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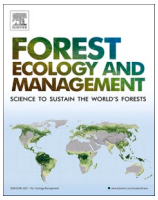

Response of natural tree regeneration to climate adaptation treatments in *Pinus resinosa*-dominated forests

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ABSTRACT

Uncertainty and emerging threats associated with climate change necessitate the development of new approaches for managing forest ecosystems. To address this need the Adaptive Silviculture for Climate Change (ASCC) Network was established to examine the efficacy of three climate adaptation strategies in important forest types across North America: 1) *resistance* to change by increasing overstory tree health through reduced inter-tree competition, 2) *resilience* by creating conditions that allow change within the natural range of variability while encouraging greater abundance of native species considered suitable for projected future climate, and 3) *transition* which involves actively facilitating systems to have a more adaptive response. The present study focused on the influence of Adaptive Silviculture for Climate Change treatments on natural regeneration in a *Pinus resinosa* Ait. (red pine)-dominated forest in northern Minnesota, USA. We aimed to answer the following research questions: 1) How do different climate adaptation strategies (resistance, resilience, and transition) influence natural regeneration relative to passive management? 2) Do impacts on the understory woody community, including trees and shrubs, differ among treatments in terms of abundance, composition, and diversity?

Naturally regenerated trees and shrubs were sampled during the 5th growing season following Adaptive Silviculture for Climate Change treatment implementation (May-August 2019). The species composition of naturally regenerated trees differed among treatments as did adaptability, quantified as a composite index that integrated disturbance response and life history traits. The transition treatment resulted in greater capacity for adaptation to future conditions in the newly regenerated cohort. All treatments increased tree species diversity and richness relative to passive management, but the greatest woody species diversity occurred in the resilience treatment. This suggests a trade-off between maximizing woody species diversity (greatest in the resilience treatment) and adaptability (greatest in transition treatment). Overall, these results affirm the potential for using silviculture to increase tree diversity and adaptability through natural regeneration in anticipation of threats posed by changing climate in a major forest type, with results serving as a model for expectations in similar ecosystems.

1. Introduction

Forest ecosystems around the globe face an uncertain future due to climate change (Millar et al. 2007). Direct impacts such as increased frequency of drought, fire, frost, flooding, and wind events, combined with indirect impacts (e.g. pests and pathogens) together create the potential for devastating losses of ecosystem services and function (Loreau et al. 2001; Frelich and Reich 2010). For example, declines in tree species diversity are expected to accelerate as climate change continues (Bellard et al. 2012; Moritz and Agudo 2013). Tree species at the edge of their current ranges may not be able to persist with changes in climate, resulting in a further decrease of functional diversity unless other, similarly functioning species, take their place (Iverson et al. 2019). The potential loss of existing tree species, coupled with the inability of some tree species to regenerate under new climatic conditions, could lead to resilience debt, where an ecosystem is unable to reorganize following disturbance (Johnstone et al. 2016; Webster et al. 2018). This could ultimately lead to state shifts that further degrade ecosystem function and health (Johnstone et al. 2016; Martínez-vilalta and Lloret 2016).

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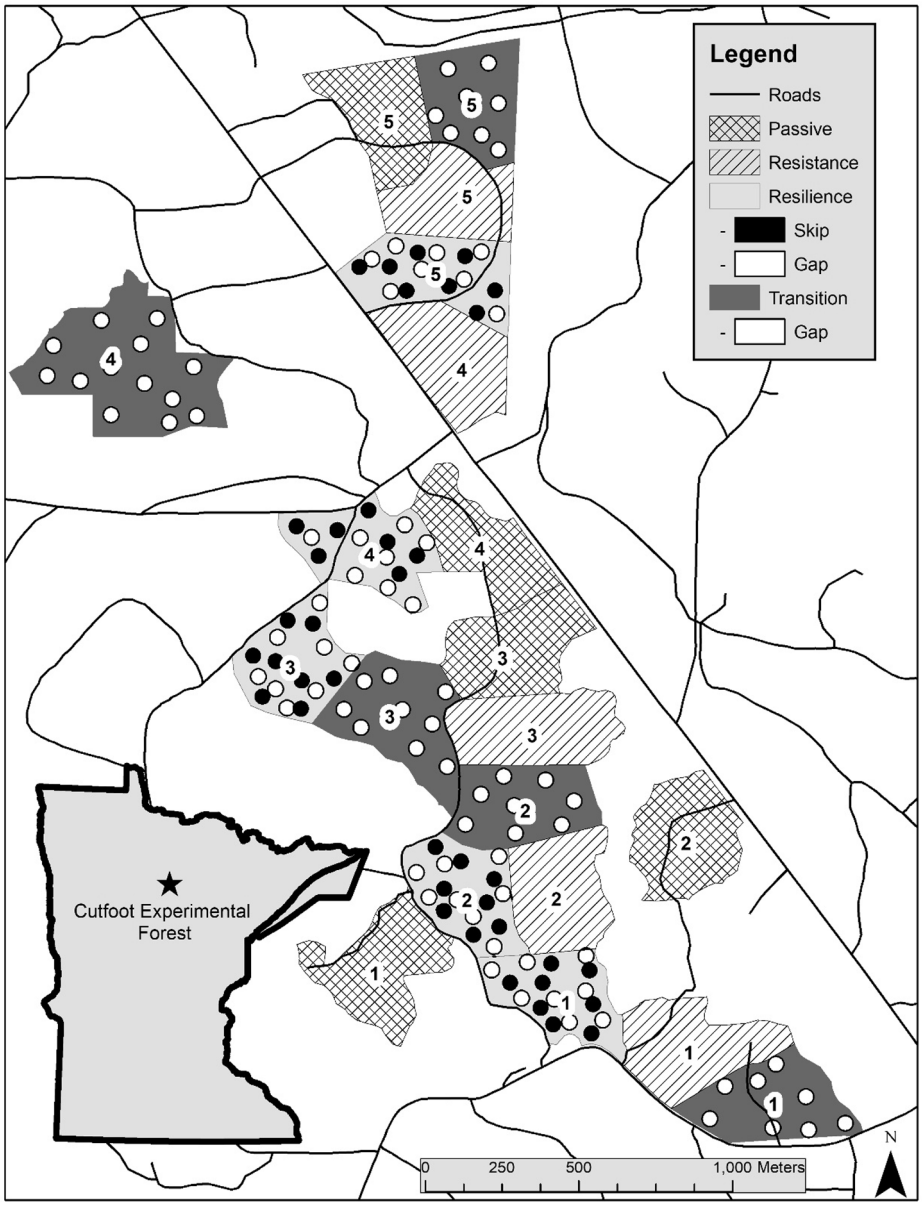

Fig. 1. Map showing location of the Red Pine ASCC on the Cutfoot Experimental Forest of the Chippewa National Forest in Northern Minnesota, USA. Numbers indicate blocks (see Section 2.2 for explanations on silvicultural treatments).

Tree regeneration in forests is a key process that both maintains forest ecosystems through time and serves as a mechanism through which change occurs, including changes that lead to greater resilience. Artificial regeneration through planting is a common method of manipulating species composition in a forest; however, natural regeneration is still a key component of succession and forest recovery following disturbance in many forests and regions (Franklin et al. 2007; Martínez-vilalta and Lloret 2016; Redmond et al. 2018), and its absence can have major implications for sustainability of ecosystem function and forest health (Martínez-vilalta and Lloret 2016). Natural regeneration allows for a continuation of successful or desired genetic legacies present on the site, natural root development, as well as spatial distributions which generally contribute to more structurally heterogenous stands. Achieving natural regeneration objectives in light of climate change can be particularly challenging because successful tree species must: 1) have the ability to establish given current climate conditions, particularly considering vulnerability to environmental stresses during the seedling stage of life (Davis et al. 1998) and 2) be suited to future conditions in order to persist and thrive over time (Matthews et al. 2011; Williams and Dumroese 2013).

To address this challenge, silvicultural strategies are needed that facilitate a degree of flexibility that enables ongoing adaptation (Millar et al. 2007). Potential approaches include efforts to facilitate *resistance* to change (through improvement of forest health and defenses), *resilience* to disturbance (by allowing change to occur but keeping the system within its range of natural variability), and *transition* (or *response)* through actions that facilitate change to a state considered more adapted to future climate (Millar et al. 2007; Millar and Stephenson 2015; Nagel et al. 2017). Natural regeneration of future climate adapted tree species may be important in all of these strategies.

It is also important to quantify how individual tree species contribute to the overall capacity of a forest to adapt. This means considering how different species interact, how they respond to disturbance, and how vulnerable they are to current and emerging threats (e.g. pests and pathogens). Recent efforts to do this have produced species-specific indices of adaptability that combine life history traits (e.g. shade tolerance and dispersal mechanisms) and disturbance response characteristics (e.g. fire tolerance and known vulnerability to disease) (Matthews

et al. 2011). Broad, regional assessments have shown potential for these indices to inform forest management decisions when climate adaptation is an objective (e.g. Kabrick et al. 2017). However, few studies have examined the effects of silvicultural strategies aimed at climate change (e.g. *resistance, resilience,* and *transition*) on the capacity of natural regeneration to contribute to ecosystem adaptability at stand scales.

The Adaptive Silviculture for Climate Change (ASCC) Network was established in 2013 to collaboratively design and experimentally assess treatments that promote adaptive capacity in forests across North America, as they respond to changing climate (Nagel et al. 2017). In the western Great Lakes region, including northern Minnesota, USA, where the first ASCC installation was established, many ecologically and economically important tree species occur near or at the edge of their historical ranges (Handler et al. 2014). Anticipated changes to climate in the region include shorter and warmer winters, altered seasonal precipitation patterns, drier growing seasons, and rising average seasonal temperatures (Swanston et al. 2018). The extension of growing seasons and increased evapotranspiration from warmer temperatures along with changes to seasonal precipitation patterns are expected to increase the potential for water stress (Dymond et al. 2014; Handler et al. 2014). There may also be implications for biological stressors (e.g. insects) and greater fire frequency and severity due to warmer and drier conditions (Handler et al. 2014).

The first installation in the ASCC network, located on the Cutfoot Experimental Forest on the Chippewa National Forest in north-central Minnesota, USA, focuses on *Pinus resinosa* Ait. (red pine)-dominated ecosystems, due to their ecological, social, and economic value (Nagel et al. 2017). Models and empirical research suggest habitat suitability and growth of *P. resinosa,* one of the most widely managed trees in the region, may decline due to anticipated changes in climate, including growing season drought (Scheller and Mladenoff 2005; Bottero et al. 2017; Iverson et al. 2019). *P. resinosa*, like other northern, sub-boreal species, faces numerous threats not just from climatic stressors, but also heavy browse pressure from *Odocoilus virginianus* Zimmerman (white tail deer), pests, and pathogens (Gilmore and Palik 2006). Additionally, a history of fire exclusion and suppression since the early 20th century has altered forest structure, composition, and regeneration dynamics. Historically, these stands often contained multiple cohorts and greater structural heterogeneity as a result of relatively frequent low to mixed severity fires and other disturbances (Fraver and Palik 2012). The lack of fire in recent years has led to a higher tree densities as well as an increase in balsam fir and native broadleaved trees and shrubs that occurred in lesser abundances historically (Hanberry et al. 2012) and now limit natural tree regeneration (Dietrich et al. 2017).

While response of artificial regeneration to climate and silvicultural treatment is essential to the ASCC experiment, the response and success of climate-adapted natural regeneration is also of great interest and is the focus of our study. Specifically, we present the short-term (5 year) responses of natural regeneration to silvicultural treatments designed to achieve climate adaptation in *P. resinosa*-dominated forests in the western Great Lakes region. We sought to answer the following questions: 1) How do different climate adaptation strategies (i.e., resistance, resilience, and transition) influence natural regeneration compared to a passive, no management, approach? 2) How do these treatments influence the understory woody community, including trees and woody shrubs, in terms of abundance, composition, and diversity of species? Ultimately, our goal is to determine if adaptation silviculture can be used effectively to encourage natural regeneration of trees species that are better adapted to future climate. We are aware of no other large-scale manipulative experiment in North America that examines natural regeneration from a climate adaptation perspective using the adaptation framework (i.e., resistance, resilience, transition) that we employed.

2. Methods

2.1. Study site

The study occurred on the Cutfoot Experimental Forest within the Chippewa National Forest (latitude 47°40′N, longitude 94°5′W) in north central Minnesota, U.S.A. (Fig. 1). The region has a cold temperate climate with mean annual temperatures of 4° C, mean annual precipitation of 70 cm, and little topographic relief (elevation 400–450 m). Soils consist of excessively to well-drained loamy sands derived from glacial outwash (Adams et al. 2008).

The study forest is classified as northern dry mesic mixed woodland (FDn33a) based on the Minnesota native plant community classification system (MN DNR, 2003). At the time of study installation, forests were even-aged, dominated by a single cohort of *P. resinosa* that regenerated following widespread logging and fires in 1918. Overstory basal area (trees $\geq$ 12.7 cm diameter at breast height of 1.37 m) ranged from 32–41 m^2ha^{-1}, with approximately 466 trees per hectare, and a mean diameter of 31 cm. In addition to *P. resinosa*, the overstory included lesser amounts of *P. strobus* L. (eastern white pine), *P. banksiana* Lamb. (jack pine), *Betula papyrifera* Marshall (paper birch), *Abies balsamea* L. (balsam fir), *Picea glauca* (Moech) Voss. (white spruce), *Populus grandidentata* Michx (bigtooth aspen), and *Quercus rubra* L. (northern red oak). *Quercus macrocarpa* Michx. (bur oak), *P. tremuloides* Michx (quaking aspen), *Prunus serotina* Ehrh (black cherry), and *Acer rubrum* L. (red maple) were also present but infrequent (Appendix A1: Table A.1). Woody understory vegetation primarily consisted of *Corylus* spp. (hazel), *Amelanchier* spp. (serviceberry), and *Lonicera* spp. (native honeysuckle).

2.2. Experimental design

The ASCC design consists of four treatments: passive, resistance, resilience, and transition (Fig. 1). The passive treatment involved no harvest and served as the study control. The resistance treatment was designed to improve forest health and maintain current overstory dominance of *P. resinosa* through reduced resource competition (Millar et al. 2007; Bottero et al. 2017). Resistance stands were thinned to a residual basal area of approximately 25 m^2ha^{-1}, with a goal of maintaining that density over time. The resilience treatment was designed to allow change generally within the historical range of variability for the ecosystem while encouraging greater abundance of native, future-adapted tree species (Nagel et al. 2017). While climate adaptation approaches such as resilience do not necessitate strict adherence to the historic range of variability, considerable overlap exists between climate adaptation and ecological silviculture frameworks (D'Amato and Palik 2021). The resilience treatment employed variable density thinning to increase overstory heterogeneity and age diversity through new cohort establishment (Franklin et al. 2007; Palik et al. 2020). In each resilience stand, 15–20 % of the area was harvested in 0.2 ha gaps, 15–20 % was left unharvested in 0.2 ha skips (uncut patches), and the remainder (the matrix) was thinned to approximately 25 m^2ha^{-1}, similar to the resistance treatment. Late in the growing season in 2015 (after harvest), the resilience gaps were site prepared with a harrow disc to expose mineral soil for natural regeneration and to reduce competition from aggressive *Corylus* clones by severing their root systems. Resilience treatment gaps were planted with a suite of native, future-adapted tree species (see Nagel et al. 2017), however the planted seedlings were not evaluated in this study. Finally, the transition treatment was designed to actively facilitate adaptation to climate change (sensu Millar et al. 2007) by creating a range of resource environments and planting both native and novel future-adapted species. The transition treatment used an expanding gap irregular shelterwood to increase resource availability and encourage regeneration, while maintaining some overstory cover (Raymond et al. 2009; Redmond et al. 2018). Approximately 15–20 % of each transition stand was harvested in 0.2 ha gaps, while the remainder

Table 1
Treatment goals and tactics.

	Passive (control)	Resistance	Resilience	Transition
Goals/ Desired outcomes	Serve as a control for study and an example of a 'no action' management approach	Maintain red pine dominance and improve forest health resisting negative impacts of changing climate	Allow change to occur within the natural historic range of variability encouraging an eventual return to reference conditions	Facilitate change to encourage a more adaptive response to changing climate
Treatment tactics	No actions	Free thinning to 90 % of original basal area with further thinning planned for future entries to maintain woodland structure and basal area	Increase heterogeneity through variable density thinning with inclusion of 0.2 ha gaps and 0.2 ha reserves (skips). Reduce stocking to 50–75 % of original basal area. Plant a suite native future adapted species within gaps.	Promote a multicohort structure through use of an expanding-gap irregular shelterwood with reduction of basal area to 20–50 % of original stocking and inclusion of 0.2 ha gaps which will be expanded over time as regeneration advances. Plant a suite of non-native and native future adapted species through treatment
Site preparation methods	No site preparation	No site preparation	Site preparation of gaps with harrow disc	Site preparation with harrow disc throughout treatment stands
Number of Sampling Plots	7 throughout each included stand	7 throughout each included stand	11 throughout each included stand. 5 within thinning matrix, 3 within skips, 3 within gaps	9 throughout each included stand. 6 within thinning matrix, 3 within gaps

Table 2
Adaptability scores (Matthews et al. 2011) of tree species found in the Red Pine ASCC site. Scores are derived from across a species' range and do not necessarily convey its adaptability in a specific location.

Species	Climate Adaptability Score
Abies balsemea	2.7
Acer rubrum	8.5
Betula papyrifera	3.4
Fraxinus nigra	1.7
Pinus banksiana	5.2
Picea glauca	3.9
Populus grandidentata	5.1
Pinus resinosa	3.9
Prunus serotina	3
Pinus strobus	3.3
Populus tremuloides	4.7
Quercus macrocarpa	6.4
Quercus rubra	5.4
Tilia americana	4.6

of each stand (the matrix) was thinned to an average of 15 m^2ha^{-1}. Site preparation using a disk harrow was applied throughout each transition treatment stand, avoiding residual trees and large dead wood on the ground. The transition treatment included planting a suite of future-adapted tree species (see Nagel et al. 2017; Muller et al., 2019), but as in the resilience treatment, artificial regeneration was not evaluated in this study. Each of the four treatments was replicated five times in a randomized complete block design (Fig. 1). The mean treatment area (hereafter stand) was 12 ha, with stands ranging in size from 10 ha to 22 ha. Following initial treatments, the remaining overstory was dominated by *P. resinosa* with lesser abundances of other species (Table 1, Appendix A: Table A.1, Fig. A.1).

2.3. Sampling methods

Woody vegetation was sampled from May to August 2019 using 170 permanent 0.2-ha macro-plots located in the study stands. In order to appropriately capture the variability in conditions intentionally created by some treatments, the density of macro-plots varied, with 7 in passive and resistance stands (as these were relatively homogenous in structure), 9 in transition stands, and 11 in resilience stands (intentionally variable) (Table 1). Within each macro-plot, 19 subplots (1 m^2) were established at even intervals four and eight meters from and around plot center for measuring tree regeneration (Appendix A: Fig. A.2). In each subplot, species, and basal diameter (diameter at 15 cm height) were recorded for all trees greater than 15 cm in height and less than 2.5 cm diameter at breast height. Focusing on this size class allowed us to examine seedlings and saplings of natural origin, including advance regeneration, that have potential to recruit to the canopy over time in each treatment. Only stems determined to be of natural origin (based on observed characteristics and planting records) were recorded. Woody shrub species were more abundant, so measurements took place in a subset (8) of the 19 subplots located in each macro-plot. Species and diameter at 15 cm were also recorded for all shrub stems > 15 cm height.

2.4. Analysis

Aboveground woody biomass was calculated for all tree seedlings and shrubs using species-specific allometric equations based on diameter at 15 cm (Perala and Alban 1993) and averaged to the macro-plot level, as was stem density of trees and shrubs. Species frequency in a macro-plot was calculated as the proportion of sampled subplots where the species was observed. Estimates of aboveground biomass, density, and frequency within each macro-plot were averaged to the treatment stand-scale. The variability intentionally created across the resilience and transition treatments necessitated oversampling in 'skips' and 'gaps'. Data from three macro plots located in these conditions were averaged to form a single observation such that sampling was proportional to the area those conditions represented within each treatment stand. This allowed us to adequately sample the 'skips' and 'gaps' given their variability without giving either condition inappropriate weight in statistical analyses. We then calculated a relative importance index of species within each stand (IV = [relative density + relative biomass + relative frequency]/3) (McCune and Grace, 2002). Relative importance provides an estimate of species abundance that is more holistic and less influenced by any single individual measure (e.g. density) (McCune and Grace, 2002). The Shannon diversity index (H'; Spellerberg and Fedor 2003) was calculated using the stand-scale relative importance index with the vegan package (Oksanen 2010) in R (R Core Team 2018). Tree and shrub species were grouped to compare the relative importance of each life form within the treatments. We also quantified *Rubus* spp. and *Corylus* spp. individually because of their high abundance on the site, differing ecological function (e.g. mast for wildlife), different shade tolerances, and known potential impact to regeneration of other species. Species richness of trees and shrubs in each macro-plot was calculated using the sum of the number of species observed across all subplots divided by the summed area of subplots sampled within each macro-plot; macro-plot values were then averaged to the stand-scale.

In order to quantify relative adaptability to changing climate, species-specific adaptability scores (Table 2), quantified based on a composite of life history traits and disturbance response (Matthews et al. 2011), were used to calculate a community-weighted mean (Curtis and

Table 3
Summary of fixed effects for mixed model ANOVA for woody species among ASCC treatments (TRT). Statistically significant results ($p < 0.10$) are shown in bold text.

			All woody species combined		*Corylus* spp.		*Rubus* spp.		Other Shrub Species		Tree Species	
	Source	df	F	P-value	F	P-Value	F	P-Value	F	P-Value	F	P-Value
Stem Densities	TRT	3	**46.28**	**<0.001**	**7.5**	**0.002**	**50.57**	**<0.001**	**67.54**	**<0.001**	2.18	0.13
Aboveground Biomass Estimates	TRT	3	1.31	0.317	1.85	0.192	**30.05**	**<0.001**	1.67	0.214	**5.6**	**0.037**
Relative Importance	TRT	3	NA	NA	**10.1**	**0.001**	**48.97**	**<0.001**	**5.68**	**0.008**	**6.15**	**0.009**
Shannon's H'	TRT	3	**6.42**	**0.008**	NA	NA	NA	NA	1.93	0.165	**10.71**	**<0.001**
Species Richness	TRT	3	**4.471**	**0.018**	NA	NA	NA	NA	1.295	0.321	**7.352**	**0.004**

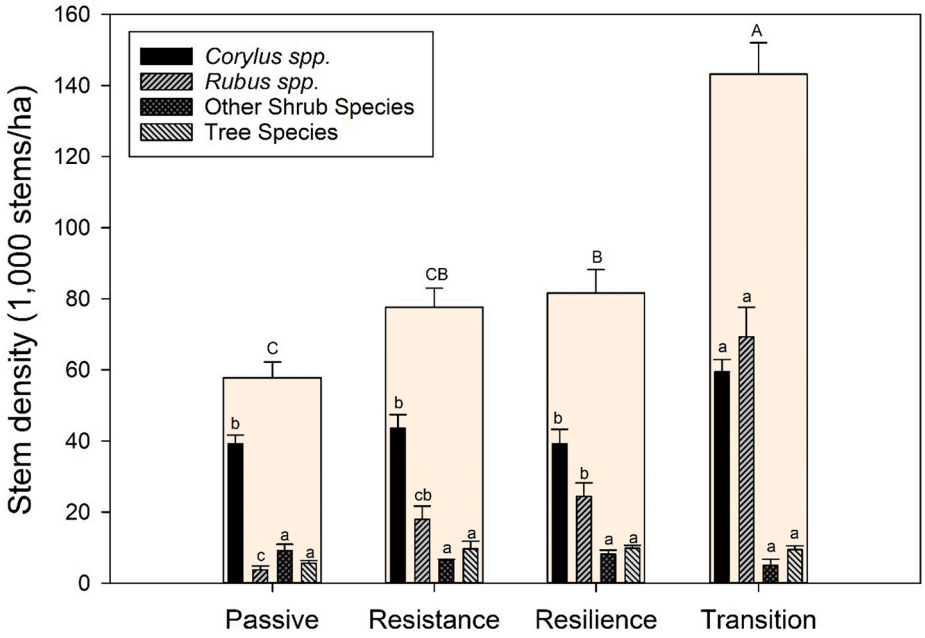

Fig. 2. Mean total density of woody species (large bars) and densities for individual groups and species (nested bars) in ASCC treatments. Values are means +/- one standard error (n = 5). Bars joined by the same upper-case letter for total density or lowercase letter for species groups were not significantly different, following Tukey-adjusted pairwise comparisons at p = 0.1.

McIntosh 1951) adaptability score for each stand:

$$CWM_i = \frac{\sum_{j=1}^{p} a_{ij} w_j}{\sum_{j=1}^{p} a_{ij}}$$

where CWM_i = mean for relative adaptability of a stand *i*, a_{ij} = abundance (relative importance in this case) of species *j* in stand *i*, w_j = weight (adaptability score) of species *j*, with *p* = all of the species present in stand *i* (McCune and Grace, 2002).

In order to determine how adaptation treatments influenced natural tree regeneration and adaptability compared to the passive treatment, change from the passive treatment for density (ΔD), above-ground biomass (ΔBM), relative importance (ΔRI), and relative adaptability (ΔAdapt) were calculated. This involved subtracting the stand-level mean for a given variable in response to the passive treatment from the stand-level mean for each of the active treatments (resistance, resilience and transition) within the same block.

Effects of treatments on stem densities, aboveground biomass, species relative importance, diversity (H'), species richness of shrubs and trees, and change (Δ) in relative importance and adaptability were analyzed with mixed-effects analysis of variance using the lmerTest package (ANOVA; Kuznetsova et al. 2017) in R (R Core Team 2018), with treatments as a fixed factor and block as a random effect. Differences between treatments were then assessed with pairwise comparisons (Tukey's HSD) using the emmeans package (Lenth 2019) in R. Data were tested for normality, and residuals visually checked to ensure homogeneity of variance; data distributions met these assumptions. Significance was determined with an alpha of 0.1 for all tests due to inherent variability and low power to detect differences in large (operational-scale) silvicultural experiments. Exact p-values are provided throughout.

Finally, we used nonmetric multidimensional scaling (NMDS) to visually examine community composition of tree species among treatments. NMDS is an ordination technique that arranges points (e.g. sites, plots) along multiple axes and allows visual identification and interpretation of patterns. NMDS differs from other methods in that it uses rank rather than numerical distances in ordination space, thus avoiding the assumption of linear relationships among variables that is rarely met with community data (McCune and Grace, 2002). NMDS was run with a random starting configuration and 500 runs with real data, followed by 249 runs of randomized data with 500 iterations total per run (McCune and Mefford 1999). All species observed during sampling occurred in greater than 5 % of plots, and therefore all were included in the NMDS. A permutation-based multivariate analysis of variance (perMANOVA) (McCune and Grace, 2002) was used to test the hypothesis that no compositional differences existed among treatments (McCune and Mefford 1999). NMDS and perMANOVA analyses were conducted in PC-Ord 7.0, and a Bray-Curtis dissimilarity index (Bray and Curtis 1957) based on the species relative importance index was used for both. Pairwise differences between treatments were calculated using an FDR adjustment for significant results (Benjamini and Hochberg 1995).

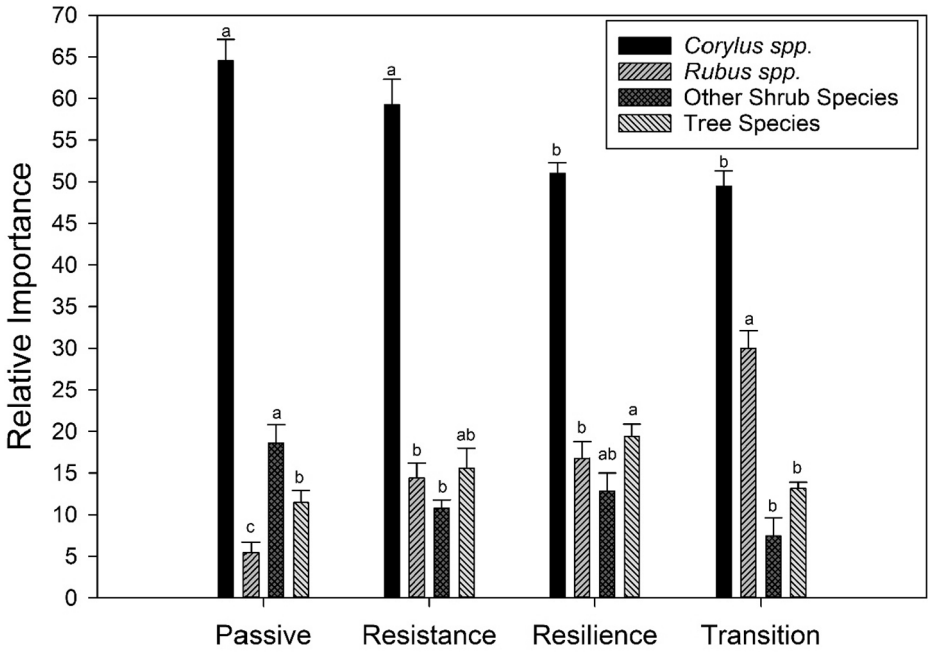

Fig. 3. Relative importance of species and groups within each treatment. Values are means +/- one standard error (n = 5). Within each group, bars joined by the same lower-case letter were not significantly different, following Tukey-adjusted pairwise comparisons (p = 0.1).

3. Results

3.1. Abundance and diversity of woody vegetation

Total density of woody species (stems > 15 cm in height and < 2.5 cm D.B.H.) differed significantly among treatments five years after implementation (Table 3). Transition treatments contained the greatest density of stems while the passive treatment contained the least (Fig. 2). Shrub density contributed the most to differences in stem density among treatments while densities of tree regeneration (all species, combined) did not differ significantly among treatments (Fig. 2). Aboveground biomass of *Rubus* spp. varied significantly among treatments, as did aboveground biomass of tree seedlings (Table 3; Appendix B: Fig. B.1).

Relative importance of individual species and guilds (e.g. trees and shrubs) varied among treatments (Table 3). Importance of *Corylus* spp. was greatest in passive and resistance treatments (Fig. 3), while *Rubus* spp. importance was greatest within the transition treatment (Fig. 3). Relative importance of other shrub species (not *Rubus* spp. or *Corylus* spp.) was highest within the passive treatment, followed by the resilience treatment (Fig. 3). The resilience treatment also contained a greater relative importance of tree species than the passive and transition treatments (Fig. 3).

Woody species diversity (H') and richness (number of species m^{-2}) varied significantly among treatments. The resilience treatment had the highest overall species diversity and the resistance treatment had the highest overall species richness (Fig. 4). The passive treatment contained the lowest tree species diversity and richness when compared to the other treatments, which did not differ from each other (Fig. 4). Shrub species diversity and richness did not differ among treatments (Fig. 4).

3.2. Change in abundance and adaptability of natural regeneration

Although the total density of natural tree regeneration did not differ among treatments (Table 3; Fig. 2), change in density of *P. serotina* did, with the transition treatment having a greater increase in density than the resistance and resilience treatments (Fig. 5). No other tree species had a significant change in density. Moreover, there were no significant differences for change in biomass from the passive treatment for individual tree species among the resistance, resilience and transition treatments (Appendix B: Table B.1, Fig. B.2). High variability may have limited the power to detect differences for species other than *P. serotina*.

Treatments more clearly influenced the relative importance of individual tree species (Fig. 5). All treatments reduced the relative importance of *A. balsamea* relative to passive management with the transition and resilience treatments leading to greater change (-ΔRI) than the resistance treatment (Fig. 5). *P. banksiana* also varied in its response to active treatments, with the resilience treatment leading to greater change in relative importance (+ΔRI) from the passive treatment than resistance and transition treatments (Fig. 5). Differences in ΔRI for *P. strobus* were observed among active treatments as well with transition leading to a decrease (−ΔRI) that differed from the increase (+ΔRI) observed in the resistance treatment (Fig. 5). Finally, differences in ΔRI for *P. serotina* followed those reported for change in density, with the transition treatment leading to a greater increase (+ΔRI) than either the resistance or resilience treatment (Fig. 5).

Change in adaptability (ΔAdapt) compared to the passive treatment varied significantly among active treatments ($F = 7.138$, $p = 0.017$; Fig. 6)). The transition treatment had the highest mean community-weighted adaptability score, due to the increased importance of species predicted to be more adaptable to future conditions (e.g. *A. rubrum, Q. rubra, Q. macrocarpa*), and decreased importance of species considered less adaptable (e.g. *A. balsamea*). The transition treatment was the only treatment to vary significantly from the passive treatment in change in relative adaptability, and it differed from both the resilience and resistance treatments (Fig. 6).

3.3. Community variation

A gradient in the composition of natural regeneration occurred across climate adaptation treatments (Fig. 7). A two-dimensional NMDS ordination provided the best solution (stress of 14.9 %). Visually, treatments overlapped minimally in ordination space, and PERMANOVA confirmed differences among them ($F = 3.811$, $p = 0.002$). Following correction for pairwise comparisons, only resistance and resilience treatments were similar ($T = 1.10$, $p = 0.376$), with all others differing from one another. Consistent with treatment comparisons

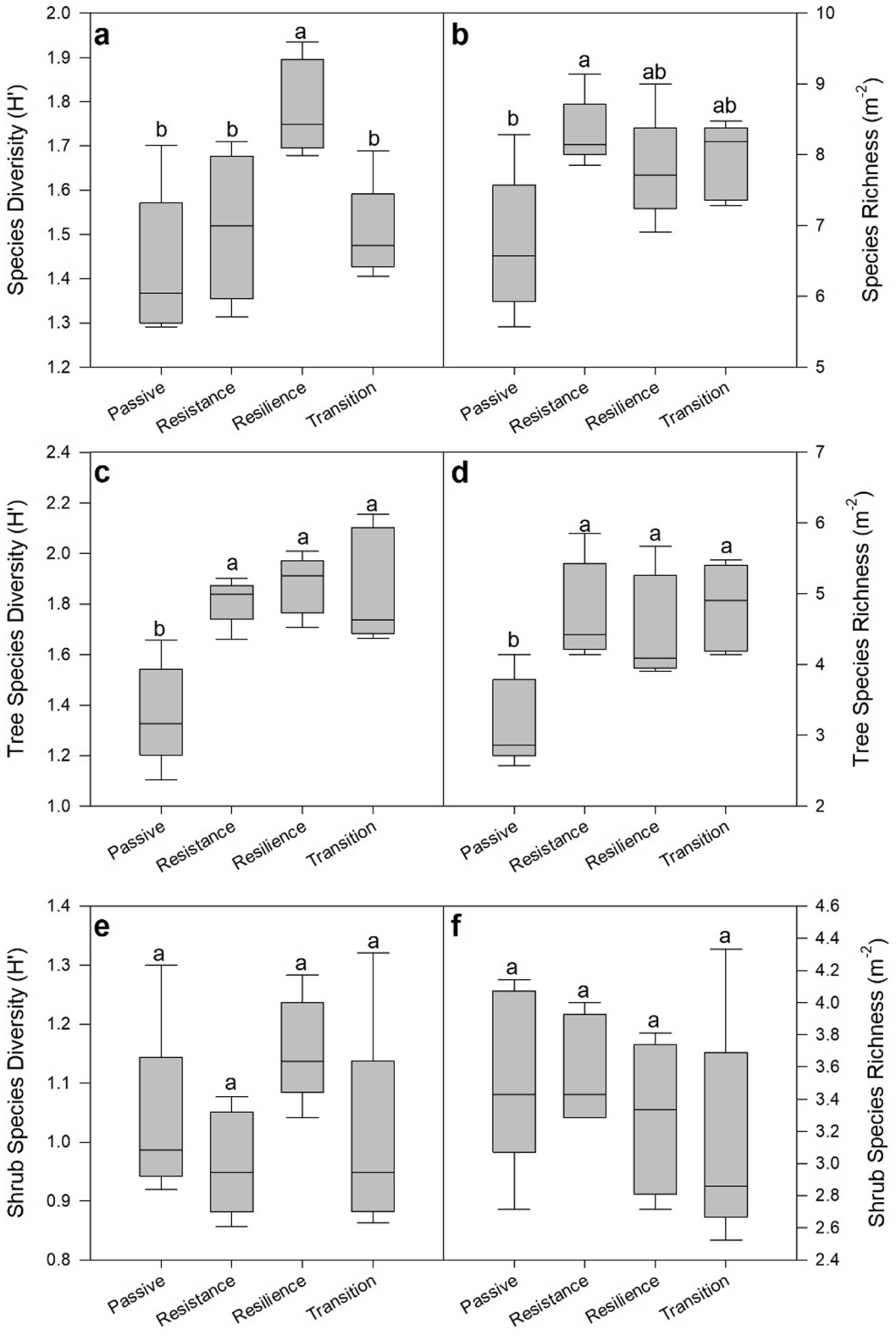

Fig. 4. Boxplots of (a) diversity of all understory woody species; (b) richness (m^{-2}) of all understory woody species; (c) diversity of tree species; (d) richness (m^{-2}) of tree species; (e) diversity of shrub species; (f) richness (m^{-2}) of shrub species. Boxplots showing 25 % quartile, median, and 75 % quartile; error bars represent 90th and 10th percentiles. Lower-case letters indicate significant differences based on Tukey-adjusted pairwise comparisons ($p = 0.1$).

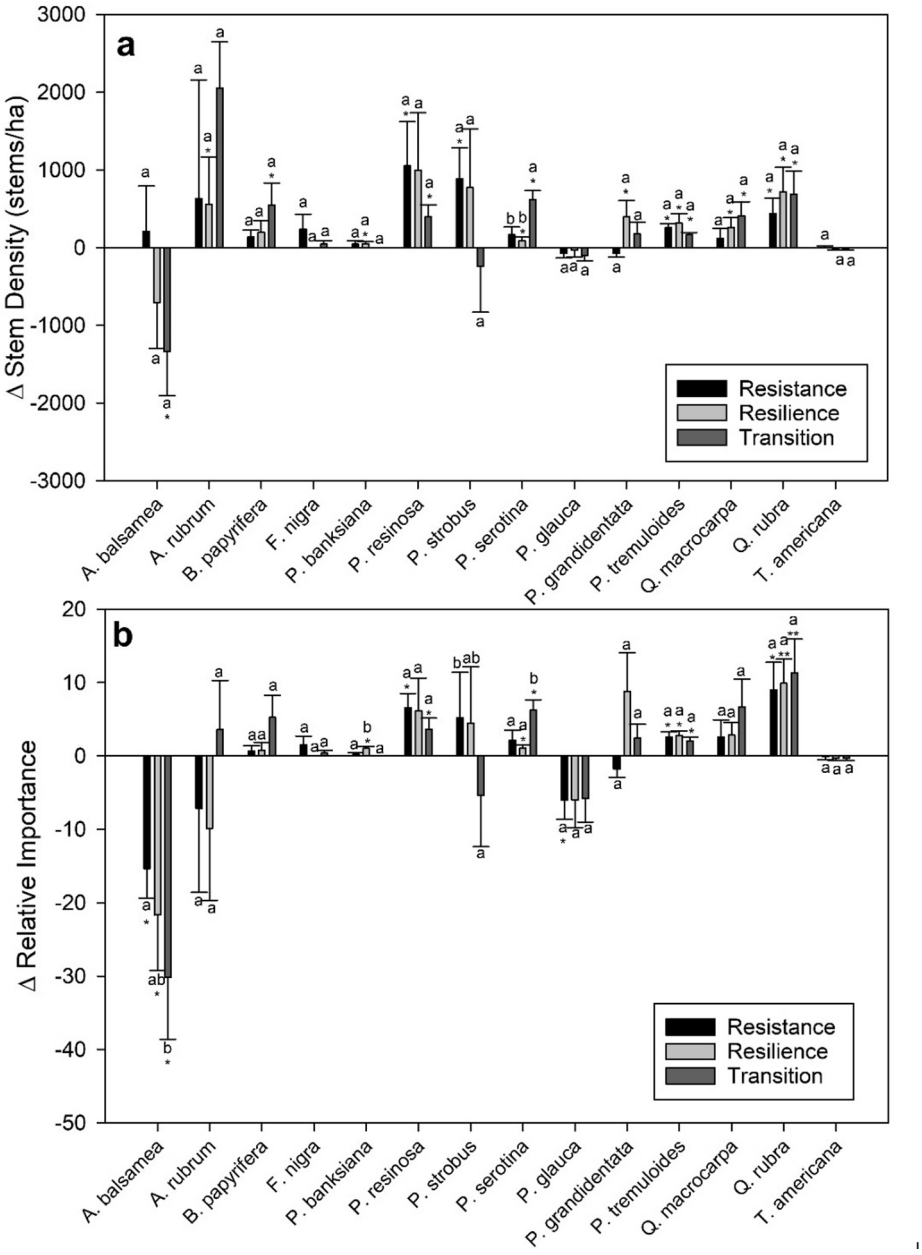

Fig. 5. (a) Change in density of tree species and (b) change in relative importance (height > 15 cm, D.B.H. < 2.5 cm) among ASCC treatments from the passive treatment. Values are means +/- one standard error (n = 5). Lower-case letters indicate significant differences based on Tukey-adjusted pairwise comparisons (p = 0.1). Symbols below letters represent a significant change from the passive treament (*=p < 0.1).

reported above, tree species diversity was correlated positively with the resilience treatment, while relative adaptability correlated positively with the transition treatment when plotted on the NMDS.

4. Discussion

In an effort to evaluate the efficacy of climate adaptation approaches in *Pinus resinosa* dominated forests in the western Great Lakes region, we sought to determine how resistance, resilience, and transition treatments (sensu Millar et al. 2007; Nagel et al. 2017) influence the composition of natural regeneration and the understory woody community broadly, compared to passive 'no-action' management. More specifically, we asked whether silvicultural approaches can be used to increase tree diversity and encourage natural regeneration of species better adapted to future climate. We assessed adaptability with scores derived from a composite of life history characteristics and vulnerabilities that applies to each species across its range (Matthews et al. 2011), rather than focusing on how well a species might fare in a specific location under future conditions. Even though the adaptability scores are not specific to how a given species might behave in the western Great Lakes region, with the exception, of *P. banksiana*, tree species in our study with a moderate to high adaptability score are also projected to maintain or increase habitat suitability in this region (Matthews et al. 2011). Altogether, our results demonstrate that silvicultural approaches for climate adaptation can successfully achieve goals for greater tree diversity and increased adaptability to future climate, although not necessarily simultaneously (i.e. trade-offs may exist between achieving objectives related to diversity and adaptability depending on the specific treatment).

The two treatments designed to encourage regeneration (resilience and transition) met the suggested minimum stocking densities for multiple species, individually, five years after treatment installation

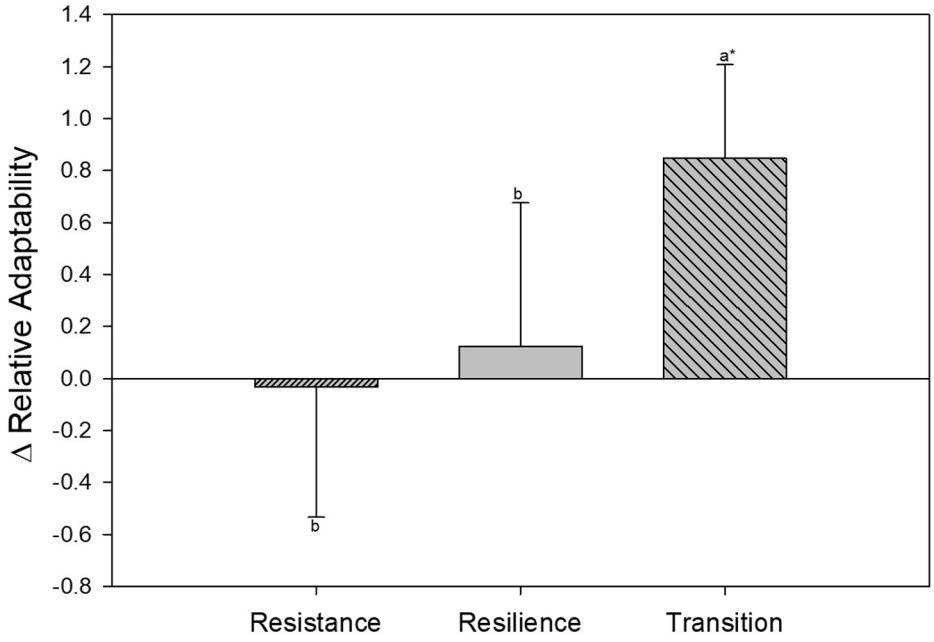

Fig. 6. Change in relative adaptability compared to the passive treatment. Values are means +/- one standard error (n = 5). Bars joined by the same lower-case letter were not significantly different following Tukey-adjusted pairwise comparisons ($p < 0.1$). Symbols (*) represent a significant difference from the passive treatment ($p < 0.1$).

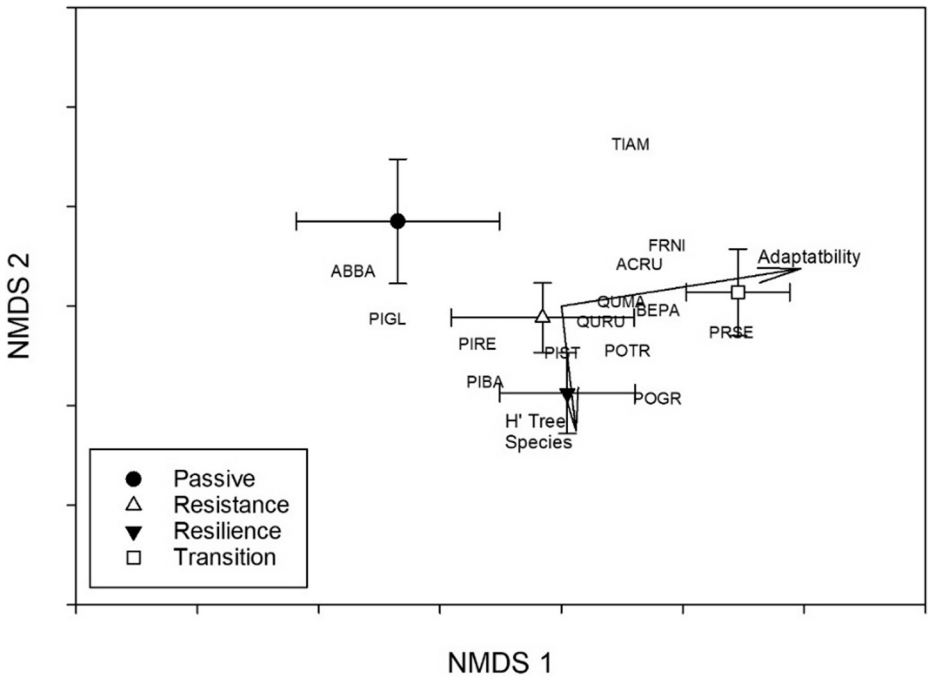

Fig. 7. Two dimensional bi-plot of NMDS ordination of adaptation treatments based on Bray-Curtis dissimilarity index of tree species relative importance. Centroid centers represent mean axis score for a treatment (n = 5), with error bars representing one standard error. Species are indicated with four-letter codes. Shannon diversity (H') and mean adaptability are plotted as vectors. Centroids that are closer together are considered to be more similar to one another in species composition than centroids that appear farther apart.

including *A. rubrum,*and *P. resinosa* in both the transition and resilience treatments, and *P. strobus* in the resilience treatment (Appendix B: Table B.2, WI DNR 2020). While total stem density of tree regeneration did not vary greatly among treatments, the density and importance of individual tree species did, leading to differences in composition, diversity, and adaptability. This suggests potential for achieving at least some climate adaptation objectives, such as increasing species diversity and/or adaptability through natural regeneration. We discuss the response of each treatment in more detail below.

4.1. Resistance

The 'resistance' approach to adaptation, designed to enhance tree vigor and resist negative effects of changing climate while maintaining largely unchanged composition uses thinning, a commonly applied silvicultural technique in *P. resinosa*-dominated forests, to maintain growth and productivity (Gilmore and Palik 2006). Traditionally, red pine stands are managed with periodic thinning to maintain stocking. The thinning applied with this treatment maintains stands at lower stocking, maintaining a more of a woodland structure within the stand. The resistance treatment in our study resulted in an increase of tree

species diversity and richness of natural regeneration, but it also led an abundance of *Corylus* spp. Comparable to the passive treatment. Abundant *Corylus* spp. Can impede tree regeneration (e.g. Roberts et al. 2017), which can negatively impact tree recruitment over the long term. *A. rubrum* was abundant across the study forest, as it is regionally (e.g. Frelich and Reich 2010; Roberts et al. 2017), with the greatest density and relative importance in the resistance treatment. However the treatment led to little difference in adaptability of regeneration from the passive treatment, likely because of the high importance of *A. balsamea* present, which is considered less adaptable to the projected warmer and drier climate (Ravenscroft et al. 2010; Matthews et al. 2011; Handler et al. 2014). In the short-term, the resistance treatment may be effective at maintaining a *P. resinosa*-dominated overstory. This treatment also helps illustrate that climate adaptation does not need to be an extreme action, and that sometimes only slight deviations from traditional silvicultural methods can positively impact the ability of a forest stand to resist the impacts of climate change. However, without further efforts to increase regeneration of *Pinus* species and decrease *A. rubrum* and competition from shrub species such as *Corylus* spp., this goal may prove difficult to achieve, considering predicted climate trajectories and increasing abundance of more competitive hardwood species (Scheller and Mladenoff 2005; Ravenscroft et al. 2010; Handler et al. 2014).

4.2. Resilience

A resilient ecosystem should have the capacity to change within its natural range of variability following a disturbance and eventually return to a prior state or function (Millar et al. 2007). The resilience treatment employed on the Red Pine ASCC led to greater overall species diversity in the woody understory community, when compared to other treatments. Resilience treatments typically emphasize the maintenance or restoration of diversity, and our results suggest that this was achieved for regenerating native tree species, even though mean adaptability of the tree seedling community was similar to that of the passive and resistance treatments (and less than that observed with the transition treatment).

Greater species diversity is expected to confer a greater capacity for resilience to future disturbances (Isbell et al. 2015), in part because it provides ecological memory links to prior reference states (Johnstone et al. 2016; Webster et al. 2018). Species diversity also helps maintain multiple pathways for ecosystem recovery following a disturbance (Halpern 1988; Bergeron et al. 2014). Building on these ideas, the resilience treatment was designed to create variability in resource and environmental conditions at the stand scale. This involved emulating conditions similar to the historical disturbance and resultant structure of *P. resinosa*-dominated forests (Fraver and Palik 2012), with stands characterized by patchy canopy cover, including gaps with exposed mineral soil reflective of early seral habitat after fire, and refugia for species less tolerant of disturbance in unharvested 'skips'. The resulting increase in species diversity and richness of natural tree regeneration in the resilience treatment, suggests it may have created the ecological memory links and potential for multiple pathways needed for this ecosystem to return to a desired state if impacted by future disturbance thereby increasing its resilience to change(Bergeron et al. 2014; Johnstone et al. 2016; Nagel et al. 2017).

4.3. Transition

Transitioning an ecosystem to a condition with greater adaptive capacity is wrought with uncertainties (Millar et al. 2007), but as related research on assisted migration in the ASCC experiment indicates, *P. resinosa* ecosystems may already be able to support both native and novel species considered better adapted to predicted future climate (Muller et al., 2019). Moreover, the present study indicates future-adapted species are regenerating and/or recruiting naturally to a greater degree in response to the transition treatment compared to the other treatments. This included *P. serotina*, a species with above average tolerances to predicted future environmental stresses (Matthews et al. 2011). Additionally, trends in abundance of *A. rubrum*, *Q. macrocarpa* and *Q. rubra*, all of which are expected to be better suited for future climate (Matthews et al. 2011; Muller et al., 2019), suggest they may also respond positively to a transition strategy like the one used in this study. *P. serotina, Q. rubra,* and particularly *Q. macrocarpa* all have moderate to high drought tolerance (Ninements and Valladares 2006), and these hardwoods may have generally better seedling survival during drought compared with the conifers common to this ecosystem (Fisichelli et al. 2014). They are also expected to respond well to the combination of disturbance (both natural and anthropogenic) and future climate conditions (Scheller and Mladenoff 2005). While trends in the abundance of these species individually were characterized by high variability, in combination (that is, as a community) they resulted in a higher overall relative adaptability of the transition treatment.

Another factor unique to this treatment that likely influenced responses is the scarification applied throughout transition stands (compared to gaps only in the resilience treatment). This likely improved seedbed conditions broadly by exposing mineral soil, and it may have reduced shrub competition immediately after harvest. However, after five growing seasons, shrub densities were highest in the transition treatment which could eventually lead to greater resource competition in the understory (Montgomery et al. 2010; Gleason et al. 2017; Redmond et al. 2018). Continued monitoring is necessary to determine how the increased density of shrubs in the transition treatment impacts tree establishment, survival and growth over the long-term. Additionally, applying site preparation during the latter half of the growing season may have influenced the composition of natural regeneration and the impact on shrubs. Assessing the influence of timing was beyond the scope of this study, and it may be worthwhile to explore with future research.

5. Management implications

Natural regeneration is an important component of sustainable forest management, particularly when resources are prohibitive for widespread use of artificial regeneration. Therefore, knowing what species are able to establish naturally, following the types of treatments we examined, including the combination of overstory manipulation and site preparation, will help inform decisions about use of these strategies to address climate adaptation. Although planting seedlings may be a more predictable way to regenerate and adapt forests to future conditions, our results suggest that the transition treatment, in particular, positively influences adaptability through natural. Overall, our results affirm the potential for using silviculture to increase tree diversity and adaptability in anticipation of threats posed by changing climate for *Pinus resinosa* forests and may be applicable to other *Pinus*-dominated or dry-mesic forest types. The collaborative research approach that has involved managers and scientists from the onset of this and other studies conducted within the ASCC network increases the likelihood that the experimental treatments are relevant and feasible (Nagel et al. 2017). In this region (e.g. White et al. 2021)and more broadly (e.g. Ontl et al. 2018), forest planning efforts increasingly consider climate adaptation. Operational-scale experimental studies like ASCC are imperative for testing ideas and informing future decision-making (Ahlering et al. 2020). Foresters have long used silviculture to achieve a variety of objectives, and, as climate continues to change, strategies focused on adaptation through manipulation of natural regeneration may have an increasingly important role to play in sustainable forest management.

CRediT authorship contribution statement

Lewis J. Wiechmann: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing. **Miranda T. Curzon:** Conceptualization, Methodology, Writing – review & editing, Supervision. **Brian J. Palik:** Conceptualization, Methodology, Writing – review & editing, Supervision.

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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Data accessibility statement

Data will be made available upon request to corresponding author.

Appendix A. Supplemental Site and Sampling Methods Information

See Table A.1 and Figs. A.1 and A.2.

Table A1
Pre- and post-treatment overstory characteristics and composition. Abbreviations: BA = mean basal area (m^2/ha), SPH = mean stems/ha, and D.B.H. = mean diameter at breast height, 1.37 m (cm). Composition is percentage of basal area.

Category	Pre-Treatment (entire study site, n = 20)	Passive (control) (n = 5)	Resistance (n = 5)	Resilience (n = 5)	Transition (n = 5)
SPH (s.e)	504.70(11.91)	506.07(18.49)	266.43(18.58)	241.31(14.37)	138.10(8.79)
DBH (s.e.)	30.86(0.57)	29.83(1.16)	33.75(1.367)	36.48(1.36)	35.42(1.15)
BA (s.e.)	41.71(0.78)	40.27(2.48)	25.18(0.20)	25.02(0.20)	15.22(0.30)
Abies balsamea	1.65 %	1.66 %	1.15 %	0.81 %	0.4 %
Acer rubrum	0.18 %	0.11 %	0.21 %	0.19 %	0.56 %
Betula papyrifera	1.78 %	1.92 %	1.08 %	1.43 %	0.69 %
Fraxinus nigra	0.01 %	0 %	0.02 %	0 %	0 %
Picea glauca	1.03 %	0.85 %	0.89 %	0.95 %	0.1 %
Pinus banksiana	4.23 %	5.47 %	5.03 %	4.09 %	1.48 %
Pinus resinosa	86.21 %	83.79 %	87.25 %	84.47 %	86.76 %
Pinus strobus	4.44 %	5.81 %	4.25 %	6.68 %	9.15 %
Populus grandidentata	0.23 %	0.08 %	0 %	1.21 %	0.36 %
Quercus macrocarpa	0.01 %	0 %	0.02 %	0 %	0.03 %
Quercus rubra	0.24 %	0.31 %	0.09 %	0.17 %	0.49 %
Ulmas americana	0.002 %	0 %	0 %	0 %	0 %

Fig. A.1. Photo examples of the four treatments on ASCC-CEF: (A.) passive (control) treatment, (B.) resistance treatment, (C.) resilience treatment looking through the matrix and a gap into a reserve ('skip'), and (D.) transition treatment looking through a gap into the matrix.

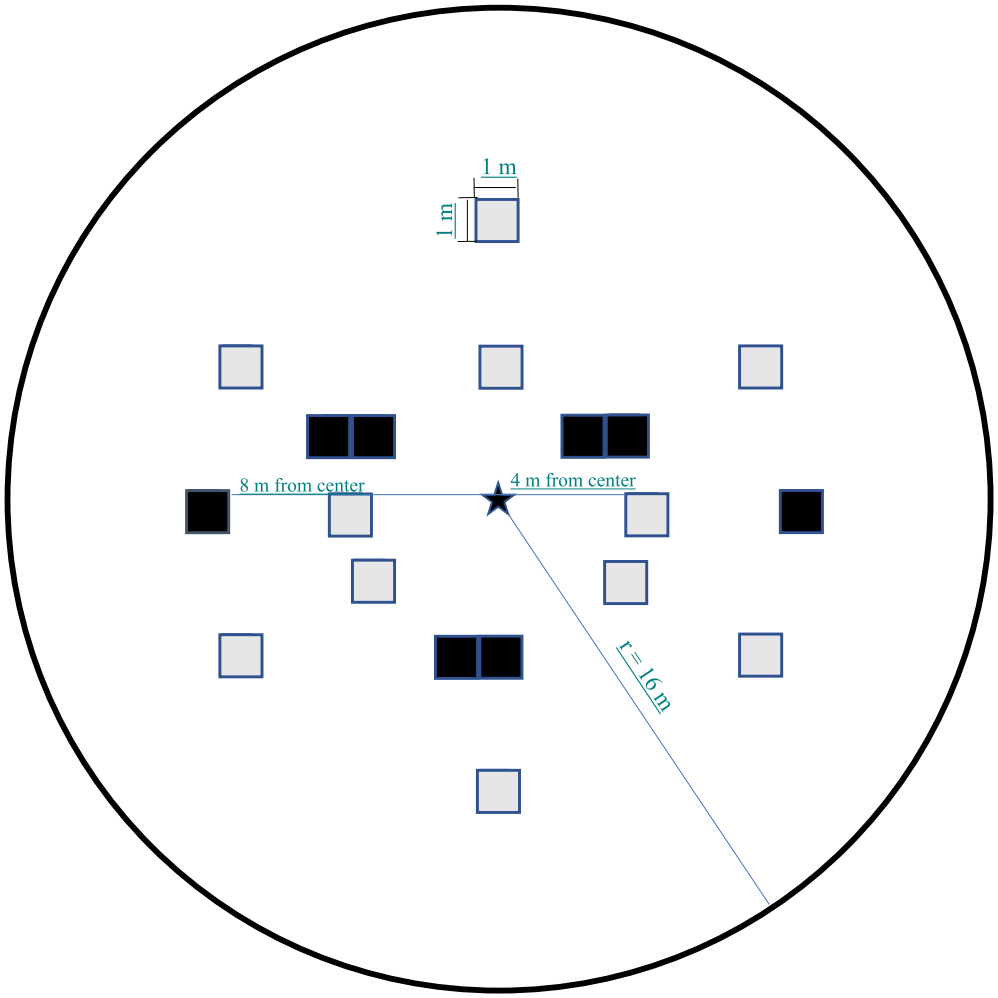

Fig. A.2. Plot layout, large circle is macro-plot boundary (16-meter radius), the star is plot center. Measurements within black boxes consisted of both shrub and tree stems. Within grey boxes measurements included just tree stems.

Appendix B. Supplemental results

See Tables B.1–B.2. And Figs. B.1–B.3.

Table B1
ANOVA results for tree species change (Δ) from the passive treatment for active treatments, resistance, resilience, and transition (TRT). Statistically significant results ($p < 0.10$) shown in bold text.

			Δ Stem Density		Δ Aboveground Biomass		Δ Relative Importance	
	Source	df	F	P-value	F	P-value	F	P-value
A. balsamea	TRT	2	1.82	0.205	1.63	0.256	**3.41**	**0.085**
A. rubrum	TRT	2	1.03	0.399	0.73	0.513	2.98	0.109
B. papyrifera	TRT	2	1.31	0.305	0.87	0.445	1.93	0.188
F. nigra	TRT	2	1.66	0.25	1.55	0.27	1.57	0.266
P. banksiana	TRT	2	0.86	0.445	1.64	0.252	**7.62**	**0.014**
P. resinosa	TRT	2	1.17	0.357	0.47	0.641	0.76	0.501
P. strobus	TRT	2	2.78	0.121	0.89	0.435	**3.49**	**0.082**
P. serotina	TRT	2	**9.51**	**0.008**	1.56	0.249	**5.68**	**0.018**
P. glauca	TRT	2	1.33	0.317	0.45	0.656	0.02	0.99
P. grandidentata	TRT	2	2.42	0.13	1.23	0.341	2.64	0.112
P. tremuloides	TRT	2	0.945	0.416	1.65	0.252	0.63	0.559
Q. macrocarpa	TRT	2	2.93	0.11	0.04	0.96	2.56	0.138
Q. rubra	TRT	2	0.35	0.717	1.79	0.209	0.091	0.914
T. americana	TRT	2	1	0.41	1	0.41	1	0.41

Table B2
Minimum density of established seedlings for adequate stocking of natural regeneration (WI DNR 2020) and density of seedlings stem/ha ± standard error within treatments (n = 5). Gray boxes indicate observed densities met the minimum recommended for full stocking.

Species	Minimum Density	Passive	Resistance	Resilience	Transition
A. balsamea	600	1533.83±710.36	1744.36±1203.34	904.76±252.26	195.49±338.35
A. rubrum	2000-5000	2120.30±761.74	2751.88±1073.27	2706.77±783.02	4200.50±1143.93
B. papyrifera	2000	105.26±35.99	240.60±72.90	353.38±152.06	751.88±338.76
F. nigra	2000-5000	*Not observed*	240.60±375.94	*Not observed*	45.11±0
P. banksiana	600-1200	*Not observed*	45.11±0	120.30±45.11	*Not observed*
P. resinosa	400-1000	15.04±0	1067.67±563.86	1037.59±879.18	458.65±156.09
P. strobus	700	842.11±568.85	1729.32±303.56	1666.67±463.73	629.07±90.05
P. serotina	1000	Not observed	165.41±132.62	135.34±56.39	659.15±111.42
P. glauca	600	120.30±66.31	45.11±37.60	120.30±43.41	30.08±0
P. grandidentata	6000	90.23±43.41	15.04±0	563.91±276.77	275.69±183.43
P. tremuloides	6000	*Not observed*	255.64±51.00	353.38±124.46	195.49±45.11
Q. macrocarpa	3100	60.15±0	180.45±189.22	368.42±115.78	496.24±178.48
Q. rubra	3100	721.80±244.33	1157.89±221.26	1483.71±336.10	1481.20±234.19
T. americana	2000-5000	15.04±0	15.04±0	*Not observed*	*Not observed*
Total stems/ha	N/A	5624.06±755.78	9654.14±824.48	9814.54±2127.65	9418.55±1078.68

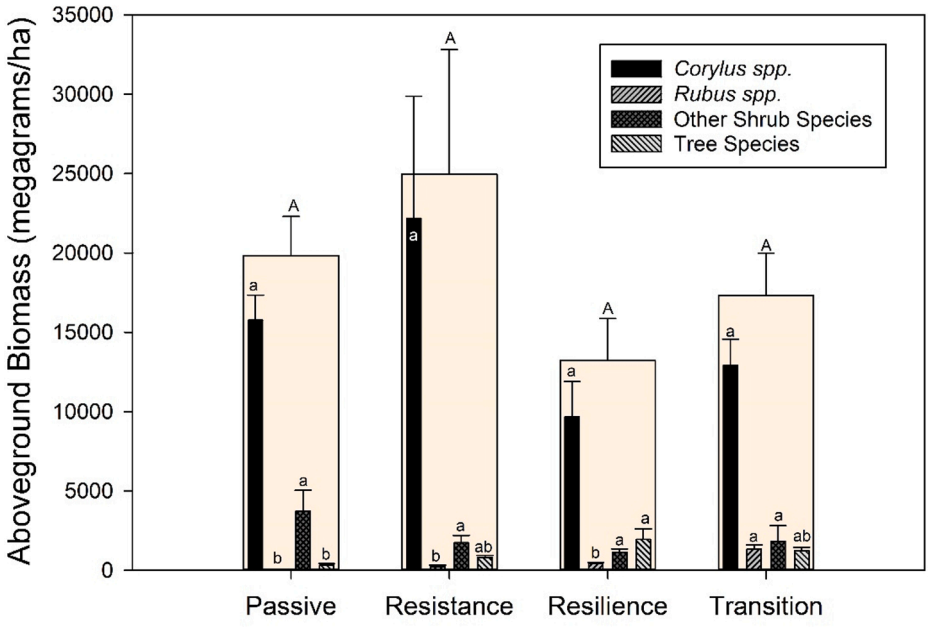

Fig. B.1. Aboveground Biomass of woody stems within each treatment, and estimates for individual groups and species. Error bars represent one standard error. Upper case letters represent significant differences among treatments for overall density and lower case letters indicate significant differences among treatments for groups following Tukey-adjusted pairwise comparisons.

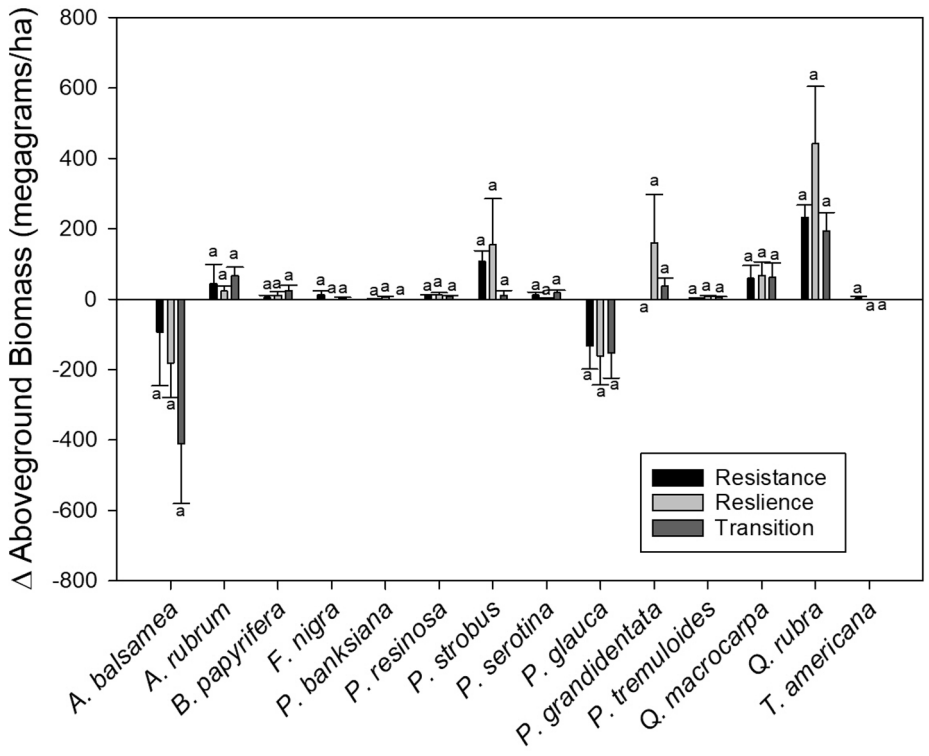

Fig. B.2. Change in aboveground biomass of tree seedling specie from the passive treatment. Error bars represent standard error. Lower case letters indicate significant differences following Tukey-adjusted pairwise comparisons.

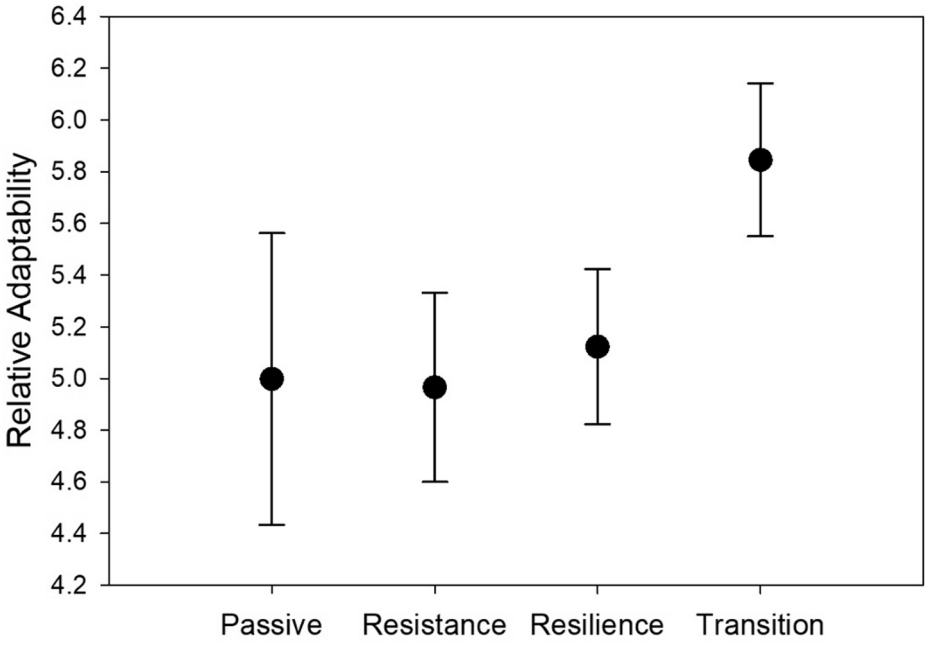

Fig. B.3. Mean Relative Adaptability Scores. Error Bars represent one standard error.

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