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Tree regeneration dynamics under a range of restoration treatments in Northeast pitch pine (*Pinus rigida*) barrens

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ABSTRACT

Fire suppression and disconnection from historic fire regimes has a distinct and significant impact on fire-dependent natural communities, including regeneration of characteristic species, whose restoration may be further complicated by climate change. Pitch pine (*Pinus rigida*) barrens are a globally rare, fire-dependent natural community found primarily in the Northeast United States. We analyzed pitch pine regeneration response across 47 sites treated with 1) harvest ($n = 6$), 2) fall prescribed fire ($n = 9$), 3) spring prescribed fire ($n = 9$), 4) mowing followed by prescribed fire ($n = 12$), and 5) controls ($n = 11$), in barrens across the Northeast, to measure the impacts of regionally common restoration treatments on desired regeneration success. Leaf litter depth, mineral soil exposure, overstory basal area and composition, understory plant cover, and tree regeneration in three size classes across these five treatment types were compared. Pitch pine small seedling abundance was adversely impacted by greater litter depth, understory cover, and abundance of shrub oak (*Quercus ilicifolia* and *Quercus prinoides*) seedlings. All treatment types had significantly more small seedlings than untreated control units. Large seedling abundance was also negatively associated with increased litter depth. Pitch pine sapling abundance increased with pitch pine overstory proportional abundance and decreased as shrub oak saplings increased. This study represents the first multi-region assessment of pitch pine restoration treatments, confirming necessary conditions for pitch pine regeneration established by previous site-level work. While no single management strategy emerged as most effective, conditions resulting from higher severity disturbances appear more conducive to pitch pine regeneration establishment and provide managers with several options to maintain these ecosystems.

1. Introduction

Fire is a keystone process in the dynamics and distribution of many natural communities (Keeley and Rundel, 2005; Bond and Scott, 2010), with recent global assessments classifying 46 % of the area of major habitat types as fire-dependent or fire-influenced (Hardesty et al., 2005). Common threats to fire-dependent natural communities include fragmentation and habitat loss, changes to fire regimes, and climate change, all of which have been linked with shifts in species richness and abundance, along with elevated extinction risk (Brown and Johnstone, 2012; Driscoll et al., 2021; Nolan et al., 2021). Moreover, altered fire regimes can impact individuals, communities, and populations, leading to changes in community composition and structure, landscape scale patterns, and ecosystem services (Forman and Boerner, 1981; Etchells et al., 2020; Lecina-Diaz et al., 2021).

In the eastern United States, the suppression and alteration of fire regimes is a primary driver of contemporary changes in the structure and composition of fire-dependent ecosystems. These changes are characterized by two main self-perpetuating and interacting themes: mesophication and densification (Nowacki and Abrams, 2008; Hanberry et al., 2014). Mesophication describes a cyclical phenomenon where lack of fire increases mesic microenvironmental conditions, reducing the prospect of fire and success of fire-dependent species, while densification refers to the conversion of open woodlands to closed canopy forests in the wake of fire suppression. Their effect has been to decrease the dominance of fire-dependent species and increase the prevalence of shade-tolerant, fire sensitive species (Arthur et al., 1998; Fralish and McArdle, 2009; Hanberry et al., 2014). This creates alternative ecosystem states that will not easily revert to fire-dependent communities, even with the reintroduction of fire (Arthur et al., 1998; Suding

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et al., 2004; Hanberry et al., 2014). Mesophication and densification inhibit the regeneration and recruitment of fire-adapted species, which require light and disturbance to establish, complicating restoration (Abrams, 1992; Stambaugh et al., 2019).

The primary impacts of global climate change on successful regeneration in these communities are through changes in temperature and moisture conditions and disturbance regimes (Westerling et al., 2006; Holden et al., 2007; Nolan et al., 2021). In particular, drought stress and heatwaves represent significant threats to seedling recruitment and retention as they may diminish available seed prior to fire events, reduce the ability of species to resprout ("resprouting exhaustion syndrome", Karavani et al., 2018), diminish recruitment success via reduced or unpredictable post-fire precipitation, and increase fire severity through more available fuels (Lamont et al., 1991; Enright et al., 2014; Aponte et al., 2016). Higher severity fires driven by climate change can eliminate local seed banks, increase dispersal distances due to larger patch sizes, and alter mycorrhizal communities necessary for recruitment and survival (Karavani et al., 2018; Etchells et al., 2020). These events also have the potential for substantial and long-term changes to community structure, which may impact habitat and future fire risk (Etchells et al., 2020; Lecina-Diaz et al., 2021). Similarly, decreased fire return intervals can reduce or eliminate fire-dependent species if there is not enough time between fires to reach reproductive maturity, by limiting the amount of regeneration advancing into the overstory, and through reduction of forest cover and shifting species dominance (Keeley et al., 1999; Brown and Johnstone, 2012; Buma et al., 2013; Stambaugh et al., 2019). Beyond shifts in fire regimes, climate change may also generate novel disturbance dynamics by influencing the distribution and virulence of both native and non-indigenous insect populations affecting these forests, which can lead to outbreaks where they were previously uncommon, expansion of epidemic range, including movement into areas with naïve host species, and extensive host mortality (Raffa et al., 2008; Lesk et al., 2017).

Pitch pine barrens are an important fire-dependent community in the Northeast United States that covers multiple seral stages of nutrient poor, droughty forest and woodland types located on sandy, glacial outwash soils dominated by pitch pine (*Pinus rigida*) and oaks (*Quercus spp.*) in the overstory and shrub oaks (*Quercus ilicifolia* and *Quercus prinoides*) and ericaceous shrubs (family Ericaceae) in the mid- and understory. These forests are found primarily from present-day New Jersey to Maine. Pitch Pine – Scrub Oak barrens are ranked G2 ('imperiled') with 6 – 20 global occurrences and estimates of community loss in the eastern United States ranging from 37 – 69 % (Noss et al., 1995). They supply essential food, habitat, and abiotic conditions to rare, threatened, and endangered plant and animal species across their range, especially Lepidoptera of conservation concern in the Northeast (Wagner et al., 2003; Schweitzer et al., 2011; Todd et al., 2013). Disconnected from ecological and cultural disturbance regimes and shaped by colonial land use, development, and fragmentation, the structure, species composition and diversity, and fuel availability of current pitch pine barrens has been greatly altered (Forman and Boerner, 1981; Milne, 1985; Motzkin et al., 1999). This lack of disturbance, especially from fire, has specifically reduced the availability of conditions favorable to the regeneration of pitch pine, namely exposed mineral soil and abundant light reaching the forest floor (Jordan et al., 2003). Restoration is additionally complicated by climate change, especially through warming winters and the range expansion of southern pine beetle (*Dendroctonus frontalis* Zimmermann, SPB), whose range was historically limited to more southern latitudes by lethal winter temperatures (Ungerer et al., 1999) but has recently begun to expand north in the past decade to deleterious effect in pitch pine barrens

Pitch pine is a primary host species in this northward expansion (Dodds et al., 2018). The high stocking conditions (i.e., densification) characterizing many pitch pine barrens due to lack of disturbance provide favorable conditions for outbreaks of SPB (Jamison et al., 2022), which can have a dramatic impact on the forest canopy causing 90 %+ mortality in overstory pines in as little as one growing season (Clark et al., 2017; Dodds et al., 2018). This same lack of disturbance limits established pitch pine regeneration, favoring a well-developed understory and mid-story of hardwood species (i.e., mesophication), which are poised to respond to SPB disturbance and dramatically shift species composition, moving this globally rare natural community type into alternative community states (Howard et al., 2011; Heuss et al., 2019). Initial studies of pitch pine barrens post-SPB outbreak found very little pine regeneration, with pine seedlings only found where SPB suppression treatment disturbed the forest floor and shrub layer (Clark et al., 2017; Heuss et al., 2019), further increasing the urgency of establishing desirable regeneration prior to outbreak to inhibit the transition to alternative community states.

Restoration treatments in pitch pine barrens have mainly focused on thinning, mowing, and the reintroduction of prescribed fire. Previous studies of repeat applications of prescribed fire have found an increased density of pine small seedlings, as well distinctive differences in tree species composition between burned and unburned stands (Olson, 2011). Shelterwood cutting coupled with repeat prescribed fire has also been shown to increase the amount of pine small seedlings, showing a positive relationship between number of burns and number of seedlings (Little and Moore, 1950). Mowing has been successful in favoring pitch pine regeneration through reducing competing vegetation and exposing mineral seedbeds (Little et al., 1958); however, effects are often short lived, due in large part to the ability of many species in this community to resprout (Bried and Gifford, 2010).

Conifer regeneration failure in other nutrient- and species-poor conifer-heath systems has been attributed to the composition, abundance, and functional traits of competing understory vegetation, along with the lack of severe disturbance to the seed bed and increased light reaching the forest floor (Mallik, 2003). For example, ericaceous leaf litter can be allelopathic, leading to nutrient imbalances in the soil, and without severe fire to consume this litter and release nutrients, regeneration conditions favor already established understory vegetation (Mallik, 2003). In pitch pine communities, ericaceous shrubs, along with shrub oaks, can rapidly recolonize sites from underground plant structures that survive low and moderate severity fires (e.g., Bried and Gifford, 2010), providing early and substantial competition to tree regeneration.

The present study investigated the impact of four regionally common restoration strategies: harvest, fall prescribed fire, spring prescribed fire, and mowing followed by prescribed fire, on pitch pine regeneration in barrens across the Northeast (MA, ME, NH, and NY). An understanding of effective treatments and significant factors influencing pitch pine regeneration is critical for the development of successful management plans to restore pitch pine barrens and improve adaptive capacity, especially considering the imminent and novel threat presented by SPB, as well as the numerous uncertainties introduced by a rapidly warming globe. The goal of this study is to understand the impact of these management strategies on environmental conditions and regeneration success in pitch pine barrens in the Northeast.

2. Methods

2.1. Study site selection and description

Pitch pine – oak barrens can be matrix communities on Long Island, New York and in southeastern Massachusetts (Swain and Kearsley, 2001; Edinger et al., 2014). Outside of coastal areas, they are found in isolated remnant stands. Pitch pine barrens occur both on coastal and inland sites and are generally relegated to nutrient poor, xeric to dry-mesic soils on sandy glacial outwash (Swain and Kearsley, 2001; Gawler and Cutko, 2010). Topography in these forests is flat to undulating. Canopy closure usually ranges from 25 % to 75 %, with areas of low canopy closure classified as woodland and those with high canopy closure as forest (Swain and Kearsley, 2001; Sperduto and Nichols, 2011). Vegetation is often patchy and heterogenous.

Study sites were located in present-day New York (NY), Massachusetts (MA), New Hampshire (NH), and Maine (ME) (Fig. 1). Units 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). All sites are largely managed with the maintenance and restoration of pitch pine barrens as a driving management objective. SPB was not present in outbreak conditions in any of the management units prior to or at the time of sampling. Sampled treatment units (i.e., experimental units) were a minimum of 1.2 ha. To control for edge effects, each unit had a minimum internal buffer of 30 m.

Four common management strategies were examined across barrens: harvest (Harvest), spring prescribed fire (SpringRx), fall prescribed fire (FallRx), and mowing followed by prescribed fire (MowRx). We were interested in areas receiving treatments between September 2015 to March 2022 and focused on regions that contained multiple units with treatments of interest within that window (Table 1). This window of time was selected given studies have shown seedlings in pine barrens to continue to appear up to seven years post disturbance (Landis et al., 2005) and it facilitated our ability to sample a minimum number of replicates in regions with less active treatment histories. Not all treatments were available in all regions. Many treatment units had experienced multiple disturbances, including previous wildfires, prescribed fires, mastication, and harvest or thinning treatments; however, we categorized units based on the most recent treatment actions. The length of active management history differed by site, with some regions having treatment histories stretching back into the 1990s and others only beginning in the mid-2010s. Many units had experienced some form of thinning to reduce canopy density and the abundance of fire-intolerant species.

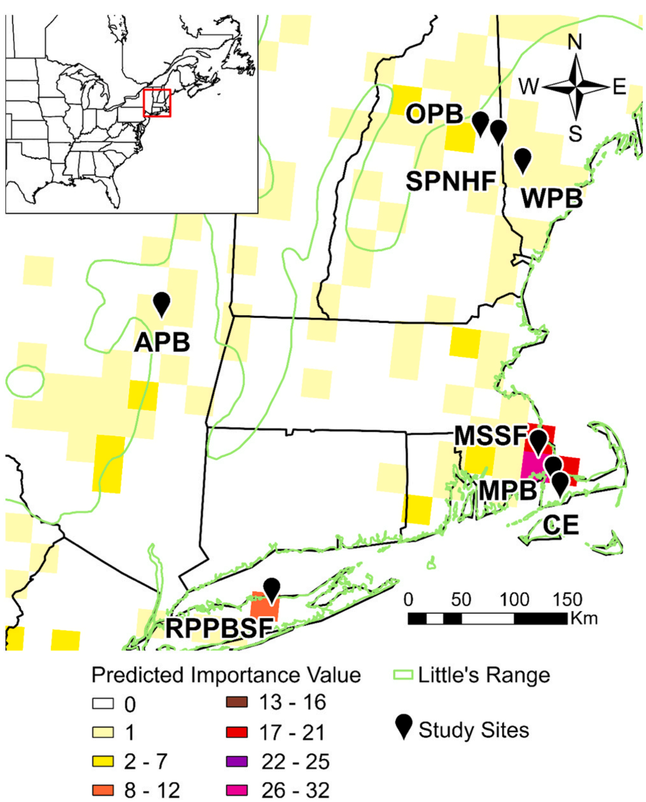

Fig. 1. Study site locations across the Northeast United States. Historic range of pitch pine is outlined in green. Projections of future range expansion and importance values are based on the Geophysical Fluid Dynamics Laboratory (GFDL) High-Emission scenario (Prasad et al., 2014). Under this scenario, suitable habitat for pitch pine is projected to expand northwards. 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).

Harvest units were treated between 2017 and 2020. Some units were treated via whole tree harvesting and in others remaining slash was dispersed and cut below four feet. Mature, fire-intolerant species were targeted for removal. This treatment type was the most regionally restricted (Table 1).

Prescribed fire units were burned following a fire plan, often allowing fires to smolder as long as possible, to remove duff and expose mineral soil, given local smoke concerns. In some units, patchy burning to create refugia and burn unit scale heterogeneity was also encouraged. Some units were cleared of smaller fuels prior to the application of prescribed fire. This is an observational study spanning multiple states and ownerships. Many sites were lacking formal assessments of fire severity and instead recorded qualitative observations of litter and duff consumption, woody shrub mortality, and mineral soil exposure. Based on these reports, conversations with managers, and on-site observations, fires assessed in this study were low to moderate in intensity and severity. Here we define severity as relating to the amount of leaf litter/duff consumed, understory plant mortality, and overstory tree mortality. Managers indicated that there was a positive correlation between days since last rain and burn weather relative humidity (RH) with fire severity.

Three prescribed fire types were examined as part of this study, being classified based on season of burning (fall or spring) or treatments (mowing) applied in conjunction with burning. Burning occurred in FallRx units between late August (8/27) and late October (10/20), from 2015 to 2021. For fall burns, average temperatures ranged from 57 to 87 °F, average relative RH from 39 to 61, and 3–8 days since last rain. Fires took place between late March (3/20) and late May (5/23), from 2016 to 2022, in SpringRx units. Average temperatures ranged from 39 to 68 °F, average RH from 29 to 87, and 0–13 days since last rain. Within MowRx units, prescribed fires were preceded by mowing, used primarily as a fuel reduction and rearrangement technique, curbing the potential for high intensity, fast moving fires. Mowing was implemented using either a Davco rotary brush-mower or FECON mower. Prescribed fire was generally applied within a year of mowing in sampled units, although up to two years prior in some units (n = 3). Units were burned between 2015 and 2021. Season of burning varied across MowRx units as most regions exhibited a preferred burning season (e.g., spring or fall), meaning there were not enough treatments across seasons and regions to analyze seasonality here. Average temperatures ranged from 42 to 86 °F, average RH from 32 to 56, and 1–13 days since last rain.

In addition to units with recent management history, experimental units that had not experienced treatment in at least 20 years (Control) were also identified. These areas were used to represent the status quo for many contemporary pitch pine barrens, which have no history of recent management or disturbance (e.g., wildfire).

2.2. Field methods

Sampling took place during the summers of 2022 and 2023. Each treatment unit had a minimum of nine sample plot locations and a maximum of thirteen, with two treatment units on Long Island, New York only having five plots each due to their small size (less than originally mapped), to maintain minimum internal buffers.

Plots (n = 498) were located on transects running in cardinal

Table 1
Number of units sampled across treatment types and regions. Regionally unavailable treatment types indicated with "n/a". Three units with a spring prescribed fire and mowing treatment and three units with a summer prescribed fire and mowing treatment were sampled, indicated with an * .

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

directions through treatment units (see Supplemental Methods). The distance between plots was variable with a minimum inter-plot distance of 10 m. Regeneration was measured at each plot using three size classes and three nested subplots for sampling efficiency (D'Amato et al., 2015; Heuss et al., 2019; Reuling et al., 2019). A 1 m^2 square frame was used to measure small seedlings, which were less than 50 cm in height. 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 measured in 10 m^2 circular subplots centered on the 1 m^2 frame. Saplings, greater than or equal to 2.5 cm and less than 10 cm dbh, were measured in 25 m^2 circular subplots centered on the same point. Counts in all regeneration classes were tallied by species. Regeneration was measured at functional height in the understory. For example, scrub oak (*Quercus ilicifolia*), which has a low and spreading form, was not pulled up to see if it met or exceeded a height class but was rather measured at the effective height within the shrub layer. A prism point, using a 2.3 m^2/ha BAF prism, was also taken at every plot with trees recorded by species and live or dead status.

Understory vegetative cover, ground cover, and leaf litter depth was also measured in the 1 m^2 frame subplots. Percent understory cover was visually estimated 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). 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 estimated using the above eight cover classes (Bechtold and Patterson, 2005; USDA, 2021). Litter depth measurements, measuring the depth of the O layer, were taken at the northwest and southeast corners of the 1 m^2 frame. Litter depths were recorded up to 15 cm and rounded to the nearest 0.5 cm. *Lymantria dispar* outbreaks in New Hampshire in 2022 and late frost in Massachusetts in 2023 impacted the foliar abundance of some plants measured in vegetative percent cover classes.

2.3. Statistical analysis

All statistical analysis was conducted in R (R Core Team, 2024) using RStudio (Posit team, 2024). Tree regeneration was divided into three species groups for analysis: pitch pine, shrub oak (including *Q. ilicifolia* and *Q. prinoides*), and other, which encompassed all other tree species. Percent cover estimates were transformed to the midpoint of the cover class (e.g., cover class 2, which encompasses 1 – 5 % was transformed to 3.0). Ericaceous species were separated into their own cover variable (see Supplemental Methods).

For small and large seedling analysis, fixed effects variables were log-transformed to reduce the effect of skew in the data. For sapling analysis, fixed effects variables were scaled to more readily compare across data collected at multiple subplot sizes.

Kruskal-Wallis tests (*tats* package; *kruskal.test* function) were used to compare total basal area (m^2/ha), pitch pine basal area (m^2/ha), proportion of pitch pine basal area (%), average leaf litter depth (cm), mineral soil exposure (%), total understory cover (%), total ericaceous understory cover (%), proportion of ericaceous vegetation (%), and pitch pine, shrub oak, and other tree species regeneration abundance across treatment types. Wilcoxon rank sum tests with Bonferroni correction (*stats* package; *wilcox.test* function) were used for post hoc comparisons to determine significant (α=0.05) differences between treatment types. This same process was used to compare average leaf litter depths across treatment units that were sampled one to three years post-treatment, four to seven years post-treatment, and control (20 + years).

Generalized linear mixed modeling (GLMM, *glmmTMB* package; *glmmTMB* function) (Brooks et al., 2017) was used to model the probability of pitch pine regeneration based on measured factors expected to influence seedbed and growing conditions. Evaluated fixed effects included treatment type, shrub oak regeneration abundance, other tree species regeneration abundance, total basal area (m^2/ha), pitch pine basal area (m^2/ha), proportion of total basal area in pitch pine (%), amount of exposed mineral soil (%), average leaf litter depth (cm), total understory cover (%), total ericaceous understory cover (%), and the relation between total basal area and proportion of pitch pine (Table 2). Plots nested within sample units were used as random effects. Region was also investigated as a random effect but was not ultimately included in final models based on lack of improvement of fit. Fixed effects were checked for issues of collinearity (*performance* package; *check_collinearity* function) (Lüdecke et al., 2021). As time between treatment and sampling varied by unit, years between treatment and sampling were log transformed and used as an offset in all models. Poisson (small seedling) and negative binomial (large seedling and sapling) distributions with a log link were used in GLMMs. Sapling models were zero inflated by region, with no pitch pine saplings recorded on Long Island, New York.

Model selection based on corrected Akaike's information criterion (AIC_c) was used to determine the best predictors of pitch pine regeneration. AIC_c comparisons were accomplished via the *dredge* function (*MuMIn* package) with models within ΔAIC_c 2 of the minimum AIC_c value considered (Burnham and Anderson, 2004; Bartoń, 2023). We only considered models with four or fewer fixed effects to maintain parsimony. Models using both basal area per hectare and pitch pine basal area per hectare were excluded due to issues of collinearity. Models were then checked and diagnosed using simulated residuals for the model (*DHARMa* package; *simulateResiduals* function) (Hartig, 2022). Models that failed residual checks were excluded. Models within ΔAIC_c 2 of the minimum AIC_c that were most parsimonious, ecologically

Table 2
Factors evaluated in generalized linear mixed models (GLMMs) to predict pitch pine regeneration probability.

Abbreviation	Definition
AVGLD	Average litter depth (cm)
MIN	Percent exposed mineral soil
BAHA	Basal area (m^2/ha)
PIRIBA	Pitch pine basal area (m^2/ha)
PIRIPROP	Proportion of pitch pine basal area
VEG	Percent understory vegetative cover
ERI	Percent ericaceous understory cover
TRTTYP	Treatment type
SOSS	Shrub oak small seedling abundance
SOLS	Shrub oak large seedling abundance
SOSA	Shrub oak sapling abundance
OTHERLS	Other tree species large seedling abundance
OTHERSA	Other tree species sapling abundance

interpretable, and practical for management decision making were prioritized in selecting best approximating models. Estimated marginal means (*emmeans* package; *emmeans* function) were calculated as a post hoc comparison to determine significant (α=0.05) differences between treatment types (Lenth, 2024). Pseudo r-squared (*performance* package; *r2_Nakagawa* function) was used as a measure of goodness of fit for small and large seedling models and adjusted r-squared (*performance* package; *r2_zeroinflated*) for sapling models, to account for zero inflation in the model (Lüdecke et al., 2021).

3. Results

Comparisons using the Kruskal-Wallis test revealed that total basal area ($h\,(4) = 153.7$, $p < 0.0001$) and pitch pine basal area ($h\,(4) = 67.4$, $p < 0.0001$) differed by treatment type (Table 3). Control units were characterized by significantly higher total basal area than all other treatment types. MowRx treatments had the lowest overall basal area, although comparable to Harvest units. Control, FallRx, and SpringRx had similar levels of pitch pine basal area, while MowRx units had significantly lower levels, although again similar to Harvest units. Proportion of total basal area in pitch pine varied by treatment type ($h\,(4) = 21.8$, $p = 0.0002$). FallRx and SpringRx units had the greatest proportion, significantly higher than Control units. Average leaf litter depth differed by treatment type as well ($h\,(4) = 78.8$, $p < 0.0001$). Harvest and Control units had greater average depth of leaf litter, substantially more than SpringRx and MowRx units. Mineral soil exposure varied by treatment ($h\,(4) = 51.8$, $p < 0.0001$), with Control units having noticeably less exposure than all other treatment types. Total understory cover also differed by treatment ($h\,(4) = 60.6$, $p < 0.0001$). FallRx units had the greatest total cover, significantly more than Control and Harvest units. Total cover by ericaceous understory vegetation varied by treatment type ($h\,(4) = 24.0$, $p < 0.0001$). Mirroring total cover, FallRx units again had the highest overall ericaceous cover, significantly more than Control, MowRx, and SpringRx units. The proportion of ericaceous cover deviated by treatment type ($h\,(4) = 52.2$, $p < 0.0001$), with MowRx units having the lowest proportion of understory vegetation in ericaceous species, substantially less than Control, FallRx, and Harvest units.

For small seedling ($h\,(4) = 34.66$, $p < 0.0001$) and large seedling ($h\,(4) = 63.0$, $p < 0.0001$) size classes, pitch pine regeneration varied by treatment type, although there was no difference between treatment types for pitch pine sapling abundance ($h\,(4) = 8.5$, $p = 0.075$). Pitch pine small seedling abundance was significantly lower in Control units as compared to FallRx, Harvest, MowRx, and SpringRx, which were not different from each other, whereas large seedlings were more abundant in Harvest units than in all other treatments. The abundance of shrub oak small seedlings ($h\,(4) = 30.4$, $p < 0.0001$), large seedlings ($h\,(4) = 135.0$, $p < 0.0001$), and saplings ($h\,(2) = 13.96$, $p = 0.0009$) varied by treatment. Across size classes, Harvest units had a low presence of shrub oak. MowRx units had moderate levels of shrub oak small seedlings and very high levels of large seedlings. FallRx units had high levels of small shrub oak seedlings and moderately high levels of large seedlings. Shrub oak saplings were more abundant in Control and FallRx units. None were recorded in MowRx or SpringRx units. Amounts of other tree species small seedlings ($h\,(4) = 54.6$, $p < 0.0001$), large seedlings ($h\,(4) = 25.2$, $p < 0.0001$), and sapling ($h\,(4) = 73.0$, $p < 0.0001$) differed by treatment as well. For small seedlings and saplings, Control units had significantly more other species recorded than all other treatment types. For large seedlings, MowRx and SpringRx units had greater abundance than Control or FallRx units.

Average leaf litter depth was impacted by time from treatment ($h\,(2) = 33.06$, $p < 0.0001$), with units sampled one to three years post-treatment having the lowest average leaf litter depth (3.28 ± 0.20^{a} cm), those sampled four to seven years post with greater average litter depth (4.27 ± 0.16^{b} cm), and Control units having the highest average litter depth (5.02 ± 0.24^{c} cm).

Table 3
Selected environmental variables compared across treatment types. Values are means with standard errors. Values within a row with different superscripts are different at the α= 0.05 level.

	Control	FallRx	Harvest	MowRx	SpringRx
Total basal area (m^2/ha)	26.78 $\pm$ 1.02^{a}	17.44 $\pm$ 1.07^{b}	12.11 $\pm$ 1.10^{cd}	9.06 $\pm$ 0.71^{c}	15.85 $\pm$ 0.94^{bd}
Pitch pine basal area (m^2/ha)	17.05 $\pm$ 0.95^{a}	14.45 $\pm$ 1.08^{ab}	9.80 $\pm$ 0.95^{bc}	7.81 $\pm$ 0.67^{c}	13.75 $\pm$ 0.90^{ab}
Proportion of total basal area in pitch pine (%)	64.06 $\pm$ 3.1^{a}	79.60 $\pm$ 2.8^{b}	69.88 $\pm$ 4.8^{ab}	68.28 $\pm$ 3.6^{ab}	80.49 $\pm$ 3.3^{b}
Average leaf litter depth (cm)	5.02 $\pm$ 0.24^{a}	4.53 $\pm$ 0.20^{ab}	5.29 $\pm$ 0.33^{a}	2.82 $\pm$ 0.17^{c}	4.05 $\pm$ 0.31^{bc}
Mineral soil exposure (%)	0.01 $\pm$ 0.01^{a}	0.20 $\pm$ 0.09^{b}	1.65 $\pm$ 1.04^{bc}	1.20 $\pm$ 0.36^{c}	0.94 $\pm$ 0.28^{c}
Total understory cover (%)	46.85 $\pm$ 2.31^{a}	72.70 $\pm$ 3.53^{b}	55.21 $\pm$ 3.41^{ac}	70.47 $\pm$ 3.58^{bc}	64.65 $\pm$ 2.65^{bc}
Total ericaceous cover (%)	21.24 $\pm$ 1.65^{a}	37.74 $\pm$ 2.62^{b}	34.10 $\pm$ 2.76^{bc}	19.88 $\pm$ 2.23^{a}	25.26 $\pm$ 2.48^{ac}
Proportion of understory cover in ericaceous species (%)	51.98 $\pm$ 3.15^{ab}	53.04 $\pm$ 4.43^{ab}	62.70 $\pm$ 3.86^{a}	30.96 $\pm$ 2.73^{c}	43.17 $\pm$ 3.88^{bc}
Pitch pine small seedlings (<50 cm)	0.009 $\pm$ 0.009^{a}	1.29 $\pm$ 0.40^{b}	0.57 $\pm$ 0.15^{b}	0.87 $\pm$ 0.46^{b}	0.57 $\pm$ 0.15^{b}
Pitch pine large seedlings (≥50 cm & <2.5 cm dbh)	0.043 $\pm$ 0.03^{a}	0.098 $\pm$ 0.05^{a}	1.30 $\pm$ 0.38^{b}	0.11 $\pm$ 0.07^{a}	0.023 $\pm$ 0.02^{a}
Pitch pine saplings (≥2.5 cm & <10 cm dbh)	0.26 $\pm$ 0.11^{a}	0.05 $\pm$ 0.03^{a}	0.05 $\pm$ 0.04^{a}	0.06 $\pm$ 0.3^{a}	0.01 $\pm$ 0.01^{a}
Shrub oak small seedlings (<50 cm)	2.39 $\pm$ 0.47^{ab}	3.74 $\pm$ 0.52^{c}	0.88 $\pm$ 0.26^{a}	2.84 $\pm$ 0.36^{bc}	1.62 $\pm$ 0.32^{ab}
Shrub oak large seedlings (≥50 cm & <2.5 cm dbh)	5.68 $\pm$ 0.77^{a}	16.08 $\pm$ 1.49^{b}	5.77 $\pm$ 1.08^{ac}	27.68 $\pm$ 1.61^{d}	12.60 $\pm$ 1.63^{bc}
Shrub oak saplings (≥2.5 cm & <10 cm dbh)	0.71 $\pm$ 0.15^{a}	0.49 $\pm$ 0.12^{a}	0.02 $\pm$ 0.02^{b}	n/a	n/a
Other species small seedlings (<50 cm)	3.74 $\pm$ 0.48^{a}	0.89 $\pm$ 0.16^{b}	1.11 $\pm$ 0.34^{b}	1.25 $\pm$ 0.31^{b}	1.21 $\pm$ 0.28^{b}
Other species large seedlings (≥50 cm & <2.5 cm dbh)	1.87 $\pm$ 0.40^{a}	2.08 $\pm$ 0.41^{ab}	2.52 $\pm$ 0.37^{bc}	4.42 $\pm$ 0.65^{c}	4.76 $\pm$ 0.91^{c}
Other species saplings (≥2.5 cm & <10 cm dbh)	0.89 $\pm$ 0.13^{a}	0.41 $\pm$ 0.14^{b}	0.14 $\pm$ 0.06^{b}	0.07 $\pm$ 0.03^{b}	0.14 $\pm$ 0.05^{b}

3.1. *Small seedlings*

Treatment type, average leaf litter depth, number of shrub oak small seedlings, and total understory cover were all influential to pitch pine small seedling abundance, as evidenced by the best approximating model, measuring goodness of fit test using a pseudo-r squared test (based on lowest AIC_c; $r^2m = 0.373$) (Table 5; see also Supplemental Results). Average leaf litter depth (estimation coefficient ± standard errors $= -1.19 \pm 0.434$, $p = 0.006$), total understory cover (-0.803 ± 0.328, $p = 0.014$), and shrub oak small seedling abundance (-0.517 ± 0.239, $p = 0.03$) all showed a negative association with pitch pine small seedling abundance (Fig. 2). A post hoc comparison of treatment types found all treatment types (FallRx, Harvest, MowRx, and SpringRx) were significantly (α=0.05) different from Control, but not from each other (Table 4). Basal area was an important factor in two of the top three models (within 2 ΔAIC_c units of the top model), showing a positive association with small seedling abundance. Pitch pine small seedlings were the most abundant of the pitch pine regeneration categories measured; however, they were only observed in 16.5 % of subplots measured.

3.2. Large seedlings

Pitch pine large seedling abundance was associated with treatment type and average litter depth based on the best approximating model. Average leaf litter depth (estimation coefficient ± standard errors = −0.9013 ± 0.249, $p = 0.0003$) was negatively associated with pitch pine large seedling abundance (Fig. 3). A post hoc comparison of treatment type indicated Harvest units were significantly different (α=0.05) from Control units (Table 4). No other treatment types were significantly different from any other. There were seven models within 2 ΔAIC_c (Table 5). Average litter depth and treatment type were the only effects showing statistically significant relationships with large seedling abundance ($r^2m = 0.137$). The null model was within 6 ΔAIC_c units of the best approximating model indicating the factors investigated did not adequately explain patterns in large seedling abundance. Pitch pine large seedlings were overall not abundant, occurring on 6.4 % of subplots measured.

3.3. Saplings

Pitch pine sapling abundance was strongly associated with the proportion of total basal area in pitch pine as supported by the best approximating model (estimation coefficient ± standard errors = 1.592 ± 0.436, $p = 0.0003$). As the proportion of basal area in pitch pine increased so did the pitch pine sapling abundance (Fig. 4). Ninety-one percent of plots with pitch pine saplings had a minimum of 86 % of their basal area in pitch pine. Conversely, as the number of shrub oak saplings increased (-0.498 ± 0.324, $p = 0.1$), pitch pine sapling abundance decreased. There were seven competing models with the best approximating model in the set (Table 5). The best approximating model explained a low level of variation in pitch pine sapling abundance (adj.

Table 4
Rates (pitch pine stem/average year/unit area) of seedlings by treatment type. Values within a row with different superscripts are different at α= 0.05 level. Small seedling predictions are for 1 m^2 and large seedling predictions are for 10 m^2.

	Control	FallRx	Harvest	MowRx	SpringRx
Small seedling model	0.0001 ± 0.0002^a	0.143 ± 0.098^b	0.096 ± 0.081^b	0.029 ± 0.020^b	0.130 ± 0.094^b
Large seedling model	0.0005 ± 0.001^a	0.009 ± 0.016^{ab}	0.172 ± 0.281^b	0.005 ± 0.009^{ab}	0.010 ± 0.017^{ab}

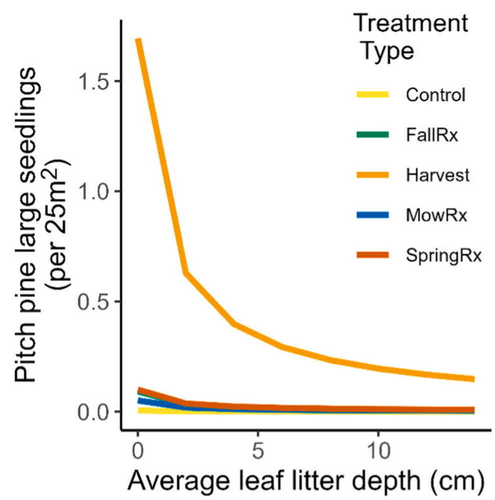

Fig. 3. Pitch pine large seedling response. Pitch pine large seedling abundance was negatively associated with average leaf litter depth. Pitch pine stem counts are corrected for time and represent one year. Harvest units were significantly different from Control units.

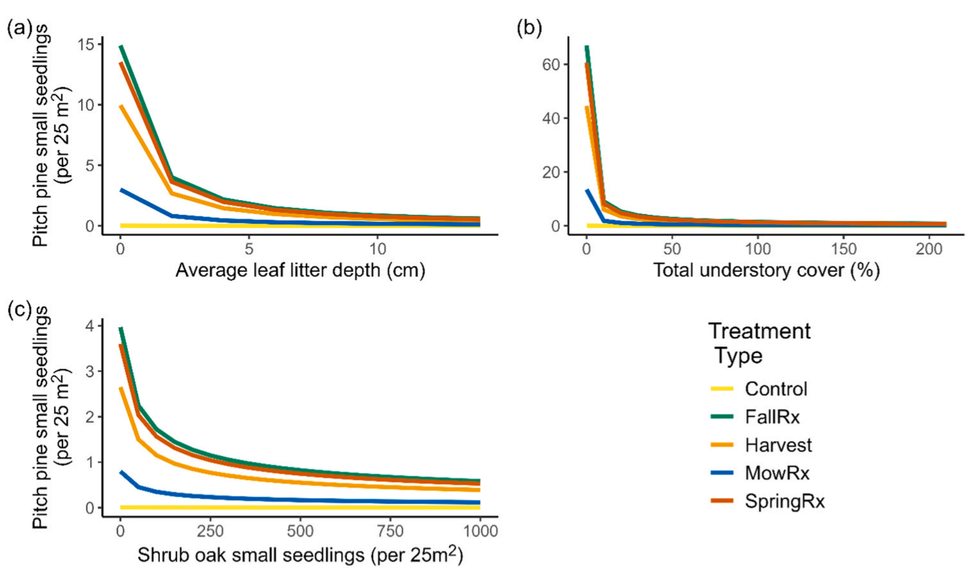

Fig. 2. Pitch pine small seedling response. Pitch pine small seedling abundance is influenced by average leaf litter depth (a), total understory cover (b), and shrub oak small seedling count (c) based on predicted values for the best approximating model. Pitch pine stem counts are corrected for time and represent one year. FallRx, Harvest, MowRx, and SpringRx treatments were all significantly different from Control, though not from each other.

Table 5
Ranking of models relating pitch pine regeneration to seedbed and growing conditions in pitch pine barrens across the northeast offset for time between treatment and sampling. Only the best approximating models and null model are presented. Models with the lowest corrected Akaike information criterion (AIC_c) and Δ_i (difference between model AIC_c and minimum AIC_c) ≤ 2 have the highest support from the data. K represents the total number of model parameters including intercept, variance, offset, random effects, and zero-inflation, where applicable. The weight (w_i) provides information about the likelihood (from 0 to 1, with 1 being the highest) that model *i* is the best supported model in the set. Variables are described in Table 2. * indicates best approximating model.

	Model	K	AIC_c	Δ_i	w_i
Small seedling abundance	−5.2343 – 1.1968xAVGLD – 0.5173xSOSS – 0.8030xVEG + TRTTYP* (6.8805xFallRx+6.4779xHarvest+5.2750xMowRx+6.7833xSpringRx)	8	723.1	0	0.2501
	−6.6845 – 1.5184xAVGLD + 0.5365xBAHA– 0.8116xVEG + TRTTYP (6.9431xFallRx+7.1001xHarvest+5.6162xMowRx+7.0329xSpringRx)	8	724.2	1.19	0.1382
	−9.5515 – 1.5035xAVGLD + 0.5973xBAHA – 0.5617xSOSS + TRTTYP (4.812xFallRx+4.551xHarvest+4.015xMowRx+4.779xSpringRx)	8	724.8	1.71	0.1063
	NULL	4	769.3	46.24	< 0.001
Large seedling abundance	−7.5746 – 1.0610xAVGLD + 0.3289xOTHERLS – 0.3207xSOLS	7	280.8	0	0.0389
	−8.0610 – 1.0979xAVGLD + 0.3107xOTHERLS	6	281.5	0.74	0.0269
	−7.4850–0.2312xERI – 0.8787xAVGLD + 0.3574xOTHERLS – 0.3062xSOLS	8	281.9	1.10	0.0224
	−7.8338 – 0.8426xAVGLD – 0.2900xSOLS + TRTTYP (3.1755xFallRx+5.7653xHarvest+2.8154xMowRx+3.1114xSpringRx)	7	282.4	1.61	0.0174
	−6.9974 – 0.7779xAVGLD – 0.1959xPIRIBA – 0.2867xSOLS	7	282.4	1.63	0.0172
	−7.2607 – 1.2775xAVGLD – 0.1212xMIN + 0.3265xOTHERLS – 0.3258xSOLS	8	282.4	1.63	0.0172
	−7.4781 – 0.7867xAVGLD – 0.1757xBAHA	6	282.7	1.93	0.0148
	−8.0011 – 0.9013xAVGLD + TRTTYP* (2.8946xFallRx+5.8075xHarvest+ 2.2997xMowRx+ 2.9793xSpringRx)	6	282.8	1.97	0.0145
	NULL	4	288.5	7.75	< 0.001
Sapling abundance	−4.5531 + 1.5920xPIRIPROP – 0.4981xSOSA*	7	228.3	0	0.0766
	−4.6435–0.2550xAVGLD + 1.7208xPIRIPROP – 0.5697xSOSA – 0.4294xVEG	9	228.5	0.16	0.0707
	−4.8051–0.4273xOTHERSS+ 1.5679xPIRIPROP – 0.5258xSOSA – 0.4295xVEG	9	228.9	0.61	0.0566
	−4.4720 – 0.2744xAVGLD + 1.7154xPIRIPROP – 0.3797xVEG	8	229.3	0.96	0.0474
	−4.3062 – 0.2513xAVGLD + 1.6312xPIRIPROP	7	229.5	1.12	0.0437
	−4.4765 – 0.2334xERI + 1.5967xPIRIPROP – 0.4980xSOSA	8	229.7	1.34	0.0392
	−4.4947 – 0.4292xOTHERSA + 1.4865xPIRIPROP	7	229.9	1.55	0.0352
	−4.6827 – 0.6894xMIN + 1.5997xPIRIPROP – 0.5007xSOSA	8	230.2	1.87	0.0295
	NULL	5	245.1	16.77	< 0.001

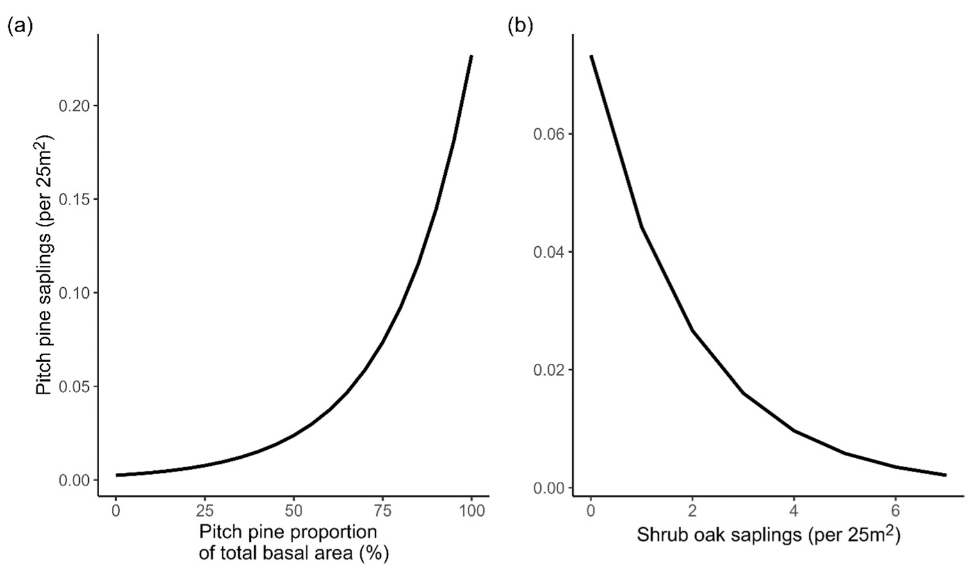

Fig. 4. Pitch pine sapling response. Pitch pine sapling abundance was positively associated with an increase in the proportion of basal area made up by pitch pine (a) and was negatively associated with the number of scrub oak saplings (b). Pitch pine stem counts are corrected for time and represent one year.

$r^2 = 0.021$). Pitch pine saplings were uncommon, occurring in less than 5 % of subplots sampled.

4. Discussion

Restoration of fire-dependent communities after the loss of cultural fire practices and long periods of fire suppression is a complicated effort that is likely to require more than solely the reintroduction of historic disturbance regimes (Suding et al., 2004). These altered communities can persist in alternative states and resist restoration due to species and trophic interactions, changes in landscape connectivity and seed availability, and long-term changes, including global climate change (Suding et al., 2004). Outcomes from this study support a growing body of research that emphasizes the importance of promoting regeneration of fire-dependent tree species as an integral facet of community restoration. Loss of mature pine overstory, whether from ice storms (Yorks and Adams, 2005), overstory removal (Olson, 2011), or novel insect outbreak (Heuss et al., 2019) in areas experiencing historic fire suppression greatly increases the risk of transition to alternative states. Further, multiple treatments are required to negatively impact advance, undesirable regeneration (Arthur et al., 1998; Dey and Hartman, 2005) and success may require more intensive methods, such as the additional application of herbicides (e.g., Bried and Gifford, 2010). Findings from this work further reinforce the need for disturbance, and particularly higher severity disturbance, to facilitate desired natural regeneration in systems with long histories of fire suppression. Previous work has indicated that a minimum of 4450 small pine seedlings per hectare should be a target outcome of restoration activities in pine barrens (Little and Moore, 1950).

Regeneration outcomes from this study provide more support for several previously established conditions determined to be important for pitch pine early regeneration. These include exposure of mineral soil and/or reduction of leaf litter (Little, 1959), reduced shrub oak cover (Boerner, 1981; Landis et al., 2005; Lee et al., 2019), and proportion of pitch pine in the overstory (Little and Moore, 1950). Other factors we documented as important include overall residual basal area and reduced understory vegetation presence. The positive influence of residual basal area on pitch pine regeneration in this study suggests that very low basal area can be a limiting factor for pitch pine survival and growth, relating both to seed source and dispersal limitations (Little, 1959, 1979), as well as an indicator of community structure (e.g., scrub oak shrubland) and subsequent competitive disadvantages to pitch pine regeneration (Landis et al., 2005; Lee et al., 2019). Seedbed conditions with reduced leaf litter depth, understory vegetation, and shrub oak abundance are indicative of areas experiencing higher disturbance severity and/or frequency, with our results indicating that pitch pine regeneration is most successful on these sites. Given the limited duration of these conditions following disturbance in these communities (Bried and Gifford, 2010; Bried et al., 2014; Lougee, 2015), there appears to be small, transient windows for regeneration success before litter depth increases and understory competition develops from resprouting and other mechanisms.

Litter depth and composition, along with increased shade and moisture in forest understories, has emerged as a limiting factor in other communities following fire suppression. Much like pitch pine barrens, fire suppression and loss of cultural fire has created denser forests with more mesophytic hardwoods in eastern oak and oak-pine systems. These mesophytic species change understory conditions, creating thick leaf litter, dense shade, and high moisture (Nowacki and Abrams, 2008; Brose et al., 2013). These changes in understory conditions act as a barrier to germination and establishment in oak, just as for pitch pine. Similar to pitch pine barrens, overstory disturbance in oak communities without established desirable regeneration present can accelerate community transition to alternative states (Nowacki and Abrams, 2008; Dey, 2014). Retention and spatial heterogeneity of trees can impact resource availability (cf. Palik et al., 2003), including light and soil nutrients, and subsequent patterns of regeneration, growth, and species diversity. In other fire-dependent, woodland systems, the impact of small increases in vegetation on light availability in open conditions was found to be exponentially larger compared to closed conditions (Boyden et al., 2012), indicating that the impacts of spatial heterogeneity may be more significant in woodland and barrens conditions than in closed canopy conditions. Resource availability and the ameliorating effects, like heat and moisture, of mature trees on understory conditions may explain the importance of areas of higher basal area to pitch pine regeneration. The effect of ericaceous cover was investigated but showed no clear and direct correlation with regeneration in this study; however, we did not investigate the composition and chemical qualities of leaf litter to develop a causal linkage with inhibition of regeneration or recruitment, which could benefit from further study (e.g., Garnett et al., 2004).

The abundance of small and large pitch pine seedlings was affected by the type of treatment applied in a given area. For small seedlings, Harvest, FallRx, MowRx, and SpringRx units all had more pitch pine seedlings than Control units, although regeneration abundance under these four treatments types did not differ significantly from each other. For large seedlings, only Harvest units differed significantly from Control units. Examining this relationship more closely, two Harvest units in Massachusetts accounted for 70.5 % of all pitch pine large seedlings recorded during the study, with 58 % occurring on subplots with exposed mineral soil. Due to the relatively low frequency and amount of exposed mineral soil recorded across treatment units (only 8 % of subplots had >1 % exposure), it was not an important predictor in modeling; however, mineral soil exposure is still a valuable ecological indicator of suitable seedbed and regeneration conditions for pitch pine. The lack of treatment effect on pitch pine sapling abundance was likely due to the timeframe of the study, which sampled areas that had experienced treatment within the last seven years, with 64 % of units treated within four years of sampling. Given the time it takes to recruit into the sapling layer, it is more likely that the pitch pine saplings we documented resulted from earlier disturbance events than those examined by this study. As all treatment types were not available in all regions, the unbalanced nature of this study may also have impacted our ability to detect differences between treatment types.

No single treatment was superior in recruiting pitch pine, indicating that many management approaches can create conditions favorable for pitch pine regeneration. Leaf litter depth and exposed mineral soil can be altered both by fire (e.g., smoldering, repeat prescribed fire) and mechanical (e.g., harvesting, mowing, bulldozing) means. Mastication can also be used prior to fire to increase levels of smoldering (Kreye et al., 2014). Both of these treatments can also reduce or remove understory vegetation, increasing mortality and slowing recovery for competing re-sprouting species (Hawver et al., 2023).

Prescribed fire has been used in some regions of this study since the mid-1990s; however, it is not wholly equivalent to historic fire, generally being more homogeneous due to altered fuel loading and ignition sources, resulting in reduced pyro-diversity, structural complexity, and refugia (Ryan et al., 2013). Nor does it necessarily occur in the same seasons or with the same frequency or intensity as historic fire (Ryan et al., 2013). Prescribed fire can be less severe than wildfire, leaving more of the humus layer intact (Boerner, 1981). The application and impact of prescribed fire is further affected by the development and fragmentation of fire-dependent ecosystems, along with social norms and preferences (Ryan et al., 2013). As a result, other treatments, including harvesting/thinning, mechanical treatments, and herbicides, are often used as part of pine barren restoration activities. Some of these fire alternatives, like mechanical treatments, can facilitate the creation of favorable seedbeds and regeneration conditions for pitch pine; however, they are not a perfect surrogate for fire and the long-term implications of their use are unknown. In particular, fire changes soil moisture, temperature, pH, ectomycorrhizal communities, and nutrient availability and can have a fertilizing effect, creating a pulse release of nutrients utilized by vegetation in burned sites (Tuininga and Dighton, 2004). Even low-intensity fires provide noticeable fertilizing effects in nutrient-poor sites (Tuininga and Dighton, 2004), such as those examined in this study.

Successful regeneration of desired species in pitch pine barrens is important to increase adaptive capacity within these landscapes. Promotion of multiple size classes can diversify possible recovery pathways following disturbance events, including SPB outbreaks. Creating or maintaining pyro-diversity at the unit and landscape scale is also important for forest structure and adaptive capacity, creating refugia and maintaining a coarse-grained landscape mosaic (Jordan et al., 2003; Ryan et al., 2013; Jamison et al., 2023). Reducing or maintaining lower basal area (<15 m^2; Jamison et al., 2022) in stands may reduce risk of SPB infestations and increase landscape scale resilience. This does not appear to be at odds with the needs of regeneration for adequate residual basal area, as no clear lower limit for basal area and pitch pine regeneration success could be identified in this study. Successful restoration of pitch pine barrens depends on the creation of an adaptive and future-oriented framework (Choi, 2007; Seastedt et al., 2008), which also takes into consideration the inherent long-term commitments of this work. Restoration is a cultural, ecological, and economic enterprise steeped in social value (Choi, 2007). Understanding of current conditions and future uncertainties, along with clear communication about values, by all stakeholders is necessary for effective management in an unprecedented future (Seastedt et al., 2008). This work, although observational in nature, highlighted multiple pathways to adaptively manage barrens to sustain future options for pitch pine, especially those management alternatives beyond the application of fire, which often faces more social and regulatory scrutiny. Future work that specifically tests the influence of seasonality and frequency of restoration treatments will be valuable to further refine recommendations for pitch pine regeneration in these communities.

CRediT authorship contribution statement

Dodds Kevin J.: Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **D'Amato Anthony W.:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization. **Stutzman Kathleen A:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122547.

Data availability

Data will be made available on request.

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