INTERACTIONS BETWEEN FOREST DISTURBANCES AND SUBCORTICAL BEETLES IN LONGLEAF PINE FORESTS

by

BENJAMIN MICHAEL GOCHNOUR

(Under the Direction of Kamal J.K. Gandhi)

ABSTRACT

Longleaf pine (*Pinus palustris* Miller) ecosystems of the southeastern U.S. are among the most biologically diverse outside of the tropics. Longleaf pine forests provide numerous ecosystem services, though these once dominant forests have been vastly reduced. Longleaf pine's evolution with and adaptation to natural disturbances make them especially resilient, however disturbance events beyond the historical range of variability are predicted under climate change. This dissertation explores the effect of disturbance agents and their interaction with subcortical beetles after disturbance events in longleaf pine forests in Georgia. We synthesize existing literature on how bark beetles respond to wind disturbances, particularly in the context of climatic changes, providing a model for understanding bark beetle-windstorm interactions. We evaluate the effects of management practices on three native *Ips* species [*I. avulsus* (Eichhoff), *Ips calligraphus* (Germar), and *I. grandicollis* (Eichhoff)] and woodboring beetles in longleaf pine following a catastrophic hurricane in windthrown stands treated with three post-windstorm management approaches: no post-storm management, prescribed fire, and salvage logging followed by prescribed fire. We found no significant difference in beetle catches between treatments likely due to an active management history in these longleaf pine stands. We further present the results of a study evaluating the response of the beetle assemblage to simulated-lightning-struck mature longleaf pine trees by sampling flight activity at different heights (0, 5, 10, and 15 m). We collected 47,343 adults and 275 species, and found patterns of vertical distribution that differed both within and between feeding guilds. Longleaf pine forests' natural resilience and adaptations to regional disturbance agents, such as hurricanes and insects, indicate that they may fare better in response to climatic changes than other pine species.

INDEX WORDS: bark beetles, disturbance, hurricanes, *Ips*, lightning, longleaf pine, prescribed fire, windstorm

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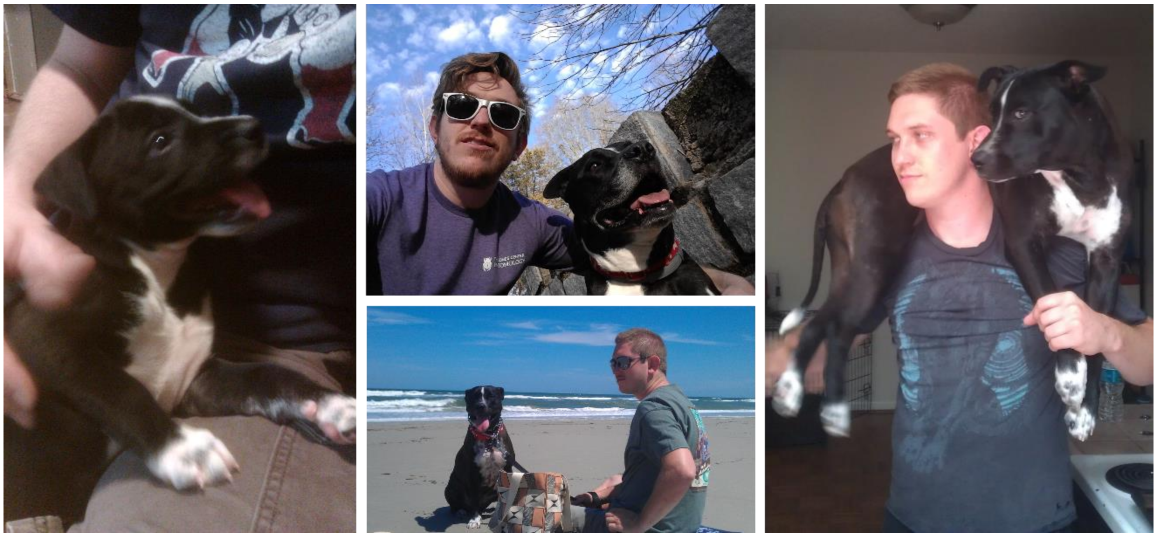
DEDICATION

For Sweet Dee, my baby, my familiar, my eternal companion.

You will always live on in my heart.

2011 – 2024



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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

1.1 Disturbance in longleaf pine ecosystems

In the southeastern U.S., there are multiple types of disturbances that affect longleaf pine (*Pinus palustris* Miller) forests (Glitzenstein et al. 1995, Brockway and Lewis 1997, Outcalt 2008, Kenney et al. 2021, Pope et al. 2023). A disturbance is defined by White and Pickett (1985) as "any relatively discrete event in time and space that disrupts ecosystem, community, or population structures and changes resources, substrate availability, or physical environment." Disturbances can be caused by biotic or abiotic factors and can have either natural or anthropogenic origins (Snow et al. 1990, Outcalt 2008). Consideration of the type and origin of disturbances is important for managing forests (Dale et al. 1998, McCay 2000, Dale et al. 2002). However, while disturbance can be something to manage for, it can also be used as a management tool through prescribed fire and salvage logging (Brockway and Lewis 1997, Kleinman and Hart 2018, Kleinman et al. 2020, Kupfer et al. 2022).

Compound disturbances result from the overlapping effects of individual disturbance agents or the interactions between legacy effects of previous disturbances with those that occur after (Gandhi et al. 2009, Kleinman et al. 2019). Moreover, some types of anthropogenic disturbance such as prescribed fire can be effectively applied as a management tool in some ecosystems, even in response to natural disturbance events (Van

Lear et al. 2005, Kleinman et al. 2017, Kleinman et al. 2020). Given the occurrence of natural disturbances and the use of frequent prescribed fire in longleaf pine ecosystems, compound disturbances are common in these forests (Kleinman et al. 2019).

While disturbance has been a natural part of longleaf pine ecosystems (Gleason 1926, Clements 1936, Sousa 1984), disturbance events beyond the historical range of variability are predicted under climate change (Dale et al. 2001, Elsner 2006, Holland and Bruyère 2014, Mitchell et al. 2014, Knutson et al. 2020). Even though longleaf forests have been shown to be more resilient to disturbance than other pine species (Platt et al. 1988, Noss 1989, Hook et al. 1991, Moser et al. 2003, Johnsen et al. 2009, Rutledge et al. 2021), the uncertainty under climate change poses a challenge for forest managers (Millar et al. 2007, Brantley et al. 2017, Clark et al. 2018). This management challenge is further complicated by the interaction of compound disturbances (Kleinman et al. 2017, Kleinman et al. 2019, Crotteau et al. 2020).

Historically, longleaf pine had an extensive range across the southeastern U.S., covering up to 37 million hectares from southeastern Virginia to central Florida and eastern Texas (Outcalt 2000, Frost 2006). Longleaf pine was found across the landscape from the dry mountain ridges of Alabama and northern Georgia (Boyer 1990), to seasonally wet coastal flatwoods and savannahs (Stout and Marion 1993, Outcalt 2000). Abiotic agents of disturbance important in longleaf pine forests include fire, windstorms, and lightning; biotic agents include subcortical beetle and disease outbreaks (Snow et al. 1990, Outcalt 2008) .

Longleaf pine ecosystems are among the most biologically diverse outside of the tropics (Provencher et al. 2003, Kirkman et al. 2004, Van Lear et al. 2005, Kaeser and

Kirkman 2009, Kirkman et al. 2016). Though longleaf pine dominates the overstory, the understory boasts enormous vascular plant diversity, namely of herbaceous species and grasses (Peet 2006). This in turn fosters high levels of faunal biodiversity, particularly insects and herpetofauna (Means 2006, Sheehan and Klepzig 2022).

However, longleaf pine is currently one of the most threatened ecosystems in the U.S. At present, it occupies less than 1 million hectares (Frost 2006), a substantial decrease from its extensive original range. Commercial logging, turpentine distillation, and replacement by commercial pine plantations, agricultural fields, and land development throughout the 19-20th centuries all contributed to the steep decline in longleaf pine (Frost 2006). Western management practices post-colonization further contributed to the loss of longleaf as fire suppression converted pine forests into later stage successional habitats (Outcalt 2000, Jose et al. 2006). Since then, efforts to restore longleaf pine ecosystems have emphasized the effective use of prescribed (or managed) fire to mimic natural cycles, and continue the long history of controlled burns by Indigenous peoples and generations of subsequent settlers (Jose et al. 2006).

Longleaf pine is a key species in native, fire-dependent southeastern ecosystems characterized by temporary drought (Noss 1989, Outcalt 2000, Van Lear et al. 2005, Jose et al. 2006). Together with some bunchgrasses, it functions as a foundation species, facilitating the development of a pyrogenic ecosystem (Brockway 2005) and altering the habitat in a way that promotes the occurrence of high-frequency, low-intensity understory fires (Noss 1989). These fires clear the understory of late successional species (Bigelow and Whelan 2019), promote flowering and resprouting of understory plants (Platt et al. 1988, Drewa et al. 2002), remove groundcover of fallen leaves and needles (Bale 2009), and reduce volume of coarse woody debris (Hanula et al. 2012), while maintaining germination and growth of longleaf pine saplings (Knapp et al. 2018). Lightning strikes initiate these fires (Allen 2002, Frost 2006), as does human activity (Kalisz et al. 1986), which has increased the frequency and prevalence of fire on the landscape (Kay 2007).

Longleaf pine's evolution with fire has resulted in frequent fire being integral to its lifecycle. The species is particularly reliant on fire during the seed and seedling stages. Seeds are large and heavy, which protects them from fire, but prevents lengthy seed dispersal over long distances (Jose et al. 2006) and promotes seed predation (Outcalt 2000), making longleaf pine seeds less competitive in fire-suppressed habitats than other pine species. For germination, the seeds also require an exposed mineral soil seedbed free of litter, as is characteristic of habitats prone to frequent fire cycles (Outcalt 2000). Additionally, longleaf seedlings exhibit a lengthy stemless phase in which root growth is favored in lieu of aboveground growth. As a result, a grass-like arrangement of needles protects the central bud from fire (Outcalt 2000). Ultimately, disturbance in the form of fire is central to longleaf pine ecosystem health.

Similar to larger scale disturbance agents, the effect of lightning on single trees plays an important role in longleaf pine forests due to the widespread and consistent occurrence of lightning strikes each year (Taylor 1974). Lightning strikes create small gaps in the canopy which contribute to forest heterogeneity, biodiversity, and regeneration (Johnson and Gjerstad 2006). They also serve as an ignition source for the frequent fires that maintain this pyrogenic ecosystem, which are primary habitats for many faunal and floral species (Van Lear et al. 2005, Outcalt 2008).

As natural disturbance agents, windstorms are also critical drivers of forest stand dynamics (Everham and Brokaw 1996, Allen et al. 2012, Mitchell et al. 2014). The southeastern U.S. is prone to windstorms in the form of hurricanes, a type of tropical cyclone, and tornados. Windstorms damage and kill trees via extreme wind speeds which result in bent, broken, or uprooted stems, broken crowns and branches, root damage, and defoliation (Gresham et al. 1991, Zampieri et al. 2020). The resulting influx of coarse woody debris and litter leads to increased concentrations and admixing of nutrients in soils which is critical for growth of many plant species (Ostertag et al. 2003). Further, changes in stand structure, age distribution, vegetative species composition, and an increase in coarse and fine woody debris in forests impacts habitat availability, altering population and community dynamics of flora and fauna (Platt et al. 2000, Batista and Platt 2003, Gandhi et al. 2007, Dodds et al. 2019, Kenney et al. 2021, Rutledge et al. 2021, Gochnour et al. 2022). As a result, hurricanes are critical disturbance agents in the southeastern U.S., providing a variety of ecosystem services affecting forest heterogeneity (Seidl et al. 2018, Hekkala et al. 2023), regeneration (Brockway and Outcalt 1998), biodiversity (Palik et al. 2002), and animal population cycles (Potterf and Bone 2017, Potterf et al. 2019).

However, catastrophic hurricanes can result in extreme changes to forest structure and function (Bigelow et al. 2021, Sharma et al. 2021, Fortuin et al. 2023, Pope et al. 2023). These storms involve high levels of windthrown trees and, in areas near the eye of the hurricane, they cause the complete removal of canopy trees, resulting in stand replacement (Zampieri et al. 2020). The occurrence of catastrophic storms is predicted to increase due to the effects of climate change (Elsner 2006, Mann and Emanuel 2006, Holland and

Bruyère 2014), and research into the outcomes of these events can aid future forest management (Zampieri et al. 2020, Sharma et al. 2021, Pope et al. 2023).

Early studies of the effects of hurricanes on longleaf pine ecosystems indicate that longleaf pine withstands wind damage better than faster-growing congeners (Gresham et al. 1991, Hook et al. 1991, Johnsen et al. 2009). These studies focused on tree species-level comparisons of damage and mortality stemming from hurricanes. For instance, a 1991 study of the effects of Hurricane Hugo on trees in the Hobcaw Forest in the lower coastal plain of South Carolina (~100 km from the eyewall of the storm) found that longleaf pine was less damaged than loblolly pine (*P. taeda* L.) or pond pine (*P. serotina* Michaux) (Gresham et al. 1991). However, the more damaging winds of the eyewall of this Category 4 storm were too strong for even longleaf to withstand, and 89% of longleaf pines were broken or uprooted (Hook et al. 1991). Similarly, Johnsen et al. (2009) found that longleaf pine suffered less mortality than loblolly pine and slash pine (*P. elliottii* Englemann) in southeast Mississippi following the effects of the eastern eyewall of Hurricane Katrina, a Category 3 storm with sustained winds of over 145 km hr^{-1} and gusts up to 225 km hr^{-1}. In summary, longleaf pines are a more wind resistant species than other southern pines, except in the extreme cases of exceptionally high sustained windspeeds.

One storm of particular significance for the context of this dissertation is Hurricane Michael, a Category 5 hurricane that made landfall in 2018 on the Florida panhandle. Previous studies on this storm have focused on variable aspects of tree susceptibility to wind damage in longleaf pine ecosystems. Zampieri et al. (2020) found that at least 28% of the total remaining longleaf pine ecosystems was impacted by Hurricane Michael in Florida alone. Mortality of longleaf pines was greatest for medium-sized trees (30-45 cm

DBH) and in areas near the eyewall of the storm (87.8% mortality) (Zampieri et al. 2020). At sites further from the storm center, mortality ranged from 4.6-15.4% (Zampieri et al. 2020). At the same time, the open canopy of longleaf-hardwood woodland fostered wind-firmness, limiting the destructive effects of the cyclone and shifting tree species composition to greater longleaf pine dominance (Bigelow et al. 2021).

Beyond distance from the eyewall, other factors influenced the extent of damage from Hurricane Michael. A survey of over 3,000 trees in longleaf pine dominated forests in southwestern Georgia found that the probability of wind damage depended on soil type and increased with diameter at breast height for all tree species (Rutledge et al. 2021) Longleaf pine exhibited the lowest variability in wind susceptibility, supporting earlier assertions about the species' wind resistance (Rutledge et al. 2021).

As illustrated through the discussion above, abiotic disturbances are drivers of ecosystem structure and change in longleaf pine forests (Glitzenstein et al. 1995, Everham and Brokaw 1996, Van Lear et al. 2005, Johnson and Gjerstad 2006, Outcalt 2008, Mitchell et al. 2014). These disturbances operate at multiple spatial and temporal scales (Glitzenstein et al. 2003, Kirkman et al. 2004, Thaxton and Platt 2006, Rutledge et al. 2021) and the resulting legacies of disturbance interact with subsequent events that, over time, constitute compound disturbance regimes that shape longleaf pine ecosystems (Brockway 2005, Estes 2006, Kleinman et al. 2017, Kleinman and Hart 2018). The effects of abiotic disturbances on trees also play a role in the maintenance of potential biotic disturbance agents such as members of the southern pine bark beetle guild (Coulson et al. 1986, Rykiel et al. 1988, Flamm et al. 1993, Schowalter 2012, McNichol et al. 2019).

1.2 Response of the southern pine bark beetle guild to disturbance in pine forests

Herbivorous insects, such as bark beetles (Coleoptera: Curculionidae: Scolytinae), play a role in pine forest ecosystem dynamics (Biedermann et al. 2019). Bark beetles construct reproductive galleries in phloem tissues of pine trees, where the beetles mate and deposit their eggs (Raffa et al. 2015). Upon hatching, the beetle larvae produce further galleries when they feed on phloem to grow and complete their lifecycles (Raffa et al. 2015). The construction of these adult and larval galleries effectively girdles pine trees, contributing to the tree's eventual death (Yousuf et al. 2014, Hornslein et al. 2019).

Bark beetles contribute to nutrient cycling, regeneration, and forest heterogeneity by speeding up tree death and decay (Winter et al. 2017). Under normal circumstances, some bark beetles attack trees that are already stressed or dying due to old age, environmental stress, or the accumulation of disease agents. However, other bark beetle species are pests, causing tree mortality and economic losses.

In the southeastern U.S., the southern pine bark beetle guild is made up of five important bark beetle pests (Nebeker et al. 2011): *Dendroctonus frontalis* Zimmermann, *Dendroctonus terebrans* (Olivier), *Ips avulsus* (Eichhoff), *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff). These subcortical beetles attack, burrow into, and breed within healthy, stressed, or dying pine trees (Flamm et al. 1993). Consequently, disturbance events that affect tree health create substantial reproductive substrate for bark beetle populations (Coulson et al. 1986, Vogt et al. 2020). Of particular concern for forest management are bark beetle outbreaks, a condition where local bark beetle population densities become large enough for the beetles to successfully attack and kill healthy trees (Gara and Coster 1968). Bark beetles exploiting the reproductive substrate produced by prior forest disturbance events can also result in an outbreak (McNichol et al. 2019). In such cases, native bark beetle species become a form of biotic disturbance themselves, capable of creating disturbance legacies and interacting with other disturbance events.

Windstorms have a significant impact on bark beetle populations by causing tree stress and death over large areas (Gochnour et al. 2022). Species in the southern pine bark beetle guild can detect and will readily attack and colonize trees damaged by windstorms (Ciesla and Bell 1968, Fredericksen et al. 1995), though there can be a lag in beetle population increases after storm events, causing population changes to manifest over several years (Gandhi et al. 2009, Spinner 2022).

In the case of fire, members of the southern pine bark beetle guild have variable responses depending on fire characteristics, host tree species, and the beetle species involved (Sullivan et al. 2003, Ritger et al. 2023). The effects of fire can lead to an increased local abundance of bark beetles (Sullivan et al. 2003, Campbell et al. 2008, Ritger et al. 2023), although this increase does not always lead to greater pine damage or mortality (McNichol et al. 2019, Palmer et al. 2024). Further, fire can increase the local abundance of bark beetle predators, dampening the population growth of bark beetle species responding to burned areas (Palmer et al. 2024). Interestingly, one beetle species, *I. grandicollis*, has repeatedly shown no differences in its response to burned versus unburned pine forests (Santoro et al. 2001, Campbell et al. 2008, Dodds et al. 2023, Ritger et al. 2023), and may even benefit from fire exclusion (Ritger et al. 2023).

Due to the widespread and consistent occurrence of lightning strikes each year, lightning serves as a significant source of reproductive substrate for bark beetles at the landscape scale (Coulson et al. 1983, Coulson et al. 1986, Rykiel et al. 1988). Lovelady et al. (1991) demonstrated a positive correlation between cumulative lightning strike events on pine trees and cumulative southern pine beetle infestations. Moreover, multiple bark beetle species regularly co-colonize lightning struck pine trees throughout the year (Coulson et al. 1986).

Lightning causes extreme trauma to struck trees which can decrease the number of beetles needed to overcome defenses and successfully colonize host trees (Flamm et al. 1993). Lightning strikes reduce trees' capacity for resin exudation and thus, decrease their ability to defend against bark beetle attack (Anderson and Anderson 1968, Hodges and Pickard 1971). In one study, the chemical components of pine resin were also seen to change after lightning strikes, with a reduction in compounds that are repellant to bark beetles and an increase in attractive compounds (Blanche et al. 1985).

Given the responses of southern bark beetle species' populations to weather related disturbances, there is potential for climate change to alter these relationships (Gan 2004, McNichol et al. 2022). Increasing temperatures and the probability of more intense disturbance events may provide opportunities for greater bark beetle population growth (Gan 2004, Allen et al. 2010, Tobin et al. 2023). While disturbance initiated bark beetle outbreaks are uncommon in longleaf pine forests, a changing climate may produce conditions that are more conducive to future outbreaks (Bowman and Chen 2022).

1.3 Dissertation outline

The goal of this dissertation is to provide information about how beetles respond to disturbances including wind, fire, lightning, and salvage logging in longleaf pine forests. Outcomes of the interactions between disturbance and members of the southern pine bark beetle guild in longleaf pine ecosystems may differ from those in forests dominated by other tree species due to longleaf forest's greater adaptation, and resilience to natural disturbance agents (Gresham et al. 1991, Outcalt 2000, Martinson et al. 2007, Johnsen et al. 2009, Rutledge et al. 2021). Moreover, the effects of climate change generate uncertainty in how compound disturbances will interact under future climatic variations. As a result, how bark beetles will respond to different management practices post-disturbance is uncertain in longleaf pine. The findings reported here add to the existing knowledge base available to longleaf forest managers to weigh the tradeoffs of different management practices.

Chapter 2 synthesizes the existing literature on how bark beetles respond to wind disturbances, particularly in the context of climatic changes. The chapter further discusses the utility and impacts of post-storm management practices on bark beetle activity. Additionally, we provide a model for understanding bark beetle-windstorm interactions. This chapter serves as a foundation for the next chapter in the dissertation, which specifically focuses on wind disturbance in longleaf pine forests.

In Chapter 3, we evaluate the effects of management practices on *I. avulsus*, *I. calligraphus*, and *I. grandicollis* in longleaf pine following a catastrophic hurricane. We sampled beetle trap catches from windthrown stands treated with three post-windstorm management approaches: no post-storm management, prescribed fire, and salvage logging followed by prescribed fire. This chapter also includes analyses of the effect of different lure combinations on woodboring beetle assemblages in the same treatment plots.

Chapter 4 narrows the focus from the stand to the single tree scale while broadening the scope to insect community responses to disturbance. We present the results of a study evaluating the activity of the beetle community and additional bark beetle predators to simulated-lightning-struck mature longleaf pine trees. We sampled flight activity at different heights (0, 5, 10, and 15 m) along the trunks of trees injured with detonation cord to characterize the spatial and temporal distributions of insects responding to lightning strikes.

Overall, the studies presented here contribute to understandings of the interplay between bark beetles and disturbance events in longleaf pine forests. In the concluding chapter (chapter 5), I summarize findings, provide management recommendations, and suggest directions for future research.

1.4 References

Allen, C. D. 2002. Lots of lightning and plenty of people: an ecological history of fire in the upland Southwest. Fire, native peoples, and the natural landscape: 143-193.

Allen, C. D., A. K. Macalady, H. Chenchouni, D. Bachelet, N. McDowell, M. Vennetier, T. Kitzberger, A. Rigling, D. D. Breshears, and E. T. Hogg. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259: 660-684.

Allen, M. S., V. Thapa, J. R. Arevalo, and M. W. Palmer. 2012. Windstorm damage and forest recovery: accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests. Plant Ecology 213: 1833-1842.

Anderson, N. H., and D. B. Anderson. 1968. *Ips* bark beetle attacks and brood development on a lightning-struck pine in relation to its physiological decline. Fla. Entomol.: 23-30.

Bale, A. M. 2009. Fire effects and litter accumulation dynamics in a montane longleaf pine ecosystem, University of Missouri-Columbia.

Batista, W. B., and W. J. Platt. 2003. Tree population responses to hurricane disturbance: syndromes in a south-eastern USA old-growth forest. J. Ecol.: 197-212.

Biedermann, P. H., J. Müller, J.-C. Grégoire, A. Gruppe, J. Hagge, A. Hammerbacher, R. W. Hofstetter, D. Kandasamy, M. Kolarik, and M. Kostovcik. 2019. Bark beetle population dynamics in the Anthropocene: challenges and solutions. Trends in ecology & evolution 34: 914-924.

Bigelow, S. W., and A. W. Whelan. 2019. Longleaf pine proximity effects on air temperatures and hardwood top-kill from prescribed fire. Fire Ecol. 15: 1-14.

Bigelow, S. W., C. E. Looney, and J. B. Cannon. 2021. Hurricane effects on climate-adaptive silviculture treatments to longleaf pine woodland in southwestern Georgia, USA. Forestry 94: 395-406.

Blanche, C., J. Hodges, and T. Nebeker. 1985. Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. Can. J. For. Res. 15: 397-399.

Bowman, K. A., and X. Chen. 2022. Current standing of longleaf pine trees under climate change. Journal of Botanical Research 4: 28-39.

Boyer, W. D. 1990. Growing-season burns for control of hardwoods in longleaf pine stands, vol. 256, US Department of Agriculture, Forest Service, Southern Forest Experiment Station.

Brantley, S. T., J. M. Vose, D. N. Wear, and L. Band. 2017. Planning for an uncertain future: Restoration to mitigate water scarcity and sustain carbon sequestration. Ecological restoration and management of longleaf pine forests: 291-310.

Brockway, D. G. 2005. Restoration of longleaf pine ecosystems, USDA Forest Service, Southern Research Station.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96: 167-183.

Brockway, D. G., and K. W. Outcalt. 1998. Gap-phase regeneration in longleaf pine wiregrass ecosystems. For. Ecol. Manage. 106: 125-139.

Campbell, J. W., J. L. Hanula, and T. A. Waldrop. 2008. Effects of prescribed fire and fire surrogates on saproxylic Coleoptera in the Southern Appalachians of North Carolina. J. Entomol. Sci. 43: 57-75.

Ciesla, W. M., and J. C. Bell. 1968. Pine engraver *Ips pini* (Coleoptera - Scolytidae) in southern Appalachian mountains. Ann. Entomol. Soc. Am. 61(1): 235-236.

Clark, K. E., E. Chin, M. N. Peterson, K. Lackstrom, K. Dow, M. Foster, and F. Cubbage. 2018. Evaluating climate change planning for longleaf pine ecosystems in the Southeast United States. J. Southeast. Assoc. Fish Wildl. Agencies 5: 160-168.

Clements, F. E. 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.

Coulson, R., P. Hennier, R. Flamm, E. Rykiel, L. Hu, and T. Payne. 1983. The role of lightning in the epidemiology of the Southern Pine Beetle. Zeitschrift für angewandte Entomologie 96: 182-193.

Coulson, R. N., R. O. Flamm, P. E. Pulley, T. L. Payne, E. J. Rykiel, and T. L. Wagner. 1986. Response of the southern pine bark beetle guild (Coleoptera: Scolytidae) to host disturbance. Environ. Entomol. 15: 850-858.

Crotteau, J. S., C. R. Keyes, S. M. Hood, and A. J. Larson. 2020. Vegetation dynamics following compound disturbance in a dry pine forest: fuel treatment then bark beetle outbreak. Ecol. Appl. 30: e02023.

Dale, V. H., S. C. Beyeler, and B. Jackson. 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. Ecol. Indic. 1: 155-170.

Dale, V. H., A. E. Lugo, J. A. MacMahon, and S. T. Pickett. 1998. Ecosystem management in the context of large, infrequent disturbances. Ecosystems 1: 546-557.

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

Dodds, K. J., M. F. DiGirolomo, and S. Fraver. 2019. Response of bark beetles and woodborers to tornado damage and subsequent salvage logging in northern coniferous forests of Maine, USA. For. Ecol. Manage. 450.

Dodds, K. J., J. Cancelliere, and M. F. DiGirolomo. 2023. Bark beetle and woodborer responses to stand thinning and prescribed fire in northeastern US coastal and inland pitch pine barrens.

Drewa, P. B., W. J. Platt, and E. B. Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83: 755-767.

Elsner, J. B. 2006. Evidence in support of the climate change–Atlantic hurricane hypothesis. Geophys. Res. Lett. 33: 1-3.

Estes, B. 2006. Impact of interacting disturbances on longleaf pine communities.

Everham, E. M., and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. 62: 113-185.

Flamm, R. O., P. E. Pulley, and R. N. Coulson. 1993. Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera, Scolytidae). Environ. Entomol. 22: 62-70.

Fortuin, C. C., C. R. Montes, J. T. Vogt, and K. J. Gandhi. 2023. Stand and tree characteristics influence damage severity after a catastrophic hurricane disturbance. For. Ecol. Manage. 532: 120844.

Fredericksen, T. S., R. L. Hedden, and S. A. Williams. 1995. Susceptibility of loblolly pine to bark beetle attack following simulated wind stress. For. Ecol. Manage. 76: 95-107.

Frost, C. 2006. History and future of the longleaf pine ecosystem. The longleaf pine ecosystem: ecology, silviculture, and restoration 438: 9-42.

Gan, J. 2004. Risk and damage of southern pine beetle outbreaks under global climate change. For. Ecol. Manage. 191: 61-71.

Gandhi, K. J. K., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. R. Spence, and S. J. Seybold. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews 15: 113-152.

Gandhi, K. J. K., D. W. Gilmore, R. A. Haack, S. A. Katovich, S. J. Krauth, W. J. Mattson, J. C. Zasada, and S. J. Seybold. 2009. Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. J. Chem. Ecol. 35: 1384-1410.

Gara, R., and J. Coster. 1968. Studies on the attack behavior of the southern pine beetle. III Sequence of tree infestation within stands.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club: 7-26.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65: 441-476.

Glitzenstein, J. S., D. R. Streng, and D. D. Wade. 2003. Fire frequency effects on longleaf pine (*Pinus palustris*, P. Miller) vegetation in South Carolina and northeast Florida, USA. Natural Areas Journal 23: 22-37.

Gochnour, B., S. Spinner, K. Klepzig, and K. Gandhi. 2022. Interactions between catastrophic wind disturbances and bark beetles in forested ecosystems, pp. 197-223, Bark beetle management, ecology, and climate change. Academic Press.

Gresham, C. A., T. M. Williams, and D. J. Lipscomb. 1991. Hurricane Hugo wind damage to southeastern US coastal forest tree species. Biotropica: 420-426.

Hanula, J. L., M. D. Ulyshen, and D. D. Wade. 2012. Impacts of prescribed fire frequency on coarse woody debris volume, decomposition and termite activity in the longleaf pine flatwoods of Florida. Forests 3: 317-331.

Hekkala, A.-M., M. Jönsson, S. Kärvemo, J. Strengbom, and J. Sjögren. 2023. Habitat heterogeneity is a good predictor of boreal forest biodiversity. Ecol. Indic. 148: 110069.

Hodges, J. D., and L. S. Pickard. 1971. Lightning in ecology of southern pine beetle, *Dendroctonus frontalis* (Coleoptera - Scolytidae). Can. Entomol. 103: 44-&.

Holland, G., and C. L. Bruyère. 2014. Recent intense hurricane response to global climate change. Climate Dynamics 42: 617–627.

Hook, D. D., M. A. Buford, and T. M. Williams. 1991. Impact of Hurricane Hugo on the South Carolina coastal plain forest. Journal of Coastal Research: 291-300.

Hornslein, N. J., C. M. Siegert, and H. J. Renninger. 2019. Changes in physiological functioning in loblolly pine trees undergoing bark beetle simulated mortality. For. Sci. 65: 312-323.

Johnsen, K. H., J. R. Butnor, J. S. Kush, R. C. Schmidtling, and C. D. Nelson. 2009. Hurricane Katrina winds damaged longleaf pine less than loblolly pine. Southern Journal of Applied Forestry 33: 178-181.

Johnson, R., and D. Gjerstad. 2006. Restoring the overstory of longleaf pine ecosystems. The longleaf pine ecosystem: 271-295.

Jose, S., E. J. Jokela, and D. L. Miller. 2006. The Longleaf Pine Ecosystem, pp. 3-8. In S. Jose, E. J. Jokela and D. L. Miller (eds.), The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer New York, New York, NY.

Kaeser, M. J., and L. K. Kirkman. 2009. Estimating total plant species richness in depressional wetlands in the longleaf pine ecosystem. Wetlands 29: 866-874.

Kalisz, P. J., A. W. Dorian, and E. L. Stone. 1986. Prehistoric land-use and the distribution of longleaf pine on the Ocala National Forest, Florida: an interdisciplinary synthesis. The Florida Anthropologist 39: 183-193.

Kay, C. E. Year. Published. Are lightning fires unnatural? A comparison of aboriginal and lightning ignition rates in the United States, pp. 16-28. *In*, Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tall Timbers Research Station, Tallahassee, FL, 2007.

Kenney, G., C. L. Staudhammer, S. Wiesner, S. T. Brantley, S. W. Bigelow, and G. Starr. 2021. Hurricane michael altered the structure and function of longleaf pine woodlands. J. Geophys. Res.-Biogeosci. 126: 17.

Kirkman, L., L. Giencke, R. Taylor, L. Boring, C. Staudhammer, and R. Mitchell. 2016. Productivity and species richness in longleaf pine woodlands: resource-disturbance influences across an edaphic gradient. Ecology 97: 2259-2271.

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

Kleinman, J. S., and J. L. Hart. 2018. Vascular flora of longleaf pine woodlands after wind disturbance and salvage harvesting in the Alabama Fall Line Hills. Castanea 83: 183-195.

Kleinman, J. S., S. A. Ford, and J. L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. For. Ecol. Manage. 403: 112-125.

Kleinman, J. S., J. D. Goode, A. C. Fries, and J. L. Hart. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. Ecosphere 10: 18.

Kleinman, J. S., J. D. Goode, J. L. Hart, and D. C. Dey. 2020. Prescribed fire effects on *Pinus palustris* woodland development after catastrophic wind disturbance and salvage logging. For. Ecol. Manage. 468: 118173.

Knapp, B. O., L. S. Pile, J. L. Walker, and G. Geoff Wang. 2018. Fire effects on a fire-adapted species: response of grass stage longleaf pine seedlings to experimental burning. Fire Ecol. 14: 1-16.

Knutson, T., S. J. Camargo, J. C. Chan, K. Emanuel, C.-H. Ho, J. Kossin, M. Mohapatra, M. Satoh, M. Sugi, and K. Walsh. 2020. Tropical cyclones and climate change assessment: Part II: Projected response to anthropogenic warming. Bulletin of the American Meteorological Society 101: E303-E322.

Kupfer, J. A., K. Lackstrom, J. M. Grego, K. Dow, A. J. Terando, and J. K. Hiers. 2022. Prescribed fire in longleaf pine ecosystems: fire managers' perspectives on priorities, constraints, and future prospects. Fire Ecol. 18.

Lovelady, C. N., P. E. Pulley, R. N. Coulson, and R. O. Flamm. 1991. Relation of lightning to herbivory by the southern pine bark beetle guild (Coleoptera, Scolytidae). Environ. Entomol. 20: 1279-1284.

Mann, M. E., and K. A. Emanuel. 2006. Atlantic hurricane trends linked to climate change. Eos 87: 233-244.

Martinson, S., R. W. Hofstetter, and M. P. Ayres. 2007. Why does longleaf pine have low susceptibility to southern pine beetle? Can. J. For. Res. 37: 1966-1977.

McCay, D. H. 2000. Effects of chronic human activities on invasion of longleaf pine forests by sand pine. Ecosystems 3: 283-292.

McNichol, B. H., C. R. Montes, B. F. Barnes, J. T. Nowak, C. Villari, and K. J. K. Gandhi. 2019. Interactions between southern *Ips* bark beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality. For. Ecol. Manage. 446: 164-174.

McNichol, B. H., S. R. Clarke, M. Faccoli, C. R. Montes, J. T. Nowak, J. D. Reeve, and K. J. Gandhi. 2022. Relationships between drought, coniferous tree physiology, and *Ips* bark beetles under climatic changes, pp. 153-194, Bark beetle management, ecology, and climate change. Elsevier.

Means, D. B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. The longleaf pine ecosystem: 157-213.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17: 2145-2151.

Mitchell, R. J., Y. Q. Liu, J. J. O'Brien, K. J. Elliott, G. Starr, C. F. Miniat, and J. K. Hiers. 2014. Future climate and fire interactions in the southeastern region of the United States. For. Ecol. Manage. 327: 316-326.

Moser, W., T. Treiman, and E. Johnson. 2003. Species choice and risk in forest restoration: A comparison of methodologies for evaluating forest management decisions. Forestry 76: 137-147.

Nebeker, T. E., R. Coulson, and K. Klepzig. 2011. Southern pine bark beetle guild. Southern Pine Beetle II. In: General Technical Report SRS-140, USDA Forest Service Southern Research Station, Asheville, NC: 199-209.

Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Natural Areas Journal 9: 211-213.

Ostertag, R., F. N. Scatena, and W. L. Silver. 2003. Forest floor decomposition following hurricane litter inputs in several puerto rican forests. Ecosystems 6.

Outcalt, K. W. 2000. The longleaf pine ecosystem of the South. Native Plants Journal 1: 42-53.

Outcalt, K. W. 2008. Lightning, fire and longleaf pine: Using natural disturbance to guide management. For. Ecol. Manage. 255: 3351-3359.

Palik, B. J., R. J. Mitchell, and J. K. Hiers. 2002. Modeling silviculture after natural disturbance to sustain biodiversity in the longleaf pine (*Pinus palustris*) ecosystem: balancing complexity and implementation. For. Ecol. Manage. 155: 347-356.

Palmer, J. F., D. R. Coyle, W. C. Heaton, J. T. Nowak, and J. A. Hartshorn. 2024. Response of *Ips* bark beetles (Coleoptera: Curculionidae: Scolytinae) to prescribed fire in South Carolina. For. Ecol. Manage. 561: 121870.

Peet, R. K. 2006. Ecological classification of longleaf pine woodlands. The longleaf pine ecosystem: 51-93.

Platt, W. J., G. W. Evans, and M. M. Davis. 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76: 353-363.

Platt, W. J., R. F. Doren, and T. V. Armentano. 2000. Effects of Hurricane Andrew on stands of slash pine (*Pinus elliottii* var. densa) in the everglades region of south Florida (USA). Plant Ecology 146: 43-60.

Pope, C. A., J. B. Cannon, S. W. Bigelow, and A. Sharma. 2023. Effects of hurricane canopy gaps on longleaf pine and upland oak sapling growth. For. Ecol. Manage. 529: 10.

Potterf, M., and C. Bone. 2017. Simulating bark beetle population dynamics in response to windthrow events. Ecological Complexity 32: 21-30.

Potterf, M., C. Nikolov, E. Kocicka, J. Ferencik, P. Mezei, and R. Jakus. 2019. Landscape-level spread of beetle infestations from windthrown- and beetle-killed trees in the non-intervention zone of the Tatra National Park, Slovakia (Central Europe). For. Ecol. Manage. 432: 489-500.

Provencher, L., A. R. Litt, and D. R. Gordon. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conserv. Biol. 17: 1660-1671.

Raffa, K. F., J.-C. Gregoire, and B. S. Lindgren. 2015. Natural history and ecology of bark beetles, pp. 1-40, Bark beetles. Elsevier.

Ritger, H. M. W., S. T. Brantley, K. D. Klepzig, and K. J. K. Gandhi. 2023. Differential effects of fire regime and site conditions on bark beetles (Coleoptera: Curculionidae) in a longleaf pine (*Pinus palustris* Mill.) ecosystem. For. Ecol. Manage. 549: 13.

Rutledge, B. T., J. B. Cannon, R. K. McIntyre, A. M. Holland, and S. B. Jack. 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. For. Ecol. Manage. 481: 13.

Rykiel, E. J., R. N. Coulson, P. J. Sharpe, T. F. Allen, and R. O. Flamm. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomenon. Landscape ecology 1: 129-139.

Santoro, A. E., M. J. Lombardero, M. P. Ayres, and J. J. Ruel. 2001. Interactions between fire and bark beetles in an old growth pine forest. For. Ecol. Manage. 144: 245-254.

Schowalter, T. D. 2012. Ecology and management of bark beetles (Coleoptera: Curculionidae: Scolytinae) in southern pine forests. J. Integr. Pest Manag. 3: 7.

Seidl, R., K. Albrich, D. Thom, and W. Rammer. 2018. Harnessing landscape heterogeneity for managing future disturbance risks in forest ecosystems. J. Environ. Manage. 209: 46-56.

Sharma, A., S. K. Ojha, L. D. Dimov, J. G. Vogel, and J. Nowak. 2021. Long-term effects of catastrophic wind on southern US coastal forests: Lessons from a major hurricane. PLoS One 16: e0243362.

Sheehan, T. N., and K. D. Klepzig. 2022. Arthropods and fire within the biologically diverse longleaf pine ecosystem. Ann. Entomol. Soc. Am. 115: 69-94.

Snow, G., W. Hoffard, C. Cordell, and A. Kais. Year. Published. Pest management in longleaf pine stands, pp. 128-134. *In*, Proceedings of the Symposium on the Management of Longleaf Pine, 1990. Gen Tech. Rep. SO-75. USDA Forest Service, Southern Forestry Experiment Station.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.

Spinner, S. C. 2022. Responses of bark beetles and their associates to a severe wind disturbance in southern pine stands. University of Georgia.

Stout, I. J., and W. R. Marion. 1993. Pine flatwoods and xeric pine forests of the southern (lower) coastal plain. Biodiversity of the southeastern United States: lowland terrestrial communities: 373-446.

Sullivan, B. T., C. J. Fettig, W. J. Otrosina, M. J. Dalusky, and C. W. Berisford. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. For. Ecol. Manage. 185: 327-340.

Taylor, A. R. Year. Published. Ecological aspects of lightning in forests, pp. 455-482. *In*, Proceedings of the Tall Timbers fire ecology conference, 1974.

Thaxton, J. M., and W. J. Platt. 2006. Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87: 1331-1337.

Tobin, P. C., K. J. Haynes, and A. L. Carroll. 2023. Spatial dynamics of forest insects, pp. 647-668, Forest Entomology and Pathology: Volume 1: Entomology. Springer International Publishing Cham.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. For. Ecol. Manage. 211: 150-165.

Vogt, J. T., K. J. Gandhi, D. C. Bragg, R. Olatinwo, and K. D. Klepzig. 2020. Interactions between weather-related disturbance and forest insects and diseases in the southern United States.

White, P. S., and S. T. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. In S. T. Pickett and P. S. White (eds.), The ecology of natural disturbance and patch dynamics. Elsevier.

Winter, M.-B., C. Bässler, M. Bernhardt-Römermann, F.-S. Krah, H. Schaefer, S. Seibold, and J. Müller. 2017. On the structural and species diversity effects of bark beetle disturbance in forests during initial and advanced early-seral stages at different scales. Eur. J. For. Res. 136: 357-373.

Yousuf, F., G. M. Gurr, A. J. Carnegie, R. A. Bedding, R. Bashford, and C. W. Gitau. 2014. Biology of the bark beetle *Ips grandicollis* Eichhoff (Coleoptera: Scolytinae) and its arthropod, nematode and microbial associates: a review of management opportunities for Australia. Austral Entomol. 53: 298-316.

Zampieri, N. E., S. Pau, and D. K. Okamoto. 2020. The impact of Hurricane Michael on longleaf pine habitats in Florida. Scientific Reports 10: 8483.

CHAPTER 2

INTERACTIONS BETWEEN CATASTROPHIC WIND DISTURBANCES AND BARK BEETLES IN FORESTED ECOSYSTEMS[1]

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Abstract

Catastrophic wind disturbances under climatic changes are causing major economic impacts and ecological changes that can persist for decades. Bark beetle (Coleoptera: Curculionidae) population and community dynamics are often linked to such wind disturbances at several spatial and temporal scales ranging from damage to individual trees to large-scale windthrow that may prompt multiyear outbreaks on the landscape scale. In this chapter, we discuss how catastrophic wind disturbances and ensuing biological legacies enhance bark beetle populations, particularly in the context of climatic changes. The high level of variability at the tree, stand, and landscape levels created by windstorms generally has positive consequences for eruptive bark beetle species, particularly in Europe. Poststorm timber salvaging to alleviate pest burdens may push biotic elements, especially those dependent on coarse woody debris and forest gaps, into different successional pathways. Climate change is undoubtedly influencing the interactions between these two major disturbance agents by increasing their intensity and severity levels and altering landscape characteristics with feedback loops. In the Anthropocene, predictive modeling of network interactions between multiple abiotic and biotic disturbances and stressors will be critical for effective mitigation, forest restoration, and sustainable forestry practices in a rapidly changing world.

KEYWORDS: bark beetles, forest management, population dynamics, thresholds, wind disturbance

2.1 Managing longleaf pine forests for compound disturbances under climate change

One of the main tools for managing longleaf pine forests is prescribed fire (Outcalt 2008, Lashley et al. 2014, Darracq et al. 2016, Bigelow et al. 2017, Kupfer et al. 2022). Its use as a form of management traces back to Indigenous peoples (Kalisz et al. 1986, Kay 2007). Early colonial settlers suppressed wildland fires, although this was relatively short lived, and current management of the remaining longleaf habitats relies heavily on frequent application of prescribed fire (Fowler and Konopik 2007). These low-intensity fires are preferrable to high-intensity fires which can cause crown fires and tree mortality (Heyward 1939).

After windstorms, salvage logging is sometimes used prior to prescribed burns to remove the influx of fuels in the form of windthrown trees (Lindenmayer and Noss 2006). By removing large, long-burning fuels before prescribed burns, salvage logging facilitates low intensity fires (Emery et al. 2020). However, salvage logging is also a form of disturbance in and of itself as it causes soil compaction and mechanical damage to standing trees (Neaves III et al. 2017, Santoro and D'Amato 2019). As a result, longleaf forest managers are faced with weighing the costs and benefits of managing with and for compound disturbances.

While bark beetles have not historically been a major concern for longleaf pine management, climate change may change this pattern (Gan 2004). While the studies on longleaf forests are limited, studies in other areas of North America have found concerning effects of climate change on bark beetle species (Bentz et al. 2010). For example, in the western U.S., the western pine beetle [*Dendroctonus ponderosae* (Hopkins)] has exhibited decreased generation times, increased overwinter survival, range expansion, and lowered thresholds for eruptive population events (Williams and Liebhold 2002, Taylor and Safanyik 2003, Raffa et al. 2008, Mitton and Ferrenberg 2012). These changes have resulted in beetle outbreaks with severe consequences for the forest ecosystems (Saab et al. 2014, Dhar et al. 2016). Given the influence of climate change on disturbance agents, it is important to monitor the responses of potentially eruptive beetle species (Weed et al. 2013).

Hurricane Michael exemplifies the potential for future disturbances in longleaf pine ecosystems to occur beyond historical ranges of variability. This catastrophic hurricane caused widespread damage to pine forests in the Southeast thus, resulting in variable forest conditions (Zampieri et al. 2020, Brandei 2022). Alongside the regular application of prescribed fire, land managers have implemented salvage logging in these areas to mitigate the effects of the storm by reducing excessive fuel loads (Kenney et al. 2021). It is unclear how the members of the southern pine bark beetle guild will respond to both the windstorm and the subsequent management practices.

The subsequent management of these areas with salvage logging and prescribed fire will further increase the diversity of outcomes post disturbance (Millar et al. 2007, Bigelow et al. 2021). The interaction between these outcomes will undoubtedly extend to the beetle populations already present in these forests with implications for further disturbance by biotic agents (Mitchell et al. 2014). Increasing our knowledge of how these disturbance agents interact in longleaf pine forests will aid in restoration efforts in the context of climate change (Temperli et al. 2012).

2.2 Introduction

2.2.1 Windthrow and subcortical beetles

Sudden increases in stressed and damaged trees may lead to positive responses by subcortical insects such as bark (Coleoptera: Curculionidae: Scolytinae) and woodboring (Coleoptera: Buprestidae and Cerambycidae) beetles which are particularly adept at exploiting such trees and stands after a windstorm event (e.g., Connola, Collins, Risley, & Smith, 1956; Dodds, DiGirolomo, & Fraver, 2019; Gandhi et al., 2009; Gardiner, 1975; Kirkendall, Biedermann, & Jordal, 2015). In particular, bark beetles are considered the most injurious insects to mature trees and appear to be very responsive to altered climatic and host conditions (Bentz et al., 2010; Safranyik et al., 2010). Many of these species are secondary colonizers which means that they attack host trees whose defense systems are weakened. There are a few primary species such as *Dendroctonus ponderosae* and *D. frontalis* that can colonize presumably healthy trees and cause much greater damage. Adult primary (and some secondary) bark beetles introduce symbiotic fungi (including nutritional mutualists and antagonistic tree pathogens) as they feed and oviposit in the phloem layer of conifer host trees (Hofstetter, Dinkins-Bookwalter, Davis, & Klepzig, 2015; Hubbard, Rhoades, Elder, & Negron, 2013). These fungi and their beetle vectors aid in the depletion of host defenses, overcoming the tree’s defense system (Kirisits, 2007). As bark beetles disrupt the transport of sugars in the phloem down to the roots, their associated fungi interrupt water and nutrient transport in the xylem, clogging the tree’s vascular system, and effectively girdling and killing the trees (Christiansen, Waring, & Berryman, 1987; Krokene, 2015).

Large bark beetle outbreaks are among the most economically impactful forest disturbances in North America and Europe. In North America alone, these outbreaks cause over $2 billion in annual economic losses (calculated variously as hectares affected, timber volume lost, and downgraded in wood quality) (Grégoire, Raffa, & Lindgren, 2015). Though some bark beetle outbreaks are closely associated with windthrow events, little is known of their combined economic impacts (Dale et al., 2001; Seidl & Rammer, 2017). There are numerous parallel (or even identical) effects of windthrow and bark beetle infestation through alterations of stand structure, while differences may include much higher abundance and diversity of woody debris on the forest floor after a windstorm as compared to a bark beetle outbreak where most of the woody debris is left standing. Both types of events lead to downgrading or complete loss of wood value. Blue staining from bark beetle associated fungi does not affect wood integrity, but it can make it less desirable and valuable (Shupe, Lebow, & Ring, 2008). If salvage operations are not quickly undertaken, insects and fungi may degrade and weaken wood structure, decreasing the volume suitable for lumber. As an example, wood value declined by 15% in initial stages of succumbing to bark beetle attack (i.e., within one year), and by another 50% as trees decay and exhibit holes, resin pockets, rot, and cracks (Hlásny et al., 2019; Loeffler & Anderson, 2017).

Likewise, both bark beetles and wind disturbances can heavily impact ecosystem services. Affected stands may become carbon sources instead of sinks and landscape level changes may occur in esthetic, recreational, carbon market, and habitat values (Daniels & Larson, 2020; Grégoire et al., 2015; Lindroth et al., 2009). Both affect timber and nontimber economics and vary from local and regional to national scales (Hlásny et al., 2019). Ecological factors such as stand resiliency and resistance, and tree physiology, as well as economic factors including forest value, commodity supply, and demand all interact and make monetary valuation of impacts difficult. While short term increases in timber supply may boost regional economies (Grégoire et al., 2015), this surge in timber volume eventually decreases the timber market price for all sellers, as “selling begets more selling and timber prices collapse” (Chow & Obermajer, 2007; Hlásny et al., 2019; Holmes, 1991). In the short run, the welfare of producers is decreased, while that of wood-using firms is increased (Pye, Holmes, Prestemon, & Wear, 2011). Over the longer term, extensive bark beetle outbreaks can reduce the standing volume of timber, ultimately causing a small but significant price increase due to timber scarcity (Pye et al., 2011). The sudden harvest of trees may also cause issues with infrastructure needed for transporting wood, and mills ill equipped to handle high volume of material, thus challenging their processing and storage capacity (Broman, Frisk, & Rönnqvist, 2009). Mills in the path of hurricanes may directly be impacted, e.g., hardwood and conifer mills showed a loss in production efficiency and in grade level of finished lumber from windthrow material after Hurricane Katrina (McConnell & Shmulsky, 2009). In areas that are more prone to windthrow, economic impacts from both windthrow and bark beetles may continue to be magnified with time.

2.2.2 Objectives of the chapter

Both windthrow and bark beetles are natural disturbance agents that cause extensive tree mortality, and their impacts and management are not mutually exclusive. Herein, we provide an overview of the interactions between catastrophic wind disturbance events and bark beetles, particularly under the context of climatic changes. We draw from many forested ecosystems around the world with a focus on European and North American conifer-dominated forests where windstorms have a significant role in extant forest patterns and processes. We will discuss the utility and impacts of poststorm management activities for these subcortical beetles. Finally, we identify gaps in current knowledge and directions for future research. If catastrophic wind disturbances become more dominant and prevalent in major forested landscapes, then a greater attention to the cascading ecological and economic issues will be needed for long-term forest preservation, restoration, and sustainability approaches.

2.3 Interactions of wind disturbance with bark beetles

Bark beetles may remain at low numbers or increase dramatically to outbreak levels after a wind disturbance event (Connola et al., 1956; Gardiner, 1975; Nikolov et al., 2014) (Figure 2.2). The progression from endemic to epidemic phase by primary bark beetles (such as *D. ponderosae* in western USA) is governed by a series of thresholds and feedbacks (Raffa et al., 2008). Wind disturbance can alter these thresholds, particularly host defenses, in forests where predisturbance stand conditions and tree vigor would otherwise have low susceptibility to bark beetles. These processes can feed back into one another, amplifying, or dampening the effects of disturbance agents and affecting the progression of bark beetle outbreaks. Further, the ecological legacies created by both wind disturbance and bark beetle outbreaks may favor or enable further susceptibility to future wind damage or bark beetle infestation (Okland, Nikolov, Krokene, & Vakula, 2016) (Figures 2.1 and 2.2).

In windthrown areas, as in general, bark beetle colonization dynamics are largely dictated by tree defense systems, and stand structure and composition. Little work has directly been done on the altered physiology of tree defenses after a windstorm (Zhao, Solheim, Langstrom, & Borg-Karlson, 2011). However, there appear to be several mechanisms by which damaged, stressed, and dying trees become more susceptible to attack by bark beetles. Trees that experience uprooting or stem breakage often die rapidly following a storm event and become readily available for colonization by bark beetles, likely having lost their ability to defend themselves from such an attack. Conifer defenses against beetles and their associated fungi include preformed and induced responses (Krokene, 2015). The defensive response begins with initial mechanical resin flow from any wound, which may ‘pitch out’ or entomb attacking beetles. Then, attacking beetles and fungi face constitutive monoterpene, resin acid, and phenolic compounds in tree tissues (Kolosova & Bohlmann, 2012; Raffa, Aukema, Erbilgin, Klepzig, & Wallin, 2005). Insect feeding and fungal growth are met with induced defense responses which see extreme elevations of these same compounds (Krokene, 2015). Trees not killed by the wind disturbance are less well defended and may show a range of responses from priming of chemical defenses to eventual depletion of resin and defensive capabilities as shown for other disturbances (such as wildfires) based on their severity levels (Hood, Sala, Heyerdahl, & Boutin, 2015). As such, trees damaged through severe defoliation, crown damage, or root damage, have a harder time recovering from disturbance if only due to the importance of functional cellular machinery to produce tree chemical defenses (Christiansen et al., 1987; Schowalter, 1985; Weslien, 1992). Even apparently undamaged trees can show reduced defenses (sometimes more so than wind-damaged trees) to bark beetle associated fungi (Zhao et al., 2011). This gradient and timeline of stress recovery by trees may facilitate bark beetle outbreaks and cause alterations in forest structure and com- position along the path of a windstorm event for several years poststorm.

2.3.1 At the tree- and stand levels

While insect behavior varies within a tree, though any subcortical tissue can be colonized by bark beetles. Branches (by *Pityophthorous* spp.), main stem (*Ips* and *Dendroctonus* spp.), and roots (*Hylastes* beetles and *Hylobius* weevils) are colonized by different numbers and species of bark beetles (Table 2.1) (Gandhi et al., 2007; Wood, 1982). Different bark beetle species may prefer shaded versus more exposed parts of the same tree, likely due to different phloem moisture and temperature levels (Gandhi et al., 2007). Such a variation of bark beetle populations and communities within a tree adds to the heterogeneity seen at higher spatial levels (Table 2.1).

At the individual tree level, wind disturbance results in structural and mechanical damage to the woody tissue (Figure 2.1). Bending of stems and branches cracks bark and wood, exposing internal tissues, and releasing tree volatiles. Needle damage and loss of trees likewise increase volatiles into the environment (Loreto & Schnitzler, 2010). Depending on timing of the disturbance, increased levels of host volatiles may have immediate impacts on the behavior of many bark beetles (Byers, 1995; Seybold, Huber, Lee, Graves, & Bohlmann, 2006). Secondary bark beetles seeking host trees cue in on increased levels of terpenes and ethanol, tracking volatile plumes back to weakened and wounded trees. Here they begin the process of host colonization, entering trees. Primary beetles generally signal other beetles to do the same through aggregation pheromones eliciting mass attacks (Pureswaran & Borden, 2005; Schroeder, 1988). However, as soon as any beetle begins to chew its way into a tree's tissues, the tree mounts a defensive response. As discussed above, these defensive systems are impaired in wind-damaged trees, which can allow successful beetle entry and establishment (Schowalter, 1985; Weslien, 1992).

Effects of wind disturbance at the stand level are characterized by percent crown damage, basal area lost, and/or increase in the type and volume of coarse woody debris. Trees in an area affected by wind may suffer broken branches and mechanical torsion, breakage of the stem, uprooting, or complete blowdown, thus leading to deadwood and coarse woody debris diversity within a stand (Peterson, 2000). Trees collide with each other as they are blown around and fall over, resulting in leaning or downed trees, creating snags, and forming canopy gaps (Foster & Boose, 1992). The sudden availability of these newly created habitats (in addition to tree damage) may, to varying degrees, elicit a positive response from bark beetles.

Globally, associations between wind damage and increased populations have been observed for many different species of bark and ambrosia beetles. After severe wind damage, Kerchev (2014) recorded *Polygraphus proximus* attacking windthrown trees in western Siberia; Gardiner (1975) documented *I. pini*, *I. borealis*, and *Trypodendron lineatum* attacks on windthrown spruce-jack pine stands in northern Ontario, Canada; Grimbacher and Stork (2009) found that bark beetle abundance was positively correlated with amounts of coarse woody debris due to Cyclone Larry in the tropical rainforests of the Atherton Tablelands, Australia; Connola et al. (1956) recorded attacks by *P. rufipennis* and *Dryocoetes piceae* in windthrown forests in the Adirondack Mountains of New York, USA; Gandhi et al. (2009) demonstrated that subcortical insects including bark beetles increased in numbers two years in stands affected by a catastrophic windthrow event in subboreal, Minnesota, USA; and *Ips typographus* (L.) has been documented to increase in numbers after many windstorms in Europe (Eriksson, Pouttu, & Roininen, 2005; Nikolov et al., 2014; Schroeder, 2001, 2010). An in-depth synopsis of such associations between bark beetles and wind damage on host trees in North American forests may be found in Gandhi et al. (2007). Likewise, these types of interactions in Europe have been addressed extensively (Thorn et al., 2014). While these insects may increase in numbers, that does not necessarily translate into increased damage to live trees within and around the windthrow areas (Bouget & Noblecourt, 2005; Gandhi et al., 2009; Schroeder, 2001, 2010). The timing of the disturbance itself, the quality of suitable host material (coniferous or not), size of the windthrown areas, various landscape characteristics, and/or the in situ short-term response of beetles may all influence the ultimate combined impacts of wind and beetles (Schroeder, 2001, 2010).

Only a few bark beetle species have been reported to drastically increase in numbers and colonize standing live trees after wind disturbance. This life history has the potential to amplify economic and ecological impacts well beyond the immediate effects of windstorms. For example, *I. typographus* (which colonizes Norway spruce, *Picea abies*) is considered a keystone species for significantly altering European landscapes (Eriksson et al., 2005; Komonen, Schroeder, & Weslien, 2011; Nikolov et al., 2014; Schroeder, 2001, 2010). In some cases, losses associated with subsequent outbreaks of *I. typographus* can exceed the losses from the wind disturbance event itself (e.g., in the Tatra Mountains of Slovakia) (Nikolov et al., 2014). Following another windstorm, approximately 80% of wind-damaged trees were killed by *I. typographus* (Janik & Romportl, 2018). Eriksson et al. (2005) likewise found that in the first summer after a severe windstorm, at the landscape level 71% of the affected areas were colonized by *I. typographus*. Similarly, *I. typographus japonicus* and *P. proximus* increased in numbers at the stand level after a windthrow in spruce trees and started attacking standing live trees two years after a storm in Hokkaido, Japan (Inouye, 1962). Recently, drought has been seen to be a significant trigger of outbreaks as well (Hlásny et al., 2021; Zimová, Merganičova´, Štěpánek, Modlinger, & Turčáni, 2021). In North America, *D. rufipennis*, *D. pseudotsugae*, and *D. confusus* have also historically initiated outbreaks from windthrown conifers and moved into standing trees to cause economic damage for many years thereafter (Gandhi et al., 2007; McMillin, Allen, Long, Harris, & Negrón, 2003). While many native bark beetle species respond to downed material, only a few are capable of building high populations that then move on to kill living trees in and around wind damaged areas.

Many characteristics at the stand level may be critical in determining the populations and communities of bark beetles in windthrown and adjacent areas (Table 2.1). There are no differences in terms of production of *I. typographus* between wind-felled and standing live residual Norway spruce trees, but more progeny emerged from tree tops than from the bottom parts of trees in Sweden (Komonen et al., 2011). In some cases, blown-over trees had higher infestation levels by bark beetles than those with broken stems (Gilbert, Nageleisen, Franklin, & Gregoire, 2005). In other studies, broken trees were colonized first by bark beetles (likely because these trees desiccate quicker and their defense systems are more impaired) and/or supported higher numbers of beetles than those that were blown over (Gardiner, 1975, 1976; Jakuš, 1998), while no differences were observed in similar studies (Wickman, 1965).

The location of trees may matter within stands. Beetle-attacked trees in shaded areas may support higher beetle brood production (McGregor, Hamel, & Oakes, 1976). Hardwood edges adjacent to coniferous forests may be associated with lower *Tomicus piniperda* populations, and vice-versa, likely due to the disruption of host finding ability by nonhost volatiles (Gilbert et al., 2005). Trees in the south and west facing areas tend to have higher beetle damage levels (presumably as these stands were drier), with increasing proportion of host trees and basal area, and with decreasing elevations (at least in early years) (Jakuš et al., 2011; Stadelmann, Bugmann, Wermelinger, & Bigler, 2014). *Ips typographus* tends to prefer colonizing trees in gaps and forest edges (Eriksson et al., 2005). Tree size may also play a role in colonization by bark beetles. Larger diameter Norway spruce trees seem to have more *I. typographus* activity (Scherstjanoi, Gimmi, Wolf, & Bugmann, 2010), while *Pityogenes chalcographus* preferred smaller diameter trees (Göthlin, Schroeder, & Lindelöw, 2000). This stand-level variability may result in different management options for greater effectiveness in controlling beetle outbreaks.

Variability in damage to individual trees within a windthrown stand creates a heterogenous matrix of potential host trees. We expect that severely damaged trees may be more easily colonized by bark beetles. Trees that are stressed and dying may become available for colonization later, although we are not aware of studies directly addressing it. This temporal variation in near-term host availability allows for a longer lasting source of more easily exploitable reproductive material for bark beetles. In general, there is a lag phase and bark beetles are typically reported to increase in numbers 2–3 years after a windstorm in and around the damaged areas (Krehan, Steyrer, & Tomiczek, 2010; Okland et al., 2016; Stadelmann et al., 2014; Wermelinger, 2004). This may reflect an inherent increase in beetle populations, but it may also be a response to increased host material released from damaged and stressed trees over time. While most of the focus has been on interactions between bark beetles and host material, these beetles likely also experience a release from natural enemies (predators and parasitoids), as they too may spread across a widely damaged landscape (Schroeder, 2007; Wermelinger, Obrist, Baur, Jakoby, & Duelli, 2013).

Standing live residual trees that survive windstorms can be damaged above and below- ground (which is especially harder to detect and quantify). In addition to the damage from the storm itself (and any subsequent bark beetle impacts), trees in wind impacted stands may experience as much as 10% reductions in stem growth in standing residual trees years after a storm (Seidl & Blennow, 2012). Similarly, presumably undamaged trees at stand edges exhibited slower growth for a few years after a storm in Europe (Zhao et al., 2011). In a study simulating mechanical stress and defoliation by wind disturbance, Fredericksen, Hedden, and Williams (1995) used a winch system to pull loblolly pine (*Pinus taeda* L.) trees in a windswept fashion and defoliated branches, and reported a 67% reduction in stem diameter growth after 1 year, likely to the loss of photosynthetic tissue. Few studies have experimentally quantified the extent of tree damage both above and belowground and how that may affect bark beetle dynamics.

Windthrow creates canopy gaps that increases the light received by trees at gap edges and in the understory, and consequently also the ambient temperatures in that area (Marešová et al., 2020). This increase in temperature may heighten tree volatile emissions, which some bark beetles use as primary attractants in locating suitable host trees (Baier & Bader, 1997). In a Norway spruce stand in the Western Carpathians, Marešová et al. (2020) showed a difference in host volatile concentrations in the air and phloem between trees at the edge of a newly formed gap and those at the interior of the forest. These differences were attributed to greater exposure to solar radiation, higher crown temperatures, and resin flow in trees at the gap edges. In combination with the increased release of tree volatiles into the air, these processes may result in a faster exhaustion of trees' defenses and greater susceptibility to and attraction of bark beetles.

Opening of forest canopy and increases in temperature conditions may positively affect bark beetle activity and development time as they are highly dependent on temperature. Increased temperature conditions within a stand may reduce the time it takes for the beetles to colonize and reproduce in a single tree before moving to another host (McKee & Aukema, 2015; Schebeck & Schopf, 2017). Fleischer, Ferenčík, Hlaváč, and Kozánek (2016) reported that when bark temperatures increased from 17.7°C to 19.5°C, the number of generations of *I. typographus* went from two to three with a corresponding increase in populations. With warmer temperatures, there may also be less mortality in the wintertime, further contributing to outbreaks (Bentz & Powell, 2014). As bark beetles respond positively to warmer temperatures, there appears to be a strong synergism of temperature with more intense windthrown events, raising questions about how long these forests can remain resilient under continued climate changes (Mezei et al., 2017; Stadelmann, Bugmann, Meier, Wermelinger, & Bigler, 2013).

2.3.2 At the landscape level

At the landscape level, different stands may show a gradient in damage severity depending on the storm type, with greater damage and mortality where windspeeds were highest and a reduction in damage and mortality moving away from the epicenter of storm (Feng et al., 2018; Wang, Qu, Hao, Liu, & Stanturf, 2010). Such patterns are typical and more distinct for tornadoes, for example, though few studies have focused on bark beetles and tornado tracks (Dodds et al., 2019). This type of pattern may result in differential beetle population growth along the damage gradient, allowing for the beetle populations to build up faster in some areas, such as increase in populations associated with differing elevations (Forster, Meier, & Gall, 2003). While we expect that higher numbers of bark beetles will reside in the most severely damaged areas, lower infestation levels per tree have been reported in the most severely damaged forests (Gilbert et al., 2005; Schroeder, 2007). It seems that the sudden pulse of large numbers of downed trees may result in beetles initially distributing themselves both actively and passively across the landscape (Gilbert et al., 2005; Schroeder, 2007).

After a wind disturbance event, successional pathways can be interrupted, returned to a previous state, or redirected completely (Figure 2.2). Large reductions in overstory shading lead to a surge in understory growth (which may also be influenced by edaphic factors) manifesting as advanced regeneration of existing overstory trees or a change in floral demographics (Arpin, Ponge, Faille, & Blandin, 1998). Depending on the physical characteristics of the regrowth, the area may end up being either more or less susceptible to subsequent wind disturbance. Changes in tree density, average stem diameter, tree height, and canopy thickness may contribute to a disturbed forest’s susceptibility to future wind events. Additionally, a change in tree demographics may lead to differences in an area’s vulnerability to severe windstorms, with hardwood species generally being more resistant to both wind disturbances and bark beetles than conifer species. In a 19-year study in the western Carpathians, Konopka, Seben, and Pajtik (2019) showed a transition in tree species composition following severe wind disturbances. The dominant Norway spruce was reduced while the European birch (*Betula* spp.) expanded its proportion of total trees and carbon biomass. Similarly, Bücking, Schüler, Beck, and Stolz (1998) found that after severe wind disturbance in France, planted spruce stands were replaced by a mix of spruce and beech (*Fagus* spp.). In general, *I. typographus* outbreaks due to windthrow events have reduced the dominance of Norway spruce (mostly in artificially established plantations) but have increased structural diversity across stands (Sommerfeld et al., 2020). This postdisturbance shift may dampen the effect of future wind disturbance in the area through the persistence of a more diverse forest that may be less prone to bark beetle outbreaks (Figure 2.2).

2.4 Postwindstorm forest management practice

Climate change may affect the role of forests as carbon sinks, as increasing natural disturbances offset management practices that aim to enhance forest carbon storage (Seidl, Rammer, & Blennow, 2014). Linking forest productivity to the effects of climate change and disturbance, Reyer et al. (2017) have shown that while climate change may increase forest productivity, the accompanied increase in disturbance may lead to more damage to forests with higher standing stocks. In addition, the maintenance of forests for their biodiversity and recreational value may further predispose them to natural disturbances as the average age of trees increases. In combination, this may increase the cost of effective management practices and the magnitude of management needed to effectively achieve management goals. Building in projected impacts of climate change into future management practices is urgently needed to mitigate the dual effects of catastrophic wind disturbance events and ensuing bark beetle outbreaks.

Ips typographus adults are among the first insects colonizing wind-felled Norway spruce in Europe (Potterf et al., 2019). While substantial numbers of these beetles are necessary to attack and kill healthy trees, wind damaged trees have little to no resistance to them. Forest managers are often forced to make quick decisions on expeditiously removing windthrown trees from high-risk areas to protect residual trees (Dobor et al., 2020a; Eriksson et al., 2005). Management actions to deal with this exigency primarily include sanitation felling, salvage logging for pulp or firewood, and—sometimes—prescribed burning (Dodds, Hanavan, & DiGirolomo, 2017). For these measures to be effective, it may be necessary to remove as much as 80% of wind-felled trees (Dobor et al., 2020b). Despite the success of some treatments, especially in drought conditions, small amounts of residual coarse woody debris can still seed a transition from endemic to outbreaking bark beetle populations and affect biodiversity within the remaining stand (Thorn et al., 2020). This, combined with the higher temperatures may render salvage logging efforts less effective at reducing bark beetle outbreaks in the future.

In other cases, windstorms may lead to little in the way of elevated bark beetle activity (Dodds et al., 2019). After a tornado resulted in massive amounts of dead wood ideal for colonization by wood-inhabiting insects, Dodds et al. (2019) found higher abundances and numbers of species of bark beetles and woodborers in disturbed stands (windthrown and salvage logged) as compared to undisturbed controls. However, there was no evidence of concerning increases in populations of tree killing bark beetles such as the spruce beetle, *D. rufipennis* as has been reported in western forests (Gandhi et al., 2007) and in much of Europe (Wermelinger, Duelli, & Obrist, 2002). Gandhi et al. (2009) studied populations and communities of subcortical insects after windthrow and poststorm managed areas (salvaged logging and prescribed burning) in a subboreal forest and reported that while numbers increased in wind disturbed areas two years after the storm, they subsequently declined on their own. There was a short-term increase in bark beetle numbers in the windthrown-burned areas indicating indirect effects of burning itself. Interestingly, wood- boring beetles (Cerambycidae) were observed colonizing residual pine trees in wind- thrown areas in exclusion of bark beetles (Gandhi, 2005). Hence, there was a change in insect colonization dynamics as cerambycid beetles are considered secondary colonizers attacking trees after bark beetles, and suggests a greater need to monitor wind-disturbed forests for other potential forest pests.

In contrast, in wind damaged stands in Europe, infestation by *I. typographus* was higher under passive management (trees left on the ground) than active protection (broken and fallen trees processed) (Grodzki & Fronek, 2019). Passively managed plots had a higher percent of female beetles and more progeny per female than did actively managed plots. Trees in actively managed plots were attacked less intensively than those in passively managed plots. In this case, active management had significant beneficial effects on the health of the remaining trees (Grodzki & Fronek, 2019). Using a mix of empirical data and modeling, Okland et al. (2016) showed that *I. typographus* populations utilized windthrown trees to reproduce up to two years postwind disturbance. Modeling the effect of salvage logging revealed that intensive salvaging during the first 2 years postwind disturbance reduces the probability of outbreaking patches in subsequent years. Even with less aggressive management activities, the patterns and means of deposition of logging residues (cut branches and treetops) may affect infestation and reproduction by a bark beetle (Kacprzyk, 2012). For example, infested logging residue from windfalls that was spread loosely over the forest floor was more heavily infested by *P. chalcographus* than piled material. Beetle reproduction, however, was significantly higher in the piled material (especially in the middle of the piles) (Kacprzyk, 2012). This even led to the suggested use of logging residue piles to trap out beetles and prevent infestation of other trees. Overall, salvage logging and sanitation felling is considered an important technique to greatly reduce infestation by *I. typographus* in windthrown European forests (Stadelmann, Bugmann, Wermelinger, Meier, & Bigler, 2013), but is also used in North American forests to reduce fuel load and potential outbreaks of pests and pathogens (Gandhi et al., 2009).

Bark beetle population levels may differ greatly within and across windthrown stands, which may be taken into account when attempting to model and manage their outbreak risk (Eriksson et al., 2005). Distances to previous *I. typographus* infestations are major determinants for risk of subsequent tree mortality (Havašová, Ferenčík, & Jakuš, 2017; Kautz, Dworschak, Gruppe, & Schopf, 2011), with 50% and 75% tree damage within 300 and 500 m, respectively, from uncleared windthrown stands (Nikolov et al., 2014). Size of the windthrow gaps may matter, as larger sizes are correlated with higher impact from bark beetles, and thus larger areas could be targeted first for salvaging (Karvemo, Rogell, & Schroeder, 2014; Schroeder, 2010). Higher basal area and dominance by host species (resource concentration hypothesis) are, of course, correlated positively with bark beetle incidence (Schroeder, 2010). *Ips sexdentatus* attacks on standing trees were correlated with areas where pine logs from the windthrow in a pine plantation were stored, indicating a spill-over effect (Rossi et al., 2009). As based on these stand and landscape attributes, a nuanced risk analysis may provide great predictive power for managing areas to lower any further economic losses, especially in the first 1–2 years after the windstorm event (Stadelmann, Bugmann, Meier, et al., 2013).

Of course, managing forests for multiple, interacting disturbances is not without its complexities. After a windstorm event, concerns may immediately go to salvaging any possible economic gains from timber, preserving sensitive habitats, or preventing an outbreak of tree killing bark beetles. None of these issues have clear-cut solutions though it may solve the bark beetle issue. For example, salvage logging of windthrown trees is less productive than logging a stand of undamaged trees and comes with higher costs (Karha et al., 2018). However, despite the increased cost and decreased productivity of processing wind damaged trees, management practices may provide real economic returns, add additional value through buffering bark beetle outbreaks following wind disturbance, and allow subsequent management of the stand through prescribed fire and timber salvage of downed materials, as is common in the southern USA. The management tradeoffs in addressing wind damage and bark beetle risks are not simple either. Trees felled by wind also serve as an excellent habitat for a diverse assemblage of wood colonizing (saproxylic) insects including harmless (to timber production) species as well as rare or threatened species (Eriksson et al., 2005). Increases in species diversity of bark beetles, their associates, and saproxylic insects dependent on dead woody debris for some part of their life cycle have been reported for a few years after the storm, and this is especially important in the European forests where windstorms are the major source of dead wood debris (Wermelinger, 2004; Wermelinger et al., 2002; Wohlgemuth, Bürgi, Scheidegger, & Schütz, 2002). In fact, bark beetle outbreaks (as a natural disturbance agent) create suitable habitats and provide a food source for many floral and faunal species along with other ecosystem services (Müller, Bussler, Gossner, Rettelbach, & Duelli, 2008). Cavity and ground-nesting birds benefited from the gaps caused by windstorms and subsequent *I. typographus* outbreaks, and there was a general increase in species diversity and abundance of birds (Przepiora, Loch, & Ciach, 2020). Hence, windthrown areas can be considered as hot-spots and repositories for biodiversity of native species (particularly early successional species), as compared to the undisturbed forests where some species have patchy distributions and persist under much lower numbers. Timber driven management where trees are harvested, decaying logs are masticated, and even weakened, and dead trees are removed, has historically resulted in substantial reductions in coarse woody debris in European forests (Fridman & Walheim, 2000). Simpler practices such as debarking to reduce populations of *I. typographus* within trees has reduced other saproxylic beetles, fungi, and parasitoid wasps along with foraging by woodpeckers (Thorn et al., 2016). Other nontarget impacts on the diversity of bird and plant species have been documented in poststorm managed forests (Jonášova´ & Prach, 2008; Thorn et al., 2016). There are further considerations on not using any kind of management in wilderness areas or in national preserves and allowing natural disturbances to operate and run their course (Hendee, Stankey, & Lucas, 1978; Zyval, Krenova, & Kindlmann, 2016). A careful and thoughtful consideration, therefore, needs to be placed on where, when, and how much management should be done, and what kinds of biological legacies to leave behind after a severe windthrow event (Thorn et al., 2020).

Positive feedback loops may occur from both management and other stressors to wind disturbances. In Czech Republic, wind damage increased over the period of 1964–91 in forests with greater than 50% Norway spruce (Modlinger & Novotny, 2015). During this time, an increase in *I. typographus* populations followed wind disturbance events with a 1–3 year delay. Gap creation via sanitation logging in response to bark beetle outbreaks further increased damage from wind disturbance with a 1–5 year delay. The reciprocal interaction between wind and bark beetle damage across a landscape may create a positive feedback loop (Figure 2.2). There is evidence that other stressors (such as drought) may affect trees' defenses to have an additive effect on bark beetle dynamics (Hlásny et al., 2021). In many instances, *I. typographus* outbreaks after windthrow were intensified during droughts even though active management was conducted (Hlásny et al., 2019; Temperli, Bugmann, & Elkin, 2013), as it is similarly for some bark beetle species in the southern USA forests (Goyer, Wagner, & Schowalter, 1998).

2.5 Conceptual model of cross-scale interactions between windthrow and bark beetles

We provide a conceptual model that broadly outlines the spatial and temporal interactions that occur among catastrophic windthrow events, forests, and bark beetle dynamics (Figure 2.2). Feedbacks between windstorms and bark beetle populations manifest through the impacts on host trees at various scales. At the tree level, wind speed, duration of sustained winds, and amount of rain deposition affects individual trees' health through mechanical stress and changes in soil structure. This can lower the threshold for beetle entry into the tree by releasing host volatiles into the surrounding environment and reducing the trees' ability to defend itself. At the stand level, storm size, speed of travel, event duration, and intensity affect patterns and severity of tree mortality and blowdown. These patterns of available host material may set the stage for an increase in beetle populations within and across stands. At the landscape scale, storm frequency and intensity can impact the frequency of bark beetle population outbreaks and their ability to spread as dependent on topographical features. The resulting availability of host material postwind disturbance can affect bark beetle populations for several years, potentially leading to population increases adjacent to subsequent wind disturbance events, allowing the population to shift from one disturbed site to another. Additionally, climatic changes can have direct impacts on host tree physiology through changes in average and extreme temperature and precipitation levels and indirect impacts through demographic shifts in dominant tree species (Figure 2.2).

Bark beetle outbreaks may in turn have similar impacts on host tree populations through infestation formation across forest stands (Figure 2.2). Larger beetle infestations and ensuing multiyear tree mortality increase windspeeds at the newly created forest edges, leading to exposure of more edge trees to environmental stressors and disturbances (Gray, Spies, & Pabst, 2012). These infested forests may enter new successional pathways, altering canopy composition and their susceptibility to future wind disturbances. Potential host replacement at the landscape level (also due to climate change) may push beetle species out of their range resulting in regime shifts for both the major abiotic and biotic disturbances (Figure 2.2).

2.6 Conclusions

Chronic effects of wind disturbance manifest as increased resource availability for bark beetles and poststorm forest heterogeneity. Windstorms often produce a gradient of damages along the path of the storm. Over longer time periods, this leads to a variety of successional stages in the forest that may develop along different ecological trajectories. This may be due to dominant tree species turnover, changes in faunal activity, or differences in abiotic factors including temperature, humidity, sunlight, and wind speeds. In addition, windstorms increase coarse woody debris deposition onto the forest floor. This woody biomass may be used by a plethora of organisms ranging from saproxylic fungi and bacteria to woodboring insects and cavity dwelling birds and mammals. When eruptive pest species such as bark beetles are presented with adequate material to colonize, outbreak may occur, leading to further forest disturbances. It is notable that bark beetles and the forests themselves are adapted to these periodic disturbance events that occur one on top of the other (compounded disturbances), and are temporally aggregated resulting in a complex matrix of damage and regrowth.

Given the rich literature we discussed above, it might be assumed that managers and researchers have the tools and information they need to effectively manage the risks, damages, and dynamic changes arising from windstorms and bark beetles. However, the context is changing for the storms themselves, tree resilience, and bark beetle dynamics. Climate change may increase these bark beetle caused disturbances to the extent that past management approaches are no longer sufficient to deal with new aspects of beetle biology and ecology including additional generations (Dobor et al., 2020a). Hence, adaptive management options need to be seriously considered in any future models. We suggest four major future areas for research as follows:

1) An emphasis on preparedness and preemptive measures such as creating risk/hazard models for a stand of particular attributes and location, and enhancing wind firmness of stands (Blennow & Sallnas, 2004; Seidl, Schelhaas, Rammer, & Verkerk, 2014) is needed as much as (or more than) new technologies and tactics to mitigate and recover from the often overwhelming impacts of large-scale catastrophic windstorms.
2) Comprehensive system models to predict positive interactions between catastrophic windstorms (and other compounded weather events) with tree killing bark beetles as based on storm (intensity, duration, area impacted, etc.) and stand attributes (age, species, size, land use history, previous disturbances, etc.). This will provide adaptive management guidelines to incorporate these predictions into timely and more effective strategies to tackle economic and ecological damage.
3) A better understanding of various management practices poststorm on multiple ecosystem services for mitigating nontarget impacts and forest restoration purposes.
4) Inclusion of an integrative and trans-disciplinary approach such as the socio-economic and human health components, as catastrophic wind disturbances can also adversely affect them through multiple means (Van Bloem & Martin, 2021).

Considering the intricately coupled human-natural systems, there are many feedback loops (e.g., storm-driven changes in land use type, and management frequency and intensity) that may have positive or negative impacts on the socio-economic components and hence poststorm management in forested landscapes.

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2.8 References

Ahrends, B., M. Jansen, and O. Panferov. 2003. Effects of windthrow on drought risk in spruce and pine forest ecosystems under climate change conditions. Wind Effects on Trees 16: 303.

Allen, M. S., V. Thapa, J. R. Arevalo, and M. W. Palmer. 2012. Windstorm damage and forest recovery: accelerated succession, stand structure, and spatial pattern over 25 years in two Minnesota forests. Plant Ecology 213: 1833-1842.

Arpin, P., J.-F. Ponge, A. Faille, and P. Blandin. 1998. Diversity and dynamics of eco-units in the biological reserves of the Fontainebleau forest (France): contribution of soil biology to a functional approach. European journal of soil biology 34: 167-177.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. For. Ecol. Manage. 63: 247-300.

Baier, P., and R. Bader. 1997. Monoterpene content and monoterpene emission of Norway spruce bark and their relation to the primary attraction of bark beetles (Coleoptera, Scolytidae), pp. 639-643. In K. H. Hoffmann and W. Volkl (eds.), Mitteilungen Der Deutschen Gesellschaft Fur Allgemeine Und Agewandte Entomologie, Band 11, Heft 1-6, Dezember 1997: Entomologists Conference, vol. 11. Deutschen Gesell Allgemeine & Angewandte Entomologie, Bremen 33.

Beatty, S. W., and E. L. Stone. 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16: 539-548.

Beaudet, M., J. Brisson, D. Gravel, and C. Messier. 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understory of an old-growth forest. J. Ecol. 95: 458-467.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60: 602-613.

Bentz, B. J., and J. A. Powell. 2014. Mountain pine beetle seasonal timing and constraints to bivoltinism. The American naturalist 184: 787-796.

Bigelow, S. W., C. E. Looney, and J. B. Cannon. 2021. Hurricane effects on climate-adaptive silviculture treatments to longleaf pine woodland in southwestern Georgia, USA. Forestry 94: 395-406.

Bigelow, S. W., M. C. Stambaugh, J. J. O'Brien, A. J. Larson, and M. A. Battaglia. 2017. Longleaf pine restoration in context: comparisons of frequent fire forests, pp. 311-338, Ecological restoration and management of longleaf pine forests. CRC Press.

Bhatia, K. T., G. A. Vecchi, T. R. Knutson, H. Murakami, J. Kossin, K. W. Dixon, and C. E. Whitlock. 2019. Recent increases in tropical cyclone intensification rates. Nature Communications 10: 1-9.

Blennow, K., and O. Sallnas. 2004. WINDA—a system of models for assessing the probability of wind damage to forest stands within a landscape. Ecol. Model. 175: 87-99.

Boose, E. R., D. R. Foster, and M. Fluet. 1994. Hurricane impacts to tropical and temperate forest landscapes. Ecological Monographs 64: 369-400.

Bouget, C., and T. Noblecourt. 2005. Short-term development of ambrosia and bark beetle assemblages following a windstorm in French broadleaved temperate forests. J. Appl. Ecol. 129: 300-310.

Brandei, T. 2022. Assessing forest resource damage following natural disasters using national forest inventory plots: A case study of Hurricane Michael.

Brazdil, R., P. Stucki, P. Szabo, L. Reznickova, L. Dolak, P. Dobrovolny, R. Tolasz, O. Kotyza, K. Chroma, and S. Suchankova. 2018. Windstorms and forest disturbances in the Czech Lands: 1801-2015. Agric. For. Meteorol. 250: 47-63.

Broman, H., M. Frisk, and M. Rönnqvist. 2009. Supply chain planning of harvest and transportation operations after the storm Gudrun. INFOR: Information Systems and Operational Research 47: 235-245.

Bücking, W., G. Schüler, M. Beck, and T. Stolz. 1998. Documentation of the structure, ground cover and regeneration of the windthrow areas. The Development of Biotic Communities after Windthrow. Ecomed, Landsberg: 75-93.

Byers, J. A. 1995. Host-tree chemistry affecting colonization in bark beetles, Springer, Boston, MA.

Canham, C. D., M. J. Papaik, and E. F. Latty. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Can. J. For. Res. 31: 1-10.

Carlton, G., and F. Bazzaz. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. Ecology 79: 1305-1319.

Chow, S., and A. Obermajer. 2007. Moisture and blue stain distribution in mountain pine beetle infested lodgepole pine trees and industrial implications. Wood science and technology 41: 3.

Christiansen, E., R. H. Waring, and A. A. Berryman. 1987. Resistance of conifers to bark beetle attack: searching for general relationships. For. Ecol. Manage. 22: 89-106.

Cobb, R. C., and M. R. Metz. 2017. Tree diseases as a cause and consequence of interacting forest disturbances. Forests 8: 147.

Connola, D. P., D. L. Collins, J. H. Risley, and W. E. Smith. 1956. Insect damage and its prevention in windthrown saw timber. The University of the State of New York, Albany, NY, USA.

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

Daniels, M. K., and E. R. Larson. 2020. Effects of forest windstorm disturbance on invasive plants in protected areas of southern Illinois, USA. Journal of Ecology 108: 199-211.

Darracq, A. K., W. W. Boone IV, and R. A. McCleery. 2016. Burn regime matters: a review of the effects of prescribed fire on vertebrates in the longleaf pine ecosystem. For. Ecol. Manage. 378: 214-221.

Dhar, A., L. Parrott, and S. Heckbert. 2016. Consequences of mountain pine beetle outbreak on forest ecosystem services in western Canada. Can. J. For. Res. 46: 987-999.

Dickens, E. D., D. J. Moorhead, C. Bates, and S. Griffin. 2018. Assessing hurricane and tornado storm damaged forest stands.

Dobor, L., T. Hlasny, W. Rammer, S. Zimova, I. Barka, and R. Seidl. 2020. Is salvage logging effectively dampening bark beetle outbreaks and preserving forest carbon stocks? J. Appl. Ecol. 57: 67-76.

Dobor, L., T. Hlasny, W. Rammer, S. Zimova, I. Barka, and R. Seidl. 2020. Spatial configuration matters when removing windfelled trees to manage bark beetle disturbances in Central European forest landscapes. J. Environ. Manage. 254: 12.

Dodds, K. J., M. F. DiGirolomo, and S. Fraver. 2019. Response of bark beetles and woodborers to tornado damage and subsequent salvage logging in northern coniferous forests of Maine, USA. For. Ecol. Manage. 450.

Donato, D. C., J. L. Campbell, and J. F. Franklin. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? J. Veg. Sci. 23: 576-584.

Emery, R. K., J. S. Kleinman, J. D. Goode, and J. L. Hart. 2020. Effects of catastrophic wind disturbance, salvage logging, and prescribed fire on fuel loading and composition in a *Pinus palustris* woodland. For. Ecol. Manage. 478: 118515.

Eriksson, M., A. Pouttu, and H. Roininen. 2005. The influence of windthrow area and timber characteristics on colonization of wind-felled spruces by *Ips typographus* (L.). For. Ecol. Manage. 216: 105-116.

Everham, E. M., and N. V. L. Brokaw. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. 62: 113-185.

Feng, Y., R. I. Negron-Juarez, C. M. Patricola, W. D. Collins, M. Uriarte, J. S. Hall, N. Clinton, and J. Q. Chambers. 2018. Rapid remote sensing assessment of impacts from Hurricane Maria on forests of Puerto Rico. PeerJ Preprints 6.

Fleischer, P., J. Ferenčík, P. Hlaváč, and M. Kozánek. 2016. Elevated bark temperature in unremoved stumps after disturbances facilitates multi-voltinism in *Ips typographus* population in a mountainous forest. Central European Forestry Journal 62: 15-22.

Forster, B., F. Meier, and R. Gall. 2003. Bark beetle management after a mass attack—some Swiss experiences. *In*, Proceedings of Ecology, Survey and Management of Forest Insects, Krakow, Poland. pp. 10-15.

Foster, D. R., and E. R. Boose. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology 80: 79-98.

Foster, D. R., D. H. Knight, and J. F. Franklin. 1998. Landscape Patterns and Legacies Resulting from Large, Infrequent Forest Disturbances. Ecosystems 1: 497-510.

Fowler, C., and E. Konopik. 2007. The history of fire in the southern United States. Human Ecology Review: 165-176.

Fredericksen, T. S., R. L. Hedden, and S. A. Williams. 1995. Susceptibility of loblolly pine to bark beetle attack following simulated wind stress. For. Ecol. Manage. 76: 95-107.

Fridman, J., and M. Walheim. 2000. Amount, structure, and dynamics of dead wood on managed forestland in Sweden. For. Ecol. Manage. 131: 23-36.

Gan, J. 2004. Risk and damage of southern pine beetle outbreaks under global climate change. For. Ecol. Manage. 191: 61-71.

Gandhi, K. J. K. 2005. The responses of sub-boreal forest insects to a catastrophic wind-disturbance event and subsequent fuel-reduction practices in northeastern Minnesota, Volumes I and II. Ph.D., University of Minnesota, USA.

Gandhi, K. J. K., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. R. Spence, and S. J. Seybold. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews 15: 113-152.

Gandhi, K. J. K., D. W. Gilmore, R. A. Haack, S. A. Katovich, S. J. Krauth, W. J. Mattson, J. C. Zasada, and S. J. Seybold. 2009. Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. J. Chem. Ecol. 35: 1384-1410.

Gardiner, L. M. 1975. Insect Attack and Value Loss in Wind-Damaged Spruce and Jack Pine Stands in Northern Ontario. Canadian Journal of Forest Resources 5: 420-462.

Gardiner, L. M. 1976. Blowdown in Ontario spruce and jack pine, Canadian Forest Industry.

Gilbert, M., L. M. Nageleisen, A. Franklin, and J. C. Gregoire. 2005. Post-storm surveys reveal large-scale spatial patterns and influences of site factors, forest structure and diversity in endemic bark-beetle populations. Landscape Ecology 20: 35-49.

Gilman, E. F., F. Masters, and J. C. Grabosky. 2008. Pruning affects tree movement in hurricane force wind. Arboriculture and Urban Forestry 34: 20.

Göthlin, E., L. M. Schroeder, and A. Lindelöw. 2000. Attacks by *Ips typographus* and *Pityogenes chalcographus* on windthrown spruces (*Picea abies*) during the two years following a storm felling. Scandinavian Journal of Forest Research 15: 542-549.

Goyer, R. A., M. R. Wagner, and S. T.D. 1998. Current and proposed technologies for bark beetle management. Journal of Forestry 96: 29-33.

Gray, A. N., T. A. Spies, and R. J. Pabst. 2012. Canopy gaps affect long-term patterns of tree growth and mortality in mature and old-growth forests in the Pacific Northwest. For. Ecol. Manage. 281: 111-120.

Grégoire, J. C., K. F. Raffa, and B. S. Lindgren. 2015. Economics and politics of bark beetles, Academic Press.

Grimbacher, P. S., and N. E. Stock. 2009. How do beetle assemblages respond to cyclonic disturbance of a fragmented tropical rainforest landscape? Oecologia 161: 591-599.

Grodzki, W., and W. G. Fronek. 2019. The European spruce bark beetle *Ips typographus* (L.) in wind-damaged stands of the eastern part of the Tatra National Park – the population dynamics pattern remains constant. Folia Forestalia Polonica 61: 174-181.

Hanson, J. J., and C. G. Lorimer. 2007. Forest structure and light regimes following moderate wind storms: Implications for multi-cohort management. Ecol. Appl. 17: 1325-1340.

Havašová, M., J. Ferenčík, and R. Jakuš. 2017. Interactions between windthrow, bark beetles and forest management in the Tatra national parks. For. Ecol. Manage. 391.

Hendee, J. C., G. H. Stankey, and R. C. Lucas. 1978. Wilderness management (No. 1365). *In* U. D. o. A. Forest Service [ed.].

Heyward, F. 1939. The relation of fire to stand composition of longleaf pine forests. Ecology 20: 287-304.

Hirano, T., K. Suzuki, and R. Hirata. 2017. Energy balance and evapotranspiration changes in a larch forest caused by severe disturbance during an early secondary succession. Agric. For. Meteorol. 232: 457-468.

Hlásny, T., Z. S., M. K., Š. P., M. R., and T. M. 2021. Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. For. Ecol. Manage. 490: 1-13.

Hlásny, T., P. Krokene, A. Liebhold, C. Montagné-Huck, J. Müller, H. Qin, K. Raffa, M. J. Schelhaas, R. Seidl, M. Svoboda, and H. Viiri. 2019. Living with bark beetles: impacts, outlook and management options (No. 8). *In* E. F. Institute [ed.].

Hofstetter, R. W., J. Dinkins-Bookwalter, T. S. Davis, and K. D. Klepzig. 2015. Symbiotic associations of bark beetles, Academic Press.

Holmes, T. P. 1991. Price and welfare effects of catastrophic forest damage from southern pine beetle epidemics. For. Sci. 37: 500-516.

Hood, S., A. Sala, E. K. Heyerdahl, and M. Boutin. 2015. Low-severity fire increases tree defense against bark beetle attacks. Ecology 96: 1876-1855.

Hubbard, R. M., C. C. Rhoades, K. Elder, and J. Negron. 2013. Changes in transpiration and foliage growth in lodgepole pine trees following mountain pine beetle attack and mechanical girdling. For. Ecol. Manage. 289: 312-317.

Inouye, M. 1962. Details of bark beetle control in the storm-swept areas in the natural forest of Hokkaido, Japan. Zeitschrift für angewandte Entomologie 51: 160-164.

Jakuš, R. 1998. Patch level variation on bark beetle attack (Col., Scolytidae) on snapped and uprooted trees in Norway spruce primeval natural forest in endemic condition: effects of host and insolation. Journal of Applied Entomology 122: 409-421.

Jakuš, R., M. Edwards-Jonášová, P. Cudlín, M. Blaženec, M. Ježík, F. Havlíček, and I. Moravec. 2011. Characteristics of Norway spruce trees (*Picea abies*) surviving a spruce bark beetle (*Ips typographus* L.) outbreak. Trees 25: 965-973.

Janda, P., V. Trotsiuk, M. Mikolas, R. Bace, T. A. Nagel, R. Seidl, M. Seedre, R. C. Morrissey, S. Kucbel, and P. Jaloviar. 2017. The historical disturbance regime of mountain Norway spruce forests in the Western Carpathians and its influence on current forest structure and composition. For. Ecol. Manage. 388: 67-78.

Janik, T., and D. Romportl. 2018. Recent land cover change after the Kyrill windstorm in the Šumava NP. Applied Geography 97: 196-211.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, M. C. Mack, R. K. Meentemeyer, M. R. Metz, G. L. W. Perry, T. Schoennagel, and M. G. Turner. 2016. Changing disturbance regimes, ecological memory, and forest resilience. Frontiers in Ecology and the Environment 14: 369-378.

Jonášová, M., and K. Prach. 2008. The influence of bark beetle outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. Biol. Conserv. 141: 1525-1535.

Kacprzyk, M. 2012. Feeding habits of *Pityogenes chalcographus* (L.) (Coleoptera: Scolytinae) on Norway Spruce (*Picea abies*) L. (Karst.) logging residues in wind-damaged stands in southern Poland. International Journal of Pest Management 58: 121-130.

Kalisz, P. J., A. W. Dorian, and E. L. Stone. 1986. Prehistoric land-use and the distribution of longleaf pine on the Ocala National Forest, Florida: an interdisciplinary synthesis. The Florida Anthropologist 39: 183-193.

Karha, K., T. Anttonen, A. Poikela, T. Palander, A. Lauren, H. Peltola, and Y. Nuutinen. 2018. Evaluation of Salvage Logging Productivity and Costs in Windthrown Norway Spruce-Dominated Forests. Forests 9: 22.

Karvemo, S., B. Rogell, and M. Schroeder. 2014. Dynamics of spruce bark beetle infestation spots: Importance of local population size and landscape characteristics after a storm disturbance. For. Ecol. Manage. 334: 232-240.

Kautz, M., D. K., G. A., and S. R. 2011. Quantifying spatio-temporal dispersion of bark beetle infestations in epidemic and non-epidemic conditions. For. Ecol. Manage. 262: 598-608.

Kay, C. E. Year. Published. Are lightning fires unnatural? A comparison of aboriginal and lightning ignition rates in the United States, pp. 16-28. *In,* Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tall Timbers Research Station, Tallahassee, FL, 2007.

Keenan, R. J., C. E. Prescott, and J. H. Kimmins. 1993. Mass and nutrient content of woody debris and forest floor in western red cedar and western hemlock forests on northern Vancouver Island. Can. J. For. Res. 23: 1052-1059.

Kenney, G., C. L. Staudhammer, S. Wiesner, S. T. Brantley, S. W. Bigelow, and G. Starr. 2021. Hurricane Michael altered the structure and function of longleaf pine woodlands. J. Geophys. Res.-Biogeosci. 126: 17.

Kerchev, I. A. 2014. Ecology of four-eyed fir bark beetle *Polygraphus proximus* Blandford (Coleoptera; Curculionidae, Scolytinae) in the west Siberian region of invasion. Russian Journal of Biological Invasions 5: 176-185.

Kirisits, T. 2007. Fungal associates of European bark beetles with special emphasis on the ophiostomatid fungi, pp. 181-235. In F. Lieutier, K. R. Day, A. Battisti, J. C. Gregoire and H. F. Evans (eds.), Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis. Springer, Dordrecht The Netherlands.

Kirkendall, L. R., P. H. W. Biedermann, and B. H. Jordal. 2015. Evolution and Divesity of Bark and Ambrosia Beetles, pp. 85-156. In R. W. Hoffstetter and F. E. Vega (eds.), Bark Beetles: Biology and Ecology of Native and Invasive Species. Academic Press, London, UK.

Knutson, T. R., J. L. McBride, J. Chan, K. Emanual, G. Holland, C. Landsea, I. Held, J. P. Kossin, A. K. Srivastava, and M. Sugi. 2010. Tropical cyclones and climate change. Tropical cyclones and climate change 3: 157-163.

Kolosova, N., and J. Bohlmann. 2012. Conifer defense against insects and fungal pathogens, pp. 85-109, Growth and defense in plants: resource allocation at multiple scales. Springer.

Komonen, A., L. M. Schroeder, and J. Weslien. 2011. *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. Journal of Applied Entomology 135: 132-141.

Konopka, B., V. Seben, and J. Pajtik. 2019. Species composition and carbon stock of tree cover at a post-disturbance area in Tatra Nationa Park, Western Carpathians. Mt. Res. Dev. 39: R71-R80.

Konôpka, B., P. Zach, and J. Kulfan. 2016. Wind–an important ecological factor and destructive agent in forests. Central European Forestry Journal 62: 123-130.

Kossin, J. P., K. R. Knapp, T. L. Olander, and C. S. Velden. 2020. Global increase in major tropical cyclone exceedance probability over the past four decades. Proceedings of the National Academy of Sciences 117: 11975-11980.

Krehan, H., G. Steyrer, and C. Tomiczek. 2010. Bark beetle calamity in 2009: arguments for different regional damage trends. Forstschutz Aktuell 49: 9-16.

Krokene, P. 2015. Conifer defenses and resistance to bark beetles, pp. 177-207. In F. Vega and R. W. Hofstetter (eds.), Bark Beetles: Biology and Ecology and Native and Invasive Species. Academic Press.

Kulakowski, D., and T. T. Veblen. 2007. Effect of prior disturbances on the extent and severity of wildfire in Colorado subalpine forests. Ecology 88: 759-769.

Kupfer, J. A., K. Lackstrom, J. M. Grego, K. Dow, A. J. Terando, and J. K. Hiers. 2022. Prescribed fire in longleaf pine ecosystems: fire managers' perspectives on priorities, constraints, and future prospects. Fire Ecol. 18.

Kuuluvainen, T., and T. Aakala. 2011. Natural forest dynamics in boreal Fennoscandia: a review and classification. Silva Fennica 45: 823-841.

Lashley, M. A., M. C. Chitwood, A. Prince, M. B. Elfelt, E. L. Kilburg, C. S. DePerno, and C. E. Moorman. 2014. Subtle effects of a managed fire regime: a case study in the longleaf pine ecosystem. Ecol. Indic. 38: 212-217.

Leckebusch, G. C., and U. Ulbrich. 2004. On the relationship between cyclones and extreme windstorm events over Europe under climate change. Global and planetary change 44: 181-193.

Lindenmayer, D. B., and R. F. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv. Biol. 20: 949-958.

Lindner, M., and M. Rummukainen. 2013. Climate change and storm damage in European forests, pp. 129. In B. Gardiner, A. R. T. Schuck, M. J. Schelhaas, C. Orazio, K. Blennow and B. Nicoll (eds.), Living with storm damage to forests, vol. 3. European Forest Institute, Joensuu, Finland.

Lindroth, A., F. Lagergren, A. Grelle, L. Klemedtsson, O. L. A. Langvall, P. E. R. Weslien, and J. Tuulik. 2009. Storms can cause Europe-wide reduction in forest carbon sink. Global Change Biology 15: 346-355.

Loeffler, D., and N. Anderson. 2017. Impacts of the mountain pine beetle on sawmill operations, costs, and product values in Montana. Forest Products 68: 15-24.

Loreto, F., and J. P. Schnitzler. 2010. Abiotic stresses and induced BVOCs. Trends in Plant Science 15: 154-166.

Lorimer, C. G., and C. R. Halpin. 2014. Classification and dynamics of developmental stages in late-successional temperate forests. For. Ecol. Manage. 334: 344-357.

Maresova, J., A. Majdak, R. Jakus, J. Hradecky, B. Kalinova, and M. Blazenec. 2020. The short-term effect of sudden gap creation on tree temperature and volatile composition profiles in a Norway spruce stand. Trees-Structure and Function 34: 1397-1409.

McCarthy, J. 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environmental Reviews 9: 1-59.

McConnell, T. E., and R. Shmulsky. 2009. Effects of Hurricane Katrina on the structure, performance, capacity, and future of the lumber industry in US Gulf States. Journal of Forest Products Business Research 6.

McGregor, M. D., D. R. Hamel, and R. D. Oakes. 1976. Status of bark beetle populations in windthrow, Flathead National Forest, Montana. Forest Environmental Protection Report 76–13. *In* N. R. USDA Forest Service, State and Private Forestry [ed.], Missoula, MT.

McKee, F. R., and B. H. Aukema. 2015. Influence of temperature on the reproductive success, brood development and brood fitness of the eastern larch beetle *Dendroctonus simplex* LeConte. Agric. For. Entomol. 17: 102-112.

McMillin, J. D., K. K. Allen, D. F. Long, J. L. HArris, and J. F. Negrón. 2003. Effects of western balsam bark beetle on spruce-fir forests of north-central Wyoming. Western Journal of Applied Forestry 18: 259-266.

Meigs, G. W., and W. S. Keeton. 2018. Intermediate-severity wind disturbance in mature temperate forests: legacy structure, carbon storage, and stand dynamics. Ecol. Appl. 28: 798–815.

Meigs, G. W., R. C. Morrissey, R. Bace, O. Chaskovskyy, V. Cada, T. Despres, D. C. Donato, P. Janda, J. Labusova, M. Seedre, M. Mikolas, T. A. Nagel, J. S. Schurman, M. Synek, M. Teodosiu, V. Trotsiuk, L. Vitkova, and M.

Svoboda. 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406: 410-426.

Mezei, P., R. Jakus, J. Pennerstorfer, M. Havasova, J. Skvarenina, J. Ferencik, J. Slivinsky, S. Bicarova, D. Bilcik, M. Blazenec, and S. Netherer. 2017. Storms, temperature maxima and the Eurasian spruce bark beetle *Ips typographus*-An infernal trio in Norway spruce forests of the Central European High Tatra Mountains. Agric. For. Meteorol. 242: 85-95.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17: 2145-2151.

Mitchell, S. J. 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry 86: 147-157.

Mitchell, R. J., Y. Q. Liu, J. J. O'Brien, K. J. Elliott, G. Starr, C. F. Miniat, and J. K. Hiers. 2014. Future climate and fire interactions in the southeastern region of the United States. For. Ecol. Manage. 327: 316-326.

Mitton, J. B., and S. M. Ferrenberg. 2012. Mountain pine beetle develops an unprecedented summer generation in response to climate warming. The American naturalist 179: E163-171.

Modlinger, R., and P. Novotny. 2015. Quantification of time delay between damages caused by windstorms and by *Ips typographus*. Central European Forestry Journal 61: 221-231.

Moore, T. W., and R. W. Dixon. 2011. Climatology of tornadoes associated with Gulf Coast-landfalling hurricanes. Geographical Review 101: 371-395.

Müller, J., B. H., G. M., R. T., and D. P. 2008. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodivers. Conserv. 17: 2979-3001.

Neaves III, C. M., W. M. Aust, M. C. Bolding, S. M. Barrett, C. C. Trettin, and E. Vance. 2017. Soil properties in site prepared loblolly pine (*Pinus taeda* L.) stands 25 years after wet weather harvesting in the lower Atlantic coastal plain. For. Ecol. Manage. 404: 344-353.

Nikolov, C., B. Konopka, M. Kajba, J. Galko, A. Kunca, and L. Jansky. 2014. Post-disaster Forest Management and Bark Beetle Outbreak in Tatra National Park, Slovakia. Mt. Res. Dev. 34: 326-335.

Nissen, K. M., G. C. Leckebusch, J. G. Pinto, and U. Ulbrich. 2014. Mediterranean cyclones and windstorms in a changing climate. Reg. Envir. Chang. 14: 1873-1890.

NOAA. 2012. The Saffir-Simpson Hurricane Wind Scale, 2012.

NOAA. 2021. NHC terms.

Okland, B., C. Nikolov, P. Krokene, and J. Vakula. 2016. Transition from windfall- to patch-driven outbreak dynamics of the spruce bark beetle *Ips typographus*. For. Ecol. Manage. 363: 63-73.

Ostertag, R., F. N. Scatena, and W. L. Silver. 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. Ecosystems 6.

Outcalt, K. W. 2008. Lightning, fire and longleaf pine: Using natural disturbance to guide management. For. Ecol. Manage. 255: 3351-3359.

Peterson, C. J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. The Science of the Total Environment 262: 287-311.

Petit, J. R., and A. Hampe. 2006. Some evolutionary consequences of being a tree. Annual Review of Ecology, Evolution, and Systematics 37: 187-214.

Potterf, M., C. Nikolov, E. Kocicka, J. Ferencik, P. Mezei, and R. Jakus. 2019. Landscape-level spread of beetle infestations from windthrown- and beetle-killed trees in the non-intervention zone of the Tatra National Park, Slovakia (Central Europe). For. Ecol. Manage. 432: 489-500.

Przepiora, F., J. Loch, and M. Ciach. 2020. Bark beetle infestation spots as biodiversity hotspots: Canopy gaps resulting from insect outbreaks enhance the species richness, diversity and abundance of birds breeding in coniferous forests. For. Ecol. Manage. 473.

Pureswaran, D. S., and J. H. Borden. 2005. Primary attraction and kairomonal host discrimination in three species of *Dendroctonus* (Coleoptera : Scolytidae). Agric. For. Entomol. 7: 219-230.

Pye, J. M., T. P. Holmes, J. P. Prestemon, and D. N. Wear. 2011. Economic impacts of the southern pine beetle. In: Coulson, RN; Klepzig, KD 2011. Southern Pine Beetle II. Gen. Tech. Rep. SRS-140. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station. 213-222. 140: 213-222.

Quine, C. P., and B. A. Gardiner. 2007. Understanding how the interaction of wind and trees results in windthrow, stem breakage, and canopy gap formation, pp. 103-155, Plant Disturbance Ecology: The process and the response.

Raffa, K. F., B. H. Aukema, N. Erbilgin, K. D. Klepzig, and K. F. Wallin. 2005. Interactions among conifer terpenoids and bark beetles across multiple levels of scale: an attempt to understand links between population patterns and physiological processes. Recent Advances in Phytochemistry: 79-118.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58: 501-517.

Reyer, C. P. O., N. Brouwers, A. Rammig, B. W. Brook, J. Epila, R. F. Grant, M. Holmgren, F. Langerwisch, S. Leuzinger, W. Lucht, B. Medlyn, M. Pfeifer, J. Steinkamp, M. C. Vanderwel, H. Verbeeck, and D. M. Villela. 2015. Forest resilience and tipping points at different spatio-temporal scales: approaches and challenges. J. Ecol. 103: 5-15.

Reyer, C. P. O., S. Bathgate, K. Blennow, J. G. Borges, H. Bugmann, S. Delzon, S. P. Faias, J. Garcia-Gonzalo, B. Gardiner, J. R. Gonzalez-Olabarria, C. Gracia, J. G. Hernandez, S. Kellomaki, K. Kramer, M. J. Lexer, M. Lindner, E. van der Maaten, M. Maroschek, B. Muys, B. Nicoll, M. Palahi, J. H. N. Palma, J. A. Paulo, H. Peltola, T. Pukkala, W. Rammer, D. Ray, S. Sabate, M. J. Schelhaas, R. Seidl, C. Temperli, M. Tome, R. Yousefpour, N. E. Zimmermann, and M. Hanewinkel. 2017. Are forest disturbances amplifying or canceling out climate change-induced productivity changes in European forests? Environ. Res. Lett. 12: 12.

Rossi, J. P., J. C. Samalens, D. Guyon, I. van Halder, H. Jactel, P. Menassieu, and D. Piou. 2009. Multiscale spatial variation of the bark beetle *Ips sexdentatus* damage in a pine plantation forest (Landes de Gascogne, Southwestern France). For. Ecol. Manage. 257: 1551-1557.

Runkle, J. R. 1982. Patterns of disturbance in some old-growth mesic forests of eastern North America. Ecology 63: 1533-1546.

Saab, V. A., Q. S. Latif, M. M. Rowland, T. N. Johnson, A. D. Chalfoun, S. W. Buskirk, J. E. Heyward, and M. A. Dresser. 2014. Ecological consequences of mountain pine beetle outbreaks for wildlife in western North American forests. For. Sci. 60: 539-559.

Safranyik, L., A. L. Carroll, J. Régnière, D. W. Langor, W. G. Riel, T. L. Shore, B. Peter, B. J. Cooke, V. G. Nealis, and S. W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. The Canadian Entomologist 142: 415-442.

Santoro, J. A., and A. W. D'Amato. 2019. Structural, compositional, and functional responses to tornado and salvage logging disturbance in southern New England hemlock-hardwood forests. For. Ecol. Manage. 444: 138-150.

Schaetzl, R. J., S. F. Burns, D. L. Johnson, and T. W. Small. 1988. Tree uprooting: review of impacts on forest ecology. Vegetatio 79: 165-176.

Schebeck, M., and A. Schopf. 2017. Temperature-dependent development of the European larch bark beetle, *Ips cembrae*. Journal of Applied Entomology 141: 322-328.

Scherstjanoi, M., U. Gimmi, A. Wolf, and H. Bugmann. 2010. Windthrow and bark beetle attacks in the Alptal after the wind storms Vivian and Lothar. Schweizerische Zeitschrift für Forstwesen 161: 36-44.

Schowalter, T. D. 1985. Adaptations of insects to disturbance, pp. 235-252. In S. T. A. Pickett and P. S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego.

Schroeder, L. M. 1988. Attraction of the bark beetle *Tomicus piniperda* and some other bark-living and wood-living beetles to the host volatiles alpha-pinene and ethanol. Entomol. Exp. Appl. 46: 203-210.

Schroeder, L. M. 2001. Tree mortality by the bark beetle *Ips typographus* (L.) in storm-disturbed stands. Integrated Pest Management Reviews 6: 169-175.

Schroeder, L. M. 2007. Escape in space from enemies: a comparison between stands with and without enhanced densities of the spruce bark beetle. Agric. For. Entomol. 9: 85-91.

Schroeder, L. M. 2010. Colonization of storm gaps by the spruce bark beetle: influence of gap and landscape characteristics. Agric. For. Entomol. 12: 29-39.

Seidl, R., and K. Blennow. 2012. Pervasive growth reduction in Norway spruce forests following wind disturbance. Plos One 7: 8.

Seidl, R., and W. Rammer. 2017. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. Landscape Ecology 32: 1485-1498.

Seidl, R., M. J. Schelhaas, and M. J. Lexer. 2011. Unraveling the drivers of intensifying forest disturbance regimes in Europe. Global Change Biology 17: 2842-2852.

Seidl, R., W. Rammer, and K. Blennow. 2014. Simulating wind disturbance impacts on forest landscapes: tree-level heterogeneity matters. Environmental Modelling & Software 51: 1-11.

Seidl, R., M. J. Schelhaas, W. Rammer, and P. J. Verkerk. 2014. Increasing forest disturbances in Europe and their impact on carbon storage. Nature Climate Change 4: 806-810.

Seidl, R., D. Thom, M. Kautz, D. Martin-Benito, M. Peltoniemi, G. Vacchiano, J. Wild, D. Ascoli, M. Petr, J. Honkaniemi, M. J. Lexer, V. Trotsiuk, P. Mairota, M. Svoboda, M. Fabrika, T. A. Nagel, and C. P. O. Reyer. 2017. Forest disturbances under climate change. Nature Climate Change 7: 395-402.

Senevirante, S. I., N. Nicholls, D. Easterling, C. M. Goodess, S. Kanae, J. Kossin, Y. Luo, J. Marengo, K. McInnes, M. Rahimi, M. Reichstein, A. Sorteberg, C. Vera, and X. Zhang. 2012. Changes in climate extremes and their impacts on the natural physical environment. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G. K. Plattner, S. K. Allen, M. Tignor and P. M. Midgley (eds.), Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation: A special Report of Working Groups I and II of the the Intergovernmental Panel on Climate Change (IPCC). Cambridge University Press, Cambridge, UK and New York, NY, USA.

Seybold, S. J., D. P. Huber, J. C. Lee, A. D. Graves, and J. Bohlmann. 2006. Pine monoterpenes and pine bark beetles: a marriage of convenience for defense and chemical communication. Phytochemistry Reviews 5: 143-178.

Shortle, W. C., and K. R. Dudzik. 2012. Wood decay in living and dead trees: a pictorial overview, pp. 1-26. *In* U. S. D. o. Agriculture [ed.]. U.S. Forest Service, Newtown Square, PA, USA.

Shupe, T., S. Lebow, and D. Ring. 2008. Causes and control of wood decay, degradation & stain., pp. 26. Louisiana Cooperative Extension Service, Louisiana State University Agriculture Center, Baton Rouge, LA.

Sommerfeld, A., W. Rammer, M. Heurich, T. Hilmers, J. Müller, and R. Seidl. 2020. Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? J. Ecol. 109: 737-749.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.

Stadelmann, G., H. Bugmann, B. Wermelinger, and C. Bigler. 2014. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. For. Ecol. Manage. 318: 167-174.

Stadelmann, G., H. Bugmann, F. Meier, B. Wermelinger, and C. Bigler. 2013. Effects of salvage logging and sanitation felling on bark beetle (*Ips typographus* L.) infestations. For. Ecol. Manage. 305: 273-281.

Stadelmann, G., H. Bugmann, B. Wermelinger, F. Meier, and C. Bigler. 2013. A predictive framework to assess spatio-temporal variability of infestations by the European spruce bark beetle. Ecography 36: 1208-1217.

Stuart-Haentjens, E. J., P. S. Curtis, T. Fahey, and V. C.S. 2015. Net primary production of a temperate deciduous forest exhibits a threshold response to increasing disturbance severity. Ecology 96.

Suvanto, S., H. M. Henttonen, P. Nojd, and H. Makinen. 2016. Forest susceptibility to storm damage is affected by similar factors regardless of storm type: Comparison of thunder storms and autumn extra-tropical cyclones in Finland. For. Ecol. Manage. 381: 17-28.

Taylor, S. W., and L. Safanyik. 2003. Effect of climate change on range expansion by the mountain pine beetle in British Columbia. *In*, Mountain Pine Beetle Symposium: Challenges and Solutions; Canadian Forest Service: Victoria, BC, Canada.

Temperli, C., H. Bugmann, and C. Elkin. 2012. Adaptive management for competing forest goods and services under climate change. Ecol. Appl. 22: 2065-2077.

Temperli, C., H. Bugmann, and C. Elkin. 2013. Cross-scale interactions among bark beetles, climate change, and wind disturbances: a landscape modeling approach. Ecological Monographs 83: 383-402.

Thorn, S., C. Bässler, T. Gottschalk, T. Hothorn, H. Bussler, K. Raffa, and J. Müller. 2014. New insights into the consequences of post-windthrow salvage logging revealed by functional structure of saproxylic beetles assemblages. PLOS One.

Thorn, S., S. A. Werner, J. Wohlfahrt, C. Bässler, S. Seibold, P. Quillfeldt, and J. Müller. 2016. Response of bird assemblages to windstorm and salvage logging—Insights from analyses of functional guild and indicator species. Ecol. Indic. 65: 142-148.

Thorn, S., C. Bässler, H. Bußler, D. B. Lindenmayer, S. Schmidt, S. Seibold, B. Wende, and J. Müller. 2016. Bark-scratching of storm-felled trees preserves biodiversity at lower economic costs compared to debarking. For. Ecol. Manage. 364: 10-16.

Thorn, S., A. Chao, K. B. Georgiev, J. Müller, C. Bässler, J. L. Campbell, J. Castro, Y.-H. Chen, C.-Y. Choi, T. P. Cobb, D. C. Donato, E. Durska, E. Macdonald, E. Feldhaar, J. B. Fontaine, P. J. Fornwalt, R. M. Hernández, R. L. Hutto, M. Koivula, E.-J. Lee, D. Lindenmayer, G. Mikusiński, M. K. Obrist, M. Perlík, J. Rost, K. Waldron, B. Wermelinger, L. Weiß, M. Żmihorski, and A. B. Leverkus. 2020. Estimating retention benchmarks for salvage logging to protect biodiversity. Nature Communications 11: 4762.

Turner, M. G., W. L. Baker, C. J. Peterson, and R. K. Peet. 1998. Factors influencing succession: lessons from large, infrequent natural disturbances. Ecosystems 1: 511-523.

Ulanova, N. G. 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135: 155-167.

Uriarte, M., J. Thompson, and J. K. Zimmerman. 2019. Hurricane María tripled stem breaks and doubled tree mortality relative to other major storms. Nature communications 10: 1-7.

Van Bloem, S. J., and P. H. Martin. 2021. Socio-ecological lessons from the multiple landfalls of Hurricane Georges. Ecosphere 14: e03373.

Vogt, J. T., J. K. Gandhi, D. C. Bragg, R. Olatinwo, and K. D. Klepzig. 2020. Interactions between weather-related disturbance and forest insects and diseases in the southern United States, pp. 1-37. *In* U. D. o. Agriculture [ed.], Asheville, NC, USA.

Walker, L. R., J. Voltzow, J. D. Ackerman, D. S. Fernandez, and N. Fetcher. 1992. Immediate impacts of Hurricane Hugo on a Puerto Rican rain forest. Ecology 73: 691-694.

Wang, W., J. J. Qu, X. Hao, Y. Liu, and J. A. Stanturf. 2010. Post-hurricane forest damage assessment using satellite remote sensing. Agric. For. Meteorol. 150: 122-132.

Weed, A. S., M. P. Ayres, and J. A. Hicke. 2013. Consequences of climate change for biotic disturbances in North American forests. Ecological Monographs 83: 441-470.

Wermelinger, B. 2004. Ecology and management of the spruce bark beetle *Ips typographus* - a review of recent research. For. Ecol. Manage. 202: 67-82.

Wermelinger, B., P. Duelli, and M. K. Obrist. 2002. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. Forest Snow and Landscape Research 77: 133-148.

Wermelinger, B., M. K. Obrist, H. Baur, O. Jakoby, and D. P. 2013. Synchronous rise and fall of bark beetle and parasitoid populations in windthrow areas. Agric. For. Entomol. 15: 301-309.

Weslien, J. 1992. Monitoring *Ips typographus* (L.) populations and forecasting damage. Journal of Applied Entomology 114: 338-340.

White, P. S., and S. T. Pickett. 1985. Natural disturbance and patch dynamics: an introduction. In S. T. Pickett and P. S. White (eds.), The ecology of natural disturbance and patch dynamics. Elsevier.

Wickman, B. E. 1965. Insect-caused deterioration of windthrown timber in Northern California, 1963–1964. PSW-20. *In* U. F. S. P. S. F. a. R. E. Station [ed.], Berkeley, CA.

Williams, D. W., and A. M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. The Bark Beetles, Fuels, and Fire Bibliography: 34.

Wohlgemuth, T., M. Bürgi, C. Scheidegger, and M. Schütz. 2002. Dominance reduction of species through disturbance—a proposed management principle for central European forests. For. Ecol. Manage. 166: 1-15.

Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph.

Xi, W., and R. K. Peet. 2011. The complexity of catastrophic wind impacts on temperate forests, IntechOpen.

Zampieri, N. E., S. Pau, and D. K. Okamoto. 2020. The impact of Hurricane Michael on longleaf pine habitats in Florida. Scientific Reports 10: 8483.

Zhang, G., H. Murakami, T. R. Knutson, R. Mizuta, and K. Yoshida. 2020. Tropical cyclone motion in a changing climate. Science Advances 6: eaaz7610.

Zhao, T., H. Solheim, B. Langstrom, and A. K. Borg-Karlson. 2011. Storm-induced tree resistance and chemical differences in Norway spruce (*Picea abies*). Annals of Forest Science 68: 657-665.

Zimová, S., K. Merganičová, P. Štěpánek, R. Modlinger, and M. Turčáni. 2021. Devastating outbreak of bark beetles in the Czech Republic: Drivers, impacts, and management implications. For. Ecol. Manage. 490: 119075.

Zyval, V., Z. Krenova, and P. Kindlmann. 2016. Conservation implications of forest changes caused by bark beetle management in the Sumava National Park. Biol. Conserv. 204: 394-402.

Table 2.1 Major sources of variation in bark beetle populations and communities due to attributes at the tree, stand, and landscape-levels.

Spatial level	**Attribute**	**Examples of variations**
Tree	Section	Crown (branches), main stem (various heights), or roots
	Aspect of fallen trees	Exposure to sun: upper, side, or lower surface
	Size	Diameter, height
	Age	Diameter, height
	Crown size	Crown to bole ratio
	Damage type	Broken (with various heights of stumps or uprooted
	Damage level	Low, moderate, or high
	Status	Standing live, standing dead (including stumps), learning live, leaning dead, or downed trees
Stand	Basal area	
	Density	
	Previous disturbance and stress history	Previous windthrow, drought, etc.
	Soil type	Interactions with drought; water holding capacity; nutrient levels
	Conifer: hardwood ratio	
	Tree species	Presence of suitable host species
	Stand diversity	
	Aspect	North, East, West, or South facing slopes
	Elevation	
Landscape	Proximity to windthrown forests	
	Amount and type of edges	
	Local climatic conditions	Temperature, Precipitation

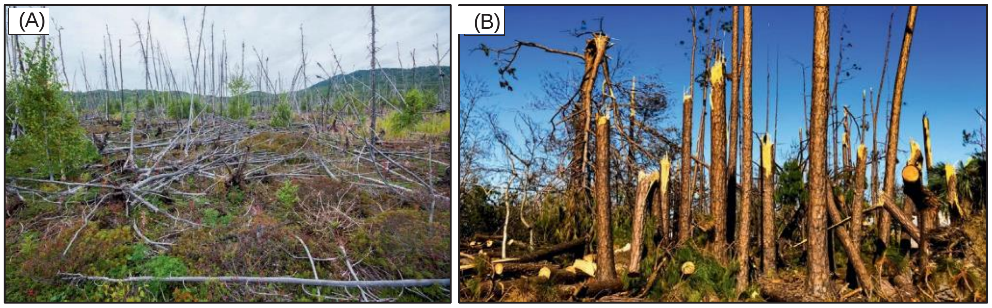

Figure 2.1 Examples of forest damage caused by catastrophic wind disturbance events in (A) Alaska, USA, and (B) pine forests in southeastern USA. *From (A) Viktor Loki, Shutterstock and (B) David Herring, Shutterstock.*

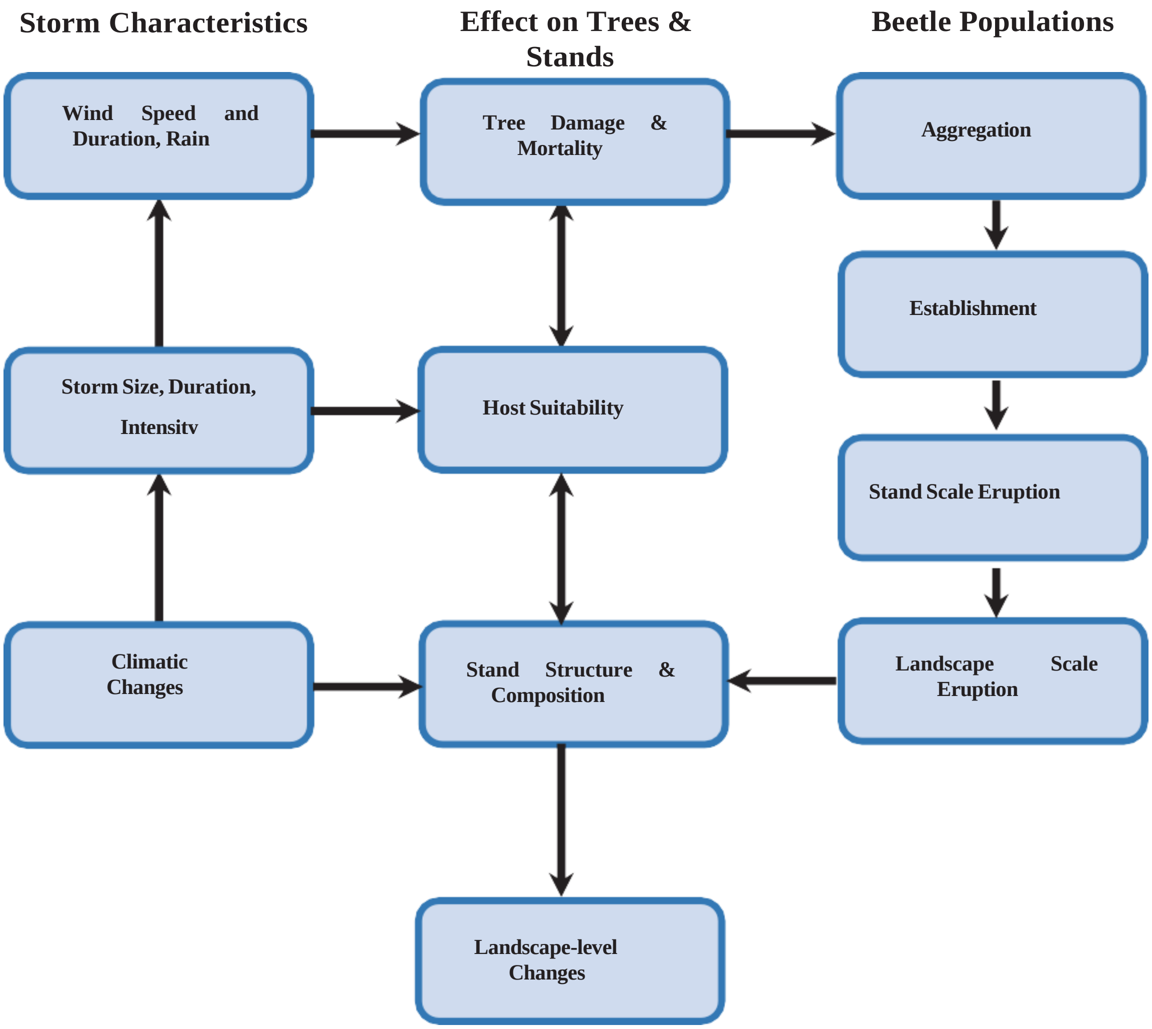

Figure 2.2 A conceptual model of interactions between the abiotic disturbance (catastrophic windstorms) and biotic components (bark beetle outbreaks) at various spatial scales.

CHAPTER 3

SHORT-TERM RESILIENCE OF LONGLEAF PINE FORESTS TO SUBCORTICAL BEETLES AFTER A CATASTROPHIC HURRICANE IN SOUTHEASTERN U.S.[2]

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[2] Gochnour, B.M., C.N. Miller, T.N., Sheehan, B. Barnes, K.D. Klepzig, C.R. Montes, and K.J.K Gandhi. To be submitted to a peer-reviewed journal

Abstract

Climate change is increasing the intensity and severity of Atlantic hurricanes in forested ecosystems. Catastrophic windstorms such as these can play a significant role in subcortical beetle (bark and woodboring beetles; Coleoptera: Buprestidae, Cerambycidae, and Curculionidae) population dynamics, where availability of damaged and stressed host trees allows for higher beetle populations. Post-hurricane management activities such as salvage-logging and prescribed burning aim to reduce fuel loads, although, they may also impact subcortical beetle populations. However, how bark beetles will respond to post-storm management activities in longleaf pine stands has yet to be assessed. Our research objective was to evaluate the effects of post-windstorm land management practices, including prescribed burning and salvage logging, on subcortical beetle populations and assemblages in pine forests. We evaluated the effects of these management practices on the trap catches and species diversity of subcortical beetles in managed pyrogenic longleaf pine (*Pinus palustris* M.) stands during the first growing season after the catastrophic Hurricane Michael significantly impacted southwestern Georgia. Treatments included stands that had experienced: (1) windthrow; (2) windthrow with subsequent prescribed fire and no salvage logging; or (3) windthrow with subsequent prescribed fire and salvage logging. Funnel and intercept panel traps baited with bark beetle pheromones (ipsenol, ipsdienol, and cis-verbenol) and host attractants (ethanol, alpha-pinene, and beta-pinene) respectively, were used to compare catches of three native *Ips* species [*I. avulsus* (Eichhoff), *Ips calligraphus* (Germar), and *I. grandicollis* (Eichhoff)] and the associated community of woodboring beetles. Our short-term results indicated that neither *Ips* beetles nor woodboring beetle species showed differences in trap catches between any forest treatments. There were also no differences in composition of woodboring beetle assemblages between treatments. Moreover, no outbreaks of either of the groups were observed in these longleaf pine forests in subsequent years, highlighting the forests' resilience to such disturbances. However, the late-fall timing of the hurricane and active management through frequent prescribed fire and gap selection thinning across the property may have influenced the relationship between the longleaf pine ecosystem and subcortical beetle activity. Results from this study may assist with adaptive management of longleaf pine forests to allow for resilience to both wind disturbances and subcortical beetle activity in the context of a changing climate.

KEYWORDS: bark beetle, Coleoptera, *Ips* beetle, prescribed fire, salvage, wind disturbance, woodboring beetles

3.1 Introduction

Windstorms are common abiotic disturbance agents in temperate forests, playing an important role in extant ecosystem patterns and processes (Thom and Seidl 2016). Wind disturbance creates canopy gaps, alters successional pathways, and influences species interactions in forested landscapes (Meigs et al. 2017). Large scale windstorms such as hurricanes can cause damage with a wide range of severity over large forest areas. Wind speeds are often highest near the center of the hurricane and result in the most severe damage. In these areas, entire stands of trees can be blown down, removing the canopy and drastically altering forest composition. Farther from the center, storm effects are more variable and the heterogeneity of forest damage in these areas can create multiple successional trajectories, resulting in greater forest heterogeneity on large scales (Xi et al. 2008). The sudden change in forest composition may also lead to habitat filtering, where certain species are extirpated from these habitats, resulting in altered ecosystem services in affected areas (Wermelinger et al. 2017).

In recent years, severe windstorms causing economic impacts over a billion dollars have increased in the U.S. (NCEI 2021). From 1980 to 2023, there were 363 severe climate and weather disasters that together resulted in a total cost exceeding 2.5 trillion USD. Of these events, 22 occurred in 2020 alone, seven of which were tropical cyclones (NCEI 2021). However, historically an average of only 6-7 North Atlantic tropical cyclones form each year, with only two making landfall in the U.S. annually (Vecchi and Knutson 2011, NOAA 2021). As the climate continues to change, future windstorms may also increase in intensity (sustained wind speed) and/or severity (magnitude of the effect on impacted land areas), resulting not only in economic costs but also carrying consequences for forest ecosystems (Elsner 2006, Holland and Bruyère 2014, Emanuel 2021).

3.1.1 Abiotic and biotic disturbances in southeastern pine forests

Pine forests (*Pinus* spp. L.) in the southeastern U.S., America's "wood-basket," produce 60% of the country's timber volume (Butler and Wear 2013, Oswalt and Smith 2014). The main pine species native to this area include longleaf pine (*P. palustris* Miller), loblolly pine (*Pinus taeda* L.), shortleaf pine (*P. echinata* Miller), and slash pine (*P. elliottii* Engelman). Prior to European colonization, longleaf pine trees dominated the landscape, covering the majority of the southeastern coastal plain from North Carolina to Louisiana, and down to peninsular Florida (Outcalt 2000, Frost 2006). However, longleaf pine stands have been removed for commercial pulp production, turpentine distillation, agricultural fields, and land development throughout the 19-20th centuries (Frost 2006). Additionally, longleaf pine has a long rotation time and a lower basal area, making it an unpopular commercial species. As a result, many of these forests were replanted with the higher-yielding loblolly pine, preferred for its fast growth, straight trunk, and height at maturity of over 30 m (Haywood et al. 2015, Susaeta and Gong 2019). Southeastern pine forests are impacted by both abiotic and biotic disturbances, including a variety of wind disturbances (Butler and Wear 2013, Oswalt and Smith 2014, Fortuin et al. 2022). Compared to other pine species, longleaf pine's higher wood density and development of a tap root both provide resilience to windstorms and other forms of disturbance (Cannon et al. 2023a). These characteristics may become invaluable (Haywood et al. 2015) as the effects of climate change increase the intensity of storm events in southeastern forests (NOAA 2021).

Biotic disturbances may be linked spatially and temporally with abiotic ones as a compounded disturbance system (Gochnour et al. 2022). Amongst biotic disturbances, bark beetle (Coleoptera: Curculionidae: Scolytinae) outbreaks are one of the most economically significant forest disturbances in North America, responsible for timber losses exceeding 2 billion USD annually (Grégoire et al. 2015). Bark beetles colonize host trees that are stressed or dying, often due to previous disturbances and wind damaged trees present an opportunity for the beetles to attack while tree defenses are compromised (Schowalter 1985, Weslien 1992), which can result in increased beetle populations within and around windthrown areas (Stadelmann et al. 2014). In fact, wind disturbance has been shown to be a critical factor in the initiation and propagation of outbreaks of *Ips typographus* (L.) in Europe (Schroeder 2001, Schroeder and Lindelow 2002, Schroeder 2010) and *Dendroctonus rufipennis* (Kirby) in the northeastern and western U.S. (Werner et al. 2006, Gandhi et al. 2007, Dodds et al. 2019). Outbreaking bark beetle populations can kill healthy trees affecting forests on a landscape scale, causing substantial economic impacts and affecting forest resilience (Komonen et al. 2011, Lausch et al. 2013). In contrast, species of *Ips* in the southeastern U.S. have not been found to outbreak on a large scale post-disturbance, though there are instances where they have formed localized spots of tree colonization in response to drought (McNichol et al. 2022). *Ips* spp. have also been found in higher numbers on wind-damaged trees in the southeastern U.S. (Vogt et al. 2020). However, climate change may alter the relationship between bark beetles and their host trees, enabling more severe outbreak events in the future (Raffa et al. 2008, Raffa et al. 2015).

3.1.2 Post-windstorm pine forest management

In longleaf pine forests, prescribed burning is a widespread management tool (Ritger et al. 2023). Longleaf pine ecosystems are pyrogenic, with flammable grasses, pine needles, and fallen trees serving as fuel for frequent, low-intensity fires that maintain an early successional stage in the understory (Noss 1989, Elliott et al. 1999, Brockway 2005). Burning can result in short term increases in available soil nitrogen, which is often a limiting factor in plant growth, although the burning of woody materials also releases nitrogen into the atmosphere, potentially causing a net loss of nitrogen for the forest (Carter and Foster 2004). Moreover, the frequent application of prescribed fire can reduce the risk of severe wildfire by consuming forest fuels, preventing them from accumulating on the forest floor (Davis and Cooper 1963).

To reduce residual coarse woody debris (i.e., fuels) on the landscape following a windstorm, management practices such as prescribed burning and salvage logging are often necessary (Kupfer et al. 2022). Salvage operations as a precursor to prescribed burns post-windstorm aim to harvest viable timber products and moderate fuel loads in the environment. Salvage logging can facilitate more consistent burns by removing large deposits of woody debris which impede the spread of low intensity fires, or remain burning and produce smoke, long after the prescribed burn was ignited (Lindenmayer and Noss 2006, Emery et al. 2020). However, salvage logging is also an anthropogenic disturbance, compressing soils and subjecting healthy trees to mechanical damage (Lindenmayer and

Noss 2006). As a result, when applied post-windstorm, salvage logging can create compound disturbance conditions. Despite this, when carefully applied and monitored, gentler, more targeted harvest techniques result in very low levels of negative impacts. These techniques, along with longleaf pine's adaptation to moderate disturbances results in a healthy, resilient forest and normal levels of regeneration (Peterson and Leach 2008, Oldfield and Peterson 2019), which may even be elevated through increased cone production after a hurricane (Cannon et al. 2023b).

Not only do these management practices result in reduced fuels and promote forest regeneration, but the practices may also reduce potential subcortical beetle reproductive substrate (logs, fallen trees, and branches) following wind disturbance events (Gandhi 2005, Gandhi et al. 2007). After severe windstorms in a northwestern Pennsylvania black cherry (*Prunus serotina* Ehrh.)-dominated forest, bark, woodborer, and ambrosia beetle abundance and damage increased in unsalvaged windthrown areas (DiGirolomo et al. 2013). In a North American sub-boreal forest in Minnesota, subcortical beetle assemblages underwent demographic shifts after a catastrophic windstorm and subsequent salvage logging and prescribed fire (Gandhi et al. 2009).

3.1.3 Beetle responses to post-windstorm management

Hurricane Michael was a category 5 storm that made landfall on the Florida panhandle and proceeded inland, causing widespread damage to forests in Alabama, Florida, and Georgia (Kenney et al. 2021, Henderson et al. 2022, Klepac and Cleary 2022). Costs associated with this storm exceeded 25 billion USD in damages, including the destruction of thousands of homes (Beven et al. 2019). This storm event resulted in the near complete removal of overstory trees in coastal forests, >50% tree death in adjacent stands, and catastrophic effects on forest ecosystems ranging into southern Georgia (Zampieri et al. 2020, Kenney et al. 2021). The hurricane, however, provided a rare opportunity to study the responses of subcortical beetles to management approaches after a catastrophic storm in the southeastern region. A study in planted loblolly pine stands found increases in woodboring beetle populations based on damage severity after Hurricane Michael (Miller et al. 2023). Woodboring beetle abundance was highest in moderate damage stands and was dominated by three species (86% of all beetles collected) (Miller et al. 2023). Meanwhile, species richness was highest in both high and low damage stands (Miller et al. 2023). However, how bark beetles respond to post-storm management activities in longleaf pine stands has yet to be assessed. Our research objective was to assess the effects of land management practices, including prescribed burning and salvage logging, on subcortical beetle populations and assemblages in pine forests, post-wind disturbance. Results from this study may assist with adaptive management of longleaf pine forests to allow for resilience to both wind disturbances and subcortical beetle activity in the context of a changing climate.

3.2 Materials and methods

3.2.1 Study site

The Jones Center at Ichauway is a 11,741 ha property in Baker County, Georgia (31.220446°N, -84.478796°W). Residing on the upper coastal plain in the southwestern corner of the state on a karst topography, it is dominated by loamy sand and sandy loam Troup soil types with a geological similarity to Ocala Limestone (Hodler and Schretter

1986, Graf 1987, Holland et al. 2019). The elevation at Ichauway ranges from 29 m to 55 m above mean sea level. This area receives around 140 cm of rainfall per year on average, the majority of which occurs in the spring and summer months (Rutledge et al. 2021). The temperature ranges from 33.33 °C highs in the summer to 1.67 °C lows in the winter. Stands at Ichauway are comprised of longleaf and slash pines, old-field loblolly pine, mixed pine hardwoods, riparian hardwood forests (*Acer, Carya, Liquidambar, Magnolia, Quercus* spp.), and isolated depressional wetlands (Goebel et al. 1997).

From the 1920's until the mid-1980's, Ichauway served as a quail hunting property for Robert W. Woodruff, a home to numerous employees and families, and a working farm and forest. Timber operations consisted only of selective harvests, using the Stoddard Neel approach to create gaps for regeneration, maintain open woodland and provide viable ecological habitats for native game and wildlife. After Woodruff's death in 1985, the property was transferred to the Robert W. Woodruff Foundation which in 1991, established The Joseph W. Jones Ecological Research Center at Ichauway.

Much of the longleaf pine grassland ecosystem present at Ichauway has not been subjected to agricultural tilling and so remains home to some of the most species-rich habitat in North America. Many of these longleaf pine stands contain trees ranging from 80 to 100 years of age and represent an example of this ecosystem akin to the historic landscape of the southeastern Coastal Plain. Vascular plant species density has been shown to be > 50 species per m^2 in some habitats with over 1,100 species identified on the property (Peet and Allard 1993). Ichauway is also home to over 370 vertebrate species, some of which are of interest to conservation scientists due to their rare or endemic nature (Smith et al. 2006). Efforts to catalog arthropod diversity are just beginning, but the Center collection already contains over 700 species in 178 families (Sheehan and Klepzig 2022).

On the 11th of October 2018, the property was subjected to severe wind disturbance from Hurricane Michael. Stands dominated by longleaf pine had on average 12.5% treefall and 14.8% tree damage (Rutledge et al. 2021). It is estimated that some 300,000 trees were lost during the storm, of which most were pines, greatly increasing the fuel load across the property. After the hurricane, both salvage logging and prescribed burning were conducted. Extensive salvage logging operations were implemented in Winter 2018 and Spring of 2019. Fallen, broken, and bent over trees, and remnant stumps were removed from most of the property. Piles of slash were left behind for later burning. At Ichauway, almost all the areas of longleaf pine woodland are burned every two years on a revolving basis. These frequent, relatively low intensity fires are intended to consume understory vegetation while leaving the pine trees virtually unharmed. This burn regime creates low basal area woodlands with open canopy conditions, and maintenance of the understory flora toward early successional and fire adapted species (Provencher et al. 2003, Ellair and Platt 2013, Shappell and Koontz 2015).

3.2.2 Study design

We selected fifteen stands within longleaf pine woodland dominated burn blocks (mapped areas delineated with firebreaks for prescribed fire treatments) based on damage from Hurricane Michael, salvage operations, and prescribed fire application. Prescribed burns at our stands were conducted within 3-7 months post-wind disturbance. These stands had a density ranging from 49.12 to 196.48 trees per hectare, with basal area ranging from

5.27 m^2 to 23.24 m^2 per hectare (Table 3.1). Coarse woody debris volume in the stands ranged from 1.9 m^3 to 149.29 m^3 per hectare post-treatment. Coarse woody debris decreased on average by 22% with the addition of fire and 47% with the addition of fire and salvage logging (Table 3.1).

To determine the impacts of salvage logging and prescribed burning on bark beetles in longleaf pine woodlands, we chose five stands for each of the three different recent management histories in 2019: 1) hurricane damage with no prescribed fire in the year following the hurricane and no salvage logging; 2) hurricane damage with prescribed fire in the year following the hurricane and no salvage logging; and 3) hurricane damage with both prescribed fire and salvage logging the year after (hereafter windthrow-only, windthrow-fire, and windthrow-fire-salvage respectively). We did not include a wind damage plus salvage logging treatment without prescribed burning in our study because this combination is not within management plans at Ichauway and is unlikely to be found in longleaf pine stands affected by Hurricane Michael. Most land managers burned their lands regardless of whether they could be salvaged, to reduce fuels from the storm and keep hardwood competition under control.

3.2.3 Subcortical beetle trapping

In Summer 2019, we created a trapping transect in each stand comprised of two Lindgren funnel traps and two cross-vane panel traps, placed alternately at ~20 m intervals along a linear transect. We used a total of 90 traps (45 each of Lindgren funnels and cross-vane panel traps) in the study. Several compounds have been identified as attractants for *Ips* species including racemic mixes of ipsenol, ipsdienol, and cis-verbenone (Wood 1982a, Allison et al. 2012) (Table 3.2). So, we baited each funnel trap with one (+/-) ipsenol bubble cap (Synergy Semiochemicals Corp., Delta, Canada), one *cis*-verbenol bubble cap (Synergy Semiochemicals Corp.), and one (+/-) ipsdienol bubble cap, IP034 (Chemtica Intl., Santo Domingo, Costa Rica) (hereafter "bark beetle bait"). We also deployed cross-vane traps each containing one ultra-high release ethyl alcohol and one *Sirex* blend (70% alpha-pinene and 30% beta-pinene) (Synergy Semiochemicals Corp.) (hereafter "tree volatile bait"). Ethyl alcohol, alpha-pinene, and beta-pinene mimic a complex of volatiles released by host trees utilized by subcortical insects as reproductive substrate (Billings 1985, Ginzel and Hanks 2005). We filled each trap collection container with propylene glycol to prevent the collection fluid from evaporating and ensure preservation of the insects collected. We operated the traps every other week from 17 April to 25 September 2019, with the contents of traps being collected each week. This resulted in 12 sampling dates and 720 individual samples. Baits were replaced once a month for the duration of the sampling period.

Trap contents were transferred to individual containers filled with 75% ethanol and were refrigerated until further processing. We then separated all insects larger than *Ips*, resulting in one fraction of the sample containing *Ips* and the other, woodboring beetles. Species of insects not from these two target groups were few and were not used in this study. We identified the three *Ips* beetles to the species level: *I. avulsus* (Eichhoff) , *I. calligraphus* (Germar), and *I. grandicollis* (Eichhoff) using Wood (1982b). Our focus was on *Ips* beetles because they respond quickly to increased woody debris on the landscape, pose the highest threat to healthy trees after wind disturbance, and are of the highest concern to land managers. Because of the large volume of *Ips* beetles captured in our study, a subsampling by volume methodology was used to estimate beetle catches. We identified all woodboring beetles to the species level (Coleoptera: Cerambycidae and Buprestidae) using Lingafelter (2007). These beetles are secondary colonizers on surviving but stressed trees and were also abundant in our stands. All our beetle identifications were verified by E. R. Hoebeke with the Georgia Museum of Natural History, University of Georgia, Athens, U.S. where we deposited a reference collection.

3.2.4 Ips Beetle Trap Catches

For all of our statistical analyses in this study, we used R statistical software (version 3.5.1; R Core Team 2021). Generalized linear models (GLMs) were used to determine whether *Ips* beetle trap catches showed differences between our treatments in the year following Hurricane Michael. Our unit of replication was the individual stand for a total of 5 replicates of three treatments across 15 stands. Our response variables were trap catches of the three *Ips* beetle species, summed for all traps and dates at the stand level for the entirety of the sampling period. Land management treatments were used as the categorical predictor variables in all GLMs. Data for each species were discrete and adhered to assumptions of normality according to Shapiro-Wilk and Levene’s tests. Our data was over-dispersed, and hence, we used negative binomial GLMs from the package *MASS* with a logarithmic link function to address this issue. For all GLMs, p-values and 95% confidence intervals (CIs) were computed using a Wald z-distribution approximation at $\alpha = 0.05$.

We used the previously mentioned subsampling and extrapolation by volume methodology to generate the count data for our *Ips* species trap catches given the high number of subcortical beetles collected in our study (estimated ~825,000 *Ips* beetles). This methodology involves cleaning the samples to remove debris and other insects larger than our target species. The volumes of the cleaned and centrifuged samples were then recorded and used to extrapolate beetle counts from a 5 mL subsample. Error terms were generated for each species through repeated subsampling of a sample whose total beetle counts were known. Using a Monte Carlo simulation, we randomly assigned error to each sample generated by extrapolation. We then repeated our analysis using the *glm.nb* function in the package *MASS* for R. This process was repeated 1,000 times and the p-values were recorded. The number of significant versus non-significant p-values served as a power analysis for the results of our GLMs.

3.2.5 Woodborer Trap Catches

We analyzed woodborer trap catches to assess the differences between our land-area treatments and to determine if there were differences in trap catches between bait types. Our response variables were the total number of woodboring beetle species and trap catches of the three most abundant species, summed at the stand level for each bait type, for the entirety of the sampling period. We performed Shapiro-Wilk tests on each response variable to assess normality, and Levene’s test to determine homogenous variance. Two-way ANOVAs with land-area treatment and bait types were performed for each of the normally distributed response variables for a total of two models. In the two cases where normality was violated, Kruskal-Wallace tests were performed. Land management treatment combinations and bait type were used as the categorical predictor variables in all statistical tests. Response variables were discrete and bounded at zero. We used t-tests and Welch's t-tests to determine trap catch differences between bait types for response variables with normally distributed data.

3.2.6 Woodborer species diversity and composition

To determine whether land management treatments affected woodborer species diversity, we generated rarefaction curves using the function *iNEXT* in the package *iNEXT* (Chao et al. 2014, Hsieh et al. 2022). Rarefaction is a technique that allows for the estimation of species richness based on sampling effort, represented by the number of collected samples or individuals. This method of species richness estimation addresses an issue in community sampling where increased sampling renders a higher number of species. Rarefaction uses random resampling from the pool of data to generate an estimate of mean species richness attained at various levels of sampling effort (Gotelli and Colwell 2001). We generated species accumulation curves with 95% confidence intervals for each of our treatment groups using the accumulated individuals from all stands to illustrate differences in estimated species richness between treatments.

We performed nonmetric multidimensional scaling (NMDS) using the function *metaMDS* in the R package *vegan* to plot woodboring beetle assemblages among treatments and bait types. We used NMDS to visualize the differences in species captured between treatments and bait types based on cumulative trap catches for each trap during the entirety of the study. NMDS functions by finding a non-parametric, monotonic relationship between our dissimilarity matrix and the Euclidean distances between our data, and then arranging the points in a reduced-dimensional space (Cox and Cox 2000).

We used an analysis of similarities (ANOSIM) test to assess differences in woodborer responses to bait type. ANOSIM is a nonparametric test that uses a ranked dissimilarity matrix to evaluate differences in species assemblages from predefined groups of samples (Clarke 1993). Our assemblage matrix was generated based on cumulative catches from each trap across all treatment groups over the course of the study. Two-dimensional NMDS models comparing catches of woodboring beetle species converged at 74 iterations with a stress value of 0.237. Evaluation of the same data in three dimensions converged at 156 iterations with a stress value of 0.168. These cumulative, individual trap catches were then grouped by treatment and then bait type for these analyses. Dissimilarity matrices were calculated using Bray-Curtis distances and were analyzed using the function *anosim* in the R package *vegan*. Significance of dissimilarity between bait types was evaluated at $\alpha < 0.05$.

3.3 Results

3.3.1 Ips beetles

Our 720 individual trap collections yielded approximately 825,000 *Ips* beetles during the sampling period. Of the *Ips* beetles trapped, approximately 17,000 were *I. avulsus*, 247,000 were *I. calligraphus*, and 560,000 were *I. grandicollis*. For *I. avulsus*, a 1,000 iteration Monte Carlo simulation which added randomized error to our samples resulted in 1,000 non-significant p-values for each of the treatments. This suggests a high degree of confidence in our results despite extrapolation error. The negative binomial model’s explanatory power was moderate (Nagelkerke's $R^2 = 0.16$) (Table 3.3). The model's intercept, corresponding to our windthrow-only treatment, was at 6.91 (95% CI

[6.60, 7.25], $p < 0.001$). Within this model, the effect of our windthrow-fire treatment was non-significant (beta = 0.10, 95% CI [-0.36, 0.56], p = 0.676). Additionally, the effect of our windthrow-fire-salvage treatment was non-significant (beta = 0.30, 95% CI [-0.16, 0.76], p = 0.199). Standardized parameters were obtained by fitting the model on a standardized version of the dataset.

For *I. calligraphus*, a 1,000 iteration Monte Carlo simulation which added randomized error to our samples resulted in 1,000 non-significant p-values for each of the treatments. The negative binomial model's explanatory power was substantial (Nagelkerke's $R^2 = 0.30$). The model's intercept, corresponding to our windthrow-only treatment, was at 9.56 (95% CI [9.35, 9.78], $p < 0.001$). Within this model, the effect of our windthrow-fire treatment was statistically non-significant (beta = 0.14, 95% CI [-0.16, 0.45], p = 0.346). Additionally, the effect of our windthrow-fire-salvage treatment was statistically non-significant (beta = 0.29, 95% CI [-0.01, 0.59], p = 0.058). Standardized parameters were obtained by fitting the model on a standardized version of the dataset.

For *I. grandicollis*, a 1,000 iteration Monte Carlo simulation which added randomized error to our samples resulted in 1,000 non-significant p-values for each of the treatments. The negative binomial model's explanatory power was weak (Nagelkerke's $R^2 = 5.62e-03$). The model's intercept, corresponding to our windthrow-only treatment, was at 10.56 (95% CI [10.18, 11.01], $p < 0.001$). Within this model, the effect of our windthrow-fire treatment was statistically non-significant (beta = -0.07, 95% CI [-0.65, 0.52], p = 0.817). Additionally, the effect of our windthrow-fire-salvage treatment was statistically non-significant (beta = -0.04, 95% CI [-0.63, 0.54], p = 0.885). Standardized parameters were obtained by fitting the model on a standardized version of the dataset.

3.3.2 Woodboring beetles

We trapped 37,330 woodboring beetles comprising of 41 species, 30 genera, and seven subfamilies within the families Buprestidae and Cerambycidae (Table 3.4). While two *Monochamus* species were likely captured in this study [*Monochamus titillator* (Fabricius) and *Monochamus carolinensis* (Olivier)], ambiguity in their morphological differentiation and their consideration as a species complex led us to treat these two species as a single entity, henceforth "*Monochamus* spp.*"*. Cerambycid beetles accounted for 99.86% of all beetles captured while buprestid beetles accounted for the remaining 0.14% of beetles. The three most abundant species, *Monochamus* spp. (65.83%), *Acanthocinus obsoletus* (Olivier) (31.37%), and *Xylotrechus sagittatus* (Germar) (1.25%) accounted for 98.45% of all cerambycid beetles. The remaining 581 individuals collected (1.55%) were represented by 38 species, including 9 singleton and 5 doubleton taxa.

Twenty beetle species, including the most abundant species, were captured in all three treatments. Two species [*Neoclytus mucronatus* (Fabricius) and *Prionus imbricornis* (L.)] were unique to our windthrow-only stands. Four species [*Buprestis apricans* Herbst, *Liopinus alpha* (Say), *Lepturges confluens* (Haldeman), and *Strangalia famelica famelica* Newman] were unique to our windthrow-fire stands. Five species [*Typocerus zebra* (Olivier), *Distenia undata* (Fabricius), *Archodontes melanopus* (L.), *Knulliana cincta cincta* (Drury), and *Knulliana cincta spinifera* (Drury)] were unique to our windthrow-fire-salvage stands. Four species [*Eupogonius tomentosus* (Haldeman), *Aegomorphus modestus* (Gyllenhal in Schoenherr), *Curius dentatus* Newman, and *Leptostylus asperatus* (Haldeman)] were found in only windthrow-only and windthrow-fire stands. Three species

[*Obrium maculatum* (Olivier), *Arhopalus rusticus* (L.), and *Orthosoma brunneum* (Forster)] were found in only windthrow-only and windthrow-fire-salvage stands. Two species [*Anelaphus parallelus* (Newman) and *Nyssodrysina haldemani* (LeConte)] were found in only windthrow-fire and windthrow-fire-salvage stands. Results of our two-way ANOVAs showed no differences between treatments for species richness or trap catches of *Monochamus* spp. However, bait type was significant for both species richness ($t = -3.387$, $df = 28$, $p = 0.002$) and *Monochamus* spp. ($t = -5.02$, $df = 20.432$, $p < 0.001$) trap catches (Table 3.5). Species richness was 39% higher in bark beetle baited traps than in tree volatile baited traps (Figure 3.1a). *Monochamus* spp. trap catches were 88% higher in bark beetle baited traps than in tree volatile baited traps (Figure 3.1b).

Kruskal-Wallace tests showed no differences between treatments for both *A. obsoletus* and *X. sagittatus*. Additionally, bait type was significant for both *A. obsoletus* ($X^2 = 21.779$, $p < 0.001$; Figure 3.1c) and *X. sagittatus* ($X^2 = 22.039$, $p < 0.001$; Table 3.5, Figure 3.1d). Trap catches for *A. obsoletus* were 2,749% higher in bark beetle baited traps than in tree volatile baited traps. Trap catches for *X. sagittatus* were 2,383% higher in tree volatile baited traps than in bark beetle baited traps.

Species rarefaction curves showed windthrow-fire stands had the highest observed species richness (31 species at 10,771 individuals). The windthrow-only and windthrow-fire-salvage stands had lower observed species richness (28 and 29 species respectively at 10,771 individuals). Rarefaction curves showed slightly different species accumulation trends between treatments, but ultimately species richness did not differ between treatments (Figure 3.2).

The NMDS for treatments were largely overlapping for woodboring beetles, and ANOSIM detected no differences in species composition between the treatment groups (R-statistic = 0.03, P = 0.935) (Figure 3.3). The bait type NMDS plots showed nonoverlapping groups by bait type and ANOSIM detected a difference in dissimilarities between woodboring beetle assemblages captured by the two different bait types (R-statistic = 0.753, P < 0.001). Tree volatile baited traps showed slightly more dispersion between traps than bark beetle baited traps.

3.4 Discussion

While wind disturbance is known to impact subcortical beetle populations, how bark beetles respond to post-windstorm management practices in longleaf pine is not well-understood. Our study addresses this gap in the context of an actively managed longleaf pine forest in the southeastern U.S. following Hurricane Michael. Based on trapping conducted within the first year following the storm, we found the following trends: 1) *Ips* beetle and woodboring beetle total trap catches, including those of the most abundant species, did not differ between different land management treatments; 2) woodborer species richness did not differ between different land management treatments; 3) woodboring beetle species richness was higher in bark beetle baited traps; 4) *Monochamus* spp. and *A. obsoletus* had greater total trap catches in bark beetle baited traps while *X. sagittatus* had greater total trap catches in tree volatile baited traps; and 5) the woodboring beetle assemblage differed by bait type.

3.4.1 Beetle response to post-storm management practices

Overall, since Hurricane Michael, we have not observed any significant outbreaks of subcortical beetles in the longleaf woodlands of Ichauway. Similarly, species diversity and occurrence of woodboring beetles did not differ between land-area treatments. These patterns could due to either widespread wind damage across the property that obscured stand-level differences leading to similarly high population levels between treatments, movement of insects to and from adjacent stands not included in the study that received different burn or salvage treatments, and/or the delay between storm damage in October 2018 and sampling initiated in May 2019, which likely rendered residual woody debris unusable for bark beetle reproduction. With property wide tree mortality at 12.5% and damaged standing trees an additional 15%, ample reproductive material was generated across the landscape (Rutledge et al. 2021), perhaps causing similar but high population levels in all of our studied stands. The forests at Ichauway are burned in a mosaic pattern with approximately half of the property burned each year leading to burned and unburned stands adjacent to and interspersed with one another. Studies have found that some insect groups are attracted to burned areas (Gerson and Kelsey 1997, Sullivan et al. 2003, Gandhi et al. 2008, Bell 2023). This may have resulted in movement of insects across the property from unburned to burned stands.

It is possible that the characteristics of these well-managed longleaf pine forests contributed to the lack of effect from land management treatments on the number of bark beetles captured in our study in post hurricane conditions. The longleaf pine forest's features, including mixed age stands and an open canopy structure, may play a role in disrupting bark beetle attack initiation and aggregation. These characteristics result from application of the Stoddard-Neel method of forest management which involves frequent return interval prescribed fire and selective harvest as the main tools for maintaining the ecosystem (Neel et al. 2011). Martinson et al. (2007) demonstrated longleaf pine forest's resistance to southern pine beetle, *Dendroctonus frontalis* Zimmermann, outbreak at the stand level, with monotypic stands of longleaf pine having rare occurrences of outbreaks compared to their more common occurrence in loblolly pine stands. Thistle et al. (2004) evaluated the behavior of tracer gasses released in the understory of a loblolly pine forest. In this work, they used the movement and detection of a gas as a proxy for the movement of pheromones, such as those used by the southern pine beetle (or for that matter *Ips* pine engravers) during aggregation in host trees. They found that tracer gas plume movement in thinned pine stands was chaotic (due to more wind movement and temperature variability), resulting in highly variable pulses of gas which (if they were beetle pheromones) would be difficult for a beetle to follow to the source. In contrast, unthinned stands had more stable microenvironments (less wind movement and stable temperatures), resulting in a cohesive, stable plume of gas which could easily be followed to its source. The applicability of these findings to bark beetle dynamics is clear. Closed canopy stands (commonly found in planted loblolly pine areas) create optimal conditions for bark beetles to find colonized host trees. Open canopy stands (prevalent in longleaf in general and dominant at Ichauway) are much less conducive to this crucial step in bark beetle tree killing behavior.

Taken together, these mechanisms may be keeping *Ips* bark beetle populations in a stable endemic phase despite evidence of the large number of beetles and potential host material present in these forests based on our high capture rates. There are estimated to be over one million pine trees on the Ichauway property, and the mixed age stands may provide a somewhat homogenous proportion of trees susceptible to attack (often due to the frequent lightning strikes in this area) in any given year. The volume of usable reproductive substrate, via downed woody material, produced by the storm may not have been enough to affect populations in a drastic way between our stands. Further, the timing of windstorms may be playing an integral role in subcortical beetle population dynamics (DiGirolomo et al. 2013). The coarse woody debris created in the storm in October 2018 would not be used by the beetles until the growing season of the following year, when populations began to build up after winter. This delay may have rendered this phloem tissue of this potential reproductive resource unusable, effectively leading to greater similarity between our treatment stands than might have been expected.

3.4.2 Woodborer response to bait type

We did find a preference for certain bait types exhibited by many of the woodboring beetle species captured in our study. Not surprisingly, tree volatile baited trap catches of *X. sagittatus* were higher by a range of 1,630 to 3,475% by tree stand than bark beetle baited trap catches. However, we captured more woodborer species in our traps baited with bark beetle pheromones than in traps baited with compounds that mimic signals given off by host pine trees. In our study, bark beetle baited trap catches of *Monochamus* spp. and *A. obsoletus* were higher by a range of 51.6 to 111.44% and 2,209.83 to 3,645.76% respectively by stand than tree volatile baited traps. This may suggest a kairomonal response by certain woodboring beetles to bark beetle's pheromones as a reliable way to find suitable host trees (Sullivan et al. 2024). When *Ips* pheromones were deployed in combination with host tree volatiles, some woodborer species responded in greater numbers than to either of the bait types alone, further indicating that woodborers are responding to bark beetle pheromones (Miller et al. 2011, Miller et al. 2015). However, individual components of combination baits can be disruptive to the capture of certain species (Stock et al. 1990, Kostyk et al. 1993, Holsten et al. 2003, Ross 2021). Ultimately, a diversity of trapping approaches may provide the most accurate representation of the forest insect communities. This is an important consideration if management decisions are made based on biodiversity assessments.

3.5 Conclusions

The effects of climate change are projected to increase the intensity and severity of future windstorms, with implications for subcortical insect population dynamics and community demographics (Seidl and Rammer 2017, Ting et al. 2019). However, in the southern coastal plain of the U.S., particularly in longleaf pine forests, the relationship is less established. Land management practices common in forests of the southeastern U.S. include prescribed fire and salvage logging, with the primary goal of these practices being fuel reduction. Larger fuels (slash, large branches, and stems) also have the capacity to serve as subcortical insect breeding material and represent the potential for local population density increases that lead to outbreak scenarios (Ciesla and Bell 1968, VillaCastillo and Wagner 1996, Hayes et al. 2008, Fettig et al. 2013).

Although several previous studies have shown alterations to subcortical beetle populations and assemblages in response to wind disturbance and subsequent management practices (Gandhi et al. 2009, Komonen et al. 2011, Novais et al. 2018, Spinner 2022, Miller et al. 2023), the responses of beetle species here showed no differences in regard to fire and salvage logging. The *Ips* beetle species we sampled exhibited similar responses across all treatment groups on this longleaf pine dominated property. We also observed no appreciable effect of prescribed fire or salvage logging on woodboring beetle assemblages. This may be due, in part, to the management of this property with prescribed fire and selective harvesting, with the goal of recreating the effects of natural disturbance regimes that occurred in these forests prior to European settlement. Longleaf pine forests' natural resilience following regional disturbance agents, such as hurricanes and insects, indicate that they may fare better in response to climatic changes than the dominant commercial pine species.

3.6 **Acknowledgements**

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3.7 References

Allison, J. D., J. L. McKenney, D. R. Miller, and M. L. Gimmel. 2012. Role of Ipsdienol, Ipsenol, and cis-Verbenol in chemical ecology of *Ips avulsus*, *Ips calligraphus*, and *Ips grandicollis* (Coleoptera: Curculionidae: Scolytinae). J. Econ. Entomol. 105: 923-929.

Bell, A. J. 2023. Like moths to a flame: A review of what we know about pyrophilic insects. For. Ecol. Manage. 528: 13.

Beven, J. L., R. Berg, and A. Hagen. 2019. National hurricane center tropical cyclone report: Hurricane Michael (AL142018). Robbie Berg and Andrew Hagen," National Hurricane Center Tropical Cyclone Report Hurricane Michael–AL142018", National Hurricane Center 17: 86.

Billings, R. 1985. Southern pine bark beetles and associated insects: Effects of rapidly-released host volatiles on response to aggregation pheromones. Zeitschrift für Angewandte Entomologie 99: 483-491.

Brockway, D. G. 2005. Restoration of longleaf pine ecosystems, USDA Forest Service, Southern Research Station.

Butler, B. J., and D. N. Wear. 2013. Forest ownership dynamics of southern forests. In: Wear, David N.; Greis, John G., eds. 2013. The Southern Forest Futures Project: technical report. Gen. Tech. Rep. SRS-GTR-178. Asheville, NC: USDA-Forest Service, Southern Research Station.: 103-121.

Cannon, J. B., C. J. Peterson, C. M. Godfrey, and A. W. Whelan. 2023a. Hurricane wind regimes for forests of North America. Proc. Natl. Acad. Sci. U. S. A. 120: 8.

Cannon, J. B., B. T. Rutledge, J. J. Puhlick, J. L. Willis, and D. G. Brockway. 2023b. Tropical cyclone winds and precipitation stimulate cone production in the masting species longleaf pine (*Pinus palustris*). New Phytol.: 13.

Carter, M. C., and C. D. Foster. 2004. Prescribed burning and productivity in southern pine forests: a review. For. Ecol. Manage. 191: 93-109.

Chao, A., N. J. Gotelli, T. Hsieh, E. L. Sander, K. Ma, R. K. Colwell, and A. M. Ellison. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological monographs 84: 45-67.

Ciesla, W. M., and J. C. Bell. 1968. Pine engraver *Ips pini* (Coleoptera - Scolytidae) in southern Appalachian mountains. Ann. Entomol. Soc. Am. 61: 235-+.

Clarke, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian journal of ecology 18: 117-143.

Cox, T. F., and M. A. Cox. 2000. Multidimensional scaling, CRC press.

Davis, L. S., and R. W. Cooper. 1963. How prescribed burning affects wildfire occurrence. Journal of Forestry 61: 915-917.

DiGirolomo, M. F., D. C. Allen, S. V. Stehman, S. L. Stout, and J. Wiedenbeck. 2013. Insect damage to wind-thrown and standing live black cherry resulting from delayed salvage after a major abiotic disturbance. Northern Journal of Applied Forestry 30: 101-108.

Dodds, K. J., M. F. DiGirolomo, and S. Fraver. 2019. Response of bark beetles and woodborers to tornado damage and subsequent salvage logging in northern coniferous forests of Maine, USA. For. Ecol. Manage. 450.

Ellair, D. P., and W. J. Platt. 2013. Fuel composition influences fire characteristics and understorey hardwoods in pine savanna. J. Ecol. 101: 192-201.

Elliott, K. J., R. L. Hendrick, A. E. Major, J. M. Vose, and W. T. Swank. 1999. Vegetation dynamics after a prescribed fire in the southern Appalachians. For. Ecol. Manage. 114: 199-213.

Elsner, J. B. 2006. Evidence in support of the climate change–Atlantic hurricane hypothesis. Geophysical Research Letters 33: 1-3.

Emanuel, K. 2021. Atlantic tropical cyclones downscaled from climate reanalyses show increasing activity over past 150 years. Nature Communications 12: 7027.

Emery, R. K., J. S. Kleinman, J. D. Goode, and J. L. Hart. 2020. Effects of catastrophic wind disturbance, salvage logging, and prescribed fire on fuel loading and composition in a Pinus palustris woodland. For. Ecol. Manage. 478: 118515.

Fettig, C. J., R. E. Burnside, C. J. Hayes, J. J. Kruse, N. J. Lisuzzo, S. R. McKelvey, S. R. Mori, S. K. Nickel, and M. E. Schultz. 2013. Factors influencing northern spruce engraver colonization of white spruce slash in interior Alaska. For. Ecol. Manage. 289: 58-68.

Fortuin, C. C., C. R. Montes, J. T. Vogt, and K. J. K. Gandhi. 2022. Predicting risks of tornado and severe thunderstorm damage to southeastern U.S. forests. Landscape Ecology 37: 1905-1919.

Frost, C. 2006. History and future of the longleaf pine ecosystem. The longleaf pine ecosystem: ecology, silviculture, and restoration 438: 9-42.

Gandhi, K. J., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. C. Zasada, and S. J. Seybold. 2008. Catastrophic windstorm and fuel-reduction treatments alter ground beetle (Coleoptera: Carabidae) assemblages in a North American sub-boreal forest. For. Ecol. Manage. 256: 1104-1123.

Gandhi, K. J. K. 2005. The responses of sub-boreal forest insects to a catastrophic wind-disturbance event and subsequent fuel-reduction practices in northeastern Minnesota, Volumes I and II. Ph.D., University of Minnesota, USA.

Gandhi, K. J. K., D. W. Gilmore, S. A. Katovich, W. J. Mattson, J. R. Spence, and S. J. Seybold. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews 15: 113-152.

Gandhi, K. J. K., D. W. Gilmore, R. A. Haack, S. A. Katovich, S. J. Krauth, W. J. Mattson, J. C. Zasada, and S. J. Seybold. 2009. Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. J. Chem. Ecol. 35: 1384-1410.

Gerson, E. A., and R. G. Kelsey. 1997. Attraction and direct mortality of pandora moths, Coloradia pandora (Lepidoptera: Saturniidae), by nocturnal fire. For. Ecol. Manage. 98: 71-75.

Ginzel, M. D., and L. M. Hanks. 2005. Role of host plant volatiles in mate location for three species of longhorned beetles. J. Chem. Ecol. 31: 213-217.

Gochnour, B., S. Spinner, K. Klepzig, and K. Gandhi. 2022. Interactions between catastrophic wind disturbances and bark beetles in forested ecosystems, pp. 197-223, Bark beetle management, ecology, and climate change. Academic Press.

Goebel, P., B. Palik, L. Kirkman, and L. West. 1997. Field guide: landscape ecosystem types of Ichauway. Newton, GA.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology letters 4: 379-391.

Graf, W. L. 1987. Geomorphic systems of North America, Geological Society of America.

Grégoire, J. C., K. F. Raffa, and B. S. Lindgren. 2015. Economics and politics of bark beetles, Academic Press.

Hayes, C. J., T. E. DeGomez, J. D. McMillin, J. A. Anhold, and R. W. Hofstetter. 2008. Factors influencing pine engraver (*lps pini* Say) colonization of ponderosa pine *Pinus ponderosa* Dougl. ex. Laws.) slash in Northern Arizona. For. Ecol. Manage. 255: 3541-3548.

Haywood, J. D., M. A. S. Sayer, and S.-J. S. Sung. Year. Published. Comparison of planted loblolly, longleaf, and slash pine development through 10 growing seasons in central Louisiana—an argument for longleaf pine, p. 383. *In,* Southern Silvicultural Research Conference, 2015.

Henderson, J. D., R. C. Abt, K. L. Abt, J. Baker, and R. Sheffield. 2022. Impacts of hurricanes on forest markets and economic welfare: The case of hurricane Michael. Forest Policy Econ. 140: 9.

Hodler, T. W., and H. A. Schretter. 1986. The atlas of Georgia, University of Georgia, Institute of Community & Area Development.

Holland, A. M., B. T. Rutledge, S. B. Jack, and J. M. Stober. 2019. The longleaf pine forest: long-term monitoring and restoration of a management dependent ecosystem. Journal for Nature Conservation 47: 38-50.

Holland, G., and C. L. Bruyère. 2014. Recent intense hurricane response to global climate change. Climate Dynamics 42: 617–627.

Holsten, E. H., P. J. Shea, and R. R. Borys. 2003. MCH released in a novel pheromone dispenser prevents spruce beetle, *Dendroctonus rufipennis* (Coleoptera: Scolytidae), attacks in south-central Alaska. J. Econ. Entomol. 96: 31-34.

Hsieh, T., K. Ma, and A. Chao. 2022. iNterpolation and EXTrapolation for Species Diversity. R Package, Version 3.0.0.

Kenney, G., C. L. Staudhammer, S. Wiesner, S. T. Brantley, S. W. Bigelow, and G. Starr. 2021. Hurricane michael altered the structure and function of longleaf pine woodlands. J. Geophys. Res.-Biogeosci. 126: 17.

Klepac, S., and J. Cleary. Year. Published. Analysis of damage patterns from Hurricane Michael, pp. 352-361. *In*, 9th Forensic Engineering Congress, Nov 04-07 2022, Denver,, CO. Amer Soc Civil Engineers, NEW YORK.

Komonen, A., L. M. Schroeder, and J. Weslien. 2011. *Ips typographus* population development after a severe storm in a nature reserve in southern Sweden. Journal of Applied Entomology 135: 132-141.

Kostyk, B. C., J. H. Borden, and G. Gries. 1993. Photoisomerization of antiaggregation pheromone verbenone - biological and practical implications with respect to the mountain pine-beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). J. Chem. Ecol. 19: 1749-1759.

Kupfer, J. A., K. Lackstrom, J. M. Grego, K. Dow, A. J. Terando, and J. K. Hiers. 2022. Prescribed fire in longleaf pine ecosystems: fire managers' perspectives on priorities, constraints, and future prospects. Fire Ecol. 18.

Lausch, A., M. Heurich, and L. Fahse. 2013. Spatio-temporal infestation patterns of *Ips typographus* (L.) in the Bavarian Forest National Park, Germany. Ecol. Indic. 31: 73-81.

Lindenmayer, D. B., and R. F. Noss. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv. Biol. 20: 949-958.

Lingafelter, S. 2007. Illustrated key to the longhorned woodboring beetles of the eastern United States. Coleopterists Society Miscellaneous Publication 3: 206.

Martinson, S., R. W. Hofstetter, and M. P. Ayres. 2007. Why does longleaf pine have low susceptibility to southern pine beetle? Can. J. For. Res. 37: 1966-1977.

McNichol, B. H., S. R. Clarke, M. Faccoli, C. R. Montes, J. T. Nowak, J. D. Reeve, and K. J. Gandhi. 2022. Relationships between drought, coniferous tree physiology, and *Ips* bark beetles under climatic changes, pp. 153-194, Bark beetle management, ecology, and climate change. Elsevier.

Meigs, G. W., R. C. Morrissey, R. Bace, O. Chaskovskyy, V. Cada, T. Despres, D. C. Donato, P. Janda, J. Labusova, M. Seedre, M. Mikolas, T. A. Nagel, J. S. Schurman, M. Synek, M. Teodosiu, V. Trotsiuk, L. Vitkova, and M. Svoboda. 2017. More ways than one: Mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. For. Ecol. Manage. 406: 410-426.

Miller, C. N., B. F. Barnes, S. Kinz, S. C. Spinner, J. T. Vogt, E. McCarty, and K. J. K. Gandhi. 2023. Woodboring beetle (Buprestidae, Cerambycidae) responses to Hurricane Michael in variously damaged southeastern US pine plantations. For. Sci. 69: 272-285.

Miller, D. R., C. Asaro, C. M. Crowe, and D. A. Duerr. 2011. Bark beetle pheromones and pine volatiles: attractant kairomone lure blend for longhorn beetles (Cerambycidae) in pine stands of the southeastern United States. J. Econ. Entomol. 104: 1245-1257.

Miller, D. R., C. M. Crowe, K. J. Dodds, L. D. Galligan, P. de Groot, E. R. Hoebeke, A. E. Mayfield, III, T. M. Poland, K. F. Raffa, and J. D. Sweeney. 2015. Ipsenol, ipsdienol, ethanol, and α-pinene: trap lure blend for Cerambycidae and Buprestidae (Coleoptera) in pine forests of eastern North America. J. Econ. Entomol. 108: 1837-1851.

NCEI, N. C. f. E. I. 2021. U.S. billion-dollar weather and climate disasters (2020).

Neel, L., P. S. Sutter, and A. G. Way. 2011. The art of managing longleaf: a personal history of the Stoddard-Neel approach, University of Georgia Press.

NOAA, N. O. a. A. A. 2021. 2021 update to data last published online in 2019 as part of the Atlantic Hurricane Database Re-analysis Project.

Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Natural Areas Journal 9: 211-213.

Novais, S., L. E. Macedo-Reis, E. J. Cristobal-Peréz, G. Sánchez-Montoya, M. Janda, F. Neves, and M. Quesada. 2018. Positive effects of the catastrophic Hurricane Patricia on insect communities. Scientific Reports 8: 9.

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

Oswalt, S., and W. B. Smith. 2014. U.S. Forest resource facts and historical trends. Forest Service, United States Department of Agriculture FS-1035.

Outcalt, K. W. 2000. The longleaf pine ecosystem of the South. Native Plants Journal 1: 42-53.

Peet, R. K., and D. J. Allard. 1993. Longleaf pine vegetation of the southern Atlantic and eastern Gulf Coast regions: a preliminary classification, pp. 45-81. *In*, Proceedings of the Tall Timbers fire ecology conference.

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

Provencher, L., A. R. Litt, and D. R. Gordon. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conserv. Biol. 17: 1660-1671.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, and T. E. Kolb. 2015. Responses of tree-killing bark beetles to a changing climate, vol. 7, Cabi Publishing-C a B Int, Wallingford.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of bark beetle eruptions. BioScience 58: 501-517.

Ritger, H. M. W., S. T. Brantley, K. D. Klepzig, and K. J. K. Gandhi. 2023. Differential effects of fire regime and site conditions on bark beetles (Coleoptera: Curculionidae) in a longleaf pine (*Pinus palustris* Mill.) ecosystem. For. Ecol. Manage. 549: 13.

Ross, D. W. 2021. 3-Methylcyclohex-2-en-1-one and the Douglas-fir beetle (Coleoptera: Curculionidae): history of successful bark beetle pheromone treatments. Can. Entomol. 153: 62-78.

Rutledge, B. T., J. B. Cannon, R. K. McIntyre, A. M. Holland, and S. B. Jack. 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. For. Ecol. Manage. 481: 13.

Schowalter, T. D. 1985. Adaptations of insects to disturbance, pp. 235-252. In S. T. A. Pickett and P. S. White (eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, San Diego.

Schroeder, L. M. 2001. Tree mortality by the bark beetle *Ips typographus* (L.) in storm-disturbed stands. Integrated Pest Management Reviews 6: 169-175.

Schroeder, L. M. 2010. Colonization of storm gaps by the spruce bark beetle: influence of gap and landscape characteristics. Agric. For. Entomol. 12: 29-39.

Schroeder, L. M., and A. Lindelow. 2002. Attacks on living spruce trees by the bark beetle *Ips typographus* (Col. Scolytidae) following a storm-felling: a comparison between stands with and without removal of wind-felled trees. Agric. For. Entomol. 4: 47-56.

Seidl, R., and W. Rammer. 2017. Climate change amplifies the interactions between wind and bark beetle disturbances in forest landscapes. Landscape Ecology 32: 1485-1498.

Shappell, L. J., and S. M. Koontz. 2015. Fire reintroduction increased longleaf pine (*Pinus palustris* L.) recruitment and shifted pine demographics in a long-unburned xeric sandhill assemblage. For. Ecol. Manage. 354: 344-352.

Sheehan, T. N., and K. D. Klepzig. 2022. Arthropods and fire within the biologically diverse longleaf pine ecosystem. Ann. Entomol. Soc. Am. 115: 69-94.

Smith, L. L., D. A. Steen, J. M. Stober, M. C. Freeman, S. W. Golladay, L. M. Conner, and J. Cochrane. 2006. The vertebrate fauna of Ichauway, Baker County, GA. Southeast. Nat. 5: 599-620, 522.

Spinner, S. C. 2022. Responses of bark beetles and their associates to a severe wind disturbance in southern pine stands. University of Georgia.

Stadelmann, G., H. Bugmann, B. Wermelinger, and C. Bigler. 2014. Spatial interactions between storm damage and subsequent infestations by the European spruce bark beetle. For. Ecol. Manage. 318: 167-174.

Stock, A. J., J. H. Borden, T. L. Pratt, H. D. Pierce, and B. D. Johnston. 1990. Endo-brevicomin - An antiaggregation pheromone for the western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera, Scolytidae). Can. Entomol. 122: 935-940.

Sullivan, B. T., C. J. Fettig, W. J. Otrosina, M. J. Dalusky, and C. W. Berisford. 2003. Association between severity of prescribed burns and subsequent activity of conifer-infesting beetles in stands of longleaf pine. For. Ecol. Manage. 185: 327-340.

Sullivan, B. T., H. L. Munro, B. F. Barnes, B. H. McNichol, W. P. Shepherd, and K. J. K. Gandhi. 2024. Potential for a minor pine bark beetle pest, *Dendroctonus terebrans* (Coleoptera: Curculionidae: Scolytinae), to mediate host location by a major pine killer, *Dendroctonus frontalis*. J. Econ. Entomol.: 12.

Susaeta, A., and P. Gong. 2019. Economic viability of longleaf pine management in the Southeastern United States. Forest Policy Econ. 100: 14-23.

Thistle, H. W., H. Peterson, G. Allwine, B. Lamb, T. Strand, E. H. Holsten, and P. J. Shea. 2004. Surrogate pheromone plumes in three forest trunk spaces: composite statistics and case studies. For. Sci. 50: 610-625.

Thom, D., and R. Seidl. 2016. Natural disturbance impacts on ecosystem services and biodiversity in temperate and boreal forests. Biological Reviews 91: 760-781.

Ting, M. F., J. P. Kossin, S. J. Camargo, and C. H. Li. 2019. Past and future hurricane intensity change along the US East coast. Scientific Reports 9: 8.

Vecchi, G. A., and T. R. Knutson. 2011. Estimating annual numbers of Atlantic hurricanes missing from the HURDAT database (1878–1965) using ship track density. Journal of Climate 24: 1736-1746.

VillaCastillo, J., and M. R. Wagner. 1996. Effect of overstory density of *Ips pini* (Coleoptera: Scolytidae) performance in ponderosa pine slash. J. Econ. Entomol. 89: 1537-1545.

Vogt, J. T., J. K. Gandhi, D. C. Bragg, R. Olatinwo, and K. D. Klepzig. 2020. Interactions between weather-related disturbance and forest insects and diseases in the southern United States, pp. 1-37. *In* U. D. o. Agriculture [ed.], Asheville, NC, USA.

Wermelinger, B., M. Moretti, P. Duelli, T. Lachat, G. Pezzatti, and M. Obrist. 2017. Impact of windthrow and salvage-logging on taxonomic and functional diversity of forest arthropods. For. Ecol. Manage. 391: 9-18.

Werner, R. A., E. H. Holsten, S. M. Matsuoka, and R. E. Burnside. 2006. Spruce beetles and forest ecosystems in south-central Alaska: a review of 30 years of research. For. Ecol. Manage. 227: 195-206.

Weslien, J. 1992. Monitoring *Ips typographus* (L.) populations and forecasting damage. Journal of Applied Entomology 114: 338-340.

Wood, D. L. 1982a. The role of pheromones, kairomones, and allomones in the host selection and colonization behavior of bark beetles. Annual Review of Entomology 27: 411-446.

Wood, S. L. 1982b. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph.

Xi, W., R. K. Peet, and D. L. Urban. 2008. Changes in forest structure, species diversity and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. Journal of Plant Ecology 1: 43-57.

Zampieri, N. E., S. Pau, and D. K. Okamoto. 2020. The impact of Hurricane Michael on longleaf pine habitats in Florida. Scientific Reports 10: 8483.

Table 3.1 Attributes of the fifteen study stands at the Jones Center at Ichauway in Georgia, U.S.

Treatment	Basal Area (m^2/hectare)[a]	Average Pine Diameter (cm)	Pine Trees per Hectare	Pine Coarse Woody Debris (m^3/hectare)[a]
Windthrow-only	5.98 ± 0.60	34.28 ± 2.46	143.43 ±10.58	47.7 ± 26.08
Windthrow-fire	3.92 ±1.04	32.91 ± 2.43	90.38 ± 23.54	37.21 ± 25.34
Windthrow-fire-salvage	5.62 ±1.25	38.39 ± 2.06	111.99 ± 24.18	25.5 ± 7.51

[a] Stand measurements were taken from a circular 0.1-hectare plot in the center of each study stand.

Table 3.2 Load and release rate for bait products used to attract bark and woodboring beetles in each trap type sampled during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S.

Bait	**Load**	**Purity (%)**	**Release rate**	**Trap type**
(+/-) - ipsenol bubble cap	100 mg	0.93	0.6-0.8 mg/day @ 25° C	Funnel
(+/-) - ipsdienol bubble cap	100 mg	0.92	0.6-0.8 mg/day @ 25° C	Funnel
cis-verbenol bubble cap	175 mg	0.95	0.6-0.8 mg/day @ 20° C	Funnel
Ultra-high release ethanol	100 mL	0.95	300 mg/day @ 25° C	Cross-vane
α and β pinene ultra-high release	200 mL	70:30	2,000 mg/day @ 25°C	Cross-vane

Table 3.3 Results of GLMs[1] evaluating the effects of land management treatment combinations on total *Ips avulsus*, *Ips calligraphus*, and *Ips grandicollis* trap catches during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S. Combinations of prescribed fire and salvage logging were our explanatory variables. Coefficient estimates, standard errors, Wald z-scores, and P-values are included for each categorical explanatory variable. Nagelkerke's R^2 values are included to illustrate the explanatory power of each model.

		GLM				
Total trap catches	**Treatment**	**Coefficient**	**Standard error**	**Wald Z**	**P**	**Nagelkerke's R^2**
Ips avulsus	Windthrow-only	9.56	0.11	88.03	< 0.001	0.30
	Windthrow-fire	0.14	0.15	0.94	0.346	
	Windthrow-fire-salvage	0.29	0.15	1.89	0.058	
Ips calligraphus	Windthrow-only	10.56	0.21	50.44	< 0.001	< 0.001
	Windthrow-fire	-0.07	0.30	-0.23	0.817	
	Windthrow-fire-salvage	-0.04	0.30	-0.15	0.885	
Ips grandicollis	Windthrow-only	6.91	0.17	41.58	< 0.001	0.16
	Windthrow-fire	0.10	0.23	0.42	0.676	
	Windthrow-fire-salvage	0.30	0.23	1.29	0.199	

[1] GLMs are negative binomial with a logarithmic link function for all response variables.

Table 3.4 List of woodboring beetle families, subfamilies, genera, and species identified during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S.

Family	**Subfamily**	**Species**	**Windthrow-only**	**Windthrow-Fire**	**Windthrow-Fire-Salvage**	**Funnel trap**	**Cross-vane trap**
Buprestidae	*Buprestinae*	*Buprestis apricans* Herbst	0	1	0	1	0
		Buprestis lineata Fabricius	5	3	2	7	3
		Buprestis maculipennis Gory	5	5	2	8	4
		Chalcophora virginiensis (Drury)	7	3	13	21	2
		Chrysobothris femorata (Olivier)	3	3	2	4	4
Cerambycidae	*Cerambycinae*	*Anelaphus villosus* (Fabricius)	0	4	1	2	3
		Curius dentatus Newman	1	1	0	1	1
		Elaphidion mucronatum (Say)	5	6	4	11	4
		Enaphalodes atomarius (Drury)	6	2	4	8	4
		Knulliana cincta cincta (Drury)	0	0	2	1	1
		Knulliana cincta spinifera (Fabricius)	0	0	1	1	0
		Neoclytus acuminatus (Fabricius)	8	6	3	11	6
		Neoclytus mucronatus (Fabricius)	1	0	0	0	1
		Neoclytus scutellaris (Olivier)	2	2	6	7	3
		Obrium maculatum (Olivier)	9	0	1	10	0
		Xylotrechus colonus (Fabricius)	7	2	6	8	7
		Xylotrechus sagittatus (Germar)	183	147	135	18	447
	Disteniinae	*Distenia undata* (Fabricius)	0	0	1	0	1
	Lamiinae	*Acanthocinus nodosus* (Fabricius)	79	41	39	128	31
		Acanthocinus obsoletus (Olivier)	4,538	3,175	3,996	11,312	397
		Aegomorphus modestus (Blais)	1	1	0	0	2
		Astylopsis arcuate (LeConte)	40	39	24	94	9
		Astylopsis sexguttata (Say)	14	24	22	55	5
		Ataxia crypta (Say)	1	2	2	4	1
		Ecyrus dasycerus (Say)	1	3	3	6	1

	Eupogonius tomentosus (Haldeman)	2	1	0	1	2
	Leptostylus asperatus (Haldeman)	1	3	0	0	4
	Leptostylus transversus (Gyllenhal)	9	15	4	16	12
	Lepturges angulatus (LeConte)	1	5	1	3	4
	Lepturges confluens (Haldeman)	0	1	0	0	1
	Liopinus alpha (Say)	0	2	0	2	0
	Monochamus spp. (Fabricius)	8,029	7,216	9,285	16,036	8,539
	Nyssodrysina haldemani (LeConte)	0	3	1	4	0
	Styloleptus biustus (LeConte)	1	5	6	11	1
Lepturinae	*Strangalia famelica famelica* Newman	0	1	0	1	0
	Typocerus zebra (Olivier)	0	0	1	1	0
Prioninae	*Archodontes melanopus* (Linné)	0	0	1	1	0
	Orthosoma brunneum (Forster)	1	0	1	1	1
	Prionus imbricornis (Linné)	1	0	0	1	0
	Prionus pocularis Dalman	9	5	11	7	18
Spondylidinae	*Arhopalus rusticus* (Linné)	3	0	5	6	2
Total Beetles		**12,973**	**10,727**	**13,585**	**27,809**	**9,521**
Total Richness		**30**	**31**	**31**	**36**	**32**

Table 3.5 Results of ANOVA and Kruskal-Wallis analyses evaluating the differences in species richness and total trap catches of *Monochamus spp.*, *Acanthocinus obsoletus*, and *Xylotrechus sagittatus* between bait types, treatments, and their interaction during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S. Asterisks indicate significance at *a* < 0.05.

Response Variable	Treatment	Analysis of Variance		
		d.f.	F value	P value
Species Richness	Bait Type	1	12.187	0.002
	Treatment	2	0.395	0.678
	Treatment x Bait Type	2	2.477	0.105
Monochamus spp.	Bait Type	1	26.201	< 0.001
	Treatment	2	1.460	0.252
	Treatment x Bait Type	2	1.094	0.351
		Kruskal-Wallis Test		
		d.f.	X^2	P value
Acanthocinus obsoletus	Bait Type	1	21.779	< 0.001
	Treatment	2	0.547	0.761
Xylotrechus sagittatus	Bait Type	1	22.039	< 0.001
	Treatment	2	1.019	0.601

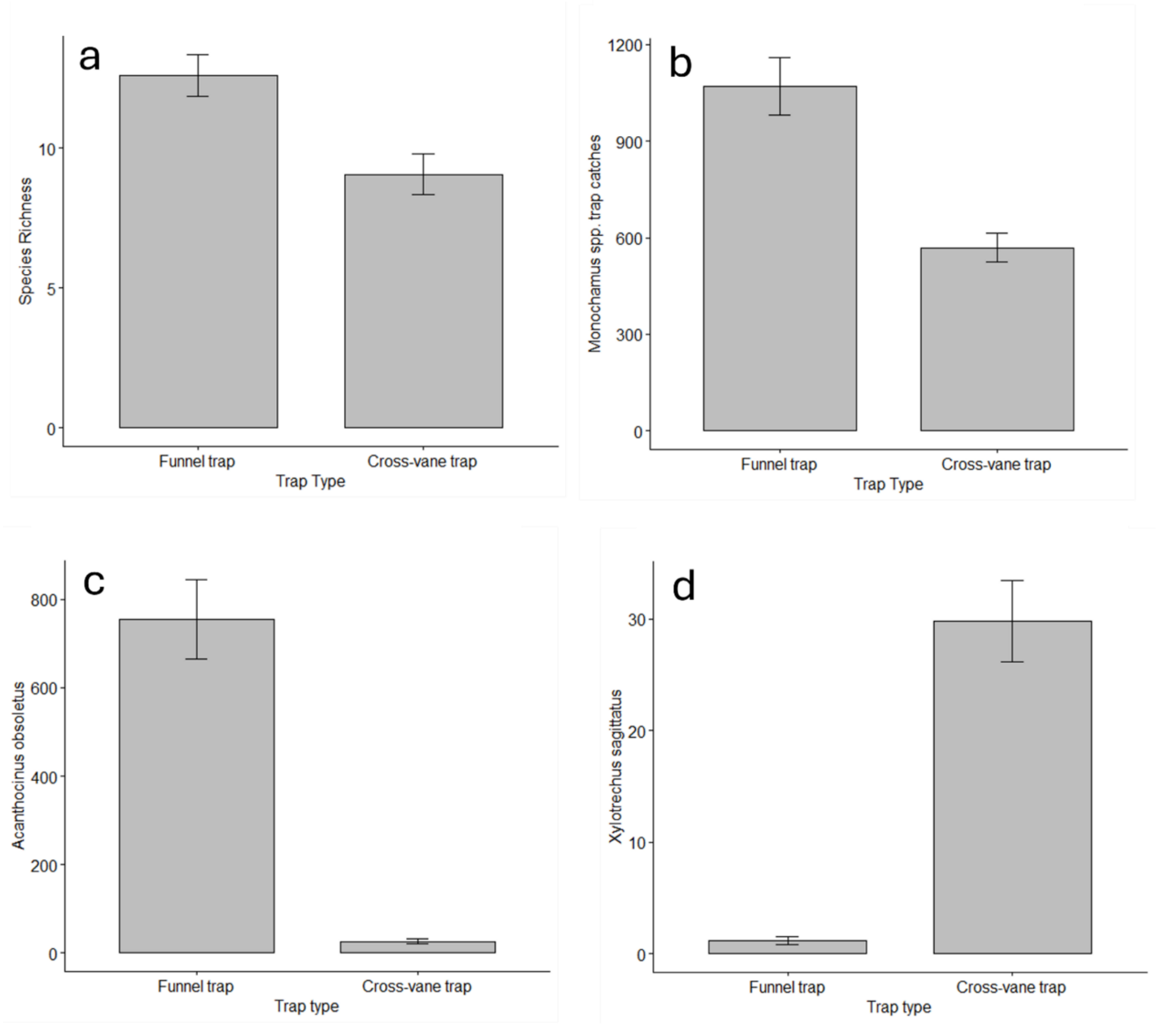

Figure 3.1 Bar plots depicting the mean and standard error by bait type for (a) woodboring beetle species richness, (b) *Monochamus* spp. trap catches, (c) *Acanthocinus obsoletus* trap catches, and (d) *Xylotrechus sagittatus* trap catches during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S.

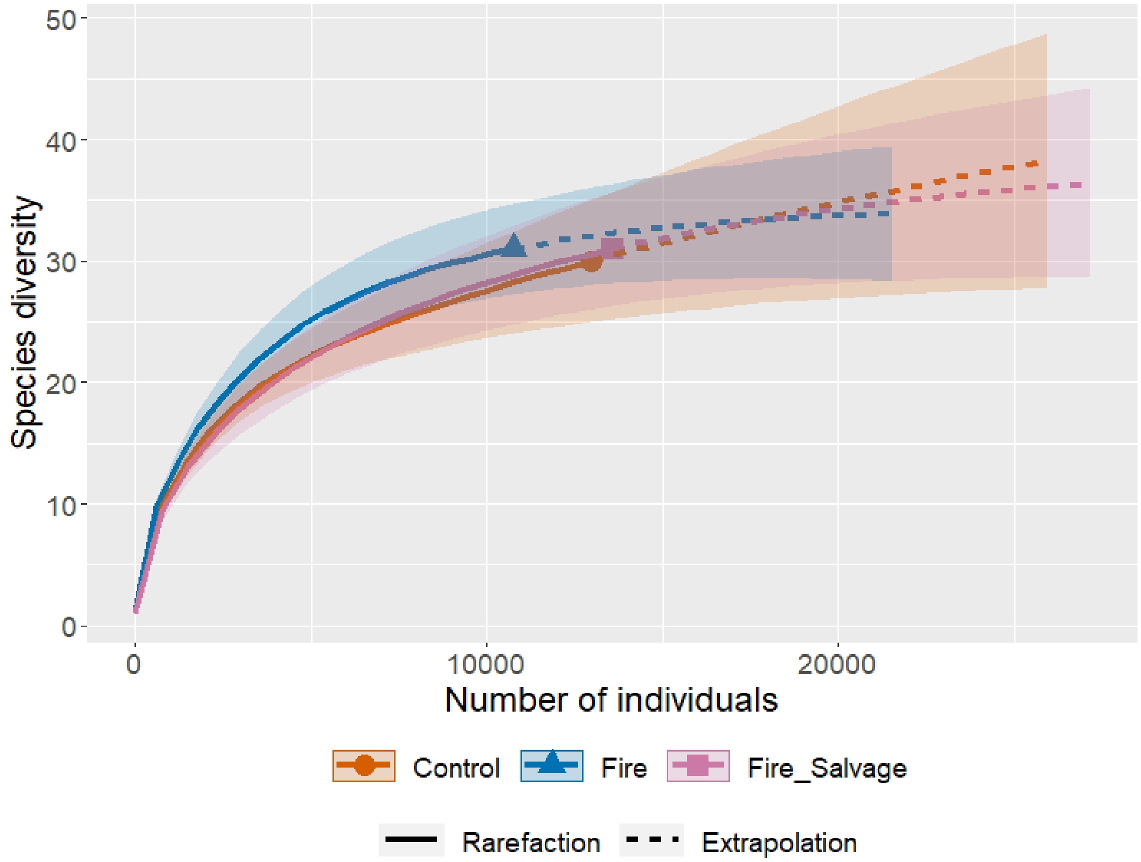

Figure 3.2 Rarefaction curves for woodborer species richness across three land management treatment combinations during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S. Shaded areas represent 95% confidence intervals.

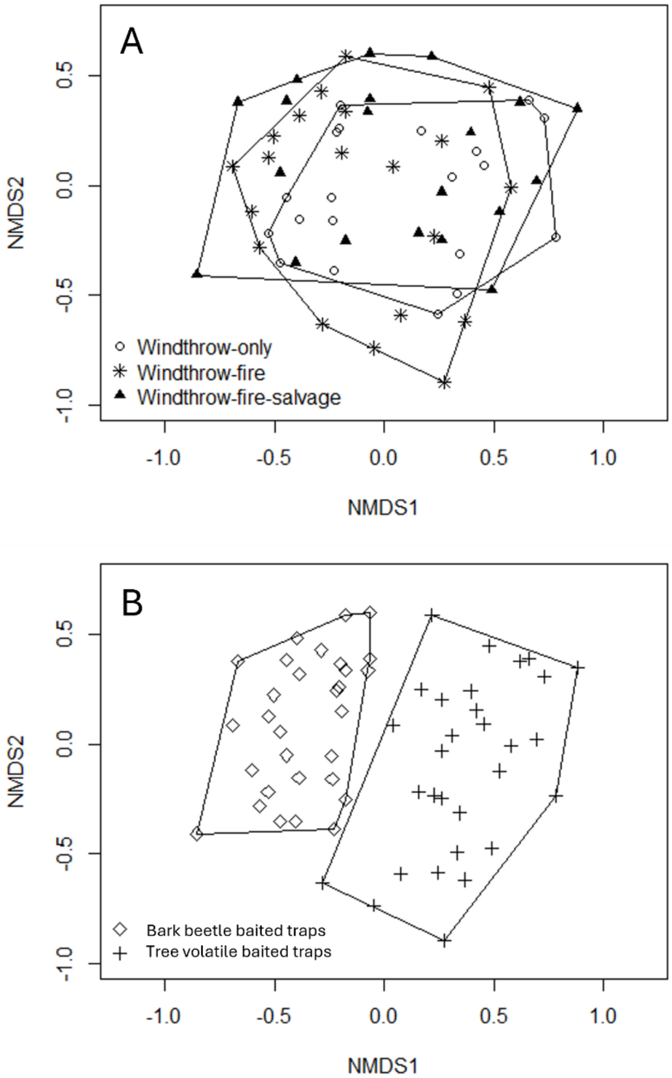

Figure 3.3 NMDS plots depicting Bray-Curtis dissimilarities in two dimensions for woodboring beetle assemblages captured by either treatment (a) or bait type (b) during May-September 2019 at the Jones Center at Ichauway in Georgia, U.S.

CHAPTER 4

VERTICAL DISTRIBUTION OF A BEETLE ASSEMBLAGE IN SIMULATED-LIGHTNING-STRUCK LONGLEAF PINE TREES[3]

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[3] Gochnour, B.M., T.N. Sheehan, K.J.K Gandhi, and K.D. Klepzig. To be submitted to a peer-reviewed journal

Abstract

Southern pine bark beetles (Coleoptera: Scolytinae) have been assumed to display well defined vertical patterns of colonization in host trees, with some species found mainly near the top of trees and others near the bottom, suggesting a partitioning of the tree resource between beetle species. In longleaf pine (*Pinus palustris* Miller) ecosystems, high insect diversity adds to the complexity of resource partitioning. Given the interest in restoration of longleaf pine forests, a better understanding of how the insect assemblage associated with stressed trees is distributed vertically can aid our ability to manage for multiple goals, including biodiversity and regulation of bark beetle populations. We assessed vertical distribution of flight activity and colonization in response to lightning-struck longleaf pine trees. We simulated lightning strikes using detonation cord and used a flight intercept trap array with unbaited cross-vane panel traps hung at four heights (0, 5, 10, 15 m) to assess the activity and vertical distribution of the insect assemblage. Additionally, we assessed successful bark beetle colonization by collecting emergence data from trunk sections associated with the four heights. In total, we collected 47,343 insects among 275 species from eight trees. Many important herbivore species and associated predatory insects showed a vertical stratification in their flight activity around treatment trees with some found more often near the bottom or top of the trees. Initial colonization dynamics of dying pine trees can have important implications for the associated community of insects that assemble around these colonization events. Early arriving herbivores may have the opportunity to exploit a larger area of the tree resource and predatory insects' flight activity may be influenced by the presence of their prey species. The confluence of hundreds of species of insects at these trees during colonization events may give us insight into larger scale, subcortical and predatory beetle population dynamics.

KEYWORDS: bark beetle, community, disturbance, generalized additive model, lightning, longleaf pine, stratification, trophic guild

4.1 Introduction

Longleaf pine (*Pinus palustris* Miller) ecosystems are among the most biodiverse outside of the tropics (Provencher et al. 2003, Kirkman et al. 2004, Van Lear et al. 2005, Kaeser and Kirkman 2009, Kirkman et al. 2016). These ecosystems are characterized by an open canopy overstory of longleaf pine trees with an understory dominated by grasses, herbs and other early successional species (Peet 2006). Longleaf pine forests are also home to a great diversity of insects (Sheehan and Klepzig 2022). However, once spanning > 365,000 km^2 from eastern Texas to central Florida and Virginia, longleaf pine forests have been reduced to <5% of their original range (Frost 2006). Recent restoration efforts have highlighted the complex and biologically diverse nature of these systems (Sheehan and Klepzig 2022).

Given interest in restoration, knowledge of how ecologically and economically important insect species interact with host trees can inform longleaf management strategies (Ritger et al. 2023). Eruptive forest pests in other pine systems (often driven by climate change), such as bark beetles (Coleoptera: Scolytinae), have recently become of more interest (Bentz et al. 2010). Bark beetles provide important ecosystem services in pine forests (Schowalter 2012), but are also known to contribute to mortality of stressed and damaged trees (Schowalter 2012, McNichol et al. 2019). Bark beetle populations are intimately related to disturbance agents, such as lightning, and their effect on forest ecosystems. Their colonization behavior, which includes tunneling into and creating reproductive galleries within the phloem tissue of stressed pine trees, effectively girdles attacked trees and along with symbiotic fungi, it contributes to tree dieback and death (Yousuf et al. 2014, Raffa et al. 2015, Hornslein et al. 2019). Disturbance events that affect tree health can create substantial reproductive resources for beetle populations (Coulson et al. 1986, Vogt et al. 2020). In particular, lightning strikes result in trees that are both attractive and vulnerable to bark beetle attacks, initiating insect colonization of individual struck trees (Anderson and Anderson 1968, Hodges and Pickard 1971, Coulson et al. 1983, Coulson et al. 1985, Coulson et al. 1986). In the southeastern U.S., the occurrence of lightning is widespread and consistent between years, leading to a reliable source of stressed trees for bark beetles at a landscape scale (Coulson et al. 1983, Coulson et al. 1986, Rykiel et al. 1988, Lovelady et al. 1991, Flamm et al. 1993). Lightning strikes cause extreme trauma to struck trees, not only resulting in stress from physical damage but also triggering the release of tree volatiles (Taylor 1974, Miller 1983). Studies on lighting-struck loblolly pine (*P. taeda* L.) have found changes in resin composition after a lightning strike, with an increase in attractive compounds and a decrease in repellant compounds (Blanche et al. 1985). These changes along with the immediate release of tree volatiles following a lightning strike, allow bark beetles and wood borers to locate lightning-struck trees (Anderson and Anderson 1968, Blanche et al. 1985).

In attacked trees, bark beetles display vertical patterns of colonization, with some species found predominantly near the top of the tree and others near the base of the tree, suggesting a partitioning of the tree resource between beetle species (Paine et al. 1981, Flamm et al. 1993, Ayres et al. 2001). Patterns of successful colonization at different heights have been associated with proportional landing rates at those same heights (Flamm et al. 1993). This indicates that beetles distribute themselves along the height of the tree prior to landing and do not significantly relocate to other heights once on the tree (Flamm et al. 1993). Consequently, we hypothesize that bark beetle colonization of lightning struck longleaf pine trees will be similarly vertically distributed and can be observed through flight activity, although no such studies exist on longleaf pines.

Bark beetles are only one group of insects aggregating around lightning-struck pine trees. While previous studies of tree colonization have focused on bark beetles, other feeding guilds and trophic levels such as root-feeding beetles, ambrosia beetles, woodboring beetles, predators, and detritivores associated with the dying and dead pines are less understood. However, studies of flight activity have shown a high degree of variability of vertical distribution within feeding guilds (Sheehan et al. 2019), indicating that a species level analysis of these patterns in relation to colonization events is important. Overlapping or complimentary patterns of flight and colonization by species within a feeding guild may lead to competition or resource partitioning respectively, with implications for local population levels (Rykiel et al. 1988, Flamm et al. 1993, Ayres et al. 2001).

Importantly, predatory beetles have been shown to have an influence on bark beetle colonization success in pine trees (Flamm et al. 1989). In the southeastern U.S., there is a diverse assemblage of predatory insects known to prey on subcortical beetle species and some exhibit a kairomonal response to subcortical beetle pheromones and host tree volatiles (Billings and Cameron 1984, Miller and Asaro 2023). Some predators have even shown the ability to partition prey resources through selective sensitivity to different prey species pheromones (Reeve et al. 2009), focusing their activity in areas of colonized trees where their specific prey is most abundant.

The high insect diversity of longleaf pine forests adds to the complexity involved in the vertical partitioning of dying trees. Given the interest in restoration of longleaf pine ecosystems, a better understanding of how insect assemblages associated with lightning-stuck trees are distributed vertically can aid our ability to manage for multiple goals, including biodiversity and regulation of bark beetle populations. We add to this knowledge by assessing vertical distribution of flight activity in response to simulated-lightning-struck longleaf pine trees. Specifically, this study addresses the following questions: 1) how is the flight activity of bark beetle species vertically distributed along the trees; 2) does this distribution correlate with patterns of successful bark beetle colonization; and 3) how is flight activity of species in other feeding guilds including ambrosia beetles, root feeding beetles, predators, and detritivores vertically distributed?

4.2 Materials and methods

4.2.1 Study location and tree selection

Our study was conducted on The Jones Center at Ichauway, an 11,741 ha property in Baker County, Georgia. It is comprised of longleaf and slash pine (*P. elliottii* Englemann) woodlands, old-field loblolly pine stands, mixed pine hardwoods, riparian hardwood forests, agricultural fields, and isolated depressional wetlands. Longleaf pine stands dominate the property and are the focus of our study. Much of the longleaf pine ecosystem at Ichauway has not been subjected to agricultural tilling and the trees are of multiple, mixed ages, ranging from new seedlings to over 100 years old. Prescribed fire and selective harvesting are used to manage these habitats, which are known to be some of the most biologically diverse areas in North America.

The stand in which our study took place is located near the center of the property (31.226591°N, -84.469767°W). This stand is characterized by moderate canopy closure of the predominant longleaf pines, scattered hardwood trees, an open midstory, and a highly diverse understory of native grasses, legumes, forbs and more. We selected eight longleaf pine trees that were approximately 20 m in height, and under 0.5 m diameter at breast height (DBH).

4.2.2 Lightning simulation and insect community sampling

We injured the trees artificially using explosives to mimic the physical trauma caused by lightning strike. We contracted an explosives expert (Controlled Blasting, Inc., Winder, Georgia) to conduct the detonation. The detonation was conducted with 164 grains/m detonating cord wrapped in a spiral configuration around each tree. This explosive cord contained a center core of pentaerythritol tetranitrate, a high explosive that detonates at approximately 7,010 m/sec. The explosion destroyed adjacent bark and phloem tissues, exposing the xylem underneath in many sections along the spiral and creating a localized cloud of bark and wood debris.

To evaluate insect flight activity adjacent to the tree trunks, we deployed a flight intercept trap array around five of the trees. We built cross-vane panel traps using plexiglass sheets attached to a Lindgren funnel trap base as described by Sheehan et al. (2019) (Figure 4.1a). We used paracord, metal clips, and a pulley system to hang the traps at four heights (0, 5, 10, and 15 m) along the trunks of the trees (Figure 4.1b). To simulate the attractiveness of a lightning struck host tree to insects, we did not bait the traps. Thus, insects found the trees aided only by the volatiles released from the trees after detonation. We used soapy water as collection fluid in the traps which we emptied and refilled every

Monday, Wednesday, and Friday, for the duration of the study during 14 May-30 July 2021. We stored insects from each sample collected in 75% ethanol before identifications.

We used emergence data to assess bark beetle colonization. We felled the three remaining trees once we saw signs of bark beetle infestation, 19 days post-detonation, and removed 1 m trunk sections at intervals matching the heights where flight intercept traps were hung. We placed each trunk section in an individual plywood rearing box measuring 0.5 m x 0.5 m x 1.2 m (*l* x *w* x *h*). The rearing boxes were housed at an on-site facility kept at a constant temperature of 21.11 °C and equipped with a 33-Liter 115-volt dehumidifier which operated continuously (Toshiba, Houston, USA). Each box was fitted with a collection device connected to a window near the top of the box (Figure 4.1c). We emptied the contents every Monday, Wednesday, and Friday, for the remaining duration of the study. We stored insects from each sample collected in 75% ethanol.

Bark beetles were the focus of the study, however, to characterize the insect assemblage associated with bark beetle colonization of lightning-struck trees, species of interest extended to all beetle taxa as well as predatory Hemipterans (Hemiptera: Anthocoridae, Lyctocoridae, and Rediviidae). Insects included in the study were identified using published keys (McNamara 1861, Horn 1873, Blanchard 1917, Liljeblad 1945, Valentine 1960, Campbell 1964, Herring 1966, Warner 1966, Halstead 1973, Herring 1976, Bright 1981, Wood 1982, Smetana 1990, Triplehorn 1990, Caterino 1999, Ohara and Mazur 2002, Leavengood 2008, Pollock 2012, Kolibáč 2013, Gomez et al. 2018, Klimaszewski et al. 2018, DiLorenzo et al. 2021, Mathison 2021, Schnepp and Anderson 2021), the reference collection at the Georgia Museum of Natural History at the University of Georgia, and with expert assistance from Rick Hoebeke (Associate Curator & Collection

Manager, Collection of Arthropods). For each sample, we recorded counts of all individuals of each identified species of interest.

4.2.3 Analysis of vertical distribution of insect assemblage

For each individual cross-vane panel trap and emergence box, we summed the data from all collection days. These cumulative catches were used for statistical analyses. For both flight intercept (n=5) and emergence data (n=3), our unit of replication was the individual tree. Height was used as categorical predictor variable in all analyses. For all of our statistical analyses in this study, we used R statistical software (version 3.5.1; R Core Team 2021).

To compare assemblage composition by height, we plotted cumulative trap catches by height categories using nonmetric multidimensional scaling (NMDS) and assessed differences using a permutational multivariate analysis of variance. NMDS functions by finding a non-parametric, monotonic relationship between the dissimilarity matrix and the Euclidean distances between data, and then arranging the points in a reduced-dimensional space (Cox and Cox 2000). We performed NMDS using the function *metaMDS* in the R package *vegan* to plot insect assemblage composition among heights. This assemblage matrix was generated based on cumulative catches from each trap over the course of the study. These cumulative, individual trap catches were then grouped by height category. Two-dimensional NMDS models comparing trap catches of insect assemblage composition converged at 362 iterations with a stress value of 0.113.

Following this, we performed a permutational multivariate analysis of variance (PERMANOVA) using functions from the package *vegan* to assess differences in insect assemblage between heights. We first calculated the ranked dissimilarity matrix using function *dist*. We then analyzed this using the function *adonis2*, a nonparametric test that uses a ranked dissimilarity matrix to evaluate differences in species assemblage from predefined groups of samples (Anderson 2001). Samples were grouped by height and blocked by tree. Finally, post-hoc pairwise comparisons between height categories were made using the function *pairwise.adonis2*. Significance of dissimilarity between height categories was evaluated at $\alpha < 0.05$.

For emergence data, we followed the procedures described above to compare assemblage composition by height using NMDS and a permutational multivariate analysis of variance. Two-dimensional NMDS models comparing trap catches of insect assemblage converged at 115 iterations with a stress value of 0.114. Significance of dissimilarity between height categories was evaluated at $\alpha < 0.05$.

4.2.4 Analysis of vertical distribution of individual species

In addition to community level analyses, we analyzed differences in cumulative trap catches by height for individual species. Representative species from several feeding guilds (bark beetles, root-feeding beetles, ambrosia beetles, predators, and detritivores) were selected for analyses. We selected species with substantial abundance ($n > 50$) in our samples and with known life history associations with bark beetle species' activity. Our data were not normally distributed and had non-homogenous variance. Hence, to determine if height had a significant effect on trap catches, we performed Kruskal-Wallis tests for each species using the function *kruskal.test* in the package *stats*. Following this, we performed Dunn's tests for each species to make post-hoc pairwise comparisons of trap catches between height categories. We used the function *dunnTest* in the package *FSA* and Dunn's test p-values were adjusted using the Benjamini-Hochberg method. Additionally, species richness by height was analyzed following the same statistical procedure. Finally, to analyze differences in insect emergence by height for individual species, we used Kruskal-Wallis and Dunn's tests.

The delay between tree death and arrival of insect species may give insight into what these species are responding to, either host tree characteristics or prey species activity. We integrated this factor into our analysis using a Generalized Additive Model (GAM). We used the *gam* function from the package *mgcv* to examine the nonlinear relationship between individual species trap catches and our explanatory variables: days-post-detonation, height category, and these variables interaction. The response variable (trap catches) followed a Poisson distribution, and smoothing parameters were selected using restricted maximum likelihood (REML).

4.3 Results

4.3.1 Vertical distribution of insect assemblage flight activity

Across the four heights (0, 5, 10, and 15 m), our flight intercept traps collected a total of 45,088 insects among 275 species (Table 4.1). Of these species, 266 were from the order Coleoptera and nine were from the order Hemiptera. As trap height increased, there was a statistically significant trend of decreasing species richness [Kruskal-Wallis χ^2 = 31.15, $p < 0.001$; Epsilon squared (rank) = 0.16, 95% CI (0.09, 1.00)] (Figure 4.2).

Results from the NMDS show that assemblage composition changed along the tree height (Figure 4.3). Cumulative trap catches clustered within height groups along a single axis (NMDS2). The groups were generally arranged along this axis with the same orientation they had along the height of the trees. Our PERMANOVA analysis further showed height to be a significant factor in insect assemblage composition ($F = 11.37$, $p < 0.001$). Post-hoc pairwise comparisons resolved significant differences between species assemblage for all height category pairs (Table 4.2).

4.3.2 Vertical distribution of individual species' flight activity

Bark beetle species showed varied patterns of vertical distribution along the height of the tree (Table 4.3; Figure 4.4). Of the 12 species of bark beetles collected, five species were found in great enough numbers for analysis ($n > 50$). Species with a trend of increasing trap catches as height increased included *Ips avulsus* (Eichhoff) [Kruskal-Wallis $\chi^2 = 13.15$, $p = 0.004$; Epsilon squared (rank) = 0.69, 95% CI (0.59, 1.00)], *I. grandicollis* (Eichhoff) [Kruskal-Wallis $\chi^2 = 9.03$, $p = .029$; Epsilon squared (rank) = 0.48, 95% CI (0.41, 1.00)] , and *Pityophthorus* spp. Eichhoff [Kruskal-Wallis $\chi^2 = 9.19$, $p = 0.027$; Epsilon squared (rank) = 0.48, 95% CI (0.28, 1.00)]. One species had significantly greater trap catches near the bottom of the trees, *Dendroctonus terebrans* (Olivier) [Kruskal-Wallis $\chi^2 = 39.88$, $p < 0.001$; Epsilon squared (rank) = 0.20, 95% CI (0.13, 1.00)]. There were no significant differences in trap catches by height for *I. calligraphus* (Germar).

Root-feeding beetles exhibited two patterns of vertical distribution along the height of the tree (Table 4.3; Figure 4.5). Of the five collected species of root-feeding beetles, four species were found in great enough numbers for analysis ($n > 50$). There were significantly greater trap catches near the bottom of trees for *Hylastes porculus* Erichson [Kruskal-Wallis $\chi^2 = 15.90$, $p = 0.001$; Epsilon squared (rank) = 0.84, 95% CI (0.81, 1.00)], *H. salebrosus* Eichhoff [Kruskal-Wallis $\chi^2 = 16.83$, $p < 0.001$; Epsilon squared (rank) = 0.89, 95% CI (0.86, 1.00)], and *H. tenuis* Eichhoff [Kruskal-Wallis $\chi^2 = 17.72$, $p < 0.001$; Epsilon squared (rank) = 0.93, 95% CI (0.92, 1.00)]. The root weevil *Pachylobius picivorus* (Germar) did not show significant differences in trap catches between heights.

Of the 18 species of ambrosia beetles collected, six species were found in great enough numbers for analysis ($n > 50$). Ambrosia beetles from the genera *Gnathotrichus*, *Myoplatypus* and *Xyleborus* exhibited a vertical distribution with greater trap catches near the bottom of trees (Table 4.3; Figure 4.6). *Gnathotrichus materiarius* (Fitch) [Kruskal-Wallis $\chi^2 = 15.87$, $p = 0.001$; Epsilon squared (rank) = 0.84, 95% CI (0.79, 1.00)]. *Myoplatypus flavicornis* (Fabricius) was trapped most often at 0 m and was rarely found at 10 m and 15 m [Kruskal-Wallis $\chi^2 = 14.66$, $p = .002$; Epsilon squared (rank) = 0.77, 95% CI (0.73, 1.00)]. Similarly, both *Xyleborus ferrugineus* (Fabricius) [Kruskal-Wallis $\chi^2 = 12.12$, $p = .007$; Epsilon squared (rank) = 0.64, 95% CI (0.57, 1.00)] and *X. pubescens* Zimmermann [Kruskal-Wallis $\chi^2 = 17.58$, $p < 0.001$; Epsilon squared (rank) = 0.93, 95% CI (0.90, 1.00)] were trapped most frequently at 0 m, with a pattern of reduced catches as tree height increased. However, *Ambrosiodmus minor* (Stebbing) and *Xyleborinus saxesenii* (Ratzeburg) showed no significant differences in trap catches between heights.

Seventeen known predators of bark beetles were analyzed. Of these, eight species showed no significant differences in trap catches between heights: *Corticeus parallelus* (Melsheimer), *Lasconotus pusillus* LeConte, *Lyctocoris elongatus* Reuter, *Platysoma cylindricum* (Paykull), *Plegaderus barbelini* Marseul, *Priocera castanea* (Newman), *Scoloposcelis flavicornis* Reuter, and *Temnoscheila virescens* (Fabricius) (Table 4.3). The other nine species exhibited varied patterns of vertical distribution (Table 4.3; Figure 4.7).

Species that were trapped significantly more often near the bottom of the tree included *Colydium nigripenne* LeConte [Kruskal-Wallis χ^2 = 13.36, p = 0.004; Epsilon squared (rank) = 0.70, 95% CI (0.65, 1.00)], *C. thoracicus* (Melsheimer) [Kruskal-Wallis χ^2 = 17.87, p < 0.001; Epsilon squared (rank) = 0.94, 95% CI (0.94, 1.00)], *Nudobius luridipennis* Casey [Kruskal-Wallis χ^2 = 7.98, p = 0.046; Epsilon squared (rank) = 0.42, 95% CI (0.25, 1.00)], *Platysoma parallelum* (Say) [Kruskal-Wallis χ^2 = 11.89, p = 0.008; Epsilon squared (rank) = 0.63, 95% CI (0.51, 1.00)], and *Plegaderus transversus* (Say) [Kruskal-Wallis χ^2 = 12.49, p = .006; Epsilon squared (rank) = 0.66, 95% CI (0.58, 1.00)]. Species trapped significantly more often near the top of the tree were *Aulonium tuberculatum* LeConte [Kruskal-Wallis χ^2 = 12.46, p = .006; Epsilon squared (rank) = 0.66, 95% CI (0.58, 1.00)], *Corticeus glaber* (LeConta) [Kruskal-Wallis χ^2 = 8.78, p = .032; Epsilon squared (rank) = 0.46, 95% CI (0.34, 1.00)], *Corticotomus cylindricus* (LeConte)[Kruskal-Wallis χ^2 = 12.15, p = .007; Epsilon squared (rank) = 0.64, 95% CI (0.50, 1.00)], and *Lasconotus referendarius* Zimmermann [Kruskal-Wallis χ^2 = 11.17, p = .011; Epsilon squared (rank) = 0.59, 95% CI (0.55, 1.00)].

Five species associated with dying pines, decaying wood, or fungi were also trapped in substantial numbers, with some showing correlations between trap catches and tree height (Table 4.3; Figure 4.8). Species found predominantly near the bottom of trees included *Colopterus unicolor* (Zieger) [Kruskal-Wallis χ^2 = 16.59, p < 0.001; Epsilon squared (rank) = 0.87, 95% CI (0.81, 1.00)], *Cossonus corticola* Say [Kruskal-Wallis χ^2 = 13.32, p = .004; Epsilon squared (rank) = 0.70, 95% CI (0.58, 1.00)], and *Oxylaemus americanus* LeConte [Kruskal-Wallis χ^2 = 13.45, p = .004; Epsilon squared (rank) = 0.71, 95% CI (0.65, 1.00)]. One species was associated with traps nearer to the top of trees, *Clypastraea fasciata* (Say) [Kruskal-Wallis χ^2 = 8.05, p = .045; Epsilon squared (rank) = 0.42, 95% CI (0.29, 1.00). *Arthrolips fasciata* (Erichson) showed no significant differences in trap catches between heights.

4.3.3 Vertical distribution of species and assemblage emergence

We collected 2,255 insects among 26 species that we were able to identify from the emergence boxes. NMDS for our emergence data showed largely overlapping groupings, although PERMANOVA showed a significant effect of height assemblage composition (R^2 = .798, F = 10.52, p = .007). However, post-hoc comparisons failed to resolve any differences between heights.

Only two species were captured in numbers high enough for statistical analysis, *I. calligraphus* (1,585 individuals) and *I. grandicollis* (221 individuals). *Ips calligraphus* showed a significant effect of height on cumulative emergence [Kruskal-Wallis χ^2 = 7.82, p = 0.049; Epsilon squared (rank) = 0.71, 95% CI (0.63, 1.00)], with significantly greater emergence at 0 m compared to 15 m. *Ips grandicollis* also showed a significant effect of height on cumulative emergence [Kruskal-Wallis χ^2 = 8.33, p = 0.04; Epsilon squared (rank) = 0.76, 95% CI (0.72, 1.00)], although post-hoc comparisons failed to resolve any differences between heights.

4.3.4 Vertical and temporal distribution of individual species' flight activity

Concerning the addition of time-since-detonation to our analysis of flight activity across height categories, we found a variety of flight activity patterns across space and time, and within each of the trophic groups (Table 4.4). In all but three of the 37 species analyzed, the interaction term was significant with most having a significance of $p < 0.001$. For those three species without a significant interaction term, *L. elongatus*, *O.americanus*, and *X. saxesenii*, the height and days-post-detonation factors were highly significant ($p < 0.001$).

The three *Ips* species and *Pityophthorus* spp. had the highest flight activity peaks at 15 m at around 30 days-post-detonation although these were often preceded by smaller peaks at lower heights suggesting initial attraction to the center of the tree trunk followed by increased activity at the top of the trees. In contrast, *D. terebrans* was found the earliest and had the highest peak at 0 m, while at other heights it showed a similar but far reduced flight activity pattern which decreased with increasing tree height category.

The four root feeding beetle species all had the earliest and highest flight activity at 0 meters at around 30 days-post-detonation and flight activity generally decreased with increasing height category. The three *Hylastes* species exhibited multiple flight activity peaks which were present at all height categories although this was most dramatic at 0 m. *Pachylobius picivorus* had reduced and delayed peaks with increasing height resulting in increasing delay of the peak at greater heights.

Ambrosia beetles tended to have slightly later peaks, around 40 days-post-detonation, in flight activity when compared to bark beetles and root feeding beetles. The exception to this was *A. minor*, which had its highest peak around 27 days-post-detonation. *Ambrosiodmus minor* also was unique in that it had a secondary delayed peak at 15 m around 65 days-post-detonation.

Predatory insects showed the most variation in their patterns of flight activity with some having peaks around 25 days-post-detonation, while other species' flight activity was still increasing as the experiment concluded. Additionally, this trophic group had species exhibiting their highest flight activity peaks at either 0, 5, 10, or 15 m height categories. This group also showed a variety of delay patterns in their activity at different heights. Some species were most active earlier at lower heights with their activity increasing up the tree with increasing days-post-detonation. Other species had an inverse flight activity pattern, arriving first at the top of the tree and moving downward over time. There were also species that had early flight activity peaks at the 5 m and 10 m height categories followed by peaks at the 0 m and 15 m height categories. This suggests an initial attraction to the middle of the tree, after which they moved toward the top and bottom of the tree.

Detritivore species had variable flight activity patterns with peaks ranging from 30 to 50 days-post-detonation. Further, these species showed initial and greatest flight activity at different heights. Although generally, these species showed the greatest flight activity at either the tops or bottoms of trees with reduced activity moving further from these height categories.

4.4 Discussion

Investigations into multispecies colonization of stressed or dying pine trees by subcortical beetles have focused on economically important beetle and host tree species. Here, we broaden this inquiry to include multiple feeding guilds and trophic levels within the assemblage of insects responding to lightning struck longleaf pine trees. Our findings include the following: 1) bark beetle species showed three distinct patterns of vertical distribution in their flight activity (species that were predominantly collected near the bottom, the top of the tree, and species that showed even distributions in flight activity between heights) in longleaf pine trees; 2) these patterns were present within other feeding guilds exploiting the tree resource; 3) predatory insects also exhibited multiple vertical distribution patterns; and 4) the assemblage of 275 insect species included in our study showed changes in its composition from the bottom of the trees to the top.

4.4.1 Vertical distribution of bark beetle species

In our assessment of bark beetle flight activity, we found multiple patterns of vertical distribution. Of the species showing significant differences in flight activity by height, three species occurred most often at the top of the tree and only one species occurred most often at the bottom. These findings align with previous studies that found phloem-feeders, including bark beetles, to be associated with the forest canopy in mixed hardwood and pine forests in Georgia (Sheehan et al. 2019). Moreover, the exception here, *D. terebrans* are known to attack mostly within 1 m of the soil line (Staeben et al. 2010), indicating a potential correlation between flight activity and colonization.

If cumulative bark beetle flight activity near a stressed tree prior to landing is correlated with colonization at different heights, the emergence data should follow patterns similar to flight activity. However, only two species emerged in numbers high enough for statistical analysis, *I. grandicollis* and *I. calligraphus*, and in both species the vertical distribution of flight activity and emergence were incongruent. Immediately after detonation, *I. calligraphus* was collected more than any other species and had by far the greatest emergence. Taken together, these observations indicate that the lack of emergence by the majority of species collected in flight traps could be due to felling the trees before many species had an opportunity to attack and colonize them, or that the emergence cages weren't the most conducive environments for emergence.

Moreover, in our flight data, *I. avulsus* was found most often at the 15 m height with decreasing numbers as height decreased and *I. calligraphus* had an even distribution at all heights. Studies of *I. avulsus* and *I. calligraphus* colonization of dying loblolly and shortleaf pine trees found similar patterns in gallery construction, where *I. avulsus* galleries dominated the upper bole while *I. calligraphus* galleries were evenly distributed along the height of the tree (Flamm et al. 1987, 1993). Additionally, Flamm et al. (1993) documented a correlation between the vertical distribution of bark beetle arrival density and successful colonization, further indicating that our emergence data may not reflect the complete colonization of the tree by later arriving species.

Despite the emergence data, it is possible that the multiple distributions of flight activity found here could still indicate a partitioning of the phloem resource by bark beetles. This result is consistent with studies of vertical resource partitioning by bark beetles in loblolly pine trees (Paine et al. 1981, Coulson et al. 1986, Ayres et al. 2001). Several hypotheses have been suggested to influence the vertical distribution of bark beetle species in colonized trees, including arrival order (Coulson et al. 1986) and seasonality (Coulson et al. 1986). Differences in our days-post-detonation flight activity data revealed that these species arrive in greater numbers earlier on at certain heights allowing for access to the phloem resource before potential competitors arrive in comparable numbers. Additionally, these temporal differences in flight activity between heights may indicate preferences for certain host characteristics such as optimal phloem thickness.

However, phloem thickness may confound the relationship between emergence and cumulative flight activity for some species by influencing their reproductive output (Haack et al. 1984, Slansky and Haack 1986, Haack et al. 1987a). For example, reproductive success for *I. calligraphus,* the largest of the three *Ips* species captured in this study, has been positively correlated with phloem thickness in slash pine (*Pinus elliottii* Engelmann var. *elliottii*) (Haack et al. 1984, Haack et al. 1987a, Haack et al. 1987b). Here, *I. calligraphus* showed an even distribution of flight activity at all heights but had significantly greater emergence from trunk sections at 0 m, where phloem is thickest. This could indicate that for some larger beetles, phloem thickness could influence the relationship between flight activity and reproductive success along the height of the tree.

Additional studies that collect both emergence data and flight activity data by height would be beneficial for testing the patterns found in this study. While studies of gallery construction are beneficial for assessing resource partitioning, emergence studies also provide a measure of reproductive success. However, both emergence and gallery construction data require destructive sampling methods. Flight activity data, on the other hand, not only allows for sampling over the full duration of tree death events but can also capture the full assemblage of species responding to stressed trees.

4.4.2 Comparing patterns of vertical distribution across feeding guilds

We found that species richness was highest at the bottom of trees and decreased with increasing trap height. We also observed a significant change in community composition along the same height gradient. This may be in part due to differences in the volume of colonizable host material between the bottoms and tops of our study trees.

Greater host volume at a given height would seem to support greater numbers of both species and total numbers of insects captured in our lowest traps.

All four of the ambrosia beetle species showing significant differences in flight activity occurred most often at the bottom of trees. This pattern may be explained by ambrosia beetles' symbiotic fungi growing better near the more humid forest floor (Sheehan et al. 2019). However, two species were evenly distributed along the height of the tree, indicating that there are likely multiple factors influencing ambrosia beetle flight distribution. Moreover, both patterns were found by Sheehan et al. (2019), however, other studies found opposite trends in some circumstances (Prochazka et al. 2018). Root-feeding beetles exhibited similar patterns as ambrosia beetles, which could be explained by their life history strategies. Additionally, root-feeding beetles and ambrosia beetles inhabit separate tree tissues, phloem and xylem respectively, which may allow for greater overlap in their activity at lower heights.

Despite the general patterns found here, with bark beetles concentrated near the tops of trees and ambrosia beetles near the bottom, there were exceptions at the species level. This is consistent with studies of beetle flight activity which assert that generalizations based on feeding guilds may mask contrasting patterns of vertical distribution exhibited by guild members (Sheehan et al. 2019). As a result, our study also illustrates the benefit of trapping at multiple heights for bark beetle detection (Sheehan et al. 2019, Ulyshen and Sheehan 2019) and in studies of species richness (Holdsworth et al. 2016, Prochazka et al. 2018).

We also found patterns of vertical stratification in many of the species captured in this study known to prey upon bark beetles (Smith and Goyer 1980, Goyer and Smith

1981). Like the tree colonizing species, some predatory species were distributed either higher or lower, while others showed an even distribution along the height of the trees. Moreover, within a single genus of predatory beetles, *Corticeus*, we found all three patterns, further indicating that species-level analysis may provide a more complete picture of vertical distributions. Across predators, these patterns could potentially be explained by a combination of predator-predator and predator-prey interactions.

Vertical stratification of predators could result in both reduced competition between predators for prey species as well as reduced intraguild predation. Interactions between known bark beetle predators, such as *Thanasimus dubius* (Fabricius) and *T. virescens*, have been shown to result in intraguild predation (Chism 2013), meaning that vertical stratification of predators might reduce such pressure. Additionally, the stratification of predators could reduce competition through a vertical partitioning of the prey resource. Competition could also be reduced through prey specialization. The ability of predatory beetle species to detect and respond to subcortical beetle pheromones is well supported (Erbilgin and Raffa 2001, Costa 2010). As a result, the patterns of predator distribution could be in response to the vertical distribution of subcortical beetle species colonizing the dying pine trees. Predators who exhibit a kairomonal response to specific subcortical beetles' pheromones may have patterns of vertical distribution resembling that of their specific prey, including an even distribution along the height of a tree. Alternatively, even patterns of vertical distribution could indicate generalist predatory strategies.

In addition to predatory beetles, we also identified nine known Hemipteran predators of bark beetles (Table 4.1). Of these species, two were found in high enough numbers to analyze: *L. elongatus* and *S. flavicornis,* which both had even distributions along the height of the trees. *Scoloposcelis flavicornis* is known to consume *I. grandicollis* eggs, larvae, and pupae. Additionally, a congener of *S. flavicornis, S mississippiensis*, was also found to prey on other bark beetle predators and cannibalize conspecifics (Schmitt and Goyer 1983). As a result, the even distribution of *S. flavicornis* may suggest a generalist predatory strategy.

Detritivores also showed three patterns of vertical distribution with most species distributed near the bottoms of trees. One species in particular, *C. corticola*, was the most numerous of all species in our study. While these beetles may not compete with subcortical insects for phloem or xylem, they may serve as an abundant prey resource for predators.

4.5 Conclusions

Studying the entire beetle assemblage responding to tree colonization events may shed light on how longleaf pine forests support such a high biodiversity of insect species. While we cannot speak to the causality of these patterns in our data, they provide a compelling framework for future research. First, a revisiting of our associated emergence study would clarify the relationship between flight activity and colonization success for subcortical beetle species. Additionally, analysis of predatory species sensitivity to specific subcortical beetle species' pheromones would support specialization of predators with congruent flight distributions to their prey. Behavioral assays of predator species interactions on trees could provide evidence of intraguild predation or avoidance between species, two mechanisms for prey resource partitioning. Further, both arrival order and seasonality have been shown to influence the distribution of tree colonizing species. These temporal aspects likely play an important role in vertical distributions due to differences in available resources for species who arrive first versus later on in the colonization process. Subcortical beetles have been shown to have distinct population peaks throughout the year, which would lead to variable proportions of beetle species aggregating around lightning struck trees at different times of year. Moreover, it is likely that several of these factors are concurrently responsible for the patterns we see in vertical distribution, and their respective magnitudes of effects would be of interest.

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4.7 References

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. Austral ecology 26: 32-46.

Anderson, N. H., and D. B. Anderson. 1968. *Ips* bark beetle attacks and brood development on a lightning-struck pine in relation to its physiological decline. Fla. Entomol.: 23-30.

Ayres, B. D., M. P. Ayres, M. D. Abrahamson, and S. A. Teale. 2001. Resource partitioning and overlap in three sympatric species of *Ips* bark beetles (Coleoptera : Scolytidae). Oecologia 128: 443-453.

Bentz, B. J., J. Régnière, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negrón, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. BioScience 60: 602-613.

Billings, R. F., and R. S. Cameron. 1984. Kairomonal responses of Coleoptera, *Monochamus titillator* (Cerambycidae), *Thanasimus dubius* (Cleridae), and *Temnochila virescens* (Trogositidae), to behavioral chemicals of southern pine bark beetles (Coleoptera: Scolytidae). Environ. Entomol. 13: 1542-1548.

Blanchard, F. 1917. Revision of the Throscidae of North America (Coleoptera). Transactions of the American Entomological Society (1890-) 43: 1-26.

Blanche, C., J. Hodges, and T. Nebeker. 1985. Changes in bark beetle susceptibility indicators in a lightning-struck loblolly pine. Can. J. For. Res. 15: 397-399.

Bright, D. E. 1981. Taxonomic monograph of the genus *Pityophthorus* Eichhoff in north and central America (Coleoptera: Scolytidae). The Memoirs of the Entomological Society of Canada 113: 1-378.

Campbell, J. M. 1964. A revision of the genus *Lobopoda* (Coleoptera: Alleculidae) in North America and the West Indies, University of Illinois at Urbana-Champaign.

Caterino, M. S. 1999. Taxonomy and phylogeny of the *Hister servus* group (Coleoptera: Histeridae): a Neotropical radiation. Systematic Entomology 24: 351-376.

Chism, S. B. 2013. Functional response of *Temnochila virescens*, effect of competition with *Thanasimus dubius* on adult *Ips grandicollis* survival, and determination of pheromone preference types. 1548889 M.S., Southern Illinois University at Carbondale Ann Arbor.

Costa, A. J.-B. 2010. Aggregation, dispersal and edge behavior of the bark beetle predator *Thanasimus dubius* (Coleoptera: Cleridae); potential use in biological control. 3408624 Ph.D., Southern Illinois University at Carbondale Ann Arbor.

Coulson, R., P. Hennier, R. Flamm, E. Rykiel, L. Hu, and T. Payne. 1983. The role of lightning in the epidemiology of the Southern Pine Beetle. Zeitschrift für angewandte Entomologie 96: 182-193.

Coulson, R., R. Flamm, T. Wagner, E. Rykiel, P. Sharpe, T. Payne, and S. Lin. 1985. Population dynamics of initiation and growth of southern pine beetle infestations.

Coulson, R. N., R. O. Flamm, P. E. Pulley, T. L. Payne, E. J. Rykiel, and T. L. Wagner. 1986. Response of the southern pine bark beetle guild (Coleoptera: Scolytidae) to host disturbance. Environ. Entomol. 15: 850-858.

Cox, T. F., and M. A. Cox. 2000. Multidimensional scaling, CRC press.

DiLorenzo, C. L., G. S. Powell, A. R. Cline, and J. V. McHugh. 2021. Carpophiline-ID: an interactive matrix-based key to the carpophiline sap beetles (Coleoptera, Nitidulidae) of Eastern North America. ZooKeys 1028: 85.

Erbilgin, N., and K. F. Raffa. 2001. Kairomonal range of generalist predators in specialized habitats: responses to multiple phloeophagous species emitting pheromones vs. host odors. Entomol. Exp. Appl. 99: 205-210.

Flamm, R., R. Coulson, P. Beckley, P. Pulley, and T. Wagner. 1989. Maintenance of a phloem-inhabiting guild. Environ. Entomol. 18: 381-387.

Flamm, R. O., P. E. Pulley, and R. N. Coulson. 1993. Colonization of disturbed trees by the southern pine bark beetle guild (Coleoptera, Scolytidae). Environ. Entomol. 22: 62-70.

Flamm, R. O., S. P. Cook, T. L. Wagner, P. E. Pulley, and R. N. Coulson. 1987. Reamergence and emergence of *Ips avulsus* and *Ips calligraphus* (Coleoptera: Scolytidae). Environ. Entomol. 16: 869-876.

Frost, C. 2006. History and future of the longleaf pine ecosystem. The longleaf pine ecosystem: ecology, silviculture, and restoration 438: 9-42.

Gomez, D. F., R. J. Rabaglia, K. E. Fairbanks, and J. Hulcr. 2018. North American Xyleborini north of Mexico: a review and key to genera and species (Coleoptera, Curculionidae, Scolytinae). ZooKeys: 19.

Goyer, R. A., and M. T. Smith. 1981. The feeding potential of *Corticeus glaber* and *Corticeus parallelus* (Coleoptera: Tenebrionidae), facultative predators of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). The Canadian Entomologist 113: 807-811.

Haack, R. A., R. C. Wilkinson, and J. L. Foltz. 1987a. Plasticity in life-history traits of the bark beetle *Ips calligraphus* as influenced by phloem thickness. Oecologia 72: 32-38.

Haack, R. A., R. C. Wilkinson, J. L. Foltz, and J. A. Corneil. 1984. Gallery construction and oviposition by *Ips calligraphus* (Coleoptera Scolytidae) in relation to slash pine phloem thickness and temperature. Can. Entomol. 116: 625-632.

Haack, R. A., R. C. Wilkinson, J. L. Foltz, and J. A. Corneil. 1987b. Spatial attack pattern, reproduction, and brood development of *Ips calligraphus* (Coleoptera: Scolytidae) in relation to slash pine phloem thickness, a field-study. Environ. Entomol. 16: 428-436.

Halstead, D. G. H. 1973. A revision of the genus *Silvanus* Latreille (sl)(Coleoptera: Silvanidae).

Herring, J. L. 1966. The genus *Orius* of the western hemisphere (Hemiptera: Anthocoridae). Ann. Entomol. Soc. Am. 59: 1093-1109.

Herring, J. L. 1976. Keys to genera of Anthocoridae of America North of Mexico, with description of a new genus (Hemiptera: Heteroptera). Fla. Entomol.: 143-150.

Hodges, J. D., and L. S. Pickard. 1971. Lightning in ecology of southern pine beetle, *Dendroctonus frontalis* (Coleoptera - Scolytidae). Can. Entomol. 103: 44-&.

Holdsworth, S., P. M. Hammond, and P. Eggleton. 2016. Assessing high compositional differences of beetle assemblages across vertical woodland strata in the New Forest, Hampshire, England. Journal of Natural History 50: 2477-2485.

Horn, G. H. 1873. Synopsis of the Histeridae of the United States. Proceedings of the American Philosophical Society: 273-360.

Hornslein, N. J., C. M. Siegert, and H. J. Renninger. 2019. Changes in physiological functioning in loblolly pine trees undergoing bark beetle simulated mortality. For. Sci. 65: 312-323.

Kaeser, M. J., and L. K. Kirkman. 2009. Estimating total plant species richness in depressional wetlands in the longleaf pine ecosystem. Wetlands 29: 866-874.

Kirkman, L., L. Giencke, R. Taylor, L. Boring, C. Staudhammer, and R. Mitchell. 2016. Productivity and species richness in longleaf pine woodlands: resource-disturbance influences across an edaphic gradient. Ecology 97: 2259-2271.

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

Klimaszewski, J., R. P. Webster, D. W. Langor, A. Brunke, A. Davies, C. Bourdon, M. Labrecque, A. F. Newton, J.-A. Dorval, and J. H. Frank. 2018. Key to tribes of Aleocharinae occurring in eastern Canada. Aleocharine Rove Beetles of Eastern Canada (Coleoptera, Staphylinidae, Aleocharinae): A Glimpse of Megadiversity: 59-71.

Kolibáč, J. 2013. Trogossitidae: A review of the beetle family, with a catalogue and keys. ZooKeys: 1.

Leavengood, J. M. 2008. The checkered beetles (Coleoptera: Cleridae) of Florida. University of Florida Gainesville.

Liljeblad, E. 1945. Monograph of the family Mordellidae (Coleoptera) of North America, north of Mexico.

Lovelady, C. N., P. E. Pulley, R. N. Coulson, and R. O. Flamm. 1991. Relation of lightning to herbivory by the southern pine bark beetle guild (Coleoptera, Scolytidae). Environ. Entomol. 20: 1279-1284.

Mathison, B. A. 2021. Click beetles (Coleoptera: Elateridae) of the southeastern United States, Florida State Department of Agriculture and Consumer Services.

McNamara, J. 1861. Family Curculionidae: snout beetles or weevils. Checklist of beetles of Canada and Alaska. Edited by Y. Bousquet. Agriculture Canada Publication: 329-356.

McNichol, B. H., C. R. Montes, B. F. Barnes, J. T. Nowak, C. Villari, and K. J. K. Gandhi. 2019. Interactions between southern *Ips* bark beetle outbreaks, prescribed fire, and loblolly pine (*Pinus taeda* L.) mortality. For. Ecol. Manage. 446: 164-174.

Miller, D. R., and C. Asaro. 2023. Predators attracted to combination of bark beetle pheromones and host kairomones in pine forests of southeastern United States. Environ. Entomol. 52: 787-794.

Miller, M. C. 1983. Lightning strike simulation for studying southern pine bark and engraver beetle attacks, vol. 296, US Department of Agriculture, Forest Service, Southern Forest Experiment Station.

Ohara, M., and S. Mazur. 2002. A revision of the genera of the tribe Platysomatini (Coleoptera, Histeridae, Histerinae) part 4: Redescriptions of the type species of *Heudister*, *Playsoma*, *Cylister*, *Cylistus*, *Nicotikis*, *Mesostrix* and *Desbordesia*. Insecta matsumurana. New series: journal of the Faculty of Agriculture Hokkaido University, series entomology. 59: 1-28.

Paine, T. D., M. C. Birch, and P. Švihra. 1981. Niche breadth and resource partitioning by four sympatric species of bark beetles (Coleoptera: Scolytidae). Oecologia 48: 1-6.

Peet, R. K. 2006. Ecological classification of longleaf pine woodlands. The longleaf pine ecosystem: 51-93.

Pollock, D. A. 2012. Review of the Eustrophinae (Coleoptera, Tetratomidae) of America north of Mexico. ZooKeys: 1.

Prochazka, J., L. Cizek, and J. Schlaghamersky. 2018. Vertical stratification of scolytine beetles in temperate forests. Insect. Conserv. Divers. 11: 534-544.

Provencher, L., A. R. Litt, and D. R. Gordon. 2003. Predictors of species richness in northwest Florida longleaf pine sandhills. Conserv. Biol. 17: 1660-1671.

Raffa, K. F., J.-C. Gregoire, and B. S. Lindgren. 2015. Natural history and ecology of bark beetles, pp. 1-40, Bark beetles. Elsevier.

Reeve, J. D., B. L. Strom, L. K. Rieske, B. D. Ayres, and A. Costa. 2009. Geographic variation in prey preference in bark beetle predators. Ecol. Entomol. 34: 183-192.

Ritger, H. M. W., S. T. Brantley, K. D. Klepzig, and K. J. K. Gandhi. 2023. Differential effects of fire regime and site conditions on bark beetles (Coleoptera: Curculionidae) in a longleaf pine (*Pinus palustris* Mill.) ecosystem. For. Ecol. Manage. 549: 13.

Rykiel, E. J., R. N. Coulson, P. J. Sharpe, T. F. Allen, and R. O. Flamm. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomenon. Landscape ecology 1: 129-139.

Schmitt, J. J., and R. A. Goyer. 1983. Consumption rates and predatory habits of *Scoloposcelis mississippensis* and *Lyctocoris elongatus* (Hemiptera: Anthocoridae) on pine bark beetles. Environ. Entomol. 12: 363-367.

Schnepp, K. E., and R. S. Anderson. 2021. *Phaenomerus foveipennis* (Morimoto)(Coleoptera: Curculionidae: Conoderinae) in the Southeastern USA. The Coleopterists Bulletin 75: 310-312.

Schowalter, T. D. 2012. Ecology and management of bark beetles (Coleoptera: Curculionidae: Scolytinae) in southern pine forests. J. Integr. Pest Manag. 3: 7.

Sheehan, T. N., and K. D. Klepzig. 2022. Arthropods and fire within the biologically diverse longleaf pine ecosystem. Ann. Entomol. Soc. Am. 115: 69-94.

Sheehan, T. N., M. D. Ulyshen, S. Horn, and E. R. Hoebeke. 2019. Vertical and horizontal distribution of bark and woodboring beetles by feeding guild: is there an optimal trap location for detection? J. Pest Sci. 92: 327-341.

Slansky, F., and R. A. Haack. 1986. Age-specific flight behavior in relation to body-weight and lipid-content of *Ips calligraphus* reared in slash pine bolts with thick or thin inner bark (phloem). Entomol. Exp. Appl. 40: 197-207.

Smetana, A. 1990. Revision of the Subfamily Xantholininae of America North of Mexico (Coleoptera: Staphylinidae). Supplementum 2. The Coleopterists' Bulletin: 83-87.

Smith, M. T., and R. A. Goyer. 1980. Relative abundance and seasonal occurrence of *Corticeus glaber* and *Corticeus parallelus* (Coleoptera: Tenebrionidae), associates of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). The Canadian Entomologist 112: 515-519.

Staeben, J. C., S. R. Clarke, and K. J. K. Gandhi. 2010. Black turpentine beetle, US Department of Agriculture, Forest Service, Pacific Northwest Region.

Taylor, A. R. 1974. Ecological aspects of lightning in forests, pp. 455-482. *In*, Proceedings of the Tall Timbers fire ecology conference.

Triplehorn, C. A. 1990. Review of the genus *Corticeus* (Coleoptera: Tenebrionidae) of America north of Mexico. Ann. Entomol. Soc. Am. 83: 287-306.

Ulyshen, M. D., and T. N. Sheehan. 2019. Trap height considerations for detecting two economically important forest beetle guilds in southeastern US forests. J. Pest Sci. 92: 253-265.

Valentine, B. D. 1960. The genera of the weevil family Anthribidae north of Mexico (Coleoptera). Transactions of the American Entomological Society (1890-) 86: 41-85.

Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: Implications for species at risk. For. Ecol. Manage. 211: 150-165.

Vogt, J. T., J. K. Gandhi, D. C. Bragg, R. Olatinwo, and K. D. Klepzig. 2020. Interactions between weather-related disturbance and forest insects and diseases in the southern United States, pp. 1-37. *In* U. D. o. Agriculture [ed.], Asheville, NC, USA.

Warner, R. E. 1966. A review of the *Hylobius* of North America, with a new species injurious to slash pine (Coleoptera: Curculionidae). The Coleopterists' Bulletin: 65-81.

Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph.

Yousuf, F., G. M. Gurr, A. J. Carnegie, R. A. Bedding, R. Bashford, and C. W. Gitau. 2014. Biology of the bark beetle *Ips grandicollis* Eichhoff (Coleoptera: Scolytinae) and its arthropod, nematode and microbial associates: a review of management opportunities for Australia. Austral Entomol. 53: 298-316.

Table 4.1 List of insect orders, families, subfamilies, and species identified from traps suspended at four heights in five simulated-lightning-struck longleaf pine trees during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

				Total catches				
Order	**Family**	**Subfamily**	**Species**	**0m**	**5m**	**10m**	**15m**	**Total**
Coleoptera	Aderidae		*Aderus brunnipennis* (LeConte)	6	21	8	4	39
			Cnopus impressus LeConte	3	7	3	9	22
	Anthicidae	Anthicinae	*Acanthinus argentinus* Pic	0	0	0	1	1
		Notoxinae	*Notoxus murinipennis* LeConte	0	0	1	0	1
	Anthribidae	Anthribinae	*Euparius marmoreus* (Olivier)	1	1	2	2	6
			Eusphyrus walshii LeConte	0	0	1	0	1
	Attelabidae	Attelabinae	*Homoeolabus analis* (Illiger)	0	2	1	0	3
	Biphyllidae		*Diplocoelus rudis* (LeConte)	8	2	0	0	10
	Bostrichidae	Bostrichinae	*Xylobiops basilaris* (Say)	3	0	0	0	3
		Dinoderinae	*Stephanopachys densus* (LeConte)	3	0	0	0	3
			Stephanopachys rugosus (Olivier)	9	14	9	4	36
		Mesocoelopodinae	*Mesocoelopus collaris* Mulsant & Rey	0	0	1	0	1
			Tricorynus sp. Waterhouse	13	22	16	29	80
	Bothrideridae		*Bothrideres geminatus* (Say)	0	2	0	1	3
			Bothrideres sp. Dejean	0	0	1	0	1
	Buprestidae	Buprestinae	*Buprestis lineata* Fabricius	2	1	2	0	5
			Buprestis maculipennis Gory	0	1	0	0	1
			Chalcophora virginiensis (Drury)	4	0	1	0	5
			Chrysobothris pusilla Gory & Laporte	0	2	0	0	2
		Polycestinae	*Mastogenius subcyaneus* (LeConte)	0	1	0	0	1
	Carabidae	Harpalinae	*Coptodera aerata* Dejean	4	5	2	0	11
			Selenophorus palliatus Fabricius	5	2	0	0	7
			Somotrichus unifasciatus (Dejean)	1	0	3	4	8
		Trechinae	*Mioptachys flavicauda* (Say)	7	6	6	1	20
			Tachyta inornata (Say)	5	0	2	1	8

Cerambycidae	Cerambycinae	*Enaphalodes atomarius* (Drury)	1	0	0	1	2
		Neoclytus scutellaris (Olivier)	1	0	0	1	2
		Obrium maculatum (Olivier)	8	0	0	0	8
		Smodicum cucujiforme (Say)	1	0	0	0	1
		Xylotrechus sagittatus (Germar)	43	33	24	34	134
	Lamiinae	*Acanthocinus nodosus* (Fabricius)	20	1	1	2	24
		Acanthocinus obsoletus (Olivier)	27	11	25	26	89
		Astylopsis arcuata (LeConte)	1	2	6	16	25
		Astylopsis collaris (Haldeman)	0	2	0	0	2
		Astylopsis perplexa (Haldeman)	0	0	0	1	1
		Astylopsis sexguttata (Say)	3	3	2	0	8
		Ecyrus dasycerus (Say)	1	0	0	0	1
		Eupogonius pauper LeConte	0	0	1	0	1
		Eupogonius tomentosus (Haldeman)	1	0	0	3	4
		Eutrichillus biguttatus (LeConte)	0	5	12	7	24
		Monochamus titillator (Fabricius)	10	9	30	64	113
	Prioninae	*Mallodon dasystomus* (Say)	0	0	1	0	1
		Prionus pocularis Dalman	15	0	0	0	15
	Spondylidinae	*Arhopalus rusticus* (Linnaeus)	11	0	0	2	13
		Asemum striatum (Linnaeus)	4	4	0	0	8
		Scaphinus muticus (Fabricius)	3	2	0	2	7
Cerylonidae	Ceryloninae	*Cerylon unicolor* (Zieger)	5	4	2	7	18
		Philothermus puberulus Schwarz	0	1	0	0	1
Chrysomelidae	Eumolpinae	*Colaspis* sp. Fabricius	0	0	1	2	3
		Demotina modesta Baly	0	0	1	0	1
		Metachroma pellucidum Crotch	3	0	1	1	5
		Paria sp. LeConte	1	0	0	0	1
Ciidae	Ciinae	*Octotemnus* sp. Mellié	1	0	1	0	2
Cleridae	Clerinae	*Priocera castanea* (Newman)	54	52	43	30	179
		Thanasimus dubius (Fabricius)	0	0	1	1	2

	Epiphloeinae	*Pyticeroides laticornis* (Say)	0	1	0	0	1
	Hydnocerinae	*Phyllobaenus verticalis* (Say)	0	2	0	0	2
	Orthopleurinae	*Neorthopleura thoracica* (Say)	2	1	2	0	5
	Peloniinae	*Cregya oculata* (Say)	0	1	0	0	1
	Tillinae	*Cymatodera inornata* (Say)	0	0	1	0	1
Coccinellidae	Coccinellinae	*Harmonia axyridis* (Pallas)	0	2	0	0	2
	Scymninae	*Diomus myrmidon* (Mulsant)	0	0	0	2	2
		Scymnus sp. Kugelann	1	0	0	1	2
Corylophidae		*Arthrolips decolor* LeConte	4	11	12	5	32
		Arthrolips fasciata (Erichson)	58	73	92	68	291
		Arthrolips misella LeConte	7	8	5	2	22
		Clypastraea fasciata (Say)	10	44	44	95	193
		Clypastraea lunata (LeConte)	0	4	9	20	33
		Sericoderus sp. Stephens	1	2	1	0	4
Cryptophagidae	Cryptophaginae	*Caenoscelis basalis* Casey	0	0	0	1	1
Curculionidae	Conoderinae	*Phaenomerus foveipennis* (Morimoto)	4	9	1	4	18
	Cossoninae	*Acamptus rigidus* LeConte	1	0	0	0	1
		Cossonus corticola Say	4,999	4,735	2,548	1,062	13,344
		Stenoscelis andersoni Buchanan	0	7	1	2	10
		Stenoscelis brevis (Boheman)	0	2	4	2	8
	Cryptorhynchinae	*Apteromechus ferratus* (Say)	2	0	0	0	2
		Acalles minutissimus (LeConte)	0	1	0	0	1
	Dryophthorinae	*Sitophilus zeamais* Motschulsky	1	2	2	1	6
	Entiminae	*Pandeleteius hilaris* (Herbst)	0	0	1	0	1
	Molytinae	*Hylobius pales* (Herbst)	6	0	1	2	9
		Pachylobius picivorus (Germar)	194	88	105	67	454
	Platypodinae	*Myoplatypus flavicornis* (Fabricius)	169	29	4	2	204
	Scolytinae	*Ambrosiodmus lecontei* Hopkins	6	0	1	0	7
		Ambrosiodmus minor (Stebbing)	94	63	56	89	302
		Ambrosiodmus rubricollis (Eichhoff)	2	0	0	0	2

	Ambrosiophilus atratus Eichhoff	1	0	0	0	1
	Cnestus mutilatus (Blandford)	0	1	6	1	8
	Coccotrypes carpophagus (Hornung)	0	0	0	2	2
	Crypturgus alutaceus Schwarz	4	15	23	14	56
	Dendroctonus terebrans (Olivier)	1,234	262	148	56	1,700
	Dryoxylon onoharaense (Murayama)	1	1	1	0	3
	Gnathotrichus materiarius (Fitch)	372	78	28	13	491
	Hylastes porculus Erichson	218	74	16	6	314
	Hylastes salebrosus Eichhoff	1,411	242	44	21	1,718
	Hylastes tenuis Eichhoff	329	131	22	7	489
	Hypothenemus sp. Westwood	3	2	0	0	5
	Ips avulsus (Eichhoff)	8	21	40	121	190
	Ips calligraphus (Germar)	257	329	311	677	1,574
	Ips grandicollis (Eichhoff)	52	186	191	211	640
	Monarthrum fasciatum (Say)	3	0	1	0	4
	Monarthrum mali (Fitch)	3	11	4	2	20
	Orthotomicus caelatus (Eichhoff)	27	19	0	0	46
	Pityoborus comatus (Zimmermann)	1	1	1	0	3
	Pityophthorus spp. Eichhoff	80	241	136	655	1,112
	Pseudopityophthorus sp. Swaine	1	0	0	0	1
	Scolytus multistriatus (Marsham)	1	0	0	0	1
	Xyleborinus saxesenii (Ratzeburg)	52	27	28	12	119
	Xyleborus affinis Eichhoff	2	0	0	0	2
	Xyleborus ferrugineus (Fabricius)	841	271	163	81	1,356
	Xyleborus pubescens Zimmermann	3,015	936	358	144	4,453
	Xylosandrus amputatus (Blandford)	0	1	0	0	1
	Xylosandrus compactus (Eichhoff)	1	0	0	0	1
	Xylosandrus crassiusculus (Motschulsky)	60	4	0	0	64
	Xylosandrus germanus (Blandford)	0	0	0	1	1
Dermestidae	*Trogoderma* sp. Berthold	0	1	0	0	1

Elateridae	Agrypninae	*Alaus myops* (Fabricius)	1	0	0	0	1
		Lacon impressicollis (Say)	0	1	0	0	1
		Pherhimius fascicularis (Fabricius)	1	0	0	0	1
	Cebrioninae	*Selonodon* sp. Latreille	1	0	0	0	1
	Dendrometrinae	*Hemicrepidius bilobatus* (Say)	3	0	0	2	5
	Elaterinae	*Blauta cribraria* (Germar)	0	1	0	0	1
		Dicrepidius palmatus Candèze	10	18	13	10	51
		Dipropus soleatus (Say)	9	2	2	2	15
		Glyphonyx bimarginatus Schaeffer	2	0	0	0	2
		Glyphonyx ferruginosus Schaeffer	6	1	1	0	8
		Megapenthes rufilabris (Germar)	11	1	1	2	15
		Melanotus communis (Gyllenhal)	0	0	0	1	1
		Melanotus decumanus (Erichson)	1	0	0	0	1
		Melanotus ignobilis Melsheimer	5	2	2	1	10
		Melanotus insipiens (Say)	0	0	1	0	1
		Melanotus spadix (Erichson)	3	2	0	3	8
	Lissominae	*Drapetes exstriatus* (Say)	1	12	1	2	16
		Drapetes quadripustulatus Bonvouloir	0	1	0	0	1
		Drapetes rubricollis LeConte	1	0	0	0	1
Endomychidae	Epipocinae	*Epipocus punctatus* LeConte	2	0	0	0	2
	Merophysiinae	*Holoparamecus depressus* Curtis	0	0	1	0	1
Erotylidae	Xenocelinae	*Cryptophilus integer* (Heer)	1	0	0	0	1
Eucnemidae	Eucneminae	*Dendrocharis* sp. Guérin-Méneville	2	0	0	0	2
	Macraulacinae	*Dromaeolus striatus* (LeConte)	1	4	1	2	8
		Fornax sp. Laporte	1	0	0	0	1
		Nematodes atropos (Say)	1	3	3	4	11
	Melasinae	*Dirrhagofarsus lewisi* (Fleutiaux)	1	0	0	0	1
		Dirrhagofarsus sp. Fleutiaux	1	0	0	1	2
		Microrhagus triangularis (Say)	0	1	0	0	1
Histeridae	Abraeinae	*Aeletes simplex* (LeConte)	6	0	0	0	6

		Plegaderus barbelini Marseul	54	40	31	17	142
		Plegaderus transversus (Say)	190	235	101	46	572
	Dendrophilinae	*Bacanius tantillus* LeConte	8	2	0	1	11
		Carcinops pumilio (Erichson)	1	1	1	0	3
		Paromalus seminulum Erichson	4	0	0	0	4
	Histerinae	*Hister defectus* LeConte	20	6	3	0	29
		Hister servus Erichson	7	8	1	0	16
		Platysoma cylindricum (Paykull)	75	87	51	91	304
		Platysoma parallelum (Say)	608	488	264	125	1,485
Hybosoridae	Ceratocanthinae	*Germarostes globosus* (Say)	1	2	0	2	5
Laemophloeidae		*Cryptolestes* sp. Ganglbauer	30	32	19	3	84
		Laemophloeus biguttatus Casey	3	4	1	1	9
		Lathropus robustulus Casey	1	0	0	0	1
		Lathropus vernalis LeConte	6	6	5	42	59
		Narthecius grandiceps LeConte	0	3	2	0	5
		Placonotus sp. Macleay	4	4	0	1	9
Latridiidae	Corticariinae	*Melanophthalma* sp. Motschulsky	22	13	15	23	73
Lycidae		*Plateros* sp. Bourgeois	0	4	2	1	7
Meloidae	Nemognathinae	*Nemognatha nemorensis* Hentz	1	0	0	0	1
Melyridae	Malachiinae	*Chaetocoelus setosus* LeConte	1	3	4	18	26
	Melyrinae	*Melyrodes cribrata* (LeConte)	2	0	0	0	2
Monotomidae	Monotominar	*Bactridium* sp. LeConte	1	2	0	0	3
Mordellidae		*Conalia helva* (LeConte)	7	5	10	10	32
		Glipodes sericans (Melsheimer)	12	1	0	0	13
		Hoshihananomia octopunctata (Fabricius)	2	0	0	0	2
		Mordella atrata Melsheimer	4	9	1	0	14
		Mordella marginata Melsheimer	6	18	15	5	44
		Mordellaria undulata (Melsheimer)	1	0	0	1	2
		Mordellistena fuscata (Melsheimer)	3	0	0	0	3
		Mordellistena liturata (Melsheimer)	0	3	3	1	7

		Mordellistena rufescens Smith	1	0	0	1	2
Murmidiidae		*Murmidius ovalis* (Beck)	4	1	3	2	10
		Mychocerinus depressus (LeConte)	0	1	0	0	1
Mycetophagidae		*Litargus balteatus* LeConte	6	8	4	3	21
		Litargus sexpunctatus (Say)	1	5	3	4	13
		Litargus tetrspilotus LeConte	0	1	1	4	6
Nitidulidae	Amphicrossinae	*Amphicrossus ciliatus* (Olivier)	0	1	0	0	1
	Carpophilinae	*Carpophilus dimidiatus* (Fabricius)	1	1	0	0	2
		Carpophilus sp. Stephens	0	2	0	0	2
	Cillaeinae	*Colopterus unicolor* Erichson	2,058	1,366	439	128	3,991
		Conotelus obscurus Erichson	21	33	4	4	62
	Epuraeinae	*Epuraea* sp. Erichson	0	1	0	0	1
	Nitidulinae	*Amphotis schwarzi* Ulke	1	0	0	1	2
		Pallodes sp. Erichson	1	0	0	0	1
		Phenolia grossa (Fabricius)	1	0	0	0	1
		Stelidota geminata (Say)	1	0	0	0	1
Passandridae		*Catogenus rufus* (Fabricius)	5	3	4	4	16
Phalacridae		*Ochrolitus rubens* (LeConte)	3	0	0	0	3
		Stilbus apicalis (Melsheimer)	0	1	1	0	2
Ptiliidae	Ptiliinae	*Ptinella* sp. Motschulsky	4	2	1	1	8
	Dorcatominae	*Byrrhodes intermedius* (LeConte)	0	1	1	0	2
		Petalium alaseriatum Ford	2	1	5	25	33
	Ernobiinae	*Ernobius granulatus* LeConte	0	0	0	2	2
	Ptininae	*Ptinus bimaculatus* Melsheimer	0	1	0	0	1
	Xyletininae	*Euvrilletta mucorea* (LeConte)	0	1	0	0	1
Scarabaeidae	Cetoniinae	*Trigonopeltastes delta* (Forster)	1	0	0	0	1
	Melolonthinae	*Diplotaxis* sp. Kirby	0	2	4	2	8
	Scarabaeinae	*Onthophagus concinnus* Laporte	1	0	0	0	1
Scraptiidae	Scraptiinae	*Canifa* sp. LeConte	0	0	1	0	1
Silvanidae	Silvaninae	*Ahasverus rectus* LeConte	50	15	14	4	83

		Cathartosilvanus imbellis LeConte	6	1	0	0	7
		Nausibius repandus LeConte	5	4	2	5	16
		Silvanus muticus Sharp	13	6	1	0	20
Sphindidae		*Sphindus americanus* LeConte	25	20	6	12	63
Staphylinidae	Aleocharinae	*Anacyptus testaceus* (LeConte)	9	0	0	1	10
		Homalota sp. Mannerheim	166	291	121	81	659
		Myrmecocephalus concinnus (Erichson)	0	2	0	0	2
		Myrmecocephalus gracilis (Verhoeff)	6	2	0	1	9
		Oligota sp. Mannerheim	63	26	21	6	116
		Oxypoda sp. Mannerheim	1	2	3	4	10
		Phloeopora sp. Erichson	5	16	8	6	35
		Placusa sp. Erichson	5	7	9	8	29
		Platystethus spiculus Erichson	0	2	2	0	4
	Osoriinae	*Nacaeus tenuis* (LeConte)	76	42	24	8	150
	Paederinae	*Rugilus angularis* (Erichson)	1	0	0	0	1
	Pselaphinae	*Batrisodes* sp. Reitter	1	0	0	0	1
		Euconnus sp. Thomson	2	0	0	0	2
	Scaphidiinae	*Baeocera* sp. Erichson	2	0	2	1	5
	Staphylininae	*Philonthus* sp. Stephens	0	0	0	1	1
	Tachyporinae	*Coproporus ventriculus* (Say)	0	2	0	0	2
		Sepedophilus crassus (Gravenhorst)	5	0	1	0	6
	Xantholininae	*Diochus schaumi* Kraatz	1	0	0	0	1
		Microlinus pusio (LeConte)	3	0	0	0	3
		Nudobius luridipennis Casey	33	21	9	13	76
Synchroidae		*Synchroa punctata* Newman	2	0	0	0	2
Tenebrionidae	Alleculinae	*Hymenorus* sp. Mulsant	8	13	14	3	38
		Lobopoda erythrocnemis (Germar)	4	5	2	5	16
		Lobopoda socia (LeConte)	0	0	1	8	9
	Diaperinae	*Corticeus glaber* (LeConte)	11	18	28	58	115
		Corticeus parallelus (Melsheimer)	50	63	40	56	209

		Corticeus thoracicus (Melsheimer)	1,153	216	98	14	1,481
		Platydema subcostata Laporte & Brullé	0	2	0	0	2
	Stenochiinae	*Alobates barbatus* (Knoch)	0	1	3	3	7
	Tenebrioninae	*Tribolium castaneum* (Herbst)	2	1	0	0	3
Terediddae		*Oxylaemus americanus* LeConte	27	18	12	1	58
Tetratomidae	Eustrophinae	*Eustrophopsis bicolor* (Fabricius)	11	5	1	7	24
Throscidae		*Aulonothroscus convergens* (Horn)	7	3	9	4	23
Trogossitidae	Trogossitinae	*Airora cylindrica* (Audinet-Serville)	0	2	0	0	2
		Corticotomus cylindricus (LeConte)	1	1	16	36	54
		Temnoscheila virescens (Fabricius)	18	13	20	26	77
		Tenebroides bimaculatus Melsheimer	3	2	0	1	6
		Tenebroides collaris (Sturm)	10	7	5	1	23
		Tenebroides semicylindricus (Horn)	2	1	1	2	6
Zopheridae	Colydiinae	*Aulonium ferrugineum* Zimmermann	1	2	7	2	12
		Aulonium tuberculatum LeConte	2	21	17	43	83
		Bitoma carinata (LeConte)	1	1	0	0	2
		Bitoma quadricollis (Horn)	2	1	3	0	6
		Bitoma quadriguttata (Say)	47	28	13	6	94
		Colydium lineola Say	9	9	3	4	25
		Colydium nigripenne LeConte	58	6	4	1	69
		Endeitoma granulata (Say)	4	1	1	4	10
		Lasconotus pusillus LeConte	53	96	72	78	299
		Lasconotus referendarius Zimmermann	72	454	548	588	1,662
		Lobogestoria gibbicollis Reitter	2	4	1	1	8
		Nematidium filiforme LeConte	1	1	0	0	2
		Paha laticollis (LeConte)	0	1	0	0	1
		Synchita fuliginosa Melsheimer	4	1	1	0	6
		Synchita parvula Guérin-Méneville	3	5	10	5	23
	Zopherinae	*Hyporhagus punctulatus* Thomson	326	144	152	191	813
		Pycnomerus haematodes (Fabricius)	6	3	3	0	12

			Pycnomerus sulcicollis LeConte	208	78	29	19	334
Hemiptera	Anthocoridae		*Calliodis temnostethoides* (Reuter)	2	1	2	2	7
			Dasyleistes assimilis (Reuter)	8	0	1	2	11
			Scoloposcelis flavicornis Reuter	41	68	57	134	300
			Xylocoris sp. DuFour	4	2	11	29	46
		Anthocorinae	*Orius insidiosus* (Say)	2	1	0	0	3
	Lyctocoridae		*Lyctocoris elongatus* Reuter	53	33	18	21	125
	Reduviidae		*Microtomus purcis* (Drury)	5	3	2	2	12
		Harpactorinae	*Apiomerus crassipes* (Fabricius)	0	1	3	3	7
			Rocconota annulicornis (Stål)	1	0	0	0	1
	Total abundance			**19,785**	**12,409**	**7,079**	**5,815**	**45,088**
	Total species			**207**	**183**	**160**	**150**	**275**

Table 4.2 Results of post-hoc Dunn’s tests comparing differences in species richness between four heights in five simulated-lightning-struck longleaf pine trees during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

Height pairings	F statistic	P value
0 m vs 5 m	4.92	0.015
0 m vs 10 m	13.57	0.004
0 m vs 15 m	27.12	0.007
5 m vs 10 m	4.54	0.045
5 m vs 15 m	15.31	0.012
10 m vs 15 m	3.45	0.049

Table 4.3 Results of Kruskal-Wallis tests to assess significance of height for species richness and individual species trap catches during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

Trophic guild	Species	d.f.	Kruskal-Wallis χ^2	P value
	Species richness	3	16.02	0.001
Bark beetles	*Dendroctonus terebrans*	3	15.78	0.001
	Ips avulsus	3	13.15	0.004
	Ips calligraphus	3	2.66	0.448
	Ips grandicollis	3	9.03	0.029
	Pityophthorus spp.	3	9.19	0.027
Root feeders	*Hylastes porculus*	3	15.89	0.001
	Hylastes salebrosius	3	16.83	<0.001
	Hylastes tenuis	3	17.72	<0.001
	Pachylobius picivorus	3	7.12	0.068
Ambrosia beetles	*Ambrosiodmus minor*	3	1.37	0.712
	Gnathotrichus materiarius	3	15.87	0.001
	Myoplatypus flavicornis	3	14.66	0.002
	Xyleborinus saxesenii	3	2.75	0.432
	Xyleborus ferrugineus	3	12.12	0.007
	Xyleborus pubescens	3	17.58	<0.001
Predators	*Aulonium tuberculatum*	3	12.46	0.006
	Colydium nigripenne	3	13.36	0.004
	Corticeus glaber	3	8.78	0.032
	Corticeus parallelus	3	3.14	0.371
	Corticeus thoracicus	3	17.87	<0.001
	Corticotomus cylindricus	3	12.15	0.007
	Lasconotus pusillus	3	1.81	0.612
	Lasconotus referendarius	3	11.17	0.011
	Lyctocoris elongatus	3	7.43	0.059
	Nudobius luridipennis	3	7.98	0.046
	Platysoma cylindricum	3	2.66	0.448
	Platysoma parallelum	3	11.89	0.008
	Plegaderus barbelini	3	6.45	0.092
	Plegaderus transversus	3	12.49	0.006
	Priocera castanea	3	1.21	0.751
	Scoloposcelis flavicornis	3	7.02	0.071
	Temnoscheila virescens	3	0.39	0.941
Detritivores	*Arthrolips fasciata*	3	2.24	0.524
	Clypastraea fasciata	3	8.05	0.045
	Colopterus unicolor	3	16.59	<0.001
	Cossonus corticola	3	13.32	0.004
	Oxylaemus americanus	3	13.45	0.004

Table 4.4 Results of General Additive Models to assess significance of height, days-post-detonation, and their interaction for individual species trap catches during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

				Height		Days post detonation		Interaction	
Trophic guild	Species	Deviance explained (%)	Adjusted R^2	EDF	P value	EDF	P value	EDF	P value
Bark beetles	*Dendroctonus terebrans*	79.9	0.63	2.8	0.002	5.7	0.004	11.3	<0.001
	Ips avulsus	55.2	0.32	1	0.733	7	<0.001	8.3	<0.001
	Ips calligraphus	60.9	0.37	2.9	<0.001	8	<0.001	16.3	<0.001
	Ips grandicollis	50.4	0.32	2.8	<0.001	7.7	<0.001	13.4	<0.001
	Pityophthorus spp.	60.1	0.24	2.8	<0.001	8.2	<0.001	16.5	<0.001
Root feeders	*Hylastes porculus*	56.8	0.36	1	0.182	5.9	0.077	3.4	0.004
	Hylastes salebrosius	67.9	0.35	2.5	0.236	5.7	0.192	11.1	<0.001
	Hylastes tenuis	57.8	0.46	2.4	0.004	7.9	<0.001	2.6	0.013
	Pachylobius picivorus	49.8	0.36	2.8	0.016	6.1	0.464	6.3	<0.001
Ambrosia beetles	*Ambrosiodmus minor*	21.6	0.09	2.2	0.041	6.1	0.659	5.2	<0.001
	Gnathotrichus materiarius	63.5	0.46	1.7	0.348	3.2	0.642	9.8	<0.001
	Myoplatypus flavicornis	63.6	0.39	1	0.34	1	0.73	7.8	<0.001
	Xyleborinus saxesenii	26	0.13	1	<0.001	7.7	<0.001	<0.001	0.529
	Xyleborus ferrugineus	62.9	0.5	2.6	0.006	6.9	0.002	7.5	<0.001
	Xyleborus pubescens	68.1	0.41	1	0.371	6.7	0.01	14.9	<0.001
Predators	*Aulonium tuberculatum*	52.5	0.27	2.7	0.059	1	0.964	5.9	<0.001
	Colydium nigripenne	50.3	0.24	1	0.335	3.9	0.943	5.3	0.004
	Corticeus glaber	41.7	0.19	1	0.933	3	0.788	6.8	<0.001
	Corticeus parallelus	28.2	0.17	1	0.805	1	0.66	8.1	<0.001
	Corticeus thoracicus	68.4	0.38	2.8	0.001	6.4	0.634	5.9	<0.001
	Corticotomus cylindricus	47.7	0.21	2.1	0.365	2.5	0.915	5.2	<0.001
	Lasconotus pusillus	52	0.32	2.1	0.738	7	<0.001	12.1	<0.001
	Lasconotus referendarius	72.4	0.44	2.5	0.058	8	<0.001	15.2	<0.001

	Lyctocoris elongatus	26.1	0.15	1.5	<0.001	5.5	<0.001	0.002	0.349
	Nudobius luridipennis	32.7	0.15	1	0.759	3.4	0.709	7.6	<0.001
	Platysoma cylindricum	41.7	0.27	2.7	0.125	1.4	0.673	9.8	<0.001
	Platysoma parallelum	61.1	0.41	1.6	0.688	7	<0.001	12.7	<0.001
	Plegaderus barbelini	35.6	0.22	1	0.824	4.3	0.228	3.8	0.002
	Plegaderus transversus	46.7	0.34	2.7	0.002	1	0.229	11.7	<0.001
	Priocera castanea	37.3	0.23	1.3	0.718	1	0.233	3.9	0.012
	Scoloposcelis flavicornis	43.1	0.24	2.5	0.359	5.1	0.172	10.2	<0.001
	Temnoscheila virescens	18.7	0.08	1	0.892	3.9	0.468	2.8	0.046
Detritivores	*Arthrolips fasciata*	32.6	0.17	1	0.77	1	0.978	12	<0.001
	Clypastraea fasciata	48.7	0.27	2.8	0.034	5.7	0.243	4.6	<0.001
	Colopterus unicolor	72.5	0.56	2.8	<0.001	7	<0.001	13	<0.001
	Cossonus corticola	68.1	0.48	2.4	0.007	9.5	<0.001	18.2	<0.001
	Oxylaemus americanus	18.4	0.07	2.2	<0.001	3.7	<0.001	<0.001	0.327

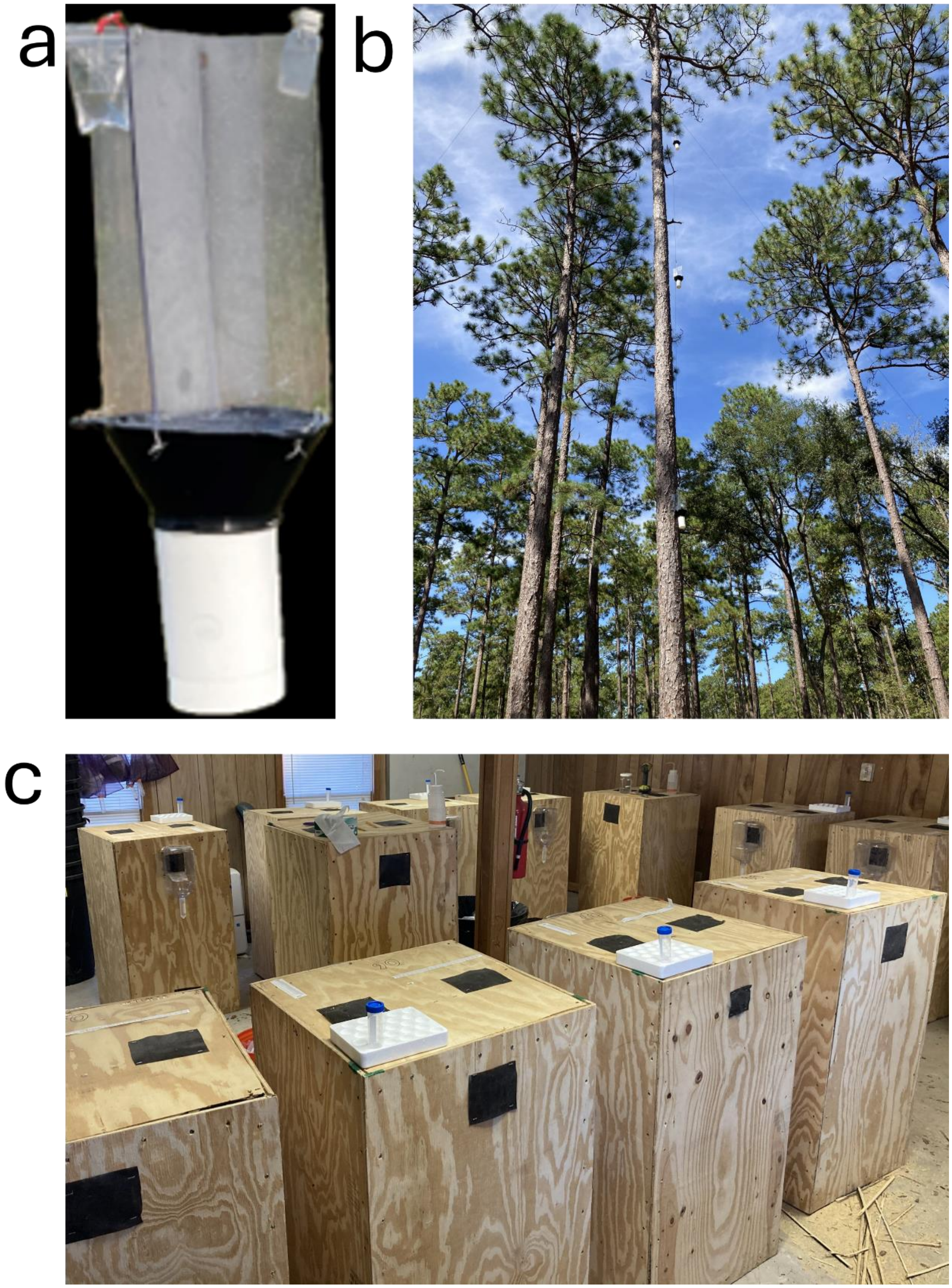

Figure 4.1 Flight intercept traps (a), vertical trap array (b), and emergence boxes (c) used to collect flight and emergence data.

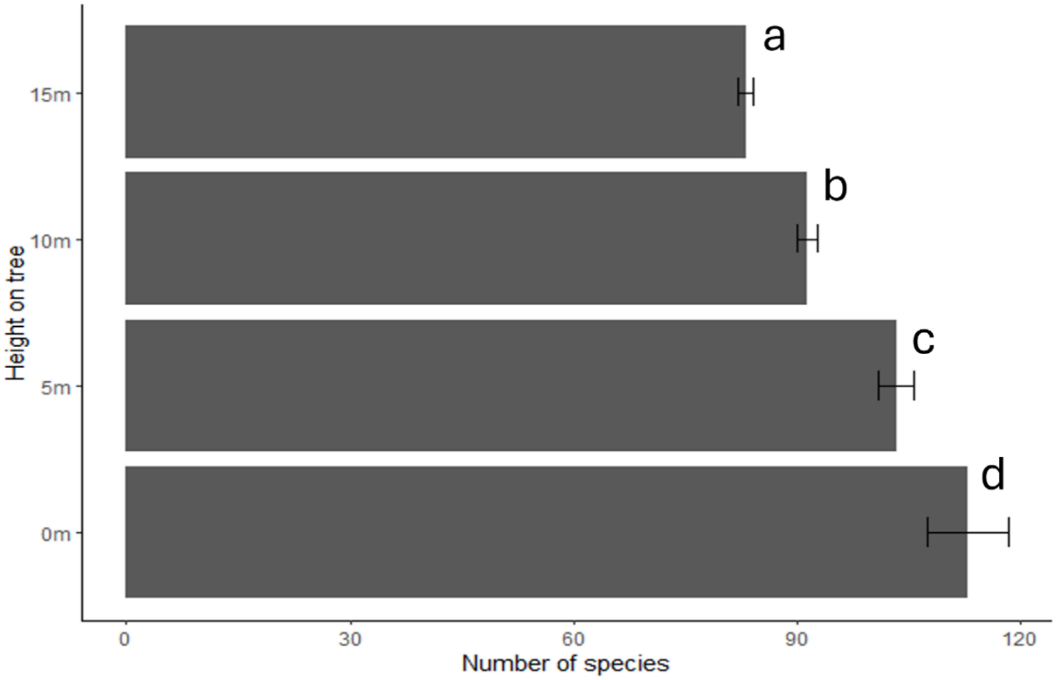

Figure 4.2 Species richness at four heights around simulated lightning struck trees during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

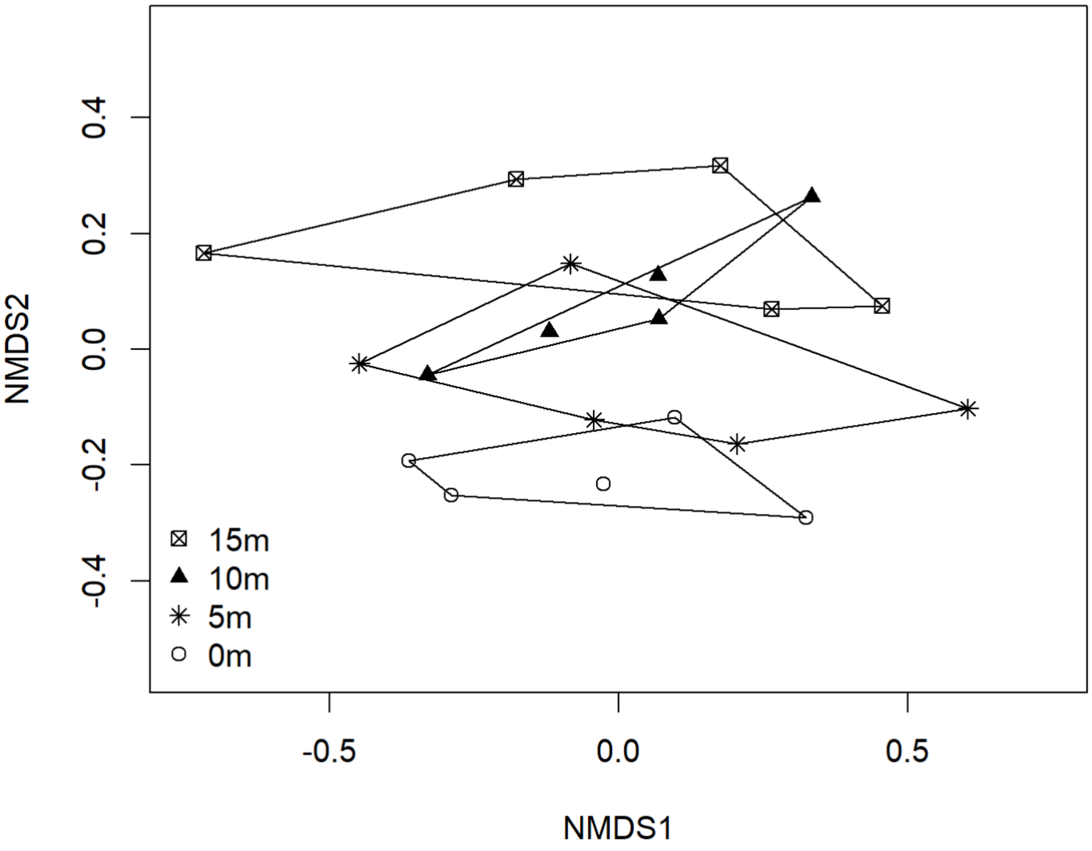

Figure 4.3 NMDS plot for insect assemblages grouped by capture in cross vane flight intercept traps at four heights along the trunks of simulated-lightning-struck longleaf pine trees during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

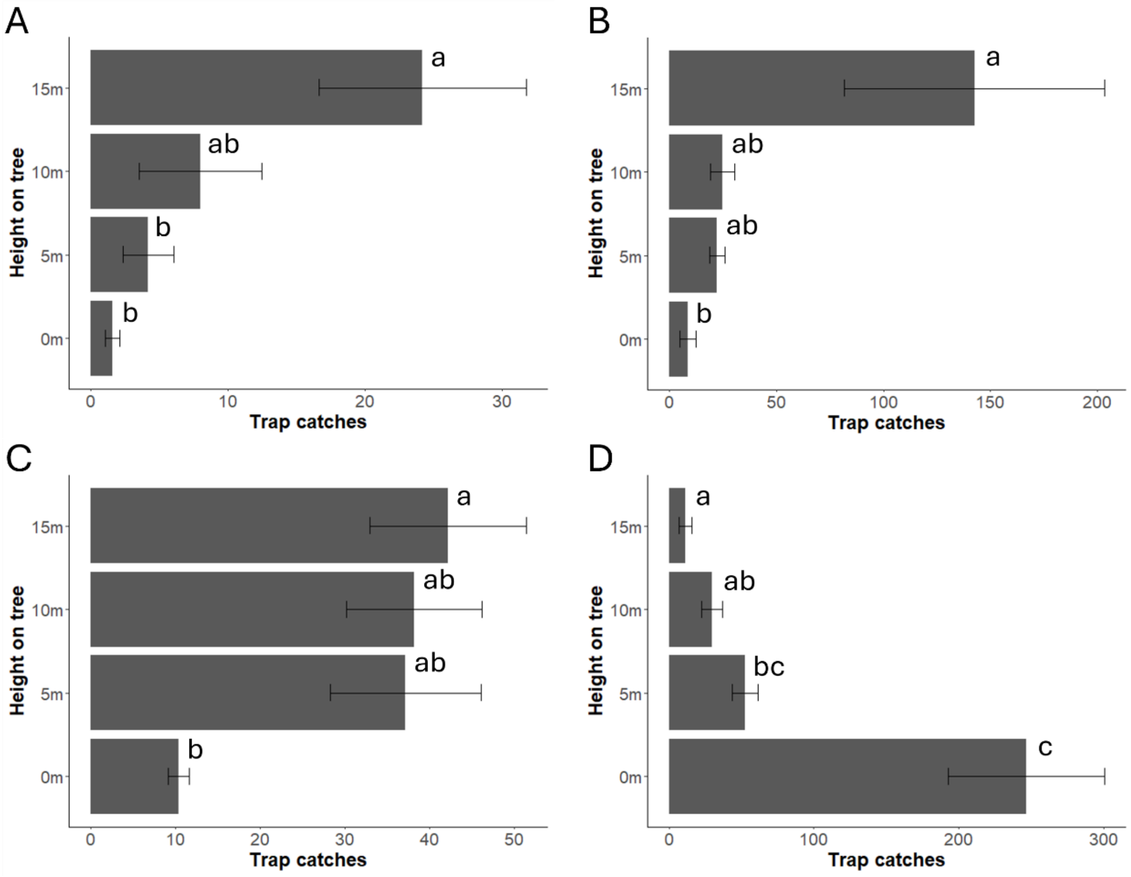

Figure 4.4 Bark beetle trap catches at four heights around simulated lightning struck trees for (a) *I. avulsus*, (b) *Pityophthorus* spp., (c) *I. grandicollis*, and (d) *D. terebrans* during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

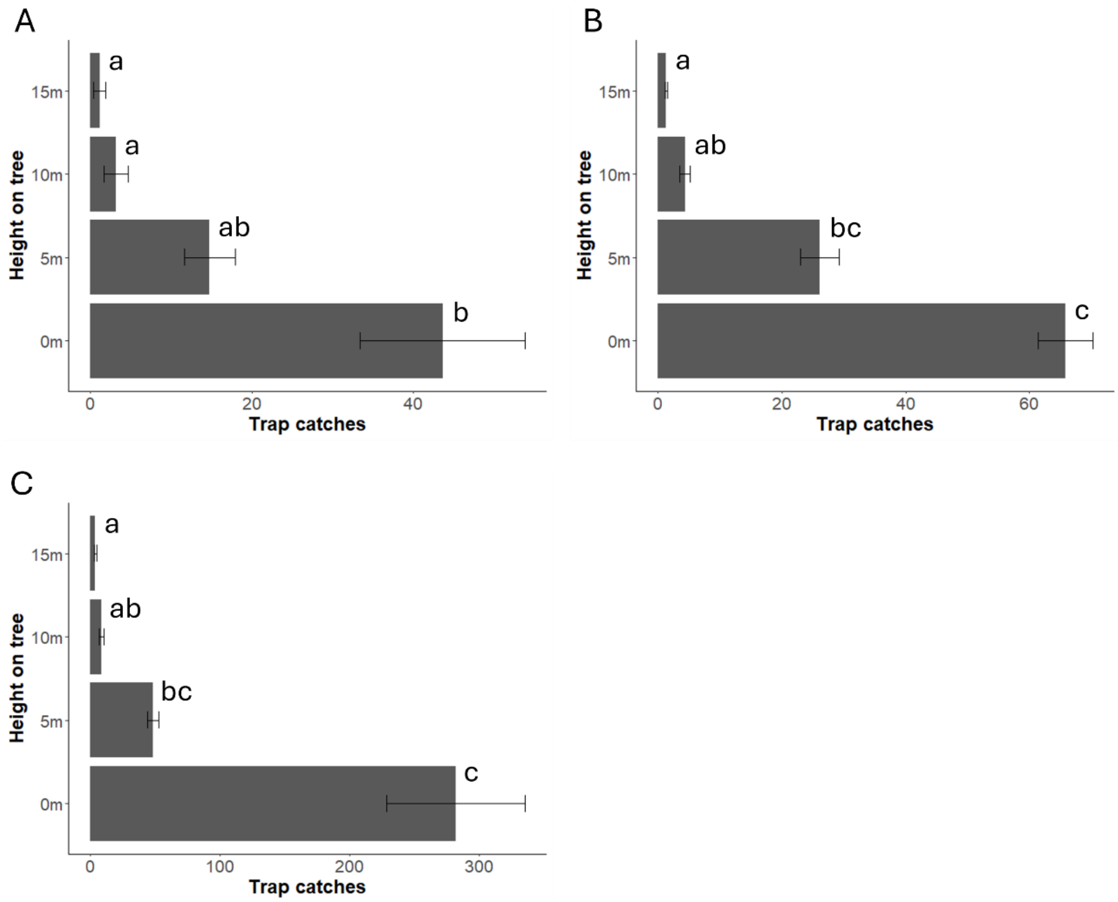

Figure 4.5 Root feeding beetle trap catches at four heights around simulated lightning struck trees for (a) *H. porculus,* (b) *H. tenuis,* and (c) *H. salebrosus* during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

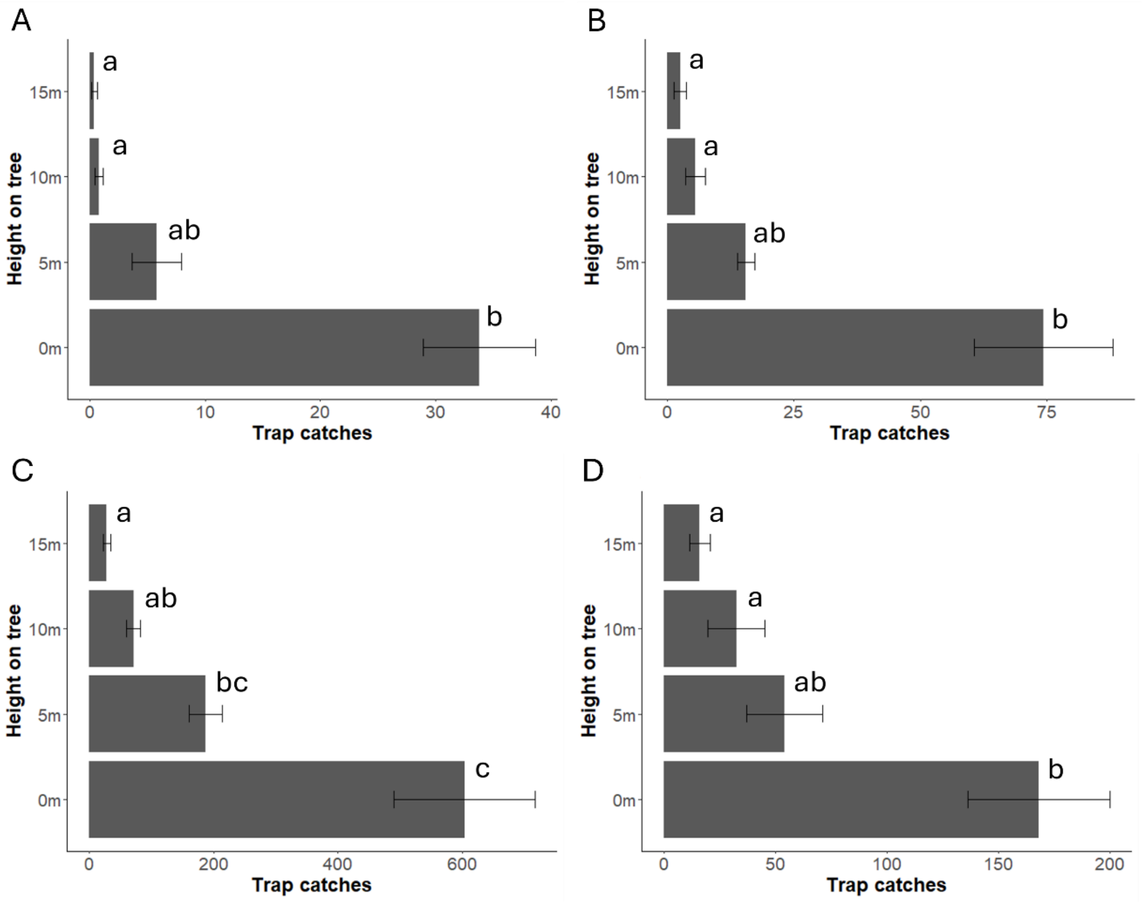

Figure 4.6 Ambrosia beetle trap catches at four heights around simulated lightning struck trees for (a) *M. flavicornis*, (b) *G. materiarius*, (c) *X. pubescens*, and (d) *X. ferrugineus* during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

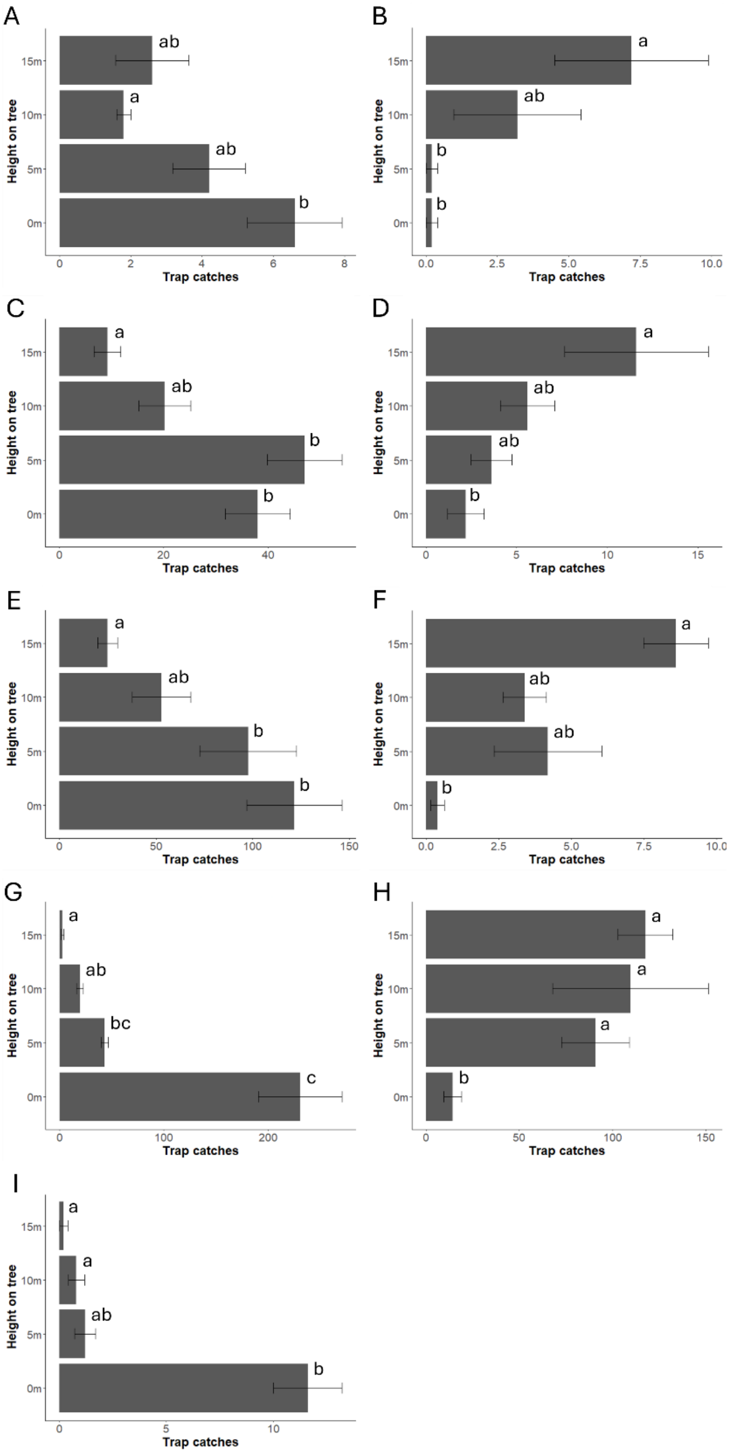

Figure 4.7 Predator beetle trap catches at four heights around simulated lightning struck trees for (a) *N. luridipennis*, (b) *C. cylindricus*, (c) *P. transversus*, (d) *C. glaber*, (e) *P. parallelum*, (f) *A. tuberculatum*, (g) *C. thoracicus*, (h) *L. referendarius*, and (i) *C. nigripenne* during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

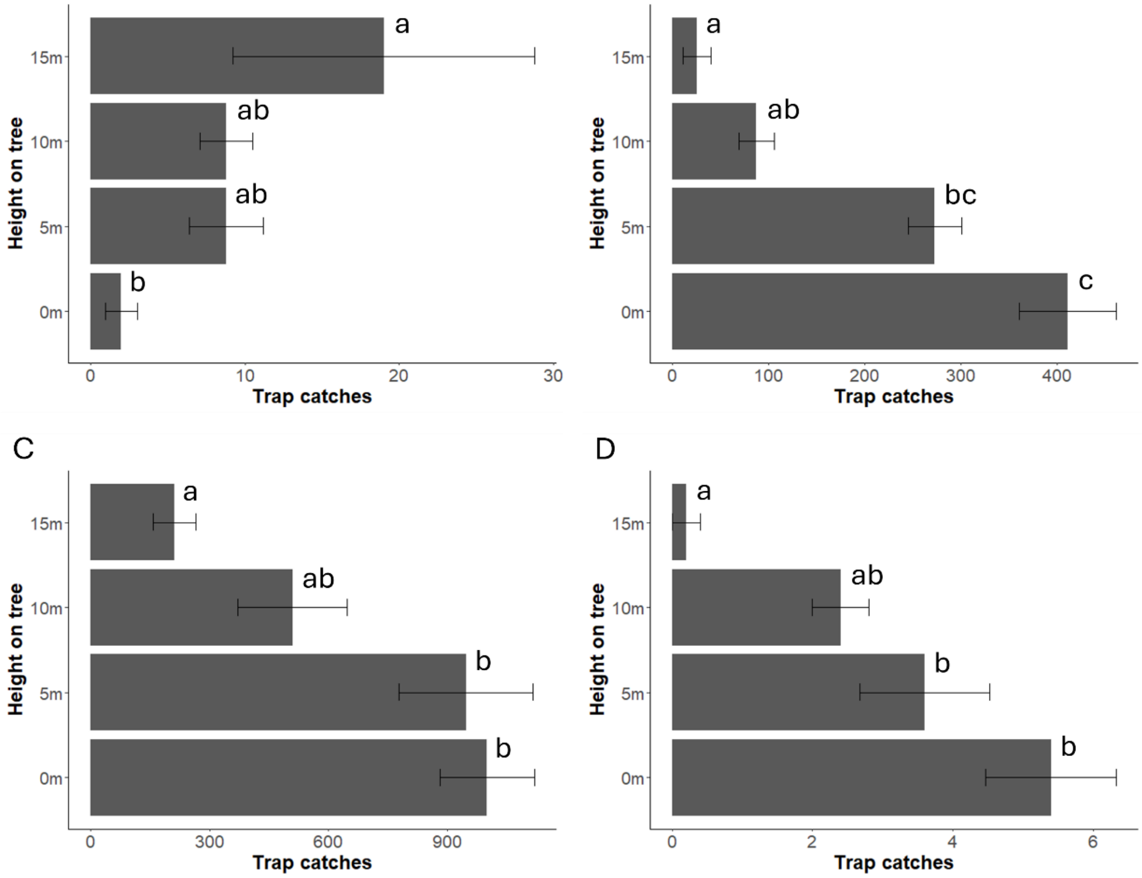

Figure 4.8 Detritivore beetle trap catches at four heights around simulated lightning struck trees for (a) *C. fasciata*, (b) *C. unicolor*, (c) *C. corticola*, and (d) *O. americanus* during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

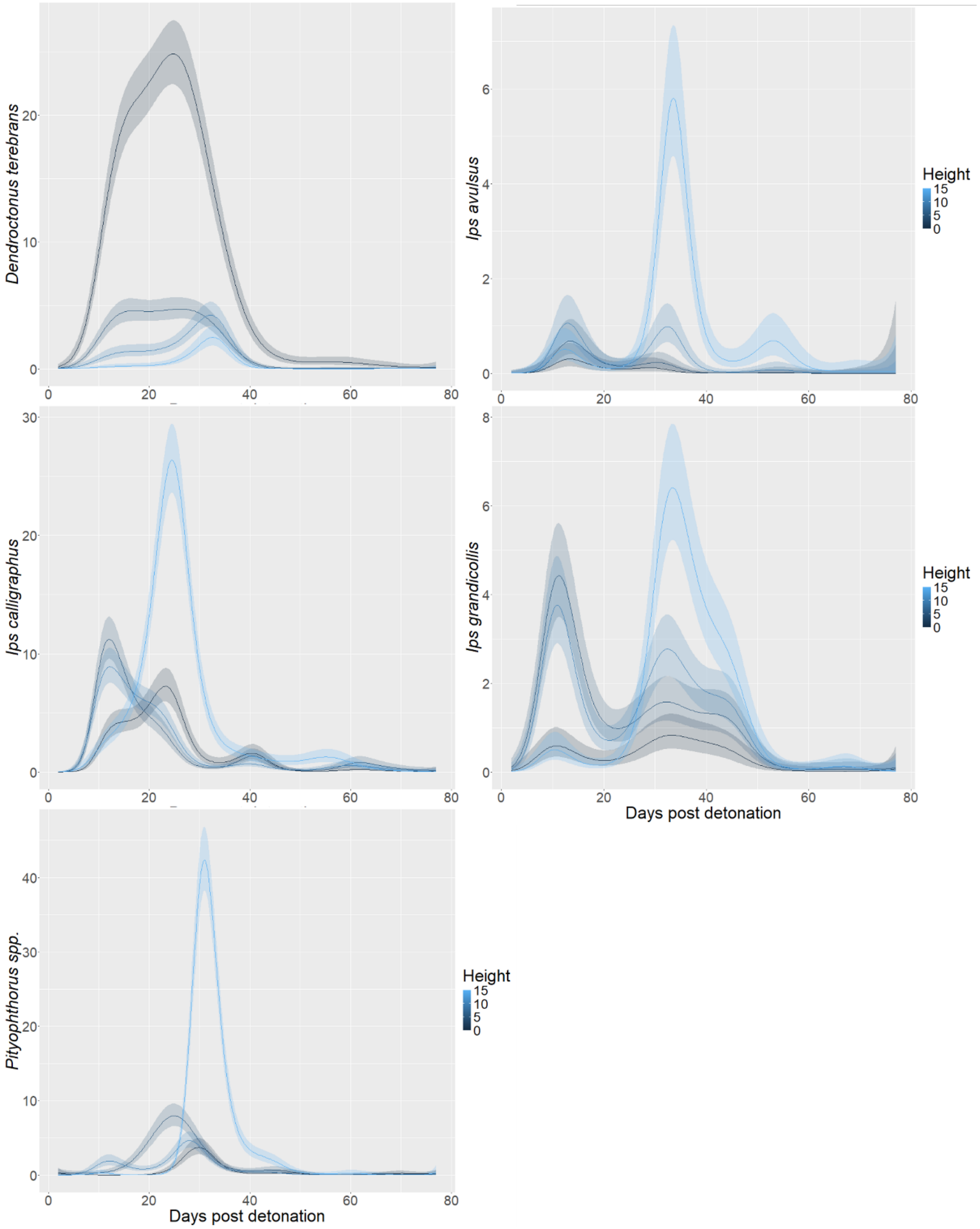

Figure 4.9 Generalized additive models for bark beetle species trap catches at four heights over 32 sampling events during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

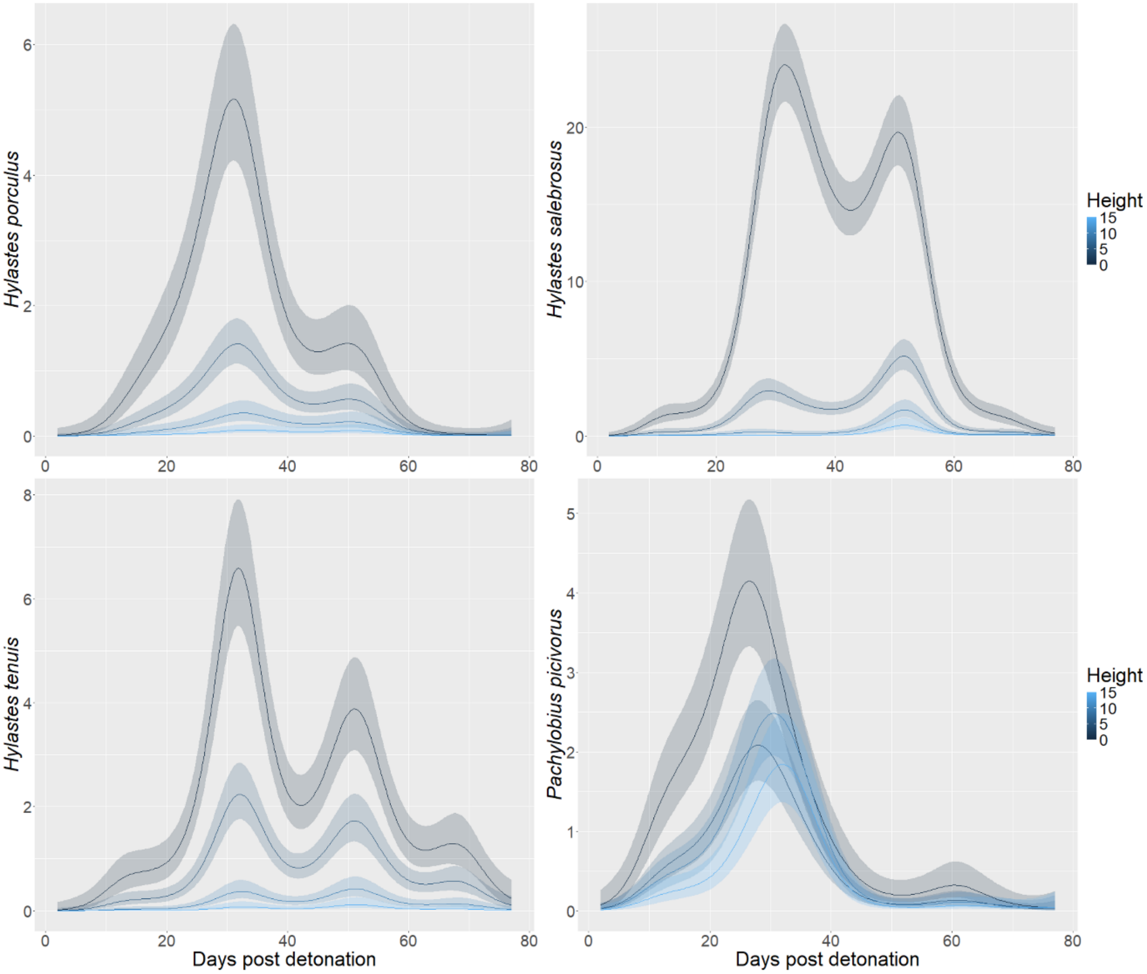

Figure 4.10 Generalized additive models for root feeding beetle species trap catches at four heights over 32 sampling events during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

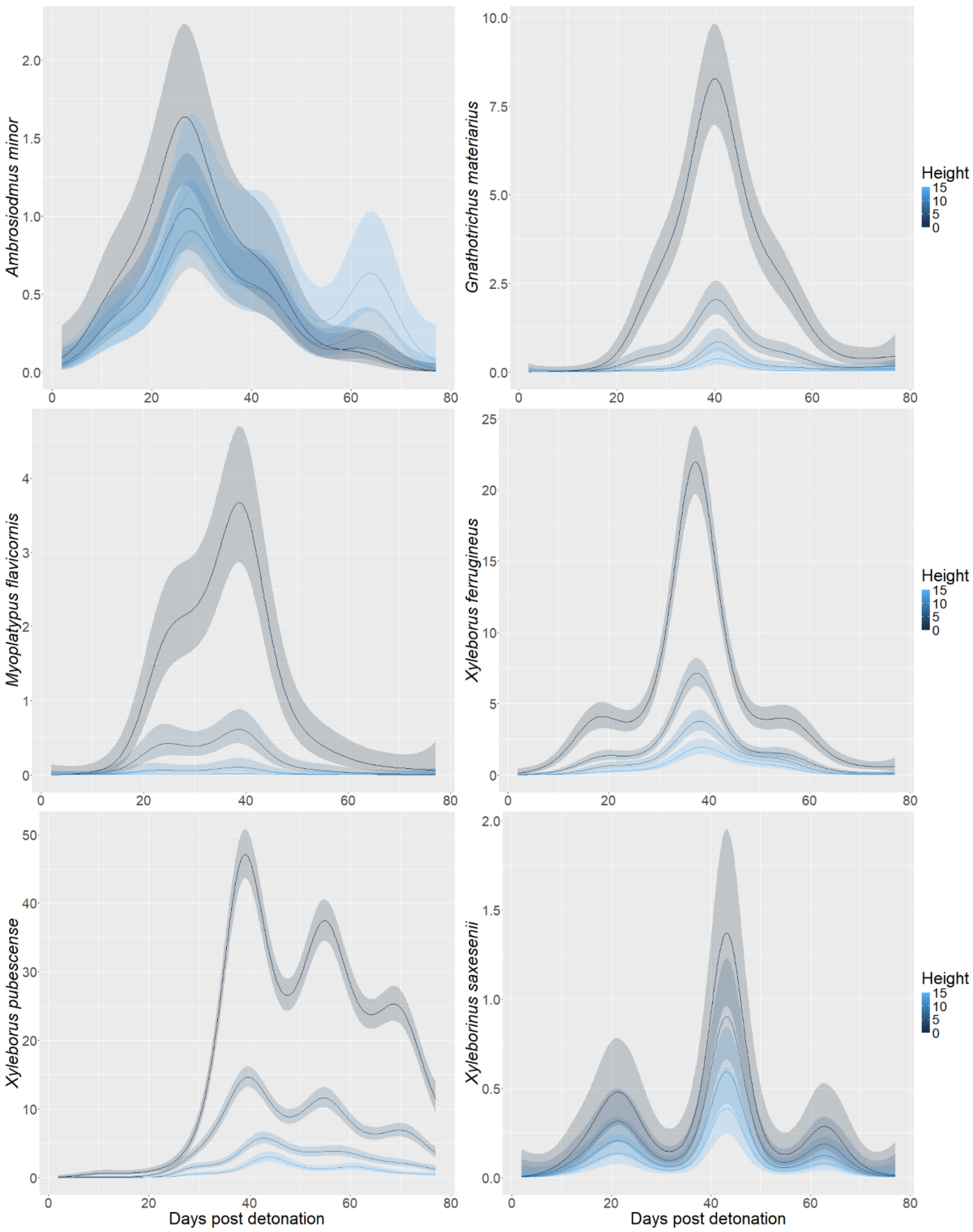

Figure 4.11 Generalized additive models for ambrosia beetle species trap catches at four heights over 32 sampling events during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

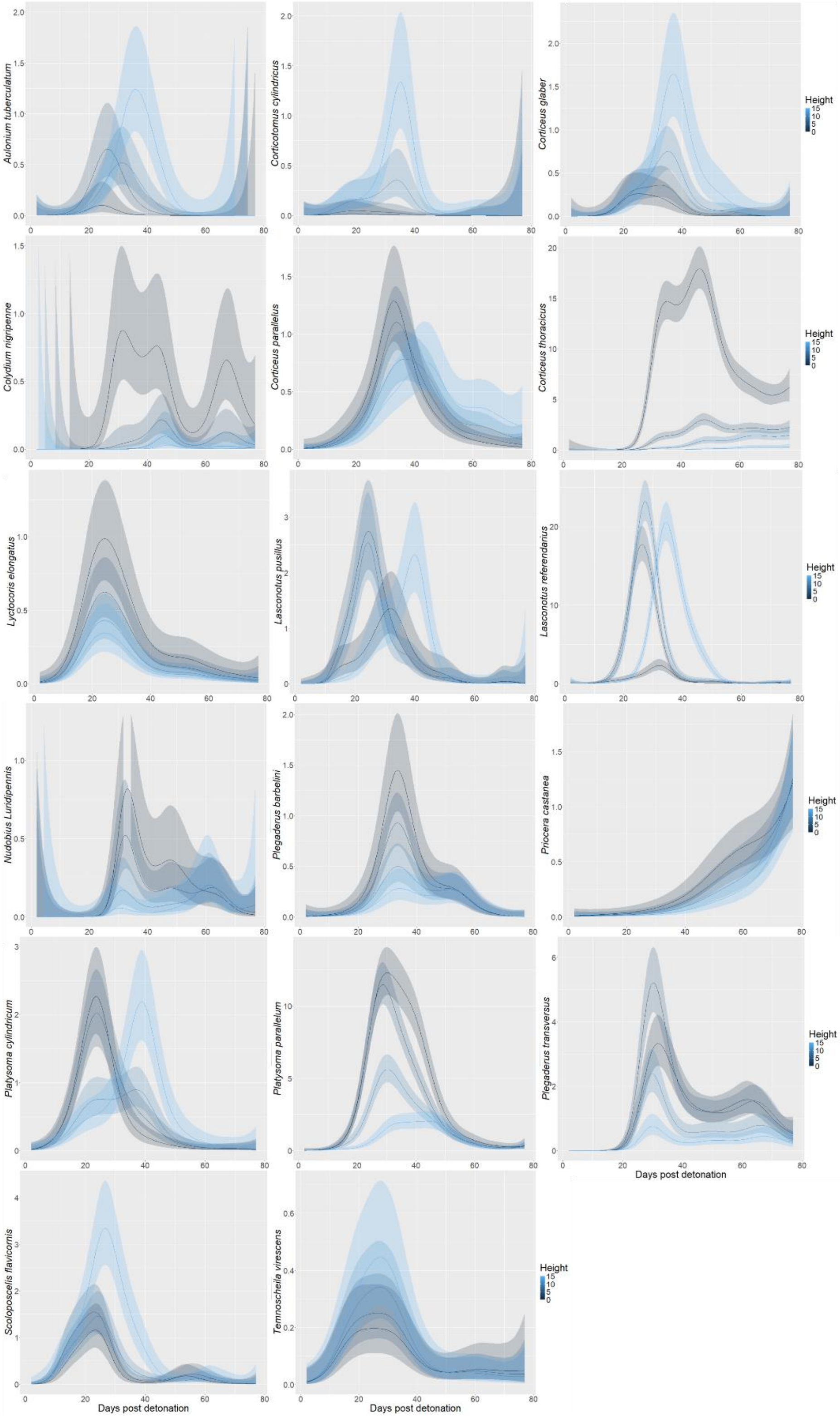

Figure 4.12 Generalized additive models for predatory insect species trap catches at four heights over 32 sampling events during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

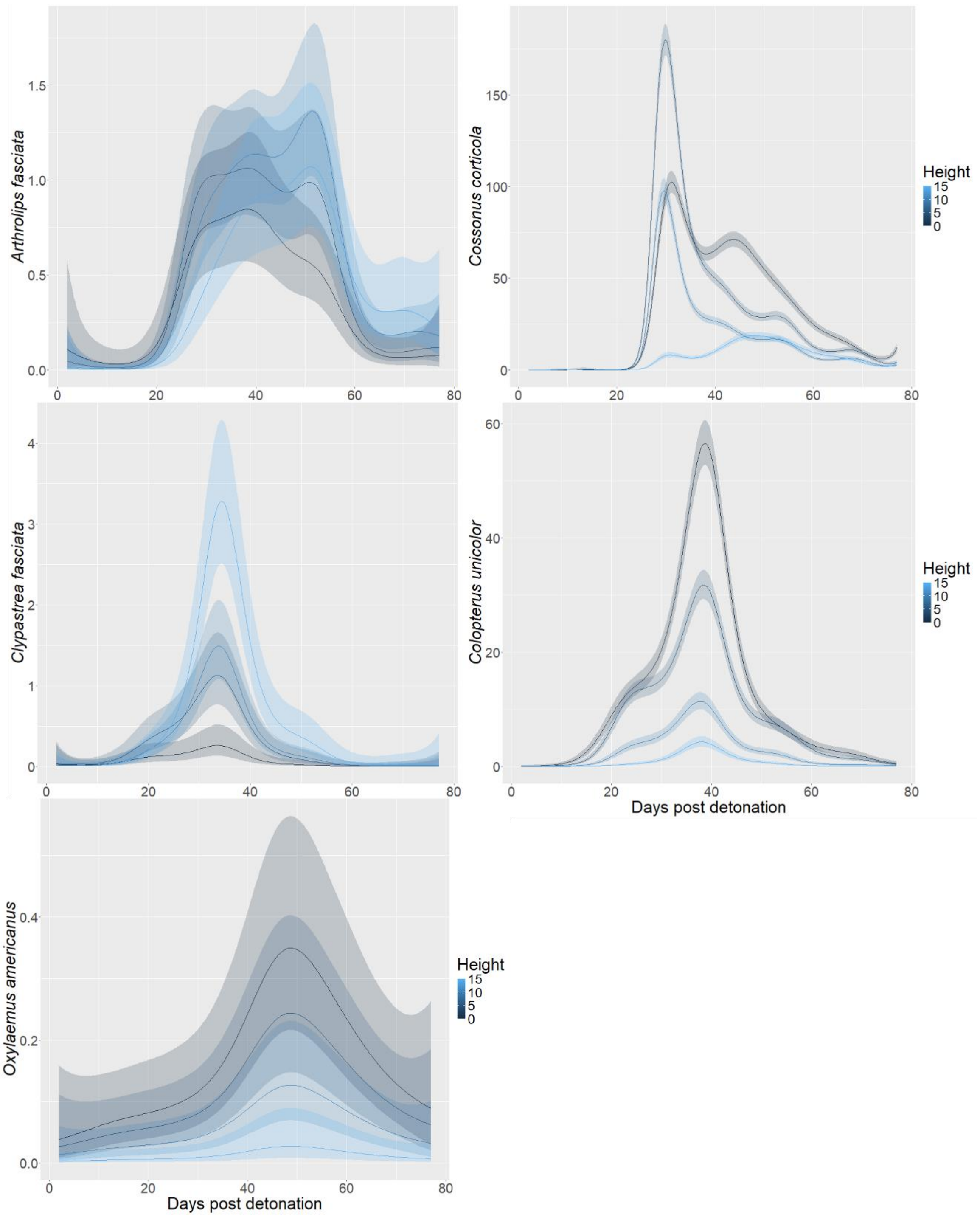

Figure 4.13 Generalized additive models for detritivore beetle species trap catches at four heights over 32 sampling events during May-July 2021 at the Jones Center at Ichauway in Georgia, U.S.

CHAPTER 5

CONCLUSIONS

5.1 Dissertation synopsis

Longleaf pine ecosystems of the southeastern U.S. are among the most biologically diverse outside of the tropics. Longleaf pine forests provide numerous ecosystem services, though these once dominant forests have been vastly reduced. In the southeastern U.S., there are multiple types of disturbances that affect longleaf pine (Glitzenstein et al. 1995, Brockway and Lewis 1997, Outcalt 2008, Kenney et al. 2021, Pope et al. 2023). While disturbance has been a natural part of these ecosystems (Gleason 1926, Clements 1936, Sousa 1984), disturbance events beyond the historical range of variability are predicted under climate change (Dale et al. 2001, Elsner 2006, Holland and Bruyère 2014, Mitchell et al. 2014, Knutson et al. 2020). Longleaf forests have been shown to be more resilient to disturbance than other pine species (Platt et al. 1988, Noss 1989, Hook et al. 1991, Moser et al. 2003, Johnsen et al. 2009, Rutledge et al. 2021), however the uncertainty from changing climates poses a challenge for forest managers (Millar et al. 2007, Brantley et al. 2017, Clark et al. 2018). This is further complicated by the interaction of compound disturbances (Kleinman et al. 2017, Kleinman et al. 2019, Crotteau et al. 2020).

The objective of this dissertation is to provide information about how beetles respond to disturbances including wind, fire, lightning, and salvage logging in longleaf pine forests in southwestern Georgia. Outcomes of the interactions between disturbance and bark beetles in longleaf pine ecosystems may differ from those in forests dominated by other tree species due to longleaf forest's greater adaptation, and resilience to natural disturbance agents (Gresham et al. 1991, Outcalt 2000, Martinson et al. 2007, Johnsen et al. 2009, Rutledge et al. 2021). As a result, how bark beetles will respond to different management practices post-disturbance is uncertain in longleaf pine. The findings reported here add to the existing knowledge base available to longleaf forest managers to weigh the tradeoffs of different management practices.

We first synthesize existing literature on how bark beetles respond to wind disturbances, providing a model for understanding bark beetle-windstorm interactions (Chapter 2). Catastrophic wind disturbances under climatic changes are causing major economic impacts and ecological changes that can persist for decades. Bark beetle population and community dynamics are often linked to such wind disturbances at several spatial and temporal scales ranging from damage to individual trees to large-scale windthrow that may prompt multiyear outbreaks on the landscape scale. We discuss how catastrophic wind disturbances and ensuing biological legacies enhance bark beetle populations, particularly in the context of climatic changes. The high level of variability at the tree, stand, and landscape levels created by windstorms generally has positive consequences for eruptive bark beetle species, particularly in Europe. Post-storm timber salvaging to alleviate pest burdens may push biotic elements, especially those dependent on coarse woody debris and forest gaps, into different successional pathways. Climate change is undoubtedly influencing the interactions between these two major disturbance agents by increasing their intensity and severity levels and altering landscape characteristics with feedback loops. In the Anthropocene, predictive modeling of network interactions between multiple abiotic and biotic disturbances and stressors will be critical for effective mitigation, forest restoration, and sustainable forestry practices in a rapidly changing world.

Climate change is increasing the intensity and severity of Atlantic hurricanes in forested ecosystems (Emanuel 2021). However, how bark beetles will respond to post-storm management activities in longleaf pine stands has yet to be assessed. Hence, our research objective in Chapter 3 was to evaluate the effects of post-windstorm land management practices on subcortical beetle populations and assemblages. We evaluated the effects of management practices on the trap catches and species diversity of subcortical beetles in managed longleaf pine stands during the first growing season after the catastrophic Hurricane Michael significantly impacted the area in 2018. Treatments included stands that had experienced: (1) windthrow; (2) windthrow with prescribed fire and no salvage logging; or (3) windthrow with prescribed fire and salvage logging. Funnel and intercept panel traps baited with bark beetle pheromones (ipsenol, ipsdienol, and cis-verbenol) and host attractants (ethanol, alpha-pinene, and beta-pinene) respectively, were used to compare catches of three native *Ips* species (*I. avulsus, I. calligraphus,* and *I. grandicollis*) and the associated community of woodboring beetles. Our results indicated that neither *Ips* beetles nor woodboring beetle species showed differences in trap catches between any land-area treatments. There were also no differences in the assemblage of woodboring beetle species between treatments. Moreover, no outbreaks of either of the groups were observed in these longleaf pine forests in subsequent years, highlighting the forests’ resilience to such disturbances. Although, the timing of the hurricane in late-fall, and active management of the property through frequent prescribed fire and gap selection thinning, may have confounded the interaction between the effects of our treatments and subcortical beetle activity in these longleaf pine forests.

Following this, we simultaneously narrow focus from the stand to the single tree scale while broadening the scope to insect community responses to disturbance (Chapter 4). Bark beetles display vertical patterns of colonization in stressed trees, with some species found mainly near the top of trees and others near the bottom, suggesting a partitioning of the tree resource between beetle species. In longleaf pine ecosystems, high insect diversity adds to the complexity of resource partitioning. We assessed vertical distribution of flight activity and colonization in response to lightning-struck longleaf pine trees. We simulated lightning strikes using detonation cord and used a flight intercept trap array with unbaited cross-vane panel traps hung at four heights (0, 5, 10. 15 m) to assess the activity and vertical distribution of the insect assemblage. Additionally, we evaluated successful bark beetle colonization by collecting emergence data from trunk sections associated with the four heights. In total, we collected 47,343 insects among 275 species of interest. Many important herbivore species showed a vertical stratification in their flight activity around treatment trees. These patterns were also present within associated predatory insects. Initial colonization dynamics of dying pine trees can have important implications for the associated community of insects that assemble around these colonization events. Given the interest in restoration of longleaf pine forests, a better understanding of how the insect assemblage associated with stressed trees is distributed vertically can aid adaptive management for multiple goals, including biodiversity and regulation of bark beetle populations.

5.2 Management recommendations and future directions for research

While our studies were restricted to a single tract of longleaf pine's remaining range in the southeastern U.S., our findings can be of use for management decision making in longleaf pine forests broadly. Salvage logging has been suggested to be an important management practice after windstorms to reduce residual deadwood which may be used by subcortical beetles as reproductive substrate. Here we found that longleaf pine stands managed with frequent fire and selective harvest practices that reproduce the historical disturbance regimes which longleaf pines are adapted to, lead to resilience following wind disturbances and bark beetles. Despite the severe effects of Hurricane Michael and the high numbers of beetles residing in these stands, there was little evidence of tree mortality associated with increases in bark beetle populations in the years following the storm. These results indicate that in well managed longleaf pine forests, specific management aimed at reducing bark beetle populations after wind disturbance may not be necessary.

However, the effect of seasonality on windstorm interactions with bark beetle populations likely played a role in the outcome of this experiment. Further investigation into the timing of windstorms in relation to peak beetle activity during the year may give insight into the importance of post-storm management effects on beetle populations.

Much of the property at Ichauway is managed using prescribed fire with a 2-year return interval. This fire regime results in resilient forests with low basal area, open canopies, and heterogenous age classes. Forests not maintained with fire would be subjected to overcrowding and competition with hardwood species. Investigating the effects of windstorms on such forests, and the responses of subcortical beetle populations therein, may give insight into the resistance and resilience to these disturbances endowed by frequent prescribed fire.

The standing dead wood created by lightning strikes serves as an important resource for subcortical beetles and the associated insect assemblage involved in tree colonization events. These events represent a nexus of life history interactions between hundreds of insect species, likely affecting their population dynamics at larger scales. Forest management that prioritizes the conservation of this dead wood niche will contribute to the maintenance of the high biodiversity characteristic of longleaf pine ecosystems.

Future studies of resource partitioning by subcortical beetles would benefit from detailed analysis of the many stages involved in the process including attraction, aggregation, attack, colonization, and emergence. There are likely factors involved at each stage that may affect the final distribution of insects in a colonized tree. These factors may include vertical stratification of flight height, arrival order, competitive exclusion, host tree characteristics, trophic interactions with predators, and demographic changes associated with seasonality. Further, assessment of the full diversity of arthropod involvement in these colonization events will add to the understanding of this incredibly complex biological happening.

5.3 Conclusion

Overall, the studies presented here contribute to understandings of the interplay between bark beetles and disturbance events in the context of climate change. The effects of climate change generate uncertainty in how compound disturbances will interact under future climatic variation. However, longleaf pine forests' relative resilience to hurricanes and bark beetles, two regional disturbance agents common in the southeastern U.S., indicate that they may fare better in response to climatic changes than other pine species. The knowledge generated from these studies may assist with adaptive management decision making in longleaf pine forests.

5.4 References

Brantley, S. T., J. M. Vose, D. N. Wear, and L. Band. 2017. Planning for an uncertain future: Restoration to mitigate water scarcity and sustain carbon sequestration. Ecological restoration and management of longleaf pine forests: 291-310.

Brockway, D. G., and C. E. Lewis. 1997. Long-term effects of dormant-season prescribed fire on plant community diversity, structure and productivity in a longleaf pine wiregrass ecosystem. For. Ecol. Manage. 96: 167-183.

Clark, K. E., E. Chin, M. N. Peterson, K. Lackstrom, K. Dow, M. Foster, and F. Cubbage. 2018. Evaluating climate change planning for longleaf pine ecosystems in the Southeast United States. J. Southeast. Assoc. Fish Wildl. Agencies 5: 160-168.

Clements, F. E. 1936. Nature and structure of the climax. J. Ecol. 24: 252-284.

Crotteau, J. S., C. R. Keyes, S. M. Hood, and A. J. Larson. 2020. Vegetation dynamics following compound disturbance in a dry pine forest: fuel treatment then bark beetle outbreak. Ecol. Appl. 30: e02023.

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

Elsner, J. B. 2006. Evidence in support of the climate change–Atlantic hurricane hypothesis. Geophysical Research Letters 33: 1-3.

Emanuel, K. 2021. Atlantic tropical cyclones downscaled from climate reanalyses show increasing activity over past 150 years. Nature Communications 12: 7027.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club: 7-26.

Glitzenstein, J. S., W. J. Platt, and D. R. Streng. 1995. Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecological Monographs 65: 441-476.

Gresham, C. A., T. M. Williams, and D. J. Lipscomb. 1991. Hurricane Hugo wind damage to southeastern US coastal forest tree species. Biotropica: 420-426.

Holland, G., and C. L. Bruyère. 2014. Recent intense hurricane response to global climate change. Climate Dynamics 42: 617–627.

Hook, D. D., M. A. Buford, and T. M. Williams. 1991. Impact of Hurricane Hugo on the South Carolina coastal plain forest. Journal of Coastal Research: 291-300.

Johnsen, K. H., J. R. Butnor, J. S. Kush, R. C. Schmidtling, and C. D. Nelson. 2009. Hurricane Katrina winds damaged longleaf pine less than loblolly pine. Southern Journal of Applied Forestry 33: 178-181.

Kenney, G., C. L. Staudhammer, S. Wiesner, S. T. Brantley, S. W. Bigelow, and G. Starr. 2021. Hurricane michael altered the structure and function of longleaf pine woodlands. J. Geophys. Res.-Biogeosci. 126: 17.

Kleinman, J. S., S. A. Ford, and J. L. Hart. 2017. Catastrophic wind and salvage harvesting effects on woodland plants. For. Ecol. Manage. 403: 112-125.

Kleinman, J. S., J. D. Goode, A. C. Fries, and J. L. Hart. 2019. Ecological consequences of compound disturbances in forest ecosystems: a systematic review. Ecosphere 10: 18.

Knutson, T., S. J. Camargo, J. C. Chan, K. Emanuel, C.-H. Ho, J. Kossin, M. Mohapatra, M. Satoh, M. Sugi, and K. Walsh. 2020. Tropical cyclones and climate change assessment: Part II: Projected response to anthropogenic warming. Bulletin of the American Meteorological Society 101: E303-E322.

Martinson, S., R. W. Hofstetter, and M. P. Ayres. 2007. Why does longleaf pine have low susceptibility to southern pine beetle? Can. J. For. Res. 37: 1966-1977.

Millar, C. I., N. L. Stephenson, and S. L. Stephens. 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17: 2145-2151.

Mitchell, R. J., Y. Q. Liu, J. J. O'Brien, K. J. Elliott, G. Starr, C. F. Miniat, and J. K. Hiers. 2014. Future climate and fire interactions in the southeastern region of the United States. For. Ecol. Manage. 327: 316-326.

Moser, W., T. Treiman, and E. Johnson. 2003. Species choice and risk in forest restoration: A comparison of methodologies for evaluating forest management decisions. Forestry 76: 137-147.

Noss, R. F. 1989. Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Natural Areas Journal 9: 211-213.

Outcalt, K. W. 2000. The longleaf pine ecosystem of the South. Native Plants Journal 1: 42-53.

Outcalt, K. W. 2008. Lightning, fire and longleaf pine: Using natural disturbance to guide management. For. Ecol. Manage. 255: 3351-3359.

Platt, W. J., G. W. Evans, and M. M. Davis. 1988. Effects of fire season on flowering of forbs and shrubs in longleaf pine forests. Oecologia 76: 353-363.

Pope, C. A., J. B. Cannon, S. W. Bigelow, and A. Sharma. 2023. Effects of hurricane canopy gaps on longleaf pine and upland oak sapling growth. For. Ecol. Manage. 529: 10.

Rutledge, B. T., J. B. Cannon, R. K. McIntyre, A. M. Holland, and S. B. Jack. 2021. Tree, stand, and landscape factors contributing to hurricane damage in a coastal plain forest: Post-hurricane assessment in a longleaf pine landscape. For. Ecol. Manage. 481: 13.

Sousa, W. P. 1984. The role of disturbance in natural communities. Annual Review of Ecology and Systematics 15: 353-391.