WINDTHROW AND SALVAGE LOGGING EFFECTS ON HERBACEOUS DIVERSITY AND COMPOSITION IN THE SOUTHEASTERN US

by

AUSTIN JAMES MENZMER

(Under the Direction of Chris J. Peterson)

ABSTRACT:

Using both natural and field experiments, this dissertation examines the impact of single and compound disturbance (windthrow and salvage logging) severity on herbaceous species diversity and composition in Georgia and Tennessee.

Following a brief review of relevant literature, I first examine the effect of varying severity on herbaceous species diversity and composition in an experimental wind disturbance of the Georgia Piedmont one, three, and four years post-disturbance. I present evidence that disturbance severity, as quantified by 50% or 100% of tree basal area felled, increases herbaceous diversity most noticeably one year post-disturbance in a closed-canopy forest, but the effect decreases three and four years post-disturbance. Herbaceous compositional dissimilarity was consistently observed between most treatments in all years without apparent connection to disturbance severity.

Next, I examine the impact of compound wind and salvage logging on herbaceous diversity and composition in a wiregrass-dominated fire frequent longleaf pine woodland of Georgia three years post-disturbance. I present evidence that varying severity did not affect a change in herbaceous diversity. However, herbaceous compositional dissimilarity was observed in two out of six treatment comparisons.

Finally, I examine the long-term impact of wind and salvage logging on herbaceous diversity and composition in the Tennessee Coastal Plain. This study built upon prior work that sampled herbaceous species two years post-disturbance; my contribution enabled a retrospective of over two decades. Twenty-two, twenty-three, and twenty-four years post-disturbance, neither herbaceous diversity nor composition varied with disturbance severity, as defined by the presence or absence of salvage logging. The nondifferences are likely due to the progression of time.

I found that single disturbance severity had the strongest impact on herbaceous diversity one year post-disturbance in a closed-canopy forest; however, a compound disturbance (wind plus salvage logging) had no apparent effects on herbaceous diversity three and twenty-plus years post-disturbance in an open-canopy woodland and closed-canopy forest. Both single and compound disturbance impacted herbaceous composition short-term but not long-term post-disturbance. At present, it appears that wind and salvage logging have temporary but not long-lasting effects on the herbaceous diversity and composition of the southeastern United States.

INDEX WORDS: single disturbance, compound disturbance, wind disturbance, salvage logging, closed-canopy forest, open-canopy woodland, disturbance severity, herbaceous species, diversity, composition

WINDTHROW AND SALVAGE LOGGING EFFECTS ON HERBACEOUS DIVERSITY AND COMPOSITION IN THE SOUTHEASTERN US

by

AUSTIN JAMES MENZMER

MS, Andrews University, 2019

A Dissertation Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

DOCTOR OF PHILOSOPHY

ATHENS, GEORGIA

2024

WINDTHROW AND SALVAGE LOGGING EFFECTS ON HERBACEOUS DIVERSITY AND COMPOSITION IN THE SOUTHEASTERN US

by

AUSTIN JAMES MENZMER

Major Professor: Chris Peterson
Committee: Jeffery Cannon
Lisa Donovan
Megan DeMarche

Electronic Version Approved:

Ron Walcott
Dean of the Graduate School
The University of Georgia
May 2024

DEDICATION

To my beautiful bride, Jolene. You are the strongest and most beautiful person that I know. We finally finished this thing!

ACKNOWLEDGEMENTS

I have always heard it said that it takes a village to raise a child, and I believe that it takes an entire city to help one earn a Ph.D. First and foremost, I want to thank my wife Jolene Menzmer for being my true teammate in every sense of the word. This is her degree as much as it is mine. It's thrilling to finally be at the finish line together! I would also like to thank my in-laws, parents, and other family and friends for their support. Professionally I would like to thank Chris Peterson for inviting me into his lab and my labmates-turned-friends Callie Oldfield, Mark Zenoble, and Rebecca Klee for the supportive community they created for me. My committee members Jeff Cannon, Megan DeMarche, Lisa Donovan, and Shu-Mei Chang have been invaluable in teaching me the ways of plant ecology. Kathrin Stanger-Hall, Peggy Brickman, and Paola Barriga deserve special mention as they mentored me in becoming a better teacher. My heart smiles at the thought of Brad Erbesfield of UGA's Disability Resource Center, who graciously helped me navigate securing needed accommodations for fieldwork.

I am grateful to have received funding for either fieldwork, conference travel, or sustenance from the Department of Plant Biology at UGA, the Graduate School of UGA, and the Georgia Botanical Society.

Chapter 2. I would like to extend thanks to my wife Jolene Menzmer and technicians Emma Guglielmo and Kathryn King for aid in fieldwork. I cannot miss mentioning the superb help of Callie Oldfield, who originated this study and who taught me the ropes of plant identification. I also extend appreciation to the UGA Warnell School of Forestry and Natural

Resources for permission to sample at the site.

Chapter 3. I would like to extend particular thanks to Jeff Cannon, Lisa Giencke, and their technicians for guidance in experimental design, aid in fieldwork, and especially for assistance in plant identification. They opened their expertise, enthusiasm, and site to me.

Chapter 4. I want to extend a special thanks to my wife Jolene Menzmer, who not only helped me originate this study but also accompanied me on all sampling trips. This is her work as much as it is mine, and I could not have done it without her teamwork. She was particularly helpful in experimental design, reminding me to drink water and eat snacks, and providing words of encouragement at just the right moment. She did a fantastic job at wrangling the data and writing it all down! I want to thank Roger McCoy and Richard Sanderson of the State of Tennessee for granting me permission to sample at Natchez Trace State Park, and former labmate Andrea Leach for the initial 2001 data collection.

TABLE OF CONTENTS

Page

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

Herbaceous species, particularly colorful wildflowers, play an important role in elevating the aesthetic beauty of our world. Many people have fond memories of childhood visits to botanical gardens or national parks with herbaceous species lining the trails. While naturalists such as John Muir enthused that we "need beauty as well as bread" (Larsen 2011), herbaceous species provide many more benefits than just being pleasing to the eye. For example, herbaceous species are more efficient at carbon sequestration than woody species (Deng et al. 2022) and herbaceous root systems can reduce soil erosion (Kervroëdan et al. 2021). Herbaceous species are a regular food source for animals such as deer (Royo et al. 2010) or squirrels (Menzmer 2019), and this layer has been estimated to comprise up to 90% of plant species richness in forests (Gilliam 2007).

The diversity and composition of plant species – two metrics by which to measure plant community health – are well-known to be impacted by natural disturbances such as wind and fire (Dale et al. 2001). The increasing frequency and severity of natural disturbances have been observed to increase carbon dioxide emissions and thus contribute to the negative effects of climate change (Chambers et al. 2007, Jones et al. 2022, Balaguru et al. 2023). To maintain healthy ecosystems, it is crucial to comprehend how natural disturbances impact species diversity and composition.

Natural disturbances have a broad range of impacts on woody and herbaceous species diversity and composition. For example, severe flooding decreased woody species diversity (De Jagar et al. 2012) while fire caused a boreal forest in Minnesota to exhibit early-successional (species that can establish shortly following a disturbance) composition post-disturbance

(Anoszko et al. 2022). Fire increased herbaceous diversity in Arkansas and South Carolina due to an increase in light availability (Lewis and Harshbarger 1976, Sparks 1988) while excess nitrogen decreased herbaceous diversity due to a decrease in evenness (Gilliam 2019). Windstorms and herbivory in closely neighboring forests have produced both increases and decreases in woody diversity following disturbance (Peterson 2021, Kruger et al. 2009). Wind has a profound impact on herbaceous diversity, especially through the creation of pits and mounds (Beatty 1984). Wind supported a shift in herbaceous composition to dominance of shade-intolerant herbs immediately following a Pennsylvania tornado (Peterson and Pickett 1995) due to increased light availability. Collins and Pickett (1988) found herbaceous cover not to vary with experimentally-created single-tree or multi-tree gaps up to three years post-disturbance, though they acknowledged that longer timespans or larger gaps may enable herbaceous cover to vary more noticeably. No matter what disturbance one chooses, these forces impact plant communities across America.

Windstorms such as thunderstorms, tornadoes, or hurricanes are common natural disturbances in the southeastern United States (Peterson and Leach 2008, Kleinman et al. 2017, Rutledge et al. 2021). Salvage logging, the practice of removing fallen trees following a natural disturbance, is often carried out after windstorms and can increase the cumulative severity of damage following a natural disturbance (Lindenmayer and Noss 2006, Lindenmayer and Ough 2006, Peterson and Leach 2008, Blair et al. 2016, Sass et al. 2018, Burton et al. 2020). Fire is another frequent event after windstorms (Cannon et al. 2019). Often compound disturbances – multiple disturbances occurring in a short timespan – can affect plant diversity and composition in ways that differ from the effects of single disturbances (Anoszko et al. 2022). For example, compound disturbances such as wind plus salvage logging and wind plus fire have increased the compositional dissimilarity between saplings and seedlings in both Pennsylvania and West Virginia (Royo et al. 2010, Royo et al. 2016, Slyder et al. 2020). In Minnesota, the abundance of late-successional trees increased following wind and fire (Anoszko et al. 2022). Frequency of vertebrates, particularly cavity-nesting birds, decreases in abundance following salvage logging (Thorn et al. 2018). It is crucial to understand how single and compound disturbances affect plant communities.

There are contradictory findings in the current body of literature on the specific effect of compound disturbances from wind and salvage logging on woody species diversity. This compound disturbance has decreased species diversity within five years post-disturbance (Royo et al. 2016, Kleinman et. al 2017) as well as increased species diversity one-to-two years post-disturbance (Peterson and Leach 2008, Slyder et al. 2020) relative to single disturbances. The latter two studies attributed the short-term increase in diversity to moderate disturbance severity and an active seedbank, while the former two attributed the longer-term decrease to competitive exclusion where a few shade-tolerant species dominate. Oldfield and Peterson (2019) found no difference in woody diversity between salvage logged and unsalvage logged plots six years following a wind disturbance, attributing this result to an overall moderate disturbance severity. While the driving factors that impact woody species (variance in disturbance severity, light availability, and competitive exclusion) are easy to list, what every author means by severity is a greater challenge.

Even though herbaceous species comprise up to 90% of forest richness (Gilliam 2007), few studies examine herbaceous species response to wind disturbance and salvage logging. Wind disturbance and salvage logging increase herbaceous diversity due to an increase in microtopographical heterogeneity, decreases in canopy cover, and an increase in seedbank germination in some studies (Elliott et al. 2002, Nelson et al. 2008, Slyder et al. 2020) while these same disturbances in other studies decreased herbaceous diversity due to variation in sampling date, competitive exclusion, or decreases in canopy cover and microtopographical heterogeneity (Rumbaitis del Rio 2006, Brewer et al. 2012, Kleinman et al. 2017, 2021). Other studies (Peterson and Leach 2008, Waldron et al. 2014, Palm et al. 2022) observe no impact of wind and salvage logging on herbaceous diversity. Moderate disturbance severity, a low number of species, and a similarity in canopy cover were credited as likely explanations for the observed lack of impact. Though few studies examine the effects of wind and salvage logging on species diversity, even fewer studies analyze the impact of wind and salvage logging on changes in the composition of herbaceous species. Those that do indicate a mix of results: Peterson & Pickett (1995) found early-successional species such as *Erechtites* and *Dennsteadtia* dominated within four years post-disturbance due to increased resource availability, Elliott et al. (2002) and Lang et al. (2009) found a mix of both early- and late-successional species due to environmental heterogeneity three and twenty-five years post-disturbance, and Mabry and Korsgren (1998) that late-successional species are most common, crediting progression of time (fifty years) post-disturbance. Environmental heterogeneity and resource availability are often the mechanisms through which disturbances affect herbaceous species.

Experimental wind disturbances provide a rare opportunity to have maximal control over the precise level of disturbance severity a given area of vegetation receives. While there are studies that utilize experimental wind disturbances to study response of woody plants (Barker-Plotkin et al. 2013, Cannon et al. 2019), none of the existing literature uses experimental wind disturbances to study the impact of disturbance severity on herbaceous species. To generalize how wind disturbance and salvage logging affect herbaceous species diversity and composition, it is helpful to examine a gradient of disturbance severity.

Few studies have examined the impacts of wind and salvage logging on herbaceous species in open-canopy woodlands as opposed to closed-canopy forests. One exception is Kleiman et al. (2017), which found that treatments with wind damage only supported higher herbaceous diversity than treatments with wind damage and salvage logging. Conducting studies that examine the impact of wind and salvage logging on herbaceous response in a variety of ecosystems would increase the generalization and applicability.

Similarly, few studies examine the effects of wind and salvage logging longer than five years post-disturbance. The exceptions are Palm et al. (2022) and Mabry and Korsgren (1998) which examine herbaceous response multiple decades post-disturbance. Palm et al. (2022) observed differences in composition but not diversity twenty years post-disturbance, crediting variation in light availability between treatments. Mabry and Korsgren (1998) observed that herbaceous composition was dominated by late-successional species fifty years post-disturbance, crediting the passage of time. These two entries in the literature generalize that over decades, wind and salvage logging are not observed to have long-lasting impacts on herbaceous diversity but possible impacts on herbaceous composition. However, as these studies were conducted in Estonia (Palm) and Massachusetts (Mabry and Korsgren), it is worth conducting such studies in other geographic regions such as the southeastern U.S. to see how consistently this compound disturbance impacts herbaceous species.

My central questions driving my dissertation are: 1) how do impacts of experimental wind disturbance alter herbaceous diversity and composition immediately after disturbance in a closed-canopy forest?; 2) how do the effects of wind and salvage logging on herbaceous species response differ (if at all) in an open-canopy woodland compared to a closed-canopy forest?; and 3) how do wind and salvage logging impact herbaceous diversity and composition in long-term timespans (i.e. 20+ years) in a closed-canopy forest?

Chapter 2 examines the short-term response (one, three, and four years post-disturbance) of herbaceous diversity and composition to a single experimental wind disturbance with quantified severity treatments in the closed-canopy forest of the Georgia Piedmont. Chapter 3 examines the short-term (3 years post-disturbance) impact of a compounded disturbance (wind and salvage logging) to herbaceous diversity and composition in an open-canopy longleaf pine woodland. Chapter 4 examines the long-term (twenty-plus years post-disturbance) response of herbaceous diversity and composition to a compound disturbance (wind and salvage logging) in a closed-canopy coastal plain forest of the Tennessee Coastal Plain. Chapter 5 summarizes individual chapter and overall dissertation conclusions.

LITERATURE CITED

Anoszko, E., L. E. Frelich, R. L. Rich, and P. B. Reich. 2022. Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere **13**:e3952.

Balaguru, K., W. Xu, C.-C. Chang, L. R. Leung, D. R. Judi, S. M. Hagos, M. F. Wehner, J. P. Kossin, and M. Ting. 2023. Increased US coastal hurricane risk under climate change. Science advances **9**:eadf0259.

Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology **65**:1406-1419.

Blair, D. P., L. M. McBurney, W. Blanchard, S. C. Banks, and D. B. Lindenmayer. 2016. Disturbance gradient shows logging affects plant functional groups more than fire. Ecological Applications **26**:2280-2301.

Brewer, J. S., C. A. Bertz, J. B. Cannon, J. D. Chesser, and E. E. Maynard. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? Ecological Applications **22**:442-458.

Burton, P. J., A. Jentsch, and L. R. Walker. 2020. The ecology of disturbance interactions. BioScience **70**:854-870.

Cannon, J. B., S. K. Henderson, M. H. Bailey, and C. J. Peterson. 2019. Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. Forest ecology and management **436**:117-128.

Chambers, J. Q., J. I. Fisher, H. Zeng, E. L. Chapman, D. B. Baker, and G. C. Hurtt. 2007. Hurricane Katrina's carbon footprint on US Gulf Coast forests. Science **318**:1107-1107.

Collins, B., K. Dunne, and S. Pickett. 1985. Responses of forest herbs to canopy gaps. The ecology of natural disturbance and patch dynamics:217-234.

Collins, B. S., and S. Pickett. 1988. Response of herb layer cover to experimental canopy gaps. American Midland Naturalist:282-290.

Dale, V. H., L. A. Joyce, S. McNulty, R. P. Neilson, M. P. Ayres, M. D. Flannigan, P. J. Hanson, L. C. Irland, A. E. Lugo, and C. J. Peterson. 2001. Climate change and forest disturbances: climate change can affect forests by altering the frequency, intensity, duration, and timing of fire, drought, introduced species, insect and pathogen outbreaks, hurricanes, windstorms, ice storms, or landslides. BioScience **51**:723-734.

De Jager, N. R., M. Thomsen, and Y. Yin. 2012. Threshold effects of flood duration on the vegetation and soils of the Upper Mississippi River floodplain, USA. Forest ecology and management **270**:135-146.

Deng, L., H. Yuan, J. Xie, L. Ge, and Y. Chen. 2022. Herbaceous plants are better than woody plants for carbon sequestration. Resources, Conservation and Recycling **184**:106431.

Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. Journal of the Torrey Botanical Society:48-59.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience **57**:845-858.

Gilliam, F. S. 2019. Excess nitrogen in temperate forest ecosystems decreases herbaceous layer diversity and shifts control from soil to canopy structure. Forests **10**:66.

Jones, M. W., J. T. Abatzoglou, S. Veraverbeke, N. Andela, G. Lasslop, M. Forkel, A. J. Smith, C. Burton, R. A. Betts, and G. R. van der Werf. 2022. Global and regional trends and drivers of fire under climate change. Reviews of Geophysics **60**:e2020RG000726.

Kervroëdan, L., R. Armand, F. Rey, and M. P. Faucon. 2021. Trait-based sediment retention and runoff control by herbaceous vegetation in agricultural catchments: A review. Land Degradation & Development **32**:1077-1089.

Kleinman, J. S., S. A. Ford, and J. L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. Forest ecology and management **403**:112-125.

Kleinman, J. S., J. D. Goode, and J. L. Hart. 2021. Ground flora cover, diversity, and life-history trait representation after wind disturbance, salvage logging, and prescribed fire in a Pinus palustris woodland. Applied vegetation science **24**:e12541.

Krueger, L. M., and C. J. Peterson. 2009. Effects of woody debris and ferns on herb-layer vegetation and deer herbivory in a Pennsylvania forest blowdown. Ecoscience **16**:461-469.

Lang, K. D., L. A. Schulte, and G. R. Guntenspergen. 2009. Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. Forest ecology and management **259**:56-64.

Larsen, R. R. 2011. The Role of Nature in John Muir's Conception of the Good Life. Antioch University.

Lewis, C. E., and T. J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina coastal plain. Rangeland Ecology & Management/Journal of Range Management Archives **29**:13-18.

Lindenmayer, D., and R. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology **20**:949-958.

Lindenmayer, D., and K. Ough. 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. Conservation Biology **20**:1005-1015.

Mabry, C., and T. Korsgren. 1998. A permanent plot study of vegetation and vegetation-site factors fifty-three years following disturbance in centralNew England, USA. Ecoscience **5**:232-240.

Menzmer, A. 2019. Seasonal Diet Variation in Thirteen-Lined Ground Squirrel (Ictidomys Tridecemlineatus) in Southwestern Michigan.

Nelson, J. L., J. W. Groninger, L. L. Battaglia, and C. M. Ruffner. 2008. Bottomland hardwood forest recovery following tornado disturbance and salvage logging. Forest ecology and management **256**:388-395.

Oldfield, C. A., and C. J. Peterson. 2019. Woody species composition, diversity, and recovery six years after wind disturbance and salvage logging of a southern Appalachian forest. Forests **10**:129.

Palm, K., F. Vodde, T. Tullus, J. Engelhart, and K. Jõgiste. 2022. Impact of different storm severity levels and post-storm management on understory vegetation richness, diversity and composition 19–20 years after wind disturbance. Forest ecology and management **524**:120506.

Peterson, C. J. 2021. First-decade biomass and carbon accumulation, and woody community change after severe wind damage in a hemlock-white pine forest remnant. Forests **12**:231.

Peterson, C. J., and A. D. Leach. 2008. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry **81**:361-376.

Peterson, C. J., and S. T. Pickett. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology **76**:763-774.

Plotkin, A. B., D. Foster, J. Carlson, and A. Magill. 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology **94**:414-423.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology **91**:93-105.

Royo, A. A., C. J. Peterson, J. S. Stanovick, and W. P. Carson. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology **97**:1566-1582.

Rumbaitis del Rio, C. M. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. Canadian journal of forest research **36**:2943-2954.

Rutledge, B. T., J. B. Cannon, R. K. McIntyre, A. M. Holland, and S. B. Jack. 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. Forest ecology and management **481**:118724.

Sass, E. M., A. W. D'Amato, and D. R. Foster. 2018. Lasting legacies of historical clearcutting, wind, and salvage logging on old-growth Tsuga canadensis-Pinus strobus forests. Forest ecology and management **419**:31-41.

Slyder, J. B., J. W. Wenzel, A. A. Royo, M. E. Spicer, and W. P. Carson. 2020. Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. New Forests **51**:409-420.

Sparks, J. C., R. E. Masters, D. M. Engle, M. W. Palmer, and G. A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. Journal of Vegetation Science **9**:133-142.

Thorn, S., C. Bässler, R. Brandl, P. J. Burton, R. Cahall, J. L. Campbell, J. Castro, C. Y. Choi, T. Cobb, and D. C. Donato. 2018. Impacts of salvage logging on biodiversity: A meta-analysis. Journal of Applied Ecology **55**:279-289.

Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. Forest ecology and management **135**:155-167.

Waldron, K., J. C. Ruel, S. Gauthier, L. De Grandpré, and C. J. Peterson. 2014. Effects of post-windthrow salvage logging on microsites, plant composition and regeneration. Applied vegetation science **17**:323-337.

CHAPTER 2

THE EFFECTS OF EXPERIMENTAL WIND DISTURBANCE SEVERITY ON HERBACEOUS SPECIES DIVERSITY AND COMPOSITION IN A GEORGIA PIEDMONT FOREST[1]

[1] AJ Menzmer, CA Oldfield, and CJ Peterson. To be submitted to *Southeastern Naturalist*.

ABSTRACT

Herbaceous species are often the most diverse component of forests, yet their responses to disturbance are far less understood than woody plant communities. Disturbances may contribute to species richness in the herbaceous layer by allowing numerous species to establish that typically are excluded from intact forests. Based on the intermediate disturbance hypothesis, I hypothesize that wind disturbance events of moderate severity will facilitate the greatest diversity of herbaceous species when compared to severe disturbances or undisturbed forests. I also predict species composition will diverge in the proportion of annuals and perennials depending on disturbance severity level. To test this, I created an experimental wind disturbance of two levels - 50% damage severity and 100% damage severity (severity based on percent basal area felled) - using chainsaws near Watkinsville, GA in 2018. In 2019, 2021, and 2022 I measured the percent cover of herbaceous species within randomly placed $1m^2$ quadrats in the 100% (moderate severity) treatment (n = 26), 50% (low severity) treatment (n = 38), and undisturbed (control) forest (n = 46). I found, in support of my hypothesis, that average Shannon diversity increased with disturbance severity; herb diversity was consistently highest during all years in the moderate severity treatment (1.07+/- 0.54 to 1.28 +/- 0.51) while the low severity and control treatments alternated between years in claiming lowest diversity. Results from MRPP analysis and NMDS ordination indicate consistent compositional dissimilarity between most treatments in most years; however, severity does not appear to be the direct cause. These results support the growing body of literature that suggests moderate disturbance severity is key in leading to high herbaceous species diversity. However, there is a need for ongoing studies of the herb layer to better understand the lasting changes of different severity wind disturbances on herbaceous diversity and composition.

INTRODUCTION

Natural disturbances such as severe windstorms and wildfires are forecasted to increase in both frequency and severity as climate warms (Jones et al. 2022, Balaguru et al. 2023). Understanding how these disruptive events can affect plant diversity (Elliott et al. 2002, Palm et al. 2022, Sparks 1988) is important in the preservation of species. Wind disturbance can cause profound shifts in forest plant diversity and composition, especially through the creation of pits and mounds (Ulanova 2000). Wind disturbance caused Minnesota tree species to exhibit both early- and late-successional species post-disturbance (Anoszko et al. 2022) due to moderate severity. Wind disturbance caused Pennsylvania herbaceous species to shift towards early-successional species post-disturbance (Peterson and Pickett 1995) due to increased light availability. Wind disturbance caused an increase in tree species richness compared to undisturbed forests and an increase in mid-successional tree species (Peterson and Pickett 1995, 2000). While it is accepted that disturbance severity impacts plant diversity and composition, the lack of studies that quantify disturbance severity presents challenges to creating generalized predictions of how severity will impact plant species.

The most common quantification of disturbance severity has been the subdividing of gaps into ‘large’, ‘mid-sized’, or ‘small’, but these qualitative names have varying quantitative measurements across studies (Anderson and Leopald 2002, Kern et al. 2014). Studies have found that herbaceous species richness, a component of herbaceous species diversity, generally increases with increasing gap size (Goldblum 1997, Anderson and Leopald 2002, Schumann 2003, Zenner 2006, Naaf and Wulf 2007, Falk 2008). Environmental heterogeneity and gaps increase compositional dissimilarity between disturbed and undisturbed treatments of forest due to niche partitioning and increased light availability (Beatty 1984, Schumann 2003, Naaf and Wulf 2007). Studying diversity directly, Kern et al. (2014) found herbaceous diversity increased between small and medium gaps, but decreased when gap size increased from medium to large gaps. A major limitation found in the existing literature is the reliance on natural wind disturbances. Notably, few studies use controlled experimental wind disturbances to isolate the effect of disturbance severity on herbaceous species and instead emphasize woody species (Barker-Plotkin et al. 2013, Cannon et al. 2019). The exception is Collins and Pickett (1988), who studied the impact of experimental wind disturbance on herbaceous cover in Pennsylvania. They created three single-tree and three multi-tree canopy gaps, sampling one year pre-disturbance and three years post-disturbance. They found that in this timeframe, the cover of herbs and ferns increased while the dominant species *Erythronium americanum* decreased. However, the cover of any herbaceous species did not vary at all with disturbance severity. The authors speculated that larger gaps may impact herbaceous cover more than the gaps used in their experimental design. Larger scale experiments that better mimic real disturbances are necessary to test the effects of severity on herbaceous species.

The term ‘severity’ in disturbance literature is used broadly but with varying definitions. A more restricted view (Frelich and Reich 1999) is that severity is measured as percent tree mortality; while broader views consider the extent of damage to understory vegetation, and forest floor (Oliver & Larson 1996). Roberts (2004) states that a severe disturbance must have substantial overstory as well as soil disturbance. Here I measure severity as percent tree basal area fallen or removed from the canopy, so that an area with 100% basal area down is a more severe disturbance than an area with a lesser percentage of basal area down.

In this study, I use four conceptual models that provide predictions of how disturbance impacts species diversity and composition.

The intermediate disturbance hypothesis (IDH, Connell 1978), known for its emphasis on how diversity is influenced by disturbance frequency, can be alternatively understood as the relationship between diversity and disturbance severity. This hypothesis predicts that in low severity situations, disturbance-intolerant species will competitively exclude other species and thus lower overall species diversity. In high severity situations, a small group of disturbance-tolerant specialists with advantageous traits like rapid growth and efficient dispersal will fill newly vacant niches, once again reducing overall species diversity. Stated otherwise, low disturbance severity fails to create environments to support competitively-inferior species due to the relatively high number of competitively-superior species still present, while high disturbance severity destroys high enough numbers of competitively-superior species that they are no longer dominant. While the original disturbance-tolerant/intolerant framing of the IDH has drawn criticism for its simplicity and lack of empirical validation, the alternative interpretation based on competitive inferiority/superiority has garnered moderate acceptance within the ecological community (Fox 2013, Sheil & Burslem 2013). Nevertheless, reviews of the IDH (Mackey & Currie 2001, Kershaw & Mallik 2013) offer mixed results. Mackey & Currie (2001) and Kershaw and Mallik (2013) noted that the unimodal pattern is most often observed where severe disturbances affect sessile species and where studies were conducted in well-drained soils. Given this study examines sessile plants in the well-drained soils of the Piedmont (Alabama Cooperative Extension System 2023), predictions of IDH may apply.

Schippers et al. (2001) used a simulation model to explore how disturbance severity influences herbaceous composition, mediated by three life history traits: adult longevity (annual/perennial), seed size (large/small), and dormancy (dormant or non-dormant). In the simulation, a disturbance was defined as the removal of organisms. The simulation found that in undisturbed communities, perennials with non-dormant small seeds dominate. Perennials with dormant small seeds dominated with mild disturbance. As disturbance severity increased, annuals dominated – first with small non-dormant seeds followed by small dormant seeds. Relevant to my study, perennial dominance was observed at lower severities and annual dominance at higher ones.

Roberts (2004) considers the impact of disturbance severity on herbaceous species' regeneration mechanisms. Following disturbances of higher severity, Roberts (2004) predicts that regeneration occurs solely through seeds due to the erosion of soil; however, as disturbance severity lowers and more of the soil is left in place post-disturbance, the importance of vegetative regeneration such as rhizomes increases. However, as wind disturbance primarily affects the tree canopy, Roberts provides the caveat that limited change in regeneration may be observed.

While not a formal model per se, studies such as Mabry and Korsgren (1998), Lang et al. (2009), and Palm et al. (2022) underscore a trend. All three studies were twenty- to fifty-year retrospectives on the impacts of wind and salvage logging on herbaceous species. The authors found that after the progression of time, the difference in diversity between treatments was negligible and composition was increasingly dominated by late-successional species as time progressed. While my study covers a much smaller timeframe, nevertheless I expect that differences in diversity may decrease and the abundance of late-successional species may increase with the progression of time.

With these models and literature in mind, I hypothesize that a) herbaceous diversity will be greatest in the moderate severity treatment and b) the differences in diversity between treatments will decrease from being significant to nonsignificant as time progresses (Hypothesis 1). I hypothesize that with increasing disturbance severity, the disturbed treatments will exhibit dissimilar species composition post-disturbance when compared to the control treatment and that the differences will decrease with time (Hypothesis 2).

METHODS

To test these hypotheses, I compared herbaceous diversity and composition in three experimental wind disturbance treatments varying in degree of tree mortality (i.e. severity). The experimental wind disturbance site is located at Watson Springs (N 33.69, W -83.28), a mature secondary pine-hardwood closed-canopy forest in the Georgia Piedmont (Warnell School of Forestry & Natural Resources 2021). Soils on the site are sandy loams of the Cecil series classified as Typic Kanhapludults (Oldfield 2021), typical of the Piedmont. The average minimum and maximum temperatures are 11 °C and 24 °C, respectively with an annual average precipitation of 129 cm (College of Agricultural and Environmental Sciences 2023).

The experiment was established in 2018 and consisted of three adjacent 70x70 meter treatments. In the first (moderate severity) treatment, all basal area from trees > 5 cm dbh were felled by chainsaws and remained in place. In the second (low severity) treatment, the basal area from half of trees > 5 cm dbh were felled by chainsaws and remained in place. The third treatment was left as an undisturbed control (Oldfield 2021). Each treatment was divided into forty-nine 100 m^2 squares, with one 1 m^2 quadrat located randomly in each square. In 2019, 2021, and 2022, I identified all herbaceous plants to species and estimated percent cover within each quadrat. When species could not be identified, they were distinguished by morphotype and percent cover data was collected. Percent cover, beyond common percentages such as 25%, 50%, or 75%, was determined by my outstretched hand representing 5% and my closed fist representing 1%. In the case of species overlapping cover, each species was given percent cover; total quadrat percent cover was allowed to exceed 100%. Unfortunately, natural causes out of my control caused the locations and markings of some quadrats to become lost. Thus, over all three years, twenty-six quadrats were sampled in the moderate severity treatment, thirty-eight quadrats in the low severity treatment, and forty-six quadrats in the control treatment. Fieldwork occurred between 1 September to 15 October 2019, 11 May to 30 June 2021, and 5 July to 18 July 2022. The phenology of the ten most common species covers this multi-season timeframe (US Forest Service 2023, Vascular Plants of North Carolina 2023, Lady Bird Johnson Wildflower Center 2023).

To test the hypothesis that diversity will be greatest in areas of moderate disturbance severity in a closed-canopy forest but decrease over time (Hypothesis 1), I calculated the diversity of each quadrat using the Shannon-Wiener (H') index. Quadrats with one or no species present were given a zero. Next, I averaged all the quadrat diversity values to compute average diversity values and standard deviations for each treatment in each year. As only one replicate of each treatment (average diversity) exists, I am limited to descriptive statistics to avoid pseudoreplication.

To test the hypothesis that the initial post-disturbance compositional dissimilarity of treatments will decrease with the progression of time (Hypothesis 2), I used both multi-response permutation procedures (MRPP) and non-metric multidimensional scaling (NMDS) to compare compositional dissimilarity between treatments. MRPP is a nonparametric analysis well suited to community ecology data and gives a measure of dissimilarity for all pairwise comparisons of the three groups (McCune and Grace 2002). I defined groups, or treatments, by the disturbance severity: moderate = 100% of the basal area removed, low = 50% of the basal area removed, and control = 0% of the basal area removed (Peck 2016). I used Sorensen distances as it is less prone to the influence of outliers (Peck 2016). MRPP produces three outputs for each pairwise comparison of groups: a test statistic (T) which indicates how large the separation between treatments is, an agreement value (A) which represents the level of within-group homogeneity, and a p-value which indicates statistical significance (Peck 2016). NMDS is an ordination approach that illustrates differences in species composition graphically – greater distance between points indicates greater compositional differences between plots. The stress value of an NMDS refers to combining multiple species on to a single dimension, and can range from 0 to 1, with the lower values indicating a better fit of the data. Stress values 0.3 or under and two dimensions for ease of interpretability are advised (Peck 2016). Observation of one species, *Polygonatum*, was removed as it was observed only once in the 2019 dataset. Additionally, a total of sixteen quadrats were removed from the 2019 analysis due to no cover present. Several sedge species were pooled into one sedge morphotype for analysis. Observation of two species, *Vaccinium arboreum*, and *Aristolochia serpentaria,* were removed as they were only observed once in the 2021 dataset.

To further examine the impact of disturbance severity on herbaceous composition, change over time in the percentage of perennials and overall herbaceous percent cover was examined. To determine if there were significant differences in the richness of annuals and perennials in the treatments over time, I utilized a binomial regression. To investigate how disturbance severity impacts the growth or decline of herbaceous percent cover in quadrats over time, I utilized a chi-squared test of independence.

RESULTS

In 2019, the average Shannon's diversity index of quadrats (hereafter, diversity) in the moderate severity treatment (n=26) was 1.28 (SD: +/- 0.51). Diversity of the low severity treatment (n=38) was 0.49 (SD: +/- 0.49), and of the control treatment (n=46) was 0.18 (SD: +/- 0.32) (Fig. 1A). In 2021, the average diversity of the moderate severity treatment was 1.12 (SD: +/- 0.56), of the low severity treatment was 0.99 (SD: +/- 0.48), and of the control treatment was 1.08 (SD: +/- 0.41) (Fig 1B). In 2022, the average diversity of the moderate severity treatment was 1.07 (SD: +/- 0.54), of the low severity treatment was 0.51 (SD: +/- 0.39), and of the control treatment was 0.81 (SD: +/- 0.56) (Fig. 1C).

The average diversity of the moderate severity treatment was consistently highest in all three years compared to the average diversity of the other two treatments. In 2019, the lowest average diversity was observed in the control treatment. In 2021 and 2022, the lowest average diversity was observed in the low severity treatment. The standard deviation ranges for all treatments in all years are overlapping, indicating likely nonsignificance.

In 2019, the MRPP output indicated significant compositional dissimilarity in both the moderate vs. low and moderate vs. control treatment comparisons (Table 2-1). The moderate vs. control treatment comparison exhibited the largest compositional dissimilarity according to T value (Table 2-1). The NMDS (Figure 2-2A) illustrates the compositional dissimilarity between these treatments. In 2021 and 2022, the MRPP output indicated all treatment comparisons were compositionally dissimilar, except for moderate vs. low in 2022. The moderate vs. control treatment comparisons again exhibited the maximum compositional dissimilarity according to T value (Table 2-1). Despite the overlap in all treatments, the NMDS figures (Figure 2-2B, C) do support the moderate vs. control treatment comparisons possessing maximum dissimilarity (Stress values: 2019, 0.12; 2021, 0.24; 2022, 0.20). With slight variation, similar species drove the compositional differences each year (Figure 2-2D, E, F). In 2019, the genera and species that contributed most strongly to compositional differences among treatments included *Smilax glauca*, *Euonymus americana*, and *Bignonia capriolata*; in 2021, *Vitis rotundifolia*, *Hypoxis hirsuta*, *Callicarpa americana*, *Dichanthelium*, *Smilax glauca*, and *Leersia virginica*; in 2022, *Vitis rotundifolia*, *Smilax glauca*, *Leersia virginica*, *Euonymus americanus*, and *Callicarpa americana*.

Significant differences were found in the richness of perennials and annuals dependent on treatment ($p < 0.01$), year ($p < 0.001$), and the interaction of treatment and year ($p < 0.01$). The percentage of perennial species decreased in the control treatment (100% in 2019 and 2021 to 93% in 2022), and increased in both the low and moderate severity treatments (low: 87% in 2019 to 100% in 2021 and 2022; moderate: 90% in 2019 to 92% in 2021 and 96% in 2022). Annual species *Viola sororia* and *Erechtities hieraciifolius* were observed growing at the moderate severity treatment in 2019 (one year post-disturbance) but not in 2021 or 2022 (three and four years post-disturbance).

Figure 2-3 presents the average percent cover (+/- two standard errors) of species that propagate using seeds and rhizomes, respectively, in each treatment and year combination. Overlapping error bars between treatments for both regeneration mechanisms suggest nonsignificant differences. The exception is the error bars of the rhizomatous species in 2021, whose values differ by less than one percent. This is a questionable difference at best.

Table 2-S1 showcases the total cover for all 110 quadrats in each year of sampling plus the overall trend in this timeframe. The chi-square test indicates significance ($\chi^2 = 40.26$, df = 4, p = 3.82e-08). Post-hoc tests indicate significance in herbaceous cover increasing and decreasing over time in the moderate severity treatment, significance in herbaceous cover observing no change in the low severity treatment, and significance in herbaceous cover increasing in the control treatment. Overall, there was an increase in cover in 51% (56/110) of quadrats, a decrease in 48% (53/110) of quadrats, and no change in cover was observed in one quadrat. Sorted by treatment, the vast majority (85%) of quadrats in the moderate severity treatment decreased in cover from 2019 – 2022. In the low severity treatment, the distribution was more equal with 55% of quadrats increasing in cover and 45% of quadrats decreasing in cover. In the control treatment, most quadrats (67%) increased in cover.

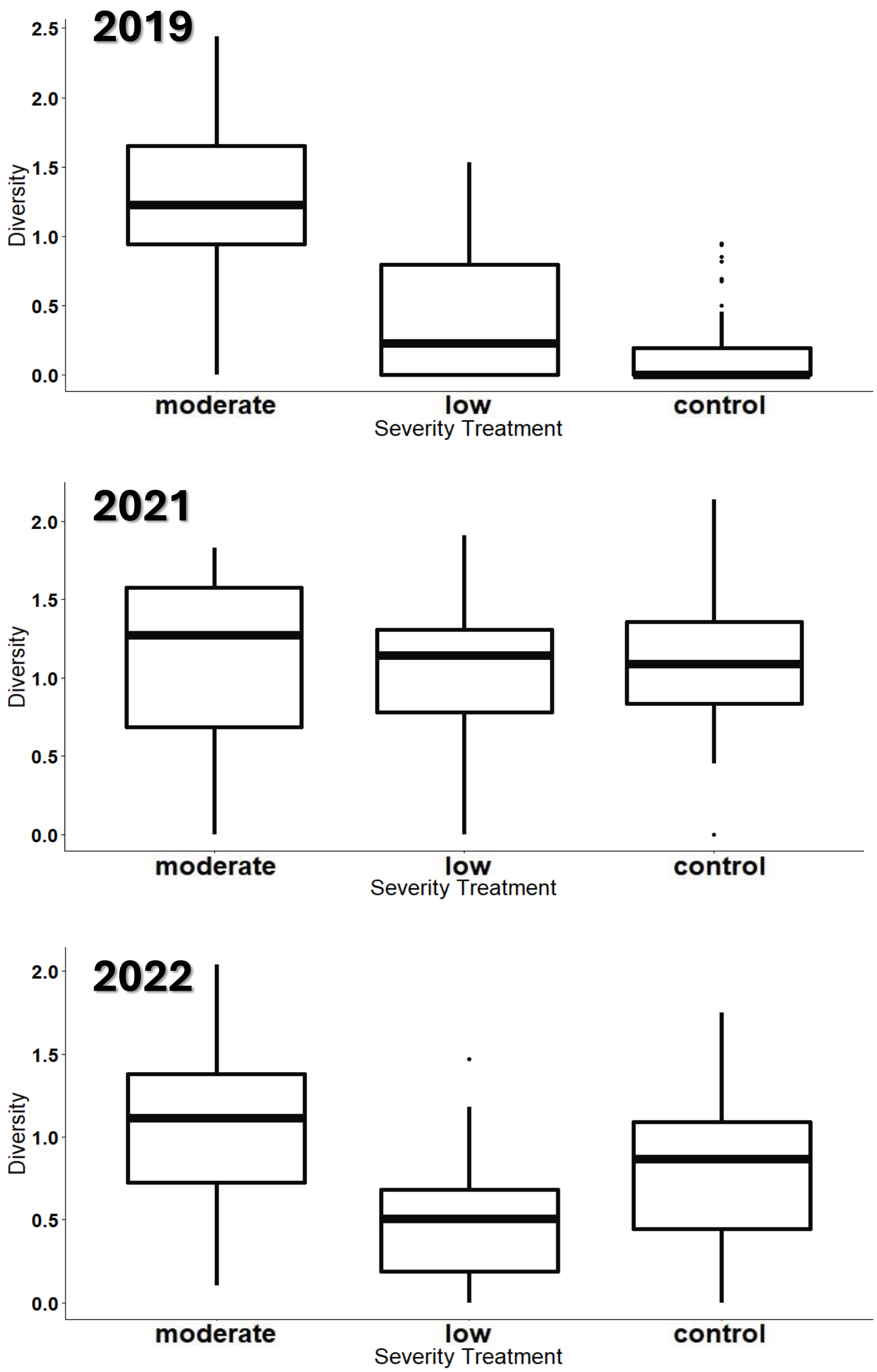


Figure 2-1. Average Shannon diversity values per severity treatment for 2019, 2021, and 2022. Moderate = 100% severity, low = 50% severity, control = 0% severity.

Table 2-1. MRPP output of the test statistic (T), effect size (A), and statistical significance (p) of the three treatment comparisons at Watson Springs in 2019, 2021, and 2022. Cutoff of significance: 0.01.

Comparison	*T*	*A*	*p*
2019 moderate vs. low	-14.02	0.07	< 0.01
2019 moderate vs. control	-22.55	0.11	< 0.01
2019 low vs. control	-1.42	0.01	0.09
2021 moderate vs. low	-3.72	0.02	< 0.01
2021 moderate vs. control	-15.28	0.06	< 0.01
2021 low vs. control	-5.41	0.02	< 0.01
2022 moderate vs. low	-2.68	0.01	0.02
2022 moderate vs. control	-10.20	0.04	< 0.01
2022 low vs. control	-6.94	0.03	< 0.01

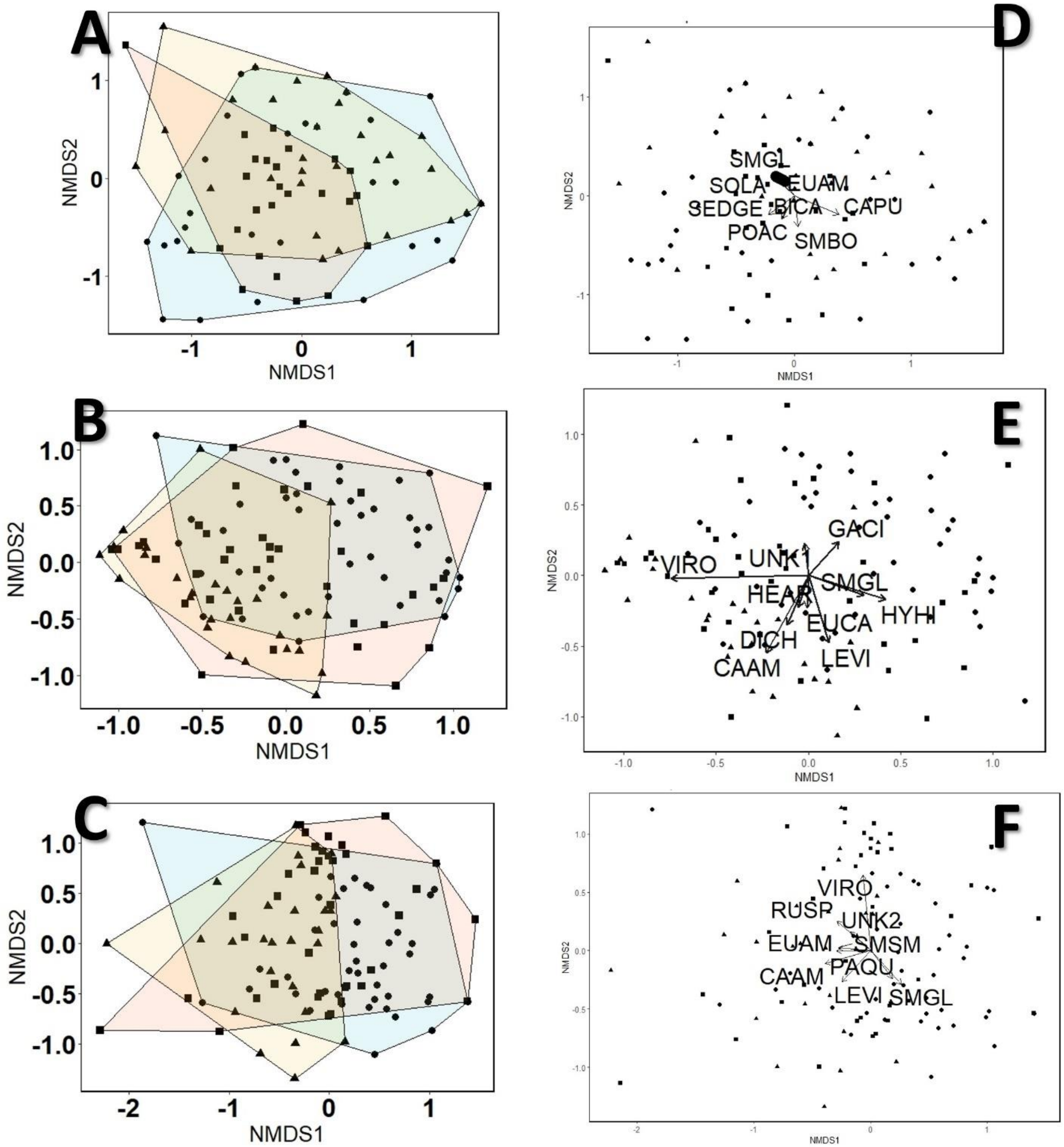
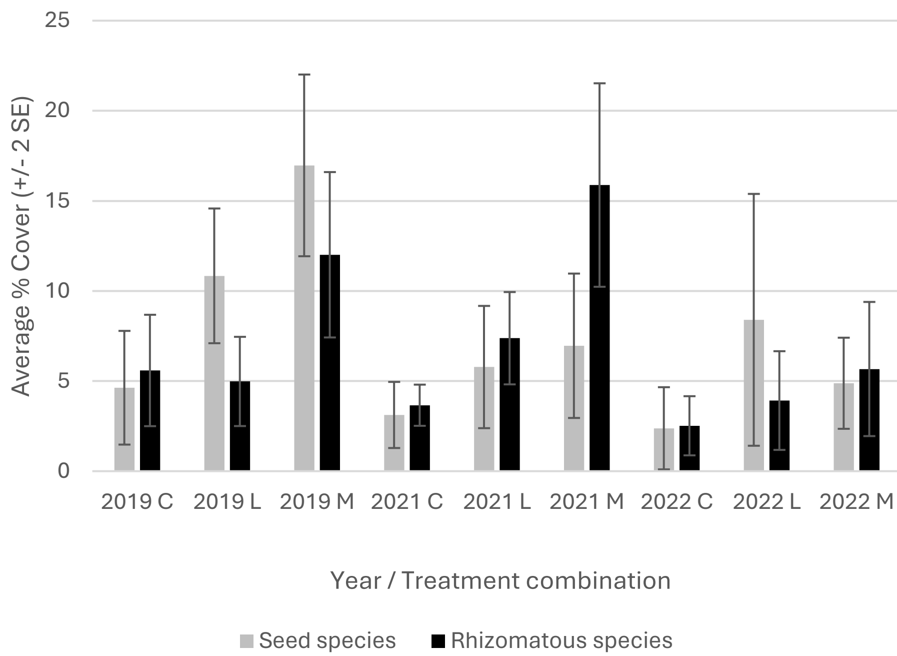


Figure 2-2. The compositional dissimilarity between treatments at Watson Springs in 2019 (A, D), 2021 (B, E), and 2022 (C, F) as displayed in NMDS graphs. Blue/circles represent the control treatment, orange/squares represent the low severity treatment, and yellow/triangles represent the moderate severity treatment. (A, B, C) show compositional overlap of treatments with each other, while (D, E, F) indicate the species that drove the compositional dissimilarity. VIRO = Vitis rotundifolia, GACI = Galium circaezans, Rose = ROSE, Smilax glauca = SMGL, Hexastylis arifolia = HEAR, Dichanthelium = DICH, Hypoxis hirsuta = HYHI, Eupatorium capillifolium = EUCA, Leersia virginica = LEVI, Callicarpa americana = CAAM, Rubus sp. =

RUSP, Smilax smalli = SMSM, Parthenocisscus quinquefolia = PIQU, Euonymous americana = EUAM. Unknown species = UNK1, UNK2. SOLA = Solanceae , SEDGE = sedge species, POAC = Poaceae , SMBO = Smilax bono-nox, CAPU = Carex purpurifera, BICA = Bignonia capriolata.

Figure 2-3. The average percent cover (plus/minus 2 standard errors) of species that propagate using seeds or rhizomes in each year/treatment combination of the experimental wind disturbance. Grey = seed species; black = rhizomatous species. C = control treatment; L = low severity treatment, M = moderate severity treatment.



DISCUSSION

This study aimed to determine how variation in wind disturbance severity may impact herbaceous species over short-term timespans. All years reveal significant dissimilarity between treatments in composition, while the impact of disturbance severity on diversity is more questionable due to overlapping error bars and pseudoreplication (Figure 2-1, Table 2-1).

In 2019, average treatment diversity exhibited a positive relationship with increasing disturbance severity as indicated by Figure 2-1. In 2021, diversity exhibited neither an overall positive nor negative relationship with increasing severity. In 2022, diversity exhibited an inconsistent relationship with increasing disturbance severity. These data support that species diversity will be greatest in areas of moderate severity (Hypothesis 1, Connell 1978) but that the differences in diversity between treatments will decrease with the progression of time. In light of the intermediate disturbance hypothesis, these data represent herbaceous species that experienced light to moderate disturbance severity – the leftmost half of the IDH curve. Webb (1999) posited that disturbance causing a heterogeneous distribution of resources such as light, moisture, and nutrients is a fundamental assumption when predicting that disturbance will increase species diversity. Higher herbaceous diversity in the moderate severity treatment is consistent with the concept that severity may have caused enough heterogeneity to effect change (Table 1). The low severity treatment exhibiting lower diversity than the undisturbed control treatment in 2022 is particularly puzzling, as I would expect the low severity treatment to likely possess increased resource heterogeneity and thus higher diversity.

Herbaceous species composition differed significantly among most treatments and years (Table 2-1), with the greatest differences between moderate and control. The compositional dissimilarity observed is likely due to changes in resource availability. The data provides mixed support for Hypothesis 2, that increasing disturbance severity will cause increasingly dissimilar species composition post-disturbance, but that the differences will decrease with time. While there are differences between treatments immediately post-disturbance in 2019 (two comparisons significant), these differences stay consistent in 2021 and 2022 (three and two comparisons significant, respectively). Based on my hypothesis, I expected that herbaceous species in the experimental wind disturbance to consistently decrease in compositional dissimilarity with the progression of time. However, more consistent decreases may be observed during longer timespans than four years post-disturbance. Peterson and Pickett (1995) found in Pennsylvania following a tornado that the composition of herbs immediately post-disturbance was comprised predominantly of shade-intolerant species (such as *Erechtites hieracifolia*) in the disturbed area. However, these species began to decline four to six years post-disturbance. Barker-Plotkin et al. (2013) found that twenty years following an experimental wind disturbance, herbaceous composition was not significantly different to pre-disturbance conditions. I observed shade-intolerant species *Viola sororia* and *Erechtities hieraciifolius* in 2019 (one year post-disturbance) but not in 2021 or 2022 (three and four years post-disturbance). This compositional trend is supported by the increasing percentage of perennials in the moderate severity treatment as time progressed. *Vitis rotundifolia* and *Smilax glauca* were two perennials that contributed to compositional dissimilarity, likely due to how common they were in the treatments. My results support the early dominance of shade-intolerant annuals in treatments of greater severity immediately post-disturbance. Subsequently, perennials increased in dominance with the simultaneous increase in time post-disturbance and decreasing effects of said disturbance, supporting the prediction of Schippers et al. (2001) that perennials will dominate in areas of lower disturbance severity.

Neither severity treatment nor time were observed to cause differences (+/- 2 SE) in the average percent cover of seeded and rhizomatous species, save for the < 0.5% differences between rhizomatous species in 2021. Rhizomatous species can be more resilient to wind disturbance than species that use seeds as a reproductive strategy, as rhizomatous species' reproductive organs are not exclusively aboveground and thus susceptible to wind damage (Yu et al. 2008, Kettenring et al. 2014). However, as wind disturbance primarily affects the tree canopy as opposed to the herbaceous layer, the nondifference of herbaceous average percent cover in each treatment is unsurprising (Roberts 2004).

The differences in total cover (Table S1) between 2019 and 2022 in each treatment underscores the likely importance of light and dispersal in herbaceous species' growth. The general decrease in herbaceous cover in the moderate severity treatment, on the surface a surprising finding, could potentially be attributed to the increasing dominance of species such as *Rubus* spp., *Vitis rotundifolia*, and *Callicarpa americana* with the progression of time post-disturbance which crowd out other herbaceous species (personal observation). The roughly equal number of quadrats with an increase or decrease in cover in the low severity treatment makes sense due to it having fifty percent of tree basal area felled; this treatment supports a mix of shade-intolerant and shade-tolerant species. Finally, many quadrats in the control treatment increasing in cover could possibly be due to edge effects, from species in the low severity treatment dispersing via seed or rhizomes. These results align with the predictions of Collins and Pickett (1988): larger gaps – likely due to greater light availability – do cause changes in herbaceous cover.

Four improvements to the experimental design of future studies come to mind when considering these results. First, due to aforementioned the quasi-closed-canopy that *Rubus* spp., *Vitis rotundifolia*, and *Callicarpa americana* appear to have created over the moderate severity treatment post-disturbance, I suggest future studies adding hemispherical photography at each quadrat each year of sampling post-disturbance. Quantification of canopy openness for each quadrat would underscore the importance of light availability in how disturbance severity affects herbaceous diversity and composition. Secondly, collecting soil moisture data in each quadrat would be beneficial in determining the impact of water on herbaceous diversity and composition. Third, while not always feasible, establishing replicate treatments in an experimental wind disturbance – not just subsampled quadrats – could provide the opportunity for true replication and greater generality. Fourth, establishing an experimental wind disturbance followed by partial salvage logging or fire could indicate how herbaceous species respond to compound disturbance at quantifiable severity levels. Cannon et al. (2019), studying in Georgia, found that the presence of both experimental wind and fire disturbance had differing impacts on sapling composition than either disturbance separately, but no studies to my knowledge have studied the impact of experimental wind disturbance in combination with fire or salvage logging on herbaceous species diversity and composition. More comprehensive data collection, prevented in my case due to logistical constraints, may help to illuminate the impact of abiotic factors such as soil moisture or light availability on herbaceous diversity and composition.

In summary, average herbaceous diversity increased with disturbance severity and compositional dissimilarities between treatments were maintained over a range of severities in a closed-canopy experimental wind disturbance one to four years post-disturbance. These findings suggest that disturbance severity – and the likely change in light availability – appears to have a noticeable effect on herbaceous diversity and composition in short-term timespans, but the impact on diversity is temporary and the impact on composition more long-lasting. These data should encourage future short-term experimental wind disturbance studies that collect both biotic and abiotic data relating to the impact of disturbance severity (as opposed to canopy gaps) with herbaceous diversity and composition. Data from such studies would provide knowledge of which herbaceous species may be most at risk because of climate change and aid scientists in making preservation recommendations.

LITERATURE CITED

Alabama Cooperative Extension System. “Alabama Soils: Piedmont Plateau”. Revised 21 August 2018. Accessed 17 November 2023. https://www.aces.edu/blog/topics/healthy-soils/alabama-soils-piedmont-plateau/

Anderson, K. L., and D. J. Leopold. 2002. The role of canopy gaps in maintaining vascular plant diversity at a forested wetland in New York State. Journal of the Torrey Botanical Society:238-250.

Anoszko, E., L. E. Frelich, R. L. Rich, and P. B. Reich. 2022. Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere **13**:e3952.

Balaguru, K., W. Xu, C.-C. Chang, L. R. Leung, D. R. Judi, S. M. Hagos, M. F. Wehner, J. P. Kossin, and M. Ting. 2023. Increased US coastal hurricane risk under climate change. Science advances **9**:eadf0259.

Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. Ecology **65**:1406-1419.

Cannon, J. B., S. K. Henderson, M. H. Bailey, and C. J. Peterson. 2019. Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. Forest ecology and management **436**:117-128.

College of Agricultural and Environmental Sciences, University of Georgia. “Iron Horse Farm Historical Data”. Revised 6 April 2023. Accessed 16 June 2023. http://www.georgiaweather.net/mindex.php?variable=HI&site=PENFIELD

Collins, B. S., and S. Pickett. 1988. Response of herb layer cover to experimental canopy gaps. American Midland Naturalist:282-290.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. Science **199**:1302-1310.

Dytham, C. 2011. Choosing and using statistics: a biologist's guide. John Wiley & Sons.

Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. Journal of the Torrey Botanical Society:48-59.

Falk, K. J., D. M. Burke, K. A. Elliott, and S. B. Holmes. 2008. Effects of single-tree and group selection harvesting on the diversity and abundance of spring forest herbs in deciduous forests in southwestern Ontario. Forest ecology and management **255**:2486-2494.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in ecology & evolution **28**:86-92.

Frelich, L. E., and P. B. Reich. 1999. Minireviews: neighborhood effects, disturbance severity, and community stability in forests. Ecosystems **2**:151-166.

Goldblum, D. 1997. The effects of treefall gaps on understory vegetation in New York State. Journal of Vegetation Science **8**:125-132.

Jones, M. W., J. T. Abatzoglou, S. Veraverbeke, N. Andela, G. Lasslop, M. Forkel, A. J. Smith, C. Burton, R. A. Betts, and G. R. van der Werf. 2022. Global and regional trends and drivers of fire under climate change. Reviews of Geophysics **60**:e2020RG000726.

Kern, C. C., R. A. Montgomery, P. B. Reich, and T. F. Strong. 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. Forest Science **60**:335-344.

Kershaw, H. M., and A. U. Mallik. 2013. Predicting plant diversity response to disturbance: applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. Critical Reviews in Plant Sciences **32**:383-395.

Kettenring, K. M., D. F. Whigham, E. L. Hazelton, S. K. Gallagher, and H. M. Weiner. 2015. Biotic resistance, disturbance, and mode of colonization impact the invasion of a widespread, introduced wetland grass. Ecological Applications **25**:466-480.

Kirkman, L. K., P. C. Goebel, B. J. Palik, and L. T. West. 2004. Predicting plant species diversity in a longleaf pine landscape. Ecoscience **11**:80-93.

Lady Bird Johnson Wildflower Center. "Vitis rotundifolia". Accessed 23 June 2023. https://www.wildflower.org/plants/result.php?id_plant=viro3

Mackey, R. L., and D. J. Currie. 2001. The diversity–disturbance relationship: is it generally strong and peaked? Ecology **82**:3479-3492.

McCune, B., et al. 2002. Analysis of ecological communities, MjM software design, Gleneden Beach, Oregon, USA.

Miller, J. H., and K. V. Miller. 2005. Forest plants of the southeast and their wildlife uses. University of Georgia Press.

Naaf, T., and M. Wulf. 2007. Effects of gap size, light and herbivory on the herb layer vegetation in European beech forest gaps. Forest ecology and management **244**:141-149.

NCSU. 2024. North Carolina Extension Gardener Plant Toolbox. Accessed 22 January 2024 https://plants.ces.ncsu.edu/

Oldfield, C.A. 2021. Windthrow and salvage logging effects on forest recovery, composition, and carbon pools in the southeastern us. Dissertation, University of Georgia, Athens, Georgia, USA.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics: Updated edition. John Wiley and sons.

Palm, K., F. Vodde, T. Tullus, J. Engelhart, and K. Jõgiste. 2022. Impact of different storm severity levels and post-storm management on understory vegetation richness, diversity and composition 19–20 years after wind disturbance. Forest ecology and management **524**:120506.

Peck J. 2016. Multivariate Analysis for Ecologists, MjM software design, Gleneden Beach, Oregon, USA.

Peterson, C. J., and S. T. Pickett. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology **76**:763-774.

Peterson, C. J., and S. T. Pickett. 2000. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos **90**:489-500.

Plotkin, A. B., D. Foster, J. Carlson, and A. Magill. 2013. Survivors, not invaders, control forest development following simulated hurricane. Ecology **94**:414-423.

Roberts, M. R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany **82**:1273-1283.

Schippers, P., J. M. Van Groenendael, L. M. Vleeshouwers, and R. Hunt. 2001. Herbaceous plant strategies in disturbed habitats. Oikos **95**:198-210.

Schumann, M. E., A. S. White, and J. W. Witham. 2003. The effects of harvest-created gaps on plant species diversity, composition, and abundance in a Maine oak–pine forest. Forest ecology and management **176**:543-561.

Sheil, D., and D. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. Trends Ecol. Evol **28**:571-572.

Sparks, J. C., R. E. Masters, D. M. Engle, M. W. Palmer, and G. A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. Journal of Vegetation Science **9**:133-142.

Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. Forest ecology and management **135**:155-167.

US Forest Service. "Parthenocissus quinquefolia". Accessed 23 June 2023. https://www.fs.usda.gov/database/feis/plants/vine/parqui/all.html

Vascular Plants of North Carolina. "Asplenium platyneuron". Accessed 23 June 2023. https://auth1.dpr.ncparks.gov/flora/species_account.php?id=4121

Warnell School of Forestry & Natural Resources. "Watson Spring Forest". Accessed 27 September 2021. https://www.warnell.uga.edu/about/centers-labs/watson-springs-forest

Webb, S. 1999. Disturbance by wind in temperate-zone forests. Ecosystems of disturbed ground:187-222.

Yu, F.-H., N. Wang, W.-M. He, Y. Chu, and M. Dong. 2008. Adaptation of rhizome connections in drylands: increasing tolerance of clones to wind erosion. Annals of botany **102**:571-577.

Zenner, E. K., J. M. Kabrick, R. G. Jensen, J. E. Peck, and J. K. Grabner. 2006. Responses of ground flora to a gradient of harvest intensity in the Missouri Ozarks. Forest ecology and management **222**:326-334.

SUPPLEMENTAL

Table 2-S1. Herbaceous species cover in each quadrat (and treatment) in each year of sampling at Watson Springs, plus the trend that cover exhibited.

Treatment	Quadrat	2019	2021	2022	Trend
Moderate	A1	116	160	60	Decrease
Moderate	A2	111	145	90	Decrease
Moderate	A3	321	130	25	Decrease
Moderate	A4	183	86	9	Decrease
Moderate	A5	110	17	25	Decrease
Moderate	A6	75	106	96	Increase
Moderate	A7	35	85	59	Increase
Moderate	B1	70	120	33	Decrease
Moderate	B2	57	165	27	Decrease
Moderate	B4	147	115	19	Decrease
Moderate	B5	182	55	64	Decrease
Moderate	B6	115	175	20	Decrease
Moderate	C1	70	150	46	Decrease
Moderate	C7	66	87	61	Decrease
Moderate	D6	175	205	70	Decrease
Moderate	D7	101	116	22	Decrease
Moderate	E1	12	45	4	Decrease
Moderate	E2	146	80	65	Decrease
Moderate	E6	40	91	24	Decrease

Moderate	E7	0	15	20	Increase
Moderate	F1	200	60	25	Decrease
Moderate	F2	115	150	30	Decrease
Moderate	F6	75	115	31	Decrease
Moderate	F7	120	185	105	Decrease
Moderate	G4	138	92	27	Decrease
Moderate	G7	35	150	47	Increase
Low	H1	6	37	1	Decrease
Low	H2	1	10	21	Increase
Low	H3	95	114	21	Decrease
Low	H5	71	52	108	Increase
Low	H7	0	10	50	Increase
Low	I1	30	37	42	Increase
Low	I2	33	95	82	Increase
Low	I4	127	36	35	Decrease
Low	I5	0	27	82	Increase
Low	I6	5	66	63	Increase
Low	J2	100	94	52	Decrease
Low	J3	0	60	30	Increase
Low	J4	40	62	85	Increase
Low	J5	30	115	42	Increase
Low	J6	10	1	1	Decrease
Low	J7	10	80	31	Increase
Low	K1	5	100	3	Decrease
Low	K2	7	49	34	Increase
Low	K3	1	93	59	Increase
Low	K4	5	70	10	Increase
Low	K6	10	38	6	Decrease
Low	L2	25	74	3	Decrease
Low	L4	35	9	14	Decrease
Low	L5	20	47	7	Decrease
Low	L6	20	20	17	Decrease

Low	L7	70	70	40	Decrease
Low	M1	3	41	10	Increase
Low	M4	75	75	55	Decrease
Low	M5	30	180	83	Increase
Low	M6	10	50	23	Increase
Low	M7	10	4	3	Decrease
Low	N1	0	73	9	Increase
Low	N2	16	19	26	Increase
Low	N3	46	38	9	Decrease
Low	N4	20	115	3	Decrease
Low	N5	15	80	81	Increase
Low	N6	5	43	10	Increase
Low	N7	3	55	1	Decrease
Control	O2	10	69	29	Increase
Control	O3	20	85	7	Decrease
Control	O4	10	8	62	Increase
Control	O5	1	36	8	Increase
Control	O6	11	87	6	Decrease
Control	O7	0	12	9	Increase
Control	P1	22	39	44	Increase
Control	P2	10	30	10	No change
Control	P3	1	45	5	Increase
Control	P4	6	115	17	Increase
Control	P5	2	35	3	Increase
Control	P6	21	10	6	Decrease
Control	P7	51	85	10	Decrease
Control	Q1	0	12	4	Increase
Control	Q2	20	75	18	Decrease
Control	Q3	25	105	34	Increase
Control	Q4	25	70	47	Increase
Control	Q5	15	7	7	Decrease

Control	Q6	5	35	2	Decrease
Control	Q7	7	37	22	Increase
Control	R1	0	35	3	Increase
Control	R4	25	70	37	Increase
Control	R5	0	55	13	Increase
Control	R6	0	2	2	Increase
Control	R7	85	12	11	Decrease
Control	S1	30	52	32	Increase
Control	S2	25	2	1	Decrease
Control	S3	0	12	13	Increase
Control	S4	10	11	16	Increase
Control	S5	1	18	15	Increase
Control	S6	11	50	5	Decrease
Control	S7	11	27	5	Decrease
Control	T1	5	22	11	Increase
Control	T2	5	24	24	Increase
Control	T3	0	3	3	Increase
Control	T4	0	14	15	Increase
Control	T5	5	11	14	Increase
Control	T6	6	9	1	Decrease
Control	T7	20	6	7	Decrease
Control	U1	1	7	13	Increase
Control	U2	20	32	22	Increase
Control	U3	0	11	8	Increase
Control	U4	0	10	6	Increase
Control	U5	5	12	26	Increase
Control	U6	0	1	1	Increase
Control	U7	10	5	1	Decrease

CHAPTER 3

WINDTHROW AND SALVAGE LOGGING ALTERS HERBACEOUS SPECIES COMPOSITION BUT NOT SHANNON DIVERSITY IN SHORT-TERM STUDY OF GEORGIA LONGLEAF PINE WOODLANDS[2]

[2] AJ Menzmer, JB Cannon, LM Giencke, and CJ Peterson. To be submitted to *Castanea*.

ABSTRACT

Fire-frequent longleaf pine woodlands of the southeastern US are imperiled ecosystems that support a high diversity of herbaceous species. However, severe disturbance from wind is expected to increase with climate change, so it is crucial to understand how wind disturbances impact plant diversity. Few studies have analyzed the effects of wind and salvage logging on herbaceous species diversity and composition in longleaf pine woodlands - a layer containing over 90% of woodland species. Here, I present a study of wiregrass-dominated longleaf pine woodlands affected by Hurricane Michael in 2018 and subsequent salvage logging and analyze how herbaceous diversity and composition differ between areas of varying damage three years post-disturbance.

In 2021, twelve sites were established and sampled at the Jones Center at Ichauway in Georgia; six in unsalvage logged stands and six in salvage logged stands. At each site we established one plot within a canopy gap created by Hurricane Michael and one within an adjacent intact woodland. Each plot contained three 1 m^2 sampling quadrats in which we recorded species presence and abundance (percent cover; diversity calculated using the Shannon index). This experimental design examined four severity treatments: unsalvage logged gap, unsalvage logged nongap, salvage logged gap, and salvage logged nongap. Herbaceous diversity did not differ between treatments with varying canopy cover or presence of salvage logging. Herbaceous composition did not differ between severity treatments except for the unsalvage logged gap vs. unsalvage logged nongap and unsalvage logged nongap vs. salvage logged gap comparisons.

These data support two conclusions: 1) wind and salvage logging plus the unexamined disturbance of fire both pre- and post-Michael does not change herbaceous diversity; 2) disturbances that occurred post-Michael such as salvage logging and fire may obscure the impact of wind disturbance on herbaceous composition. This work suggests that disturbances at present levels of severity have minimal impact on composition and null impact on the diversity of herbaceous species three years post-disturbance.

INTRODUCTION

Natural disturbances are one of several factors that can shape plant species diversity (Elliott et al. 2002, Palm et al. 2022, Sparks 1988). The frequency and intensity of hurricanes and fires, both common natural disturbances in the southeastern U.S., are forecasted to increase as a result of climate change (Jones et al. 2022, Balaguru et al. 2023). Therefore, understanding natural disturbances' impact on plant diversity is increasingly important.

Single disturbances have a broad range of impacts on plant diversity and composition. For example, fire increased herbaceous diversity in Arkansas and South Carolina due to an increase in light availability (Lewis and Harshbarger 1976, Sparks 1988) while wind caused tree species in Minnesota to exhibit a mixed composition that includes both early and late successional species post-disturbance (Anoszko et al. 2022). Wind disturbances in particular can impact plant diversity in forests through the creation of pits and mounds (Ulanova 2000).

Between 1979 – 2011 an increase in windstorms such as tornados has been observed in the southeastern United States (Gensini and Brooks, 2018). Salvage logging, the practice of removing fallen trees following a natural disturbance, is often carried out after windstorms and can increase the cumulative severity of damage following a natural disturbance (Lindenmayer and Noss 2006, Lindenmayer and Ough 2006, Peterson and Leach 2008a, Blair et al. 2016, Leverkus et al. 2018, Taeroe et al. 2019, Burton et al. 2020). Fire is another frequent event after windstorms, as wind damage can increase forest fuels (Cannon et al. 2019). Often compound disturbances – multiple disturbances occurring in a short timespan – can affect plant diversity and composition in ways that differ from the effects of single disturbances (Thorn et al. 2018, Anoszko et al. 2022). For example, compound disturbances have increased herbaceous diversity and compositional differences between wind and wind plus salvage logging treatments in Pennsylvania and Germany (Fischer 1992, Fischer et al. 2002, Royo et al. 2016, Slyder et al. 2020). Compound disturbances have also increased compositional differences of herbaceous species between burned and unburned canopy gap treatments in West Virginia (Royo et al. 2010) and increased the abundance of late-successional trees in a Minnesota forest following wind and fire (Anoszko et al. 2022), both cases due to increased environmental heterogeneity.

Severity is a common term in disturbance literature but there is little agreement on the definition. For example, Frelich and Reich (1999) define severity as the mortality level of tree species, while Oliver and Larson (1996) define severity as a gradient focusing on how much vegetation is destroyed. The definition increases in complexity when considering the impact of multiple – or compound – disturbances. Following Oliver and Larson (1996), my definition of severity is the amount of vegetation destroyed. For this study, I consider the compound disturbance of wind plus salvage logging as having higher severity than the single disturbances of either wind or salvage logging.

The existing literature is inconsistent on the impacts of wind and salvage logging on woody species diversity. This compound disturbance has been observed to both increase (Peterson and Leach 2008a, Slyder et al. 2020) and decrease (Kleinman et al. 2017) diversity within five years post-disturbance in Pennsylvania and Tennessee. Royo et al. (2016) sampled woody species diversity for multiple consecutive years following a wind and salvage logging operation in Pennsylvania and found that an initial decrease in diversity was diminished five years post-disturbance. Kleinman et al. (2017) and Royo et al. (2016) credited the decrease in diversity to competitive exclusion where a few shade-tolerant species dominate, whereas Peterson and Leach (2008a) and Slyder et al. (2020) credited the increase in diversity to moderate disturbance severity and an active seedbank. Environmental heterogeneity – and subsequently diversity – will likely decrease in areas of compound disturbance such as wind and salvage logging when compared to the single disturbance of wind due to salvage operations increasing biotic homogenization (Brewer et al. 2012).

Only a few studies have analyzed the impact of wind disturbance and salvage logging on herbaceous species diversity in closed-canopy forests, despite the herbaceous layer comprising up to 90% of plant species richness (Gilliam 2007, Kleinman et al. 2019). In some cases, this disturbance combination has caused herbaceous diversity to increase due to higher environmental heterogeneity, lower canopy cover, or higher levels of seed germination from seedbank (Elliott et al. 2002, Nelson et al. 2008, Slyder et al. 2020). In other cases, this disturbance combination has caused herbaceous diversity to decrease due to decreases in both environmental heterogeneity and resource availability (Brewer et al. 2012, Kleinman et al. 2017). Still other studies credit moderate disturbance severity, a low number of species present, and lack of difference in canopy openness between treatments as explanations for why this compound disturbance had no impact on herbaceous diversity (Peterson and Leach 2008b, Waldron et al. 2014, Palm et al. 2022). Fewer studies still have analyzed herbaceous response to wind and salvage logging in longleaf pine woodlands which have higher light availability compared to closed-canopy forests. The effect of salvage logging on light availability will be lower in an open-canopy woodland than in a closed-canopy forest (Kleinman et al. 2017). Here, I present a study of wiregrass-dominated longleaf pine woodlands affected by Hurricane Michael in 2018 and subsequent salvage logging and analyze how herbaceous diversity and composition differ between areas of varying damage three years post-disturbance.

Three conceptual models provide predictions of how disturbance impacts species diversity and composition. The intermediate disturbance hypothesis (IDH, Connell 1978), known for its emphasis on how diversity is influenced by disturbance frequency, can be alternatively understood as the relationship between diversity and disturbance severity. This hypothesis predicts that after low severity disturbance, disturbance-intolerant species will competitively exclude other species and thus lower overall species diversity. After high severity disturbance, a small group of disturbance-tolerant specialists with advantageous traits like rapid growth and efficient dispersal will fill newly vacant niches, once again reducing overall species diversity. Stated otherwise, low disturbance severity fails to create environments to support competitively-inferior species due to the relatively high number of competitively-superior species still present, while high disturbance severity destroys high enough numbers of competitively-superior species that they are not a major player in the environment. While the original disturbance-tolerant/intolerant framing of the IDH has drawn criticism for its simplicity and lack of empirical validation, the alternative interpretation based on competitive inferiority/superiority has garnered moderate acceptance within the ecological community (Fox 2013, Sheil & Burslem 2013). Nevertheless, reviews of the IDH (Mackey & Currie 2001, Hughes et al. 2007, Kershaw & Mallik 2013) offer mixed results. Hughes et al. (2007) credited limited support for IDH to dissimilar experimental designs. Mackey & Currie (2001) and Kershaw and Mallik (2013) noted that the unimodal pattern is most often observed where severe disturbances affect sessile species and where studies were conducted in well-drained soils. Given this study examines sessile plants in the Coastal Plain's well-drained soils (Georgia Museum of Natural History 2021), therefore utilizing the IDH is worthwhile.

Schippers et al. (2001) used a simulation model to explore how disturbance severity influences herbaceous composition, mediated by three life history traits: adult longevity (annual/perennial), seed size (large/small), and dormancy (dormant or non-dormant). In the simulation, a disturbance was defined as the removal of organisms. Each disturbance simulation consisted of a 1600-cell grid filled with one plant in each cell. Each of the eight strategies (combinations of the above life history traits) was represented with two hundred plants each. The simulation found that in undisturbed communities, perennials with non-dormant small seeds dominate. Perennials with dormant small seeds dominated when 10% of the 1600 cells experienced disturbance. At levels of 20% disturbance and higher, annuals dominated – first with small non-dormant seeds followed by small dormant seeds. Relevant to my study, perennial dominance was observed at lower severities and annual dominance at higher ones.

It is worthwhile noting that both Connell (1978) and Schippers et al. (2001) make the same broader prediction: that disturbance-intolerant species dominate at lower severities while disturbance-tolerant species dominate at higher severities. While Connell (1978) used tree species in describing the framework, his predictions are virtually identical to Schippers et al. (2001) if applied to herbaceous species. Both frameworks – one focused on diversity and the other on composition – are useful models for understanding the effects of disturbances on herbaceous plant communities.

As regeneration mechanism information was unavailable for all species in this study, an unpublished database (Jeffery Cannon, pers. comm., 2021) of species' dispersal modes must suffice as the basis for hypothesizing how varying disturbance severities impact species with differing dispersal modes.

I hypothesize that herbaceous diversity will be highest in areas that have experienced wind damage but not salvage logging, and lowest in areas that have experienced both wind damage and salvage logging or neither disturbance (Hypothesis 1). I hypothesize that species composition will become increasingly dissimilar between undisturbed and disturbed areas increasing disturbance severity (Hypothesis 2). Finally, I hypothesize that species that use abiotic factors (such as gravity or wind) for dispersal will be impacted less by disturbance severity than species that use biotic factors (such as ants or vertebrates) (Hypothesis 3).

METHODS

To test the hypotheses, I compared the diversity and composition of herbaceous species at an open-canopy woodland with four treatments representing combinations of hurricane wind damage and salvage logging disturbance: unsalvage logged nongap, unsalvage logged gap, salvage logged nongap, and salvage logged gap. The study was conducted at the Jones Center at Ichauway (31.22°, -84.47°) which contains stands of second-growth longleaf pine woodlands with wiregrass understory. The Jones Center has been a research and conservation preserve since the 1990s, and before that was managed with frequent fire since the 1920s (Jones Center at Ichuaway 2022). Soils present are those of the Neilhurst and Red Bay series (Kirkman et al. 2001, USDA 2004, 2018). The average minimum and maximum temperatures at the site are 5 °C and 34 °C, with annual precipitation of 131 cm (Kirkman et al. 2001). All treatments had an understory dominated by wiregrass (*Aristida stricta*), were burned every ~2 years but not since 2020, and were impacted by Hurricane Michael in 2018 which created a complex mosaic of gaps and undamaged areas (Arko et al. 2024). The experimental design consisted of twelve blocks (six salvage logged and six unsalvage logged). Within each block I established a plot within a hurricane-created gap, and a paired plot >60 m away in an intact portion of the same stand.

Within each plot, I placed three 1 m^2 quadrats 5 m from the plot center spaced at 120 degrees (Figure 3-1). In June 2021, I identified all herbaceous species rooted within each quadrat and recorded the corresponding percent cover. Unidentified plants were given a unique name and percent cover data was still collected.

To analyze diversity, the Shannon-Wiener (H') values of each plot were calculated from averaged quadrat percent cover, followed by average diversity values per treatment. To determine the differing impacts of severity on average diversity, I used a nested ANOVA with wind disturbance nested in salvage logging (Dytham 2011). Severity treatments were broken down into logging (salvage logged/unsalvage logged) and canopy cover (gap/intact). To determine dissimilarity in species composition between treatments, I used both multi-response permutation procedures (MRPP) and non-metric multidimensional scaling (NMDS). MRPP is a nonparametric analysis well suited to community ecology data and gives a measure of dissimilarity for all pairwise comparisons of groups (McCune and Grace 2002). Groups were defined by the disturbance severities: unsalvage logged nongap, unsalvage logged gap, salvage logged nongap, and salvage logged gap (Peck 2016). I used Sorensen distances as it is less prone to the influence of outlying data points (Peck 2016). MRPP produces three outputs for each pairwise comparison of treatments: a test statistic (T) which indicates how large the separation between treatments is, an agreement value (A) which represents the level of within-group homogeneity, and a p-value which indicates statistical significance (Peck 2016). NMDS is an ordination approach that illustrates differences in species composition graphically – greater distance between points indicates greater compositional differences between plots. The stress value of an NMDS refers to combining multiple species onto a single dimension and can range from 0 to 1. Lower values indicating a better fit of the data - stress values 0.3 or under and two dimensions for ease of interpretability are advised (Peck 2016). An unpublished database was used in assigning species' dispersal modes (Jeffery Cannon, pers. comm., 2021). Binomial regression was used to determine significance between abiotic and biotic dispersal modes.

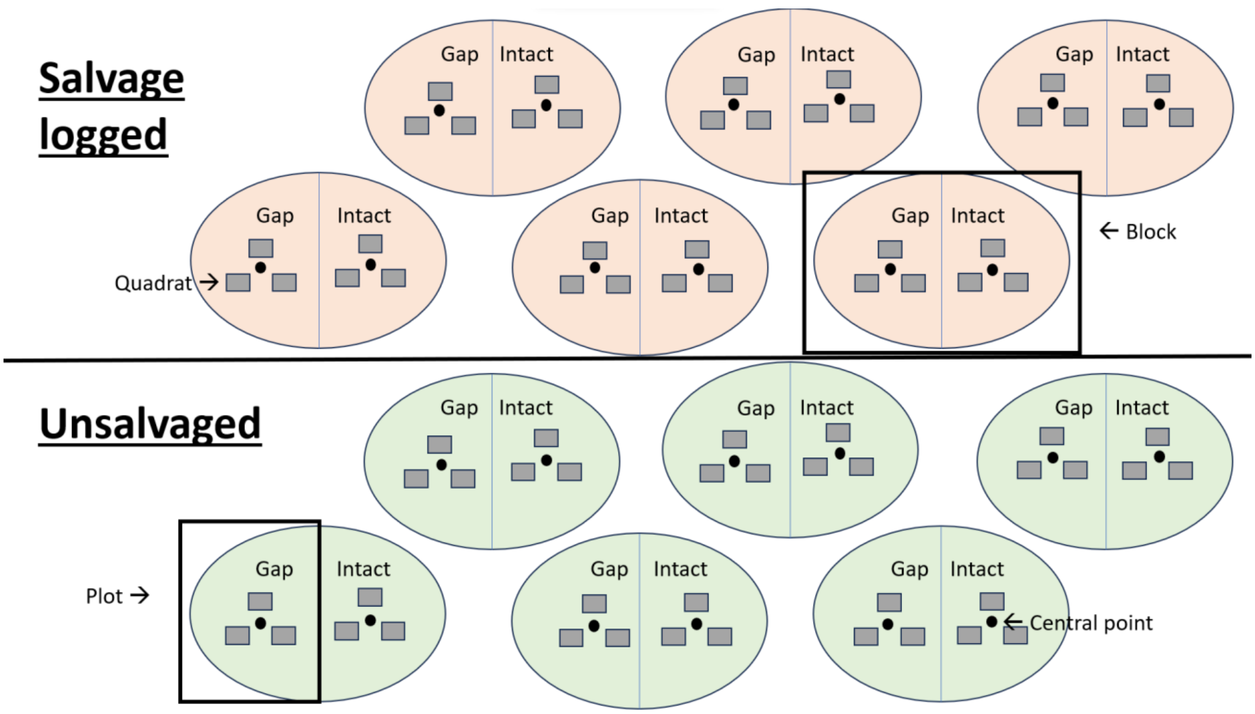


Figure 3-1. Experimental design of the Jones Center. Quadrats – in groups of three – were all an equidistant five meters away from a central point. Gap and intact plots were a minimum of sixty meters away from each other; distances between sites were much greater.

RESULTS

The average Shannon-Weiner index (hereafter diversity) of the unsalvage logged nongap treatment was 2.89 (SD: +/- 0.42), of the unsalvage logged gap treatment was 3.05 (SD: +/- 0.30), of the salvage logged nongap treatment was 3.13 (SD: +/- 0.35), of the salvage logged gap treatment was 3.01 (SD: +/- 0.41) (Figure 3-2). The nested ANOVA results produced no significant p-values ($p < 0.05$) for salvage logging or wind disturbance (Table 3-1). This indicates no difference in diversity between the severity treatments.

Significant compositional dissimilarity was observed for two (unsalvage logged gap vs. unsalvage logged nongap, unsalvage logged nongap vs. salvage logged gap) out of six treatment comparisons ($p = 0.02$ and < 0.01, respectively). The NMDS (Figure 3-3) supports the conclusion that these two treatment comparisons exhibit minimal similarity. The species that contributed most strongly to compositional differences among treatments included *Rubus cuneifolius*, *Aristida stricta*, *Toxicodendron pubescens*, and *Pteridium aquilinum*.

Perennials such as *Aristida stricta* and *Dyschoriste oblongifolia* dominated composition in all treatments. Perennials comprised 90% of species in the unsalvage logged nongap treatment, 89% of species in the unsalvage logged gap treatment, 93% of species in the salvage logged nongap treatment, and 91% in the salvage logged gap treatment.

No significant difference was found between species that used biotic (ants or vertebrates) or abiotic (gravity or wind) dispersal modes ($\chi^2 = 1.01$, df = 3, $p = 0.80$). Gravity was the most common dispersal mode among species across all severity treatments (Figure 3-4). Wind was the second most common dispersal mode except for the salvage logged nongap treatment where vertebrate dispersal was most common. Species that utilized ants and vertebrates as dispersal modes were of roughly equal percentages, though less common than gravity or wind. There were a small number of species that utilized other dispersal methods. Across all severity treatments, the percentage of species that utilized gravity or wind as dispersal modes varied by 6%; the percentage of species that utilized ants, 4%; and the percentage of species that utilized vertebrates, 8%.

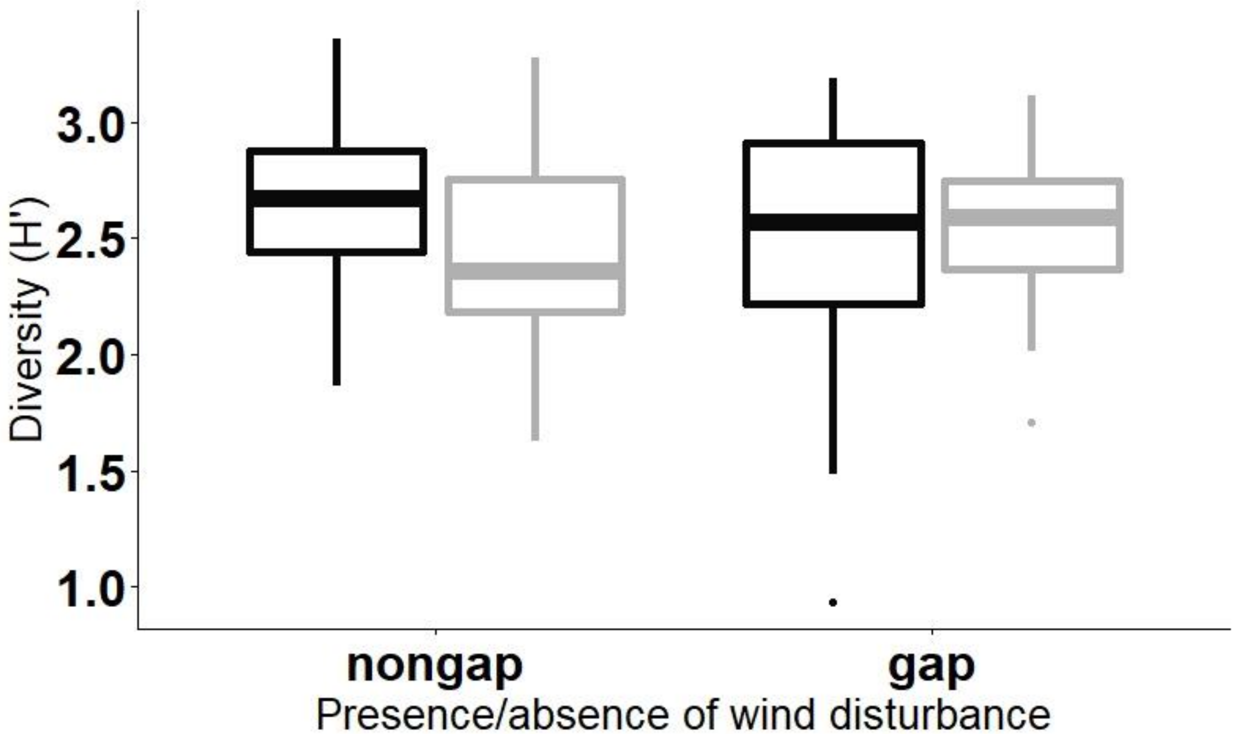


Figure 3-2. How logging (salvage logged=black, unsalvage logged=grey) affects average diversity in treatments with regards to the presence or absence of wind disturbance (gap/nongap).

Table 3-1. Nested ANOVA results for Jones Center data examining the impact of salvage logging (salvage logged/unsalvage logged) and wind disturbance (gap/intact) on average diversity, the latter being nested inside of the former.

	Df	*Sum Sq*	*Mean Sq*	*F value*	*P value*
Salv. Logging	1	0.0585	0.05851	0.426	0.522
Salv. Logging: Wind Disturbance	2	0.1143	0.05714	0.416	0.665
Residuals	20	2.7486	0.13743		

Table 3-2. MRPP output of the test statistic (T), effect size (A), and statistical significance (p) of the four treatment comparisons at the Jones Center in 2021.

Comparison	*T*	*A*	*p*
unsalv gap vs. salv gap	0.17	-0.01	0.53
unsalv nongap vs. salv nongap	-1.26	0.01	0.11
salv gap vs. salv nongap	-0.49	0.01	0.27
unsalv gap vs. unsalv nongap	-2.52	0.04	**0.02**
unsalv gap vs. salv nongap	0.08	-0.01	0.50
unsalv nongap vs. salv gap	-4.05	0.06	**< 0.01**

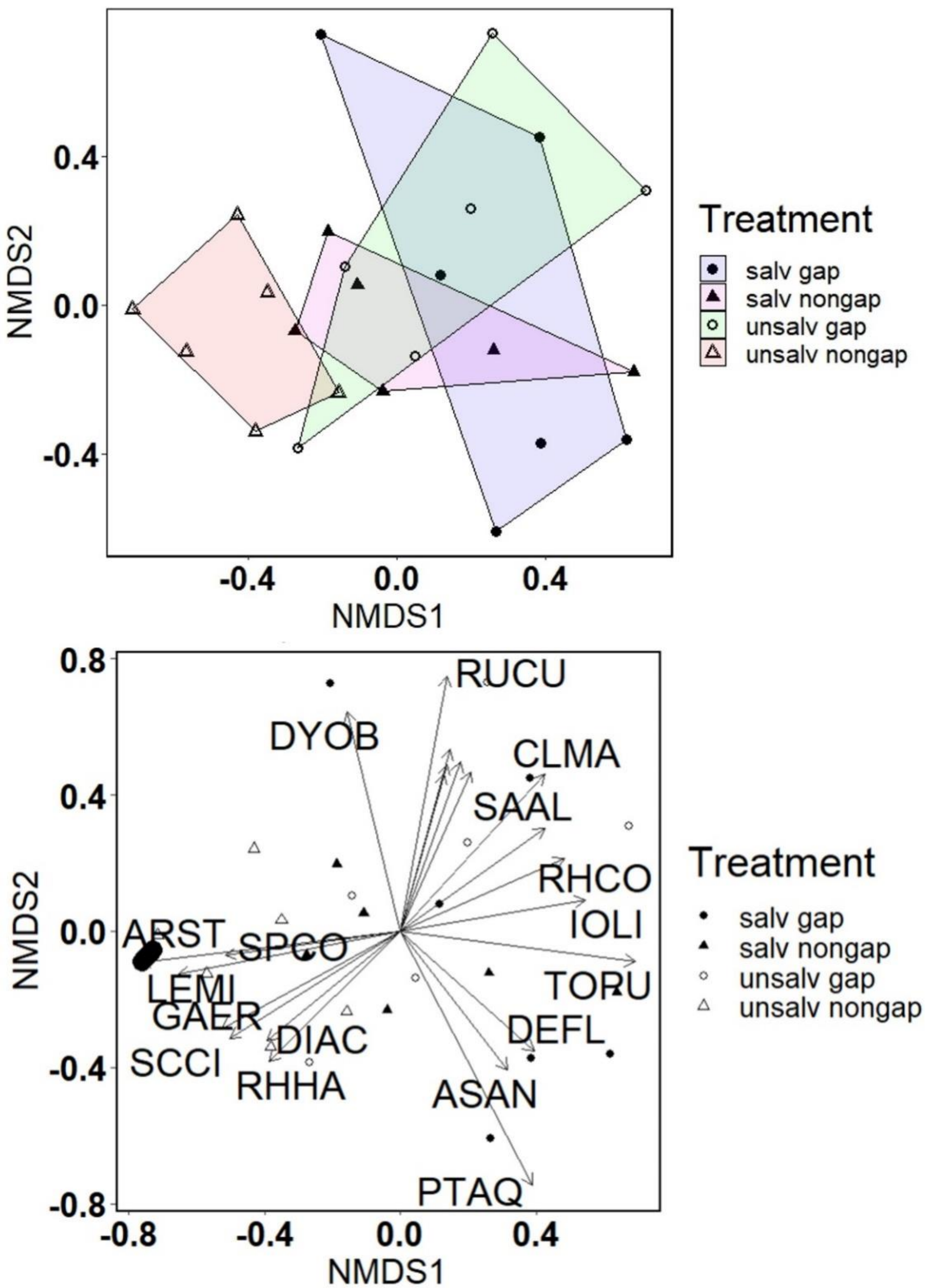


Figure 3-3. The compositional dissimilarity between Jones Center treatments in 2021. Circles denote gap treatments, while triangles denote intact woodland (nongap) treatments. Salvage logged treatments are denoted by filled-in shapes, while unsalvage logged treatments are denoted by hollow shapes. Stress: 0.20 Contributing species were Toxicodendron pubescens (TOPU), Ionactis linariifolia (IOLI), Rhus copallinum (RHCO), Sassafras albidum (SAAL), Dyschoriste oblongifolia (DYOB), Rubus cuneifolius (RUCU), Clitoria mariana (CLMA), Desmodium floridanum (DEFL), Asminia angustifolia (ASAN), Pteridium aquilinum (PTAQ), Aristida stricta (ARST), Sporobolus compositus (SPCO), Lechea minor (LEMI), Galactia erecta

(GAER), Scleria ciliata (SCCI), Dichanthelium aciculare (DIAC), and Rhynchospora harveyi (RHHA).

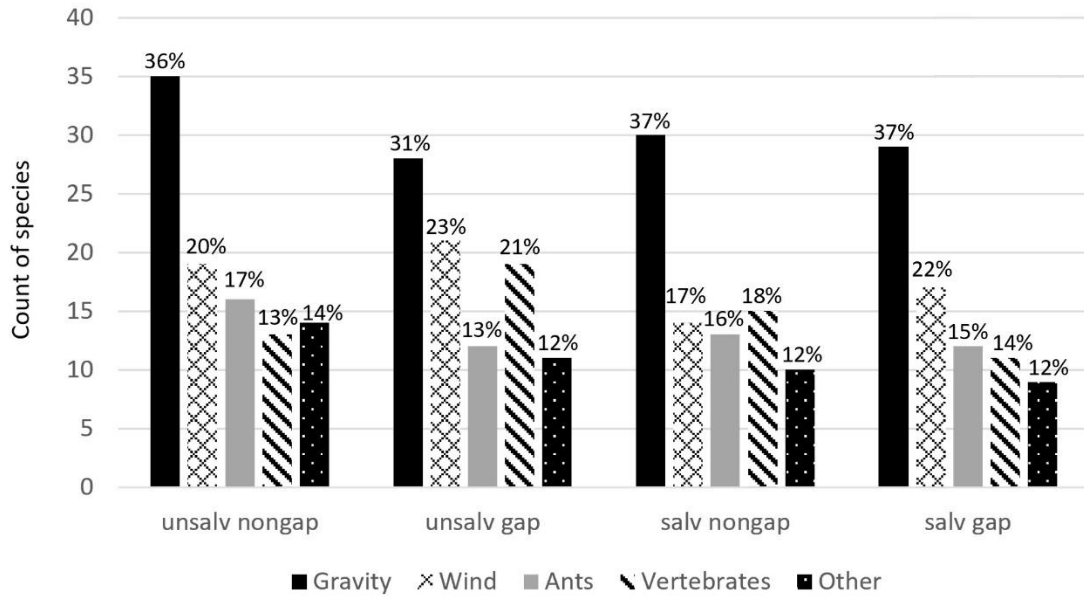


Figure 3-4. Dispersal mode for species found at Jones Center as sorted by severity treatment, with the percentage of species per treatment that utilized a given dispersal type. The unsalvage logged nongap treatment had 97 species, unsalvage logged gap treatment 91, salvage logged nongap 82, and salvage logged gap treatment 78.

DISCUSSION

This study investigated how the compound disturbance of wind and salvage logging impacts herbaceous species in an open-canopy, fire-frequent longleaf pine woodland three years post-disturbance. In this case, I found no significant differences between treatments in diversity and but differences in composition between two out of six treatment comparisons (Figure 3-2, Table 3-1, Table 3-2).

The diversity results fail to support Hypothesis 1, that herbaceous species diversity would be highest in areas that have experienced wind damage but not salvage logging. The open-canopy nature of the study site could partially explain why the presence/absence of gaps had minimal effects on herbaceous diversity (Table 3-1). Webb (1999) posited that disturbance causing a heterogeneous distribution of resources such as light, moisture, and nutrients is a fundamental assumption when predicting that disturbance will increase species diversity. I conclude that the compound disturbance of wind and salvage logging in the open-canopy woodland did not cause enough environmental heterogeneity in topography or light for herbaceous diversity to vary between severity treatments (Table 3-1). These results are consistent with the findings of Peterson and Leach (2008b) while contrasting with the findings of Elliott et al. (2002), Slyder et al. (2020), Nelson et al. (2008), Brewer et al. (2012) and Kleinman et al. (2017). These differences are likely due to the varying severity of disturbances examined in these studies. Peterson and Leach (2008b), studying salvage logged and unsalvage logged portions of a closed-canopy forest two years following a thunderstorm in Tennessee, observed no difference in herbaceous diversity between treatments. This was attributed to the salvage logged treatment not being severe enough to cause high enough levels of habitat heterogeneity to be significantly different from the unsalvage logged treatment. While a Category 2 hurricane (Rutledge et al. 2021) plus subsequent salvage logging may well be classified as a severe rather than moderate compound disturbance, the progression of time may decrease the impact on herbaceous species diversity. Other studies reporting changes in herbaceous diversity due to wind and salvage logging credit homogenization of habitat or flora (Brewer et al. 2012, Kleinman et al. 2017), the presence of a seedbank (Slyder et al. 2020), or a decrease in canopy cover (Nelson et al. 2008). While the Jones Center is known to have an herbaceous seedbank (Kaeser and Kirkman 2012), the relative lack of canopy cover and the likely microtopographical homogeneity – from salvage operations leveling pits – are possible causes of the similarity in average diversity between severity treatments.

No significant compositional differences between severity treatments were observed save for the unsalvage logged gap vs. unsalvage logged nongap and unsalvage logged nongap vs. salvage logged gap comparison (Table 3-2, Figure 3-3). These results provide mixed support for Hypothesis 2, that with increasing disturbance severity disturbed and undisturbed treatments will exhibit increasingly dissimilar composition post-disturbance. The creation of gaps from wind disturbance likely supports dissimilar species composition, but additional disturbance from salvage logging obscures compositional dissimilarity at intermediate severity levels. In treatments of higher – compound – disturbance levels, compositional differences are evident when compared to treatments of low severity.

Disturbance severity was observed to have no discernable effect on the percentage of perennials in each treatment. Considering the prediction of Schippers et al. (2001) that perennials will dominate at lower severity disturbances, I would argue that the passage of time between disturbance and data collection may preclude the most accurate understanding of immediate post-disturbance composition. While my one year of data collection occurred three years post-disturbance, the significant compositional difference between the unsalvage logged gap vs. unsalvage logged nongap and unsalvage logged nongap and salvage logged gap treatments in 2021 underscores the importance that wind disturbance alone – and extreme severity compound disturbance – has on herbaceous composition in disturbed areas. Species driving these differences include *Dichanthelium aciculare*, *Aristida stricta*, *Pityopsis graminifolia*, and *Dyschoriste oblongifolia*. All of these species grow by seed in pine-dominated landscapes with sandy soils. All but *Aristida stricta* are well adapted to the frequent fire disturbances of the Coastal Plain

Two studies of wind and salvage logging discuss herbaceous composition following disturbance (Elliott et al. 2002, Palm et. al 2022). Elliott et al. (2002) recorded four percent more early-successional species in disturbed (wind + salvage logging) as opposed to undisturbed forest. Unfortunately, the authors did not separate undisturbed and disturbed treatments in their experimental design, making it unclear if wind disturbance or salvage logging caused the greater dominance of early-successional species in the disturbed forest stands. Palm et al. (2022) in Estonia found significant compositional dissimilarity between all treatments of varying severity levels (undisturbed, moderate wind, heavy wind, and salvage logged). They attributed the difference to higher levels of light availability. However, both studies occurred in closed-canopy forests. My results indicate that wind, more than salvage logging, creates a change in herbaceous composition in the open-canopy woodland.

Disturbance severity appears to have had minimal impact on dispersal mechanisms of herbaceous species (Figure 3-4). All treatments had between 78 – 97 species in total. Dispersal types that netted at least 10 species per treatment are gravity, wind, ants, and vertebrates, listed in decreasing order of abundance. The data does not support my prediction that animal-dispersed seeds would be most impacted by disturbance. The percentages of change between dispersal types across treatments is relatively minimal (2-4%). These plant abundance data suggest that food sources for animals may not be severely impacted by wind disturbance or salvage logging, decreasing the disturbance severity felt by animals.

In conclusion, average herbaceous diversity did not vary with wind or wind plus salvage logging in an open-canopy woodland three years post-disturbance while herbaceous compositional dissimilarity was only observed when salvage logging was absent. These data should encourage future short-term studies that simultaneously collect biotic and abiotic data centering on the impact of disturbance severity (wind and wind+salvage logging) on herbaceous diversity and composition during several consecutive years post-disturbance in open-canopy woodlands. Possible directions could include examining at the impact of fire and wind on herbaceous species, how changing light availability and soil moisture levels post-disturbance may impact herbaceous species, and how changing diversity and composition post-disturbance of herbaceous species may impact herbivores. Data from such studies would aid in providing an explanation for patterns exhibited in this study, helping scientists to better predict which groups of herbaceous species to focus conservation efforts on.

LITERATURE CITED

Arko, A. D., J. B. Cannon, A. Himes, and A. Polinko. 2024. The effects of a moderate severity hurricane on gap characteristics in a longleaf pine (Pinus palustris Mill.) woodland. Forest ecology and management **551**:121502.

Anoszko, E., L. E. Frelich, R. L. Rich, and P. B. Reich. 2022. Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere **13**:e3952.

Blair, D. P., L. M. McBurney, W. Blanchard, S. C. Banks, and D. B. Lindenmayer. 2016. Disturbance gradient shows logging affects plant functional groups more than fire. Ecological Applications **26**:2280-2301.

Balaguru, K., W. Xu, C.-C. Chang, L. R. Leung, D. R. Judi, S. M. Hagos, M. F. Wehner, J. P. Kossin, and M. Ting. 2023. Increased US coastal hurricane risk under climate change. Science advances **9**:eadf0259.

Brewer, J. S., C. A. Bertz, J. B. Cannon, J. D. Chesser, and E. E. Maynard. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? Ecological Applications **22**:442-458.

Burton, P. J., A. Jentsch, and L. R. Walker. 2020. The ecology of disturbance interactions. BioScience **70**:854-870.

Cannon, J. B., S. K. Henderson, M. H. Bailey, and C. J. Peterson. 2019. Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. Forest ecology and management **436**:117-128.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. Science **199**:1302-1310.

Dytham, C. 2011. Choosing and using statistics: a biologist's guide. John Wiley & Sons.

Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. Journal of the Torrey Botanical Society:48-59.

Fischer, A. 1992. Long term vegetation development in Bavarian Mountain Forest ecosystems following natural destruction. Vegetatio **103**:93-104.

Fischer, A., M. Lindner, C. Abs, and P. Lasch. 2002. Vegetation dynamics in central European forest ecosystems (near-natural as well as managed) after storm events. Folia Geobotanica **37**:17-32.

Fox, J. W. 2013. The intermediate disturbance hypothesis should be abandoned. Trends in ecology & evolution **28**:86-92.

Frelich, L. E., and P. B. Reich. 1999. Minireviews: neighborhood effects, disturbance severity, and community stability in forests. Ecosystems **2**:151-166.

Gensini, V. A., and H. E. Brooks. 2018. Spatial trends in United States tornado frequency. NPJ climate and atmospheric science **1**:38.

Georgia Museum of Natural History. "Physiographical Regions of Georgia". Revised 2021. Accessed 17 November 2023. https://gawildlife.uga.edu/index.php?page=information/regions

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience **57**:845-858.

Hughes, A., J. E. Byrnes, D. L. Kimbro, and J. J. Stachowicz. 2007. Reciprocal relationships and potential feedbacks between biodiversity and disturbance. Ecology letters **10**:849-864.

Jones Center at Ichauway. "About Us". Revised 2022. Accessed 2 October 2022. https://www.jonesctr.org/about-us/

Jones, M. W., J. T. Abatzoglou, S. Veraverbeke, N. Andela, G. Lasslop, M. Forkel, A. J. Smith, C. Burton, R. A. Betts, and G. R. van der Werf. 2022. Global and regional trends and drivers of fire under climate change. Reviews of Geophysics **60**:e2020RG000726.

Kaeser, M. J., and L. K. Kirkman. 2012. Seed longevity of 12 native herbaceous species in a fire-maintained pine savanna after 8 years of burial. Forest ecology and management **281**:68-74.

Kershaw, H. M., and A. U. Mallik. 2013. Predicting plant diversity response to disturbance: applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. Critical Reviews in Plant Sciences **32**:383-395.

Kirkman, L. K., R. J. Mitchell, R. C. Helton, and M. B. Drew. 2001. Productivity and species richness across an environmental gradient in a fire-dependent ecosystem. American Journal of Botany **88**:2119-2128.

Kirkman, L. K., P. C. Goebel, B. J. Palik, and L. T. West. 2004. Predicting plant species diversity in a longleaf pine landscape. Ecoscience **11**:80-93.

Kleinman, J. S., S. A. Ford, and J. L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. Forest ecology and management **403**:112-125.

Kleinman, J., J. Goode, A. Fries, and J. Hart. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. Ecosphere **10**:e02962.

Leverkus, A. B., D. B. Lindenmayer, S. Thorn, and L. Gustafsson. 2018. Salvage logging in the world's forests: Interactions between natural disturbance and logging need recognition. Global Ecology and Biogeography **27**:1140-1154.

Lewis, C. E., and T. J. Harshbarger. 1976. Shrub and herbaceous vegetation after 20 years of prescribed burning in the South Carolina coastal plain. Rangeland Ecology & Management/Journal of Range Management Archives **29**:13-18.

Lindenmayer, D., and R. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology **20**:949-958.

Lindenmayer, D., and K. Ough. 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. Conservation Biology **20**:1005-1015.

Mackey, R. L., and D. J. Currie. 2001. The diversity–disturbance relationship: is it generally strong and peaked? Ecology **82**:3479-3492.

McCune, B., et al. 2002. Analysis of ecological communities, MjM software design, Gleneden Beach, Oregon, USA.

Nelson, J. L., J. W. Groninger, L. L. Battaglia, and C. M. Ruffner. 2008. Bottomland hardwood forest recovery following tornado disturbance and salvage logging. Forest ecology and management **256**:388-395.

Oliver, C. D., and B. C. Larson. 1996. Forest stand dynamics: Updated edition. John Wiley and sons.

Palm, K., F. Vodde, T. Tullus, J. Engelhart, and K. Jõgiste. 2022. Impact of different storm severity levels and post-storm management on understory vegetation richness, diversity and composition 19–20 years after wind disturbance. Forest ecology and management **524**:120506.

Peck J. 2016. Multivariate Analysis for Ecologists, MjM software design, Gleneden Beach, Oregon, USA.

Peterson, C. J., and A. D. Leach. 2008a. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecological Applications **18**:407-420.

Peterson, C. J., and A. D. Leach. 2008b. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry **81**:361-376.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology **91**:93-105.

Royo, A. A., C. J. Peterson, J. S. Stanovick, and W. P. Carson. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology **97**:1566-1582.

Rutledge, B. T., J. B. Cannon, R. K. McIntyre, A. M. Holland, and S. B. Jack. 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. Forest ecology and management **481**:118724.

Schippers, P., J. M. Van Groenendael, L. M. Vleeshouwers, and R. Hunt. 2001. Herbaceous plant strategies in disturbed habitats. Oikos **95**:198-210.

Sheil, D., and D. Burslem. 2013. Defining and defending Connell's intermediate disturbance hypothesis: a response to Fox. Trends Ecol. Evol **28**:571-572.

Slyder, J. B., J. W. Wenzel, A. A. Royo, M. E. Spicer, and W. P. Carson. 2020. Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. New Forests **51**:409-420.

Sparks, J. C., R. E. Masters, D. M. Engle, M. W. Palmer, and G. A. Bukenhofer. 1998. Effects of late growing-season and late dormant-season prescribed fire on herbaceous vegetation in restored pine-grassland communities. Journal of Vegetation Science **9**:133-142.

Taeroe, A., J. H. de Koning, M. Löf, A. Tolvanen, L. Heiðarsson, and K. Raulund-Rasmussen. 2019. Recovery of temperate and boreal forests after windthrow and the impacts of salvage logging. A quantitative review. Forest ecology and management **446**:304-316.

Thorn, S., C. Bässler, R. Brandl, P. J. Burton, R. Cahall, J. L. Campbell, J. Castro, C. Y. Choi, T. Cobb, and D. C. Donato. 2018. Impacts of salvage logging on biodiversity: A meta-analysis. Journal of Applied Ecology **55**:279-289.

Waldron, K., J. C. Ruel, S. Gauthier, L. De Grandpré, and C. J. Peterson. 2014. Effects of post-windthrow salvage logging on microsites, plant composition and regeneration. Applied vegetation science **17**:323-337.

USDA. "Red Bay series". Revised 2018. Accessed 18 March 2024. https://soilseries.sc.egov.usda.gov/OSD_Docs/R/RED_BAY.html

USDA. "Neilhurst series". Revised 2004. Accessed 18 March 2024. https://soilseries.sc.egov.usda.gov/OSD_Docs/N/NEILHURST.html

CHAPTER 4

MODERATE WINDTHROW AND SALVAGE LOGGING DO NOT ALTER HERBACEOUS DIVERSITY OR COMPOSITION IN LONG-TERM STUDY OF TENNESSEE COASTAL PLAIN FOREST[3]

[3] AJ Menzmer, BJ Menzmer, and CJ Peterson. To be submitted to *Castanea*.

ABSTRACT

The southeastern United States supports high plant biodiversity in forested systems. However, maintaining this biodiversity in the face of climate change will require understanding how natural disturbances facilitate the coexistence of plant species. Few long-term studies have analyzed the effects of varying disturbance severity (from multiple natural and/or anthropogenic disturbances) on herbaceous species diversity and composition. Here, I present a study of a coastal plain forest that weathered a moderate-severity windstorm and subsequent salvage logging in 1999 and analyze how herbaceous diversity and composition have changed between sampling in 2001 and 2021 - 2023. In 2001, sixteen 30x30 meter plots were established at Natchez Trace State Park in Tennessee; eight in unsalvage logged stands and eight in salvage logged stands. Average herbaceous diversity, composition, canopy openness, and soil moisture did not differ between unsalvage logged and salvage logged stands (aka severity treatments). In 2021 - 2023, I collected the same types of data in these plots to make historical comparisons. While the number of subplots sampled differed between years of sampling, average plot-wide comparisons are still valid. I found herbaceous diversity and soil moisture did not vary between severity treatments (2021 - 2023) or between years (2001 to 2021 - 2023). Composition did not differ between severity treatments (2001 and 2021 - 2023). Canopy openness did not differ between severity treatments (2021 - 2023) but did decrease over time (2001 to 2021 - 2023). These data support two conclusions: 1) low-to-moderate severity disturbances (whether from single or multiple disturbances) may not alter herbaceous diversity and composition, and 2) the herbaceous layer, in absence of additional major disturbances, supports similar levels of diversity and composition over long periods of time, as demonstrated by similar values in both 2001 and 2021 - 2023. This long-term study supports the validity of many short-term (< 5 years post-disturbance) studies' post-disturbance conclusions.

INTRODUCTION

Windstorms are common natural disturbances that are increasing in frequency in the southeastern United States (Brooks 2013, Gensini and Brooks, 2018). Salvage logging, the practice of removing fallen trees following a natural disturbance, frequently follows windstorms and can increase the cumulative severity of damage following a natural disturbance (Lindenmayer and Noss 2006, Lindenmayer and Ough 2006, Peterson and Leach 2008a, Blair et al. 2016, Taeroe et al. 2019, Burton et al. 2020). Few studies look at the implications of compound disturbances – multiple disturbances occurring shortly after each other – for plant diversity, as opposed to single disturbances. Often compound disturbances affect diversity and composition in ways that differ from single disturbances (Royo et al. 2010, Royo et al. 2016, Leverkus et al. 2018, Slyder et al. 2020, Anoszko et al. 2022).

Despite the herbaceous layer accounting for up to 90% of plant species richness in forests (Gilliam 2007), only a handful of studies have analyzed the long-term recovery of herbaceous species to wind and salvage logging (Thorn et al. 2018, Kleinman et al. 2019). The long-term studies that do exist are Palm et al. (2022), Lang et al. (2009), and Mabry and Korsgren (1998): they examined herbaceous response to wind and salvaging twenty, twenty-five, and fifty-years post-disturbance. Palm et al. (2022) found no significant difference in average diversity but significant compositional dissimilarity between all treatments of varying severity levels (undisturbed, moderate wind, heavy wind, and salvage logged). They credited the differences in composition to varying levels of light availability. Lang et al. (2009) did not examine herbaceous diversity but did find significant compositional dissimilarity between salvage logged and unsalvage logged severity treatments, crediting the difference to microtopographic variation. The salvage logged treatment had a higher percentage of early-successional species than the unsalvage logged treatment. Mabry and Korsgren (1998) found late-successional species dominating the landscape as opposed to early-successional species, likely due to time since the initial disturbance. These studies conclude that differences in severity will have no long-lasting impact on herbaceous diversity. These studies also provide mixed evidence for the impact of severity on herbaceous composition, due to increasing time post-disturbance (Mabry and Korsgren 1998), variation in topography (Lang et al. 2009), and shade from canopy trees (Palm et al. 2022). None of these studies looks at the long-term recovery of herbaceous species in the southeastern United States. This study makes a valuable contribution to evaluating the long-term effects of wind and salvage logging on herbaceous species.

Roberts (2004) considers the impact of disturbance severity on herbaceous species' regeneration mechanisms. Following disturbances of higher severity, Roberts (2004) predicts that regeneration occurs solely through seeds due to the erosion of soil; however, as disturbance severity lowers and more of the soil is left in place post-disturbance, the importance of vegetative regeneration such as rhizomes increases. However, as wind disturbance primarily affects the tree canopy, Roberts provides the caveat that limited change in regeneration may be observed.

I hypothesize that a) diversity will be highest following the single disturbance of wind as opposed to the compound disturbance of wind plus salvage logging and b) as light levels decrease from increasing canopy growth, overall differences in diversity will decrease as sun-tolerant species die out (Hypothesis 1). Furthermore, I hypothesize that as time progresses, the compositional dissimilarity of herbaceous species between severity treatments will decrease as the canopy closes and sun-tolerant species become less abundant (Hypothesis 2). Finally, I hypothesize that species that use rhizomes for dispersal will be impacted less by wind and salvage logging than species that use seeds for dispersal (Hypothesis 3).

METHODS

To test Hypotheses 1 and 2, I compared herbaceous diversity and composition in two treatments of varying severity over 22 years following wind and salvage logging. The study site was located at Natchez Trace State Park & Forest (N 35.72, W -88.29), a coastal plain pine-hardwood closed-canopy forest. Prior to 1935, Natchez Trace experienced frequent agricultural and logging disturbances, before becoming part of a federal reclamation project and being switched to state management in 1955 (Oldfield and Peterson 2021). Soils are predominantly from the Lexington series with loamy and sandy sediments (USDA 2013). The average minimum and maximum temperatures are 5 °C and 26 °C, with annual precipitation of 124 cm (Franklin and Kupfer 2004). Wind damage from a downburst in 1999 and subsequent salvage logging provide an opportunity to study the effects of salvage logging on herbaceous species diversity and composition (Peterson and Leach 2008b).

In 2001, sixteen 30x30 meter plots were established in Natchez Trace State Park and Forest (Peterson and Leach 2008b). Eight plots were set up in salvage logged stands and eight in unsalvage logged stands (2 sites x 2 treatments x 8 plots). A total of 369 0.5m^2 circular quadrats were set up within the thirty-two plots in which to collect herbaceous species data. The identity and percent cover of all herbaceous species in each quadrat was recorded. Canopy openness – a substitute for light availability – was collected through hemispherical photography at each quadrat. Over time, the specific locations of the original circular quadrats from 2001 were lost. However, the locations of each plot were still known.

In 2021, I set up four 1x1 m^2 quadrats, arranged in the four directions on the compass, in each plot. Each quadrat was an equidistant five meters from a central location. The identity and percent cover of all herbaceous species in each quadrat was recorded. In addition, hemispherical photography was conducted to measure canopy openness. Photographs were taken at ~ 0.30 m high in the center of the quadrat using a Cannon EOS Rebel T3i with an Altura Photo 8mm f/3.0 Professional for Canon Wide Angle Aspherical Fisheye Lens. Photography occurred on cloudy days to minimize the risk of sun flares. Gap Light Analyzer was utilized in calculating canopy openness values. Repeated sampling occurred in 2022 and 2023.

To determine differences in diversity between severity treatments, the percent cover for each species was averaged between quadrats to the plot level. The Shannon-Wiener diversity index (H') was then calculated for each plot followed by average diversity values for each treatment. To incorporate all four years of data (2001 + 2021 – 2023) in one analysis looking at the impact of disturbance severity on diversity, I used Friedman's test as the assumption of homogeneity of variances was not supported (Dytham 2011). To make a fair comparison of the $0.5m^2$ 2001 quadrats with the $1m^2$ quadrats of 2021 – 2023, the percent cover of two 2001 quadrats was summed before quadrat diversity was calculated.

To determine dissimilarity in species composition between treatments, I used both multi-response permutation procedures (MRPP) and non-metric multidimensional scaling (NMDS). MRPP is a nonparametric analysis well suited to community ecology data and gives a measure of dissimilarity for all pairwise comparisons of the three treatments (McCune and Grace 2002). I also include a second matrix that pairs the quadrats with the grouping variable of treatments. Groups are defined by disturbance severity treatments: salvage logged and unsalvage logged. I used Sorensen as my distance measure, due to it being less prone to the influence of outliers (Peck 2016). MRPP output for each pairwise comparison of treatments includes a test statistic (T) which indicates how large the separation between treatments is, an agreement value (A) which represents the level of within-group homogeneity, and a p-value which indicates statistical significance (Peck 2016). NMDS is an ordination approach that illustrates differences in species composition graphically – greater distance between points indicates greater compositional differences between plots. The stress value of an NMDS refers to combining multiple species onto a single dimension, and can range from 0 to 1, with the lower values indicating a better fit of the data. Stress values 0.3 or under and two dimensions for ease of interpretability are advised (Peck 2016). A graph is produced that illustrates compositional dissimilarity between treatments along unitless axes (McCune and Grace 2002).

To determine how well herbaceous species with varying regeneration mechanisms respond to wind and salvage logging, I compared the average percent cover of species that utilized seeds vs. rhizomes as a means of reproduction in each treatment/year combination. Communities where the percent cover is primarily from species that reproduce using seeds may be more susceptible to wind and salvage logging than communities made up of species that use rhizomes, as these disturbances predominantly affect above-ground vegetation (Roberts 2004).

To determine differences in average canopy openness between severity treatments, I utilized a chi-squared test of independence.

While my quadrats – set up in 2021 - vary in specific location and number compared to the quadrats of Peterson and Leach (2008a), I am still able to compare average plot diversity values between years. To apply a more granular analysis to my 2021 – 2023 data, I calculated the diversity, richness, and total percent cover of each quadrat. This data was analyzed with a chi-squared test of independence.

RESULTS

The average diversity in each treatment each year is presented below in Figure 4-1. The results indicate that disturbance severity does not alter average herbaceous diversity (Friedman's test, χ^2=17.87, df=15, p=0.27).

The granular analysis revealed that quadrat diversity decreased in almost half of the quadrats while simultaneously increasing in slightly over a third of the quadrats between 2021 and 2023 (Table 4-S1). In this same time frame, quadrat richness decreased in around forty percent of the quadrats but increased in a quarter of the quadrats (Table 4-S2). Total percent cover decreased between 2021 and 2023 in around a third of the quadrats while almost half increased in total percent cover in this same time frame (Table 4-S3). However, the chi-squared test of independence indicated a nonsignificant difference in diversity, richness, and cover between the number of quadrats that increased, decreased, or exhibited no change ($p \geq 0.05$).

MRPP output is presented in Table 4-1; in all years herbaceous composition did not differ between treatments (all p values ≥ 0.05). Figure 4-2 displays the combined NMDS graph for all years (Stress: 0.1726). NMDS 1 predominantly captures the effects of time while NMDS 2 predominantly captures the effects of treatment. Contributing species include *Vitis rotundifolia*, *Rubus* spp., *Pueraria montana*, and *Uvularia sessifolia* (Figure 4-S1). The overlapping treatments of the NMDS, especially from 2021 – 2023, support the nonsignificant p values of the MRPP output.

Figure 4-3 presents the average percent cover of rhizomatous and seed species in each treatment and year. Overlap between treatments (plus/minus two standard errors) was observed in all years for seeded and rhizomatous species; statistical significance is unlikely. Not included in Figure 4-3 is that the 2022 unsalvage logged treatment recorded an average percent cover (+/- SE) of 17.50% (+/- 4.23%) of species that reproduce via spores. All herbaceous species, in both treatments and all years, were perennials except for *Amphicarpacea bracteata* in the salvage logged treatment of 2023.

Figure 4-4 presents the average canopy openness values of each treatment/year combination with two standard deviations of error for each value. Differences in canopy openness between treatments were significant in 2001 ($t= -2.34$, $df=14$, $p = 0.03$) but not for 2021, 2022, or 2023 ($p \geq 0.05$).

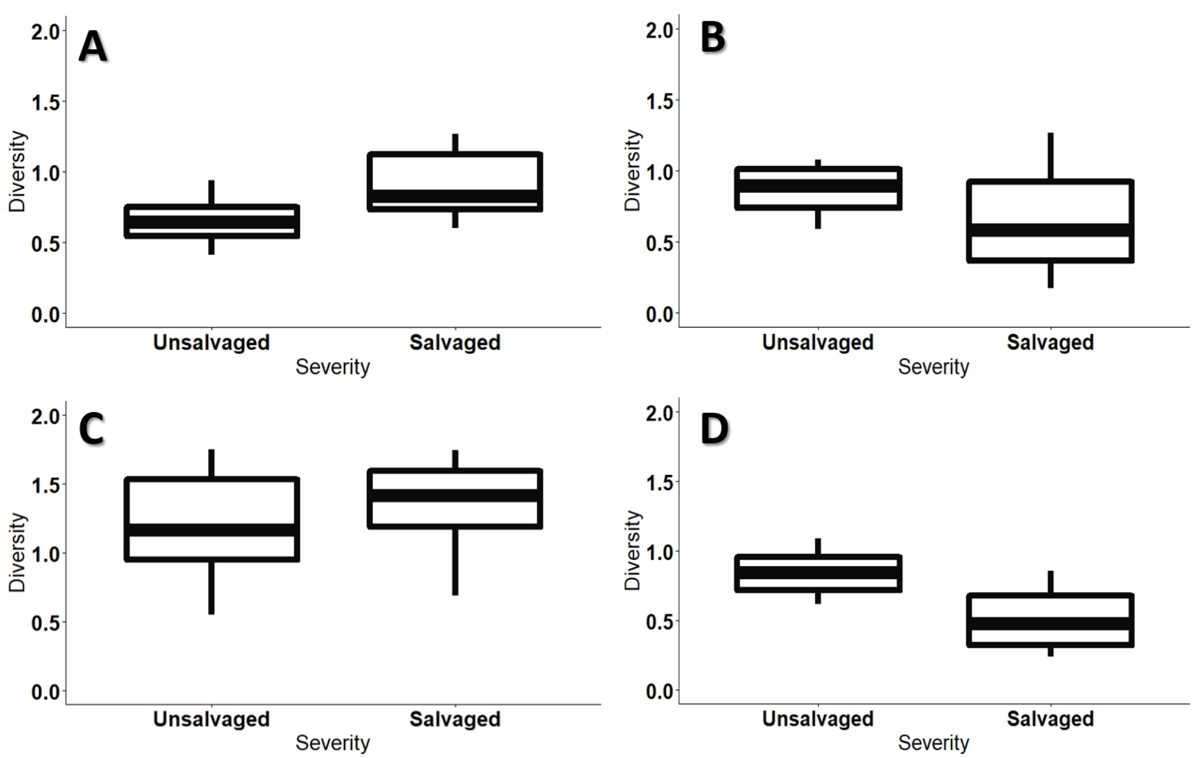


Figure 4-1. Disturbance severity plotted against average herbaceous diversity in unsalvage logged and salvage logged treatments at Natchez Trace in 2001 (A), 2021 (B), 2022 (C), and 2023 (D).

Table 4-1. MRPP output of the test statistic (T), effect size (A), and statistical significance (p) of the unsalvage logged vs. salvage logged treatment comparison of compositional dissimilarity at Natchez Trace in 2001, 2021, 2022, and 2023.

Comparison	*T*	*A*	*p*
2001 unsalvage logged vs. salvage logged	-0.38	< 0.01	0.45
2021 unsalvage logged vs. salvage logged	-1.06	< 0.01	0.87
2022 unsalvage logged vs. salvage logged	-1.66	0.02	0.06
2023 unsalvage logged vs. salvage logged	-1.77	0.02	0.05

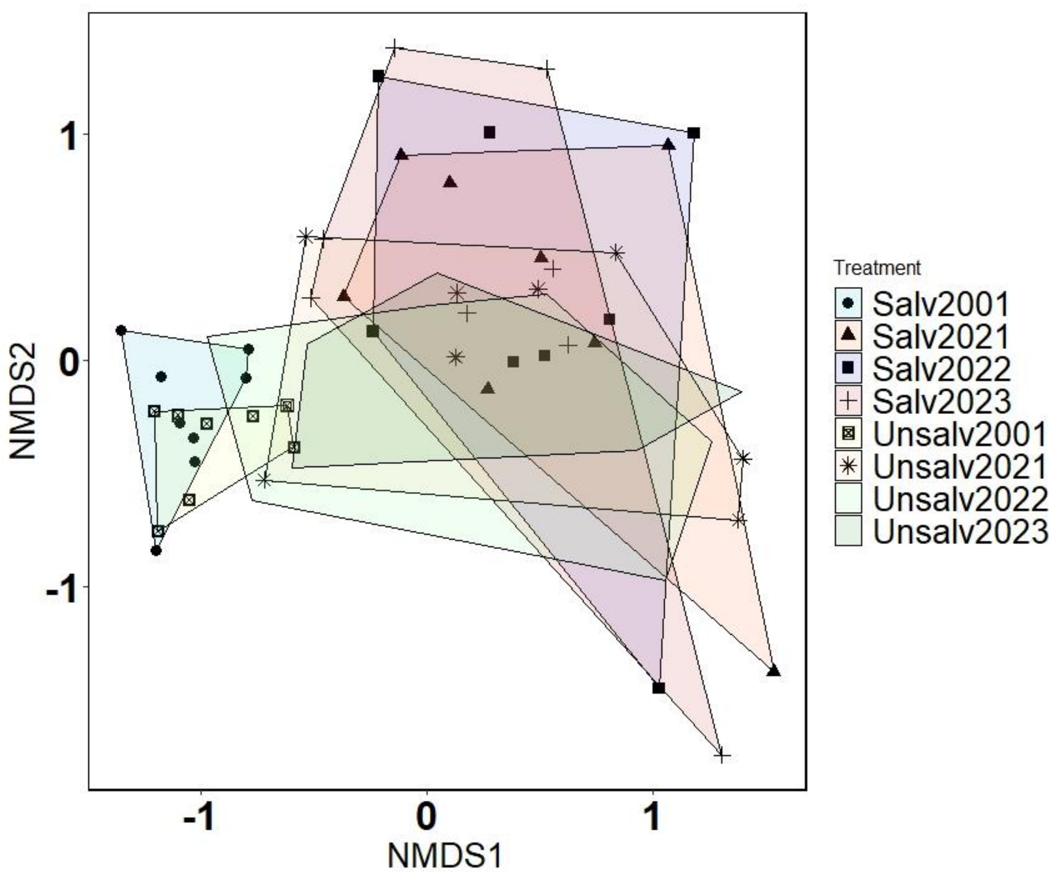


Figure 4-2. The herbaceous compositional dissimilarity between unsalvage logged and salvage logged treatments at Natchez Trace in 2001, 2021, 2022, and 2023.

Figure 4-3. The average percent cover (plus/minus two standard errors) of species that propagate using seeds or rhizomes in each treatment/year combination of the long-term closed-canopy forest. Grey = seed species; black = rhizomatous species.

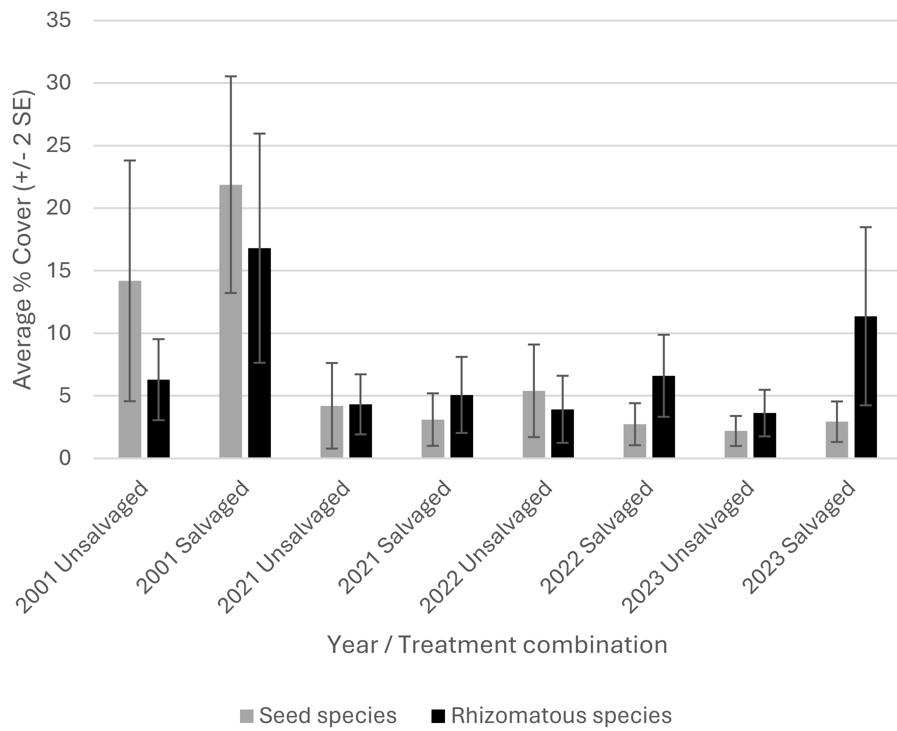
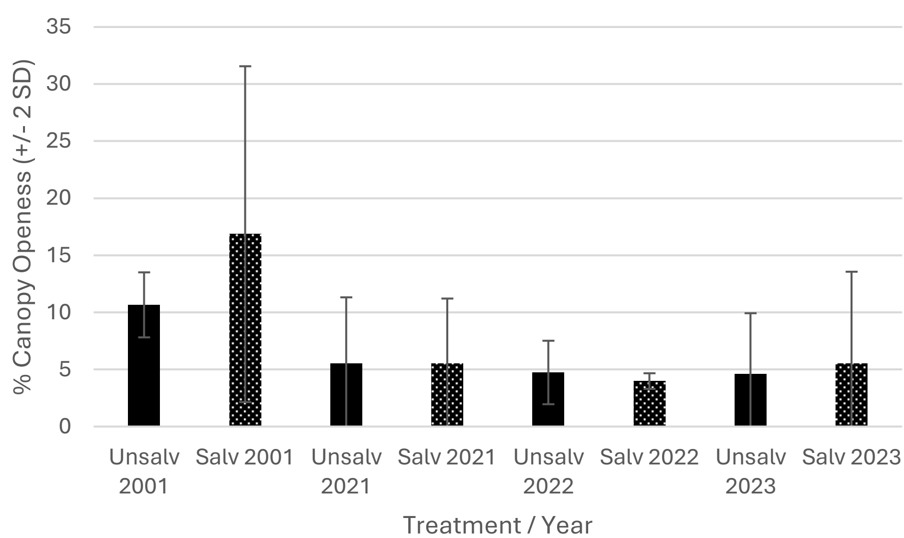


Figure 4-4. The average canopy openness in each treatment/year combination, plus/minus two standard deviations. Solid black = unsalvage logged (unsalv) treatments; Dotted black = salvage logged (salv) treatments.



DISCUSSION

Few studies examine the herbaceous response to wind and salvage logging more than three years post-disturbance save Mabry and Korsgren (1998), Lang et al. (2009), Kleinman et al. (2017), and Palm et al. (2022). My study examined the long-term impact of wind and salvage logging on herbaceous diversity and composition over several consecutive years. Comparing the 2001 herbaceous dataset of Peterson and Leach (2008b) with my herbaceous dataset from 2021, 2022, and 2023 in the same plots provides a rare opportunity to analyze how disturbance severity impacts herbaceous diversity and composition over long timespans.

The data from all four years of sampling revealed no significant difference in average diversity between treatments. Hypothesis 1 was not supported. This indicates consistency both in the short-term (two years) and long-term (twenty-two to twenty-four years) post-disturbance. This consistency is supported by the granular analysis I did of the 2021 – 2023 data. The number of unsalvage logged and salvage logged quadrats that showed an increase or decrease in diversity, richness, and total percent cover, respectively, was remarkably similar and nonsignificant. This consistency points to either a) disturbance severity having minimal impact on herbaceous diversity at all or b) the impact of disturbance severity on herbaceous diversity being more ephemeral (one-year post-disturbance maximum, data nonexistent) than initially thought.

My results of diversity are consistent with those of Palm et al. (2022) but inconsistent with those of Kleinman et al. (2017). Palm et al. (2022), studying herbaceous species twenty years post-disturbance in Estonia, found no significant difference in average diversity between all treatments of varying severity levels (undisturbed, moderate wind, heavy wind, and salvage logged). The authors attributed the lack of difference in all treatments to insufficient light. At Natchez Trace, average canopy openness was measured in 2021 – 2023 but varied less than a percentage point between treatments. This similarity provides grounds for explaining the lack of difference in diversity between treatments. Kleinman et al. (2017), sampling herbaceous species five years following a tornado, observed the unsalvage logged treatment had the greatest diversity in comparison with the undisturbed and salvage logged treatments. The authors reasoned that the high diversity in the unsalvage logged treatment was due to the greater amount of coarse woody debris present which caused higher moisture levels. Peterson and Leach (2008b) suggest the salvage logged treatments of Natchez Trace were of very low severity and reported similar levels of coarse woody debris between salvage logged and unsalvage logged treatments. The lack of diversity or compositional dissimilarity between treatments at Natchez Trace may be credited to a lack of environmental heterogeneity that results from moderate wind and salvage logging disturbance. These studies in conjunction with the results from Natchez Trace underscore the importance of varying levels of light and coarse woody debris in facilitating a heterogenous environment suited for greater herbaceous diversity.

The data from all four years of sampling revealed no significant compositional dissimilarity between treatments. Hypothesis 2 was not supported. The MRPP outputs for each year provide low T and low A values (Table 2). This suggests that species composition is highly variable between the plots and that groups of species are not distinguishable, even in 2001 two years post-disturbance. While Schippers et al. (2001) does predict that perennial herbaceous species will dominate following low severity disturbances, ephemeral annuals may have existed one year post-disturbance before data collection began.

My results of composition are consistent with those of Mabry and Korsgren (1998) but in contrast with those of Lang et al. (2009), Kleinman et al. (2017) and Palm et al. (2022). Fifty years following a 1938 hurricane and immediate salvage logging in Massachusetts, Mabry and Korsgren (1998) found late-successional species dominating the landscape as opposed to early-successional species. The authors attributed the pattern to the progression of time. Twenty-five years post-disturbance, Lang et al. (2009) recorded a greater dominance of early-successional species in the salvage logged treatment as opposed to unsalvage logged treatment, crediting high frequencies of a few select species. Five years following a 2011 tornado in Alabama, Kleinman et al. (2017) found compositional dissimilarity between all three treatments and attributed the difference to the abundance of coarse woody debris. Finally, Palm et al. (2022) in Estonia found significant compositional dissimilarity between all treatments of varying severity levels (undisturbed, moderate wind, heavy wind, and salvage logged). They attributed the difference to the richness of microsites. While microsite diversity was observed at Natchez Trace two years post-disturbance (Peterson & Leach 2008b), the progression of time may obscure the effects of microsites on species composition. Alternative explanations for the lack of compositional dissimilarity could include the recent similarity in average canopy openness or likely similarity in coarse woody debris.

Analysis of regeneration mechanisms used by herbaceous species in each treatment/year combination indicates that neither mechanism dominates regeneration two nor twenty-plus years post-disturbance. This may be attributed to the moderate nature of the wind disturbance and even subsequent salvage logging, supporting Roberts (2004)'s caveat. Analysis of average canopy openness in each treatment/year combination indicates a significant difference in the light availability two years post-disturbance, but this difference disappears twenty-plus years post-disturbance. Minimal variation in abiotic factors such as light between treatments supports the minimal variation in biotic factors between treatments.

I suggest that future studies strive to sample herbaceous diversity and composition one year after disturbances of varying severities – using either categorical or continuous scales – to ascertain whether disturbances have ephemeral effects on the herbaceous layer. Perhaps there is a severity threshold under which the effects of disturbance – either single or compound – cannot be seen (Peterson and Leach 2008b) or a time threshold beyond which effects of disturbance are also blurred. Furthermore, the replication in this study (n=8) is relatively small; increasing the sample size in future studies may tease out differences undetected by this study.

In a long-term study of the impacts that moderate wind disturbance followed by moderate salvage logging have on herbaceous species in a closed-canopy forest, no variation was found either in diversity or composition. This long-term study supports the legitimacy of short-term (< 5 years) studies' post-disturbance conclusions. Additionally, this study strikes a bright note in the otherwise disturbing narrative of global warming: moderate-severity compound disturbances over the long-term do not appear to currently have negative impacts on biodiversity of herbaceous species in this closed-canopy forest.

LITERATURE CITED

Anoszko, E., L. E. Frelich, R. L. Rich, and P. B. Reich. 2022. Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere **13**:e3952.

Blair, D. P., L. M. McBurney, W. Blanchard, S. C. Banks, and D. B. Lindenmayer. 2016. Disturbance gradient shows logging affects plant functional groups more than fire. Ecological Applications **26**:2280-2301.

Brooks, H. E. 2013. Severe thunderstorms and climate change. Atmospheric research **123**:129-138.

Burton, P. J., A. Jentsch, and L. R. Walker. 2020. The ecology of disturbance interactions. BioScience **70**:854-870.

Dytham, C. 2011. Choosing and using statistics: a biologist's guide. John Wiley & Sons.

Franklin, S. B., and J. A. Kupfer. 2004. Forest communities of Natchez Trace State Forest, western Tennessee Coastal Plain. Castanea **69**:15-29.

Gensini, V. A., and H. E. Brooks. 2018. Spatial trends in United States tornado frequency. NPJ climate and atmospheric science **1**:38.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience **57**:845-858.

Kleinman, J. S., S. A. Ford, and J. L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. Forest ecology and management **403**:112-125.

Kleinman, J., J. Goode, A. Fries, and J. Hart. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. Ecosphere **10**:e02962.

Lang, K. D., L. A. Schulte, and G. R. Guntenspergen. 2009. Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. Forest ecology and management **259**:56-64.

Leverkus, A. B., D. B. Lindenmayer, S. Thorn, and L. Gustafsson. 2018. Salvage logging in the world’s forests: Interactions between natural disturbance and logging need recognition. Global Ecology and Biogeography **27**:1140-1154.

Lindenmayer, D., and R. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conservation Biology **20**:949-958.

Lindenmayer, D., and K. Ough. 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. Conservation Biology **20**:1005-1015.

Mabry, C., and T. Korsgren. 1998. A permanent plot study of vegetation and vegetation-site factors fifty-three years following disturbance in central New England, USA. Ecoscience **5**:232-240.

McCune, B., et al. 2002. Analysis of ecological communities, MjM software design, Gleneden Beach, Oregon, USA.

Oldfield, C. A., and C. J. Peterson. 2021. Aboveground Biomass and Carbon Accumulation 19 Years Post-Windthrow and Salvage Logging. Forests **12**:173.

Palm, K., F. Vodde, T. Tullus, J. Engelhart, and K. Jõgiste. 2022. Impact of different storm severity levels and post-storm management on understory vegetation richness, diversity and composition 19–20 years after wind disturbance. Forest ecology and management **524**:120506.

Peck J. 2016. Multivariate Analysis for Ecologists, MjM software design, Gleneden Beach, Oregon, USA.

Peterson, C. J., and A. D. Leach. 2008a. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecological Applications **18**:407-420.

Peterson, C. J., and A. D. Leach. 2008b. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry **81**:361-376.

Royo, A. A., R. Collins, M. B. Adams, C. Kirschbaum, and W. P. Carson. 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. Ecology **91**:93-105.

Royo, A. A., C. J. Peterson, J. S. Stanovick, and W. P. Carson. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology **97**:1566-1582.

Schippers, P., J. M. Van Groenendael, L. M. Vleeshouwers, and R. Hunt. 2001. Herbaceous plant strategies in disturbed habitats. Oikos **95**:198-210.

Slyder, J. B., J. W. Wenzel, A. A. Royo, M. E. Spicer, and W. P. Carson. 2020. Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. New Forests **51**:409-420.

Taeroe, A., J. H. de Koning, M. Löf, A. Tolvanen, L. Heiðarsson, and K. Raulund-Rasmussen. 2019. Recovery of temperate and boreal forests after windthrow and the impacts of salvage logging. A quantitative review. Forest ecology and management **446**:304-316.

Thorn, S., C. Bässler, R. Brandl, P. J. Burton, R. Cahall, J. L. Campbell, J. Castro, C. Y. Choi, T. Cobb, and D. C. Donato. 2018. Impacts of salvage logging on biodiversity: A meta-analysis. Journal of Applied Ecology **55**:279-289.

USDA. "Lexington Series". Revised 2013. Accessed 17 March 2024. https://soilseries.sc.egov.usda.gov/OSD_Docs/L/LEXINGTON.html

SUPPLEMENTAL

Table 4-S1. Diversity values for each of the sixty-four 1x1m^2 quadrats at Natchez Trace in 2021, 2022, and 2023 along with an overall trend of increase, decrease, or no change with time progression. Quadrats 1A – 8D are unsalvage logged, while quadrats 9A – 16D are salvage logged. Bright red indicates the lowest diversity values, yellow moderate diversity values, and bright green indicates the highest diversity values.

Quadrat	2021	2022	2023	Trend
1A	1.079	1.061	1.055	Decrease
1B	0.377	0.315	0.633	Increase
1C	0	1.04	1.04	Increase
1D	0.895	1.163	0.693	Decrease
2A	0.841	0	0.595	Decrease
2B	1.055	0	0.95	Decrease
2C	1.215	0.349	1.119	Decrease
2D	0.895	0.943	0.687	Decrease
3A	0.827	0.349	0.578	Decrease
3B	0.921	0.916	1.184	Increase
3C	0.598	0.982	1.231	Increase
3D	1.011	0.956	1.368	Increase
4A	0.402	0.678	0.716	Increase
4B	0.693	0	0	Decrease
4C	0	0.287	0.685	Increase
4D	1.649	1.216	1.359	Decrease
5A	0.693	0.637	0.693	No change
5B	0.084	0.188	0	Decrease
5C	0.693	0.693	0.693	No change
5D	1.55	1.211	1.089	Decrease
6A	0.847	1.106	0.974	Increase
6B	0.684	0.349	0.349	Decrease
6C	1.465	1.359	1.523	Increase
6D	1.04	0.302	1.04	No change

7A	1.359	0.887	0.539	Decrease
7B	0.947	0.453	0.851	Decrease
7C	0.619	0.895	0.918	Increase
7D	1.304	0.302	0.603	Decrease
8A	1.273	0.451	1.082	Decrease
8B	0.5	0.598	0.637	Increase
8C	1.512	1.474	1.334	Decrease
8D	0.6	0.721	0.759	Increase
9A	0.637	0	0	Decrease
9B	0.852	0.655	0.97	Increase
9C	0	0	0	No change
9D	0	0	0	No change
10A	0.595	1.41	0.661	Increase
10B	0.41	0	0	Decrease
10C	1.099	0	0	Decrease
10D	0.978	0.794	0.8	Decrease
11A	1.472	0.761	0.743	Decrease
11B	1.277	0.562	1.402	Increase
11C	0.562	0.5	0.21	Decrease
11D	0.684	0.762	0.76	Increase
12A	0.696	0.343	0.817	Increase
12B	1.056	0.876	0.927	Decrease
12C	1.543	1.163	0.882	Decrease
12D	1.503	1.452	0.797	Decrease
13A	0.898	0.877	0.873	Decrease
13B	0.163	0	0.729	Increase
13C	0.855	1.04	0.983	Increase
13D	0	0	0	No change
14A	0.76	0.562	0.277	Decrease
14B	1.099	0.509	0.377	Decrease

14C	0	0.693	0	No change
14D	0.903	1.041	0.562	Decrease
15A	0	0.693	0.693	Increase
15B	0.683	0.693	1.265	Increase
15C	0	0.562	0.234	Increase
15D	0	0	0.191	Increase
16A	0	0.637	0	No change
16B	0.956	1.061	0.76	Decrease
16C	0	0	0.562	Increase
16D	0	0	0	No change

Table 4-S2. Richness values for each of the sixty-four 1x1m^2 quadrats at Natchez Trace in 2021, 2022, and 2023 along with an overall trend of increase, decrease, or no change with time progression. Quadrats 1A – 8D are unsalvage logged, while quadrats 9A – 16D are salvage logged. Bright red indicates the lowest richness values, yellow moderate richness values, and bright green indicates the highest richness values.

Quadrat	2021	2022	2023	Trend
1A	3	3	3	No change
1B	2	3	3	Increase
1C	1	3	3	Increase
1D	4	4	2	Decrease
2A	6	1	4	Decrease
2B	3	1	3	No change
2C	4	2	6	Increase
2D	4	3	2	Decrease
3A	5	2	3	Decrease
3B	3	4	4	Increase
3C	2	4	4	Increase
3D	3	3	5	Increase
4A	3	3	4	Increase
4B	2	1	0	Decrease
4C	1	2	4	Increase
4D	7	5	7	No change
5A	2	2	2	No change
5B	2	3	1	Decrease
5C	2	2	2	No change
5D	5	4	4	Decrease
6A	5	7	4	Decrease
6B	3	2	2	Decrease
6C	5	5	5	No change
6D	3	3	3	No change
7A	5	4	4	Decrease

7B	5	5	5	No change
7C	4	4	4	No change
7D	5	3	3	Decrease
8A	4	2	3	Decrease
8B	2	2	2	No change
8C	5	5	4	Decrease
8D	3	3	3	No change
9A	2	1	0	Decrease
9B	4	2	3	Decrease
9C	0	0	0	No change
9D	0	0	1	Increase
10A	4	6	4	No change
10B	2	1	0	Decrease
10C	3	1	0	Decrease
10D	5	4	4	Decrease
11A	6	4	4	Decrease
11B	4	2	5	Increase
11C	2	2	2	No change
11D	3	3	3	No change
12A	5	3	3	Decrease
12B	6	3	4	Decrease
12C	6	4	3	Decrease
12D	6	5	4	Decrease
13A	3	4	3	No change
13B	2	1	4	Increase
13C	4	4	3	Decrease
13D	1	1	1	No change
14A	3	2	2	Decrease
14B	3	3	2	Decrease
14C	1	2	1	No change

14D	5	4	2	Decrease
15A	1	2	2	Increase
15B	2	2	4	Increase
15C	1	2	2	Increase
15D	1	1	2	Increase
16A	1	2	1	No change
16B	3	3	3	No change
16C	1	1	2	Increase
16D	1	1	1	No change

Table 4-S3. Total percent cover for each of the sixty-four 1x1m^2 quadrats at Natchez Trace in 2021, 2022, and 2023 along with an overall trend of increase, decrease, or no change with time progression. Quadrats 1A – 8D are unsalvage logged, while quadrats 9A – 16D are salvage logged. Bright red indicates the lowest total percent cover values, yellow moderate total percent cover values, and bright green indicates the highest total percent cover values.

Quadrat	2021	2022	2023	Trend
1A	7	9	5	Decrease
1B	8	27	19	Increase
1C	1	4	4	Increase
1D	14	19	14	No change
2A	39	90	31	Decrease
2B	5	2	5	No change
2C	9	9	22	Increase
2D	14	10	9	Decrease
3A	26	27	17	Decrease
3B	16	17	22	Increase
3C	7	20	20	Increase
3D	6	7	21	Increase
4A	39	17	31	Decrease
4B	2	2	0	Decrease
4C	7	12	21	Increase
4D	19	30	36	Increase
5A	2	3	2	No change
5B	61	78	50	Decrease
5C	2	2	2	No change
5D	7	15	10	Increase
6A	46	51	18	Decrease
6B	9	9	9	No change
6C	9	10	9	No change
6D	8	17	4	Decrease
7A	10	21	37	Increase

7B	88	73	53	Decrease
7C	36	14	24	Decrease
7D	22	97	49	Increase
8A	9	6	8	Decrease
8B	5	7	9	Increase
8C	14	12	14	No change
8D	11	12	14	Increase
9A	6	1	0	Decrease
9B	27	11	15	Decrease
9C	0	0	0	No change
9D	0	0	1	Increase
10A	36	63	81	Increase
10B	7	2	0	Decrease
10C	3	1	0	Decrease
10D	21	13	23	Increase
11A	20	32	35	Increase
11B	7	4	15	Increase
11C	8	15	37	Increase
11D	9	24	25	Increase
12A	61	71	57	Decrease
12B	55	23	53	Decrease
12C	15	16	16	Increase
12D	22	17	37	Increase
13A	39	28	25	Decrease
13B	52	70	45	Decrease
13C	28	42	30	Increase
13D	1	1	1	No change
14A	11	4	2	Decrease
14B	3	14	8	Increase
14C	1	2	2	Increase

14D	27	16	4	Decrease
15A	2	2	2	No change
15B	7	10	15	Increase
15C	3	8	16	Increase
15D	4	2	21	Increase
16A	5	6	4	Decrease
16B	7	15	11	Increase
16C	0	3	4	Increase
16D	1	1	1	No change

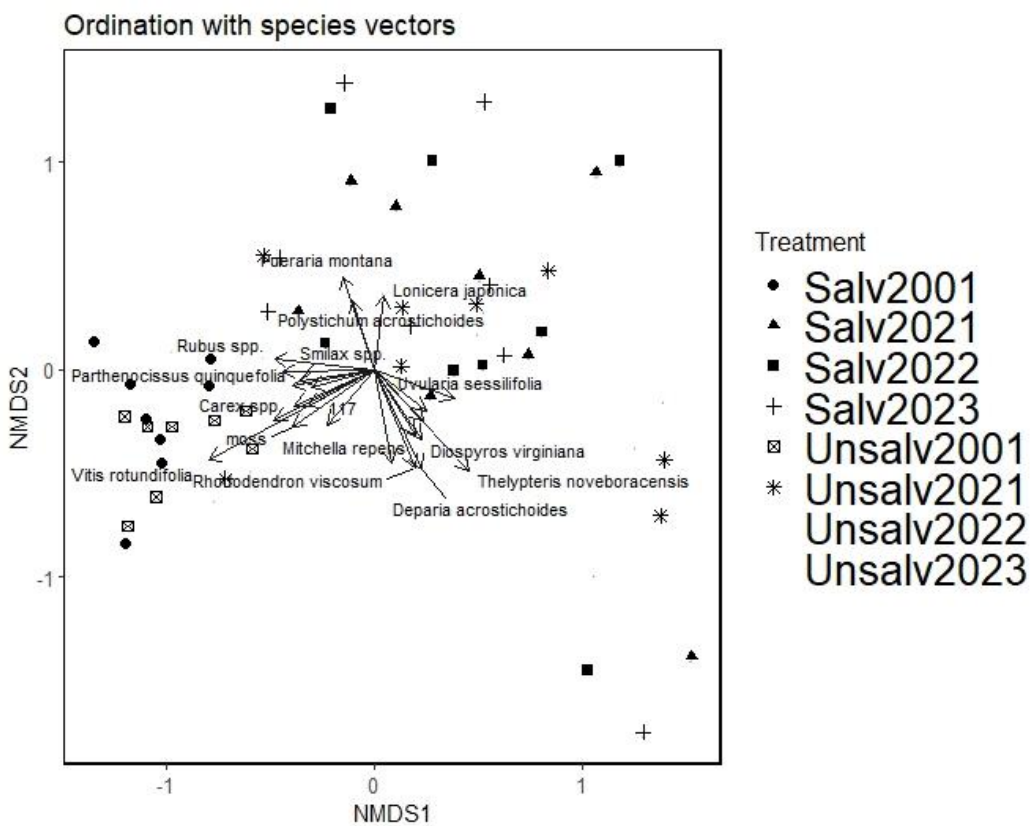


Figure 4-S1. NMDS graph for 2001, 2021, 2022, and 2023 sampling at Watson Springs (Salv = salvage logged; Unsalv = unsalvage logged) with species vectors. Small font size necessary to include all species on graph.

CHAPTER 5
CONCLUSIONS

As natural disturbances increase in both frequency and severity, it is important to comprehend how they impact herbaceous diversity and composition. The herbaceous layer harbors up to 90% of plant species richness in forests (Gilliam 2007), but are sensitive to changes in richness (and therefore diversity and composition) because of disturbances (Elliott et al. 2002, Kern et al 2014, Kleinman et al. 2017). Compound disturbances are more likely to result in long-term shifts in herbaceous species than single disturbances (Lindenmayer and Ough 2006, Anoszko et al. 2022) due to decreased environmental heterogeneity. Increasing comprehension of how wind and salvage logging – both separately and in unison – impact herbaceous species in a variety of habitats and timespans is vital to the preservation of herbaceous species.

This dissertation produces both short-term and long-term predictions of the effects of wind disturbance, and wind disturbance plus ensuing salvage logging, on herbaceous species by measuring diversity and composition over time. I studied the impacts of quantified severity through an experimental wind disturbance at Watson Springs Forest one, three, and four years post-disturbance. To study the impact of wind and salvage logging in an open-canopy woodland, I established a new study at the Jones Center at Ichuaway three years post-disturbance. To assess the long-term impact of wind disturbance and salvage logging, I performed follow-up work at the site of an earlier study at Natchez Trace State Park over twenty years post-disturbance.

The study in Chapter 2 analyzed if quantifying disturbance severity would aid in understanding how wind disturbance impacts herbaceous diversity and composition in a short-term timespan. The study site was an experimental wind disturbance set up in a closed-canopy forest on the Georgia Piedmont. Three severity treatments – each 70 x 70 meters – were set up: moderate and low severity plus an undisturbed control. One replicate of each treatment was created. I found that average Shannon diversity increased with disturbance severity; herb diversity was consistently highest during all years in the moderate severity treatment (1.07+/-0.54 to 1.28 +/- 0.51) while the low severity and control treatments alternated between years in claiming lowest diversity. The impact of disturbance severity on herbaceous diversity was most pronounced one year post-disturbance. These data support my hypothesis that the impact of disturbance severity on herbaceous diversity is highest one year post-disturbance and decreases with the progression of time. In all three years of sampling, compositional differences between treatments were consistent, providing mixed support for my hypothesis that compositional differences between treatments would be highest one year post-disturbance and decrease with time. The data suggests that factors other than disturbance severity (and indirectly, light availability) are the chief drivers of herbaceous composition at the experimental wind disturbance. The inclusion of abiotic data collection in the experimental design of future studies may explain surprising patterns that pseudoreplication and biotic data by itself is unable to unravel.

The study in Chapter 3 analyzed how wind and salvage logging – a compound disturbance – impacts herbaceous diversity and composition in an open-canopy woodland of Georgia three years post-disturbance. Four treatments of varying severities were created: unsalvage logged nongap (where neither wind created a canopy gap or salvage logging occurred), unsalvage logged gap, salvage logged nongap, and salvage logged gap. Six replicates of each treatment were created. No significant differences in diversity were observed between treatments. These data do not support my hypothesis that diversity would be highest in treatments that experienced wind disturbance but not salvage logging. This lack of difference may be attributed to the open-canopy nature of the site, with higher levels of light availability across all treatments in comparison to treatments in a closed-canopy forest. Significant differences in composition were observed in the unsalvage logged gap vs. unsalvage logged nongap and unsalvage logged nongap vs. salvage logged gap comparisons. These results indicate that while wind disturbance may cause compositional dissimilarity to herbaceous species, salvage logging at moderate severities obscures the impact of wind. One possible explanation for the obscuring is that salvage logging operations decrease microtopographical heterogeneity through the partial leveling of mounds created by wind disturbance. However, at high enough levels, there is enough environmental heterogeneity to cause compositional dissimilarity with areas of lower severity. These data support my hypothesis that with increasing disturbance severity disturbed and undisturbed treatments will exhibit increasingly dissimilar composition post-disturbance. In summary, no significant differences between treatments in diversity were observed possibly due to high light availability. Compositional differences were observed at low and high but not moderate severities, possibly due to microtopographical homogenization by dragging logs across mounds. The inclusion of abiotic and biotic data collection in multiple consecutive years post-disturbance, as opposed to one year of sampling three years post-disturbance, may reveal possibly ephemeral impacts of wind and salvage logging on herbaceous species in an open-canopy woodland that is outside the scope of this study.

The study in Chapter 4 analyzed the long-term impact of wind and salvage logging on herbaceous diversity and composition over two decades post-disturbance in the Tennessee Coastal Plain. The site was a closed-canopy, pine-hardwood forest in western Tennessee. Two treatments of varying disturbance severity (unsalvage logged and salvage logged) were established in 2001 two years post-disturbance. Later sampling occurred in 2021 – 2023, twenty-two to twenty-four years post-disturbance. Eight replicates of each treatment were created. While the exact locations of the 2001 sampling quadrats were lost to time, the locations of the replicates of each treatment were not. Data from the 2021 – 2023 sampling quadrats was averaged to produce a fair comparison to the averaged 2001 data. No differences in diversity between salvage logged and unsalvage logged treatments were observed in any year. These data do not support my hypothesis that significant differences in diversity between treatments would be evident immediately post-disturbance and that these differences would disappear over time. Rather, the data supports consistency between two years and twenty-plus years post-disturbance. This is likely due to the moderate severity of this compound disturbance, producing higher levels of coarse woody debris and minimal variation in light availability. Similarly, no significant dissimilarity was observed in composition between any treatments in any year. Similar contributing factors to the nonexistent difference in diversity between treatments could be used for the nonexistent difference in composition. Lack of heterogeneity of environment in both treatments from moderate disturbance severity would necessitate similar species composition. If possible, initiating data collection one year rather than two-years post-disturbance may capture the possible ephemeral effects of wind and salvage logging on herbaceous species. However, the consistency of results from the present long-term study offer two notes of hope: 1) the legitimacy of conclusions from short-term studies (< 5 years post-disturbance) is supported, and 2) at present, moderate-severity compound disturbances do not appear to have long-lasting negative impacts on herbaceous diversity and composition.

In totality, the present dissertation has presented evidence that disturbance severity (as quantified by 50% of 100% of basal area felled) does impact herbaceous diversity in the short-term post-disturbance in a closed-canopy forest. However, in an open-canopy woodland short-term post-disturbance or a closed-canopy forest long-term post-disturbance, disturbance severity is not observed to impact herbaceous diversity. The present dissertation also has presented evidence that disturbance severity does directly impact composition in closed-canopy forests in the short-term but not the long-term. Chapter 4 presented no compositional dissimilarity between treatments, while in Chapter 2, differences were present but did not exhibit patterns that indicated direct impact by varying disturbance severity. Chapter 3 presented that disturbance may indeed impact herbaceous composition in open-canopy woodlands when severity is low (undisturbed vs. wind) or high (undisturbed vs. wind and salvage logging), but that these differences may be masked by salvage logging decreasing the microtopographical heterogeneity that wind disturbance creates. I suggest that future studies collect both abiotic and biotic data over multiple consecutive years post-disturbance – ideally starting with one year post-disturbance – to gain a deeper understanding of what factors impact herbaceous response to disturbance and how to protect this layer of the forest in the face of climate change.

LITERATURE CITED

Anoszko, E., L. E. Frelich, R. L. Rich, and P. B. Reich. 2022. Wind and fire: Rapid shifts in tree community composition following multiple disturbances in the southern boreal forest. Ecosphere **13**:e3952.

Elliott, K. J., S. L. Hitchcock, and L. Krueger. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. Journal of the Torrey Botanical Society:48-59.

Gilliam, F. S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience **57**:845-858.

Kern, C. C., R. A. Montgomery, P. B. Reich, and T. F. Strong. 2014. Harvest-created canopy gaps increase species and functional trait diversity of the forest ground-layer community. Forest Science **60**:335-344.

Kleinman, J. S., S. A. Ford, and J. L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. Forest ecology and management **403**:112-125.

Lindenmayer, D., and K. Ough. 2006. Salvage logging in the montane ash eucalypt forests of the Central Highlands of Victoria and its potential impacts on biodiversity. Conservation Biology **20**:1005-1015.