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Early tree regeneration response following adaptive silviculture treatments in northern hardwood ecosystems

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ABSTRACT

Climate change poses threats to forests, creating a need for adaptation to novel and changing conditions. This need has led to the creation of adaptation frameworks including the *resistance, resilience, transition* (RRT) framework, which proposes management strategies along a gradient of change and adaptation. Although management within this framework is grounded in theory and past management experience, little is known about how these approaches may influence regeneration, a critical phase in forest development. To address this gap, we examined five-year outcomes of treatments implemented using the RRT framework as part of the Adaptive Silviculture for Climate Change network in northern hardwood forests. The *resistance* approach employed traditional single-tree selection, *resilience* single-tree and group selection, and the *transition* variable density thinning and irregular shelterwood. All treatments reflected multi-aged regeneration methods with varying levels of canopy gap formation and retention with our study goal to determine how treatments influenced natural and planted regeneration composition, abundance, and functional identity, as well as projected compatibility with future climate conditions. We found that the seedling size class reflected recent adaptive silviculture treatments while sapling composition was associated with longer-term historic management in all treatments. Treatments shifted regeneration composition toward desired future conditions, with *resistance* resulting in a regeneration profile similar to the canopy, while *transition* regeneration composition diverged from the overstory with the highest proportion of shade-intolerant species. *Resilience* included regeneration conditions found in both *resistance* and *transition* offering the potential to absorb a broad range of climate change and disturbance impacts. Functional trait profiles of regeneration in each treatment showed slight differences, with assisted migration plantings in *transition* contributing to its divergence from the other treatments, highlighting the value of including planted species in adaptation treatments. As a whole, the adaptive treatments resulted in regeneration profiles that aligned well with objectives related to the RRT framework, although changes were small in some cases and it may require second, or even third, entries for stands to continue on adaptation-oriented trajectories.

1. Introduction

Conditions brought on by global change are expected to significantly impact forests. Rising temperatures, shifts in seasonality, and an increase in extreme weather events such as droughts and convective storms are expected to alter the capacity for forests to sustain current functions and ecological conditions (IPCC, 2015; Seidl et al., 2017; Swanston et al., 2018). More specifically, changes to temperature and precipitation patterns may shift the location of where individual tree species can successfully regenerate, as well as limit survival and growth (Zhu et al., 2012). In addition, extreme events, such as droughts and strong storms, may physiologically stress and physically damage trees, reducing function (Allen et al., 2010; Clark et al., 1999; Contosta et al., 2019; Rogers et al., 2017). These changing climate and disturbance regimes compound the growing impacts of abiotic stressors, namely invasive insects and pathogens, which can cause large-scale mortality to individual tree species and generate drastic and lasting impacts on forest health, structure, and species composition (Kautz et al., 2017; Lovett et al., 2016). Adaptation to these novel and changing conditions will be necessary to sustain forest functions and conditions that are consistent with long-term societal expectations and needs (Domke et al., 2023; Hagerman and Pelai, 2018; Messier et al., 2014).

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Regeneration represents a crucial adaptation pathway for forests, as trees that establish following a disturbance may be the dominant organisms in that forest for centuries (Seidl and Turner, 2022). The long life span of trees means that mature trees may occupy growing space in circumstances under which they can no longer successfully regenerate (Qiu et al., 2021) generating potential climate mismatches in areas currently dominated by sexually mature overstory trees (Iverson et al., 2019b). In addition to being an important life stage, regeneration is also a vulnerable phase. Trees undergo ontogenetic changes in their ability to withstand variability in local climatic conditions (Davis and Botkin, 1985), with seedlings being the most vulnerable stage of tree development (Beckage et al., 2005) largely due to their high sensitivity to changes in moisture and temperature relative to mature individuals (Clark et al., 1999; Gustafson et al., 2020). Individuals that successfully recruit to sapling and canopy tree stages have survived numerous factors including animal predation, variable light and moisture conditions, often strongly influenced by microsite, and competition (Kozlowski, 2002), as well as the interactive impacts of these stressors (Niinemets, 2010). Natural disturbances, climate-change related shifts to natural patterns, and management all have the capacity to influence regeneration composition, with past management often supporting reduced diversity, and climate change-related disturbances disproportionally impacting one or a select few species (Dey et al., 2018). Each species has a unique set of adaptations that define how it will respond to climate change, therefore a forest occupied by a diversity of plant species is likely to have a greater number of response pathways to disturbances brought on by climate change than more simplified systems (Oliver et al., 2015) although in the case of extreme disturbances, even diverse forests may respond negatively (e.g., Shovon et al., 2024).

Northern hardwood forests, which dominate a large proportion of the temperate region of northeastern North America, have a specific set of vulnerabilities to global change. This includes structurally and compositionally simple conditions resulting from historic, intensive land uses and timber-focused management (Neuendorff et al., 2007; Schulte et al., 2007), including a reduction in the presence of shade-intolerant canopy tree species (Ducey et al., 2023). The greatest density of non-indigenous insects and pathogens also occurs in this region, with organisms including emerald ash borer (*Agrilus planipennis*; McCullough, 2020), hemlock woolly adelgid (*Adelges tsugae*; Orwig and Foster, 1998), beech bark disease (*Cryptococcus fagisuga & Neonectria spp.* complex; Cale et al., 2017), and beech leaf disease (*Litylenchus crenatae mccannii*; Reed et al., 2022), currently or threatening to functionally eliminate individual species from the forest. Further, climate related stressors such as warmer temperatures, reduced snowpack, and changing precipitation patterns may reduce growth and vigor of canopy trees (Luce et al., 2016; Reinmann et al., 2019). Multi-cohort and mixed species management approaches that strive to counter past trends by increasing structural and compositional diversity may offer a pathway toward greater resilience to disturbance by creating a diverse set of potential disturbance recovery pathways (Falk et al., 2022; Taylor et al., 2020). This includes increasing variation in post-harvest regeneration conditions, such as varied light and seedbed conditions, to support regeneration from a diversity of species that may ultimately result in a more diverse forest canopy (Henry and Walters, 2023).

The presence and arrangement of functional traits in plants can offer another lens to assess the influence of diversity on resilience and ecosystem productivity and can add depth to descriptions of species-specific climate sensitivities and how these relate to forest resilience (Aubin et al., 2016; Boisvert-Marsh et al., 2020). Plant communities with differing species composition and disturbance history reflect these influences in the presence and abundance of various functional traits, or their functional identity (Curzon et al., 2020; Keyser et al., 2020; Wilfahrt et al., 2014). Functional identity at a stand-scale may change in response to new disturbance regimes or changes to growing conditions; any changes to a forest's functional identity will also affect how it influences ecosystem processes (Lelli et al., 2019; Wilfahrt, 2018). Functional diversity can also be described with a number of metrics that quantify different aspects of trait variation, such as dispersion, divergence, and redundancy, and these can be combined for a more complete picture of this diversity (Laliberté and Legendre, 2010; Mason et al., 2005; Villéger et al., 2008). As with species composition, aspects of functional diversity change in response to disturbance, including forest management, creating a potential avenue for forest managers to influence functional diversity.

Given the threats posed by climate change, forest managers are seeking management options that support adaptation and a number of adaptive frameworks and related research projects have emerged to address this need. One such effort is the Adaptive Silviculture for Climate Change project (ASCC; Nagel et al., 2017). The ASCC project includes a network of sites across varied ecosystems within which scientists and managers apply a common framework to site-specific constraints and climate change concerns and develop specific management goals and prescriptions through the process of science co-production (Norström et al., 2020). The framework examines three approaches to climate change adaptation with different goals based on responding to varying levels of change: resistance, resilience, and transition. Under this framework a resistance approach supports current forest structure and function while defending against expected changes, a resilience approach creates a forest that can accommodate some change and adapt, but can ultimately still return to a desired reference condition, and a transition approach intentionally accommodates change and enables response to new and changing conditions (Millar et al., 2007; Nagel et al., 2017).

Although these approaches build from past management experience in specific regions, key knowledge gaps exist regarding outcomes of these methods in terms of conferring adaptation potential and diverse functional conditions, limiting their translation to wider practice. In light of this, we propose to use the three adaptation approaches outlined above (resistance, resilience, transition) to examine five-year natural forest regeneration responses in a northern hardwood forest and compare them to unmanaged forests. We ask the following questions: 1) How do the three adaptation treatments influence regeneration abundance, composition, and diversity? 2) How are the species in each treatment projected to respond to climate change? 3) How do the treatments affect forest vulnerability and adaptive capacity as represented by functional diversity and trait profiles? Addressing these questions can help us understand how each adaptive silviculture treatment might direct the development of the forest toward a desired future condition that can better respond to the changing climate.

2. Methods

2.1. Site description

This study took place at the ASCC installment at the Second College Grant in northern New Hampshire, a 10,800-hectare forest owned and managed by Dartmouth College (Fig. 1). Within the Second College Grant, the study encompasses 160 ha of northern hardwood forest, dominated by sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and yellow birch (*Betula allegheniensis* Britt.), with smaller components of red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill), red maple (*Acer rubrum* L.), and white pine (*Pinus strobus* L.) Mean annual temperature ranges from a minimum in January of −12° C to a maximum in July of 17° C with annual precipitation averaging 117.9 cm (PRISM Climate Group, 2021). Elevations vary from 484 to 650 m above sea level. Soils are coarse, loamy, glacially-derived tills and exhibit moderate variation across the research area.

2.2. Treatment descriptions

The resistance prescription is single-tree selection (Table 1): trees

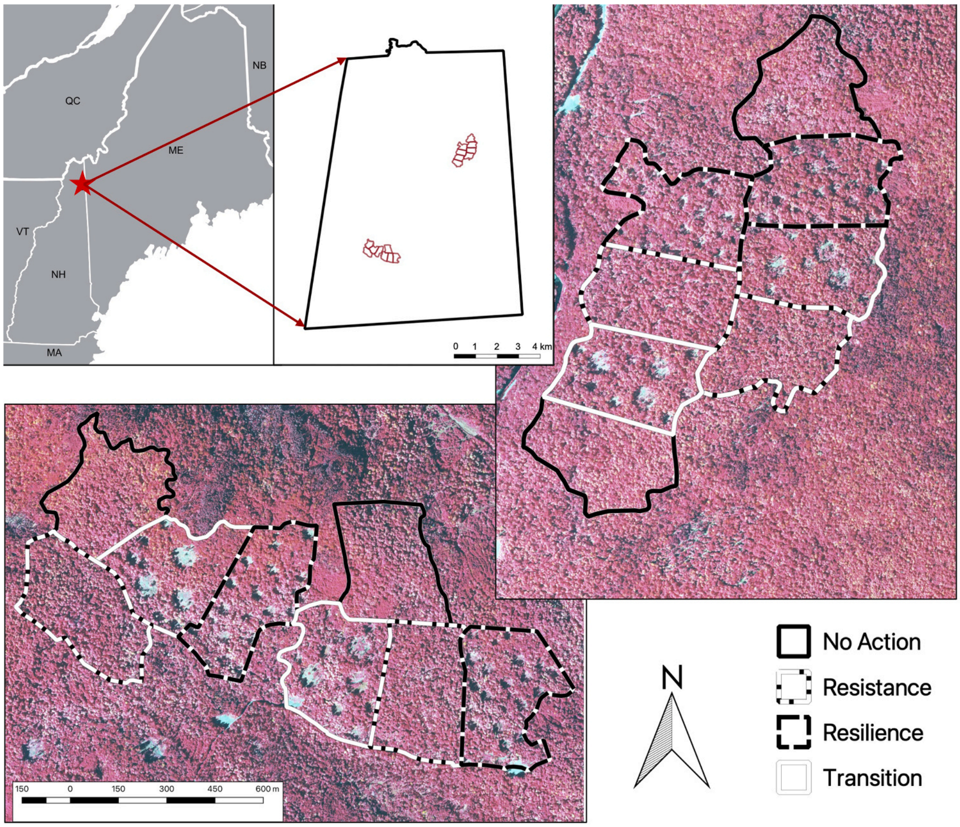

Fig. 1. Second College Grant location and treatments.

Table 1
Silvicultural prescriptions in Adaptive Silviculture for Climate Change Treatments at Second College Grant, New Hampshire.

	Resistance	Resilience	Transition
Silvicultural prescription	Single tree selection with occasional groups of 2–3 canopy trees removed, 20 year cutting cycle, target basal area 16–18 m^2ha^{-1}	Hybrid single-tree/group selection with 20% of area in gaps (0.04 and 0.1 ha), 20% in reserves, remaining matrix thinned, 20 year cutting cycle, target basal area 16–18 m^2ha^{-1} as stand average, with variation through space	Irregular shelterwood and variable density thin: 20% of area in gaps (0.1 and 0.4 ha), 10–20% uncut during first entry, matrix single tree selection, target basal area 16–18 m^2ha^{-1} through matrix for 14–16 m^2ha^{-1} as across-stand average
Desired future species composition	Maintain current: Sugar maple 55%, beech 25%, yellow birch 10%. Retain individuals of other species: red maple, red spruce	High species diversity, reduced sugar maple component (< 30–40%), increase in other species (emphasis on wind, ice, and drought resistant species and trees)	Dominance of currently onsite species adapted to future climate change (yellow birch, red maple, beech); increased proportion of future-adapted species not currently onsite

were removed across all size classes based on Arbogast guidelines for a reverse-j diameter distribution (Arbogast, 1957), with an emphasis on maintenance of current species composition, residual stems with lower risk to insects, pathogens, and ice storm impacts, and basal area of 16–18 m^2ha^{-1}. The resilience treatment is a hybrid single-tree and group selection system designed to diversify natural regeneration and specifically encourage red spruce and yellow birch regeneration in canopy gaps. This treatment calls for 20% of the harvest area in gaps 0.04 and 0.1 ha in size, 20% of the harvest area in permanent reserves of similar size to the gaps and the remaining matrix forest reduced to a residual basal area of 16–18 m^2ha^{-1}. The transition treatment is a combined continuous cover irregular shelterwood and variable density thinning, with 20% of the harvest area in gaps 0.1 and 0.4 ha in size, 10–20% of the area retained in uncut patches, and the matrix forest reduced to a density of 16–18 m^2ha^{-1} via single-tree marking. A major goal of the treatment is an eventual shift in species dominance toward those expected to be better adapted to future growing conditions, both through natural regeneration and planting. In each treatment block, plantings took place following harvest in two 0.4 ha gaps and two 0.1 ha gaps. Species planted include a combination of present but locally uncommon species (population enrichment): red spruce, white pine, bigtooth aspen (*Populus grandidentata* Michx.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and species with a nearby range that are not onsite (assisted range expansion): black birch (*Betula lenta* L.), bitternut hickory (*Carya cordiformis* (Wangenh.)), and American chestnut B3F3 (*Castanea dentata* (Marshall) Borkh.). With the exception of *C. dentata*, which was direct-seeded, all planted trees were bare-root nursery seedlings and all were planted in spring 2018 in areas outside of plots used for monitoring natural regeneration (Clark et al., 2021). The four treatments were replicated in four 10-ha blocks and harvesting took place in the late summer and fall of 2017 by method of hand felling and cable skidding.

2.3. *Field methods*

We installed a network of nested measurement plots with varying number of plots per treatment. In no action and resistance, where treatments were applied more uniformly, 10 plots were established at random locations per replicate, while in resilience and transition we used a random stratified procedure, intentionally locating plots within gaps, reserves, and matrix forest, resulting in 14 and 15 plots in each replicate of the resilience and transition treatments, respectively. At the treatment level, the stratified plots were weighted such that the weight of each plot type (gap/reserve/matrix) approximated the treatment area encompassed by that condition. Each measurement plot included overstory measurement in a 0.04 ha (11.3 m radius) plot, where each tree was identified to species and measured at DBH (1.3 m above base) and height and decay class was noted for snags. We measured regeneration of saplings from 2.5 to 9.9 cm DBH in three nested 0.004 ha (3.59 m radius) subplots along azimuths of 0°, 120° and 240° at 5.5 m from plot center. Measurements of seedlings (>30.5 cm tall and <2.5 cm DBH) and shrub species took place in 1.26 m radius subplots in the same locations as the sapling plots. Our analyses are based on measurements from pre-harvest and five years post-harvest. Planted seedlings have been tracked and measured annually on an individual basis since planting (Clark et al., 2021).

2.4. *Data analysis*

2.4.1. *Species diversity*

All analyses were performed in R version 4.3 (R Core Team, 2022). Species composition was analyzed for natural regeneration only, while all other analyses include both naturally regenerated and planted tree species, with planted seedling abundance weighted based on the number of stems present in proportion to natural regeneration abundance.

We assessed species abundance outcomes for the most common and ecologically important naturally regenerated species: *A. rubrum*, *A. saccharum*, *B. allegheniensis*, *F. grandifolia,* and grouped less common species by shade tolerance and life form. The conifer group is primarily *P. rubens* and *A. balsamea,* with very few individuals of *T. canadensis*. The intolerant hardwood group includes *P. serotina, Prunus pensylvanica* L.f., *Populus tremuloides, Populus grandidentata, Fraxinus americana, Fraxinus nigra, Betula papyrifera,* and *Betula cordifolia.* We fit linear mixed effects models to assess regeneration abundance with treatment as a fixed effect, pre-treatment abundance as a covariate, block as a random effect, and abundance five years post-treatment as a response variable with the R package *nlme* (Pinheiro et al., 2020). We carried out post-hoc analyses with the *emmeans* package in R (Lenth, 2023).

We evaluated compositional diversity with the Shannon diversity index using the *vegan* package in R (Oksanen et al., 2022), in both seedling and sapling classes for each treatment, calculated as:

$$-\sum p_i \ln(p_i)$$

where p_i is the proportion of individuals for the *i*th species. Differences between treatments were assessed using linear mixed effects models with treatment as a fixed effect and block as a random effect.

We assessed beta diversity across plots in each treatment in both seedling and sapling classes using Whittaker's Beta (β_w), calculated as:

$$\beta_w = \frac{S}{\overline{\alpha}} - 1$$

where S is the total number of species and $\overline{\alpha}$ is the average number of species per site (Koleff et al., 2003; Whittaker, 1960). Treatment means were calculated using the *betadiver* and *betadisper* functions in *vegan* and differences assessed with ANOVA and Tukey's HSD.

2.4.2. *Adaptability and compatibility indices*

We followed the approach outlined by Kabrick et al., (2017) to assess the suitability of individual tree species to future climate scenarios using data available in regional vulnerability assessments (e.g., Janowiak et al., 2018) and the Climate Change Tree Atlas (Iverson et al., 2019b; Peters et al., 2020). The adaptability index combines trait (e.g., drought tolerance) and disturbance response (e.g., pest vulnerability) characteristics to estimate the ability of a given species to respond to change. This index ranges from 0 to 8.5, with scores <3.3 indicating low adaptability, 3.3–5.2 moderate adaptability, and >5.2 high adaptability. The compatibility index calculates a ratio of future (2070–2099) to current importance value for each species. Importance values are calculated as the weighted average of a species relative basal area and relative density in a given region based on FIA data. The predicted future importance values are reported in the Climate Change Tree Atlas (CCTA; Peters et al., 2020, accessed 9/3/2023) and values used for this study were derived from the predictions for the 1° grid square the Second College Grant falls within (S44°E71°). The CCTA future importance values are based off the average of three different model outputs: Community Climate System Model, Geophysical Fluid Dynamics Model, and Hadley Global Environment Model under two future scenarios: low emissions (RCP 4.5) and high emissions (RCP 8.5) (Iverson et al., 2019a). A ratio of future:actual suitable habitat range is then calculated and ranked into 5 categories: 1 = large decrease in importance (ratio < 0.5), 2 = small decrease (0.5–0.8), 3 = no change (ratio 0.8–1.2), 4 = small increase (1.2–2), and 5 = large increase (>2). For all indices (adaptability, compatibility – low emissions, compatibility – high emissions), scores were weighted by the relative abundance of each species in a plot, then averaged by treatment. Two of the planted species, *C. dentata* and *C. cordiformis,* did not have listed adaptability and compatibility indices in the CCTA, so were excluded from this analysis. We used t-tests to assess whether the change from pre- to post-harvest was significantly different than zero.

2.4.3. *Functional trait diversity*

We chose 13 functional traits to describe treatment functional identity: maximum height, growth rate, leaf size, wood density, wood decay rate, vegetative productivity, seed mass, shade tolerance, drought tolerance, waterlogging tolerance, leaf longevity, leaf mass per unit area, and nitrogen content per leaf mass. These were chosen based on data availability and relevance to adaptive capacity, and species values come from Paquette and Messier (2011). We calculated functional identity for each treatment as the community-weighted mean, or mean trait value weighted by species abundance, using the *FD* package (Laliberté et al., 2014). We used non-metric multidimensional scaling to examine differences in functional identity between treatments and from pre- to post-harvest and quantified these outcomes using NMDS and multi response permutation procedure (MRPP) in the *vegan* package. To determine differences between means we used the *pairwiseAdonis* package (Martinez, 2017).

We calculated four functional diversity indices: dispersion, which describes trait variability, divergence, which describes the spread of traits, evenness, which describes trait distribution, and redundancy, which describes trait replication across different species in a community (Laliberté and Legendre, 2010; Ricotta et al., 2016; Villéger et al., 2008). Functional richness was originally included in the analysis, but ultimately removed because it requires more species than traits for robust results and our data did not consistently achieve this ratio between pre- and post-harvest species composition (Villéger et al., 2008). To determine how the adaptation treatments influenced these indices, we subtracted pre-harvest from post-harvest values and compared treatments using linear mixed-effects models.

3. Results

3.1. *Regeneration composition*

Following harvest, seedling composition was notably different among treatments (Fig. 2A). The no action approach had the lowest abundance across all species. *Acer rubrum*, *A. saccharum*, and *F. grandifolia* showed statistically different abundances among treatments, but with slightly different patterns. Both *F. grandifolia* and *A. rubrum* were least abundant in no action and most abundant in transition, with the other two treatments falling between, although

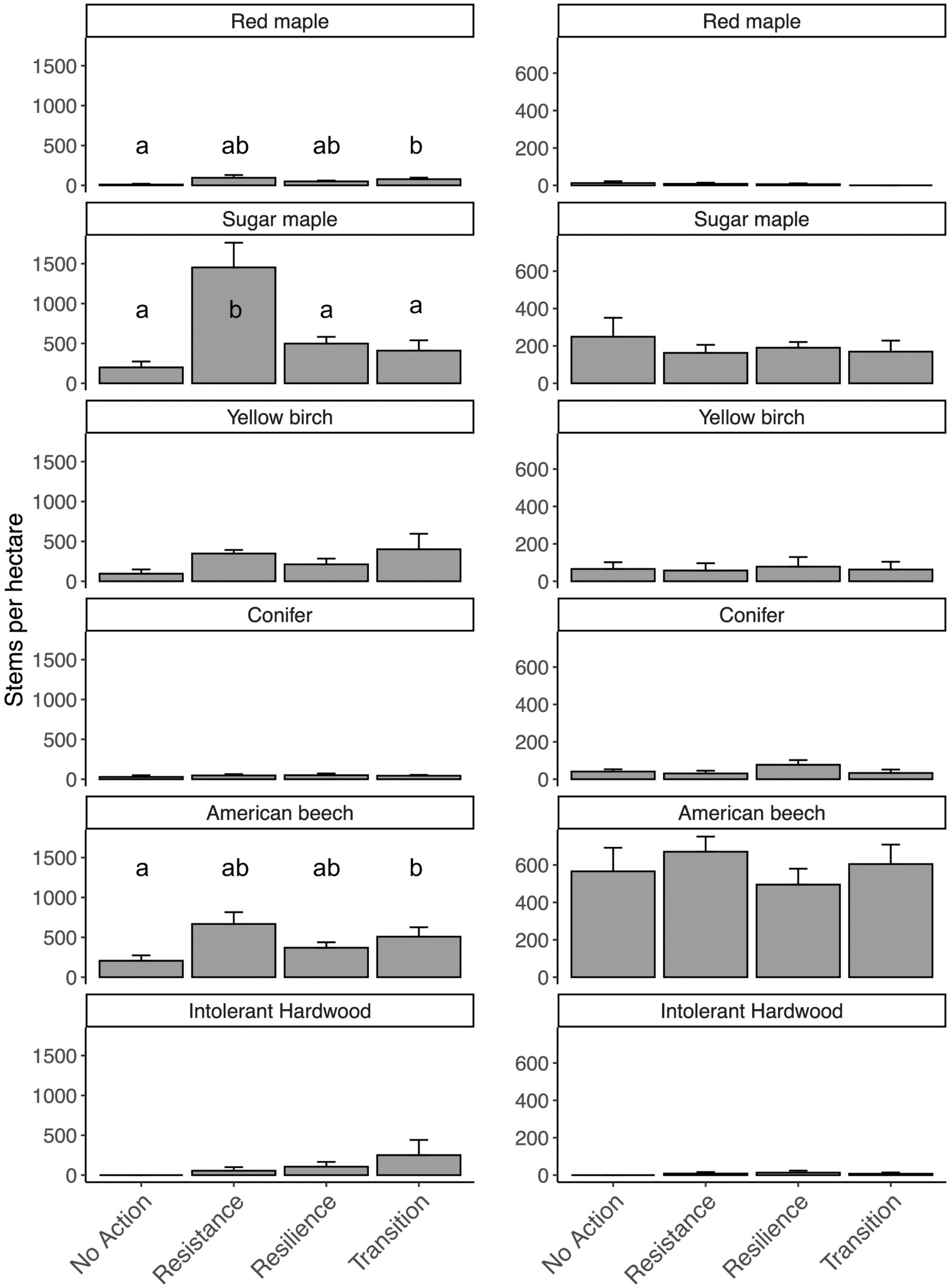

Fig. 2. Natural regeneration of seedlings (left) and saplings (right) by species in four adaptation treatments at the NEASCC installation, Second College Grant, NH. Bars represent standard error. Within species group, different letters indicate statistically different abundance at $p < 0.05$.

A. rubrum was less abundant than *F. grandifolia* across all treatments. *Acer saccharum* seedlings were considerably more abundant than the other three treatments under the resistance approach. Despite lack of statistical significance, *B. alleghеniensis* was generally most abundant in the transition treatment. The conifer group had consistently low abundance across all treatments. There were no differences in sapling abundance among treatments (Fig. 2B.)

3.2. Regeneration diversity

In the seedling class, species richness was higher in all active management treatments, with an average of eight species present across plots in the resistance treatment, nine in resilience, and 18 in transition. Richness was lowest in no action, with five species present, although Shannon diversity was not significantly different among treatments

Table 2
Mean species richness and Shannon diversity mean (se) seedling and sapling regeneration averaged across measurement plots in four adaptation treatments at Second College Grant, NH. Letters indicate significant differences at $p < 0.05$.

	Postharvest			
	No Action	Resistance	Resilience	Transition
Seedlings				
Species Richness	5 (0.00) a	8 (0.95) b	9 (0.75) b	18 (0.96) c
Shannon Diversity	0.68 (0.14) a	0.88 (0.12) a	0.87 (0.15) a	0.85 (0.15) a
Saplings				
Species Richness	5 (0.25) a	6 (0.50) ab	9 (0.75) b	5 (0.25) a
Shannon Diversity	0.78 (0.11) ab	0.72 (0.12) ab	0.82 (0.15) a	0.63 (0.13) b

(Table 2). In the sapling class, the resilience treatment had the highest Shannon diversity and transition the lowest, with no action and resistance falling between the two. Resilience also had the highest sapling species richness, at nine species present, while no action and transition had an average of five species present and resilience six. There were no differences in beta diversity among treatments in the sapling class, while the seedling class showed higher beta diversity in transition (Fig. 3).

3.3. Adaptability and compatibility indices

Both pre- and post-harvest, adaptability indices fell into the moderate category for both regeneration classes (Fig. 4). The seedling size class reflected the influence of harvest treatment more so than the sapling class, although differences between treatments were minimal. Under the high-emissions model, compatibility was lowest in no action, and highest in transition, with the other two treatments falling between, while the low emissions model led to minimal difference among treatments. However, compatibility scores remained below 3 in all treatments. Post-harvest, the adaptability score increased in all three active management treatments in the seedling class and decreased in the sapling class. Under the high-emissions scenario, the compatibility scores in the seedling class increased in no action and resilience and decreased in resistance and transition, while under low emissions, only resilience and transition changed significantly following harvest. In the sapling class, compatibility scores increased under high emission in no action, resistance, and transition, with no significant changes under low emissions Table 3.

3.4. Functional diversity

In both the seedling and sapling classes, functional indices showed little variation among treatments with the exception of functional evenness. In the seedling class, the resistance and resilience treatments had higher functional dispersion and redundancy after harvest, but there were no differences between the treatments (Fig. 5). Aside from functional evenness, sapling functional indices showed little to no change under management.

There were distinct functional profiles in pre-and post-harvest communities, as well as between treatments, as indicated by the arrangement of treatments in the final NMDS solution, which had stress of 0.05 (Fig. 6). These differences were confirmed by the MRPP analysis, which indicated significant differences between pre- and post-harvest functional profiles in resilience and transition, with no differences in no action and resilience. The traits that aligned most closely with no action and pre-harvest conditions were leaf size, wood density, maximum height, and shade tolerance, while the resilience and transition post-harvest aligned with high growth rate and leaf nitrogen content.

4. Discussion

Climate change threatens to alter forest health and function, with particular concerns focusing on how the regeneration layer, which is the future canopy, may be poised to withstand future climate conditions. Climate-adaptive forest management offers opportunities for managers to potentially assist forests in adapting to novel and changing conditions by making management decisions to direct composition of natural regeneration, but there is a gap between the theories that support these management approaches and empirical knowledge of their outcomes (Nagel et al., 2017). To build this body of knowledge, we compared five-year post-harvest regeneration composition in three active adaptive

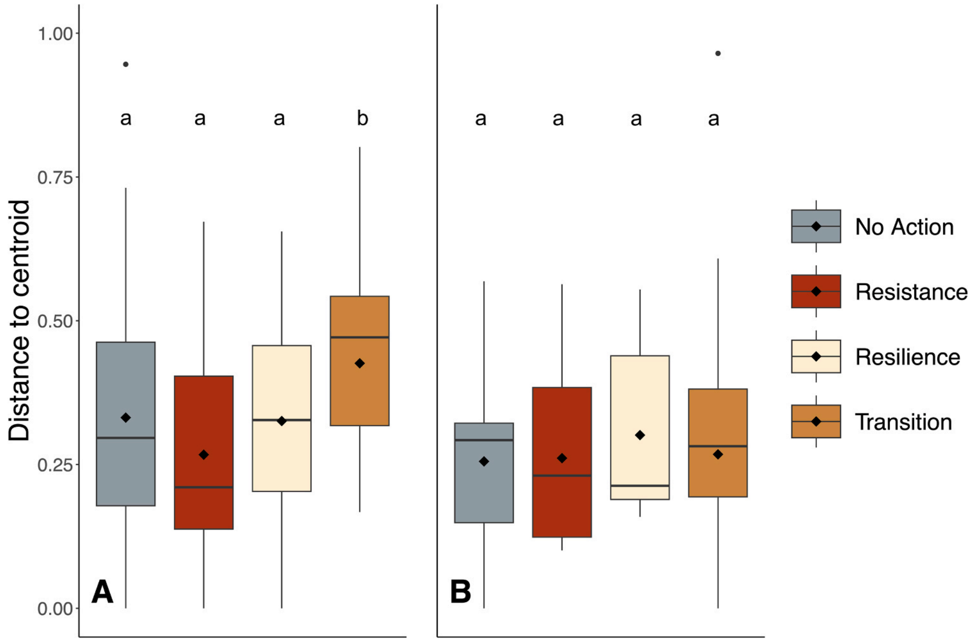

Fig. 3. Boxplots of species dissimilarity among measurement plots in four adaptation treatments in the seedling (A) and sapling (B) classes. The y-axis indicates the distance of observations to the group centroid. The central bar represents the median, box edges the first and third quartiles, and the diamond shapes the mean group distance to centroid. Boxes with different lowercase letters have significantly different mean distance to centroid based on ANOVA ($p < 0.05$).

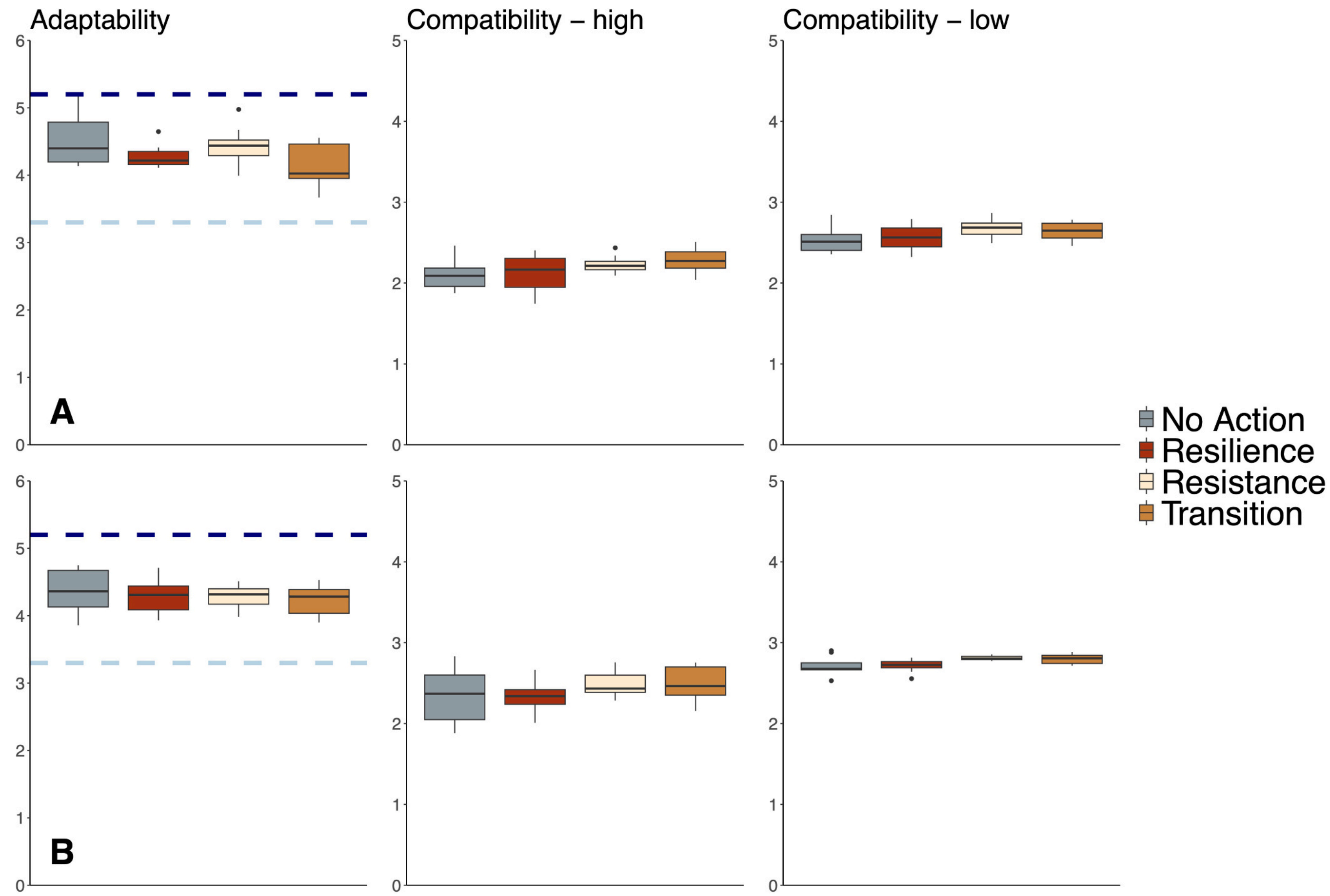

Fig. 4. Boxplots of adaptability and compatibility indices of naturally regenerated and planted seedlings (A) and saplings (B) following three adaptation treatments and no action approach. Central bar represents the median, box edges represent first and third quartiles. Whiskers represent minimum and maximum values, and points represent outliers. Adaptability indices are divided into three categories: low (<3.3; below light blue line), moderate (3.3<5.2; between light and dark blue lines), high (>5.2; above dark blue line). Compatibility index has 5 levels: 1: large decrease in future importance; 2: small decrease in future importance; 3: no chance in future importance; 4: small increase in future importance; 5: large increase in future importance.

Table 3
Mean (sd) Adaptability and compatibility indices of naturally regenerated and planted tree species change from pre- to post- harvest.

	Change		
	Adaptability	Compatibility - high	Compatibility - low
Seedlings			
No Action	-0.02 (0.35)*	0.12 (0.14)*	-0.16 (0.20)*
Resistance	0.27 (0.17)*	-0.15 (0.10)*	0.00 (0.05)*
Resilience	0.21 (0.15)*	0.28 (0.19)*	0.19 (0.06)*
Transition	0.23 (0.15)*	-0.12 (0.09)*	-0.12 (0.07)*
Saplings			
No Action	-0.11 (0.13)*	0.15 (0.11)*	0.03 (0.07)
Resistance	-0.20 (0.07)*	0.14 (0.07)*	0.01 (0.04)
Resilience	-0.19 (0.08)*	0.06 (0.09)*	0.02 (0.11)
Transition	-0.09 (0.10)*	0.13 (0.10)*	0.06 (0.09)

* indicates change significantly different than 0 at $p < 0.05$

management techniques and a passive approach to assess and compare treatment outcomes based on desired future conditions outlined before the harvest. We found that treatments did move regeneration composition toward desired future conditions, although shifts in functional diversity and identity, as well as projected adaptability and compatibility with future conditions, did not fully match with expected outcomes. The results described here, although short-term in nature, can inform climate-adaptive management of northern hardwood forests based on a set of desired future conditions that include adaptation to changing climate and disturbance regimes.

4.1. Adaptation treatment influence on regeneration abundance, composition, and diversity

The patterns exhibited by regeneration in each treatment and size class reflect multiple influences, vulnerabilities and responses to factors such as competition and canopy release effects, and likely include varying legacies of past stand disturbance (Harris et al., 2022). Divergence between seedling and sapling layer as a response to forest management, as we found, is not uncommon (e.g., Bédard et al., 2022; Reuling et al., 2019), as seedlings tend to reflect more recent management while sapling composition shows responses to a longer history of disturbance. The sapling composition we found across all four treatments can be described as a response to historic management activity, namely single-tree selection harvests, that perpetuated lower light conditions (Katz et al., 2010; Plotkin et al., 2013). Conversely, the seedling composition, which exhibited variation between treatments particularly with regards to shade-intolerant species, is more reflective of new pathways created by the adaptive management tactics. Seedling composition is also a response to seedbed conditions: in addition to sunlight, early successional species often require bare soil to germinate and yellow birch often regenerates on downed wood, while sugar maple regenerates well through leaf litter (Bolton and D'Amato, 2011). Therefore, management choices such as harvesting equipment and timing of harvest, both of which impact ground conditions, must be

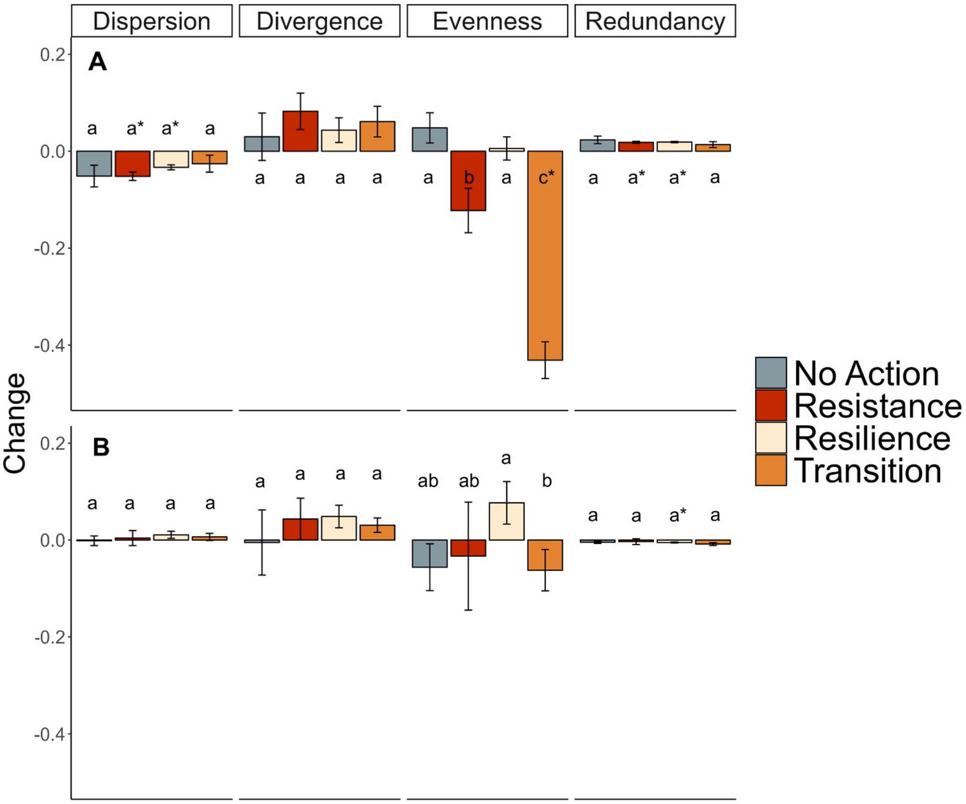

Fig. 5. Change in functional diversity indices in seedling (A) and sapling (B) size classes following four adaptation treatments. Bars represent standard error. Within each index, different letters represent statistical differences among treatments at $p < 0.05$. * indicates change significantly different from 0 based on t-test.

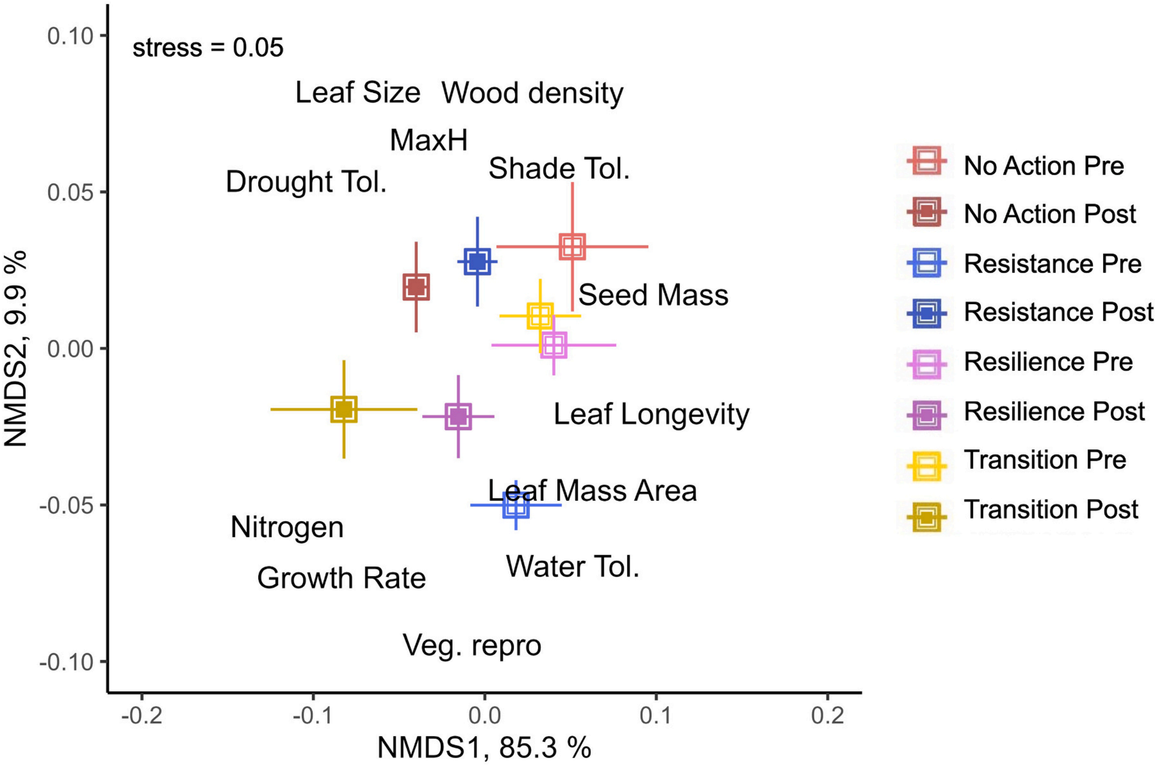

Fig. 6. NMDS biplots of forest functional trait profiles among the different ASCC treatments at Second College Grant, pre- and post-harvest. Presented are the first two axes of a three-dimensional ordination. Points represent the location of each treatment in 3-dimensional space and bars are standard error. Text represents functional traits arranged in space by weighted average scores.

considered when designing adaptation treatments. For example, winter harvests, which have the benefit of limiting negative impacts such as soil compaction, erosion, and rutting, may not create the desired ground conditions to shift species composition.

While both the resilience and transition seedling species composition diverged from overstory composition, resistance regenerated high amounts of sugar maple, consistent with canopy composition. Abundance of sugar maple and general dearth of shade intolerant species is a typical management legacy in northern hardwoods where single-tree selection has been the predominant management approach, especially on higher quality sites and those with reduced deer browse pressure (Henry et al., 2021; Knapp et al., 2019). The canopy gaps incorporated into the resilience and transition treatment provided conditions for natural regeneration of less common, shade-intolerant species, in line with the objectives of these approaches, although it is worth noting that these are early results: many of the dominant species in the seedling class are short-lived early successional species that will eventually cede dominance to longer-lived, and possibly more shade-tolerant species (Martin et al., 2021). Some studies in this forest type have found that yellow birch may be poised to ascend to the canopy (Bilodeau-Gauthier et al., 2020; Halpin et al., 2017), particularly in the larger canopy gaps like those created in the transition treatment, while other long term gap studies point to the eventual continued dominance of sugar maple as canopy gaps close through time (Knapp et al., 2019). As such, second or even third entries might be needed in areas treated with smaller canopy gaps to keep these less tolerant species as a significant component of the future stand (Arseneault et al., 2011; Leak, 2006, 1999).

Differences among treatments further reflect the specific canopy conditions created by each treatment, including spatial variation. Each adaptation treatment was developed with specific future conditions in mind, resulting in a unique set of stand-wide conditions that is reflected in the seedling composition and diversity and linked to the treatment objectives. Diverse structural conditions are often related to forest resilience as they can support greater ecosystem productivity, and diversity of pathways toward recovery from disturbance (Seidl and Turner, 2022; Yachi and Loreau, 1999). Single-tree selection, the resistance tactic, was originally developed to create uniformity across stands and regulate timber production (Arbogast, 1957), including dominance by commercially-important shade-tolerant species (Keyser and Loftis, 2013; Leak and Sendak, 2002; Neuendorff et al., 2007). Correspondingly, the resistance treatment, which is based on single-tree selection, tends toward low-light understory conditions and uniformity, supporting regeneration of shade tolerant sugar maple and minimal variation throughout the stand. At the other end of the spectrum, 20% of the harvest area in transition is allocated to open regeneration environments in the 0.4 ha gaps, and as such, short-lived shade tolerant species account for a substantial proportion of the regeneration. Resilience represents a balance between these two treatments, employing single-tree, group selection, and patch retention that includes elements of conditions found in both of the other active management treatments, with canopy gaps that support more intolerant regeneration, thinned areas to support tolerant regeneration, and reserves to carry forward current closed canopy conditions, including shade-tolerant sapling layers developed under previous management regimes. The resultant overstory spatial patterns in resilience include high resource conditions in canopy gaps, low light conditions in reserves, and moderate conditions in the thinned matrix, each of which may support a unique developmental trajectory (Getzin et al., 2008; Lian et al., 2022; Wikle and D'Amato, 2023). In the context of adaptive capacity, the resilience treatment may offer the greatest diversity of conditions across an individual stand, and an ability to absorb and respond to many climate change impacts, while resistance and transition treatments might be most appropriate for specific cases where there are compelling reasons to either maintain the current forest type (resist), such as refugia or unique conditions or actively facilitate change (transition) in cases where extreme changes are projected or the shade-tolerant components of the forest are particularly vulnerable (Millar et al., 2007).

4.2. *Species composition projected response to climate change*

While the changes exhibited in the adaptability and compatibility indices across treatments were small, they reflect general expectations associated with the vulnerability of species currently present on site. The compatibility index describes whether individual species are likely to increase on site with a changing climate, and few northern hardwood species fit this projection; under a high-emissions scenario, sugar maple, yellow birch, and beech may all decrease in importance or remain at similar importance levels (Iverson et al., 2019a), while those projected to increase (white pine, hemlock, northern red oak) are present in only low abundances across these sites, and generally only where planted. Although higher severity harvests often result in greater divergence between canopy and regeneration composition (Keyser et al., 2020), natural regeneration is limited to the canopy species present and by their dispersal ability. As a result, large changes in these communities are not likely without supplemental planting. The current dominance of maple, birch, and beech reflects the suitability of historic and current climate and disturbance patterns for their growth and survival. Nevertheless, a rapidly changing climate may lead to conditions where mature trees occupy an environment that is no longer conducive to regeneration of the same species, while species that may be better climatically adapted to site conditions are not present as a seed source for natural regeneration (Decker et al., 2021; Zhu et al., 2012). This highlights the value of the assisted migration plantings in this study – not to create a new forest, but rather to plan ahead for a greater diversity of seed sources in the future (Duveneck and Scheller, 2015).

4.3. *Functional diversity and identity*

Functional evenness was the only functional diversity measure with notable differences between treatments and from pre- to post-harvest, with a reduction in this index occurring in resistance and transition in the seedling size class. Lower functional evenness describes uneven resource use across a site, often indicating underutilized niche space, or some level of available resources on site (Mason et al., 2005; Villéger et al., 2008) sometimes realized by a decrease in productivity or accumulated biomass compared to sites with high evenness. In other words, stands with reduced functional evenness leave some resources "on the table," which could mean reduced biomass accumulation or resources available for an invading species (Ali et al., 2018). There are many reasons why functional evenness might be negatively influenced by harvesting. The reduced functional evenness in resistance may be a result of the uniformity of understory conditions, where competition and past management have supported the dominance of sugar maple at the expense of other species that might use available resources. Conversely, the reduced functional evenness in transition may be due to the stark differences in resource availability between large canopy gaps, reserve patches, and matrix forest, leaving unoccupied trait space even five years post-harvest. The minimal variation among the other indices is supported by other studies of functional diversity under various forest management that similarly report that management does not always result in significant changes to functional diversity when there are only a few dominant species, particularly when harvests are low to moderate in severity (Curzon et al., 2017; Keyser et al., 2020).

The differences among functional profiles in each treatment provide greater context for the relationship between adaptive capacity and functional traits. Adaptive capacity is generally not contingent on a single trait, but rather presence and relationships of multiple traits, and further, many functional traits represent tradeoffs between various adaptation strategies (Wilfahrt, 2018). For example, high nitrogen content per leaf mass, which was aligned with the resilience and transition treatments post-harvest, supports fast growth, but at the expense of protection from herbivory, while fast relative growth rate provides for a competitive advantage conferred by access to sunlight, but may result in a sacrifice of wood density, creating vulnerability to embolism under drought conditions (Funk et al., 2017; Wilfahrt et al., 2014). The value of specific traits for adaptive capacity may also require further context than simply presence of a species, as seed mass, a trait often associated with drought adaptation, was aligned with pre-harvest conditions but driven largely by the beech component, which is primarily root sprouts that will never reach reproductive size due to the current impacts of beech bark disease and projected expansion of beech leaf disease (Cale et al., 2017). Another caveat to linking functional identity to adaptive capacity relates to contributions that we did not measure, such as phenotypic and genetic diversity, which will influence the adaptive abilities of individual trees and may vary based on location within a species' range (Aitken et al., 2008; Royer-Tardif et al., 2021). Despite these caveats, the divergence of post-harvest functional trait profiles between treatments reflects moderate success of the treatments at directing the stands toward a desired future. In particular, while the assisted migration plantings may have resulted in minimal changes in stand-wide species composition, the addition of novel and/or redundant traits into the system had a noticeable effect. The two traits that supported the divergence of post-harvest transition treatment from the other treatments are nitrogen content per leaf mass and growth rate, and trees with higher values of these traits include planted species *P. grandidentata, P. serotina, P. strobus, and Q. rubra* (Paquette and Messier, 2011), all of which are projected to gain future habitat in our study region under changing climate.

4.4. Management implications and conclusions

The adaptive silviculture treatments examined here offer potential pathways forward for managers seeking to manage forests toward adaptation by providing insight into how specific prescriptions may achieve desired future conditions linked to adaptive capacity. Each treatment resulted in a unique set of conditions that aligned with goals related to resistance, resilience, and transition, aligning our outcomes with other studies in the ASCC network (e.g., Wiechmann et al., 2022), emphasizing the value of outlining and managing toward ecosystem-specific desired future conditions to improve adaptive capacity (Nagel et al., 2017). In this northern hardwood ecosystem, silviculture with a focus on natural regeneration was able to achieve many goals related to climate adaptation, but management with a focus on transition benefited from assisted migration plantings to further shift species and functional composition away from current conditions. While each treatment led to unique regeneration composition, differences among treatments were small and some may be ephemeral, illustrating the importance of both long-term monitoring to better understand the relationships between silvicultural prescriptions and desired future conditions, and repeated entries to continue to influence forest composition and structure, particularly as changing environmental conditions evolve.

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CRediT authorship contribution statement

Anthony W D'Amato: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Kevin S Evans**: Writing – review & editing, Methodology, Investigation, Conceptualization. **Jessica L Wikle**: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

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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