N nor inorganic N varied systematically with vegetation cover or fire frequency, C:N ratio was influenced by both current vegetation cover (Fig. 3a) and fire frequency (Fig. 5a). Forest floor C:N was 42–48% greater in pine sites than in all other cover types (barrens, brush, and deciduous

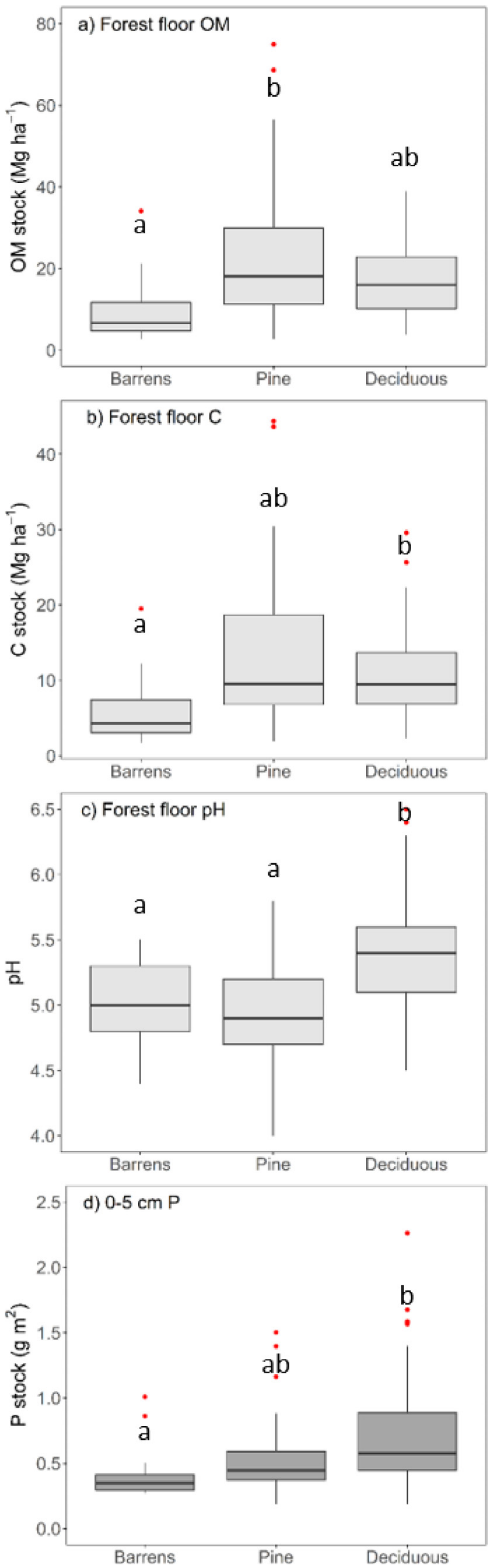

Fig. 4. Historic vegetation cover best explained variation in 4 soil properties, among the forest floor (a-c) and upper mineral soil (d) horizons. Boxes with different letters indicate significantly different groups ($p < 0.05$) according to Tukey's posthoc tests.

forest), and C:N of unburned and low burn frequency sites was 16% greater than C:N of moderate burn frequency sites and 23% greater than C:N of high burn frequency sites (Fig. 5a). Forest floor base cation stocks were most frequently related to vegetation cover type. Brush sites had more than double the K, Ca, and Mg stocks of pine sites, and K and Ca were also elevated in brush sites relative to barrens sites (Fig. 3b-d). Variation in Ca:Mg ratio was related to fire frequency, with moderately burned sites having nearly 20% greater Ca:Mg than unburned sites (Fig. 5b). Forest floor pH was more acidic at historic barrens and pine sites than sites with a history of deciduous forest cover (Fig. 4c), and pH appeared to increase with fire frequency (Fig. 5c).

3.2. Mineral soil nutrients

Nutrient stocks in mineral soils generally showed different responses to vegetation cover and fire frequency than the forest floor (see Supplementary Table S1). Current vegetation cover was consistently influential with respect to differences in the mineral soil nutrients, providing explanation for variation in 4 and 3 models for the 0–5 cm and 5–10 cm mineral soil horizons, respectively (Fig. 3e-k). In contrast, historic vegetation showed very little relation to mineral soil characteristics and was only included in 1 model (Fig. 4d). Fire frequency was also related to some mineral soil characteristics in both the upper and lower horizon (Fig. 5d-i).

5–10 cm mineral soil C stocks (i.e. 5–10 cm depth) were > 50% greater at barrens sites than deciduous forest sites, but no statistically significant differences were observed for upper (0–5 cm) soil C stocks or for organic matter in either mineral soil horizon (Fig. 3i, Table S1). Mineral soil total N was 32% greater at barrens sites than at deciduous forest sites for both upper (Fig. 3e) and lower mineral soil (57% difference), and 5–10 cm mineral soil inorganic N was nearly 40% greater at sites with low fire frequency than sites with moderate fire frequency (Fig. 5h). Upper mineral soil C:N ratios were 13% greater at pine sites than barrens sites (Fig. 3f), similar to the pattern observed for forest floor C:N. Upper mineral soil extractable P was greater at sites with moderate fire frequency relative to all other fire frequency groups (Fig. 5d), and historically deciduous sites also had 65% greater 0–5 cm soil extractable P than historically barrens sites (Fig. 4d). Pine site 0–5 cm mineral soil K stocks were nearly 40% lower than barrens K stocks (Fig. 3g), and 0–5 cm Ca:Mg was more than 50% greater in pine sites than in all other vegetation cover types (Fig. 3h). Upper mineral soil Mg stocks were elevated in moderate and high burn frequency sites relative to low burn frequency sites (33% and 22% difference, respectively; Fig. 5f), and unburned sites had lower pH (4.51) than all other fire frequency groups (Fig. 5g). Cation stocks and pH of lower mineral soils did not vary significantly among any of the groups tested (Table S1).

3.3. Multidimensional patterns in soil nutrient status

Non-metric multidimensional scaling (NMDS) ordination revealed relatively little separation in ordination space among current vegetation cover types or among sites with varying burn history, and NMDS plots revealed a pattern of increasing overlap in ordination space with increasing soil depth (Fig. 6). Stress values increased with depth, from 0.04 for the forest floor, to 0.09 and 0.10 for the 0–5 cm and 5–10 cm mineral soil, respectively. PERMANOVA results indicated significant dissimilarity in burn frequency groups ($F = 2.96_{3,117}$, $p = 0.03$), but variance explanation was poor ($R^2 = 0.07$), and vegetation cover provided only a slightly better ordination fit ($F = 4.38_{3,117}$, $p < 0.01$, $R^2 = 0.10$) (Fig. 6a-b). Although mineral soils overlapped among burn frequency and vegetation cover groups in ordination space, PERMANOVA indicated statistically significant dissimilarities. For the 0–5 cm mineral soils, burn frequency groups were more dissimilar in ordination space ($F = 6.19_{3,119}$, $p < 0.01$, $R^2 = 0.14$) than vegetation cover ($F = 2.77_{3,119}$, $p < 0.01$, $R^2 = 0.07$) groups (Fig. 6c-d). The 5–10 cm

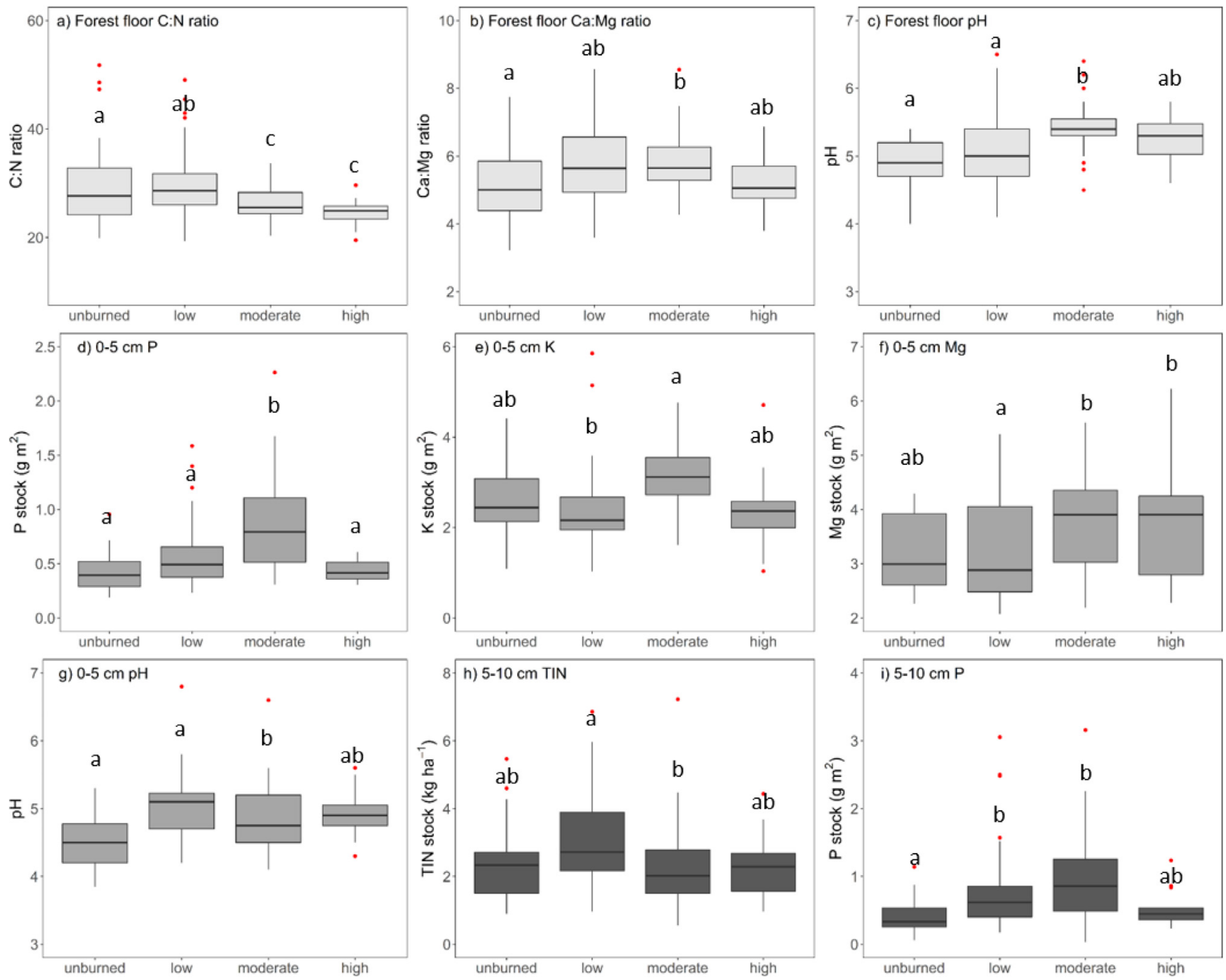

Fig. 5. Prescribed fire frequency best explained variation in 9 soil properties, among the three distinct horizons. Boxes with different letters indicate significantly different groups ($p < 0.05$) according to Tukey's posthoc tests. Light gray indicate forest floor samples (a-d), medium gray indicates 0–5 cm mineral soils (e-h), and dark gray indicates 5–10 cm mineral soils (j-l).

mineral soils also showed greater dissimilarity among burn frequency groups ($F = 3.37_{3,120}$, $p < 0.01$) relative to vegetation cover groups ($F = 2.10_{3,120}$, $p = 0.02$), although neither provided high variance explanation ($R^2 = 0.08$ and 0.05, respectively) (Fig. 6e-f). Extant barrens sites of different vegetation cover history showed separation in ordination space for the forest floor horizon (Fig. 7a), although PERMANOVA results were marginally non-significant ($F = 2.84_{2,\ 38}$, $p = 0.054$, $R^2 = 0.13$). Neither upper nor lower mineral soil characteristics of barrens sites differed by vegetation history (Fig. 7 b-c; $p = 0.14$ and $p = 0.83$, respectively).

4. Discussion

How do individual components of soil fertility relate to vegetation cover and recent burn history?

Patterns of individual soil properties identified some key differences between barrens sites and contrasting vegetation cover types which are characterized by greater woody plant densities. Previous studies have suggested that low pH, soil moisture deficiency, and poor nutrient status, specifically of Ca, Mg, and N, limit tree growth in pine barrens (David et al., 1988; Heikens and Robertson, 1994; Sweet, 1880). In our study, we observed lower soil C, OM, K, Ca, and pH at barrens sites relative to other cover types, especially brush and deciduous forest. At Moquah, sites with barrens vegetation are associated with low fuel loads which result in minimal fuel consumption and low inputs of fire-generated ash relative to other cover types (Quigley et al., 2019). This pattern may explain why barrens sites had lower forest floor pH than deciduous forest sites and depleted K and Ca stocks relative to brush sites. In contrast, mineral soils of barrens sites had greater total C and organic N stocks than deciduous forest mineral soils, which may be driven by differences in how these contrasting plant communities cycle nutrients. Along grassland-to-forest gradients, fine-root biomass decreases with increasing tree cover (Reich et al., 2001). Therefore, it is possible that barrens-to-forest gradients may have similar trends, and fine root turnover or increased inputs from root exudates may explain the elevated mineral soil C and N at barrens sites. N-fixing plants are also important components of many native fire-prone communities and may influence the rate of N recovery after fire (Neary et al., 1999). For example, sweet fern, a characteristic ground-layer plant in barrens communities, is associated with symbiotic N-fixation and may influence N recovery in barrens habitat. Furthermore, as a fire-adapted species, sweet fern is able to establish on very dry soils with low OM and N concentrations (Hendrickson, 1986), and this positive feedback may be important for barrens persistence. Further investigations of N mineralization in relation to plant composition will provide valuable insight into the role of N fixers in nutrient limitation of pine barrens soils.

Many of the nutrient stocks measured, however, did not differ between barrens sites versus brush, pine, or deciduous sites, and this may

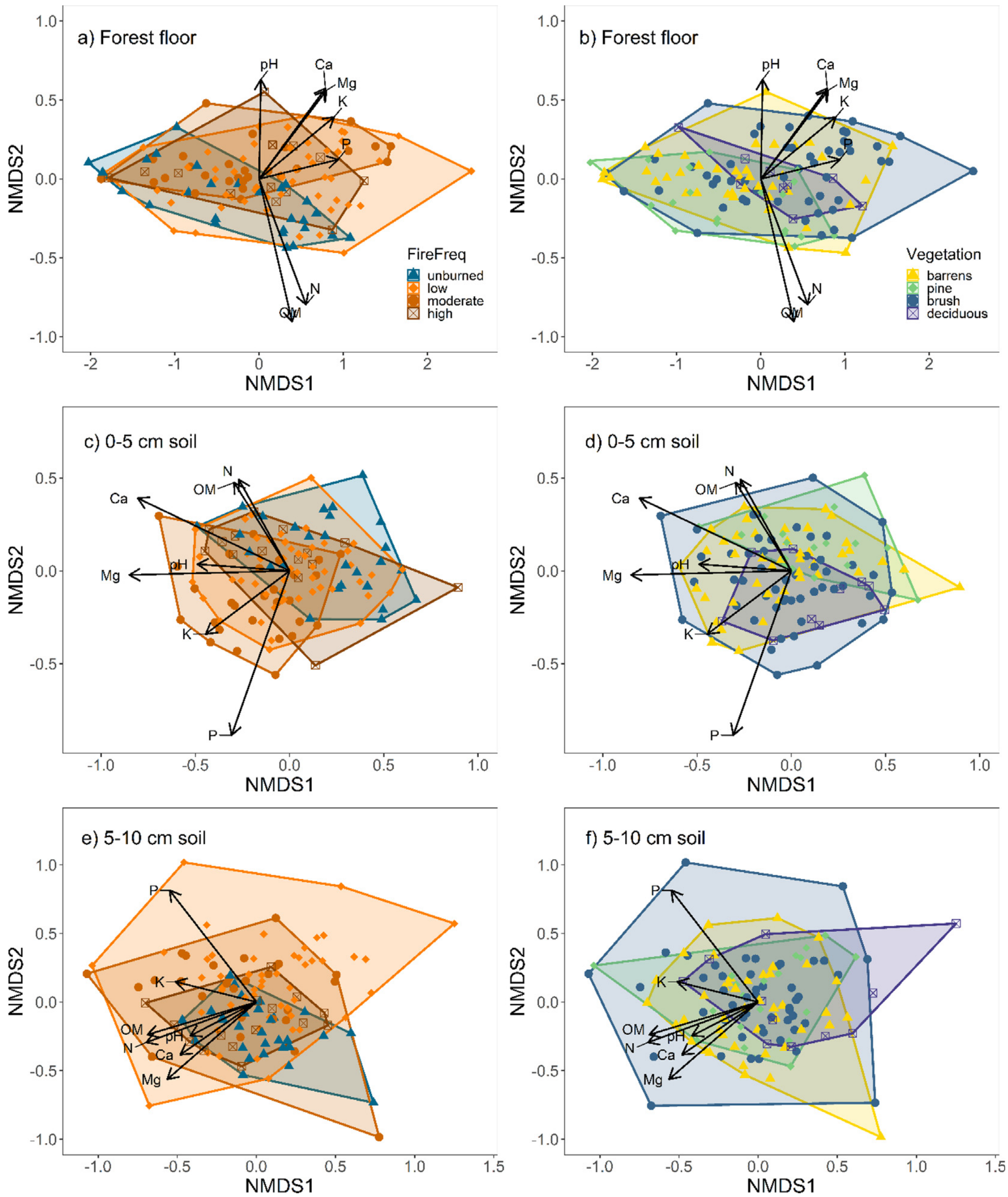

Fig. 6. Non-metric Multi-dimensional scaling (NMDS) ordination of forest floor samples (n = 125) from Moquah Barrens, Wisconsin, USA. Vectors in panel a show individual statistically significant soil properties ($p < 0.05$) included in the ordination with arrow lengths standardized by eigenvalues. Panels b and c show sites grouped by current vegetation cover (b) and burn frequency (c).

be explained by differential plant nutrient uptake. Rapid postfire vegetation regrowth may diminish the effects of fire on soil nutrient stocks (Likens et al., 1978), which is especially true for sandy soils prone to nutrient leaching (Hole, 1976). Other fire-dependent habitats, including California chaparral and New Jersey pine barrens, are dominated by plant species capable of rapid regrowth or re-sprouting and profuse nutrient uptake immediately following fire (Boerner, 1982), and the same is likely true of Wisconsin pine barrens plant communities. Some nutrient stocks may also have been depleted in forested areas prior to this study due to widespread timber harvesting from the late 1860s through 1930 (Radeloff et al., 1999). For example, whole-tree harvesting is known to result in ecosystem P loss in hardwood forests (Yanai, 1998). Thus, historical management practices beyond prescribed fire may have had lasting effects on soil properties such as those differences observed between forested and open-canopy landscapes in the Moquah Barrens. In this case, inherent differences in soil properties among extant vegetation cover types may be obscured, and we address this question in a later section (see: *How do past vegetation states create soil legacies?*).

Fire effects on soil are often ephemeral, and the recently burned plots included in this study were last burned 2–15 years prior. Fire-associated changes in nutrient stocks may have dissipated within this time period due to a variety of processes including leaching, mineralization, plant uptake, deposition, and redistribution. Nonetheless, we observed some lasting effects of fire frequency on soil properties, namely between long-unburned sites and burned sites. For instance, fire tends to increase soil pH due to cation inputs from ash (Simard et al., 2001), and our frequently burned sites generally had higher forest floor and mineral soil pH than long-unburned sites. Soil pH is an important factor influencing the availability and exchange rates of essential nutrients, and a pH difference of ~0.5 could impact nutrient availability and turnover in the acidic soils characteristic of the Moquah Barrens.

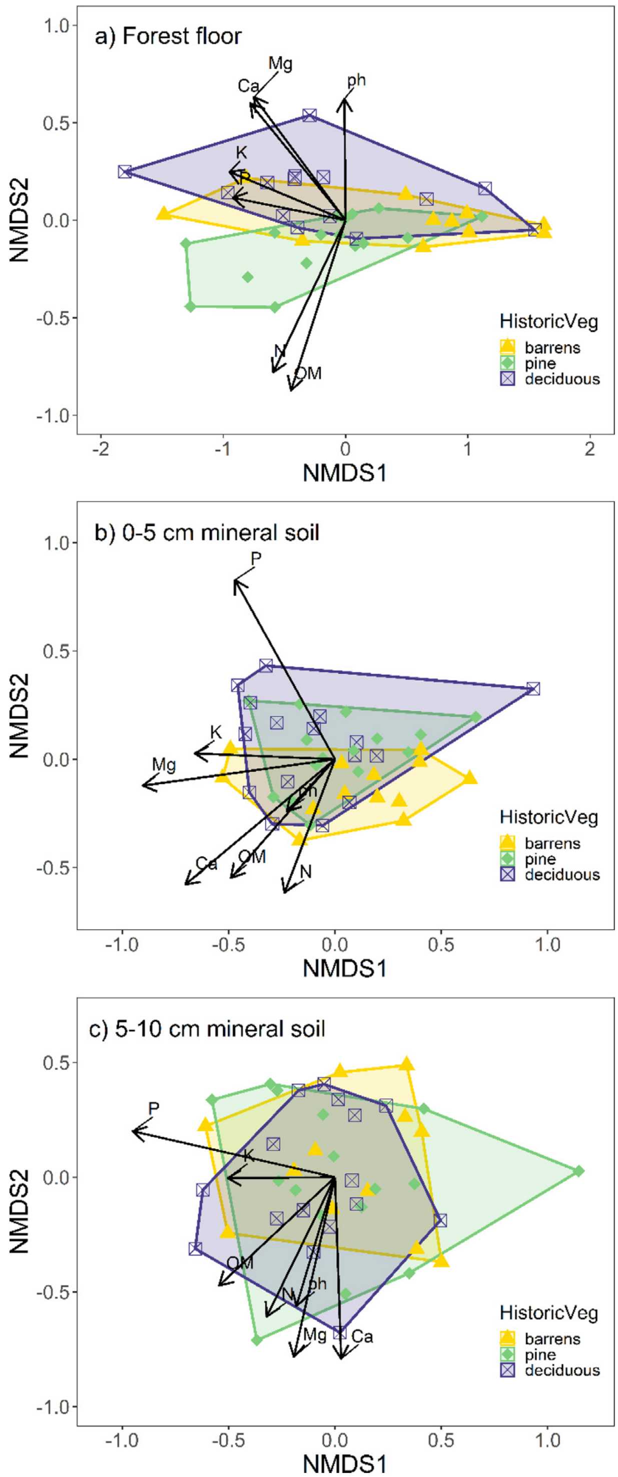

Fig. 7. Non-metric multi-dimensional scaling (NMDS) for sites with barrens vegetation cover (n = 44) grouped by historic vegetation cover. Panels show ordination of forest floor (a), 0–5 cm mineral soil (b), and 5–10 cm mineral soil properties.

Sites with moderate and high burn frequency also had greater mineral soil Mg stocks than unburned sites, likely from repeated ash deposits after fires. Additional studies reported that fuel loads are positively related to postfire ash and soil cation stocks and pH (Pietikaeinen and Fritze, 1995; Quigley et al., 2019). In contrast, high frequency fire in loblolly and shortleaf pine stands decreased soil Ca and Mg (Liechty and Hooper, 2016), suggesting that additional factors such as soil texture may influence soil chemical response to fire. Soil P binds tightly to mineral soil and is less susceptible to leaching than other elements, but net losses of P may also occur during high intensity fires (Certini, 2005). Although prescribed fires in the Moquah Barrens are generally of low intensity and severity, we observed depleted mineral soil P stocks in unburned sites relative to burned sites which could have important consequences for soil microbial communities, nutrient availability, and litter decomposition (Hou et al., 2012). Additional relationships between prescribed burn frequency and soils may be obscured by the uneven distribution of vegetation cover types among burn frequency groups (Table 1), and continued monitoring of study will help disentangle these two factors.

We were surprised by the overall lack of relationship between prescribed burn frequency and soil C and N, since these elements have low volatilization temperatures and have been shown to significantly decline over decadal scales under frequent fire regimes (Pellegrini et al., 2017). Under prolonged fire exclusion, C accumulation in forest floor horizons has been reported for a variety of ecosystems (Choromanska and Deluca, 2002; Miesel et al., 2012), and fire-induced soil C losses may persist for up to 50 years depending on rates of plant colonization (Parker et al., 2001). Similarly, N contained in surface soils may be lost during organic matter combustion, with a pronounced decrease occurring during fires of high intensity or severity (Choromanska and Deluca, 2002; Giovannini et al., 1990). The decline in forest floor C:N with fire frequency suggests that changes in organic matter composition may be evident even in the absence of statistically significant effects on total C or N. Furthermore, although total C and N stocks were not related to fire frequency, additional measures of C and N may be more ecologically informative. For instance, pyrogenic C, which includes a range of C-rich fire-generated compounds, may contribute to a soil C sink via its increased chemical stability relative to OM that is unaltered by fire (Pingree and DeLuca, 2017; Santin et al., 2015). Pyrogenic C may show fire frequency-dependent patterns across the landscape as has been observed in other ecosystems (Reisser et al., 2016). Likewise, although point measurements of total N did not differ among sites with contrasting fire history, N mineralization rates may be influenced by fire (Wang et al., 2012). This is an important avenue for further research.

How do overall soil conditions differ among vegetation cover types and/or along gradients of burn frequencies?

Ordination and NMDS plots revealed that sites with differing current vegetation cover and burn history show a great deal of overlap in multivariate soil conditions (Fig. 6). As expected, greater overall differences were observed in the organic forest floor horizon than in mineral soils, and this was supported by a decrease in stress values with increasing soil depth (forest floor $k > $ 0–5 cm $k > $ 5–10 cm k). We expected greater similarity in the mineral soil chemical composition than forest floor because glacial outwash soils are inherently nutrient-limited and because low severity prescribed fires typically affect only the surface horizons. The ordination axes were likewise most informative for the forest floor (Fig. 6a-b), with the first axis defined primarily by cations (P, K, Ca, and Mg) and the second axis defined primarily by OM, N, and pH. However, even forest floor NMDS plots showed a surprising amount of overlap among sites with different vegetation cover types. This indicates that barrens vegetation may not be strictly limited by the soil edaphic conditions measured in this study, as has been assumed (Heikens and Robertson, 1994; Sweet, 1880). Although savannas and grasslands are among the most nutrient-limited biomes globally (Fisher et al., 2012; Lee et al., 2010), the role of nutrient limitation in maintaining these habitats in highly heterogeneous Lake States pine barrens remains unclear.

In our study, variation in soil chemical composition was more restricted in the forest/woodland types relative to brush and barrens, which can be visualized in Fig. 6. In specific, separation between pine and deciduous systems was most apparent, particularly in the forest floor and upper mineral soil (Fig. 6b, d). All deciduous forest sites included in this study were historically deciduous forest, and pine sites were limited to pine forest history (i.e. no conversion of barrens to forest). In contrast, brush sites represented a transitional type spanning both deciduous and pine history, and barren sites included both restored barrens (i.e. harvested deciduous or pine sites) and natural barrens remnants. The observed patterns in ordinations of current barrens sites indicate that the legacy of past conditions may obscure differences in soil fertility in subsequent stages of restoration. For example, multivariate forest floor space of natural barren sites falls intermediate to restored barrens of pine history and deciduous history, respectively. In general, the high amount of overlap in Fig. 7a suggests potential for successful restoration of forest and woodland sites to natural barrens type soil conditions.

How do past vegetation states create soil legacies?

Historic vegetation and land management practices can have lasting effects on soils and vegetation communities, as has been observed with agricultural legacies in soils of forests and pine woodlands (Bizzari et al., 2015; Flinn and Marks, 2007), and studies of the effects of afforestation of previously open lands on belowground C and N (Li et al., 2012). In this study, the legacy of historic vegetation was strongest within the forest floor – specifically the amount of OM and total C observed. Forest floors in sites with a pine history had consistently higher OM and total C than those of barrens history, and deciduous forest history sites had intermediate levels of these variables (Fig. 5). In our study, sites with barrens history were limited to extant barrens vegetation (Table 1), so the effect of historic vegetation on the forest floor likely represents the contrast between persistent barrens and sites with historic forest in various stages of restoration (i.e., forest, woodland, brush, and restored barrens). Nonetheless, our results are consistent with global patterns of belowground C storage, where conifer forests often have a more developed forest floor relative to deciduous forests (Vesterdal et al., 2013). More generally, the afforestation of open lands tends to enhance development of the organic layer (Li et al., 2012).

Development of the forest floor is an important factor underlying mesophication of xeric systems (Nowacki and Abrams, 2008). For example, a recent study of remnant long leaf pine (*Pinus palustris*) woodlands associated with sandy soils reported a positive relationship between topsoil OM and water retention (Bizzari et al., 2015). Low soil OM may contribute to excessively well drained soil conditions at barrens sites and provide native barrens plants a competitive advantage by limiting seedling recruitment (Iacona et al., 2010), as poor soil water retention can contribute to limited tree growth in pine barrens (Sweet, 1880). Our results indicate that the development of the forest floor persists as a legacy potentially affecting restoration efforts, and this legacy may be influenced by its previous vegetation state. As such, our finding that burn frequency had little influence over C and OM in the forest floor is significant. It is possible that the application of late dormant season (spring) burns, when soil moisture can be elevated and soil temperatures are generally cool, may preclude significant combustion of the forest floor. If so, the legacy of past forest floor development may persist for longer periods under the current burn regime.

Although ordinations of the forest floor of barrens sites showed separation with respect to historic vegetation, mineral soil characteristics of barrens sites did not differ by vegetation history (Fig. 6b and c). This result is somewhat surprising given the widespread practice of furrowing in the installation of pine plantations in the region, but we provide two possible explanations for the lack of observed differences. First, our soils represent point samples taken at a specific location relative to center of each plot, and, even at furrowed sites, sampling may not have occurred directly over furrows. Second, mineral soils at Moquah are coarse sands subject to very high levels of leaching, which may wash out any potential differences over time. Regardless of underlying cause, it appears that the most important legacies of past vegetation states and management history in this system lie within the development of the forest floor.

5. Conclusions

In 1959, John Curtis predicted that the practice of excluding fire from barrens would result in conversion of open-canopy lands to late-successional ‘climax’ hardwood forests, a prediction that, accelerated by plantation establishment on barrens habitat, has come to fruition throughout the Lake States region and threatens the survival of a number of regionally and globally-sensitive species that depend on barrens habitat (Addis et al., 1995; Curtis, 1959; Hamerstrom Jr., 1963). Prior knowledge of pre-settlement landscape conditions and disturbance regimes in this region is limited, though we do know that forests in this area were far more open prior to Euro-American settlement than they are today (Radeloff et al., 1999). Our study provides foundational information to help land managers restore soil conditions that limit tree growth in barrens habitat and to improve future restoration efforts via adaptive management (Niemuth and Boyce, 1998).

Dimensions of soil conditions relevant to barrens restoration are influenced by a suite of factors, including current and historic vegetation cover, as well as prescribed burn management. We identified several soil properties (i.e., C, OM, K, Ca, and pH) that were characteristically lower in extant barrens soils relative to adjacent soils that support later-successional communities with higher woody plant densities. These differences across current vegetation types were complicated by both vegetation history (specifically in the development of a persistent forest floor) and fire frequency (specifically via cation enrichment affecting soil fertility and pH in the surface layers). The challenge of disentangling effects of these driving factors was also evident by the degree of overlap between vegetation classes and burn histories that increased with depth in the soil profile. When interpreted within the context of mesophication, our findings suggest that although woody densification is widely observed in pine barrens, the underlying soil features characteristic of glacial outwash sands may allow for prescribed fire and additional management to successfully restore barrens habitat. More specifically, restoration of pine plantations to barrens could benefit from fire activities that enhance consumption of the forest floor, while restoration of deciduous forest and brush habitats will likely be more related to the effective control of hardwood regeneration, after which soil conditions may return to a more archetypical barrens state. Given these study results, managers may see immediate signs of restoration reflected in vegetation structure but can expect restoration of other ecosystem components, like soils, to take time and require repeated treatments.

CRediT authorship contribution statement

Kathleen M. Quigley: Methodology, Software, Validation, Formal analysis, Investigation, Resources, Data curation, Writing - original draft, Visualization. **Randall Kolka:** Supervision, Methodology, Conceptualization, Investigation, Resources, Writing - review & editing. **Brian R. Sturtevant:** Investigation, Resources, Supervision, Project administration, Writing - review & editing. **Matthew B. Dickinson:** Methodology, Resources, Writing - review & editing. **Christel C. Kern:** Methodology, Resources, Writing - review & editing. **Deahn M. Donner:** Writing - review & editing, Supervision, Project administration. **Jessica R. Miesel:** Supervision, Methodology, Conceptualization, Investigation, Resources, Writing - review & editing.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118163.

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