

INFLUENCE OF COARSE WOODY DEBRIS ON SEEDLINGS AND SAPLINGS IN A
PINUS PALUSTRIS WOODLAND

by

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ABSTRACT

Coarse woody debris (CWD) has beneficial effects on plant growth and establishment. Longleaf pine (*Pinus palustris* Mill.) stands support relatively low amounts of CWD — 2 to 30 m³ ha⁻¹. In April 2011, an EF3 tornado passed through the Oakmulgee Ranger District of the Talladega National Forest in the Fall Line Hills of Alabama. This disturbance resulted in the large addition of CWD to a longleaf pine woodland, and a rare opportunity to analyze how CWD can influence a managed, pine woodland. The goal of this study was to examine the effect of CWD on woody plant richness, density, and growth rate (quantified by height) in a longleaf pine woodland that experienced a catastrophic wind disturbance. A total of three 1 m² quadrats were established against either side of a piece of CWD (> 3 m in length and ≥ 10 cm in diameter). Another quadrat was established at least 3 m away from the focal CWD piece. For each plot, the presence and height of every woody plant (< 5 cm dbh) were recorded. Sapling density, oak and hickory density, and organic matter were all found to be significantly higher in quadrats adjacent to CWD than away (all $p < 0.05$). There was also a significant relationship between CWD decay class and average plant height, richness, density, and organic matter (all $p < 0.05$). Results from this study help to inform managers about the ecological functions of CWD in longleaf pine systems and other pine woodlands.

LIST OF ABBREVIATIONS AND SYMBOLS

<i>A</i>	within-group agreement
°C	Celsius
cm	centimeter
CWD	coarse woody debris
DC	decay class
dbh	diameter at breast height
EF	enhanced fujita
h	hour
ha	hectare
km	kilometer
m	meter
mm	millimeter
MkC2	Maubila flaggy loam
MRPP	multi response permutation procedure
MsF	Maubila-Smithdale complex
NCDC	National Climatic Data Center
NMS	non-metric multi-dimensional scaling
NWS	National Weather Service
<i>p</i>	probability of occurrence within the null hypothesis of finding a test result as extreme or more extreme than the observed results

pH potential hydrogen

PRISM parameter-elevation regression on independent slopes model

Quad quadrat

r^2 coefficient of determination

r_s Spearman correlation coefficient

spp. species

SE standard error

T test statistic

US United States

USA United States of America

USDA United States Department of Agriculture

vs. versus

% percent

\pm plus or minus

> greater than

\geq greater than or equal to

< less than

* statistically significant at $p < 0.05$

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CONTENTS

ABSTRACT.....	ii
LIST OF ABBREVIATIONS AND SYMBOLS.....	iii
ACKNOWLEDGEMENTS.....	v
LIST OF TABLES.....	viii
LIST OF FIGURES.....	ix
1. INTRODUCTION.....	1
1.1 Coarse Woody Debris as a Biological Legacy.....	1
1.2 Coarse Woody Debris and Forest Management.....	3
1.3 CWD in the Longleaf Pine (<i>Pinus palustris</i>) Ecosystem.....	4
1.4 Research Significance.....	5
1.5 Objectives & Hypotheses.....	6
2. METHODS.....	8
2.1 Study Site.....	8
2.2 Field Methods.....	11
2.3 Analytical Methods.....	14
3. RESULTS.....	18
3.1 Coarse Woody Debris Influence on Plant Traits.....	18
3.2 Effect of Coarse Woody Debris on Soil Traits.....	19
3.3 Coarse Woody Debris Characteristics and Plant Attributes.....	21

3.4 Effect of Coarse Woody Debris Decay Class on Organic Matter	24
3.5 Site Quality & Plant Community	26
3.6 Relationship Between Soil and Plant Features	27
4. DISCUSSION.....	29
4.1 Oak and Hickory Density Higher Near Coarse Woody Debris	29
4.2 Coarse Woody Debris and Seedling Height	30
4.3 Coarse Woody Debris Characteristics and Plant Community Traits.....	31
4.4 Influence of Coarse Woody Debris on Plant Community and Soil Traits.....	33
4.5 Conclusions.....	34
REFERENCES	36

LIST OF TABLES

1. Decay class system modified to account for the relatively rapid decomposition of sapwood, but typical decomposition of heartwood that is characteristic of southern U.S. pines (Schowalter *et al.*, 1998; Ulyshen *et al.*, 2018).....14
2. Summary statistics for the MRPP with CWD decay class as the grouping variable23

LIST OF FIGURES

1. Map depicting the CWD sampled on the Oakmulgee Ranger District of the Talladega National Forest, expressed as black dots, and the soil map units of the study site.....	10
2. Representation of how six 1 m ² quadrats were established around a piece of CWD	13
3. Bar graphs illustrating the difference between (a) oak and hickory density, (b) mean plant height, and (c) mean organic matter depth near CWD and away (all $p < 0.05$)	20
4. Bar graphs illustrating how (a) density, (b) plant height, and (c) organic matter depth significantly varied by CWD decay class (all $p < 0.05$)	25
5. Three-dimensional non-metric multidimensional scaling based on light intensity categories	27

1. INTRODUCTION

1.1 Coarse Woody Debris as a Biological Legacy

All forests experience natural disturbances that modify their structure, composition, and function (Foster, 1983; Frelich, 2002; Oliver & Larson, 1996). These disturbances leave biological legacies that influence forest ecosystem processes and patterns (Dale *et al.*, 2005; Foster *et al.*, 1998; Franklin *et al.*, 2007). Specifically, biological legacies include structures that alter species establishment and growth which can impact forest succession and development (Seidl *et al.*, 2014; Turner, 2010). Deadwood is an example of a structural, biological legacy that can have a significant influence on forest ecosystem function (Foster *et al.*, 1998; Franklin *et al.*, 2000). For example, hollows and crevices found in large deadwood provide critical breeding habitats for some animal species (Gibbons & Lindenmayer, 2002; Kunz *et al.*, 2003; Newton, 1994; van der Hoek *et al.*, 2017). Additionally, the presence of deadwood can affect the hydrology (Harmon *et al.*, 1986), carbon and nitrogen storage (Laiho & Prescott, 2004; Woodall & Liknes, 2008), and pedogenesis in forest ecosystems (Hartmann *et al.*, 2012). Deadwood can help maintain soil fertility (Brais *et al.*, 2006), protect soil from erosion (Pinno & Das Gupta, 2018; Vázquez *et al.*, 2011), and increase water runoff retention (Ludwig *et al.*, 2005). Furthermore, deadwood can serve as a water reservoir in areas that experience drought and intense fires (Amaranthus *et al.*, 1989). The ability of deadwood to drive ecosystem processes has caused it to be increasingly incorporated into forest management plans (Gao *et al.*, 2015; Kuuluvainen *et al.*, 2019; Stokland *et al.*, 2004; Vanderkerkhove *et al.*, 2009).

Coarse woody debris (CWD), which includes standing dead trees and logs, is a common biological legacy of forest disturbances (Franklin & MacMahon, 2000; Stokland *et al.*, 2012; Triska & Cromack, 1980). CWD accumulates gradually with stand age as a function of endogenous disturbances, but superimposed over the background of tree mortality rates are periodic exogenous disturbances that add CWD in pulses (Hart & Kleinman, 2018; Rahman *et al.*, 2008; Vitoková *et al.*, 2018). Temperate rainforests are considered to have some of the highest volumes of downed CWD, upwards of 300 m³ ha⁻¹, because these systems are highly productive (Lindenmayer *et al.*, 1999; Spies *et al.*, 1988). Xeric conifer forests that are maintained with frequent fire contain some of the lowest amounts of CWD — often less than 30 m³ ha⁻¹ (James & Hardt, 1996; Robertson & Bowser, 1999; Ulyshen *et al.*, 2018).

The successful germination and establishment of seedlings are influenced by the composition of the forest floor substrate (Cornett *et al.*, 2000; Haskell *et al.*, 2012; Stroheker *et al.*, 2018). CWD can aid in the establishment of some plant species by providing a substrate with high moisture and nutrient contents (Zielonka, 2006; Zimmerman *et al.*, 1995), less interspecific competition (Harmon & Franklin, 1989), and a reduced risk of pathogenic soil fungi (Cheng & Igarashi, 1987; Sakamoto & Miyamaoto, 2005). Additionally, CWD can provide shelter to seedlings and saplings from wind, animal browsing, and harsh environmental conditions (Bailey *et al.*, 2012; Goldin & Brookhouse, 2015). The moisture retained under CWD is also hypothesized to protect mycorrhizal fungi and related microflora from fire, and the protection of these species may allow them to re-establish more readily following fire (Perry *et al.*, 1989).

Variability in CWD characteristics are important for maintaining biological diversity in forest ecosystems (McWinn & Crossley, 1996). CWD diameter and size are factors that help determine habitat suitability of downed wood for faunal species (Stokland *et al.*, 2004). Large

volumes of CWD across a range of decay stages, species, and size classes are vital for the health and genetic diversity of saproxylic species (Sebek *et al.*, 2013). Saproxylic fungi influence soil quality, and in their absence soil conditions can become inadequate for seedling growth and recruitment (Hartmann *et al.*, 2012). Nonvascular species, primarily lichen, benefit from CWD in early stages of decay, and CWD in later decay stages typically benefit bryophytes and vascular species (Botting & DeLong 2009; Kumar *et al.*, 2017; McCullough, 1948). Furthermore, CWD texture and pH, which influence plant colonization and use, vary by species and CWD size (Pereira *et al.*, 2014; Shorohova *et al.*, 2016).

1.2 Coarse Woody Debris & Forest Management

In general, actively managed forests have lower volumes of CWD than forests that do not experience frequent silvicultural interventions (Dieler *et al.*, 2017; Larrieu *et al.*, 2012; Nagel *et al.*, 2017; Pedlar *et al.*, 2002; Siitonen *et al.*, 2000). European studies have found that the amount of CWD in a managed forest is about 2% to 30% of what would be found in an unmanaged counterpart (Fridman & Walheim, 2000; Keren & Diaci, 2018). In a managed North American forest, CWD volume can decrease up to 15% of what would be expected prior to silvicultural interventions (Harmon, 2001). This difference in volume between managed and unmanaged conditions is largely explained by tree harvesting that reduces the abundance of large snags and logs (Kruys *et al.*, 1999). Over an extended period, some silvicultural systems may reduce the volume of CWD and other biological legacies to a degree that native forest diversity is impacted (Angers *et al.*, 2005; Kenefic & Nyland 2007; Mahon *et al.*, 2008; McGee *et al.*, 1999).

Other explanations for the difference in CWD volumes between unmanaged and managed forests are related to natural disturbances. After a disturbance that increases CWD in an

unmanaged forest, the CWD is retained and allowed to serve various functions as decay proceeds (McComb & Lindenmayer, 1999). However, after a disturbance in a managed forest, silvicultural interventions may occur, such as salvage logging, and result in the extraction of the majority of large CWD fragments (Michalová *et al.*, 2017; Priewasser *et al.*, 2013). Additionally, some ecosystems are managed with prescribed fire, and this practice can decrease CWD volume (Aponte *et al.*, 2014; Collins *et al.*, 2014).

Over the past few decades, native forest diversity has increasingly become a priority in forest management (Butchart *et al.*, 2010; Hunter & Hunter, 1999; Pereira *et al.*, 2012; Wilson, 1988). CWD can have a strong influence on forest diversity and can provide critical ecosystem functions (Harmon *et al.*, 1986; McWinn & Crossley, 1996). The relationship between CWD and biodiversity has caused its quantity and spatial distribution to be a gauge for sustainable forest management (Forest Europe, 2015; Stokland *et al.*, 2012; Vitoková *et al.*, 2018). The exact principles of sustainable forest management vary by region, however, the conservation of biodiversity is a common touchstone (Rametsteiner & Simula, 2003; Siry *et al.*, 2005). Some typical CWD management practices are to leave existing snags and create new ones, add CWD for erosion control, retain trees of small commercial value to provide for future CWD, avoid crushing CWD with harvesting equipment, and redistribute CWD when found in areas with extremely high CWD volumes (Hagan & Grove, 1999).

1.3 CWD in the Longleaf Pine (*Pinus palustris*) Ecosystem

The amount of CWD in the southeastern U.S. varies from more than 100 m³ ha⁻¹ in mixed hardwood stands to less than 5 m³ ha⁻¹ in pine-dominated stands (James & Hardt, 1996). The longleaf pine (*Pinus palustris* Mill.) ecosystem, located in the southeastern U.S., is highly

diverse and endangered as a result of land-use changes and fire suppression (Kirkman *et al.*, 2004; Ulyshen *et al.*, 2018). Similar to old-growth conifer forests found in the western U.S., the old-growth longleaf pine forests in the Southeast contain some of the lowest amounts of woody debris — typically varying from 2 to 30 m³ ha⁻¹ (Robertson & Bowser, 1999; Ulyshen, 2018; Ulyshen *et al.*, 2018). These low woody debris volumes are often explained by the subtropical climate that facilitates wood-decomposing microbes, saprotrophic fungi, and frequent fires (Aponte *et al.*, 2014; Collins *et al.*, 2014; Guyette *et al.*, 2012; Jackson *et al.*, 2017; Ryan & Williams, 2011). Termites, particularly of the genus *Reticulitermes*, also play an important role in the decomposition rates of CWD in longleaf pine forests (Hanula *et al.*, 2012; Ulyshen *et al.*, 2018). Additionally, longleaf pine stands generally have relatively low basal areas, and mortality events primarily comprise individual trees (Palik & Pederson, 1996).

Pine CWD can provide different ecosystem functions than hardwood CWD. Coniferous tree species typically have bark that has a lower pH and is drier than the bark of broadleaved species (Culberson, 1955; Hauck & Javkhan, 2009). Furthermore, coniferous logs generally decay more slowly than hardwood logs, and this attribute provides additional time for species to colonize (Harmon, 1989; Harmon *et al.*, 1986; Shorohova & Kapitsa, 2014).

1.4 Research Significance

Many studies have examined how CWD positively affects biodiversity in forest systems, however, the question has not been thoroughly addressed in longleaf pine forests (Harmon *et al.*, 1986; Stokland *et al.*, 2012; Ulyshen *et al.*, 2018). The longleaf pine ecosystem is one of the most endangered in the United States because of land-use changes and fire suppression (Frost, 2007; Kirkman *et al.*, 2004; Noss *et al.*, 1995). Studies surrounding CWD have predominately

been conducted in boreal forests while the biodiverse subtropical ecosystems, such as the longleaf pine ecosystem, have received relatively little attention (Dirzo & Raven, 2003; Hansen *et al.*, 2008; Seibold *et al.*, 2015). This study is a unique analysis of how the presence of CWD can impact microsite conditions and plant community composition in the endangered longleaf pine ecosystem. Furthermore, these results will help realize the importance of CWD retention, and this has implications for the management of harvest entries and salvaging operations.

Data from this study were collected in a forest stand that was impacted by a catastrophic wind disturbance. Globally, windstorms, hurricanes, and tornadoes are some of the most common natural disturbance types (Everham & Brokaw, 1996). The results from this study will provide information on the influence that CWD can have on an ecosystem post wind disturbance, therefore, contributing to the understanding of biological legacies and management of naturally-disturbed forests.

1.5 Objectives & Hypotheses

To advance scientific knowledge of how CWD impacts plant regeneration and biodiversity, it is essential to further the understanding of its effects on microenvironmental characteristics that may influence seedling germination and establishment. In this analysis, how the presence of CWD affects plant communities and the composition of the forest floor substrate was examined. The goal of this study was met by answering the following questions: (1) Does CWD affect seedling (< 1 m height) and sapling (≥ 1 m height, < 5 cm dbh) presence, density, or species richness? (2) Does CWD influence the height of woody seedlings and saplings? (3) Does CWD impact bulk density, soil water content, or organic matter volume of the surrounding soil? And, (4) Are features (e.g. woody plant density, soil attributes) of the forest

floor affected by characteristics of the CWD such as the decay stage, amount present, or size? These questions were answered in a managed longleaf pine forest that experienced a catastrophic wind disturbance and is subject to frequent prescribed fire.

CWD is favorable for the establishment and growth of a variety of plant species in a range of forest types by providing shelter and increased water retention, therefore, (1) it was hypothesized that the CWD found in this study site would benefit woody plant density (Han *et al.*, 2018; Harmon *et al.*, 1986; Vítková *et al.*, 2018). Additionally, (2) it was anticipated that the shelter provided by CWD would influence woody plant species assemblages. The growth of individual species can be enhanced by CWD, and (3) it was speculated that it would benefit the growth, measured by height, of certain individuals in this study by providing shelter and a more favorable microclimate (Orman *et al.*, 2016; Orman & Szewczyk, 2015). (4) It was also predicted that the decay stage and concentration of CWD would help to determine the microenvironmental plant community and soil features. Past studies have found that CWD can begin to have negative impacts on plant diversity when it reaches severely late decay stages and is found in excessive amounts (Orman *et al.*, 2016; Pinno & Das Gupta, 2018). Furthermore, CWD in intermediate to late decay stages has been shown to support a higher number of tree seedlings than CWD in the very early stages of decay (Harmon & Franklin, 1989; Zielonka, 2006).

2. METHODS

2.1 Study Site

This study was conducted on the Oakmulgee Ranger District of the Talladega National Forest in Bibb County, Alabama, USA. The Oakmulgee Ranger District is in the Fall Line Hills (Fenneman, 1938). The Fall Line Hills comprise sedimentary rock belts that serve as a transition zone for the Coastal Plain and Appalachian Highlands (Shankman & Hart, 2007). The geologic composition of the area is primarily from the Late Gordo Formation — chert and quartz pebbles, cross-bedded and gravelly sands, and carbonaceous clay (Szabo *et al.*, 1988). Soils are mainly derived from the Maubila series which is described as deep and moderately well drained with a subangular blocky structure (USDA, 2019). Specifically, data were collected over an area with two variations of the Maubila series, the Maubila flaggy loam and the Maubila-Smithdale complex (USDA, 2019) (**Figure 1**). The two soil delineations both have 14 cm of available water storage, and the minimum water table depth for both is 23 cm (USDA, 2019).

The regional climate of the study area is humid mesothermal, characterized by year-round rainfall, long, hot summers, and brief, mild winters (Thorntwaite, 1948). The 30-year normal annual precipitation and temperature are 1,369 mm and 17 °C (PRISM, 2019). February has the highest precipitation at 140 mm, and October has the lowest at 84 mm (PRISM, 2019). The coldest month is January with a mean temperature of 0.5 °C and the warmest month is July with a mean temperature of 27 °C (PRISM, 2019).

The study was conducted in the central longleaf pine belt of Alabama (Harper, 1943), and the plant communities liken to the Oak (*Quercus*) – Pine (*Pinus*) forest region (Braun, 1950).

Longleaf pine historically dominated the forest canopy of the study area, however, loblolly pine (*Pinus taeda* L.), shortleaf pine (*Pinus echinata* Mill.), and various hardwood species can reach subcanopy and canopy positions (Beckett & Golden, 1982; Cox & Hart, 2015). The ecosystem supports a diverse herbaceous layer and an open mid-story (Kleinman & Hart, 2018; Walker & Silletti, 2007). Fire is a dominant force in the advancement of longleaf pine systems by maintaining the characteristically diverse understory and preventing succession to hardwood dominance (Van Lear *et al.*, 2005). Additionally, longleaf pine woodlands require frequent low-intensity surface fires to decrease inter-specific competition and expose bare mineral soil for seed germination (Platt *et al.*, 1988).

Prior to widespread European settlement, Native Americans inhabited lands around the Black Warrior River — located to the north and west of the study area. Moundville, a cultural center for the Mississippian Indians until 1700, is located only 13 km from the border of the Oakmulgee Ranger District (Maxham, 2000). Europeans settled the region in the 1820s, and in the early 1900s the Kaul Lumber Company extensively logged the area (Cox & Hart, 2015; Reed, 1905). The industrial-scale harvesting led to the deterioration of the longleaf pine system, and foresters falsely concluded that fire exclusion would be the best practice to curtail additional degradation (Harper, 1943; Reed, 1905). Following federal acquisition in 1935, longleaf pine restoration has been a priority on the District (Cox & Hart, 2015). Longleaf pine recovery efforts comprise regeneration harvests with site preparation and outplanting, thinning of undesirable trees and shrubs, and a prescribed fire rotation of 2 – 5 years (USDA, 2002).

Tornadoes occur frequently in Bibb County, Alabama (Harper, 1943; Reed, 1905). The National Climatic Data Center has recorded 27 tornado events in the area since 1950, and three of these events were of EF3 or greater magnitude (NCDC, 2019). One high-intensity tornado

took place on 27 April 2011 and passed through the Oakmulgee Ranger District. The tornado was an EF3 long-tracked wedge tornado, one of the 362 confirmed tornadoes of the 2011 Super Outbreak, with estimated maximum wind speeds of 233 km / h (NWS, 2011).

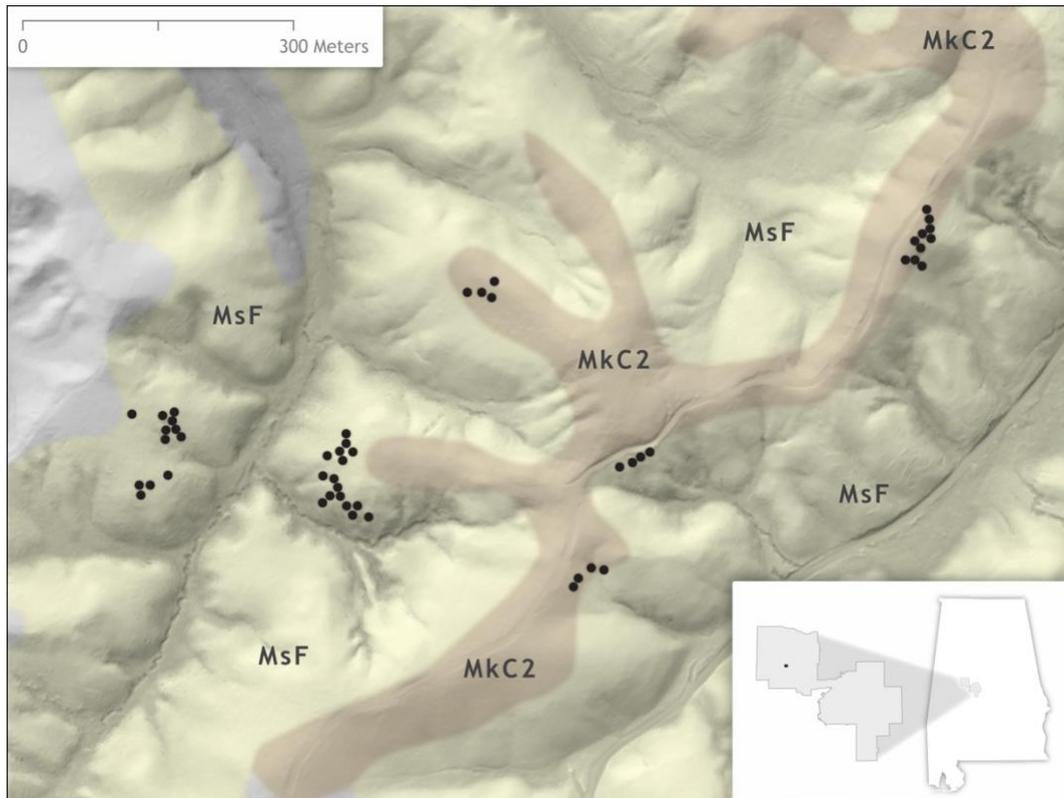


Figure 1. Map depicting the CWD sampled on the Oakmulgee Ranger District of the Talladega National Forest, expressed as black dots, and the soil map units of the study site. MsF soil map unit represents the Maubila-Smithdale complex, and MkC2 indicates areas of the Maubila flaggy loam.

2.2 Field Methods

In the summer of 2019, 350 quadrats were established in wind disturbed areas that were not salvage harvested on the Oakmulgee Ranger District of the Talladega National Forest — 300 quadrats contiguous to CWD and 50 quadrats located away from CWD. CWD sampling only occurred in a single compartment on the district to ensure consistency in prescribed fire. Transects, beginning from random starting points, were used to locate and sample the CWD that met the following criteria: > 3 m in length and ≥ 10 cm in diameter.

A group of three 1 m² quadrats, of equal distance from one another, were placed on the ground on both sides of the CWD to analyze site characteristics — resulting in six quadrats surrounding one CWD plot (**Figure 2**). This sampling scheme was modified from Chečko *et al.* (2015). The quadrats were uniformly established by placing quadrat 1 on the downslope side of the CWD, and then moving clockwise to assign the five remaining quadrats. A seventh quadrat was established at least 2 m away from the focal log and any other CWD. The location of the seventh quadrat, in relation to the CWD plot, varied because additional CWD was occasionally present near the focal log. Initially, the seventh quadrat was established at least 2 m away from and in line with quadrat 2. If there was a log or snag less than 2 m away from this placement, the quadrat was moved to be in line with quadrat 5. If quadrat 5 still had CWD near it, the seventh quadrat was moved to be in line with another quadrat in the following order — quadrat 1, quadrat 6, quadrat 3, and quadrat 4 — until it was established away from additional CWD. All quadrats were further subdivided into 25 cm sections for data collection — section 1 was closest to the CWD and section 4 was the farthest away.

For every quadrat, multiple attributes of the focal CWD were recorded: tree species, diameter, length, presence of rot, decay class, and azimuth. The area where data were collected

was under a uniform prescribed fire plan, therefore, all of the CWD analyzed was subjected to prescribed fire. However, if the CWD had visual signs of combustion where a quadrat was established, it was scored as charred (Donato *et al.*, 2009; Knapp *et al.*, 2005). CWD was also categorized as being either on the ground or elevated. Decay class was determined by using a system that accounted for the relatively rapid decomposition of sapwood, but common decomposition of heartwood that occurs in pines of the southeastern U.S. (**Table 1**) (Schowalter *et al.*, 1998; Ulyshen *et al.*, 2018).

For every 1 m² quadrat, including the seventh quadrat, the presence, height, and quadrat section of each woody plant seedling and sapling were noted. Organic matter depth was documented to the quarter of a cm by placing a ruler in the middle of each of the four quadrat sections (i.e. four readings quadrat⁻¹). This method allowed for the calculation of an organic matter average for each quadrat and the understanding of how organic matter depth changed with distance from CWD. Organic matter measurements were not taken in portions of a section where pieces of bark had recently sloughed off during CWD decay. The slope aspect and topographic position for each quadrat were recorded. The microtopography was reported using the terrain shape index method introduced by McNab (1989). To examine how the amount of CWD influenced plant and soil traits, quadrats located alongside CWD were classified as ungrouped, grouped, or extremely grouped. A quadrat was considered grouped if CWD or a stump was less than 1 m away from the quadrat edge and classified as extremely grouped if the additional CWD was within the quadrat boundaries. This method was adapted from Pinno & Das Gupta (2018) and Chećko *et al.* (2015).

Soil samples were taken from the top of the soil profile with a 4 cm by 7.5 cm steel pipe with a volume of 94.25 cm³. Samples were collected at the center of each of the seven quadrats.

Rocks occasionally impeded soil sample collection and forced the collection to occur closer to a quadrat edge than the true center. Samples were collected by removing all organic matter from the top of the soil, hammering down the steel pipe, removing the sample with a trowel, and then placing the sample in a double sealed plastic bag. This sampling method was modified from LaFevor (2014). After collection, the samples were transferred to a separate bag for protection and moved to the laboratory to be weighed, dried at 105 °C for 24 h, and then reweighed (Tome *et al.*, 1996). The samples were then dry sieved to remove all organic matter and rocks which were subsequently weighed.

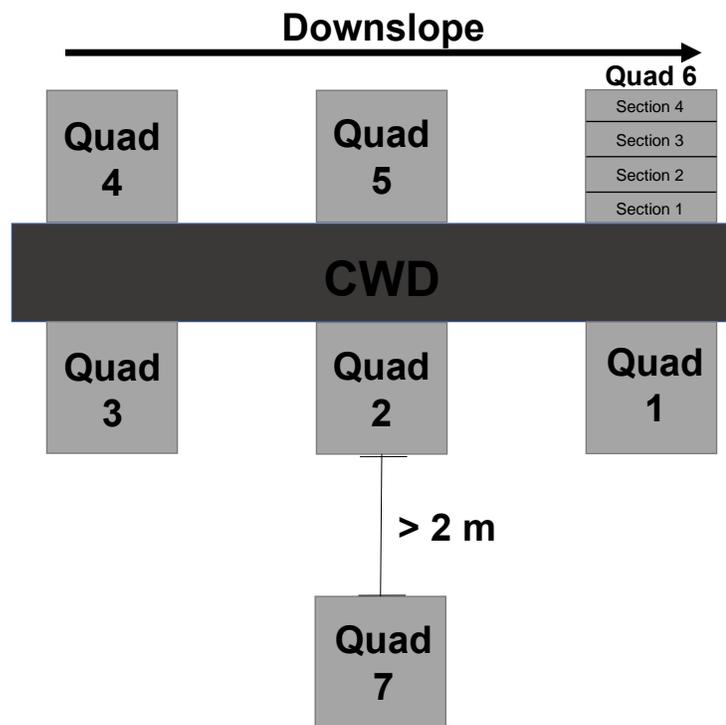


Figure 2. Representation of how six 1 m² quadrats were established around a piece of CWD. Quadrat 7 is shown colinear to quadrat 2 and at least 2 m away from the focal piece of CWD. Quadrat 6 illustrates how quadrats were further subdivided into 25 cm sections.

Table 1. Decay class system modified to account for the relatively rapid decomposition of sapwood, but typical decomposition of heartwood that is characteristic of southern U.S. pines (Schowalter *et al.*, 1998; Ulyshen *et al.*, 2018). This study did not record any CWD in decay class 7.

Decay Class (DC)	Shape	Bark	Sapwood	Heartwood
DC 1	Round	Present, Unbroken	Newly dead, Standard color	Not discernible
DC 2	Round	Present, Slackened	Mainly intact, but partially soft in sections	Not discernible
DC 3	Round	Remnant to removed	Slightly soft	Not Discernible
DC 4	Round to oval	Remnant to removed	Breaks under foot, but not crumbly	Not discernible or starting to become visible
DC 5	Oval	Removed	Breaks in hand, Crumbly	Noticeable in sections
DC 6	Round, Solely heartwood	Removed	Removed	No decomposition
DC 7	Oval, Solely heartwood	Removed	Removed	Decomposing

2.3 Analytical Methods

Plant species density and richness were calculated for each quadrat. Density was treated as the sum of woody seedlings and saplings in each quadrat, and richness was calculated as the number of woody seedling and sapling species. Organic matter depth was averaged by quadrat by taking the mean of the four organic matter depths recorded in the four quadrat sections. Dry bulk density and wet bulk density were determined for all soil samples by taking the dry or wet weight and dividing it by the volume of the steel pipe used for data collection. Soil water content was calculated by subtracting the soil wet weight by the dry weight and dividing the difference by the dry weight. Vegetation analyses consisted of total plant density and richness, and density of particular taxonomic groups — pine, oaks and hickories (*Carya*), and all other remaining

hardwood species. Individual plants were also classified as either seedlings (< 1 m in height) or saplings (\geq 1 m in height, < 5 cm dbh).

For this study, significance was determined at a $p < 0.05$. To assess differences in microsites, the six quadrats adjacent to a piece of CWD were classified as “near” and the seventh quadrat at least 2 m away from CWD was classified as “away”. Data were not normally distributed. Therefore, the Welch’s *F*-Test and the Kruskal-Wallis one-way analysis of variance test were completed in R to statistically analyze the differences in plant, soil, and organic matter traits near CWD and away (R Core Team, 2017). The specific statistical test that was used for each analysis was dependent on the assumption of homoscedasticity — when variances were not equal the Welch’s *F*-Test was applied.

When examining how CWD characteristics influenced the local plant community, soil traits, and organic matter depth, the Kruskal-Wallis test or the Welch’s *F*-Test were also used. Post-hoc pairwise comparisons were completed using the Games-Howell post-hoc test. This test does not assume equal variances or sample sizes and is a common approach when dealing with nonparametric data (Ruxton & Beauchamp, 2008; Toothaker, 1993). Plant, site, and soil variables were tested to find any significant environmental differences between CWD species, decay class, and ground placement (suspended or grounded). How the quadrat section, the cardinal direction of the quadrat, the quadrat slope position relative to CWD, the amount of CWD near a quadrat, and the presence of rot or char influenced vegetation, organic matter, and soil measurements were also examined. Additionally, site characteristics, such as topographic classification and organic matter depth, were tested with plant and soil measurements.

All data were log transformed to run correlation and linear regression analyses. The log transformed data still failed normality tests, however, it significantly improved the problem of

heteroscedasticity. The nonparametric Spearman (r_s) correlation coefficient was applied to investigate relationships between multiple measurement variables. Linear regression was used following correlation analysis. CWD length, azimuth, and diameter were tested to be correlated with organic matter depth and seedling and sapling density, richness, and height. Correlation and regression analyses were also used to find the relationship between certain site attributes — slope azimuth, degree slope, and average organic matter depth — and plant density, richness, and height. The linear relationships between vegetation variables and soil measurements were also examined.

Non-metric multidimensional scaling (NMS) ordination and multi-response permutation procedure (MRPP) were conducted in PC-ORD v. 6.0 to further understand the influence of CWD and site characteristics on plant species assemblages (McCune & Medford, 2011; Mielke & Berry, 2001). A MRPP, with a post-hoc pairwise comparison, was utilized to examine plant community differences between CWD decay class. NMS ordination was applied to investigate the CWD attributes and site qualities that may be driving differences in species assemblages. For the analysis, the number of individuals by species for each quadrat was aggregated by CWD and side of log. This resulted in two sampling units per CWD — three quadrats on one side of the log were aggregated and three quadrats on the other side were aggregated. Quadrats away from CWD were not included in this analysis because they were not associated with any CWD characteristics. Taxa that were only represented by one or two individuals were removed from the analysis — Florida maple (*Acer floridanum* (Chapm.) Pax), tulip-poplar (*Liriodendron tulipifera* L.), American witch-hazel (*Hamamelis virginiana* L.), and chestnut oak (*Quercus montana* Willd.). Additionally, count data were relativized by maximum species, and Bray-Curtis dissimilarity was used as the distance measure.

NMS ordination treatment categories were assigned based on associated CWD azimuth, slope azimuth, and cardinal direction of the plot relative to CWD. These data were in the form of aspect values, therefore, they were converted into 45°-wide azimuth arcs that were utilized to build four categories of light intensity. This was done to test the hypothesis that shelter provided by CWD may influence woody plant species assemblages. The light intensity categories were (1) high light, (2) medium high, (3) medium low, and (4) low light. For example, a high light plot was established near a log running north to south, on a south facing slope, and on the western side of the log. A plot that received a treatment of 4, or low light, could be established near a log running east to west, on an east facing slope, and on the northern side of the log. Once light categories were assigned to the plots, NMS ordination was applied to relate differences in plant communities by 14 environmental variables: CWD species, CWD length, presence of rot, degree slope, topographic position, decay class, diameter, proximity to additional CWD, elevation of CWD, char score, the plot slope position relative to CWD, average organic matter depth, organic matter weight, and soil water content.

3. RESULTS

3.1 Coarse Woody Debris Influence on Plant Traits

In the study area, there were not any CWD in decay class 7, and woody plant data contained 36 different species. Of the 339 quadrats that had species present, winged sumac (*Rhus copallinum* L.) had the highest frequency of occurrence (55%), followed by sparkleberry (*Vaccinium arboreum* Marshall, 37%) and longleaf pine (*Pinus palustris*, 33%). Woody plant data included 11 unique oak species, two unique pine species, and two unique hickory species (*Carya* spp.). Florida maple (*Acer floridanum*) and tulip-poplar (*Liriodendron tulipifera*) were the only species to be represented by a single individual.

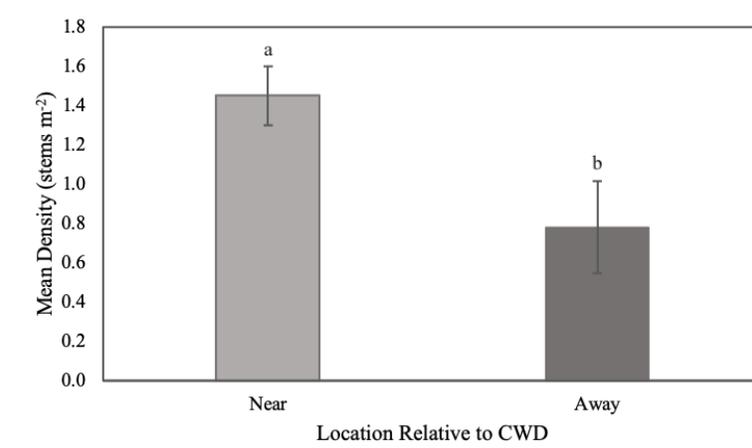
Mean woody plant species richness in 1 m² quadrats near CWD was 2.40 ± 0.70 (SE), and mean species richness in 1 m² quadrats away from CWD was 2.30 ± 0.20 . Adjacent to CWD the mean plant density was 9.00 woody stems m⁻² ± 0.07 and away it was 10.60 woody stems m⁻² ± 0.20 . Total plant density was not different by proximity to CWD, however, sapling density was found to be significantly higher in quadrats adjacent to CWD. Sapling density near CWD was 2.63 stems m⁻² ± 0.31 , and away from CWD sapling density was 1.79 stems m⁻² ± 0.26 . Additionally, oak and hickory density was found to be significantly higher in quadrats adjacent to CWD than in quadrats away from CWD. Mean density of oak and hickory stems in quadrats contiguous to CWD was 4.00 stems m⁻² ± 0.30 and mean density of oak and hickory stems discontinuous to CWD was 2.80 stems m⁻² ± 0.60 (**Figure 3a**).

Total plant height was significantly greater in quadrats near CWD than away. The mean height for woody stems in quadrats adjacent to CWD was 41.30 cm \pm 0.70 (SE), and the mean height in quadrats away from CWD was 29.70 cm \pm 1.30 (**Figure 3b**). When separated into seedlings and saplings, analyses determined that seedling height was significantly higher near CWD than away, but sapling height was not significantly different.

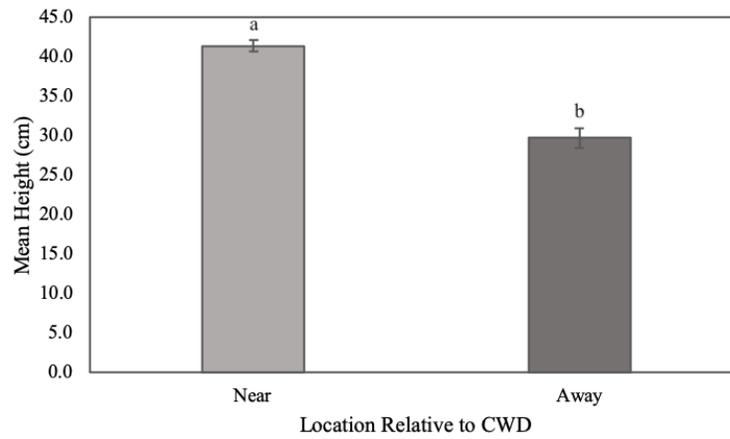
3.2 Effect of Coarse Woody Debris on Soil Traits

Mean organic matter depth was significantly higher near CWD than away. The mean organic matter depth adjacent to CWD was 1.70 cm \pm 0.05 (SE), and the mean away from CWD was 1.20 cm \pm 0.07 (**Figure 3c**). Furthermore, organic matter was found to significantly differ with distance from CWD. Section 1, the section directly adjacent to CWD, had the highest mean organic matter depth at 1.80 cm \pm 0.07, followed by section 2 (1.60 cm \pm 0.06). Post-hoc tests determined that section 3 (1.50 cm \pm 0.05) and section 4 (1.50 cm \pm 0.05) had significantly lower organic matter depths than section 1. Soil wet bulk density, dry bulk density, soil water content, and organic matter weight did not significantly differ between quadrats that were far from CWD and quadrats that were contiguous to CWD.

(a)



(b)



(c)

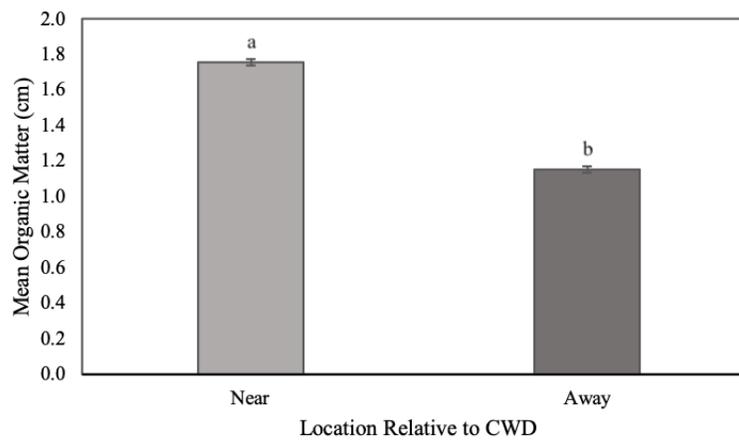


Figure 3. Bar graphs illustrating the difference between (a) oak and hickory density, (b) mean plant height, and (c) mean organic matter depth near CWD and away (all $p < 0.05$).

3.3 Coarse Woody Debris Characteristics & Plant Attributes

Quadrats near CWD that were pine had significantly lower richness and density values than ones adjacent to CWD that were hardwood. Mean plant richness near pine CWD was 2.40 ± 0.07 (SE) and near hardwood CWD it was 3.00 ± 0.30 . Pine CWD had a mean plant density of $8.90 \text{ stems m}^{-2} \pm 0.40$ and hardwood CWD had a mean density of $11.50 \text{ stems m}^{-2} \pm 1.30$. In contrast, seedling and sapling heights were significantly higher near pine CWD than hardwood CWD.

Quadrats adjacent to uncharred CWD had significantly higher plant density, richness, and height than quadrats near charred CWD. Seedling density and sapling density were significantly higher near uncharred CWD. Seedling richness, mean organic matter depth, and oak and hickory density were also significantly higher in quadrats adjacent to uncharred CWD. CWD that were entirely touching the ground had significantly greater plant heights and organic matter depths than pieces of CWD that were elevated.

Seedlings and saplings were significantly taller in quadrats that were considered extremely grouped. Extremely grouped quadrats, or quadrats where additional CWD was within the quadrat boundary, had a mean woody plant height of $47.40 \text{ cm} \pm 1.70$ (SE). Woody plants in quadrats that were not near any additional CWD had a mean height of $40.20 \text{ cm} \pm 1.00$ and plants with CWD within a meter from a quadrat edge had a mean height of $39.80 \text{ cm} \pm 1.40$. Post-hoc tests confirmed that plants were significantly shorter in ungrouped quadrats and quadrats that had additional CWD $< 1 \text{ m}$ away from a quadrat edge than in extremely grouped quadrats.

Plant density was significantly different by CWD decay class. Decay class 2 had the highest plant density with $16.30 \text{ stems m}^{-2} \pm 2.50$ (SE), and decay class 6 had the lowest with

7.20 stems $m^{-2} \pm 0.80$ (**Figure 4a**). Post-hoc tests determined that only decay class 2 and decay class 6 had significantly different densities from one another. Woody plant height was significantly associated with CWD decay class categories. The greatest heights were associated with decay class 5 (47.70 cm \pm 1.10) and decay class 6 (41.80 cm \pm 2.90) (**Figure 4b**). The lowest heights were found near decay class 1 (25.20 cm \pm 1.80) and decay class 3 (32.80 cm \pm 1.80). Woody plants near CWD in decay class 1 were determined to have significantly lower heights than any of the other decay classes. Decay class 5 had significantly taller heights than any other decay class, except for decay class 6. Additionally, plant heights found near decay class 3 were significantly different from decay class 6.

A MRPP was completed with decay class as the grouping variable. The MRPP confirmed that species assemblages were significantly different across varying decay classes (**Table 2**). The plant community composition of decay class 1 was significantly different from decay classes 2, 4, 5, and 6. Species composition in decay class 2 was significantly different from decay classes 3 and 5 as well as quadrats that were away from CWD. Quadrats near CWD in decay classes 4, 5, and 6 significantly varied from quadrats near CWD in decay class 3. Plant communities adjacent to CWD in decay class 4 were also significantly distinct from ones near CWD in decay classes 5 and 6 as well as assemblages that were not near any CWD. Species composition adjacent to CWD in decay class 5 was significantly different from decay class 6, and plant communities near CWD in both decay classes 5 and 6 were significantly distinct from ones that were not near any CWD.

A significant negative correlation was found between plant density and CWD length and diameter ($r_s = -0.1$). Additionally, there was a significant negative correlation between height and

CWD length ($r_s = -0.1$). Plant richness did not closely correlate with CWD length or diameter ($r_s = -0.09$).

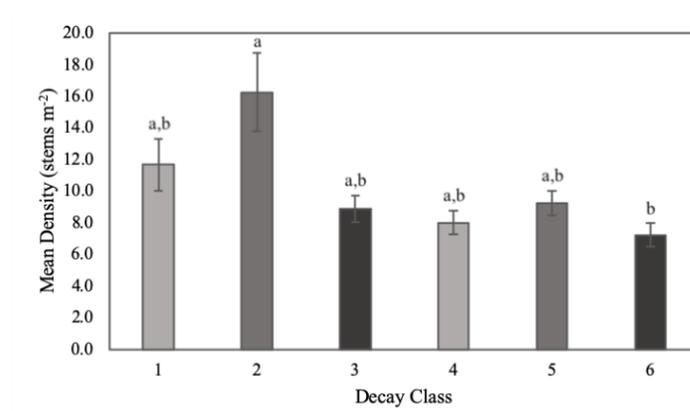
Table 2. Summary statistics for the MRPP with CWD decay class as the grouping variable. Column one expresses the different decay classes that were represented by the data (1–6). “Away” indicates data that were collected away from CWD.

Decay Class Pairwise Comparisons	<i>T</i>	<i>A</i>	<i>p</i>
1 vs. 2	-8.19	0.03	0.00*
1 vs. 3	0.43	0.00	0.58
1 vs. 4	-7.11	0.02	0.00*
1 vs. 5	-8.07	0.04	0.00*
1 vs. 6	-4.00	0.03	0.00*
1 vs. Away	-0.44	0.00	0.24
2 vs. 3	-3.59	0.01	0.01*
2 vs. 4	-1.94	0.00	0.05
2 vs. 5	-7.09	0.02	0.00*
2 vs. 6	-1.79	0.01	0.06
2 vs. Away	-2.62	0.01	0.02*
3 vs. 4	-3.32	0.01	0.01*
3 vs. 5	-6.00	0.03	0.00*
3 vs. 6	-2.30	0.01	0.03*
3 vs. Away	-0.53	0.00	0.24
4 vs. 5	-7.60	0.02	0.00*
4 vs. 6	-2.50	0.01	0.03*
4 vs. Away	-2.15	0.01	0.04*
5 vs. 6	-2.26	0.02	0.03*
5 vs. Away	-6.57	0.05	0.00*
6 vs. Away	-2.59	0.04	0.02*

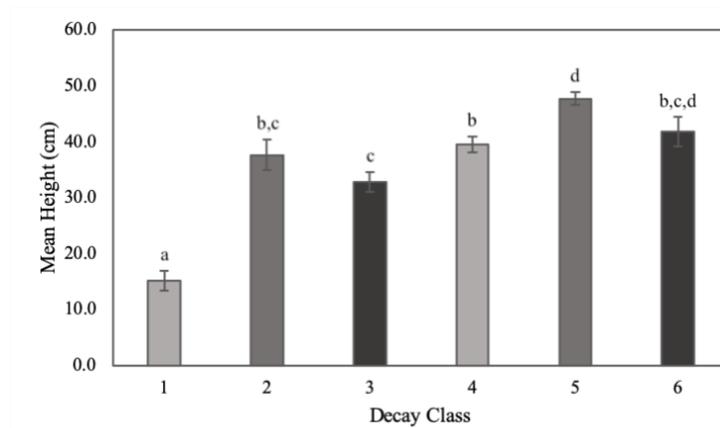
3.4 Effect of Coarse Woody Debris Decay Class on Organic Matter

Mean organic matter depth and decay class categories were significantly related. The lowest mean organic matter depths were recorded next to CWD in decay class 1 at $1.30 \text{ cm} \pm 0.10$ (SE), and the second lowest were found near CWD in decay class 3 at $1.40 \text{ cm} \pm 0.10$ (**Figure 4c**). The two highest mean organic matter depths were found near CWD in decay class 6 ($2.10 \text{ cm} \pm 0.30$) and decay class 2 ($2.00 \text{ cm} \pm 0.20$). Post-hoc tests determined that the quadrats surrounding CWD in decay class 1 had significantly lower organic matter depths than quadrats near decay class 5. Additionally, organic matter depth near CWD in decay class 5 was significantly higher than the depth recorded near CWD in decay class 4.

(a)



(b)



(c)

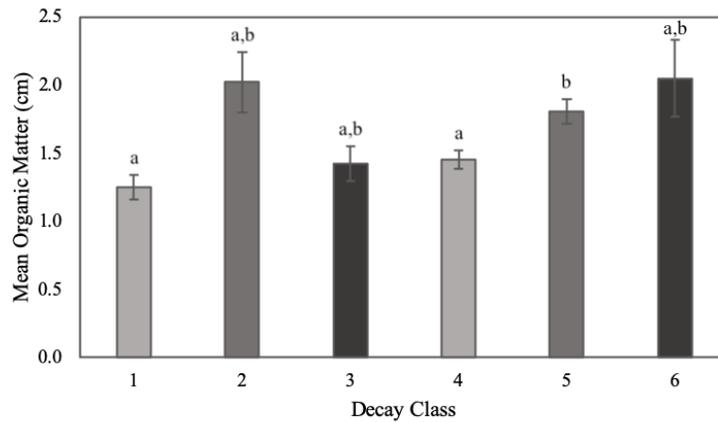


Figure 4. Bar graphs illustrating how (a) density, (b) plant height, and (c) organic matter depth significantly varied by CWD decay class (all $p < 0.05$). Letters indicate significant differences between groups determined by Games – Howell post-hoc tests (all $p < 0.05$).

3.5 Site Quality & Plant Community

Organic matter and plant density had a significant positive correlation ($r_s = 0.1$). Regression analysis on organic matter and plant density was significant, but the test found a low coefficient of determination ($r^2 = 0.02$). Plant height was also positively correlated with mean organic matter depth ($r_s = 0.2$), and regression analysis determined the relationship to be significant with a low coefficient of determination ($r^2 = 0.03$).

The NMS analysis that utilized treatments of high sun, medium high sun, medium low sun, and low sun did not illustrate a clear driver in species assemblages. Axis 1 of the ordination explained 30% of the variance in plant community composition, and axis 2 explained 20% of the variance (**Figure 5**). Although slight relationships were found between plant communities and the fourteen environmental variables tested, none of the environmental variables significantly correlated with axis 1 or 2.

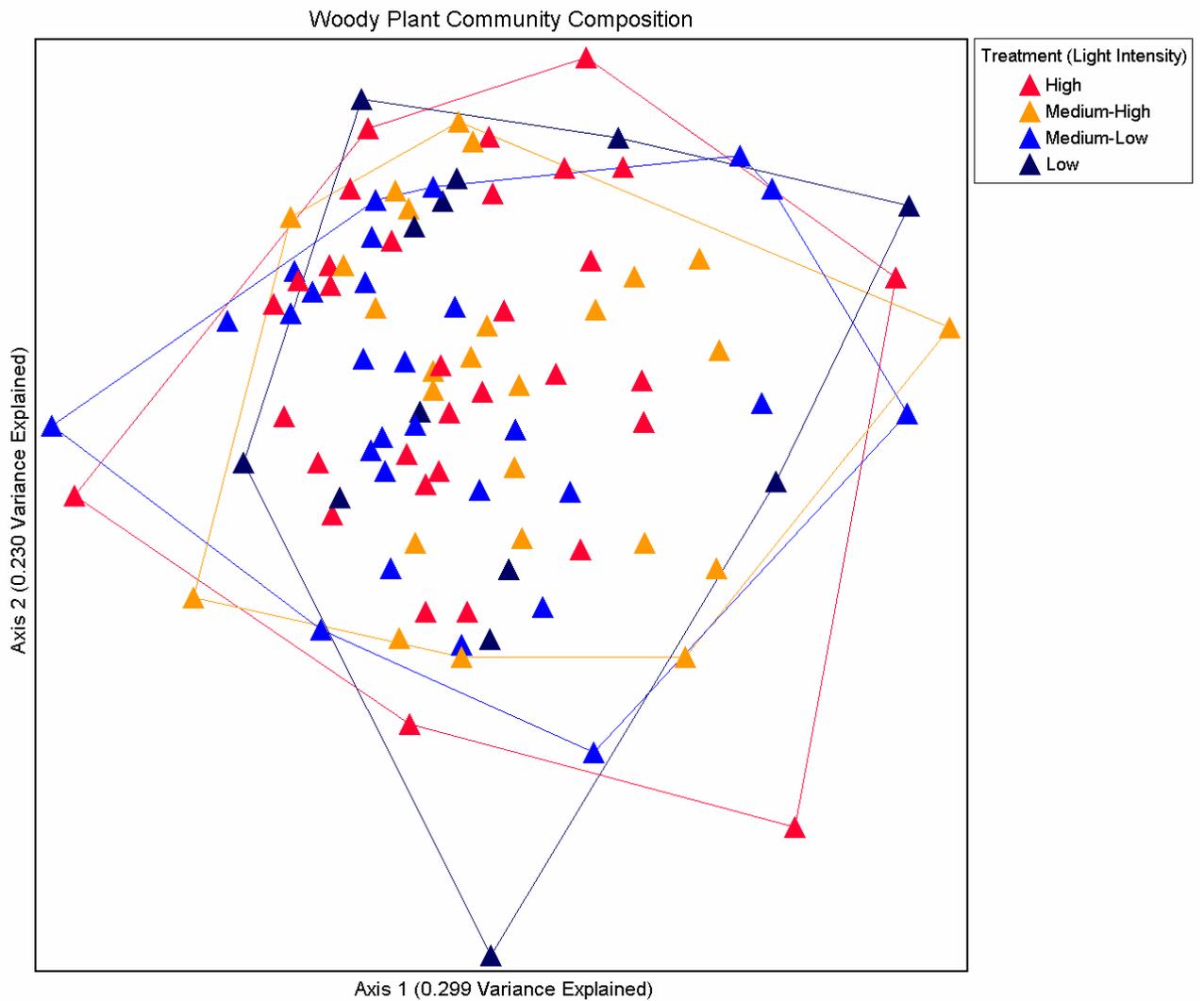


Figure 5. Three-dimensional non-metric multidimensional scaling based on light intensity categories. No clear relationship is illustrated between sun treatment and plant community assemblages.

3.6 Relationship Between Soil & Plant Features

Plant density and dry soil weight were found to have a significant positive correlation ($r_s = 0.1$). Richness and wet and dry soil weight also had a significant positive correlation ($r_s = 0.1$). Height had a significant negative correlation with soil wet weight, soil dry weight, and organic matter weight ($r_s = -0.1$). Richness also had a significant negative correlation with

organic matter weight ($r_s = -0.1$). Density had a significant negative correlation with soil water content ($r_s = -0.1$). In contrast, plant height had a significant positive correlation with soil water content ($r_s = 0.1$).

Soil wet bulk density had a significant positive correlation with plant density ($r_s = 0.2$). The subsequent regression was significant with a low coefficient of determination ($r^2 = 0.03$). Dry bulk density also had a significant positive correlation with plant density ($r_s = 0.2$), and the regression analysis illustrated a slightly significant relationship between the two variables ($r^2 = 0.03$). Plant height had a significant negative correlation with wet and dry bulk density ($r_s = -0.1$).

4. DISCUSSION

4.1 Oak & Hickory Density Higher Near Coarse Woody Debris

Oak and hickory density was significantly higher in quadrats adjacent to CWD than quadrats that were established away from CWD. This oak and hickory density difference between near CWD and away was largely driven by saplings. Oak and hickory saplings were found in 11% of the quadrats that were contiguous to CWD and only 2% of the quadrats that were not near any CWD. Previous studies have found similar results with the presence of CWD benefiting particular plant species (Fukasawa, 2019; Orman *et al.*, 2016; Raymond *et al.*, 2018). Oak seedlings are able to sprout aggressively after prescribed fires (Dey & Hartman, 2005; Fan *et al.*, 2012). When oak shoots are killed they will often have suppressed buds beneath the soil surface (Olson & Boyce, 1971). CWD has been found to protect mycorrhizal fungi and fungal hyphae from fire, and aid in the re-establishment of these species post fire (Ford *et al.*, 2018; Perry *et al.*, 1989). Oak root and bud systems could have been protected from prescribed fires by CWD, allowing them to re-sprout more readily after fire than systems located away from CWD.

Alternatively, the CWD may have served as an obstruction to trap oak and hickory seeds as it did with organic matter (Harmon *et al.*, 1986). When only examining quadrats that had oaks and hickories present, there were significantly higher organic matter depths adjacent to CWD than away from CWD. Near CWD, organic matter depth was $1.90 \text{ cm} \pm 0.10$ (SE), and organic matter depth away from CWD was $1.30 \text{ cm} \pm 0.10$. This was similar to the overall trend in organic matter being significantly deeper near CWD. Organic matter cover can aid in the germination of acorns by preserving their moisture content (Barrett, 1931; Korstian, 1927). The

potential increase in oak and hickory seeds retained near CWD and the greater organic matter cover may have increased the density of oak and hickory seedlings near CWD.

4.2 Coarse Woody Debris & Seedling Height

The increase in mean woody plant height adjacent to CWD was primarily driven by seedlings. Past CWD studies conducted in various forest types have found that CWD presence can improve individual growth rates (Bace *et al.*, 2011; Holeska *et al.*, 2007; Orman & Szewczyk, 2015). The difference in height found in this study may be a result of the CWD sheltering seedlings from browsing or by the CWD forming a microsite with a more favorable microclimate (Bailey *et al.*, 2012; Whyte & Lusk, 2019). CWD has been shown to provide a windbreak for seedlings located one to seven barrier heights on the leeward side of the log and one barrier height on the windward side (Bird *et al.*, 2007). The mean diameter for CWD in this study was 20.80 cm \pm 0.10 (SE), therefore, seedlings about 1.40 m on the leeward side of CWD could be protected and seedlings 0.20 m on the windward side could be protected. This study was conducted in a stand that experienced a catastrophic wind disturbance, thus, the CWD sampled did not have any trees nearby that could potentially serve as windbreaks. The protection of seedlings from wind may be one factor contributing to greater plant heights adjacent to CWD.

A sheltering object can alter temperature and humidity values over a relatively short distance when compared to wind velocity (Cleugh & Hughes, 2002). The presence of CWD could have resulted in a more favorable microclimate for seedling growth by reducing temperature changes and increasing humidity through decreased evapotranspiration (Bailey *et al.*, 2012). Seedlings were found most often on south facing slopes (45%) and west facing slopes (36%). South facing slopes receive more sun than north facing slopes, and vegetation on west

facing slopes must bear the harsh afternoon sun. The increased humidity and temperature stability provided by CWD could have decreased desiccation in seedlings and facilitated growth (Battaglia & Reid, 1993).

4.3 Coarse Woody Debris Characteristics & Plant Community Traits

Seedlings were significantly taller in quadrats that had additional CWD within a quadrat. The two soil map units of the study site, Maubila flaggy loam and Maubila-Smithdale complex, are considered to have high erodibility, and CWD can protect soil from erosion (Pinno & Das Gupta, 2018; USDA, 2019). A large aggregation of CWD could have helped protect the soil in the study site from erosion, therefore, aiding plant growth. Furthermore, the extremely grouped CWD would have led to a reduction in growing space, but potentially an increase in favorable microsite conditions. A high concentration of CWD may have positively affected plant growth by providing increased shelter and beneficial soil qualities while encouraging individual growth to surpass CWD heights and achieve greater sunlight availability.

Plant density peaked near CWD in decay class 2 and decreased in later decay stages. The majority of past research has shown that as decay advances CWD becomes a more favorable substrate, resulting in an increase in plant density (Andersson & Hytteborn, 1991; Chećko *et al.*, 2015; Kumar *et al.*, 2018; Orman & Szewczyk, 2015). However, when CWD is severely decayed a decrease in plant density has been observed (Orman *et al.*, 2016). The high plant density found in quadrats adjacent to CWD in decay class 2 may be related to the decay class being better able to protect root and bud systems from prescribed fire because the logs are still intact and in early stages of decay (Harmon *et al.*, 1986). Decayed logs are more easily consumed by fire, therefore, CWD in later decay stages may not have been able to protect root and bud systems as

efficiently as CWD in decay class 2 (Brown *et al.*, 1985; Pyne *et al.*, 1996). The majority of CWD in the study resulted from a catastrophic wind disturbance that occurred in 2011, therefore, the observed decrease in plant density in later decay stages may simply be a function of time. As time progressed post-disturbance, the CWD would become more decayed and there would be increased competition among seedlings that would result in fewer individuals (Harmon, 1989).

Woody plant density, oak and hickory density, plant richness, mean height, and organic matter depth were all documented to be higher near uncharred CWD than charred CWD. The formation of char can be variable and depend on factors such as fire intensity and duration and soil porosity and moisture (Knicker, 2007). For instance, more energy is required to combust moist fuels than dry fuels because water must be removed from the substance before carbonization can begin (Frandsen, 1987; Nelson, 2001). Fire intensity is also influenced by a myriad of factors including fuel moisture, fuel bed structure, and weather (Alexander, 1982; Martin & Sapsis, 1992). The carbonization process can begin to take place above 200 °C, and above 300 °C roots, seeds, and soil nutrients can be consumed (Frandsen, 1991; Freitas *et al.*, 1999). The area around CWD that was scored as charred likely experienced more extreme temperatures than CWD that did not have visual signs of char, and these high temperatures could have burned a greater amount of fuel and consumed root and bud systems belowground. The CWD that did not have char did not experience the threshold temperature of 200°C, or it did not encounter extreme temperatures for an adequate duration. An area not reaching the critical temperature for charring could have resulted in the facilitation of individual establishment after fire. There was not a clear relationship between uncharred CWD and other CWD characteristics, specifically decay stage, size, and sun versus shade treatment. Therefore, it is difficult to

conclude whether the fire was influenced by the presence of CWD or if the char variation was a result of natural fire pattern variability.

4.4 Influence of Coarse Woody Debris on Plant Community & Soil Traits

No significant difference between plant density and richness near CWD versus away was found in this study. Furthermore, soil measurements taken during this study were not found to significantly differ between areas near CWD and away. Soil properties can be a dominant factor in plant community characteristics, leading to the presence of CWD to only influence minor changes (Brais *et al.*, 2006; Pinno & Das Gupta, 2018). The close similarity of soil variables measured in this study may help to explain why total plant density and richness were not distinct by proximity to CWD.

Another potential explanation for the lack of division in plant density and richness near CWD and away is that plant communities found in forest types with historically low volumes of CWD may predominately respond to soil and site characteristics rather than the presence of CWD. The longleaf pine ecosystem in the southeastern U.S. typically supports some of the lowest volumes of CWD when compared to other forest types and regions (Ulyshen, 2018; Ulyshen *et al.*, 2018). Little has been reported on the role of CWD in longleaf pine woodlands specifically, however, one herpetofaunal study was completed on an upland pine stand in the southeastern U.S. Coastal Plain. Davis *et al.*, (2009) found that the amphibians and reptiles of the study site were lacking a reliance on CWD for habitat. It was concluded that the herpetofaunal must have adapted to the characteristically low CWD volumes that are typical of the longleaf pine ecosystem that historically dominated the site. The results from this study suggest a similar relationship between CWD and woody plants. It may be that ecosystems in the southeastern U.S.

that do not have historically high volumes of CWD may support plant and animal populations that have largely adapted to survive without CWD, but can still benefit from its presence.

Slight distinctions in woody plant assemblages were found using NMS ordination, however, the analysis could not determine which variables examined in this study caused these distinctions. The separation of woody plant assemblages may be due to various re-sprouting abilities of species in the study site. Additionally, it may be related to soil characteristics. One area of CWD research that was beyond the scope of this investigation was the influence of downed wood on soil nutrients. Carbon and nitrogen soil content increases with the presence of CWD (Blońska *et al.*, 2017; Harmon *et al.*, 1986; Stutz & Lang, 2017). Soil base saturation and pH can also potentially be increased by CWD (Stutz & Lang, 2017). It is possible that there were underlying soil nutrient qualities influencing the minor differences in plant assemblages illustrated in ordination.

4.5 Conclusions

CWD retention has become a consideration in forest management because of its many ecological functions: protecting soil from erosion (Vázquez *et al.*, 2011), increasing water runoff retention (Ludwig *et al.*, 2005), providing a beneficial substrate for plants (Stroheker *et al.*, 2018), creating a favorable microclimate (Bailey *et al.*, 2012), serving as critical habitat for breeding animals (Gibbons & Lindenmayer, 2002), and increasing biological diversity (McWinn & Crossley, 1996). This study illustrated that retaining high, localized amounts of CWD can positively influence plant height. The results from this examination also found a relationship between CWD decay stage and woody plant density, height, and species composition. Quadrats adjacent to CWD in decay class 2 had the greatest woody plant density, quadrats near CWD in

decay class 5 had the greatest plant heights, and differences between woody plant composition was found across varying decay classes. Similar to past findings, these results suggest that management aimed to promote native forest diversity should retain CWD volumes with varying amounts and decay stages because these characteristics help dictate local plant traits (Hagan & Grove, 1999; Harman *et al.*, 1986).

This study did illustrate a relationship between CWD and oak and hickory density in a longleaf pine forest. Additionally, the majority of CWD in the study site (59.33%) did not show signs of combustion, and uncharred CWD was related to a higher oak and hickory density. These findings may inform managers of longleaf pine stands to retain relatively low amounts of CWD to prevent invasion by oak and hickory.

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