

A REVIEW AND CASE STUDY OF MULTIPLE INTERACTING DISTURBANCES IN  
FOREST ECOSYSTEMS

by

JONATHAN S. KLEINMAN

JUSTIN L. HART, COMMITTEE CHAIR

MICHAEL K. STEINBERG

MATTHEW C. LAFEVOR

ARVIND A.R. BHUTA

DANIEL C. DEY

A DISSERTATION

Submitted in partial fulfillment of the requirements  
for the degree of Doctor of Philosophy  
in the Department of Geography  
in the Graduate School of  
The University of Alabama

TUSCALOOSA, ALABAMA

2021

Copyright Jonathan Samuel Kleinman 2021  
ALL RIGHTS RESERVED

## ABSTRACT

Strategies to enhance ecosystem resilience are increasingly needed in forest management plans. Natural and managed disturbances that alter ecosystem resilience to other perturbations are called compound disturbances. This dissertation first synthesized the literature on compound disturbances in forest ecosystems. I used a systematic review to catalogue case studies of compound forest disturbances and identify trends in the types, timing, environmental settings, and ecological consequences of each disturbance combination. The review emphasized that the detection of positive, negative, and neutral disturbance impacts on ecosystem resilience were often contingent on which response variables were used to monitor forest recovery. To illustrate and investigate this and other key concepts described in the review, I then examined a combination of wind disturbance, salvage logging, and prescribed fire in the Alabama Fall Line Hills. A range of woody plant, ground flora, and ground surface material metrics were collected before and after prescribed fire in *Pinus palustris* Mill. woodlands differentially impacted by an EF3 tornado and salvage logging. In support of the review, salvage logging and prescribed fire had different effects on post-wind disturbance recovery depending on which response variables were assessed. *Pinus palustris* saplings exhibited the greatest densities in salvage-logged sites and were more resistant to prescribed fire than most other sapling species. This indicated that recovery toward *P. palustris* canopy dominance was not negatively affected by salvage logging

and was enhanced by prescribed fire. Ground flora diversity and community dissimilarity, however, were reduced in salvage-logged sites before and after prescribed fire. Nonetheless, prescribed fire did impose some consistent selective pressures on understory plants with common life-history strategies. Overall, this dissertation supported the use of prescribed fire to promote *P. palustris* woodland recovery. Leaving some wind-disturbed zones unlogged was also recommended to support ground flora resilience. Moving forward, a diversity of response variables should be measured to achieve comprehensive assessments of disturbance effects on ecosystem resilience.

## DEDICATION

To Dad, who taught me how to read my biology textbook.

## ACKNOWLEDGEMENTS

I am grateful for my advisor and mentor, Justin Hart, who has given so much to my personal and professional development. This dissertation was a team effort and would not have been possible without the collective efforts of the Forest Dynamics Lab. Special thanks to Scott Ford who worked shoulder to shoulder with me in the establishment of monitoring plots, and to Davis Goode who was a steadfast and considerate partner on many expeditions. To other lab mates, field technicians, and research assistants, past and present, thank you for your support.

Thank you Michael Steinberg, Matthew LaFevor, Arvind Bhuta, and Daniel Dey for the considerable amount of time and effort you invested as committee members. I appreciate the insights and expertise that you each contributed to this dissertation and even more so the times we shared outside of the university. These experiences were enabled by the University of Alabama Graduate School and Department of Geography, which have been great sources of community and comradery. To Doug Sherman in particular, thank you for the trust and challenge. And to my parents, Julie and Danny Kleinman, thank you for your endless gifts of love, wisdom, and encouragement.

This work was supported by a participating agreement with the USDA Forest Service, Oakmulgee Ranger District. The Southern Appalachian Botanical Society and Biogeography Specialty Group of the American Association of Geographers provided additional funding.

## CONTENTS

ABSTRACT.....	ii
DEDICATION.....	iv
ACKNOWLEDGEMENTS.....	v
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
CHAPTER 1 INTRODUCTION.....	1
CHAPTER 2 ECOLOGICAL CONSEQUENCES OF COMPOUND DISTURBANCES IN FOREST ECOSYSTEMS: A SYSTEMATIC REVIEW....	7
Abstract.....	7
Introduction.....	8
Methods.....	10
Results and Discussion.....	14
Synthesis.....	32
References for Chapter 2.....	37
CHAPTER 3 PRESCRIBED FIRE EFFECTS ON <i>PINUS PALUSTRIS</i> WOODLAND DEVELOPMENT AFTER CATASTROPHIC WIND DISTURBANCE AND SALVAGE LOGGING.....	45
Abstract.....	45
Introduction.....	46
Methods.....	49
Results.....	55

Discussion.....	68
Management Implications.....	73
References for Chapter 3 .....	76
<b>CHAPTER 4 GROUND FLORA COVER, DIVERSITY, AND LIFE-HISTORY TRAIT REPRESENTATION AFTER WIND DISTURBANCE, SALVAGE LOGGING, AND PRESCRIBED FIRE IN A <i>PINUS PALUSTRIS</i> WOODLAND.....</b>	<b>85</b>
Abstract.....	85
Introduction.....	86
Methods.....	90
Results.....	103
Discussion.....	115
Conclusions.....	122
References for Chapter 4 .....	124
<b>CHAPTER 5 OVERALL CONCLUSION.....</b>	<b>132</b>
<b>REFERENCES .....</b>	<b>137</b>



## LIST OF TABLES

<b>Table 2.1.</b> Articles reviewed sorted by disturbance combinations, types of compound interactions, and time between disturbance events .....	16
<b>Table 3.1.</b> Summary of mixed ANOVAs to assess impacts of pre-fire conditions, time relative to prescribed fire, and their interaction on ground surface categories .....	59
<b>Table 3.2.</b> Summary of mixed ANOVAs to assess impacts of pre-fire conditions, time relative to prescribed fire, and their interaction on sapling and seedling density .....	62
<b>Table 3.3.</b> Density of saplings documented in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	63
<b>Table 3.4.</b> Density of seedlings documented in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	65
<b>Table 3.5.</b> Average richness and Shannon diversity of saplings and seedlings documented in mature, wind-disturbed, and salvage-logged plots .....	67
<b>Table 4.1.</b> Plant trait designations of the ground flora taxa documented in differentially disturbed <i>Pinus palustris</i> woodlands .....	95
<b>Table 4.2.</b> Descriptions of the life-history traits used to define the 155 ground flora taxa documented in differentially disturbed <i>Pinus palustris</i> woodlands ....	101
<b>Table 4.3.</b> Mean $\pm$ standard error foliar cover, richness, and Shannon diversity of ground flora in mature, wind-disturbed, and salvage-logged woodlands.....	105
<b>Table 4.4.</b> Indicator values of plant taxa most representative of mature, wind-disturbed, and salvage-logged sites before and after prescribed fire .....	109
<b>Table 4.5.</b> Positive and negative associations between life-history traits and disturbance categories before and after prescribed fire .....	111
<b>Table 4.6.</b> Summary of mixed ANOVAs used to assess impacts of pre-fire conditions, time, and their interaction on the foliar cover and richness of ground flora in each growth habit and life form. ....	112

## LIST OF FIGURES

<b>Figure 1.1.</b> <i>Pinus palustris</i> woodland in the Fall Line Hills of Alabama, USA .....	4
<b>Figure 2.1.</b> Article selection diagram.....	11
<b>Figure 2.2.</b> Frequency of 288 screened articles that referred to multiple forest disturbances.....	15
<b>Figure 2.3.</b> Response variables used to assess forest recovery .....	21
<b>Figure 2.4.</b> Geographic distribution of the compound disturbances reviewed .....	22
<b>Figure 3.1.</b> Study area in the Oakmulgee District, Talladega National Forest, Alabama, USA .....	50
<b>Figure 3.2.</b> Average volume of coarse woody debris, sapling density, and seedling density in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	57
<b>Figure 3.3.</b> Volume of coarse woody debris categorized as decay class II and decay class III in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	58
<b>Figure 3.4.</b> Average cover of ground surface categories documented in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	60
<b>Figure 4.1.</b> Plot locations in mature, wind-disturbed, and salvage-logged woodlands. Inset illustrates how quadrats were nested within each plot.....	93
<b>Figure 4.2.</b> NMS solutions before and after prescribed fire.....	106
<b>Figure 4.3.</b> Average dissimilarity of ground flora assemblages in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	108
<b>Figure 4.4.</b> Foliar cover and richness of ground flora representing each growth habit and life form in mature, wind-disturbed, and salvage-logged plots before and after prescribed fire .....	113
<b>Figure 4.5.</b> Photographs of live <i>Symplocos tinctoria</i> shoots and live <i>Styrax grandifolius</i> shoots growing from the same rootstocks as fire-killed shoots.....	119

## CHAPTER 1

### INTRODUCTION

Forest ecosystems exist in a constant state of recovery. Disturbances impact living and abiotic forest patterns and processes, and can accelerate or retrogress stand development along a trajectory from stand initiation to the expression of complex, multi-aged stands (Oliver and Larson 1996, Hart and Cox 2017). At a landscape-scale, a diversity of ecosystem goods and services are provided by the coexistence of forest stands in multiple stages of development. For example, after stand-regenerating disturbance events, early-successional forests support high biological diversity and complex food webs (Swanson et al 2011). Stands of mature trees provide society with natural, renewable wood products, and some trees are best unharvested to support other ecological and cultural functions (Lindenmayer and Laurance 2017).

Though forests exhibit a dynamic range of conditions throughout stand development, resilience is the ecosystem property in which intrinsic structures, feedbacks, and functions persist after disturbance (Holling 1973). Forest ecosystem resilience is of paramount concern as forests globally are subject to more frequent and severe natural and anthropogenic perturbations (Turner 2010, Trumbore et al. 2015). Climate-driven changes in natural disturbance regimes and mounting pressures on forest resources may compromise the capacity of some forests to recover. Science is therefore needed to inform strategies to manage naturally-disturbed ecosystems before, during, and after unplanned perturbations (Dale et al. 2001).

Compound disturbances are those that alter ecosystem resilience to other perturbations (Paine et al. 1998). Compound disturbance effects are often expressed as altered or delayed

recovery trajectories, however, compound disturbances can also enhance ecosystem resilience by buffering effects of other perturbations (Buma 2015, Cannon et al. 2017). Understanding the consequences of compound disturbances can therefore help guide strategies to enhance ecosystem resilience to future disturbance regime scenarios. To improve our understanding of compound disturbances, the second chapter of this dissertation synthesized the growing literature on the topic, with a focus on forest ecosystems (Kleinman et al. 2019). I used a systematic review to catalogue and categorize forest disturbance combinations by types, timing, environmental settings, and ecological consequences.

To further enhance our understanding of multiple interacting disturbances, I examined a case study of catastrophic wind disturbance, salvage logging, and prescribed fire in Alabama, USA (Kleinman et al. 2020, Kleinman et al. 2021). Catastrophic wind disturbances impact terrestrial ecosystem worldwide and will become more common in some regions including the southeastern USA (Webster et al., 2005, Gensini and Brooks, 2018). Managers must therefore be increasingly prepared to consider the socioeconomic and ecological implications of post-wind disturbance salvage logging, which is commonly applied to remove dead and damaged trees. Salvage logging can reduce risks of subsequent high-severity wildfires and insect outbreaks and simultaneously provide a partial return on otherwise lost standing timber value. However, though forest recovery is not necessarily negatively impacted by salvage logging (Royo et al. 2016), many caution against consequences including biodiversity loss (Swanson et al. 2011), habitat homogenization (Lindenmayer et al. 2017), and even total ecosystem collapse (Van Nieuwstadt et al. 2001).

This dissertation directly addressed four limitations in our understanding of salvage logging that are consistently highlighted in the literature. First, compared to salvage

logging conducted after wildfires, much less is known about post-wind disturbance operations (Royo et al. 2016, Thorn et al. 2018). Second, more research focus is needed on non-arboreal plant assemblages (i.e. ground flora), which typically host greater floristic diversity than canopy strata and are often more sensitive indicators of disturbance (Roberts 2004, Gilliam 2007, Leverkus et al. 2018). Third, repeated measurements are required for a more comprehensive understanding than single “snapshots” of recovery. Finally, little is known about the resilience of salvaged stands to subsequent disturbances (D’Amato et al. 2011, Buma and Wessman 2012, Taboada et al. 2018), especially with respect to prescribed fire effects in salvage-logged sites (Palik and Kastendick 2009).

The critically endangered *P. palustris* ecosystem, which occupies less than 5% of its pre-settlement extent, provides an ideal model ecosystem to study disturbance effects. *Pinus palustris* ecosystems host nearly monospecific, *P. palustris*-dominated canopies situated above open midstories (Figure 1.1). As such, post-disturbance investigations of canopy recovery can focus on the vertical stratification of a single species, *P. palustris*. In contrast, *P. palustris* ecosystems support some of the most species-rich ground flora assemblages outside of the tropics (Walker and Peet 1983), and the expression of species-specific life-history strategies in the understory can provide more sensitive indicators of disturbance effects (Dale et al. 2002).

Frequent low-intensity fires, which were historically ignited by Native Americans and lightning strikes, are an integral component of *P. palustris* stand dynamics. Today, land managers use prescribed fires to induce shoot mortality of woody stems that would otherwise outcompete fire-resistant *P. palustris* for canopy dominance and to maintain suitable seedbed conditions for fire-adapted ground flora. Though prescribed fires are well-studied in *P. palustris* ecosystems, uncertainty exists regarding prescribed fire effects after stand-regenerating



Figure 1.1. *Pinus palustris* woodland in the Fall Line Hills of Alabama, USA

disturbance events. Catastrophic canopy removal and corresponding reductions in canopy-derived fine fuels can challenge the application of prescribed fires, which require an uninterrupted fine fuel bed (O'Brien et al. 2008). Moreover, the release of understory hardwoods can also disrupt flammable fuel bed continuity (Mitchell et al. 2009). However, a growing literature highlights the importance of relatively flammable, fire-facilitating hardwoods in the perpetuation of prescribed fire in *P. palustris* ecosystems (Fill et al. 2015, Kane et al. 2008, Hiers et al. 2014, Emery and Hart 2020).

The third and fourth chapters of this dissertation used a permanent plot network to collect woody-plant, ground-flora, and ground surface-material metrics before and after prescribed fire in *P. palustris* woodlands differentially impacted by an EF3 tornado and salvage logging. In chapter three, I focused on the composition and density of woody stems to examine the impacts of interacting disturbances on *P. palustris* stand development (Kleinman et al. 2020). To gain a more comprehensive understanding of disturbance effects on floristic dynamics, I focused on ground flora succession in chapter four (Kleinman et al. 2021). Specifically, I used trait-based analyses to enable a more detailed assessment of disturbance effects than aggregate metrics of foliar cover and diversity.

Overall, this dissertation provides a framework for understanding the intricacies of multiple interacting disturbances in the context of global change and human responses to altered disturbance regimes. Assessments of operational-scale management actions (i.e. salvage logging and prescribed fire) on ecosystem recovery can inform the management of the critically endangered *P. palustris* ecosystem and fire-adapted forests worldwide. Limitations in our understanding of compound disturbances in general and post-disturbance salvage logging in particular are addressed. Research focus on ground flora succession and prescribed fire effects

in salvage-logged sites provides an understudied perspective on interacting disturbances and contributes to a more holistic understanding of disturbance effects on ecosystem recovery.



## CHAPTER 2

### ECOLOGICAL CONSEQUENCES OF COMPOUND DISTURBANCES IN FOREST ECOSYSTEMS: A SYSTEMATIC REVIEW

#### **Abstract**

Investigations of compound disturbances that alter forest resilience (i.e. recovery time or trajectory) have escalated over the past two decades. We used a systematic approach to identify and describe the ecological consequences of discrete forest disturbance events involved in compound interactions. Fire, wind disturbance, and salvage logging were the most common disturbance types investigated. Most compound interactions occurred in North America and involved five or fewer years between disturbances. Common and interrelated disturbance legacies that facilitated compound interactions included reduced seed source availability, deadwood deposition and extraction, and increased light and growing space availability. Forest recovery was assessed with a diversity of metrics including woody and herbaceous plants, soil properties, and carbon stocks, which sometimes determined if and what kind of compound interaction was detected. Distinctions between recovery time and trajectory, forest succession and development, and species-specific and community-level responses also influenced the detection and direction of compound interactions. Moving forward, we advocate a more holistic approach to quantify ecosystem recovery that considers multiple response variables. Other opportunities to improve compound disturbance ecology include increased emphasis on understudied disturbance types, regions, and forest types. We also encourage more research on buffering interactions that increase forest resilience, which were underrepresented in this review.

## Introduction

Disturbances modify forest composition, structure, and function, and leave legacies that impact the rate and trajectory of forest recovery (Oliver and Larson 1996, Franklin et al. 2002). Natural disturbances include biotic events, such as insect outbreaks and invasive pathogens, and abiotic events, such as fires, floods, ice storms, and damaging wind events. Forest succession and development are also directed by human impacts that range from exploitative logging and land-use change to deliberate silvicultural entries designed to achieve desired conditions. The widespread occurrence of more frequent and severe natural disturbances has been attributed, in part, to precipitation and temperature anomalies associated with global change (Dale et al. 2001, Seidl et al. 2017, Sommerfeld et al. 2018). Coupled with growing human demands, recognition of altered disturbance regimes has motivated interest in multiple interacting disturbances (Turner 2010, Buma 2015). Interacting disturbances may cause unexpected rates and trajectories of forest recovery and reduce resistance and resilience to future perturbations (Paine et al. 1998, Bigler et al. 2005). Understanding disturbance interactions is therefore critical to forecast changes in ecosystem properties and implement management strategies.

Buma (2015) distinguished two types of disturbance interactions: linked and compound (*sensu* Simard et al. 2011). Linked interactions alter forest resistance (i.e. capacity to endure disturbance without changing), and compound interactions alter forest resilience (i.e. capacity to recover to pre-disturbance conditions; Cannon et al. 2017). Forest resilience includes engineering resilience, which is inversely related to recovery time, and ecological resilience, which describes the amount of energy required to direct recovery toward an alternative state (Holling 1973, Angeler and Allen 2016). Thus, linked interactions describe the influence of one disturbance on forest response to (i.e. resistance to) another disturbance, and compound

interactions describe the combined effects of multiple disturbances on altering the rate or trajectory of forest recovery (Paine et al. 1998, Simard et al. 2011). Interacting disturbances are also defined by whether resistance and/or resilience are decreased or increased (Cannon et al. 2017, Kane et al. 2017). When one disturbance enhances the impact of another by decreasing resistance or resilience, the interaction is amplifying. Alternatively, buffering interactions describe situations when one disturbance reduces the impact of another by increasing resistance or resilience (Cannon et al. 2019).

Disturbance interaction mechanisms are mediated by disturbance legacies, which include changes in the spatial arrangement of physical site conditions and life-history strategies represented by residual organisms and propagules (Franklin et al. 2000, Johnstone et al. 2016). For example, in one of six vignettes used to formalize the compound disturbance concept, Paine et al. (1998) described how ash deposits from a volcanic eruption thinned native vegetation in Hawaii Volcanos National Park. Volcanic legacies, including ash deposits and reduced vegetation cover, facilitated invasion of an exotic plant that grows faster than natives, yields abundant seed, and fixes high levels of nitrogen that is incorporated in the soil (Vitousek and Walker 1989, Vitousek 1990). Thus, the eruption reduced resistance to the invasion (a linked interaction), which altered post-eruption successional trajectories and nutrient dynamics (a compound interaction).

Though identification of linked interactions is possible during or soon after the disturbance events of interest, impacts of compound disturbances take longer to manifest. Forest recovery is a continuous process, and initial post-disturbance conditions may not indicate long-term recovery trajectories (Gill et al. 2017). Despite theoretical advances to describe changing disturbance regimes and alternative states, quantification of ecosystem resilience remains a

tenuous task from an operational perspective (Seidl et al. 2016). Moreover, determination of whether disturbances impact resilience can depend on which response variables are considered (Carpenter et al. 2001).

The goal of this review is to identify and describe the ecological consequences of compound forest disturbances. A systematic review of the literature is used to create a catalog of disturbance combinations and compare them based on different manifestations of compound interactions. Although forest recovery can be assessed with a diversity of response variables, limited use of these metrics restricts understanding of disturbance impacts. As such, we are particularly interested in how compound disturbances are quantified, and how the consideration of different response variables influences how compound interactions are identified and described. Compound disturbances are also compared by geographic regions and forests types, and disturbance legacies and mechanisms of change (Peters et al. 2011). This review provides a framework for future investigations, and, by identifying generalities in the literature, improves our ability to define, forecast, and manage for compound disturbances.

## **Methods**

### ***Article Selection***

A keyword-driven approach was used to search the Web of Science Core Collection database with the terms: (“compound\* disturbance\$” OR “compound\* perturbation\$” OR “disturbance interaction\$” OR “interacting disturbance\$” OR “multiple disturbance\$” OR “multiple perturbation\$” OR “repeat\* disturbance\$”) AND (forest OR savanna OR woodland). This search yielded 328 records published through April 2019, which were screened and assessed for eligibility (Figure 2.1; Moher et al. 2009). After database searching, identified

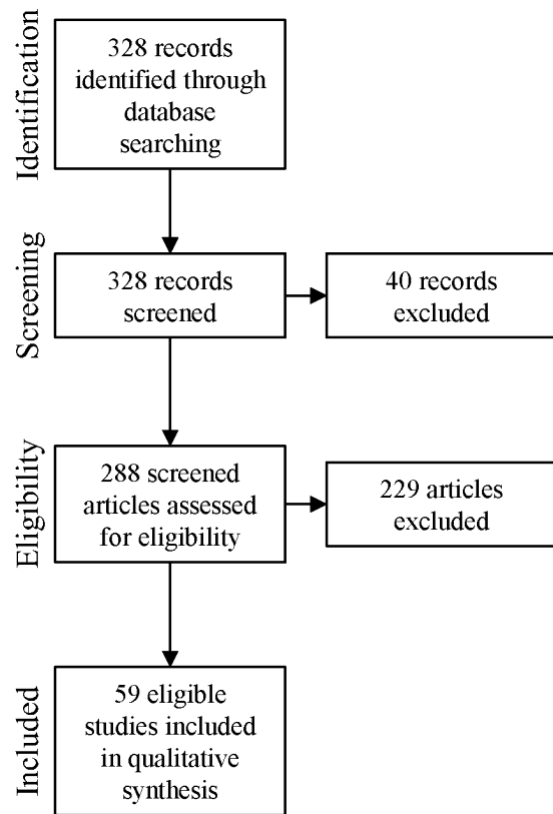


Figure 2.1. Article selection diagram adapted from the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (Moher et al. 2009).

records were vetted by titles, abstracts, and keywords to remove those that did not match the focus of this investigation. Specifically, 40 records were excluded that did not pertain to forest ecosystems and/or used the terms compound, interacting, multiple, or repeat to refer to something other than multiple disturbance events (e.g. organic compound). After screening, 288 articles remained that referred to multiple forest disturbances. The full texts of these articles were reviewed to exclude those that did not meet eligibility criteria for inclusion in the review framework. Excluded articles consisted of review papers and short communications, studies focused on non-discrete disturbances like climate change and chronic herbivory, disturbance reconstructions, and those that did not measure post-disturbance recovery with empirical data (e.g. prospective simulation models). After eligibility assessment, 59 full-length research articles remained that used empirical data to measure forest recovery after multiple, discrete, disturbance events with overlapping spatial distributions. These articles were included in a review framework designed to compare disturbance combinations by forest types and locations, disturbance types and timing, and attributes of disturbance interactions.

### ***Review Framework***

Forest types and locations were assigned based on study area descriptions and coordinates. Because authors utilized a variety of classification schemes, North American forest types were standardized to a classification scheme adapted from Barbour and Billings (2000). Based on dominant tree taxa and geographic locations, reviewed North American forest types included Boreal (B), Coastal Plain (CP), Eastern Deciduous (ED), Pacific Coastal–Cascadian (PCC), Piedmont (P), Rocky Mountain (RM), Subtropical (ST), and Tropical (T). Forest type descriptions outside North America were indicated as Intercontinental (IC). Although not

displayed in the review framework, pre-disturbance forest ages and stages of development were also recorded. However, of the 59 articles reviewed, only 25 specified age and 25 described developmental stage. Moreover, developmental stages were most commonly reported as mature, old-growth, or second-growth. With the exception of Sass et al. (2018) who described stem exclusion and Gill et al. (2017) who described understory reinitiation, forest disturbances were not discussed in the context of stand development models (e.g. Oliver and Larson 1996, Franklin et al. 2002).

To indicate inter-disturbance recovery time, the years disturbance events occurred were listed in the review framework. Most disturbances fit one of seven disturbance type categories: bark beetles, drought, fire, moths, wind, salvage logging, or intensive forest management. Bark beetles included *Dendroctonus brevicomis* (Stevens-Rumann et al. 2015), *D. ponderosae* (Harvey et al. 2014a, Harvey et al. 2014b, Agne et al. 2016), *D. pseudotsugae* (Harvey et al. 2013, Stevens-Rumann et al. 2015), and *D. rufipennis* (Kulakowski et al. 2013, Carlson et al. 2017). Droughts consisted of discrete periods of exceptionally dry conditions, triggered by anomalously high temperatures and low moisture availability (Peters et al. 2011, Keith et al. 2012). Fire included prescribed fires and wildfires. Moths consisted of a *Lymantria monacha* outbreak (Bottero et al. 2013), and successive *Epirrita autumnata* and *Operophtera brumata* outbreaks (Karlsen et al. 2013). Wind events included blowdown (Buma and Wessman 2011, D'Amato et al. 2011), downbursts (Peterson and Leach 2008a, Lang et al. 2009), hurricanes (Robertson and Platt 2001, Teh et al. 2009, Bonilla-Moheno 2012, Sass et al. 2018), tornadoes (Gagnon and Platt 2008, White et al. 2014, Kleinman et al. 2017, Oldfield and Peterson 2019), and a catastrophic storm (Bottero et al. 2013). Salvage logging was conducted after wind and before fire, after wind without subsequent fire, and after fire. Intensive forest management (IFM,

*sensu* Stokely et al. 2018) was used to describe clearcut harvesting, experimental manipulation, and other related silvicultural entries (e.g. replanting and herbicide application). A psyllid insect (*Cardiaspina* spp.) outbreak was also described (Keith et al. 2012).

Response variables related to forest recovery were recorded to determine how impacts of compound interactions were described and to identify which forest recovery metrics were most often utilized. This process also contributed to an “outcome-level assessment” in which study results were assessed in relation to the type of supporting data collected (Moher et al. 2009). Forest recovery response variables were restricted to those that measured forest resilience (i.e. recovery time or trajectory), not resistance (i.e. disturbance probability, extent, intensity, or severity). For instance, post-disturbance plant establishment (e.g. seedling composition and density) was considered a metric of forest recovery, but disturbance-mediated plant mortality, which is a metric of disturbance severity, was not (Keeley 2009). In the review framework, the “+” sign indicated amplifying compound interactions in which one disturbance enhanced the impact of another disturbance by reducing forest resilience. Alternatively, the “-” sign indicated buffering compound interactions in which one disturbance reduced the impact of another disturbance by increasing forest resilience (Cannon et al. 2017). Disturbances that did not interact to impact resilience were marked “0.”

## **Results and Discussion**

### ***Wind and Fire***

Investigations of compound forest disturbances have escalated over the past two decades (Figure 2.2). Wind disturbance and fire composed the most well-documented disturbance combination (Table 2.1). Consistent with the other disturbance combinations reviewed,



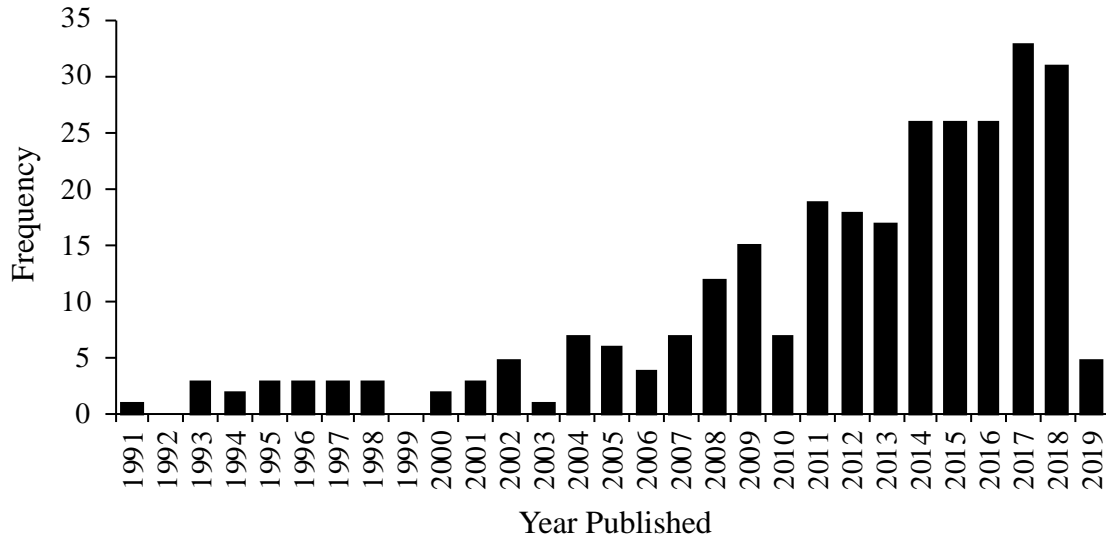


Figure 2.2. Frequency of the 288 screened articles that referred to multiple forest disturbances displayed by year of publication. Year 2019 is incomplete because database searching ended April 2019.

Table 2.1. Articles reviewed in this study sorted by the most common disturbance combinations, types of compound interactions (buffering –, amplifying +, neutral 0), and time between disturbance events. Intensive forest management (IFM) was used to describe experimental manipulation, logging, and other silvicultural entries. North American forest types included Boreal (B), Coastal Plain (CP), Eastern Deciduous (ED), Pacific Coastal–Cascadian (PCC), Piedmont (P), Rocky Mountain (RM), Subtropical (ST), and Tropical (T). Studies located outside of North America are indicated as Intercontinental (IC). Articles that described multiple disturbance combinations are distinguished by scenario numbers.

<i>Combination (disturbance 1 and disturbance 2)</i>	<i>Compound interaction</i>	<i>Forest type and location</i>	<i>Disturbance 1 dates</i>	<i>Disturbance 2 dates</i>	<i>Reference</i>	<i>Scenario</i>
Wind and fire	–/+	P – Georgia, USA	2012	2013	Cannon et al. (2019)	
	+	CP – South Carolina, USA	1989	1990	Smith et al. (1997)	
	+	CP – Louisiana, USA	2000	2004	Gagnon and Platt (2008)	
	+	RM – Colorado, USA	1997	2002	Buma and Wessman (2011)	I
	+	RM – Colorado, USA	1997	2002	Buma and Wessman (2012)	I
	+	RM – Colorado, USA	1997	2002	Buma et al. (2014)	I
	+	RM – Colorado, USA	1997	2002	Gill et al. (2017)	
	+	RM – Colorado, USA	1997	2002	Kulakowski et al. (2013)	I
	+	B – Minnesota, USA	1999	2007	Bradford et al. (2012)	I
	+	B – Minnesota, USA	1999	2007	D'Amato et al. (2011)	I
	0	B – Minnesota, USA	1999	2007	Mitchell et al. (2012)	I
Post-wind salvage logging and fire	–	RM – Colorado, USA	1999–2001	2002	Buma and Wessman (2011)	II
	–	RM – Colorado, USA	1999–2001	2002	Buma and Wessman (2012)	II
	+	RM – Colorado, USA	1999–2001	2002	Buma et al. (2014)	II
	+	B – Minnesota, USA	1999–2002	2007	Bradford et al. (2012)	II
	+	B – Minnesota, USA	1999–2002	2007	D'Amato et al. (2011)	II
	+	B – Minnesota, USA	1999–2002	2007	Mitchell et al. (2012)	II
	+	IC – Victoria, Australia	2003 and/or 2007	2007 and/or 2013	Fairman et al. (2017)	
Repeat fires	+	IC – León, Spain	1998	2012	Taboada et al. (2018)	I

<i>Combination (disturbance 1 and disturbance 2)</i>	<i>Compound interaction</i>	<i>Forest type and location</i>	<i>Disturbance 1 dates</i>	<i>Disturbance 2 dates</i>	<i>Reference</i>	<i>Scenario</i>
Bark beetle outbreaks and fire	+	PCC – Oregon, USA	1987	2002	Donato et al. (2016)	
	+	IC – Victoria, Australia	1939	1983 and/or 2009	Bowd et al. (2018)	I
	+	IC – Victoria, Australia	1939	1983 and/or 2009	Bowd et al. (2019)	I
	0	IC – Catalonia, Spain	1994	1998	Bonfil et al. (2014)	
	0	RM – New Mexico, USA	1977, 1996, and/or 2000	2011	Haire et al. (2017)	
	0	PCC – California, USA	2000	2012	Nemens et al. (2018)	
	0	PCC – Oregon, USA	1987	2002	Donato et al. (2009)	
	+	RM – Colorado, USA	2004–2013	2013	Carlson et al. (2017)	
	+	RM – Wyoming, USA	1995–2004	2008	Harvey et al. (2013)	
	0	RM – Wyoming, USA	2006–2008	2008	Harvey et al. (2014a)	I
	0	RM – Idaho, USA	2009–2011	2011	Harvey et al. (2014b)	I
	0	RM – Wyoming, USA	2003–2009	2011	Harvey et al. (2014a)	II
	0	RM – Montana, USA	2001–2008	2011	Harvey et al. (2014b)	II
	0	RM – Idaho and Montana, USA	1999–2004	2007	Stevens-Rumann et al. (2015)	
Fire and salvage logging	0	PCC – Oregon, USA	1997–2004	2012	Agne et al. (2016)	
	0	RM – Colorado, USA	1940–1949	2002	Kulakowski et al. (2013)	II
	+	B – Alberta, Canada	2001	2001–2002	Cobb et al. (2007)	I
	+	B – Alberta, Canada	2001	2001–2002	Kishchuk et al. (2015)	
	+	IC – Victoria, Australia	1939 and 2009	2009–2010	Bowd et al. (2018)	II
	+	IC – Victoria, Australia	1939 and 2009	2009–2010	Bowd et al. (2019)	II
	+	PCC – California, USA	2002	2003	Knapp and Ritchie (2016)	
	+	IC – Canary Islands, Spain	2008	2009	Hernández- Hernández et al. (2017)	
+	IC – León, Spain	1998 and 2012	1999	Taboada et al. (2018)	II	

<i>Combination (disturbance 1 and disturbance 2)</i>	<i>Compound interaction</i>	<i>Forest type and location</i>	<i>Disturbance 1 dates</i>	<i>Disturbance 2 dates</i>	<i>Reference</i>	<i>Scenario</i>	
Wind and salvage logging	+	IC – León, Spain	1998 and 2012	1999 and 2014	Taboada et al. (2018)	III	
	0	IC – León, Spain	2012	2013 or 2014	Taboada et al. (2018)	IV	
	+	CP – Alabama, USA	2011	2011	Kleinman et al. (2017)		
	+	ED – Alabama, USA	2011	2011	White et al. (2014)		
	+	ED – Wisconsin, USA	1977	1978–1979	Lang et al. (2009)		
	+	ED – New Hampshire, USA	1938	ca. 1938–1943	Sass et al. (2018)	I	
	+	CP – Tennessee, USA	1999	ca. 1999–2002	Peterson and Leach (2008a)		
Repeat IFM	+	ED – Georgia, USA	2011	2012–2013	Oldfield and Peterson (2019)		
	+	IC – Aosta Valley, Italy	1990	1992–1993	Bottero et al. (2013)	I	
	– / +	IC – Catalonia, Spain	1992	2002	López et al. (2009)		
	+	RM – British Columbia, Canada	1993–1994	1993–1994	Kranabetter et al. (2017)		
	+	PCC – Washington, USA	1999–2000	2000	Peter and Harrington (2009)		
	+	PCC – British Columbia, Canada	2002	2002–2003	Starzomski and Srivastava (2007)		
	+	CP – Florida, USA	2007	2008 and 2010	Ober and DeGroot (2014)		
	+	IC – Guangxi Zhuang Autonomous Region, China	1991	1998	Wen et al. (2010)		
	IFM and fire	+	IC – Jämtland County, Sweden	1985	1996–1998	Strengbom and Nordin (2012)	
		+	CP – Georgia, USA	1998–1999	1998–2003	Kirkman et al. (2007)	
+		ED – Alabama, USA	2005 or 2006	2006 or 2007	Sutton et al. (2013)		
+		CP – Mississippi, USA	1999	2000, 2003, and 2006	Igley et al. (2014)		
+		B – Ontario, Canada			Pidgen and Mallik (2013)		
+		B – Alberta, Canada	1999	2001	Cobb et al. (2007)	II	
+		CP – Louisiana, USA	1984–1985	1987 and 2000	Coleman et al. (2008)		

<i>Combination (disturbance 1 and disturbance 2)</i>	<i>Compound interaction</i>	<i>Forest type and location</i>	<i>Disturbance 1 dates</i>	<i>Disturbance 2 dates</i>	<i>Reference</i>	<i>Scenario</i>
Fire and IFM	+	B – British Columbia, Canada	1997–2004	2010	Ton and Krawchuk (2016)	
	+	IC – KwaZulu-Natal, South Africa	2005	2005–2006	Schutz et al. (2011)	
	+	IC – Catalonia, Spain	1994 and/or 1998	1999	Bonfil et al. (2014)	II
	+	IC – Victoria, Australia	1939 and 1983	2009–2010	Bowd et al. (2018)	III
	+	IC – Victoria, Australia	1939 and 1983	2009–2010	Bowd et al. (2019)	III
IFM and wind	+	IC – Victoria, Australia	1939	1980–1985 or 2009–2010	Bowd et al. (2018)	IV
	+	IC – Victoria, Australia	1939	1980–1985 or 2009–2010	Bowd et al. (2019)	IV
	+	ST – Río Grande, Puerto Rico	1989	1989 and 1998	Teh et al. (2009)	
	+	ED – New Hampshire, USA	1929	1938	Sass et al. (2018)	II
	Drought and psyllid insect outbreak	+	IC – New South Wales, Australia	2002–2003	2002–2003	Keith et al. (2012)
Drought and fire	- / +	GH – Moscow, Idaho			Sparks et al. (2018)	
Repeat drought	+	IC – Western Australia, Australia	2006–2007	2010–2011	Matusick et al. (2016)	
IFM and drought	+	T – Oaxaca, Mexico	1990	1997–1998	Valdés et al. (2006)	
Fire and wind	+	ST – Florida, USA	1989	1992	Robertson and Platt (2001)	
Repeat wind	+	T – Quintana Roo, Mexico	2005	2005	Bonilla-Moheno (2012)	
Repeat moth outbreaks	+	IC – Finmark County, Norway	2002–2004	2005–2006	Karlsen et al. (2013)	
Moth outbreak and salvage logging	+	IC – Aosta Valley, Italy	1984–1990	1991–1992	Bottero et al. (2013)	II

the most common forest recovery response variables involved woody plants, but a range of other variables were also measured (Figure 2.3). Also consistent with the broader literature, the occurrence and direction of compound wind-and-fire interactions sometimes depended on which response variables were considered. This concept was exemplified by an experimental wind-and-fire study in which rapid *Rhus copallinum* recruitment indicated an amplifying interaction, but increased biomass of sapling regrowth indicated a buffering interaction (Cannon et al. 2019). Enhanced *R. copallinum* establishment paralleled other compound interactions where clonal regrowth of sprouting plants was observed. Indeed, based on clonal *Arundinaria gigantea* densities, Gagnon and Platt (2008) reported that wind and fire could result in dense, monotypic bamboo stands.

Outside of the southeastern United States, two other well-studied wind-and-fire combinations occurred in the Minnesota sub-boreal and Colorado Rocky Mountains (Figure 2.4). In both locations, clonal *Populus tremuloides* sprouted prolifically. However, a range of other forest responses were observed. In Minnesota, although post-fire seedling densities indicated a potential transition to a *Populus tremuloides*-dominated state, multivariate analyses did not indicate compositional differences in shrub and tree regeneration (D'Amato et al. 2011). Net forest carbon loss was attributed to wind-induced increases in deadwood and forest floor carbon pools, which were subsequently consumed by fire (Bradford et al. 2012). Nonetheless, despite increased fire severity on wind-and-fire impacted sites (Fraver et al. 2011), forest floor and soil mercury levels were comparable to fire-only sites (Mitchell et al. 2012).

In Colorado, altered canopy succession and carbon stock recovery also signaled amplifying compound interactions. Wind-induced fuel loading was linked with larger burned patches, greater fire temperature and duration, and increased *Pinus contorta* cone consumption

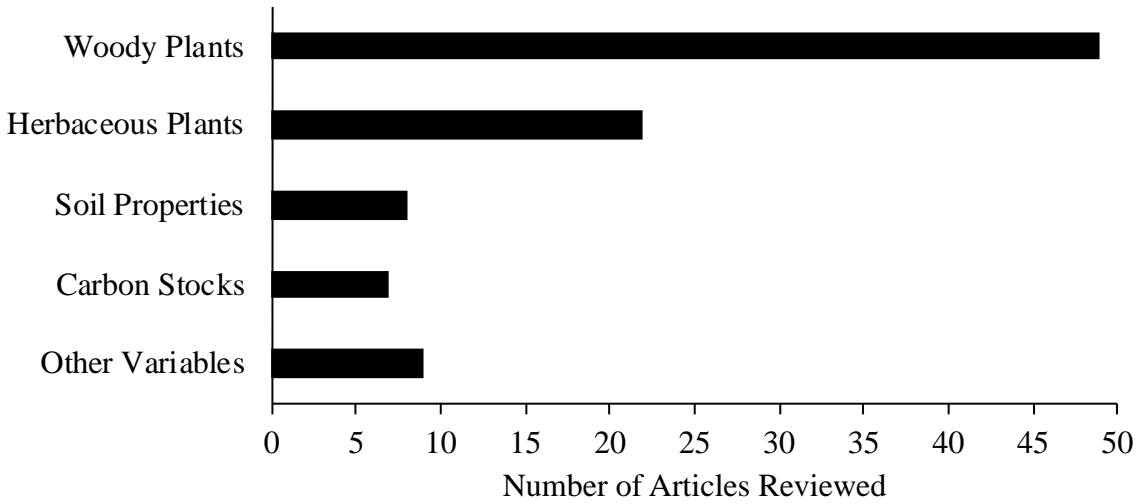


Figure 2.3. Response variables used to assess forest recovery displayed by the frequency of reviewed articles that utilized them. Soil properties included microtopographic variability and forest floor litter, fibric, and humic horizons. Other variables included arthropods, bryophytes, fungi, and herpetofauna.

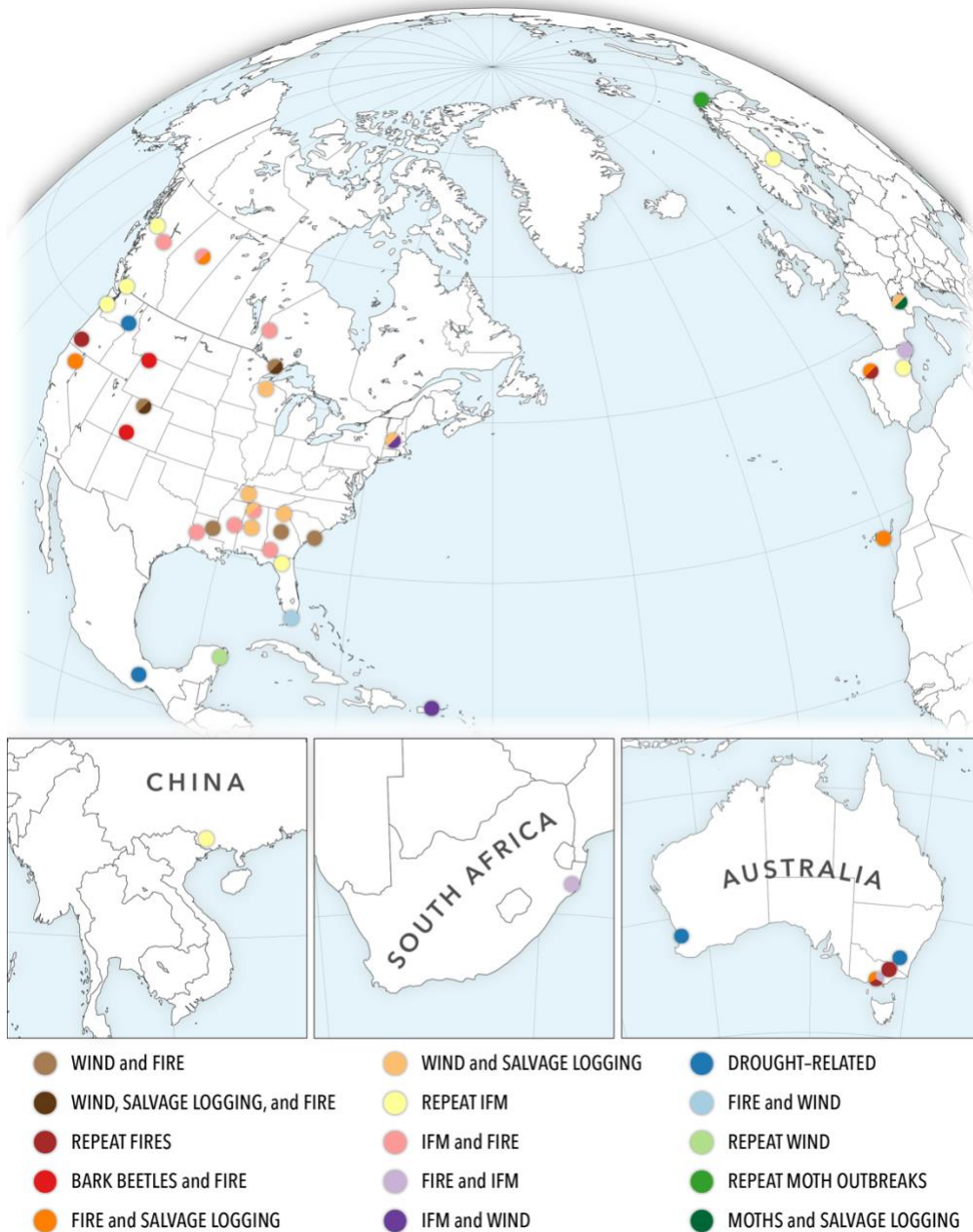


Figure. 2.4. Geographic distribution of the compound forest disturbances reviewed. Study location (circle) colors correspond to disturbance combination descriptions. Divided circles indicate study locations where multiple types of compound disturbance combinations occurred. Intensive forest management (IFM) includes experimental manipulation, logging, and other silvicultural entries.



(Buma and Wessman 2011). Because of cone consumption and greater dispersal requirements, a paucity of post-fire *P. contorta* seedlings was observed, which indicated a potential transition to a *P. tremuloides*-dominated state (Buma and Wessman 2012, Kulakowski et al. 2013). Wind-and-fire impacted sites also exhibited greater successional instability over a 13-year period compared to unburned wind-disturbed sites (Gill et al. 2017). Regarding black carbon (i.e. decay-resistant charcoal), Buma et al. (2014) predicted a net loss over the fire-return interval on wind-and-fire impacted sites, where black carbon formation was likely offset by consumption.

### ***Post-Wind Salvage Logging and Fire***

Some wind-and-fire investigations also examined impacts of salvage logging between wind and fire. Compound interactions were documented in all instances, however, in the Colorado combination, response variable selection determined whether interactions were amplifying or buffering. Regarding post-fire tree regeneration, a buffering compound interaction was observed. By reducing fuel loading, salvage logging reduced fire intensity and *Pinus contorta* cone consumption (Buma and Wessman 2011). As such, post-fire *P. contorta* regeneration was greater on salvaged sites, exemplifying increased forest resilience (Buma and Wessman 2012). Regarding black carbon, however, the compound interaction was amplifying, with the greatest net losses expected on salvaged sites where a considerable amount of carbon was extracted (Buma et al. 2014).

In Minnesota, post-wind salvage logging and fire exhibited all amplifying compound interactions. By removing deadwood, salvage logging homogenized post-fire plant communities and was expected to have lasting impacts on forest recovery (D'Amato et al. 2011). Reduced downed woody debris and standing snag carbon pools also indicated potential for altered or

delayed forest carbon recovery (Bradford et al. 2012). Moreover, drier conditions, exposed mineral soil, and potentially compacted litter on salvaged sites increased forest floor susceptibility to mercury emission and volatilization (Mitchell et al. 2012).

### ***Repeat Fires***

Forest resilience to successive wildfires was indicated by persistence of remotely-sensed refugial plant communities (Haire et al. 2017), persistence of “core” plant species (Donato et al. 2009), and the sustained ability of sprouting plants to recharge underground carbon stocks and regrow after fire (Bonfil et al. 2004, Nemens et al. 2018). By contrast, Fairman et al. (2017) attributed reduced *Eucalyptus pauciflora* resprouting ability to a reduction of viable growth buds and increased vulnerability of immature stems to recurring fire. Sites subject to multiple fires also exhibited potential to transition from shrub- to grass-dominated understories and develop toward more open woodland- or savanna-like structures. Taboada et al. (2018) documented a species-specific response in which resprouting shrubs persisted after successive fires, but *Pinus pinaster*, which reproduces from serotinous cones, had insufficient time to replenish the canopy seed bank between fires. Bowd et al. (2018) also documented an increased abundance of resprouting plants and reduced populations of on-site seeders after multiple fires. Although Donato et al. (2009) documented unique plant assemblages in twice-burned sites, differences reflected additional species, not losses. Nonetheless, deadwood biomass was substantially reduced in twice-burned sites, and a deadwood biomass discrepancy was predicted to last for over 100 years of stand development (Donato et al. 2016). Bowd et al. (2019) also documented long-lasting impacts, in which altered soil properties endured over 80 years after a single fire, and multiple fires had amplifying effects.

### ***Bark Beetles and Fire***

In this review, only two beetle-and-fire investigations reported compound interactions (Harvey et al. 2013, Carlson et al. 2017). Forest resilience was attributed to ample inter-disturbance recovery time and species-specific recovery strategies. Agne et al. (2016) discussed how 8–15 years between disturbances was likely long enough for advanced regeneration to reach larger size classes. Kulakowski et al. (2013) documented comparable post-fire tree regeneration on sites unaffected or impacted by bark beetles over 50 years prior. Whereas *Pseudotsuga menziesii* failed to provide viable seed for post-fire regeneration (Harvey et al. 2013), serotinous *Pinus contorta* cones persisted on beetle-killed trees and contributed to post-fire seedling establishment (Harvey et al. 2014a, Harvey et al. 2014b). Another reason proposed for undetected interactions was that high severity fires had similar impacts regardless of pre-fire beetle outbreaks (Stevens-Rumann et al. 2015). Indeed, Harvey et al. (2013), who documented a compound interaction, only observed this interaction in areas burned by light surface fires. Tree regeneration was low regardless of beetle outbreaks where fires were more severe. Compared to the tree regeneration-focused articles, Carlson et al. (2017) used a more generalized, Landsat-based approach to detect negative relationships between pre-fire beetle outbreak severity and understory vegetation recovery.

### ***Fire and Salvage Logging***

A unique suite of response variables was used to detect compound fire-and-salvage logging interactions. Deadwood extraction yielded suitable conditions for early-successional species associated with open habitats, thereby delaying bryophyte recovery (Hernández-

Hernández et al. 2017), and reducing the compositional variability of ground beetles (Cobb et al. 2007). Kishchuk et al. (2015) attributed delayed recovery of carbon and soil organic matter to removal of charred material that would have otherwise been incorporated in forest floor recovery. However, foliar nutrition and regeneration growth converged, reinforcing that detection of compound interactions can depend on the response variables assessed. Similarly, Knapp and Ritchie (2016) attributed reduced shrub cover and richness to mechanical impacts of salvage logging, but noted that, of the multiple functional groups and life-history categories assessed, only shrubs were significantly impacted. Bowd et al. (2018) reported that, although on-site seeders persisted in salvaged sites, resprouting species exhibited significant reductions. Soil nutrient levels and ecologically important exchangeable cations were reduced as well (Bowd et al. 2019). Disturbance frequency also influenced whether fire and salvage logging exhibited interactions. Taboada et al. (2018) reported that, after a single fire, salvage logging did not impact forest recovery, but with two fires, reduced seedling establishment was amplified by salvage logging.

### ***Wind and Salvage Logging***

The detection of compound wind-and-salvage logging interactions without subsequent fire depended on which response variables were assessed and which aspects of forest resilience were considered. For instance, Sass et al. (2018) observed parallel successional trajectories in unlogged and logged wind-disturbed sites, but noted persistent salvage-mediated structural differences, including reduced microtopographic variability. Similarly, Peterson and Leach (2008b) noted that salvage logging altered microsite conditions, but not herbaceous plant assemblages. In a companion study, salvage logging compacted soil, but did not alter the

percentage of soil surface disrupted (Peterson and Leach 2008a). Furthermore, variation in woody plant diversity and compositional dissimilarity was mostly driven by wind severity, not salvage logging.

In a *Pinus palustris* woodland, salvage-mediated habitat homogenization was associated with reduced ground flora diversity and macrofungal richness and fruiting abundance (Ford et al. 2018, Kleinman and Hart 2018). However, salvaged sites hosted the greatest *P. palustris* sapling densities, indicating that recovery toward pre-disturbance canopy conditions was not delayed (Kleinman et al. 2017). In contrast, Bottero et al. (2013) attributed reduced *Picea abies* seedling establishment to the removal and piling of logs that may have otherwise served as germination sites (i.e. nurse logs). Oldfield and Peterson (2019) also documented delayed succession on salvaged sites, which, compared to unlogged sites, hosted more mid-successional species and fewer late-successional species. Nonetheless, sapling and tree density and diversity were unaffected.

Distinction between recovery time and trajectory also influenced detection of compound interactions. White et al. (2014) predicted that sites differentially impacted by wind and logging would transition from *Quercus* to *Acer* dominance. Yet, despite similar successional trajectories, salvage logging accelerated this transition by damaging *Quercus* saplings. In contrast, Lang et al. (2009) noted that, after 25 years, areas differentially disturbed by wind and salvage logging converged by most metrics of plant recovery, but exhibited different recovery trajectories. Salvaged sites recovered from residual stump sprouts and roots suckers instead of the seedlings, saplings, and trees that persisted in unlogged areas. Moreover, salvage logging was associated with persistent soil compaction and homogenization, reduced microtopography variability, and increased representation of disturbance-adapted plants (Lang et al. 2009).

### ***Repeat Intensive Forest Management***

Experimental, rather than observational, approaches can limit possible autocorrelation and pseudoreplication involved with “natural experiments,” and are well-suited to test forest responses to multiple levels of disturbance severity (Foster et al. 2016). Strengbom and Nordin (2012) reported that experimental N enrichment had minimal impacts on vascular plant and bryophyte communities until coupled with subsequent clear-cut harvesting. Experimental approaches can also be used to examine subtle differences across treatments not possible in an uncontrolled setting. For example, Starzomski and Srivastava (2007) experimentally manipulated a moss-covered rock outcrop to demonstrate how reduced habitat connectivity lowered ecological resilience to microarthropod extraction.

A diversity of response variables can be utilized in experimental studies to detect a range of forest responses to compound disturbances. For instance, although Kranabetter et al. (2017) documented impacts of organic matter removal and soil compaction on plant and fungal community dissimilarity, beetle communities exhibited a negligible response. In plantations subject to repeated experimental raking, changes in arthropod abundance manifested differentially across arthropod orders of interest (Ober and DeGroot 2014). López et al. (2009) described a tradeoff between aboveground growth and carbon stock renewal in twice-thinned stands. Whereas increased biomass and densities of resprouting individuals signaled a buffering interaction, reduced lignocarbon reserves indicated an amplifying interaction. Wen et al. (2010) surveyed understory plant communities in plantations subject to one or two rotations of continuous cropping. Compared to first rotation stands, second rotation stands hosted altered understory plant communities, characterized by reduced plant diversity and cover of woody

growth forms. Peter and Harrington (2009) also documented reduced understory plant cover and diversity in clearcut stands subject to annual herbicide application, which consequently accelerated establishment of planted seedlings.

### ***Intensive Forest Management and Fire***

Because prescribed fire is another form of intensive management, the combination of prescribed fire after other silvicultural entries can also be described as “repeat intensive forest management.” These combinations illustrated how compound disturbances can sometimes be utilized to achieve desired conditions. In particular, Kirkman et al. (2007) demonstrated how incomplete overstory removal and prescribed fire could induce desired compositional shifts in a forest plantation without sacrificing structural and functional continuity. Iglay et al. (2014) documented a tradeoff between desired structure and diversity, in which herbicide and prescribed fire achieved target midstory hardwood reductions but also reduced understory plant diversity. Sutton et al. (2013) reported that sites subject to experimental thinning and prescribed burning hosted distinct herpetofaunal assemblages associated with reduced canopy cover and litter depth. Pidgen and Mallik (2013) also reported divergent recovery trajectories, in which some trees, shrubs, and other plants with vegetative regeneration strategies had insufficient time (ca. two years) to recovery between clearcut harvesting and prescribed fire.

The combination of logging and wildfire also induced a range of forest responses. Although Coleman et al. (2008) reported that logged sites exhibited comparable post-fire plant assemblages and successional trajectories to unlogged sites, subtle species-specific and structural differences were observed. In contrast, Cobb et al. (2007) documented conspicuous differences in beetle assemblages, characterized by reduced compositional variability, and Ton and

Krawchuk (2016) documented distinct differences in plant assemblages, characterized by increased representation of disturbance-adapted species. Altered recovery trajectories were also indicated by a reduction of post-fire *Pinus contorta* seedling densities, attributed to clearcut-mediated seed source reductions (Ton and Krawchuk 2016).

### ***Fire and Intensive Forest Management***

Mechanical impacts of clearcut logging in fire-regenerated stands induced comparable effects to post-fire salvage logging. Key soil metrics including organic carbon and available phosphorous and potassium were reduced (Bowd et al. 2019), in addition to a reduction of resprouting plants (Bowd et al. 2018). Resprouting plants also exhibited a range of response variable-specific responses to experimental post-fire defoliation. For example, although leaf biomass allocation increased in resprouting *Acacia karroo* saplings, root carbohydrate reserves, shoot diameter, and stem biomass were reduced (Schutz et al. 2011). Bonfil et al. (2004) reported that, although *Quercus cerriodes* was resilient to fire and low intensity manipulation (i.e. clipping), *Q. ilex* was not. Nonetheless, the number and growth of both *Q. cerriodes* and *Q. ilex* were reduced by high-intensity post-fire manipulation (i.e. cutting or concentrated burning with a propane torch).

### ***Intensive Forest Management and Wind***

The literature on forest responses to logging and subsequent wind disturbance is expansive and unresolved (Albrecht et al. 2012, Coates et al. 2018). However, we reviewed only two articles that assessed logging followed by wind disturbance, indicating the inherent limitations of our restricted inclusion criteria. Consistent with the other articles reviewed, the



detection of compound forest clearing and wind disturbance interactions was contingent on the response variables considered. Like post-hurricane salvage logging, sites clearcut prior to a hurricane followed comparable successional trajectories to unlogged sites, but exhibited persistent structural differences (Sass et al. 2018). Teh et al. (2009) reported that, whereas soil carbon and nutrient pools were resilient to experimental gap formation and multiple hurricanes, post-hurricane fine root production was reduced in cleared sites.

### *Drought*

Response variable selection also influenced the detection and direction of drought-related interactions. Sparks et al. (2018) documented a buffering interaction in which severely water-stressed saplings exhibited enhanced post-fire recovery, indicated by increased rates of bud production. However, post-fire height and diameter growth decreased with increasing drought severity, indicating an amplifying interaction. Valdés et al. (2006) noted that, although drought reduced total fine-root and ectomycorrhizal-root biomass after seed tree harvesting and prescribed fire, soil inoculum potential remained relatively stable. Another response variable-specific interaction was documented by Matusick et al. (2016), in which successive droughts induced a structural transformation, but the relative abundance of dominant tree species remained stable. Keith et al. (2012) also examined forests subject to successive droughts, but the compound interaction of interest involved the combined impacts of insect attack and drought. Whereas forests undergoing drought alone still served as carbon sinks, simultaneous drought and insect stress resulted in net carbon losses (Keith et al. 2012).

### ***Other Combinations***

In addition to the drought-related combinations, four disturbance combinations were unique to individual studies in the review framework. Robertson and Platt (2001) monitored epiphytic bromeliads in subtropical hammocks differentially impacted by pre-hurricane lightning fire. Because burned bark and branches provided less stable substrates, the hurricane disproportionately dislodged epiphytes in burned sites, thereby delaying recovery toward pre-disturbance epiphytic distributions. Although resprouting conferred structural resilience to two hurricanes in quick succession, compositional shifts in the relative abundance of more and less resistant species were observed (Bonilla-Moheno 2012). Karlsen et al. (2013) described consecutive moth outbreaks that induced understory shrub-to-grassland transitions. However, transitions only occurred in nutrient-limited sites, as nutrient-rich sites hosted a higher diversity of understory plants that contributed to forest resilience. Like post-wind salvage logging, Bottero et al. (2013) attributed reduced *Picea abies* seedling establishment after a moth outbreak and salvage logging to the removal and piling of logs that may have otherwise served as germination sites.

### **Synthesis**

Forest responses to compound disturbances range from accelerated or delayed recovery toward pre-disturbance conditions to succession and development toward alternative states. Although compound interactions were detected in most articles reviewed, an “outcome reporting bias” likely increased chances of detecting articles that reported significant interactions (Moher et al. 2009). For instance, all of the wind and salvage logging combinations exhibited compound interactions, but post-wind salvage logging can be conducted in ways that maintain forest

resilience (Royo et al. 2016). Consistent with a recent review of wind and fire interactions (Cannon et al. 2017), a paucity of buffering interactions that increased forest resilience were identified. Moreover, the detection of buffering interactions was contingent on which response variables were assessed. All disturbance combinations that exhibited buffering compound interactions also exhibited amplifying interactions that reduced forest resilience in some capacity. For example, although post-wind salvage logging enhanced *Pinus contorta* recovery (buffering interaction; Buma and Wessman 2011, 2012), it also amplified black carbon stock reductions (amplifying interaction; Buma et al. 2014). Whereas experimental wind and fire enhanced sapling regrowth (buffering interaction), *Rhus copallinum* recruitment increased disproportionately (amplifying interaction; Cannon et al. 2019). We contend more research on buffering interactions is needed to improve understanding of compound disturbances, and encourage researchers to examine a broader range of response variables to achieve a more complete understanding of compound interactions.

Indeed, the response variables used to assess forest recovery often determined if a compound interaction was detected. These distinctions most commonly involved differential recovery related to the expression of species-specific life-history strategies (Buma and Wessman 2012, Knapp and Ritchie 2016, Bowd et al. 2018), but also involved a distinction between recovery time and trajectory (Lang et al. 2009, White et al 2014) and forest succession and development (Bonilla-Moheno 2012, Matusick et al. 2016, Sass et al. 2018). Other disturbance combinations only exhibited compound interactions at specific forest strata (Bradford et al 2012, Mitchell et al. 2012) or scales, such as changes in individual species but not overall communities (Coleman et al. 2008). We hope some of the less commonly reported metrics, such as bryophyte,

beetle, and/or fungal assemblages, inspire future studies to conduct more comprehensive investigations of forest ecosystem recovery.

Compound disturbance interactions were recorded in only six countries outside of North America, indicating the need for more research on this topic outside of North America. Within North America, however, investigations were well-distributed, indicating that no particular region or forest type has disproportionately influenced our conceptual understanding of compound disturbances. Regarding disturbance types, however, a disproportionate focus on fire, wind, and salvage logging indicated the need for more research focus on other understudied disturbance types such as floods, ice storms, and landslides.

Commonly reported disturbance legacies that facilitated compound interactions included seed source reduction, deadwood accumulation and reduction, and increased light and growing space availability. For instance, reduced post-fire regeneration was attributed to seed source reduction by a preceding fire (Taboada et al. 2018), bark beetle outbreak (Harvey et al. 2013), and clearcut logging operation (Ton and Krawchuk 2016). Salvage-mediated deadwood extraction resulted in reduced black carbon formation (Buma et al. 2014) and delayed carbon and soil organic matter recovery (Kishchuk et al. 2015). Deadwood extraction also homogenized plant communities (Kleinman et al. 2017), and delayed bryophyte community recovery by improving habitat suitability for early-successional assemblages associated with open habitat (Hernández-Hernández et al. 2017). Kranabetter et al. (2017) attributed increased representation of invasive plants and reduced fungal richness, in part, to organic matter removal, which increased mineral soil exposure and reduced soil moisture and soil porosity. Cobb et al. (2007) attributed reduced compositional variability of ground beetles in logged areas, in part, to absence of species adapted to damp microclimates beneath logs. By defoliating shrubs, moths facilitated

grass proliferation in response to increased light and nutrient availability from moth excreta and elimination of allelopathic shrubs (Karlsen et al. 2013).

Inter-disturbance recovery time also influenced the occurrence of compound interactions (Pidgen and Mallik 2013, Carlson et al. 2017, Taboada et al. 2018). In particular, Bowd et al. (2018) and Taboada et al. (2018) described how on-site seeders had insufficient time to mature and reproduce between successive fires. Although compound interactions generally involved five or fewer years between successive disturbance events, and this five-year benchmark may help characterize compound disturbances, it should not be considered a defining principle. Indeed, D'Amato et al. (2011) and Bradford et al. (2012) documented compound interactions between wind and fire separated by eight years, and Harvey et al. (2014a) and Harvey et al. (2014b) did not document compound interactions between bark beetle outbreaks and fires separated by 0–3 years. Nonetheless, over half of the compound interactions documented involved a year or less between disturbance events.

Based on our systematic review, we make the following observations and recommendations:

- Progress in compound disturbance ecology has been largely influenced by disturbance combinations involving fire, wind, and salvage logging. A disproportionate focus on these disturbance types may bias our understanding of compound interactions, and we encourage more research on other understudied disturbance types.
- Most compound disturbances exhibited amplifying interactions that reduced forest resilience. To understand ways forest resilience is enhanced, we recommend more research focus on buffering interactions.

- A disproportionate amount of research has been conducted in North America. To ensure understanding of compound disturbances is not biased toward the climates and lifeforms of this continent, more work is needed in other understudied regions and forest types.
- Compound disturbances were most often mediated by disturbance legacies involving reduced seed source availability, deadwood accumulation and reduction, and increased light and growing space availability.
- To date, compound forest disturbance investigations have typically examined events separated by five or fewer years. To advance understanding of compound disturbances, we recommend more studies are developed to investigate longer inter-disturbance recovery periods.
- Assessments of forest recovery were focused primarily on woody plant-based metrics. To achieve a more complete understanding of compound interactions, we recommend the use of a diversity of other metrics including arthropods, bryophytes, carbon stocks, fungi, herbaceous plants, herpetofauna, mammals, and soil properties, which were also encountered in this review.
- Ultimately, efforts to quantify ecosystem resilience to interacting disturbances are contingent on the response variables measured. Going forward, we encourage the development of a more holistic resilience framework that considers multiple response variables.

## References for Chapter 2

- Agne, M.C., Woolley, T., Fitzgerald, S. 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. *Forest Ecology and Management* 366, 73–86.
- Albrecht, A., Hanewinkel M., Bauhus J., Kohnle, U. 2012. How does silviculture affect storm damage in forests of south-western Germany? Results from empirical modeling based on long-term observations. *European Journal of Forest Research* 131, 229–247.
- Angeler, D.G., Allen, C.R. 2016. Quantifying resilience. *Journal of Applied Ecology* 53, 617–624.
- Barbour, M. G., Billings, W.D. 2000. *North American terrestrial vegetation*, Second edition. Cambridge University Press, Cambridge, United Kingdom.
- Bigler, C., Kulakowski, D., Veblen, T. T. 2005. Multiple disturbance interactions and drought influence fire severity in rocky mountain subalpine forests. *Ecology* 86, 3018–3029.
- Bonfil, C., Cortes, P., Espelta, J.M., Retana, J. 2004. The role of disturbance in the co-existence of the evergreen *Quercus ilex* and the deciduous *Quercus cerrioides*. *Journal of Vegetation Science* 15, 423–430.
- Bonilla-Moheno, M. 2012. Damage and recovery of forest structure and composition after two subsequent hurricanes in the Yucatan Peninsula. *Caribbean Journal of Science* 46, 240–248.
- Bottero, A., Garbarino, M., Long, J.N., Motta, R. 2013. The interacting ecological effects of large-scale disturbances and salvage logging on montane spruce forest regeneration in the western European Alps. *Forest Ecology and Management* 292, 19–28.
- Bowd, E.J., Banks, S.C., Strong, C.L., Lindenmayer, D.B. 2019. Long-term impacts of wildfire and logging on forest soils. *Nature Geoscience* 12, 113–118.
- Bowd, E.J., Lindenmayer D.B., Banks, S.C., Blair, D.P. 2018. Logging and fire regimes alter plant communities. *Ecological Applications* 28, 826–841.
- Bradford, J.B., Fraver, S., Milo, A.M., D'Amato, A.W., Palik, B., Shinneman, D.J. 2012. Effects of multiple interacting disturbances and salvage logging on forest carbon stocks. *Forest Ecology and Management* 267, 209–214.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6.
- Buma, B, Poore, R.E., Wessman, C.A. 2014. Disturbances, their interactions, and cumulative effects on carbon and charcoal stocks in a forested ecosystem. *Ecosystems* 17, 947–959.

- Buma, B., Wessman, C.A. 2011. Disturbance interactions can impact resilience mechanisms of forests. *Ecosphere* 2.
- Buma B, Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecology and Management* 266, 25–33.
- Cannon, J.B., Henderson, S.K., Bailey, M.H., Peterson, C.J. 2019. Interactions between wind and fire disturbance in forests: Competing amplifying and buffering effects. *Forest Ecology and Management* 436, 117–128.
- Cannon, J.B., Peterson, C.J., O'Brien J.J., Brewer, J.S. 2017. A review and classification of interactions between forest disturbance from wind and fire. *Forest Ecology and Management* 406, 381–390.
- Carlson, A.R., Sibold, J.S., Assal T.J., Negron, J.F. 2017. Evidence of compounded disturbance effects on vegetation recovery following high-severity wildfire and spruce beetle outbreak. *Plos One* 12.
- Carpenter, S., Walker, B., Anderies, J.M., Abel, N. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* 4, 765–781.
- Coates, K.D., Hall, E.C., Canham, C.D. 2018. Susceptibility of trees to windthrow storm damage in partially harvested complex-structured multi-species forests. *Forests* 9, 199.
- Cobb, T.P., Langor, D.W., Spence, J.R. 2007. Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera : Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forest Research* 37, 1310–1323.
- Coleman, T.W., Meeker, J.R., Clarke, S.R., Rieske, L.K. 2008. The suppression of *Dendroctonus frontalis* and subsequent wildfire have an impact on forest stand dynamics. *Applied Vegetation Science* 11, 231–242.
- D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L. 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management* 262, 2070–2078.
- Dale, V.H., et al. 2001. Climate change and forest disturbances. *Bioscience* 51, 723–734.
- Donato, D.C., Fontaine, J.B., Campbell, J.L. 2016. Burning the legacy? Influence of wildfire reburn on dead wood dynamics in a temperate conifer forest. *Ecosphere* 7, 13.
- Donato, D.C., Fontaine, J.B., Robinson, W.D., Kauffman, J.B., Law, B.E. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. *Journal of Ecology* 97, 142–154.



- Fairman, T.A., Bennett, L.T., Tupper, S., Nitschke, C.R. 2017. Frequent wildfires erode tree persistence and alter stand structure and initial composition of a fire-tolerant sub-alpine forest. *Journal of Vegetation Science* 28, 1151–1165.
- Ford, S.A., Kleinman, J.S., Hart, J.L. 2018. Effects of wind disturbance and salvage harvesting on macrofungal communities in a *Pinus* woodland. *Forest Ecology and Management* 407, 31–46.
- Foster, C.N., Sato, C.F., Lindenmayer, D.B., Barton, P.S. 2016. Integrating theory into disturbance interaction experiments to better inform ecosystem management. *Global Change Biology* 22, 1325–1335.
- Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D. 2000. Threads of continuity. *Conservation in Practice* 1, 8–17.
- Franklin, J.F., et al. 2002. Disturbances and structural development of natural forests ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155, 399–423
- Fraver, S., Jain, T., Bradford, J. B., D'Amato, A.W., Kastendick, D., Palik, B., Shinneman, D., Stanovick, J. 2011. The efficacy of salvage logging in reducing subsequent fire severity in conifer-dominated forests of Minnesota, USA. *Ecological Applications* 21, 1895–1901.
- Gagnon, P.R., Platt, W.J.. 2008. Multiple disturbances accelerate clonal growth in a potentially monodominant bamboo. *Ecology* 89, 612–618.
- Gill, N.S., Jarvis, D., Veblen, T.T., Pickett, S.T.A., Kulakowski, D. 2017. Is initial post-disturbance regeneration indicative of longer-term trajectories? *Ecosphere* 8.
- Haire, S.L., Coop, J.D., Miller, C. 2017. Characterizing spatial neighborhoods of refugia following large fires in northern New Mexico USA. *Land* 6, 24.
- Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G. 2013. Influence of recent bark beetle outbreak on fire severity and postfire tree regeneration in montane Douglas-fir forests. *Ecology* 94, 2475–2486.
- Harvey, B.J., Donato, D.C., Romme, W.H., Turner, M.G.. 2014a. Fire severity and tree regeneration following bark beetle outbreaks: the role of outbreak stage and burning conditions. *Ecological Applications* 24, 1608–1625.
- Harvey, B.J., Donato, D.C., Turner, M.G.. 2014b. Recent mountain pine beetle outbreaks, wildfire severity, and postfire tree regeneration in the US Northern Rockies. *Proceedings of the National Academy of Sciences of the United States of America* 111, 15120–15125.

- Hernández-Hernández, R., Castro, J., Aguilar, M.D., Fernandez-Lopez, A.B., Gonzalez-Mancebo, J.M.. 2017. Post-fire salvage logging imposes a new disturbance that retards succession: The case of bryophyte communities in a Macaronesian laurel forest. *Forests* 8.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4, 1–23. Iglay et al. (2014)
- Johnstone, J.F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14, 369–378.
- Kane, J.M., Varner, J.M., Metz, M.R., van Mantgem, P.J. 2017. Characterizing interactions between fire and other disturbances and their impacts on tree mortality in western U.S. *Forests. Forest Ecology and Management* 405, 188–199.
- Karlsen, S.R., Jepsen, J.U., Odland, A., Ims, R.A., Elvebakk, A. 2013. Outbreaks by canopy-feeding geometrid moth cause state-dependent shifts in understorey plant communities. *Oecologia* 173, 859–870.
- Keeley, J.E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18, 116–126.
- Keith, H., van Gorsel, E., Jacobsen, K.L., Cleugh, H.A. 2012. Dynamics of carbon exchange in a *Eucalyptus* forest in response to interacting disturbance factors. *Agricultural and Forest Meteorology* 153, 67–81.
- Kirkman, L.K., Mitchell, R.J., Kaeser, M.J., Pecot, S.D., Coffey, K.L. 2007. The perpetual forest: using undesirable species to bridge restoration. *Journal of Applied Ecology* 44, 604–614.
- Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., Sidders, D. 2015. Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. *Canadian Journal of Forest Research* 45, 141–152.
- Kleinman, J.S., Ford, S.A., Hart, J.L. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. *Forest Ecology and Management* 403, 112–125.
- Kleinman, J.S., Hart, J.L. 2018. Vascular flora of longleaf pine woodlands after wind disturbance and salvage harvesting in the Alabama Fall Line Hills. *Castanea* 83, 183–195.
- Knapp, E.E., Ritchie, M.W. 2016. Response of understory vegetation to salvage logging following a high-severity wildfire. *Ecosphere* 7.

- Kranabetter, J.M., Haeussler, S., Wood, C. 2017. Vulnerability of boreal indicators (ground-dwelling beetles, understory plants and ectomycorrhizal fungi) to severe forest soil disturbance. *Forest Ecology and Management* 402, 213–222.
- Kulakowski, D., Matthews, C., Jarvis, D., Veblen, T.T. 2013. Compounded disturbances in sub-alpine forests in western Colorado favour future dominance by quaking aspen (*Populus tremuloides*). *Journal of Vegetation Science* 24, 168–176.
- Lang, K.D., Schulte, L.A., Guntenspergen, G.R. 2009. Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. *Forest Ecology and Management* 259, 56–64.
- López, B.C., Gracia, C.A., Sabate, S., Keenan, T. 2009. Assessing the resilience of Mediterranean holm oaks to disturbances using selective thinning. *Acta Oecologica-International Journal of Ecology* 35, 849–854.
- Matusick, G., Ruthrof, K.X., Fontaine, J.B., Hardy, G.E.S. 2016. *Eucalyptus* forest shows low structural resistance and resilience to climate change-type drought. *Journal of Vegetation Science* 27, 493–503.
- Mitchell, C.P.J., Kolka, R.K., Fraver, S. 2012. Singular and combined effects of blowdown, salvage logging, and wildfire on forest floor and soil mercury pools. *Environmental Science & Technology* 46, 7963–7970.
- Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., Grp, P. 2009. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. *Plos Medicine* 6.
- Nemens, D.G., Varner, J.M., Kidd, K.R., Wing, B. 2018. Do repeated wildfires promote restoration of oak woodlands in mixed-conifer landscapes? *Forest Ecology and Management* 427, 143–151.
- Ober, H.K., DeGroot, L.W. 2014. Repeated raking of pine plantations alters soil arthropod communities. *Forests* 5, 689–714.
- Oldfield, C.A., Peterson, C.J. 2019. Woody species composition, diversity, and recovery six years after wind disturbance and salvage logging of a southern Appalachian forest. *Forests* 10, 13.
- Oliver, C.D., Larson, B.C. 1996. *Forest stand dynamics*, Update edition. John Wiley and Sons, New York, New York, USA.
- Paine, R.T., Tegner, M.J., Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545.

- Peter, D.H., Harrington, C. 2009. Six years of plant community development after clearcut harvesting in western Washington. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere* 39, 308–319.
- Peters, D.P.C., Lugo, A.E., Chapin, F.S., Pickett, S.T.A., Duniway, M., Rocha, A.V., Swanson, F.J., Laney, C., Jones, J. 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2.
- Peterson, C.J., Leach, A.D. 2008a. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. *Ecological Applications* 18, 407–420.
- Peterson, C.J., Leach, A.D. 2008b. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry* 81, 361–376.
- Pidgen, K., Mallik, A.U. 2013. Ecology of compounding disturbances: The effects of prescribed burning after clearcutting. *Ecosystems* 16, 170–181.
- Robertson, K.M., Platt, W.J. 2001. Effects of multiple disturbances (fire and hurricane) on epiphyte community dynamics in a subtropical forest, Florida, USA. *Biotropica* 33, 573–582.
- Royo, A.A., Peterson, C.J., Stanovick, J.S., Carson, W.P. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology* 97, 1566–1582.
- Sass, E.M., D'Amato, A.W., Foster, D.R. 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.
- Schutz, A.E.N., Bond, W.J., Cramer, M.D. 2011. Defoliation depletes the carbohydrate reserves of resprouting *Acacia* saplings in an African savanna. *Plant Ecology* 212, 2047–2055.
- Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hick, J.A. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53, 120–129.
- Seidl, R., et al. 2017. Forest disturbances under climate change. *Nature Climate Change* 7, 395–402.
- Simard, M., Romme, W.H., Griffin, J.M., Turner, M.G. 2011. Do mountain pine beetle outbreaks change the probability of active crown fire in lodgepole pine forests? *Ecological Monographs* 81, 3–24.
- Smith, G.F., Nicholas, N.S., Zedaker, S.M. 1997. Succession dynamics in a maritime forest following Hurricane Hugo and fuel reduction burns. *Forest Ecology and Management* 95, 275–283.

- Sommerfeld, A., et al. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications* 9.
- Sparks, A.M., Talhelm, A.F., Feltrin, R.P., Smith, A.M.S., Johnson D.M., Kolden, C.A., Boschetti, L. 2018. An experimental assessment of the impact of drought and fire on western larch injury, mortality and recovery. *International Journal of Wildland Fire* 27, 490–497.
- Starzomski, B.M., Srivastava, D.S. 2007. Landscape geometry determines community response to disturbance. *Oikos* 116, 690–699.
- Stevens-Rumann, C., Morgan, P., Hoffman, C. 2015. Bark beetles and wildfires: How does forest recovery change with repeated disturbances in mixed conifer forests? *Ecosphere* 6.
- Stokely, T.D., Verschuyf, J., Hagar, J.C., Betts, M.G. 2018. Herbicides and herbivory interact to drive plant community and crop-tree establishment. *Ecological Applications* 28, 2011–2023.
- Strengbom, J., Nordin, A. 2012. Physical disturbance determines effects from nitrogen addition on ground vegetation in boreal coniferous forests. *Journal of Vegetation Science* 23, 361–371.
- Sutton, W.B., Wang, Y., Schweitzer, C.J. 2013. Amphibian and reptile responses to thinning and prescribed burning in mixed pine-hardwood forests of northwestern Alabama, USA. *Forest Ecology and Management* 295, 213–227.
- Taboada, A., Fernandez-Garcia, V., Marcos, E., Calvo, L. 2018. Interactions between large high-severity fires and salvage logging on a short return interval reduce the regrowth of fire-prone serotinous forests. *Forest Ecology and Management* 414, 54–63.
- Teh, Y.A., Silver, W.L., Scatena, F.N. 2009. A decade of belowground reorganization following multiple disturbances in a subtropical wet forest. *Plant and Soil* 323, 197–212.
- Ton, M., Krawchuk, M.A. 2016. The effects of disturbance history on ground-layer plant community composition in British Columbia. *Forests* 7, 17.
- Valdés, M., Asbjornsen, H., Gomez-Cardenas, M., Juarez, M., Vogt, K.A. 2006. Drought effects on fine-root and ectomycorrhizal-root biomass in managed *Pinus oaxacana* Mirov stands in Oaxaca, Mexico. *Mycorrhiza* 16, 117–124.
- Vitousek, P.M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57, 7–13.
- Vitousek, P.M., Walker, L.R. 1989. Biological invasion by *Myrica fava* in Hawaii: plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs* 59, 247–65.

Wen, Y.G., Ye, D., Chen, F., Liu, S.R., Liang, H.W. 2010. The changes of understory plant diversity in continuous cropping system of *Eucalyptus* plantations, South China. *Journal of Forest Research* 15, 252–258.

White, S.D., Hart, J.L., Cox, L.E., Schweitzer, C.J. 2014. Woody regeneration in a southern Appalachian *Quercus* stand following wind disturbance and salvage logging. *Castanea* 79, 223–236.

## CHAPTER 3

### PRESCRIBED FIRE EFFECTS ON *PINUS PALUSTRIS* WOODLAND DEVELOPMENT AFTER CATASTROPHIC WIND DISTURBANCE AND SALVAGE LOGGING

#### **Abstract**

Scientifically informed strategies to manage naturally disturbed forests are critical to support the sustained provisioning of ecosystem goods and services. In fire-adapted ecosystems, catastrophic canopy removal can disrupt surface fuel continuity and challenge the continued use of low-intensity prescribed fire. Although salvage logging is used globally after natural disturbance events, little information is available on how salvage logging interacts with subsequent use of prescribed fire. This study investigated the impacts of operational-scale prescribed fire on *Pinus palustris* (longleaf pine) stand development in areas differentially impacted by an April 2011 EF3 tornado and a subsequent salvage logging operation. Twenty 0.04-ha nested plots were systematically established in mature, wind-disturbed, and salvage-logged sites ( $n = 60$ ) to measure seedlings, saplings, woody fuels, organic litter, and mineral soil before and after prescribed fire. Prescribed fire-induced fine fuel consumption, mineral soil exposure, and substantial sapling density reductions were observed throughout the treatment area. Prescribed fire effects were not apparently impacted by salvage logging, which did not alter the amount of fine fuels available for prescribed fire consumption. Despite overall sapling density reductions, fire-resistant *P. palustris* saplings exhibited increased densities on wind-disturbed and salvage-logged sites. *Pinus palustris* seedlings, however, exhibited marked post-fire reductions, which contrasted with a strong resprouting response observed among top-killed

hardwood species. Concerning woody plant recovery, this study indicated that salvage logging was not detrimental to *P. palustris* stand development and that prescribed fire effectively enhanced recovery in unlogged and logged wind-disturbed sites.

## **Introduction**

Forest disturbances alter the spatial arrangement of ecosystem components, thereby influencing successional, developmental, and functional processes (Oliver and Larson 1996, Franklin et al. 2002). Of particular concern are forest disturbances that interact to impact the sustained provisioning of ecosystem goods and services (Turner 2010, Thom and Seidl 2016). Wind disturbance and fire represent major components of terrestrial disturbance regimes worldwide (MacDonald 2003) and have substantial socioeconomic impacts on forest ecosystems in the United States (Dale et al. 2001). Salvage logging is commonly applied after natural disturbances to partially capture the economic value of wood products in damaged or dead trees, and to reduce risk and severity of subsequent disturbance events (Leverkus et al. 2018, Müller et al. 2019).

Despite its widespread social and economic importance, the ecological effects of salvage logging remain unresolved (Stanturf et al. 2007). Salvage logging, by definition, extracts deadwood that may otherwise contribute to the structural diversity of early-successional forests and serve as critical habitat in ecosystem recovery (Franklin et al. 2000, Swanson et al. 2011, Lindenmayer et al. 2019). Salvage logging can also damage residual trees, saplings, and seedlings, thereby altering post-disturbance successional trajectories (White et al. 2014, Knapp and Ritchie 2016). As debate continues on how to manage forests after natural disturbance events (Stokstad 2006, Lindenmayer et al. 2017), a growing literature challenges the



presumption that salvage logging always leads to negative ecological consequences (Lang et al. 2009, Fidej et al. 2016, Royo et al. 2016). For example, Peterson and Leach (2008) and Sass et al. (2018) report similar successional pathways in unlogged and logged sites despite altered microsite conditions. Salvage logging can also facilitate coexistence of species that would not otherwise persist after natural disturbances alone (Royo et al. 2016, Slyder et al. 2019).

Recent reviews of the salvage logging literature underscore that our current understanding is disproportionately based on post-fire operations (Leverkus et al. 2018, Thorn et al. 2018). Compared to fire, however, wind disturbances leave distinct legacies that influence forest recovery that may be differentially impacted by salvage logging (Johnstone et al. 2016). For instance, wind disturbances deposit, but do not consume, forest floor litter and debris, and typically do not remove understory vegetation (Roberts 2004, Gilliam et al. 2006). Moreover, although salvage logging is often justified as risk reduction, few studies have assessed the resilience of salvaged stands to subsequent disturbance events (D'Amato et al. 2011, Buma and Wessman 2012, Taboada et al. 2018). Because wind-deposited fuel loads can amplify fire effects, post-wind disturbance salvage logging may attenuate high-intensity fires and positively impact post-fire forest recovery (Buma 2015). Low-intensity fires, however, often require fuel bed continuity, and may be inhibited by interrupted canopy-derived leaf litter input and the potential release of less flammable plant species in wind-disturbed sites (Cannon et al. 2017). Although salvage logging can have additional impacts on plant communities and surface fuel dynamics, relatively little is known about low-intensity fire effects on sites salvage-logged after wind disturbance (Palik and Kastendick 2009). This study investigated low-intensity prescribed fire effects on *Pinus palustris* (longleaf pine) stand development in wind-disturbed sites that

were either salvage logged or not logged, as well as mature sites not impacted by catastrophic wind disturbance but subject to the same prescribed fire regime.

Prior to European settlement, *P. palustris* ecosystems occupied ca. 37 million ha across the southeastern United States and experienced frequent, low-intensity surface fires ignited by lightning strikes and Native Americans (Frost 2006). Restricted to less than 5% of its pre-settlement extent, the *P. palustris* ecosystem is now managed with prescribed fires with strong federal, state, and private support (Noss et al. 1995, Melvin 2015). Prescribed fires facilitate a positive feedback in *P. palustris* ecosystems in which highly flammable, canopy-derived *Pinus* litter sustains frequent fires, which inhibit canopy recruitment of less fire-resistant species (Platt et al. 1988, O'Brien et al. 2008, Mitchell et al. 2009). Fire-maintained *P. palustris* stands, in turn, sustain a suite of ecosystem services, including quality habitat for federally endangered *Leuconotopicus borealis* Vieillot (red-cockaded woodpeckers), terrestrial carbon storage, and valuable, drought-tolerant timber (Kush et al. 2004, Samuelson et al. 2019). Conceptual understanding of *P. palustris* stand dynamics can be used to guide the management of other fire-adapted forests, such as neotropical *Pinus* forests of the Caribbean, *P. echinata* (shortleaf pine) forests of the North American Interior Highlands, and *P. ponderosa* (ponderosa pine) forests across the North American Intermountain West (Bigelow et al. 2018). Indeed, prescribed fire application in the southeastern United States provides a model for the management of federally endangered *Strix occidentalis* (spotted owl) habitat ranging from British Columbia to Mexico (Stephens et al. 2019).

The overarching objective of this study was to assess the impacts of operational-scale prescribed fire on *P. palustris* stand development on sites differentially impacted by an EF3 tornado and a subsequent salvage logging operation. Baseline data indicated that *P. palustris*

saplings were substantially outnumbered by other species in mature, wind-disturbed, and salvage-logged sites (Kleinman et al. 2017, Ford et al. 2018). We therefore questioned whether prescribed fire would effectively enhance *P. palustris* recovery through shoot mortality of less fire-resistant species. In other words, it was unclear whether prescribed fire would reduce hardwood sapling densities on sites impacted by catastrophic canopy removal where canopy-derived *Pinus* litter may be insufficient to sustain low-intensity fire (O'Brien et al. 2008, Mitchell et al. 2009). Nonetheless, a growing literature in vegetation-fire feedbacks recognizes the importance of flammable fuels derived from other fire-adapted plants such as pyrophytic *Quercus* (oak) spp. (Kane et al. 2008, Hiers et al. 2014, Fill et al. 2015). We therefore hypothesized that wind-disturbed and salvage-logged sites, which hosted relatively high *Quercus* seedling and sapling densities and herbaceous vegetation cover (Kleinman et al. 2017), would experience prescribed fire-induced sapling density reductions. We also hypothesized that deadwood extraction on salvage-logged sites would have negligible impacts on prescribed fire effects. Specifically, we did not expect that low-intensity prescribed fire, carefully scheduled to avoid extreme weather conditions, would be altered by the presence or absence of larger (i.e. merchantable) pieces of deadwood targeted by salvage logging.

## **Methods**

### ***Study Area***

This study was conducted in the Oakmulgee District of the Talladega National Forest in Bibb County, Alabama (32°55'30"N, 87°24'00"W; Figure 3.1). Situated in the Fall Line Hills ecoregion (level III), the Oakmulgee District occurs within the *Quercus-Pinus* forest region of the United States (Braun 1950, Griffith et al. 2001). The Fall Line Hills physiographic transition

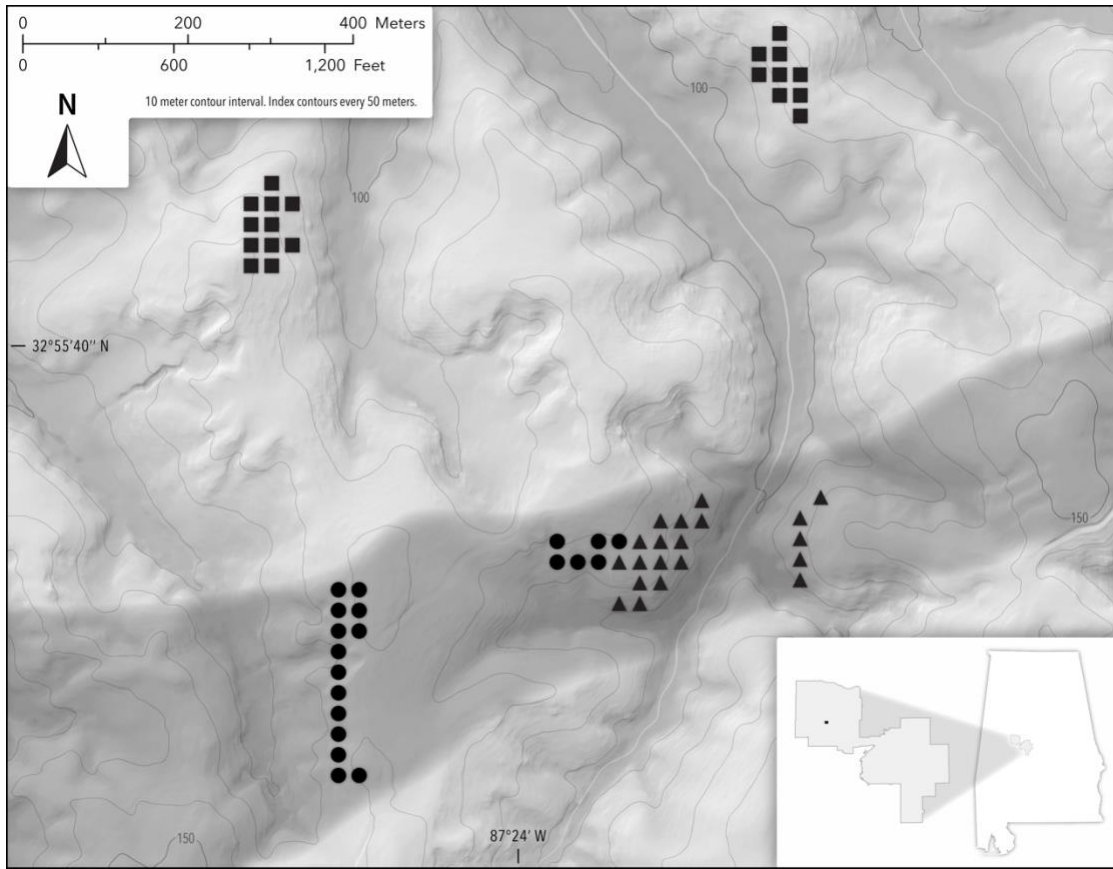


Figure 3.1. Study area in the Oakmulgee District, Talladega National Forest, Alabama, USA (shaded on inset map). Tornado path is shaded, with symbols indicating plot locations in mature (squares), wind-disturbed (triangles), and salvage-logged (circles) sites.

zone spans the inland border of the Coastal Plain, where deeply eroded, marine-deposited sediments meet the steep slopes and ridges of the adjacent Appalachian Highlands (Fenneman 1938). This environmental gradient supports plant assemblages characteristic of the Coastal Plain and Appalachian Highlands (Shankman and Hart 2007, Kleinman and Hart 2018). In the Oakmulgee District, *P. palustris*-dominated woodlands occur on fire-maintained upper slopes and south-facing lower slopes, and a diversity of *Quercus* spp. and other hardwoods coexist with *P. echinata* (shortleaf pine) and *P. taeda* (loblolly pine) in the overstories of unburned sites and bottomlands (Beckett and Golden 1982).

Hillslopes and ridges in the study area contain deep, moderately-well drained soils derived from the Cretaceous-aged Gordo Formation (GSA 2006, USDA NRCS 2020). Maubila series soils consist of a sandy loam or loam surface layer up to 10 cm deep and clay-based substrata over 200 cm deep to bedrock (USDA NRCS 2008). The area exhibits a humid mesothermal climate, characterized by long, hot summers and year-round precipitation (Thorntwaite 1948). Mean temperature is 17.2 °C, with mean January and July temperatures of 6.6 °C and 26.9 °C, respectively, and mean annual precipitation is 1376.21 mm (PRISM 2020). The frost-free period is ca. 230 days from March to November (USDA NRCS 2008).

The USDA Forest Service manages *P. palustris* woodlands in the Oakmulgee District with prescribed fires every 2–5 years. Prescribed fires reduce fuel loads, maintain fire-adapted ground flora assemblages, top-kill fire-sensitive woody plants that would otherwise outcompete *P. palustris* for canopy dominance, and increase availability of substrate (i.e. bare soil) suitable for *P. palustris* and herbaceous plant germination. On 27 April 2011, an EF3 tornado with estimated wind speeds of 233 kph and a maximum width of 1609 m tracked through the Oakmulgee District (NWS 2011). Within seven months, wheeled feller bunchers and chainsaws

were used to salvage wind-damaged trees, which were transported with wheeled skidders to ramp sites for processing by a stationary knuckleboom loader. Salvage logging occurred near pre-existing road networks, leaving some wind-disturbed sites unlogged. Thus, the presence of areas unimpacted by the tornado, wind-disturbed but unlogged, and salvage-logged, combined with an active prescribed fire program, provided the opportunity to assess the impacts of multiple interacting disturbances on *P. palustris* woodland development.

### ***Experimental Design and Field Methods***

In March 2016, at the start of the sixth growing season post-wind disturbance, satellite imagery, geospatial data, and ground reconnaissance were used to select sites with analogous pre-disturbance conditions (Kleinman et al. 2017, Ford et al. 2018). Sites with the greatest possible similarity in pre-disturbance biophysical conditions were selected so observed differences in site conditions could be attributed to the disturbance events of interest, not pre-disturbance variability. Although less robust than experimental inference, such space-for-time substitutions are necessary to advance understanding of “natural experiments” (e.g. tornadoes) in which experimental replicability is not always practical (Pickett 1989, Hargrove and Pickering 1992, Davies and Gray 2015). Selected sites were *P. palustris*-dominated woodlands that originated in the early 1930s after industrial-scale logging and federal acquisition of the land. Sites occur within a 1 km<sup>2</sup> expanse of the same watershed on upper- and mid-slope positions with Maubila series soils. Sites are located in the same Forest Service-delineated compartment, which ensures they experience the same prescribed fire regime. The most recent prescribed fires in the compartment occurred May 2010 before the tornado, April 2014 before field sampling, and April 2018 before and after field data collection. As such, data collected May–July of 2016

and 2017 are referred to as “before fire” or “pre-fire” data, and data collected June 2018 are referred to as “after fire” or “post-fire” data. We note, however, that pre- and post-fire data must be interpreted with caution because, based on the timing of study initiation, impacts of the April 2014 prescribed fire cannot be distilled from April 2018 prescribed fire effects.

We delineated three pre-fire disturbance categories in the selected sites (Kleinman et al. 2017, Ford et al. 2018). Mature sites exhibited no visible tornado damage, and had a basal area of  $21.7 \text{ m}^2\text{h}^{-1}$  and 90% canopy cover. Wind-disturbed sites included areas directly impacted by the tornado that were left unlogged, and had a residual basal area of  $1.1 \text{ m}^2\text{h}^{-1}$  and 14% canopy cover. Salvage-logged sites were impacted by the tornado and exhibited obvious signs of salvage logging, including mechanically cut stems, and had a residual basal area of  $0.6 \text{ m}^2\text{h}^{-1}$  and 5% canopy cover. The relatively sharp transition zone (ca. 70 m) between sites unimpacted by the April 2011 EF3 tornado and sites that experienced catastrophic canopy removal was avoided to reduce potential variability in disturbance severity along the forest edge (Goode et al. 2020). Twenty nested plots were systematically established with 25-m spacing in each disturbance category ( $n = 60$ ). Nested plots consisted of a  $400\text{-m}^2$  plot and ten nested  $1 \times 1 \text{ m}$  quadrats ( $10 \text{ m}^2$ ). Center quadrats were positioned at the center of each  $400\text{-m}^2$  plot, and the other nine quadrats were spaced evenly along the  $0^\circ$ ,  $120^\circ$ , and  $240^\circ$  azimuths from plot center.

The largest sampling units ( $400\text{-m}^2$  plots) were used to survey saplings (live woody stems  $> 1 \text{ m}$  in height and  $< 5 \text{ cm}$  at  $1.37 \text{ m}$  above root collar) and downed coarse woody debris (CWD) in 2016 and 2018. Coarse woody debris included deadwood  $\geq 10 \text{ cm}$  diameter categorized as logs (i.e. dead stems disconnected from roots) and uprooted stems (dead stems with uplifted root networks; USDA 2016). Logs were measured for diameter at both ends and uprooted stems were measured for diameter at  $1.37 \text{ m}$  from root plate. Coarse woody debris was

also measured for length and assigned a decay class from I to V according to increasing degree of decay (USDA 2016).

In 2016 and 2018, saplings were identified and tallied in each 400-m<sup>2</sup> plot, and seedlings, defined as live woody stems  $\leq 1$  m in height of seed or sprout origin, were identified and tallied in nested 1-m<sup>2</sup> quadrats. Nested quadrats were also used to estimate the percent cover of ground surface categories in 2017 and 2018. Ground surface categories included CWD, fine woody debris (FWD, woody material  $< 10$  cm diameter), bare mineral soil, and organic litter (dead, nonwoody material), which was further distinguished as *Pinus* litter, Poaceae (grass) litter, or other litter (i.e. broadleaves and duff). Ground surface categories were assigned a cover class from 0–10 adapted from the North Carolina Vegetation Survey (NCVS), where 0 = absent, 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100% (Peet et al. 1998).

### ***Analytical Methods***

Mixed (split-plot) ANOVAs were used to assess differences in response variables between background disturbance categories (mature, wind-disturbed, and salvage-logged) and across time (before and after prescribed fire). When disturbance categories and time failed to exhibit significant interactions, main effects were assessed with one-way ANOVAs and Tukey HSD tests (levels of  $P < 0.05$  considered significant). Changes in aboveground biomass were used to assess prescribed fire severity and infer qualities of prescribed fire intensity (i.e. physical energy released; Keeley 2009). Specifically, the volume of CWD and the percent cover of ground surface categories were compared between disturbance categories before and after prescribed fire. To assess impacts of prescribed fire on woody plant reproduction in areas



differentially impacted by wind disturbance and salvage logging, sapling and seedling density, richness, and Shannon diversity were compared before and after prescribed fire. All response variables were standardized to the hectare level and transformed as necessary for statistical analyses to meet assumptions of homoscedasticity.

To calculate CWD volume ( $\text{m}^3\text{ha}^{-1}$ ), a conic paraboloid equation was used for logs (Fraver et al. 2007), and species-specific allometric equations were used for uprooted stems (Woodall et al. 2011, Parker and Hart 2014, Ford et al. 2018). Based on decay dynamics of species in the study area, CWD in decay classes II and III were likely deposited by the wind event and were therefore referred to as wind-deposited CWD (Russell et al. 2014, Ulyshen et al. 2018). Proportions of wind-deposited CWD in decay classes II and III were compared between 2016 and 2018 to assess impacts of decay on CWD volume reductions. To calculate plot-level ground surface cover values, quadrat-level NCVS rankings were converted to corresponding range midpoints, averaged per plot, and reconverted to NCVS cover classes (Peet et al. 1998). Seedling densities were summed across quadrats to determine plot-level densities, and, together with sapling densities, were compared by species to assess disturbance impacts on woody plant competition and vertical stratification.

## **Results**

### ***Fire Severity***

The volume of CWD was significantly impacted by the interaction of pre-fire disturbance history and time relative to prescribed fire ( $P < 0.001$ ). Before prescribed fire, CWD volume was  $5.7 \text{ m}^3\text{ha}^{-1}$  on mature sites,  $179.0 \text{ m}^3\text{ha}^{-1}$  on wind-disturbed sites, and  $19.9 \text{ m}^3\text{ha}^{-1}$  on salvage-logged sites. After prescribed fire, CWD volume was reduced by only 3% on mature

sites, but dropped 22% and 29% on wind-disturbed and salvage-logged sites, respectively (Figure 3.2). On mature sites, CWD in decay classes II and III accounted for 70% (i.e. 4.0 m<sup>3</sup>ha<sup>-1</sup>) of the CWD volume documented on these sites in 2016, and may be considered background mortality. On wind-disturbed and salvage-logged sites, CWD in decay classes II and III (i.e. wind-deposited CWD) accounted for 99.8% and 98.9% of the CWD volume documented on these sites in 2016 and 2018, respectively. Over the duration of the study, the proportion of wind-deposited CWD categorized as decay class II decreased and the proportion categorized as decay class III increased (Figure 3.3). In 2016, decay class II stems composed 93% of the volume of wind-deposited CWD on wind-disturbed and salvage-logged sites, but only 59% in 2018. This reduction was counterbalanced by decay class III stems, which composed 7% of the volume of wind-deposited CWD on wind-disturbed and salvage-logged sites in 2016 and 41% in 2018.

Based on ground cover estimates taken on nested quadrats, the percent surface cover of CWD was also reduced, albeit almost imperceptibly, after prescribed fire ( $P = 0.048$ , Table 3.1, Fig. 3.4). From 2017 to 2018, average CWD cover changed from  $0.4\% \pm 0.2\%$  (standard error, SE) to  $0.3\% \pm 0.2\%$  (SE) on mature plots,  $10.0\% \pm 1.5\%$  (SE) to  $7.8\% \pm 1.2\%$  (SE) on wind-disturbed plots, and  $3.6\% \pm 0.9\%$  (SE) to  $2.4\% \pm 0.8\%$  (SE) on salvage-logged plots. Excluding the surface cover of CWD, which was lower on salvage-logged plots compared to wind-disturbed plots ( $P = 0.006$ ), surface cover categories did not significantly differ between wind-disturbed and salvage-logged plots before prescribed fire. Mature plots, however, were characterized by less exposed mineral soil and Poaceae litter cover ( $P < 0.001$  and  $P = 0.005$ , respectively), and more *Pinus* litter cover ( $P < 0.001$ ), than wind-disturbed and salvage-logged

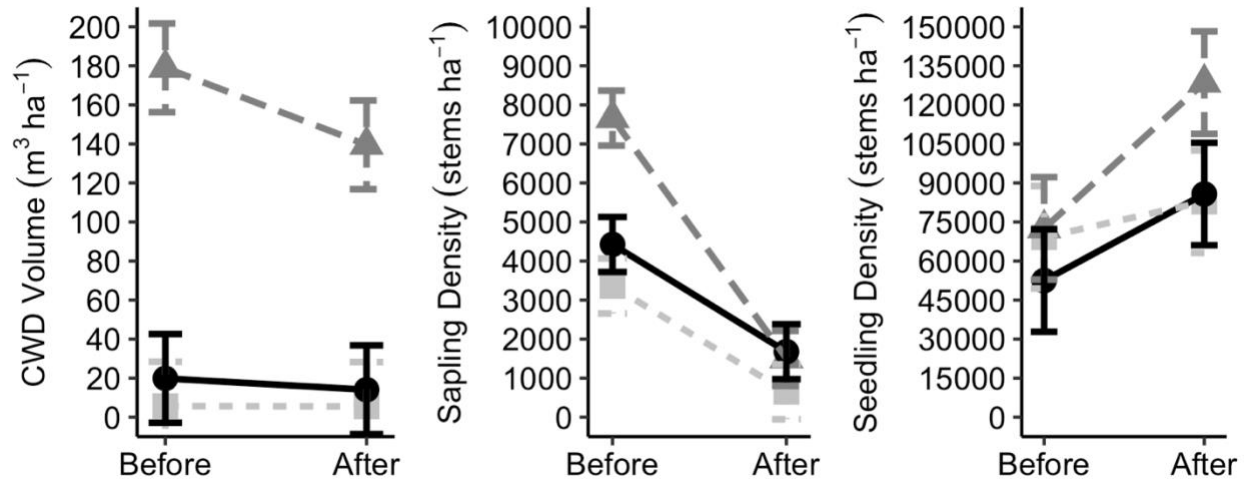


Figure. 3.2. Disturbance category and time relative to prescribed fire had significant interactions on the average volume of coarse woody debris (CWD,  $P < 0.001$ ), sapling density ( $P < 0.001$ ), and seedling density ( $P = 0.008$ ) documented in mature (light gray squares, short-dashed lines), wind-disturbed (dark gray triangles, long-dashed lines), and salvage-logged (black circles, solid lines) plots before (2016) and after (2018) prescribed fire.

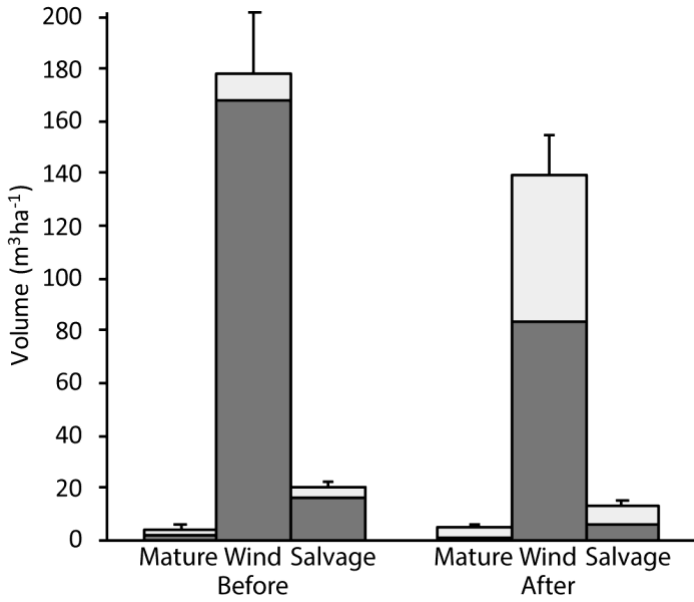


Figure. 3.3. Volume ( $\text{m}^3\text{ha}^{-1}$ ) of coarse woody debris (CWD) categorized as decay class II (dark gray bars) and decay class III (light gray bars) in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Table 3.1. Summary of mixed ANOVAs used to assess the impacts of pre-fire conditions (mature, wind-disturbed, and salvage-logged), time relative to prescribed fire (before and after), and their interaction on ground surface cover categories. Statistically significant values ( $P < 0.05$ ) are indicated with bold text.

Surface Cover (%)	Pre-Fire Condition (C)			Time (T)			C × T		
	<i>F</i> -values	<i>P</i> -values	df	<i>F</i> -values	<i>P</i> -values	df	<i>F</i> -values	<i>P</i> -values	df
Coarse Woody Debris	88.72	< <b>0.001</b>	2	4.085	<b>0.048</b>	1	0.634	0.534	2
Fine Woody Debris	6.595	<b>0.003</b>	2	0.096	0.758	1	1.269	0.289	2
Bare Mineral Soil	89.92	< <b>0.001</b>	2	74.22	< <b>0.001</b>	1	0.764	0.47	2
<i>Pinus</i> Litter	185.1	< <b>0.001</b>	2	29.816	< <b>0.001</b>	1	1.452	0.243	2
Poaceae Litter	27.43	< <b>0.001</b>	2	59.376	< <b>0.001</b>	1	2.305	0.109	2
Other Litter	7.634	<b>0.001</b>	2	30.911	< <b>0.001</b>	1	6.818	<b>0.002</b>	2

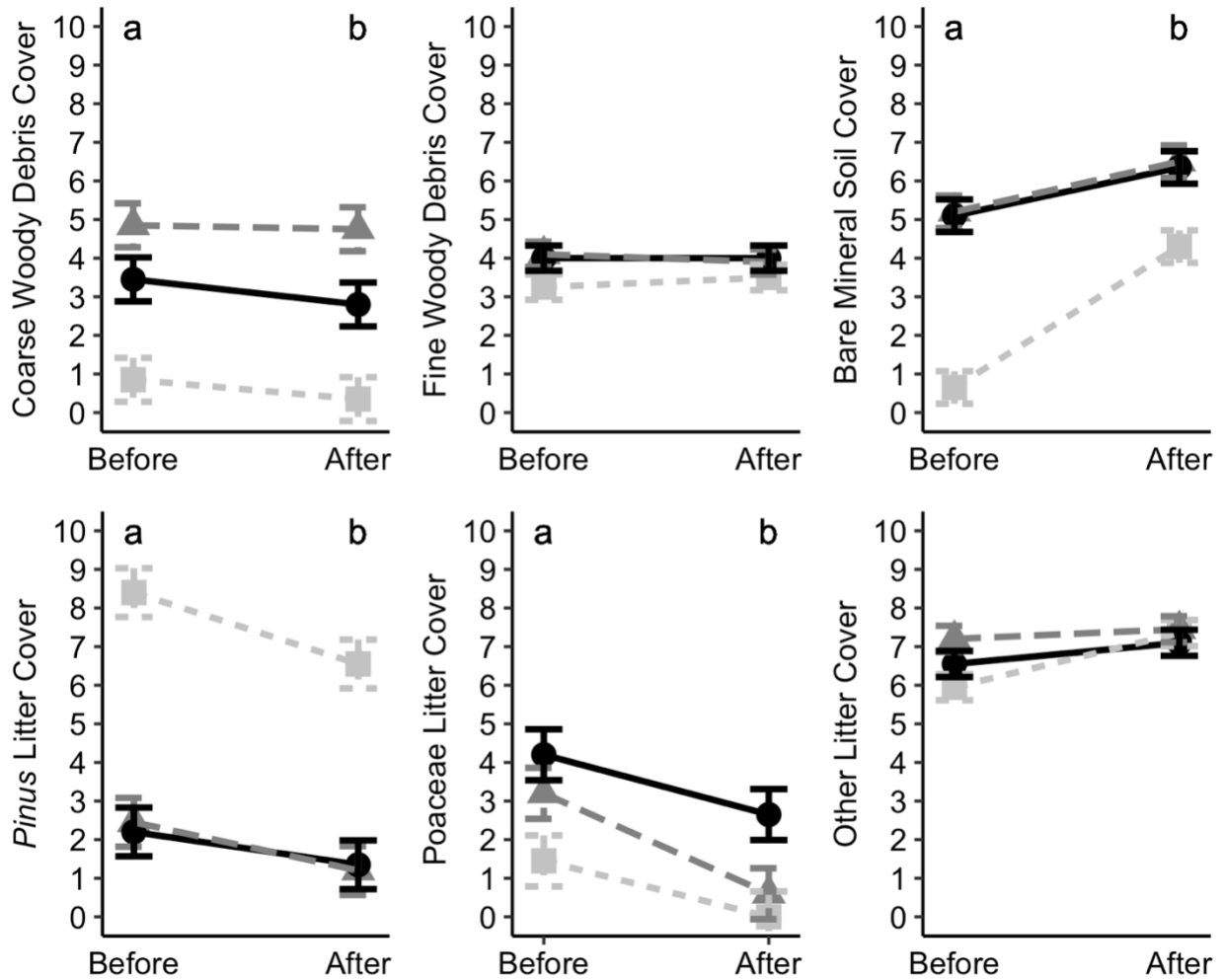


Figure 3.4. Average cover of ground surface categories documented in mature (light gray squares, short-dashed lines), wind-disturbed (dark gray triangles, long-dashed lines), and salvage-logged (black circles, solid lines) plots before (2017) and after (2018) prescribed fire. Cover classes are adapted from Peet et al. (1998), where 0 = absent, 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100%. Lower-case letters indicate significant before-and-after differences in the percent cover of coarse woody debris ( $P = 0.048$ ), bare mineral soil ( $P < 0.001$ ), *Pinus* litter ( $P < 0.001$ ), and Poaceae litter ( $P < 0.001$ ).

plots. After prescribed fire, all disturbance categories exhibited increased bare mineral soil exposure and reduced *Pinus* and Poaceae litter cover ( $P < 0.001$ ).

### ***Woody Plant Regeneration***

The interaction of pre-fire disturbance history and time relative to prescribed fire significantly impacted the density of saplings ( $P < 0.001$ ) and seedlings ( $P = 0.008$ ; Table 3.2, Figure 3.2). After prescribed fire, reduced sapling densities were observed on mature, wind-disturbed, and salvage-logged sites (Table 3.3), which coincided with increases in seedling densities (Table 3.4). Changes were most pronounced on wind-disturbed sites where prescribed fire reduced sapling density by 6,156 stems  $\text{ha}^{-1}$ , compared to reductions of 2,709 stems  $\text{ha}^{-1}$  and 2,746 stems  $\text{ha}^{-1}$  on mature and salvage-logged sites, respectively. Despite overall sapling density reductions, the density of *P. palustris* saplings increased after prescribed fire on wind-disturbed and salvage-logged sites. Before prescribed fire, *P. palustris* saplings were outnumbered by 21 other species on wind-disturbed sites and 13 other species on salvage-logged sites. After prescribed fire, however, *P. palustris* saplings were outnumbered by only seven and three other species on wind-disturbed and salvage-logged sites, respectively. In contrast to *P. palustris*, these other species (i.e. *Liquidambar styraciflua*, *Quercus coccinea*, *Q. falcata*, *Q. nigra*, *Q. stellata*, *Rhus copallinum*, and *Vaccinium arboreum*), all exhibited marked post-fire sapling density reductions compared to pre-fire measurements. After prescribed fire, mature, wind-disturbed, and salvage-logged sites also exhibited reduced sapling species richness ( $P < 0.001$ ) and Shannon diversity ( $P = 0.015$ ) values (Table 3.5). Nonetheless, sapling species richness and Shannon diversity remained lowest in mature sites before and after prescribed fire ( $P < 0.001$ ). Compared to salvage-logged sites, wind-disturbed sites hosted greater pre-fire

Table 3.2. Summary of mixed ANOVAs used to assess the impacts of pre-fire conditions (mature, wind-disturbed, and salvage-logged), time relative to prescribed fire (before and after), and their interaction on sapling (woody stems > 1 m height and < 5 cm diameter) and seedling (woody stems < 1 m height) density (stems ha<sup>-1</sup>), richness (*S*), and Shannon diversity (*H'*). Statistically significant values ( $P < 0.05$ ) are indicated with bold text.

Regeneration Layer	Metric	Pre-Fire Condition (C)			Time (T)			C × T		
		<i>F</i> -values	<i>P</i> -values	d f	<i>F</i> -values	<i>P</i> -values	d f	<i>F</i> -values	<i>P</i> -values	d f
Sapling	Density	23.02	< <b>0.001</b>	2	301.3	< <b>0.001</b>	1	13.74	< <b>0.001</b>	2
	Richness	51.38	< <b>0.001</b>	2	106.3	< <b>0.001</b>	1	1.053	0.356	2
	Shannon Diversity	47.53	< <b>0.001</b>	2	6.274	<b>0.015</b>	1	0.775	0.466	2
Seedling	Density	3.215	<b>0.048</b>	2	31.38	< <b>0.001</b>	1	5.27	<b>0.008</b>	2
	Richness	6.101	<b>0.004</b>	2	34.82	< <b>0.001</b>	1	0.02	0.98	2
	Shannon Diversity	3.417	<b>0.04</b>	2	40.851	< <b>0.001</b>	1	0.517	0.599	2



Table 3.3. Density (stems ha<sup>-1</sup>) of saplings (woody stems > 1 m height and < 5 cm diameter) documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Species	Saplings ha <sup>-1</sup>					
	Mature		Wind		Salvage	
	2016	2018	2016	2018	2016	2018
<i>Acer floridanum</i> (Chapm.) Pax	–	–	49	–	–	–
<i>Acer rubrum</i> L.	649	10	249	5	181	23
<i>Acer saccharum</i> Marshall	–	–	1	–	–	–
<i>Aesculus pavia</i> L.	–	–	1	–	–	–
<i>Asimina parviflora</i> (Michx.) Dunal	–	–	5	–	–	–
<i>Callicarpa americana</i> L.	60	–	26	–	8	–
<i>Carya glabra</i> (Mill.) Sweet	4	–	166	34	9	1
<i>Carya tomentosa</i> (Lam.) Nutt.	19	3	130	24	31	6
<i>Castanea dentata</i> (Marshall) Borkh.	–	1	–	–	–	–
<i>Castanea pumila</i> (L.) Mill.	5	–	–	–	4	3
<i>Cornus florida</i> L.	54	–	8	5	43	4
<i>Diospyros virginiana</i> L.	158	79	324	31	109	26
<i>Fagus grandifolia</i> Ehrh.	1	–	–	–	–	–
<i>Hamamelis virginiana</i> L.	–	–	58	5	1	–
<i>Ilex opaca</i> Aiton	–	–	–	–	1	–
<i>Liquidambar styraciflua</i> L.	114	19	541	76	254	68
<i>Liriodendron tulipifera</i> L.	–	–	1	–	11	1
<i>Magnolia macrophylla</i> Michx.	–	–	10	–	5	1
<i>Magnolia virginiana</i> L.	–	–	–	–	5	5
<i>Nyssa sylvatica</i> Marshall	3	20	10	53	65	24
<i>Oxydendrum arboreum</i> (L.) DC.	144	181	570	50	103	74
<i>Pinus echinata</i> Mill.	–	–	4	–	–	3
<i>Pinus palustris</i> Mill.	30	11	34	56	75	123
<i>Pinus taeda</i> L.	14	5	21	29	35	93
<i>Prunus serotina</i> Ehrh.	–	–	3	–	1	–
<i>Prunus umbellata</i> Elliott	–	–	–	3	–	–
<i>Quercus alba</i> L.	34	4	389	45	51	8
<i>Quercus coccinea</i> Münchh.	48	15	544	140	88	49
<i>Quercus falcata</i> Michx.	60	10	443	141	430	208
<i>Quercus hemisphaerica</i> Bartram ex Willd.	–	1	19	6	18	4
<i>Quercus incana</i> Bartram	4	–	9	–	24	3
<i>Quercus laevis</i> Walter	6	–	16	1	61	21
<i>Quercus margarettae</i> W.W. Ashe ex Small	9	–	48	8	94	24
<i>Quercus marilandica</i> Münchh. var. <i>marilandica</i>	43	8	38	23	235	104

Species	Saplings ha <sup>-1</sup>					
	Mature		Wind		Salvage	
	2016	2018	2016	2018	2016	2018
<i>Quercus montana</i> Willd.	–	–	50	6	1	3
<i>Quercus nigra</i> L.	8	–	469	71	379	91
<i>Quercus rubra</i> L.	3	5	4	11	4	1
<i>Quercus stellata</i> Wangenh.	29	10	115	69	96	46
<i>Quercus velutina</i> Lam.	19	10	291	43	75	28
<i>Rhus copallinum</i> L.	380	114	1366	363	500	238
<i>Rhus glabra</i> L.	–	–	25	31	3	–
<i>Sassafras albidum</i> (Nutt.) Nees	3	–	24	3	45	6
<i>Styrax grandifolius</i> Aiton	–	30	146	25	3	6
<i>Symplocos tinctoria</i> (L.) L'Hér.	–	–	216	–	10	–
<i>Vaccinium arboreum</i> Marshall	1448	116	1203	138	1325	375
<i>Vaccinium elliotii</i> Chapm.	14	–	1	–	23	–
<i>Vaccinium pallidum</i> Aiton	–	–	9	–	–	–
<i>Vaccinium stamineum</i> L.	4	–	29	13	23	14
<b>TOTAL</b>	<b>3360</b>	<b>651</b>	<b>7661</b>	<b>1505</b>	<b>4425</b>	<b>1679</b>

Table 3.4. Density (stems ha<sup>-1</sup>) of seedlings (woody stems < 1 m height) documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Species	Seedlings ha <sup>-1</sup>					
	Mature		Wind		Salvage	
	2016	2018	2016	2018	2016	2018
<i>Acer floridanum</i> (Chapm.) Pax	–	–	200	650	–	–
<i>Acer rubrum</i> L.	1950	4200	400	650	400	350
<i>Aesculus pavia</i> L.	–	–	–	150	–	–
<i>Asimina parviflora</i> (Michx.) Dunal	500	750	350	800	200	600
<i>Callicarpa americana</i> L.	200	–	200	250	200	200
<i>Carya glabra</i> (Mill.) Sweet	200	300	850	300	–	50
<i>Carya tomentosa</i> (Lam.) Nutt.	800	850	1150	1700	1100	550
<i>Cornus florida</i> L.	2600	950	150	–	1050	350
<i>Diospyros virginiana</i> L.	500	850	700	2100	250	1450
<i>Gaylussacia dumosa</i> (Andrews) Torr. & A.Gray	4500	13350	100	800	8700	22250
<i>Hamamelis virginiana</i> L.	–	–	–	350	–	–
<i>Hydrangea quercifolia</i> Bartram	50	–	–	–	–	–
<i>Juniperus virginiana</i> L.	–	–	–	–	50	–
<i>Liquidambar styraciflua</i> L.	–	–	2000	4100	350	1050
<i>Liriodendron tulipifera</i> L.	–	100	250	100	–	50
<i>Nestronia umbellula</i> Raf.	150	–	–	–	–	–
<i>Nyssa sylvatica</i> Marshall	3300	700	4300	4650	2100	2500
<i>Oxydendrum arboreum</i> (L.) DC.	850	600	650	1600	200	1000
<i>Pinus</i> L.	6250	100	2150	950	8000	2400
<i>Pinus palustris</i> Mill.	18100	1900	4050	2350	6500	3500
<i>Prunus serotina</i> Ehrh.	–	–	50	150	–	–
<i>Prunus umbellata</i> Elliott	–	–	250	450	200	250
<i>Quercus alba</i> L.	1250	5550	1500	5250	–	200
<i>Quercus coccinea</i> Münchh.	450	500	600	300	250	100
<i>Quercus falcata</i> Michx.	1250	4400	2700	9800	2450	6450
<i>Quercus hemisphaerica</i> Bartram ex Willd.	450	500	50	200	50	–
<i>Quercus incana</i> Bartram	–	600	–	–	200	–
<i>Quercus laevis</i> Walter	200	–	150	50	400	250
<i>Quercus margarettae</i> W.W. Ashe ex Small	950	1300	900	600	950	950
<i>Quercus marilandica</i> Münchh. var. <i>marilandica</i>	200	550	300	600	650	950
<i>Quercus montana</i> Willd.	–	–	400	1600	–	–
<i>Quercus nigra</i> L.	450	650	1350	2250	1750	2150
<i>Quercus rubra</i> L.	850	800	150	500	–	–
<i>Quercus stellata</i> Wangenh.	2800	850	600	250	100	50

Species	Seedlings ha <sup>-1</sup>					
	Mature		Wind		Salvage	
	2016	2018	2016	2018	2016	2018
<i>Quercus velutina</i> Lam.	550	–	900	1000	250	150
<i>Rhododendron canescens</i> (Michx.) Sweet	–	–	950	1000	–	–
<i>Rhus copallinum</i> L.	2300	12700	8900	32400	4500	16150
<i>Rhus glabra</i> L.	–	–	100	250	–	–
<i>Sassafras albidum</i> (Nutt.) Nees	600	600	550	550	350	2300
<i>Styrax grandifolius</i> Aiton	–	–	7950	11650	550	700
<i>Symplocos tinctoria</i> (L.) L'Hér.	–	–	4600	5750	600	850
<i>Vaccinium arboreum</i> Marshall	15950	26700	18800	30700	9950	17700
<i>Vaccinium elliotii</i> Chapm.	950	1450	400	–	–	–
<i>Vaccinium pallidum</i> Aiton	–	–	250	100	–	–
<i>Vaccinium stamineum</i> L.	–	1000	2650	1650	200	250
<b>TOTAL</b>	<b>69150</b>	<b>82800</b>	<b>72550</b>	<b>128550</b>	<b>52500</b>	<b>85750</b>

Table 3.5. Average richness and Shannon diversity of saplings (woody plants > 1 m height and < 5 cm dbh) and seedlings (woody plants < 1 m height) documented in mature, wind-disturbed, and salvage-logged plots. Sapling values reflect 400-m<sup>2</sup> plot averages and seedling values reflect 10-m<sup>2</sup> plot averages. Different capital letters denote significant differences between years ( $P < 0.05$ ), and lower-case letters denote significant differences between pre-fire conditions ( $P < 0.05$ ) within years based on Tukey's pairwise comparisons.

Regeneration Layer	Metric	Time	Pre-Fire Condition						
			Mature		Wind		Salvage		
Sapling	Richness	2016	A	9.6 ± 1.0	a	19.6 ± 0.7	b	16.3 ± 0.7	c
		2018	B	5.0 ± 0.6	a	14.0 ± 0.8	b	12.3 ± 0.9	b
	Shannon Diversity	2016	A	1.2 ± 0.1	a	2.3 ± 0.1	b	2.1 ± 0.1	c
		2018	B	1.1 ± 0.1	a	2.2 ± 0.1	b	2.0 ± 0.1	b
Seedling	Richness	2016	A	9.3 ± 0.6	a	11.9 ± 0.7	b	9.3 ± 0.5	a
		2018	B	7.4 ± 0.8	a	10.0 ± 0.7	b	7.5 ± 0.6	a
	Shannon Diversity	2016	A	1.7 ± 0.1		1.9 ± 0.1		1.8 ± 0.1	
		2018	B	1.3 ± 0.1		1.7 ± 0.1		1.5 ± 0.1	

values of sapling species richness ( $P = 0.015$ ) and Shannon diversity ( $P = 0.013$ ), however, prescribed fire negated these differences.

Contrary to the sapling stratum, *P. palustris* seedling densities were reduced after prescribed fire by 42% and 46% in wind-disturbed and salvage logged sites, respectively. Mature sites exhibited an even greater *P. palustris* seedling density reduction of 90%. This relative seedling density reduction was exceeded only by other *Pinus* spp. (i.e. combined *P. echinata* and *P. taeda* seedling densities), which were reduced by 98% in mature sites, and 56% and 70% in wind-disturbed and salvage-logged sites, respectively. Other species with noteworthy seedling density reductions included *Cornus florida*, *Q. laevis*, and *Q. stellata*, which exhibited reduced post-fire seedling densities in all three disturbance categories. Whereas *P. palustris* composed the majority of seedlings counted on mature plots prior to prescribed fire, six other seedling species outnumbered *P. palustris* on mature plots after prescribed fire. Four of these species (i.e. *Gaylussacia dumosa*, *Q. alba*, *Q. falcata*, and *Rhus copallinum*), exhibited more than doubled seedling densities after prescribed fire in all disturbance categories. Although total seedling densities increased after prescribed fire, seedling richness and Shannon diversity values were reduced in every disturbance category ( $P < 0.001$ , Table 5). Nonetheless, seedling richness remained greatest on wind-disturbed plots before ( $P = 0.027$ ) and after prescribed fire ( $P = 0.037$ ).

## **Discussion**

Global recognition of more frequent and severe forest disturbance events has motivated mounting interest in strategies to manage naturally disturbed forests (Seidl et al. 2017, Sommerfeld et al. 2018). Of all catastrophic wind disturbances that impact forest ecosystems,

tornadoes reach the greatest wind speeds and mortality rates (Everham and Brokaw 1996) and are becoming increasingly frequent in the southeastern United States (Gensini and Brooks 2018). Forest managers and policy makers must therefore be increasingly prepared to consider the potential ecological consequences of post-wind disturbance salvage logging. Results and recommendations of this study may be used to develop strategies to manage other forests subject to catastrophic canopy removal, especially fire-adapted forests managed with low-intensity prescribed fires.

Based on before- and after-prescribed fire data collected in areas differentially impacted by catastrophic wind disturbance and salvage logging, salvage logging did not alter the amount of fine fuels available for prescribed fire consumption. With the exception of CWD, the percent cover of surface fuel categories did not significantly differ between wind-disturbed and salvage-logged sites before prescribed fire. To echo Fraver et al. (2017), these results can be attributed to the retention of slash on salvaged sites where merchantable deadwood extraction, not fuels reduction, was the primary management objective. Considering that larger fuels (i.e. CWD) have a negligible impact on fire ignition and rate of spread compared to fine fuels with a higher surface-area-to-volume ratio (Rothermel 1972), we contend that prescribed fire intensity was largely unaffected by deadwood extraction on salvage-logged sites. Nonetheless, these results must be interpreted with caution because an earlier (April 2014) prescribed fire, conducted before this study was initiated, likely altered fine fuels in the study area and may have been differentially impacted by salvage logging.

Although slight post-fire reductions in the percent cover and volume of CWD were observed, these reductions could be attributed to decay processes other than prescribed fire consumption (Cornwell et al. 2009). Between the 2016 and 2018 deadwood surveys,

approximately one-third of the CWD volume documented on wind-disturbed and salvage-logged sites transitioned from decay class II to decay class III. Compared to decay class II stems, decay class III stems have sapwood that can be broken apart by hand (USDA 2016). This decay class transition was not surprising considering that, during 2016 baseline data collection, Ford et al. (2018) documented 97% of saproxylic (i.e. wood-decomposing) fungi occurrences on decay class II stems. Ulyshen et al. (2018) also described how wood-decomposing microbes, favored by hot and humid conditions, likely accelerated wood decay rates in frequently burned *P. palustris* stands. Though prescribed fires that consume large volumes of CWD have been reported in other forest types (Randall-Parker and Miller 2002, Knapp et al. 2005), results of this study align more closely with Hanula et al. (2012), who documented frequent low-intensity prescribed fires with negligible impacts on CWD volumes in a *P. palustris* flatwood ecosystem.

Contrary to CWD, sapling densities were substantially reduced after prescribed fire, indicating that prescribed fire top-killed woody plants throughout the treatment area. A ubiquitous increase in exposed mineral soil combined with *Pinus* and Poaceae litter reductions further corroborated the efficacy of prescribed fire in all disturbance categories. However, whereas canopy-derived *Pinus* litter likely sustained prescribed fire in mature sites (Platt et al. 1988, Mitchell et al. 2009), the pre-fire surface cover of *Pinus* litter averaged less than 2% on wind-disturbed and salvage-logged sites. Yet, wind-disturbed and salvage-logged sites exhibited fire-mediated sapling mortality, indicating that other fuels must have sustained the prescribed fire. These results supported recent advancements in our conceptual understanding of frequently burned *P. palustris* stands in which fire-adapted plants besides *P. palustris* produce pyrogenic fuels (Fill et al. 2015). In fact, wind-disturbed and salvage-logged sites contained relatively high seedling and sapling densities of all *Quercus* species identified by Kane et al. (2008) as “fire



facilitators” (i.e. *Q. falcata*, *Q. laevis*, *Q. margarettae*, and *Q. stellata*). Nonetheless, *Q. nigra*, which has low litter flammability, also exhibited relatively high densities, demonstrating the complexity of fuel bed composition and flammability (Heirs et al. 2014). Based on fuels collected on the same plots described herein, Emery and Hart (in review) found that wind-disturbed and salvage-logged sites also contained other highly flammable fuels derived from species such as *Gelsemium sempervirens* (L.) St.-Hil. and *Vaccinium stamineum*.

Despite overall sapling density reductions, *P. palustris* exhibited increased post-fire sapling densities on wind-disturbed and salvage-logged sites. Thus, prescribed fire enhanced *P. palustris* recovery on these sites through shoot mortality of less fire-resistant species. Indeed, *P. palustris* saplings are particularly fire-resistant, in part because of thick bark and tufts of long needles to protect aboveground meristematic tissues (Brockway et al. 2006). Fire-induced competition reduction and corresponding increases in resource availability may have also stimulated *P. palustris* seedling recruitment to the sapling stratum (Grelen 1978, Ramsey et al. 2003). However, although prescribed fire increased *P. palustris* sapling densities and reduced hardwood sapling densities, *P. palustris* saplings remained outnumbered by other species on wind-disturbed and salvage-logged sites. Nonetheless, we expect that continued application of prescribed fire will continue to relegate hardwood species to smaller size classes (Bond and Midgley 2001, Grady and Hoffmann 2012), and thereby facilitate the stratification of *P. palustris* saplings above less fire-resistant woody plants (Bigelow and Whelan 2019). Indeed, many studies show that a regime of repeated prescribed fires is needed produce desired compositional and structural changes (Boyer 1990, Waldrop and Lloyd 1991, and others cited in Knapp et al. 2009). Observationally, *P. palustris* sapling appeared taller than most other saplings, and we therefore recommend that future studies quantify sapling heights to demonstrate how *P. palustris*

saplings, despite being outnumbered, stratify above less fire-resistant competitors with repeated application of prescribed fire. Counter to wind-disturbed and salvage-logged sites, mature sites hosted fewer *P. palustris* saplings after prescribed fire. However, we observed no fire-killed *P. palustris* saplings on mature plots, which would have been discernable based on burnt terminal buds. As such, sapling density reductions on mature sites were attributed to *P. palustris* sapling growth to the tree size class (i.e.  $\geq 5$  cm diameter), not prescribed fire-mediated mortality.

In fire-prone ecosystems globally, plants can persist with two non-exclusive post-fire regeneration strategies: seeding and resprouting (Morais et al. 2014, Pausas and Keely 2014). *Pinus palustris* exemplifies the seeding strategy, whereby fire-resistant juveniles recruit to canopy positions and produce seed-bearing cones. Resprouting occurs when top-killed individuals produce new shoots from surviving tissues at or below ground level. Study area-wide reductions in sapling densities and corresponding increases in seedling densities exemplified a post-fire resprouting response. For instance, on wind-disturbed sites, *Vaccinium arboreum* and *Rhus copallinum* were each reduced by over 1000 sapling stems  $\text{ha}^{-1}$  after prescribed fire, but gained over 10,000 and 20,000 seedling stems  $\text{ha}^{-1}$ , respectively. Although *V. arboreum* is better-known for a third post-fire strategy (i.e. colonization), in which animal- or water-dispersed seeds are transported from unburned sites (Tirmenstein 1991), Olson and Platt (1995) also described post-fire *V. arboreum* (and *R. copallinum*) resprouting. Our observations also corresponded with Cannon et al. (2019), who reported rapid clonal establishment of *R. copallinum* on wind-and-fire impacted sites, and Hiers et al. (2014), who described the resprouting ability of most *Quercus* species documented in this study. Results of this study can also be conceptualized through resistance- and resilience-based disturbance-response syndromes (Batista and Platt 2003): *P. palustris* saplings survived prescribed fire and exhibited modest post-

fire recruitment (resistant syndrome), whereas most hardwood species experienced shoot mortality, yet exhibited prolific post-fire clonal recovery (resilient syndrome).

Though some *P. palustris* seedlings can also resprout after prescribed fire (Knapp et al. 2018), we observed marked post-fire *P. palustris* seedling reductions, especially on mature sites. Grace and Platt (1995) and Jack et al. (2010) described how prescribed fire-induced *P. palustris* mortality rates were greatest among smaller seedling size classes and in areas with greater surface *Pinus* litter loads, which facilitated prescribed fires of greater intensities. We therefore suspect that mature sites, which contained the greatest surface *Pinus* litter cover and the highest pre-fire *P. palustris* seedling densities, experienced the greatest prescribed fire intensities and, consequently, the greatest *P. palustris* seedling mortality rates. *Pinus palustris* seedlings and saplings are also especially vulnerable to fire-induced mortality during shoot elongation (i.e. the “candling stage”) in the early growing season. Although prescribed fires are purposefully conducted when wind speeds are sufficient to maintain flame heights below lethal levels for candling *P. palustris* saplings, the timing of prescribed fire in the early growing season could have also amplified mortality of candling *P. palustris* seedlings.

### **Management Implications**

We recognize that assessments of whether and how disturbances impact forest resilience can depend on which response variables are assessed (Kleinman et al. 2019). Indeed, we did not measure carbon stocks (Buma et al. 2014), insects (Cobb et al. 2007), soil properties (Kishchuk et al. 2015), or a multitude of other ecosystem components that may be negatively impacted by salvage logging (Lindenmayer et al. 2017). However, with respect to woody plant recovery, this study supported other studies that suggested that negative ecological consequences of salvage

logging are not necessarily a certainty (Peterson and Leach 2008, Lang et al. 2009, Fidej et al. 2016, Royo et al. 2016, Sass et al. 2018, Slyder et al. 2019). In 2016, salvage-logged sites hosted the greatest *P. palustris* sapling densities, indicating that salvage logging did not alter short-term recovery toward pre-disturbance canopy conditions (Kleinman et al. 2017, Ford et al. 2018). However, *P. palustris* saplings were substantially outnumbered by other species at this time, and it was unclear whether prescribed fire would effectively induce shoot mortality of woody competitors in areas lacking a continuous canopy-derived *Pinus* litter fuel bed. It was also unclear how deadwood extraction would impact prescribed fire effects on salvage-logged sites. Here we report that, despite a paucity of *Pinus* litter on wind-disturbed and salvage-logged sites, prescribed fire enhanced *P. palustris* recovery by top-killing less fire-resistant species.

The response variables we measured to assess prescribed fire effects (i.e. fine fuel consumption, mineral soil exposure, and sapling density reductions) were not apparently impacted by deadwood extraction on salvage-logged sites. The efficacy of prescribed fire in wind-disturbed and salvage-logged sites was attributed primarily to pyrogenic fine fuels derived from broadleaved plants such as fire-facilitating *Quercus* species (Kane et al. 2008, Heirs et al. 2014, Fill et al. 2015). We therefore highlight the importance of alternative pyrogenic fuel sources to maintain prescribed fires, especially after stand-regenerating events, and recommend retention of fine fuels on salvage-logged sites to facilitate continued use of prescribed fire. We also suspect that prescribed fire, conducted in April, was particularly effective at top-killing hardwood saplings shortly after they had invested energy into aboveground growth (Glitzenstein et al 1995, Drewa et al. 2006). As such, we support the continued use of early growing-season fires to promote *P. palustris* recovery, yet acknowledge inconclusive evidence regarding timing of prescribed fire within the growing season (Reilly et al. 2017).

Although prescribed fire improved post-disturbance stand development toward *P. palustris* dominance, *P. palustris* saplings remained ubiquitously outnumbered by other hardwood species. Whereas some of these species (i.e. *Rhus copallinum* and *Vaccinium arboreum*) do not typically transcend understory positions, *Quercus* spp. (especially *Q. coccinea* and *Q. falcata*) were particularly abundant, and may achieve canopy positions without more intensive management to supplement prescribed fire such as mechanical removal and/or selective herbicide application. Nonetheless, contrary to *P. palustris*, these species all exhibited marked post-fire sapling density reductions, and repeated use of prescribed fire may effectively control these species over time. In addition to repeated use of prescribed fire, a shorter prescribed fire-return interval might also enhance *P. palustris* recovery. For example, in mature sites, transition from a four- to two-year prescribed fire-return interval would help maintain lower *Pinus* litter fuel loads, which would in turn support less intense fires and consequently lower *P. palustris* seedling mortality rates (Jack et al. 2010). A shorter prescribed fire-return interval would also increase the likelihood of exposed bare mineral soil, which is required for successful *P. palustris* seed germination (Brockway et al. 2006), corresponding with *P. palustris* cone production, which occurs at rather sporadic intervals (Chen et al. 2018).

### References for Chapter 3

- Batista, W.G., Platt, W.J. 2003. Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. *Journal of Ecology* 91, 197–212.
- Beckett, S., Golden, M.S. 1982. Forest vegetation and vascular flora of Reed Brake Research Natural Area, Alabama. *Castanea* 47, 368–392.
- Bigelow, S.W., Stambaugh, M.C., O'Brien, J.J., Larson, A.J., Battaglia, M.A.. 2018. Longleaf pine restoration in context comparisons of frequent fire forests. In: Kirkman, L. W., Jack, S.B. *Ecological restoration and management of longleaf pine forests*. CRC Press, Taylor & Francis Group, Boca Raton, FL, pp 311–338.
- Bigelow, S.W., Whelan, A.W. 2019. Longleaf pine proximity effects on air temperatures and hardwood top-kill from prescribed fire. *Fire Ecology* 15:27.
- Bond, W.J., Midgley, J.J. 2001. Ecology of sprouting in woody plants: the persistence niche. *Trends in Ecology and Evolution* 16, 45–51
- Boyer, W.D. 1990. Growing season burns for control of hardwoods in longleaf pine stands. Res. Pap. SO-256. New Orleans, LA: U.S. Department of Agriculture, Forest Service, Southern Forest Experiment Station. 7 p.
- Braun, E.L., 1950. *Eastern Deciduous Forests of North America*. The Blackburn Press, Caldwell, NJ, pp. 596.
- Brockway, D.G., Outcalt, K.W., Boyer, W.D., 2006. Longleaf pine regeneration ecology and methods. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. Springer, New York, NY, pp. 95–133.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6:70.
- Buma, B., Poore, R.E., Wessman, C.A. 2014. Disturbances, their interactions, and cumulative effects on carbon and charcoal stocks in a forested ecosystem. *Ecosystems* 17, 947–959.
- Buma, B., Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecology and Management* 266, 25–33.
- Cannon, J.B., Henderson, S.K., Bailey, M.H., Peterson, C.J. 2019. Interactions between wind and fire disturbance in forests: competing amplifying and buffering effects. *Forest Ecology and Management* 436, 117–128.

- Cannon, J. B., Peterson, C.J., O'Brien, J.J., Brewer, J.S. 2017. A review and classification of interactions between forest disturbance from wind and fire. *Forest Ecology and Management* 406, 381–390.
- Chen, X., Brockway, D.G., Guo, Q. 2018. Characterizing the dynamics of cone production for longleaf pine forests in the southeastern United States. *Forest Ecology and Management* 429, 1–6.
- Cobb, T.P., Langor, D.W., Spence, J.R. 2007. Biodiversity and multiple disturbances: boreal forest ground beetle (Coleoptera : Carabidae) responses to wildfire, harvesting, and herbicide. *Canadian Journal of Forest Research* 37, 1310–1323.
- Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F.A., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? *Global Change Biology* 15, 2431–2449.
- D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L. 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in subboreal pine systems. *Forest Ecology and Management* 262, 2070–2078.
- Dale, V.H., Joyce, L.A., McNulty, S., Neilson, R.P., Ayres, M.P., Flannigan, M.D., Hanson, P.J., Irland, L.C., Lugo, A.E., Peterson, C.J., Simberloff, D., Swanson, F.J., Stocks, B.J., Wotton, B.M. 2001. Climate change and forest disturbances. *Bioscience* 51, 723.
- Davies, G.M., Gray, A. 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution* 5, 5295–5304.
- Drewa, P.B., Thaxton, J.M., Platt, W.J. 2006. Responses of root-crown bearing shrubs to differences in fire regimes in *Pinus palustris* (longleaf pine) savannas: Exploring old-growth questions in second-growth systems. *Applied Vegetation Science* 9, 27–36.
- Everham, E.M., Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. *The Botanical Review* 62, 113–185.
- Fenneman, N.M., 1938. *Physiography of Eastern United States*. McGraw-Hill, New York, NY, pp. 714.
- Fidej, G., Rozman, A., Nagel, T.A., Dakskobler, I., Diaci, J. 2016. Influence of salvage logging on forest recovery following intermediate severity canopy disturbances in mixed beech dominated forests of Slovenia. *iForest* 9, 430–436.
- Fill, J.M., Platt, W.J., Welch, S.M., Waldron, J.L., Mousseau, T.A. 2015. Updating models for restoration and management of fiery ecosystems. *Forest Ecology and Management* 356, 54–63.

- Ford, S.A., Kleinman, J.S., Hart, J.L. 2018. Effects of wind disturbance and salvage harvesting on macrofungal communities in a *Pinus* woodland. *Forest Ecology and Management* 407, 31–46.
- Franklin, J. F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D. 2000. Threads of continuity. *Conservation in Practice* 1, 8–17.
- Franklin, J.F., Spies, T.A., Van Pel, R., Carey, A.B., Thronburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forests ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155, 399–423.
- Fraver, S., Dodds, K.J., Kenefic, L.S., Morrill, R., Seymour, R.S., Sypitkowski, E., 2017. Forest structure following tornado damage and salvage logging in northern Maine, USA. *Canadian Journal of Forest Research* 47, 560–564.
- Fraver, S., Ringvall, A., Jonsson, B.G., 2007. Refining volume estimates of down woody debris. *Canadian Journal of Forest Research* 37, 627–633.
- Frost, C.C., 2006. History and future of the longleaf pine ecosystem. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds.), *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. Springer, New York, NY, pp. 9–42.
- Gilliam, F.S., Platt, W.J., Peet, R.K., 2006. Natural disturbances and the physiognomy of pine savannas: A phenomenological model. *Applied Vegetation Science* 9, 83–96.
- Gensini, V.A., Brooks, H.E. 2018. Spatial trends in United States tornado frequency. *Climate and Atmospheric Science* 1:38.
- Glitzenstein, J.S., Platt, W.J., Streng, D.R., 1995. Effects of fire regime and habitat on tree dynamics in North Florida longleaf pine savannas. *Ecological Monographs* 65, 441–476.
- Goode J.D., Kleinman, J.S., Hart, J.L., Bhuta, A.R.R. 2020 Edge influence on composition and structure of a *Pinus palustris* woodland following catastrophic wind disturbance. *Canadian Journal of Forest Research* 50, 332–341.
- Grace, S.L., Platt, W.J. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology* 83, 75–86.
- Grady, J.M., Hoffman, W.A. 2012. Caught in a fire trap: recurring fire creates stable size equilibria in woody resprouters. *Ecology* 93, 2052–2060
- Grelen, H.E. 1978. May burns stimulate growth in longleaf pine seedlings. Research Note SO-234. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 5 p.



- Griffith, G.E., Omernik, J.M., Comstock, J.A., Lawrence, S., Martin, G., Goddard, A., Hulcher, V.J., Foster, T., 2001. Ecoregions of Alabama and Georgia (Color Poster with Map, Descriptive Text, Summary Tables, and Photographs; Map Scale 1:17,000,000). US Geological Survey, Reston, Virginia.
- GSA (Geological Survey of Alabama), 2006. Geologic map of Alabama, digital version 1.0: Alabama Geological Survey Special Map 220A [adapted from Szabo, M.W., Osborne, W.E., Copeland, C.W., Jr., Neathery, T.L., 1988. Geologic map of Alabama (1:250,000): Alabama Geological Survey Special Map 220].
- Hanula, J.L., Ulyshen, M.D., Wade, D.D., 2012. Impacts of prescribed fire frequency on coarse woody debris volume, decomposition and termite activity in the longleaf pine flatwoods of Florida. *Forests* 3, 317–331.
- Hargrove, W.W., Pickering, J. 1992. Pseudoreplication: a *sine qua non* for regional ecology. *Landscape Ecology* 6, 251–258.
- Hiers, J.K., Walters, J.R., Mitchell, R.J., Varner, J.M., Conner, L.M., Blanc, L.A., Stowe, J. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. *Journal of Wildlife Management* 78, 383–393.
- Jack, S.B., Hiers, J.K., Mitchell, R.J., Gagnon, J.L. 2010. Fuel loading and fire intensity—effects on longleaf pine seedling survival. In: Stanturf, J.A. (Ed.), *Proceedings of the 14th biennial southern silvicultural research conference*. Gen. Tech. Rep. SRS–121. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 275–279.
- Johnstone, J.F., et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14, 369–378.
- Kane, J.M., Varner, J.M., Hiers, J.K.. 2008. The burning characteristics in southeastern oaks: discriminating fire facilitators from fire impeders. *Forest Ecology and Management* 256, 2039–2045.
- Keeley, J.E. 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire* 18, 116–126.
- Kishchuk, B.E., Thiffault, E., Lorente, M., Quideau, S., Keddy, T., Sidders, D. 2015. Decadal soil and stand response to fire, harvest, and salvage-logging disturbances in the western boreal mixedwood forest of Alberta, Canada. *Canadian Journal of Forest Research* 45, 141–152.
- Kleinman, J.S., Ford, S.A., Hart, J.L. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. *Forest Ecology and Management* 403, 112–125.

- Kleinman, J.S., Goode, J.D., Fries, A.C., Hart, J.L. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. *Ecosphere* 10: e02962.
- Kleinman, J.S., Hart J.L. 2018. Vascular flora of longleaf pine woodlands after wind disturbance and salvage harvesting in the Alabama Fall Line Hills. *Castanea* 83, 183–195.
- Knapp, B.O., Pile, L.S., Walker, J.L., Wang, G.G. 2018. Fire effects on a fire-adapted species: response of grass stage longleaf pine seedlings to experimental burning. *Fire Ecology* 14, 2
- Knapp, E.E., Estes, B.L., Skinner, C.N. 2009. Ecological effects of prescribed fire season: a literature review and synthesis for managers. Gen. Tech. Rep. PSW-GTR-224. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 80 p.
- Knapp, E.E., Keeley, J.E., Ballenger, E.A., Brennan, T.J. 2005. Fuel reduction and coarse woody debris dynamics with early and late season prescribed fire in a Sierra Nevada mixed conifer forest. *Forest Ecology and Management* 208, 383–397.
- Knapp, E.E., Ritchie, M.W. 2016. Response of understory vegetation to salvage logging following a high-severity wildfire. *Ecosphere* 7, e01550.
- Kush, J.S., Meldahl, R.S., McMahon, C.K., Boyer, W.D. 2004. Longleaf pine: a sustainable approach for increasing terrestrial carbon in the southern United States. *Environmental Management* 33: S139–S147.
- Lang, K.D., Schulte, L.A., Guntenspergen, G. R. 2009. Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. *Forest Ecology and Management* 259, 56–64.
- Leverkus, A.B., et al. 2018. Salvage logging effects on regulating and supporting ecosystem services—A systematic map. *Canadian Journal of Forest Research* 48, 983–1000 .
- Lindenmayer, D., Thorn, S., Banks, S. 2017. Please do not disturb ecosystems further. *Nature Ecology and Evolution* 1, 0031.
- Lindenmayer, D.B., Westgate, M.J., Scheele, B.C., Foster, C.N., Blair, D.P. 2019. Key perspectives on early successional forests subject to stand-replacing disturbances. *Forest Ecology and Management* 454.
- MacDonald, G. 2003. *Biogeography: Introduction to Space, Time and Life*. John Wiley and Sons, New York, NY. 518 p.
- Melvin, M. 2015. National prescribed fire use survey report. Washington, DC: Coalition of Prescribed Fire Councils Inc. Technical Report 02-15.

- Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G. 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. *Journal of Forestry* 107, 391–397.
- Marais, K.E., Pratt, R.B., Jacobs, S.M., Jacobsen, A.L., Esler, K.J. 2014. Postfire regeneration of resprouting mountain fynbos shrubs: differentiating obligate resprouters and facultative seeders. *Plant Ecology* 215, 195–208.
- Müller, J., Noss, R. Thorn, S., Bäessler, C., Leverkus, A.B., Lindenmayer, D. 2019. Increasing disturbance demands new policies to conserve intact forest. *Conservation Letters* 12:e12449.
- Noss, R.F., LaRoe III, E.T., Scott, J.M., 1995. Endangered ecosystems of the United States: A preliminary assessment of loss and degradation. *Biological Report 28*. USDI National Biological Service, Washington, D.C.
- NWS (National Weather Service), 2011. Sawyerville-Eoline (Greene, Hale and Bibb Counties) EF-3 tornado April 27 2011. Retrieved February 10, 2020 from NWS Weather Forecast Office, Birmingham, AL. [https://www.weather.gov/bmx/event\\_04272011sawyerville](https://www.weather.gov/bmx/event_04272011sawyerville).
- O'Brien, J.J., Hiers, J.K., Callaham, M.A., Jr., Mitchell, R.J., Jack, S. 2008. Interactions among overstory structure, seedling life history traits and fire in frequently burned neotropical pine forests. *Ambio* 37, 542–547.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics, Update Edition*. John Wiley and Sons, New York, NY, pp. 520.
- Olson, M.S., Platt, W.J., 1995. Effects of habitat and growing season fires on resprouting of shrubs in longleaf pine savannas. *Vegetatio* 119, 101–118.
- Palik, B., Kastendick, D. 2009. Woody plant regeneration after blowdown, salvage logging, and prescribed fire in a northern Minnesota forest. *Forest Ecology and Management* 258, 1323–1330.
- Parker, R.P., Hart, J.L., 2014. Patterns of riparian and in-stream large woody debris across a chronosequence of southern Appalachian hardwood stands. *Natural Areas Journal* 34, 65–78.
- Pausas, J.G., Keeley, J.E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204, 55–65.
- Peet, R.K., Wentworth, T.R., White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63, 262–274.
- Peterson, C.J., Leach, A.D. 2008. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry* 81, 361–376.

- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. p. 110–135. In: Likens, G.E. (ed.). Long-term studies in ecology: Approaches and alternatives. Springer-Verlag, New York, New York.
- Platt, W.J., Evans, G.W., Rathbun, S.L., 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). American Naturalist 131, 491–525.
- PRISM Climate Group, 2020. Data explorer: time series values for individual locations. Retrieved February 10, 2020 from Northwest Alliance for Computational Science and Engineering, Oregon State University, OR.<<http://www.prism.oregonstate.edu/explorer/>>.
- Ramsey, C.L., Jose, S., Brecke, B.J., Merritt, S. 2003. Growth response of longleaf pine (*Pinus palustris* Mill.) seedlings to fertilization and herbaceous weed control in an old field in southern USA. Forest Ecology and Management 172, 281–289.
- Randall-Parker, T., Miller, R. 2002. Effects of prescribed fire in ponderosa pine on key wildlife habitat components: preliminary results and a method for monitoring. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Eds.), Proceedings of the symposium on ecology and management of dead wood in western forests. USDA Forest Service General Technical Report PSW GTR-181, Albany, CA, pp. 823–834.
- Reilly, M.J., Outcalt, K., O'Brien, J.J., Wade, D. 2017. Effects of repeated growing season prescribed fire on the structure and composition of pine–hardwood forests in the Southeastern Piedmont, USA. Forests 8:8.
- Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. Canadian Journal of Botany 82, 1273–1283.
- Rothermel, R.C. 1972. A mathematical model for predicting fire spread in wildland fuels. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, Res. Pap. INT-115.
- Royo, A.A., Peterson, C.J., Stanovick, J.S., Carson, W.P., 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? Ecology 97, 1566–1582.
- Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., Skog, K.E., 2014. Residence times and decay rates of downed woody debris biomass/carbon in eastern US forests. Ecosystems 17, 765–777.
- Samuelson, L.J., Stokes, T.A., Ramirez, M.R., Mendonca, C.C. 2019. Drought tolerance of a *Pinus palustris* plantation. Forest Ecology and Management 451, 117557.

- Sass, E.M., D'Amato, A.W., Foster, D.R. 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.
- Seidl, R., et al. 2017. Forest disturbances under climate change. *Nature Climate Change* 7, 395–402.
- Shankman, D., Hart, J.L., 2007. The Fall Line: a physiographic-forest vegetation boundary. *Geographical Review* 97, 502–519.
- Slyder, J.B., Wenzell, J.W., Royo, A.A., Spicer, M.E., Carson, W.P. 2019. Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. *New Forests* 62, 12 p.
- Sommerfeld, A., et al. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications* 9:4355.
- Stanturf, J.A., Goodrick, S.L., Outcalt, K.W. 2007. Disturbance and coastal forests: A strategic approach to forest management in hurricane impact zones. *Forest Ecology and Management* 250, 119–135.
- Stephens, S.L., et al. 2019. Is fire "for the birds"? How two rare species influence fire management across the US. *Frontiers in Ecology and the Environment* 17, 391–399.
- Stokstad, E. 2006. Salvage logging research continues to generate sparks. *Science* 311, 761–761.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9, 117–125.
- Taboada, A., Fernandez-Garcia, V., Marcos, E., Calvo, L. 2018. Interactions between large high-severity fires and salvage logging on a short return interval reduce the regrowth of fire-prone serotinous forests. *Forest Ecology and Management* 414, 54–63.
- Thom, D., Seidl, R. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. *Biological Reviews* 91, 760–781.
- Thorn, S., Bässler, C. et al. 2018. Impacts of salvage logging on biodiversity: a meta-analysis. *Journal of Applied Ecology* 55, 279–289
- Thornthwaite, C.W., 1948. An approach toward rational classification of climate. *Geographical Review* 38, 55–94.
- Tirmenstein, D.A. 1991. *Vaccinium arboreum*. In: *Fire Effects Information System*, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire

- Sciences Laboratory (Producer). Retrieved February 10, 2020  
<<https://www.fs.fed.us/database/feis/plants/shrub/vacarb/all.html>>.
- Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849.
- Ulyshen, M.D., Horn, S., Pokswinski, S., McHugh, J.V., Hiers, J.K. 2018. A comparison of coarse woody debris volume and variety between old-growth and secondary longleaf pine forests in the southeastern United States. *Forest Ecology and Management* 429, 124–132.
- USDA, Forest Service, 2016. Forest Inventory and Analysis National Core Field Guide, Volume 1: Field Data Collection Procedures for Phase 2 Plots, Version 7.1, 432 p.
- USDA NRCS (United States Department of Agriculture, Natural Resources Conservation Service), 2008. Soil Survey of Bibb County, Alabama.
- USDA NRCS (United States Department of Agriculture, Natural Resources Conservation Service), 2020. Web Soil Survey. Retrieved February 10, 2020  
<<http://websoilsurvey.nrcs.usda.gov/>>.
- Waldrop, T.A., Lloyd, F.T. 1991. Forty years of prescribed burning on the Santee Fire Plots: effects on overstory and midstory vegetation. Pages 45–50. In: Nodvin, S.C., Waldrop, T.A. (eds). *Fire and the environment: ecological and cultural perspectives*. General Technical Report SE-GTR-69. Asheville, NC: USDA Forest Service, Southeastern Forest Experiment Station. 429 p.
- White, S.D., Hart, J.L., Cox, L.E., Schweitzer, C.J. 2014. Woody regeneration in a southern Appalachian *Quercus* stand following wind disturbance and salvage logging. *Castanea* 79:223–236.
- Woodall, C.W., Heath, L.S., Domke, G.M., Nichols, M.C., 2011. Methods and equations for estimating aboveground volume, biomass, and carbon for trees in the US forest inventory, 2010.

## CHAPTER 4

### GROUND FLORA COVER, DIVERSITY, AND LIFE-HISTORY TRAIT REPRESENTATION AFTER WIND DISTURBANCE, SALVAGE LOGGING, AND PRESCRIBED FIRE IN A *PINUS PALUSTRIS* WOODLAND

#### **Abstract**

Salvage logging and prescribed fire are commonly applied in forests worldwide, yet little is known about the combined impacts of these management actions on early-successional ecosystems. We questioned how operational-scale prescribed fire would affect ground flora cover, species diversity, and life-history trait expression in *Pinus palustris* woodlands differentially impacted by an EF3 tornado and salvage logging. Fall Line Hills, Alabama, USA (32°55'30" N, 87°24'00" W). The composition and foliar cover of woody and herbaceous plants  $\leq 1$  m height were monitored before and after prescribed fire in 600 1-m<sup>2</sup> quadrats distributed throughout mature, wind-disturbed, and salvage-logged *P. palustris* woodlands. Plant taxa were categorized by growth habit and life form to aid interpretation of multivariate analyses used to illustrate differences in ground flora assemblages between disturbance categories. Prescribed fire reduced ground flora cover, but not diversity, which remained greatest in wind-disturbed sites that were not salvage logged. Though ground flora assemblages remained disparate between disturbance categories, prescribed fire imposed some consistent selective pressures on plants with common life-history strategies. Post-fire understory tree cover reductions coincided with increased shrub cover throughout the treatment area. Nonetheless, differences in graminoid cover were exaggerated after prescribed fire, and representation of the geophyte life form was relatively constant across space and time. Prescribed fire did not counteract salvage-mediated

reductions in ground flora diversity. Retention of downed deadwood maximized early-successional plant diversity in wind-disturbed sites. Trait-based ground flora analyses enabled a more detailed understanding of disturbance effects than aggregate metrics of foliar cover and diversity. In ecosystems with high floristic diversity, grouping plants by common life-history traits can provide a simple and effective means to monitor impacts of management actions on ecosystem recovery.

## **Introduction**

Plant diversity and community organization are shaped by natural and anthropogenic disturbance agents, each with unique impacts on plant succession and development (White and Jentsch, 2001). After a disturbance, the composition and spatial arrangement of residual ecosystem components are called disturbance legacies (Franklin *et al.*, 2000; Peters *et al.*, 2001). Disturbance legacies such as woody debris and the life-history strategies of residual species constitute the ecological memory of an ecosystem and influence recovery processes (Johnstone *et al.*, 2016; Webster *et al.*, 2018). Climate-driven changes in disturbance regimes globally have amplified interest in promoting forest ecosystem resilience (Turner 2010; Seidl *et al.*, 2016). Resilience describes the capacity of a perturbed ecosystem to maintain its intrinsic structures, feedbacks, and functions (Holling, 1973), and is measured by rates and trajectories of recovery (Angeler and Allen, 2016). Management actions taken before, during, or after unplanned perturbations can enhance or diminish ecosystem resilience.

Catastrophic wind disturbances including hurricanes and tornadoes impact many terrestrial ecosystems and are projected to become more frequent in some regions such as the southeastern United States (Webster *et al.*, 2005, Gensini and Brooks, 2018). These large,



infrequent disturbances have disproportionate impacts on ecosystem composition and structure, and require heightened attention in long-term management strategies (Dale *et al.*, 1998; Stanturf *et al.*, 2007). Post-disturbance salvage logging is a common management practice that removes dead and damaged trees. Salvage logging can therefore provide a partial return on otherwise lost standing timber value and potentially reduce the severity of subsequent disturbances like insect outbreaks and wildfires (Buma and Wessman, 2012; Müller *et al.*, 2019). Despite its potential socioeconomic benefits and widespread application, the ecological consequences of salvage logging are not fully understood (Leverkus *et al.*, 2018; Thorn *et al.*, 2018).

In some cases, post-disturbance salvage logging can qualify as a compound disturbance interaction in which one disturbance alters ecosystem resilience to (i.e. capacity to recover from) another disturbance (Paine *et al.*, 1998; Buma, 2015). Salvage logging can negatively impact the recovery of biological communities from birds (Georgiev *et al.*, 2020) to bryophytes (Hernández-Hernández *et al.*, 2017) and induce long-lasting ecosystem state shifts (Van Nieuwstadt *et al.*, 2001; Lindenmayer *et al.*, 2017). However, negative ecological consequences of salvage logging are not inevitable, especially with respect to woody plant recovery (Royo *et al.*, 2016; Taylor *et al.*, 2017). To achieve a more comprehensive understanding of post-disturbance salvage logging and compound disturbance interactions, greater research focus is needed on the recovery of non-woody plants (Leverkus *et al.*, 2018; Kleinman *et al.*, 2019). Indeed, the forest disturbance ecology literature is focused primarily on metrics of tree regeneration despite understory plant communities often hosting markedly more floristic diversity than canopy strata (Roberts, 2004; Gilliam, 2007).

After stand-regenerating wind events, some plants may be more or less suited to grow in microsites sheltered by woody debris or on patches of exposed, dry soil on unearthed root

mounds (Beatty, 1984; Logan *et al.*, 2020). Salvage logging operations that alter these structural legacies can homogenize early-successional ecosystems and the diverse biological communities they support (Swanson *et al.*, 2011; Lindenmayer *et al.*, 2019). Salvage logging is therefore often associated with reduced understory plant diversity and community dissimilarity (Purdon *et al.*, 2004; Rumbaitis del Rio, 2006; Brewer *et al.*, 2012). Nonetheless, Peterson and Leach (2008) reported no differences in understory plant diversity between unlogged and salvage-logged sites despite altered microsite conditions, and Orczewska *et al.* (2019) reported increased understory plant diversity in salvage-logged sites. In the latter example, however, increased plant diversity corresponded with the colonization and spread of disturbance-adapted plants that impeded recovery of late-successional species.

Trait-based assessments of understory plants can be used to determine floristic indicators of disturbance that are not always detected by metrics of foliar cover and diversity (Dale *et al.*, 2002). Measurements of species-specific life-history traits illustrate how plants survive, colonize, and compete in disturbance-impacted areas (Donato *et al.*, 2009; Pidgen and Mallik, 2013). For example, Knapp and Ritchie (2016) described how recently germinated shrubs were more susceptible to the mechanical impacts of salvage logging than forbs and graminoids. Non-native plant invasion is also facilitated by disturbances that liberate previously occupied growing space, and may be amplified by salvage logging through soil disturbance, propagule distribution, and mechanical damage of competing vegetation (Miller *et al.*, 2015).

The North American Coastal Plain is a global biodiversity hotspot with over 1800 endemic vascular plants (Noss *et al.*, 2015). The *Pinus palustris* (longleaf pine) ecosystem once occupied ca. 37 million ha of the North American Coastal Plain, but has been reduced to less than 5% of its former extent (Frost, 2006). Remnant patches of the *P. palustris* ecosystem are

managed with frequent, low-intensity prescribed fires that perpetuate *P. palustris*-dominated canopies and diverse understory plant communities (Outcalt, 2006). Specifically, prescribed fires induce shoot mortality of hardwoods that could otherwise outcompete *P. palustris* for canopy positions and enhance seedbed suitability and growing conditions for fire-adapted understory plants (Mitchell *et al.*, 2009). Cultural and institutional support of prescribed fire is strong in the North American Coastal Plain, which provides a model for prescribed fire management in other fire-adapted forests in the North American Interior Highlands and Intermountain West (Bigelow *et al.*, 2018). Fire science in the *P. palustris* ecosystem may also inform a growing international interest in prescribed fire management in regions such as southern Europe (Fernandes *et al.*, 2013; Fuentes *et al.*, 2018) and southwestern Australia (Burrows and McCaw, 2013).

The overarching objective of this study was to assess how operational-scale prescribed fire influenced floristic assemblages in *P. palustris* woodlands differentially impacted by an April 2011 EF3 tornado and a subsequent salvage logging operation. The presence and foliar cover of understory plants were monitored before and after prescribed fire in mature, wind-disturbed, and salvage-logged sites to assess changes in plant community composition, species diversity, and life-history trait expression. A baseline study attributed greater floristic diversity in wind-disturbed sites to microsite variability associated with fallen trees, and reduced plant diversity in salvage-logged sites to habitat homogenization associated with deadwood extraction (Kleinman *et al.*, 2017). In this study, we hypothesized that (1) floristic diversity would remain greatest after prescribed fire in wind-disturbed sites that were not logged. However, we also hypothesized that (2) prescribed fire would promote some plant community convergence by imposing consistent selective pressures on plants with common life-history strategies.

## Methods

### *Study Area*

This study was conducted in the Oakmulgee District of the Talladega National Forest in Bibb County, Alabama, USA (32°55'30" N, 87°24'00" W). The Oakmulgee District occurs in the *Quercus-Pinus* forest region of the United States (Braun, 1950) in the remnant central *P. palustris* hills of Alabama (Harper, 1943). In the Fall Line Hills physiographic transition zone, species from the Coastal Plain coexist with species from the adjacent Appalachian Highlands on steep, stream-carved slopes and ridges (Fenneman, 1938; Shankman and Hart, 2007). In the study area, *P. palustris*-dominated woodlands occur on upper slopes and south-facing lower slopes maintained with prescribed fire every 2–5 years (Beckett and Golden, 1982; Cox and Hart, 2015). Understory plant communities are characterized by *Pteridium latiusculum* {syn: *P. aquilinum*} and *Schizachyrium scoparium*, and a diversity of *Quercus* spp. and other hardwoods occur in sub-canopy strata (Teague *et al.*, 2014; Kleinman and Hart, 2018). Hillslopes and ridges contain deep, moderately-well drained soils developed from the Cretaceous-aged Gordo Formation (GSA, 2006; USDA NRCS, 2008; USDA NRCS, 2020a). The climate is humid mesothermal, with long, hot summers and year-round precipitation (Thornthwaite, 1948). Mean monthly temperature is highest in July (26.9 °C) and lowest in January (6.6 °C), with a mean annual temperature of 17.2 °C and mean annual precipitation of 1376.21 mm (PRISM, 2020).

On 27 April 2011, the Oakmulgee District was impacted by an EF3 tornado with estimated maximum wind speeds of 233 kph and a maximum path width of 1609 m (National Weather Service, 2011). The tornado was one of 362 tornadoes that impacted the eastern United States during the 25–28 April 2011 Super Outbreak. After the storm, plans to salvage potentially

hazardous damaged and deadwood from tornado-impacted areas were developed. From July–November 2011, wheeled feller bunchers and chainsaws were used to cut uprooted trees and logs, which were transported with wheeled skidders to a stationary knuckleboom loader. However, because the salvaged-wood market was oversupplied after the 2011 Super Outbreak, some wind-disturbed sites were not logged. This presented an opportunity to assess the individual and interacting effects of wind disturbance, salvage logging, and prescribed fire on *P. palustris* stand dynamics.

### ***Field Methods***

In March 2016, we opportunistically delineated three disturbance categories: mature, wind-disturbed, and salvage-logged (Kleinman *et al.*, 2017; Ford *et al.*, 2018). Mature sites were not impacted by the tornado, wind-disturbed sites were directly impacted by the tornado but not logged, and salvage-logged sites were directly impacted by the tornado and salvage logged. The density of live woody stems  $\geq 5$  cm diameter at 1.37 m above root collar was 325 stems ha<sup>-1</sup> in mature sites and 31 stems ha<sup>-1</sup> in both wind-disturbed and salvage-logged sites (Kleinman *et al.*, 2017; Ford *et al.*, 2018). Although the conditions of this “natural experiment” (i.e. tornado and salvage logging) precluded experimental replicability, care was taken to select sites with comparable pre-disturbance conditions. We therefore used a space-for-time substitution to gain insight on the impacts of catastrophic wind disturbance and salvage logging that would not otherwise be attainable with traditional methods of experimentation (Pickett, 1989; Hargrove and Pickering, 1992; Davies and Gray, 2015). In other words, selection of sites with comparable pre-disturbance conditions enabled observed differences between sites to be attributed to the disturbance events of interest, not pre-disturbance disparities. Prior to the tornado, all sites were

in stands that established in the early 1930s, were dominated by *P. palustris*, shared upper- and mid-slope positions with Maubila-series soils, and occurred within a 1 km<sup>2</sup> expanse of each other. Sites also occurred in the same Forest Service-delineated compartment, which ensured that sites experienced the same prescribed fire regime, including operational-scale prescribed fires in May 2010, April 2014, and April 2018. Thus, recurring fire was a background condition in all sites, but, based on the timing of our field surveys, data collected May–July 2016 were considered “before” fire data and data collected June 2018 were considered “after” fire data.

Within each of the three disturbance categories, 20 nested plots ( $n = 60$ ) were systematically established with 25-m spacing (Figure 4.1). Nested plots consisted of a 400-m<sup>2</sup> fixed-radius plot and ten nested 1-m<sup>2</sup> quadrats (10 m<sup>2</sup>). Quadrats were positioned with one at the center of each 400-m<sup>2</sup> plot and the other nine spaced evenly along the 0°, 120°, and 240° azimuths from plot center. Within each 1-m<sup>2</sup> quadrat, we recorded the composition and foliar cover of all ground flora, defined as live woody and herbaceous plants  $\leq 1$  m in height. Excluding Poaceae (grasses), ground flora were identified to the finest taxonomic resolution possible and assigned a cover class from 1–10. This cover class system was adapted from the North Carolina Vegetation Survey (NCVS), where 1 = trace, 2 = 0–1%, 3 = 1–2%, 4 = 2–5%, 5 = 5–10%, 6 = 10–25%, 7 = 25–50%, 8 = 50–75%, 9 = 75–95%, and 10 = 95–100% (Peet *et al.*, 1998).

Data collected at the 400-m<sup>2</sup> plot-scale were used to interpret associations between biophysical site conditions and variation in ground flora assemblages. These data included the density of saplings (i.e. live woody stems  $> 1$  m in height and  $< 5$  cm diameter at 1.37 m above root collar) and volume of coarse woody debris (i.e. downed deadwood  $\geq 10$  cm diameter). Coarse woody debris volume was calculated with conic-paraboloid and species-specific

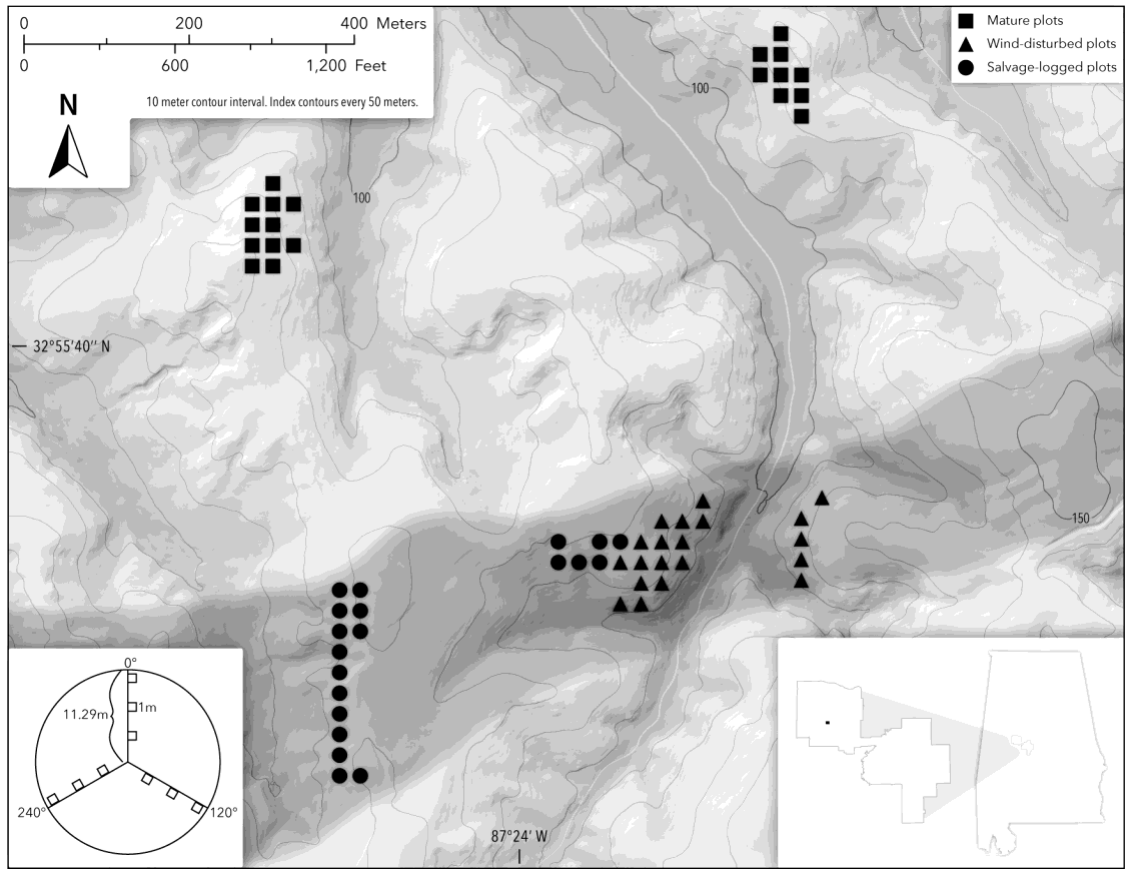


Figure 4.1. Plot locations in mature, wind-disturbed, and salvage-logged *Pinus palustris* woodlands in the Oakmulgee District, Talladega National Forest, Alabama, USA (shaded on bottom-right inset map). Bottom-left inset illustrates how ten 1-m<sup>2</sup> quadrats were nested within each 400-m<sup>2</sup> fixed-radius plot.

allometric equations derived from diameter measurements taken at both ends of logs (i.e. dead stems disconnected from roots) and at 1.37 m from root plate on uprooted stems (i.e. dead stems with uplifted root networks; Ford *et al.*, 2018; Kleinman *et al.*, 2020). Percent slope and aspect were also measured to examine potential effects on ground flora assemblages.

### ***Analytical Methods***

Taxonomic concepts were standardized to Weakley (2015). Each taxon encountered was evaluated in the context of four life-history categories to achieve a detailed understanding of disturbance effects on floristic dynamics (Table 4.1). Life-history categories included native status, duration, growth habit, and Raunkiaer (1934) life form (Table 4.2). Plant trait designations were guided by the USDA Fire Effects Information System and PLANTS databases (USDA Forest Service 2020; USDA NRCS 2020b), herbarium specimens (Keener *et al.*, 2020), published floras (Oosting, 1942; Gibson, 1961; Palmquist *et al.*, 2014), and, ultimately, field observations. Although many other trait-based classification schemes have been proposed (Pulsford *et al.*, 2016), the Raunkiaer (1934) system based on locations of perennating plant parts is particularly informative in fire-prone ecosystems where the height and depth of radiant heat have major implications for plant persistence (Rowe, 1983). Post-fire resprouting ability is also important in fire-prone ecosystems (Pausas and Keeley, 2014). Information on plant resprouting ability was therefore recorded and used to interpret results, but was not assessed statistically because of limited data availability, especially for non-woody plants.

To derive plot-level ground flora cover values, quadrat-level NCVS rankings were transformed to corresponding range midpoints and averaged per plot. Plot-level cover values were grouped by constituent life-history traits to calculate the foliar cover and richness of each



Table 4.1. Native status, duration, growth habit, and life form of the 155 ground flora taxa documented in differentially disturbed *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA.

Family	Latin name and authority	Native Status	Duration	Growth Habit	Raunkiaer Life Form
AGAVACEAE	<i>Yucca filamentosa</i> L.	Native	Perennial	Shrub	Chamaephyte
ALTINGIACEAE	<i>Liquidambar styraciflua</i> L.	Native	Perennial	Tree	Phanerophyte
ANACARDIACEAE	<i>Rhus copallinum</i> L.	Native	Perennial	Shrub	Phanerophyte
	<i>Rhus glabra</i> L.	Native	Perennial	Shrub	Phanerophyte
	<i>Toxicodendron pubescens</i> Mill.	Native	Perennial	Shrub	Phanerophyte
	<i>Toxicodendron radicans</i> (L.) Kuntze	Native	Perennial	Vine	Phanerophyte
ANNONACEAE	<i>Asimina parviflora</i> (Michx.) Dunal	Native	Perennial	Shrub	Phanerophyte
APIACEAE	<i>Angelica venenosa</i> (Greenway) Fernald	Native	Perennial	Forb	Hemicryptophyte
	<i>Eryngium yuccifolium</i> Michx.	Native	Perennial	Forb	Geophyte
APOCYNACEAE	<i>Asclepias tuberosa</i> L.	Native	Perennial	Forb	Hemicryptophyte
ARISTOLOCHIACEAE	<i>Endodeca serpentaria</i> (L.) Raf.	Native	Perennial	Forb	Geophyte
	<i>Hexastylis arifolia</i> (Michx.) Small	Native	Perennial	Forb	Hemicryptophyte
ASTERACEAE	<i>Ageratina aromatica</i> (L.) Spach	Native	Perennial	Forb	Hemicryptophyte
	<i>Ambrosia artemisiifolia</i> L.	Native	Annual	Forb	Therophyte
	<i>Chrysopsis mariana</i> (L.) Elliott	Native	Perennial	Forb	Hemicryptophyte
	<i>Cirsium</i> Mill.	Native	Biennial	Forb	Hemicryptophyte
	<i>Conyza canadensis</i> (L.) Cronquist	Native	Annual	Forb	Therophyte
	<i>Coreopsis major</i> Walter	Native	Perennial	Forb	Hemicryptophyte
	<i>Elephantopus tomentosus</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Erechtites hieraciifolius</i> (L.) Raf. ex DC.	Native	Annual	Forb	Therophyte
	<i>Eupatorium album</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Eupatorium capillifolium</i> (Lam.) Small	Native	Perennial	Forb	Hemicryptophyte
	<i>Eupatorium hyssopifolium</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Eupatorium</i> L.	Native	Perennial	Forb	Hemicryptophyte
<i>Eupatorium rotundifolium</i> L.	Native	Perennial	Forb	Hemicryptophyte	
<i>Gamochoaeta argyrinea</i> G.L.Nesom	Native	Annual	Forb	Therophyte	

<b>Family</b>	<b>Latin name and authority</b>	<b>Native Status</b>	<b>Duration</b>	<b>Growth Habit</b>	<b>Raunkiaer Life Form</b>
	<i>Helianthus</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Hieracium gronovii</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Lactuca canadensis</i> L.	Native	Biennial	Forb	Hemicryptophyte
	<i>Liatris</i> Schreb.	Native	Perennial	Forb	Geophyte
	<i>Nabalus</i> Cass.	Native	Perennial	Forb	Hemicryptophyte
	<i>Pityopsis graminifolia</i> (Michx.) Nutt.	Native	Perennial	Forb	Hemicryptophyte
	<i>Pseudognaphalium helleri</i> (Britton) Anderb.	Native	Annual	Forb	Therophyte
	<i>Pseudognaphalium obtusifolium</i> (L.) Hilliard & Burt	Native	Annual	Forb	Therophyte
	<i>Rudbeckia hirta</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Sericocarpus linifolius</i> (L.) Britton, Sterns, & Poggenb.	Native	Perennial	Forb	Hemicryptophyte
	<i>Sericocarpus tortifolius</i> (Michx.) Nees	Native	Perennial	Forb	Hemicryptophyte
	<i>Solidago</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Solidago odora</i> Aiton	Native	Perennial	Forb	Hemicryptophyte
	<i>Symphyotrichum cordifolium</i> (L.) G.L.Nesom	Native	Perennial	Forb	Hemicryptophyte
	<i>Symphyotrichum</i> Nees	Native	Perennial	Forb	Hemicryptophyte
	<i>Symphyotrichum patens</i> (Aiton) G.L Nesom	Native	Perennial	Forb	Hemicryptophyte
	<i>Trilisa odoratissima</i> (J.F.Gmel.) Cass.	Native	Perennial	Forb	Hemicryptophyte
	<i>Vernonia angustifolia</i> Michx.	Native	Perennial	Forb	Hemicryptophyte
BLECHNACEAE	<i>Lorinseria areolata</i> (L.) C.Presl	Native	Perennial	Forb	Geophyte
CAMPANULACEAE	<i>Lobelia puberula</i> Michx.	Native	Perennial	Forb	Hemicryptophyte
CONVOLVULACEAE	<i>Calystegia catesbeiana</i> Pursh	Native	Perennial	Vine	Hemicryptophyte
	<i>Ipomoea pandurata</i> (L.) G.Mey.	Native	Perennial	Vine	Geophyte
	<i>Stylisma humistrata</i> (Walter) Chapm.	Native	Perennial	Vine	Geophyte
CORNACEAE	<i>Cornus florida</i> L.	Native	Perennial	Tree	Phanerophyte
CUPRESSACEAE	<i>Juniperus virginiana</i> L.	Native	Perennial	Tree	Phanerophyte
CYPERACEAE	<i>Rhynchospora globularis</i> (Chapm.) Small	Native	Perennial	Graminoid	Hemicryptophyte
	<i>Scleria triglomerata</i> Michx.	Native	Perennial	Graminoid	Geophyte

<b>Family</b>	<b>Latin name and authority</b>	<b>Native Status</b>	<b>Duration</b>	<b>Growth Habit</b>	<b>Raunkiaer Life Form</b>
DENNSTAEDTIACEAE	<i>Pteridium latiusculum</i> (Desv.) Hieron. ex R.E.Fr.	Native	Perennial	Forb	Geophyte
DIOSCOREACEAE	<i>Dioscorea villosa</i> L.	Native	Perennial	Vine	Geophyte
EBENACEAE	<i>Diospyros virginiana</i> L.	Native	Perennial	Tree	Phanerophyte
ERICACEAE	<i>Gaylussacia dumosa</i> (Andrews) Torr. & A.Gray	Native	Perennial	Shrub	Chamaephyte
	<i>Oxydendrum arboreum</i> (L.) DC.	Native	Perennial	Tree	Phanerophyte
	<i>Rhododendron canescens</i> (Michx.) Sweet	Native	Perennial	Shrub	Phanerophyte
	<i>Vaccinium arboreum</i> Marshall	Native	Perennial	Tree	Phanerophyte
	<i>Vaccinium elliotii</i> Chapm.	Native	Perennial	Shrub	Phanerophyte
	<i>Vaccinium pallidum</i> Aiton	Native	Perennial	Shrub	Chamaephyte
	<i>Vaccinium stamineum</i> L.	Native	Perennial	Shrub	Phanerophyte
	EUPHORBIACEAE	<i>Acalypha</i> L.	Native	Annual	Forb
<i>Cnidoscolus stimulosus</i> (Michx.) Engelm. & A.Gray		Native	Perennial	Forb	Hemicryptophyte
<i>Euphorbia pubentissima</i> Michx.		Native	Perennial	Forb	Hemicryptophyte
<i>Tragia smallii</i> Shinnery		Native	Perennial	Forb	Hemicryptophyte
<i>Tragia urens</i> L.		Native	Perennial	Forb	Hemicryptophyte
FABACEAE	<i>Centrosema virginianum</i> (L.) Benth.	Native	Perennial	Vine	Hemicryptophyte
	<i>Chamaecrista fasciculata</i> (Michx.) Greene	Native	Annual	Forb	Therophyte
	<i>Clitoria mariana</i> L.	Native	Perennial	Vine	Hemicryptophyte
	<i>Crotalaria sagittalis</i> L.	Native	Annual	Forb	Therophyte
	<i>Desmodium</i> Desv.	Native	Perennial	Forb	Hemicryptophyte
	<i>Lespedeza hirta</i> (L.) Hornem.	Native	Perennial	Forb	Hemicryptophyte
	<i>Lespedeza procumbens</i> Michx.	Native	Perennial	Forb	Hemicryptophyte
	<i>Lespedeza repens</i> (L.) W.Barton	Native	Perennial	Forb	Hemicryptophyte
	<i>Lespedeza violacea</i> (L.) Pers.	Native	Perennial	Forb	Hemicryptophyte
	<i>Mimosa microphylla</i> Dryand.	Native	Perennial	Vine	Hemicryptophyte
	<i>Stylosanthes biflora</i> (L.) Britton, Sterns, & Poggenb.	Native	Perennial	Forb	Hemicryptophyte
	<i>Tephrosia virginiana</i> (L.) Pers.	Native	Perennial	Forb	Hemicryptophyte

<b>Family</b>	<b>Latin name and authority</b>	<b>Native Status</b>	<b>Duration</b>	<b>Growth Habit</b>	<b>Raunkiaer Life Form</b>
FAGACEAE	<i>Castanea dentata</i> (Marshall) Borkh.	Native	Perennial	Tree	Phanerophyte
	<i>Castanea pumila</i> (L.) Mill.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus alba</i> L.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus coccinea</i> Münchh.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus falcata</i> Michx.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus hemisphaerica</i> Bartram ex Willd.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus incana</i> Bartram	Native	Perennial	Tree	Phanerophyte
	<i>Quercus laevis</i> Walter	Native	Perennial	Tree	Phanerophyte
	<i>Quercus margaretta</i> W.W. Ashe ex Small	Native	Perennial	Tree	Phanerophyte
	<i>Quercus marilandica</i> Münchh. var. <i>marilandica</i>	Native	Perennial	Tree	Phanerophyte
	<i>Quercus montana</i> Willd.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus nigra</i> L.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus rubra</i> L.	Native	Perennial	Tree	Phanerophyte
	<i>Quercus stellata</i> Wangenh.	Native	Perennial	Tree	Phanerophyte
<i>Quercus velutina</i> Lam.	Native	Perennial	Tree	Phanerophyte	
GELSEMIACEAE	<i>Gelsemium sempervirens</i> (L.) St.-Hil.	Native	Perennial	Vine	Phanerophyte
HAMAMELIDACEAE	<i>Hamamelis virginiana</i> L.	Native	Perennial	Tree	Phanerophyte
HYDRANGEACEAE	<i>Hydrangea quercifolia</i> Bartram	Native	Perennial	Shrub	Phanerophyte
HYPERICACEAE	<i>Hypericum gentianoides</i> (L.) Britton, Sterns, & Poggenb.	Native	Annual	Forb	Therophyte
	<i>Hypericum hypericoides</i> (L.) Crantz	Native	Perennial	Shrub	Phanerophyte
IRIDACEAE	<i>Iris verna</i> L.	Native	Perennial	Forb	Geophyte
JUGLANDACEAE	<i>Carya glabra</i> (Mill.) Sweet	Native	Perennial	Tree	Phanerophyte
	<i>Carya tomentosa</i> (Lam.) Nutt.	Native	Perennial	Tree	Phanerophyte
LAMIACEAE	<i>Callicarpa americana</i> L.	Native	Perennial	Shrub	Phanerophyte
	<i>Scutellaria elliptica</i> Muhl. ex Spreng. var. <i>elliptica</i>	Native	Perennial	Forb	Hemicryptophyte
LAURACEAE	<i>Sassafras albidum</i> (Nutt.) Nees	Native	Perennial	Tree	Phanerophyte
LILIACEAE	<i>Lilium michauxii</i> Poir.	Native	Perennial	Forb	Geophyte

<b>Family</b>	<b>Latin name and authority</b>	<b>Native Status</b>	<b>Duration</b>	<b>Growth Habit</b>	<b>Raunkiaer Life Form</b>
LINACEAE	<i>Linum virginianum</i> L.	Native	Perennial	Forb	Hemicryptophyte
MAGNOLIACEAE	<i>Liriodendron tulipifera</i> L.	Native	Perennial	Tree	Phanerophyte
	<i>Magnolia macrophylla</i> Michx.	Native	Perennial	Tree	Phanerophyte
MELASTOMATACEAE	<i>Rhexia mariana</i> L. var. <i>mariana</i>	Native	Perennial	Forb	Geophyte
NYSSACEAE	<i>Nyssa sylvatica</i> Marshall	Native	Perennial	Tree	Phanerophyte
OROBANCHACEAE	<i>Agalinis purpurea</i> (L.) Pennell	Native	Annual	Forb	Therophyte
	<i>Aureolaria flava</i> (L.) Farw.	Native	Perennial	Forb	Hemicryptophyte
	<i>Aureolaria pectinata</i> (Nutt.) Pennell	Native	Annual	Forb	Therophyte
OSMUNDACEAE	<i>Osmunda spectabilis</i> Willd.	Native	Perennial	Forb	Geophyte
	<i>Osmundastrum cinnamomeum</i> (L.) C.Presl	Native	Perennial	Forb	Hemicryptophyte
OXALIDACEAE	<i>Oxalis</i> L.	Native	Perennial	Forb	Hemicryptophyte
PASSIFLORACEAE	<i>Passiflora lutea</i> L.	Native	Perennial	Vine	Hemicryptophyte
PHYTOLACCACEAE	<i>Phytolacca americana</i> L.	Native	Perennial	Forb	Geophyte
PINACEAE	<i>Pinus</i> L.	Native	Perennial	Tree	Phanerophyte
	<i>Pinus palustris</i> Mill.	Native	Perennial	Tree	Phanerophyte
PLANTAGINACEAE	<i>Plantago aristata</i> Michx.	Native	Annual	Forb	Therophyte
	<i>Veronica arvensis</i> L.	Not Native	Annual	Forb	Therophyte
POACEAE	–	Native	Perennial	Graminoid	Hemicryptophyte
POLYGALACEAE	<i>Persicaria</i> Mill.	Native	Perennial	Graminoid	Hemicryptophyte
	<i>Polygala nana</i> (Michx.) DC.	Native	Annual	Forb	Therophyte
RHAMNACEAE	<i>Berchemia scandens</i> (Hill) K.Koch	Native	Perennial	Vine	Phanerophyte
ROSACEAE	<i>Amelanchier arborea</i> (F.Michx.) Fernald	Native	Perennial	Tree	Phanerophyte
	<i>Potentilla simplex</i> Michx.	Native	Perennial	Forb	Hemicryptophyte
	<i>Prunus alabamensis</i> C.Mohr	Native	Perennial	Tree	Phanerophyte
	<i>Prunus serotina</i> Ehrh. var. <i>serotina</i>	Native	Perennial	Tree	Phanerophyte
	<i>Prunus umbellata</i> Elliott	Native	Perennial	Tree	Phanerophyte
	<i>Rubus</i> L.	Native	Perennial	Shrub	Hemicryptophyte

<b>Family</b>	<b>Latin name and authority</b>	<b>Native Status</b>	<b>Duration</b>	<b>Growth Habit</b>	<b>Raunkiaer Life Form</b>
RUBIACEAE	<i>Diodella teres</i> (Walter) Small	Native	Annual	Forb	Therophyte
	<i>Galium pilosum</i> Aiton	Native	Perennial	Forb	Hemicryptophyte
	<i>Houstonia caerulea</i> L.	Native	Perennial	Forb	Hemicryptophyte
	<i>Mitchella repens</i> L.	Native	Perennial	Forb	Hemicryptophyte
SANTALACEAE	<i>Nestronia umbellula</i> Raf.	Native	Perennial	Shrub	Phanerophyte
SAPINDACEAE	<i>Acer floridanum</i> (Chapm.) Pax	Native	Perennial	Tree	Phanerophyte
	<i>Acer rubrum</i> L.	Native	Perennial	Tree	Phanerophyte
	<i>Aesculus pavia</i> L. var. <i>pavia</i>	Native	Perennial	Tree	Phanerophyte
SMILACACEAE	<i>Smilax bona-nox</i> L.	Native	Perennial	Vine	Phanerophyte
	<i>Smilax glauca</i> Walter	Native	Perennial	Vine	Phanerophyte
	<i>Smilax pumila</i> Walter	Native	Perennial	Vine	Chamaephyte
	<i>Smilax rotundifolia</i> L.	Native	Perennial	Vine	Phanerophyte
	<i>Smilax smallii</i> Morong	Native	Perennial	Vine	Phanerophyte
SOLANACEAE	<i>Physalis</i> L.	Native	Perennial	Forb	Geophyte
STYRACACEAE	<i>Styrax grandifolius</i> Aiton	Native	Perennial	Shrub	Phanerophyte
SYMPLOCACEAE	<i>Symplocos tinctoria</i> (L.) L'Hér.	Native	Perennial	Tree	Phanerophyte
TETRACHONDRACEAE	<i>Polypremum procumbens</i> L.	Native	Annual	Forb	Therophyte
VIOLACEAE	<i>Viola</i> L.	Native	Perennial	Forb	Hemicryptophyte
VITACEAE	<i>Muscadinia rotundifolia</i> (Michx.) Small	Native	Perennial	Vine	Phanerophyte
	<i>Parthenocissus quinquefolia</i> (L.) Planch.	Native	Perennial	Vine	Phanerophyte
XYRIDACEAE	<i>Xyris</i> L.	Native	Perennial	Forb	Hemicryptophyte

Table 4.2. Descriptions of the life-history traits used to define the 155 ground flora taxa documented in differentially disturbed *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA. Trait definitions follow the USDA PLANTS database (USDA NRCS 2020b) and Raunkiaer (1934).

<b>Trait</b>	<b>State</b>	<b>Description</b>
Native Status	Natives	Native to Alabama, USA
	Non-natives	Not native to Alabama, USA
Duration	Annuals	Complete life cycle within one growing season
	Biennials	Complete life cycle in two growing seasons
	Perennials	Live more than two growing seasons
Growth Habit	Forbs	Herbaceous plants (lack persistent aboveground woody tissue)
	Graminoids	Herbaceous plants with grass-like morphology
	Vines	Woody or herbaceous plants with climbing or trailing morphology
	Shrubs	Woody perennials < 5 meters height
	Trees	Woody perennials > 5 meters height
Life Form	Geophytes	Perennating organs belowground (bulbs, rhizomes, and tubers)
	Therophytes	Perennating tissue stored in seed (annuals)
	Hemicryptophytes	Perennating buds at ground level
	Chamaephytes	Perennating buds aboveground but < 0.5 m height
	Phanerophytes	Perennating buds > 0.5 m height

growth habit and life form and summed to derive total foliar cover. Plot-level cover values were reconverted to corresponding NCVS values to calculate Shannon diversity at the 10-m<sup>2</sup> scale. Plot-level metrics, which included total foliar cover, richness, and Shannon diversity and the foliar cover and richness of each growth habit and life form, were transformed as needed to achieve homoscedasticity and compared between background disturbance categories (mature, wind-disturbed, and salvage-logged) and across time (before and after prescribed fire) with 3 × 2 mixed ANOVAs. One-way ANOVAs and Tukey HSD tests were used to assess main effects when disturbance categories and time did not exhibit significant interactions (levels of  $p < 0.05$  considered significant).

To visualize differences in ground flora assemblages between disturbance categories, we conducted nonmetric multidimensional scaling (NMS) with PC-ORD version 7 (McCune and Mefford, 2016). Multivariate analyses were conducted separately on before- and after-fire datasets, which included the composition and NCVS cover class of all ground flora documented per plot. To moderate the influence of rare and exceptionally large plants on apparent differences in ground flora assemblages, datasets were modified to exclude taxa with single-plot occurrences and relativized by maximum by dividing plot-level cover values by the maximum values recorded per taxon (Peck, 2016). NMS scree plots were used to select the optimal number of axes in NMS solutions, which were run 250 times with real data, applied Sørensen distance, and were cross-checked for conformity with other solutions. One-way PerMANOVAs with Sørensen distance were used to validate observed differences in ground flora assemblages. To assess relationships between biophysical site conditions and ground flora assemblages, biplot overlays were used to illustrate correlations ( $r^2$  cutoff of 0.25) between ordination axes and five environmental variables: disturbance category, transformed slope aspect (Beers *et al.*, 1996),



percent slope, sapling density, and coarse woody debris volume. To determine if floristic assemblages became more or less variable over time, values of average dispersion (i.e. scatter) between plots per disturbance category were calculated with NMS dissimilarity matrices and assessed with a  $3 \times 2$  mixed ANOVA.

Indicator species analysis was used to identify plant taxa most representative of distinct floristic assemblages based on the relative frequency and abundance of individual taxa per disturbance category (Dufrêne and Legendre, 1997). Indicator species were compared based on the life-history traits they represented. Life-history traits represented by all ground flora were then assessed with fourth-corner analysis to determine associations between each plant trait and disturbance category (Dray and Legendre, 2008). Fourth-corner analysis relates an (R) matrix of environmental characteristics (i.e. plots and associated disturbance categories) to a species trait matrix (Q) by way of a species abundance matrix (L) with five potential models. The first model was used to permute the presence or absence of each taxon independently and apply a randomization procedure to determine the significance of each plant trait and disturbance category association (Dray and Dufour, 2007; Dray and Legendre, 2008).

## **Results**

We documented 155 plant taxa in the 600 1-m<sup>2</sup> quadrats distributed throughout mature, wind-disturbed, and salvage-logged sites. Only one quadrat, nested in a salvage-logged plot before prescribed fire, contained a non-native plant, *Veronica arvensis*. However, *Lygodium japonicum*, an aggressive non-native climbing fern, was observed in three wind-disturbed plots after prescribed fire, although not within the limits of any nested quadrats. Most plants documented were perennials (136 taxa), followed by annuals (17 taxa) and biennials (2 taxa).

Over half of plants documented were forbs (79 taxa), and the next-most common growth habits were trees (38 taxa), vines (18 taxa), shrubs (14 taxa), and graminoids (4 taxa). Metrics of graminoid richness must be interpreted with caution, however, because Poaceae were not identified beyond family. The most well-represented life forms were hemicryptophytes (60 taxa) and phanerophytes (59 taxa), followed by therophytes (17 taxa), geophytes (15 taxa), and chamaephytes (4 taxa).

Prescribed fire reduced the foliar cover ( $p < 0.001$ ), but not species richness or Shannon diversity, of ground flora assemblages throughout the treatment area (Table 4.3). Despite overall foliar cover reductions, wind-disturbed and salvage-logged sites maintained greater foliar cover than mature sites before and after prescribed fire ( $p < 0.001$ ). Though foliar cover was comparable on wind-disturbed and salvage-logged sites, ground flora richness and Shannon diversity remained greatest in wind-disturbed sites before ( $p = 0.033$  and  $p = 0.019$ , respectively) and after ( $p = 0.002$  and  $p = 0.002$ , respectively) prescribed fire.

Three-dimensional NMS solutions explained 70% and 69% (non-metric  $R^2$  values) of variation in ground flora assemblages before and after prescribed fire, respectively (Figure 4.2). One-way PerMANOVAs verified observed differences in the composition and foliar cover of ground flora between disturbance categories each year ( $p < 0.001$ ). In the before-fire NMS solution, axis 1 was positively associated with coarse woody debris volume ( $r^2 = 0.25$ ) and sapling density ( $r^2 = 0.65$ ), which corresponded to the location of wind-disturbed plots in ordination space. In the after-fire NMS solution, coarse woody debris volume was positively associated with axis 3 ( $r^2 = 0.35$ ), which also corresponded to the location of wind-disturbed plots in ordination space. Sapling density, however, was positively associated with axis 2 after prescribed fire ( $r^2 = 0.29$ ), which did not correspond to any one particular disturbance category.

Table 4.3. Mean  $\pm$  standard error (SE) foliar cover (%), richness (taxa per 10 m<sup>2</sup>), and Shannon diversity of ground flora in mature, wind-disturbed, and salvage-logged *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA. Different capital letters indicate significant differences between years ( $p < 0.05$ ) and lower-case letters indicate significant differences between pre-fire conditions ( $p < 0.05$ ) within years based on Tukey's pairwise comparisons.

Metric	Time		Mature		Wind		Salvage	
Foliar Cover (%)	2016	A	40.0 $\pm$ 4.5	a	73.7 $\pm$ 3.8	b	70.3 $\pm$ 3.7	b
	2018	B	24.8 $\pm$ 3.1	a	46.2 $\pm$ 2.8	b	45.8 $\pm$ 2.5	b
Richness	2016	A	25.1 $\pm$ 1.3	a	33.7 $\pm$ 1.3	b	29.1 $\pm$ 1.2	a
	2018	A	24.5 $\pm$ 1.7	a	33.9 $\pm$ 1.6	b	26.3 $\pm$ 1.2	a
Shannon Diversity	2016	A	3.0 $\pm$ 0.1	a	3.3 $\pm$ 0.0	b	3.1 $\pm$ 0.0	a
	2018	A	3.0 $\pm$ 0.1	a	3.3 $\pm$ 0.0	b	3.0 $\pm$ 0.1	a

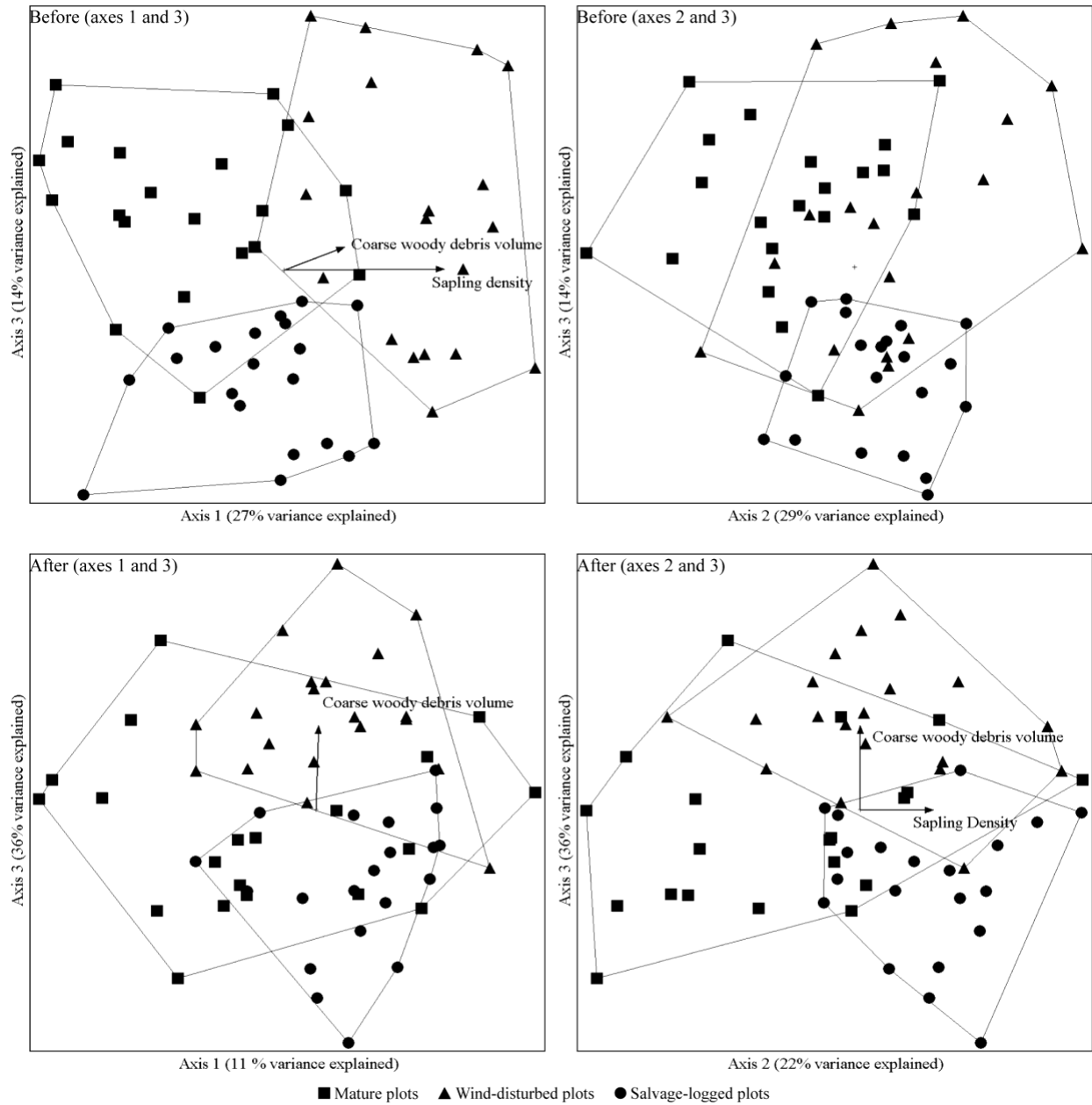


Figure 4.2. Three-dimensional NMS solutions before (top two panels) and after (bottom two panels) prescribed fire based on the composition and foliar cover of ground flora documented in mature, wind-disturbed, and salvage-logged plots. Convex hulls (loops) include plots in the same disturbance category and biplot overlays (arrows) indicate associations between environmental variables and ordination axes.

The dispersion of plots in ordination space was impacted by the interaction of background disturbance category and time relative to prescribed fire ( $p < 0.001$ ; Figure 4.3). Before prescribed fire, wind-disturbed sites exhibited the greatest variability in ground flora assemblages, followed by mature sites and salvage-logged sites. After prescribed fire, mean dispersion remained lowest in salvage-logged sites, but mature sites exhibited the greatest variability in ground flora assemblages.

Indicator species analysis identified 49 taxa most representative of the ground flora assemblages observed in each disturbance category (Table 4.4). Before prescribed fire, two indicators were associated with mature sites, 20 were associated with wind-disturbed sites, and 11 were associated with salvage-logged sites. After prescribed fire, one indicator was associated with mature sites, 21 were associated with wind-disturbed sites, and 12 were associated with salvage-logged sites. Among the 49 indicators, the most well-represented growth habits were forbs (19 taxa) and trees (17 taxa), and the most well-represented life forms were phanerophytes (25 taxa) and hemicryptophytes (15 taxa).

Based on the growth habits and life forms represented by all ground flora, fourth-corner analysis identified a variety of relationships between disturbance categories and life-history traits (Table 4.5). Mature sites were negatively associated with graminoids and shrubs, and positively associated with vines before and after prescribed fire. These results generally corresponded with individual assessments of how the foliar cover and richness of ground flora representing each life-history trait were impacted by pre-fire disturbance history, time relative to prescribed fire, and their interaction (Table 4.6, Figure 4.4). Mature sites exhibited the lowest graminoid cover before and after prescribed fire ( $p < 0.001$ ). Although shrub cover increased after prescribed fire throughout the treatment area ( $p < 0.001$ ), shrub cover remained lowest on mature sites. Vine

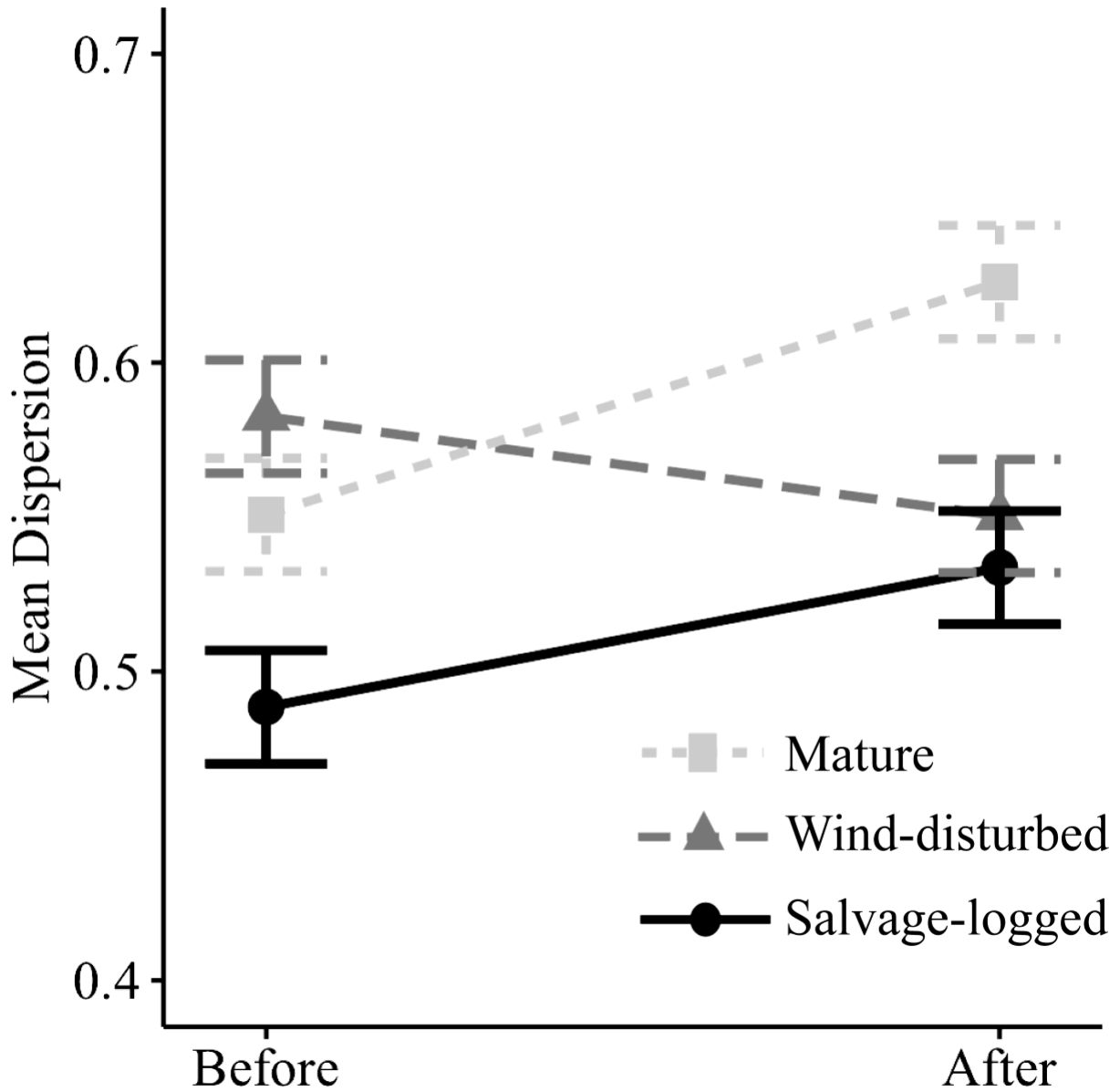


Figure 4.3. Disturbance category and time had a significant interaction ( $p < 0.001$ ) on the average dissimilarity (i.e. dispersion) of ground flora assemblages documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire.

Table 4.4. Indicator values (average relative frequency and abundance) with corresponding *p*-values (\* = < 0.05, \*\* = < 0.01, \*\*\* = < 0.001) of plant taxa most representative of mature, wind-disturbed, and salvage-logged sites before (2016) and after (2018) prescribed fire in *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA.

Indicator species	Before	After	Growth Habit	Raunkiaer Life Form
Mature				
<i>Acer rubrum</i>	35.4*		Tree	Phanerophyte
<i>Cornus florida</i>	30.7*		Tree	Phanerophyte
<i>Solidago odora</i>		40.1*	Forb	Hemicryptophyte
Wind-disturbed				
<i>Scleria triglomerata</i>		32.5*	Graminoid	Geophyte
<i>Conyza canadensis</i>	58.2***		Forb	Therophyte
<i>Erechtites hieracifolius</i>		39.2**	Forb	Therophyte
<i>Eupatorium capillifolium</i>	25**		Forb	Hemicryptophyte
<i>Eupatorium rotundifolium</i>		32.4**	Forb	Hemicryptophyte
<i>Lactuca canadensis</i>	67.3***	56.2***	Forb	Hemicryptophyte
<i>Lespedeza violacea</i>		22.5*	Forb	Hemicryptophyte
<i>Osmundastrum cinnamomeum</i>	20*	20*	Forb	Hemicryptophyte
<i>Phytolacca americana</i>	20*		Forb	Geophyte
<i>Pityopsis graminifolia</i>		45.7***	Forb	Hemicryptophyte
<i>Scutellaria elliptica</i>	20*		Forb	Hemicryptophyte
<i>Solidago</i> spp.		33.3**	Forb	Hemicryptophyte
<i>Symphotrichum</i>	41.6**		Forb	Hemicryptophyte
<i>Parthenocissus quinquefolia</i>	20*	25**	Vine	Phanerophyte
<i>Smilax smallii</i>	20*		Vine	Phanerophyte
<i>Rhus copallinum</i>	45.1**	43.6**	Shrub	Phanerophyte
<i>Rhus glabra</i>		30**	Shrub	Phanerophyte
<i>Rubus</i> spp.		31*	Shrub	Hemicryptophyte
<i>Styrax grandifolius</i>	39.6***	50.9***	Shrub	Phanerophyte
<i>Vaccinium stamineum</i>	51.1***		Shrub	Phanerophyte
<i>Carya glabra</i>	36.8**		Tree	Phanerophyte
<i>Carya tomentosa</i>		35*	Tree	Phanerophyte
<i>Liquidambar styraciflua</i>	30.5*	37.2**	Tree	Phanerophyte
<i>Liriodendron tulipifera</i>	20*		Tree	Phanerophyte
<i>Nyssa sylvatica</i>	40*	33.1*	Tree	Phanerophyte
<i>Prunus umbellata</i>		22.5*	Tree	Phanerophyte
<i>Quercus alba</i>	53.1***	51.3***	Tree	Phanerophyte
<i>Quercus coccinea</i>	39.7**		Tree	Phanerophyte
<i>Quercus falcata</i>		41.4*	Tree	Phanerophyte
<i>Quercus velutina</i>	38.4**	46.4***	Tree	Phanerophyte

Indicator species	Before	After	Growth Habit	Raunkiaer Life Form
<i>Symplocos tinctoria</i>	30**	40***	Tree	Phanerophyte
Salvage-logged				
Poaceae	43.9**	46.8***	Graminoid	Hemicryptophyte
<i>Agalinis purpurea</i>	61***	45***	Forb	Therophyte
<i>Coreopsis major</i>	43.4**	44.7**	Forb	Hemicryptophyte
<i>Diodella teres</i>	25.7*	35**	Forb	Therophyte
<i>Hypericum gentianoides</i>	24.5*		Forb	Therophyte
<i>Tephrosia virginiana</i>	55.3***	52.1***	Forb	Hemicryptophyte
<i>Tragia smallii</i>		40.3*	Forb	Hemicryptophyte
<i>Gelsemium sempervirens</i>	46***	47.5***	Vine	Phanerophyte
<i>Smilax glauca</i>		40.7*	Vine	Phanerophyte
<i>Stylisma humistrata</i>	22.5*		Vine	Geophyte
<i>Gaylussacia dumosa</i>	34.4*	36*	Shrub	Chamaephyte
<i>Pinus</i> spp.		32.8*	Tree	Phanerophyte
<i>Quercus falcata</i>	41.8*		Tree	Phanerophyte
<i>Quercus laevis</i>		20.8*	Tree	Phanerophyte
<i>Quercus nigra</i>	46.6**	34*	Tree	Phanerophyte



Table 4.5. Positive (+) and negative (-) associations with corresponding *p*-values (\* = < 0.05, \*\* = < 0.01, \*\*\* = < 0.001) between life-history traits and background disturbance categories before (2016) and after (2018) prescribed fire in *Pinus palustris* woodlands in the Fall Line Hills of Alabama, USA.

Trait	State	Time	Mature	Wind	Salvage	
Growth						
Habit	Graminoid	Before	(-) <sup>***</sup>		(+) <sup>***</sup>	
		After	(-) <sup>***</sup>		(+) <sup>**</sup>	
	Forb	Before			(+) <sup>*</sup>	
		After				
	Vine	Before	(+) <sup>*</sup>	(-) <sup>***</sup>		
		After	(+) <sup>*</sup>	(-) <sup>***</sup>		
	Shrub	Before	(-) <sup>*</sup>	(+) <sup>**</sup>		
		After	(-) <sup>**</sup>	(+) <sup>*</sup>		
	Tree	Before			(-) <sup>**</sup>	
		After		(+) <sup>**</sup>	(-) <sup>**</sup>	
	Life Form	Geophyte	Before			
			After			
		Therophyte	Before	(-) <sup>***</sup>		(+) <sup>***</sup>
			After			
Hemicryptophyte		Before	(-) <sup>*</sup>		(+) <sup>**</sup>	
		After			(+) <sup>**</sup>	
Chamaephyte		Before				
		After		(-) <sup>**</sup>	(+) <sup>**</sup>	
Phanerophyte		Before	(+) <sup>**</sup>		(-) <sup>***</sup>	
		After			(-) <sup>**</sup>	

Table 4.6. Summary of mixed ANOVAs used to assess impacts of pre-fire conditions (mature, wind-disturbed, and salvage-logged), time relative to prescribed fire (before and after), and their interaction on the foliar cover and richness of ground flora in each growth habit and life form.

Metric	Trait	State	Pre-Fire Condition (C)			Time (T)			C × T		
			F-values	P-values	df	F-values	P-values	df	F-values	P-values	df
Foliar Cover	Growth Habit	Graminoid	26.09	< <b>0.001</b>	2	2.833	0.098	1	2.16	0.125	2
		Forb	4.742	<b>0.012</b>	2	0.104	0.748	1	1.598	0.211	2
		Vine	20.68	< <b>0.001</b>	2	99.472	< <b>0.001</b>	1	4.574	<b>0.014</b>	2
		Shrub	17.97	< <b>0.001</b>	2	11.302	<b>0.001</b>	1	0.345	0.71	2
		Tree	5.206	<b>0.008</b>	2	141.318	< <b>0.001</b>	1	1.078	0.347	2
	Life Form	Geophyte	1.419	0.25	2	0.012	0.913	1	0.703	0.499	2
		Therophyte	31.15	< <b>0.001</b>	2	0	0.995	1	9.753	< <b>0.001</b>	2
		Hemicryptophyte	27.21	< <b>0.001</b>	2	0.347	0.558	1	4.537	<b>0.015</b>	2
		Chamaephyte	3.299	<b>0.044</b>	2	2.384	0.128	1	2.216	0.118	2
		Phanerophyte	9.166	< <b>0.001</b>	2	96.61	< <b>0.001</b>	1	1.58	0.215	2
Richness	Growth Habit	Graminoid	3.38	<b>0.041</b>	2	8.34	<b>0.005</b>	1	1.382	0.259	2
		Forb	6.03	<b>0.004</b>	2	3.822	0.056	1	3.253	<b>0.046</b>	2
		Vine	2.586	0.084	2	3.247	0.077	1	0.551	0.58	2
		Shrub	8.211	< <b>0.001</b>	2	0.36	0.551	1	0.12	0.887	2
		Tree	7.514	<b>0.001</b>	2	39.08	< <b>0.001</b>	1	1.275	0.287	2
	Life Form	Geophyte	0.904	0.411	2	3.46	0.068	1	0.299	0.742	2
		Therophyte	27.98	< <b>0.001</b>	2	2.088	0.154	1	8.047	< <b>0.001</b>	2
		Hemicryptophyte	4.751	<b>0.012</b>	2	10.552	<b>0.002</b>	1	1.222	0.302	2
		Chamaephyte	3.491	<b>0.037</b>	2	0	1	1	1.153	0.323	2
		Phanerophyte	12.1	< <b>0.001</b>	2	26.484	< <b>0.001</b>	1	1.558	0.219	2

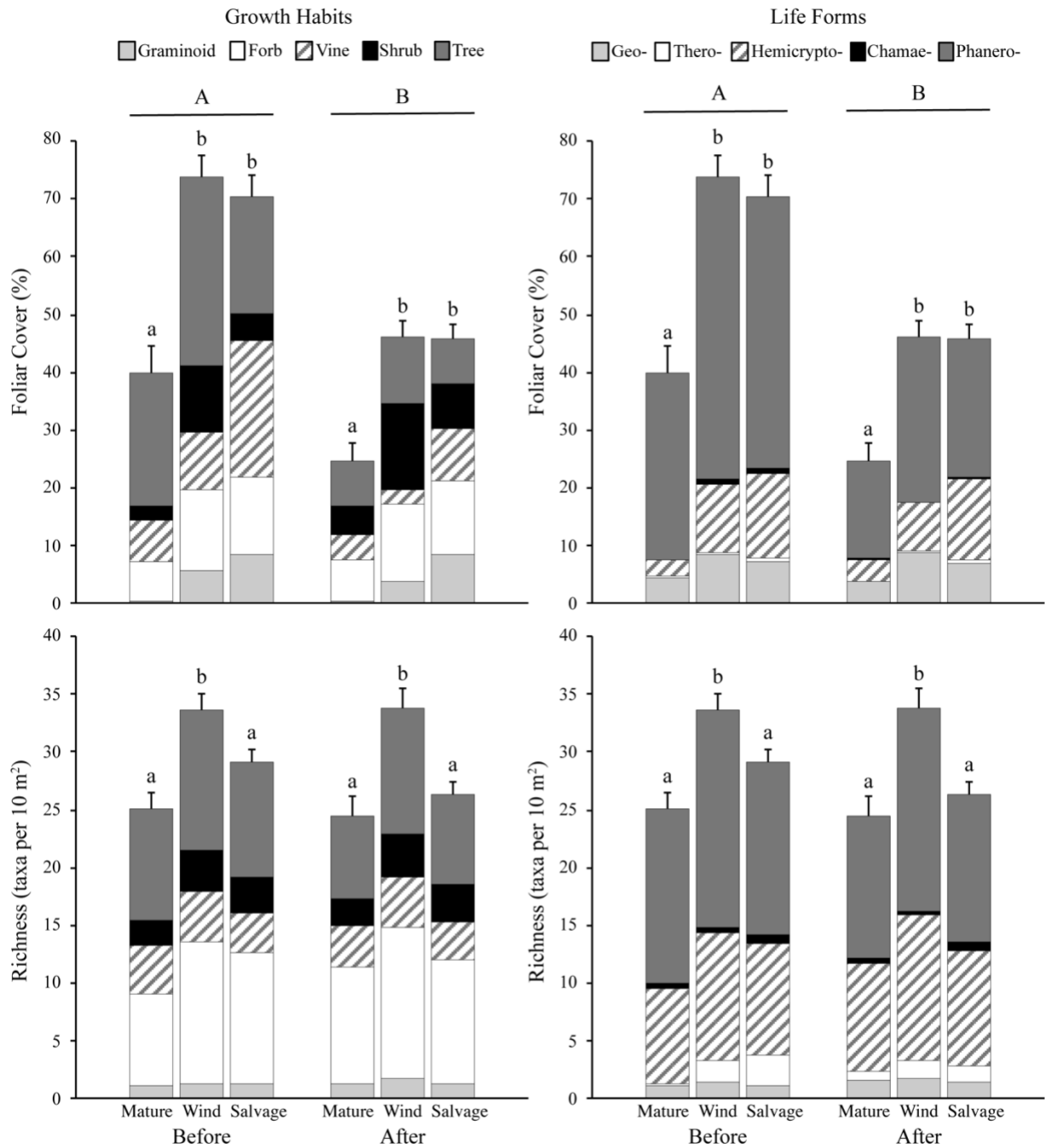


Figure 4.4. Foliar cover (%) and richness (taxa per 10 m<sup>2</sup>) of ground flora representing each growth habit and life form documented in mature, wind-disturbed, and salvage-logged plots before (2016) and after (2018) prescribed fire. Different capital letters denote significant differences between years ( $p < 0.05$ ), and lower-case letters denote significant differences between pre-fire conditions ( $p < 0.05$ ) within years based on Tukey's pairwise comparisons.

cover was impacted by the interaction of disturbance category and time ( $p < 0.001$ ), and showed greater post-fire reductions on wind-disturbed and salvage-logged sites compared to mature sites. In contrast to growth habits, significant fourth-corner associations between mature sites and life forms did not persist after prescribed fire. Prior to prescribed fire, mature sites were negatively associated with therophytes and hemicryptophytes. The interaction of disturbance category and time impacted therophyte richness ( $p < 0.001$ ) and hemicryptophyte cover ( $p = 0.015$ ), which both increased slightly after prescribed fire on mature sites, yet, were slightly reduced on wind-disturbed and salvage-logged sites. Although fourth-corner analysis also detected a positive pre-fire relationship between mature sites and phanerophytes, wind-disturbed sites hosted greater values of phanerophyte cover and richness before ( $p = 0.001$  and  $p = 0.003$ , respectively) and after ( $p = 0.006$  and  $p < 0.001$ , respectively) prescribed fire.

For wind-disturbed sites, fourth-corner analysis identified negative relationships with vines and positive relationships with shrubs before and after prescribed fire. Prior to prescribed fire, vine cover was substantially lower on wind-disturbed sites compared to salvage-logged sites, and after prescribed fire, wind-disturbed sites contained the lowest vine cover. Shrub cover was greatest on wind disturbed sites before ( $p = 0.001$ ) and after ( $p = 0.044$ ) prescribed fire, and compared to mature sites, shrub richness was also greater in wind-disturbed sites before ( $p = 0.004$ ) and after ( $p = 0.001$ ) prescribed fire. Although a positive fourth-corner association between mature sites and trees was only detected with post-fire data, tree richness was greatest in wind-disturbed sites before ( $p = 0.023$ ) and after ( $p = 0.009$ ) prescribed fire. Pre-fire tree cover was also greatest on wind-disturbed sites ( $p = 0.049$ ), but after treatment-area wide tree cover reductions ( $p < 0.001$ ), the foliar cover of trees did not significantly differ between disturbance categories. The only fourth-corner association detected between wind-disturbed sites and life

forms was a negative post-fire chamaephyte relationship. Though foliar cover and richness of chamaephytes averaged less than 1% and one taxon per 10 m<sup>2</sup>, respectively, on plots throughout the treatment area, post-fire chamaephyte richness was greater on salvage-logged sites compared to wind-disturbed sites ( $p = 0.028$ ).

Salvage-logged sites showed positive fourth-corner associations with graminoids and negative associations with trees before and after prescribed fire. The foliar cover of graminoids was consistently greatest on salvage-logged sites, although only significantly greater than wind-disturbed sites after prescribed fire ( $p = 0.037$ ). In contrast, salvage-logged sites contained significantly lower tree cover than wind-disturbed sites before prescribed fire ( $p = 0.015$ ), but not after. Tree richness, however, remained lower on salvage-logged sites compared to wind-disturbed sites before ( $p = 0.023$ ) and after ( $p = 0.009$ ) prescribed fire. Although fourth-corner analysis detected a positive post-fire relationship between salvage-logged sites and forbs, forb cover and richness did not significantly differ between wind-disturbed and salvage-logged sites. In terms of life forms, salvage-logged sites exhibited a positive fourth-corner relationship with hemicryptophytes and a negative relationship with phanerophytes before and after prescribed fire. Hemicryptophyte cover was consistently greatest on salvage-logged sites, and, compared to wind-disturbed sites, phanerophyte cover was lower on salvage-logged sites before and after prescribed fire. Salvage-logged sites also exhibited a positive pre-fire fourth-corner relationship with therophytes and a positive post-fire fourth-corner relationship with chamaephytes.

## **Discussion**

Prescribed fire reduced the foliar cover of ground flora assemblages throughout the treatment area. Floristic diversity, however, was relatively unchanged. Similar results were

reported by Fuentes *et al.* (2018), who documented significantly reduced cover, but not diversity, of understory plants after prescribed fire in a *P. halepensis* forest of Northeastern Spain. In support of our first hypothesis, wind-disturbed sites hosted the greatest ground flora richness and Shannon diversity before and after prescribed fire, which was attributed to a complexity of microsites and microclimatic conditions associated with coarse woody debris. Indeed, ground flora assemblages in wind-disturbed sites were correlated with coarse wood debris volume before and after prescribed fire. Ground flora assemblages on wind-disturbed sites were also correlated with sapling density before, but not after, prescribed fire. These results corresponded with a companion study that documented only slight post-fire coarse woody debris volume reductions, yet substantial prescribed fire-mediated sapling density reductions in the same study area (Kleinman *et al.*, 2020). Whereas prescribed fire offset differences in sapling densities between wind-disturbed and salvage-logged sites, ground flora assemblages remained disparate. In other words, prescribed fire did not remedy salvage-mediated differences in understory plant recovery.

Legacies of deadwood extraction persisted on salvage-logged sites. In addition to reduced ground flora diversity, salvage-logged sites exhibited the lowest mean dispersion of ground flora assemblages. Metrics of mean dispersion indicated how variable, not necessarily how diverse, ground flora assemblages were within disturbance categories. Specifically, mean dispersion values indicated how dissimilar ground flora assemblages were between plots in each disturbance category. The relatively low dispersion observed in salvage-logged sites indicated that deadwood extraction homogenized ground flora assemblages. Early stages of plant succession are most often limited by moisture and nutrient availability (Muller, 2014). Whereas downed deadwood contributed to a complex mosaic of sheltered, moist microsites and decomposition-derived soil organic matter in wind-disturbed sites, mechanical extraction of

deadwood resulted in more uniform growing conditions in salvage-logged sites. Moreover, direct impacts of salvage logging machinery, log skidding, and additional soil disturbance likely contributed to the loss of some ground flora that were observed in wind-disturbed sites but absent from salvage-logged sites (Brewer et al. 2012).

Interestingly, post-fire dispersion of ground flora assemblages was greatest in mature sites. This demonstrated that, after prescribed fire, mature sites hosted ground flora assemblages that were most dissimilar from one plot to the next. Working within 1 km of the study area, Goode *et al.* (2020) also documented greater ground flora variability in the interior forest compared to the tornado swath and forest edge. Variability between ground flora assemblages in mature sites was attributed primarily to gap-scale disturbances such as lightning strikes and single-tree blowdown events (Palik and Pederson, 1996). Though mature sites typically hosted a continuous *P. palustris*-dominated canopy and uninterrupted *Pinus* litter-composed fuel bed, it was not uncommon to encounter a canopy gap (Kleinman *et al.*, 2017). The density of snapped, uprooted, and standing dead stems (snags) > 5 cm diameter at 1.37 m height was 25 stems ha<sup>-1</sup> in mature sites (2016 data). We contend that canopy gaps supported early-successional ground flora within a matrix of mature woodlands, and thereby contributed to greater intra-stand variability than sites that experienced catastrophic canopy removal. Moreover, fire-induced fuel consumption on mature sites facilitated establishment and growth of therophytes and hemicryptophytes. Therophytes typically complete their short life cycles on recently exposed ground (Raunkiaer, 1934), and hemicryptophyte shoot penetration of the litter layer may be enhanced with litter mass reductions (Facelli and Pickett, 1991).

Although ground flora assemblages remained dissimilar between disturbance categories, prescribed fire imposed consistent plant trait selection throughout the treatment area, which

supported our second hypothesis. Prior to prescribed fire, wind-disturbed sites hosted the greatest foliar cover of ground flora classified as trees (i.e. woody plants with the potential to grow over 5 m height), which was likely a legacy of canopy tree removal and competitive release. Reduced understory tree cover on salvage-logged sites may have been a legacy of stem damage from salvage logging machinery. Despite these pre-fire differences, prescribed fire reduced understory tree cover throughout the treatment area and thereby negated differences in understory tree cover between disturbance categories. Nonetheless, post-fire tree richness remained greatest in wind-disturbed sites. Persistent differences in understory tree richness were attributed to the post-fire resprouting abilities of trees in the study area. Whereas woody plant biomass can take two or more years to recover to pre-fire conditions, the ability to resprout enables woody plant persistence in fire-adapted ecosystems (Peterson *et al.*, 2007). For the trees in this study for which physiological information was available, only *Symplocos tinctoria* was listed as not having the ability to resprout (USDA Forest Service, 2020; USDA NRCS, 2020b). However, we contend that *S. tinctoria*, which was an indicator of wind-disturbed sites before and after prescribed fire, can indeed produce new shoots from surviving rootstocks after aboveground mortality (Figure 4.5).

Prescribed fire-induced understory tree cover reductions coincided with increased shrub cover throughout the treatment area. We suspect that shrubs captured some of the growing space previously occupied by top-killed understory trees. Like trees, the large majority of shrubs in the study area can resprout, with two listed exceptions of *Rhododendron canescens* and *Styrax grandifolius* (USDA Forest Service, 2020; USDA NRCS, 2020b). Nonetheless, *S. grandifolius* was an indicator of wind-disturbed sites before and after prescribed fire, and can in fact regenerate from underground rhizomes after fire (Hill, 2007; Figure 4.5). Barefoot *et al.* (2019)





Figure 4.5. (A) Full-shot and (B) close-up photographs of live *Symplocos tinctoria* shoots growing from the same rootstock as fire-killed shoots. (C) Full-shot and (D) close-up photographs of live *Styrax grandifolius* shoots growing from the same rootstock as fire-killed shoots.

also reported *S. grandifolius* as an indicator of mechanically thinned mixed *Pinus*-hardwood stands subject to a three-year prescribed fire rotation. *Rhus copallinum* was the other indicator shrub of wind-disturbed sites before and after prescribed fire. *Rhus copallinum* can rapidly resprout in sites impacted by wind and fire disturbances (Cannon *et al.*, 2019), and composed the greatest post-fire densities of seedlings (live woody stems < 1 m height) and saplings in wind-disturbed sites (Kleinman *et al.*, 2020). On salvage-logged sites, the subshrub *Gaylussacia dumosa* was a significant indicator before and after prescribed fire. The underground rhizomes of *G. dumosa* are resistant to fire and are stimulated to resprout after aboveground foliar consumption (Coladonato, 1992). *Gaylussacia dumosa* was also the only indicator species representative of the chamaephyte growth habit, and its common occurrence corresponded with greater levels of post-fire chamaephyte richness on salvage-logged sites.

Like understory trees, prescribed fire reduced the foliar cover of phanerophytes throughout the treatment area. This reduction counteracted a pre-fire disparity between salvage-logged and mature sites in the foliar cover of phanerophytes. Whereas trees and vines were distinguished by growth habit, the phanerophyte life form included all trees and some vines. *Gelsemium sempervirens* was a particularly widespread woody vine, and was a significant indicator of salvage-logged sites before and after prescribed fire. Emery and Hart (2020) used laboratory burns to assess the flammability of fuels collected in the study area, and classified *G. sempervirens* vines and leaves in a moderate-high flammability group. We contend that the substantial vine cover reductions observed in salvage-logged sites largely represented *G. sempervirens* consumption.

Though prescribed fire counteracted some differences in woody plant cover, differences in graminoid cover were exaggerated. Graminoid cover was consistently lowest on mature sites

with intact canopies and consequently lower understory light availability. Although pre-fire graminoid cover was comparable on wind-disturbed and salvage-logged sites, post-fire graminoid cover was greatest on salvage-logged sites. These results corresponded with others who attributed increased cover of light-demanding graminoids to the reduction of shade (Peterson *et al.*, 2007; Policelli *et al.*, 2019). The removal of standing and leaning deadwood maximized understory light availability in salvage-logged sites (Kleinman *et al.*, 2017). Although the Poaceae (grass) family was a significant indicator of salvage-logged sites, the sedge *Scleria triglomerata* was a significant indicator of wind-disturbed sites. These results were attributed to the photosynthetic pathways of the constituent indicators. Peterson *et al.* (2007) described how C<sub>4</sub> grasses and sedges exhibited the greatest responses to increased light availability, whereas C<sub>3</sub> grasses and sedges were associated with partial shading. Though Poaceae were not identified beyond family in this study, the most common graminoids in the study area were C<sub>4</sub> bunchgrasses (e.g. *Schizachyrium scoparium*; Becket and Golden, 1982; Teague *et al.*, 2014). In contrast, *S. triglomerata*, which utilizes a C<sub>3</sub> photosynthetic pathway (Bruhl and Wilson, 2007), was perhaps better adapted to grow in the partial shade near downed woody debris in wind-disturbed sites (Percy and Ehleringer, 1984).

Among all growth habits and life forms assessed, geophytes were least impacted by disturbance category and time relative to prescribed fire. We suspect that the relatively consistent representation of geophytes across space and time reflected a long-term legacy of recurrent low-intensity fire in the study area. Although belowground perennating tissues are primarily recognized as a drought-survival adaptation (Raunkiaer, 1934), the geophytic life-history strategy also confers resilience in fire-adapted ecosystems where underground growth buds are protected from surface fires (Ruiters *et al.*, 1993; Dale *et al.*, 2002). Moreover,

compared to life forms with surface-level and aboveground growth buds, geophytes may have been better protected from the mechanical impacts of salvage logging in the understory.

## **Conclusions**

With changing disturbance regimes in forest ecosystems worldwide, it is increasingly important to consider how management actions impact ecosystem resilience (Turner, 2010; Seidl *et al.*, 2016). Though many response variables can be used to assess ecosystem recovery rates and trajectories, forest resilience is most often assessed by metrics of tree regeneration. Ground flora assemblages, however, can indicate disturbance effects with greater sensitivity than woody plant-based metrics, in part, because of the greater diversity of life-history traits they represent (Roberts, 2004; Gilliam, 2007). For example, here we report that, although prescribed fire offset differences in sapling densities between unlogged and logged wind-disturbed sites (Kleinman *et al.*, 2020), ground flora assemblages remained disparate. It is therefore critical to consider the “resilience of what” in assessments of post-disturbance management actions on ecosystem recovery (Carpenter *et al.*, 2001; Kleinman *et al.*, 2019).

Within the ground flora stratum, a variety of response variable-specific outcomes were observed. Salvage logging reduced ground flora diversity, but did not alter foliar cover. Prescribed fire reduced foliar cover, but did not alter ground flora diversity. Because salvage-logged sites continued to support homogenized ground flora assemblages with reduced floristic diversity, we recommend leaving some wind-disturbed zones unlogged to serve as ground flora refugia if ground flora resilience is a management objective. Indeed, a key silvicultural strategy to combat global change is to increase representation of a broad range of functional traits to enhance ecosystem adaptation potential.

Beyond aggregate metrics of foliar cover and diversity, this study demonstrated the efficacy of trait-based plant community analyses to achieve a detailed understanding of natural and anthropogenic disturbance effects on floristic dynamics. Prescribed fire reduced understory tree cover throughout the treatment area, which corresponded with increased shrub cover, and exaggerated the disproportionate cover of graminoids on salvage-logged sites. Prescribed fire also facilitated establishment and growth therophytes and hemicryptophytes in mature sites, and increased chamaephyte representation in salvage-logged sites. The geophyte life form, however, was apparently unaffected by catastrophic wind disturbance, salvage logging, and prescribed fire. In species-rich ecosystems like the *P. palustris* ecosystem, grouping ground flora by common growth habits and life forms can provide a simple and effective method to monitor post-disturbance ecosystem recovery (Dale *et al.*, 2002).

## References for Chapter 4

- Angeler, D.G., Allen, C.R. 2016. Quantifying resilience. *Journal of Applied Ecology* 53, 617–624.
- Barefoot, C.R., Willson, K.G., Hart, J.L., Schweitzer, C.J., Dey, D.C. 2019. Effects of thinning and prescribed fire frequency on ground flora in mixed *Pinus*-hardwood stands. *Forest Ecology and Management* 432, 729–740.
- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65, 1406–1419.
- Beckett, S., Golden, M.S. 1982. Forest vegetation and vascular flora of Reed Brake Research Natural Area, Alabama. *Castanea* 47, 368–392.
- Beers, T.W., Dress, P.E., Wensel, L.C. 1966. Aspect transformation in site productivity research. *Journal of Forestry* 64, 691–692.
- Bigelow, S.W., Stambaugh, M.C., O'Brien, J.J., Larson, A.J. and Battaglia, M.A. 2018. Longleaf pine restoration in context comparisons of frequent fire forests. In: Kirkman, L.K., Jack, S.B. (Eds), *Ecological restoration and management of longleaf pine forests*. Boca Raton, FL: CRC Press, Taylor & Francis Group, pp. 311–338.
- Braun, E.L. 1950. *Eastern Deciduous Forests of North America*. Caldwell, NJ: The Blackburn Press, pp. 596.
- Brewer, J.S., Bertz, C.A., Cannon, J.B., Chesser, J.D., Maynard, E.E. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? *Ecological Applications* 22, 442–458.
- Bruhl, J.J. and Wilson, K.L. 2007. Towards a comprehensive survey of C<sub>3</sub> and C<sub>4</sub> photosynthetic pathways in Cyperaceae. *Aliso* 23, 99–148.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6:70.
- Buma, B., Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecology and Management* 266, 25–33.
- Burrows, N., McCaw, L. 2013. Prescribed burning in southwestern Australian forests. *Frontiers in Ecology and the Environment* 11: e25–e34.
- Cannon, J.B., Henderson, S.K., Bailey, M.H., Peterson, C.J. 2019. Interactions between wind and fire disturbance in forests: competing amplifying and buffering effects. *Forest Ecology and Management* 436, 117–128.

- Carpenter, S., Walker, B., Anderies, J.M., Abel, N. 2001. From metaphor to measurement: Resilience of what to what? *Ecosystems* 4, 765–781.
- Coladonato, M. 1992. *Gaylussacia dumosa*. In: Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Retrieved June 16, 2020  
<<https://www.fs.fed.us/database/feis/plants/shrub/gaydum/all.html>>.
- Cox, L.E., Hart, J.L. 2015. Two centuries of forest compositional and structural changes in the Alabama Fall Line Hills. *American Midland Naturalist* 174, 218–237.
- Dale, V.H., Beyeler, S.C., Jackson, B. 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. *Ecological Indicators* 1, 155–170.
- Dale, V.H., Lugo, A.E., MacMahon, J.A., Pickett, S.T.A. 1998. Ecosystem management in the context of large, infrequent disturbances. *Ecosystems* 1, 546–557.
- Davies, G.M., Gray, A. 2015. Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution* 5, 5295–5304.
- Donato, D.C., Fontaine, J.B., Robinson, W.D., Kauffman, J.B., Law, B.E. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. *Journal of Ecology* 97, 142–154.
- Dray, S., Dufour, A.B. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software* 22, 1–20.
- Dray, S., Legendre, P. 2008. Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology* 89, 3400–3412.
- Dufrêne, M., Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67, 345–366.
- Emery, R.K., Hart, J.L. 2020. Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. *Fire* 3: 39.
- Facelli, J.M., Pickett, S.T.A. 1991. Plant litter: its dynamics and effects on plant community structure. *The Botanical Review* 57, 1–32.
- Fenneman, N.M. 1938. *Physiography of Eastern United States*. New York, NY: McGraw-Hill, pp. 714.

- Fernandes, P.M., Davies, G.M., Ascolia, D., Fernández, C., Moreira, F., Rigolot, E. et al. 2013. Prescribed burning in southern Europe: developing fire management in a dynamic landscape. *Frontiers in Ecology and the Environment* 11: e4–e14.
- Ford, S.A., Kleinman, J.S., Hart, J.L. 2018. Effects of wind disturbance and salvage harvesting on macrofungal communities in a *Pinus* woodland. *Forest Ecology and Management* 407, 31–46.
- Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D. 2000. Threads of continuity. *Conservation in Practice* 1, 8–17.
- Frost, C.C. 2006. History and future of the longleaf pine ecosystem. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds), *The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration*. New York, NY: Springer, pp. 9–42.
- Fuentes, L., Duguay, B., Nadal-Sala, D. 2018. Short-term effects of spring prescribed burning on the understory vegetation of a *Pinus halepensis* forest in Northeastern Spain. *Science of the Total Environment* 610–611, 720–731.
- Gensini, V.A., Brooks, H.E. 2018. Spatial trends in United States tornado frequency. *Climate and Atmospheric Science* 1:38.
- Georgiev, K.B., Chao, A., Castro, J., Chen, Y., Choi, C., Fontaine, J.B. et al. 2020. Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. *Journal of Applied Ecology* 57, 1103–1112.
- Gibson, D. 1961. Life-forms of Kentucky flowering plants. *The American Midland Naturalist* 66, 1–60.
- Gilliam, F.S. 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* 57, 845–858.
- Goode J.D., Kleinman, J.S., Hart, J.L., Bhuta, A.R.R. 2020. Edge influence on composition and structure of a *Pinus palustris* woodland following catastrophic wind disturbance. *Canadian Journal of Forest Research* 50, 332–341.
- GSA (Geological Survey of Alabama). 2006. Geologic map of Alabama, digital version 1.0: Alabama Geological Survey Special Map 220A [adapted from Szabo, M.W., Osborne, W.E., Copeland, C.W., Jr. and Neathery, T.L. (1988) *Geologic map of Alabama (1:250,000)*: Alabama Geological Survey Special Map 220].
- Hargrove, W.W. and Pickering, J. 1992. Pseudoreplication: a *sine qua non* for regional ecology. *Landscape Ecology* 6, 251–258.
- Harper, R.M. 1943. *Forests of Alabama*. Geological Survey of Alabama, Monograph 10. Wetumpka, AL: Wetumpka Printing Company, pp. 230.



- Hernández-Hernández, R., Castro, J., Aguilar, M.D., Fernandez-Lopez, A.B., Gonzalez-Mancebo, J.M. 2017. Post-fire salvage logging imposes a new disturbance that retards succession: the case of bryophyte communities in a Macaronesian laurel forest. *Forests* 8:252.
- Hill, S.R. 2007. Conservation Assessment for the Bigleaf Snowbell (*Styrax grandifolius* Ait.). INHS Technical Report 2007, 65, 1–35.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Johnstone, J.F., Allen, C.D., Franklin, J.F., Frelich, L.E., Harvey, B.J., Higuera, P.E. et al. 2016. Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14, 369–378.
- Keener, B.R., Diamond, A.R., Davenport, L.J., Davison, P.G., Ginzburg, S.L., Hansen, C.J. et al. 2020. Alabama Plant Atlas. Retrieved August 10, 2020 <<http://floraofalabama.org/>>.
- Kleinman, J.S., Ford, S.A. and Hart, J.L. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. *Forest Ecology and Management* 403, 112–125.
- Kleinman, J.S., Goode, J.D., Fries, A.C., Hart, J.L. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. *Ecosphere* 10:e02962.
- Kleinman, J.S., Hart J.L. 2018. Vascular flora of longleaf pine woodlands after wind disturbance and salvage harvesting in the Alabama Fall Line Hills. *Castanea* 83, 183–195.
- Kleinman, J.S., Goode, J.D., Hart, J.L., Dey, D.C. 2020. Prescribed fire effects on *Pinus palustris* woodland development after catastrophic wind disturbance and salvage logging. *Forest Ecology and Management* 468, 118173.
- Knapp, E.E., Ritchie, M.W. 2016. Response of understory vegetation to salvage logging following a high-severity wildfire. *Ecosphere* 7, e01550.
- Leverkus, A.B., Rey Benayas, J.M., Castro, J., Boucher, D., Brewer, S., Collins, B.M. et al. 2018. Salvage logging effects on regulating and supporting ecosystem services—A systematic map. *Canadian Journal of Forest Research* 48, 983–1000 .
- Lindenmayer, D., Thorn, S., Banks, S. 2017. Please do not disturb ecosystems further. *Nature Ecology and Evolution* 1, 0031.
- Lindenmayer, D.B., Westgate, M.J., Scheele, B.C., Foster, C.N., Blair, D.P. 2019. Key perspectives on early successional forests subject to stand-replacing disturbances. *Forest Ecology and Management* 454.

- Logan, A.T., Goode, J.D., Keellings, D.J., Hart, J.L. 2020. Microsite influence on woody plant regeneration in a *Pinus palustris* woodland following catastrophic disturbance. *Forests* 11, 588.
- McCune, B., Mefford, M. J. 2016. PC-ORD. Multivariate analysis of Ecological Data, Version 7.0 for Windows. Wild Blueberry Media, Corvallis, OR, USA.
- Miller, J.H., Manning, S.T., Enloe, S.F. 2015. A management guide for invasive plants in southern forests. Asheville, NC: USDA Forest Service SRS-GTR-131, pp. 120.
- Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G. 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. *Journal of Forestry* 107, 391–397.
- Muller, R.N. 2014. Nutrient relations of the herbaceous layer in deciduous forest ecosystems. In: Gilliam, F.S. (Ed), *The Herbaceous Layer in Forests of Eastern North America*, 2nd edition. New York, NY: Oxford University Press, pp. 13–34.
- Müller, J., Noss, R. Thorn, S., Bässler, C., Leverkus, A.B., Lindenmayer, D. 2019. Increasing disturbance demands new policies to conserve intact forest. *Conservation Letters* 12:e12449.
- Noss, R.F., Platt, W.J., Sorrie, B.A., Weakley, A.S., Means, D.B., Costanza, J., Peet, R.K. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American Coastal Plain. *Diversity and Distributions* 21, 236–244.
- National Weather Service. 2011. Sawyerville-Eoline (Greene, Hale and Bibb Counties) EF-3 Tornado April 27, 2011. Retrieved August 7, 2020 <[https://www.weather.gov/bmx/event\\_04272011sawyerville](https://www.weather.gov/bmx/event_04272011sawyerville)>.
- Oosting, H.J. 1942. An ecological analysis of the plant communities of Piedmont, North Carolina. *The American Midland Naturalist* 28, 1–126.
- Orczewska, A., Czortek, P. and Jaroszewicz, B. 2019. The impact of salvage logging on herb layer species composition and plant community recovery in Białowieża Forest. *Biodiversity and Conservation* 28, 3407–3428.
- Outcalt, K.W. 2006. Prescribed burning for understory restoration. In: Jose, S., Jokela, E.J., Miller, D.L. (Eds), *The Longleaf Pine Ecosystem: Ecology, Silviculture and Restoration*. New York, NY: Springer Science, pp. 326–329.
- Paine, R.T., Tegner, M.J., Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545.
- Palik, B.J., Pederson, N. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. *Canadian Journal of Forest Research* 26, 2035–2047.

- Palmquist, K.A., Peet, R.K., Weakley, A.S. 2014. Changes in plant species richness following reduced fire frequency and drought in one of the most species-rich savannas in North America. *Journal of Vegetation Science* 25, 1426–1437.
- Pausas, J.G., Keeley, J.E. 2014. Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* 204, 55–65.
- Pearcy, R.W., Ehleringer, J. 1984. Comparative ecophysiology of C<sub>3</sub> and C<sub>4</sub> plants. *Plant, Cell and Environment* 7, 1–13.
- Peck, J.E. 2016. *Multivariate Analysis for Ecologists: Step-by-Step using PC-ORD*. Glendeden Beach, OR: MjM Software Design, pp. 192.
- Peet, R.K., Wentworth, T.R., White, P.S. 1998. A flexible, multipurpose method for recording vegetation composition and structure. *Castanea* 63, 262–274.
- Peters, D.P.C., Lugo, A.E., Chapin, F.S., Pickett, S.T.A., Duniway, M., Rocha, A.V et al. 2011. Cross-system comparisons elucidate disturbance complexities and generalities. *Ecosphere* 2:81.
- Peterson, D.W., Reich, P.B., Wrage, K.J. 2007. Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science* 18, 3–12.
- Peterson, C.J., Leach, A.D. 2008. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry* 81, 361–376.
- Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (Ed), *Long-term studies in ecology: Approaches and alternatives*. New York, NY: Springer-Verlag, pp. 110–135.
- Pidgen, K., Mallik, A.U. 2013. Ecology of compounding disturbances: the effects of prescribed burning after clearcutting. *Ecosystems* 16, 170–181.
- Policelli, N., Picca, P., Gómez Villafañe, I.E. 2019. Is prescribed fire a suitable management tool to reduce shrub encroachment in palm savannas? *Restoration Ecology* 27, 109–119.
- PRISM Climate Group. 2020. Data explorer: time series values for individual locations. Retrieved February 10, 2020 <<http://www.prism.oregonstate.edu/explorer/>>.
- Pulsford, S.A., Lindenmayer, D.B., Driscoll, D.A. 2016. A succession of theories: purging redundancy from disturbance theory. *Biological Reviews* 91, 148–167.
- Purdon, M., Brais, S., Bergeron, Y. 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. *Applied Vegetation Science* 7, 49–60.

- Raunkiaer, C. 1934. *The Life Forms of Plants and Statistical Plant Geography*. Oxford: Clarendon Press.
- Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82, 1273–1283.
- Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. In: Wein, R.W. and MacLean, D.A. (Eds) *The Role of Fire in Northern Circumpolar Ecosystems*. New York: John Wiley & Sons., pp. 135–154.
- Royo, A.A., Peterson, C.J., Stanovick, J.S., Carson, W.P. 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology* 97, 1566–1582.
- Ruiters, C., McKenzie, B., Raitt, L.M. 1993. Life-history studies of the perennial geophyte *Haemanthus pubescens* L. subspecies *pubescens* (Amaryllidaceae) in lowland coastal fynbos, South Africa. *International Journal of Plant Sciences* 154, 441–449.
- 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.
- Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hick, J.A. 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *Journal of Applied Ecology* 53, 120–129.
- Shankman, D., Hart, J.L. 2007. The Fall Line: a physiographic-forest vegetation boundary. *Geographical Review* 97, 502–519.
- Stanturf, J.A., Goodrick, S.L., Outcalt, K.W. 2007. Disturbance and coastal forests: A strategic approach to forest management in hurricane impact zones. *Forest Ecology and Management* 250, 119–135.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J. 2011. The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9, 117–125.
- Taylor, A.R., MacLean, D.A., McPhee, D., Dracup, E., Keys, K. 2017. Salvaging has minimal impacts on vegetation regeneration 10 years after severe windthrow. *Forest Ecology and Management* 406, 19–27.
- Teague, J., Palmquist, K.A., Peet, R.K., Carr, S. 2014. *Pinus palustris* / *Schizachyrium scoparium* - *Pteridium aquilinum* Woodland [Version Date: November 7, 2014]. United

- States National Vegetation Classification. Federal Geographic Data Committee, Washington, D.C.
- Thorn, S., Bäessler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L. et al. 2018. Impacts of salvage logging on biodiversity: a meta-analysis. *Journal of Applied Ecology* 55, 279–289.
- Thornthwaite, C.W. 1948. An approach toward rational classification of climate. *Geographical Review* 38, 55–94.
- Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849.
- USDA Forest Service. 2020. Fire Effects Information System (FEIS). Retrieved August 10, 2020 <<https://www.feis-crs.org/feis/>>.
- USDA NRCS. 2008. Soil Survey of Bibb County, Alabama. Retrieved August 10, 2020 <[http://soils.usda.gov/survey/printed\\_surveys/](http://soils.usda.gov/survey/printed_surveys/)>.
- USDA NRCS. 2020a. *Web Soil Survey*. Retrieved August 10, 2020 <<http://websoilsurvey.sc.egov.usda.gov/>>.
- USDA NRCS. 2020b. *The PLANTS Database*. Retrieved August 10, 2020 <<http://plants.usda.gov/>>.
- Van Nieuwstadt, M.G.L., Sheil, D., Kartawinata, K. 2001. The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Conservation Biology* 15, 1183–1186.
- Weakley, A.S. 2015. Flora of the southern and mid-Atlantic states. Working draft of 21 May 2015. ([http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora\\_2015-05-29.pdf](http://www.herbarium.unc.edu/FloraArchives/WeakleyFlora_2015-05-29.pdf)). University of North Carolina, North Carolina Botanical Garden, Chapel Hill, North Carolina.
- Webster, P.J., Holland, G.J., Curry, J.A. Chang, H.-R. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309, 1844–1846.
- Webster, C.R., Dickinson, Y.L., Burton, J.I., Frelich, L.E., Jenkins, M.A., Kern, C.C. et al. 2018. Promoting and maintaining diversity in contemporary hardwood forests: confronting contemporary drivers of change and the loss of ecological memory. *Forest Ecology and Management* 421, 98–108.
- White, P.S., Jentsch, A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Progress in Botany* 62, 399–449.

## CHAPTER 5

### OVERALL CONCLUSION

This dissertation improved our theoretical and applied understanding of multiple interacting disturbances in forest ecosystems. The second chapter presented a systematic review of compound forest disturbances, i.e. disturbances with the capacity to alter forest ecosystem resilience to other perturbations. The third and fourth chapters examined a case study of catastrophic wind disturbance, salvage logging, and prescribed fire in the Fall Line Hills of Alabama, USA. Repeated surveys were used to monitor woody plant development and ground flora succession in differentially disturbed *Pinus palustris* woodlands. The critically endangered, fire-adapted *P. palustris* ecosystem provided an ideal model to study how humans can impact recovery in naturally disturbed ecosystems. Emphasis on nonwoody plant responses to disturbance across multiple spatiotemporal scales improved understanding of post-disturbance forest recovery processes. This work can be used to guide management decisions involving stand regeneration, woody debris extraction, and prescribed fire in other fire-adapted forests.

A concept emphasized in chapter two was that determination of whether and how a disturbance impacted forest resilience was often contingent on which response variables were assessed (Kleinman et al. 2019). A single disturbance combination may simultaneously exhibit positive, negative, and neutral impacts on ecosystem resilience depending on which aspects of recovery are considered. This has important implications in forest ecosystems where recovery is most often assessed in terms of the composition, density, and vertical distribution of trees in small size classes (i.e. seedlings and saplings). Yet, forest ecosystems also support nonwoody

plants, animals, and fungi in addition to watershed, carbon storage, and nutrient cycling functions that may be overlooked in some post-disturbance investigations. These ecosystem components can be differentially impacted by the same disturbance combination, and must therefore be considered for comprehensive assessments of forest recovery.

In support of chapter two, the third and fourth chapters of this dissertation demonstrated that salvage logging and prescribed fire had different effects on post-wind disturbance recovery depending on which response variables were assessed. Chapter three focused on woody plants, and found that salvage-logged sites hosted the greatest *P. palustris* sapling densities before and after prescribed fire (Kleinman et al. 2020). This indicated that recovery toward *P. palustris* canopy dominance was not inherently hindered by salvage logging, and supported a growing literature that also highlights how salvage logging is not necessarily detrimental to woody plant recovery (Fidej et al. 2016, Royo et al. 2016, Taylor et al. 2017, Slyder et al. 2019).

Counter to conceptual models of low-intensity fire after catastrophic canopy removal in *P. palustris* ecosystems, prescribed fire induced shoot mortality throughout the treatment area. Though canopy removal and corresponding reductions in canopy-derived *Pinus* litter can challenge the application of prescribed fire (O'Brien et al. 2008, Mitchell et al. 2009), flammable fuels derived from pyrophytic broadleaved species likely sustained the fire (Hiers et al. 2014, Fill et al. 2015, Emery et al. 2020). Whereas sapling densities were ubiquitously reduced, *P. palustris* saplings were fire-resistant. This indicated that recovery toward *P. palustris* canopy dominance was enhanced by prescribed fire, and supported the paradigm that frequent low-intensity fires are critical to perpetuate *P. palustris* canopy dominance (Platt et al. 1988, Van Lear et al. 2005).

Chapter four focused on ground flora succession, and reported that salvage logging reduced the floristic diversity and compositional dissimilarity of ground flora assemblages (Kleinman et al. 2021). Thus, in contrast to woody plant development, salvage logging negatively impacted early-successional ground flora communities. These results supported many others that caution against negative ecological impacts of salvage logging (Van Nieuwstadt et al. 2001, Swanson et al. 2011, Lindenmayer et al. 2017). Post-disturbance management decisions must therefore consider tradeoffs between potential socioeconomic benefits of salvage logging and the ecological impacts it can have on ecosystem components other than woody plants. Ground flora community homogenization was associated with deadwood extraction in salvage-logged sites. Indeed, deadwood is an important post-disturbance legacy that facilitates recovery of many ecosystem components (Franklin et al. 2002). Ground flora assemblages in salvaged sites were likely also impacted by mechanical impacts of logging machinery, log skidding, and additional soil disturbance (Brewer et al. 2012).

Although prescribed fire did not remedy the negative effects of salvage logging on ground flora assemblages, prescribed fire did impose some consistent selective pressures on understory plants with common life-history strategies. These results corroborated others who endorsed consideration of species-specific life-history strategies to achieve more sensitive indicators of disturbance effects on floristic dynamics (Dale et al. 2002, Donato et al. 2009). In *P. palustris* ecosystems and other ecosystems with high floristic diversity, grouping plants by common life-history strategies can provide an effective strategy to monitor disturbance effects on floristic dynamics. Moreover, the indicator species identified in chapter four may help discern the disturbance history of other sites in which historical records are not as well-preserved. Future work could achieve a deeper understanding of disturbance effects on floristic dynamics



by considering additional plant qualities such as seed abundance and dispersal vector, shade tolerance, growth rate, and coefficients of conservatism (Swink and Wilhelm 1994, Pidgen and Mallik 2013).

The objective of this dissertation was to advance scientific understanding of multiple interacting forest disturbances to ultimately improve strategies to enhance ecosystem resilience. Based on the case study described in chapters three and four, it was recommended that deadwood is retained in some zones after stand regenerating disturbances to facilitate ground flora recovery. To further improve development of operational guidelines, future research can examine the most efficient size and location of these unlogged refugia to maximize benefits for desired ecosystem qualities. There is also much to investigate with respect to the timing and techniques used in salvage logging operations. Indeed, this dissertation treated salvage logging as a binary response variable, but in reality, salvage logging operations can span a gradient of disturbance severity (Peterson and Leach 2008).

Continued monitoring is also needed to inform long-term planning efforts. In recent salvage logging reviews, 70% of studies reviewed by Thorn et al. (2018) spanned less than five years, and 79% of studies reviewed by Leverkus et al. (2018) measured response variables at only one or two times. Moreover, Royo et al. (2016) hypothesized that ephemeral salvage logging effects are often overstated by short-term studies. This dissertation reported monitoring data from three growing seasons (2016, 2017, and 2018), and two additional growing seasons of field data have since been collected (2019 and 2020). It is possible that recovery trajectories in unlogged and salvaged-logged sites converge over time, and the five-year dataset collected provides a strong foundation to track long-term salvage logging effects.

Overall, this dissertation indicated that a diversity of response variables should be measured to achieve comprehensive assessments of disturbance effects on ecosystem resilience. In fire-adapted ecosystems subject to catastrophic disturbance events, this work indicated that salvage logging does not necessarily negatively impact canopy recovery. However, ground flora assemblages were negatively impacted. As such, retention of unlogged refugia is recommended to support ground flora resilience. Though prescribed fire did not remedy salvage logging effects on ground flora recovery, prescribed fire did effectively facilitate woody plant recovery. Thus, continued application of prescribed fire is also recommended to promote *P. palustris* ecosystem recovery after catastrophic disturbance events.

## REFERENCES

- Brewer, J.S., Bertz, C.A., Cannon, J.B., Chesser, J.D., Maynard, E.E. 2012. Do natural disturbances or the forestry practices that follow them convert forests to early-successional communities? *Ecological Applications* 22, 442–458.
- Buma, B. 2015. Disturbance interactions: characterization, prediction, and the potential for cascading effects. *Ecosphere* 6:70.
- Buma, B., Wessman, C.A. 2012. Differential species responses to compounded perturbations and implications for landscape heterogeneity and resilience. *Forest Ecology and Management* 266, 25–33.
- Cannon, J.B., Peterson, C.J., O'Brien J.J., Brewer, J.S. 2017. A review and classification of interactions between forest disturbance from wind and fire. *Forest Ecology and Management* 406, 381–390.
- D'Amato, A.W., Fraver, S., Palik, B.J., Bradford, J.B., Patty, L. 2011. Singular and interactive effects of blowdown, salvage logging, and wildfire in sub-boreal pine systems. *Forest Ecology and Management* 262, 2070–2078.
- Dale, V.H., et al. 2001. Climate change and forest disturbances. *Bioscience* 51, 723–734.
- Dale, V.H., Beyeler, S.C., Jackson, B. 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. *Ecological Indicators* 1, 155–170.
- Donato, D.C., Fontaine, J.B., Robinson, W.D., Kauffman, J.B., Law, B.E. 2009. Vegetation response to a short interval between high-severity wildfires in a mixed-evergreen forest. *Journal of Ecology* 97, 142–154.
- Emery, R.K., Hart, J.L. 2020. Flammability characteristics of surface fuels in a longleaf pine (*Pinus palustris* Mill.) woodland. *Fire* 3, 39.
- Emery, R.K., Kleinman, J.S., Goode, J.D., Hart, J.L. 2020. Effects of catastrophic wind disturbance, salvage logging, and prescribed fire on fuel loading and composition in a *Pinus palustris* woodland. *Forest Ecology and Management* 478, 118515.
- Fidej, G., Rozman, A., Nagel, T.A., Dakskobler, I., Diaci, J. 2016. Influence of salvage logging on forest recovery following intermediate severity canopy disturbances in mixed beech dominated forests of Slovenia. *iForest* 9, 430–436.

- Fill, J.M., Platt, W.J., Welch, S.M., Waldron, J.L., Mousseau, T.A. 2015. Updating models for restoration and management of fiery ecosystems. *Forest Ecology and Management* 356, 54–63.
- Franklin, J.F., Spies, T.A., Van Pel, R., Carey, A.B., Thronburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forests ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management* 155, 399–423.
- Gensini, V.A., Brooks, H.E. 2018. Spatial trends in United States tornado frequency. *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.
- Hart, J.L., Cox, L.E. 2017. Incorporating intermediate-severity disturbances in oak stand development. *Forests* 8, 284.
- Hiers, J.K., Walters, J.R., Mitchell, R.J., Varner, J.M., Conner, L.M., Blanc, L.A., Stowe, J. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. *Journal of Wildlife Management* 78, 383–393.
- Holling, C.S. 1973. Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics* 4:1–23.
- Kane, J.M., Varner, J.M., Hiers, J.K.. 2008. The burning characteristics in southeastern oaks: discriminating fire facilitators from fire impiders. *Forest Ecology and Management* 256, 2039–2045.
- Kleinman, J.S., Goode, J.D., Fries, A.C., Hart, J.L. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. *Ecosphere* 10, e02962.
- Kleinman, J.S., Goode, J.D., Hart, J.L. 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.
- Kleinman J.S., Goode, J.D., Hart, J.L., Dey, D.C. 2020. Prescribed fire effects on *Pinus palustris* woodland development after catastrophic wind disturbance and salvage logging. *Forest Ecology and Management* 468, 118173.
- Leverkus, A.B., Rey Benayas, J.M., Castro, J., Boucher, D., Brewer, S., Collins, B.M. et al. 2018. Salvage logging effects on regulating and supporting ecosystem services—A systematic map. *Canadian Journal of Forest Research* 48, 983–1000.

- Lindenmayer, D.B., Laurance, W.F. 2017. The ecology, distribution, conservation and management of large old trees. *Biological Reviews* 92, 1434–1458.
- Lindenmayer, D., Thorn, S., Banks, S. 2017. Please do not disturb ecosystems further. *Nature Ecology and Evolution* 1, 0031.
- Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G. 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. *Journal of Forestry* 107, 391–397.
- O'Brien, J.J., Hiers, J.K., Callaham, M.A., Jr., Mitchell, R.J., Jack, S. 2008. Interactions among overstory structure, seedling life history traits and fire in frequently burned neotropical pine forests. *Ambio* 37, 542–547.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics, Update Edition*. John Wiley and Sons, New York, NY, pp. 520.
- Paine, R.T., Tegner, M.J., Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1, 535–545.
- Palik, B., Kastendick, D. 2009. Woody plant regeneration after blowdown, salvage logging, and prescribed fire in a northern Minnesota forest. *Forest Ecology and Management* 258, 1323–1330.
- Peterson, C.J., Leach, A.D. 2008. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. *Ecological Applications* 18, 407–420.
- Pidgen, K., Mallik, A.U. 2013. Ecology of compounding disturbances: The effects of prescribed burning after clearcutting. *Ecosystems* 16, 170–181.
- Platt, W.J., Evans, G.W., Rathbun, S.L., 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). *American Naturalist* 131, 491–525.
- Roberts, M.R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82, 1273–1283.
- Royo, A.A., Peterson, C.J., Stanovick, J.S., Carson, W.P., 2016. Evaluating the ecological impacts of salvage logging: can natural and anthropogenic disturbances promote coexistence? *Ecology* 97, 1566–1582.
- Slyder, J.B., Wenzell, J.W., Royo, A.A., Spicer, M.E., Carson, W.P. 2019. Post-windthrow salvage logging increases seedling and understory diversity with little impact on composition immediately after logging. *New Forests* 62, 12 p.
- Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B., Swanson, F.J., 2011. The forgotten stage of forest succession: early-

- successional ecosystems on forest sites. *Frontiers in Ecology and the Environment* 9, 117–125.
- Swink, F., Wilhelm, G. 1994. *Plants of the Chicago Region*, 4th ed., Indiana Academy of Science, Indianapolis, 921 pp.
- Taboada, A., Fernandez-Garcia, V., Marcos, E., Calvo, L. 2018. Interactions between large high-severity fires and salvage logging on a short return interval reduce the regrowth of fire-prone serotinous forests. *Forest Ecology and Management* 414, 54–63.
- Taylor, A.R., MacLean, D.A., McPhee, D., Dracup, E., Keys, K. 2017. Salvaging has minimal impacts on vegetation regeneration 10 years after severe windthrow. *Forest Ecology and Management* 406, 19–27.
- Thorn, S., Bässler, C., Brandl, R., Burton, P.J., Cahall, R., Campbell, J.L. et al. 2018. Impacts of salvage logging on biodiversity: a meta-analysis. *Journal of Applied Ecology* 55, 279–289.
- Trumbore, S., Brando, P., Hartmann, H. 2015. Forest health and global change. *Science* 349, 814–18.
- Turner, M.G. 2010. Disturbance and landscape dynamics in a changing world. *Ecology* 91, 2833–2849.
- Van Lear, D.H., Carroll, W.D., Kapeluck, P.R., Johnson, R. 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. *Forest Ecology and Management* 211, 150–165.
- Van Nieuwstadt, M.G.L., Sheil, D., Kartawinata, K. 2001. The ecological consequences of logging in the burned forests of East Kalimantan, Indonesia. *Conservation Biology* 15, 1183–1186.
- Walker, J., Peet, R.K. 1983. Composition and species diversity of pine-wiregrass savannas of the Green Swamp, North Carolina. *Vegetatio* 55, 163–179.
- Webster, P.J., Holland, G.J., Curry, J.A. Chang, H.-R. 2005. Changes in tropical cyclone number, duration, and intensity in a warming environment. *Science* 309, 1844–1846.