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Stand spatial structure outcomes of forest adaptation treatments in northern hardwood forests in North America

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Abstract

Spatial arrangement of trees is determined by a complex suite of factors, including disturbance history, competition, and resource availability. These spatial patterns drive adaptive capacity by influencing arrangement of growing space, neighborhood competitive relationships, and disturbance response, with irregular patterns supporting higher adaptive capacity. While spatial structure in relation to disturbance and climate change resilience has been studied in dry conifer forests and old-growth temperate forests, it has never been explored in the context of climate adaptive management in mesic, second-growth forests. To address this gap, we analyzed tree spatial patterns in second-growth northern hardwood forests under four different climate adaptation management approaches: no action; resistance or resilience to impacts of climate change; and transition to future-adapted forest types. We used spatial point statistics approaches to describe how patterns differed among the four treatments. We found that the treatments focused on future adaptation led to patterns with variable tree spacing and clumping, while those focused on perpetuating current conditions resulted in less pattern variation. This indicates that adaptation strategies that include uneven-aged regeneration methods that restore and maintain tree spatial patterns historically generated by gap dynamics can be successful in altering resource availability patterns and adaptation space in forest stands.

Key words: spatial pattern, forest adaptation, climate change resilience, structural complexity, silviculture, northern hardwood forest

Introduction

Forest ecosystems and their ecological processes are defined by the presence and arrangement of tree species, sizes, and elements of stand structure, all of which can reflect a combination of anthropogenic factors and natural processes (Brown et al. 2011; Law et al. 2009; Peters et al. 2022). These patterns of forest structure in turn, influence ecosystem function and process and forest dynamics in a complex manner (Ali 2019). For example, tree regeneration and recruitment depend on light and nutrient availability patterns determined by canopy structure (Gough et al. 2019; Hakkenberg et al. 2016), as does understory plant diversity (Curzon et al. 2020; Duguid et al. 2013). Further, spacing and arrangement of trees may either facilitate or limit movement of pests and pathogens (Fettig et al. 2007), and structural complexity in canopy tree size and arrangement impacts water and nutrient dynamics (Felipe-Lucia et al. 2018; Gallardo 2003; Schneider et al. 2019; Yuan et al. 2020).

The scale of spatial patterns offers an additional layer of insight into forest processes: these can be divided into two broad categories, global and local. Global patterns are those evaluated at the stand scale and describe dominant patterns across a specified area, while local analyses work to classify different pattern elements, such as tree clusters, within a stand or study area (Dale and Fortin 2014; Larson and Churchill 2012). When these two scales of analysis are used together, they can provide a more complete picture of a given spatial pattern and can offer opportunities to explore links between stand-scale patterns and neighborhood relationships (Larson and Churchill 2012). At both scales, resource availability, microsite variability and disturbance history can affect tree spatial arrangement by influencing where trees can establish and grow, with stand age, competitive dynamics, and mortality patterns modifying these arrangements over the course of forest development (Boyden et al. 2012; Canham et al. 2006; Ehbrecht et al. 2021; Franklin et al. 2002; Rodman et al. 2017). For example, young forest stands undergo intensive competition leading to self-thinning that generally creates uniform tree arrangement at a global scale (Kenkel 1988; Oliver 1981), but as they mature, mortality patterns shift away from density dependence leading to less uniform patterns (Aakala et al. 2012; Larson et al. 2015). Shade tolerance and tree size are two factors that may further influence spatial pattern, as shade tolerant species may tolerate aggregation better, while large trees may repel other trees (Gonzalez-Akre et al. 2016; Lutz et al. 2014). Natural disturbances may also generate aggregated spatial arrangements, due to their often patchy impact (Drever et al. 2006; Frelich and Reich 1999), while management for timber production has historically led to uniform tree arrangement (Kuehne et al. 2018; Puettmann et al. 2009); legacies of these disturbances persist for many years (Després et al. 2017; Pederson et al. 2014).

There has been a recent emphasis on better quantifying and describing overstory tree spatial arrangement, specifically related to increasing the understanding surrounding how forest structure and tree spatial arrangement relate to disturbance vulnerability (Larson et al. 2012; Velázquez et al. 2016). Of increasing importance and interest, spatial patterning of trees and structural complexity have been linked to resilience and recovery in the face of global change (Allen et al. 2016). In many forested areas, past management activity has led to forests that are more structurally and compositionally simple than historic conditions (Fuller et al. 1998; Shifley et al. 2014); forests in this state are likely to have increased vulnerability to climate-change-related disturbances (Oliver et al. 2015; Tilman et al. 2014). Consequently, adaptive forest management approaches are being explored to provide guidance to forest managers on how to increase forest adaptive capacity (Millar et al. 2007). Structural complexity has been linked to forest adaptive capacity, with complexity contributing to successful disturbance recovery, therefore increasing structural complexity is often a component of climate-adaptive management (Liang et al. 2016; Senf et al. 2019). Complexity can include varying combinations of light, moisture, and temperature conditions such as those caused by canopy gaps, retention in openings, or thinned canopies that support diversity of regeneration conditions (Aussenac 2000; Larson and Churchill 2012; Raymond et al. 2018), which can be represented by both local and global scale aggregation. Diverse structural elements, such as large trees (Glick and Matlack 2021), cavity trees (Martin and Raymond 2019), or intermingled trees representing multiple species and sizes providing numerous layers of crown depth (del Río et al. 2016) can also contribute to complexity. At localized scales, diverse tree neighborhoods can increase resilience to drought through differential occupation of functional trait space (Gazol and Camarero 2016). In the event of a novel disturbance, any of these structural elements or others may present the suite of conditions necessary for successful disturbance recovery to occur, as well as providing necessary support for fungal, animal and plant species to persist (Aguilar-Cruz et al. 2020; Mullally et al. 2019; Oliver et al. 2010).

These factors contributing to adaptive capacity can be related to quantified patterns of canopy tree structural arrangement. Global analyses place canopy tree arrangement on a gradient with uniformity at one end and aggregation at the other, with spatial randomness falling in the middle. Cluster analysis of trees can provide further granularity to patterns of aggregation at a local scale, by describing size of aggregated patches (Larson and Churchill 2012; LeFevre et al. 2020). Uniform arrangement, especially when combined with lower species and size diversity, may be associated with lower adaptive capacity, and irregular arrangement with higher capacity, as forests with a diversity of structural and compositional arrangements are more likely to see at least some of those arrangements present resilience to various disturbances (Anderson-Teixeira et al. 2013; Halpern 1988; Sánchez-Pinillos et al. 2019). Uniform arrangement, rather than random or aggregated, has also been linked to poorer outcomes in vegetation restoration projects (Fivash et al. 2022). While an abundant body of research exists on describing these spatial patterns, there is much less information linking quantified outcomes to the implementation of specific silvicultural treatments (Larson and Churchill 2012). Further, these patterns have been explored primarily in dry conifer forests (e.g., Clyatt et al. 2016; Larson et al. 2012; Sánchez Meador et al. 2009), but little research has been done to link spatial patterns specifically to adaptation management approaches in mesic forests.

The purpose of this study is to quantify the spatial outcomes of adaptation treatments applied to northern hardwood forests in northeastern North America by examining factors that contribute to diverse microhabitats and adaptation pathways. This study takes advantage of a large-scale adaptation experiment that is part of the Adaptive Silviculture for Climate Change network (ASCC; Nagel et al. 2017) to examine spatial patterns of trees following the application of four adaptation approaches: no action, resistance, resilience, and transition. We analyze the spatial patterns and associations of three dominant species in this forest type: sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and beech (*Fagus grandifolia* Ehrh.), as well as patterns across all species. We ask two questions. (i) How does tree spatial arrangement differ at local and global scales under four different climate adaptation approaches? (ii) How do spatial patterns of three dominant tree species in northern hardwood forests compare with each other across these adaptation approaches? This exploration is necessary for understanding how adaptation treatments impact canopy tree arrangement and associated adaptation pathways. Our assessment of tree arrangement by species will provide valuable baseline information on how each of these species interacts with its environment in response to natural and anthropogenic drivers.

Methods

Site description and field methods

We conducted this research at the Second College Grant, a 10 800-ha forest owned and managed by Dartmouth College in northern New Hampshire, USA. The forest is in the temperate-boreal transition zone, and within the 162-ha study area is northern hardwood forest, dominated by sugar maple, American beech, and yellow birch, with smaller components of red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill) and white pine (*Pinus strobus* L.). Mean annual temperature ranges from − 12 °C (January) to 17 °C (July) and annual precipitation is 117.9 cm (PRISM Climate

Group 2021). Soils are coarse loamy glacially derived tills and similar across the research area (NRCS 2020), and elevations vary from 484–650 m above sea level. Prior to the start of this project, the study area last experienced management in the form of a thinning between 1996 and 2000 (Jevon et al. 2019).

This study was conducted within the ASCC project (Nagel et al. 2017), an international, co-produced study designed by managers and scientists to test climate change adaptation techniques at a replicated, operational scale. The ASCC study at the Second College Grant assesses four approaches to global change adaptation: no action, resistance, resilience, and transition, each in four replicates of 10 hectares (Fig. 1). Broadly, a resistance approach aims to perpetuate current forest conditions through managing for tree health, vigor, and regeneration of current species, the resilience approach introduces variation into a system but allows for return to a reference condition, transition actively facilitates change, while no action offers an opportunity to observe how the forest responds to climate change absent active management (Millar et al. 2007; Nagel et al. 2017). The ASCC silvicultural prescriptions at the Second College Grant are as follows and are described in detail in Wikle et al. (*in review*): resistance is based on single-tree selection methods with emphasis on retention of healthy and resistant individuals, resilience is a hybrid single-tree/group selection that includes gaps and reserves 0.04 and 0.1 ha in area and a thinned matrix, and transition is a continuous cover irregular shelterwood that includes gaps in sizes of 0.1 and 0.4 ha, reserves of 0.04 and 0.1 ha, and a thinned matrix. In large canopy gaps (0.4 ha), one to three trees were retained as biological legacies, while in the smaller canopy gaps, canopy tree retention was uncommon.

We installed a 100 × 100-m (1 ha) stem mapped plot in each treatment and block for 16 plots total. In each 1 ha plot, we recorded diameter at breast height (DBH: 1.37 m), species, and x and y coordinates for each living tree $\geq$ 10 cm DBH and tagged each tree for future measurements. In resilience and transition, plots were intentionally centered on gaps of 0.1 and 0.4 ha, respectively, to capture the spatial variation created by these treatments. In no action and resistance, plot centers were located randomly using Random Points in QGIS 3.16 (QGIS 2020) and adjusted as necessary on the ground to avoid streams and wetlands that would alter the integrity of plots for describing post-management conditions.

Data analysis

Global patterns

We used the pair correlation function (PCF), $g(r)$, to quantify tree arrangement in each treatment. PCF is a modification of Ripley's K ($K(r)$; Ripley 1977), a common method used to analyze spatial point patterns by predicting a number of individuals within a given distance r of a focal individual. However, K(r) measures cumulatively from each focal tree, which may bias outcomes, especially at greater distances. Conversely, the PCF is non-cumulative, using concentric circles, so can better identify spatial patterns at specific scales (Larson and Churchill 2012; Perry et al. 2006; Wiegand and Moloney 2004). Pair correlation tests against a null model of complete spatial randomness (CSR; defined as Poisson distribution with mean λ), or rejection of CSR with point patterns falling on either side of CSR as either aggregated (positive values) or uniformly distributed (negative values; Diggle 2013). We evaluated for significance by comparing our observed data with 999 Monte Carlo envelope simulations of the null model (Grabarnik et al. 2011; Wiegand and Moloney 2015, 2004). We chose 999 simulations because envelope testing of spatial point patterns lends itself to high probability of type 1 error if a low number of simulations is chosen. Type 1 error probabilities reduce to 0.03–0.09 when 999 simulations are used (Grabarnik et al. 2011). Departure from the null model at distance r occurs if the actual distribution fell outside the simulation envelopes. As each treatment was replicated four times, we performed our analyses on pooled data using the pool and pool.envelope functions in the spatstat package (Baddeley and Turner 2005) using the methods described in Baddeley et al. (2015).

The mark variogram function, $\gamma_m(r)$ was used to evaluate spatial patterns of tree diameter, specifically if the dbh of each tree in a point pattern is similar or different to nearby trees. Similar to our PCF calculation, we pooled our plots by treatment and plotted the normalized mark variogram against 999 simulations of the null model of no relationship between tree sizes based on distance between trees. If there is no relationship between tree spacing and size, the observed values fall within the confidence band. If values are less than one, diameters are similar to each other, while if they are greater than one, tree diameters are negatively autocorrelated (Ghalandarayeshi et al. 2017; Pommerening and Särkkä 2013).

We used the mark mingling function, $\widehat{v}(r)$, to examine global patterns related to species mingling, specifically, whether neighboring pairs of trees across the plot tend toward conspecific or heterospecific aggregation (Hui and Pommerening 2014; Pommerening et al. 2011). This function can be calculated as follows:

$$(1)\qquad \widehat{v}(r) = \frac{1}{\mathbf{EM}} \sum_{x_1, x_2 \in W}^{\neq} \frac{1\left(m\left(x_1\right) \neq m\left(x_2\right)\right) k_h\left(\parallel x_1 - x_2 \parallel - r\right)}{2\pi r A\left(W_{x_1} \cap W_{x_2}\right)}$$

where x_1 and x_2 are two points in the point pattern within observation window W, k_h is the Epanechnikov kernel function, and $A\left(W_{x_1} \cap W_{x_2}\right)$ is the area of intersection of W_{x_1} *and* W_{x_2}. **EM** is expected mingling, and is used as a normalization term, calculated as follows:

$$(2)\qquad \mathbf{EM} = \sum_{i=1}^{s} \frac{n_i\left(n - n_i\right)}{n\left(n - 1\right)}$$

where s is the number of species, n is the number of trees, and n_i is the number of species i (Hui and Pommerening 2014). We tested this function following methods outlined in Pommerening et al. (2021), where a null hypothesis is constructed using random superposition. We simulated 2499 random shifts of species populations by shifting approxi-

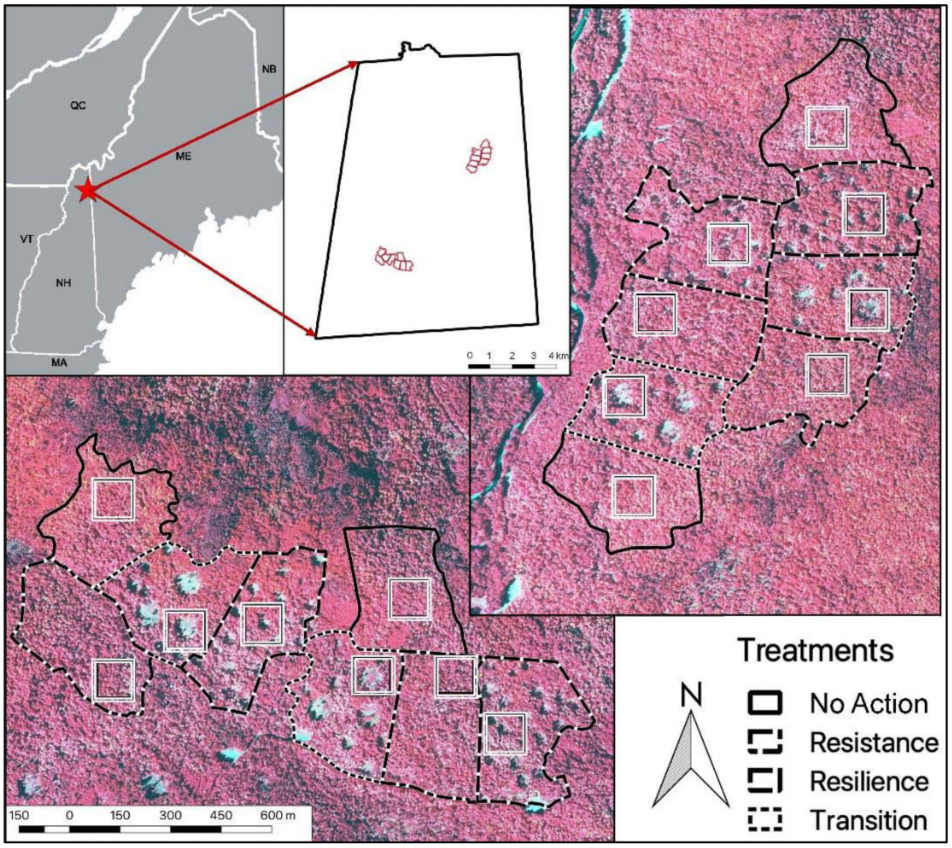


Fig. 1. Spatial plot locations within New England Adaptive Silviculture for Climate Change installation at Dartmouth College Second College Grant, NH, USA. See methods for treatment descriptions. This map was created using 2016 New Hampshire color infrared aerial imagery acquired from the National Agriculture Imagery Program (NH Granit 2019) in QGIS 3.16 (QGIS 2020).

mately half of the trees in each of our 16 plots by adding the same random values to the x and y coordinates of these individuals. We carried out these analyses using R and C++ code provided by Hui and Pommerening (2014). We pooled the outcome by treatment as with our PCF and mark variogram analyses.

Local patterns

We executed analysis of clustering at multiple spatial scales to deepen our understanding of tree aggregation in our treatments by supplementing our point pattern analysis with a spatial clump detection algorithm (Larson and Churchill 2008; Plotkin et al. 2002) that detects clumps based on a given inter-tree distance, *d*. Under this algorithm, two trees are linked if they are closer than *d* distance apart. Clusters occur when two trees are connected by other linked trees, even if each individual pair of trees are not within *d* distance of each other (Plotkin et al. 2002). The inter-tree distance can be selected by calculating crown overlap for each pair of tree, with changing distance based on each pair of neighbors, or can be chosen by selecting a single limiting distance that fits with the ecology of the ecosystem (Larson and Churchill 2008; Plotkin et al. 2002). We performed sensitivity analysis by plotting mean clump size against limiting distance and selected our limiting distance of five meters based on when mean clump size began to increase drastically (Larson et al. 2012). We used R code provided by Larson and Churchill (2008) to perform the cluster analysis. To compare treatments, we created five clump size groups based on similar analyses: individual, 2–4, 5–9, 10–15, and 16 + trees, and compared proportion of trees in each group size among treatments. We chose not to use an edge correction based on evidence that this correction offers no improvement when describing patterns of tree clumping (Churchill et al. 2013; Plotkin et al. 2002; Yamada and Rogerson 2003).

We evaluated the arrangement of the three most common species: sugar maple, beech, and yellow birch. Unfortunately, there were not enough individuals of beech and yellow birch present in plots to perform PCF analysis, so we used the Clark-Evans index of aggregation (R) with a Donnelly edge correction to assess spatial arrangement for each of these three species (Clark and Evans 1954). The Clark-Evans index is calculated as follows:

$$(3) \qquad R = \frac{\bar{r}_{observed}}{E\,(r)} where: E\,(r) = \frac{1}{2 * \sqrt{\frac{N}{A}}}$$

where *r* is the distance in any specified units from a given individual to its single nearest neighbor, N is the number of trees, and A is the area of the observation window. The Clark-Evans index evaluates distance to nearest neighbor, where $R > 1$ (max 2.1491) when the mean distance to the nearest neighbor within the observation window is maximized and spacing is uniform. When $R < 1$, mean distance to nearest neighbor is shorter and points are aggregated, and $R = 1$ indicates CSR.

We also conducted neighborhood analyses by species. The species mingling index (Kuehne et al. 2015; Pommerening 2002) presents a method to quantify whether tree neighborhood relationships are conspecific or heterospecific and was calculated as:

$$Mi = \frac{1}{k}\sum_{j=1}^{k} 1\left(\text{species}_i \neq \text{species}_j\right) \tag{4}$$

where k = number of neighbors. We calculated this index using the spatstat and ForestSAS (Chai 2019) packages in R.

Results

The no action plots had an average of 482 trees per hectare and 25.9 $\mathrm{m^2 ha^{-1}}$ of basal area (Table 1). Despite different silvicultural prescriptions, resistance and resilience had similar density (394 and 413 trees per hectare, respectively) and basal area (19.1 and 19.2 $\mathrm{m^2 ha^{-1}}$, respectively) as compared to no action. Transition had the lowest stem density and basal area, with 349 trees per hectare and 13.6 $\mathrm{m^2 ha^{-1}}$ of basal area. The treatments influenced species composition, with sugar maple importance highest in no action and resistance and lower in resilience and transition. American beech showed the opposite trend, with importance value high in the gap-centered plots and lower in no action and resistance. Yellow birch showed similar patterns to beech, with highest importance value in resilience and transition. In no action and resistance, these three species accounted for over 90% of the stems present, while they made up 89% of stems in resilience and 83% in transition. Other species found in the transition treatment include red spruce (6.8%) and red maple (*Acer rubrum* L; 5.9%), which were often deliberately left as retention trees in harvest gaps given their ecological and adaptation values.

The stem maps reflect different structural arrangements based on treatment. The various-sized canopy gaps are apparent in the stem maps of resilience and transition treatments, although slightly obscured by higher density of retained small-diameter beech in two of the replicates (bottom panels in Fig. 2). In no action, despite not receiving treatments in the present study, impacts of past management in the form of skid trails are still visible in the stem maps. The resistance treatment shows reduced stem density from the no action. In resilience and transition, retention patches (i.e., "skips") and thinned matrix areas are also apparent by visual assessment.

Pooled point pattern analysis indicated CSR at all distances in no action (Figs. 3, S1). Resistance showed spatial aggregation at distances less than two meters and resilience at less than three meters. In the transition treatment, spatial aggregation was indicated below four meters, and spacing became more uniform above 22 meters, with the intervening distances falling into the CSR envelope. The trend toward uniformity at long distances in the transition treatment is likely a "virtual repulsion" effect, rather than descriptive of conditions, as many trees have no neighbors at long distances due to the gap resulting in fewer than expected neighbors at extended distances (Wiegand and Moloney 2004). Minimal notable patterning emerged for aggregation by diameter (Fig. S2). In no action, aggregation of trees of similar diameter was indicated at distances of less than five meters. Otherwise, trees of different diameters were interspersed randomly in all treatments at all calculated distances. Mark mingling, the global test for aggregation by species, revealed slight differences by treatment (Fig. S3). The no action and resistance treatments had aggregation by species only at distances of one meter or less, while resilience and transition showed conspecific aggregation at distances up to 10 m. When not pooled by treatment, more within treatment variation is visible (Fig. S4)

Each treatment showed different patterns of clustering (Fig. 4). No action had the highest mean clump size and resistance the lowest. Resilience and transition fell between no action and resistance. Transition had the highest number of individual trees while no action and resilience had the greatest number of clumps containing 16 trees or more. Clumps of 10–15 trees were the least common in all treatments, while clumps of 2–4 and 5–9 were most common. The transition treatment had the fewest clumps of 2–4 trees and no action the fewest clumps of 5–9 trees.

When examined at plot scales for aggregation, notable visual differences occur between treatments in regard to extent and arrangement of open space (Fig. 5). No action and resistance look similar despite lower tree density in resistance; both showed more homogenous stand conditions in comparison to the other two treatments, with long narrow spacing between clumps and widely distributed single trees further than 5 meters from a neighbor. Resilience and transition reflect the creation of gaps, with larger, round openings that have higher edge to area ratios, and more open space, although individual tree retention within transition gaps influenced the extent of open space such that resilience had more space that was greater than 15 m distance from any tree despite smaller gap size than transition.

Species mingling differed among treatments, as well as among species, with sugar maple mingling least with other species, although management slightly increased mingling, with the two gap treatments displaying the highest mingling values (Fig. 6). Yellow birch consistently had the highest mingling through all treatments, with minimal change among them. Beech had the highest mingling value in no action and lowest in transition, with similar values in resistance and resilience. When individual species were assessed for aggregation, differences were apparent among treatments, as well as by species (Table 2). Sugar maple had an aggregated distribution for all treatments, although was most aggregated in the transition treatment. Yellow birch was spatially aggregated in all treatments, with minimal changes among them. Beech exhibited CSR in the uncut treatment, with aggregation occurring similarly in each of the three treatments.

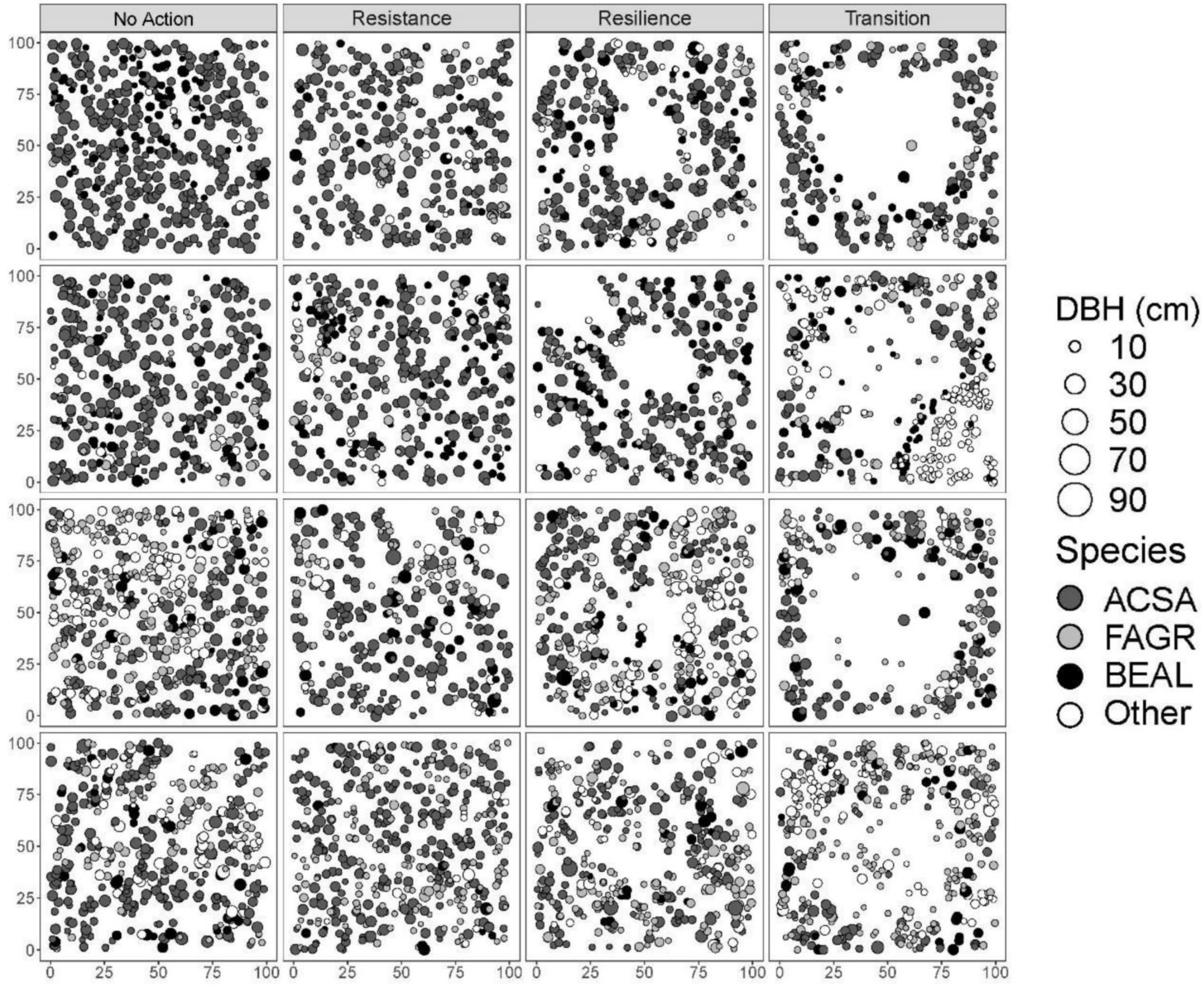
Table 1. Structure and composition of trees in replicated 1 ha spatial plots representing four climate adaptation silviculture approaches. For each column, values sharing the same letter are not significantly different (Tukey HSD).

	Mean (sd)		Importance value (%)[1]			
Treatment	Trees per hectare	Basal area (m^2ha^{-1})	*Acer saccharum*	*Betula allegheniensis*	*Fagus grandifolia*	Other[2]
No Action	482 (30) a	25.9 (2.7) a	64.3	11.0	14.6	10.1
Resistance	394 (58) ab	19.1 (1.6) b	67.9	9.9	18.2	4
Resilience	413 (25) ab	19.2 (2.3) b	54.3	13.9	20.9	10.9
Transition	349 (77) b	13.6 (0.1) c	41.6	15.1	26.0	17.3

[1] Importance value calculated based on relative density and relative basal area of species

[2] Other species included *Picea rubens, Abies balsamea, Acer rubrum, Fraxinus americana, Populus spp., Prunus spp., and Tsuga canadensis*

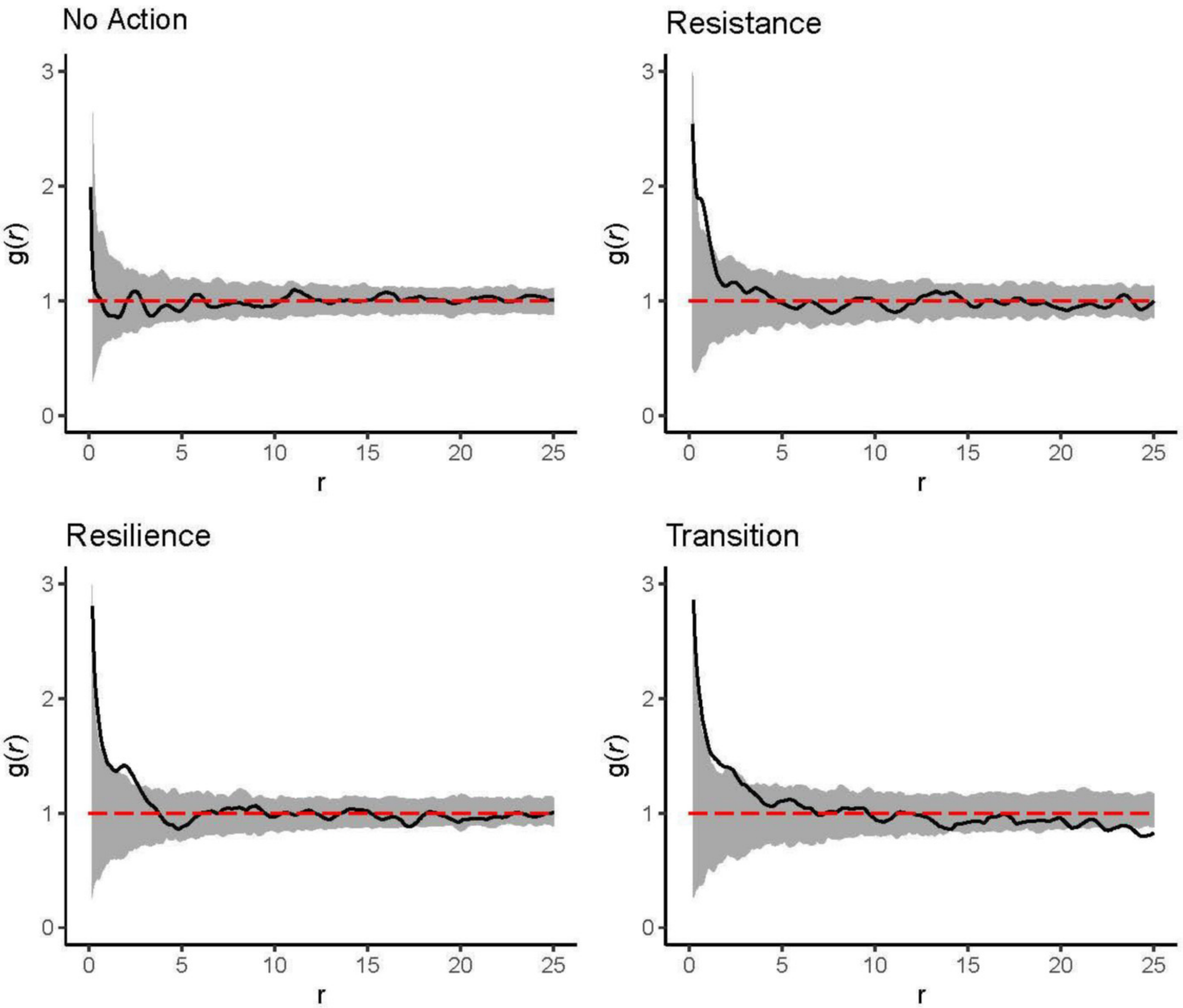
Fig. 2. Stem maps of 16 plots reflecting 4 forest adaptation treatments within New England Adaptive Silviculture for Climate Change installation at Dartmouth College Second College Grant, NH. Symbol color indicates species and size reflects diameter at breast height. ACSA = *Acer saccharum*; BEAL = *Betula alleghaniensis*; FAGR = *Fagus grandifolia;* see Table 1 for species included in "Other" category.



Discussion

Arrangement of canopy trees is an important facet of forest ecosystem structure and function and thus increasingly important to understand as forests face threats brought on by global change. In this study we assessed spatial arrangement of trees and three dominant tree species in relation to forest adaptation treatments to explore relationships between forest management strategies and heterogeneity in overstory trees, which may reflect adaptive capacity. Adaptation approaches generated distinct spatial patterns in canopy trees when analyzed at the local scale, including the spatial aggre-

Fig. 3. Replicated pair correlation function for all trees in each of 4 adaptation treatments representing spatial distribution at distance r. Black line is observed data and shaded area represents complete spatial randomness (CSR) derived from 999 Monte Carlo simulations. Observations falling within this envelope at a given distance indicate CSR, while observations above indicate aggregation and those below, uniform arrangement.



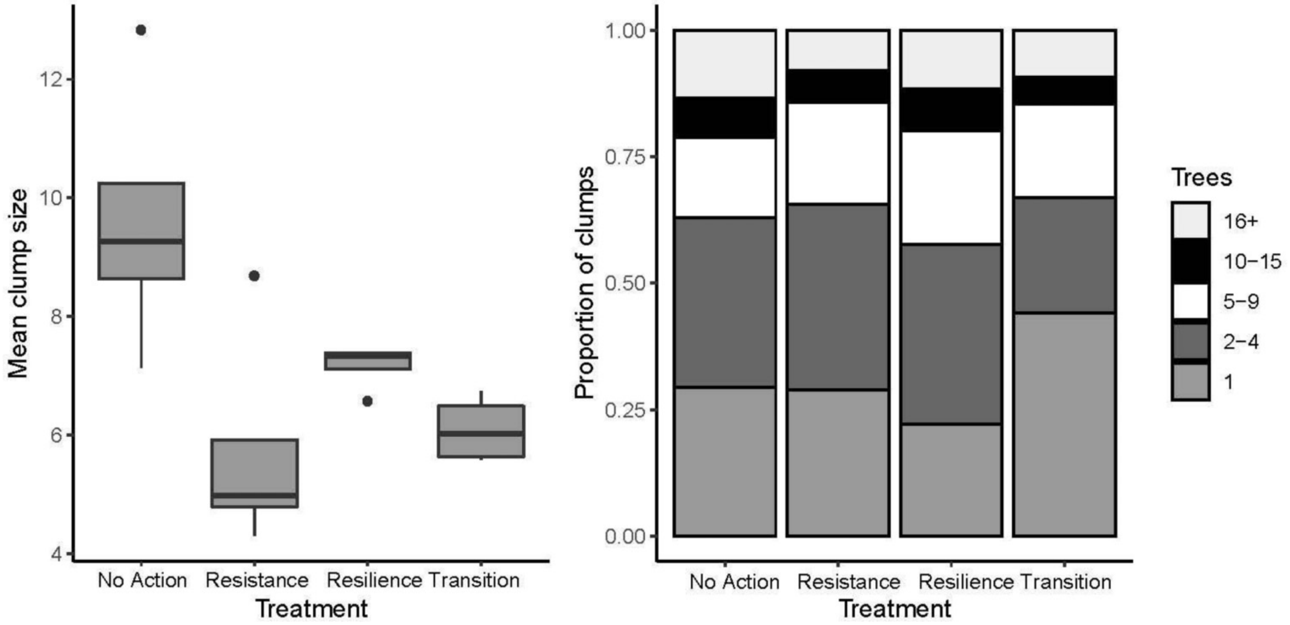
gation and species mingling of the dominant canopy species in these forests. These findings build upon previous work in fire-dependent ecosystems of the western US by highlighting the spatial linkages to future adaptive capacity to global change generated by adaptation treatments in mesic, temperate forests.

Canopy tree patterns—global scale

The dominance of complete spatial randomness (CSR) at most distances is likely reflective of the interplay between stand developmental dynamics and the influence of both historic and adaptive silvicultural treatments. More specifically, tree–tree competition in these forests can generate more uniform patterns, whereas intermediate-scale disturbances, such as those imposed by the silviculture treatments examined, create aggregation, leaving resulting patterns falling between uniformity and aggregation (cf. Davis et al. 2005). It is important to note here that even passively managed areas had a management legacy, as do the majority of forests across the northern hardwood region (Fuller et al. 1998; Niering 1998; Webster et al. 2018), so the patterns in our no action treatment reflect this legacy, despite passive management going forward. As such, the patterns we found differ from those documented for forests without a long history of management, where spatial patterns trend toward aggregation due to competition, complex topography, habitat heterogeneity, uneven resource distribution, and patchiness of disturbances (Lara-Romero et al. 2016; Lin et al. 2011; Piao et al. 2013; Rozas et al. 2009).

The fine-scale aggregation occurring at distances less than 4 m in all three active management treatments describes conditions wherein trees are irregularly spaced, with concomitant irregularity in resource use and availability. It is possible that these patterns are at least partially driven by canopy gaps, which are characterized by patches of trees adjacent to open areas, given that the aggregation distance is shortest in resistance, but longer in resilience and transition. These aggregated patterns may promote adaptive capacity in several ways. For example, the patchy open space provided

Fig. 4. Boxplot of clump size distribution representing median (line across box), first and third quartiles (upper and lower box lines), and extreme values (points) (A) and distribution of clump sizes at 5-meter inter-tree distance (B) in each of four adaptive silviculture treatments.



by tree clustering and heterogenous growth conditions creates available growing space where new seedlings can establish, adding to compositional, age, and size diversity (Tinya and Ódor 2016). Further, irregular spacing between trees can lead to asymmetric competition based on access to light or belowground resources, which may selectively increase the size of large diameter trees and accelerate stand development (Getzin et al. 2008). These spatial patterns may also begin to approximate conditions found in old-growth northern hardwood forests, as similar patterns of local aggregation have been found resulting from periodic wind disturbance, which leads to fine-scale (<5 m) aggregation with close spacing and CSR at greater distances (Peterson 2020). Given that the size and extent of harvest gaps and retention levels used in this study were informed by natural disturbance patterns (Clark et al. 2021), these similarities with spatial structures in natural systems are not unexpected.

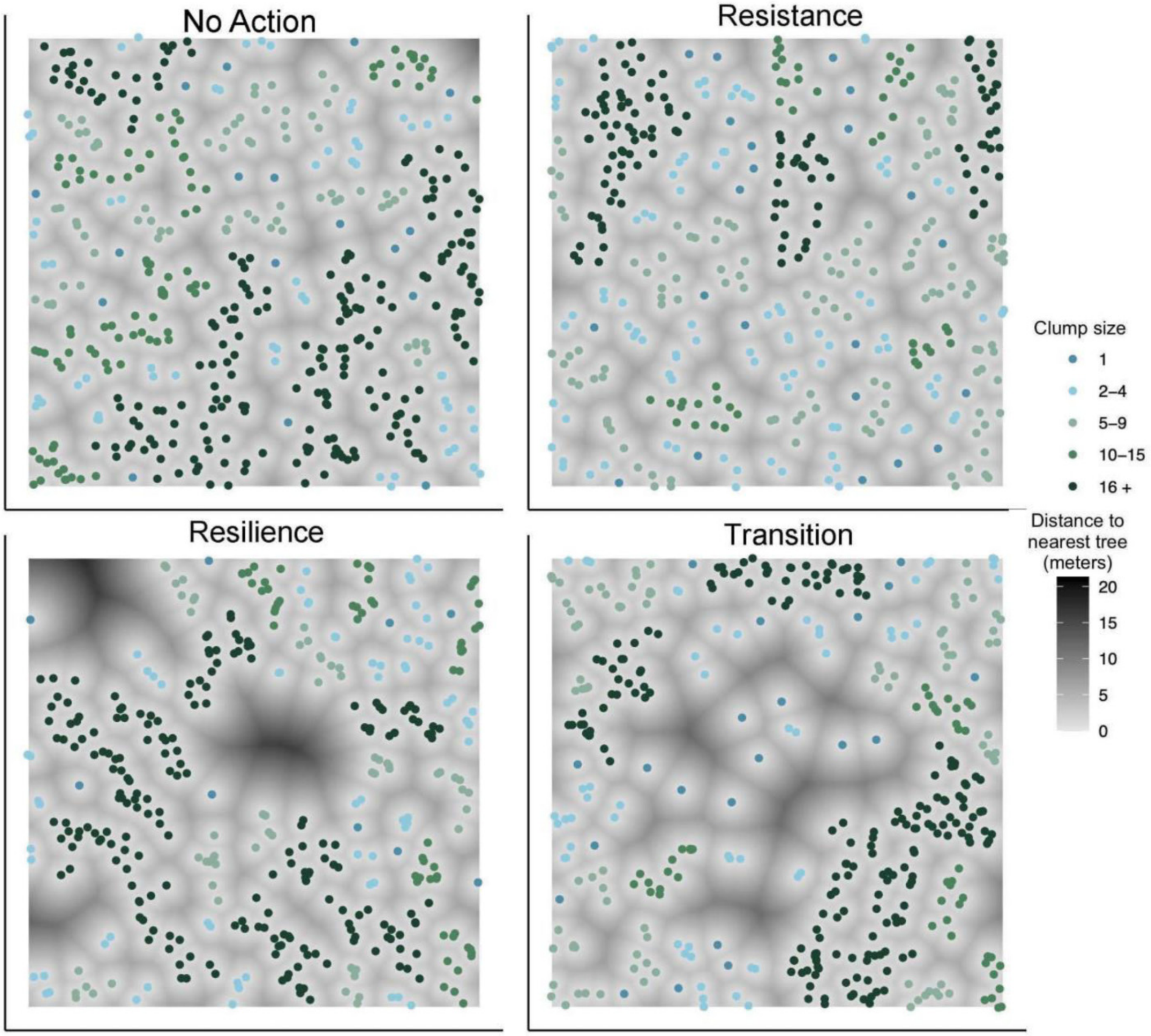
The dominant spatial pattern of CSR with some fine-scale aggregation found in our study is consistent with other point pattern analyses in moist temperate forests, although we found less aggregated patterning than some other studies that focus on the species level (Orwig et al. 2021; Pederson et al. 2014; Wang et al. 2010). Dry conifer forests, specifically those that represent historic reference conditions, that is, patterns shaped by frequent, low-severity natural disturbance, also exhibit similar patterning to that found in our study (Clyatt et al. 2016; Rodman et al. 2016), likely due to similarities in frequency and severity of natural disturbances in both systems, despite different agents of disturbance. Conversely, tropical, species-rich forests trend toward spatial aggregation at multiple scales, both generally and at the species level (Du et al. 2017; Seidler and Plotkin 2006), driven by seed dispersal limitation, as well as the high species diversity and coincident rare species, which have been shown to exhibit greater aggregation than common species (Condit et al. 2000; Lin et al. 2011); in other words, systems with a similar scale of natural disturbance seem to tend toward similar global scale spatial patterning.

Mark mingling was the global-scale analysis that provided the greatest differentiation between treatments, with the two treatments incorporating canopy gaps separating from the others. We suspect that these outcomes are shaped by the presence of the gaps themselves, as many trees in these plots have fewer neighbors within the 15-meter threshold. When the unpooled results are examined (Figs. S1 and S3), it becomes clear as well that specific site characteristics, such as a small patch of red spruce in transition block two and gap retention of beech in resilience and transition blocks three and four, may be influencing these patterns as well.

Tree clustering—neighborhood scale

While the global scale analyses failed to reveal large differences in spatial pattern between active management treatments, the clump detection algorithm highlighted different spatial characteristics in each of the adaptation approaches. The high relative quantity of individual trees found in transition reflects the low tree density and legacy retention in canopy gaps, where the presence of individual trees can support links to beneficial fungal networks, greater seed source availability and subsequent species diversity, continuation of ecological processes, and shelter for amelioration of harsh growing conditions (Fedrowitz et al. 2014; Lindenmayer et al. 2012). Conversely, the comparatively low proportion of individual trees in resilience, driven by canopy gaps with no retention, may avoid potential downsides of individual tree retention such as slowed growth of regeneration and

Fig. 5. Stem maps showing example tree patterns in 1-ha stem mapped plots in four climate adaptive silviculture treatments. Solid circles indicate trees that belong to clumps at an inter-tree distance of 5 m while open circles indicate trees that are farther than 5 m from the nearest neighbor. Background color describes distance to nearest tree with darker colors indicating greater distance to the nearest neighbor.



promotion of primarily shade-tolerant regeneration in gaps due to greater competition for light, moisture, and nutrients (Halpern and Urgenson 2021; Knapp et al. 2019). The predominance of individual trees and small clumps (two–four trees) in all treatments partially reflects the chosen limiting distance for the clump detection algorithm, but also supports the global pattern of fine-scale aggregation with dispersion at greater distances. Another notable pattern revealed by the cluster analysis is that while resistance and resilience had similar non-spatial outcomes, such as basal area and density, spatial mapping illustrated the considerable differences in resource conditions across each treatment. This emphasizes that spatial forest structural targets such as spacing are as important as non-spatial targets such as density when designing silvicultural treatments, especially those with an emphasis on adaptation, as tree arrangement has considerable influence on patterns of resource availability (Kuehne et al. 2015; LeFevre et al. 2020).

Individual species patterns

At the plot-wide scale, the pattern of CSR that we found may be trait-influenced: northern hardwood forests are comprised of both shade tolerant and intolerant species and some research indicates that patterns of uniformity have been supported by shade intolerant species, and aggregation by shade tolerant species in hardwood forests (Aldrich et al. 2003; Petritan et al. 2014; Williamson 1975). As a result, the combination of these two characteristics might lead to a distribution that spans the boundaries in between these conditions and presents as spatially random, as observed in our study.

The species-level patterns we found in our study are at least partially explained by germination and growth characteristics, most notably in the passively managed plots. The aggregation of yellow birch in all treatments may be reflective of its specific regeneration needs i.e., in gaps on downed wood or exposed mineral soil (Bolton and D'Amato 2011;

Fig. 6. Mingling index by species in each of four adaptation treatments, with mean index value at top of each bar. Mingling is based on an individual tree and 4 nearest neighbors. A value of 0 indicates all four nearest neighbors are conspecific, while a value of 1 indicates all 4 neighbors differ in species. The scale represents a corresponding percentage of neighbors that are a different species.

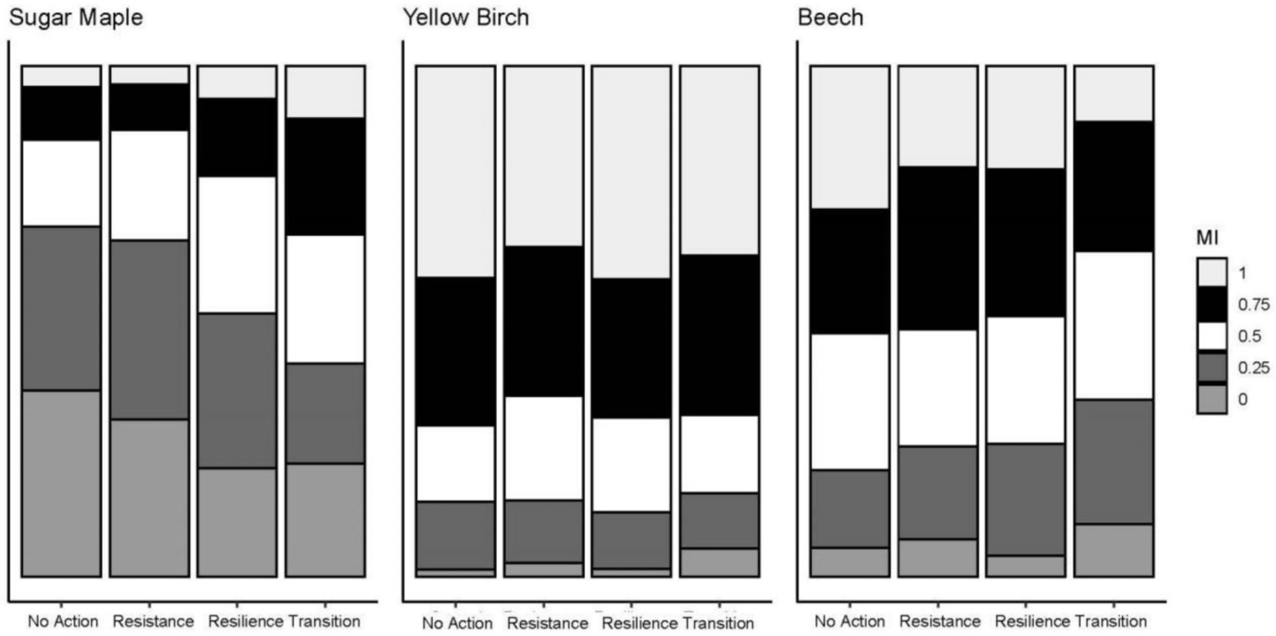


Table 2. Clark-Evans index of tree arrangement for three most common overstory species following four adaptation silviculture approaches. Values > 1 indicate overdispersion, <1 indicate aggregation, and = 1 indicates complete spatial randomness

Treatment	*Acer saccharum*	*Betula alleghensiensis*	*Fagus grandifolia*
No Action	0.92	0.76	1.01
Resistance	0.93	0.78	0.84
Resilience	0.83	0.77	0.80
Transition	0.74	0.75	0.78

Gauthier et al. 2016; Poznanovic et al. 2014) and its high mingling with other species, minimally affected by treatment, is likely due to its lower comparative abundance relative to the shade-tolerant canopy species favored by historic fine-scale disturbance on these sites. When viewed through an adaptive capacity lens, this mingling highlights a valuable stand-level adaptative capacity trait, species diversity at the neighborhood level (Pommerening and Uria-Diez 2017), which can indicate differential niche occupation and resource use at the scale of tree-tree interactions. Sugar maple patterns of uniformity and low levels of mingling can similarly be explained by regeneration and growth characteristics; sugar maple is shade-tolerant and germinates well through leaf-litter (Bolton and D'Amato 2011; Cleavitt et al. 2011), so may be less limited by a need for microsites or high light conditions. These characteristics may lead to more uniform distribution in space resulting in a potential decrease in adaptive capacity due to lower stand-level diversity of growing space and occupation of functional trait space (cf. Curzon et al. 2017). The increased aggregation and decrease in mingling exhibited by beech with management is a surprising outcome, as forests in the aftermath stage of beech bark disease, such as those examined in this study, tend toward sprout-origin regeneration, which is generally aggregated (Giencke et al. 2014). However, this management-induced aggregation may reflect historic preferential removal of other species other than the low value beech, which would result in clumps of unharvested beech that might exclude regeneration of other species, and ultimately work in counter to adaptation goals by creating reduced species and structural diversity.

The adaptive management techniques led to different patterns for each dominant species. Sugar maple became more aggregated and intermingled with other species, while beech became more aggregated but decreased in mingling. Notably, the transition approach had a considerable increase in species mingling and aggregation around sugar maple in parallel with reduced importance value, which may support increased occupation of trait space (Gazol and Camarero 2016) and patchy canopy openings, both conditions expected to increase adaptive capacity. Species patterns in resistance remained similar to those in no action, while resilience supported some metrics in common with no action (similar levels of mingling and importance in beech), and others in common with transition (greater aggregation and mingling of sugar maple). Taken together, these outcomes illustrate that each adaptation approach created a unique set of structural conditions reflecting management goals of adaptive capacity and further, exemplify how adaptive management may interact with current arrangement and interactions between tree species to reorganize spatial patterns and relative distribution.

Conclusion

Analysis of tree spatial patterns provides a novel and valuable lens into structures supporting forest adaptive capacity and potential pathways to disturbance response. By combining multiple spatial analyses, we were able to provide a unique perspective on outcomes of adaptation treatments, and further, contribute to the limited body of spatial data available in mesic forest systems. Global scale analyses of spatial patterns revealed influences of management on tree pattern, but minimal differences between management techniques, while local analyses teased apart distinctive patterns in each of the four adaptation approaches. At a species level, response to adaptive management differed by treatment. Our results indicate that adaptive management can alter spatial patterns and tree neighborhood environments, resulting in conditions that include elements known to increase adaptive capacity. Further, we have highlighted the value of emphasizing and understanding spatial objectives in management where goals include increasing the diversity of resource conditions and enhancing disturbance recovery options. This includes applying regeneration methods, such as hybrid single-tree/group selection and irregular shelterwoods, which combine canopy gaps and variable intensities of retention, to generate a range of within-stand adaptation pathways to future change.

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Data availability

Data collected and analyzed during this study are available in the OSF repository at: https://osf.io/xz3jv/?view_only=027a2f51b6144d6cbe4a3e1f9f33ae01

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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