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Understory Plant Community Response to a Range of Restoration Scenarios in Northeast US Pitch Pine (*Pinus rigida*) Barrens

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ABSTRACT

Aims: Fire-dependent pine and oak-pine ecosystems of the eastern United States have been significantly impacted by their disconnection from historic disturbance regimes, particularly fire, along with changes in land use and policies of fire suppression. Climate change presents additional challenges to these communities, especially through the introduction and expansion of novel stressors. Understory plants in these communities provide important wildlife habitat, along with social and cultural value. Restoration management in northeast pitch pine (*Pinus rigida*) barrens has mainly utilized prescribed fire and mechanical treatments, including mowing and thinning. This study compared the effect of these regionally common management activities on the composition, diversity, and abundance of understory plant species.

Location: Pitch pine barrens in Maine, Massachusetts, New Hampshire, and New York, United States.

Methods: We employed systematic grid sampling, using plots to measure species diversity and estimate abundance, along with other relevant environmental conditions, in the summers of 2022 and 2023. We sampled at 47 sites across three ecoregions. We used nonmetric multi-dimensional scaling to examine gradients in understory plant community composition across treatment types within ecoregions.

Results: Distinct understory community assemblages and structures were associated with different restoration strategies. This included a higher abundance of species that can endure fire and resprout from buried plant parts in prescribed fire units, whereas fire-sensitive species and those slow to recolonize after fire events were most abundant in untreated control units. Within prescribed fire treatments, the abundance of some fire-adapted species reflected relationships with fire severity, including *Vaccinium angustifolium* being associated with mowing followed by fire and *Gaylusaccia baccata* with areas experiencing fall burns. Restoration treatments also generated unique understory structural conditions related to treatment severity and frequency, including greater shrub densities important for several threatened wildlife species.

Conclusions: Impacts to understory plant community composition and structure demonstrate the importance of reinstating disturbance events, particularly fire, within pitch pine barrens to restore desired conditions and support cultural and ecological objectives.

1 | Introduction

Forests provide habitat for a wide array of species, with most plant species diversity found in forest understories (Gilliam 2007). This biodiversity is a critical component in many aspects of ecosystem function (Nilsson and Wardle 2005). Natural disturbances, like fire, wind and ice storms, floods, and insect outbreaks, strongly influence biodiversity, including understory plant species, with subsequent changes to ecosystem structure, function, and level of services (Viljur et al. 2022). A recent review by Viljur et al. (2022) demonstrated that species benefiting from disturbance are those that favor open canopy conditions, with heterogeneous landscapes of disturbed and undisturbed patches supporting higher overall biodiversity. These patterns also vary temporally, with species richness often reaching peak levels within 10 years post-disturbance (Viljur et al. 2022). As such, the suppression of or disconnection from historic disturbance regimes can negatively impact forest biodiversity, especially the presence and abundance of disturbance-dependent species (e.g., Livingston et al. 2016; Bassett et al. 2020). Studies of restoration activities in areas experiencing fire suppression have shown more severe disturbance (e.g., thinning and burning vs. thinning only or burning only) increases effectiveness at re-establishing desired conditions (e.g., Schwilk et al. 2009; Strahan et al. 2015); however, results can be short-lived without repeat disturbance (Bassett et al. 2020). Long periods of fire suppression can substantially change fire-dependent communities, transitioning them to alternate states, which may require more than the re-application of historic disturbance regimes to restore previous conditions, if restoration is even possible (Suding et al. 2004; Lettow et al. 2014).

The suppression and alteration of fire regimes in the coterminous eastern United States has resulted in the mesophication and densification of fire-dependent communities (Nowacki and Abrams 2008; Hanberry et al. 2014). Mesophication refers to a self-perpetuating phenomenon where increases in fire-sensitive vegetation and mesic understory conditions further inhibit fire and the recruitment of pyrophytic species, while densification describes the transformation of open canopy woodlands, savannas, and grasslands into closed canopy forests, resulting from the absence of fire. While changes to tree species composition and community structure have been the primary focus of work examining these dynamics, fire suppression also impacts understory plant communities (Oakman et al. 2021). Community succession in the absence of disturbance can increase the diversity and abundance of shade-tolerant plants, leading to greater alpha diversity, where early- and mid-successional plants exist together, following expectations of peak species richness in mid-successional communities (Horn 1974; Li and Waller 2015). However, the homogenization of light availability resulting from increased canopy closure and lack of disturbance can negatively impact beta diversity, leading to landscape-scale plant community homogenization, and losses in the abundance and richness of early successional, shade-intolerant species over time (Lettow et al. 2014; Li and Waller 2015; Livingston et al. 2016; Bassett et al. 2020).

Pitch pine (*Pinus rigida*) barrens are a globally rare (ranked G2; NatureServe 2024) fire-dependent ecosystem found in northeast North America and are affected by the abovementioned mesophication and densification dynamics due to extended periods of fire suppression. Generally, their overstories range from 20% to 60% canopy closure and are dominated by pitch pine (*Pinus rigida*) with occasional tree oaks (*Quercus* spp.) and a mid and understory of abundant *Quercus ilicifolia* and *Quercus prinoides* and shrub Ericaceae species, although definitions differ slightly by state (e.g., Swain and Kearsley 2001; Edinger et al. 2014). These communities are underlain by sandy glacial outwash, a significant factor impacting their fragmentation and development. This, along with the lack of disturbance, has led to substantial losses in community distribution, occurrence, and condition over the past two centuries, including in the vegetative composition and structural condition of pitch pine barrens (Widoff 1987; Jordan et al. 2003; Howard et al. 2011).

It is likely that several factors, including climate, lightning, vegetation, and human stewardship, along with their interaction, were responsible over time for the creation and maintenance of fire-dependent natural communities, including pitch pine barrens, across the eastern United States (Abrams and Nowacki 2015). Oral traditions and present-day management affirm the importance of cultural fire practices by Tribal Nations, which are a continent-wide disturbance regime characteristic of other woodland and barren communities (Kimmerer and Lake 2001; Steen-Adams et al. 2019; Dockry et al. 2023). Pitch pine barrens provide important sources of food, medicine, and materials (LeCompte 2018; Anchor QEA LLC, The Nature Conservancy, and Fine Arts and Sciences LLC 2019; Steen-Adams et al. 2019) and were sustained in large part by low-intensity surface fires set by Tribal Nations in the coterminous northeast, as further supported by numerous primary source European observers (Day 1953; Stewart 2002), pollen and charcoal analyses (Foster et al. 2002), and fire-scar analyses (Marschall et al. 2016). European colonization eliminated these practices and today, fire suppression, along with development and fragmentation, is the major source of change for pitch pine barrens (Widoff 1987; Motzkin et al. 1999).

Many plants in pitch pine barrens possess traits that allow them to evade, resist, or endure fire (Rowe 1983). Plants that evade fire may store their seeds in the canopy (e.g., serotiny) or forest floor, while those that resist can exhibit traits like thick, insulating bark and branch pruning (Rowe 1983; Schwilk and Ackerly 2003). Those that endure will often resprout from buried plant parts able to survive low and moderate severity fires (Matlack et al. 1993). The physical characteristics of plants in these systems, like their leaf litter flammability and packing ratios, can influence the severity and intensity of fire (Patterson et al. 1983; Schwilk and Ackerly 2003). Across the northeast, barrens communities have strong similarities. However, the presence, diversity, and abundance of shrub and herbaceous species have clear regional affinities in barrens understories, reflecting their ecoregion designations. Ecoregions are areas of similarity in biotic and abiotic factors, including climate, soils, land surface form, and vegetation (Omernik 1987).

Understory communities in pitch pine barrens provide significant ecological value. Historically, the frequency of disturbance in these communities made them more dependable locations for the creation and maintenance of early successional habitat, contributing both locally and regionally to species richness and biodiversity (Lorimer 2001; Lorimer and White 2003). Many species, including several rare, threatened, and endangered lepidopterans, birds, mammals, reptiles, and amphibians, utilize the high-quality early successional habitat available in frequently disturbed pitch pine barrens (Stewart and Rossi 1981; Fuller and DeStefano 2003; Wagner et al. 2003; Gifford et al. 2010). Declines in the abundance of many of these specialists have been linked with loss of early successional habitat across the northeast (Litvaitis et al. 1999). Subsequently, recommendations for restoration strategies focus on the creation and maintenance of early successional habitat and landscape-scale heterogeneity in pine barrens communities (e.g., Litvaitis et al. 1999; Jordan et al. 2003; Bried et al. 2014).

Much of the work examining the restoration and maintenance of pitch pine barrens has focused on the impacts of restoration activities on tree regeneration (e.g., Šrůtek et al. 2008; Lee et al. 2019); however, the response of understory plant communities to restoration techniques has not been studied as fully (Jamison et al. 2023). Previous work has shown that repeated fire reduces shrub cover and impacts shrub species dominance, while a single surface fire can have little lasting effect on species composition (Buell and Cantlon 1953; Matlack et al. 1993). Frequent prescribed fire coupled with reductions in overstory basal area can increase the presence of herbaceous species, including *Carex pensylvanica* and *Baptisia tinctoria*, the latter being an important food source for the critically imperiled Frosted Elfin (*Callophrys irus*) (Little and Moore 1949; Buell and Cantlon 1953).

Our study investigated the effect of four regionally common restoration strategies (harvest, fall prescribed fire, spring prescribed fire, and mowing followed by prescribed fire) on understory communities in pitch pine barrens across the northeast United States to inform management decision-making. As these communities provide essential habitat for rare and endangered species, including the federally endangered Karner Blue Butterfly (*Lycaeides melissa samuelis*), and are sites important to cultural heritage, an understanding of the effects of different restoration strategies on understory plant composition, abundance, and diversity is essential for successful restoration and the support of ecological, cultural, and social values. We therefore investigated a range of site-level conditions to create a rough understanding of disturbance severity represented by these four restoration strategies and the response of understory species abundance, diversity, and richness to them, as they are applied regionally.

2 | Methods

2.1 | Study Area

This study took place in three of the most common biophysical settings for pitch pine barrens in the northeast United States: coastal barrens, inland barrens, and northern barrens. These communities form on xeric, excessively drained soils resulting from glaciation, often the beds of former glacial lakes (e.g., inland barrens like the Albany Pine Bush, NY) or terminal glacial moraines (e.g., coastal barrens including the Central Pine Barrens of Long Island, NY). Coastal barrens can form matrix communities (Swain and Kearsley 2001; Edinger et al. 2014), while inland and northern barrens are usually smaller, occupying disconnected and fragmented pockets of their former range. There are fewer than 20 pitch pine barrens remaining, with an estimated loss of 48% of barrens across their range and greater than 99% loss in local areas (Noss et al. 1995; Motzkin et al. 1999).

Study sites were located in present-day New York (NY), Massachusetts (MA), New Hampshire (NH), and Maine (ME). Sites were selected based on management histories and discussions with local managers at the Albany Pine Bush Preserve (Albany Pine Bush, APB), Massachusetts Department of Conservation and Recreation (Myles Standish State Forest, MSSF), Massachusetts Department of Fisheries and Wildlife (Mashpee Pine Barrens, MPB), Massachusetts National Guard (Camp Edwards, CE), the Nature Conservancy (Ossipee Pine Barrens, OPB & Waterboro Pine Barrens, WPB), New York State Department of Environmental Conservation (Rocky Point Pine Barrens State Forest, RPPBSF), and Society for the Protection of New Hampshire Forests (Harmon Property, SPNHF) (Figure 1).

The restoration techniques we investigated included harvest (Harvest), spring prescribed fire (SpringRx), fall prescribed fire (FallRx), and mowing followed by prescribed fire (MowRx). Areas received treatment between September 2015 and March 2022. Sites in each region without a history of recent management (≥ 20 years) were also assessed as controls. These control units represent the conditions of pitch pine barrens without active management, common for many barrens in the northeast. All treatments were not applied equally between regions (Table 1).

Harvest units underwent treatments where either commercial or non-commercial timber harvests were applied between 2017 and 2020. In some locations, whole-tree harvesting was used, and elsewhere slash was cut below four feet and dispersed. Often, removals targeted mature, fire-intolerant tree species. Prescribed fire treatments (FallRx, SpringRx, MowRx) were burned following a prescribed fire plan, which varied across sites and regions. Prescribed fire plans often used smoldering to remove leaf litter and expose mineral soil within the constraints of local smoke concerns. Burning was also used in some cases to create refugia and burn unit scale heterogeneity by encouraging patchiness in burn intensity and duration. Some units were cleared of fuels prior to burning. Prescribed fire treatments in this study were low to moderate in severity and intensity. Sites assessed were burned in the spring (late March to late May; 2016–2022; SpringRx), in the fall (late August to late October; 2015–2021; FallRx) or were mowed prior to prescribed burning (2014–2021; MowRx) (See Appendix S1 for additional information). Burning of previously mowed units took place across a range of seasons, and assessment of the influence of the seasonality of fire was not possible here due to limited sample size. In MowRx units, prescribed fire generally took place within 1 year of mowing, although up to 2 years in some units ($n = 3$). Mowed sites were treated using a Davco rotary brush-mower or a FECON mower. This technique is used primarily to rearrange fuels and reduce the potential for high-intensity and fast-moving fires.

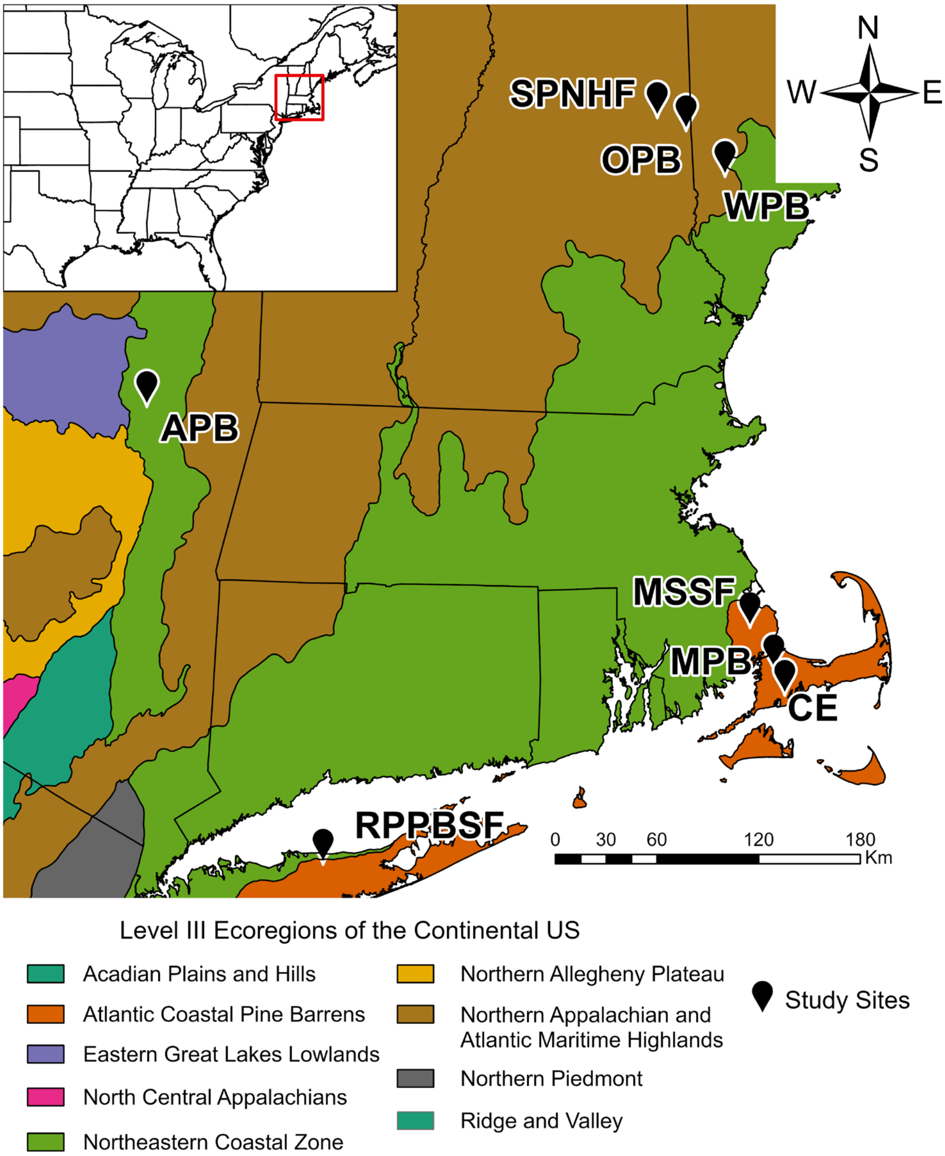

FIGURE 1 | Study sites across the northeast United States and their location with Level III Ecoregions based on United States Environmental Protection Agency (2013) data indicated. Study sites included the Albany Pine Bush (APB), Myles Standish State Forest (MSSF), Mashpee Pine Barrens (MPB), Camp Edwards (CE), Ossipee Pine Barrens (OPB), Waterboro Pine Barrens (WPB), Rocky Point Pine Barrens State Forest (RPPBSF), and Society for the Protection of New Hampshire Forests (SPNHF).

2.2 | Field Methods

Sampling took place from early June to mid-August in 2022 and 2023. For regions in which sampling spanned multiple years, we concentrated sampling in the same months to avoid temporal differences in floristic composition. Treatment units were a minimum of 1.2 ha and were sampled along a grid with a minimum inter-plot distance of 10 m. Units had a minimum of nine plots and a maximum of 13, with two sites on Long Island having only five plots due to smaller-than-originally-indicated unit size. An internal buffer of at least 30 m was used to reduce the impact of edge effects.

At each plot, a 1 m^2 frame was used to estimate understory plant cover, ground cover, and leaf litter depth ($n = 498$). Percent understory cover was recorded for each species present using eight cover classes: (1) < 1%; (2) 1%–5%; (3) 6%–10%; (4) 11%–20%; (5) 21%–40%; (6) 41%–60%; (7) 61%–80%; (8) 81%–100% (Bechtold and Patterson 2005; USDA 2021). *Lymantria dispar* outbreaks in 2022 in New Hampshire and late frost in 2023 in southeast Massachusetts impacted the foliar abundance of some understory plants. Plant nomenclature follows the U.S. Department of Agriculture NRCS PLANTS database (2021). *Amelanchier* spp., non-native *Lonicera* spp., *Rubus* spp., and *Cornus* spp. (*Cornus amomum*, *C. acemose*, and *C. sericea*) were not identified to species. Two grass specimens were identified only to family Poaceae and another two grass specimens only to genus. Additionally, two tree species, two shrub species, two *Carex* species, and eight forb species were identifiable only to genus and one to tribe as well. Percent ground cover was classified into nine type classes (i.e., lichen, trash/junk, moss, road/trail, rock, water, mineral soil, wood, and litter/duff) and abundance was characterized using the above eight cover classes. Measurements of the depth of the O layer, to characterize litter depth, were taken at the northwest

TABLE 1 | Number of individual treatment units sampled within each region across treatment types.

	Control	Harvest	FallRx	MowRx	SpringRx	*n*
Northern Barrens						
Ossipee, NH	2	n/a	3	3	n/a	8
Waterboro, ME	2	n/a	3	n/a	n/a	5
Inland Barrens						
Albany, NY	2	n/a	n/a	6*	3	11
Coastal Barrens						
Long Island, NY	3	3	n/a	n/a	3	11
Southeast, MA	2	3	3	3	3	14
n	11	6	9	12	9	47

Note: Treatments that were unavailable regionally are indicated with an "n/a." Three units of spring fire followed by mowing and three units of summer fire followed by mowing were sampled and are designated with an "*." FallRx indicates prescribed fire applied in the fall, MowRx indicates prescribed fire following by mowing, and SpringRx indicates prescribed fire applied in the spring.

and southeast corners of the 1 m^2 frame and were recorded up to 15 cm, rounding to the nearest 0.5 cm. Large seedlings, greater than or equal to 50 cm in height and less than 2.5 cm dbh (diameter at breast height = 1.3 m height), were counted in 10 m^2 circular subplots centered on the 1 m^2 frame. Basal area, using a 2.3 m^2/ha BAF prism, was taken at every plot center, with each tree recorded as live or dead by species.

2.3 | Statistical Analysis

All statistical analysis was conducted in R (R Core Team 2024) using RStudio (Posit team 2024). Percent cover estimates for each species were transformed to the midpoint of the cover class (e.g., cover class 2, which encompasses 1%–5% was transformed to 3.0). The data were then divided into three ecoregions, based on similarities of species, and analyzed separately. Sites on Long Island, NY, and southeast MA were grouped as Coastal Barrens. Sites in NH and ME were grouped as Northern Barrens, and sites at the Albany Pine Bush (NY) were grouped as Inland Barrens.

To create a rough measure of disturbance severity (M. R. Roberts 2004), we compared total basal area (m^2/ha), average leaf litter depth (cm), total understory cover (%), mineral soil exposure, and woody material cover (%) across treatment types in each ecoregion. Environmental variables were modeled using generalized linear and linear mixed modeling (GLMM, *glmmTMB*, package; *glmmTMB* function) by treatment type with plots nested within sites as a random effect (Brooks et al. 2017). Normal distributions were used for modeling, except for basal area, which used a negative binomial distribution. Due to the small sample size, we were unable to use an offset to account for differences in time between treatment and sampling. These models were then compared using a Type III Wald Chi-square test (*Anova* function; *car* package) (Fox and Weisberg 2019). Where significant differences ($\alpha = 0.05$) were found, post hoc comparisons between treatments were made using Tukey's HSD test (*stats* package; *TukeyHSD* function) (R Core Team 2024). Where data failed to meet expectations of normality and homoscedasticity and transformations were inadequate or models failed to converge, environmental variables were averaged to the site level. These site-wide averages were compared using ANOVA (*stats* package; *aov* function) and significant differences were compared using Tukey's HSD test, as described above. Where site-wide averages also failed to meet expectations of normality and homoscedasticity and transformations were inadequate, the non-parametric Kruskal–Wallis test (*stats* package; *kruskal.test* function) was used instead and Dunn's test of multiple comparisons (*dunn.test* package; *dunn.test* function) was then used to determine significant differences among treatments (Dinno 2024).

Understory species were categorized by plant guild (i.e., ferns/fern-allies, forbs, grasses, sedges, shrubs/vines, and trees) and the total cover for each guild in each plot was used to compare the abundance of guilds across treatment types within regions using the same process described above, along with large seedling abundance. For each ecoregion, alpha diversity (*vegan* package; *specnumber* function), represented by species richness per plot, gamma diversity (*vegan* package; *specpool* function), the total species count, and bootstrap estimates of species richness (Dixon 2001), Shannon–Wiener diversity index (*vegan* package; *diversity* function), and *Pielou's J* (Pielou 1969), a measure of evenness, was calculated for each available treatment type (Oksanen et al. 2024). These were again compared using the process described above. Beta diversity was measured across plots using the Sørenson dissimilarity coefficient and Podani family calculations within treatment types (*adespatial* package; *beta.div.comp* function) and broken down into its replacement and richness difference components (Dray et al. 2023).

Nonmetric multi-dimensional scaling (NMDS) was used to examine gradients in the composition of understory communities across restoration treatments within ecoregions (*vegan* package; *metaMDS* function) (Oksanen et al. 2024). NMDS is a distance-based iterative ordination technique that uses ranked distances to present values along a number of predetermined axes focusing on a reduction in "stress" (McCune and Grace 2002). Values were calculated using Bray–Curtis distances. Species were restricted to those that occurred in at least 5% of plots for each ecoregion. Plots within each unit were averaged to create an average species composition and cover for each individual unit. Average cover for each species was standardized (*vegan* package;

decostand function), dividing by the total average cover across all units, to reduce the distance between common and rare species (Oksanen et al. 2024). NMDS ordinations were run starting with six axes with subsequent stepwise reductions in axes. A stress level <0.2 was considered acceptable. Vector fitting (*vegan* package; *envfit* function), which uses permutations of regression to test for goodness of fit, was used to examine the relationship between NMDS axes and eight environmental factors: lichen cover (%), moss cover (%), mineral soil exposure (%), woody material cover (%), leaf litter cover (%), average litter depth (cm), basal area (m^2/ha), and pitch pine basal area (m^2/ha), all of which had been averaged for each unit (Oksanen et al. 2024). The same procedure was used to determine significant relationships within the ordination space with individual species. Indicator species analysis (*labdsv* package; *indval* function) was then used to identify species with significant fidelity to specific treatment applications (D. Roberts 2023). Finally, a PER-MANOVA (*vegan* package; *adonis2* function) was used to assess differences in community composition between treatment types, followed by pairwise comparisons of treatment types (*pairwiseAdonis* package: *pairwise.adonis2* function) (Martinez Arbizu 2017; Oksanen et al. 2024). PER-MANOVA is a non-parametric test that compares the centroids and dispersion within and between groups using random permutations.

3 | Results

We observed 160 vascular plants (Appendix S2) in the understory across the three ecoregions and 47 sites. This included 21 tree species, 61 forbs, 47 shrubs/vines, 17 grasses (family Poaceae), 6 sedges (family Cyperaceae), and 8 ferns/fern-allies. All species of grasses, sedges, and ferns/fern-allies were native. Five of the 61 forb species were non-native, along with four of the 47 shrub/vine species and two of the 21 tree species. Four herbaceous species were annuals, 56 were perennials, and one was only identified to tribe and could not therefore be classified. *Quercus ilicifolia* and *Carex pensylvanica* were the only species present in every treatment type of every region across the study. Initial analyses of community composition across all sites indicated a strong ecoregion effect that limited our ability to evaluate the outcomes of restoration treatments on vegetation structure and composition within ecoregions (Appendix S3). As a result, we conducted our analyses separately for each ecoregion.

3.1 | Coastal Barrens

For Coastal Barrens, total basal area (*Wald* X^2 $(4)=14.09$, $p=0.007$) diverged by treatment type (Table 2), with control units having the highest basal area, significantly higher than MowRx units. Understory cover (*Wald* X^2 $(4)=41.56$, $p<0.001$) varied substantially by treatment type in this region. MowRx units had lower average leaf litter depth (*Wald* $X^2=9.8$, $p=0.044$) than Control units. Mineral soil exposure (H $(4)=5.87$, $p=0.209$) did not differ by treatment type. Woody material cover (H $(4)=9.60$, $p=0.048$) varied by treatment type, with Harvest units having more woody material than Control and MowRx units. Shrub cover (*Wald* X^2 $(4)=28.09$, $p<0.001$) was higher in FallRx, Harvest, and SpringRx units than in Control units in Coastal Barrens. However, *Quercus ilicifolia* and *Quercus prinoides* large seedlings counts were significantly higher (*Wald* X^2 $(4)=18.33$, $p=0.001$) in MowRx units than in Control, FallRx, and Harvest units in Coastal Barrens. We were unable to test for differences in sedge cover due to failed model convergence. Neither total understory cover by ferns and fern-allies ($F_{4,18}=1.38$, $p=0.282$) nor total forb cover (H $(4)=4.03$, $p=0.402$) varied between treatment types. Grass cover (H $(4)=4.63$, $p=0.327$) was very low in this region and showed no significant variance by treatment type. Total understory cover by tree species ($F_{4,18}=0.946$, $p=0.460$) across treatment types revealed no significant differences in this region.

Average species richness (*Wald* X^2 $(4)=20.79$, $p=0.003$) and average diversity (*Wald* $X^2=14.41$, $p=0.006$) differed across treatment types in Coastal Barren, with Control units displaying fewer species and diversity than FallRx and MowRx units. Average evenness (H $(4)=1.82$, $p=0.770$) did not diverge by treatment type. There were 66 unique species recorded across all plots in Coastal Barrens. SpringRx treatments had the greatest species richness, with 39 species recorded, and Control had the lowest, with only 23.

There were distinct patterns in understory plant community composition across treatments, as reflected in the NMDS ordination for Coastal Barrens, which was best explained by a two-axis solution (final stress $=0.165$) (Figure 2). These differences were confirmed by PER-MANOVA ($F_4=2.49$, $p<0.001$), which indicated MowRx unit understories were significantly ($\alpha=0.05$) different from SpringRx, Harvest, and Control units. Both Harvest and FallRx units were marginally different from Control unit understories. Indicator species analysis (Table 4) found *Pteridium aquilinum* and *Gaylussacia baccata* had high fidelity to FallRx units. *Quercus prinoides*, *Rubus* spp., *Kalmia angustifolia*, and *Vaccinium angustifolium* were indicators of MowRx unit understories, and *Smilax glauca* was an indicator of Harvest unit understories.

3.2 | Inland Barrens

For Inland Barrens, MowRx and SpringRx units had significantly lower total basal area (*Wald* X^2 $(2)=13.18$, $p=0.001$) than Control units (Table 2). Understory cover (*Wald* X^2 $(2)=1.2$, $p=0.538$) did not vary by treatment type. We were unable to test for differences in average leaf litter depth due to failed model convergence. Mineral soil exposure (H $(2)=2.82$, $p=0.245$) did not vary significantly by treatment type, nor did cover by woody material (H $(2)=0.68$, $p=0.711$). Shrub cover (*Wald* X^2 $(2)=8.32$, $p=0.016$) was significantly greater in SpringRx and MowRx units than Control units. Sedge cover (*Wald* X^2 $(2)=7.27$, $p=0.026$) varied substantially, although subsequent pairwise comparisons revealed no significant differences between treatment types in Inland Barrens. Total understory cover by ferns/fern-allies ($F_{2,8}=0.29$, $p=0.764$) and total cover by forbs ($F_{2,8}=0.52$, $p=0.611$) did not differ by treatment type. Cover by grasses (H $(2)=4.57$, $p=0.102$) did not vary by treatment type, nor did total understory cover by tree species (H $(2)=2.74$, $p=0.254$) in this region.

Species richness (*Wald* X^2 $(2)=0.15$, $p=0.929$) was not significantly different across treatment types in this region (Table 3);

TABLE 2 | Selected environmental variables compared across treatment types within ecological regions.

	Control	FallRx	Harvest	MowRx	SpringRx
Coastal Barrens					
Total basal area (m^2/ha)	24.9 ± 1.27[a]	19.1 ± 1.31[ab]	12.1 ± 1.10[ab]	8.7 ± 1.43[b]	17.4 ± 1.14[ab]
Total understory cover (%)	34.0 ± 2.44[c]	76.2 ± 6.46[a]	55.2 ± 3.41[ab]	42.5 ± 4.95[bc]	60.7 ± 3.51[a]
Average litter depth (cm)	6.42 ± 0.33[a]	5.74 ± 0.27[ab]	5.29 ± 0.33[ab]	3.86 ± 0.45[b]	5.42 ± 0.37[ab]
Mineral soil exposure (%)	0.0 ± 0.0[a]	0.15 ± 0.13[a]	1.41 ± 1.21[a]	0.26 ± 0.18[a]	0.88 ± 0.52[a]
Woody material cover (%)	2.11 ± 0.54[b]	2.29 ± 0.45[ab]	6.20 ± 1.51[a]	2.07 ± 0.56[b]	3.00 ± 0.32[ab]
Total shrub cover (%)	25.13 ± 2.09[c]	53.98 ± 4.84[a]	41.85 ± 3.62[ab]	33.70 ± 4.50[bc]	41.09 ± 2.61[ab]
Total sedge cover (%)	0.27 ± 0.11	0.02 ± 0.02	0.64 + 0.39	0.53 ± 0.27	0.50 ± 0.19
Total fern/fern-ally cover (%)	0.49 ± 0.29[a]	13.25 ± 6.70[a]	4.36 ± 2.40[a]	1.32 ± 0.58[a]	4.01 ± 3.10[a]
Total forb cover (%)	2.64 ± 1.61[a]	6.99 ± 1.94[a]	2.80 ± 1.49[a]	3.97 ± 0.75[a]	4.05 ± 1.89[a]
Total grass cover (%)	0.0 ± 0.0[a]	0.0 ± 0.0[a]	0.14 ± 0.13[a]	0.15 ± 0.13[a]	0.45 ± 0.33[a]
Tree cover (%)	5.47 ± 2.23[a]	2.25 ± 0.64[a]	4.23 ± 0.97[a]	3.11 ± 2.87[a]	9.37 ± 4.18[a]
Inland Barrens					
Total basal area (m^2/ha)	35.40 ± 2.03[a]	n/a	n/a	9.83 ± 1.05[b]	13.39 ± 1.58[b]
Total understory cover (%)	58.20 ± 6.25[a]	n/a	n/a	74.56 ± 4.12[a]	71.17 ± 3.76[a]
Average litter depth (cm)	2.54 ± 0.40	n/a	n/a	1.90 ± 0.15	1.80 ± 0.20
Mineral soil exposure (%)	0.05 ± 0.0[a]	n/a	n/a	2.19 ± 0.87[a]	1.27 ± 1.00[a]
Woody material cover (%)	4.00 ± 3.50[a]	n/a	n/a	1.68 ± 0.65[a]	2.00 ± 1.12[a]
Total shrub cover (%)	26.03 ± 5.56[b]	n/a	n/a	49.36 ± 3.50[a]	52.42 ± 4.74[a]
Total sedge cover (%)	4.53 ± 2.87[a]	n/a	n/a	8.85 ± 1.81[a]	2.30 ± 1.14[a]
Total fern/fern-ally cover (%)	6.08 ± 2.98[a]	n/a	n/a	3.88 ± 1.40[a]	4.24 ± 2.16[a]
Total forb cover (%)	10.95 ± 8.45[a]	n/a	n/a	4.32 ± 0.83[a]	6.35 ± 3.01[a]
Total grass cover (%)	0.0 ± 0.0[a]	n/a	n/a	1.57 ± 0.55[a]	2.61 ± 2.18[a]
Tree cover (%)	10.63 ± 1.48[a]	n/a	n/a	6.63 ± 3.78[a]	3.24 ± 1.77[a]
Northern Barrens					
Total basal area (m^2/ha)	25.09 ± 1.80[a]	16.64 ± 1.44[ab]	n/a	7.82 ± 1.25[b]	n/a
Total understory cover (%)	56.20 ± 3.64[a]	71.04 ± 4.22[a]	n/a	89.28 ± 9.02[a]	n/a
Average litter depth (cm)	4.55 ± 0.34[a]	3.95 ± 0.24[a]	n/a	3.66 ± 0.26[a]	n/a
Mineral soil exposure (%)	0.0 ± 0.0[b]	0.20 ± 0.18[ab]	n/a	0.14 ± 0.07[a]	n/a
Woody material cover (%)	3.80 ± 1.19[a]	3.62 ± 0.97[a]	n/a	1.63 ± 0.41[a]	n/a
Total shrub cover (%)	30.85 ± 3.70[b]	39.38 ± 2.66[ab]	n/a	65.13 ± 7.37[a]	n/a
Total sedge cover (%)	9.45 ± 2.25[a]	8.51 ± 1.60[a]	n/a	5.43 ± 0.86[a]	n/a
Total fern/fern-ally cover (%)	6.47 ± 1.35[a]	11.78 ± 3.49[a]	n/a	12.13 ± 5.65[a]	n/a
Total forb cover (%)	6.56 ± 2.69[a]	9.12 ± 3.26[a]	n/a	6.14 ± 0.84[a]	n/a
Total grass cover (%)	0.01 ± 0.01[a]	0.19 ± 0.17[a]	n/a	0.20 ± 0.15[a]	n/a
Tree cover (%)	2.61 ± 0.93[a]	1.96 ± 0.77[ab]	n/a	0.31 ± 0.01[b]	n/a

Note: Values are means with standard errors. Statistically significant differences ($p < 0.05$; Tukey's HSD or Dunn's test of multiple comparison) between treatment types are denoted with different lowercase letters. Treatment types that were not available in an ecoregion are indicated with "n/a." FallRx indicates prescribed fire applied in the fall, MowRx indicates prescribed fire following by mowing, and SpringRx indicates prescribed fire applied in the spring.

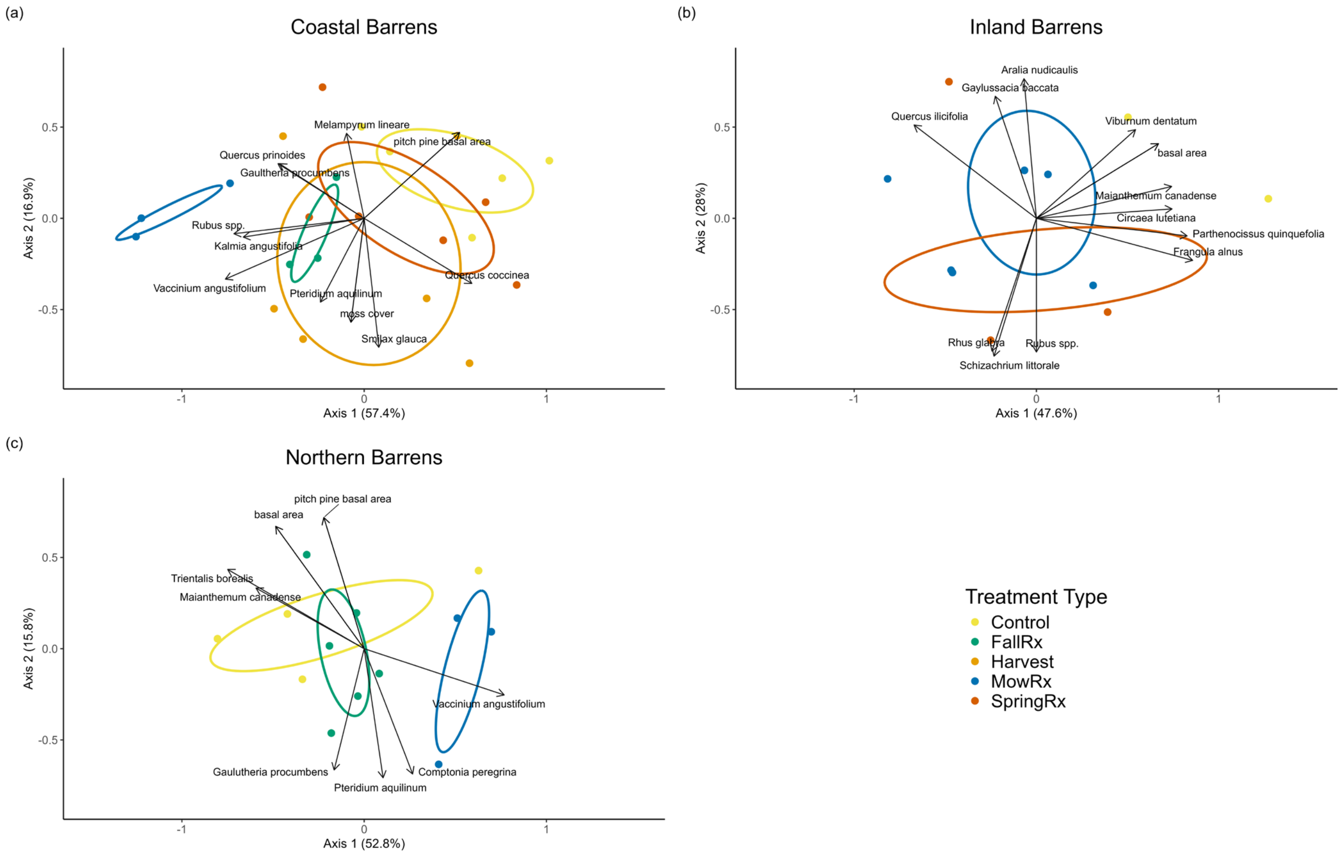

FIGURE 2 | NMDS showing significant species and environmental factors in Coastal Barrens (a); Inland Barrens (b); and Northern Barrens (c). Points represent average understory composition for individual units. Biplot vectors display understory species and environmental factors with significant ($\alpha = 0.05$) correlation with the main axes based on permutations of the goodness of fit test.

neither was evenness (H (2) = 0.47, p = 0.791). We were unable to test for differences in species diversity due to failed model convergence. There were 109 unique species observed across all plots in Inland Barrens. MowRx treatments had the greatest species richness, with 80 species recorded, and Control the least, with only 42.

Understory plant community composition and abundance demonstrated marked tendencies in Inland Barrens, as shown by the NMDS ordination (Figure 2), which was best explained using a two-axis solution (final stress = 0.120). Indicator species analysis revealed *Quercus ilicifolia* as an indicator of MowRx unit understories (Table 4) and *Viburnum dentatum*, *Maianthemum canadense*, and *Prunus serotina* with high fidelity to Control unit understories.

3.3 | Northern Barrens

For Northern Barrens, total basal area (*Wald* X^2 (2) = 7.38, p = 0.025) differed by treatment type, with Control units having significantly higher basal area than MowRx units (Table 2). Total understory cover (*Wald* X^2 (2) = 1.65, p = 0.439) and average leaf litter depth (*Wald* X^2 (2) = 1.42, p = 0.491) did not differ between treatments in this region. Control units had significantly less exposed mineral soil (H (2) = 6.61, p = 0.037) than MowRx units. Woody material cover (H (2) = 2.08, p = 0.354) did not vary by treatment type in Northern Barrens. Control units had less total shrub cover (*Wald* X^2 (2) = 7.80, p = 0.020) than MowRx treatments. Meanwhile, sedge cover (*Wald* X^2 (2) = 0.032, p = 0.984) did not change significantly between treatment types. Neither total cover by ferns and fern-allies ($F_{2,10}$ = 0.36, p = 0.708) nor total forb cover (H (2) = 0.027, p = 0.986) differed between treatments. Total understory cover by grass (H (2) = 1.93, p = 0.381) was quite low and did not vary among treatments in Northern Barrens. Total understory cover by tree species (H (2) = 5.98, p = 0.050) was marginally less (adjusted p = 0.058) in MowRx units than Control units.

Species richness (*Wald* X^2 (2) = 0.67, p = 0.714) did not vary across treatment type in this region (Table 3). Species diversity (*Wald* X^2 (2) = 0.50, p = 0.777) and evenness (H (2) = 0.19, p = 0.911) also did not differ significantly by treatment type. There were 49 unique species identified across all plots in Northern Barrens. Here, Control treatments had the greatest richness with 37 species recorded, and MowRx had the lowest, with only 22.

Clear affinities in understory plant community composition in Northern Barrens were illustrated by NMDS ordination (Figure 2), which employed a two-axis solution (stress = 0.151). PER-MANOVA analysis supported this divergence (F = 1.85, df = 2, p = 0.029) and post hoc pairwise analysis revealed significant differences between the understories of MowRx and FallRx units. *Pinus rigida* basal area (m^2/ha) and basal area (m^2/ha) were higher in the portion of the ordination space containing Control and FallRx units (Figure 2). *Vaccinium angustifolium*

TABLE 3 | Measures of diversity compared across treatment types within ecological regions.

	Control	FallRx	Harvest	MowRx	SpringRx
Coastal Barrens					
Observed species richness (Bootstrap)	23 (24–26)	28 (29–34)	25 (26–29)	33 (36–41)	38 (41–46)
Average species richness/plot	5.49 ± 0.20[c]	7.27 ± 0.30[ab]	5.96 ± 0.25[bc]	8.03 ± 0.34[a]	6.69 ± 0.26[abc]
Average diversity/plot *Shannon–Wiener Index*	1.06 ± 0.05[b]	1.39 ± 0.06[a]	1.14 ± 0.05[ab]	1.43 ± 0.06[a]	1.27 ± 0.05[ab]
Average evenness/plot *Pielou's J*	0.72 ± 0.02[a]	0.76 ± 0.01[a]	0.72 ± 0.02[a]	0.73 ± 0.01[a]	0.73 ± 0.03[a]
Total beta diversity	0.321	0.292	0.332	0.355	0.317
Replacement contribution to beta diversity (%)	54.5%	51.4%	61.6%	48.4%	60.5%
Richness contribution to beta diversity (%)	45.5%	48.6%	38.4%	51.6%	39.5%
Number of plots (sites)	51 (5)	33 (3)	56 (6)	33 (3)	54 (6)
Inland Barrens					
Observed species richness (Bootstrap)	42 (45–50)	n/a	n/a	80 (89–95)	65 (74–80)
Average species richness/plot	8.65 ± 0.63[a]	n/a	n/a	9.32 ± 0.36[a]	8.79 ± 0.41[a]
Average diversity/plot *Shannon–Wiener Index*	1.40 ± 0.12	n/a	n/a	1.45 ± 0.07	1.47 ± 0.08
Average evenness/plot *Pielou's J*	0.69 ± 0.03[a]	n/a	n/a	0.69 ± 0.04[a]	0.72 ± 0.05[a]
Total beta diversity	0.432	n/a	n/a	0.407	0.412
Replacement contribution to beta diversity (%)	66.2%	n/a	n/a	64.8%	79.3%
Richness contribution to beta diversity (%)	33.8%	n/a	n/a	35.2%	20.7%
Number of plots (sites)	20 (2)	n/a	n/a	69 (6)	33 (3)
Northern Barrens					
Observed species richness (Bootstrap)	37 (41–47)	30 (31–35)	n/a	22 (23–26)	n/a
Average species richness/plot	7.41 ± 0.42[a]	7.28 ± 0.24[a]	n/a	6.62 ± 0.30[a]	n/a
Average diversity/plot *Shannon–Wiener Index*	1.31 ± 0.07[a]	1.32 ± 0.04[a]	n/a	1.21 ± 0.06[a]	n/a
Average evenness/plot *Pielou's J*	0.71 ± 0.03[a]	0.72 ± 0.03[a]	n/a	0.71 ± 0.06[a]	n/a
Total beta diversity	0.338	0.320	n/a	0.296	n/a
Replacement contribution to beta diversity (%)	61.9%	57.4%	n/a	36.3%	n/a
Richness contribution to beta diversity (%)	38.1%	42.6%	n/a	63.7%	n/a
Number of plots (sites)	46 (4)	69 (6)	n/a	34 (3)	n/a

Note: Values are means with standard errors. Statistically significant differences ($p < 0.05$; Tukey's HSD or Dunn's test of multiple comparison) between treatment types are denoted with different lowercase letters. Treatment types that were not available in an ecoregion are indicated with 'n/a'. FallRx indicates prescribed fire applied in the fall, MowRx indicates prescribed fire following by mowing, and SpringRx indicates prescribed fire applied in the spring.

was a significant indicator of MowRx unit understories, while *Pinus strobus* was an indicator of Control units (Table 4).

4 | Discussion

The timing, severity, frequency, and extent of disturbance interact with plant functional traits to influence the structure and composition of understory plant communities (Rowe 1983; M. R. Roberts 2004). As such, suppression of historic fire regimes in fire-dependent forests across North America has resulted in substantial changes not only to overstory conditions and tree regeneration (Abrams 2005; Fralish and McArdle 2009; Howard et al. 2011), but also to understory plant communities (Lettow et al. 2014; Li and Waller 2015; Livingston et al. 2016). Our work augments the growing area of research into management

TABLE 4 | Indicator species analysis across treatment types within ecoregions.

Species	Response mechanism	Treatment type	*p*
Coastal Barrens			
Pteridium aquilinum	Endure	FallRx	0.031
Gaylussacia baccata	Endure	FallRx	0.002
Quercus prinoides	Endure	MowRx	0.003
Rubus spp.	Endure, Invade, Evade	MowRx	0.001
Kalmia angustifolia	Endure	MowRx	0.018
Vaccinium angustifolium	Endure, Invade, Evade	MowRx	0.029
Smilax glauca	Endure	Harvest	0.017
Inland Barrens			
Quercus ilicifolia	Endure	MowRx	0.026
Viburnum dentatum	Avoid	Control	0.016
Maianthemum canadense	Avoid, Endure, Evade	Control	0.013
Prunus serotina	Avoid, Endure	Control	0.035
Northern Barrens			
Vaccinium angustifolium	Endure, Invade, Evade	MowRx	0.007
Pinus strobus	Avoid, Resist, Invade	Control	0.016

Note: The treatment type FallRx indicates prescribed fire applied in the fall and MowRx indicates prescribed fire following by mowing.

techniques to restore understory plant communities in fire-dependent systems and highlights distinct understory community assemblages and structures associated with different restoration strategies in pitch pine barrens. This includes the abundance of several ecologically and culturally important species, including ericaceous shrub species (*Vaccinium angustifolium* and *Gaylussacia baccata*) and scrub oak (*Quercus ilicifolia*). The management approaches we investigated can serve to restore important sources of stable early successional habitat and landscape-scale heterogeneity, along with cultural and social values (Jordan et al. 2003; Gifford et al. 2010; Anchor QEA LLC, The Nature Conservancy, and Fine Arts and Sciences LLC 2019).

Disturbance severity can be characterized by the impact of a disturbance on the forest canopy, forest floor, and soil, and understory vegetation (M. R. Roberts 2004). High severity disturbances, like a crown fire, reduce the forest canopy, consume leaf litter, expose mineral soil, and remove understory vegetation, while low severity disturbances, like an ice storm, act on only one or two facets of this framework, for example, opening the overstory with little impact to the forest floor or existing understory vegetation (M. R. Roberts 2004). These impacts interact with the functional traits of understory species to influence understory plant community dynamics over time. In this study, patterns in overstory basal area, exposed mineral soil, and levels of understory cover across treatments reflected a range of disturbance severities from no disturbance in Control units to low- to moderate-severity disturbance in Harvest, SpringRx, FallRx, and MowRx units, respectively. NMDS and PER-MANOVA analysis of understory communities by treatment type reflected these differential disturbance effects with clear differences in understory plant community composition and abundance between treatments.

Species assemblages characterizing restoration treatments were largely reflective of species response traits to treatment disturbance severity. Plant responses to fire include evading, avoiding, resisting, or enduring disturbance, as well as invading post-disturbance, although species are not limited to one response mechanism (Rowe 1983). All species indicative of prescribed fire treatments (Table 4) were primarily enduring, although some also invade and evade. These enduring species, like *Quercus prinoides* and *Pteridium aquilinum*, tend to be top-killed by low- and moderate-severity fires but resprout from buried structures that survive, including rhizomes and root collars (Matlack and Good 1989; Matlack et al. 1993). These species can also spread clonally, quickly capitalizing on disturbance events (Matlack and Good 1989; Matlack et al. 1993). Differences in species between treatments receiving prescribed fire likely were related to the level of disturbance severity a given treatment represented. For example, MowRx represented the greatest disturbance severity. This may have favored species, such as *Vaccinium* spp. and *Quercus ilicifolia*, that have been demonstrated to increase with repeated or high-severity fire (Buell and Cantlon 1953; Abrahamson 1984). In contrast, *Gaylussacia* spp. have been found to decrease under these regimes (Buell and Cantlon 1953; Abrahamson 1984; Matlack et al. 1993) and were associated with the lower severity FallRx treatment. The more uniform environment created by mowing treatments could also create greater consistency across a burn, which may have impacted species response.

Restoration treatments also were associated with unique understory structural conditions, which presumably were related to treatment severity and frequency. As with previous work examining prescribed fire effects on understory communities, fire largely increased the abundance of resprouting shrubs (Buckman 1964; Richburg et al. 2004; Schwilk et al. 2009). The only exception was for MowRx units in Coastal Barrens. This may have been due to a late spring frost event in 2023 that impacted foliar cover estimates at the time of sampling, especially for *Quercus ilicifolia* and *Quercus prinoides*, as their large seedlings (≥ 50 cm in height and < 2.5 cm in DBH) counts were significantly higher in MowRx units than in Control, FallRx, or Harvest units. Increases in forb, graminoid, and shrub cover have also been associated with high frequency or severe fire (Buell and Cantlon 1953; Matlack and Good 1989; Wayman and North 2007; Schwilk et al. 2009; Goodwin et al. 2018); however, these changes can be short-lived without repeat disturbance (Goodwin et al. 2018; Bassett et al. 2020). While some treatment types showed an increase in cover of forbs, grasses, or sedges when compared with Control units, this was not statistically significant (Table 2). Units sampled for the study ranged from 1 to 7 years post treatment, which may have obscured the short-term and long-term effects of disturbance on understory guilds. Additionally, no units had histories of very high (i.e., annual to biennial) treatment frequencies, so we could not directly test for the influence of fire frequency.

The impacts of treatment on species richness and diversity were not consistent across ecoregions. Previous work has shown that, following fire suppression, alpha diversity can increase (e.g., Li and Waller 2015) or decrease (e.g., Livingston et al. 2016). In Coastal and Inland Barrens, observed species richness was lower in Control units, with 21.7% and 35.7% of species observed distinct from those observed in treated units, respectively. For Northern Barrens, Control unit species richness was higher, with 40.5% of species observed distinct from those in treated units. Previous work has indicated that increases in shade-tolerant mid-successional species can drive elevated alpha and gamma diversity and, where coupled with a decrease in beta diversity, result in overall homogenization of the understory plant community (Li and Waller 2015). Such a dynamic likely contributed to the greater richness in Control units, with species unique to these areas often being mid- to late-successional, mesic species like *Fagus grandifolia* and *Acer pensylvanicum*. Treated units in Inland Barrens shared 33 species that were distinct from those found in Control units; however, only one or two species in Northern and Coastal Barrens, respectively, were shared among all treatment types that were also absent from Control units. Collectively, species replacement tended to be a larger contributor to beta diversity; however, in MowRx units in two ecoregions, beta diversity was driven by richness differences. As turnover was less important in these units, species composition was more uniform with pockets of greater richness, which may be a result of greater habitat homogeneity created by higher severity disturbances (Stevens et al. 2019) or by the conditions created via mowing. As this was an opportunistic, observational study, there is no pre-treatment data available against which to compare post-treatment species diversity and abundance. Other studies of pitch pine barrens have found a strong link between community structure and composition and post-colonial land use history (Patterson et al. 1983; Motzkin et al. 1999; Copenheaver et al. 2000). Expectations of species composition and structural attributes in pitch pine barrens are tied closely with disturbance severity and frequency, with areas experiencing the highest frequency and severity of disturbance (e.g., fire) maintained as stable and open grasslands, while those at the opposite end of the spectrum densifying, mesophying, and transitioning to alternative states (Jordan et al. 2003).

Common management techniques used to restore pitch pine barrens impact stand environmental conditions and structure, with subsequent effects on species richness and abundance. Management using prescribed fire clearly encourages the dominance of fire-dependent species, especially resprouting shrubs, although the severity and frequency of fire can also impact forb and graminoid richness and abundance. Many of the conditions and species associated with restoration treatments reflect important habitat conditions for rare and declining species (Wagner et al. 2003; Gifford et al. 2010) or culturally important foods for Tribal Nations whose ancestral homelands overlap with pine barrens communities. To this end, fire has long been used as a management approach by Tribal Nations to unlock nutrients stored in leaf litter, facilitate resprouting in shrubs, control detrimental insect and disease populations, and encourage the production of soft mast and spread of plants of cultural significance through clonal growth and rhizome spread (White 1975; Anderson 2005; LeCompte 2018; Steen-Adams et al. 2019). Nations, including the Salish, Confederated Tribes of Warm Springs, Gitkasn, and Wet'suwet'en, use prescribed fire to increase the presence and abundance of *Vaccinium* spp. mast and *Pteridium aquilinum* rhizomes, species significant both for food and cultural value (White 1975; Gottesfeld 1994; Steen-Adams et al. 2019). Collaboration and discourse between western forest ecology and restoration methodologies and indigenous knowledge would benefit their restoration as well as other species of cultural importance in these ecosystems (Dockry et al. 2023). This study has documented the influence of management activities on resulting understory communities, with future work needed on specific species of interest and their relationship with the seasonality, frequency, heterogeneity, and severity of management techniques.

Author Contributions

A.W.D., K.J.D., and K.A.S. conceived the research. A.W.D., K.J.D., and K.A.S. designed the research and field methodology. K.A.S. conducted fieldwork, analyzed the data, and wrote the first draft, with regular advice from other authors; all authors were involved in the writing and editing of the final manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data are available on the *Figshare* repository: https://doi.org/10.6084/m9.figshare.27993479.v1.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Supplemental methods for prescribed fire treatments. **Appendix S2:** Average abundance by treatment type of all vascular plant species surveyed. **Appendix S3:** Initial NMDS of all regions.