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Describing a landscape mosaic: Forest structure and composition across community types and management regimes in inland northeastern pitch pine barrens

Elizabeth-Ann K. Jamison [a,*], Anthony W. D'Amato [a], Kevin J. Dodds [b]

[a] Rubenstein School of Environment and Natural Resources, University of Vermont, Aiken Center, 81 Carrigan Drive, Burlington, VT 05405, United States
[b] USDA Forest Service, Northeastern Area State & Private Forestry, 271 Mast Rd, Durham, NH 03824, United States

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ABSTRACT

Pitch pine (*Pinus rigida* Mill.) barrens are a globally rare, fire-dependent ecosystem of great ecological, social, and cultural significance found primarily in the northeastern US. In many cases, fire has been excluded from these systems leading to habitat degradation and biodiversity loss as pine barrens landscapes homogenize into closed-canopy forests of shade-tolerant, mesophytic species. This study aims to support the adaptive management of pine barrens ecosystems in the face of mesophication by contributing baseline information on their structure and composition. Specifically, we (1) assessed how stand conditions differ between community types and management strategies at the two sites and (2) placed this work in the broader context of pine barrens ecology and management. We sampled overstory structure and composition across five community types (successional northern sandplain grasslands, pitch pine-scrub oak barrens, pitch pine-scrub oak thicket, pitch pine-scrub oak woodland, and pitch pine-oak forest) and four management strategies (burning, thinning, burning and thinning, and no management). Differences in structure and composition between communities supported the concept of pine barrens as a landscape mosaic maintained by multiple unique disturbance regimes. Results suggest that burning, thinning, and their combination are all effective in maintaining conditions historically associated with pine barrens communities, and that a lack of active management may lead to a transition away from these characteristics. The range of pine barrens conditions documented in this and previous studies underscores the importance of management regimes that utilize a diversity of treatments applied at frequencies and intensities consistent with historic disturbance regimes for each pitch pine community type. Such strategies would maintain the mosaic of habitat conditions required to support the suite of species endemic to these communities, and would confer resilience to emerging stressors, such as southern pine beetle (*Dendroctonus frontalis*), which often generates greatest impacts in unmanaged, homogeneous forests.

1. Introduction

Many of the world's terrestrial ecosystems are influenced by fire, and those with long histories of repeated fire often exhibit exceptionally high species richness and endemism (He et al., 2019). From Siberia's taiga forests to the eucalyptus forests of Australia, fire is a major ecological and evolutionary force that operates across spatiotemporal scales to drive patterns in biodiversity (Hardesty et al., 2005; He et al., 2019; Pausas et al., 2017). Fire regimes (fire interval, intensity, size, seasonality, and spread) affect plant community structure and composition (Bond et al., 2005; He et al., 2019; Pausas and Keeley, 2009) and are, in turn, affected by edaphic and climatic factors; a process which forms a complex feedback network between fire, vegetation, biogeochemistry, and climate (Archibald et al., 2018; Krawchuk and Moritz, 2011; Rogers et al., 2015). This cycle reinforces site-specific ecological, environmental, and fire characteristics and creates a global landscape mosaic (He et al., 2019).

Changes to fire regimes have become a global conservation issue (Hardesty et al., 2005). Many unique fire-dependent savannas, grasslands, shrublands, barrens, and woodlands around the world are experiencing degradation and biodiversity loss as a result of fire exclusion or suppression (Durigan and Ratter, 2016; Scheller et al., 2005). This results from a multitude of factors, including the removal of Indigenous people and their land management practices from these systems

* Corresponding author.
E-mail address: elizabethjamison5@gmail.com (E.-A.K. Jamison).

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(Christianson et al., 2022; Kimmerer and Lake, 2001), expansion of the wildland urban interface, lack of effective fire management, and concerns among the public and decision-makers about fire escape and smoke mitigation (Black et al., 2020; Durigan and Ratter, 2016; Knowlton, 2013; van Wagtendonk, 2007). These factors are magnified by lower levels of research and conservation interest and engagement in restoring fire-dependent ecosystems, particularly grasslands and savannas (Bond and Parr, 2010).

One fire-dependent ecosystem of great ecological, social, and cultural significance is the pitch pine (*Pinus rigida* Mill.) barrens of the northeastern United States. This ecosystem occurs on sandy, nutrient poor soils along the Atlantic Coast from New Jersey to Maine and inland throughout the northeastern US. It is a biodiverse mosaic of barrens, woodland, wetland, shrubland, and grassland communities that are broadly referred to as “pine barrens”. (Bried et al., 2014; Edinger et al., 2014). Pitch pine and oaks (*Quercus rubra* L., *Q. velutina* Lam., *Q. coccinea* Münchh., or *Q. alba* L.) are the dominant tree species which grow in variable proportions and densities over understories of scrub oak (*Quercus ilicifolia* Wang.), heath shrubs, and grasses (Edinger et al., 2014; Jordan et al., 2003). Relative to other forest types and regions of the northeastern US, pitch pine barrens historically experienced fairly frequent landscape- and stand-scale fire and wind events resulting in a comparatively greater amount of young and open woodland conditions in these areas (Lorimer and White, 2003). These early-successional communities provide habitat for many rare and declining wildlife species, including the endangered Karner blue butterfly (*Lycaeides melissa samuelis*), the pine barrens treefrog (*Hyla andersonii*), and shrubland bird species like the prairie warbler (*Setophaga discolor*) (Bried and Gifford, 2010; Gifford et al., 2010; NJFAC, 2006). As such, there is considerable interest in generating management strategies that can maintain these historic barrens conditions and associated species (Bried et al., 2014).

Pitch pine is a highly fire-adapted species with thick insulating bark, semi-serotinous cones, and the ability to epicormically sprout (Gucker, 2007; Jordan et al., 2003). Fire is critical for pitch pine regeneration, as it is a shade intolerant species that requires bare mineral soil for germination (Lee et al., 2019; Little and Garrett, 1990). In the absence of fire, organic material accumulates, pitch pine loses dominance, and pine barrens convert to closed canopy mesic forest through successional replacement by longer-lived oaks and less fire-adapted species like red maple (*Acer rubrum* L.) or white pine (*Pinus strobus* L.) (Forman and Boerner, 1981; Howard et al., 2011; Jordan et al., 2003; Kurczewski and Boyle, 2000; Milne, 1985; Scheller et al., 2008; Seischab and Bernard, 1991). This process of “mesophication” is consistent with patterns documented with the cessation of fire in other temperate fire-dependent communities (Nowacki and Abrams, 2008). Loss of overstory pitch pine to emerging stressors, such as the northward expansion of southern pine beetle (*Dendroctonus frontalis* Zimmermann; Lesk et al., 2017), has accelerated these trends, as hardwood species now largely dominate areas impacted by this insect (Heuss et al., 2019). As a result, management strategies focused on restoring and maintaining historical pine barrens conditions are now not only viewed as critical to achieving biodiversity objectives, but also for increasing resilience to this emerging threat (Dodds et al., 2018; Jamison et al., 2022).

As with many other fire-dependent ecosystems, the primary strategies used to maintain and restore pine barrens communities rely on prescribed burning and thinning in combination with mowing and/or herbicide treatment to mimic historic disturbance regimes (Bried et al., 2015, 2014,2011; Bried and Gifford, 2010; Gifford et al., 2010; Howard et al., 2011; Jordan et al., 2003). Despite the proven effectiveness of these approaches, substantial economic, operational, and social obstacles exist to their implementation due to a lack of local markets for low-quality wood (Dodds et al., 2018), public resistance to forest management practices in an expanding wildland-urban interface (Blanchard and Ryan, 2007; Radeloff et al., 2005; Ryan, 2012), and complex impacts of climate change (Kretchun et al., 2014; Lesk et al., 2017; Li and Waller, 2017; Lucash et al., 2014). As such, there is a need for a greater understanding of how these systems are changing with and without active management to guide, improve, and support adaptation strategies (Alagona et al., 2012; Manning et al., 2011; Wortley et al., 2013).

This study aims to support the adaptive management of pine barrens ecosystems in the face of emerging stressors and management obstacles that accelerate ecosystem loss to mesophication. Specifically, our objective is to add to current day information available on the structure and composition of northeastern pitch pine barrens by (1) assessing how stand conditions differ between community types and management strategies in two large, inland pitch pine barrens (Albany Pine Bush, New York and Ossipee Pine Barrens, New Hampshire) and (2) placing this work in the broader context of pine barrens ecology and management. Rather than implying that pine barrens ecosystems should be managed to maintain or create characteristics documented in this paper, we present a snapshot of present-day communities that have resulted from known management and site histories. This information can assist future conservation initiatives in identifying communities in danger of being lost, generating benchmarks for management, and ensuring that management achieves desired outcomes.

2. Materials and methods

2.1. Study area and design

The Albany Pine Bush (APB) in New York (NY) and the Ossipee Pine Barrens (OPB) in New Hampshire (NH) were selected as study sites because they are two of the northernmost examples of pitch pine barrens that have not been altered by southern pine beetle in species composition or stand structure (Dodds et al., 2018). The APB and OPB are representative of other northeastern pitch pine barrens, forming on nutrient-poor, well-to-excessively drained sand deposits that have been heavily impacted by past land use (Motzkin et al., 1999). Additionally, once considered wastelands, these barrens have become increasing attractive for residential, commercial, and industrial development (Barnes, 2003), which amplifies threats of land conversion, fire suppression, and habitat fragmentation (APBPC, 2017; Lougee, 2015). Consistent with other pine barrens, the APB and OPB support rare and endangered butterflies, moths, birds, amphibians, reptiles, and plant assemblages and are managed with conservation and restoration objectives (APBPC, 2017; Lougee, 2015).

Existing spatial data provided from each site were used to select stands for sampling. The intent was to capture a variety of community types (classifications were given by land managers and from Edinger et al., 2014), including (1) successional northern sandplain grasslands, (2) pitch pine-scrub oak barrens, (3) pitch pine-scrub oak thicket, (4) pitch pine-scrub oak woodland, and (5) pitch pine-oak forest (Table 1). Communities of similar structure dominated by pitch pine, oak, red maple, and white pine were grouped into the “pitch pine-oak forest” community type. Sample stands were also distributed across four different management strategies including (1) burned, (2) thinned, (3) burned and thinned, and (4) no management. Mowing is commonly used to support burning and thinning operations at both the APB and OPB and was therefore not specified as a management strategy on its own, but was part of the overall management regime occurring in these management types. A total of 75 stands were sampled (50 in the APB and 25 in the OPB), but community types or management strategies with too few replications were excluded from analysis. In total, 69 stands (49 in the APB and 20 in the OPB) were assessed (Fig. 1, Fig. 2, Table 1).

2.2. Field methods

Field work was conducted at the APB and OPB from June - August 2020. Within sample stands, three 400 m^2 fixed-radius plots were randomly established with a distance of at least 40 m between plot centers. Species, status (live or snag), crown class (dominant, codominant, intermediate, or suppressed), and diameter at breast height (DBH;

Table 1
Pine barrens community types and management strategies in sample stands at the Albany Pine Bush (APB) and the Ossipee Pine Barrens (OPB). Community type absence is indicated with "na".

Community type	Burned		Thinned		Burned and thinned		Unmanaged		Community total	
	APB	OPB	APB	OPB	APB	OPB	APB	OPB	APB	OPB
Successional northern sandplain grassland	2	na	0	na	1	na	0	na	*3*	*na*
Pitch pine-scrub oak thicket	5	0	0	1	2	1	0	0	*7*	*2*
Pitch pine-scrub oak barrens	8	na	1	na	12	na	0	na	*21*	*na*
Pitch pine-scrub oak woodland	na	3	na	2	na	5	na	4	*na*	*14*
Pitch pine-oak forest	8	0	2	0	2	2	6	2	*18*	*4*
Management total	*23*	*3*	*3*	*3*	*17*	*8*	*6*	*6*	***49***	***20***

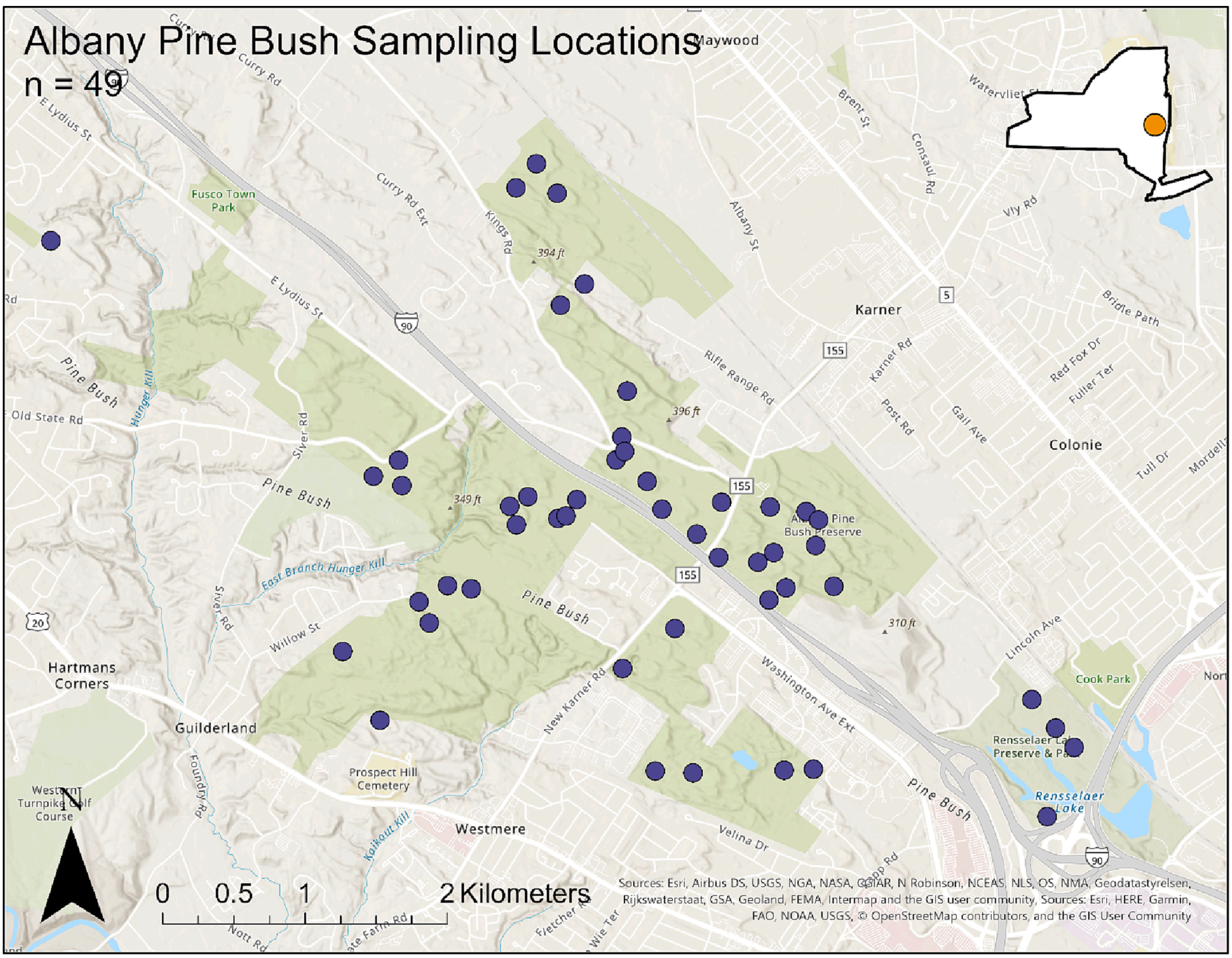

Fig. 1. Map of sampling locations at the Albany Pine Bush in New York, USA.

1.37 m) were recorded for every living tree and snag >7.5 cm in diameter occurring within these plots to characterize patterns in overstory structure and composition.

2.3. Statistical analyses

Statistical analyses were conducted in R (R Core Team, 2021). Following Janowiak et al. (2008), size class distributions characterizing each community were assessed by regressing the base 10 logarithm of trees per hectare (TPHA) across all combinations of three variables that represented 5-cm diameter class midpoints: DBH, DBH^2, and DBH^3 (*stats* package; *glm* function) (R Core Team, 2021). The combination with the highest adjusted R^2 and the lowest residual standard error was selected as the optimal model. Size class distribution shapes were then assigned based on the variables included in the optimal model and the sign of their coefficients (Janowiak et al., 2008).

The *vegan* package in R was used to run a series of multivariate analyses on forest compositional and structural conditions across management strategies and community types. Nonmetric multidimensional scaling (NMDS; *metaMDS* function) was used to examine gradients in structure and composition across management strategies and community types (Kenkel and Orloci, 1986). The analysis was run on a Bray-Curtis dissimilarity matrix of key pine barrens conditions (Howard et al., 2011) that were averaged at the site level and square root transformed to minimize the effect of large values on the overall ordination solution. The 12 structural and compositional conditions included in the

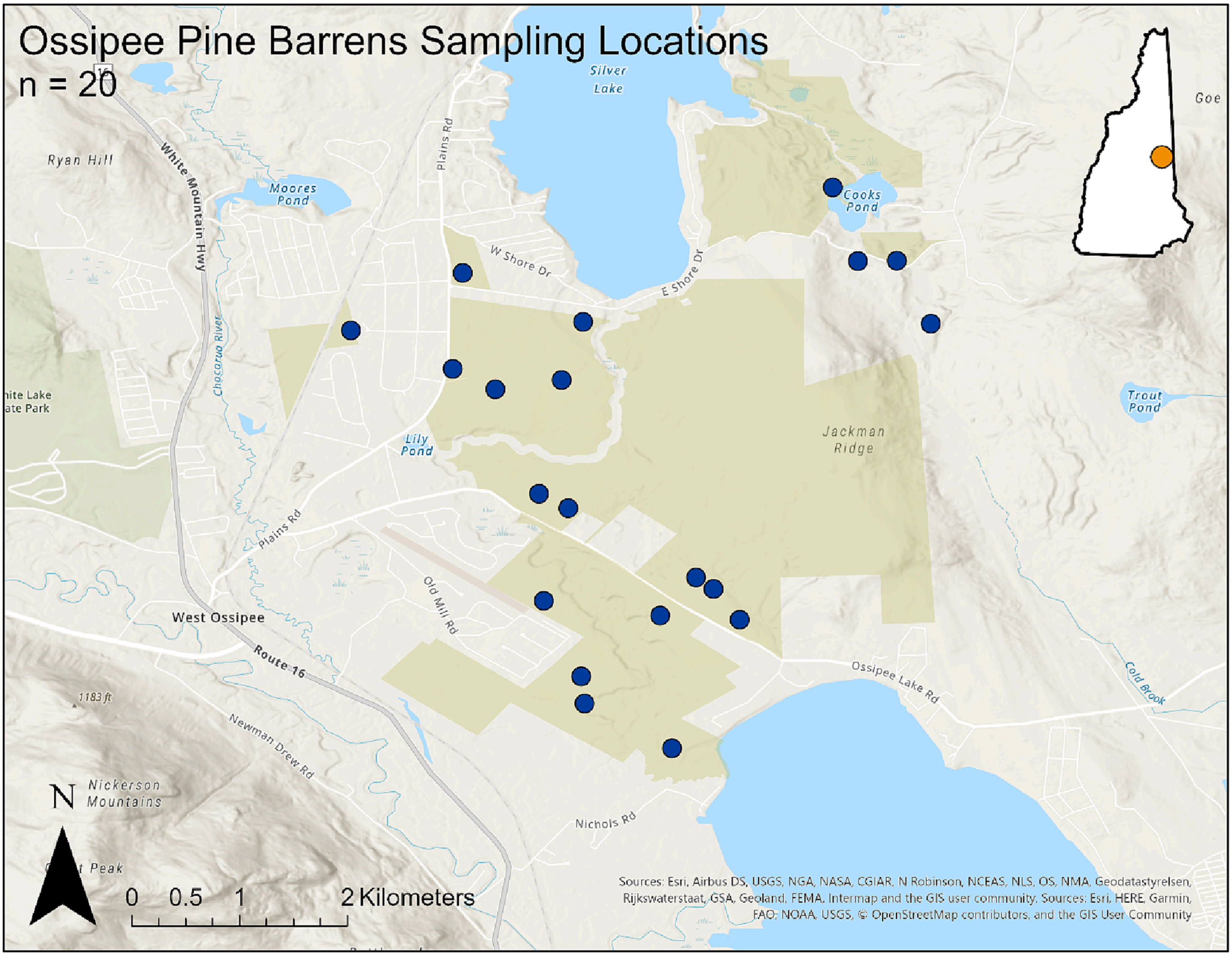

Fig. 2. Map of sampling locations at the Ossipee Pine Barrens in New Hampshire, USA.

analysis were (1) basal area of pitch pine, (2) basal area of white pine, (3) basal area of oak, (4) basal area of red maple, (5) total basal area of hardwoods, (6) stand basal area, (7) TPHA, (8) proportional basal area of pitch pine, (9) proportional basal area of pine, (10) quadratic mean diameter (QMD), (11) proportion of trees >40 cm in diameter, and (12) the standard deviation of basal areas in each of the three plots (Howard et al., 2011). To assess the contribution of each stand condition to the ordination structure, we used the *envfit* function, which calculates vector loadings on NMDS axes for each stand condition (equivalent to vector direction cosines), performs rank correlations between loadings and NMDS axis scores, and assesses statistical significance using a permutation test with 999 permutations. The resulting vectors indicate direction of increasing stand condition values and correlation strength with axis scores (vector length is scaled by R^2 values). The ordination was rotated so that the proportion pitch pine vector runs along NMDS1 in the positive direction.

We used permutational multivariate analysis of variance (PERMANOVA; *adonis* function) to test if stand structure and composition differed between management strategy and community groups or their interaction (Anderson, 2001). The analysis was performed on the same dissimilarity matrix used for our NMDS and was based on 999 permutations. Statistical significance was determined at $\alpha = 0.05$ and the *betadisper* function (an analogue to the Levene's test) confirmed the assumption of homogeneity of variances. Lastly, pairwise PERMANOVA tests were used to evaluate differences in stand structure between management strategy and community pairs. Bonferroni-corrected significance levels were adjusted for multiple comparisons.

3. Results

3.1. Stand density and tree size distributions

The five sampled natural communities can broadly be divided into two groups based on level of canopy closure and tree density: the pitch pine-oak forest and pitch pine-scrub oak woodland form a more closed canopy group (which contains the only unmanaged stands) and the pitch pine-scrub oak barrens, pitch pine-scrub oak thicket, and successional northern sandplain grasslands form a more open canopy group (all of which were actively managed). The closed canopy group had a higher mean basal area and TPHA, but a lower QMD than the open canopy group (Appendix A.1). Size class distribution patterns were right-skewed in the closed canopy group and bell-shaped in the open canopy group (Fig. 3, Fig. 4). Consistent with these trends, unmanaged stands exhibited higher stand basal area and TPHA, and lower QMD and proportion pitch pine than actively managed stands (Appendix A.2). Furthermore, unmanaged stands had a right-skewed diameter distribution while actively managed stands had a bell-shaped diameter distribution (Fig. 5).

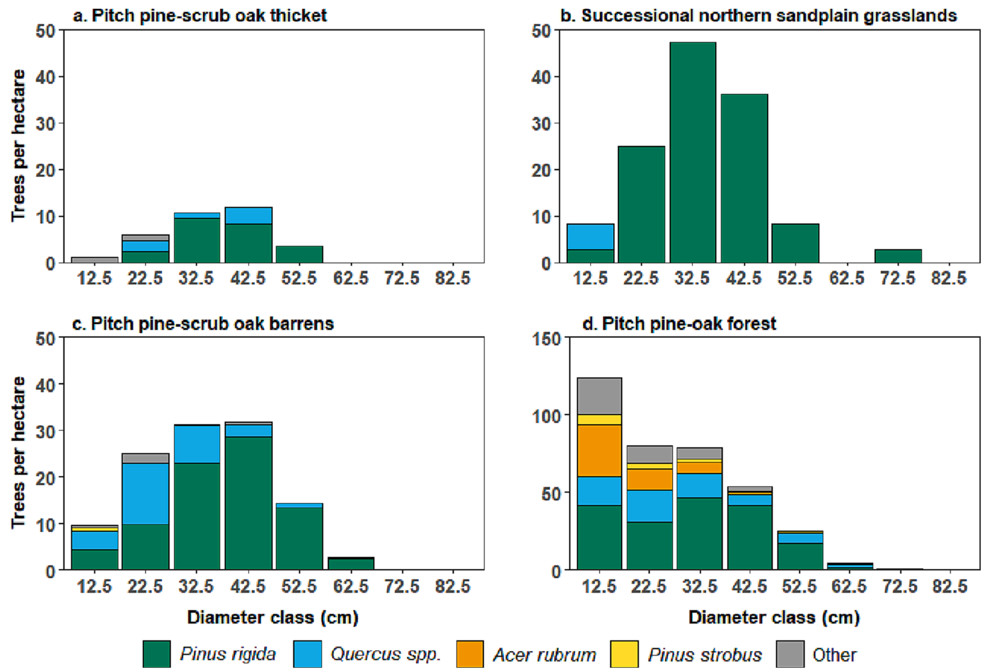

Fig. 3. Size class distributions of the four pine barrens communities sampled in the Albany Pine Bush: (a) pitch pine-scrub oak thicket, (b) successional northern sandplain grasslands, (c) pitch pine-scrub oak barrens, and (d) pitch pine-oak forest. Size class bins are 10 cm. Trees per hectare values are averaged across sample stands.

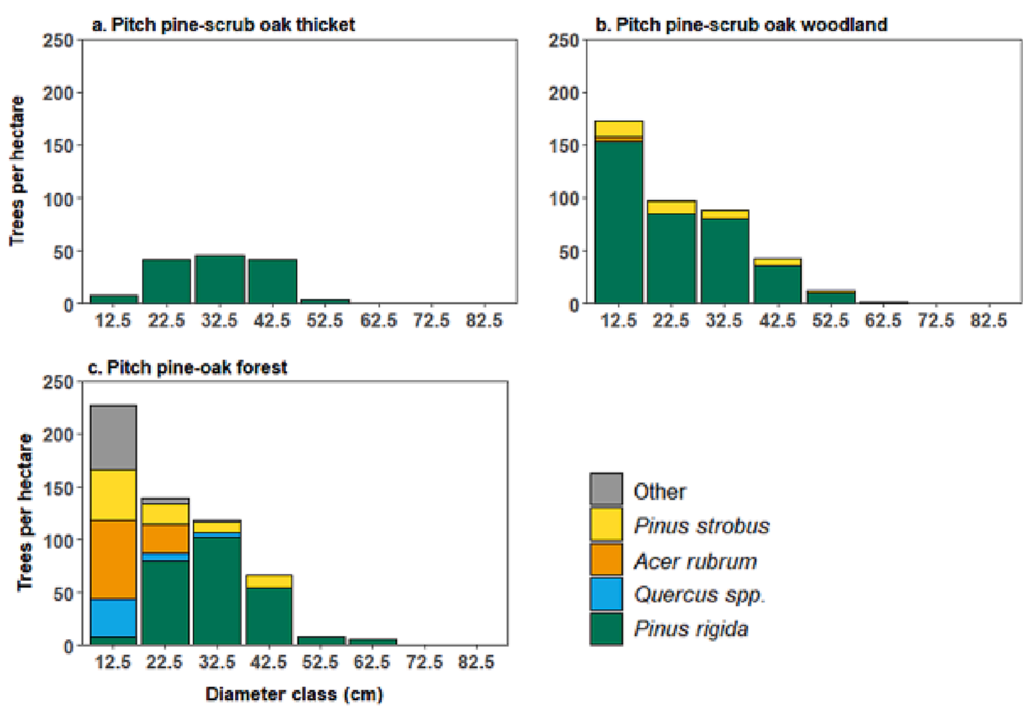

Fig. 4. Size class distributions of the three pine barrens communities sampled in the Ossipee Pine Barrens: (a) pitch pine-scrub oak thicket, (b) pitch pine-scrub oak woodland, and (c) pitch pine-oak forest. Size class bins are 10 cm. Trees per hectare values are averaged across sample stands.

3.2. Compositional and structural conditions across community types and management regimes

Forest structure and composition differed significantly between community types (PERMANOVA $p = 0.001$) and management strategies (PERMANOVA $p = 0.001$), but there was not an interaction between these factors (PERMANOVA $p = 0.068$, Table 2).

Pairwise PERMANOVA indicated significant differences between six community pairs: (1) pitch pine-oak forest, (2) pitch pine-scrub oak thicket, and (3) pitch pine-scrub oak barrens all differed from each other; pitch pine-scrub oak woodland differed from (4) pitch pine-scrub oak thicket and (5) pitch pine-scrub oak barrens; and (6) successional northern sandplain grasslands differed from pitch pine-oak forest (Appendix A.3). These distinctions were illustrated by the separation between community types in the NMDS ordination space (stress = 0.101, Fig. 6). Forests and thickets were located in opposing portions of

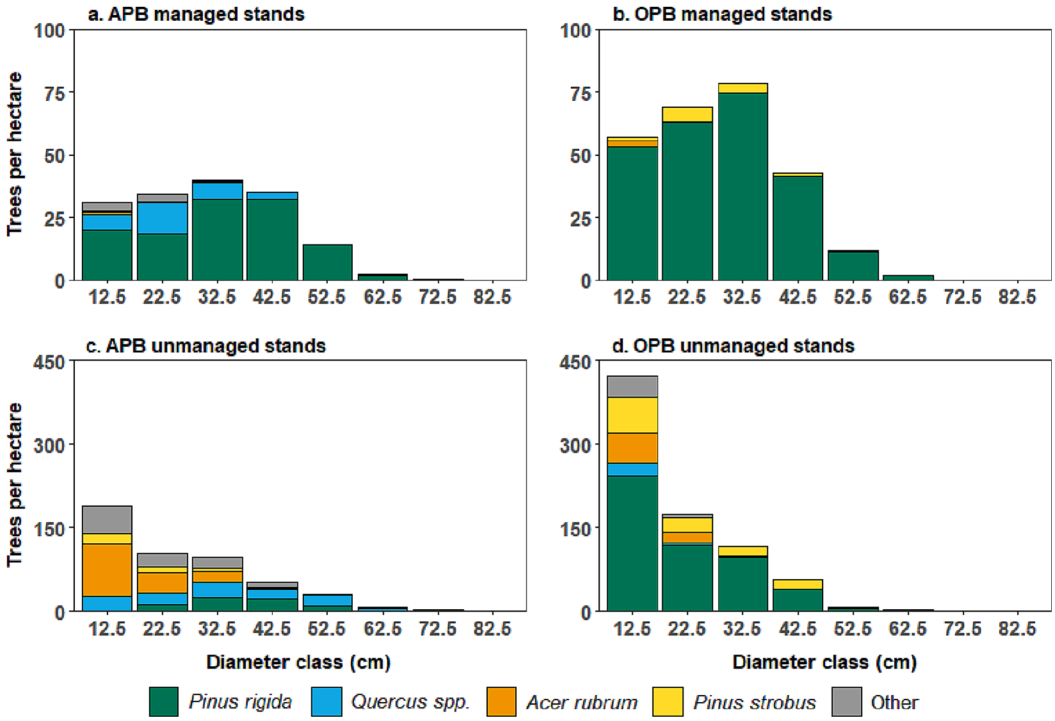

Fig. 5. Size class distributions of actively managed (a, b) and unmanaged stands (c, d) in the Albany Pine Bush (APB; a, c) and the Ossipee Pine Barrens (OPB; b, d). Size class bins are 10 cm. Trees per hectare values are averaged across sample stands.

Table 2
PERMANOVA results for overstory conditions in the Albany Pine Bush and Ossipee Pine Barrens by community type, management strategy, and site groupings. Analysis was performed on a Bray-Curtis dissimilarity matrix using 999 permutations. Significant values (*) are based on α = 0.05.

Group	DF	SS	F	R^2	*p*
Community type	4	0.77	15.16	0.31	0.001*
Management strategy	3	0.81	21.20	0.32	0.001*
Site (APB or OPB)	1	0.08	6.26	0.03	0.011*
Management × community	8	0.15	1.45	0.06	0.126
Community × site	1	0.02	1.45	0.01	0.214
Management × site	1	0.03	2.22	0.01	0.124

the ordination; forests in the bottom left quadrant (characterized by high hardwood and red maple basal area), and thickets in the upper right quadrant (characterized by high QMD and proportion pitch pine; Fig. 6). Forests overlapped with woodlands in the bottom right quadrant (associated with high pitch pine basal area) and with barrens in the upper left quadrant (characterized by high QMD and oak basal area). Thickets also overlapped with woodlands and barrens and were localized further in the portions of the ordination associated with high QMD and/or proportion pitch pine. The sample size of grasslands was not large enough to generate a hull, but the three points for these communities were contained within the hulls of barrens, thickets, and woodlands.

There were significant differences in overstory characteristics between actively managed stands (stands treated with prescribed fire, thinning, or a combination) and unmanaged stands (stands that received no active management; PERMANOVA $p = 0.006$) but not between different active management strategies (Appendix A.4). This was evident in the separation of actively managed and unmanaged groups in the NMDS ordination space, and the general overlap between all active management strategies (Fig. 7). Actively managed stands were localized in the top half of the ordination (associated with high QMD) while unmanaged stands were localized in the bottom half of the ordination (associated with high stand basal area). Actively managed stands also tended to have a higher proportional pitch pine basal area than unmanaged stands, which had more hardwoods, red maple, and white pine.

4. Discussion

4.1. Succession of pine barrens communities

Pitch pine communities have been organized into successional stages, some more transient than others, which are dependent on specific environmental and anthropogenic disturbances and the interaction of disturbance with site conditions (Jordan et al., 2003). Although we did not assess pitch pine communities or disturbance regimes at such fine scales, the diversity of overstory characteristics observed in this study suggest that pitch pine communities at the APB and OPB align with this previously described successional trajectory (presented as a conceptual diagram in Fig. 8). The successional northern sandplain grasslands community is the earliest successional variant of inland pine barrens (APBPC, 2017) and has been described as a transient, short-lived state that relies on frequent fire and/or mechanical removal of woody plants to persist (Edinger et al., 2014). In the absence of frequent fire, grasslands transition to pitch pine-scrub oak barrens and pitch pine-scrub oak thicket, which are similar community types maintained by fire every 6–15 years, but thickets contain tall, dense shrubs presumably due to lower fire frequencies (Bried and Gifford, 2010, 2008). Under a fire return interval of 20–40 years (Jordan et al., 2003), barrens and thicket progress to the pitch pine-scrub oak woodland community, with these communities exhibiting a greater tree density (NHESP, 2007). Pitch pine-oak forests are the latest successional stage we sampled. This community type represent conditions developing under relatively low disturbance, allowing for increases in tree density and oak dominance (Buell and Cantlon, 1950; Good and Good, 1984; Parshall et al., 2003). Such conditions were historically maintained by a moderate intensity fire interval of 40–200 years or a low intensity fire interval of 5–40 years (Jordan et al., 2003). At the OPB, the dominance of less pyrophilic species such as white pine and red maple suggest these systems are in a

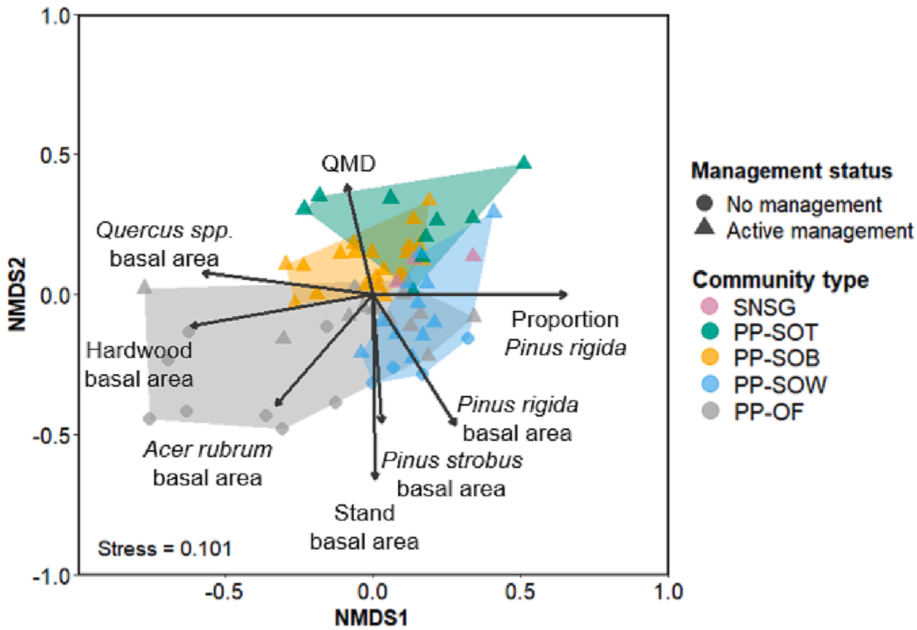

Fig. 6. Nonmetric multidimensional scaling ordination based on stand-level composition and structure in the Albany Pine Bush and the Ossipee Pine Barrens. Hulls delineate community type and point shape depicts the management status of the stand. Vectors represent stand conditions with unique and significant loadings with vector direction indicating increasing stand condition value and vector length indicating correlation with axis scores (R^2 value). PP-OF = pitch pine-oak forest. PP-SOB = pitch pine-scrub oak barrens. PP-SOT = pitch pine-scrub oak thicket. PP-SOW = pitch pine-scrub oak woodland. SNSG = successional northern sandplain grasslands.

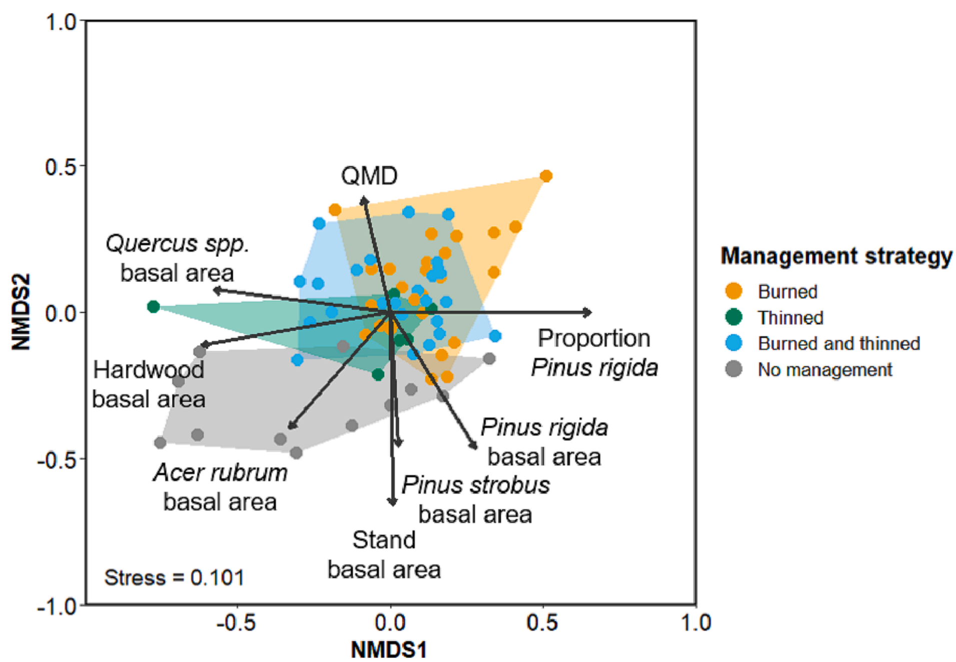

Fig. 7. Nonmetric multidimensional scaling ordination based on stand-level composition and structure in the Albany Pine Bush and the Ossipee Pine Barrens. Hulls delineate management strategy. Vectors (from *envfit* function) are stand conditions with unique and significant loadings. Vector direction indicates increasing stand condition value and vector length indicates correlation with axis scores (R^2 value).

later successional state than those at the APB (Howard et al., 2011; Palus et al., 2018). The general tendency of pine barrens systems to transition to closed canopy systems dominated by less fire-adapted species over time underscores the importance of restoring disturbance if maintenance of the full range of barrens conditions is a conservation goal.

The distinction between unmanaged and actively managed pitch pine-oak forests at both the APB and the OPB further demonstrates the successional trend of pine barrens communities. Relative to their actively managed counterparts, unmanaged pitch pine-oak forests had greater tree densities dominated by less pyrophilic species (oak, red maple, white pine, and others) with remaining highly pyrophilic pitch pine concentrated in large size classes. These findings are consistent with previous research that has shown pitch pine-oak communities transition to dense forests dominated by less fire-adapted species in the absence of disturbance (Alexander et al., 2021; Forman and Boerner, 1981; Howard et al., 2011; Jordan et al., 2003; Kurczewski and Boyle, 2000; Milne, 1985; Palus et al., 2018; Scheller et al., 2008; Seischab and Bernard, 1991). As this transition proceeds, it becomes increasingly difficult to reintroduce fire due to the accumulation of mesophytic litter and the establishment of a cool, moist microclimate which decrease flammability (Nowacki and Abrams, 2008).

Consistent with the patterns we documented, many formerly open-canopy, fire-dependent communities in the eastern United States have transitioned to closed-canopy forests of shade-tolerant, fire-sensitive

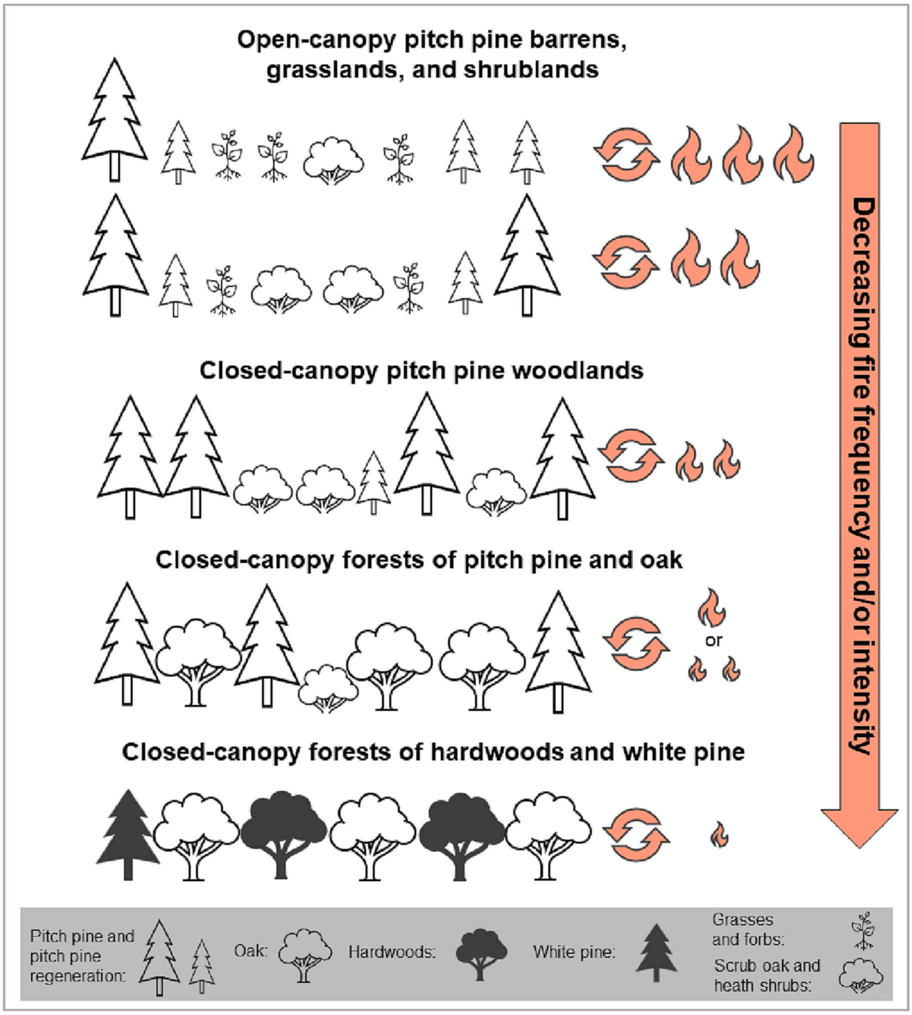

Fig. 8. Conceptual diagram of ecological succession in northeastern pitch pine-dominated communities under different disturbance regimes. Circular arrows indicate a disturbance regime that maintains a community type, while the large downward arrow shows the direction of succession as fire frequency and/or intensity decreases. The number of fire symbols corresponds to fire frequency and the size of fire symbols corresponds to fire intensity. Adapted from Jordan et al. (2003).

plants (Bried et al., 2014; Nowacki and Abrams, 2008). This trend has been referred to as "mesophication": a positive-feedback cycle in which conditions brought by canopy closure and mesophytic species (shading, mesophytic litter, cool and moist microclimates) increasingly favor mesophytic species over shade-intolerant, disturbance-dependent species (Nowacki and Abrams, 2008). Mesophication was initiated by the forced removal of Native Americans from the Northeast, resulting in the reduction or elimination of traditional Indigenous land management practices, such as cultural burning (Christianson et al., 2022; Kimmerer and Lake, 2001), and exacerbated by fire suppression policies of the 1920s, the effects of which have been referred to as "one of the unrecognized ecological catastrophes of landscape history" (Frost, 1998). Since then, mesophication has caused rapid composition and structural changes and biotic homogenization in fire-adapted ecosystems, including loss of more open, woodland conditions in many regions (Hanberry et al., 2012; Li and Waller, 2015; Nowacki and Abrams, 2008; Palus et al., 2018). Although this history has shaped pine barrens succession on a broad scale, the distinction between community types described in this study likely reflects the recent fine-scale differences in land-use and management histories at the two sites. Therefore, it is difficult to know how the patchwork mosaic that exists today relates to the precolonial landscape when fire was more frequent, and patchwork was primarily determined by differences in topography and soil drainage.

4.2. Effects of management practices on pine barrens communities

The threat of ecosystem conversion stemming from fire exclusion has led to an increased emphasis on conservation and restoration strategies that preserve fire-dependent communities such as pine barrens (Quigley et al., 2021; Scheller et al., 2005; Vander Yacht et al., 2019). Results of this study indicate that burning, thinning, and their combination can all maintain the unique and ecologically important overstory conditions of fire-dependent ecosystems. Thinning has previously proven highly effective in creating open-canopy barrens for ecological health and reduced crown fire threat (Bried et al., 2015, 2014; King et al., 2011; Patterson and Crary, 2007), and clear-cuts have been used as an operationally efficient tool in mimicking fire-generated openings and restoring the native pine barrens landscape (Radeloff et al., 2000). Like thinning, fire is effective in encouraging the maintenance of an open canopy of fire-dependent tree species (Jordan et al., 2003; Kurczewski and Boyle, 2000), but it also generates additional structural, ecological, and chemical effects. For example, fire impacts ectomycorrhizal communities (Tuininga and Dighton, 2004), provides cues for seed germination and recruitment (Keeley et al., 1985; Keeley and Fotheringham, 2000), removes hardwood litter (Kirkman et al., 2001), and increases the availability and heterogeneity of ecologically important dead and charred wood (Eriksson et al., 2013). Furthermore, research has shown that fire may limit tree growth and maintain barrens conditions by reducing soil nutrient stocks, organic matter, and soil water retention (Boerner, 1982; Nave et al., 2011; Neill et al., 2007; Quigley et al., 2021, 2020, 2019). We did not capture these effects in our study, which may explain the lack of distinction we observed between stands managed with and without fire.

Similarly, because we only sampled overstory conditions, this study does not capture diversity in structure or composition of understory communities and tree regeneration. Effective management must also take these factors into account, particularly because tall, dense shrub thickets that develop in the absence of disturbance do not provide open barrens habitat of grasses, forbs, scrub oak, and other native shrubs (Bried and Gifford, 2010). Dense shrub thickets can also prevent pitch pine regeneration (Landis et al., 2005; Lee et al., 2019), which may explain the low number of pitch pine we observed in pitch pine-scrub oak thickets. Prescribed burning and mowing are effective both in reducing scrub oak densities to desired levels and promoting pitch pine regeneration (Bried and Gifford, 2010; Lee et al., 2019; Little and Garrett, 1990; Patterson and Crary, 2007). Although we were unable to directly compare the effects of fire to those of mowing, previous research suggests that these treatments can be applied in combination to meet ecologic, economic, and fuel reduction objectives. Patterson and Crary (2007) determined that mechanical pretreatment followed by growing season burning and/or additional mechanical treatment is optimal (Poulos et al., 2020; Rooney and Leach, 2010). Herbicide has also been proposed as a cost-effective management strategy for pine barrens understories; particularly in initiating an early shrubland state in a dense thicket, after which frequent, low-intensity burning can maintain low shrub densities (Bried and Gifford, 2010).

4.3. Management strategies for pine barrens communities

Effectively managing these complex components of a disturbance-dependent ecosystem requires a diversity of tools optimized for site-specific objectives (Bassett et al., 2020; Bried et al., 2015; Bried and Gifford, 2010; Swengel, 1998). Therefore, rather than implying that management with fire, thinning, and their combination generate identical results, the results of this study indicate that land managers have multiple tools available when influencing pine barrens communities. This allows for flexibility when working within site requirements or restrictions; a factor that is particularly important when managing disturbance-dependent ecosystems situated within densely populated regions (APBPC, 2017; Blanchard and Ryan, 2007; Dodds et al., 2018; Ryan, 2012).

This study did not assess management frequency or intensity which are important components of disturbance regimes (He et al., 2019). However, our classification of management regimes as burning, thinning, and burning and thinning is broad enough to be adjusted and combined with other treatments (like mowing or herbicide application) to achieve fine scale management objectives. Future studies could build on this work by examining the effects of management frequency and intensity across soil texture and moisture gradients over time in order to identify disturbance regimes that promote distinct pine barrens communities. Moreover, our work only focused on the tree community responses to these treatments; however, trees are only a minor component of the thickets, barrens, and grasslands included in this work. Future work that more holistically examines the impacts of management on vascular plant communities in these systems will be important for guiding restoration strategies for these mosaics.

The restoration of the relationship between people, fire, and ecosystems is another essential component of long-term, effective management of fire-dependent communities (Larson et al., 2021). The wildland-urban interface in pine barrens is expanding rapidly, and community members who are unfamiliar with the ecological and fuel reduction benefits of prescribed burning are less likely to support management efforts (Blanchard and Ryan, 2007; Ryan et al., 2013; Ryan, 2012). Thus, education on management techniques and forest regeneration can increase local support for and acceptance of prescribed burns on public lands (Ryan et al., 2013; Ryan, 2012). Management of fire-dependent ecosystems can also be improved by engaging with Indigenous communities (Huffman, 2013; Larson et al., 2021), descendants of whom likely created historic barrens and grasslands in the Northeast (Motzkin and Foster, 2002; Patterson and Sassaman, 1988; Welch et al., 2000). Traditional fire knowledge and practice continues to grow, and engaging practitioners can help to restore socio-ecological systems and solve fire-related problems of global significance (Huffman, 2013; Larson et al., 2021).

5. Conclusion

Results support the concept of pine barrens as a landscape mosaic of communities maintained by unique disturbance regimes (Forman and Boerner, 1981). When disturbance is removed, the mosaic homogenizes as communities densify and transition toward forests of shade-tolerant, mesophytic species at the expense of open-canopy grasslands and shrublands (Bried et al., 2014; Nowacki and Abrams, 2008). Therefore, pine barrens communities are created and maintained by human or environmental disturbance (Lee et al., 2019).

We found that prescribed fire, thinning, and their combination are effective in maintaining open-canopy conditions and pitch pine dominance. However, previous research has shown that fire plays a particularly important role in this system (Jordan et al., 2003; Kurczewski and Boyle, 2000; Quigley et al., 2021, 2020, 2019). Management plans should apply fire with other treatments at frequencies and intensities consistent with community-specific historic disturbance regimes to maintain the ecologically important range of habitat conditions associated with pine barrens.

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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.

Data availability

Data will be made available on request.

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Appendix 1. Structural characteristics of five pine barrens communities in the Albany pine Bush and the Ossipee pine Barrens. Characteristics were averaged across sampled stands. Standard error is in parentheses. ba = basal area per hectare (m2/ha)

Community type	Structural characteristics										
	n	Trees/ha	Stand ba	*Pinus rigida* ba	*Pinus strobus* ba	*Quercus* spp. ba	*Acer rubrum* ba	Hardwood ba	Proportion *Pinus rigida*	QMD (cm)	Proportion > 40 cm
Pitch pine-scrub oak thicket	9	57 (19.3)	5.5 (1.6)	4.9 (1.8)	0 (0)	0.6 (0.4)	0 (0)	0.6 (0.3)	0.8 (0.1)	35.5 (1.4)	0.3 (0.1)
Successional northern sandplain grassland	3	114 (13.9)	11 (3.8)	11 (3.8)	0 (0)	0 (0)	0 (0)	0 (0)	1 (0)	33.9 (3.9)	0.2 (0.1)
Pitch pine-scrub oak barrens	21	115 (12)	12.1 (1.1)	10.1 (1.1)	0 (0)	1.9 (0.6)	0 (0)	2 (0.6)	0.8 (0.1)	37.7 (1)	0.4 (0)
Pitch pine-scrub oak woodland	14	414 (77.2)	21.8 (2.2)	19.1 (2)	2.6 (1.1)	0 (0)	0.1 (0)	0.1 (0)	0.9 (0.1)	28.9 (1.9)	0.2 (0)
Pitch pine-oak forest	22	411 (53.7)	27 (1.9)	17.2 (2.2)	1.6 (0.8)	4.8 (1.6)	1.8 (0.6)	8 (2.1)	0.6 (0.1)	31 (1.4)	0.2 (0)

Appendix 2. Structural characteristics of unmanaged stands and stands managed using burning, thinning, and burning and thinning in the Albany pine Bush and the Ossipee pine Barrens. Characteristics were averaged across sampled stands. Standard error is in parentheses. ba = basal area per hectare (m^2/ha)

Management strategy	Structural characteristics										
	n	Trees/ha	Stand ba	*Pinus rigida* ba	*Pinus strobus* ba	*Quercus* spp. ba	*Acer rubrum* ba	Hardwood ba	Proportion *Pinus rigida*	QMD (cm)	Proportion > 40 cm
Burned	26	201.3 (42.8)	14.5 (1.8)	13.7 (1.8)	0.1 (0.1)	0.4 (0.2)	0.1 (0.1)	0.7 (0.2)	0.9 (0)	34.4 (1.4)	0.3 (0)
Thinned	6	205.6 (17.3)	19.3 (3.2)	16.1 (4.2)	1.2 (0.8)	1.8 (1.6)	0.1 (0.1)	1.9 (1.6)	0.7 (0.1)	34.4 (2.8)	0.3 (0.1)
Burned and thinned	25	162.3 (21.1)	14.4 (1.5)	12.1 (1.4)	0.2 (0.2)	2.1 (0.7)	0 (0)	2.2 (0.7)	0.8 (0.1)	35.2 (1)	0.3 (0)
Unmanaged	12	632.6 (74.9)	32 (2.4)	15.2 (3.4)	4.8 (1.5)	6.5 (2.6)	3.1 (1)	11.6 (3.4)	0.4 (0.1)	26.5 (1.5)	0.1 (0)

Appendix 3. Pairwise PERMANOVA results for community types in the Albany pine Bush and Ossipee pine Barrens. Significant values (*) are based on Bonferroni-corrected p-values (α = 0.05) to adjust for inflated type 1 error. PP-OF = pitch pine-oak forest. PP-SOB = pitch pine-scrub oak barrens. PP-SOT = pitch pine-scrub oak thicket. SNSG = successional northern sandplain grasslands. PP-SOW = pitch pine-scrub oak woodland

Community pairs	F	R^2	*p*
PP-OF vs PP-SOB	37.55	0.48	0.01*
PP-OF vs PP-SOT	36.61	0.56	0.01*
PP-OF vs SNSG	8.68	0.27	0.03*
PP-OF vs PP-SOW	0.55	0.02	1
PP-SOB vs PP-SOT	10.17	0.27	0.02*
PP-SOB vs SNSG	0.49	0.02	1
PP-SOB vs PP-SOW	22.85	0.41	0.01*
PP-SOT vs SNSG	3.78	0.27	0.66
PP-SOT vs PP-SOW	23.35	0.53	0.01*
SNSG vs PP-SOW	5.34	0.26	0.21

Appendix 4. Pairwise PERMANOVA results for management strategies in the Albany pine Bush and Ossipee pine Barrens. Significant values (*) are based on Bonferroni-corrected p-values (α = 0.05) to adjust for inflated type 1 error. B = burned. BT = burned and thinned. T = thinned. None = no management

Management pairs	F	R^2	*p*
B vs BT	0.55	0.01	1
B vs None	20.31	0.36	0.006*
B vs T	2.10	0.07	0.798
BT vs None	32.87	0.48	0.006*
BT vs T	2.29	0.07	0.642
None vs T	21.64	0.57	0.006*

Appendix 5. Stand condition loadings on NMDS axes from the *envfit* function. The function calculates stand condition loadings on each NMDS axis, performs rank correlations between stand condition loadings and NMDS axis scores, and assesses statistical significance using a permutation test with 999 permutations. Significant values (*) are based on $\alpha = 0.05$. Basal area is in m^2/ha

Stand condition	NMDS1 loading	NMDS2 loading	R^2	*p*
Pitch pine basal area	0.51	−0.86	0.55	0.001*
White pine basal area	0.06	−1.00	0.39	0.001*
Oak basal area	−0.99	0.13	0.63	0.001*
Red maple basal area	−0.64	−0.77	0.49	0.001*
Hardwood basal area	−0.98	−0.18	0.73	0.001*
Stand basal area	0.01	−1.00	0.80	0.001*
Trees per hectare	0.17	−0.99	0.70	0.001*
Proportion pitch pine	1.00	0.00	0.79	0.001*
Proportion pine	0.98	−0.17	0.64	0.001*
Quadratic mean diameter	−0.22	0.98	0.30	0.001*
Proportion of trees > 40 cm in diameter	−0.32	0.95	0.19	0.002*
Standard deviation in basal area between plots	0.22	−0.98	0.10	0.026*

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