RESPONSES OF BARK BEETLES AND THEIR ASSOCIATES TO A SEVERE WIND DISTURBANCE IN SOUTHERN PINE STANDS

by

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(Under the Direction of Kamal J.K. Gandhi and Elizabeth McCarty)

ABSTRACT

Bark beetles (Coleoptera: Scolytinae) are commonly reported to reach epidemic levels in wind disturbed stands due to increases in resources such as weakened or recently killed trees. Hurricanes are important wind disturbance agents and can cause spatially heterogeneous damage across a forest, which may impact insect population responses to the disturbances. In 2018, Hurricane Michael struck the Florida Panhandle, damaging over 1.2 million hectares of forests. In the growing season following Hurricane Michael, I conducted a study to determine how populations of bark and root-feeding beetles and their predators responded to different severities of hurricane damage [low (≤20%), moderate (21-40%), and high (≥41 %)]. Over 200,000 bark and root-feeding weevils were captured during of this study. Results indicate insect populations were similar among stands with different wind damage severities. This study may inform foresters engaged in post-hurricane management activities such as salvage harvesting to prevent economic losses from insects.

INDEX WORDS: Bark beetles, Disturbance, Forest management, Hurricane, Population ecology

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DEDICATION

I would like to dedicate this thesis to my late grandfather, George Foster III. George was an avid outdoorsman who spent countless hours in the woods hunting, fishing, and working. He studied forestry in college and worked in the forestry industry in Arkansas and Louisiana. I am grateful for his support, encouragement, and everything he taught me about the natural world.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 INTRODUCTION

Southeastern U.S. forests extend from eastern Texas and Oklahoma to Florida and Virginia, covering an area of approximately 93 million hectares (Butler and Wear, 2013). These forests are among the most productive in the world and are aptly termed as the "Wood Basket of the World" (Oswalt et al. 2019). Roughly half of these 93 million hectares are pine-dominated forests, which contribute the majority of timber harvests in the region (Hanson et al. 2010; Wear et al. 2013). Important pine species in the Southeast include loblolly (*Pinus taeda* L.), slash (*P. elliottii* Engelm.), longleaf (*P. palustris* Mill.), and shortleaf pine (*P. echinata* Mill.) (Gaby 1985). The Southeast yields billions of cubic feet of timber products annually and produces 17% of the world's industrial roundwood (Wear et al. 2016). The forestry industry's impacts on the economy of the Southeast are significant, creating hundreds of thousands of jobs and generating billions of dollars in revenue and income annually in the region (Hanson et al. 2010).

Natural disturbances like droughts, windstorms, and insect outbreaks frequently impact southern pine forests and alter stand structure, species composition, and economic values (Klos et al. 2009; Oswalt et al. 2008; Oswalt et al. 2016). Bark beetles (Curculionidae: Scolytinae) are important components of forested ecosystems and often act as disturbance agents (Hicke et al. 2016). These beetles are associated with a variety of other insects that can impact forests and influence bark beetle populations, like predators and other herbivores (Stephen 2011). Bark beetle outbreaks can occur following disturbance events (Connola et al. 1956; Gardiner 1975; Gochnour et al. 2022). Outbreaks arising from a previous weather-related disturbance event can compound the long-term impacts of the initial disturbance (Nikolov et al. 2014).

Wind disturbances are among the most important and widespread type of weather-related disturbance in southeastern U.S. forests (Vogt et al. 2020). Wind disturbances can range from small, frequent thunderstorms that impact small areas to infrequent catastrophic hurricanes that impact large regions (Meigs and Keeton 2018). A single hurricane can damage hundreds of millions of trees and cause billions of dollars in losses for the timber industry (Oswalt et al. 2008; Prestemon and Holmes 2010). Hurricanes and other tropical cyclones are common in the Southeast and can have significant and extensive impacts on pine forests.

One of the most impactful recent hurricanes was Hurricane Michael. This storm made landfall in Florida in 2018 as a category five hurricane (Beven et al. 2019). In Florida and Georgia alone, an estimated two million hectares of forest were damaged by the storm's catastrophic winds (Florida Forest Service 2018; Georgia Forestry Commission 2018). Wind disturbances can make forests more susceptible to other disturbances such as insects and diseases (Temperli et al. 2013). Many forest owners were concerned that the forest damage caused by Hurricane Michael might precipitate an outbreak of bark beetles, exacerbating the initial hurricane damage (Florida Forest Service 2018). That fear was well founded, as the Florida Forest Service reported several outbreaks of pine bark beetles (*Ips* spp.) in 2019 in the Florida Panhandle (Florida Forest Service 2019). Understanding how bark beetles respond to catastrophic wind disturbances like Hurricane

Michael in southern pine forests will be crucial in planning management operations that minimize potential economic losses from pests following future catastrophic windstorms in the Southeast.

The economic losses associated with catastrophic wind damage in high-value southern pine forests and the costs of restoring these forests are considerable (Florida Forest Service 2018). Epidemic outbreaks of bark beetles following hurricanes could substantially increase these economic losses by causing mortality, further degrading already-damaged timber, and complicating expensive restoration efforts. Salvage logging may allow foresters to recover some value while simultaneously minimizing the risk of bark beetle outbreaks. Proper planning of salvage operations to recover timber values before beetle outbreaks occur will be crucial in minimizing economic losses from pest damage. However, there has been little research into how bark beetle populations react to wind disturbances in forests in the region.

1.2 LITERATURE REVIEW

1.2.1 Bark Beetle Ecology

Bark beetles belong to Scolytinae, a subfamily containing roughly 6,000 species within the family of true weevils, Curculionidae (Kirkendall et al. 2015). These insects are found in a wide range of ecosystems throughout the world, including the temperate and boreal forests of the northern hemisphere and the tropical rainforests of Australia (Connola et al. 1956; Gardiner 1975; Grimbacher and Stork 2009; Kerchev 2014). Bark beetles exploit a wide variety of resources, including fruits, seeds, and herbaceous plants; however, the most economically important species are phloem feeders that attack trees and other woody plants (Raffa et al.

2015). Well-known forest pests in this group include *Ips* spp., *Dendroctonus frontalis* (Zimmerman), and *D. terebrans* (Oliver). The *Ips* spp. of the southern pine bark beetle guild (*I. avulsus* Eichhoff, *I. calligraphus* Germar, and *I. grandicollis* Eichhoff) are among the most ecologically important species of bark beetles in the Southeast (Nebeker 2011).

The economic damages caused by bark beetles are a result of their feeding and brooding habits. The most serious injury to trees is the destruction of phloem, which can significantly disrupt nutrient translocation throughout the host tree and result in mortality (Hubbard et al. 2013). Though the life cycles of these insects can vary substantially between species, many commonalities exist among phloem-feeding bark beetles. Mature beetles typically emerge from their brood galleries to search for mates and new hosts in the spring or summer. Emerging adults usually find suitable host trees within several hours or days and bore entrance holes into the bark to create mating chambers. Upon entering the host tissues, many species inoculate their host with symbiotic fungi or microbes that assist in host colonization (Hemingway et al. 1977; Zhou et al. 2001). Adults then mate in these newly excavated mating chambers and females bore brood galleries where they oviposit. Once the eggs have hatched, larvae begin feeding and create new galleries in their hosts' phloem as they develop. Larvae develop through 2-5 instars, after which they pupate in their feeding galleries or pupation chambers that they create within the phloem. After pupation, adult beetles begin maturation feeding to complete development. Maturation feeding is an important process in which adult beetles feed on phloem after pupation to acquire the nutritional resources needed to complete development before emergence (McNee et al. 2000). Once fully matured, adults bore exit holes through the bark of their natal host to search for mates and new hosts, beginning the cycle anew.

Bark beetles must overcome their host tree’s diverse arsenal of defense mechanisms throughout their life cycle. A well-documented example of this struggle between herbivore and host plant can be found in coniferous trees. Conifers have evolved well-developed, vigorous defenses to protect themselves against herbivores due to their long history of coevolution with diverse groups of natural enemies including dinosaurs (Chin and Gill 1996; Franceschi et al. 2005; Prasad et al. 2005). These defenses can interfere with bark beetle feeding and development in a variety of ways. Invading beetles may be suffocated or physically pushed out of entrance holes by resin flows induced by bark beetle-mediated tree wounding (Berryman et al. 1989). Beetle-attacked conifers also produce a plethora of chemicals that can repel or kill the beetles (Schiebe et al. 2012).

Bark beetles exhibit several means of overcoming these defense mechanisms. Some bark beetle species engage in mass attacks in which large numbers of adult beetles attack individual trees, often overwhelming the defenses of a healthy host (Paine et al. 1997). Other species may attack weakened or recently killed trees to avoid the vigorous defenses of healthy hosts (Louis et al. 2016). These insects can even use the toxic defense compounds of their hosts to their advantage by utilizing these chemicals as precursors to their communication pheromones (Seybold et al. 2000). Additionally, many bark beetle species have fungal or microbial symbionts, which can weaken the defenses of their hosts (Hemingway et al. 1977). *Dendroctonus terebrans* and *Ips* spp. are associated with a variety of fungal pathogens, such as *Ceratocysis* spp., *Leptographium* spp., and *Ophiostoma* spp., that can weaken pines (Klepzig and Six 2004; Rane and Tattar 1987).

Bark beetles rely on a variety of chemical cues for locating suitable hosts and mates. Volatile organic compounds (VOCs) are used by these insects for locating host trees (Pureswaran et al. 2004). Plant VOCs are gaseous chemicals, typically monoterpenes and ethanol in conifers, that diffuse from plant cells due to vapor pressure (Lerdau et al. 1997). High levels of tree stress can lead to elevated emissions of these VOCs, which bark beetles can easily follow to find the weakened hosts (Raffa 2001). Bark beetles also produce their own chemical signals for intraspecific communication and attracting or locating mates. Once colonizing adults locate a new host and excavate a mating chamber, beetles release sexual or aggregation pheromones to attract mates and other conspecifics, respectively (Allison et al. 2012). Aggregation pheromones are also used to initiate mass attacks in aggressive species of bark beetles, such as the southern pine beetle (Sullivan 2011). Conversely, some bark beetle species also emit anti-aggregation pheromones to reduce intraspecific competition once they have reached optimal colonization densities within their host (Raffa 2001). Sexual, aggregation, and anti-aggregation pheromones and host VOCs play a large role in the dynamics of bark beetle outbreaks.

Bark beetles typically persist in small, endemic populations that cause little economic damage (Smith et al. 2011). However, under certain conditions, these populations can erupt into large-scale outbreaks that can cause widespread alterations and substantial economic losses in forests (Marini et al. 2017). The transition from small, endemic populations to large, epidemic outbreaks can be triggered by several different phenomena. Abiotic disturbances, like windstorms or droughts, can weaken and stress trees throughout a stand and make these trees more susceptible to bark beetle attack (Louis et al. 2016). Increased quantities of susceptible host trees can allow bark beetle populations to grow to numbers that exceed the insects' typical endemic population levels (de Groot et al. 2018). Unusually warm temperatures can also contribute to the formation and dynamics of bark beetle outbreaks. Increased temperature can accelerate the development of immature beetles and create conditions advantageous for locating hosts and mass swarming along with creating more stressed trees in the stands (Vakula et al. 2015).

Bark beetle outbreaks can substantially alter ecosystems, affecting everything from forest hydrology and soil structure to nutrient cycling and vertebrate assemblages (Lynch et al. 2021; Martin et al. 2006; Pugh and Small 2012). Vast areas of forest are converted from carbon sinks to sources, impacting global carbon cycling (Kurz et al. 2008). The early abscission of young, nitrogen-rich needles may also occur, resulting in locally altered soil nutrient cycling (Morehouse et al. 2008). Higher rates of snowmelt have been attributed to increases in snow accumulation and solar radiation on the forest floor caused by the decrease in canopy cover associated with bark beetle-mediated-tree mortality, which ultimately leads to altered hydrological cycles (Pugh and Small 2012). Additionally, animal communities are modified by altered habitat and resource availability. For example, outbreaks of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) altered the abundance and diversity of forest-dwelling birds in Utah (Martin et al. 2006). Bark beetle outbreaks can also influence reptile distributions, mammal populations, and the diversity of other insects within affected stands (Gandhi et al. 2022).

In addition to their ecological impacts, bark beetle outbreaks often cause significant economic impacts. Outbreaks can significantly reduce the economic value of timber stands due to widespread tree mortality and the degradation of wood quality caused by bark beetle feeding (Connola et al. 1956). The southern pine beetle causes an estimated $43 million in damage per year on average, and the mountain pine beetle is expected to cause a 1.34% decrease in Canada's GDP between 2009 and 2054 (Corbett et al. 2015; Pye et al*.* 2011). The value of homes near infested stands and the recreational value of forests are reduced, leading to decreased revenues from real estate, recreation, and tourism (Holmes and Koch 2019; Rosenberger et al. 2013). The propensity of bark beetle populations to grow to epidemic levels following disturbance events like windstorms can compound the economic damages of the initial disturbance (Nikolov et al*.* 2014).

1.2.2 Bark Beetle Associates

1.2.2.1 Predators

Bark beetles interact with a wide variety of other organisms, including other herbivores and predators. Predators play an important role in bark beetle ecology and may impact outbreak dynamics (Reeve 1997). A variety of organisms prey on bark beetles, including birds like woodpeckers and other insects (Wegensteiner et al. 2004). Notable insect predators of bark beetles include flies (Diptera), such as long-legged flies (Dolichopodidae) and lance flies (Lonchaeidae: *Lonchaea* spp.), and beetles such as checkered beetles (Cleridae), bark-gnawing beetles (Trogossitidae), and hister beetles (Histeridae) (Kenis et al. 2015). Predation by carnivorous insects can be a significant source of bark beetle mortality and may slow the colonization of host trees by these pests (Reeve 1997).

One such predator is *Temnoscheila virescens* (Fabricius) (Coleoptera: Trogossitidae). This insect belongs to the superfamily Cleroidae, which contains many bark beetle predators, including the dubious checkered beetle (*Thanasimus dubius* Fabricius). *Temnoscheila virescens* is a common bark beetle predator that has been reported throughout the Southeast and other parts of the eastern U.S. (Billings and Cameron 1984; Kulhavey and Gover 1989; Mignot and Anderson 1970). Adults hide in bark crevices and attack *Ips* spp. as they attempt to enter the phloem of host trees (Chism 2013). Larvae live in the galleries created by *Ips* spp. in the phloem and feed on immature bark beetles (Mignot and Anderson 1970). This predator is closely linked to *Ips* spp. through its chemical ecology. Though *T. virescens* has been observed to feed on non-*Ips* spp. prey items in laboratory settings, the insect showed strong responses to the *Ips* spp. pheromones - ipsenol and ipsdienol (Billings and Cameron 1984; Lawson and Morgan 1993). Additionally*, T. virescens* showed no response to southern pine beetle pheromones such as frontalin, further suggesting that this insect is an obligate predator of *Ips* spp. (Billings and Cameron 1984).

Temnoscheila virescens is an efficient predator of *Ips* spp. and has even been used as a biological control agent of the *I. grandicollis* in exotic pine plantations in Australia (Lawson and Morgan 1993). While these beetles cannot completely stop an *Ips* spp. attack, predation by *T. virescens* can reduce the number of adult *I. grandicollis* that successfully enter the phloem by 66.7% (Chism 2013). However, these impacts may diminish at high predator densities. In laboratory experiments, adult *T. virescens* commonly cannibalized one another when no other prey items were available, and they preyed on dubious checkered beetle adults under high predator densities (Chism 2013; Mignot and Anderson 1970). This suggests *T. virescens* populations are controlled by prey and competitor densities. This density dependence may influence this predator's response to bark beetle outbreaks.

1.2.2.2 Root-Feeding Weevils

Root-feeding weevils comprise another important group of insects associated with bark beetles. These beetles belong to Hylobiini, a tribe within Curculionidae. Well known representatives include the large pine weevil (*Hylobius abietis* L.) and the pine root collar weevil (*H. radicis* Buchanan). These insects are associated with recently cut pine stumps, dying pines, and regenerating pine stands (Drooz 1985; Rieske and Raffa 1990). In the Southeast, *H. pales* (Herbst) and *Pachylobius picivorus* (Germar) are common root-feeding pests of conifers. Root-feeding weevils can cause high rates of pine mortality and injury, making them one of the most important groups of pinophagous, or pine feeding, insects in eastern North America (Nord et al. 1982).

Adult root-feeding weevils congregate near stressed, recently cut pine stumps or the base of dying pines in the spring to mate. *Hylobius pales* and *P. picivorus* females oviposit in feeding niches on roots up to 30 cm below ground (Flavell 1974; Salom et al. 1987). Following eclosion, larvae feed on the phloem of their respective oviposition sites. Pupation occurs in chip cocoons under the bark (Price 2008). Once fully mature, adults emerge and disperse to locate feeding resources in the late summer (Roberts and Douce 1999). Mature weevils feed on the inner bark of young, tender pine shoots and stems, often targeting seedlings (Nord et al. 1982). After feeding, adults enter diapause, though they may remain active through the year during warm winters (Roberts and Douce 1999).

Once sexually mature, adult weevils seek out suitable brooding material in the spring by utilizing chemical cues, much like bark beetles. Root-feeding weevils are attracted to semiochemicals emitted by recently cut stumps and stressed or dead pines such as turpentine and ethanol (Rieske and Raffa 1990). Turpentine is likely used for host recognition, while ethanol may aid the weevils in locating sufficiently weakened hosts (Rieske and Raffa 1991). Peak attraction to these chemicals usually occurs during ovipositional periods in spring and decreases thereafter (Rieske and Raffa 1990). However, *H. pales* and *P. picivorus* respond dissimilarly to different ratios of ethanol and turpentine, with *H. pales* responding to higher ethanol ratios than *P. picivorus* (Rieske and Raffa 1991). These different responses may allow these insects to partition common resources.

Root-feeding weevils are major pests of regenerating pine forests throughout eastern North America. These weevils are common pests of first year pine plantations in recently cut sites in the Southeast and Christmas tree farms in the Midwest (Nord et al. 1982; Rieske and Raffa 1991). The feeding damage caused by these insects can reduce the commercial quality of trees by disfiguring stems (Corneil and Wilson 1984; Drooz 1985). Damage from *H. pales* and *P. picivorus* feeding can commonly cause 30-60% seedling mortality within a regenerating stand, though mortality rates can reach as high as 90% if not properly managed (Nord et al. 1982). In addition to their feeding damage, root-feeding weevils can also act as vectors of weak tree pathogens. Several Ophiostomatoid fungi have been isolated from *H. pales* and *P. picivorus*, including *Leptographium* spp., *Ophiostoma* spp., and *Pesotum* spp. (Zanzot et al. 2010). In the Southeast, *P. picivorus* and *H. pales* are strongly associated with two species of *Leptographium, L. procerum* and *L. terebrantis* (Eckhardt et al. 2007). *Hylobius pales* has been identified as the principal vector of *L. procerum* in Virginia pine (*P. virginiana*) forests (Salom et al. 1994). These pathogens may weaken trees and make them more susceptible to bark beetle attacks.

1.2.3 Wind Disturbances

Wind, much like bark beetle outbreaks, is an important disturbance agent and can cause significant economic losses and alterations to forests (Batista and Platt 2003; Oswalt et al. 2008; Prestemon and Holmes 2010). Wind disturbances may be defined as discrete events in time in which strong winds disrupt ecosystem processes and functioning. In the Southeast, common wind disturbances include derechos, tornadoes, and tropical cyclones like hurricanes. These disturbances vary in intensity and frequency, ranging from infrequent, catastrophic disturbances like hurricanes to frequent, less-intense events, like thunderstorm-associated downbursts (National Hurricane Center 2021). Wind disturbances can cause substantial injuries or mortality in individual trees, leading to alterations in species composition and stand structure across the affected landscape (Busing et al. 2009; Gresham et al. 1991). High winds can snap stems or branches, uproot entire trees, and cause defoliation, thus resulting in elevated tree stress or mortality (Foster and Boose 1992).

Wind-associated weather events frequently damage commercially important forests and can cause substantial economic losses to forest owners. In southern pine forests, Hurricanes Hugo, Frances, Ivan, Katrina, and Rita caused over $7 billion in timber losses between 1989 and 2005 when adjusted for 2021 inflation (Prestemon and Holmes 2010; US Inflation Calculator 2021). Severe windstorms can also result in considerable property damage and loss of human life, causing socio-economic impacts that can cripple communities for years (Sutter and Simmons 2010; Zoraster 2010). Additionally, wind disturbances may create conditions that make forests more susceptible to other disturbances, like insect outbreaks. This susceptibility can lead to further economic losses and ecological alterations (Nikolov et al. 2014).

Wind disturbances have far-reaching impacts on forests that can be seen at the individual tree-level all the way to the landscape-level. Effects may be relatively short-term or manifest as legacies that persist for decades or centuries (Foster et al. 1998; Ostertag et al. 2003). Individual trees can be subjected to a multitude of wind-related injuries during a windstorm. High winds cause stress along the entire tree. Physical stress can cause the tree to bend, placing strain on and injuring plant tissues (Wood 1994). Stems and branches can snap and entire trees may be uprooted as a result of this physical strain (Mitchell 2013). Wind-related injuries such as total uprooting or stem breakage may result in rapid tree death or increased stress in surviving trees, possibly leading to delayed mortality (Everham and Brokaw 1996). Wounding caused by these injuries can facilitate the entry of economically damaging insects and pathogens, such as bark beetles and their fungal symbionts, which can worsen the initial damage (Shortle and Dudzik 2012). Tree deformities caused by wind damage and the colonization of wounded trees by pests can degrade timber quality and economic values (Connola et al. 1956).

The damage and mortality inflicted upon these trees can also have significant impacts on biotic communities at the landscape level by altering resource and habitat availability and distribution. Large influxes of leaf litter and woody debris caused by wind disturbances can alter nutrient availability in forest soils for recovering vegetation (Van Bloem et al. 2005). Increases in nutrients were documented in Puerto Rican forests following Hurricane Georges, where forest floor litter mass increased by as much as 150% relative to pre-disturbance conditions, resulting in elevated nutrient concentrations in soils (Ostertag et al. 2003). Changes in nutrient availability benefit both surviving and newly established vegetation following a wind-disturbance; however, this benefit is often short lived. Nutrient concentrations returned to pre-hurricane levels within ten months of Hurricane Georges (Ostertag et al. 2003). The surge of weakened or recently killed trees following a windstorm provides subcortical insects with greater amounts of nutritional resources and suitable substrates (de Groot et al. 2018; Louis et al. 2016).

Wind disturbances can also significantly alter forest structure. A readily observable example of wind-mediated alterations in structure is the formation of canopy gaps resulting from windthrown trees. Canopy gap formation creates new habitats within a forest influencing species composition, age structure, and biodiversity (Mitchell 2013). The effects of strong wind vary among trees of different species and age classes due to differences in tensile strength, rooting characteristics, and tree size and shape (Coutts 1986; Everham and Brokaw 1996). These differences can lead to disparate mortality rates among different species or size classes of trees, altering species compositions and age structures throughout a stand. For instance, in the aftermath of Hurricane Michael, mortality increased with tree size in longleaf pine stands (Zampieri et al. 2020). Following Hurricane Hugo, conifers were less likely to be damaged by winds than hardwood species (Gresham et al. 1991). In addition to the changes in forest structure, the wind-mediated uprooting of trees can alter soil biogeochemical processes and physically modify the forest floor by creating pit and mound topography (Bowden et al. 1993; Clinton and Baker 2000). The long-lasting legacies of wind disturbance often results in a heterogeneous mosaic of age structures, species compositions, and habitat types across the landscape (Mitchell 2013).

This mosaic of wind-related damage results from the spatial heterogeneity of disturbance severity (Foster 1988). Wind disturbance damage heterogeneity is caused by meteorological factors together with biotic and abiotic landscape traits. The intensity and direction of winds can change as the windstorm passes through the landscape and lead to patterns of dissimilar damage (Everham and Brokaw 1996). These patterns are prominent following tropical cyclones, as wind direction and speed often change as the cyclone moves across the landscape (Boose et al. 1994). Rainfall rates also vary spatially during a severe wind disturbance event. Variation in rainfall can lead to different patterns of damage across a forest because moisture impacts soil strength and consequently, rooting stability (Anthes 1982; Huang et al. 2019). More predictable patterns of damage arise from a stand's proximity to the eye of a cyclonic storm, which can produce a gradient of wind damage radiating away from the path of the storm's eye (Hook et al. 1991). Abiotic stand and landscape factors also contribute to this mosaic of windstorm damage. Topographic position, soil characteristics, aspect, disturbance history, and slope are often spatially variable within a forest and can influence patterns of wind damage, contributing to the spatial heterogeneity of windstorm impacts (Everham and Brokaw 1996). The spatial disparity in damage is partially driven by variability in tensile strength of stems, rooting depth, age, and tree species across a landscape (Coutts 1986). The sum of these factors creates a complex mosaic of variable windstorm damage across a forest.

Hurricanes form in the tropics, where oceanic water surface temperatures and atmospheric conditions are conducive to cyclone development (Boose et al. 1994). Hurricanes are characterized as low-pressure systems that circulate around a central eye with windspeeds exceeding 119 km per hour (National Hurricane Center 2021). These powerful storms can impact millions of hectares of forests and cause billions of dollars in economic damage (Beven et al. 2019; Florida Forest Service 2018). Extensive damage could be readily seen after Hurricane Katrina, where approximately 575 million trees were damaged or killed in Mississippi alone, resulting in a loss of forest products valued at over $1.7 billion (Oswalt et al. 2008; Prestemon and Holmes 2010). Similar damages were inflicted by Hurricane Laura in Louisiana, where >300,000 hectares of forests were damaged, causing over $1 billion in economic losses to the state's timber industry (Powell 2020). Fortunately for southeastern forest owners, major hurricanes, which are defined as those with wind speeds exceeding 179 km/h, are infrequent and typically only strike in 14-to-52-year intervals, depending on location (National Hurricane Center 2021). However, there is mounting evidence suggesting that the intensity of major hurricanes is increasing and that hurricanes are moving more slowly over land due to global climate change (Zhang et al. 2020). Increases in intensity may lead to altered disturbance regimes that exceed forests' ecological resilience, creating a serious need for further research into post-hurricane forest management to ensure the recovery and persistence of southeastern U.S. forests (Johnstone et al. 2016; Reyer et al. 2015; Seidl et al. 2011).

1.2.4 Hurricane Michael

Hurricane Michael was one of the most powerful hurricanes to hit the U.S. in recorded history. The storm was the 4th strongest hurricane and had the 3rd lowest minimum central pressure of a hurricane to make landfall in the U.S. since 1900 (Beven et al. 2019; Janssen et al. 2019). This storm was responsible for 59 deaths and $25 billion in damage, making it one of the most economically devastating hurricanes to hit the U.S. (Beven et al. 2019). Nearly two million hectares of forests were damaged by the storm, resulting in billions of dollars in losses to the local timber industry (Florida Forest Service 2018; Georgia Forestry Commission 2018). Hurricane Michael also seriously altered sensitive ecosystems, like longleaf pine savannas and coastal sand dunes, threatening the recovery of endangered species such as the red-cockaded woodpecker (*Leuconotopicus borealis* Vieillot) and the gopher tortoise (*Gopherus polyphemus* Daudin) (Chapman 2018; Clark et al. 2019). The destructive impacts of this catastrophic storm can be explained in part by understanding the factors that influenced the formation of the storm and its path.

Hurricane Michael began as a large area of disturbed weather that formed over the Caribbean Sea on 2 October 2018 (Beven et al. 2019). The system's circulation and convection had become organized into a tropical depression by 7 October 2018 after absorbing the remnants of another storm and becoming embedded in a cyclonic gyre (Beven et al. 2019; Callaghan 2019). The storm strengthened to a hurricane by 8 October as it was pushed northeast-ward towards the Florida Panhandle by mid-latitude westerlies (Beven et al. 2019; Callaghan 2019). On 10 October 2018, Hurricane Michael made landfall between Tyndall Air Force Base and Mexico Beach, Florida as a category five storm with maximum sustained wind speeds of 259 km per hour and a minimum low pressure of 919 millibars (Beven et al. 2019). Moving northward through the Florida Panhandle and Georgia, Hurricane Michael quickly decreased from a Category 5 storm to a Category 4 storm and eventually weakened to a tropical storm as it approached Macon, Georgia (Beven et al. 2019). The storm then passed through South Carolina on 11 October 2018 and transitioned to an extratropical cyclone as it traveled through North Carolina the next day (Beven et al. 2019). The system regained hurricane force winds by 13 October 2018 as it traveled across Virginia and into the Atlantic Ocean (Beven et al. 2019). After continuing northeastward through the Atlantic, the storm finally dissipated off the coast of Portugal on 15 October 2018 (Beven et al. 2019).

Hurricane Michael heavily impacted the southern timber industry, causing roughly $2 billion in timber losses (Florida Forest Service 2018; Georgia Forestry Commission 2018). The storm damaged >1 million hectares of forests in Florida and approximately 800,000 hectares of forests in Georgia, resulting in estimated losses of $1.3 billion and $762 million, respectively (Florida Forest Service 2018; Georgia Forestry Commission 2018). Over 17% of Florida's forests were impacted by this hurricane (Florida Forest Service 2018; Hodges et al. 2017). In southwest Georgia, ≥50% of the stems on roughly 32,375 hectares were broken by Hurricane Michael's strong winds (Georgia Forestry Commission 2018). While this storm indiscriminately damaged all forests along its path, southern pine forests sustained the most damage due to their widespread abundance in the region (Florida Forest Service 2018; Georgia Forestry Commission 2018). In Florida and Georgia, 647,497 and 485,623 hectares of pine forests were damaged, respectively (Florida Forest Service 2018; Georgia Forestry Commission 2018). Additionally, roughly 607,000 hectares of hardwood forests and over 364,000 hectares of upland mixed pine-hardwood forests were damaged in Florida and Georgia (Florida Forest Service 2018; Georgia Forestry Commission 2018). The damage to hardwood and mixed pine-hardwood forests resulted in a combined $913,759,841 in economic losses (Florida Forest Service 2018; Georgia Forestry Commission 2018). The extent to which these forests will recover to pre-Hurricane Michael conditions is unclear; however, the estimated financial costs of recovery are great (Chapman 2018). The costs of debris removal, reforestation, and overall recovery of hurricane-damaged forests in Florida alone are expected to reach several hundred million dollars (Florida Forest Service 2018). Further compounding this uncertainty and the future costs of recovery are the risk of epidemic bark beetle outbreaks, which could further affect the southern timber industry and hamper recovery efforts.

1.2.5 Insect Responses to Wind Disturbance

Bark beetle abundance commonly increases in forests following severe wind disturbances due to the increases in weakened or recently killed host trees. This response has been documented throughout the world in many different ecosystems. In the boreal forests of northern Ontario, *I. borealis* (Swaine) and *I. perturbatus* (Eichhoff) were prevalent in windthrown jack pine-white spruce stands following a severe windstorm (Gardiner 1975). Increases in subcortical insects were observed following severe wind disturbance in subboreal forests in northern Minnesota (Gandhi et al. 2010). Outbreaks of the European spruce bark beetle (*I. typographus* L.) occurred throughout the Tatra Mountains in Slovakia after the Alzbeta windstorm struck the region (Nikolov et al. 2014). Similar responses were documented in the tropical rainforests of Australia, where bark beetles invaded wind damaged forests following Cyclone Larry (Grimbacher and Stork 2009). These wind disturbance-triggered outbreaks are influenced by many biotic and abiotic factors.

Bark beetle infestations following wind disturbances can be primarily attributed to altered microclimates, increased host VOC emissions, and increases in suitable feeding and brooding resources (Louis et al. 2016; Marešová et al. 2020). These factors can lead to devastating bark beetle outbreaks that may persist for years (Jakuš et al. 2002; Schroeder and Lindelow 2002). Wind disturbance-associated bark beetle outbreaks often exhibit variability in space and time due to the spatiotemporal heterogeneity of suitable resources (Forster et al. 2003; Jakuš et al. 2002). While wind disturbances lead to an increase in bark beetle resources, the availability of these resources may fluctuate over time. Many of the effects of wind disturbance do not occur during or immediately after the storm and may lag behind the initial damage (Jones-Held et al. 2019). Weakened trees can continuously decline until death and may not die for months or years after the disturbance (Henkel et al. 2016). Stems, branches, or crowns of snags may break, and leaning, live trees may fall at different times following the initial disturbance and injure nearby trees (Jones-Held et al. 2019). These delayed effects may change resource availability for bark beetles through time and in turn influence outbreak dynamics. Additionally, resource quality varies through time. The phloem of recently killed host trees and slash degrades over time due to moisture loss, eventually rendering the substrate unusable by bark beetles (DeGomez et al. 2008; Redmer et al. 2001). Delayed tree injuries may also alter host tree VOC emission rates through time, affecting bark beetles' ability to locate suitable host trees (Fineschi et al. 2013; Hietz et al. 2005).

Bark beetle outbreaks following wind disturbance often exacerbate the damage inflicted upon affected forests (Nikolov et al. 2014). Following a severe wind disturbance in northern Ontario, these factors led to a 10% and a 20% loss of merchantable timber one and two years after the storm, respectively (Gardiner 1975). Swift management actions should be taken to minimize financial loss and prevent further damage to commercially valuable trees from bark beetle infestations (Stadelmann et al. 2013). Due to the spatial and temporal complexities of wind disturbance-related bark beetle outbreaks, management activities may be carefully planned to address the unique situation of each stand. This may necessitate different insect suppression strategies in stands with different severities of hurricane damage.

Salvage logging is a useful tool to minimize bark beetle damage following wind disturbances (Gardiner 1975). This treatment harvests weakened, fallen, or recently killed trees to save value that would be otherwise lost while simultaneously removing important bark beetle resources. Salvage logging can also prevent the buildup of bark beetle populations that could potentially move to relatively less damaged stands nearby (Forster et al. 2003). Ideally, management practices like salvage logging could be performed immediately following the wind disturbance in every affected stand to prevent bark beetle outbreaks (Gardiner 1975). However, swift management action is often not practical due to constraints such as a lack of storage space, transportation capabilities, labor, and mill availability arising from the massive influx of salvaged wind-damaged timber (Broman et al. 2009). These limitations force forest owners to make tough decisions and to readjust management priorities (Forster et al. 2003). Efforts focusing on minimizing economic losses from bark beetles must direct management activities to stands with the greatest economic value and the greatest risk of bark beetle outbreaks. The proper timing of actions aimed at protecting wind-damaged stands from bark beetle infestations could possibly vary depending on the severity of wind damage that occurred in the stand. Understanding the bark beetle population dynamics in stands that experienced different severities of wind damage will help inform the proper planning of salvage logging, allowing forest owners to minimize economic losses and ecological alterations following a catastrophic wind disturbance.

1.3 THESIS OBJECTIVES

The goal of this study is to understand how bark beetles (*Ips* spp. and *D. terebrans*), root-feeding weevils (*H. pales* and *P. picivorus*), and bark beetle predators (*T. virescens*) respond to catastrophic wind disturbances in the Southeast. This objective will be accomplished by comparing trap catches of the *D. terebrans*, *H. pales*, *I. avulsus*, *I. calligraphus*, *I. grandicollis*, *P. picivorus*, and *T. virescens* among stands with low (≤20% damage), moderate (21-40% damage), and high (≥41%) severities of hurricane damage in the first growing season after Hurricane Michael made landfall. The results will provide forest managers with information to help make decisions regarding the prioritization of salvage harvesting in stands with different levels of wind damage, with the goal of minimizing potential economic losses from herbivorous insect outbreaks following a catastrophic wind disturbance in the Southeast.

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FIGURES

Figure 1.1: Target bark beetle species: **A.** *Dendroctonus terebrans*, **B.** *Ips avulsus*, **C.** *I. calligraphus*, and **D.** *I. grandicollis*. Images courtesy of Pest and Diseases Image Library, Bugwood.org (Figure 1A, 1D), Natasha Wright, Braman Termite & Pest Elimination Bugwood.org (Figure 1C), and Seth Spinner (Figure 1B).

Figure 1.2: The bark beetle associate target species: **A.** *Hylobius pales*, **B.** *Pachylobius picivorus*, and **C.** *Temnoscheila virescens*. Images courtesy of Jennifer C. Girón Duque, Museum of Texas Tech University, Bugwood.org (Figures 2A-B) and John Ott, Bugguide.com (Figure 2C).

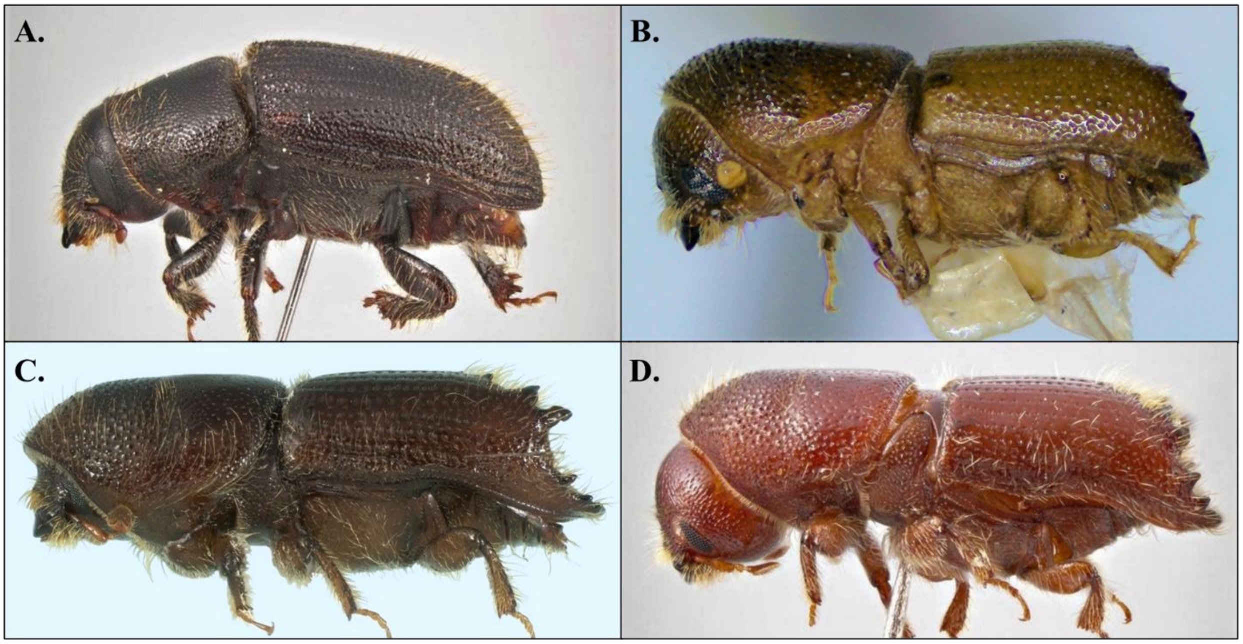

Figure 1.1

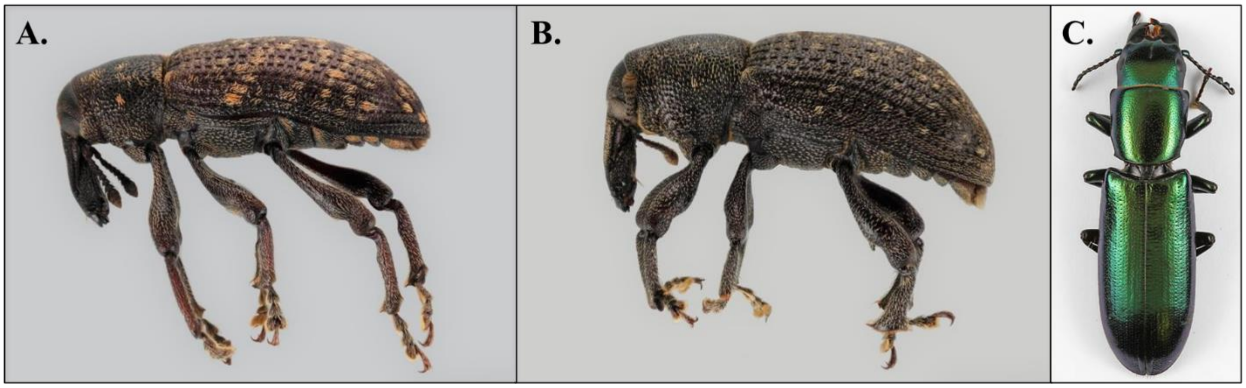

Figure 1.2

CHAPTER 2

SHORT-TERM RESPONSES OF BARK BEETLES AND THEIR ASSOCIATES TO VARIATION IN HURRICANE SEVERITY IN A SOUTHERN PINE FOREST [1]

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[1] S.C. Spinner, B.F. Barnes, E.P. McCarty, and K.J.K Gandhi. To be submitted to *Forest Ecology and Management*.

ABSTRACT

Wind disturbances and herbivorous insect outbreaks commonly alter forests in the southeastern U.S. Hurricanes are among the most important disturbances that impact forests of the Southeast. Hurricane damage is often spatially heterogeneous, resulting in a mosaic of stands with different levels of wind damage. Hurricane Michael made landfall in Florida, USA in 2018 and damaged over 1.2 million hectares of forest, resulting in ~$2 billion US in damage to commercial timber. Bark beetles (Coleoptera: Scolytinae) commonly invade wind disturbed stands and reach epidemic levels due to the increase in important resources, such as weakened or recently killed trees. The spatial heterogeneity of hurricane damage could potentially lead to different distributions of these resources across a forest, and hence differential responses by bark beetles and associated insects. Our research objective was to determine how bark and root-feeding beetles and their associates responded to different levels of wind damage in southern pine forests. We trapped insects in stands with either low (≤20%), moderate (21-40%), or high (≥41 %) damage during the first year after Hurricane Michael. The results demonstrate that trap catches of these insects did not differ among stands with different wind damage severities. The observed similarities in insect populations may have been caused by inadequate phloem quality during bark beetle emergence due to the timing of the wind disturbance (late fall). These results suggest that post-hurricane management activities, such as salvage harvesting, may not need to be based on hurricane damage severity to minimize additional economic losses from subcortical insects following a late season hurricane in southern pine stands.

INDEX WORDS: Bark beetles, Disturbance, Forest management, Hurricane, Population ecology

2.1 INTRODUCTION

The forests of the southeastern U.S. are vast, encompassing approximately 93 million hectares and accounting for 29% of the total forested land in the country (Conner and Hartshell 2002; Smith et al. 2009). These forests stretch from Texas to Virginia and Florida and are the dominant land cover-type in the region (Hanson et al. 2010). Southeastern forests are among the most diverse temperate forests in the world, supporting approximately 3,000 plant, 600 bird, 170 amphibian, 197 reptile, and 250 mammal species (Miller 2001; Griep and Collins 2002). Coniferous trees (Pinales) especially pines (*Pinus* spp.), dominate roughly half of this forested land with other half dominated by hardwood species (Hanson et al. 2010). Common conifers in the region include loblolly (*P. taeda* L.), slash (*P. elliotti* Englem.), longleaf (*P. palustris* Mill.), and shortleaf pine (*P. echinata* Mill.) (Gaby 1985). Southeastern forests are also extremely economically productive, yielding 17% of the world's industrial roundwood (Wear et al. 2016). Hence, they represent a valuable national resource.

Southeastern forests are commonly impacted and altered by natural disturbances such as droughts, storms, and herbivorous insect outbreaks (Klos et al. 2009; Oswalt et al. 2008; Oswalt et al. 2016). Hurricanes and bark beetle outbreaks are among the most important disturbance agents in southeastern forests, where they can cause hundreds of millions or, in the case of some severe hurricanes, billions of dollars in economic damages (Prestemon and Holmes 2010; Pye et al. 2011). Bark beetles (Coleoptera: Curculionidae: Scolytinae) that reproduce in tree cortical tissue can cause significant economic losses e.g., southern pine beetle (*Dendroctonus frontalis* Zimmerman) outbreaks that result in millions of dollars of damage per year (Price et al.

1992; Pye et al. 2011). The interaction between these two disturbance agents can even magnify such impacts on these forests, leading to long-term resilience and sustainability issues.

Bark beetles play important roles in forested ecosystems especially after abiotic disturbances such as windthrow (Nikolov et al. 2014). These insects are disturbance agents, influencing stand structure and succession (Audley et al. 2020; Collins et al. 2011). They can affect everything from soil structure to nutrient cycling and forest hydrology (Lynch et al. 2021; Pugh and Small 2012). Bark beetles injure or kill their host trees through feeding and brooding behaviors (Ciesla 2011). Common species that colonize trees early in the Southeast include *D. terebrans* (Oliver), *I. avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff). Bark beetles can also introduce microbial symbionts that cause further injury to host trees and degrade wood quality (Howell et al. 2018; Zhou et al. 2001).

Windstorms are also important disturbance agents in southeastern forests (Batista and Platt 2003; Oswalt et al. 2008; Prestemon and Holmes 2010). Wind disturbances have wide ranging impacts that affect forests on different spatial and temporal scales. At the stand and landscape levels, wind disturbances can alter species composition, age structure, and nutrient cycling (Foster and Boose 1995; Ostertag et al. 2003). These impacts can leave ecological legacies that may persist for years (Foster et al. 1998). At the individual tree level, strong winds can break limbs, crowns, and stems, uproot trees, or cause defoliation, which can result in tree mortality (Gresham et al. 1991). These injuries reduce tree vigor and can lessen the defensive responses of host trees, making wind-damaged trees susceptible to insect and disease infestations (Louis et al. 2016).

Most bark beetle species attack dying, stressed, or recently killed trees to take advantage of the reduced defenses of these hosts (Louis et al. 2016). Due to the great number of stressed or recently killed trees following a wind disturbance, bark beetle populations can erupt into large outbreaks, further damaging the disturbed forests. This phenomenon has been observed in tropical, temperate, and boreal forests around the world (Connola et al. 1956; Gardiner 1975; Grimbacher and Stork 2009; Kerchev 2014; Nikolov et al. 2014). Additionally, tree injuries caused by wind disturbances can increase the emission of volatile organic compounds (VOCs) from hosts trees and attract large numbers of bark beetles to a stand (Fineschi et al. 2013; Hietz et al. 2005; Pureswaran et al. 2004). Severe wind disturbances paired with subsequent bark beetle outbreaks can cause serious economic damages and impact forests for years following the initial disturbance (Nikolov et al. 2014).

Other tree-attacking insects may also take advantage of the increases in weakened or recently killed host trees following a wind disturbance. Two species of root-feeding weevils, *Hylobius pales* (Herbst) and *Pachylobius picivorus* (Germar) (Coleoptera: Curculionidae), are known to attack pines stressed or recently killed by disturbances such as fire, drought, and harvesting activities (Nord et al. 1982; Rieske and Raffa 1991). Larvae of root-feeding weevils develop in the roots of these dying pines and feed on phloem while adults feed on the bark of young pine stems (Nord et al. 1982). This damage can cause stem disfigurement and reduce the commercial quality of affected trees (Corneil and Wilson 1984; Drooz 1985). These feeding behaviors have made root-feeding weevils considerable pests in pine plantations throughout eastern North America (Rieske and Raffa 1990; Rieske and Raffa 1991).

Bark beetle populations can be regulated by top-down factors like their natural enemies (Reeve 1997). *Temnoscheila virescens* (Fabricius) (Coleoptera: Trogossitidae) is a common predator of *Ips* spp. in the Southeast (Mignot and Anderson 1970). Adult *T. virescens* beetles attack adult *Ips* spp. on the outer bark of pines, while larvae live in the phloem and prey on immature stages of *Ips* spp. (Mignot and Anderson 1970). *T. virescens* can significantly reduce the number of *I. grandicollis* adults to enter a host tree (Chism 2013). While *T. virescens* has been observed feeding on a variety of non-bark beetle prey in laboratory settings, the prey finding strategies of this insect suggest that it is an obligate *Ips* spp. predator (Billings and Cameron 1984; Lawson and Morgan 1993). *Temnoscheila virescens* responds almost exclusively to *Ips* spp. attractants but shows little to no response to southern pine beetle pheromones, suggesting that this predator is an *Ips* spp. specialist (Billings and Cameron 1984). Although there has been little research investigating the responses of *T. virescens*, *H. pales*, or *P. picivorus* to wind disturbances, these insects may respond to changes in prey and host material availability.

Hurricanes are among the most important wind disturbance agents in southeastern forests (Vogt et al. 2020). These storms can impact millions of hectares of forests and cause billions of dollars in economic damages (Prestemon and Holmes 2010). While hurricanes are common and natural disturbance agents in southeastern forests, the intensity of hurricanes is increasing due to anthropogenic climate change (Zhang et al. 2020). Increased storm intensity will pose a threat to southeastern forests and complicate forest management in the region. Hurricane damage severity is often spatially heterogeneous due to meteorological factors and landscape characteristics, like a stand’s proximity to the eye of the storm and topography (Everham and Brokaw 1996; Lugo 2008). The resulting mosaic of hurricane damage severity may lead to unequal distributions of insect resources and could possibly influence insect distributions. This heterogeneity may complicate post-hurricane management efforts aimed at minimizing losses from pests as insect populations could potentially vary among stands exhibiting different severities of hurricane damage.

Hurricane Michael was one of the most powerful hurricanes to strike the southeastern U.S. The hurricane made landfall near Mexico Beach, Florida on 10 October 2018 and damaged forests from Florida to Virginia (Beven et al. 2019). Hurricane Michael was the fourth strongest hurricane to hit the U.S. in recorded history (Beven et al. 2019). Over two million hectares of forests were damaged in Florida and Georgia alone, causing nearly $2 billion in economic losses (Florida Forest Service 2018; Georgia Forestry Commission 2018). Crowns, stems, and branches were snapped, and entire trees were uprooted by the storm's strong winds (Chapman 2018). The hurricane damage may have made the impacted forests more susceptible to biotic disturbance agents, such as bark beetle outbreaks. The Florida Forest Service reported several outbreaks of *Ips* spp. in the Florida Panhandle in 2019 (Florida Forest Service 2019). As forest owners attempt to prepare for future catastrophic hurricanes, understanding how bark beetles and their associates respond to hurricane damage in southern pine forests will be key to managing these insects and minimizing economic losses.

It is critical to understand how bark beetles and their associates respond to hurricanes in the Southeast to reduce economic damages and ecological alterations and to promote forest recovery. Salvage harvesting is an important tool to minimize economic losses and to reduce the risk of bark beetle outbreaks following a disturbance (Gardiner 1975). Ideally, salvage harvesting would occur immediately following a wind disturbance. However, this is often nearly impossible due to mill availability, transport capabilities, and other logistical constraints (Broman et al. 2019). The spatial heterogeneity of hurricane damage further complicates this matter. Due to the spatial heterogeneity of insect resources, stands with specific severities of damage may need to be prioritized over others to prevent bark beetle outbreaks. However, there has been little to no research into how these insects respond to hurricane damage in southeastern U.S. forests. The objective of this study is to assess bark and root-feeding beetle and predator population responses to catastrophic hurricane damage by comparing trap catches of four different bark beetle species, two root-feeding weevil species, and one bark beetle predator species among stands with different severities of hurricane damage. The results of this study will provide forest owners with information to help make decisions regarding the prioritization of salvage harvesting in the first year after disturbance in southeastern U.S. pine stands that endured different levels of hurricane damage. This information could potentially help reduce economic losses associated with bark and root-feeding beetles and minimize insect damage following catastrophic hurricanes in southeastern U.S. forests.

2.2 METHODS

2.2.1 Study Sites

Our study sites were slash pine plantations in the Florida Panhandle near Panama City, Florida. There were 14 sites, all with similar forest structures [age class (21 - 30 years) and pre-hurricane basal area (8.6 – 14.8 m^2)] (Table 1), species compositions, and soil types. Sites were at least one km apart from one another to ensure sampling independence. The sites had 20-70%

hurricane damage as estimated by foresters. Damage was visually assessed by foresters and was based on the proportion of broken canopy, uprooted trees, and broken stems in each site. These sites were classified as low tree damage (≤20%), moderate damage (21-40%), or high damage (≥41%). Insect populations were monitored in four low damage sites, three moderate damage sites, and seven high damage sites. We were unable to locate more low and moderate damage sites because the eye of Hurricane Michael passed directly over our study sites and the stands in this forest were heavily damaged by the storm. Some stands were not accessible to foresters for damage assessment due to the large amount of fallen trees blocking roads prior to insect sampling. In accessible stands, foresters made visual estimates of the damage in each stand. Damage in inaccessible stands was estimated by comparing satellite imagery of inaccessible stands to imagery of accessible stands where visual assessments were made. Undisturbed stands were not included in the study because the hurricane's path was >550 km wide and there were no undamaged stands in the vicinity. Sampling further away would have introduced the confounding effect of geographic variation.

2.2.2 Insect Sampling

Insects were sampled by Lindgren funnel traps and flight intercept panel traps (Miller and Crowe 2011). Two of each trap type (four traps total per site) were placed in an alternating fashion 30 m apart from each other along a transect inside each stand. The Lindgren funnel traps were baited with *Ips* pheromones [(-)-ipsenol, (+/-)-ipsdienol, and *cis*-verbenol] (Table 2) to capture *Ips* spp. and *T. virescens.* Flight intercept panel traps were baited with high-release ethanol and α-pinene (Table 2) to capture *D. terebrans*, *H. pales*, and *P. picivorus*. The collection cup in each trap was filled with propylene glycol to preserve samples in the field until they were collected. Traps were installed on 14 May 2019 and removed 17 September 2019. The trapped insects were removed every 2-3 weeks and baits were changed once a month.

Captured insects were frozen at -18 to -14° C in the lab until they could be sorted. Sorted beetles were then stored in vials and preserved with 75% ethanol until they could be identified. The target species were *D. terebrans, H. pales*, *I. avulsus, I. calligraphus*, *I. grandicollis*, *P. picivorus,* and *T. virescens*. Target species were identified to species level using taxonomic keys: *D. terebrans* (LaBonte and Valley 2013), *H. pales* (Warner 1966), *Ips* spp. (LaBonte and Valley 2011), *P. picivorus* (Anderson 2002), and *T. virescens* (Baron 1971). Representative specimens of each target species were confirmed by a bark beetle taxonomist at the Georgia Museum of Natural History at the University of Georgia. A reference collection of the target species was also deposited at the museum.

2.2.3 Sub-Sampling of Ips spp.

A subsampling method was used for samples with a volume greater than 11 ml due to the high number of captured *I. calligraphus* and *I. grandicollis*. To subsample, samples were placed in a small container, drained of ethanol, and lightly packed using the bottom of a vial. Beetles were subsampled from the container using a 2.5 ml scoop. All the target species in the scoop were identified to species level. This process was repeated four times, until approximately 10 ml of beetles had been identified. The volume of the remaining, unidentified beetles was then measured using a 1.25, 2.5, or 5 ml scoop. The total volume was multiplied by the number of *I.*

calligraphus and the number of *I. grandicollis* identified in the 10 ml subsample to estimate the total number of these species in the entire sample. Other target species (*D. terebrans, H. pales, I. avulsus, P. picivorus,* and *T. virescens*) were not subsampled. Instead, large insects, such as *H. pales*, *P. picivorus*, and *T. virescens* were removed prior to subsampling, whereas the smaller insects *D. terebrans* and *I. avulsus* were removed after subsampling.

Five samples were used to test the accuracy of this subsampling method. A sample was first subsampled in the manner previously described to test the accuracy of this method. After the beetles from 10 ml subsample were identified, the volume of the remaining beetles was measured and the estimated numbers of each species in the entire sample were calculated. Then, the beetles remaining after subsampling were identified and counted, giving the actual number of *I. calligraphus* and *I. grandicollis* in the sample. The estimated numbers of each species from the subsampling method were then compared to the actual numbers of each species. Accuracy rates were calculated from these values:

$$[100 - ((\left|\text{estimated number of beetles} - \text{actual number of beetles}\right| \\ / \text{actual number of beetles}) * 100)]$$

Accuracy rates ranged from 93.3 to 98.2%. This subsampling technique was approximately 95% accurate on average.

2.2.4 Statistical Analyses

There were ten response variables for these trap catches: total bark beetles, total root-feeding weevils, *D. terebrans*, *H. pales*, *I. avulsus*, *I. calligraphus*, *I. grandicollis*, *P. picivorus*, and

T. virescens. Data were standardized to the number of beetles caught per 14 days to account for varying lengths of time between sample collections. For each response variable, trap catches from the entire sampling season were summed to yield a total trap catch for each site and then standardized to 14 days [(sum of trap catches/sum of days that traps were operational) X 14]. Data were aggregated across the entire growing season rather than at each sampling date to account for multiple generations of the target species per year. These data aggregation yielded a sample size of 14, or one sample per site.

One way Analysis of Variance (ANOVA) tests (*alpha-level < 0.05*) were used to compare each of the ten response variables among the three wind damage categories using the statistical software R (version 4.0.2). *Dendroctonus terebrans*, *I. avulsus*, and *I. grandicollis* trap catch data did not meet ANOVA assumptions of normality and were transformed. *Dendroctonus terebrans* and *I. avulsus* trap catch data were square root transformed, and a Box-Cox transformation from the R-package MASS was applied to *I. grandicollis* trap catch data. Normality of residuals was tested using Shapiro-Wilk Tests and Bartlett Tests.

2.3 RESULTS

2.3.1 Bark Beetles

2.3.1.1 Total Bark Beetles

A total of 224,139 bark beetles were collected and identified. The overall trap catch, or the number of bark beetles per 14 days, was 453 beetles. Trap catches peaked during 7-19 August 2019, with a bark beetle trap catch of 700 bark beetles. Bark beetle trap catch did not differ among the three wind damage categories ($F_{2,11} = 1.388$, $p = 0.29$) (Figure 1).

2.3.1.2 Dendroctonus terebrans

Dendroctonus terebrans was the least frequently captured insect, making up only 0.41% of total bark beetle trap catches. A total of 1,204 individuals were collected. *Dendroctonus terebrans* trap catch peaked in the period between 7-19 August 2019 at seven beetles. Trap catches during other sampling periods were <2 beetles. *Dendroctonus terebrans* trap catches were similar among the wind damage categories ($F_{2,11} = 0.99$, $p = 0.402$) (Figure 2A).

2.3.1.3 Ips avulsus

During this study, 4,104 *I. avulsus* were captured, accounting for 1.54% of the total bark beetle trap catch. This species was also trapped at the greatest rate in the period between 7-19 August 2019. *Ips avulsus* trap catches did not vary among the wind damage categories ($F_{2,11} = 0.746$, $p = 0.497$) (Figure 2B).

2.2.1.4 Ips calligraphus

Ips calligraphus was the most frequently captured bark beetle, making up 75.44% of all captured bark beetles. A total of 186,850 individuals were captured. Trap catches of *I. calligraphus* peaked between 7-19 August at 579 beetles. *Ips calligraphus* catches did not significantly differ among the wind damage categories ($F_{2,11} = 2.323$, $p = 0.144$) (Figure 2C).

2.2.1.5 Ips grandicollis

A total of 51,157 *I. grandicollis* were captured. This species comprised 22.82% of the captured bark beetles. Unlike the previously mentioned species, *I. grandicollis* trap catches peaked between 14-28 May 2019. *I. grandicollis* trap catches were similar among the wind damage categories ($F_{2,11} = 1.521$, $p = 0.261$) (Figure 2D).

2.3.2 Root-feeding Weevils

2.3.2.1 Total Root-Feeding Weevils

Root-feeding weevils were captured at lower rates than bark beetles, with only 3,064 root-feeding weevils collected compared to 224,139 bark beetles. The overall root-feeding weevil trap catch in 2019 was seven individuals per 14 days. The greatest root-feeding weevil trap catches occurred during the sampling period between 20 August and 3 September 2019 at 12 weevils. Root-feeding weevil trap catches did not significantly differ among stands with different severities of hurricane damage ($F_{2,11} = 1.172$, $p = 0.345$) (Figure 3A).

2.3.2.2 Hylobius pales

H. pales was more common than *P. picivorus* in our samples, comprising approximately 83% of the total captured root-feeding weevils. We captured 2,552 individuals. *Hylobius pales* trap catches peaked between 20 August and 3 September 2019 with a trap catch of ten weevils.

Trap catches were similar among the wind damage categories ($F_{2,11} = 1.203$, $p = 0.337$) (Figure 3B).

2.3.2.3 Pachylobius picivorus

Pachylobius picivorus was less common in our samples than *H. pales*. A total of 512 *P. picivorus* were captured. More *P. picivorus* were captured between 7-19 August 2019 than any other period. *Pachylobius picivorus* trap catches did not significantly differ among stands with different wind damage severities ($F_{2,11} = 1.351$, $p = 0.299$) (Figure 3C).

2.3.3 Predator

2.3.3.1 Temnoscheila virescens

The bark beetle predator *T. virescens* was the most frequently captured bark beetle associate included in this study. A total of 6,302 individuals were captured. Trap catches peaked in the period between 20 August and 3 September 2019, which immediately followed the period of the greatest bark beetle trap catches (7-19 August). The trap catch was 34 *T. virescens* during this period. *Temnoscheila virescens* trap catches were similar among the different wind damage categories ($F_{2,11} = 0.811$, $p = 0.469$) (Figure 3D).

2.4 DISCUSSION

Assessing the responses of bark beetles and associated insects to different severities of wind damage is a novel research question and these insect responses have not been previously assessed for a hurricane in the Southeast. This study demonstrated that bark beetle trap catches in the first growing season after Hurricane Michael did not differ among southern pine stands with low, moderate, and high severity hurricane damage. Further, root-feeding weevil and bark beetle predator trap catches were similar among stands with different hurricane damage severities in the first growing season after wind disturbance. Several studies have compared bark beetle populations between wind-disturbed and undisturbed stands. Subcortical beetle trap catches were greater in wind disturbed stands than in undisturbed stands in subboreal forests in Minnesota following a severe wind disturbance (Gandhi et al. 2010). Similarly, bark beetles and woodboring insects were more abundant in disturbed stands than undisturbed stands following a tornado in northern Maine (Dodds et al. 2019). Abundances of saprophagous insect (e.g., Tenebrionidae, Anthicidae, Corylophidae, etc.) differed depending on the severity of anthropogenic disturbance in the Mediterranean forests of central Chile (Garcia-Lopez et al. 2016).

A lack of suitable phloem may have resulted in the observed similarities among insect populations in stands with different severities of wind damage after Hurricane Michael. The suitability of phloem for bark beetle development decreases rapidly after the connection between the stem and roots is severed (Hrosso et al. 2020; Wermelinger et al. 2013). Since Hurricane Michael occurred at the end of the growing season in October, the phloem of windthrown trees may have been too degraded by the time the next growing season began and bark and root-feeding beetles were searching for suitable host material. Personal observations indicated that many trees either already experienced bark beetle emergence or were never colonized because the phloem was too dry. Our study sites were located in a region that experiences a subtropical climate with an average temperature of 15.7° C between October and February (Climate Data 2022). These warm late-season temperatures may have contributed to the desiccation of phloem during periods of bark beetle inactivity (Hayes et al. 2008). The lack of adequate amounts of suitable phloem needed to support growing insect populations across the wind disturbed forests after the late season storm Hurricane Michael may have resulted in the observed similarities among populations of bark beetles and their associates in stands with different damage severities.

The phloem of windthrown trees is an ephemeral resource that can only support bark beetles for a limited amount of time (Wermelinger et al. 2013). Phloem moisture is a limiting factor for bark beetle development and can influence bark beetle success and performance (Anderbrant et al. 1985; Anderson 1948; Haack et al. 1984; Haack et al. 1987; Pelltonen and Helovaara 1999). For example, nearly twice as many *I. pini* (Say) emerged from trees with moist phloem than damaged trees with dry phloem following an ice storm in western North America (Anderson 1948). Additionally, phloem moisture decreases rapidly after felling, eventually reaching a point that negatively impacts or precludes bark beetle development (Redmer et al. 2001; Villa-Castillo and Wagner 1996). For instance, the phloem of slash from thinning operations in Montana became too dry for bark beetle development within eight weeks, and the phloem of slash generated by logging operations in the Tatra mountains of Europe only remained suitable for bark beetle development through the first growing season (Gara et al. 1999; Kula et al. 2011).

The timing of these coarse woody debris-generating activities can influence the rate of phloem desiccation and subsequent phloem-feeding insect population responses.

The effect of felling timing on phloem quality has long been understood by foresters in the western U.S. engaged in *I. pini* management. In Montana, slash created in October was too dry for bark beetle development by the time adults emerged the next growing season (Gara et al. 1999). Felling timing can also impact bark beetle reproductive success. The number of *I. pini* offspring reared from trees felled in November and January was only 55% of the number of offspring reared from logs felled in July in red pine stands in Wisconsin (Redmer et al. 2001). Likewise, logs cut in the winter had negative effects on bark beetle populations in ponderosa pine (*Pinus ponderosa* Douglas) forests in Arizona (Hayes et al. 2008). These timing effects have been recognized and integrated into *I. pini* management plans. In western U.S. forests, management recommendations are that slash be created between August and January to allow adequate time for the phloem to desiccate before *I. pini* adults emerge the next growing season (Buckhorn 1957; Gara et al. 1999; Sartwell 1970). Slash created outside of this period will be of adequate quality for bark beetle development and allow for insect population growth (Buckhorn 1957; Sartwell 1970).

Bark beetle and associated insect trap catches were similar in stands with different severities of hurricane damage following Hurricane Michael. Future wind disturbance studies may be improved by surveying more sites, especially low and moderate damage sites, to increase sample size and to allow for a balanced design. Insect population responses in undisturbed sites could also be assessed to compare insect responses between undisturbed and disturbed sites. Additionally, greater numbers of root-feeding weevils could be captured in future studies if turpentine is used, as this chemical is more attractive to these insets than α-pinene (Raffa and Hunt 1988). Greater root-feeding weevil trap catches could also be achieved by using pitfall traps in addition to the traps used in this study. *Hylobius pales* and *P. picivorus* travel mainly by walking when searching for mates and suitable oviposition sites, while flight is primarily used for dispersing to new stands (Rieske and Raffa 1990). Because flight intercept panel traps were used, root-feeding weevils dispersing between sites were primarily targeted rather than individuals searching for mates and brooding resources within the study sites. Another confounding factor could be the damage categorization that was conducted by the foresters in their typical operational way for future salvaging efforts. It is possible that there were differences between damage categories in the volume and type of coarse woody debris, along with the remote sensing methods used for damage categorizations in inaccessible sites. However, the goal of the project was to assess damage less than a year after the storm, and it was logistically not possible to conduct mapping efforts before the growing season began in these lower coastal plains.

In future studies, phloem moisture of slash can be measured throughout the year following felling to quantify the rate of phloem desiccation in southern pine forests and to understand how populations of bark beetles and their associates respond to decreases in phloem quality. Additionally, future studies may seek to compare phloem degradation and insect responses between a late season disturbance and an early or mid-season disturbance to understand how the timing of a disturbance influences target insects in southeastern U.S. pine forests.

2.5 CONCLUSIONS

Our results indicate that management actions, like salvage harvesting, may not need to be prioritized based on hurricane damage severity to minimize bark and root-feeding beetle damage following a late season hurricane in southern pine forests. However, beetle population responses to damage categories should not be extrapolated to early or mid-season hurricanes. Anthropogenic disturbances that damage trees that occur during times of bark beetle activity, such as spring or summer, can provide suitable resources for population growth (Buckhorn 1957). This may also be true of wind disturbances in the Southeast. The results from our study may help guide foresters and landowners in complicated management decisions about the prioritization of salvage harvesting following a late season hurricane in southern pine forests.

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Table 2.1: Summary of stand characteristics with age, size, percent damage, and damage category of each stand.

Site	Stand Age in Years (in 2018)	Stand Area (Hectares)	Damage (%)	Damage Category
1	21	115.9	40	Moderate
2	21	115.9	40	Moderate
3	26	53.7	50	High
4	26	53.7	50	High
5	30	56.3	20	Low
6	20	29.9	30	Moderate
7	28	44.3	20	Low
8	28	44.3	20	Low
9	30	56.3	20	Low
10	21	16.2	60	High
11	28	72.6	70	High
12	26	149.9	50	High
13	29	78.3	50	High
14	30	85.3	50	High

Table 2.2: Composition, source, purity, release device, load, and release rate of each of the lures used to trap bark beetles and their associates.

Compound	Source[1]	Purity (%)	Release Device	Device Load	Release Rate @ 25° C
(-)-ipsenol	Synergy Semiochemicals	≥95	Polymer membrane bubble cap	100 mg	0.6 – 0.8 mg/day
(+/-)-ipsdienol	Synergy Semiochemicals	≥95	Polymer membrane bubble cap	100 mg	0.6 – 0.8 mg/day
cis-verbenol	Synergy Semiochemicals	≥95	Polymer membrane bubble cap	200 mg	1.2 mg/day
ethanol	Synergy Semiochemicals	≥95	UHR[2] polymer membrane pouch	78.9 g	200-400 mg/day
α-pinene	Synergy Semiochemicals	≥95	UHR[2] polymer membrane pouch	172 g	2,000 mg/day

[1] Synergy Semiochemicals Corporation, Delta, British Columbia, Canada

[2] Ultra High Release

LIST OF FIGURES

Figure 2.1: Map showing approximate location of study sites in the Florida Panhandle, USA. Sites were located within the area enclosed by the red square. Imagery sourced from Google Earth.

Figure 2.2: Total bark beetle trap catch data from the first growing season after Hurricane Michael in each wind damage category. Boxes contain the 25th to the 75th percentiles of the data. End points of the whiskers represent minimum and maximum trap catches. The solid lines in each box represents the median. Dashed lines indicate the arithmetic mean.

[a] Number of beetles collected per 14 days.

Figure 2.3: Distribution of trap catch data for **A**. *D. terebrans*, **B**. *I. avulsus*, **C**. *I. calligraphus*, and **D**. *I. grandicollis* from the first growing season after Hurricane Michael in each wind damage category. Boxes contain the 25th to the 75th percentiles of the data. End points of the whiskers represent minimum and maximum trap catches. The solid lines in each box represents the median. Dashed lines indicate the arithmetic mean.

[a] Number of beetles per 14 days

Figure 2.4: Distribution of trap catch data for **A**. total root-feeding weevils, **B**. *H. pales*, **C**. *P. picivorus*, and **D**. *T. virescens* from the first growing season after Hurricane Michael in each wind damage category. Boxes contain the 25th to the 75th percentiles of the data. End points of the whiskers represent minimum and maximum trap catches. The solid lines in each box represents the median. Dashed lines indicate the arithmetic mean.

[a] Number of beetles per 14 days

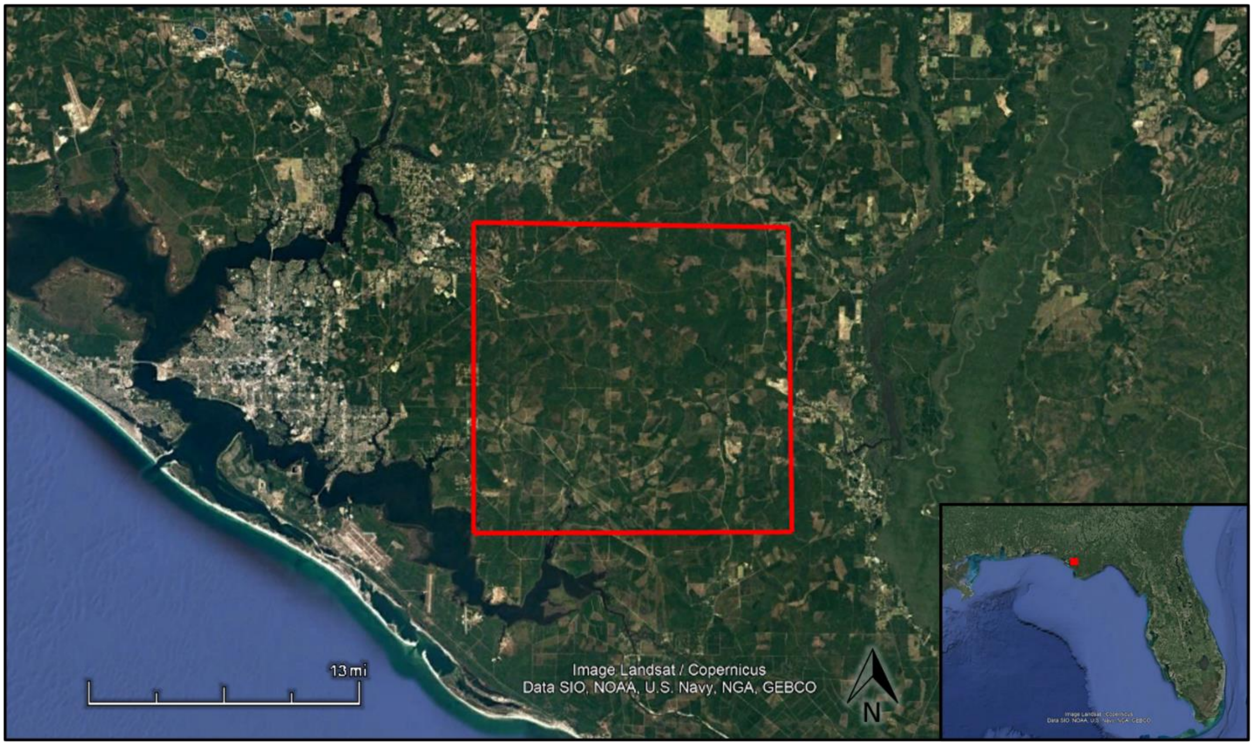
13 mi
Image Landsat / Copernicus
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
N
Image Landsat / Copernicus
Data SIO, NOAA, U.S. Navy, NGA, GEBCO

Figure 2.1

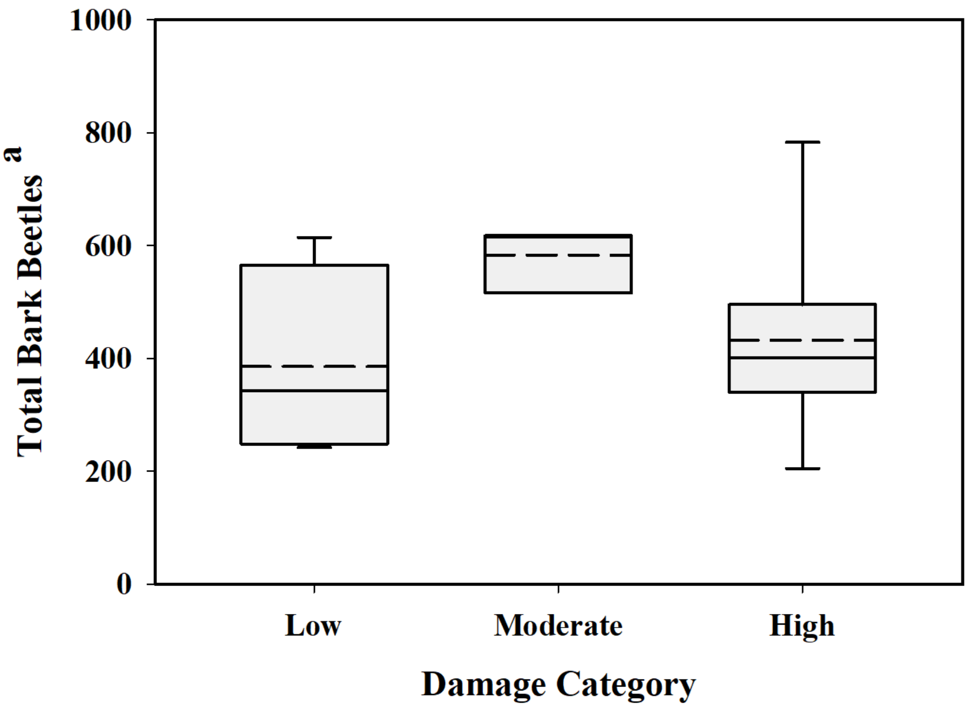
1000
800
600
400
200
0
Total Bark Beetles a
Low
Moderate
High
Damage Category

Figure 2.2

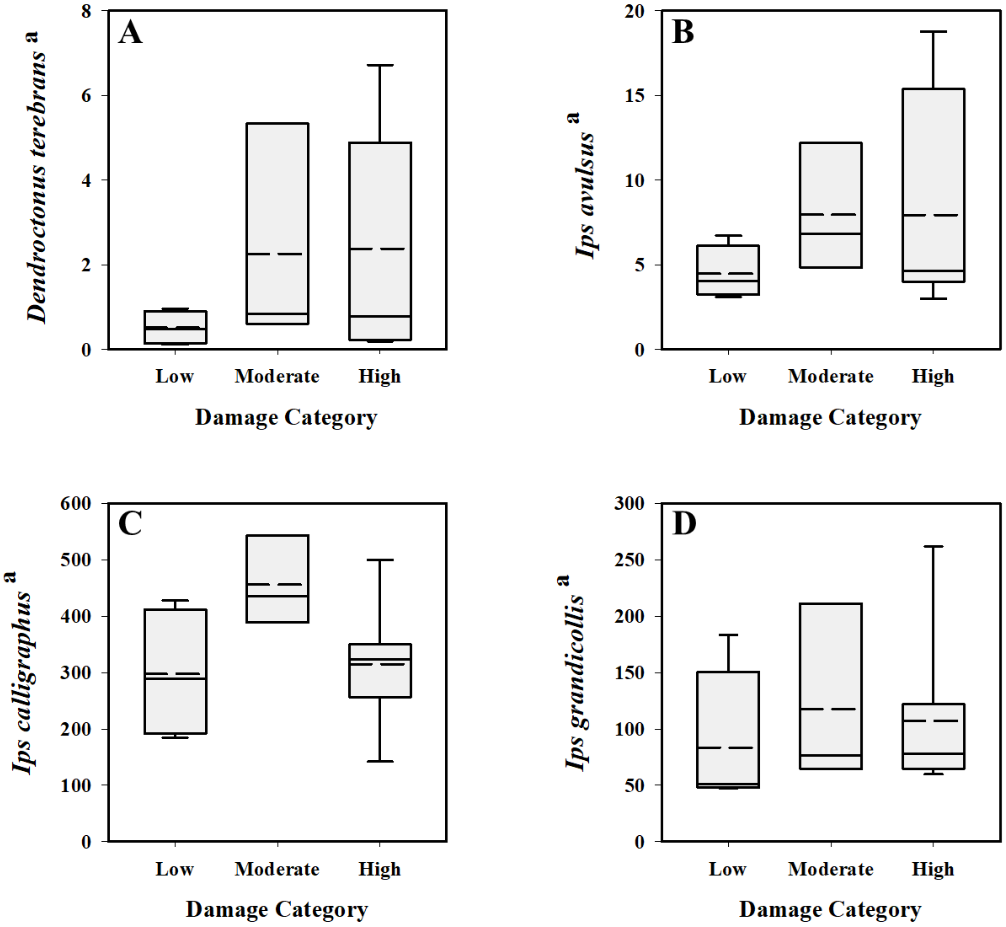
A
B
C
D
Dendroctonus terebrans a
Ips avulsus a
Ips calligraphus a
Ips grandicollis a
0
2
4
6
8
0
5
10
15
20
0
100
200
300
400
500
600
0
50
100
150
200
250
300
Low
Moderate
High
Damage Category

Figure 2.3

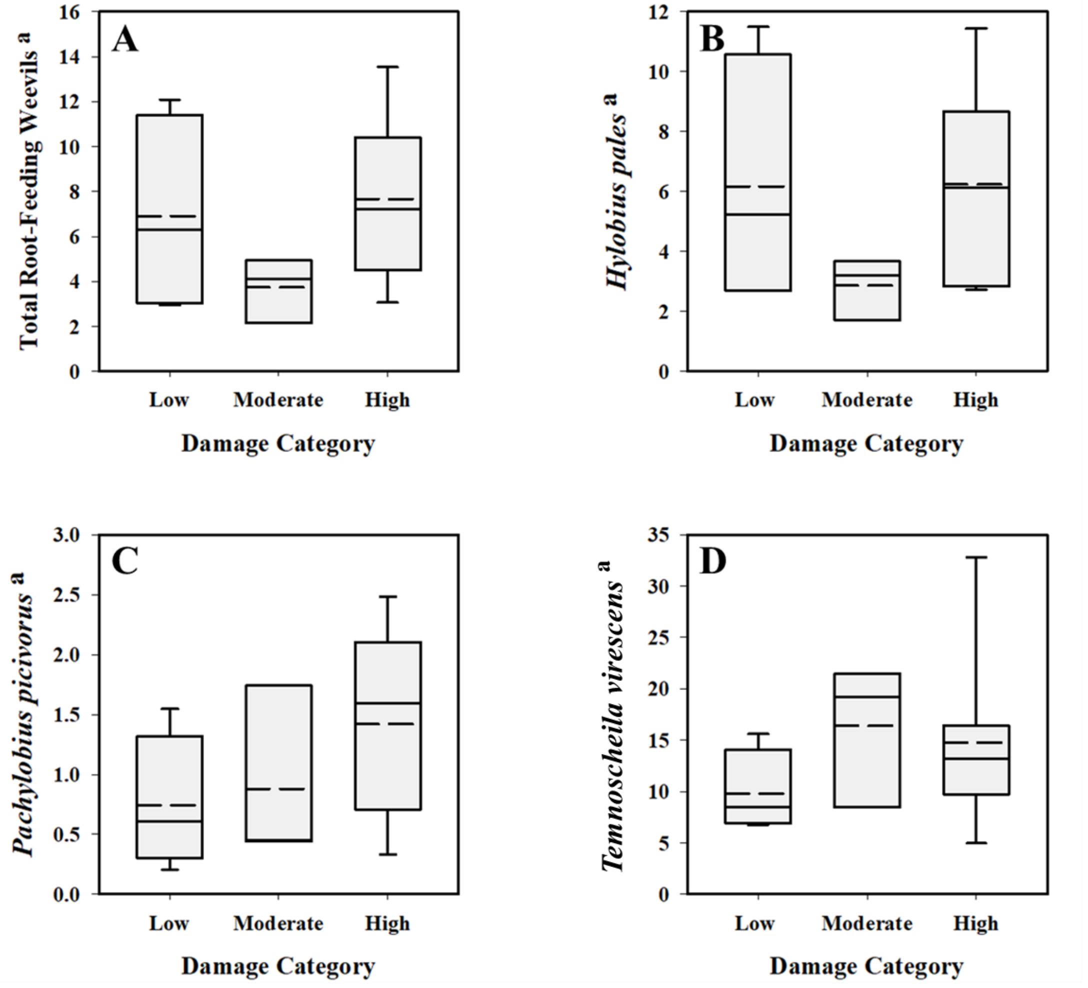
A
Total Root-Feeding Weevils a
0
2
4
6
8
10
12
14
16
Low
Moderate
High
Damage Category
B
Hylobius pales a
0
2
4
6
8
10
12
Low
Moderate
High
Damage Category
C
Pachylobius picivorus a
0.0
0.5
1.0
1.5
2.0
2.5
3.0
Low
Moderate
High
Damage Category
D
Temnoscheila virescens a
0
5
10
15
20
25
30
35
Low
Moderate
High
Damage Category

Figure 2.4

CHAPTER 3

THESIS CONCLUSIONs

3.1 CONCLUSION

Wind disturbances can significantly alter forested ecosystems and cause substantial economic damages (Batista and Platt 2003; Oswalt et al. 2008; Prestemon and Holmes 2010). The tree injuries sustained during these events can weaken trees and predispose them to attack by bark beetles and other phloem-feeding insects, potentially leading to insect outbreaks (de Groot et al. 2018; Louis et al. 2016; Nikolov et al. 2014). The severity of some wind disturbances, such as hurricanes, is spatially heterogeneous, leading to a mosaic of different damage levels across a forest (Foster 1988). These variable patterns of forest damage were prominent in the Florida Panhandle following Hurricane Michael, a category five storm that caused approximately $2 billion US in economic damage to standing timber (Florida Forest Service 2018; Georgia Forestry Commission 2018). This spatial heterogeneity could lead to uneven distributions of important bark beetle (Coleoptera: Curculionidae: Scolytinae) and root-feeding weevil (Coleoptera: Curculionidae: Molytinae) resources such as coarse woody debris, dying trees, and stumps. The purpose of this study was to determine if there were differences in populations of bark and root-feeding beetles and their associates among southern pine stands with different severities of damage following a catastrophic wind disturbance.

Bark beetle populations were similar among southern pine stands with different severities of hurricane damage. No previous studies have sought to quantify the population responses of these insects to different severities of wind disturbance. However, several studies have compared subcortical insect populations between windthrown stands and nearby undamaged stands and found greater population sizes or greater levels of insect damage in wind disturbed sites (Dodds et al. 2019; Gandhi et al. 2010; Nikolov et al. 2014). Additionally, populations of two species of root-feeding weevils (*Hylobius pales* Herbst and *Pachylobius picivorus* Germar) and *Temnoscheila virescens* (Fabricius), a bark beetle predator, did not differ among stands with different severities of wind damage. The responses of these insects to different severities of wind disturbance have not been documented prior to this study.

The similarity in insect populations among stands with different levels of damage may stem from a lack of adequate resources. Bark beetles require phloem to complete certain stages of their life cycles (Raffa et al. 2015). Phloem is an ephemeral resource that degrades rapidly after being severed from the root system, e.g., during windthrow or cutting (Hrosso et al. 2020; Wermelinger et al. 2013). Phloem degradation can reduce bark beetle performance and brood production and can even preclude bark beetle development as phloem deterioration progresses (Anderbrant et al. 1985; Anderson 1948; Pelltonen and Helovaara 1999). The impacts of phloem degradation on bark beetles have been studied in extensively in the western U.S., where slash management techniques that promote rapid phloem degradation are used to manage *Ips pini* (Say) (e.g., Gara et al. 1999, Hayes et al. 2008, and Villa-Castillo and Wagner 1996). In western Ponderosa forests, performing slash-creating management activities like thinning in periods of *I. pini* inactivity such as fall or early winter, typically leads to lower rates of bark beetle emergences than when these treatments are implemented during periods of beetle activity, like spring or summer (Buckhorn 1957; Sartwell 1970). This phenomenon occurs because the phloem of slash and trees felled in the fall or early winter has desiccated and degraded beyond the limit at which bark beetles can colonize the material by the time these insects emerge the next growing season (Gara et al. 1999).

Hurricane Michael made landfall in October, near end of the growing season and during a period of relatively lesser bark beetle activity. Because of the timing of this storm, the phloem of windthrown host material generated by the disturbance may have been too degraded to support growing insect populations by the time of the next bark beetle emergence. This phloem degradation may have reduced the reproductive success of phloem-feeding insects or precluded their development entirely, resulting in the observed similarities among populations in stands with different severities of hurricane damage. Alternatively, the insects may have emerged and left the sites due to a lack of suitable resources before we began sampling.

Even though we trapped a significant number of beetles (233,505), no differences in insect populations were detected among stands with different severities of damage. Additionally, we did not detect or receive reports of insect outbreaks in the study area during or after the study. Future studies documenting the responses of bark beetles and their associates to a mixed-severity disturbance could improve on this study by surveying more study sites and using a balanced experimental design. Greater insight may be gained if subcortical insect populations in damaged stands are compared with populations in nearby undisturbed stands. Also, root-feeding weevil trap catches could be improved by using pitfall traps baited with turpentine in addition to flight intercept panel traps (Hunt and Raffa 1989; Rieske and Raffa 1990).

Future research may focus on how the timing of disturbance influences subsequent responses of bark beetles and their associates. Understanding how phloem-feeding insects respond to early or mid-season coarse woody debris generating events in southern pine forests could greatly aid in post-hurricane forest management in the Southeast. Additionally, greater understanding of post-hurricane bark beetle dynamics could be gained through future studies that measure the phloem quality of coarse woody debris generated by disturbances that occurred at different times of the year and quantify the population responses of bark beetles and their associates to these changes in phloem quality

The study findings may help guide foresters in making decisions regarding the prioritization of post-wind disturbance salvage harvesting. Our results suggest that the prioritization of salvage harvesting operations may not be based on the severity of hurricane damage in a stand to minimize economic losses from insects following a late season hurricane in the Southeast. However, this should not be extrapolated to early on mid-season hurricanes, as the population dynamics of bark beetles and their associates may differ with disturbance timing. Further research is needed to determine the responses of these insects to wind disturbances occurring during these periods to aid in post-hurricane bark beetle management activities following early or mid-season hurricanes.

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