EDGE INFLUENCE ON COMPOSITION AND STRUCTURE

OF A *PINUS PALUSTRIS* WOODLAND FOLLOWING

CATASTROPHIC WIND DISTURBANCE

by

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ABSTRACT

Forest edges are an important legacy of natural and anthropogenic disturbances. Edges of forest fragments are influenced by adjacent non-forested ecosystems, resulting in compositional and structural differences at the edge. Edge influence 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 forest structures, which contain fewer trees ha^{-1} than forests and are typically less light limited. The goal of our study was to examine edge influence of a tornado created edge in a longleaf pine (*Pinus palustris* Mill.) woodland. In 2011, an EF-3 tornado impacted a restored longleaf pine woodland, resulting in a distinct woodland edge. To quantify distance of edge influence into the stand, nine transects were installed perpendicular to the tornado swath, with 11 plots on each transect at variable distances from the edge. Biotic and abiotic response variables were measured at the appropriate spatial scales. To determine the distance of edge influence, the magnitude of edge influence was calculated at each distance, and compared to the reference forest using a non-parametric randomization test. Edge influence on forest structure was negative, with a maximum distance of 70 m. Ground flora richness and diversity experienced a positive edge influence, with higher richness and diversity in the tornado swath and edge, however, ground flora communities at the edge were not compositionally distinct from the tornado swath or the interior. Results of this study add to our understanding of edge influence on woodland forest structure and naturally created edges.

LIST OF ABBREVIATIONS AND SYMBOLS

°C   Celsius

cm   centimeter

CWD   coarse woody debris

dbh   diameter at breast height

DEI   distance of edge influence

DEM   digital elevation model

EF   enhanced fujita

EI   edge influence

GC   gini coefficient

$H´$ Shannon diversity

ha   hectare

ISA   indicator species analysis

m   meter

M_i mingling index

MEI   magnitude of edge influence

n   sample size

NCVS North Carolina vegetation survey

NMS   non-metric multi-dimensional scaling

p   Probability of occurrence under the null hypothesis of obtaining a value as extreme or more extreme than the observed value

r^2 pearson correlation coefficient

RTEI   randomization test of edge influence

SE   standard error

sp.   species

USDA   United States Department of Agriculture

USGS   United States Geological Survey

%   percent

±   plus or minus

=   equal to

>   greater than

≥   greater than or equal to

<   less than

≤   less than or equal to

*   statistically significant at $p < 0.01$

ACKNOWLEDGEMENTS

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1. INTRODUCTION

1.1 Forest edge influence

Forest edges in fragmented landscapes are becoming increasingly abundant as a result of anthropogenic and natural disturbance. Edges of forest fragments are influenced by adjacent non-forested ecosystems, resulting in compositional and structural differences along a gradient from the edge to the interior of forest fragments (Harper *et al.* 2005). Edge influence (EI) is the manifestation of biotic and abiotic interactions between ecosystems separated by an sharp gradient following natural or anthropogenic disturbance (Murcia 1995). This transition results in detectable forest compositional, structural, and functional difference between the two adjacent ecosystems (Matlack 1993). The effects of the interactions between the intact forest and the adjacent non-forested ecosystem following disturbance can be classified into three types of edge influence: direct biotic effects, indirect biotic effects, and abiotic effects (Murcia 1995). Direct biotic effects include altered species composition, abundance, and structure. Indirect biotic effects include altered species interactions, parasitism, and herbivory. Abiotic effects result altered in environmental conditions such as light structure and soil temperature.

Edge ecosystems can be advantageous or deleterious for land managers, depending on the desired forest conditions. Although edge ecosystems may be more species rich than interior forests, edges may be more susceptible to exotic species invasions, density dependent mortality, and parasitism (Matlack 1994, Fraver 1994, Yates et al. 2004, Joshi et al. 2015).   These conditions are facilitated by altered microenvironmental dynamics of forest edges, which may include increased light availability, lower soil and litter moisture, and higher wind speeds

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(Brothers and Springarn 1992, Young and Mitchell 1994). Indeed, changes in microenvironmental conditions at the forest edge may favor unique plant communities not found in the interior forest (Noss and Cooperrider 1994). For example, increased light availability at the edge, which diminishes with distance from the edge, may favor early successional species not found in the interior (Fraver 1994). Also, trees growing along the forest edge are often more vulnerable to wind damage relative to trees in forest interior positions (Chen *et al.* 1992). Common plant response to environmental changes at the edge include increased presence of exotic species (Fraver 1994), increased species diversity and/or richness (Marchand and Houle 2006), and increased sapling and tree density (Palik and Murphy 1990, Chen *et al.* 1992, Landenberger and Ostergren 2002). Edge orientation may be a factor in the distance of edge influence, with south facing slopes typically having a greater distance of penetration of edge influence on plant communities than north facing slopes in the northern hemisphere outside the tropics (Palik and Murphy 1990).

Successional and development pathways of the edge ecosystem may differ between intact forest and adjacent non-forested ecosystem as a result of altered microclimatic conditions and resource availability (Murcia 1995). Edge influence is often measured by distance (the penetration of edge influence into the interior forest), and magnitude (the steepness of the environmental gradient at the edge) (Harper and McDonald 2005). Edge influence on plant composition and structure is influenced by multiple interacting factors. An important determinant of distance of edge influence may be the canopy structure of the dominant overstory individuals and edge type. For example, distance of edge influence was greater in a mixed-wood boreal forest (Harper and McDonald 2002) than in a mixed-mesophytic hardwood forest (Matlack 1994). The contrast in forest composition and structure between the adjacent disturbed and

undisturbed forest influences the magnitude and distance of edge influence. Depending on the edge type, the contrast between undisturbed and disturbed forest will be reduced or enhanced, resulting in edge softening or expansion (Matlack 1994, Harper and McDonald 2005). Three different measures of edge development include edge sealing, softening, and expansion. Edge sealing commonly occurs at maintained edges (i.e. agricultural), resulting in decreased distance of edge influence and increased magnitude of edge influence. Edge expansion occurs on unmaintained edges, resulting in increased distance and decreased magnitude.

Forest habitat fragmentation is often considered deleterious for maintenance of historical species assemblages in forest fragments (Santo-Silva *et al.* 2016). Forest fragmentation is a product of natural or anthropogenic disturbance, resulting in isolated patches of forest. Residual fragment size must be large enough to support native plant communities and mitigate negative edge influence (Laurence *et al.* 1998). Although forest edges may increase the structural complexity and compositional diversity of forests at a landscape scale, small forest fragments may result in the exclusion of species native to the interior forest by invading edge influence. Guidelines to mitigate edge influence and conserve native species assemblages are based on forest type, edge type, and fragment size and shape (Murcia 1995, Laurence *et al.* 1998). For example, in tropical forests, minimum residual fragment size was found to be 100–400 ha to conserve native plant species assemblages in interior forest (Laurence *et al.* 1998).

Edge influence 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. Edge influence 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 research of edge influence on woodland

composition and structure, and more specifically, edges created by catastrophic tornado disturbance.

1.2 Natural disturbance

Natural disturbances alter the composition and structure of forest ecosystems and thereby, influence successional and developmental pathways (White and Picket 1985, Oliver and Larson 1996, Hart and Cox 2017). Disturbances vary widely, but are most often classified based on size, severity, and frequency and range from frequent, gap-scale events to infrequent, catastrophic events (Oliver and Larson 1996). Second to fire, wind disturbance is the most widespread disturbance agent in terrestrial ecosystems and is arguably the most prevalent disturbance agent in forests of eastern North America (MacDonald 2003, Peterson *et al.* 2016). Tornadoes are capable of producing the fastest wind speeds in nature, and occur approximately 1,250 times per year in the U.S. (National Weather Service 2018). However, tornado severity and width 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 along their path, which influences overstory removal in forest ecosystems (Bech et al. 2009, Cannon et al. 2016, Peterson et al. 2016). Tornadoes have also been found to disproportionally uproot or snap certain overstory species (Shirakura et al. 2006). On 27 April 2011, an EF-3 tornado directly multiple fire- restored *Pinus palustris* stands in the Oakmulgee Ranger District of the Talladega National Forest, Alabama, USA (NWS 2011). The tornado had a total path length of 116 km, a maximum path width of 1.6 km, and produced wind speeds up to 233 km/h (NWS 2011). This storm provided an opportunity to assess the edge influence on unaffected interior forest.

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1.3 Research significance

Other studies have assessed herbaceous plant response (Kleinman *et al.* 2017, Kleinman et al. 2018) and macrofungal response (Ford *et al.* 2018) to catastrophic wind disturbance in *P. palutris* woodlands. However, no research has quantified the edge influence on structure and composition following a catastrophic tornado in woodlands. The results of this study will fill a void in the literature of edge influence in woodlands following tornado disturbance. Most research has focused on EI on forests, which typically contain more trees ha^{-1} and are more light limited than woodlands. As more forests are converted to woodlands, it is important to understand the influence of edges on woodland composition and structure. Similarly, the majority of edge research has focused on anthropogenic edges, such as clear cut and agricultural edges. Naturally created edges, such as those created by tornados are often less linear than anthropogenic edges. Because tornados do not uniformly remove overstory individuals, these edges may differentially influence undisturbed woodlands.

The distance of edge influence will aid in the understanding of the ecological effects of forest fragmentation in *P. palustris* woodlands. The area of residual forest fragments should be large enough to accommodate historical species assemblages in *P. palustris* woodland without significant edge influence (Murcia 1995). Many studies have recommended guidelines for minimum fragment size to maintain interior species and prevent migration of edge influence on the interior forest (see Laurence *et al.* 1998). Results from this study will offer guidelines for residual forest fragment size to reduce the loss of historical species assemblages in the interior forest by invading edge influence.

1.4 Objectives and hypotheses

The overarching goal of this study is to examine edge influence on woodland composition and structure following a catastrophic wind event. The specific objectives of this study are to (1) quantify the plant species composition and diversity, and the structural complexity of a *P. palustris* woodland from the edge of a tornado path to the interior forest, (2) determine the relationship between direct and indirect biotic and abiotic ecological processes in response to edge influence, and (3) determine the distance of edge influence (the width of the edge ecosystem) caused by the disturbance event.

We hypothesize that sapling and herbaceous diversity will decrease with increasing distance from the edge. Kleinman *et al.* (2017) found that sapling diversity was greater on tornado disturbed sites compared to the interior forest. The sapling and herbaceous species composition of the edge ecosystem will likely be a matrix of advanced regeneration from the tornado disturbed forest and the low sapling diversity from the interior forest. We also hypothesize that overstory structural complexity will decrease with increasing distance from the edge. Structurally complex forests are commonly defined by continuous vertical distribution of foliage, an abundance of stems with variable diameters at breast height (dbh), crown classes and heights, an abundance of coarse woody debris (CWD) in varying stages of decay, and compositionally diverse understory, midstory, and overstory (McElhinny, 2005). The edge of the tornado path should be composed of CWD of variable modes of death (snapped, uprooted, snag) and decay classes. The edge should also be composed of remnant trees unaffected, but possibly damaged by the tornado with varying dbh and height. We hypothesize that canopy openness will decrease with increasing distance from the edge. The variability of microenvironmental conditions from the edge to the interior forest may be conducive habitat for species not found in

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the interior forest (Noss and Cooperrider 1994). Increased light availability may result in a higher abundance of early successional species closer to the edge.

1.5 Study site

This study was conducted in the Oakmulgee Ranger District of the Talladega National Forest in west-central Alabama. The Oakmulgee Ranger District is situated in the Fall Line Hills (Fenneman 1938), a transition zone between Coastal Plains and Appalachians 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 formation. The Coker formation is primarily 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 quart pebbles (Szabo 1988). Soils in the study area are classified in the Maubila-Smithdale complex, which are deep and moderately well drained. (USDA NRCS 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 by the Kaul Lumber Company, and acquired by the USDA Forest Service in 1935 (Reed 1905, Cox and Hart 2015). Prior to European settlement, the Native Americans inhabited areas around the Black Warrior River, located to the north and west of the study site. Moundville, a social and political center of the Mississippian Indians until 1700, is located 13 km from the border of the Oakmulgee Ranger District (Maxham 2000). The Oakmulgee Ranger District is managed for re-introduction of *P. palustris* to suitable sites currently dominated by *Pinus taeda* and xeric hardwood species (USDA Forest Service 2005).

Management for *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 2–5-year rotation (USDA Forest Service 2005).

Pinus palustris ecosystems are among the most ecologically threatened ecosystems in the United States (Noss et al. 1995), occupying less than 1 million ha of its former 37 million ha range (Jose *et al.*, 2007). The ecosystem is dominated by *P. palustris* in the canopy with an open midstory and a diverse herbaceous layer (Frost 2007). Fire is the most common disturbance agent in *P. palustris* woodlands, and is required for restoration of historical species assemblages and structure (Van Lear *et al.* 2005). Restoration and maintenance of *P. palustris* woodlands requires frequent low-intensity surface fires, which promote natural regeneration of *P. palustris* by reducing inter-specific competition and exposing bare mineral soil for seeds to germinate (Platt et al.1988). The *P. palustris* ecosystem is also known for its high faunal diversity, with a higher richness of turtles, frogs, and snakes than most other forest types in North America (Keister 1971).

The climate of the region is classified as humid mesothermal, with long, hot summers and short, mild winters (Thornthwaite 1948). Mean annual temperature is 17.4 °C with the lowest monthly mean of 7.2 °C in January and highest 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 in October (70.1 mm) (PRISM 2017).

2. METHODS

2.1 Transect locations and installation

Georeferenced stand and compartment shapefiles were acquired from the USDA Forest

Service and uploaded to ArcMap v. 10.3. Aerial imagery from June 2011 was used to determine

the location of the Sawyerville-Eoline EF-3 tornado in the Oakmulgee Ranger District using

Google Earth Pro. The edge was determined by visually locating the start of continual canopy at

the edge of the tornado swath, disregarding residual trees that were not killed by the tornado, but

which were evident within the tornado swath. Aerial imagery and ground reconnaissance

confirmed that the tornado did not remove all overstory individuals along the track. A polygon of

the tornado swath was created to locate suitable edge for sampling. To determine suitable

topographic location for sampling, a 1/3 arc second digital elevation model (DEM) was

downloaded from the USGS National Map database (US Geological Survey, 2018). The DEM

raster file was reclassified to produce locations with elevations > 110 m. Contour lines were also

produced from the DEM raster file. The ArcMap document, which contained the tornado swath

polygon, USFS compartments and stands, contour lines, and roads was used to determine

suitable sampling locations. Based on laboratory reconnaissance, a compartment was selected

that contained the most edge habitat. The Oakmulgee Ranger District utilizes prescribed fire as a

silvicultural tool at the compartment scale, and thus a single compartment was selected that was

most recently treated with prescribed fire in April 2018. Twenty potential transect locations were

located based on the selection criteria and the locations were uploaded as data points to the

ArcPad application on a Trimble Juno T-41/5 data collector (Trimble Navigation Limited, 2017).

In the field, potential sampling points were located and confirmed to be situated at the

edge of the tornado swath. Selection criteria were based on laboratory reconnaissance (on the

Trimble data collector), continual canopy cover into the interior woodland (confirmed by the

aerial imagery and in the field), and the location in which uprooted trees no longer occurred as a

result of the tornado. Although laboratory reconnaissance indicated 20 possible sampling

locations, nine were utilized for data collection. Following the tornado, a salvage harvesting

operation occurred to mitigate the risks of potential hazards associated with the abundance of

dead trees, and to reclaim economic losses. The remaining 11 potential sampling locations were

determined to be unsuitable because of evidence of salvage harvesting and/or topographic

variability into the interior woodland that might bias results.

To quantify edge influence on woodland composition and structure, nine vegetation

sampling transects were established with eleven 10×10m plots at set distances from the edge

installed along each transect (**Figure 1**). Transects were installed perpendicular to the edge into

the interior woodland. 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). Species-

area curves were produced for the ground flora and overstory strata to determine if sampling area

was an adequate representation of the plant communities in this study. Sampling area was

determined to be an adequate representation of plant communities at 60 sample units.

Furthermore, sampling distance from the edge into the tornado swath

(-20 – 0 m) was representative of plant communities in the tornado swath. In an ongoing study (unpublished data), ground flora taxa were identified in the same tornado swath. Of the 113 taxa identified in the ongoing study, we documented a 79% overlap in identified taxa (89/113). 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. Plots along transects were established using ground tapes and sighting compasses.
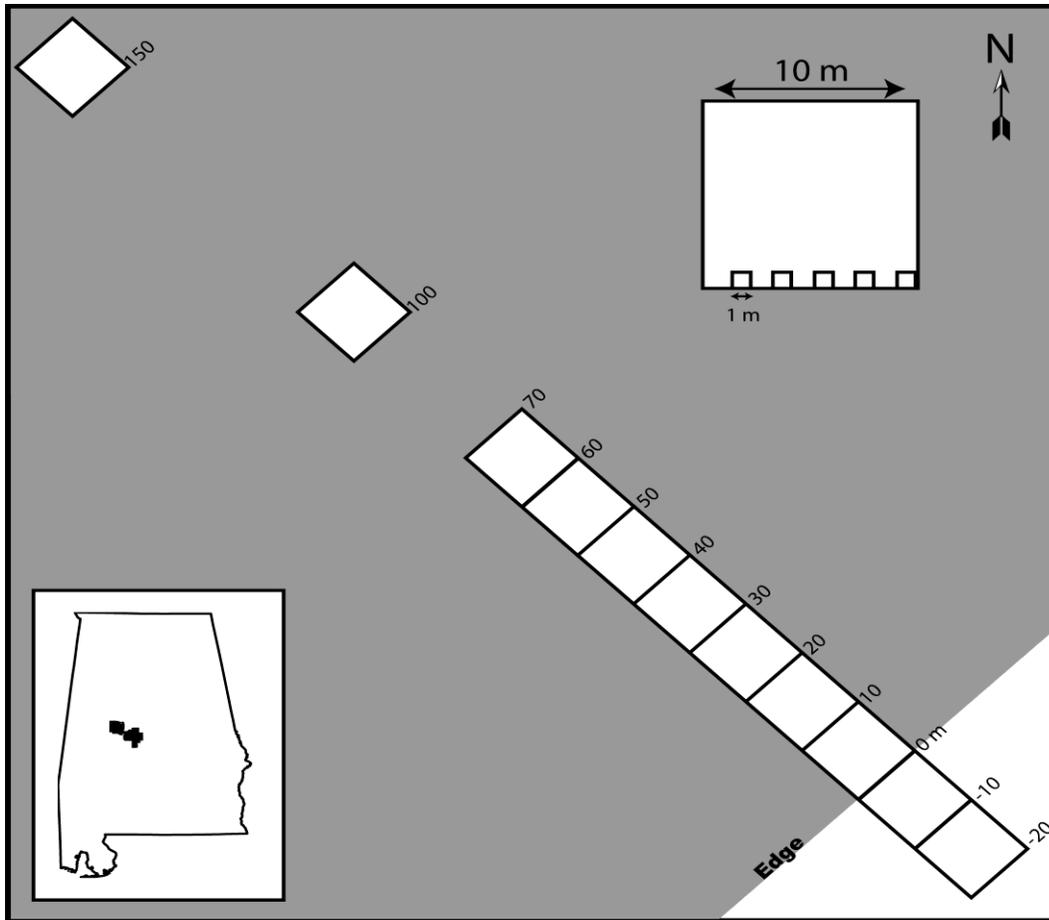
Figure 1. Sampling design and transect installation to quantify edge influence in the Oakmulgee Ranger District of the Talladega National Forest, Bibb County, AL. Overstory, saplings, and abiotic variables were measured in 10 × 10 m plots. Ground flora and ground surface substrate were measured in each 1 × 1 m quadrat.

2.2 Field methods

To quantify woodland composition and structure from the edge-to-interior gradient, trees, coarse woody debris, saplings, and light structure were sampled in each 10 × 10 m plot. Trees were defined as live woody stems ≥ 5 cm at 1.37 m above the root collar (diameter at breast height, dbh), and 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) based on canopy height and amount of intercepted light relative to adjacent trees. Trees

were also mapped to calculate spatially implicit structural and compositional metrics by measuring the distance and azimuth to each tree from the same corner of each plot using a sighting compass and Haglöf hypsometer. Saplings were defined as live woody stems < 5 cm dbh and $\geq$ 1 m height, and were identified to species and tallied for abundance. Coarse woody debris was defined as non-living upright or downed woody stems $\geq$ 10 cm diameter. 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 ($m^2\,ha^{-1}$). Logs were measured for diameter and both ends and length. Uprooted stems were measured for dbh (1.37 m above root collar) and length. If logs or uprooted stems crossed plot boundaries, measurements were taken at the location in which the individual crossed plot boundary line. Volume ($m^3\,ha^{-1}$) was calculated for logs with the equation for a conic paraboloid (Fraver et al. 2007) and was calculated for uprooted stems with species-specific allometric equations (Woodall et al. 2011). All CWD was assigned a decay class from I to V based on level of decay (FIA 2005), with I being least decayed and V being most decayed. To quantify light structure from the edge-to-interior gradient, one hemispherical canopy photograph was taken at the center of each 10×10 m plot using a fish eye lens fitted on an Olympus Stylus TG-3 digital camera mounted on a self-leveling tripod at 1.4 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 during overcast conditions to reduce glare for image analysis.

Ground flora (herbaceous and woody plants < 1 m height) and ground surface substrate were sampled in five 1×1 m nested quadrats within each 10×10 m plot (55 quadrats transect^{-1}).

Ground flora was identified to the lowest taxonomical 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 was assigned a value from 1 to 10 using the North Carolina Vegetation Survey (NCVS), where 1 = solitary or few, 2=0–1%, 3 = 1–2%, 4 = 2-5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100% (Peet et. al 1998). Ground surface substrate was categorized by cover type (adapted from USDA 2016, Wentworth 1922), and assigned a percent cover using NCVS cover classes. Ground substrate included fine woody debris (< 10 cm diameter, detached from CWD), *Pinus* litter (dead, non-woody material), non-*pinus* litter, bare ground, moss, gravel (sediment, < 6.4 cm diameter), and rock (sediment > 6.4 cm diameter).

2.3 Analytical methods

To quantify the edge influence following the tornado, EI was divided into two types: biotic and abiotic. Edge influence on biotic communities included living plants divided into three woodland strata: overstory (trees), midstory (saplings), and understory (ground flora). Edge influence on abiotic factors included coarse woody debris, light structure, and ground surface substrate. To quantify edge influence on plant communities, compositional diversity and structural complexity metrics were calculated for the three woodland strata at each distance from the edge. All metrics were calculated at the 10×10 m plot level for trees and saplings, and at the 1×1 quadrat level for ground flora.

Overstory compositional diversity metrics calculated included species richness, evenness, Shannon diversity (H') and the mingling index. The mingling index (Pommerening 2002) indicates the degree of species intermingling by comparing a reference tree to its four nearest neighbors on a scale of 0–1. A value of 0 indicates the four nearest neighbors are the same species as the reference tree. A value of 1 indicates the four nearest neighbors are different species (Aguire et al. 2003). The mingling index was calculated in R v. 3.5.1 using the Mingling function in the "spatstat" package (Baddeley et al. 2015). Overstory structural metrics calculated included basal area (m^2 plot^{-1}), tree density (number of stems plot^{-1}), quadratic mean diameter, Shannon height diversity, and the Gini coefficient (Gini 1912). Shannon diversity of tree height describes the vertical complexity of the overstory, with higher values indicating more vertical complexity. Shannon height diversity requires trees heights to be placed into classes (Staudhammer and Lemay 2001). Tree heights were placed into 1 m classes to best differentiate between smaller height differences. The Gini coefficient (GC) describes the spatial distribution of the basal area on a scale of 0–1. A GC of 1 indicated the basal area of stems is evenly distributed, and a GC of 0 indicates and uneven distribution (Matlack *et al.* 1994, Cox *et al.* 2016). The GC was calculated using the inequality package in R v. 3.5.1 (Zeileis 2014)

For the sapling stratum, density (number of stems plot^{-1}), 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), and further divided by taxonomical groups and growth habits for analysis. Percent cover, H', and richness for all ground flora were calculated. Seedling density (number of stems quadrat^{-1}) was calculated for all seedlings, *Pinus palustris* seedings, and *Quercus* seedlings. All ground flora was grouped into one of five life form categories using the USDA plant classification (https://plants.usda.gov/java/, accessed

October 2018) to determine EI on ground flora based on growth habit. Categories included forbs, graminoids, vines, shrubs, and trees. Shrubs and trees were categorized based on *in situ* observation of species growth habits. Taxa that occurred in greater than 10% of all quadrats were individually assessed for edge influence.

To quantify edge influence on abiotic factors, variables were calculated to describe changes in deadwood structure, light structure, and ground surface substrate cover. Coarse woody debris metrics calculated included volume (m^3 $plot^{-1}$), and density (number of pieces $plot^{-1}$) further divided by species and decay class. To describe light structure, canopy openness $plot^{-1}$ (%) was determined using the software WinSCANOPY. The software classifies individual pixels in each canopy photograph as canopy or sky. Canopy openness is quantified as the number of pixels unobstructed by vegetation while accounting for angular distortion from the fisheye lens. To quantify changes in ground substrate cover, the percent cover of each cover type was determined for each 1×1 m quadrat and utilized for statistical analysis. The cover types analyzed for EI included *Pinus* litter, non-*Pinus* litter, fine woody debris, and bare mineral soil. The remaining cover types were likely not affected by edge formation, because they were likely present prior to disturbance (i.e. rocks and gravel) or were previously quantified (CWD).

Once all biotic and abiotic variables were calculated, a non-parametric randomization test of edge influence (RTEI, Harper and McDonald 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 different distances from the edge. MEI standardizes edge influence across variables and among different scales of measurement. Positive MEI values indicate higher values at the edge, and negative MEI values indicate lower values at the edge. For example, if basal area showed a negative MEI, basal area was reduced at

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the edge compared to the reference forest. When MEI is tested at each distance from the edge, DEI is estimated by a set of distances in which MEI is significantly different than 0 (reference forest). The RTEI used 1000 permutations for a confidence level of 95% (p < 0.05) as recommend by Harper and McDonald (2011). RTEI was used for the determination of DEI and MEI for all biotic and abiotic metrics. A 95% confidence interval (p < 0.05) was used for all statistical analysis, unless otherwise noted.

To visualize and characterize differences in ground flora cover from the edge-to-interior gradient, cluster analysis, non-metric multidimensional scaling (NMS) ordination, multi-response permutation procedure (MRPP, Mielke and Berry 2001), and indicator species analysis (ISA, Dufrene and Legendre 1997) 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 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 – 0 m (hereafter swath), 0 – 20 m (hereafter edge), and 30 – 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 seven environmental variables: (1) live tree density (stems plot^{-1}), (2) sapling density (stems plot^{-1}), (3) canopy openness (%), (4) CWD volume (m^3 plot^{-1}), (5) *pinus* litter cover (%), (6) bare ground cover (%), and (7) other litter cover (%). Plot level NCVS cover values in the main matrix were relativized by maximum to account for taxa with large growth form. 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 was 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 difference in ground flora cover between clusters, an MRPP was conducted. A post-hoc pairwise comparison was used to determine significant difference in ground flora communities between clusters. ISA was used to compare average relative frequency and abundance of each unique taxon per cluster to identify taxa strongly associated with swath, edge, and interior plots. Constrained seriation with Monte Carlo simulation was used to visualize changes in ground flora taxa along the edge-to-interior gradient. This method freezes columns (distance from the edge) and allows rows (species) to move until the best diagonal representation of species is achieved (MacQuarrie and Lacroix 2003).

3. RESULTS

3.1 EI on overstory composition

Overall, edge influence on overstory composition was minimal but significant, with maximum edge influence of 10 m into the interior woodland. Of the 23 unique overstory taxa. *Pinus palutris* occurred on 62% of plots, and *Pinus taeda* occurred on 42% of plots. Eight unique *Quercus* spp., three unique *Pinus* spp., and two unique *Carya* spp. were recorded. Mean overstory species richness ranged from 1.0 ± 1.0 (SE) in the tornado swath to 3.4 ± 1.0 in the

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interior woodland. Overstory species richness experienced a significantly negative edge influence. Species richness was significantly reduced from the tornado swath to 10 m into the interior woodland (**Figure 2**). Magnitude of edge influence on overstory species richness was negative up to the 150 m plot, indicating that all plots had a reduced species richness when compared to the interior plot. However, only significant reductions in species richness were documented up to 10 m into the interior woodland (**Figure 2**). A similar, but stronger edge influence was documented on overstory H'. Mean overstory H´ was 0.301 ± 0.358 (SE) for the tornado swath and increased to 1.00 ± 0.397 (SE) into the interior woodland (**Figure 3**). MEI on overstory H' was negative, indicating H' was reduced at all distances. However, only a significant MEI was recorded from -20–10 m into the interior woodland (**Table 1**). Overstory mingling index (M_i) ranged from 0.28 ± 0.39 (SE) to 0.77 ± 0.31 (SE). The highest mingling index was recorded at a distance of 30 m into the woodland. No discernable pattern of Mi was recorded from the edge-to-interior gradient. The M_i was lower in the tornado swath, increasing from 30–60 m, and decreased in the interior woodland. *Pinus palustris* had the lowest mean M_i of 0.32, indicating that approximately 70% of the four nearest neighbors of *P. palustris* were of the same species. *Liriodendrum tilipifera* also had relatively low M_i value of 0.38. The remaining 21 species each had M_i values greater than 0.60. *Quercus* and *Carya* spp. had a mean M_i of 0.93, indicating these species were highly interspersed among other species. No significant edge influence on species mingling was documented.
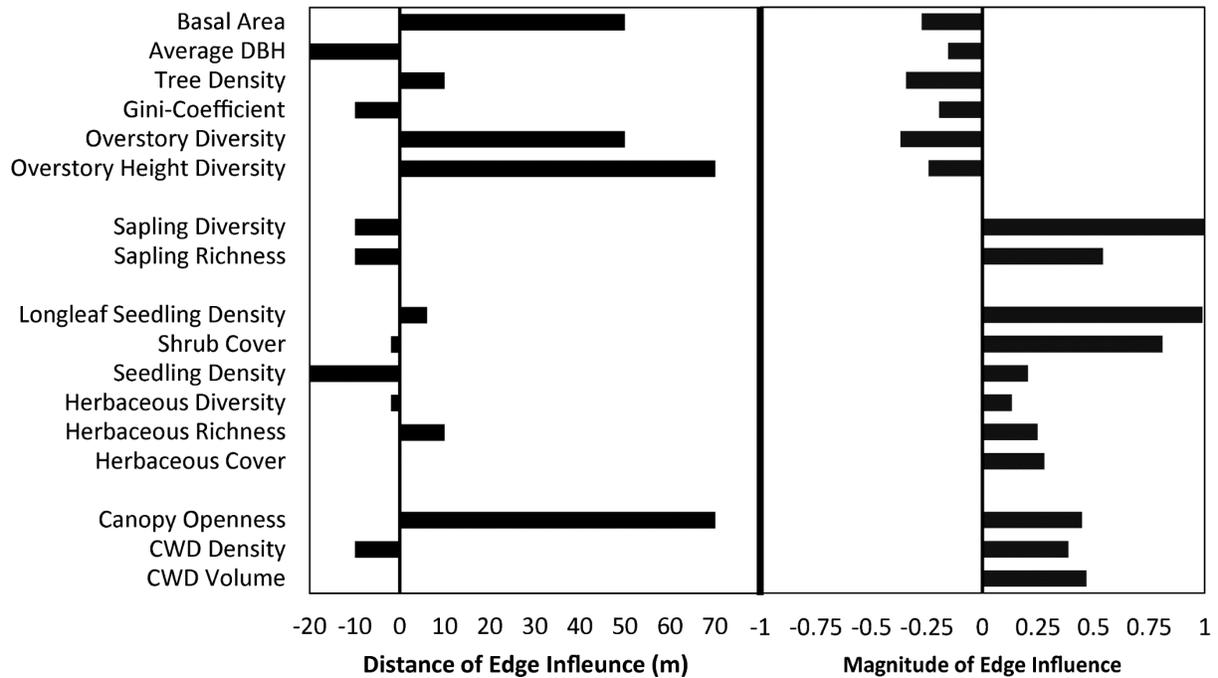
Figure 2. Distance of edge influence (DEI) and magnitude of edge influence (MEI) of calculated response variables. Positive MEI indicated significantly higher values at the edge, and negative MEI indicated significantly lower values at the edge. DBH is measured diameter 1.4 m above root collar. CWD is coarse woody debris.

3.2 EI on overstory structure

Overall, edge influence showed great variability on woodland structure, with DEI estimates ranging from 0–70 m into the interior woodland (**Table 1**). No edge influence was documented on mean tree diameter. Mean dbh was 13.9 ± 15.82 cm in the tornado swath (-20–0 m) and 19.0 ± 5.6 cm in the interior woodland (150 m). Edge influence on basal area was significantly negative, with reduced basal area occurring from -20–10 m and from 40–70 m (**Figure 2**). From 10–40 m, MEI on basal area was negative, but DEI was not significant (p > 0.05). MEI was higher in the tornado swath (-0.71 and -0.51) than from 40–70 m (mean MEI -0.23), indicating that the edge influence was more abrupt closer to the tornado swath (**Table 1**). Tree density experienced a similar significant DEI from -20–10 m but was not significantly reduced from 40–70 meters as was basal area. We documented a mean of 2.0 ± 1.9 (SE) trees plot^{-1} in the tornado swath, and 9.5 ± 4.2 trees plot^{-1} in the interior woodland. The distribution of basal area as quantified by the Gini coefficient showed no significant DEI. However, the tornado swath plots were found to have a significantly reduced GC (DEI -20 – 0 m). Edge influence on overstory height H´ showed the greatest sustained DEI of any structural variable. Overstory height H´ was significantly lower from -20–70 m compared to the interior woodland (**Figure 3**).

Table 1. Significant (p < 0.05) magnitude of edge influence (MEI) with distance from the edge. The edge is represented by the dashed line (0 m).

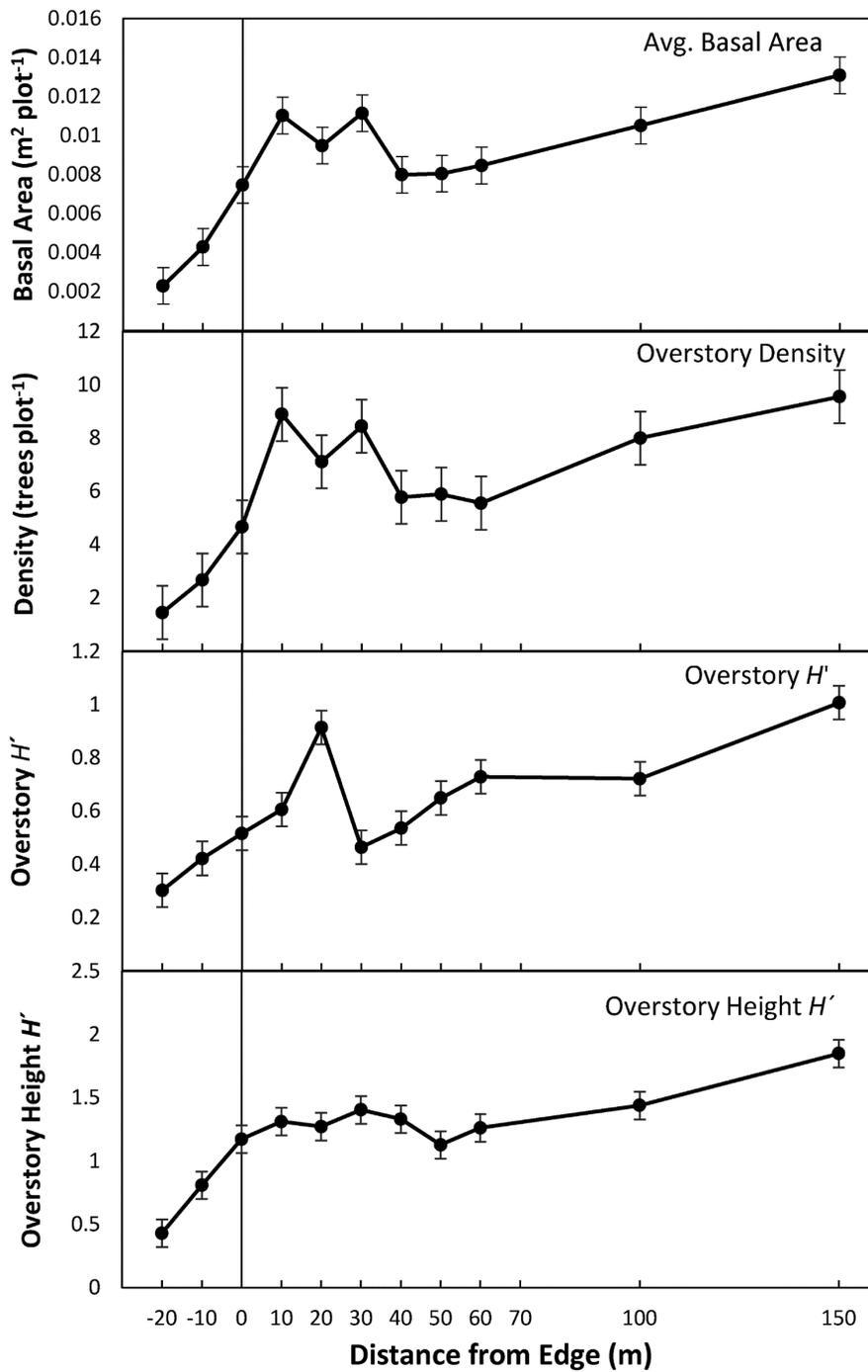| Distance (m)	Sapling Density	Sapling Richness	CWD Density	CWD Volume	Gini Coefficient	Overstory Diversity	Overstory richness	Basal Area	Overstory Density	Height Diversity	Canopy Openness
-20 - 10	0.542	0.897	0.386	0.467	-0.216	-0.539	-0.550	-0.703	-0.737	-0.623	0.446
-10 - 0				0.334	-0.231	-0.410	-0.348	-0.508	-0.564	-0.391	0.361
0 - 10						-0.323	-0.265	-0.274	-0.344	-0.224	0.270
10 - 20										-0.170	0.232
20 - 30										-0.185	0.193
30 - 40										-0.137	0.188
40 - 50								-0.242		-0.163	0.149
50 - 60								-0.239		-0.243	0.181
60 - 70								-0.215		-0.189	0.113
100 - 110											
150 - 160											

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

3.3 EI on saplings

We documented 185 saplings ha^{-1} and a sapling species richness of 24. *Pinus palustris*

had the highest relative density with 24.0% of saplings. *Quercus falcata* had the second highest

relative density with 12.5%. The *Quercus* genus had eight unique species recorded in the sapling

layer, with 29% of saplings belonging to this genus. Interpretation of descriptive statistics

revealed that the majority of *Pinus palutris* saplings (90%) occurred at distances ≥ 20 m from the

edge into the interior woodland. In contrast, the majority of *Quercus* saplings (86%) occurred

from -20 – 10 m into the woodland. *Rhus copallinum* also frequently occurred in the disturbed

plots (-20 – 0m).

RTEI results revealed non-significant DEI and MEI on sapling composition (**Table 1**).

Edge influence on sapling density was significantly positive only at the distance of -20 m from

the edge (20 m into the tornado swath). Edge influence on sapling richness and diversity

exhibited a similar DEI. Both richness and diversity were significantly positive at -20 m from the

edge. MEI values for both sapling richness and diversity were among the highest calculated for

all biotic and abiotic variables (**Table 1**). MEI was calculated at 0.9 for sapling richness and 1.0

for sapling diversity at -20 m from the edge. High MEI values indicate a high disparity between

sapling communities in the tornado swath and sapling communities in the interior woodland.

However, sapling composition at the edge was not significantly distinct from the interior

woodland.

3.4 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 (**Table 2**). Excluding grasses (*Poaceae*), *Gelsemium sempervirens*

(vine) was the most abundant species (found in 54% of quadrats), followed by the shrubs *Rhus coppalinum* (49% of quadrats) and *Vaccinium arboreum* (39% of quadrats). The highest species richness in any 1 m^2 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. For example, 1 m^2 quadrats with species richness $\geq$ 15 most commonly occurred at distances of -20 – 30 m. RTEI results revealed significantly positive edge influence on ground flora species richness (**Figure 4**). Ground flora richness was significantly greater at distances of -20 – 16 m when compared to the interior woodland. Ground flora H´ showed a similar trend along the edge-to-interior gradient, with significant positive edge influence occurring from -20 – 2 m into the interior. Ground flora richness averaged 9.6 species quadrat $^{-1}$ in the tornado swath and edge (as determined by RTEI), and richness averaged 6.7 species quadrat^{-1} in the interior woodland. Although DEI was significant, MEI on ground flora richness and diversity was relatively low compared to other biotic and abiotic response variables.

Table 2. Constrained seriation for all herbaceous taxa (non-woody plants < 1 m height) observed, with columns representing distance from the edge (m). An "x" represents presence at given distance. Asterisks indicate indicator species of the tornado swath.

Species	-20	-10	0	10	20	30	40	50	60	100	150
Coreopsis auriculata L.	x										
Sanicula canadensis L.	x										
Angelica venenosa (Greenway) Fernald	x										
Magnolia acuminata (L.) L.	x										
Pycnanthemum albescens Torrey & A. Gray	x										
Aurerolaria pectinata (Nutt.) Pennell	x										
Gamochaeta argyrinea G.L. Nesom		x	x								
Sericocarpus linifolius (L.) Britton, Sterns & Poggenb	x		x								
Lobelia cardinalis L.		x									
Ambrosia artemisiifolia L.		x									
Chrysopsis mariana (L.) Elliot		x									
Passiflora lutea L.		x									
Lespedeza virginica (L.) Britton	x		x								
Crotalaria sagittalis L.		x									
Hieracium gronovii L.		x									
Chamaecrista fasciculata (Michx.) Greene	x			x							
Desmodium Desv.	x	x	x	x							
Houstonia caerulea L.	x	x	x		x						
Rudbeckia hirta L.			x	x							
Conyza canadensis (L.) Cronquist *	x	x		x			x				
Lespedeza hirta (L.) Hornem *	x	x	x					x			
Lactuca canadensis L.	x	x	x		x			x			
Elephantopus tomentosus L.	x		x	x	x			x			
Ipomoea pandurata (L.) G. Mey	x	x	x		x						x
Conoclinium coelestinum (L.) DC.	x		x	x						x	
Lespedeza repens (L.) W.P.C Barton	x	x	x	x	x	x			x	x	
Lespedeza violacea (L.) Pers.	x		x								x
Eupatorium album L.		x		x					x		
Liatris Gaertn. Ex Shreb.				x		x					
Lespedeza procumbens Michx.		x				x	x				
Coreopsis major Walter	x	x	x	x	x	x	x	x		x	
Eupatorium rotundifolium L. *	x	x	x	x		x	x	x		x	
Desmodium rotundifolium DC.	x	x	x	x	x					x	x
Parthenocissus quinquefolia (L.) Planch	x	x	x	x	x	x	x	x			x
Clitoria mariana L.	x	x	x	x	x	x	x		x	x	

Species	1	2	3	4	5	6	7	8	9	10	11
Cnidoscolus urens (L.) Arthur var stimulosus (Michx.) Govaerts	x			x		x	x				
Calystegia catesbeiana Pursh	x	x		x		x	x	x			
Solidago altissima L. *	x	x	x	x	x		x			x	x
Solidago odora Aiton	x	x	x	x	x	x	x	x	x	x	
Physalis L.	x	x		x		x	x				x
Hexasylis arifolia (Michx.) Small	x									x	
Helianthus hirsutus Raf.				x		x					
Aristolochia serpentaria L.	x	x		x	x		x	x	x		
Mimosa microphylla Dryand.		x	x	x				x	x		
Symphyotrichum Nees *	x	x	x	x	x		x	x		x	x
Pityopsis graminifolia (Michx.) Nutt. *	x	x	x	x	x	x	x	x		x	x
Sericocarpus tortifolius (Michx.) Nees	x	x	x	x	x	x	x	x		x	x
Tephrosia virginiana (L.) Pers.		x	x	x	x	x	x	x			x
Oxalis L. *	x	x		x						x	x
Vernonia angustifolia Michx.	x		x			x	x	x		x	
Smilax smallii Morong		x	x	x	x	x				x	x
Ruellia caroliniensis (J.F. Gmel.) Steud.	x	x		x	x	x	x	x	x		x
Viola L.						x					
Erechtites hieraciifolius (L.) Raf. Ex DC.	x	x	x	x	x	x	x	x	x	x	x
Muscadinia rotundifolia (Michx.) Small	x	x	x	x	x	x	x	x	x	x	x
Poaceae *	x	x	x	x	x	x	x	x	x	x	x
Euphorbia pubentissima Michx. *	x	x	x	x	x	x	x	x	x	x	x
Cirsium Mill	x						x			x	
Pteridium latiusculum (Desv.) Hieron. Ex R. E. Fr. = (syn: P. aquilinum)	x	x	x	x	x	x	x	x	x	x	x
Galium L.	x	x		x	x	x	x	x		x	x
Gelsemium sempervirens (L.) W.T. Aiton	x	x	x	x	x	x	x	x	x	x	x
Smilax bona-nox L.	x	x	x	x	x		x	x	x	x	x
Smilax glauca Walter	x	x	x	x	x	x	x	x	x	x	x
Acalypha L.*	x	x	x	x	x	x	x	x	x	x	x
Smilax torundifolia L.	x	x	x	x	x	x	x	x	x	x	x
Tragia smallii Shinners	x	x	x	x		x	x	x	x	x	x
Scutellaria alabamensis Alexander			x	x	x		x				x
Scleria triglomerata Michx.		x	x	x	x		x		x	x	x
Lobelia puberula Michx.		x									x
Vitis aestivalis Michx. Var. aestivalis	x	x		x			x	x	x	x	x
Dichanthium tenue (R. Br.) A. Camus				x	x				x	x	
Nabalus L.		x							x	x	
Symplocos tinctoria (L.) L'Her.			x	x	x			x	x	x	x
Yucca filamentosa L.	x			x			x	x	x	x	x
Solidago L.			x								x
Eupatorium L.				x						x	

Berchemia scandens (Hill) K. Koch	x	x	x	x	x	x
Asclepias tuberosa L.			x			
Physalis heterophylla Nees			x			
Eupatorium capillifolium (Lam.) Small			x			
Scutellaria elliptica Muhl. Ex Spreng. Var. elliptica		x	x	x	x	x
Toxicodendron radicans (L.) Kuntze				x		
Toxicodendron pubescens Mill.			x			x
*Mitchella repen*s L.						x
Eryngium yuccifolium Michx. Dunal						x

Table 3. Constrained seriation for all tree and shrub taxa (woody plants < 1 m height) observed, with columns representing distance from the edge (m). An "x" represents presence at given distance. Asterisks indicate indicator species of the tornado swath.

Species	-20	-10	0	10	20	30	40	50	60	100	150
Ilex decidua Walter	x										
Sideroxylon lanuginosum Michx.	x										
Pinus Taeda L.	x										
Celtis laevigata Willd.	x										
Cornus florida L.	x	x									
Prunus umbellata Elliott	x	x		x							
Symphyotrichum patens (Aiton) G.L. Nesom	x	x	x	x							
Styrax grandifolius Aiton			x								
Vaccinium pallidum Aiton			x	x							
Hypericum hypericoides (L.) Crantz *	x	x	x	x		x		x			
Liquidambar styraciflua L. *	x	x	x	x	x		x	x			
Alnus rubra Bong					x						
Rhus glabra L.					x						
Quercus marilandica Munchh.		x	x	x		x	x	x			
Nyssa sylvatica Marshall	x	x		x	x	x	x				x
Quercus hemisphaerica W. Bartram ex Willld.		x		x		x			x		
Pinus echinata Mill.		x	x	x	x	x		x	x		
Rubus L. *	x	x	x	x	x	x	x			x	x
Carya glabra (Mill.) Sweet	x	x	x	x	x	x	x	x	x	x	
Quercus coccinea Munchh.	x	x	x	x		x	x	x	x	x	
Celtis occidentalis L.	x			x	x		x				x
Pinus palustris Mill. *	x	x	x	x	x	x	x	x	x		x
Vaccinium stamineum L.	x	x	x	x	x	x	x		x	x	x
Quercus nigra L.	x	x	x	x	x	x	x		x	x	x
Liriodendron tulipifera L.	x		x	x						x	x
Vaccinium arboreum Marshall	x	x	x	x	x	x	x	x	x	x	x
Carya tomentosa (Lam.) Nutt.	x	x	x	x	x	x	x	x	x	x	x
Quercus alba L.	x	x	x	x	x	x	x	x	x	x	x
Quercus falcata Michx.	x	x	x	x	x	x	x	x	x	x	x
Quercus stellata Wangenh.	x	x	x	x	x	x	x	x	x	x	x
Quercus velutina Lam.	x	x	x	x	x	x	x	x	x	x	x
Rhus copallinum L. *	x	x	x	x	x	x	x	x	x	x	x
Rosa carolina L.					x		x				
Diospyros virginiana L	x	x	x	x	x	x	x	x	x	x	x
Sassafra albidum (Nutt.) Nees	x	x	x	x	x	x	x	x	x	x	x
Callicarpa americana L.	x		x	x	x	x	x	x	x	x	x
Asimina parviflora Michx. Dunal	x		x	x	x	x	x	x	x	x	x

	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11
Aesculus pavia L.		x	x					x	x	x	
Rhamnus cathartica L			x								x
Oxydendrum arboreum (L.) DC.	x		x		x	x	x	x	x	x	x
Quercus montana Willd.		x			x				x		x
Vaccinium elliottii Chapm.							x				
Acer rubrum L.	x			x					x	x	x
Quercus rubra L.		x				x		x	x	x	
Quercus laevis Walter								x			
Ilex opaca Aiton						x				x	
Gaylussacia dumosa (Andrews) Torr. & A. Gray var. bigeloviana Fernald						x			x		x
Castanea dentata (Marshall) Borkh.							x		x	x	
Vaccinium corymbosum L.									x		

For tree seedlings, *Pinus palustris* occurred in 21% of quadrats, followed by *Quercus falcata* (17% of quadrats) and *Carya tomentosa* (15% of quadrats). Mean seedling density ranged from 13.5 ± 15.6 (SE) to 3.4 ± 5.22 (SE) seedlings quadrat^{-1} from plots in the tornado swath to plots in the interior. No significant edge influence was recorded on total seedling density, with no discernable pattern of seedling density from the edge-to-interior gradient. MEI values were positive from -20 – 0 m, indicating a greater density of seedlings in the tornado swath and edge, but no significant DEI was recorded. However, we did document a significantly positive edge influence on *Pinus palustris* seedlings. *Pinus palutris* seedling density was significantly greater than the interior woodland at distances of -20 – 6 m and 10 – 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 to the interior (**Figure 4**). MEI on *P. palustris* seedling density was the highest magnitude recorded in this study. We documented no EI on *Quercus* and *Carya* seedling density. Similarly, we documented no edge influence on total seedling richness and diversity (DEI of -20 m).

Edge influence on total ground flora cover was positive, with increased total cover from -20 – 2 m (**Figure 4**). Mean ground flora cover at distances in which MEI was significant was 53% $\pm$ 28 (SE) and was 23% $\pm$ 29 (SE) in the interior woodland. When ground flora was categorized into growth forms, we documented no specific edge influence on tree, forb, or vine cover, and positive edge influence on shrub and graminoid cover. Tree, forb, and vine abundance showed no significant difference at any distance from the edge, even into the tornado swath. Shrub cover was significantly greater in the tornado swath (-20 – 0 m), but showed no EI. Graminoid cover was significantly greater in the tornado swath and up to 6 m into the interior. Most individual taxa showed no significant EI. Grasses (*Poacaea*) experienced a significantly

positive edge influence distances of -20 – 6 m from the edge. Edge influence was also significantly positive on *Gelsemium sempervirens* (-20 – 6 m) and *Rhus copalinum* (-20 – 2 m). All other abundant individual ground flora taxa experienced no significant edge influence.
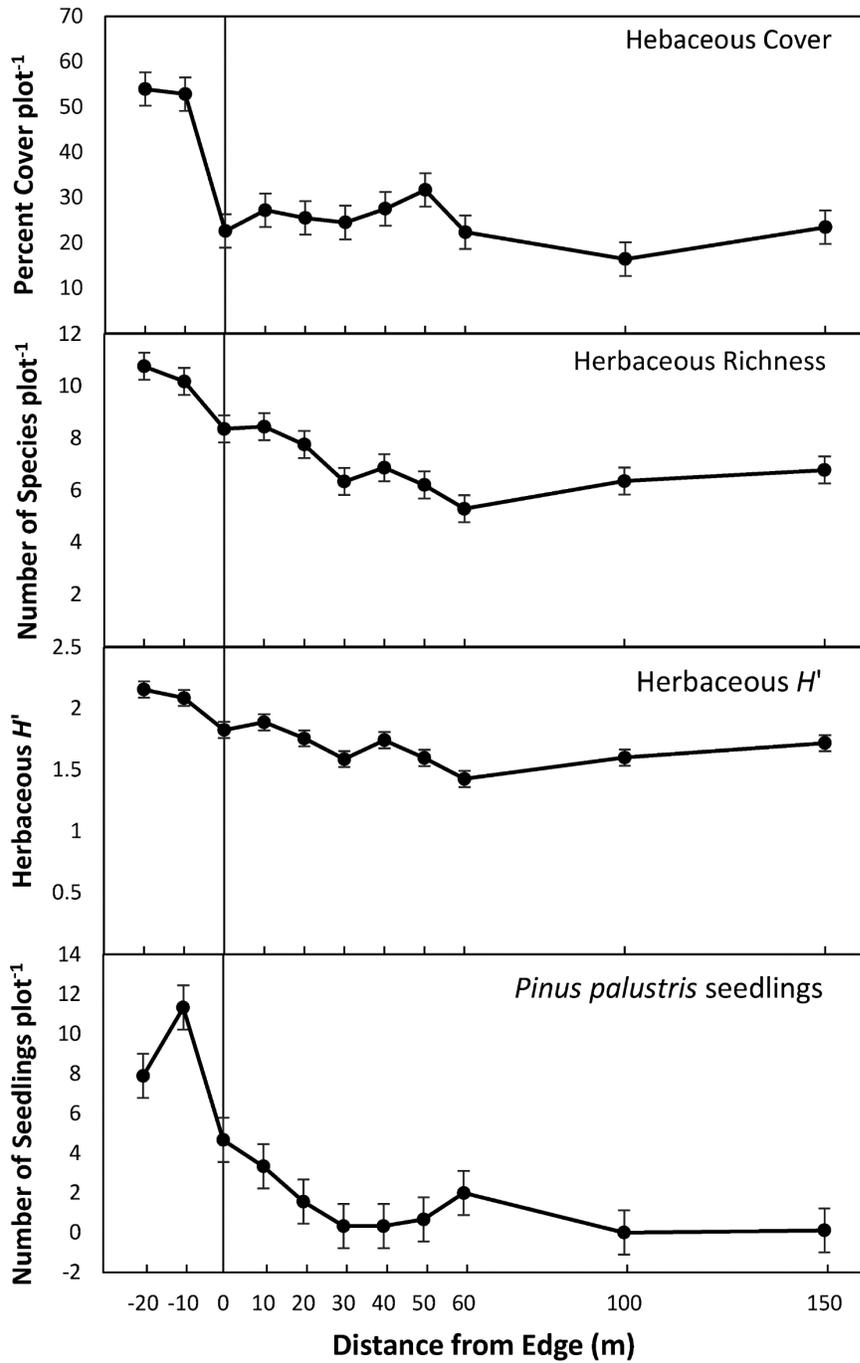
Figure 4. Average ground flora response variables from the edge-to-interior gradient, with vertical bars as standard error. *H´* is Shannon diversity.

The three axis NMS solution revealed decreasing variability of ground flora abundance from in

the interior cluster (distances 30 – 150 m) to the tornado swath cluster (distances -20 – 0 m),

(**Figure 5**). The interior cluster had the greatest variability in ground flora communities. Axis 1

explained 31% of the variation in ground flora abundance and was positively correlated with

percent canopy openness ($r^2 = 30\%$). Axis 2 explained 20% of variation and was positively

correlated with percent canopy openness ($r^2 = 50\%$). Interior plots were the most variable in

ordination space, indicating a large number of unique plant assemblages that occurred in the

interior woodland. Tornado swath plots were less variable in ordination space, and generally

occurred in the upper half of the graph, corresponding to the negative range of axis 1 and 3, and
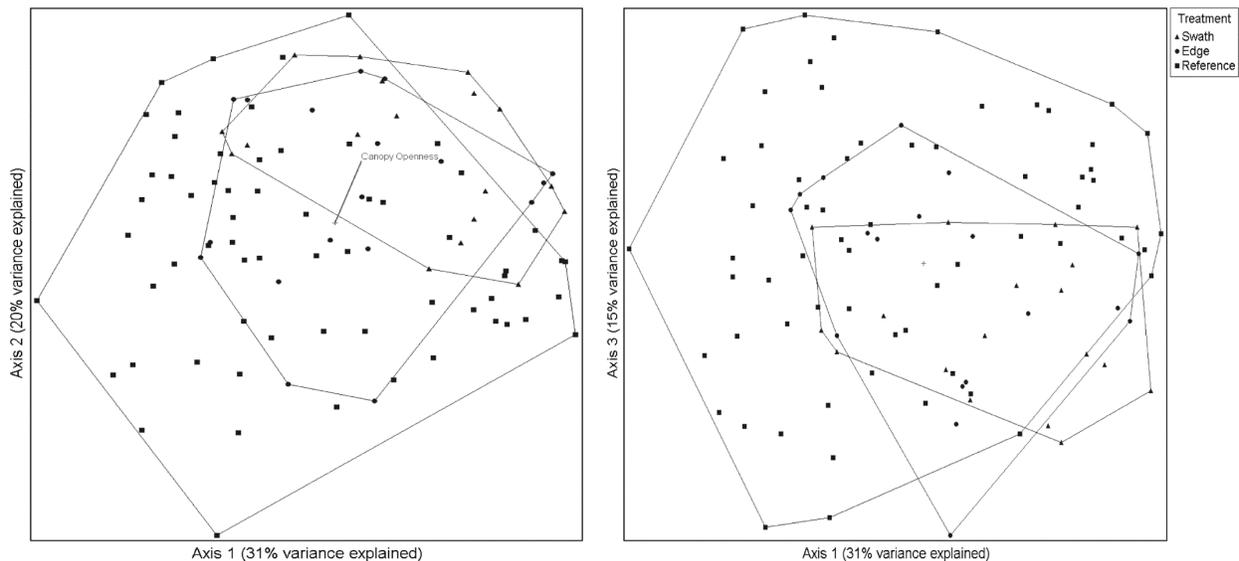
the positive range of axis 2.

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

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) nor communities in the interior

woodland (p = 0.051).

Indicator species analysis for ground flora revealed 15 indicator species of the tornado

swath, 0 of the edge, and 0 of the interior woodland. Of the 15 indicators of tornado swath, four

were woody and included *Pinus palustris*, *Liquidambar styraciflua*, *Hypericum hypericoides*,

and *Rhus copalinum*. The remaining 11 indicator species were herbaceous and included

Acalypha spp., *Conyza canadensis*, *Euphorbia pubentissima*, *Eupatorium rotundifolium*,

Lespedeza hirta, *Oxalis* spp., *Pityopsis graminifolia*, *Poacaea* spp., *Rubus* spp., *Solidago*

altissima, and *Symphiatrichum* spp. (**Table 2 and 3**). *R. copalinum* had the greatest indicator

value (IV, 51.3), followed by *Syphiatrichum* (IV = 48.8) and *P. palustrus* (IV = 46.7).

3.5 EI on abiotic variables

Edge influence on coarse woody debris volume and density, and snag density was not

significant (**Figure 1**). However, the tornado swath contained significantly greater volume and

density of CWD. We documented a significantly greater CWD volume from -20 – 0 m and

greater CWD density from -20 – -10 m. No significant difference was recorded in snag density

from the edge to interior gradient. *Pinus palustris* was the most abundant CWD species,

occurring at all distances from the edge. Logs accounted for 56% of all CWD documented,

followed by snags, which accounted for 24% of CWD. We recorded 85 snags, in which 30

(40%) were *Cornus florida* and 25 (30%) were *Pinus palustris*. Of all snags recorded, 80%

occurred at distances > 20 m from the edge. The opposite trend was documented with downed

CWD (logs and uproots), in which 68% occurred from -20 – 40 m. Edge influence on light

structure was significantly positive from the edge-to-interior gradient (**Table 1**). We noted

significantly higher percent canopy openness from -20 – 70 m into the interior woodland.

Canopy openness ranged from 58% ± 14 in the tornado swath to 22% ± 4 in the interior

woodland and showed a decreasing trend from the edge-to-interior gradient. Ground surface

substrate cover exhibited minimal edge influence. *Pinus* litter experienced a significant negative

edge influence from -20 – 8 m into the interior. Conversely, the category "other litter" and bare

mineral soil exhibited no significant edge influence.

4. DISCUSSION

4.1. Depth of edge influence

Edge influence on *Pinus palsutris* woodland composition and structure was significant.

Both positive and negative magnitude of edge influence was recorded for response variables.

Overstory compositional diversity and structure experienced a negative edge influence (reduced

values at the edge). Compositionally, the overstory interior forest was more diverse than the

edge, which may be attributed to the higher probability of overstory mortality at the edge during

and after disturbance (Matlack 1994). In the interior woodland, shade tolerant and late-

successional tree species have the ability to recruit and persist in the midstory. 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 did occur, but many

were stump sprouts, which likely indicated establishment prior to disturbance (i.e. *Liquidambar

styraciflua*). Although results indicated that overstory diversity was lower up to 150 m into the

woodland, only significant EI was recorded from the edge to 10 m into the woodland. Most edge

research lacks quantification of overstory compositional diversity along the edge-to-interior

gradient. Edge influence on overstory structure, and understory composition and diversity are

often most frequently analyzed. Also, many studies quantify edge influence on response

variables as a function of time since edge formation (Harper and McDonald 2002, Dupuch and

Fortin 2013, Harper et al. 2015), and edge influence on response variables as a function of edge

orientation (Chen et al. 1992, Prieto et al. 2014, Dabros et al. 2017), but lack insight on

successional trajectories, or how overstory composition responds to edge formation. Overstory

response may not be as immediately evident after edge formation as understory change, but the overstory should eventually respond to changes in abiotic conditions at the edge with time since disturbance. Relative to the interior woodland, the low diversity at the edge is also a function of significantly less trees than that of the interior. A gradient of low to high overstory diversity was indeed documented on overstory compositional diversity, with low diversity in the tornado swath (as a function of high overstory mortality) and increasing diversity from the edge to the interior woodland. We hypothesize that, until saplings in the tornado swath stratify into the canopy, overstory richness and diversity will remain lower than that of the interior.

Although edge influence on overstory compositional diversity has been little researched, edge influence on overstory structure has been well documented in an abundance of forest and edge types (Harper et al. 2005, Broadbent et al. 2013). We documented a negative edge influence on overstory structure up to 70 m into the interior woodland. Height diversity experienced the greatest structural edge influence (70 m), and basal area and tree density experienced a negative edge influence of 10 m into the interior woodland. The reduction in structural attributes indicates that the tornado not only had immediate impact on woodland structure, but also residual impacts (secondary responses). Secondary responses 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 (sensu Chen et al. 1992, Oosterhoorn and Kapelle 2000, Harper and McDonald 2002, Harper and McDonald 2015).

The horizontal distribution of basal area over the edge-to-interior gradient as quantified by the Gini Coefficient showed no significant edge influence. The GC has been used to effectively differentiate stands of different horizontal structures (i.e. even aged vs. uneven aged;

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Peck et al 2014). Accordingly, the GC was not significantly different at any point along the edge to interior gradient. Basal area was more evenly distributed in the tornado swath and edge than the interior woodland. However, the interior woodland had a relatively low GC compared to Peck et al. (2014), who found that uneven aged stands reveal a relatively high GC compared to even aged stands. For comparison, the GC of the interior woodland was 0.25 and was 0.15 at the edge, with both values characteristic of even-aged stands. The lower GC at the edge could be attributed to overstory mortality of a wide range of size classes. We would expect the absence of primary and secondary mortality in the interior woodland to increase the GC, with more individuals with a higher variability in basal area. However, we contend that both the edge and interior were even-aged because the GC was not significantly different between the edge and interior woodland.

The tornado created edge had a similar 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 sub-canopy positions. We recorded more shade tolerant individuals in the interior forest (i.e. *Vaciunium arboreum*, *Cornus florida*) that likely increased vertical complexity. Managers are increasingly prioritizing structurally complex forests with variability in horizontal and vertical structure. Our results indicated that the edge ecosystems in woodland forest structure are indeed less complex than interior in terms of live overstory structure. However, no significant EI was recorded on CWD structure, which is an important characteristic of structurally complex systems (McElhinney 2005). Snag density, log volume, and log density all showed no significant edge influence. One possible explanation for this could be attributed to stochastic gap-scale disturbances, which are commonly caused by pest outbreaks or strong wind events. Although we noted high mortality in the tornado swath and at the edge,

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canopy gaps in the interior were encountered in sampling because of their abundance on the landscape. Canopy gaps form by the death of one or a small cluster of overstory individuals (Runkle 1985). Canopy gaps are subject to some degree of edge influence on the surrounding intact forest, depending on the size and orientation of the gaps. Canopy gaps have also been found to occur more frequently in close proximity to the edge of intact forests (Camargo and Kapos 1995). We attribute the absence of EI on CWD to stochastic background disturbance in the forest 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. Analysis of CWD by decay class also revealed non-significant EI, but we did record a greater density of CWD in advanced stages of decay (i.e. DC III & IV) in the interior woodland, and a greater density of CWD that experienced less decay (i.e. DC I & II) at or near the edge (-20 – 20 m). These results may indicate a delayed secondary edge response to the tornado, such a snag blowdown at the edge as a result of exposure to more harsh conditions.

4.2 Influence on ground flora communities

In general, edge influence on ground flora communities was positive, with higher diversity and richness in the tornado swath and at the edge. For all ground flora species, the positive edge influence was mostly evident from 20 m into the tornado swath to 18 m into the interior. Although Shannon diversity and cover showed significant but minimal edge influence, increased herbaceous richness did penetrate relatively deep into the interior woodland. High herbaceous richness has been well documented in *P. palustris* woodland ecosystems (Kirkman and Gienke 2017), with Asteraceae, Poaceae, and Fabaceae among the families with the highest

number of rare species. With the addition of disturbance, micro-habitats associated with pit-and-mound topography and CWD accumulation increase niche space for unique species assemblages. Catastrophic wind disturbance has been found to increase herbaceous diversity and richness in *P. palustris* woodlands (Kleinman et al. 2017). Results from this study indicated that total herbaceous richness, cover, and diversity were all significantly higher in the tornado swath (-20 – 0 m) than in the reference woodland, with species richness experiencing the most EI.

The ground flora of edges of forests fragments are typically compositionally distinct from the adjacent forested and non-forested areas, depending on the steepness of the microclimatic gradient at the edge, and successional stage of the edge (Alignier et al. 2014), among other factors. We used cluster analysis, NMS, and the MRPP post-hoc test to visualize edge influence in ordination space and determine that the ground flora assemblages at edge of the tornado swath were not statistically different from those of the interior woodland or the tornado swath. This result confirmed the hypothesis ground flora communities were influenced by the tornado swath and the interior woodland. Although ground flora of the tornado swath was compositionally distinct from the interior forest, we hypothesize that the edge was influenced by the tornado swath as well as the intact forest. Although less understood than edge influence, forest influence is the influence of the intact forest on the adjacent disturbed forest. (Baker et al. 2013). We contend that the ground flora composition at the edge consists 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 forest can likely be attributed to (1) woodland light structure, (2) gap-scale disturbance, and (3) topographic variability. Woodlands contain fewer

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trees ha^{-1} and basal area ha^{-1} than forests, which allows more light penetration through the relatively open canopy. Gap-scale disturbances were also frequently observed and were hypothesized to be caused by pests outbreaks, evident by clusters of snags, or other stochastic wind events. Gap-scale disturbances inherently allow for greater light penetration in the understory. For example, the outlying plots in the NMS graph, specifically the plot in the top-middle of the graph had the highest snag density in the study, which explains its location close to the swath plots in ordination space (**Figure 5**). 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.

Whereas the interior woodland was more variable in ground flora communities, we contend the tornado swath was less variable because of more homogenous conditions. We hypothesize that a particular group of species well adapted to the relatively harsh conditions of the tornado swath were able to outcompete other species found in the interior, thus the edge contained both early successional, disturbance adapted species found in the swath and interior species common to restored *P. palustris* woodlands. Indicator species analysis identified 15 species that were significant indicators of the tornado swath cluster. Of the 15 species identified, six were among those that were disturbance obligate and have been confirmed to occur in disturbed *P. palustris* woodlands by Kleinman et al. (2018). These disturbance-adapted species included *Conyza canadensi*, *Eupatorium rotundifolium*, *Liquidambar styraciflua*, *Oxalis*, *Rhus copalinum*, and *Rubus.* The remaining nine indicator species had been documented in undisturbed *P. palustris* woodlands, but were found to have a higher abundance in the tornado

swath cluster in this study. We hypothesize that the increased light availability, CWD, and pit-and-mound microtopography that occurred in the tornado swath was more conducive to higher abundances of these species. We hypothesize that no indicator species were identified in the interior forest cluster because of the high variability in ground flora communities as previously discussed. The relatively high biophysical variability was conducive to conditions that led to no one species having a significantly greater abundance than another. Since ground flora communities at the edge were not significantly different from the interior or swath clusters, no species had significantly greater abundances to warrant indication of the edge ecosystem.

Edge influence on individual ground flora taxa was minimal, with few species experiencing identifiable trends from the edge-to-interior gradient. *Rhus copalinum* experienced edge influence from -20 – 2 m, which corresponds to increased light availability for this disturbance-adapted, early successional species. One particularly notable species that experienced positive edge influence was *Pinus palustris*. *Pinus palustris* seedlings had a significantly higher density up to 22 m into the interior forest. *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 understory light availability necessary *P. palustris* seedling establishment. Edge influence 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. The increased light as a result of edge formation likely created a conducive environment for *P. palustris* seedling regeneration and establishment. Thinning operations are commonly utilized to improve growing conditions for desirable trees, with increased seedling germination as a consequence of decreased overstory density and basal area (Harrington 2011). We contend that the decreased basal area and tree density as a function of edge was similar to thinning, which increased

favorable conditions for *P. palustris* seedling establishment. We hypothesize that the residual

individuals that survived the tornado, which were majority *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 approx. 33 m from source overstory individuals (Croker and Boyer 1975).

The survival of vigorous overstory *P. palustris* allowed seed deposition to occur in favorable

conditions for *P. palustris* establishment, compared to 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 the fire was

indeed effective as evidenced by the reduced number of saplings three months post-fire.

Kleinman et al (2017) noted an abundance of saplings three years-post fire, which was thought to

reduce the probability of *P. palustris* establishment.

4.3 Edge influence on woodland structure

Edge influence is a well-documented process with broad ecological applications.

However, a paucity of research has quantified edge influence on woodland forest structures.

Woodlands are typically less light limited than forests, which likely affected the distance

magnitude of edge influence when compared to other forests types. To our knowledge, DEI of

canopy openness is among the greatest distance recorded among most other edge studies.

Matlack (1993) suggested that abiotic variables commonly measured to quantify edge influence,

such as air temperature and soil moisture, were a function of light availability. Light structure

along the edge-to-interior gradient has been quantified with the use of various methods, but

reported maximum DEI estimates of light structure has not been found to exceed 40m. (Brothers

and Spingarn 1992, Matlack 1993, Gehlhausen et al. 2000, Marchand and Houle 2006).

However, we did not note a corresponding increase in herbaceous cover and diversity corollary to increased light availability. We attribute this to two potential explanations: (1) the MEI on canopy openness was among the lowest of any quantified biotic or abiotic variable analyzed for EI, and (2) the increased abundance of *pinus* litter from the edge-to-interior gradient. Although canopy openness was significantly higher from -20 – 70 m compared to the interior woodland, MEI was relatively low from 20 – 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 herbaceous regeneration and prevented growth of abundant forbs and graminoids (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 forest edge. The structural contrast between the forested and non-forested area is of a higher MEI with increased disturbance severity (i.e. more overstory mortality). The tornado was indeed catastrophic in severity but did not cause complete overstory mortality. Although we noted a distinct edge on the areal imagery and in the field, the residual overstory individuals in the tornado swath likely affected the distance and magnitude of edge influence. For example, McIntire and Fortin (2006) found that overstory mortality was greater following severe wildfire (89% overstory mortality), compared to *Dendroctonus ponderosae* (mountain pine beetle) outbreak (43% overstory mortality), which affected the abruptness of the natural edge, with residual overstory individuals affected estimates of DEI and MEI. 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. Chabrerie 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 as DEI will increase as saplings and smaller trees recruit into larger size classes in the tornado swath, and the overstory begins to stratify.

In fact, we hypothesize that the edge is expanding into the tornado swath, which commonly occurs on unmaintained edges (Harper *et al.* 2005). The frequent use of prescribed fire every 2–5 years, with adequate fuels for consumption, likely prevents edge sealing by topkilling hardwood saplings and promoting *P. palustris* establishment and recruitment. As the overstory begins to stratify into the newly formed canopy, edge influence should dissipate, and forest influence on the tornado swath will likely occur. I contend that forest influence on the disturbed tornado swath is already occurring, as evidenced by negative DEI estimates. Forest influence is broadly defined as the influence of mature, undisturbed forests on disturbed areas (Keenan and Kimmins 1993, Baker et al. 2013). Forest influence has broad implications for seed dispersal, microclimatic gradients, and establishment facilitation (Baker et al. 2013). Our results indicated forest influence on sapling density, diversity, richness, and seedling density. Forest influence on sapling diversity and richness was 10 m into the tornado swath, whereas 0 – 10 m into the tornado swath was not significantly different in regard to sapling density, diversity, and richness when compared to the reference woodland. Seedling density experienced the same forest influence as saplings. However, edge influence on woodland structure and composition remained the predominant ecological process. With time, we would expect to see a decrease in distance and magnitude of edge influence, and an increased distance and magnitude of forest influence.

4.4 Management implications

      For managers who intend to increase ground flora richness and diversity to enhance ecosystem services, results from this study indicate that tornado created edges were conducive to increased ground flora richness and diversity. 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 the 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 habitat heterogenization to increase variability in ground flora communities.

      Forest edges and fragments have wide-ranging implications for wildlife and endangered species management. For example, The *Leuconotopicus borealis* Vieillot (Red-Cockaded Woodpecker, RCW) is an endangered species that requires the composition and structure of *P. palustris* woodland to serve as habitat for cavity excavation and foraging (Blanc and Walters 2008). *Leuconotopicus borealis* forages over large, contiguous tracts of open canopy, mature *P. palustris* woodlands (Smith et al. 2017). Edges in *P. palustris* woodlands may be detrimental to the RCW population for several reasons. If fire exclusion occurred, sapling density would be likely increase at the edge, particularly hardwood species. Hardwood midstory removal is commonly applied to restore habitat in for *L. borealis*. Edges also reduce the amount of contiguous foraging area by creating disjunct forest fragments. Although edge influence may be

detrimental to *L. borealis* population, other wildlife may benefit from edge creation and influence. Edges with increased sapling density offer alternate browsing locations, which may reduce browse stress in the interior forest for herbivore populations.

Natural disturbance-based silviculture is commonly implemented to enhance forest diversity and complexity and increase resilience to future disturbance. To emulate catastrophic tornado disturbance, we recommend variable retention harvesting, which would support *P. palustris* regeneration and establishment, and promote compositional and structural diversity with residual overstory individuals. With overstory retention, residual overstory *P. palustris* provide a seed source for regeneration and fuel to ensure the effectiveness of fire. 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 believe that edge influence in this forest type is directly related to the ability of prescribed fire to reset understory and midstory communities. Because sampling occurred four months post-fire, we suggest continual monitoring of edge influence with time since fire. We hypothesize that lack of fire will likely lead to edge sealing, as hardwood saplings begin to compete for increased light at the edge. Prescribed fire is essential to mitigate detrimental edge influence and achieve management goals to restore *P. palustris* dominance in the tornado swath. However, the edge influence 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 seven years post disturbance. In *P. palustris* woodland

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ecosystems, we suggest maintaining a 70 m buffer around forest fragments to maintain interior

woodland conditions and mitigate potential negative edge influence.

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