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ORIGINAL PAPER

Three-dimensional light structure of an upland *Quercus* stand post-tornado disturbance

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Abstract Light is the most common limiting factor in forest plant communities, influencing species composition, stand structure, and stand productivity in closed canopy stands. Stand vertical light structure is relatively simple under a closed canopy because most light is captured by overstory trees. However, wind disturbance events create canopy openings from local to landscape scales that increase understory light intensity and vertical light structural complexity. We studied the effects of an EF-1 tornado on horizontal and vertical (i.e. three-dimensional) light structure within a *Quercus* stand to determine how light structure changed with increasing disturbance severity. We used a two-tiered method to collect photosynthetic photon flux density at 4.67 m and 1.37 m above the forest floor to construct three-dimensional light structure across a canopy disturbance severity gradient to see if light intensity varied with increasing tornado damage. Results indicate that increased canopy disturbance closer to the tornado track increased light penetration and light structure heterogeneity at lower forest strata. Increased light intensity correlated with increased sapling density that was more randomly distributed across the plot and had shifted light capture higher in the stand structure. Light penetration through the overstory was most strongly correlated with decreased stem density in the two most important tree species (based on relative dominance and relative density) in the stand, *Quercus alba* L. ($r = -0.31$) and *Ostrya virginiana* (Mill.) K. Koch ($r = -0.27$, $p < 0.01$), and indicated that understory light penetration was most affected by these two species. As managers are increasingly interested in patterning silvicultural entries on natural disturbances, they must understand residual stand and light structures that occur after natural disturbance events. By providing spatial light data that quantifies light structure post-disturbance, managers can use these results to improve planning required for long-term management. The study also provides comparisons with anthropogenic disturbances to the midstory that may offer useful comparisons to natural analogs for future silvicultural consideration.

Keywords Photosynthetic photon flux density · Midstory · Blowdown · Heterogeneity

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Introduction

Plant growth in closed canopy stands is often regulated by light intensity, as photosynthetically active radiation (PAR) usually limits understory growth (Scharenbroch et al. 2012). Increased light intensity to midstory and ground flora strata often results in increased vegetation cover, abundance, and diversity in these layers (Phillips and

Waldrop 2008; Willms et al. 2017). Light intensity may also determine which understory tree species aptly compete and recruit into the overstory (O'Hara 1986; Gottschalk 1987; Walters and Yawney 2004). Vertical light structure is considered the vertical profile of light transmission and light intensity within a stand. Vertical light structure in closed canopy stands affects, and may be affected by, vertical stand structure and overstory composition in an interdependent relationship that is temporally dynamic (Canham et al. 1994; Messier et al. 1999). Natural disturbances alter vertical structure and light conditions through the creation of canopy openings that increase light intensity in the understory (Pickett and White 1985; Franklin et al. 2002; Lin et al. 2003). Wind disturbances create overstory openings that vary in spatial extent from small, localized canopy gaps to catastrophic, stand-scale overstory removal (Hanson and Lorimer 2007; Richards and Hart 2011). Through the removal of canopy trees, wind disturbances disrupt growth patterns, alter light environments, and may release residual stems to fill vacated growing space through lateral and vertical extension (Pickett and White 1985; Oliver and Larson 1996).

Spatial heterogeneity caused by gap formation is an important byproduct of wind disturbance events. Scientists have researched biotic and abiotic heterogeneity to quantify how gap shape complexity, edge-ratios, and gap continuity are affected by disturbance severity. Wind disturbances have been studied to determine general gap characteristics to differentiate wind events from other types of disturbances (Lindemann and Baker 2001; Xi et al. 2008). Hurricane and thunderstorm blowdown events increase the number, average size, and variability of forest gaps because of large tree mortality that alters tree spatial patterns and canopy openings (Evans et al. 2007; Xi et al. 2008). Evans et al. (2007) indicated that variations in gaps may be caused by abiotic factors such as elevation, topographic position, and elevation variability, and biotic factors, including stand age and structure. Cannon et al. (2016) determined that tornadoes created comparable spatial patterns of gap frequency and size to other windstorm events. The study also found that variations in gap creation were influenced by differences in topographic features on the landscape, similar to hurricanes and other wind events. These studies determined effects of abiotic characteristics on wind disturbance severity, but have not quantified the effects on biotic characteristics, particularly from tornadoes.

Tornadoes are localized wind events that occur about 1350 times per year in the U.S. (National Weather Service 2018). Tornado windspeeds vary from 105 to 480 km h^{-1}, although most tornadoes do not reach more than 200 km h^{-1}. A tornado generally creates a defined swath of moderate-to-high severity disturbance that decreases as distance from the tornado track increases (Peterson and Rebertus 1997; Cox et al. 2016). This disturbance pattern usually creates a high number of small, low disturbance severity patches and a low number of large, high disturbance severity patches that result in increased spatial heterogeneity across the landscape. Tornado impact research in forests has primarily focused on structural and compositional changes in stands post-disturbance. Past studies have shown overstory susceptibility to blowdown, in which larger trees are more likely to be snapped or uprooted than smaller trees during tornado events (Peterson and Rebertus 1997; Peterson 2000; White et al. 2015). Tree species are also related to blowdown vulnerability, depending upon wood properties such as strength, elasticity, and modulus of rupture for each species (Peterson 2007). Because changes in overstory composition may alter understory light intensity (Canham et al. 1994; Messier et al. 1998), tornadoes can considerably alter current and future light structure to create heterogeneous light conditions at intra-stand spatial scales.

In closed canopy stands, large overstory trees capture most available light and thus govern stand structure and composition of sub-canopy strata. By removing overstory trees, tornadoes can have significant impacts on canopy openness, light structure, and stand development (Brewer et al. 2012; White et al. 2015). Overstory removal by tornado disturbances may increase stem densities in the regeneration layer and release residual midstory stems, which in turn, affects light structure in lower strata (Nelson et al. 2008; White et al. 2015). Cowden et al. (2014) and Kleinman et al. (2017) reported increased light intensity at 1.37 m (i.e., breast height) after tornado disturbances, which was attributed to the removal of leaves and stems that block PAR from reaching the understory. However, to our knowledge, light structure has not been studied between 1.37 m and the canopy nor in multiple strata after a tornado in hardwood stands. Similarly, no research has attempted to quantify changes in vertical light structure over a disturbance severity gradient created by a tornado in closed canopy hardwood stands. As tornadoes are common in eastern U.S. forest ecosystems that are usually dominated by or contain *Quercus* species (Johnson et al. 2009), *Quercus*-dominant forest structure will be governed by tornado disturbance events in many stands and should be quantified to improve stand development models. Similarly, managers are increasingly interested in patterning silvicultural entries on natural disturbances, which indicates that this type of research is needed to quantify general residual light structures after natural wind disturbance events to help set objectives for long-term management plans for *Quercus* stands.

The overall objective of this study was to quantify how a tornado affected vertical and horizontal light structure in a

Quercus alba L. stand over a disturbance severity gradient. More specifically, our goals were to quantify and map three dimensional changes (i.e., horizontal and vertical changes) in light structure and light heterogeneity, as well as to determine which specific changes in stand structure (e.g., basal area, tree and sapling density) most strongly correlate with altered light structure over the disturbance severity gradient. It was hypothesized that increased disturbance severity closer to the tornado track would increase light penetration through the canopy and heterogeneity of light structure in the stand. This would move the active layer of energy exchange nearer to the forest floor because of leaf and stem removal associated with reduced basal area and tree density. It was also predicted that codominant and dominant trees would influence light intensity to the midstory and that midstory, stem density would influence light penetration from the midstory to the ground level.

Materials and methods

Study area

The study was conducted in the Sipsey Wilderness in the William B. Bankhead National Forest in northern Alabama, USA. The Sipsey Wilderness is 10,085 hectares of unmanaged forest situated on the Cumberland Plateau of the Appalachian Plateau physiographic province (Fenneman 1938). This portion of the Cumberland Plateau is classified as a transition area between mixed mesophytic forest to the north and *Pinus* L.–*Quercus* L. forests further south (Braun 1950). *Quercus* is the most abundant genus within 14 ecological community types in the Sipsey Wilderness, as delineated by Zhang et al. (1999). Ecological communities range from predominately *Pinus virginiana* Mill. on xeric sites to predominately *Fagus grandifolia* Ehrh. and *Acer saccharum* Marshall on mesic sites, with *Quercus* either dominating or occurring in most delineated forest communities. The underlying bedrock is sandstone, stratified shale, and siltstone (Szabo et al. 1988). Geological formations within this region are classified as sandstone conglomerate, mixed with layers of siltstone and shale (Smalley 1979). The soil type is Typic Hapludults, which are well drained and moderately deep (USDA Soil Conservation Services 1959).

Regional climate is humid mesothermal, consisting of long, hot summers and short, mild winters (Thornthwaite 1948). Annual precipitation averages 138 cm with a monthly mean of 13.8 cm in January and 11.3 cm in July (PRISM Climate Group 2017). Average annual temperature is 15 °C, with a monthly mean of 26 °C in July and 5 °C in January. Smalley (1979) determined the region to have an average growing season of 220 days, spanning from late-March to late-November. On 20 April 2011, a quasi-linear convection system developed in the area, producing an EF-1 tornado that tracked 5 km and affected a portion of the Sipsey Wilderness (National Weather Service 2011). Wind speeds were estimated at 153 km h^{-1} and included 145 km h^{-1} straight-line winds.

Field methods

We used U.S. Forest Service (USFS) stand delineations and aerial photography in ArcMap version 10.2 (Environmental Systems Research Institute, Redlands, CA, U.S.) to select a 182 ha *Q. alba* stand within the Sipsey Wilderness that was partially disturbed by the 20 April 2011 EF-1 tornado. According to USFS records, the stand was established in 1900 and had no recorded history of previous broad-scale natural or anthropogenic disturbances. A two hectare (200 m $\times$ 100 m) rectangular plot was established perpendicular to the tornado swath. The design allowed us to quantify the disturbance severity gradient from highest intensity in the tornado track to less affected areas of the stand. The plot was established 25 m from the stand boundary to eliminate edge effects of neighboring stands and non-forested areas. The plot was primarily composed of *Q. alba* (55% basal area, BA), *F. grandifolia* (7% BA), *Ostrya virginiana* (Mill.) K. Koch (6% BA), and *A. saccharum* (4% BA), but also contained 24 tree species under 4% BA (Cox et al. 2016). The plot was oriented perpendicular to slope contour and the elevation changed by 37 m along the long axis of the plot (ca. 19% slope). The plot was divided into two 100 m $\times$ 100 m (1 ha) squares. It was assumed, and visually affirmed, that the northern hectare (furthest from the tornado track) had minimal wind damage from the tornado itself and is henceforth referred to as the minimal disturbance hectare (Cox et al. 2016). Areas of minimal disturbance contained 23.5 m^2 ha^{-1} BA, while areas of greater disturbances averaged 18.5 m^2 ha^{-1} BA. Although residual basal area was different over the gradient of disturbance, we contend that the plot had similar pretreatment composition, as it was installed in one stand that had uniform disturbance history over the past 110 years, similar dominant deadwood species composition, and similar live composition in areas outside the plot. The plot was subdivided into twenty 100 m $\times$ 10 m rows that ran parallel to the tornado swath, which were also parallel to the slope contour. Data from the minimal disturbance hectare were used to compare variable averages and standard errors with each row from the disturbed hectare to indicate changes caused by the tornado.

The plot was also subdivided into 200 10 m $\times$ 10 m subplots (100-m^2). Within each subplot, all live stems $\geq$ 5 cm diameter at breast height (1.37 m) were identified to species, measured for dbh, and given a crown cover class (overtopped, intermediate, codominant, and dominant, c.f., Oliver and Larson 1996). Saplings (stems $\geq$ 1 m and $\leq$ 5 cm dbh) were identified to species and tallied for frequency. Tree and sapling data collected at the subplot level were adjusted to represent densities at the hectare level. To perform tree species-specific analyses, tree data were subdivided into crown cover classes, then further subdivided by species and analyzed against light variables. Tree importance values were calculated at the plot level using the following equation:

$$\text{Tree Importance Value} = \text{Relative Denstiy} + \text{Relative Dominance} \quad (1)$$

Relative density was the number of stems of a species relative to the total number of stems in the plot. Relative dominance was defined as the total basal area of a species relative to the total basal area of the plot.

Hemispherical photography and synchronized ceptometers estimated light intensity above and below the midstory, respectively. Here, we defined the midstory stratum between 1.37 m and 4.67 m above the ground. Vegetation below 1.37 m was defined as the ground stratum. By assuming light intensity was 100% at the top of the canopy, we quantified and analyzed a three-level vertical light structure (above the canopy, at 4.67 m, and at 1.37 m) across the plot.

The plot was subdivided into 800 5 m $\times$ 5 m quadrats (25-m^2 each) to quantify ground photosynthetic photon flux density (PPFD) using two synchronized ceptometers (AccuPAR LP-80, Decagon Devices, Pullman, WA, U.S.), at breast height that captured an instantaneous evaluation of light intensity. To collect the data, one ceptometer was placed in full sunlight, while the other simultaneously recorded PPFD 80 times following a logarithmic spiral pattern from the center to the outward edge of each quadrat (Keasberry et al. 2016). The 80 recordings were compiled across the four 5 m $\times$ 5 m quadrats within each 10 m $\times$ 10 m subplot and averaged to calculate ground PPFD. In each 10 m $\times$ 10 m subplot, one hemispherical photo was taken per subplot at 4.67 m above the ground using a Panasonic Lumix (DMC-LX5) camera with a fish-eye lens attached to a self-leveling tripod with a Mid-O Mount 10MP (Regent Instruments 2011) attached to a 4.27 m pole. The width of the camera and lens accounted for the extra 0.40 m in height. The field data were collected June–July 2014 during the fourth growing season after the disturbance.

Analytical methods

Hemispherical photos were analyzed using WinSCANOPY v.2014a (Regent Instruments 2014) to calculate PPFD reaching most of the midstory, as some midstory stems were taller but not within the canopy. WinSCANOPY solar diffuse radiation parameters were set based on standard overcast sky assumptions (Anderson 1971), and direct radiation parameters based on growing season conditions that were estimated every five days with sun position calculated every 3 min. Atmospheric transmissivity was set at 0.60 with a 0.51 ratio for Rad to PAR conversion factor based on the default parameters in WinSCANOPY as defined by Regent Instruments (2014). We categorized image pixels as canopy or sky based on a grayscale level threshold that was set to approximate the amount of light reaching the C stratum. From this, WinSCANOPY estimated PPFD above and below the canopy, from which we derived a percent that reached the C stratum. Because we used different instruments to measure PPFD at the ground flora and midstory heights, a correction factor from Chianucci and Cutini (2013) was used to adjust the hemispherical photo PPFD results through the formula:

$$\text{Ceptometer PPFD} = (\text{Hemispherical PPFD} + 1.27)/1.3 \quad (2)$$

A four-percentage point correction factor was used to accurately compare canopy openness data collected by a fish-eye lens and a GSR densitometer, as quantified by Paletto and Tosi (2009), to adjust our canopy openness results.

Using ArcGIS v.10.5, ground PPFD categories were created using four natural breaks within the ceptometer PPFD results to delineate each subplot: negligible ground PPFD (0–5%), low ground PPFD (5–11%), moderate ground PPFD (11–19%), and high ground PPFD (> 19%; Keasberry et al. 2016). Midstory PPFD categories were similarly determined through four modified natural breaks within the hemispherical PPFD results, but were titled differently to account for an increased average light intensity at this stratum: low midstory PPFD (0–10%), moderate midstory PPFD (10–25%), high midstory PPFD (25–40%), and very high midstory PPFD (> 40%). Midstory interception was quantified by computing the difference between hemispherical PPFD at 4.67 m and the ceptometer PPFD at 1.37 m. This difference measured the amount of light the midstory intercepted, an indirect indication of the amount of vegetation within that 3.30 m vertical space. Five modified natural breaks were created to categorize midstory light interception: negative midstory (where ceptometer PPFD was higher than hemispherical PPFD, < 0% difference), no midstory (0–2.5% difference), little midstory (2.5–5% difference), moderate midstory (5–15% difference), and substantial midstory (> 15% difference). Canopy interception was quantified using the following equation:

$$\text{Canopy interception} = 1 - \text{midstory light intensity} \quad (3)$$

Light and vegetation data were not normal or homoscedastic after performing tests for normality and homogeneity of variance. Thus, Mann–Whitney U tests were used to determine significant differences in light intensity between the minimally disturbed and disturbed hectares. Kruskal–Wallis tests were used to determine significant changes in canopy openness, total basal area, tree density, and sapling density between the rows of the disturbed hectare. Kruskal–Wallis tests were also used to determine significant differences within canopy openness, tree basal area, tree density, tree density by species and cover class, and sapling density between the four ground PPFD categories, four midstory PPFD categories, and five midstory interception categories. Dunn's post hoc pairwise comparison tests were used to determine significant differences between light intensity and interception at different strata, canopy openness, tree basal area and density, and sapling density within rows of the disturbed hectare. Dunn's tests were also used to determine differences between variables within ground PPFD, midstory PPFD, and midstory interception categories. Spearman correlations were calculated to compare ground and midstory PPFD, midstory light interception, basal area, tree and sapling density, and tree density by species and cover class.

We recognize that use of these tests in spatially-related data induce dependent replicates because of protocol designed to capture a gradient of disturbance within a large sampling unit. Dependent replicates caused unavoidable pseudo-replication that may have affected the significance of results and increased the chance of stochastic error. However, spatially-oriented statistical tests were included that calculated autocorrelation within variables and regression that provided similar trends to the Kruskal–Wallis results. Similarly, logical issues behind pseudo-replication may not be a major cause for concern in this study. The expected results from analyses likely exceed the background variation and we primarily provide deductive discussion points and conclusions, as recommended by other researchers (Oksanen 2001; Davies and Gray 2015).

After logarithmic transformation, ground PPFD, midstory PPFD, and sapling and tree density were confirmed to be normal through Jaque–Bera tests (Jarque and Bera 1980). We performed Getis-Ord Gi hotspot analyses, Moran's I tests, and geographically weighted regression (GWR) using ArcGIS v. 10.5 to determine how spatial patterns and autocorrelation may have affected light, sapling, and tree density variables. Because these statistics account for spatial patterns in the data, spatial autocorrelation was not a concern in these analyses. Plot level disturbance severity delineations (minimal, light, and moderate disturbance) from Cox et al. (2016) were used to stratify variables spatially and perform Moran's I tests within each disturbance class. All statistical tests were performed using R v. 3.2.2 (R Core Team. Released 2015. R: A Language and Environment for Statistical Computing, Version 3.2.2. Vienna, Austria, https://www.R-project.org) and SPSS v. 22 (IBM Corp. Released 2013. IBM SPSS Statistics for Windows, Version 22.0. Armonk, NY: IBM Corp.).

Results

As expected, basal area was lowest in the rows closest to the tornado track (8.94 m^2 ha^{-1} $\pm$ 2.53 SE) as compared to the minimally disturbed hectare (23.02 m^2 ha^{-1} $\pm$ 1.64 SE), which indicated that disturbance was highest near the tornado and decreased with increased distance. As disturbance increased with closer proximity to the track, light penetrated deeper into the stand structure, with midstory and ground light intensity increasing by 23% and 13%, respectively (Fig. 1).

Overall, the average difference in light recorded between 4.67 m and 1.37 m was 6.5%, with a midstory PPFD average of 14.1% $\pm$ 0.9 SE and ground PPFD average of 7.6% $\pm$ 0.5 SE. The minimal disturbance hectare had significantly lower light infiltration compared to the disturbed hectare, including ground PPFD (5.1% $\pm$ 0.5 SE vs. 10.0% $\pm$ 0.9 SE), midstory PPFD (8.5% $\pm$ 0.6 SE vs. 19.6% $\pm$ 1.6 SE), midstory light interception (3.4% $\pm$ 0.6 SE vs. 9.6% $\pm$ 1.4 SE), and canopy openness (5.6% $\pm$ 0.3 SE vs. 12.6% $\pm$ 0.9 SE, $p < 0.001$). Ground PPFD, midstory PPFD, and sapling densities tended to increase with decreased distance from the tornado track (Fig. 2). Variance within rows increased as distance from the tornado track decreased (Fig. 2). Ground PPFD standard error increased from about 0.53% in the minimal disturbance hectare to 3.61% in the row closest to the tornado. Midstory PPFD standard error increased from 0.62 to 5.56% from the minimal disturbance hectare to the row closest to the tornado, respectively.

Spatially, Moran's I indicated moderate to high clustering for ground PPFD (index = 0.35), midstory PPFD (0.52), sapling density (0.72), and tree density (0.32, $p < 0.001$). Spatial patterns for each variable differed by disturbance severity class. Ground PPFD became more randomly distributed in light and moderate disturbance (0.08, 0.14 respectively, $p > 0.05$) as compared to clustered distributions in minimally disturbed plots (0.24, $p < 0.01$). Tree density patterns also followed this trend, with random distribution in disturbed plots (light disturbance: 0.09, moderate disturbance: 0.19, $p > 0.05$) compared to clustered distributions in minimally disturbed plots (0.38, $p < 0.001$). Alternatively, midstory PPFD distribution became increasingly more clustered as

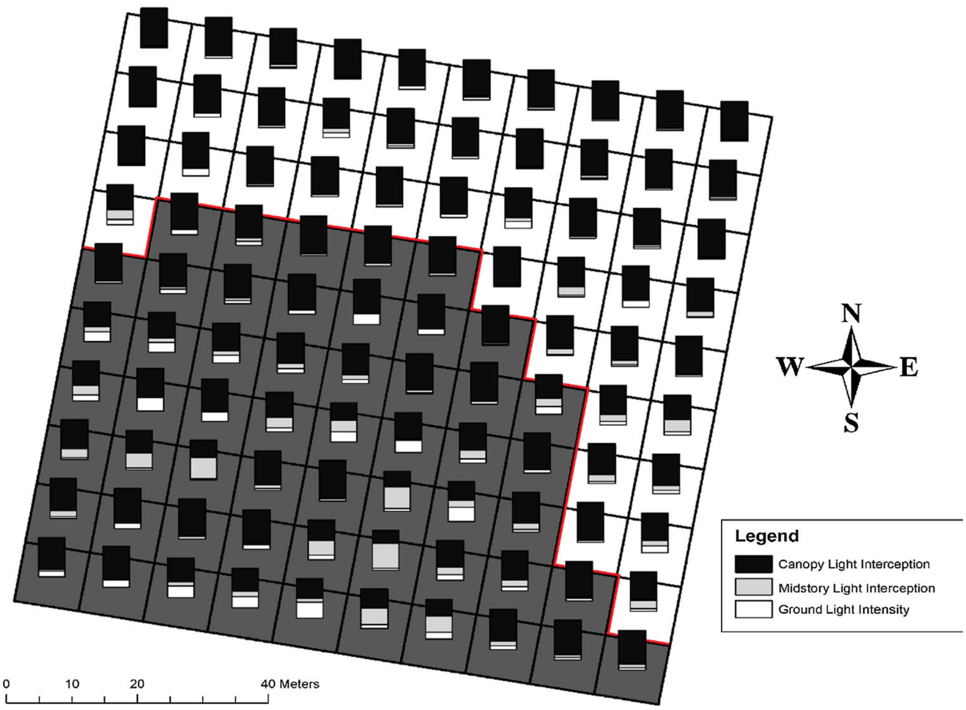

Fig. 1 Light intensity in the disturbance hectare by subplot, indicating the amount of light reaching and/or being intercepted by each stratum. Subplots further south in the hectare were closer to the wind disturbance and generally experienced greater light intensity penetrating further into the stand structure. Shading indicates moderate disturbance, while no shading indicates light disturbance, as delineated by Cox et al. (2016)

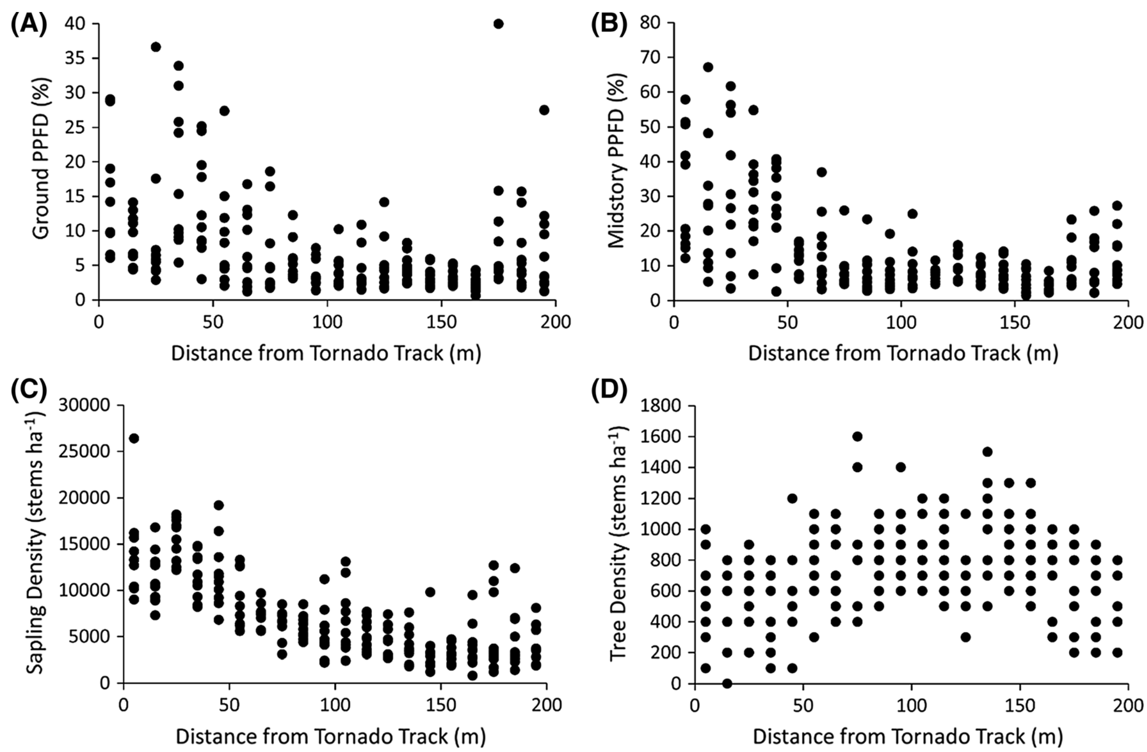

Fig. 2 Representations of changes in vertical light and stand structure with decreased distance from the tornado track. Ground PPFD (**a**) and midstory PPFD (**b**) tended to increase with increased disturbance and had greater heterogeneity in light intensity compared to plots over 100 m from the tornado track. Sapling density (**c**) also increased with increased disturbance, while tree density (**d**) decreased with decreased distance from the tornado track

disturbance increase, as Moran's I increased from 0.19 in minimally disturbed plots to 0.34 in moderately disturbed plots ($p < 0.05$). Sapling density patterns had the greatest change in distribution, from highly clustered in minimally disturbed plots (0.61) to more randomly distributed in moderately disturbed plots (0.32, $p < 0.001$). Tree density best explained variability within midstory light intensity via GWR ($r^2 = 0.569$, $p < 0.001$). Midstory light intensity strongly explained spatial arrangements of sapling density after the tornado, with an $r^2 = 0.733$ ($p < 0.001$). A Getis-Ord Gi hotspot analysis of sapling frequency revealed significant hotspots in subplots nearest the tornado track, while subplots furthest away from the track had significantly fewer saplings (Fig. 3). However, tree density better explained ground light intensity ($r^2 = 0.400$, $p < 0.001$) than sapling density ($r^2 = 0.280$, $p < 0.001$).

Sapling frequency and canopy openness increased as ground PPFD increased, averaging more than 40 more saplings and 13% greater canopy openness in subplots with high PPFD intensity compared to subplots with negligible PPFD intensity (Table 1). Tree density and total basal area decreased as ground PPFD intensity increased. High ground PPFD subplots averaged almost 300 fewer trees ha^{-1} and half the basal area as compared to negligible PPFD (Table 1). Decreased tree density occurred most drastically in codominant and overtopped trees, which were 90 and 125 trees ha^{-1} lower from negligible ground PPFD to high PPFD subplots, respectively.

Similar but more pronounced trends occurred from data analyzed by midstory PPFD categories. Sapling density increased by 250% between low and very high midstory light intensity, which increased from 6 to 52% (Table 2). Canopy openness also increased six-fold, from 5% in subplots with low light intensity to 30% in subplots with very high light intensity. Basal area was different between the two lower midstory light categories and two higher light categories, which corresponded with a decrease of 400 trees ha^{-1} (Table 2). Likewise, codominant and overtopped tree densities decreased by 136 and 199 trees

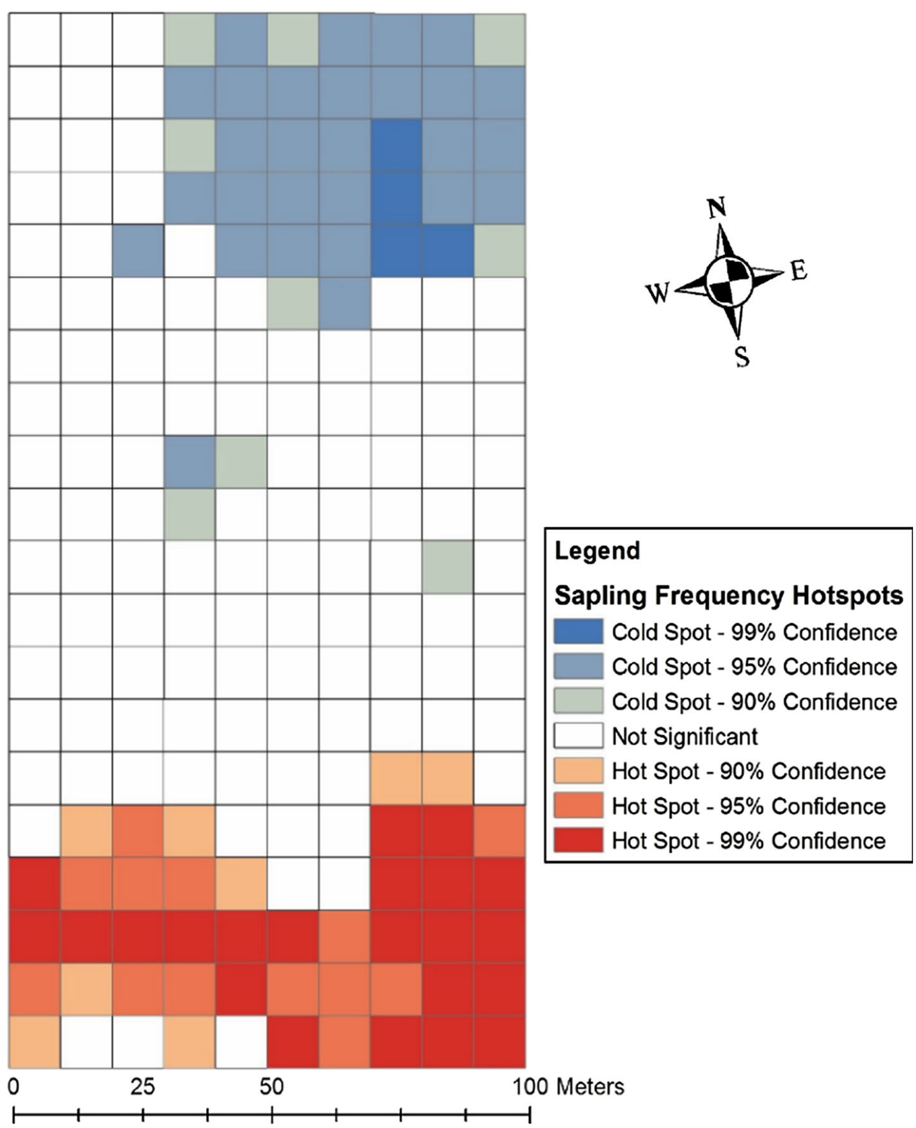

Fig. 3 The results of a Getis-Ord Gi hotspot analysis on sapling frequency. The spatial pattern represented provides evidence that sapling frequency followed the disturbance gradient from low furthest from the tornado track to high nearest the tornado track

Table 1 Results of a Kruskal–Wallis analysis, summarizing the mean values (± standard error) of canopy openness (%), basal area (m^2 ha^{-1}), tree and sapling density (stems ha^{-1}), and tree density by cover classes (stems ha^{-1}) based on intensity of ground PPFD (%)

Variable	Negligible	Low	Moderate	High	Significance
Ground PPFD	3.06 (± 0.10)^{a}	7.46 (± 0.25)^{b}	14.31 (± 0.46)^{c}	28.85 (± 1.69)^{c}	$p < 0.001$
Canopy openness	6.17 (± 0.54)^{a}	9.84 (± 1.07)^{b}	14.09 (± 1.44)^{c}	19.44 (± 2.13)^{c}	$p < 0.001$
Basal area	23.78 (± 1.68)	17.77 (± 1.69)	17.26 (± 2.97)	13.35 (± 3.18)	$p = 0.025$
Sapling density	582 (± 349)^{a}	865 (± 722)^{b}	832 (± 859)^{b}	985 (± 979)^{b}	$p < 0.001$
Tree density	819 (± 29)^{a}	653 (± 35)^{b}	567 (± 46)^{b}	533 (± 81)^{b}	$p < 0.001$
Tree cover class					
Dominant	25 (± 5)	29 (± 7)	33 (± 12)	13 (± 13)	$p = 0.628$
Codominant	179 (± 13)^{a}	125 (± 15)^{ab}	96 (± 15)^{b}	87 (± 29)^{b}	$p = 0.001$
Intermediate	317 (± 17)	287 (± 21)	258 (± 20)	260 (± 39)	$p = 0.273$
Overtopping	298 (± 20)^{a}	211 (± 25)^{b}	179 (± 35)^{b}	173 (± 37)^{ab}	$p = 0.003$

Negligible PPFD = 0–5%, low PPFD = 5–11%, moderate PPFD = 11–19%, and high PPFD > 19%. Dunn's post hoc pairwise comparison test letters indicate significance when α < 0.05 between individual categories

Table 2 Results of a Kruskal–Wallis analysis, summarizing the mean values (± standard error) of canopy openness (%), basal area (m^2 ha^{-1}), tree and sapling density (stems ha^{-1}), and tree density by cover classes (stems ha^{-1}) based on midstory light intensity (%)

Variable	Low	Moderate	High	Very high	Significance
Midstory PPFD	5.85 (± 0.20)^{a}	15.65 (± 0.58)^{b}	31.56 (± 1.31)^{bc}	52.19 (± 2.37)^{c}	$p < 0.001$
Canopy openness	4.79 (± 0.18)^{a}	9.71 (± 0.56)^{b}	18.44 (± 1.17)^{c}	30.18 (± 2.25)^{c}	$p < 0.001$
Basal area	23.09 (± 1.50)^{a}	21.68 (± 2.14)^{a}	11.16 (± 2.32)^{b}	8.49 (± 2.86)^{b}	$p < 0.001$
Sapling density	5313 (± 296)^{a}	8354 (± 655)^{b}	10,933 (± 956)^{bc}	12,750 (± 682)^{c}	$p < 0.001$
Tree density	823 (± 026)^{a}	675 (± 031)^{b}	471 (± 047)^{c}	442 (± 15)^{bc}	$p < 0.001$
Tree cover class					
Dominant	24 (± 4)	29 (± 7)	19 (± 9)	42 (± 22)	$p = 0.901$
Codominant	186 (± 13)^{a}	125 (± 14)^{b}	62 (± 19)^{b}	50 (± 29)^{b}	$p < 0.001$
Intermediate	314 (± 17)	300 (± 19)	233 (± 29)	250 (± 50)	$p = 0.155$
Overtopping	299 (± 19)^{a}	221 (± 25)^{ab}	157 (± 31)^{b}	100 (± 27)^{b}	$p < 0.001$

Low intensity = 0–10% difference, moderate = 10–25%, high = 25–40% and very high > 40%. Dunn's post hoc pairwise comparison test letters indicate significance when α < 0.05 between individual categories

ha^{-1}, respectively and accounted for most of the decrease in tree density in the high light intensity categories.

When analyzed by midstory interception, sapling density in subplots with substantial midstory had 116 saplings per subplot as compared to 48 saplings in subplots with no midstory light interception (Table 3). Canopy openness also increased from 5% in subplots with negligible interception to 21% in subplots with a substantial midstory. Tree density and basal area decreased in substantial light interception subplots, with 58% fewer trees and 48% less basal area in subplots with substantial midstory as compared to a negligible midstory.

Spearman correlation analyses resulted in 29 significant correlations between ground and midstory PPFD, midstory light interception, basal area, tree density, sapling density, and dominant, codominant, intermediate, and overtopped trees (Table 4). Tree density most strongly correlated with basal area and midstory PPFD. Sapling density correlated with midstory PPFD, ground PPFD, and midstory light interception by 51%, 34%, and 39%, respectively ($p < 0.001$). Neither tree density nor basal area strongly correlated with sapling density. Although midstory PPFD had a relatively strong correlation with midstory light interception, ground PPFD was not correlated with midstory light interception. Dominant and intermediate trees did not correlate well with most other variables.

When categorized by species, codominant *Q. alba* and overtopped *O. virginiana* were most strongly correlated with changes in midstory light intensity and interception (Table 5). Both increased as *Q. alba* and *O. virginiana* density decreased, with 89 and 135 fewer trees ha^{-1}, respectively, between low and very high light intensity categories. On average, decreased codominant *Q. alba* represented 65% of all codominant stems removed between

Table 3 Results of a Kruskal–Wallis analysis, summarizing the mean values (± standard error) of canopy openness (%), basal area (m^2 ha^{-1}), tree and sapling density (stems ha^{-1}), and tree density by cover classes (stems ha^{-1}) based on midstory interception (%, the difference between PPFD at 4.67 m from the PPFD at 1.37 m)

Variable	Negative	Negligible	Little	Moderate	Substantial	Significance
Midstory interception	− 3.89 (± 1.04)[a]	1.39 (± 0.11)[b]	3.71 (± 0.11)[c]	8.57 (± 0.38)[d]	26.66 (± 2.32)[e]	$p < 0.001$
Canopy openness	6.10 (± 0.74)[a]	5.15 (± 0.45)[a]	6.41 (± 0.60)[a]	9.92 (± 0.84)[b]	20.76 (± 1.87)[c]	$p < 0.001$
Basal area	21.40 (± 2.70)[a]	22.30 (± 2.30)[a]	25.71 (± 2.56)[a]	20.47 (± 2.19)[a]	10.64 (± 1.94)[b]	$p < 0.001$
Sapling density	6561 (± 624)[ab]	4868 (± 535)[a]	5828 (± 440)[ab]	8082 (± 712)[b]	11,653 (± 726)[c]	$p < 0.001$
Tree density	739 (± 44)[a]	817 (± 45)[a]	830 (± 39)[a]	688 (± 38)[a]	470 (± 50)[b]	$p < 0.001$
Tree cover class						
Dominant	25 (± 10)	32 (± 7)	19 (± 6)	28 (± 7)	27 (± 11)	$p = 0.821$
Codominant	161 (± 20)[a]	185 (± 20)[a]	188 (± 20)[a]	128 (± 17)[ab]	53 (± 14)[b]	$p < 0.001$
Intermediate	268(± 24)	342 (± 31)	323 (± 24)	280 (± 21)	257 (± 28)	$p = 0.125$
Overtopping	278 (± 28)[a]	259 (± 35)[ab]	300 (± 29)[a]	252 (± 29)[ab]	133 (± 24)[b]	$p = 0.006$

Negative midstory < 0% difference, Negligible midstory = 0–2.5%, little midstory = 2.5–5%, moderate midstory = 5–15% and substantial midstory > 15%. Dunn's post hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ between individual categories

Table 4 Results of Spearman correlation analysis determining the strength and significance of correlations between light variables basal area, tree and sapling density, and tree density by cover class

Variables	1	2	3	4	5	6	7	8	9
1. Ground PPFD	–								
2. Midstory PPFD	0.572***	–							
3. Midstory light interception	0.016	0.749***	–						
4. Basal area	− 0.222**	− 0.290***	− 0.222**	–					
5. Tree density	− 0.344***	− 0.448***	0.290***	0.574***	–				
6. Sapling density	0.339***	0.509***	0.392***	− 0.221**	− 0.250***	–			
7. Dominant cover class	− 0.034	− 0.024	0.009	0.327***	0.027	0.012	–		
8. Codominant cover class	− 0.255***	− 0.426***	− 0.329***	0.577***	0.482***	− 0.321***	− 0.211	–	
9. Intermediate cover class	− 0.132	− 0.159*	− 0.067	0.059	0.487***	− 0.04	− 0.04	− 0.055	–
10. Overtopped cover class	− 0.252***	− 0.284***	− 0.199**	0.373***	0.731***	− 0.079	− 0.03	0.212**	− 0.006

*Indicates $\alpha < 0.05$, **$\alpha < 0.01$, and ***$\alpha < 0.001$

low and very high light categories. Overtopped *O. virginiana* stems represented 68% of all overtopped stems removed in the same categories. Similarly, tree density decreased by approximately 95 ha^{-1} and 126 ha^{-1} for *Q. alba* and overtopped *O. virginiana*, respectively, between negligible to substantial light interception categories. On average, codominant *Q. alba* represented 72% of all codominant stems removed between negligible and substantial light interception categories. Overtopped *O. virginiana* stems represented 67% of all overtopped stems removed in the same categories.

Discussion

As expected, increased disturbance severity resulted in increased light intensity along the disturbance gradient. Horizontally, subplots closer to the tornado track had greater damage and reduced overstory structure, as indicated by greater canopy openness. An increasingly open overstory coincided with increased light intensity in understory strata, with an approximate 3 percentage point increase in midstory light intensity for every 1 m^2 decrease in basal area. Vertically, greater disturbance coincided with

Table 5 Results of Kruskal–Wallis and Spearman correlation tests indicating significant decreases in codominant *Q. alba* (n = 171) and overtopped *O. virginiana* (n = 297) densities (stems ha^{-1} ± standard error) as midstory light intensity and light interception by the midstory increases

Category	Codominant *Q. alba* Importance value = 72.1	Overtopped *O. virginiana* Importance value = 45.5
Midstory light intensity		
Low (0–10% PPFD)	114 (± 13)[a]	185 (± 17)[a]
Moderate (10–25% PPFD)	64 (± 13)[ab]	121 (± 21)[ab]
High (25–40% PPFD)	24 (± 10)[b]	86 (± 27)[b]
Very high (> 40% PPFD)	25 (± 18)[b]	50 (± 23)[b]
Significance	$p = 0.001$	$p = 0.001$
Spearman correlation	$r = -0.31$	$r = -0.27$
Midstory light interception		
Negative (< 0% interception)	89 (± 19)[a]	181 (± 29)[a]
Negligible (0–2.5% interception)	112 (± 19)[a]	151 (± 25)[ab]
Little (2.5–5% interception)	135 (± 22)[a]	184 (± 31)[a]
Moderate (5–15% interception)	60 (± 14)[ab]	142 (± 22)[ab]
Substantial (> 15% interception)	17 (± 8)[b]	67 (± 19)[b]
Significance	$p < 0.001$	$p = 0.019$
Spearman correlation	$r = -0.25$	$r = -0.20$

As the two most important species in the study site, the increased light intensity and interception in the midstory followed expected trends in the decreased density of each species. All Spearman correlations are significant at $\alpha < 0.05$ level. Dunn's post hoc pairwise comparison test letters indicate significance when $\alpha < 0.05$ between individual categories

deeper light penetration into the stand structure that highlighted reduced light interception by overstory trees, greater interception by the midstory, and greater light intensity in the understory. Heterogeneity, as measured by increased variability, also changed within vertical light structure, as midstory PPFD became increasingly clumped and ground PPFD became more randomly dispersed with greater disturbance severity. Midstory PPFD may have become spatially clumped because of the removal of large overstory trees that were more prone to blowdown during wind disturbances (Peterson and Rebertus 1997; Peterson 2000; White et al. 2015). Multiple gap-scale canopy openings would create pockets of greater light intensity that would cause clumped spatial results. Sapling density increased in pockets of greater midstory PPFD and prevented light from reaching the ground PPFD level to create randomly dispersed light structure at that stratum that may be more akin to pre-disturbance conditions.

Alterations to each stratum emphasized an increase in vertical light structure complexity in a more heterogeneous stand. Cox et al. (2016) categorized three levels of disturbance severity (minimal, light, and moderate disturbance) using basal area across the same two-hectare study plot. Our light structure results followed the trends presented in that study, with greater light intensity lower in the stand structure as increased disturbance severity created larger overstory gaps. Lhotka and Loewenstein (2009) and Grayson et al. (2012) reported similar increases in light intensity with decreased tree biomass, as they found negative relationships between basal area and ground PAR. Other studies have also indicated greater heterogeneity at stand and landscape scales that experience greater tornado and hurricane disturbance (Xi et al. 2008; Cannon et al. 2016). Although both studies indicated that variations in disturbance were caused by differences in abiotic and biotic factors across the landscape, these potential confounding variables were controlled for in our study design. Thus, this study provides unique detail to the heterogeneity that occurs, specifically from an EF-1 tornado over a gradient of disturbance severity.

After 3 years, disturbed subplots had greater sapling density that altered understory vertical light structure by moving light interception higher in the understory (Fig. 1). Increased disturbance across the hectare resulted in a greater density of advanced reproduction that intercepted more light at the midstory. Increased sapling density with greater disturbance corroborates past regeneration results after a tornado (Nelson et al. 2008; White et al. 2015). Saplings only had a secondary role in regulating light at the ground stratum compared to the overstory, indicated by sapling density steadily increasing with increased light intensity below the sapling stratum (i.e. ground light intensity, Table 1). Similarly, midstory light interception, a secondary measure of sapling density, had minimal correlation with ground light intensity (Table 4).

The overstory maintained primary control over ground light intensity before the disturbance and some control of light structure post-disturbance. Our results indicate that light intensity in the understory was relatively unaffected by midstory growth three years after the wind disturbance (Table 4). Instead, tree density was more highly correlated to ground PPFD than sapling density. Specific overstory species had greater influence on light intensity because of canopy dominance and abundance. The removal of codominant and overtopped trees, specifically codominant *Q. alba* and overtopped *O. virginiana*, was most correlated with increases in light intensity in the understory. As the two most important species in the plot, these results were not unexpected, but confirmed that pre-disturbance light structure was most influenced by dominant and densely populated tree species. The influence of the overstory on light structure was reduced with increasing disturbance and will likely remain low until the canopy begins to close again. However, individual crown cover classes may have changed from pre-disturbance conditions as previously overtopped, intermediate, or codominant trees may have been released to attain an advanced crown cover class. Basal area was reduced by as much as 15 m^2 ha^{-1}, presumably altering crown cover classifications because of decreases in large, overstory stems.

Although prior studies have documented changes in light structure after wind disturbance events, this study is unique in specifically quantifying changes in stand horizontal and vertical light structure over a natural gradient of canopy damage. Similar anthropogenic-based studies have evaluated ground layer light intensity before and after midstory thinnings in eastern U.S. hardwood forests (Lhotka and Loewenstein 2009; Schweitzer and Dey 2015; Pinchot et al. 2017). We found an average difference of 6.5% between the midstory and ground PPFD. In comparison, Lhotka and Loewenstein (2009) and Pinchot et al. (2017) both reported 7.0% increases in ground PPFD after a full midstory removal. Schweitzer and Dey (2015) observed an average increase of 8.5% after midstory removal. Lhotka and Loewenstein (2009) also reported similar light intensity at 1.37 m following removal of one half of the midstory, (canopy openness = 14% ± 1.0 and ground light level = 7% ± 0.4) to our low-level disturbance (canopy cover = 14% ± 1.1 and ground light level = 7% ± 0.3, respectively). This indicates that light structure at breast height resulting from a low severity wind disturbance can be simulated by a partial midstory thinning.

Changes to vertical light structure at levels above 4.67 m may have occurred but were not quantified in this study. To gather a more comprehensive understanding of vertical light profile changes in disturbed stands, methods used in other studies, such as Onoda et al. (2014) and Fotis and Curtis (2017), could be used with our plot design. Doing so would provide an in-depth analysis of light and plant growth in each stratum within a stand and across a canopy disturbance severity gradient. Such analyses would also provide researchers a finer spatial resolution of vertical light structure that may offer more detailed explanations of how disturbance severity and light structure may favor the regeneration of certain species after a natural disturbance.

These results only covered a portion of the natural disturbance severity gradient that may occur from a tornado disturbance, as Cox et al. (2016) delineated disturbance up to moderate severity and lacked catastrophic data. Past research indicates that tornado damage from more destructive tornadoes may contain equal amounts of catastrophic and moderate disturbance across the gradient (Cannon et al. 2016). Our plot may not have been large enough to capture the full disturbance and light gradient for more powerful tornadoes that should be studied in the future. Researchers may also want to use this vertical light data collection method to quantify the effects of other types of natural disturbances on forest light structure. This could include fire, ice, animal, and pathogen-based disturbances. Doing so may refine comparisons between disturbance types to help improve management plans that strive to match natural analogs (Franklin et al. 2002; Hanson and Lorimer 2007; Hart 2016).

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