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Forest Ecology

# Spatial Patterns of Canopy Disturbance and Shortleaf Pine in a Mixedwood Forest

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## Abstract

The spatial structure of forest ecosystems is dominated by the horizontal and vertical distribution of trees and their attributes across space. Canopy disturbance is a primary regulator of forest spatial structure. Although the importance of tree spatial pattern is widely acknowledged as it affects important ecosystem processes such as regeneration and recruitment into the overstory, quantitative reference spatial conditions to inform silvicultural systems are lacking. This is especially true for mixedwood forests, defined as those that contain hardwoods and softwoods in the canopy. We used data from a preexisting network of plots in a complex-stage mixedwood stand to investigate the influence of canopy disturbance on stand and neighborhood-scale spatial patterns. We reconstructed canopy disturbance history and linked detected stand-wide and gap-scale disturbance events to establishment and spatial patterns of shortleaf pine. The majority of shortleaf pine establishment coincided with stand-wide or gap-scale disturbance. Shortleaf pine was clustered at the stand scale but was randomly distributed at the neighborhood scale (i.e. five tree clusters), which was a legacy of the historical disturbance regime. These results may be used to improve natural disturbance-based silvicultural systems to restore and maintain mixedwood forests for enhanced resilience and provisioning of ecosystem goods and services.

**Study Implications:** Shortleaf pine was clustered into compositionally distinct patches within the oak-pine stand. Based on our findings, we recommend managers of stands with patchy species composition consider silvicultural systems that focus on patches. This approach acknowledges the effects of intrastand spatial variability of biophysical conditions and interactions with stochastically occurring canopy disturbances on regeneration and recruitment. Patch clearcuts with reserves could be implemented with the openings correspondent to microsites that favor regeneration of shortleaf pine. Similar potential approaches could be seedtree, irregular shelterwood, and other regeneration methods suited to stand conditions and the silvics of the species of interest.

**Keywords:** oak-pine, silviculture, neighborhood, intermediate-severity disturbance, disturbance history

The spatial structure of forest ecosystems is primarily defined by the horizontal and vertical distribution of trees and their attributes, such as basal area, across ecologically meaningful spatial units (e.g., neighborhoods and stands). The spatial patterns of forest structural components influence forest succession and development through neighborhood effects (Frelich et al. 1998), tree establishment and growth (Palik et al. 2003, Boyden et al. 2005), and mortality (Das et al. 2008). Variability in tree spatial patterning also affects many biotic and abiotic ecosystem functions and processes such as understory light availability (Sprugel et al. 2009), herbaceous plant communities (Laughlin et al. 2006), and soil properties (Bruckner et al. 1999). Forest disturbance is a primary control of forest spatial structure (Whittaker 1975, Schwarz et al. 2003). After forest disturbance events, the spatial arrangement of residual trees is an important biological legacy as disturbance-regulated tree spatial patterns influence subsequent stand developmental and successional pathways (Hart and Kleinman 2018, Lindenmayer et al. 2019).

Although the importance of disturbance on spatial structure within forest ecosystems is appreciated, few studies have directly linked contemporary tree spatial patterns to prior canopy disturbance events (see Frelich and Reich 1995, Franklin et al. 2002, Boyden et al. 2005, Ford et al. 2017). This is especially true for mixedwood stands, defined as stands of hardwood and softwood species in which neither group constitutes >75–80% of the overstory composition (Helms 1998, Kabrick et al. 2017). Composition in mixedwood stands is strongly influenced by the disturbance regime that maintains unique, disturbance-dependent habitat types; thus, natural disturbance patterns should be integrated into management systems (Franklin 1980, Hessburg et al 1999, Larson and Churchill 2012). Although the importance of tree spatial patterns is increasingly acknowledged in forest management, there exists a lack of quantitative reference spatial patterns necessary to inform management efforts, especially in mixedwood forest types. Specifically, more information is needed on the linkage between canopy disturbance events and tree spatial patterns to augment natural disturbance-based silvicultural systems that emulate the effects of natural disturbance processes (Mitchell et al. 2003, Palik et al. 2020).

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Mixed oak-shortleaf pine (*Pinus echinata* Mill.) stands of the eastern United States are excellent model ecosystems to examine the role of disturbance on the spatial patterns of canopy trees in mixedwood stands. These mixed oak-shortleaf pine systems, like other broadleaved–needle-leaved systems, require complex management techniques to restore and perpetuate proportional species mixtures. Shortleaf pine is the most widely distributed pine species in the eastern United States and this species co-occurs with a wide range of hardwood species. Furthermore, these systems evolved within a disturbance regime that is characteristic of most forests of the region. Second to fire, wind is the most extensive disturbance in the temperate zone (MacDonald 2003) and is the most prevalent disturbance agent in disturbance regimes in forests of the eastern United States (Peterson et al. 2016). For these reasons, the results from tree spatial pattern analyses in mixed oak-shortleaf pine forests may offer insight into the spatial patterns of other mixed broadleaved–needle-leaved forests globally. Although shortleaf pine is the most widespread pine species in the eastern United States, it has experienced extensive habitat loss as a result of altered disturbance regimes such as fire exclusion, conversion to loblolly pine (*Pinus taeda* L.) plantations, insect outbreaks, and lack of active management (Oswalt 2012). On upland sites east of the Mississippi River, area classified as mixed oak-shortleaf pine has declined by 52% since 1980 (Oswalt et al. 2012), with a notable lack of shortleaf pine in smaller size classes in most of these forests. Mixed oak-shortleaf pine forests have been considered a mid-successional forest type that exists in a dynamic state between early-successional pine forests and mid- to late-successional hardwood forests (Cooper 1989). Thus, management is required to perpetuate these increasingly desired species mixtures (Pretzsch et al. 2017).

In response to anticipated stresses and perturbations attributed to global change, forest managers increasingly wish to promote forest ecosystem resilience (Janowiak et al. 2014, Nagel et al. 2017). Management designed to enhance native forest diversity is a primary means to achieve this goal. Diverse forest communities contain native plant species with a wide range of life history strategies and functional traits, which enhance resilience to disturbance (Enright et al. 2014). For many forest managers in the eastern United States, this means an increased focus on managing for mixed oak and pine species assemblages. Indeed, the ecology and management of mixedwood forests are becoming major research foci (Kabrick et al. 2017, Willis et al. 2019, Aldea et al. 2020). In addition to increasing species richness, pine trees in hardwood stands enhance vertical structural complexity and ecosystem functions because pine species typically have high live crown ratios, support year-round foliage, and have relatively acidic litter, wood, and bark (Harmon et al. 1986, Schulte et al. 2007, Fahey and Lorimer 2013). Furthermore, pine litter increases fire temperature and heating duration in mixed fuel complexes, which may help maintain pine-hardwood stands (Ellair and Platt 2013, Emery and Hart 2020).

In mixed oak-shortleaf pine forests of the eastern United States, we hypothesize that an intermediate-severity disturbance regime combined with periodic surface fire perpetuates this mixedwood composition. These spatially extensive disturbance events may facilitate establishment of new shortleaf pine cohorts and develop compositionally distinct neighborhoods (0.04–0.2 ha) within the stand-wide species matrix. To date, no studies have reported spatial reference conditions in mixed oak-shortleaf pine stands. The goal of this study was to determine the influence of canopy disturbance on the spatial distribution of shortleaf pine at the stand and neighborhood scales in a mixed oak-shortleaf pine stand. The specific objectives were to (1) reconstruct the canopy disturbance history and recruitment strategies of shortleaf pine, (2) quantify the stand and neighborhood-level spatial patterns of shortleaf pine, and (3) relate disturbance history and establishment trends to the spatial patterns of shortleaf pine in a mixed oak-shortleaf pine stand. Results of this study aid our understanding of the influence of disturbance on stand and neighborhood-scale spatial patterns in mixedwood stands. Our results may be used to improve natural disturbance-based silvicultural systems to restore and maintain mixedwood forests for enhanced resilience and provisioning of ecosystem goods and services.

## Methods

### Study Site

This study occurred in the Savage Gulf Natural Area (SGNA) in Grundy and Sequatchie Counties, Tennessee (Figure 1). The SGNA area is a 6,309 ha reserve managed as a Class II Natural-Scientific Area by the Tennessee Department of Environment and Conservation. Because of its biodiversity and unique geological characteristics, the reserve is listed as a National Natural Landmark by the US Department of the Interior. The SGNA has been designated for recreation and research since the State of Tennessee acquired the parcel in 1973. Prior to state acquisition, parts of the reserve experienced anthropogenic disturbance, such as logging and land-clearing for agriculture (Manning 1993). The area was permanently settled by European immigrants in 1870, and the construction of rail lines and mills followed settlement. The selected study site within the SGNA appeared to be relatively undisturbed, as evidenced by lack of logging roads, cut stumps, and rail beds. See Hart et al. (2012) for a detailed description of prior land use.

The reserve is situated on the Cumberland Plateau section of the Appalachian Plateaus physiographic province, the westernmost physiographic province of the Appalachian Highland realm (Fenneman 1938). The Appalachian Plateaus province is bordered by the Ridge and Valley to the east and the Interior Low Plateau to the west. The Cumberland Plateau section is characterized by broad, uncut plateau remnants not yet maturely dissected that are situated between deep valleys (Fenneman 1938). In this study, vegetation sampling plots were established on the weakly dissected plateau landtype association of the true plateau subregion as classified by Smalley (1986). This landtype association is characterized by broad undulating to rolling ridges with gentle to moderately steep-sided slopes, dissected by young valleys (Smalley 1986). Referred to as tablelands, this distinct landform is extensive throughout the Cumberland Plateau physiographic section. The natural area is dissected by Savage Creek, a deeply incised tributary to the Collins River. The tablelands above are dissected by many bedrock streams that flow into Savage Creek. The underlying geology of the SGNA is in the Crab Orchard and Crooked Forked groups, which are primarily composed of sandstone, conglomerate, siltstone, shale, and coal. Soils of the study site belong to the Beersheba, Jefferson, Lily, Lonewood, and Ramsey soil series (USDA NRCS 2020). These series are characterized by moderately deep to very deep, well-drained soils. Soils of these series are primarily derived from sandstone, shale, siltstone, or quartzite. Soil textures are loam, silt loam, and sandy loam, and slopes range from 2 to 40% (USDA NRCS 2020).

The regional climate of the SGNA is humid mesothermal (Thornthwaite 1948), with long, moderately hot summers and

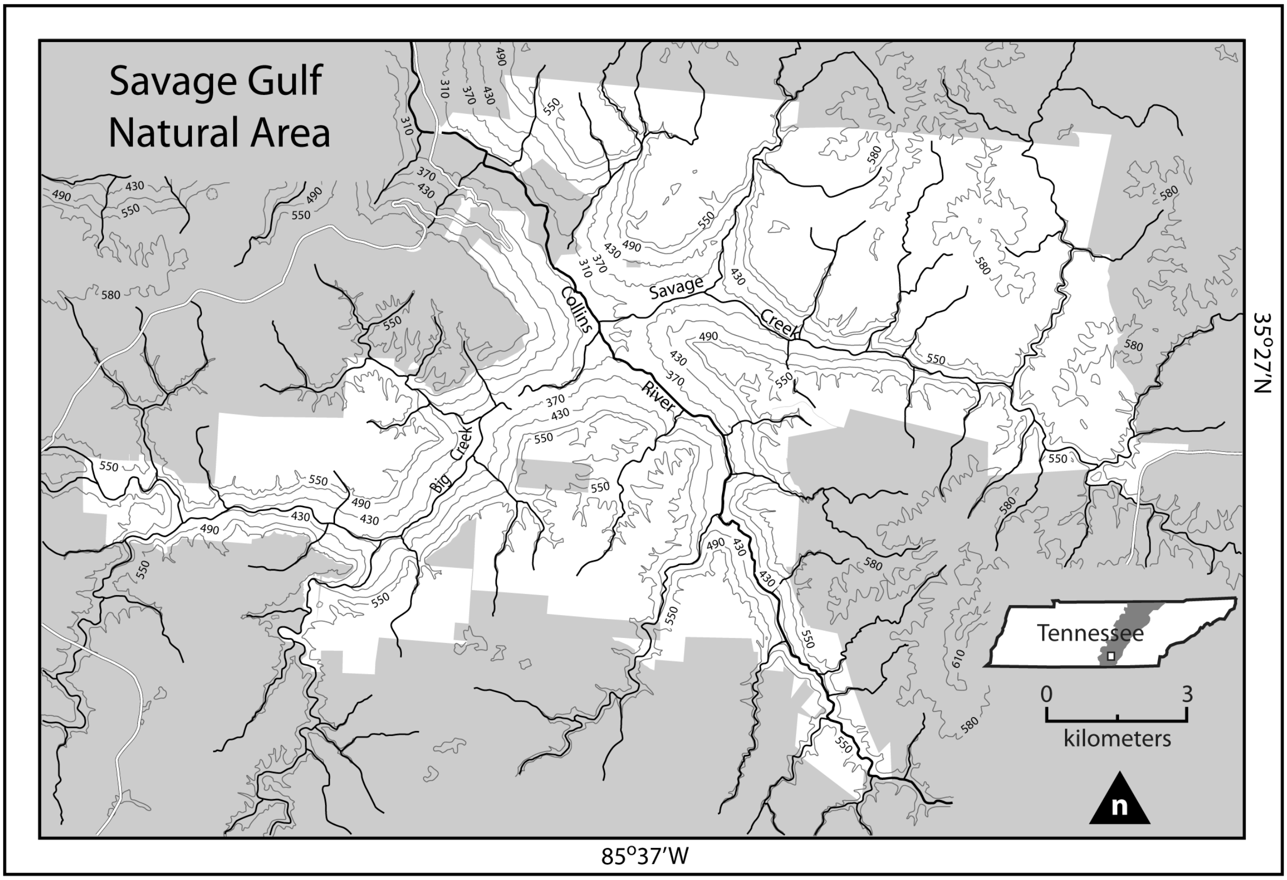

**Figure 1.** Map of Savage Gulf Natural Area (SGNA) in Tennessee, USA. Plots were located in the northern tablelands of the SGNA.

short, mild winters. Mean annual temperature is 13.5°C, with the lowest monthly mean temperature of 2.8°C in January and the highest monthly mean temperature of 23.4°C in July (PRISM 2018). The amount of precipitation is typically steady throughout the year with a mean annual precipitation of 1,474.2 mm. October receives the lowest mean precipitation (85.6 mm) and March receives the greatest mean precipitation (132.6 mm, PRISM 2018). The most frequent current natural disturbance agent in Grundy County, Tennessee, is wind disturbance, with 103 recorded wind-related storm events from 1950 to 2019 that caused significant tree or structural damage (NOAA Storm Events Database 2020). Of these 103 severe wind events, seven were tornado events.

The Cumberland Plateau supports diverse plant communities that are intermediate between mixed mesophytic, mixed hardwood, and mixed pine-hardwood forest types (Hinkle 1978, 1989). The uplands of the Cumberland Plateau were found to support 12 plant community types (Hinkle 1989), which ranged from red maple (*Acer rubrum* L.), river birch (*Betula nigra* L.), and American holly (*Ilex opaca* Aiton) on floodplain terraces to red maple, white oak (*Quercus alba* L.), and blackgum (*Nyssa sylvatica* Marshall) on poorly drained swales to Virginia pine (*Pinus virginiana* Mill.) and blackjack oak (*Quercus marilandica* Münchh) on dry ridgetops. On upland sites of the Cumberland Plateau, including the tablelands of the SGNA, plant community composition is largely a function of fine-scale topographic characteristics, soil water availability, and canopy disturbance history (Hinkle 1978, Smalley 1986, Hart et al. 2012). On the weakly dissected broad undulating uplands of the Cumberland Plateau, site index is ca. 65 for shortleaf pine and 60 for upland oaks (Smalley 1986). The contemporary plant community of the SGNA tablelands is dominated by white oak, red maple, and shortleaf pine (Hart et al. 2012). At the genus level, oak is the most dominant (46% basal area), followed by pine (17% basal area), and maple (16% basal area). Oak and pine represent 70% of canopy trees, and sourwood (*Oxydendrum arboreum* L.) and red maple represent the majority of understory trees (Hart et al. 2012).

## Field Methods

In the summer of 2008, plots were established to quantify species composition and structure, stand development, and canopy disturbance history of an upland old-growth mixed oak-pine forest (Hart et al. 2012). A 600 ha site within the SGNA was selected for this purpose. Plot locations were systematically selected within the old-growth remnant by overlaying a 240 × 240 m fishnet with ArcGIS v. 9. Plot coordinates were uploaded to a handheld GPS receiver for navigation in the field, and 87 0.04 ha fixed radius vegetation sampling plots were inventoried. In each plot, the species, crown class, and diameter at breast height (dbh, 1.37 m above root collar) were recorded for all trees (stems ≥ 5 cm dbh). Crown class was assigned for each tree based on the amount and direction of intercepted light and assigned one of four categories: dominant, codominant, intermediate, and overtopped (Oliver and Larson 1996). The distance and azimuth of each tree was recorded from plot center to calculate spatially explicit metrics for neighborhood-level analyses. A sighting compass was used to measure the azimuth from plot center to each tree, and a digital hypsometer and transponder were used to measure the distance from plot center to each tree. Saplings (woody stems ≥ 1.4 m height, <5 cm dbh) were identified to species and tallied for abundance in a nested 0.004 ha circular plot located 7.2 m due north of plot center. To determine stand age, disturbance history, and recruitment strategies, increment borers were used to extract one core from all trees ≥20 cm dbh and the four trees ≥5 cm dbh and <20 cm dbh nearest plot center.

## Analytical Methods

### Disturbance History Reconstruction

Tree core samples from oak and pine individuals were air-dried and glued to wooden mounts with cells vertically aligned (Stokes and Smiley 1996). Each sample was sanded with progressively finer abrasives to reveal the cellular structure of the wood (Orvis and Grissino-Mayer 2002). Tree rings were then dated to the calendar year of establishment under a stereo-zoom microscope. Pith estimators (Villalba and Veblen 1997) were used to estimate inner dates on ring series that did not contain pith but showed substantial ring curvature. Once all rings were dated on each series, raw-ring width was measured to the nearest 0.001 mm using a Velmex measuring stage (Velmex Incorporated 2009) interfaced with Measure J2X software (Voor Tech Consulting 2008). Ring widths were measured for all oak series ($n$ = 200) and pine series ($n$ = 129). The oak and pine chronologies were statistically analyzed using the software COFECHA (Grissino-Mayer 2001), a program that uses segmented time-series correlation analysis to ensure each ring is assigned the correct calendar year of formation. Segments that fell below a predetermined threshold ($r$ = 0.32) were flagged by COFECHA (Holmes 1983, Grissino-Mayer 2001). Flagged series were inspected for potential dating errors and adjusted if necessary.

Once all series were accurately dated and each annual growth ring was measured, dendrochronological techniques were applied to both the oak and pine chronologies to quantify the magnitude, frequency, and spatial distribution of canopy disturbance events. Typically, canopy disturbance events are identified by detected release episodes, which are defined as changes in radial growth patterns (Nowacki and Abrams 1997, Rentch et al. 2002, Hart et al. 2012). For consistency with the oak chronology published by Hart et al. (2012), we used the running mean method proposed by Nowacki and Abrams (1997) for the pine chronology. Release events were identified as periods in which the raw-ring width of a given year was ≥25% (minor) or ≥50% (major) of the mean ring width of the preceding and superseding ten years, sustained for at least three years (Hart and Grissino-Mayer 2009, Hart et al. 2012). Stand-wide disturbances (SWD) were identified as release events for a given year (±2 years) detected in at least 25% of oak and pine individuals at least 10 years of age at the time of the release, or a simultaneous release detected in at least 25 percent of plots (Hart and Grissino-Mayer 2009, Hart et al. 2012).

To reconstruct canopy recruitment strategies of shortleaf pine, all shortleaf pine with inner pith dates (i.e., tree core sample contained pith) were classified into two groups, gap origin or understory origin, based on the first 40 years of radial growth of each individual (Rentch et al. 2002). If the mean radial growth of the first 20 years was greater than the mean radial growth of the subsequent 20 years, the individual was classed as gap origin. If the mean radial growth of the first 20 years was less than the mean radial growth of the subsequent 20 years, the individual was classed as understory origin (Lorimer et al. 1988, Hart et al. 2012). To determine the relationship between canopy disturbance and shortleaf pine establishment, all detected SWD events and localized gap-scale canopy disturbance events were linked to the plot in which they occurred. On each plot, the date of establishment for shortleaf pine individuals was linked to the year of associated disturbance (±2 years) to determine whether shortleaf pine established as a result of an SWD or localized gap-scale disturbance. For each shortleaf pine, if no relationship existed between detected SWD or gap-scale disturbance and establishment date within the same plot, the analysis was expanded to include SWD disturbances detected in the four surrounding plots. We quantified plot-level disturbance frequency as the ratio of total detected disturbances to the age of the oldest tree on the plot (Goode et al. 2020).

### Multiscale Spatial Analyses

To determine the spatial distribution of shortleaf pine at the stand scale (i.e., total sampled area), we calculated spatially explicit measures of spatial autocorrelation. To test for significant spatial clustering at the stand scale, global Moran's I was calculated based on shortleaf pine relative dominance (% basal area plot$^{-1}$). Moran's I is a weighted correlation coefficient that detects deviations from spatial randomness (Moran 1950). Global Moran's I was calculated twice based on two predefined weighted neighbor matrices. For the first calculation, we used a weighted neighbor matrix with a distance band of 250 m, which included plots perpendicular to the focal plot in the calculation of the Moran's statistic. For the second calculation, we used a weighted neighbor matrix with a distance band of 340 m, which included plots perpendicular and diagonal to the focal plot in the calculation of the Moran's statistic. To visualize significant high and low clusters and outliers of shortleaf pine relative dominance throughout the stand, we mapped significant local indicators of spatial autocorrelation ($p < 0.05$). The analyses for stand-level spatial distribution of shortleaf pine were conducted with the spatial dependence (spdep) package in R version 1.2.5001 (Bivand et al. 2015).

To investigate neighborhood scale spatial structure of shortleaf pine, we calculated nearest neighbor-based indices to describe the fine-scale variation in tree species, size distribution, and spatial distribution in five-tree neighborhoods. These indices included the mingling, dominance, and uniform angle index (Pommerening 2002, Li et al. 2012) and have proven useful for the analysis of neighborhood-scale spatial structure in mixed-species forests (Hui et al. 1999, Graz 2004, 2006). Species mingling ($M_i$) is a measure of species interspersion in a five-tree neighborhood (Pommerening 2002) and is defined as the proportion of $n$ nearest neighbors that are of a different species from the focal tree. Mingling assumes five values that range from 0 to 1. A value of 0 indicates that the four nearest neighbors are of the same species, and a value of 1 indicates that the four nearest neighbors are of a different species than the focal tree. Dominance ($U_i$), a measure of diameter differentiation in a five-tree neighborhood, is the proportion of $n$ nearest neighbors that have a smaller diameter than the focal tree (Aguirre et al. 2003). Dominance assumes one of five values when the number of nearest neighbors is four. A value of 0 indicates that the four nearest neighbors of a focal tree have a larger diameter than the focal tree, and a value of 1 indicates that the four nearest neighbors have a smaller diameter than the focal tree. The uniform angle index (UAI, $W_i$) describes the spatial distribution of a five-tree neighborhood. The angle between two adjacent neighbors of the focal tree is compared to a standard angle (72°, Agguire et al. 2003). The UAI is the proportion of angles that are smaller than the standard angle. Similarly, UAI assumes values of 0 to 1. A value of 0 indicates a regular distribution and a value of 1 indicates an irregular (clumped) distribution. Because each of these metrics has the same five potential values (0.00, 0.25, 0.50, 0.75, 1.00), a bivariate distribution can be used to visualize the relationship between calculated neighborhood structural metrics in five-tree neighborhoods (Li et al. 2012). We created three combinations of bivariate distribution for all recorded trees in the stand (mingling × dominance, uniform angle × dominance, mingling × uniform angle) and three combinations of bivariate distributions for all shortleaf pine as the focal tree. All neighborhood indices were calculated with the forestSAS package in R (Chai 2016).

To visualize and explore differences in overstory composition across the stand, we conducted nonmetric multidimensional scaling (NMS) in PC-ORD v. 7 (McCune and Mefford 2011). Treatments were delineated based on the median value of pine relative dominance (% basal area) plot$^{-1}$. Once plots were assigned to one of the two treatment categories (pine or hardwood), NMS ordination was used to graphically interpret differences in overstory composition in relation to five environmental variables: (1) number of detected SWD, (2) disturbance return ratio, (3) aspect, (4) terrain shape index, and (5) elevation. These five environmental variables captured disturbance and site factors that influenced the possible distinctions between pine and hardwood overstory communities. Terrain shape index is a quantitative measure of the geometric shape of the land surface (McNab 1989). Negative values indicate degrees of surface convexity, and positive values indicate degrees of surface concavity. An NMS scree plot was used to determine the number of axes in the final solution, permuted 250 times with real data, and cross-checked for consistency with other solutions. A biplot overlay was displayed to assess correlation between ordination axes and environmental variables, with an $r^2$ cutoff of 0.25. To test for significant difference in overstory composition between treatments, a distance-based multiresponse permutation procedure was conducted in PC-ORD v. 7 (MRPP, Mielke and Berry 2001).

## Results

### Age Structure, Disturbance History, and Shortleaf Pine Recruitment Strategies

The median age of shortleaf pine at the time of sampling was 69 years (17.5 SD). The oldest shortleaf pine recorded had an inner pith date of 1722, and the youngest shortleaf pine recorded had an inner pith date of 1975. The age structure distribution for shortleaf pine was unimodal, with the largest establishment pulse in the 1940s (Figure 2). The first pulse of shortleaf pine establishment began in the 1880s, peaked in the 1940s, and declined until 1970. The majority (79%) of shortleaf pine individuals established between the 1920 and 1950 (Figure 2).

We detected 233 release events in the shortleaf pine chronology, of which 83% were classified as minor and 17% were classified as major. The majority of shortleaf pine (86%) experienced at least one release post establishment, and 49% experienced two or more releases post establishment. The median number of releases experienced by shortleaf pine was 2.0 releases individual$^{-1}$ (1.2 SD). The most releases experienced by an individual shortleaf pine was six releases. The decade with the most release events experienced by shortleaf pine was the 1970s, in which 32% of all releases were detected, followed by the 1950s (24% of releases). Comparatively, in the oak chronology, the number of detected releases was steady (Hart et al. 2012), with no distinct spike in release frequency (Figure 2). The majority of shortleaf pine established in a gap environment (87%), in which the mean of the first 20 years of growth was greater than the mean of the subsequent 20 years.

The combined oak and pine chronologies resulted in the detection of 525 release events and five stand-wide disturbance events that coincided with shortleaf pine establishment. These five stand-wide disturbance events occurred in 1880–1886 (31% of trees at least 10 years of age and 16% of plots), 1903–1912 (30% of trees and 22% of plots), 1937–1945 (18% of trees and 25% of plots), 1953–1961 (26% of trees and 37% of plots), and 1968–1976 (36 percent of trees and 57% of plots). For a list of stand-wide disturbance events prior to the first shortleaf pine establishment pulse, see Hart et al. (2012). The stand-wide disturbance frequency was 29 years, and gap-scale disturbance frequency was 1.2 years. The majority of shortleaf pine establishment coincided with local or stand-wide disturbance events detected in the same plot or a surrounding plot (Table 1). Specifically, 38% of shortleaf pine individuals established coincident with a detected stand-wide disturbance, and 41% of shortleaf pine individuals established coincident with a localized gap-scale disturbance event. The remaining 21% of shortleaf pine could not confidently be associated with a known canopy disturbance event.

### Stand-Scale Spatial Distribution of Shortleaf Pine

Shortleaf pine dominance (basal area plot$^{-1}$) was significantly clustered (Moran's Index: 0.142, $p = 0.030$) within the mixed oak-shortleaf pine stand. Significant clustering occurred at 250 m but dissipated at greater distances. Shortleaf pine dominance was uniformly distributed at 340 m (Moran's Index: 0.044, $p = 0.270$). We documented both high and low clusters of shortleaf pine dominance in areas of 250 × 250 m. The mapping of local indicators of spatial autocorrelation revealed high and low clusters and high and low outliers (Figure 3). High-high clusters indicated that the focal plot had high shortleaf pine dominance and was surround by plots (within 250 m) that also had high shortleaf pine dominance. High-low outliers indicated that the focal plot had high shortleaf pine dominance and was surrounded by plots with low shortleaf pine dominance. Low-low clusters indicated that the focal plots had low shortleaf pine dominance and was surround by plots that also had low shortleaf pine dominance. Low-high outliers indicated that the focal plot had low shortleaf pine dominance but was surrounded by plots with high shortleaf pine dominance. Of the 87 plots analyzed

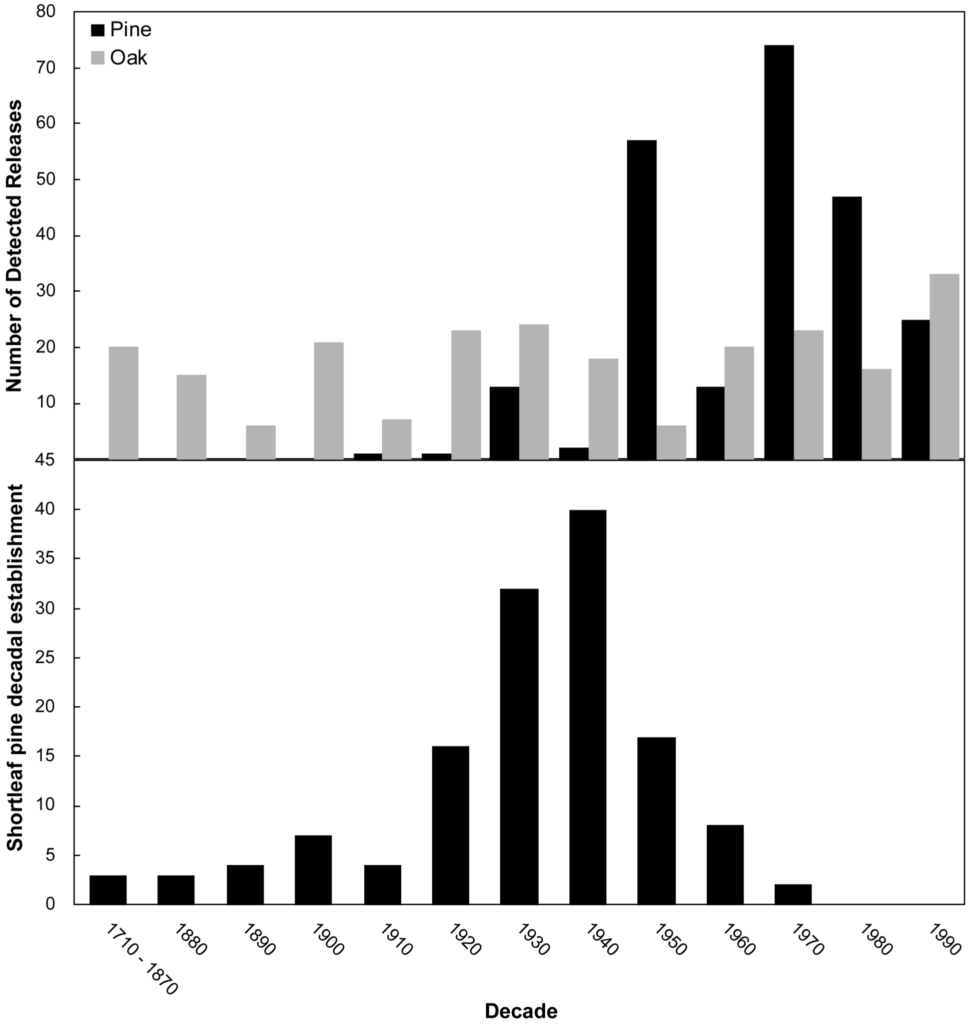

**Figure 2.** Number of detected releases by decade in the oak (gray) and pine (black) chronologies (top figure) and shortleaf pine (n = 129) establishment date by decade (bottom figure) in a mixed oak-shortleaf pine stand at Savage Gulf Natural Area, Tennessee.

for spatial autocorrelation, 13 were significantly clustered or were a significant outlier ($p < 0.05$).

## Neighborhood-Scale Distribution of Shortleaf Pine

The mingling-dominance distribution of shortleaf pine was skewed towards high mingling values and high dominance values (Figure 4a). This indicated that, for a focal shortleaf pine, the four nearest neighbors were primarily composed of a different species and had a smaller diameter. Nearly 40% of shortleaf pine trees had nearest neighbors of different species ($M_i = 1.0$) and were the dominant tree ($U_i = 1.0$). This combination was four times greater than any other bivariate distribution combination. When all trees were analyzed as the focal tree, the $M_i$-$U_i$ frequency distribution was skewed towards higher mingling values, but trees had relatively uniform dominance distribution and tended to cooccur with different species that were relatively similar in dominance (Figure 4b). For all trees, 11% had a combination of $M_i = 1.0$ and $U_i = 1.0$.

The mingling-uniform angle index ($M_i - W_i$) bivariate distribution of shortleaf pine focal neighborhoods indicated that the majority of shortleaf pine had three or four nearest neighbors of a different species ($M_i \geq 0.75$) and shortleaf pine neighborhoods were spatially randomly distributed ($W_i = 0.5$, Figure 4c). For all trees, there were more neighborhoods in which the reference tree had three or four nearest neighbors of the same species ($M_i \leq 0.25$), but the majority of neighborhoods were intermingled with different species, similar to shortleaf pine neighborhoods (Figure 4d). Similarly, for all trees, the majority of neighborhoods were randomly distributed, but more neighborhoods were slightly clumped or slightly regular ($W_i = 0.75$ and 0.25, respectively) than shortleaf pine neighborhoods. The most frequent combination (approximately 20%) was neighborhoods in which the reference tree shared four nearest neighbors of a different species ($M_i = 1.0$), and the reference tree was randomly distributed ($W_i = 0.50$).

The most frequent combination (>30%) of the uniform angle index-dominance bivariate distribution ($W_i - U_i$) of shortleaf pine neighborhoods was randomly distributed trees ($W_i = 0.5$) that were dominant ($U_i = 1.0$, Figure 4e). Nearly all shortleaf pine trees were the most dominant individuals ($U_i \geq 0.75$) and were slightly clumped ($W_i = 0.5$–$0.75$). For all trees, the majority were randomly distributed ($W_i = 0.5$), and dominance values were uniformly distributed across $W_i = 0.5$ (Figure 4f).

**Table 1.** Decadal establishment of shortleaf pine in relation to stand-wide disturbance (SWD) or localized gap-scale disturbance (Gap) detected within the same plot or one of the four surrounding plots at Savage Gulf Natural Area, Tennessee. Unknown (UNK) is shortleaf pine establishment that did not coincide with SWD or gap-scale disturbance occurrence in the same plot or surrounding plots.

| | SWD (25% Plots OR 25% Trees) | | | | | | Surrounding Plots | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1880–1886 | 1903–1912 | 1937–1945 | 1953–1961 | 1968–1976 | Local | SWD | Gap | UNK | TOTAL |
| 1880 | — | — | — | — | — | — | 2 | — | 1 | 3 |
| 1890 | — | 2 | — | — | — | — | - | — | — | 2 |
| 1900 | — | - | — | — | — | — | 2 | — | 5 | 7 |
| 1910 | — | 1 | — | — | — | 1 | 1 | - | 1 | 4 |
| 1920 | — | — | — | — | — | 5 | 4 | - | 6 | 15 |
| 1930 | — | — | 3 | — | — | 9 | 9 | 6 | 6 | 33 |
| 1940 | — | — | 6 | 1 | — | 15 | 9 | 2 | 7 | 40 |
| 1950 | — | — | — | 1 | — | 7 | 3 | 3 | 1 | 15 |
| 1960 | — | — | — | 1 | — | 4 | 3 | — | — | 8 |
| 1970 | — | — | — | — | — | 1 | 1 | — | — | 2 |
| TOTAL | 0 | 3 | 9 | 3 | 0 | 42 | 34 | 11 | 27 | 129 |

### Overstory Community Ordination

The three-dimensional NMS solution and MRPP revealed two distinct clusters of overstory plant communities (Figure 5) based on the relative dominance ($m^2ha^{-1}$) of pine individuals plot$^{-1}$. The final solution had a three-axis stress of 12.97 and explained 86% of the variability in the data. Axis 1 explained 26% of the variance in overstory plant community composition, Axis 2 explained 25% of the variance, and axis 3 explained 18% of the variance. Axis 2 was negatively correlated with the number of detected stand-wide disturbances (SWD, $r^2 = -0.26$), which corresponded to the location of pine plots in ordination space and indicated that SWD was an influential environmental driver of pine community composition. The remaining four environmental variables were not correlated ($r^2 < 0.10$) with any of the three ordination axes. Visually, the two communities (hardwood versus pine) formed two unique clusters in ordination space (i.e., the two-dimensional space between axes), and the MRPP corroborated that hardwood and pine communities were significantly different in ordination space ($p < 0.01$).

## Discussion

### Influence of Disturbance on Shortleaf Pine Establishment

Shortleaf pine is a moderately shade-intolerant species that requires canopy openings typically larger than a single tree canopy gap to establish (Clabo and Clatterbuck 2020, Mohler et al. 2021). Although shortleaf pine seedlings are able to survive for extended periods within gaps with variable levels of overstory retention (Schnake et al. 2021), shortleaf pine is usually less shade-tolerant than cooccurring oak species. We hypothesized that stand-wide disturbance (i.e., intermediate-severity disturbance) was one necessary component of the historical disturbance regime to facilitate establishment of shortleaf pine. Intermediate-severity disturbance impacts can vary spatially, with high-severity mortality contained within a portion of the stand or a high frequency of low-severity canopy gaps spread throughout the stand (Hart and Kleinman 2018). Our results indicated that although stand-wide events coincided with the establishment of shortleaf pine, most of the SWD events were detected in plots adjacent to shortleaf pine establishment. However, 21% of shortleaf pine were not linked to a detected SWD or gap-scale disturbance event. This may be attributed to the disjunct arrangement and small size of sampling plots. Stand-wide or gap-scale disturbance may have been detected in unsampled trees directly outside plots or in between plots that facilitated the establishment or release of the 21% of trees not associated with detected disturbance. Furthermore, variability in radial growth patterns within trees could have underrepresented the number of release episodes and canopy disturbance events when only one increment core was extracted from each canopy tree (Buchanan and Hart 2011). For these reasons, we contend that SWD detected in an adjacent plot likely influenced abiotic conditions in or outside of the focal plot to facilitate shortleaf pine establishment. The pulse of shortleaf pine establishment in the 1930s and 1940s corresponded with the detected stand-wide disturbance in the late 1930s (25% of plots) and subsequent canopy ascension corresponding to the stand-wide disturbance in the 1950s (37% of plots, 26% of trees experienced a release). Thus, based on the timing of stand-wide canopy disturbances and establishment and subsequent canopy recruitment of shortleaf pine, we contend that canopy disturbance influenced shortleaf pine demography in the stand. However, we acknowledge other potentially confounding environmental factors, such as domestic livestock grazing and herbivory that were not analyzed in relation to shortleaf pine establishment and recruitment. Open-range grazing was prohibited in Tennessee in 1947 (Todd 1980).

The majority of canopy shortleaf pine established in a high light environment, which could be attributed to a localized canopy gap or a detected stand-wide disturbance. In fact, only 13% of shortleaf pine individuals established in the understory of a closed canopy, based on radial growth trends. Of these individuals, all experienced at least one release after the first 20 years of growth. Therefore, results indicated that a combination of stochastic gap-scale disturbance and stand-wide disturbance (i.e., intermediate-severity disturbance) is conducive, perhaps essential, for the establishment and recruitment of spatially distinct neighborhoods of shortleaf pine. Shortleaf pine recruitment began in the late 1800s, with the first large pulse of recruitment in the 1920s. Shortleaf pine recruitment peaked in the 1940s and steadily declined until the 1970s, despite a high rate of canopy disturbance during this decline in shortleaf pine recruitment. The lack of pine individuals that recruited prior to 1900 was likely associated with selective logging that favored larger diameter stems when a rail system was installed through portions of the tableland of the study site in the early 1900s (Hart et al. 2012). The selective logging combined with the two stand-wide disturbance events that occurred between 1900 and 1940 created conditions favorable for recruitment of a new cohort of shortleaf pine. Concurrent with selective logging and detected stand-wide disturbance events between 1900 and 1940 was an increase in the frequency of fire (Stambaugh et al. 2020). Between 1834 and 1935, the mean fire interval for the SGNA was 2.5 years. Notably, a fire in 1936 scarred a high percentage of trees sampled by Stambaugh et al. (2020) and was hypothesized to have occurred during the summer (fire scar on middle and late earlywood). The timing of this fire may have resulted in a higher rate of shoot mortality in small size class stems compared to a dormant season fire (Robertson and Hmielowski 2014). This fire, combined with the stand-wide disturbance of 1935, likely facilitated the establishment pulse of shortleaf pine that began in the 1940s. When fire exclusion began in the 1940s, the mean fire interval for the SGNA increased to 13.7 years (Stambaugh et al. 2020), but two stand-wide disturbance events were detected in 1953 and 1968. Although stand-wide disturbance events were detected during this period, the lack of shortleaf pine regeneration and recruitment after the 1940s was likely a function of the absence of fire. However, these stand-wide events released some previously established shortleaf pine into the canopy. Although the spatial scale of the canopy openings cannot be elucidated from our results (constrained by the noncontiguous plot layout), larger canopy gaps are known to support regeneration and recruitment of shade-intolerant yellow pine species. (Mohler et al. 2021).

## Spatial Distribution of Shortleaf Pine

Results indicated that the contemporary stand-level spatial distribution of shortleaf pine can be attributed, at least in part, to the historical canopy disturbance events. Shortleaf pine basal area was significantly clustered at the stand scale and ranged from 0 to 1.71 $m^2 plot^{-1}$ (400 $m^2$ plot size). The clustered stand-level distribution of shortleaf pine was influenced by episodic stand-wide disturbance and stochastic gap-scale disturbance. The significantly high clusters of shortleaf pine relative dominance occurred in a group of four plots near the southern edge of the tablelands. Relative dominance of shortleaf pine in this group of four plots ranged from 27% to 71% basal area $plot^{-1}$. Although this group of plots was a statistically high cluster of shortleaf pine relative dominance, only one of the four plots had a shortleaf pine relative dominance >50%. These four plots experienced stand-wide disturbance in the 1920s and 1930s, which led to the establishment of most of the shortleaf pine trees on these plots. Mean fire frequency during these two decades was 2.5 years (Stambaugh et al. 2020). Therefore, we suspect that the combination of stand-wide disturbance and fire in quick succession likely created conditions favorable for shortleaf pine establishment. These same plots also experienced stand-wide disturbance in the 1950s, which facilitated recruitment of shortleaf pine into the canopy. Although not statistically significant, another cluster of shortleaf pine neighborhoods occurred approximately 750 m north of the southern edge of the study site, with a range of shortleaf pine relative dominance from 33% to 49%. Shortleaf pine trees in both the significant and insignificant clusters were of similar age and experienced a similar sequence of canopy disturbances that led to shortleaf pine dominance. However, these plots were not documented as high clusters because the contrast between plots with lower shortleaf pine relative dominance was not as severe as the significantly high cluster plots, which indicated more uniform co-occurrence of pine and oak species in this portion of the study site. It can be inferred from our results that the stand studied here is a mosaic of randomly distributed shortleaf pine, clusters of high shortleaf pine relative dominance (>30%), and clusters of low shortleaf pine relative dominance (<5%). Although results indicated only four high clusters of shortleaf pine relative dominance, there were plots that were categorized as outliers in the analysis. We documented one high cluster of shortleaf pine (22% relative dominance) surrounded by plots that had few-to-no shortleaf pine stems. Conversely, there were plots that had no shortleaf pine but were surrounded by plots with 25% to 40% shortleaf pine relative dominance. These findings reinforce the documented patchy nature of the various species components of mixedwood stands related to differences in topography, soil, and other biotic and abiotic factors (Palik and D'Amato 2019). However, the ordination analysis revealed a lack of correlation between overstory community composition and environmental variables. We did not measure other biotic and abiotic factors in the field that could have influenced the evident differences in overstory community composition.

The spatial distribution of shortleaf pine differed at the stand and neighborhood scale. Although not statistically tested, differences were evident in the comparison of shortleaf pine distributed across the stand and shortleaf pine distributed within five tree neighborhoods. Although clustered within the stand, shortleaf pine was not spatially or compositionally clustered within five tree neighborhoods, as evidenced by the mingling and uniform angle indices calculated at this spatial scale. The majority of mingling index values in neighborhoods with shortleaf pine as the reference tree ranged from 0.75 to 1.00, which indicated that three or more of the four nearest neighbors were compositionally distinct. Furthermore, the majority of nearest neighbors to the focal shortleaf pine were shade tolerant individuals, (e.g., sourwood, red maple, American holly). In the five tree neighborhoods analyzed in this study, neighborhoods with shortleaf pine as the reference tree were compositionally and structurally distinct from all tree neighborhoods. Shortleaf pine neighborhoods had a higher frequency of dominance over conspecific neighboring trees and were randomly distributed at the neighborhood scale. In contrast, focal trees in all tree neighborhoods were less likely to be the dominant tree in the neighborhood or have four conspecific neighbors. However, all tree neighborhoods did have a similar random spatial distribution to shortleaf pine neighborhoods. These results indicate that shortleaf pine neighborhoods are unlikely to self-perpetuate without intervention, which we posited can be largely attributed to fire exclusion that allowed fire-sensitive, shade-tolerant individuals to persist

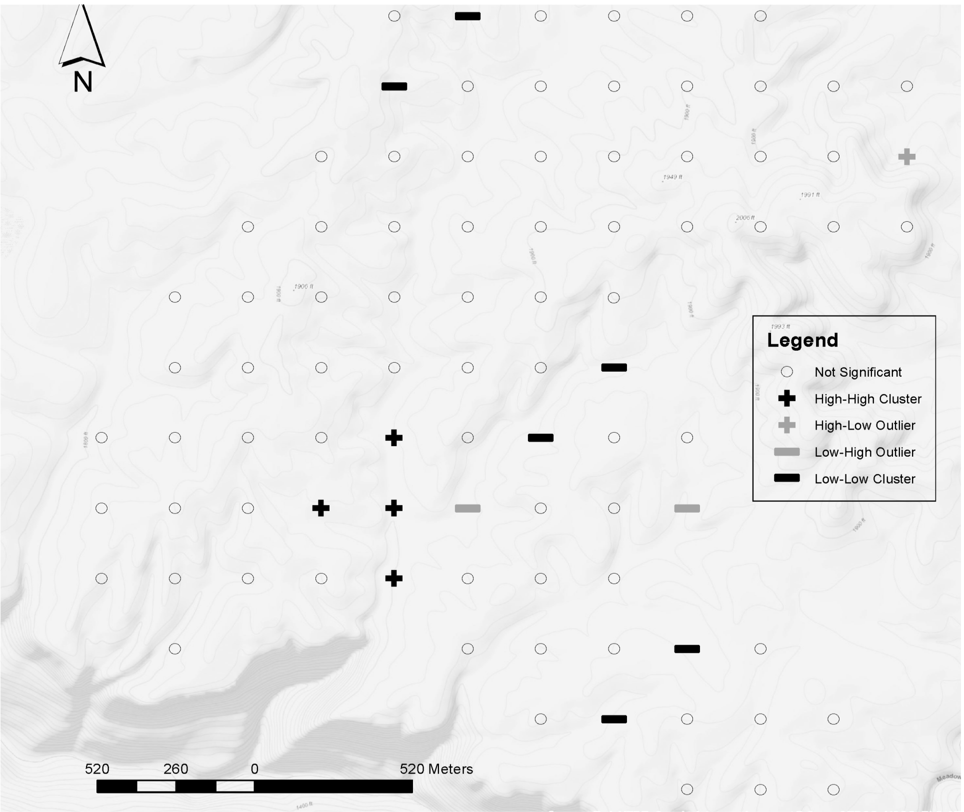

**Figure 3.** Local indicators of spatial autocorrelation (overlayed on sampling plot locations) based on shortleaf pine relative dominance (proportional $m^2 plot^{-1}$) in a mixed oak-shortleaf pine stand at Savage Gulf Natural Area, Tennessee. High-high clusters are plots that had high shortleaf pine dominance and were surround by plots that also had high shortleaf pine dominance. High-low outliers indicated were plots that had high shortleaf pine dominance and were surrounded by plots with low shortleaf pine dominance. Low-low clusters were plots that had low shortleaf pine dominance and were surrounded by plots that also had low shortleaf pine dominance. Low-high outliers were plots that had low shortleaf pine dominance but were surrounded by plots with high shortleaf pine dominance.

in the subcanopy and preclude shortleaf pine establishment and recruitment.

Analysis of all tree neighborhoods resulted in similar bivariate distribution to other mixed-species forests where dominant individuals (oak and pine species) are highly mixed with other species (Pommerening 2002, Li et al. 2012). Additionally, unmanaged forests have been previously found to be more likely to develop random neighborhood spatial patterns (Hui et al. 2007). These neighborhood structural metrics may be useful in the visualization and comparison of neighborhood composition and spatial structure, but also may help guide management activities. Because mixed-species management is becoming increasingly desirable (Willis 2019), bivariate distributions of neighborhood spatial pattern and composition may guide treatments to achieve desired neighborhood structure, composition, and spatial pattern. For example, marking guidelines for thinning treatments may include skipping shortleaf pine neighborhoods with $U_i \geq 0.75$ (focal tree is larger than at least three of four nearest neighbors) and thinning in neighborhoods with $U_i \leq 0.5$ (focal tree is smaller than at least half of four nearest neighbors) to release shortleaf pine.

## Management Implications

Increasingly, managers wish to promote mixedwood stands where species assemblages of conifers and hardwoods are hypothesized to exhibit enhanced forest resilience and adaptation potential to global change (Pretzsch et al. 2017). For managers who intend to restore or perpetuate mixedwood stands, reconstruction of the historical disturbance regime (e.g., canopy openings and fire) that shaped patterns of stand development and succession may inform management plans and silvicultural prescriptions (Keane et al. 2009, Stephens et al. 2010). For example, the size, arrangement, and timing of silvicultural entries can be patterned after the processes that have historically created and maintained desired species mixtures. Some authors have proposed that mixedwood stands should consist of hardwood and softwood species in which neither group constitutes >75–80 percent of the overstory composition (Helms 1998, Kabrick et al. 2017). However, in some mixedwood stands, such as the one studied here, species composition is patchy rather than uniform. Thus, stand boundaries are fundamental to the classification of these stand types and these patterns are scale-dependent. The stand studied here contained patches that were shortleaf pine-dominated and our results revealed that the species was spatially clustered through the study area. This large stand contained patches of shortleaf pine in an otherwise oak-dominated stand, which was confirmed through statistical analysis, aerial imagery examination, and field observation. The stand-level distribution of shortleaf pine was significantly clustered as a function, in part, of the historical disturbance regime of stand-wide canopy disturb-

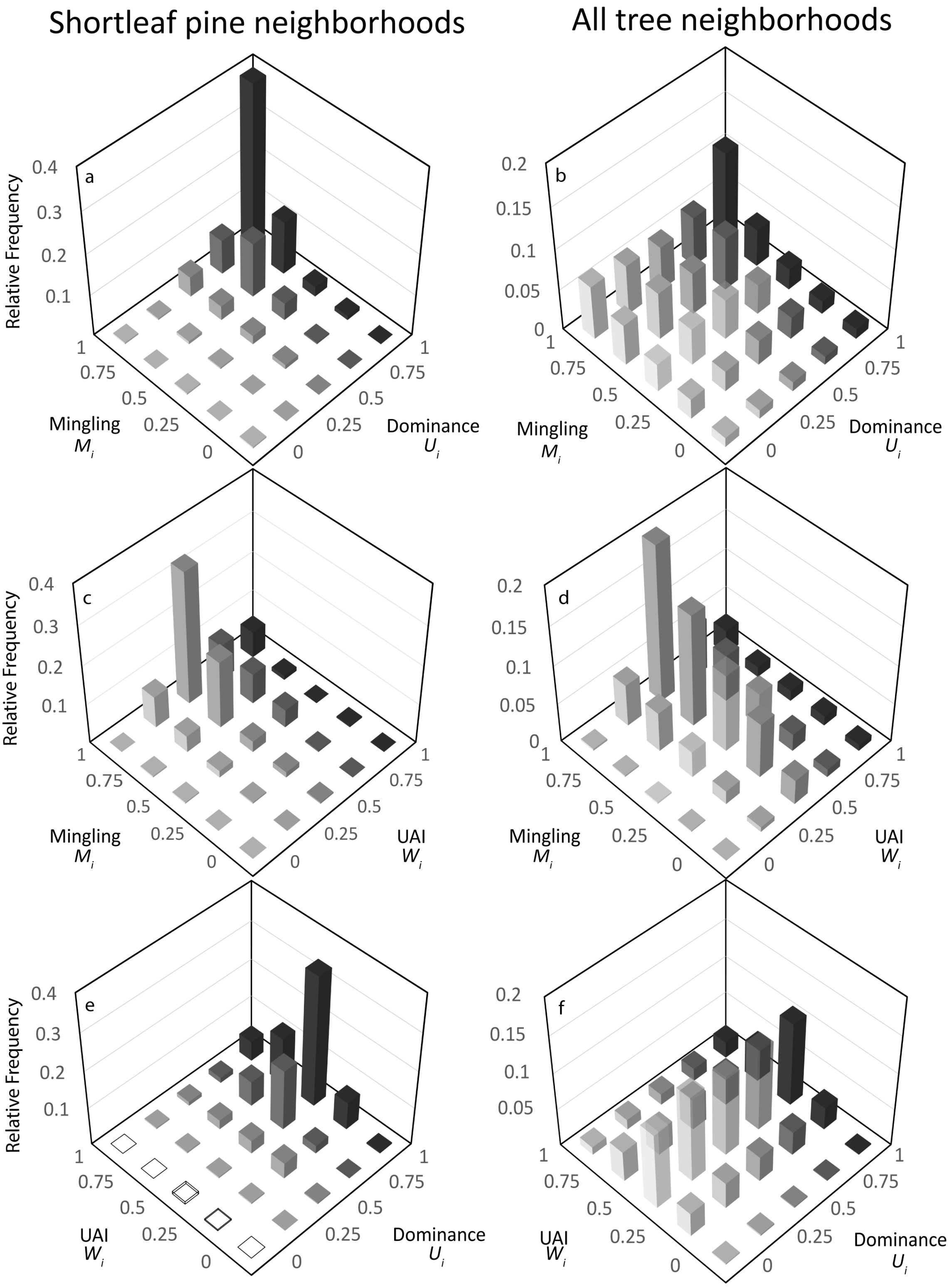

**Figure 4.** Bivariate distributions of neighborhood compositional (mingling), structural (dominance), and spatial (UAI, uniform angle index) metrics of shortleaf pine neighborhoods (right), and all trees (left) of a mixed oak-shortleaf pine stand at Savage Gulf Natural Area, Tennessee.

ance events every 20–40 years and low-intensity surface fire every 1–8 years (Hart et al. 2012, Stambaugh et al. 2020). We hypothesize the combination of these two disturbance processes facilitated the creation of a patchy mosaic of compositionally distinct hardwood and softwood neighborhoods throughout the stand. The NMS analysis confirmed this, with significantly different plot-level overstory community composition when plots were categorized by level of pine species relative dominance. Furthermore, stand-wide disturbance was weakly associated with pine plots, which supports our hypothesis that shortleaf pine establishment and recruitment benefit from intermediate-severity disturbance events. Thus,

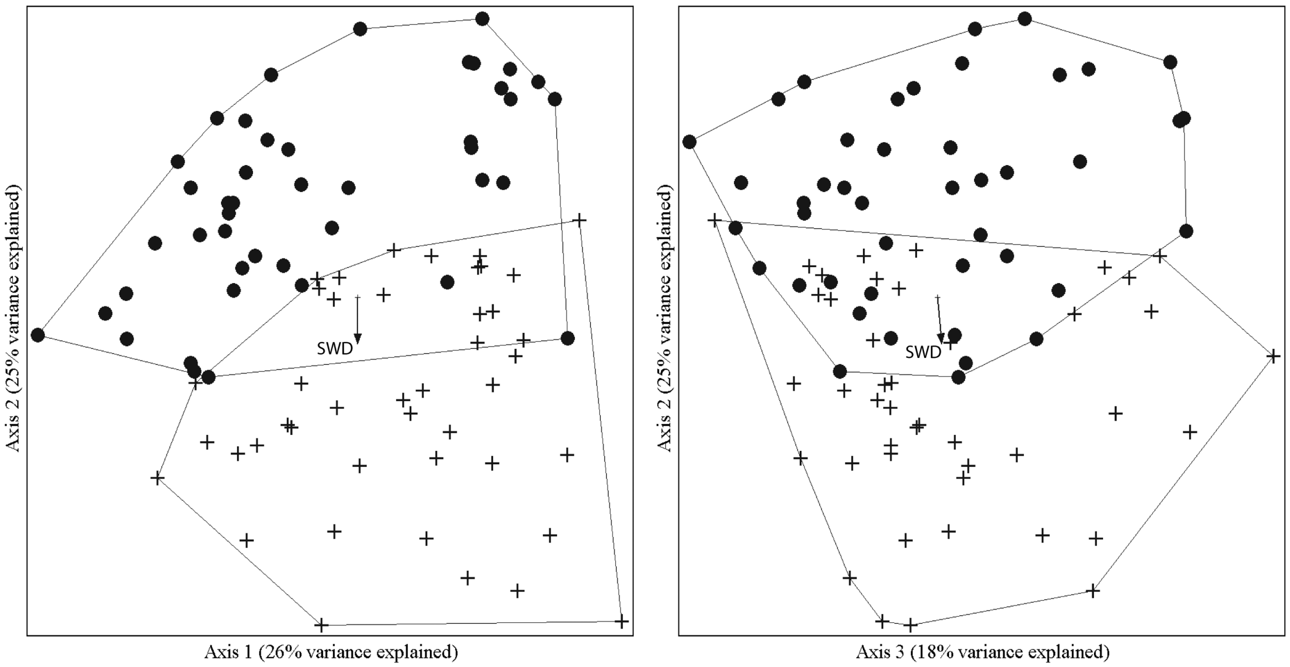

**Figure 5.** Three-dimensional nonmetric multidimensional scaling of overstory plant communities at Savage Guld Natural Area, Tennessee. Black circles represent oak neighborhoods and gray crosses represent pine neighborhoods. Polygons (convex hulls) connect plots of the same treatment, and the arrow (biplot) represents strength (length of arrow) and correlations ($r^2 \geq 0.25$) between frequency of intermediate-severity disturbance (ISD) and ordination axes. A three-axis solution best explained the variability in overstory community composition based on pine and hardwood dominance.

the stand contained patches that were dominated by shortleaf pine, patches that contained no shortleaf pine stems and were oak-dominated, and some patches that contained relatively equal mixtures of both taxa.

We suggest that silvicultural systems use an approach that acknowledges spatial patterns of tree composition. In stands with patchy species composition, we recommend an approach that specifically addresses the spatial patterns (i.e., patchiness) of the species assemblage, rather than implement a silvicultural system that uniformly treats the stand as a spatially homogenous blend of taxa. For example, in conjunction with prescribed fire, patch clearcuts with reserves of sizes ≤ 5 ha could be used to regenerate shortleaf pine on microsites within the broader stand that would favor this species, such as sites with dry and/or nutrient-poor soils where shortleaf pine is most competitive. For landowners who desire shortleaf pine on better quality sites, chemical or mechanical site preparation in combination with prescribed fire may be necessary to enhance shortleaf pine regeneration. Patch seedtree or irregular shelterwood harvests with reserves could be used on sites where shortleaf pine is already an established component and is retained at densities sufficient for natural regeneration. Artificial regeneration or enrichment plantings may be used to enhance shortleaf pine regeneration. Such approaches are consistent with inherent spatial patterns of species coexistence and the historical disturbance regime in some mixedwood systems.

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## Literature Cited

Aguirre, O., G. Hui, K. von Gadow, and J. Jiménez. 2003. An analysis of spatial forest structure using neighbourhood-based variables. *For. Ecol. Manage.* 183(1–3):137–145.

Aldea, J., I. Barbeito, E. Holmström, and M. Löf. 2020. *Program and book of abstracts of the IUFRO mixed species forests: Risks, resilience and management.* Lund, Sweden 25–27 March 2020. Report 54. Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, Alnarp.

Bivand, R., M. Altman, L. Anselin, R. Assunção, O. Berke, A. Bernat, and G. Blanchet. 2015. *Package 'spdep'*. Available online at ftp://garr. tucows. com/mirrors/CRAN/web/packages/spdep/spdep. pdf; last accessed September 14, 2020.

Boyden, S., D. Binkley, and W. Shepperd. 2005. Spatial and temporal patterns in structure, regeneration, and mortality of an old-growth ponderosa pine forest in the Colorado Front Range. *For. Ecol. Manage.* 219(1):43–55.

Bruckner, A., E. Kandeler, and C. Kampichler. 1999. Plot-scale spatial patterns of soil water content, pH, substrate-induced respiration and N mineralization in a temperate coniferous forest. *Geoderma* 93(3–4):207–223.

Buchanan, M.L., and J.L. Hart. 2011. A methodological analysis of canopy disturbance reconstructions using Quercus alba. *Can. J. For. Res.* 41(6):1359–1367.

Chai, Z.Z. 2016 *forestSAS, an R package for forest spatial structure analysis systems*. Available online at https://github.com/Zongzheng/forestSAS; last accessed October 14, 2020.

Clabo, D.C., and W.K. Clatterbuck. 2020. Establishment and early development of even-age shortleaf pine–hardwood mixtures using artificially regenerated shortleaf pine and various site preparation and release treatments. *For. Sci.* 66(3):351–360.

Cooper, A.W. 1989. Ecology of the pine-hardwood type. P. 3–8 in *Proceedings of Pine-Hardwood Mixtures: A symposium on management and ecology of the type*. USDA Forest Service Gen. Tech. Rep. SE-58, Southeastern Forest Experiment Station, Asheville, NC.

Das, A., J. Battles, P.J. van Mantgem, and N.L. Stephenson. 2008. Spatial elements of mortality risk in old-growth forests. *Ecology* 89(6):1744–1756.

Ellair, D.P., and W.J. Platt. 2013. Fuel composition influences fire characteristics and understorey hardwoods in pine savanna. *J. Ecol.* 101(1):192–201.

Emery, R.K., and J.L. Hart. 2020. Flammability characteristics of surface fuels in a longleaf pine (Pinus palustris Mill.) woodland. *Fire* 3(3):39.

Enright, N.J., J.B. Fontaine, B.B. Lamont, B.P. Miller, and V.C. Westcott. 2014. Resistance and resilience to changing climate and fire regime depend on plant functional traits. *J. Ecol.* 102(6):1572–1581.

Fahey, R.T., and C.G. Lorimer. 2013. Restoring a midtolerant pine species as a component of late-successional forests: Results of gap-based planting trials. *For. Ecol. Manage.* 292:139–149.

Fenneman, N.M. 1938. *Physiography of the eastern United States*. MacGraw-Hill Co. Inc., New York.

Ford, S., J. Kleinman, and J. Hart. 2017. Spatial patterns of canopy disturbance, structure, and species composition in a multi-cohort hardwood stand. *Forests* 8(3):93.

Franklin, J.F., T.A. Spies, R. Van Pelt, A.B. Carey, D.A. Thornburgh, D.R. Berg, D.B. Lindenmeyer, *et al.* 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *For. Ecol. Manage.* 155(1–3):399–423.

Franklin, J.F., and R.H. Waring. 1980. Distinctive features of the northwestern coniferous forest: Development, structure, and function. P. 59–86 in *Forests: Fresh perspectives from ecosystem analysis*. Oregon State University Press, Corvallis.

Frelich, L.E., and P.B. Reich. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecol. Monogr.* 65(3):325–346.

Frelich, L.E., S. Sugita, P.B. Reich, M.B. Davis, and S.K. Friedman. 1998. Neighbourhood effects in forests: Implications for within-stand patch structure. *J. Ecol.* 86(1):149–161.

Goode, J.D., C.R. Barefoot, J.L. Hart, and D.C. Dey. 2020. Disturbance history, species diversity, and structural complexity of a temperate deciduous forest. *J. For. Res.* 31(2):397–414.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: A manual and tutorial for the computer program COFECHA. *Tree-Ring Res.* 57:205–211.

Graz, F.P. 2004. The behavior of the species mingling index Msp in relation to species dominance and dispersion. *Eur. J. For. Res.* 123:87–92.

Graz, F.P. 2006. Spatial diversity of dry savanna woodlands – assessing the spatial diversity of a dry savanna woodland stand in northern Namibia using neighborhood-based measures. *Biodivers. Con serv.*15:1143–1157.

Hart, J.L., S.L. Clark, S.J. Torreano, and M.L. Buchanan. 2012. Composition, structure, and dendroecology of an old-growth Quercus forest on the tablelands of the Cumberland Plateau, USA. *For. Ecol. Manage.* 266:11–24.

Hart, J.L., and H.D. Grissino-Mayer. 2009. Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. *Plant Ecol.* 201:131–146.

Hart, J.L., and J.S. Kleinman. 2018. What are intermediate-severity forest disturbances and why are they important? *Forests* 9(9):579.

Harmon, M.E., J.F. Franklin, F.J. Swanson, P. Sollins, S.V. Gregory, J.D. Lattin, N.H. Anderson, *et al.* 1986. Ecology of coarse woody debris in temperate ecosystems. P. 133–302 in *Advances in ecological research*. Vol. 15. Academic Press, Orlando, FL.

Helms, J.A. 1998. *Dictionary of forestry.* Society of American Foresters, Bethesda, Maryland, USA. p. 210.

Hessburg, P.F., B.G. Smith, and R.B. Salter. 1999. Detecting change in forest spatial patterns from reference conditions. *Ecol. Appl.* 9(4):1232–1252.

Hinkle, C.R. 1978. *The relationship of forest communities and selected species to edaphic and topographic factors on the Cumberland Plateau of Tennessee*. Doctoral dissertation, University of Tennessee, Knoxville.

Hinkle, C.R. 1989. Forest communities of the Cumberland Plateau of Tennessee. *J. Tenn. Acad. Sci.* 64:123–129.

Holmes, R.L. 1983. *Program COFECHA user's manual.* Laboratory of Tree-Ring Research, University of Arizona, Tucson.

Hui, G.Y., K.V. Gadow, and M. Albert. 1999. The neighborhood pattern – a new structure parameter for describing distribution of forest tree position. *Sci. Silvae Sinicae* 35:37–42.

Hui, G.Y., K.V. Gadow, Y.B. Hu, and H. Xu. 2007. *Structure-based forest management.* China Forestry Press, Beijing. 29–36 p.

Janowiak, M.K., C.W. Swanston, L.M. Nagel, L.A. Brandt, P.R. Butler, S.D. Handler, P.D. Shannon, *et al.* 2014. A practical approach for translating climate change adaptation principles into forest management actions. *J. For.* 112(5):424–433.

Kabrick, J.M., K.L. Clark, A.W. D'Amato, D.C. Dey, L.S. Kenefic, C.C. Kern, B.O. Knapp, *et al.* 2017. Managing hardwood-softwood mixtures for future forests in eastern North America: Assessing suitability to projected climate change. *J. For.* 115(3):190–201.

Keane, R.E., P.F. Hessburg, P.B. Landres, and F.J. Swanson. 2009. The use of historical range and variability (HRV) in landscape management. *For. Ecol. Manage.* 258(7):1025–1037.

Larson, A.J., and D. Churchill. 2012. Tree spatial patterns in fire-frequent forests of western North America, including mechanisms of pattern formation and implications for designing fuel reduction and restoration treatments. *For. Ecol. Manage.* 267:74–92.

Laughlin, D.C., M.M. Moore, J.D. Bakker, C.A. Casey, J.D. Springer, P.Z. Fulé, and W.W. Covington. 2006. Assessing targets for the restoration of herbaceous vegetation in ponderosa pine forests. *Restor. Ecol.* 14(4):548–560.

Li, Y., G. Hui, Z. Zhao, and Y. Hu. 2012. The bivariate distribution characteristics of spatial structure in natural Korean pine broad-leaved forest. *J. Veg. Sci.* 23(6):1180–1190.

Lindenmayer, D.B., M.J. Westgate, B.C. Scheele, C.N. Foster, and D.P. Blair. 2019. Key perspectives on early successional forests subject to stand-replacing disturbances. *For. Ecol. Manage.* 454:117656.

Lorimer, C.G., L.E. Frelich, and E.V. Nordheim. 1988. Estimating gap origin probabilities for canopy trees. *Ecology* 69(3):778–785.

MacDonald, G. 2003. *Biogeography: Introduction to space, time and life*. John Wiley and Sons, New York. 518 p.

Manning, R. 1993. *The historic Cumberland Plateau: An explorer's guide*. University of Tennessee Press, Knoxville, Tennessee.

McCune, B., and M.J. Mefford. 2011. *PC-ORD: Multivariate analysis of ecological data. Version 4 for Windows. User's guide.* MjM Software, Wagga Wagga, Australia.

McNab, W.H. 1989. Terrain shape index: Quantifying effect of minor landforms on tree height. *For. Sci.* 35(1):91–104.

Mielke, P.W., and K.J. Berry. 2001. Description of MRPP. P. 9–65 in *Permutation methods*. Springer, New York.

Mitchell, R.J., J.F. Franklin, B.J. Palik, L.K. Kirkman, L.L. Smith, R.T. Engstrom, and M.L. Hunter Jr. 2003. Natural disturbance-based silviculture for restoration and maintenance of biological diversity. In *Final report to the National Commission of Science for Sustainable Forestry*. No. 120. Washington D.C., USA.

Mohler, C., M. Bataineh, D.C. Bragg, R. Ficklin, M. Pelkki, and M. Olson. 2021. Long-term effects of group opening size and site preparation method on gap-cohort development in a temperate mixedwood forest. *For. Ecol. Manage.* 480:118616.

Moran, P.A. 1950. Notes on continuous stochastic phenomena. *Biometrika* 37(1/2):17–23.

Nowacki, G.J., and M.D. Abrams. 1997. Radial-growth averaging criteria for reconstructing disturbance histories from presettlement-origin oaks. *Ecol. Monogr.* 67(2):225–249.

Oliver, C.D., and B.C. Larson. 1996. *Forest stand dynamics: Updated edition.* John Wiley and Sons, New York.

Orvis, K.H., and H.D. Grissino-Mayer. 2002. Standardizing the reporting of abrasive papers used to surface tree-ring samples. *Tree-Ring Res.* 58:47–50.

Oswalt, C.M. 2012. Spatial and temporal trends of the shortleaf pine resource in the eastern United States. P. 33–37 in *Proceedings of the Shortleaf Pine Conference: East meets west, bridging the gap with research and education across the range,* Kush, J., R.J. Barlow, and J.C. Gilbert (eds.). Alabama Agricultural Experiment Station Spec. Rep. No. 11. Auburn University, Auburn, AL.

Nagel, L.M., B.J. Palik, M.A. Battaglia, A.W. D'Amato, J.M. Guldin, C.W. Swanston, M.K. Janowiak, *et al.* 2017. Adaptive silviculture for climate change: A national experiment in manager-scientist partnerships to apply an adaptation framework. *J. For.* 115(3):167–178.

National Oceanic and Atmospheric Administration (NOAA). 2020. *Storm events database—event details. National Centers for Environmental Information.* Available online at https://www.ncdc.noaa.gov/stormevents/; last accessed August 25, 2020.

Palik, B., R.J. Mitchell, S. Pecot, M. Battaglia, and M. Pu. 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. *Ecol. Appl.* 13(3):674–686.

Palik, B.J., and A.W. D'Amato. 2019. Variable retention harvesting in Great Lakes mixed-pine forests: Emulating a natural model in managed ecosystems. *Ecol. Proc.* 8(1):1–15.

Palik, B.J., A.W. D'Amato, J.F. Franklin, and K.N. Johnson. 2020. *Ecological silviculture: Foundations and applications.* Waveland Press, Long Grove, Illinois.

Peterson, C.J., J.B. Cannon, and C.M. Godfrey. 2016. First steps toward defining the wind disturbance regime in central hardwoods forests. P. 89–122 in *Natural disturbances and historic range of variation.* Springer, Cham, Switzerland.

Pommerening, A. 2002. Approaches to quantifying forest structures. *Forestry* 75(3):305–324.

Pretzsch, H., D.I. Forrester, and J. Bauhus (eds.). 2017. *Mixed-species forests: Ecology and management.* Springer, Verlag Germany, Heidelberg.

PRISM Climate Group. 2018. *Data explorer: Time series values for individual locations, from Northwest Alliance for Computational Science and Engineering, Oregon State University.* Available online at www.prism.oregonstate.edu/explorer/; last accessed April 26, 2021.

Rentch, J.S., F. Desta, and G.W. Miller. 2002. Climate, canopy disturbance, and radial growth averaging in a second-growth mixed-oak forest in West Virginia, USA. *Can. J. For. Res.* 32(6):915–927.

Robertson, K.M., and T.L. Hmielowski. 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. *Oecologia* 174(3):765–776.

Schnake, D.K., S.D. Roberts, J.L. Willis, J.D. Kushla, and I.A. Munn. 2021. Overstory retention and stock type impact survival and growth of underplanted shortleaf pine beneath a hardwood canopy. *For. Sci.* 67(2):219–230.

Schwarz, P.A., T.J. Fahey, and C.E. McCulloch. 2003. Factors controlling spatial variation of tree species abundance in a forested landscape. *Ecology* 84(7):1862–1878.

Schulte, L.A., D.J. Mladenoff, T.R. Crow, L.C. Merrick, and D.T. Cleland. 2007. Homogenization of northern US Great Lakes forests due to land use. *Landsc. Ecol.* 22(7):1089–1103.

Smalley, G.W. 1986. *Classification and evaluation of forest sites on the northern Cumberland Plateau.* USDA Forest Service, Southern Research Experiment Station (General Technical Report SO-38).

Sprugel, D.G., K.G. Rascher, R. Gersonde, M. Dovčiak, J.A. Lutz, and C.B. Halpern. 2009. Spatially explicit modeling of overstory manipulations in young forests: Effects on stand structure and light. *Ecol. Mod.* 220(24):3565–3575.

Stambaugh, M.C., J.M. Marschall, and E.R. Abadir. 2020. Revealing historical fire regimes of the Cumberland Plateau, USA, through remnant fire-scarred shortleaf pines (Pinus echinata Mill.). *Fire Ecol.* 16(1):1–15.

Stephens, S.L., C.I. Millar, and B.M. Collins. 2010. Operational approaches to managing forests of the future in Mediterranean regions within a context of changing climates. *Environ. Res. Lett.* 5(2):024003.

Stokes, M.A., and T.L. Smiley. 1996. *An introduction to tree-ring dating: Tucson.* University of Arizona Press, Tucson, AZ. ISBN: 0816516804.

Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geogr. Rev.* 38(1):55–94.

Todd, R.W. 1980. *Tennessee fencing and animal restraint laws. Research reports.* Available online at https://trace.tennessee.edu/utk_agresreport/2.

USDA NRCS. 2020. *Web soil survey.* Available online at http://websoilsurvey. sc.egov.usda.gov/; last accessed October 3, 2020.

Villalba, R., and T.T. Veblen. 1997. Improving estimates of total tree ages based on increment core samples. *Ecoscience* 4(4):534–542.

Willis, J.L., J.S. Gordon, S. Tanger, M.A. Blazier, A.B. Self, and A. Brodbeck. 2019. Managing mixed stands: Reassessing a forgotten stand type in the southeastern United States. *Forests* 10(9):751.

Whittaker, R.H., and H. Klomp. 1975. The design and stability of plant communities. P. 169–183 in *Unifying concepts in ecology*. Springer, Dordrecht.