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Structural outcomes of climate adaptation treatments in two contrasting northern temperate forests

Jessica L. Wikle [a,*], Anthony W. D'Amato [a], Brian J. Palik [b], Christopher W. Woodall [c], Kevin S. Evans [d], Linda M. Nagel [e]

[a] *Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, VT, USA*
[b] *USDA Forest Service, Northern Research Station, Grand Rapids, Minnesota, USA*
[c] *USDA Forest Service, Northern Research Station, Durham, New Hampshire, USA*
[d] *Dartmouth College Woodlands, Dartmouth College, Milan, NH, USA*
[e] *Quinney College of Natural Resources, Utah State University, Logan, Utah, USA*

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ABSTRACT

Forest managers require climate adaptation strategies that are regionally relevant and translatable into planning processes. Adaptation frameworks, such as the resistance, resilience, transition framework, can guide the development of these strategies. However, there are limited examples of how these concepts can be operationalized with concomitant estimates of changes in forest structural complexity and diversity, which may support adaptive capacity. To address this knowledge gap, two operational-scale, replicated experiments were studied to understand how application of the resistance, resilience, transition framework influences stand structure in two contrasting northern forests: mixed pine and mesic hardwoods. We found that treatments corresponding to each adaptation approach (resistance, resilience, transition) manifested differently in each forest type. In mixed-pine, there were greater differences in structural diversity metrics among treatments; there were fewer differences among treatments in the mesic hardwood forest, which had comparatively greater pre-treatment structural variation. In both forests, our analyses demonstrate that management strategies associated with greater emphasis on change and adaptation (i.e., resilience and transition) created a quantifiably more heterogeneous arrangement of structural elements across treatment units, supporting shifts in stand-scale understory resource patterning. These results underscore the importance of accounting for the influence of pre-treatment stand conditions on outcomes of adaptation treatments and that stand-wide averaging of plot measurements may serve to obscure stand-scale diversity metrics. The variation in structural conditions across stands that we found is expected to contribute to forest response to novel disturbances by providing multiple recovery pathways. Based on these findings, application of adaptive silvicultural treatments can generate varying levels of structural heterogeneity at the stand-scale which in turn can confer adaptation potential; however, ecological memory strongly influences post-management stand conditions.

1. Introduction

Changing disturbance and climate patterns influenced by global change threaten to limit the productivity and function of forests worldwide through mechanisms such as drought, increased storm intensity, and changing temperature patterns and seasonality (Seidl et al., 2017). The impacts of these changes may be exacerbated by legacies of past management, including outcomes of timber-focused forestry, which have increased forest vulnerability by simplifying forest structure and reducing compositional diversity, a factor that contributes to greater vulnerability to current and emerging stressors, as well as eliminating habitat for key plant and animal species (D'Amato and Palik, 2021). This vulnerability may ultimately limit the ability of forests to function as they have historically and continue to provide desired ecosystem services (Messier et al., 2014). Growing concerns about impacts of emerging novel climatic conditions combined with legacies of past land use have prompted some managers to seek ways to alter management to increase forest adaptive capacity to global change (Bradford et al.,

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* Corresponding author.
E-mail address: jessica.wikle@uvm.edu (J.L. Wikle).

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2018).

The adaptive capacity of a forest is contingent upon structural complexity and heterogeneity at multiple scales (D'Amato and Palik, 2021; Thurman et al., 2020). Diversity in age classes and tree size may buffer forests from effects of wind and ice storm events (Allen et al., 2012) while retained biological legacies are key elements of ecological memory (cf. Johnstone et al., 2016) and can perpetuate ecosystem processes, protect young trees, and benefit wildlife species (Franklin et al., 1997). Spatial variation of structure in the form of canopy gaps and intact patches allows for a diversity of structural conditions; these may include microsites that may encourage regeneration of less common species and support existing conditions or features of interest (Brodie and Harrington, 2020). Given these mechanisms, forest adaptation treatments emphasize increasing diversity and heterogeneity in forest structure and composition at multiple spatial scales (Churchill et al., 2013; D'Amato and Palik, 2021).

In concert with this greater emphasis on forest structural complexity has been a growing body of literature on methods for measuring complexity. A number of metrics exist to quantify structural complexity, each linking to unique features and adaptations, and typically some combination of these metrics is required for a complete picture of complexity (McElhinny et al., 2005). Diameter class diversity is one such metric that can be quantified in multiple ways with higher values linked to greater presence of microhabitats within stands and microclimate temperature modulation in forests (Ehbrecht et al., 2019; McElhinny et al., 2005), features that support adaptive capacity. Another important structural metric relates to tree spacing, which influences factors such as competition, resource availability, and fire spread (Churchill et al., 2013). In recent years spatial counterparts to structural indices have emerged; these tend to be correlated to non-spatial metrics but offer greater granularity into forest structure patterns (Kuehne et al., 2015). In general, these metrics link to greater disturbance recovery capacity with each microhabitat or distinct condition supporting a unique disturbance recovery pathway (Puettmann and Messier, 2020). More specifically, these structural metrics may describe particular features of adaptive capacity that vary based on ecosystem, creating a need for thoughtful interpretation. For example, when considering size class diversity, high diversity paired with high stand density may indicate a stratified temperate hardwood forest resistant to novel disturbance, but in a fire-prone ecosystem describe a fire-vulnerable stand with dense ladder fuels (Ziegler et al., 2017). In the case of aggregation, a forest stand that includes both tree groups and open space may support a greater number of microhabitat conditions, but each of those clumps or openings may individually be vulnerable to wildfire, insect outbreak, or invasion by exotic plant species (Churchill et al., 2017). For these reasons, context is critical when drawing connections between complexity and adaptive capacity.

Frameworks have been proposed for management to confer greater adaptive capacity to forests (Millar et al. 2007; Messier et al. 2019). The most cited of these is the *resistance, resilience, transition* (response sensu Millar et al. 2007) framework, hereafter, RRT (Nagel et al. 2017). Broadly, *resistance* focuses on tactics to minimize the impacts of climate change and other stressors, with intent to maintain current species composition, forest structure, and function. *Resilience* allows for gradual or small changes but remains within the range of natural variation. Finally, *transition* actively facilitates responses to changing conditions, including shifting dominant species and structures. These strategies represent a gradient of change, with resistance maintaining current conditions, resilience introducing variation, and transition fostering change.

There is conceptual support for the RRT framework, (Conroy et al., 2011; Millar et al., 2007); however, little empirical evidence exists for how RRT approaches can be operationalized in a given ecosystem, or the specific tactics necessary to achieve desired outcomes. To address these needs, the Adaptive Silviculture for Climate Change network (ASCC; Nagel et al., 2017) was established as a multi-ecosystem, large-scale experimental test of adaptation strategies in a variety of North American forest ecosystems. The ASCC network employs the RRT framework, as well as a no action, or passive, treatment. The RRT prescriptions are co-produced locally (Hallett et al., 2017) by managers and scientists familiar with historical management approaches, ecological conditions, and site constraints. There is a need for evaluating the efficacy of localized RRT strategies at achieving adaptation goals, and how this varies depending on the ecosystem.

To address this need, we assessed post-harvest outcomes of RRT adaptation strategies in two ecologically and economically important forest types in the United States: a New England northern hardwood forest and a lower density mixed-pine woodland in the western Great Lakes region, using measures of structural complexity as a proxy for adaptive capacity. We asked the following questions: *1) How do adaptation (approaches arranged along an RRT gradient of increasing facilitation of change) meet objectives of enhancing structural features that may support adaptive capacity; and 2) How do these adaptation approaches differ in outcome in two different forest types?* We hypothesize that: 1) greater stand-level variation in structural, and disturbance severity indices will occur in resilience and transition treatments than in control and resistance treatments, as a result of treatments applied either uniformly (resistance, control) or variably (resilience, transition) across the treatment area, and 2) north temperate red pine (*Pinus resinosa* Ait.) forests, with lower initial species and structural diversity, will show greater response to adaptation treatments than northern hardwoods, which has greater initial diversity. Answering these questions will provide guidance for managers applying adaptation strategies in similar forest ecosystems and represents, to our knowledge, the first multi-ecosystem evaluation of structural outcomes of RRT strategies.

2. Methods

2.1. Study ecosystems and treatments

Second College Grant (SCG) is a 10,800-ha forest in northern New Hampshire, USA owned and managed by Dartmouth College. The forest is in the temperate-boreal transition zone, and within the 160-ha study area, primarily northern hardwood forest (Table 1). The SCG experimental design was a randomized block, consisting of 4 40-ha blocks with each of four treatments covering 10 ha (Fig. 1). In addition to the RRT treatments (described below), a no action treatment was included in each block. Harvesting took place in late summer and fall of 2017 using hand felling and cable skidding.

The SCG resistance prescription consists of single-tree selection with removal across all diameter classes based on Arbogast guidelines for single-tree selection to achieve a reverse-j diameter distribution (Table 2; Arbogast, 1957), while maintaining current species relative composition and 16–18 m^2 ha^{-1} of basal area. The resilience treatment is a hybrid single-tree and group selection system with 20 % of the area in 0.04 and 0.1-ha gaps, 20 % in permanent reserves (skips) of equal size to the gaps, and the remaining matrix thinned to 16–18 m^2 ha^{-1}, with trees of all sizes removed and emphasis on retention of disease-resistant beech and trees exhibiting healthy crown and vigorous growth across all species. Transition is a variable density thinning/continuous cover irregular shelterwood, with 20 % of the area in 0.1 – 0.4-ha gaps (large enough to promote regeneration of less tolerant species such as yellow birch), 10–20 % in uncut patches similar in size to gaps, and the remaining matrix reduced to a basal area of 16–18 m^2 ha^{-1} through single-tree selection. Gaps are located near mature yellow birch and red spruce to encourage regeneration of these species, and some gaps are planted with species projected to be better adapted to future climate change and/or disturbance regimes. These include the following present but locally uncommon species (population enrichment): red spruce (*Picea rubens* Sarg.), white pine (*Pinus strobus* L.), bigtooth aspen (*Populus grandidentata* Michx.), black cherry (*Prunus serotina* Ehrh.), northern red oak (*Quercus rubra* L), eastern hemlock (*Tsuga canadensis* (L.)

Table 1
Study site descriptions of Second College Grant and Cutfoot Experimental Forest.

	Elevation (m.a.s.l)	Mean annual temperature[a]	Annual precipitation (cm)[a]	Soils[b]	Dominant species	Historic disturbance regime	Global change concerns
Second College Grant	484–650	-12° C (Jan.), 17° C (July)	117.9	Coarse loamy glacially-derived tills	*Acer saccharum* Marsh., *Fagus grandifolia* Ehrh., and *Betula alleghaniensis* Britt., with smaller components of *Picea rubens* Sarg.), *Abies balsamea* (L.) Mill, and *Pinus strobus* L.	Small-scale gap disturbances with occasional large wind events. [c] Timber focused management leading to simplified structure and composition[d]	Changing precipitation regimes, stronger and more frequent storms, invasive plants and pests[f]
Cutfoot Experimental Forest	399–424	-20° C (Jan.), 27° C (July)	68.8	Loamy sands derived from glacial outwash, somewhat excessively drained	*Pinus resinosa* Ait., with smaller components of *Pinus strobus* L., *Pinus banksiana* Lamb., and various hardwoods	Mixed-severity fire, both natural and applied by Indigenous peoples, generating spatially complex woodland structures[e]	Drought stress, encroachment of fire-sensitive hardwoods, simplified forest structure, increased wildfire risk[f]

[a] Prism Climate Group, 2021
[b] NRCS, 2020
[c] Hanson and Lorimer, 2007
[d] Fraver et al., 2009
[e] Stambaugh et al., 2021
[f] Swanston et al., 2018

Carrière), and three 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.). These plantings are detailed in Clark et al., (2021).

The Cutfoot Experimental Forest (CEF) ASCC site is on the Chippewa National Forest in northcentral Minnesota, USA. It is a red pine-dominant woodland, with other species present (Table 1.) and prior to harvest, the stands were even-aged and fully stocked based on Benzie (1977). The experimental design, encompassing 200 ha, was a randomized block, consisting of 5 40-ha blocks with each of four treatments covering 10 ha (Fig. 1). As with SCG, a no action treatment was included in each block, along with RRT treatments, as described below. Harvesting occurred during the winter of 2014 and 2015 using a tracked feller buncher and grapple skidder.

The CEF resistance prescription is a uniform thinning, with residual basal area of 23–28 m^2 ha^{-1} (Table 2). Both before and after harvesting, red pine accounted for a minimum of 90 % of the basal area, and each minor species comprised less than one percent of total basal area. The resilience treatment consists of a variable density thinning with 15 % of the stand area in 0.2-ha gaps, 15 % in 0.2-ha uncut skips, and the matrix reduced to a basal area of 23–28 m^2 ha^{-1} through single-tree marking, primarily from below. An overall resilience treatment objective was to retain red pine dominance but at a lower relative basal area than the resistance treatment, with minor species increasing in relative basal area. The transition treatment consisted of the first entry of an expanding-gap irregular shelterwood with 15 % of the stand area in 0.2-ha gaps, and the remaining matrix single-tree marked to 14–18 m^2 ha^{-1}, with selection based on species targets and removal from below. The resilience gaps and transition stands had site preparation with a disk harrow to sever root systems of *Corylus cornuta* Marsh., expose mineral soil, and improve regeneration conditions, and were planted with a suite of native and novel species predicted to be future-adapted: eastern white pine, red maple (*Acer rubrum* L.), northern red oak, bur oak (*Quercus macrocarpa* Michx), white oak (*Quercus alba* L.), bitternut hickory, black cherry, and ponderosa pine (*Pinus ponderosa* C. Lawson); described in Muller et al., (2019).

2.2. *Field sampling*

Plots were installed pre-harvest at both sites, with a variable number of plots based on treatment (Table 3). For the no action and resistance treatments, each stand contained 10 (SCG) or 7 (CEF) nested plots randomly located throughout the unit. For the resilience and transition treatments a random stratified procedure was used, with plots located in gaps, skips, and thinned matrix, to capture within-treatment variability. At SCG, there were 14 and 15 plots for resilience and transition, respectively, while at CEF, both treatments had 11 plots.

At SCG, plots were measured in 2019, two years after harvest. Overstory trees (living and dead) $\geq$ 10 cm diameter at breast height (DBH=1.3 m) were tallied in a circular 0.04-ha plot, with each tree identified to species and measured for diameter. For snags, height and decay class was noted. Saplings (2.5–9.9 cm DBH) were recorded in three nested 0.004-ha subplots located along azimuths of 0°, 120° and 240° at a distance of 5.5 m from the main plot center. Regeneration taller than 30.5 cm tall and smaller than 2.5 cm DBH was tallied in 1.26 m radius subplots nested within each sapling plot.

At CEF, plots were measured in 2016, two years after harvest. Living and dead overstory trees $\geq$ 12.7 cm DBH were tallied in a circular 0.08-ha main plot. Each tree was identified to species and measured for diameter (as above). For snags, decay class was recorded, and height determined if the snag was snapped. Saplings (8.8–12.7 cm DBH) were measured in a nested 0.04-ha plot located at main plot center. Regeneration (taller than 30.5 cm and $\leq$ 8.9 cm DBH) was recorded in three nested 0.004-ha subplots located at center of the main plot and at azimuths of 90° and 270°, 8 m from plot center.

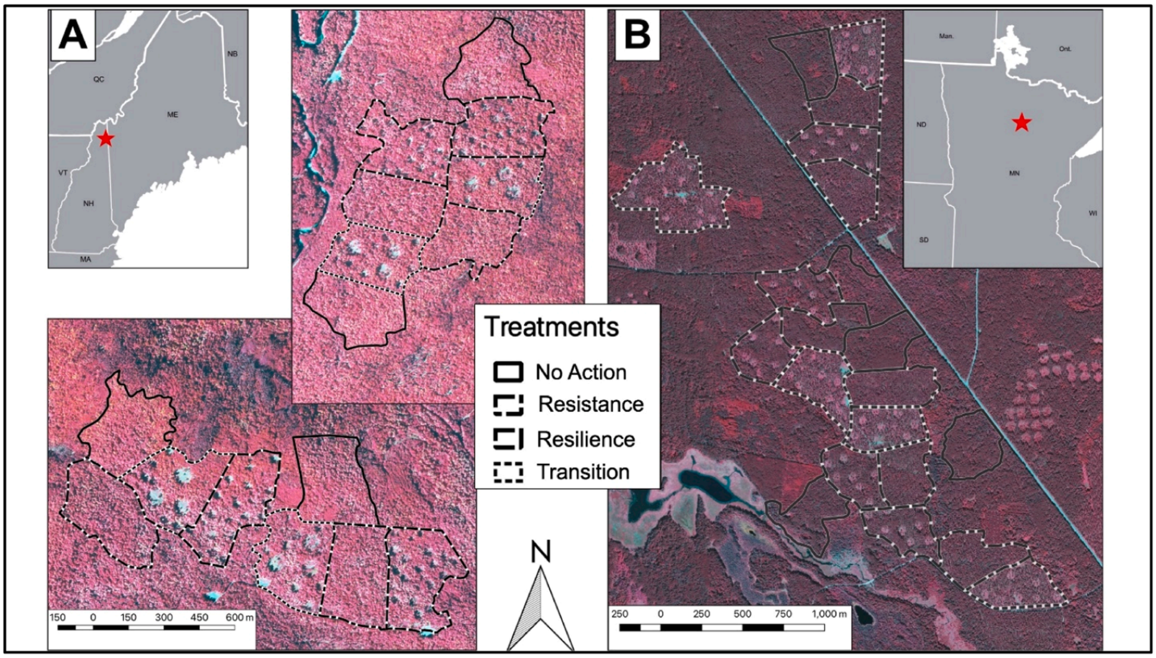

Fig. 1. Location and treatment layout of Adaptive Silviculture for Climate Change project at Second College Grant (A) and Cutfoot Experimental Forest (B). Maps created in QGIS 3.16. Source: NH 2108 NAIP CIR (SCG; NH Granit, 2018); MN 2017 NAIP CIR (CEF; Minnesota Geospatial Commons, 2017).

2.3. Data analysis

2.3.1. Forest structure

All analyses were carried out in R version 4.1.3 (R Core Team, 2019). We quantified structure using spatial and non-spatial metrics, chosen based on links to adaptive capacity, support of use in literature, and compatibility with our data collection (Table S1). We assessed diameter distributions with the following non-spatial metrics: i) Gini coefficient of tree diameters (Gd; Weiner and Solbrig, 1984), with the *reldist* package (Handcock, Mark S., 2016); ii) Shannon diversity of diameter classes (Hd; Staudhammer and LeMay, 2001), with the *vegan* package (Oksanen et al., 2019); and iii) coefficient of variation of DBH values (CVd). The Clark-Evans aggregation index, which measures clustering of trees, was used to assess spatial patterns (Clark and Evans, 1954). We used the following spatially explicit measures based on four nearest neighbors to examine overstory structure; i) DBH differentiation index (DDI), which is a measure of tree size interspersion; ii) mean directional index (MDI), which examines spatial arrangement of trees; and iii) species mingling index (MI), which is a spatial approach to species composition (Kuehne et al., 2015), all assessed using the *spatstat* package (Baddeley and Turner, 2005). We calculated a structural complexity index (SCI; Zenner and Hibbs, 2000), which is determined using all trees in a plot. SCI represents a spatially explicit counterpart to the Gini index and was calculated by performing two Delaunay triangulations on each plot using *spatstat* – one with tree diameter as marks, and one without – and calculating the ratio of 3D:2D triangulation.

2.3.2. Disturbance severity index

We calculated total aboveground biomass at each site (trees, saplings, and snags) both pre- and post-harvest within each sample plot following Chojnacky et al., (2014). We used these values to calculate a disturbance severity index for all treatments including no action (DSI; Kurth et al., 2019), defined as the change in total aboveground biomass at the plot level in the time span from before harvest to two years after harvest, standardized by dividing the total change by pre-harvest biomass. We interpreted the distribution of DSI within a given treatment as a reflection of understory resources available based on variation and pattern in harvest severity (or stand development in the case of no action), with lower values corresponding to low understory resource availability (i.e., areas containing an undisturbed canopy) and higher values corresponding to high resource availability to the understory (i.e., harvest openings).

2.3.3. Statistical methods

We used non-metric multidimensional scaling (NMDS) as a visualization tool to examine gradients in structural variation across treatments. We included the mean as well as the coefficient of variation (CV) of each index as column values, and treatment blocks as rows. We used scree plots of stress in response to dimensionality to select an appropriate number of dimensions for each model, selecting dimensions based on the point beyond which there was minimal stress reduction. Stress is calculated as the relationship between original data distances and ordination distances and represent NMDS model fit, with values less than 0.2 indicating good fit (McCune et al., 2002). Scree plots indicated use of three dimensions for SCG and two for CEF. Distance matrices were created using Bray-Curtis dissimilarities. We calculated the percentage of variability encompassed by each axis by performing a linear regression between the distance in ordination space for each axis and the distance in original space and described the axis variability using the incremental r^2 value. The NMDS models were performed using the *metaMDS* function in the *vegan* package.

We fit linear mixed effects models to compare differences in structural indices across the four treatments. We also compared differences among the micro-treatments encompassed by the four treatments: these include gap, thin16 (thinning to 16–18 m^2 ha^{-1}), single tree selection, and uncut at SCG; and gap, thin11 (thinning to 11–18 m^2 ha^{-1}), thin23 (thinning to 23–28 m^2 ha^{-1}), and uncut at CEF (Table 3). For all models, treatment or microtreatment was the fixed effect, block was the random effect, we evaluated alternative error distributions (negative binomial, gamma) and selected the error structure that provided the best model fit, and used“weights” option to allow for unequal variance structure between treatment levels. All models were fit using the *nlme* package (Pinheiro et al., 2020) and tested for normality using the plot function. We used Tukey’s pairwise tests to analyze differences between treatments using the *multcomp* package (Hothorn et al., 2008). Results were considered significant at $p < 0.05$. We used Levene’s test in the *car*

Table 2
Silvicultural prescriptions and desired future conditions in Adaptive Silviculture for Climate Change Treatments at Second College Grant (SCG), NH and Cutfoot Experimental Forest (CEF), MN.

	Resistance		Resilience		Transition	
	SCG	CEF	SCG	CEF	SCG	CEF
Silvicultural prescription	Single-tree selection	Uniform thinning	Single-tree/group selection	Variable density thinning	Irregular shelterwood/variable density thinning	Expanding gap irregular shelterwood
Prescription details	Occasional groups of 2–3 canopy trees removed, retain resistant individuals	10–15 year cutting cycle	20 % of area in gaps (0.04–0.1 ha), 20 % in reserves, thinned matrix, 20 year cutting cycle	15 % in 0.2 ha gaps, 15 % in 0.2 ha reserves, thinned matrix, 10–15 year cutting cycle	20 % of area in gaps (0.1–0.4 ha), 10–20 % uncut during first entry, thinned matrix	15 % of stand in 0.2 ha gaps
Canopy Structure	Reverse-J diameter distribution, multi-age/size	Even aged, consistently at or just below full stocking	Multiple age classes, uneven-aged, ultimately ~5 cohorts, stand scale heterogeneity in structure	Multiple age classes, more large trees, increased diversity and heterogeneity of stand structures	Uneven-aged, irregular vertical and horizontal structure, 50 % canopy cover across stand on average	Multi-cohort, structural complexity across stand, more large trees, fully stocked
Composition	Maintain current: Sugar maple > beech > yellow birch > red maple > red spruce > other	Red pine 90 % of basal area, each minor species no more than 1 %	High species diversity, reduced sugar maple component, increase in other species	Retain red pine dominance, but increased representation of future-adapted species currently present on site	Dominance of currently onsite species adapted to future climate change (yellow birch, red maple, beech); increased proportion of future-adapted species not currently onsite	Red pine present, but not dominant; increased proportion of future-adapted native and novel species
Target Basal Area	Minimum 16–18 m^2ha^{-1}	23–28 m^2ha^{-1}	Minimum 16–18 m^2ha^{-1} as stand average, with variation through space	23–28 m^2ha^{-1} average, with range from 0 (gaps) – 45+ (reserves) across stand	16–18 m^2ha^{-1} through matrix for 14–16 m^2ha^{-1} as across-stand average	14–18 m^2ha^{-1} between canopy gaps

package (Fox and Weisberg, 2019) to compare standard deviation across treatment levels as an assessment of stand-level variation in each treatment. To assess treatment-level differences in the distribution of DSI with each plot represented as a separate observation, we used the Kolmogorov-Smirnov test in the base R stats package and conducted pairwise comparisons.

3. Results

3.1. Second College Grant

3.1.1. Treatment level structure

The NMDS (stress = 0.02) illustrated differing amounts of variation within treatments (Fig. 2a). The first axis, which explained 94.1 % of the variation, reflected separation among treatments driven by CV values, or treatment scale variation. Correspondingly, no action and resistance were found in the negative portion of this axis, which was characterized by higher structural index values and lower CV values, whereas resilience and transition were found in the positive portion, which was associated with high CV values. The second axis described only a small portion of model variability and was associated most strongly with MI, with a high CV value found in the positive portion of the axis and high index value in the negative portion. No action and resistance overlapped on the NMDS, as did resilience and transition.

All RRT treatments reduced overstory basal area, density, and biomass in comparison to no action, with transition having the greatest reduction, although the basal area reduction in resistance was not statistically significant (Table 4, Fig. 3a). QMD remained highest in no action and decreased along the RRT gradient. All treatments reduced the number and basal area of snags and number of large trees (> 40 cm DBH). Structural indices varied minimally among treatments, with only DDI, MI, and SCI decreasing along the gradient of change (Table S3). However, these same indices exhibited variation within treatments with Levene's test of variance indicating significant differences for DDI, with transition significantly different than the other three treatments. Indices of variation in tree size (Hd, Gd and CVd) were all highest in resistance, but otherwise decreased along the change gradient (Table S3). In general, index values were smaller along the change gradient, with transition consistently exhibiting lower values.

3.1.2. Disturbance severity index

The plot-level DSI ranged from −0.1 – 0.46 in no action, −0.06 – 0.5 in resistance, −0.1–0.94 in resilience, and −0.07 – 0.96 in transition (Fig. 4a). These values represent change created by harvest activities, with the exception of no action, which reflects changes occurring through natural processes. The distributions for DSI, which reflect removed aboveground biomass and therefore variation in understory resource environments (e.g., light availability) at a stand scale, for no action, resistance, and resilience were statistically different from one another, while transition only differed significantly from no action.

3.1.3. Within treatment structure

When analyzed by micro-treatment, all structural indices in gaps were significantly lower than other components, but otherwise no differences were significant, with the exception of Gd, which was highest in single tree selection and lowest in uncut (Table S2). The differences detected for gap conditions may be an artifact of the analysis requirements as a number of analyses for gap plots (17/32) reported null structural values due to a need for more than three trees to calculate the index. Levene's test of variance showed significant differences ($p < 0.05$) among treatments for Gd, CVd, CE, DDI, and MDI, with gaps consistently having the largest standard deviations (Table S2).

Table 3
Summary of micro-treatments, or within-stand structural conditions making up ASCC treatments, percentage of treatment area covered by each, and number of plots used to assess each treatment and its components at SCG and CEF ASCC sites.

Treatment	SCG			CEF		
	Micro-treatment	Plots	Percent of treatment area	Micro-treatment	Plots	Percent of treatment area
No Action						
	uncut	40	100	uncut	35	100
Resistance						
	sts	40	100	thin23	35	100
Resilience						
	thin16	24	60	thin23	15	70
	gap	16	20	gap	15	15
	uncut	17	20	uncut	25	15
Transition						
	thin16	28	60	thin11	30	85
	gap	16	20	gap	15	15
	uncut	16	20			
Total Plots		197			170	

Notes: uncut = no trees were harvested, sts = single tree selection, thin16 = thinning to 16–18 m^2ha^{-1}, gap = canopy gap 0.04 – 0.2 ha in size, thin23 = thin to 23–28 m^2ha^{-1}, thin11 = thin to 11–18 m^2ha^{-1}

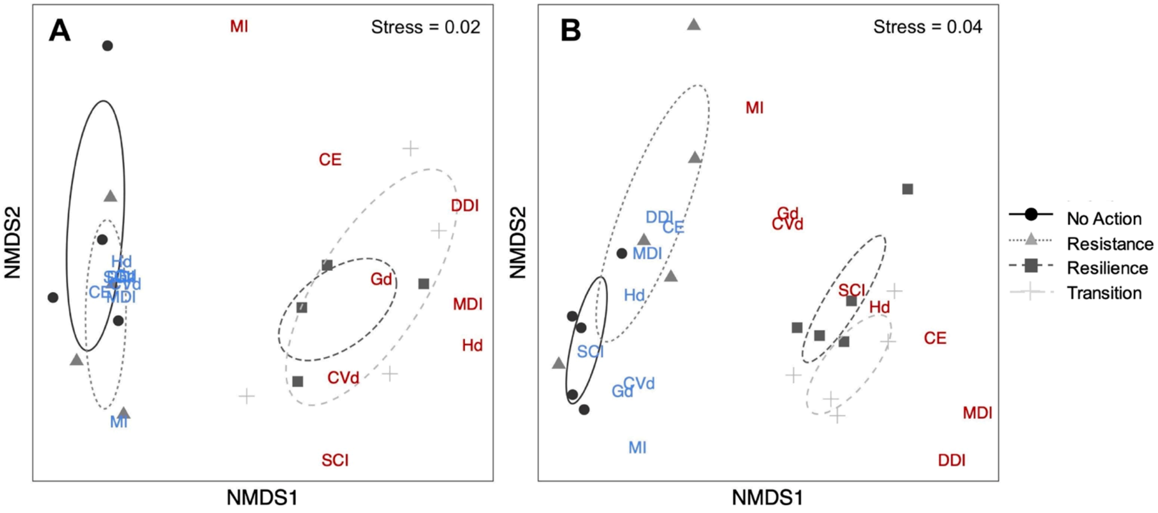

Fig. 2. NMDS biplots of forest structural indices among the different ASCC treatments at Second College Grant (A) and Cutfoot Experimental Forest (B). Presented are the first two axes of a three-dimensional ordination (A) and two-dimensional ordination (B). Elli pses represent the standard deviation of treatments. Text represents structural indices arranged in space by weighted average scores: blue indicates mean and red indicates coefficient of variation for each index.Abbreviations are as follows: Hd = Shannon diversity of diameter classes, Gd = Gini coefficient of diameter classes, CVd = Coefficient of variation for tree diameters, DDI = diameter differentiation index, MDI = mean directional index, CE = Clark-Evans index of aggregation, SCI = structural complexity index, MI = species mingling index.

3.2. *Cutfoot Experimental Forest*

3.2.1. *Treatment level structure*

Similar to SCG, the NMDS for structural indices (stress = 0.04) reflected CV values describing separation among treatments, with no action and resistance similar to each other and resilience and transition also grouped by similarity (Fig. 2b). The first axis (93.5 % variability) illustrated divergence based on CV for the indices, with no action and resistance treatments found in the negative portion of the axis with corresponding higher structural index values, and resilience and transition associated with high coefficient of variation values. The second axis highlighted differences described by MI, Gd and CVd.

Treatments resulted in a reduction in aboveground biomass, basal area, and trees per hectare, with the greatest reduction in the transition treatment (Table 4, Fig. 3b). The density of snags and large trees diminished along the change gradient, while QMD increased along the same gradient. Both Gd and CVd were highest in no action and lowest in resilience (Table S4). Hd as well as spatially explicit DDI, SCI and MDI exhibited a decrease along the change gradient. CE was highest in resistance, indicating high uniformity in these plots. Levene's test indicated significant differences in standard deviation in snag basal area only, with no action having the highest variation.

3.2.2. *Disturbance severity index*

The distribution of DSI differed across treatments. The range of values in no action ranged from −0.06–0.101, in resistance from 0.177 – 0.503, in resilience from −0.03 – 0.889, and in transition from 0.348 – 0.967. Each treatment exhibited a distribution of DSI values, and potential understory resource patterns, that was statistically different from each of the other treatments (Fig. 4b).

3.2.3. *Within treatment*

When analyzed by micro-treatment, gaps differed significantly from all other treatments, but differences were minimal. Retention of trees was more common in gaps, with only 1/30 gaps having fewer than 3 trees, so fewer null values (compared to SCG) were generated through spatial index calculation. Notably, the areas thinned to a lower density had higher DDI, Gd, and CVd than higher density thinning, despite uncut areas exhibiting the highest values. Levene's test indicated differing standard deviation in MDI only.

Table 4
Mean ± standard deviation (min-max) of stand metrics at the treatment level two years following treatment at the Second College Grant and Cutfoot Experimental Forest.

	No Action	Resistance	Resilience	Transition
Second College Grant				
Quadratic mean diameter (cm)	25.1 ± 0.87 (16.6–32.1)^{a}	25.2 ± 0.91 (19.4–33.0)^{a}	23.9 ± 2.06 (12.4–34.7)^{ab}	22.9 ± 0.97 (10.8–43)^{b}
Basal area (m^{2} ha^{-1})	23.8 ± 2.94 (6.9–44.4)^{a}	19.9 ± 2.19 (11.0–34.3)^{ab}	19.4 ± 1.22 (1.2–35.3)^{b}	17.6 ± 1.03 (1.0–34.3)^{b}
Live aboveground biomass (Mg ha^{-1})	175.1 (47–335.9)^{a}	148.7 (78.3–311.5)^{ab}	143.1 (1–273.1)^{ab}	129.9 (1–250.6)^{b}
Dead aboveground biomass (Mg ha^{-1})	5.9 (0.01–28.3)	7.5 (0.79–20.8)	5.6 (0.40–29.8)	7.1 (0.31–26.4)
Trees per hectare	492 ± 19 (199–922)^{a}	413 ±42 (174–723)^{b}	396 ± 39 (25–798)^{b}	394 ± 45 (25–748)^{b}
Snag basal area(m^{2}ha$^{-1)}$	2.4± 1.1 (0–12.4)^{a}	2.7 ± 1.1 (0–11.5)^{a}	1.4 ± 1.2 (0–11.5)^{b}	1.7 ± 1.0 (0–15.2)^{ab}
Snags per hectare	51 ± 22 (0–249)^{ab}	51 ± 9 (0–199)^{a}	28 ± 18 (0–150)^{b}	34 ± 14 (0–125)^{b}
Trees per hectare >40 cm dbh	31 ± 14 (0–75)^{ab}	31 ± 3 (0–75)^{a}	26 ±12 (0–100)^{ab}	24 ± 3 (0–75)^{b}
Cutfoot Experimental Forest				
Quadratic mean diameter (cm)	33.9 ± 2.6 (23.4–40.5)^{a}	36.5 ± 2.8 (29.2–49.4)^{b}	39.3 ± 2.7 (29.0–60.4)^{c}	39.9 ± 2.3 (25.4–53.4)^{bc}
Basal area (m^{2} ha^{-1})	38.9 ± 5.7 (26.4–56.4)^{a}	24.7 ± 0.3 (20.8–29.8)^{b}	24.5±0.6 (4.3–53.1)^{b}	14.9 ± 0.7 (0.6–25.5)^{c}
Live aboveground biomass (Mg ha^{-1})	203.7 (121.9–301.0)^{a}	128.7 (106.5–164.8)^{b}	131.9 (23.3–277.2)^{b}	82.4 (4.0–133.6)^{c}
Dead aboveground biomass (Mg ha^{-1})‡	12.0 (0.5–39)	6.6 (0–26.1)	4.6 (0–30.3)	4.8 (0–22.2)
Trees per hectare	441 ± 37 (282–798)^{a}	245 ± 36 (123–381)^{b}	220 ± 29 (25–688)^{b}	122 ± 18 (12–270)^{c}
Snag basal area(m^{2}ha$^{-1)}$	4.8 ± 2.5 (0.4–12.5)^{a} $^{\mathit{a}}$	2.5 ± 1.3 (0–8.8)^{ab} $^{\mathit{ab}}$	1.6 ± 0.7 (0–9.0)^{b} $^{\mathit{b}}$	1.7 ± 0.7 (0–9.9)^{b} $^{\mathit{b}}$
Snags per hectare	109 ± 34 (12–307)^{a}	47 ± 23 (0–160)^{b}	30 ± 20 (0–147)^{b}	27 ± 10 (0–135)^{b}
Trees per hectare >40 cm dbh	106 ± 33 (0–184)^{a}	75 ± 24 (25–123)^{bc}	82 ± 22 (0–221)^{b}	59 ± 9 (90–111)^{c}

Notes: Values with different letters are statistically different at alpha < 0.05. Values with different italic letters indicate statistically different standard deviations at alpha < 0.05.

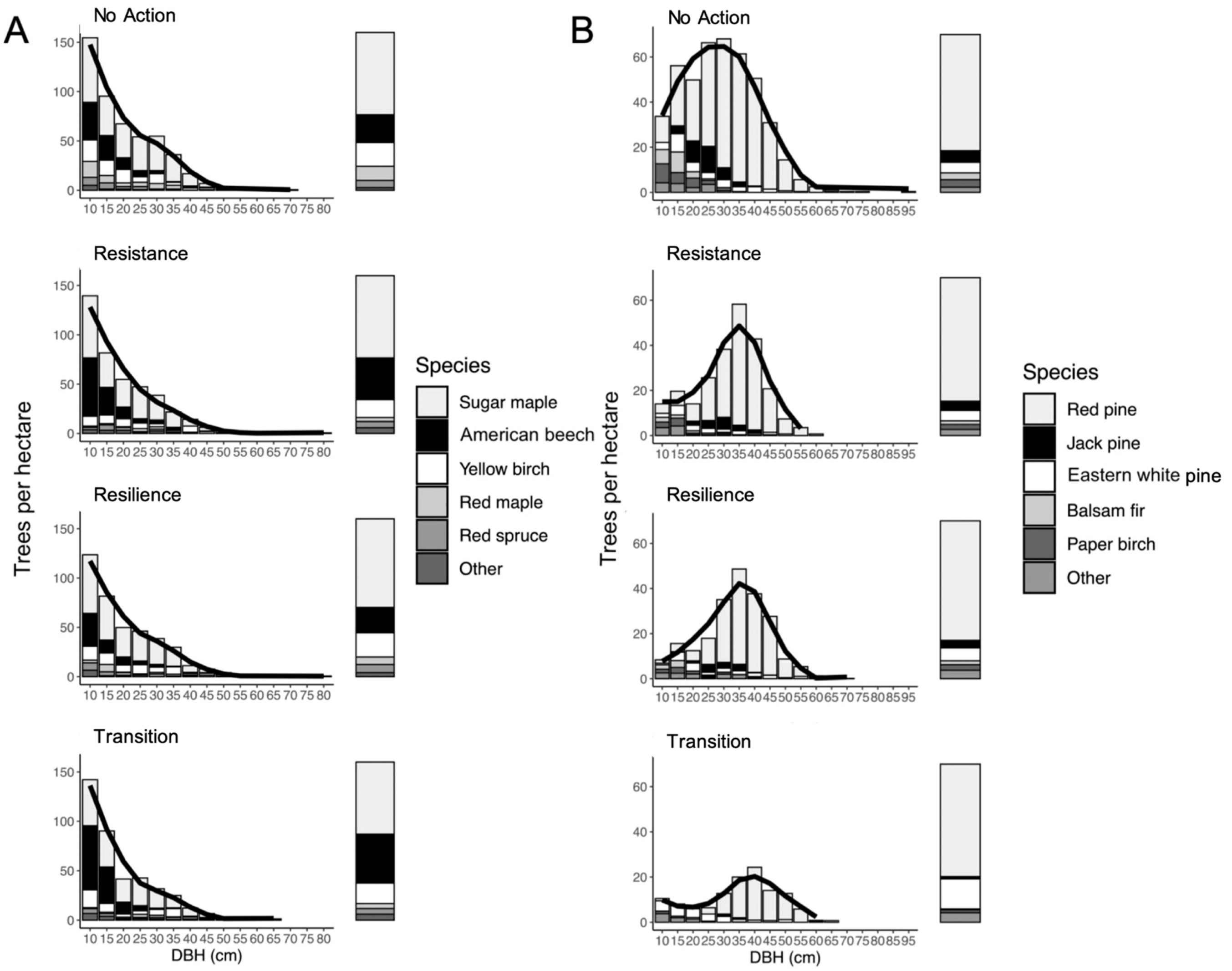

Fig. 3. Diameter distribution and species composition following adaptive silviculture treatments at Second College Grant (A) and Cutfoot Experimental Forest (B).

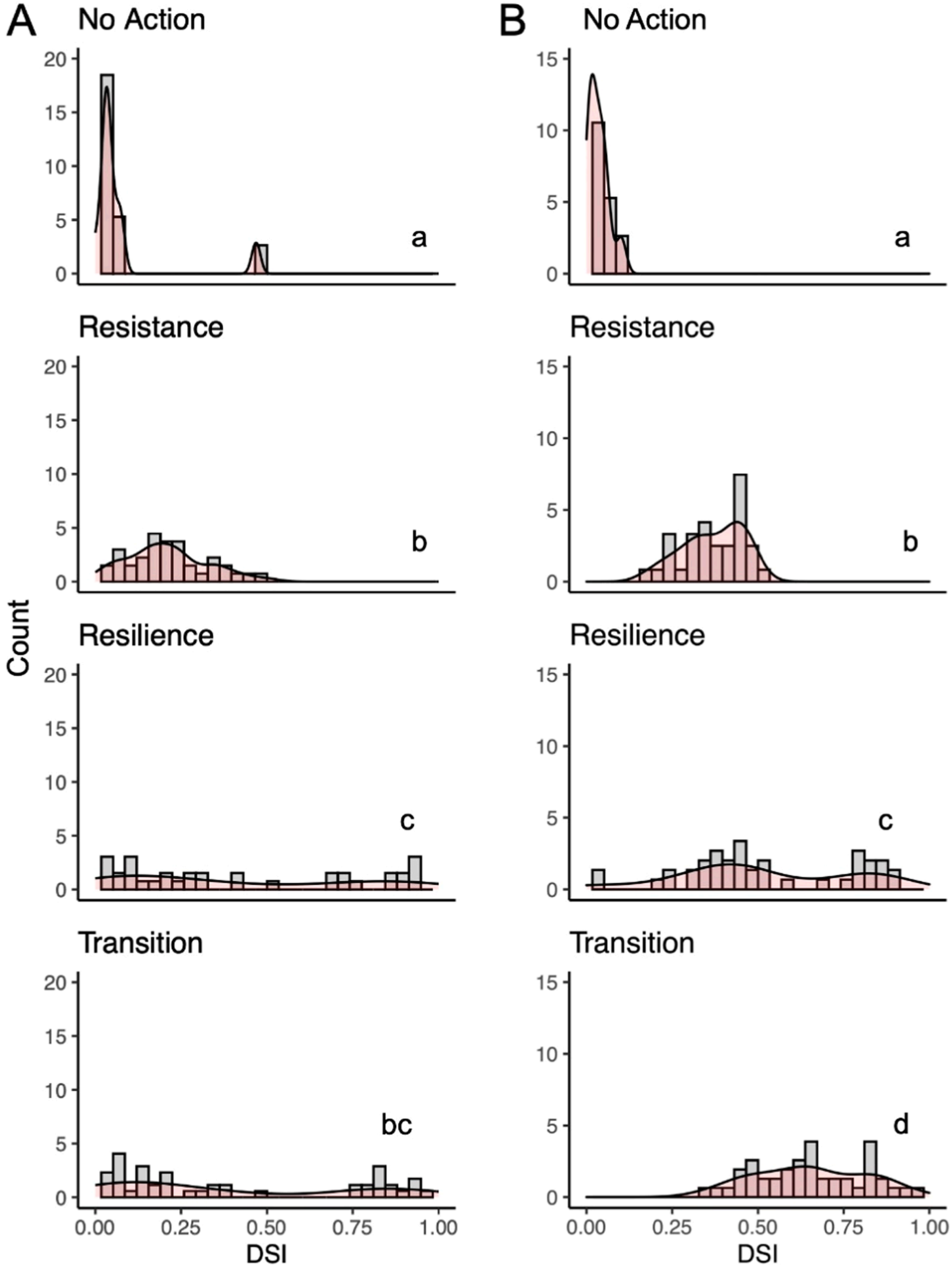

Fig. 4. Histograms of plot-level disturbance severity (DSI) across adaptive treatments and no action at Second College Grant (A) and Cutfoot Experimental Forest (B). DSI is calculated as the scaled change in aboveground biomass in the two-year time span encompassing pre- to post-harvest, with values including living and dead mature trees and saplings. Higher values describe greater reduction in aboveground biomass as a result of treatment or other disturbances. Letters indicate significant differences ($p < 0.05$) among distributions at a site based on Kolmogorov-Smirnov test.

4. Discussion

Developing quantifiable links between the outcomes of management and adaptive capacity of forest ecosystems is critical for applying strategies to manage forests in an era of global change (Thurman et al., 2020). A key step in this development is evaluating the structural outcomes of silvicultural treatments based on resilience theory and adaptation principles within operational-scale and real-world contexts. To this end, we assessed metrics of forest structure to understand how adaptation strategies tailored to local conditions may influence adaptive capacity by increasing structural complexity in two different forest ecosystems. Our findings highlight that in a short time frame after an initial harvest, adaptive silviculture treatments led to a broad range of stand-wide conditions, and possible disturbance recovery pathways, that are influenced by forest type characteristics and ecological memory associated with past management and pre-treatment stand conditions. The outcomes we present provide insight into application of adaptation treatments, thus characterizing actionable options for managing in the face of climate change.

4.1. Adaptation treatments and structural complexity

4.1.1. Structural indices

The pattern of diversity indices exhibiting lower values in resilience and transition point toward lower stand-scale adaptive capacity under these treatments. However, mean values only tell part of the story as many of the harvest gaps in the resilience and transition treatments included legacy tree retention, the importance of which is not adequately represented through our calculated indices. Gaps with biological legacies represent a combination of high resource regeneration conditions (e.g., higher light or nutrient availability) and lifeboating ecological processes that can contribute to increased adaptive capacity (Franklin et al., 1997). This outcome highlights a limitation of some canopy structural indices, in that they can downplay the value of gaps, producing low calculated diversity metrics (Saunders and Wagner, 2008), or failing to differentiate between treatments, a limitation not unique to our study (Kuehne et al., 2019). The ecological value of the gaps is further supported by the high standard deviation of structural indices, most notably at SCG, indicating that there is high variability among the gaps, each with its own distinctive structural characteristics that may offer unique responses to novel disturbance,. This within-stand variation drove the divergence of these more variable treatments (resilience and transition), from no action and resistance in our NMDS analysis. High variability between plots in a treatment unit reflects a different type of diversity than uniformly high values of plot-level diversity indices across that same unit: large differences between plots in the same stand signify that spatial variability exists across that stand, whereas uniformly high values with minimal variation reflect more similar stand-wide conditions. This spatial variation in structure may contribute to adaptive capacity by increasing system stability, slowing disease spread, adding response pathways to disturbances, and supporting ecosystem function (Franklin and Van Pelt, 2004).

While treatment-level averaging of structural indices diminished some of the nuance of plot-level variation, when analyses include standard deviation or coefficient of variation, our results suggest that adaptive silviculture treatments designed with the objectives of creating greater stand-level structural complexity do achieve these objectives, with gaps and skips creating spatial variability. Inclusion of gaps, especially those of varying size and with different levels of tree retention, along with skips, creates a broad diversity of stand conditions and notable distinctions among treatments (Kern et al., 2017). This underscores that harvest prescriptions such as variable density thinning and irregular shelterwood, systems often associated with ecological forestry, create stand-level complexity that can contribute to adaptive capacity (D’Amato and Palik, 2021; Franklin et al., 1997).

4.1.2. Disturbance severity index

We found that treatments with more emphasis on facilitating change led to a greater diversity of DSI values, signifying loss of aboveground biomass and thus potential light, nutrient, or moisture availability at the stand scale. Further, the within-stand variability that had been obscured by stand-level averaging of structural metrics was captured by an examination of plot-scale DSI. This range of conditions created by management for variability leaves a stand with a variety of disturbance recovery pathways. The fence and corridor concept (Moritz et al., 2011) describes creation of canopy gaps (with and without retention), skips, and a thinned matrix as generating patches of high resistance that may perpetuate through intense disturbance, intentional patches of greater vulnerability that will carry the stand forward into regeneration, and corridors of connectivity, which may leave the forest less susceptible to a stand-replacing event (Churchill et al., 2013). The concept is transferrable between forest types, although function may change. For example, a skip in a conifer forest may be a more vulnerable patch with density that is conducive to bark beetle damage or fire, while the same skip in northern hardwoods may limit invasive plant species, exclude recalcitrant understory plants, and perpetuate a historical stand type into the future. Conversely, a gap is a barrier to fire movement in a fire-dependent system, while in a northern hardwood forest it may produce a young regenerating patch that is less vulnerable to an ice storm or shoulder-season wet snowstorm. Given the uncertainties presented by climate change, managing for a range of conditions such as gaps, skips, and matrix forest creates a variety of adaptation or recovery pathways which increases the likelihood of some forest structures and functions persisting under novel disturbance.

4.2. Forest type influences response to adaptation treatments

We found that treatment-level differences (i.e., among no action, resistance, resilience, transition) in structural indices were minimal in the northern hardwood forest (SCG), whereas significant differences existed among treatments for most indices in the red pine woodland (CEF). In general, SCG also had higher structural diversity values in all treatments compared to CEF. Ecological memory, realized through pre-harvest age and size structure, can explain much of this variation. The red pine forests had lower pre-treatment compositional and structural diversity than northern hardwood forests, due to differences in past management and shade tolerance among species. The red pine woodlands we examined are generally even-aged (Stambaugh et al., 2021), establishing after severe post-logging wildfire, so changes caused by adaptation treatments are likely to be greater in relative value then in the northern hardwood forest, which are comparatively more complex to start, in part due to shade-tolerant species occupying space in the understory (D’Amato et al., 2011).

Even with the generally higher diversity values in the northern hardwood forest, some structural indices may be hard to interpret accurately, for example those describing diameter distribution. Northern hardwood forests often have high size-class diversity due to a prevalence of shade-tolerant species, but may still be lacking in age-class diversity and presence of very large old trees, characteristics that can confer adaptive capacity (Schwartz et al., 2005). As such, the different responses between the forest types examined make sense, with the even-aged red pine forest showing low size-class diversity, but higher response to harvesting, while northern hardwoods had high initial size-class diversity, with treatments having a limited ability to increase this diversity. This underscores the value of understanding and accounting for ecological memory represented by pre-harvest conditions when planning adaptive management and assessing outcomes, as well as finding ways to meet adaptation-related targets that are not easily accounted for by structural metrics (e.g., age, value of large trees).

Given that both study sites are part of the ASCC network, certain broad similarities exist in the adaptation treatments (Nagel et al., 2017), but localized prescriptions and evaluations of their outcomes serve to amplify ecosystem differences, while providing valuable detail to inform future adaptation practices. We found structural metrics reflected specific localized treatments; removal of smaller diameter classes based on silvicultural prescriptions led to increased QMD at CEF, while selection for healthy individuals of varying sizes can explain the decreasing QMD along the change gradient at SCG. Many of the structural metrics that we examined here have been explored primarily in conifer-dominant forests (e.g., Kuehne et al., 2015; Young et al., 2017) and interpretation of structural metrics in more stratified, multi-aged forests, like northern hardwoods, could be more complicated.

Finding simple metrics to describe adaptive capacity may be limited by several factors. One of these is measurement plot size – larger plots may better encompass changes that are not easily apparent in smaller plots, and stand-wide averaging of smaller plots may make it difficult to discern potential stand-scale variation, indicating a need for different assessment techniques (Saunders and Wagner, 2008). An additional limitation is that indices largely based on canopy measurements only represent part of the picture when it comes to adaptive capacity – quantifying the growing space made available by harvesting and subsequent regeneration is also critical. Adaptive management approaches such as those outlined in our study can, through natural or planted regeneration, either support the current species mix or begin to move a forest toward future adaptation by increasing species, genetic, and age class diversity (Aitken et al., 2008; Wikle et al., in review). In the post-harvest timespan represented here, we were able to provide an assessment of the range of canopy structure and conditions, which will influence the adaptive capacity of the forest (Getzin et al., 2008), with resilience and transition approaches creating a greater diversity of canopy structural conditions. A longer timescale and ultimate assessment of regeneration will provide a more complete understanding of adaptive capacity conferred by these adaptive treatments.

5. Conclusion

Assessment of structural outcomes of adaptation strategies is beneficial for understanding how theoretical concepts of complexity and adaptive capacity can be put into action. We found that treatments designed to increase stand-scale structural heterogeneity achieved stated goals, with those goals and outcomes influenced by characteristics of the two forest types examined, but that description and quantification of this outcome is not simple. Further, adaptation treatments led to a range of structural environments and shifts in biomass pools, which may support a variety of understory resource availability conditions, setting the stage for continued diversity of structure and composition as the forest matures. This suggests that multiple treatments designed for specific forest types and local contexts best create alternative disturbance recovery pathways and hedge against uncertainty of future climate. Operational scale examples of adaptation theory in practice, such as those we present here for two important eastern North American forest ecosystems, provide managers wanting to apply these strategies with expectations for structural outcomes. Our findings highlight the complexity of interpreting outcomes of adaptation treatments, but also provide quantifiable metrics that can be used to guide applications of these adaptation strategies.

CRediT authorship contribution statement

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

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Declaration of Competing Interest

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

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121932.

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