

# Edge influence on composition and structure of a *Pinus palustris* woodland following catastrophic wind disturbance

Jonathan D. Goode, Jonathan S. Kleinman, Justin L. Hart, and Arvind A.R. Bhuta

**Abstract:** Forest edges are an important legacy of natural and anthropogenic disturbances. Edges of intact forest fragments are influenced by adjacent non-forested ecosystems, resulting in compositional and structural differences at the edge and into the intact forest. Edge influence (EI) is the altered biotic and abiotic interactions that occur along the edge-to-interior gradient in disturbed forests. Few studies have analyzed natural disturbance created edges, particularly in woodland structures, which contain fewer trees per hectare and are typically less light-limited than forests. The goal of our study was to examine the EI of a tornado-created edge in a *Pinus palustris* Mill. (longleaf pine) woodland in Alabama. In 2011, an EF-3 tornado impacted a restored *P. palustris* woodland, resulting in a distinct edge. We installed transects perpendicular to the edge to quantify biotic and abiotic response variables and calculate the distance of EI. Reduced structural forest complexity and basal area (negative EI) were evident 70 m into the interior woodland. Ground flora richness and diversity experienced a positive EI, with higher richness and diversity at the edge. Results of this study add to our understanding of EI on woodland composition and structure and naturally created edges and may help guide natural disturbance based silvicultural systems.

**Key words:** edge influence, *Pinus palustris*, longleaf pine, biological legacies, woodland structure, ground flora.

**Résumé :** Les bordures des forêts sont d'importants legs des perturbations naturelles et anthropiques. Les bordures des fragments de forêt intacte sont influencées par les écosystèmes adjacents non boisés, ce qui entraîne des différences de composition et de structure en bordure et à l'intérieur de la forêt intacte. L'effet de bordure (EB) est la modification des interactions biotiques et abiotiques qui survient le long d'un gradient, de la bordure vers l'intérieur des forêts perturbées. Peu d'études ont analysé les bordures créées par des perturbations naturelles, particulièrement dans la structure des boisés qui contiennent moins d'arbres à l'hectare et qui sont typiquement moins privés de lumière que les forêts. Le but de notre étude consistait à examiner l'EB d'une bordure créée par une tornade dans un boisé de pin des marais (*Pinus palustris* Mill.) en Alabama. En 2011, une tornade de catégorie F3 a frappé un boisé restauré de pin des marais créant une bordure distincte. Nous avons installé des transects perpendiculaires à la bordure pour quantifier les variables de réactions biotiques et abiotiques et calculer la distance de l'EB. Une réduction de la surface terrière et de la complexité structurale de la forêt (EB négatif) était évidente à 70 m à l'intérieur du boisé. L'EB était positif dans le cas de la diversité et de la richesse de la flore du sol et l'effet était le plus prononcé en bordure du boisé. Les résultats de cette étude ajoutent à notre compréhension de l'EB sur la composition et la structure des boisés, ainsi que des bordures d'origine naturelle, et ils peuvent contribuer à orienter les systèmes sylvicoles écosystémiques. [Traduit par la Rédaction]

**Mots-clés :** effet de bordure, *Pinus palustris*, pin des marais, legs biologiques, structure du boisé, flore du sol.

## 1. Introduction

Forest edges in fragmented landscapes are increasingly abundant as a result of anthropogenic and natural disturbances. Edges of intact forest fragments are influenced by adjacent non-forested ecosystems, resulting in compositional and structural differences along a gradient from the edge to the forest interior (Harper et al. 2005). Edge influence (EI) is the manifestation of biotic and abiotic interactions that occur along the edge-to-interior forest gradient as a result of natural or anthropogenic disturbance (Murcia 1995). Altered biotic and abiotic conditions along the edge-to-interior gradient influence forest composition, structure, and function in this transitional zone (Matlack 1993).

Altered abiotic conditions are the primary drivers of changes in plant community composition and structure along the edge-to-interior gradient (Cadenasso et al. 1997). Altered microenvironmental dynamics of forest edges include increased light availability, lower soil

and litter moisture, and higher wind speeds (Brothers and Spingarn 1992, Young and Mitchell 1994). Such changes in microenvironmental conditions at the forest edge may favor unique plant communities not found in the interior forest (Laurance 1991; Noss and Cooperrider 1994). For example, increased light availability at the edge may favor early successional species that are absent from the interior (Fraver 1994). Trees growing along the forest edge are often more susceptible to wind damage compared with trees in forest interior positions (Chen et al. 1992). Furthermore, reduced air moisture content at the edge has been linked to reduced decay rates of coarse woody material (Crockatt and Bebbler 2015).

EI is often measured by distance (the penetration of EI into the interior forest) and magnitude (the steepness of the environmental gradient at the edge; Harper et al. 2005). Canopy structure of dominant overstory individuals and edge type (e.g., maintained vs. unmaintained edges) are important drivers of EI distance. Few

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studies have recorded EI distances of up to 140 m such as Comargo and Kapos (1995) and Laurance (1991) in tropical forests and Chen et al. (1992) in temperate rainforests. EI magnitude (i.e., patch contrast) describes the contrast in forest composition and structure between adjacent disturbed (edge) and undisturbed (interior) forest.

Woodlands typically contain fewer trees per hectare and are less light limited relative to forests, in which most studies of EI have occurred. Thus, the abiotic variability along the edge-to-interior gradient would likely be less pronounced in woodlands than in a closed-canopy forest (Harper et al. 2015). On the continuum from grasslands to closed-canopy forests, woodlands occur between savannas and forests. Savannas generally have <30% overstorey cover, more grass cover, and fewer trees per hectare compared with woodlands (Dey and Kabrick 2015). In *Pinus palustris* Mill. woodlands of the southeastern United States, canopy openness ranges from 50% in developing stands to 20%–30% in mature stands with high spatial variability of understorey light availability (Palik et al. 1997). Natural variability of abiotic conditions in woodlands affects distance and magnitude of EI compared with closed-canopy systems. For instance, in temperate woodlands of southeastern Australia, Wright et al. (2010) found that EI on daytime temperature and vapor pressure had a similar distance, yet reduced magnitude, compared with closed-canopy forests.

EI has been studied in tropical (e.g., Prieto et al. 2014), temperate (e.g., MacQuarrie and Lacroix 2003), and boreal (e.g., Harper et al. 2004) forest types. EI has also been studied on different natural and anthropogenic edges such as agricultural edges (Gehlhausen et al. 2000), harvest-created edges (Dupuch and Fortin 2013), and fire edges (Harper et al. 2014). However, there exists a paucity of EI research on woodland composition and structure and, more specifically, edges created by catastrophic wind disturbance (see Pohlman et al. 2008). Because of the structural difference among savannas, woodlands, and forests, it is important to understand the influence of edges on woodland (or open-canopy forest) composition and structure (see Dodonov et al. 2013).

Wind disturbance is among the most widespread disturbance agents in forest ecosystems and is arguably the most prevalent disturbance agent in forests of eastern North America (Macdonald 2001; Peterson et al. 2016). Tornadoes have the potential to be the most severe type of wind disturbance and are capable of producing the fastest wind speeds in nature; however, tornado severity and width may vary along the tornado track and by storm event and may be influenced by topography (Karstens et al. 2013; Lyza and Knupp 2014). Tornadoes often change rotational velocity, intensity, and size, which can influence overstorey removal in forest ecosystems (Bech et al. 2009; Cannon et al. 2016; Peterson et al. 2016). The Mid-West (Tornado Alley) and Southeast (Dixie Alley) regions of the United States experience the greatest number of tornado events in the world, with an average of 1253 occurrences each year (National Climatic Data Center (NCDC) 2019). Furthermore, tornado frequency is predicted to increase in the southeastern United States in the future (Gensini and Brooks 2018).

The overarching goal of this study was to examine EI on woodland composition and structure following a catastrophic tornado. Specifically, the objectives of this study were to (i) quantify plant species composition and diversity and the structural complexity of a *P. palustris* woodland from the edge of a tornado path to the interior woodland, (ii) determine how altered abiotic conditions influence plant composition and structure along the edge-to-interior gradient, and (iii) determine the distance of EI (the width of the edge ecosystem) caused by the disturbance event. Results from this study further our understanding of the biotic and abiotic components that occur at the edge of woodland fragments and offer insight to managers who wish to emulate patterns of natural disturbance and its influence on plant composition and diversity in silvicultural systems.

## 2. Materials and methods

### 2.1. Study area

This study was conducted in the Oakmulgee Ranger District of the Talladega National Forest in west-central Alabama, USA. The Oakmulgee Ranger District is situated in the Fall Line Hills (Fenneman 1938), a transition zone between the Coastal Plain and the Appalachian Highlands (Shankman and Hart 2007). The Fall Line Hills region in Alabama is characterized by steep, dissected slopes with sandy soils (Fenneman 1938). The district is geologically composed of the Tuscaloosa Coker and Gordo formations. The Coker formation is composed of micaceous very fine to medium sand, micaceous clay, and gravel beds of quartz and chert. The Gordo formation is composed of cross-bedded and gravely sands, carbonaceous clay, and chert and quartz pebbles (Szabo and Wheat 1988). Soils in the study area are classified in the Maubila–Smithdale complex, which are deep and moderately well drained (U.S. Department of Agriculture, Natural Resource Conservation Service (USDA NRCS) 2017).

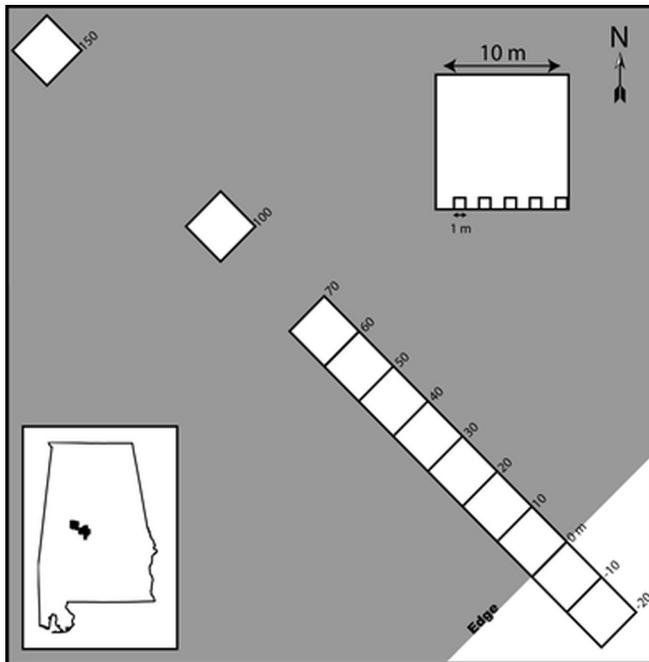
The climate of the region is humid mesothermal, with long, hot summers and short, mild winters (Thorntwaite 1948). Mean annual temperature is 17.4 °C, with the lowest monthly mean of 7.2 °C in January and the highest monthly mean of 26.9 °C in July. Mean annual precipitation is 1369 mm, with the highest amount of rain occurring in March (155.7 mm) and lowest amount occurring in October (70.1 mm) (PRISM Climate Group 2018). On 27 April 2011, an EF-3 tornado directly impacted restored *P. palustris* stands in the Oakmulgee Ranger District. The tornado had a total length of 116 km, maximum wind speeds of 233 km·h<sup>-1</sup>, and a maximum path width of 1.61 km (National Weather Service (NWS) 2011). The majority of overstorey stems in the tornado swath were snapped or uprooted, with a residual basal area of 1.09 m<sup>2</sup>·ha<sup>-1</sup> (Kleinman et al. 2017).

The Oakmulgee Ranger District of the Talladega National Forest is located within the central *P. palustris* belt in Alabama (Harper 1943). The area was settled by Europeans in the 1820s, logged extensively in the early 1900s, and federally acquired in 1935 (Reed 1905; Cox and Hart 2015). The district is managed for re-introduction of *P. palustris* to suitable sites currently dominated by *Pinus taeda* L. and xeric hardwood species (U.S. Department of Agriculture (USDA), Forest Service 2005). Restoration and maintenance of *P. palustris* in the Oakmulgee Ranger District involves regeneration harvests, site preparation, outplanting of *P. palustris*, thinning of undesirable tree species, and prescribed burning on a 2- to 5-year rotation (USDA Forest Service 2005), which promotes natural regeneration of *P. palustris* by reducing interspecific competition and exposing bare mineral soil for seeds to germinate (Platt et al. 1988). Previous studies of restored *P. palustris* in the Oakmulgee Ranger District have found basal area of 21–22 m<sup>2</sup>·ha<sup>-1</sup>, *P. palustris* relative density of 47%–92%, and *P. palustris* relative dominance of 75%–97% (Kleinman et al. 2017; Goode et al. 2019).

### 2.2. Edge determination

In the laboratory, we selected a USDA Forest Service delineated forest compartment that was dominated by *P. palustris* in woodland structure and contained abundant edge habitat created by the tornado. The edge was determined by visually locating the start of continuous canopy at the edge of the tornado swath, disregarding residual trees that were not killed by the tornado but were evident within the tornado swath. Aerial imagery analysis and ground reconnaissance confirmed that the tornado did not remove all overstorey individuals within the track. In the field, potential sampling points were located and visually confirmed to be situated at the edge of the tornado swath. Selection criteria were based on laboratory reconnaissance (aerial imagery), continuous canopy cover into the interior woodland (confirmed by the aerial imagery and visually in the field), and the location in which uprooted trees no longer occurred as a result of the tornado. Easily

**Fig. 1.** Sampling design and transect installation to quantify edge influence in the Oakmulgee Ranger District of the Talladega National Forest, Bibb County, Alabama, USA. A total of nine transects were installed along the edge-to-interior gradient between azimuths of 330° and 350°. Overstory, saplings, and abiotic variables were measured in 10 × 10 m plots. Ground flora and ground surface substrate were measured in each 1 × 1 m quadrat.



accessible portions of the tornado-affected compartment were salvage harvested after the tornado to mitigate the risks of potential hazards associated with the abundance of dead trees and to reclaim economic losses. We intentionally avoided salvage-harvested areas so that the influence of coarse woody material could be analyzed. The Oakmulgee Ranger District utilizes prescribed fire at the compartment scale so that all sites within a single compartment have the same fire history. The compartment in which the study was based was most recently burned in April 2018.

### 2.3. Field methods

Data were collected in May–July 2018, 7 years after the tornado event. To quantify EI on woodland composition and structure, nine vegetation sampling transects were established with eleven 10 × 10 m plots at set distances from the edge installed along each transect (Fig. 1). A singular southeast-facing edge was used for sampling. Transects were installed perpendicular to the edge into the interior woodland on azimuths between 330° and 350°. Transect azimuths varied because of the geometric ruggedness of the edge. Transects were spaced at least 30 m apart to reduce autocorrelation effects. Along each transect, plots were installed at 10 and 20 m into the tornado swath (henceforth referred to as –10 and –20 m) and 0, 10, 20, 30, 40, 50, 60, 100, 150 m into the interior woodland (Chen et al. 1992; Harper and Macdonald 2002; Dabros et al. 2017). Plots were established into the tornado swath to capture the gradient from tornado-disturbed to interior woodland conditions (Harper et al. 2004). Transect length was determined in the field and set at 150 m because of the topographic variability in the study area, which could have potentially biased results. Distances greater than 150 m from the edge were of a dissimilar topographic position or in stands of different composition and structure and were consequently unsuitable for comparisons.

To quantify woodland composition and structure from the edge-to-interior gradient, trees, coarse woody material, saplings, and understory light availability were sampled in each 10 × 10 m plot. Trees, defined as live woody stems ≥ 5 cm diameter at 1.37 m above the root collar (diameter at breast height, dbh), were identified to species, measured for dbh and height, and assigned one of four crown classes (overtopped, intermediate, co-dominant, and dominant; Oliver and Larson 1996). Saplings, defined as live woody stems < 5 cm dbh and ≥ 1 m height, were identified to species and tallied for density. Coarse woody material (CWM) was defined as non-living upright or downed woody stems ≥ 10 cm diameter at any point of the segment. Standing dead stems were classified as snags (largely intact crown) or snapped stems (broken above dbh). Downed stems were classified as logs (downed stems disconnected from root network) and uprooted stems (downed stems with root network intact). Standing dead stems were measured for dbh to calculate basal area (m<sup>2</sup>·ha<sup>-1</sup>). Logs were measured for diameter at both ends and length. Uprooted stems were measured for dbh and length. If logs or uprooted stems crossed plot boundaries, measurements were taken at the location where the individual crossed the plot boundary line. Volume (m<sup>3</sup>·ha<sup>-1</sup>) was calculated for logs with the equation for a conic paraboloid (Fraver et al. 2007) and for uprooted stems with species-specific allometric equations (Woodall et al. 2011). All CWM was assigned a decay class from I to V based on increasing level of decay (Forest Inventory and Analysis National Program (FIA) 2005). To quantify understory light availability from the edge-to-interior gradient, one hemispherical canopy photograph was taken at the center of each 10 × 10 m plot using a fisheye lens fitted on an Olympus Stylus TG-3 digital camera mounted on a self-leveling tripod at 1.37 m above the ground. The camera was calibrated to be used with WinSCANOPY software for photograph analysis (WinSCANOPY, Regent Instruments, Quebec City, Quebec, Canada). Photographs were captured in late afternoon and (or) during overcast conditions to reduce glare for image analysis.

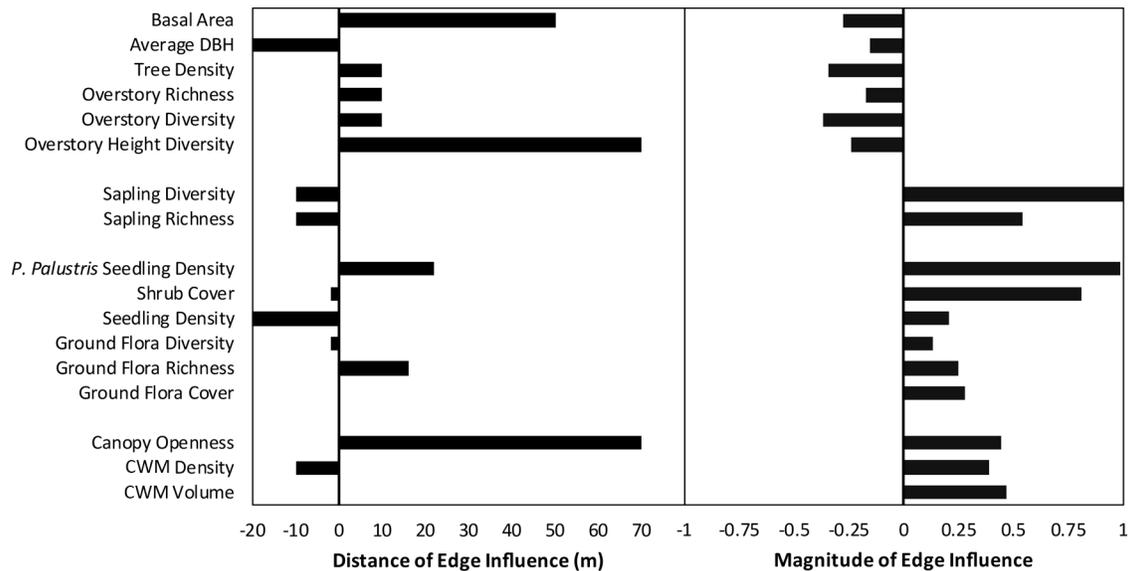
Ground flora (herbaceous and woody plants < 1 m height) and *Pinus* litter cover were quantified in five 1 × 1 m nested quadrats situated on the southwestern border of each 10 × 10 m plot (55 quadrats per transect; see Fig. 1). Ground flora was identified to the lowest taxonomic level possible by examining reproductive structures. Photographs and collections were made when necessary to aid in identification of plants in the laboratory. The percent cover of ground flora taxa was estimated within each 1 × 1 m quadrat using different-sized panel estimators that covered 1% and 5% of the quadrat as guides. Percent cover of ground flora taxa and *Pinus* litter was assigned a value from 1 to 10 using North Carolina Vegetation Survey (NCVS) protocol (Peet et al. 1998).

### 2.4. Analytical methods

To quantify the EI following the tornado, EI was divided into two types: biotic and abiotic. EI on biotic communities included living plants divided into three woodland strata: overstory (trees), midstory (saplings), and understory (ground flora). EI on abiotic factors included CWM, understory light availability, and *Pinus* litter. To quantify EI on plant communities, metrics were calculated for the three woodland strata at each distance from the edge. All metrics were calculated at the 10 m<sup>2</sup> plot scale for trees and saplings and at the 1 m<sup>2</sup> quadrat scale for ground flora.

Overstory diversity metrics included species richness, evenness, and Shannon diversity ( $H'$ ). Overstory structural complexity metrics included basal area (m<sup>2</sup> per plot), tree density (number of stems per plot), and Shannon diversity of tree height. These structural complexity metrics were chosen because they best describe the horizontal and vertical distributions of trees in the stand (McElhinney et al. 2005). Shannon height diversity describes the vertical complexity of the overstory, with higher values indicating more vertical complexity. To calculate Shannon height diversity,

**Fig. 2.** Distance of edge influence (DEI) and magnitude of edge influence (MEI) of calculated response variables. Positive MEI indicated significantly higher values at the edge, and negative MEI indicated significantly lower values at the edge. DEI is the total distance in which MEI was significant ( $p < 0.05$ ). DBH, the measured diameter at breast height (1.4 m above root collar); CWM, coarse woody material.



all trees were placed into 1 m height classes (Staudhammer and Lemay 2001).

For the sapling stratum, density (number of stems per plot),  $H'$ , and richness were calculated. Ground flora metrics were divided by seedlings (woody stems < 1 m height) and herbaceous plants (non-woody stems < 1 m height). Percent cover,  $H'$ , and richness for all ground flora were calculated. Seedling density (number of stems per 1 m<sup>2</sup> quadrat) was calculated for all seedlings, *P. palustris* seedlings, and *Quercus* seedlings.

To quantify EI on abiotic factors, variables were calculated to quantify understory light availability and *Pinus* litter cover at each distance along the edge-to-interior gradient. CWM metrics calculated included volume (m<sup>3</sup> per plot) and density (number of pieces per plot), which were further categorized by species and decay class. To describe understory light availability, canopy openness per plot (%) was determined using the software WinSCANOPY.

Once all biotic and abiotic variables were calculated, a non-parametric randomization test of EI (RTEI; Harper and Macdonald 2011) was used to determine the distance of edge influence (DEI). The basis of the RTEI is the calculation of the magnitude of edge influence (MEI) and the statistical comparison of MEI at all sampled distances to the reference plot (from 20 m into the tornado swath to 100 m into the reference woodland). MEI standardizes EI across variables and among different scales of measurement. Calculation of MEI relativizes response variables at a given distance with response variables in the reference plot to produce values from -1 to 1. Positive MEI values indicate higher values at a given distance from the edge, and negative MEI values indicate lower values at a given distance from the edge. For example, if basal area showed a significantly negative MEI, basal area was reduced at each significant distance compared with the reference woodland. DEI is determined as the maximum distance in which MEI is significantly different from 0 (reference woodland, 150 m plot). The RTEI used 1000 permutations for a confidence level of 95% ( $p < 0.05$ ) as recommend by Harper and Macdonald (2011). RTEI was used for the determination of DEI and MEI for all biotic and abiotic metrics from 20 m into the tornado swath to 100 m into the interior woodland. A 95% confidence interval ( $p < 0.05$ ) was used for all statistical analysis, unless otherwise noted. Plot 11 (150 m) on each transect was used as reference conditions for statistical analyses.

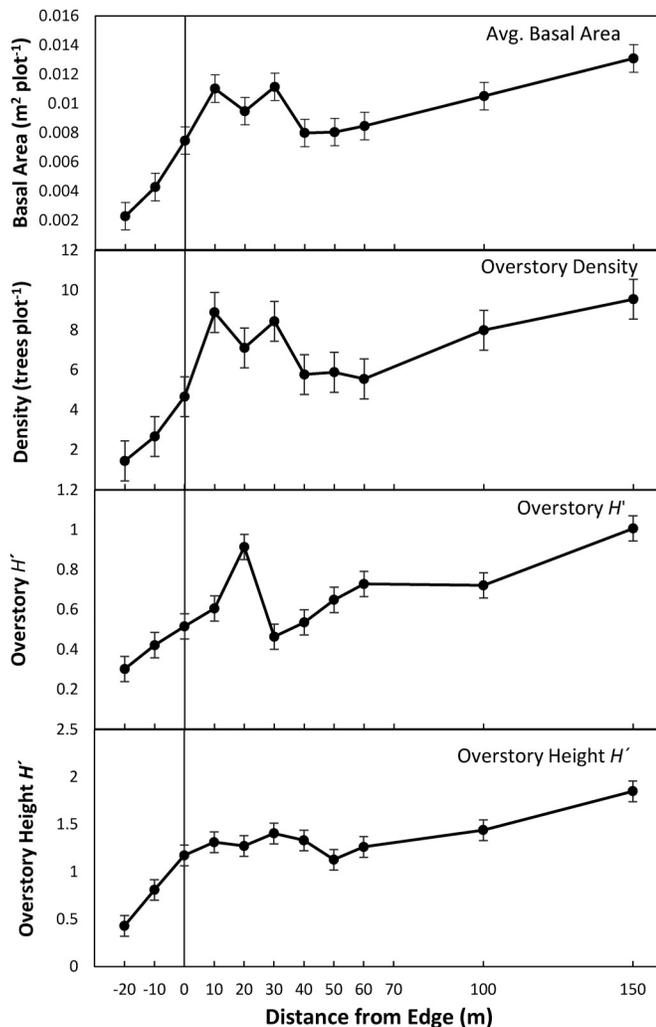
To visualize and characterize differences in ground flora cover from the edge-to-interior gradient, cluster analysis, non-metric multidimensional scaling (NMS) ordination, and multi-response permutation procedure (MRPP; Mielke and Berry 2001) were conducted using PC-ORD v. 6.0 (McCune and Medford 2011). To prepare data for cluster analysis, percent cover values were averaged per plot across each of the nine transects, resulting in one transect with average percent ground flora cover values in each of the 11 plots. Cluster analysis was used to group plots based on the composition and percent cover of ground flora communities. The cluster analysis utilized Euclidean distance and Ward's method in the calculation of the dendrogram. The dendrogram displayed three clusters with 34.4% information remaining. Upon interpretation, distinct clusters were noted at -20 to 0 m (hereafter swath), 0 to 20 m (hereafter edge), and 30 to 150 m (hereafter interior). Once clusters were visually determined, NMS ordination was used to graphically interpret differences in the composition and percent cover of ground flora in relation to five environmental variables: (i) live tree density (stems per plot); (ii) sapling density (stems per plot); (iii) canopy openness (%); (iv) CWM volume (m<sup>3</sup> per plot); and (v) percent *Pinus* litter cover. Plot-level NCVS cover values in the main matrix were relativized by maximum (i.e., the proportion of the maximum cover class documented for each species) to reduce the influence of species with large growth forms. Taxa with single occurrences were eliminated from the main matrix so that unique plant assemblages were not based on single occurrences of one individual. An NMS scree plot was used to determine the number of axes to use in the final solution. Sorenson (Bray-Curtis) distance and 250 runs with real data were performed in the final NMS ordination. Convex hulls were used to group plots based on previously determined clusters. A biplot overlay was displayed to assess correlation between axes and environmental variables, with an  $r^2$  cutoff of 0.40. To test for significant differences in ground flora composition and percent cover between clusters, an MRPP with post hoc pairwise comparisons was conducted.

### 3. Results

#### 3.1. EI on overstory and sapling composition and structure

Overall, EI on overstory composition was minimal but significant, with maximum EI of 10 m into the interior woodland. Mean

Fig. 3. Average overstory response variables from the edge-to-interior gradient, with vertical bars as standard error.  $H'$  is Shannon diversity.



( $\pm$ SE) overstory species richness ranged from  $1.0 \pm 1.0$  in the tornado swath to  $3.4 \pm 1.0$  in the interior woodland. Overstory species richness was reduced (negative EI) from the tornado swath up to 10 m into the interior woodland (Fig. 2). A similar but stronger negative EI was documented on overstory  $H'$  (DEI: 10 m). Mean ( $\pm$ SE) overstory  $H'$  was  $0.301 \pm 0.358$  for the tornado swath and increased to  $1.000 \pm 0.397$  into the interior woodland (Fig. 3). MEI on overstory  $H'$  was negative, indicating  $H'$  was reduced at all distances.

Overall, EI was highly variable on woodland structure, with DEI estimates ranging from 0 to 70 m into the interior woodland. EI on basal area was significantly negative, with reduced basal area occurring from -20 to 10 m and from 40 to 70 m (Fig. 3). Tree density exhibited a negative DEI from -20 to 10 m. We documented a mean ( $\pm$ SE) of  $2.0 \pm 1.9$  trees·plot<sup>-1</sup> in the tornado swath and  $9.5 \pm 4.2$  trees·plot<sup>-1</sup> in the interior woodland. EI on overstory height  $H'$  was negative and showed the greatest sustained DEI of any structural variable (DEI: 70 m).

We documented 185 saplings·ha<sup>-1</sup> representing 24 different species. RTEI results revealed non-significant DEI and MEI on sapling composition (Fig. 2). EI on sapling density, richness, and diversity was significantly positive only at the distance of -20 m

from the edge (20 m into the tornado swath), which indicated no penetration of EI on sapling metrics into the interior woodland. MEI values for both sapling richness and diversity were among the highest calculated for all biotic and abiotic variables (Fig. 2). MEI was 0.9 for sapling richness and 1.0 for sapling diversity at -20 m from the edge. High MEI values indicated a high disparity between sapling communities in the tornado swath and sapling communities in the interior woodland.

EI was not significant on CWM volume and density or snag density (Fig. 2); however, the tornado swath contained a significantly greater volume and density of CWM. We documented a significantly greater CWM volume from -20 to 0 m and greater CWM density from -20 to -10 m. No significant EI was recorded in snag density from the edge-to-interior gradient. *Pinus palustris* was the most abundant CWM species, occurring at all distances from the edge. Logs accounted for 56% of all CWM documented, followed by snags, which accounted for 24% of CWM. We recorded 85 snags in which 30 (40%) were *Cornus florida* L. and 25 (30%) were *P. palustris*. Of all snags recorded, 80% occurred at distances > 20 m from the edge into the interior. The opposite trend was documented with downed CWM (logs and uproots), with 68% occurring from -20 to 40 m.

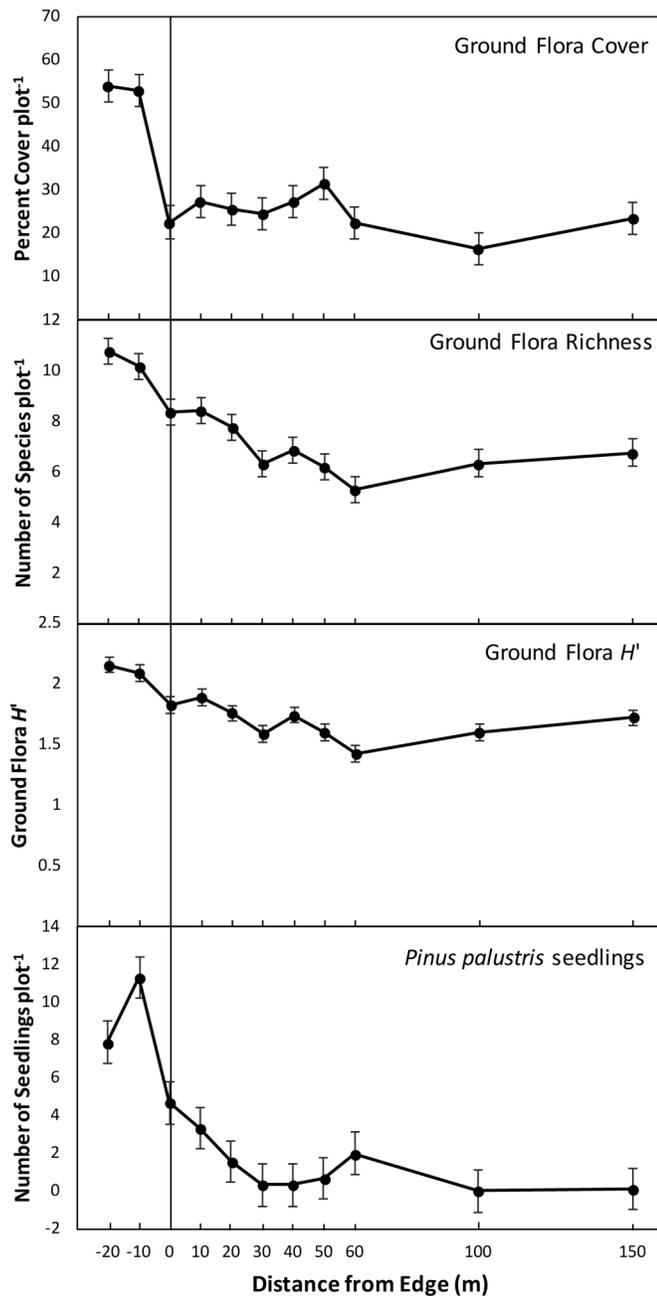
EI on understory light availability was significantly positive from the edge-to-interior gradient (Fig. 2). We noted significantly higher percent canopy openness from -20 to 70 m into the interior woodland. Canopy openness ranged from  $58\% \pm 14\%$  in the tornado swath to  $22\% \pm 4\%$  in the interior woodland and showed a decreasing trend from the edge-to-interior gradient. *Pinus* litter exhibited a significantly negative EI from -20 to 8 m into the interior.

### 3.2. EI on ground flora communities

We identified 73 herbaceous taxa (70 forb, 3 graminoid), 50 woody taxa (31 tree, 19 shrub), and 13 vine taxa (Supplementary Tables 1 and 2). The highest species richness in any 1 m<sup>2</sup> quadrat was 21 species, found 14 m into the tornado swath. In general, the tornado swath contained higher species richness, and species richness decreased with distance from the edge into the intact woodland. For example, 1 m<sup>2</sup> quadrats with species richness  $\geq 15$  most commonly occurred at distances of -20 to 30 m. RTEI results revealed significantly positive EI on ground flora species richness (Fig. 4). Ground flora richness was significantly greater at distances of -20 to 16 m when compared with the interior woodland. Ground flora  $H'$  showed a similar trend along the edge-to-interior gradient, with significant positive EI occurring from -20 to 2 m into the interior. Ground flora richness averaged 9.6 species·(1 m<sup>2</sup> quadrat)<sup>-1</sup> in the tornado swath and edge (as determined by RTEI), and richness averaged 6.7 species·(1 m<sup>2</sup> quadrat)<sup>-1</sup> in the interior woodland. For tree seedlings, *P. palustris* occurred in 21% of quadrats, followed by *Quercus falcata* Michx. (17% of quadrats) and *Carya tomentosa* (Lam.) Nutt. (15% of quadrats). Mean ( $\pm$ SE) seedling density ranged from  $13.5 \pm 15.6$  to  $3.4 \pm 5.2$  seedlings·quadrat<sup>-1</sup> from plots in the tornado swath to plots in the interior. MEI values were positive from -20 to 0 m, indicating a greater density of seedlings in the tornado swath and edge. We documented a significantly positive EI on *P. palustris* seedlings at distances of -20 to 6 m and 10 to 22 m. MEI values were greater than 0.9 for all significant distances, which indicated a large discrepancy between *P. palustris* seedling establishment in the tornado swath and edge compared with the interior (Fig. 4). MEI on *P. palustris* seedling density was the highest magnitude recorded in this study. EI on total ground flora cover was positive, with increased total cover from -20 to 2 m (Fig. 4). Mean ( $\pm$ SE) ground flora cover at distances in which MEI was significant was  $53\% \pm 28\%$  and was  $23\% \pm 29\%$  in the interior woodland.

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2019-0292>.

Fig. 4. Average ground flora response variables from the edge-to-interior gradient, with vertical bars as standard error.  $H'$  is Shannon diversity.



The three-axis NMS solution revealed decreasing variability of ground flora communities from the interior cluster (distances of 30 to 150 m) to the tornado swath cluster (distances of -20 to 0 m) (Fig. 5). The interior cluster had the greatest variability in ground flora communities. Interior plots were the most variable in ordination space, indicating that a large number of unique plant assemblages occurred in the interior woodland. Tornado swath plots were less variable in ordination space and generally occurred in the lower half of the graph, corresponding to the positive range of axes 1 and 3 and the negative range of axis 2. MRPP results confirmed significant difference in ground flora assemblages across the three clusters. The post hoc pairwise comparison revealed that ground flora communities in the tornado swath were significantly different from ground flora communities in the

interior woodland ( $p < 0.001$ ); however, ground flora communities in the edge were not significantly different from communities in the tornado swath ( $p = 0.063$ ) or from communities in the interior woodland ( $p = 0.051$ ).

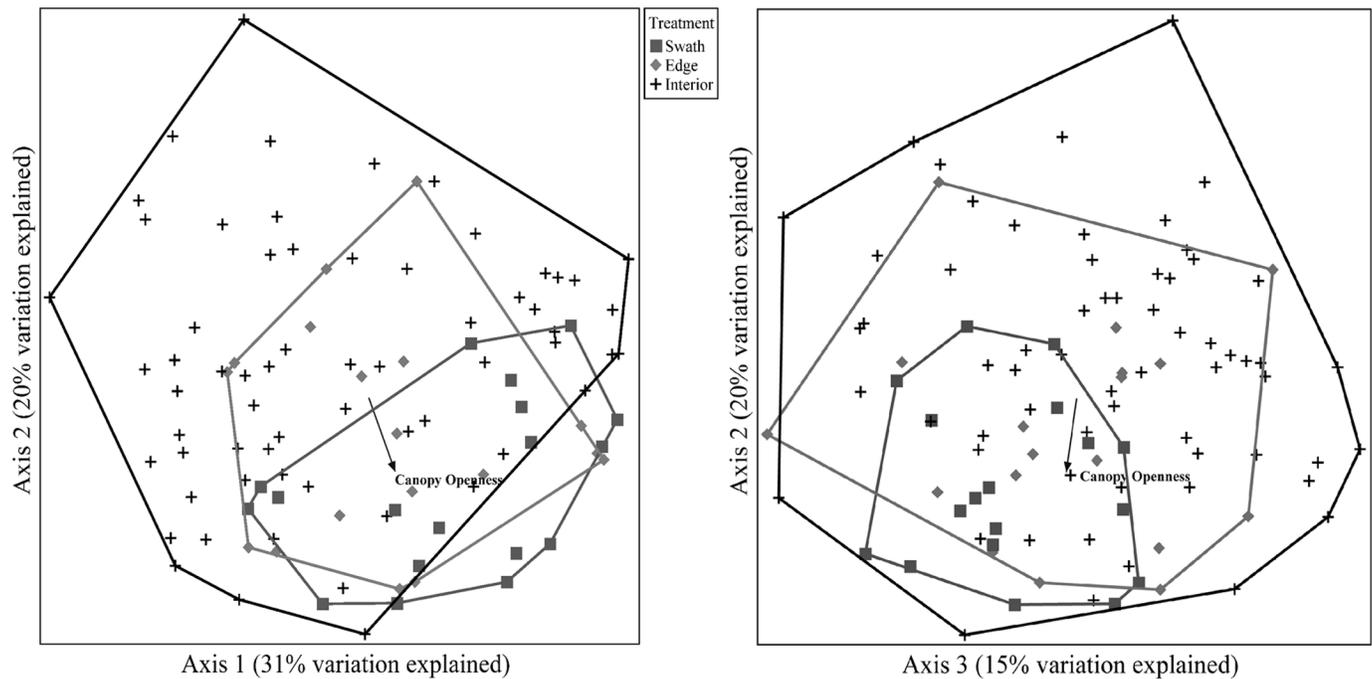
## 4. Discussion

### 4.1. Depth of EI

Overstory compositional diversity and structural complexity experienced a negative EI (reduced values at the edge). Compositionally, the overstory of the interior woodland was more diverse than the edge, which may be attributed to the higher probability of overstory mortality at the edge during and after tornado disturbance (Matlack 1994). The reduction in structural attributes indicated that the tornado had not only an immediate impact on woodland structure, but also residual impacts (secondary responses). Secondary responses may include delayed overstory mortality, damaged individuals, recruitment of new stems into the canopy, and vulnerability to pests (Harper et al. 2015). Decreased overstory density and basal area at the edge of forest fragments have been documented in other studies (Chen et al. 1992; Oosterhoorn and Kappelle 2000; Harper and Macdonald 2002; Harper et al. 2015). We speculate that most of the structural differences at the edge were primarily influenced by the tornado and few were secondary responses to edge formation. The tornado directly reduced basal area and stem density at the edge and into the interior woodland. As a result, vertical and horizontal overstory structure was simplified and this reduction reduced the vertical and horizontal complexity of the overstory at the edge. We noted a secondary response in the form of snags created by the tornado that were subsequently toppled by higher wind exposure at the edge. Of the three plant strata analyzed (overstory, saplings, and ground flora), the overstory had the greatest delay in observable edge response. In the interior woodland, shade-tolerant and late-successional tree species can recruit and persist in the mid-story. At the edge, early-successional and ruderal species typically dominate as a response to increased light availability (Murcia 1995). Early-successional species at the edge of the tornado swath occurred, but many were stump sprouts, which indicated establishment prior to disturbance (e.g., *Liquidambar styraciflua* L.), based on the number of sapling clumps in proximity to the edge. Studies have quantified EI on response variables as a function of time since edge formation (Harper and Macdonald 2002; Dupuch and Fortin 2013; Harper et al. 2015) and as a function of edge orientation (Chen et al. 1992; Prieto et al. 2014; Dabros et al. 2017), but they have lacked insight on successional trajectories or on how overstory composition responds to edge formation. Overstory response may not be as immediately evident after edge formation compared with understory change, but the overstory will respond to modifications in abiotic conditions at the edge with time since disturbance. We suggest that until saplings in the tornado swath stratify into the canopy, overstory richness and diversity will remain lower compared with the interior.

The tornado-created edge had an influence on vertical complexity as quantified by Shannon height diversity. Height diversity was greatest in the interior woodland, which contained a greater density of trees in subcanopy positions. We recorded more shade-tolerant individuals in the interior woodland (i.e., *Vaccinium arboretum* Marsh., *Cornus florida*) that increased vertical complexity. Managers are increasingly prioritizing structurally complex forests with variability in horizontal and vertical structures. Our results indicated that the edge ecosystems in woodlands are indeed less complex than interior woodlands in terms of live overstory structure. However, no significant EI was recorded on CWM, which is an important characteristic of structurally complex systems (McElhinney et al. 2005). Although the majority of overstory stems were removed in the tornado swath, tree damage also occurred at the edge. Tops of trees were removed, and large limbs

**Fig. 5.** Three-dimensional non-metric multidimensional scaling based on ground flora communities in three clusters (treatments) determined by cluster analysis. Squares represent tornado swath plots, diamonds represent edge plots, and crosses represent interior woodland plots. Polygons (convex hulls) connect plots of the same cluster, and the arrow (biplot) represents strength (length of arrow) and correlations ( $r^2 \geq 0.40$ ) between canopy openness (%) and ordination axes.



were snapped near the edge, which may have caused delayed mortality of trees that survived but were heavily damaged. However, snag density, log volume, and log density all showed no significant EI. One possible explanation for this could be attributed to stochastic gap-scale disturbances, which are commonly caused by pest outbreaks or strong wind events in this region. Although we noted high mortality in the tornado swath and at the edge, canopy gaps in the interior were encountered in field sampling. Canopy gaps form by the death of one or a small cluster of overstory individuals (Runkle 1985) and can occur more frequently in close proximity to forest edges (Camargo and Kapos 1995). We attribute the absence of EI on CWM to stochastic background disturbance in the woodland interior. In fact, snag density increased with greater distance from the edge, likely indicating that snags that occurred on or near the edge were blown down from increased exposure to stronger winds at the edge (Chen et al. 1992). Analysis of CWM by decay class also revealed non-significant EI. However, we did record a greater density of CWM in advanced stages of decay (i.e., DC III and DC IV) in the interior woodland and a greater density of CWM in the less advanced decay classes (i.e., DC I and DC II) at or near the edge (–20 to 20 m). These results may indicate a delayed secondary edge response to the tornado such as snag blowdown at the edge as a result of exposure to higher wind speeds.

#### 4.2. Influence on herbaceous plant communities

In general, EI on ground flora communities was positive, with higher diversity and richness in the tornado swath and at the edge. Although Shannon diversity and cover showed significant but minimal EI, increased herbaceous richness penetrated relatively deep into the interior woodland. High herbaceous richness has been well documented in *P. palustris* woodland ecosystems (Kirkman and Giencke 2017), with Asteraceae, Poaceae, and Fabaceae among the families with the highest number of species. With the addition of disturbance, microhabitats associated with pit-and-mound topography and CWM accumulation increase niche

space for unique species assemblages. Tornado disturbance has been found to increase herbaceous diversity and richness in *P. palustris* woodlands (Kleinman et al. 2017). Our analyses revealed that the ground flora assemblages at the edge of the tornado swath were not statistically different from those of the interior woodland or the tornado swath and were, in fact, influenced by the tornado swath and interior. Although ground flora of the tornado swath was significantly different from that of the interior woodland, it was likely composed of a subset of the overall ground flora community, which included plants well adapted to the microenvironmental conditions of the tornado swath.

The ground flora composition at the edge consisted of a matrix of species that occurred in the tornado swath and in the interior woodland. The NMS graph visually confirmed the transition of ground flora communities from the tornado swath to the interior. Visually, the plots in the tornado swath were less variable in ordination space relative to the interior plots. The high amount of variability in the interior woodland can likely be attributed to (i) woodland understory light availability, (ii) gap-scale disturbance, and (iii) topographic variability. Woodlands allow more light penetration through the relatively open canopy. Gap-scale disturbances were also frequently observed and were hypothesized to be caused by pest outbreaks, evident by clusters of snags, or other stochastic wind events. Gap-scale disturbances inherently allow for greater light penetration into the understory. We also attribute the variability in ground flora communities to topographic variability in the study site (Shankman and Hart 2007). The region is highly dissected as a result of sand formations that support steep slopes (Fenneman 1938). The combination of these three factors contributed to the high variability in ground flora communities observed in the interior woodland.

One particularly notable seedling species that experienced positive EI was *P. palustris* (DEI: 22 m). *Pinus palustris* is known to be a shade-intolerant species (Pecot and Jack 2017). Common to *P. palustris* woodland ecosystems are hardwood midstories that reduce un-

derstory light availability necessary for *P. palustris* seedling establishment. EI on understory light availability was significantly positive, with a greater amount of light able to reach the understory up to 70 m into the interior. Compared with other studies of understory light availability in *P. palustris* woodlands, the interior woodland here had a denser canopy than other Coastal Plain *P. palustris* woodlands (Palik et al. 1997; Brockway and Outcalt 1998; McGuire et al. 2001). The increased light as a result of edge formation likely created an environment conducive to *P. palustris* seedling establishment. Because basal area was significantly reduced in the edge ecosystem at variable distances from the edge, the edge resembled a variable density thinning in which trees were removed in non-uniform patterns. Thinning operations are commonly utilized to improve growing conditions for desirable trees, with increased seedling germination as a possible consequence of decreased overstory density and basal area (Harrington 2011). We contend that the decreased basal area and tree density as a function of EI was similar to a thinning of sufficient intensity to increase favorable conditions for *P. palustris* seedling establishment. The residual individuals that survived the tornado, the majority of which were *P. palustris*, supplied seed for regeneration at the edge and in the tornado swath. Seed dispersal of *P. palustris* has been found to be no more than ca. 33 m from source overstory individuals (Croker and Boyer 1976). The survival of vigorous overstory *P. palustris* in the tornado swath and at the edge allowed seed deposition to occur in favorable conditions for *P. palustris* establishment compared with conditions in the reference woodland. The residual overstory individuals were also effective in producing adequate fuel to ensure the efficacy of fire in the reduction of non-desirable, fire-intolerant saplings. We contend that fire was indeed effective as evidenced by the reduced number of saplings 3 months after fire compared with Kleinman et al. (2017), who noted an abundance of hardwood saplings 3 months after fire. Frequent prescribed fire has also been linked to increased ground flora species richness and diversity in *P. palustris* woodlands (Walker and Silletti 2006).

#### 4.3. EI on woodland structure

EI is a well-documented process with broad ecological applications; however, a paucity of research has quantified EI on temperate woodland structures. To our knowledge, DEI of canopy openness was among the greatest distance recorded in the EI literature. Matlack (1993) suggested that abiotic variables commonly measured to quantify EI such as air temperature and soil moisture were a function of light availability. Understory light availability along the edge-to-interior gradient has been quantified with the use of various methods, but reported maximum DEI estimates of understory light availability have not been found to exceed 40 m (Brothers and Spingarn 1992; Matlack 1993; Gehlhausen et al. 2000; Marchand and Houle 2006). Even with increased understory light availability, we did not note an increase in herbaceous cover and diversity corollary to increased light availability. We attribute this to two potential explanations: (i) the MEI on canopy openness was among the lowest of any quantified biotic or abiotic variable analyzed for EI; and (ii) the increased *Pinus* litter from the edge-to-interior gradient. Although canopy openness was significantly higher from -20 to 70 m compared with the interior woodland, MEI was relatively low from -20 to 70 m (<0.2 MEI) and was well below the mean MEI of canopy openness in the studies reviewed by Harper et al. (2005). An increase in *Pinus* litter also may have inhibited ground flora regeneration and growth (Harrington and Edwards 1999; Barefoot et al. 2019).

Abruptness of created edges is often related to the amount of tree mortality as a consequence of disturbance severity (Franklin et al. 2015). Higher tree mortality in the disturbed area may affect the abruptness of the woodland edge. The structural contrast between the forested and non-forested areas is of a higher magnitude with increased disturbance severity (i.e., more overstory

mortality). The tornado was indeed catastrophic in severity but did not cause complete overstory mortality, which resulted in a ragged edge. The trees that survived within the tornado swath were in closer proximity to the edge than the center of the swath. Therefore, the disturbance area adjacent to the edge more likely resembled intermediate-severity disturbance. Willson et al. (2020) found that increased tornado disturbance severity resulted in greater light penetration lower into the understory. The intermediate-severity disturbance on the periphery of the tornado swath softened the edge and reduced DEI and MEI values (Harper et al. 2005), particularly the MEI on understory light availability. Therefore, the type and severity of natural disturbance may affect edge dynamics as a result of differential patch contrast between the disturbed and undisturbed areas. For example, McIntire and Fortin (2006) found that overstory mortality was greater following severe wildfire (89% overstory mortality) compared with *Dendroctonus ponderosae* Hopkins, 1902 (mountain pine beetle) outbreak (43% overstory mortality), which affected the abruptness of the natural edge, with estimates of DEI and MEI affected by residual overstory individuals. Although overstory mortality in the disturbed area affects the structural attributes of the edge-to-interior gradient, post-disturbance management of the disturbed area also affects the successional pathways of the edge. Chabrierie et al. (2013) found that edges were more abrupt when the non-forested area was intensively managed for agricultural purposes. Our results indicate that MEI will decrease and DEI will increase as saplings and smaller trees recruit into larger size classes in the tornado swath and the overstory begins to stratify.

#### 5. Management implications

For managers who intend to increase ground flora richness and diversity to enhance ecosystem services, results from this study indicate that an entry patterned after the tornado may be conducive to achieve these goals. However, the interior woodland contained more variability in ground flora assemblages relative to the edge and tornado swath. This result can partially be explained by habitat heterogeneity in the interior woodland. Although the edge was influenced by biotic and abiotic conditions from the interior and tornado swath, the interior had the highest ground flora variability because of an abundance of both canopy gaps and low light environments, as well as topographic and microsite variability. The relatively low variability in ground flora assemblages in the tornado swath was likely attributed to the homogenization of conditions such as light availability. If biodiversity enhancement is a management goal, silvicultural entries into woodlands should maximize stand-level habitat heterogenization to increase variability in ground flora communities.

Natural disturbance based silviculture is increasingly implemented to enhance forest diversity and structural complexity and increase resilience to future disturbance. To emulate the patterns of catastrophic tornado disturbance, we recommend variable retention harvesting combined with variable density thinning, which would support *P. palustris* regeneration and establishment and promote compositional and structural diversity with residual overstory individuals. Variable retention harvesting is used to regenerate a new age class and retain structural legacies at variable spatial arrangements for at least one rotation (Mitchell and Beese 2002; O'Hara and Nagel 2013). Variable retention harvesting utilizes aggregate or dispersed spatial patterns for residual trees, based on management objectives. To emulate the patterns of catastrophic tornado disturbance, we recommend dispersed retention of 35–40 canopy trees-ha<sup>-1</sup>. Harvest openings could be configured so that the total area of the edge is minimized, and openings should be 200–275 m wide to mimic the width of the tornado disturbed swath and to ensure that at least half of the total area of the cutblock is within one tree height of retained trees. We also recommend variable density thinning at the edge of

cutblocks to mimic the patterns of negative EI on basal area from the edge-to-interior gradient and thus reduce the magnitude of EI and promote structural heterogeneity in the edge ecosystem. We noted variable reductions in basal area along the edge-to-interior gradient, with significantly less basal area ranging from 10 m to 70 m along transects. To emulate the natural exogenous disturbance patterns, thinning intensity should be variable with distance from the edge, with maximum entry distance of 70 m from the edge of the cutblock into the interior woodland. Based on our findings, we suggest that cutblocks should be spaced at least 300 m apart (from cutblock edge to cutblock edge) to maintain interior woodland conditions that are sufficiently large to support native interior species.

It could also be argued that catastrophic wind events such as tornadoes that do not cause complete overstory mortality create edges that are indeed beneficial to *P. palustris* regeneration. The increased light availability that resulted from the creation of the edge created microenvironmental conditions conducive to *P. palustris* establishment and recruitment. We speculate that EI in this forest type is directly related to the efficacy of prescribed fire to inhibit succession towards non-desirable species. Fire exclusion would likely lead to edge sealing, as hardwood saplings compete for increased light at the edge. Prescribed fire is essential to mitigate detrimental EI and achieve management goals to restore *P. palustris* dominance in the tornado swath. However, the EI on structural complexity and compositional diversity of the overstory was negative. For managers who intend to manage for ecological services such as increasing forest complexity and diversity, edges may initially have a negative influence on composition and structure, as was evident with negative overstory composition and structure metrics 7 years after disturbance. In *P. palustris* woodland ecosystems, we suggest maintaining a 70 m buffer around forest fragments to maintain interior woodland conditions and mitigate potential negative EI.

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