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Digital Object Identifier: https://doi.org/10.13023/etd.2023.265

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THE LONG-TERM EFFECTS OF WILDFIRE SEVERITY ON OAK-PINE COMMUNITIES AND THEIR MICROCLIMATES

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in Forest and Natural Resource
Sciences in the College of Agriculture, Food and Environment
at the University of Kentucky

By

Scott Glenn Culbert

Lexington, Kentucky

Co- Directors: Dr. Mary Arthur, Professor Emeritus of Forest Ecology

and Dr. Jacob Muller, Assistant Professor of Hardwood Silviculture
and Climate Adaptation

Lexington, Kentucky

2023

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ABSTRACT OF THESIS

THE LONG-TERM EFFECTS OF WILDFIRE SEVERITY ON OAK-PINE COMMUNITIES AND THEIR MICROCLIMATES

In the eastern U.S., fire-dependent tree species have historically dominated upland forest communities, but are now experiencing widespread regeneration challenges as a result of 20th century fire suppression policies, and are being replaced by mesophytic species. Wildfires that contain areas of high burn severity may provide an important means of mitigating these challenges and facilitating fire-dependent species regeneration and recruitment into larger size classes. One mechanism by which high-severity fire can accomplish this is by modifying understory microclimate characteristics to be more conducive to these species' growth. A wildfire within the Daniel Boone National Forest, Kentucky, USA, provided the opportunity to consider how wildfire may alter the regeneration of fire-dependent oak (*Quercus* spp.) and yellow pine (*Pinus echinata* Mill., *P. rigidia* Mill., *P. viginiana* Mill.) forests, and evaluate the long-term microclimate conditions following varying levels of burn severity. In this thesis, I examined the effects of burn severity on forest community structure and composition twelve years post-burn, and compared my results to those from previous measurement years. Likewise, I analyzed forest microclimate conditions across a range of burn severities throughout the 2022 growing season. Overall, I found that burn severity was negatively related to the importance of mesophytes (i.e. species known to facilitate the process of mesophication) and positively related to pyrophytes (i.e. species who positively benefit and are adapted to a frequent fire regime). At year 6, oak and pine recruitment of seedlings and saplings into larger size classes was positively related to burn severity, but by year twelve, only pine recruitment was related. This is likely due to the impact of burn severity on forest structure, and thus on understory microclimates, diminishing over time with forest regrowth. In this, I observed that the reduced canopy stem density that was caused by increased burn severity was still related to increased understory temperatures and vapor pressure deficits, but the midstory densification that has occurred increasingly with increased burn severity has largely obscured these effects. Based on this, burn severity is only partially related to microclimate conditions twelve years post-fire. At moderate burn severities where there was a meaningful amount of delayed canopy stem mortality that occurred, understory microclimates are experiencing more open growing conditions with greater light levels, greater temperatures, lower relative humidity, and greater vapor pressure deficits. Increased burn severity also increased the probability of non-native invasive plant (NNIP) presence, particularly Chinese silvergrass (*Miscanthus sinensis* Andersson). Overall, my results indicate that areas that experience increased burn severity can have lasting effects of increasing the competitive status of pyrophytes relative to mesophytes, and promoting yellow pine recruitment into canopy size classes. To bolster oak recruitment, understory microclimates may need to be modified between year six and year twelve to create more

open growing conditions. Additional natural disturbance, prescribed fire, or a thinning treatment that reduces midstory stem densities may accomplish this. Creating microclimate conditions that promote the growth of fire-dependent species may be important for adapting eastern U.S. forests to climate change and help avoid degraded forest health in the future. However, any action that occurs should be coupled with NNIP monitoring and control efforts to mitigate their establishment and proliferation at high-severity burn sites.

KEYWORDS: Fire, Recruitment, Mesophication, Climate Change, Adaptation, Regeneration

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Date

THE LONG-TERM EFFECTS OF
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MICROCLIMATES

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I dedicate the work within this thesis to my parents, Glenn and Shelly Culbert, who are unendingly supportive of my dreams; to my sister, Taylor Culbert, who is a constant inspiration to me; and to Richard Idema and Matthew Bauer, who have pushed me to reach beyond my comfort zone and develop my passions.

Any success I may enjoy in life is attributable to you.

ACKNOWLEDGMENTS

The following thesis is a work of my own, but none of it would have been possible without the wisdom, time, and attention of several important people. Foremost, I would like to thank my advisors and mentors, Dr. Jacob J. Muller and Dr. Mary A. Arthur, for not only pushing me to develop as a scientist, writer, and professional, but challenging me to grow in my ethics and values. They both exemplify what it means to be an exceptional human being, and I feel incredibly fortunate to have had the privilege to learn from them. Next, I would like to thank Dr. Claudia A. Cotton for her mentorship, feedback, advice, and guidance as a committee member. Together, these three individuals have pushed me to become a better thinker and shaped the research projects in this thesis. There is no one else I could have asked for to help guide my personal and intellectual growth.

This project would not have been possible without numerous contributions from several entities and individuals. First, I owe many thanks to the USDA Forest Service for allowing me to conduct research on the Daniel Boone National Forest and supporting my work with field personnel. In terms of field support, this project would not have been possible without the extensive assistance I received from Dr. Mary A. Arthur, Logan Baker, Jason Brown, Jordan Lucas, Dr. Claudia A. Cotton, Rebecca Davenport, Dr. Jacob J. Muller, Lauren Sherman, David Taylor, Maria Topmiller, Joanna Sorrell, and Mac A. Cherry. I would also like to thank Millie Hamilton for her daily support in the lab and for her assistance with data entry and proofing. Likewise, I want to thank Zachary Hackworth for his knowledge and time spent helping me with my data analysis and being a great resource for ideas. I would also like to thank the previous graduate students in the University of Kentucky Forest Ecology Lab whose work I have been able to build from, namely Devin Black, Jordan Winkenbach, and Zach Poynter; I have never met you, yet my work here has been thoroughly enhanced by the time and effort you have put into this project before me.

I would like to extend my sincerest gratitude to the cohort of graduate students that enriched my time here at the UK. The friendship and community that you have provided has profoundly impacted me and I will miss you all dearly. Lastly, I would like to thank my family and friends who have provided me with everlasting support throughout this process and who have pushed me to pursue my dreams.

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CHAPTER 1. ECOLOGICAL AND DISTURBANCE REGIME HISTORY OF CENTRAL MIXED-HARDWOOD FORESTS

The eastern broadleaf and Appalachian forests of the eastern United States are some of the most complex forest types in North America (Wharton and Barbour, 1973), with exceptionally high biodiversity that is largely attributable to the region's extraordinary landscape heterogeneity (Braun, 1950). This region extends from the Mississippi River east to the Appalachian Mountains, and from northern Alabama to western Pennsylvania and New York (Arthur et al., 2021). The structure, composition, and distribution of these forests, in addition to the physiology of the species that constitute them, have been strongly shaped by Native American use of fire (Lafon et al., 2017), but as a result of Euro-American settlement and subsequent land-use changes, these ecosystems vary substantially from how they did prehistorically. Of these land-use changes, the fire suppression era of the late 19th and early 20th centuries has caused profound shifts in forest structure and species composition away from fire-adapted communities towards those composed of species that facilitate mesophication. This change poses a significant threat to future forest health and ecosystem resiliency to anthropogenic climate change and has prompted land managers to reintroduce fire into these forests in an attempt to restore fire-adapted forest communities across the landscape. Incorporating characteristics of wildfire, such as variable fire severity, in fire reintroductions may play an important role in achieving this by altering forest structure so that understory conditions are more conducive to these species' growth.

Fire histories of this region have been recreated from fire-scars, witness trees, and sediment and soil charcoal studies (Lafon et al., 2017), which have illuminated a rich past

of fire in this region. Prior to Native American population expansion ~13,000 y.b.p., late growing season fires started by summer thunderstorms were likely the dominant source of ignitions on the landscape (Petersen and Drewa, 2006). During this time until early Native American Clovis culture (12,500 y.b.p.) (Fowler and Konopik, 2007), there was a climatic transition from Late-Glacial to Interglacial, where species and fire regimes changed rapidly, generally migrating north as temperatures increased (Clark et al., 1996). In what is now the Central Hardwoods Forest region, forests were primarily composed of spruce (*Picea* spp.), along with spruce/pine (*Pinus* spp. L.), white pine (*P. strobus* L.), and northern hardwood communities (Clark et al., 1996). By ~10,000 y.b.p., Native American presence on the landscape (Fowler and Konopik, 2007) and climatic changes resulted in widespread expansions of jack pine (*P. banksiana* Lamb.), which is hypothesized to have facilitated high-severity fire events with return intervals of 50-200 years, similar to what is seen in today's jack pine stands of northern Canada (Clark et al., 1996). At this time, the characteristic use of fire is believed to have been for creating conditions that improved the hunting of megafauna (Fowler and Konopik, 2007).

Over the next 2000 years, the climate of this region became warmer and drier, with Paleo-Indian (10,500-9,500 y.b.p.) and Archaic (8,000-2,800 y.b.p.) cultures progressively utilizing fire for widespread land clearing and maintenance of forest communities, in addition to hunting (Fowler and Konopik, 2007). It is believed that these climatic and land use changes shifted fire regimes from infrequent high-severity fire to frequent low-severity surface fires (Clark et al., 1996; Lafon et al., 2017). Indeed, charcoal and pollen records indicate that species compositions transitioned away from spruce and jack pine dominance to communities composed primarily of eastern white pine, along with paper birch (*Betula*

papyrifera Marsh.), aspens (*Populus* spp.), cedar (most likely northern white cedar, *Thuja occidentalis* L.), and firs (*Abies* spp.) (Clark et al., 1996; Delcourt et al., 1998). Further increases in temperatures, precipitation (Prentice, 1991), and Native American populations (Delcourt et al., 1998) throughout the Archaic cultural period coincided with additional shifts in dominant species compositions to the mesic and mixed hardwoods that are more reminiscent of present-day forest communities (Clark et al., 1996; Delcourt et al., 1998; Fowler and Konopik, 2007). These communities were primarily composed of hemlock (*Tsuga* spp.), beech (*Fagus* spp.), maples (*Acer* spp.), hickories (*Carya* spp.), and oaks (*Quercus* spp. L.) (Clark et al., 1996; Delcourt et al., 1998).

Over the next several millennia, the relative proportion of fire-tolerant species increased considerably (Fowler and Konopik, 2007), where by ~4,000 y.b.p., American chestnut (*Castanea dentata* (Marsh.) Borkh) and oaks were the dominant forest species in the region (Delcourt and Delcourt, 1997; Delcourt et al., 1998). Also throughout this period, human use of the landscape intensified, with plant husbandry and domestication becoming a common practice, aided by the use of fire (Lafon et al., 2017) that was also being used to manage for oak, pine, hickory, and chestnut dominance (Delcourt et al., 1998), some of which species provided food sources (Fowler and Konopik, 2007). Overall, prior to ~4,000 y.b.p., fire histories and forest community reconstructions are coarse in their resolution and there is likely much historic variability that has been lost over time, but it is clear that between 10,000 and 4,000 y.b.p., fire was an integral driver of species compositions and distributions throughout the eastern U.S., and these have been intentionally and effectively managed by Native American cultures.

The greater availability of preserved pollen and charcoal for the last 4000 y.b.p. has increased the temporal resolution of prehistoric forest reconstructions and allowed for a finer-scale understanding of the relationships between prehistoric species compositions, fire, and Native American communities, which has generally shown that fire has been a regular occurrence in upland and bottomland ecosystems for the past 4000 years (Fesenmyer and Christensen, 2010). In the late Archaic cultural period, extensive use of upland forests by Native Americans coincided with increases in local fire near settlements (Delcourt et al., 1998), which maintained fire-adapted pine, hickory, oak, and American chestnut communities that provided food sources and attracted game animals (Delcourt and Delcourt, 1997; Fesenmyer and Christensen, 2010; Fowler and Konopik, 2007). A transition to Woodland culture (2,800-1,300 y.b.p.), where local fire use continued to increase (Delcourt and Delcourt, 1997; Delcourt et al., 1998), maintained these species' dominance in forest communities despite increases in regional wetness (Clark et al., 1996; Lafon et al., 2017). More localized uses of fire during this cultural period are associated with increased agricultural plant domestication, early maize cultivation, and more sedentary lifestyles, in which fire was also being used to prepare seedbeds (Fowler and Konopik, 2007). The Mississippian culture (1,300-400 y.b.p.) that followed was more centered around settled communities and agriculture, which brought large increases in overall Native American populations and coincided with a distinct increase in charcoal accumulation and few changes in forest species compositions (Fowler and Konopik, 2007). Therefore, the picture that emerges from charcoal reconstructions and anthropological data over the last four millennia suggests that as Native American populations increased and lifestyles transitioned to be more sedentary and agriculture-based, the use of fire on the

landscape increased in ways that progressively managed for pyrophytic oak, pine, chestnut, and hickory communities, making these species' dominance relatively stable over time. These fires were likely low-severity surface fires that burned every 1.9 to 19.5 years (median 5.4), depending on the forest community (Lafon et al., 2017).

Fire as a selective force has altered species physiology in addition to composition over the past decamillenium, where present-day species have a range of adaptations that aid in the survival of, the positive response to, and the facilitation of fire events. Bark properties are the primary protective trait of trees, as it shields against vascular cambium damage (Hengst and Dawson, 1994), which is particularly beneficial for withstanding fire events. Several upland oak and pine species have thick bark as adults and as juveniles they preferentially allocate carbon to bark accumulation rather than height development to confer a protective advantage (Varner et al., 2016). Bark roughness also protects against fire damage, as increased bark surface area can displace radiant heat (Hengst and Dawson, 1994). The American chestnut was known to have extremely rough bark, and oak and pine species have notably rougher bark than beech and maple, whose bark confers little resistance to heat damage (Hengst and Dawson, 1994). When wounds do occur from fire events, these fire-adapted species have also developed the ability to rapidly close wounds, which reduces the chances of decay and infection (Varner et al., 2016). In addition to developing resistance to fire damage, fire-adapted species have evolved to facilitate fire events through high litter flammability. The American chestnut is widely considered to have the most flammable litter among eastern U.S. tree species (Varner et al., 2016), followed by pines and oaks (Varner et al., 2021), which is attributed to their leaf litter physically retaining less water and drying quicker and senesced leaves curling, which

increases fuel aeration (Kane et al., 2021; Varner et al., 2021). Fire-intolerant species, such as eastern hemlock (*T. canadensis* (L.) Carr.), maples, and beech, have substantially less flammable litter (Varner et al., 2021) as it packs more densely, absorbs more water, and is slower to dry (Kane et al., 2021). Another fire adaptation that has widely evolved among eastern U.S. trees is vegetative resprouting following top kill. This adaptation appears to be less specific to fire (Bond and Midgley, 2001), as species such as red maple (*A. rubrum* L.) have strong resprouting capacities (Albrecht and McCarthy, 2006). Despite this, fire-adapted oaks and pines allocate more carbon to belowground root storage (Huddle and Pallardy, 1999) and are able to resprout more persistently over time compared to these fire-intolerant species (Brose et al., 2006). Thus, the oak, pine, American chestnut, and hickory species of the eastern U.S. have evolved physiological and morphological adaptations to tolerate, facilitate, and positively respond to the fire events and fire regimes that have been established over multiple millennia by intentional Native American burning as a means of land management.

European settlement and the reduction of Native American populations by 90-95% via disease and genocide marked the first large deviation of fire regimes from what had been established for several millennia. When Native American populations were reduced, widespread burning decreased resulting in a brief period of forest densification (Fowler and Konopik, 2007) before Euro-American populations expanded (Abrams et al., 2021). By the 1800s, early settlers were using fire in similar ways and for similar purposes as Native American cultures, which included reducing forest understory stem densities, preparing fields for crops, and promoting early successional plants, among other uses (Fowler and Konopik, 2007). Over time, Euro-American settler's use of fire diverged from

that of Native Americans and was used more frequently to improve cattle forage and to benefit permanent-field agriculture, with some areas being burned on an annual basis (Fowler and Konopik, 2007). These changes shortened mean fire return intervals (FRI), though fires remained low-severity surface fires typically (Abrams et al., 2021; Fowler and Konopik, 2007).

The second deviation in the fire regimes of eastern U.S. forests began in the mid-19th century, when extensive unregulated industrial logging occurred, in what is called the "Great Cutover" (Abrams et al., 2021). During this time, forest communities were primarily regarded for their commercial value and as a means of industrialization, and the lumber derived from them was used for building materials, the charcoal iron industry, railroads, mining props, shipbuilding, manufacturing, and domestic uses (Abrams, 1992; Abrams et al., 2021; Fowler and Konopik, 2007). With advances in industrial technologies (i.e. the locomotive), extracting forests from rugged mountain terrain became economically feasible (Brose et al., 2001), allowing for nearly any forest to be harvested. Fowler and Konopik (2007) describe the process of this industrial logging beginning with systematically cutting all saw timber and smaller timber, followed by burning the leftover logging debris, or slash, to clear the land for grazing livestock, both of which inhibited woody vegetation re-establishment. The height of forest extraction lasted from 1850 to 1920 and resulted in the elimination of approximately 99% of original eastern U.S. forests, with 0.5% of old-growth forests remaining, and an estimated 66 million ha (~50%) of forestland converted to agriculture (Abrams et al., 2021). Accordingly, nearly all of the forests in the eastern U.S. today are second-growth forests that regenerated following this period of unregulated logging. The logging debris that was left over by this process was

oftentimes not burned intentionally, however, and when left behind, dried, creating abundant and easily ignitable fuel (Abrams et al., 2021; Brose et al., 2001). The locomotives that ran through these areas of slash served as an abundant ignition source with sparks emitting from their engines (Brose et al., 2001), which ignited the slash and caused wildfires that spread to adjacent uncut forests (Abrams et al., 2021; Brose et al., 2001; Fowler and Konopik, 2007). These wildfires were larger in extent, more intense, and substantially more destructive than the fires of Native Americans or early Euro-American settlers (Brose et al., 2001). The Great Cutover, combined with decades of these fires, likely benefitted fire-adapted species, like American chestnut and oaks, that have strong resprouting capacities relative to fire-intolerant species (Abrams, 1992).

These fires, along with the Peshtigo Fire of 1871 in Wisconsin and the Great Fire of 1910 in Montana, gained national attention and progressively changed the public perception of fire in the U.S. During the late 19th century, state-level policies were passed that enacted fire suppression mandates and criminalized those who started forest fires (Brose et al., 2001). In 1905, the U.S. Forest Service was established and one of its primary responsibilities was fire suppression on all federal forest reserves (van Wagtendonk, 2007). A series of devastating wildfires in 1910 solidified the narrative that fires needed to be suppressed in forestlands, and by the 1930s, an entire infrastructure and industry built around fire suppression had been developed that included fire watchtowers, networks of fire wardens, development of wildland fire-fighting techniques and technologies, and propaganda campaigns (Abrams et al., 2021; Brose et al., 2001). In 1934, the U.S. Forest Service enacted their 10 a.m. policy that mandated all fires on federal lands were to be extinguished by 10 a.m. of the next day (Ryan et al., 2013; van Wagtendonk, 2007). While

a minor amount of burning still occurred in private lands throughout this fire suppression era (Abrams et al., 2021; Fowler and Konopik, 2007), the 10 a.m. policy exemplifies the popular opinion and approach to fire in forestlands of the time.

Fire suppression policies were widely successful throughout the eastern U.S. and fire use across the landscape declined considerably as a result of them. These policies remained in effect until the 1980s (van Wagtendonk, 2007), though even after these policies were abandoned, fire occurrences and use across the landscape remained sparse (Nowacki and Abrams, 2008). During this period, the amount of area burned in the eastern U.S. was reduced from approximately 11 million ha in 1940 to about 1 million ha after 1960 (Nowacki and Abrams, 2008). This cessation of burning caused FRIs to increase to levels that far exceed any historic estimates. In the Great Smokey Mountains, mean FRIs increased from 12.7 years to over 2,000 years (Harmon, 1982). Increases in FRIs to this degree were not uncommon, where in West Virginia and western Virginia, post-suppression era FRIs were 1,001 years (Lafon et al., 2017). To accompany these changes in fire frequency, the landscapes of the eastern U.S. became more fragmented from increased human populations and forests became denser, leading to reduced fire sizes and fewer ignitions, respectively (Lafon et al., 2017). Thus, the third and perhaps largest deviation from historic fire regimes was the near-complete cessation of fire from forestlands, which brought with it a cascade of ecological impacts that are still reverberating today.

Another important change to eastern U.S. forests that coincided with the fire suppression era was the functional extinction of the American chestnut via the invasive fungus *Cryphonectria parasitica* (Murrill) Barr. This chestnut blight is an ascomycete that

was discovered in New York in 1904 and quickly spread across the range of the American chestnut (Elliott and Swank, 2008). Prior to this, the American chestnut was the most important tree species in eastern U.S. forests, comprising 22% of total density and 36% of total basal area (Elliott and Swank, 2008). After infestation, nearly all American chestnut trees died throughout the eastern U.S. The pathogen does not affect the roots of the tree though (Paillet, 2002), so evidence of this species in today's forests are the vegetative sprouts that still regenerate, only to become infected again and die back to the ground (Paillet, 2002; Parker et al., 1993). The extent of the ecological impacts caused by this loss may never be known because it occurred before modern ecological principles were developed (Paillet, 2002), but we do know that the American chestnut was a keystone species, in that it provided a food source and habitat to humans and numerous wildlife species (Hepting, 1974; Wilson, 2001). Additionally, it is considered to have been one of the most fire-adapted species (Kane et al., 2020) and its absence from ecosystems makes them less fire-prone and reduces their ability to positively respond to fire events. Consequently, the loss of the American chestnut altered fire regimes, reduced ecosystem biodiversity, and changed forest structures and species compositions in substantial ways that may never be truly realized.

The ecological impacts of Euro-American settlement, extensive unregulated logging, loss of the American chestnut, and the fire suppression era on forest ecosystems and fire regimes caused lasting changes to species compositions and forest structures throughout the eastern U.S. The oak, pine, American chestnut, and hickory species that initially regenerated following the Great Cutover grew to dominate forest communities. However, they rely upon periodic forest disturbances, such as fire, to effectively

regenerate, recruit into larger size classes, and maintain canopy dominance (Abrams and Nowacki, 1992). While fire was suppressed, fire-intolerant species were no longer being selectively culled by burning and were able to regenerate in forest understories that grew much more densely (Abrams, 1992; Fei et al., 2011; Hutchinson et al., 2008). These species include maples, beeches, yellow-poplar, and birches (*Betula* spp.) which in a frequent fire regime are typically restricted to mesic coves and bottomlands, but in the absence of fire, have been able to establish on sub-mesic and xeric sites (Abrams, 1998). The dense conditions of forest understories favored these fire-intolerant species that are typically more shade-tolerant, and over time they grew to dominate forest midstories (Abrams, 1992; Blankenship and Arthur, 2006; Hutchinson et al., 2008; Nowacki and Abrams, 1991) while pyrophytic oaks, pines, and hickories, which are oftentimes shade-intolerant, are unable to acquire the light they need to recruit into larger size classes (Abrams, 1992).

These fire-intolerant species facilitate forest mesophication, a process in which the heavy shade these species cast limits understory air movement, increases humidity, and decreases light availability and temperatures (Nowacki and Abrams, 2008). These conditions select for shade-tolerant species, eventually resulting in a positive feedback loop, where conditions become continually improved for shade-tolerant mesophytic species (Nowacki and Abrams, 2008). The mesophication of forest understory microclimates reduces the flammability of forest litter via increasing dampness and promoting moisture-accelerated decomposition (Alexander and Arthur, 2014; Kane et al., 2021), creating conditions that inhibit future fire events that are essential for maintaining fire-adapted communities. In many forests, this may result in permanent transitions to

alternative stable states, where returning to historic forest compositions and structures may be impossible (Nowacki and Abrams, 2008).

Today, the forests in this region can often be characterized as having canopies composed of fire-adapted oaks, pines, and hickories that regenerated after the Great Cutover, whose seedlings are able to establish and persist in the understory, but as a result of mesophication, those seedlings are unable to recruit into larger size classes (Abrams, 2003; Dyer and Hutchinson, 2019). If this pattern continues, pyrophytic species, particularly oaks and pines, may constitute a minor component of forest ecosystems, which would be unprecedented based on the last 6,000 years and would have vast ecological ramifications. Already, ecosystems across the region have grown more homogenous (Nowacki and Abrams, 2008) and oak species' importance has declined substantially (Fei et al., 2011). Oak species are a fundamental driver of ecosystem processes in these forests (Fralish, 2004), and if they cannot regenerate into canopy size classes, the communities they create will be lost. Such a loss will negatively affect numerous wildlife species that depend on their mast (McShea, 2000; McShea and Healy, 2002; Tallamy, 2021), while also altering ecosystem nutrient cycling (Alexander and Arthur, 2014), forest hydrology (Alexander and Arthur, 2010), and community diversity (Hanberry et al., 2020; Nowacki and Abrams, 2008).

In an effort to reverse these forest changes and prevent alternative stable states from developing, land managers have reintroduced fire into forest ecosystems, primarily through prescribed burning (Brose et al., 2001). These are purposeful burns that are administered under a predetermined set of weather conditions, and are generally low-severity surface fires (Brose et al., 2001). If administered only once or without any additional silvicultural

treatments, they are largely ineffective at creating meaningful changes in forest structure or composition in ways that benefit pyrophytic species' regeneration (Brose et al., 2013). This is because a single low-severity fire prompts sprouting by both pyrophytic and mesophytic species (Arthur et al., 2015; Kuddes-Fischer and Arthur, 2002) and is oftentimes unable to kill larger stems to create light gaps necessary for oak and pine recruitment (Kuddes-Fischer and Arthur, 2002; Royse et al., 2010).

Burns that are repeated multiple times and those that are combined with silvicultural treatments tend to be more successful in promoting oak and pine regeneration and recruitment (Brose et al., 2013). Multiple fires can enhance oak and pine seedling and sapling regeneration, limit mesophytic competitors (Alexander et al., 2008; Green et al., 2010; Holzmueller et al., 2009; Keyser et al., 2017; Signell et al., 2005), and increase light gaps (Hutchinson et al., 2012a), but few studies have shown multiple prescribed fires to specifically enhance the recruitment of oak and pine saplings into midstory size classes. This is likely either because multiple fires may still not reduce light levels enough, or longer fire-free periods are needed, to allow for recruitment (Thomas-Van Gundy et al., 2015). Burning combined with silvicultural prescriptions aimed to increase understory light levels, such as a shelterwood thinning, have been shown to enhance oak and hickory regeneration relative to mesophytic competitors (Brose and Lear, 1998; Iverson et al., 2017, 2008), but the evidence for this combination of treatments benefiting oak and pine recruitment is also sparse. In fact, Albrecht and McCarthy (2006) found that mechanical thinning and burning did not release oak seedlings and saplings from growth suppression. However, thinning treatments combined with multiple burns spaced out enough to allow for a sufficient fire-free interval may lead to recruitment of oak and pine species into sub-

canopy sizes (Hutchinson et al., 2012b). So, to overcome the ecological impacts of the fire suppression era and to foster oak and pine growth into larger size classes, intensive long-term forest management that involves a combination of multiple burns and thinning treatments may be needed (Arthur et al., 2021; Dey, 2014)

There is a growing recognition of the ecological benefits of incorporating attributes of wildfire, such as increased burn severity, into forest management plans (Hiers et al., 2020), as it may alleviate some of the logistical and financial challenges of intensive forest management while also restoring fire-dependent communities. Wildfires often create a spatial mosaic that is heterogeneous in burn severity (Hutchinson et al., 2008), which prompts greater ranges of ecological responses compared to prescribed fires. Areas with increased burn severity are more likely to undergo forest structural changes, such as decreased density and basal area in the canopy and midstory (Black et al., 2018; Schwartz et al., 2016), which increases light availability (Reilly et al., 2006) and prompts understory regeneration (Brose and Lear, 1998). Because of this, increased burn severity has been directly shown to increase the recruitment of oak (Black et al., 2018) and pine (Black et al., 2018; Saladyga et al., 2022) seedlings and saplings into larger size classes. Additionally, the structural and compositional changes that result from increased burn severity have been shown to benefit wildlife populations, particularly avian communities (Brown et al., 2014; Greenberg et al., 2013; Rose and Simons, 2016). Accordingly, inclusion of high-severity fire may be an important aspect of burn prescriptions for land managers whose goal is to limit the mesophication process, restore fire-dependent communities, and increase forest biodiversity.

The mechanism by which fire-caused forest structural changes promote oak and pine regeneration and recruitment is through modifying understory microclimate conditions to be warmer and drier with greater light levels (Refsland and Fraterrigo, 2018; Stevens et al., 2015). Understory microclimates are the near-surface climate conditions (e.g. air and soil temperatures, vapor pressure deficit, solar radiation, humidity, soil moisture, wind speed, etc.) that drive biological processes (Chen et al., 1999). These conditions are altered by forest structure and composition, where dense amounts of forest cover composed of species that cast heavy shade can substantially buffer or modify large-scale climate conditions to create microclimate conditions that are substantially different (Aussenac, 2000). Consequently, there is a positive relationship between forest moderating capacity and canopy density (von Arx et al., 2013), where decreased density causes beneath canopy light availability to increase (Kovács et al., 2020; Ma et al., 2010), air and soil temperatures to increase (Ma et al., 2010; Morecroft et al., 1998; Wolf et al., 2021), relative humidity to decrease (Ma et al., 2010; von Arx et al., 2013), and soil moisture to increase via reduced transpiration (von Arx et al., 2013). These conditions impact the survival and growth of seedlings and saplings (Aussenac, 2000; von Arx et al., 2013), indicating that the increased regeneration and recruitment of fire-adapted species associated with increased burn severity is likely due to microclimate conditions being altered in ways that are increasingly favorable for their growth.

Changes to forest structures that influence microsite growing conditions have important implications for future forest compositions and may be instrumental in combatting the destabilizing effects of anthropogenic climate change. Due to projected increases in temperature, drought severity, and wildfire, oak and pine species are expected

to be favored in future climate scenarios (Iverson et al., 2019). Though, because present-day forests are currently transitioning from dominance of fire-adapted species to mesophytic species, decreased ecosystem health and degraded future conditions may likely occur unless forests are actively managed in ways that benefit fire-adapted species in forest understories (Vose and Elliott, 2016). Active management that incorporates characteristics of wildfire, like increased burn severity, may play an important role in promoting these species that are adapted to climate change. Delineating the ecological implications of wildfire events and their management utility is also increasing in importance due to prescribed burn windows becoming shorter (Vose et al., 2021) and wildfire events predicted to increase in frequency and size in the eastern U.S. (Lafon and Quiring, 2012). Because of this, examining and understanding the role of wildfire is an essential component to informing land management practices so that forest ecosystem biodiversity and future health can be safeguarded.

This thesis represents an effort to elucidate the effects of wildfire in the Cumberland Plateau physiographic region; building on previous research by Black et al. (2018). Specifically, I investigate the long-term changes in forest community and structure at varying levels of burn severity (Chapter 2) and examine if the structural changes that are related to burn severity have an influence on understory microclimate conditions twelve years following a wildfire (Chapter 3). The results of this thesis are intended to expand scientific understanding of fire ecology, while providing land managers with practical information for considering the role wildfire plays in present day forests, and how aspects of wildfire may be incorporated into land management practices to restore fire-adapted forest communities.

CHAPTER 2. HIGHER SEVERITY FIRE INCREASES THE LONG-TERM COMPETITIVE STATUS OF PYROPHYTES IN AN UPLAND OAK-PINE FOREST, KENTUCKY, USA

2.1 Abstract

In the eastern U.S., oak (*Quercus* spp. L.) species have historically dominated upland forest communities but are now experiencing widespread regeneration challenges, in part due to 20th century fire exclusion policies, leading to replacement by mesophytic species. Fire events that burn at higher severities may play an important role in ameliorating these challenges by facilitating oak stem recruitment into larger size classes. A wildfire in the Daniel Boone National Forest, Kentucky, USA provided the opportunity to monitor forest vegetation response for twelve years post-burn and to investigate the long-term impacts of burn severity on oak-pine community regeneration. I examined the effects of burn severity on species diversity, basal area, stem density, stem recruitment into the midstory (2-10 cm diameter at breast height (DBH); 0.79-3.94 in DBH), and non-native invasive plant (NNIP) populations. After twelve years, burn severity was positively related to midstory species diversity, basal area, and stem density. Burn severity was positively related to midstory recruitment of yellow pine (*Pinus echinata* Mill., *P. rigidia* Mill., *P. virginiana* Mill.) and unrelated to recruitment of oak and mesophytic species. Likewise, burn severity was negatively related to the relative importance of midstory mesophyte species and positively related to the relative importance of midstory pyrophyte species. Increased burn severity dramatically increased the probability of invasive species presence, particularly Chinese silvergrass (*Miscanthus sinensis* Andersson). Earlier results found that up to six years post-fire, burn severity was significantly and positively related to oak sapling recruitment (Black et al., 2018). My results indicate that, 6 years later, higher burn severity was no longer

associated with oak midstory recruitment, but was associated with increased recruitment and importance of other pyrophytic species, particularly yellow pines. My results also suggest that a single high-severity fire can provide long-term recruitment benefits to yellow pine species and increase the competitive status of pyrophytes relative to mesophytes. To re-stimulate recruitment of oak into the small midstory, it may be necessary to reintroduce fire between six and twelve years following a high-severity burn. To safeguard the ecosystem benefits of increased burn severity, non-native invasive plant control methods must be employed for several years following high-severity fire.

2.2 Introduction

In the eastern United States, fire was a common occurrence until the early 20th century when fire suppression policies, such as the U.S. Forest Service 10 AM Policy of 1935, were adopted (Delcourt and Delcourt, 1997; Ryan et al., 2013). Prehistorically, lightning ignitions were responsible for periodic fire events across the landscape (Petersen and Drewa, 2006); when Native American populations expanded approximately 13,000 y.b.p., anthropogenic burning became the dominant source of fire ignitions (Delcourt and Delcourt, 1997), with median fire return intervals of 5.4 years (Lafon et al., 2017). The selective pressures of these natural and anthropogenic fire regimes strongly shaped vegetation physiology, structure, composition, and distribution (Delcourt and Delcourt, 1997; Delcourt et al., 1998; Stambaugh et al., 2015). Euro-American settlement marked the first major alteration to these established fire regimes (Abrams and Nowacki, 1992), and the cessation of fire throughout the 20th century caused profound impacts on ecosystem

dynamics, especially in oak-pine dominated forests of the eastern U.S. (Hutchinson et al., 2008).

Several oak and pine species, including white oak (*Quercus alba* L.), chestnut oak (*Q. montana* Willd.), scarlet oak (*Q. coccinea* Muenchh.), and yellow pines (*Pinus echinata* Mill., *P. rigidia* Mill., *P. viginiana* Mill.), rely upon periodic fire events to create a suite of favorable conditions that support successful understory regeneration, recruitment into larger size classes, and maintenance of canopy dominance (Abrams and Nowacki, 1992; Nowacki and Abrams, 1991). In the absence of fire, these pyrogenic species are experiencing widespread recruitment failures (Abrams, 1992), and are largely being replaced by later successional fire-intolerant species, including red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall), American beech (*Fagus grandifolia* Ehrh.), birch (*Betula* L. spp.), and yellow poplar (*Liriodendron tulipifera* L.) (Abrams, 1992; Fei et al., 2011; Hutchinson et al., 2008). These species facilitate forest mesophication, a process in which they cast heavy shade and limit air movement, causing understory microclimate conditions to be cooler, more humid, and less flammable. This process creates a positive feedback loop for selection in favor of shade-tolerant mesophytic species and against pyrogenic species, resulting in ecosystem transitions to alternative stable states (Nowacki and Abrams, 2008).

As a result, eastern U.S. oak forests can be characterized as having canopy layers dominated by oak species that regenerated prior to fire cessation (ca. 1870-1930), whose seedlings are able to establish and persist in the understory, but are unable to recruit into midstory sizes where mesophytic species grow densely and are more competitive (Abrams, 2003; Dyer and Hutchinson, 2019). Now, oak species' overall importance has dramatically

declined (Fei et al., 2011) and if current recruitment challenges continue, they may comprise an unprecedentedly minor component of future forests. Such a transformation has extensive ecological implications, as oaks play a keystone role in biotic and abiotic ecosystem processes (Fralish, 2004). For instance, acorn mast is essential for many wildlife populations, including mice, squirrels, turkeys, deer, and bears (McShea, 2000; McShea and Healy, 2002), as well as some insect populations, such as acorn weevils (*Curculio* spp.), ants (*Temnothorax* spp.), and acorn moths (*Blastobasis glanulella)* (Tallamy, 2021). Decreases in oak dominance will also substantially alter precipitation distribution below the canopy (Alexander and Arthur, 2010), along with the nutrients it carries (Alexander and Arthur, 2014, 2010), and will decrease the compositional, structural, and spatial diversity (Hanberry et al., 2020; Nowacki and Abrams, 2008) that has defined this ecoregion (Braun, 1950; Wharton and Barbour, 1973).These shifts are also associated with decreased ecosystem resilience and adaptive capacities to climate change (Iverson et al., 2019)

With the aim of curtailing these forest changes, land managers have reintroduced fire primarily through prescribed burning, or burning combined with thinning treatments (Brose et al., 2001). However, there is a growing recognition of the ecological benefits of incorporating attributes of wildfire into management plans (Hiers et al., 2020), particularly for restoring fire-dependent species and alleviating oak-pine recruitment issues (Black et al., 2018; Saladyga et al., 2022). Wildfire events often create a heterogeneous mosaic of burn severity (Hutchinson et al., 2008) that prompts a greater range of ecological responses than prescribed fires, which are typically lower in severity and more spatially homogenous (Brose et al., 2001). Patches with increased burn severity are more likely to experience

decreased density and basal area in the midstory and overstory initially following a fire, which increases understory light availability (Reilly et al., 2006). These changes to forest structure are essential for promoting growth of understory pyrogenic species (Kuddes-Fischer and Arthur, 2002), and have been shown to directly increase the recruitment of oak (Black et al., 2018) and pine (Black et al., 2018; Saladyga et al., 2022) saplings. At my research site in the Cumberland Plateau, Black et al. (2018) found that increased burn severity bolstered the competitive status of oaks and pines in the understory at six years post-fire. This may indicate that a single higher severity fire can create long-term changes in forest conditions that allow pyrogenic oaks and pines to maintain forest dominance (Black et al., 2018).

Despite the potential benefits of higher burn severity, non-native invasive plant (NNIP) establishment and proliferation following fire events complicates its use as a management tool. The increasingly disturbed soil, reduced space competition, increased available moisture, and greater light conditions associated with high-severity fire can provide an effective pathway for NNIPs in central and southern Appalachian mixed hardwood forests, especially for princess tree (*Paulownia tomentosa* [Thunb.] Siebold & Zucc. Ex. Steud) and Chinese silvergrass (*Miscanthus sinensis* Andersson) (Black et al., 2018; Miller et al., 2010). Princess tree is known to alter forest flammability and inhibit the germination and growth of native seedlings (Williams and Wang, 2021), particularly in upland xeric ecosystems (Kuppinger et al., 2010). Chinese silvergrass dramatically increases forest litter flammability, can increase organic matter decomposition rates, and has been shown to severely suppress tree growth (Stewart et al., 2009). Due to these impacts, both of these species have been listed as a moderate to severe ecosystem threat

throughout the eastern U.S. (Clemson University Cooperative Extension, 2011; Georgia Exotic Pest Plant Council, 2018; Heffernan et al., 2014; Indiana Invasive Species Council, 2022; Kentucky Exotic Pest Plant Council, 2015; North Carolina Invasive Plant Council, n.d.; Pennsylvania Invasive Species Council, 2021; Tennessee Invasive Plant Council, 2023) and are a primary concern when considering the use of fire as a management tool.

Nevertheless, understanding the ecological implications and management utility of wildfire events is becoming increasingly important in the eastern U.S., as wildfire events are anticipated to increase in frequency and size (Lafon and Quiring, 2012) and prescribed burning windows are becoming narrower with anthropogenic climate change (Vose et al., 2021). A key difference between wildfire and prescribed fire is the range of burn severities that occur in wildfires (Hutchinson et al., 2008), so understanding ecological responses at varying levels of burn severity has the potential to inform management strategies to better meet long-term objectives. In 2010, a wildfire that was ignited accidentally by campers within the USDA Forest Service Daniel Boone National Forest (DBNF), Kentucky, USA, provided an opportunity to study changes in species composition and forest structure at varying levels of burn severity. Black et al. (2018) analyzed the vegetation response to this wildfire up to six years post-burn, and identified that further research was needed to determine whether the observed results would persist.

The objective of this study was to analyze the current and long-term trends in forest stand structure and species composition and compare them to the findings of Black et al (2018). I hypothesized that: (H1) the relationships between species diversity, forest community assemblage, and forest structure with burn severity do not vary between or among years; (H2) burn severity is negatively related to stem density and basal area for all

live trees (≥ 2 cm DBH; ≥0.79 in DBH); (H3) burn severity is positively related to the recruitment of fire-adapted xeric species in midstory (2-10 cm DBH; 0.79-3.94 in DBH) and canopy (10+ cm DBH, 3.95+ cm DBH) size classes; (H4) burn severity has no relationship with the recruitment of shade-tolerant mesophytic species in midstory and canopy size classes; (H5) for trees <2cm DBH (<0.79 in DBH), burn severity is positively related to species diversity of small seedling (<50 cm height; <19.7 in height) and large seedling (>50 cm height; >19.7 in height) species diversity; and (H6) burn severity is positively related to the presence of and area occupied by NNIP species.

2.3 Methods

2.3.1 Study Area

The study was conducted on the Fish Trap Fire (FTF), which was an accidental wildfire that occurred in the fall of 2010. The study site is located within the Red River Gorge Geological Area (RRGGA) of the Daniel Boone National Forest (DBNF), in Powell County, Kentucky, which is part of the Cumberland Plateau physiographic region. Generally, this region's climate can be described as continental, having moderately cold winters and warm, humid summers (Wharton and Barbour, 1973), with a mean annual precipitation of 136.47 cm (53.73 in) and a mean annual temperature of 13.1˚C (55.6˚F) (NOAA, 2023). During winter, the average temperature is 2.3˚C (36.1˚F), whereas in summer, the average temperature is 23.1˚C (73.5˚F) (NOAA, 2023).

Topographically, this study area is characterized by highly dissected uplands and streams of the Red River watershed (Braun, 1951). The elevation ranges between 177 and 439 m (580.7 -1440.3 ft). Ridgetop soils are primarily Alticrest and Ramsey soil series

derived from Pennsylvanian sandstones and conglomerates and shales of the lower Breathitt formation (Soil Survey Staff, 2021). This Pennsylvanian sandstone also typifies the rock outcrops and cliffs that are common to this study area. Alticrest is a well-drained sandy loam and Ramsey is an excessively drained sandy loam (Soil Survey Staff, 2021). The slopes are dominated by the Helewacha soil series, consisting of parent material that is coarse loamy colluvium (Soil Survey Staff, 2021). Due to this underlying geology, the RRGGA contains numerous natural sandstone arches, cliffs, rock shelters, and other geologic formations (Braun, 1951). These formations, along with the area's complex topography, provide a myriad of site conditions and habitat types that produce exceptionally high biodiversity, making the forest type here one of the most complex in North America (Braun, 1951; Wharton and Barbour, 1973).

In the RRGGA, the composition of woody vegetation communities ranges from those communities common to xeric uplands, which are typically dominated by scarlet oak, chestnut oak, black oak (*Q. velutina* Lam.), white oak, and yellow pines, to mesic cove communities, dominated by eastern hemlock (*Tsuga canadensis* (L.) Carrière), yellow-poplar, sugar maple, eastern white pine (*P. strobus* L.), magnolias (*Magnolia* spp. L.) and hickories (*Carya* spp. Nutt.) (Black et al., 2018; Wharton and Barbour, 1973). This study focused on xeric uplands and ridgetops, as this was primarily where the FTF burned. These xeric uplands often have midstories composed of red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* A.P. DC.), black gum (*Nyssa sylvatica* Marshall var. *silvatica*), and sassafras (*Sassafras albidum* (Nutt.) Nees) (Black et al., 2018). Here, the understory shrub community is largely dominated by green briar (*Smilax* spp. L.), mountain-laurel (*Kalmia latifolia* L.) and *Vaccinium* spp. L. (Black et al., 2018).

2.3.2 Fish Trap Fire

The Fish Trap Fire was ignited accidentally on October 24, 2010 by campers, and was not fully extinguished until November 9, 2010, having burned 673.8 ha (1665.0 acre) in the DBNF, Kentucky, USA (37°49' N, 83°40' W). In 2011, a fine-scale plot-level assessment of burn severity was conducted using composite burn index (CBI) (Key and Benson, 2006) to quantify the impacts of the fire on site characteristics, such as trees, shrubs, herbs, and substrates (Key and Benson, 2006). This scale ranges from 0 to 3, spanning the possible range of severity between unburned and greatest burned effect, respectively (Key and Benson, 2006). The post-hoc use of CBI was determined to be an accurate measure of burn severity (Upadhaya, 2015), with CBI and post-fire differenced normalized burn ratio (ΔNBR) values strongly related ($r_s = 0.90$, $p = 1.19e\text{-}09$, $F_{1,25} = 87.67$, $R^2 = 0.77$). Likewise, Black et al. (2018) found CBI to have no relationship with Landsat-derived pre-burn normalized differenced vegetation index (NDVI) or topographic wetness index (TWI), and concluded that CBI variation was a function of the effects of the fire, rather than pre-fire landscape variability.

The burn severity of the Fish Trap Fire was highly heterogeneous, ranging from high-severity stand-replacing fire to unburned areas (Black et al., 2018). The most severely burned areas, which occupied <10% of total area burned, experienced nearly 100% loss of vegetation within the year following the fire, and had patches where the litter layer burned down to mineral soil (Black et al., 2018). In areas where there was substantial mortality of large trees, the soil was much wetter for several years following the fire allowing for the successful establishment of species not commonly found on xeric uplands (David Taylor,

DBNF Forest Botanist, Winchester, Kentucky USA, personal communication). This phenomenon was likely due to a combination of factors including a significant reduction in transpiration coupled with clay lenses in some places within the burn area, and the resinous discharge of species such as pitch pine (*P. rigida* Mill) that created some areas with soil hydrophobicity and altered soil moisture concentrations (Claudia Cotton, DBNF Forest Soil Scientist, Winchester, Kentucky USA, personal communication). As a result, the Fish Trap Fire directly and indirectly modified forest structural and compositional characteristics to varying degrees based on burn severity (Black et al., 2018).

2.3.3 Data Collection

In August of 2011, researchers established 30 permanent research plots across the Fish Trap Fire containment boundary, which were monumented with rebar and referenced with GPS coordinates (Figure 2.1). These research plots were selected at random across the burned area, resulting in a relatively even distribution of plots across the gradient of burn severity, with 35% of plots being unburned to low burn severity (CBI 0 to 1), 35% moderate (CBI 1 to 2), and 30% high (CBI 2 to 3) severity (Black et al., 2018). Data collection occurred in 2011, 2013, 2016, and 2022, yielding measurements for one, three, six, and twelve years post-fire, respectively. The results of this data collection through 2016 were published in Black et al. (2018), and data collection methods have remained largely identical through time. Out of the 30 plots established, five were removed from analysis in 2016 and 2022 due to data inconsistencies, non-xeric site types, or being impacted by recreational use, yielding 25 plots. Non-xeric sites were excluded from analysis because the majority of the burned area, and nearly all of the research plots, were on xeric uplands,

so excluding these sites ensured that comparisons were being made between plots that are similar in site productivity and biophysical context. Overall, the omission of these plots did not substantially affect the distribution of plots across the severity gradient.

At each research plot, a circular nested plot design was used to assess forest composition and structure. Each plot's spatial resolution was 500 m^2 (0.05 ha, 0.12 acre). For all stems ≥ 2 cm (0.79 in) diameter at breast height (DBH) within each plot I recorded tree species, DBH, canopy vigor, number of basal sprouts, and number of sprouts browsed by wildlife. Canopy vigor was visually assessed on a scale of 0 to 3, with 0 indicating dead, 1 indicating >50% canopy dieback, 2 indicating 25-50% canopy dieback, and 3 indicating <25% canopy dieback. Additionally, within a 25 m^2 (0.006 acre) circular microplot sharing the same plot center as the larger plot, stems <2 cm (0.79 in) DBH were counted, identified to species, and recorded as small (<50 cm (19.7 in) height) or large (≥ 50 cm (19.7 in) height). To accompany these data, along two 25.2 m (82.7 ft) transects oriented N to S and E to W, ground cover was recorded every 10 cm (3.9 in) as mineral soil, rock, moss, litter, vegetation, or woody debris. Lastly, the presence of any non-native invasive woody or non-woody plant species (NNIP) occurring within the entire plot was recorded, and within the microplot, their presence, percentage of ground cover occupied, and maximum height were recorded. Collection of NNIP data prior to 2016 was focused on princess tree (*Paulownia tomentosa* [Thunb.] Siebold & Zucc. Ex. Steud*)*, which was known to establish after the FTF. However, in 2016, floristic surveys revealed the presence of several other NNIPs. Thus, the NNIP data for princess tree is consistent throughout all sampling years, and data on other NNIPs are robust for 2016 and 2022.

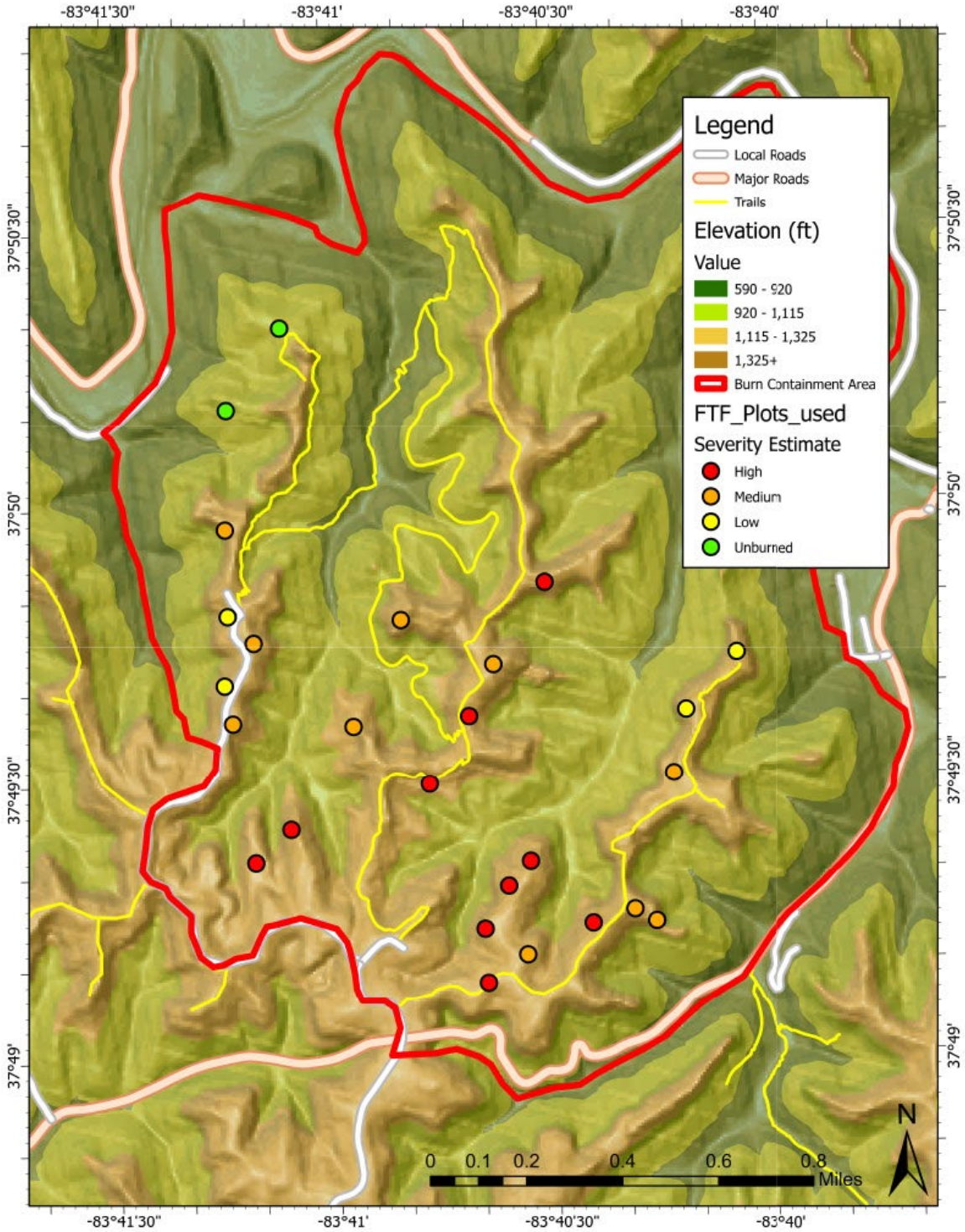

Figure 2.1 Locations of the permanent field plots at the location of the Fish Trap Fire, a wildfire that burned in 2010 on the Cumberland Platea, Kentucky, USA.

2.3.4 Statistical Analysis

From the measurements described in Section 2.3.3, several metrics were calculated to provide information on the vegetation response to the FTF. For stems ≥2 cm (0.79 in) DBH these include basal area (m^2/ha; ft^2/acre), stem density (stems/ha; stems/acre), relative importance values, Shannon's Diversity Index (SHDI), Simpson's Diversity Index, and species richness. The formula used for calculating relative importance values was:

$$\frac{R_{ba} + R_{sd}}{2} * 100$$

where R_{ba} and R_{sd} are the basal area and stem density of a given species relative to all species measured in a given plot.

To assess the relationship between fire severity and forest vegetation measurements, linear regression was used. Prior to any regression modeling, statistical assumptions of data independence and normality were assessed for all variables being analyzed. After model generation, statistical assumptions (homoscedasticity, outliers, and normally distributed residuals) were assessed for each model. Any violations of these assumptions were corrected by transforming the data with a square-root or natural log transformation. Linear regression models were generated using R (R Core Team, 2023), and for each calculated metric, linear, square-root, and 2nd, 3rd, and 4th degree polynomial models were generated. From these models, Akaike's Information Criteria (AIC) was used to determine which model best described the metric's relationship with burn severity. The resulting best-fit model was then plotted using the ggplot2 and ggpubr packages in R (Kassambara, 2022; R Core Team, 2023; Wickham, 2016).

To analyze stem recruitment over time, species were grouped into one of four categories related to fire: pyrophytes, mesophytes, intermediates, and no relationship (Table 2.1). Species were placed in categories based on their fire tolerances, adaptive traits, response to fire events, and ecological impacts on post-fire environments, as well as similar categorizations in recent literature (Arthur et al., 2021; Saladyga et al., 2022). Thus, pyrophytes are species that have physiological tolerances to fire, have evolved characteristics to promote fire events, and are known to be more successful in frequent fire regimes. Mesophytes are species that are known to facilitate the process of mesophication through having branch architecture and leaf morphology that casts heavy shade and limits understory air movement and whose litter is notably fire-inhibiting. Intermediate species are those that do not have traits associated with fire tolerance, but are also not known to facilitate mesophication. For each of these species groupings, recruitment was calculated as the difference in number of stems per area between 2022 and previous measurement years at a given size class. Size classes were midstory (2-10 cm DBH; 0.79-3.94 in DBH) and canopy (10+ cm DBH; 7.87+ in DBH). Recruitment was calculated from 2011 to 2022, and for more recent recruitment from 2016 to 2022. Linear regression was used to explore the relationship of recruitment to burn severity.

For stems <2 cm (0.79 in) DBH, linear regression was used to assess the relationships of species abundance and species diversity with burn severity, and generalized linear models (GLM) with a Poisson distribution were used to model species richness in R (R Core Team, 2023). Similarly, GLM with a binomial distribution was used to predict the presence of NNIPs in year twelve post-fire, based on burn severity and groundcover.

Table 2.1 Species groupings of all tree species found since 2011 at the FTF study site, Daniel Boone National Forest, Kentucky. Groupings are based on previous categorizations (Arthur et al., 2021; Saladyga et al., 2022) and species' fire tolerances, adaptive traits, response to fire events, and ecosystem impacts (i.e. if they facilitate mesophication or not).

Pyrophytes	Mesophytes	Intermediates	No Relationship
Carya glabra (Mill.)	*Acer rubrum* L.	*Amelanchier arborea* (Michx. F.) Fernald	*Aralia spinosa* L.
Carya tomentosa (Poir.) Nutt.	*Acer saccharum* Marshall	*Cornus florida* L.	*Hamamelis virginiana* L.
Kalmia latifolia L.	*Betula lenta* L.	*Fraxinus americana* L.	*Ilex opaca* Ait.
Pinus echinata Mill.	*Fagus grandifolia* Ehrh.	*Nyssa sylvatica* var. *silvatica*	*Magnolia macrophylla* Michx.
Pinus rigida Mill.	*Liriodendron tulipifera* L.	*Ostrya virginiana* (Mill.) K. Koch	*Malus* sp. Mill.
Populus grandidentata Michx.	*Magnolia acuminata* L.	*Pinus virginiana* Mill.	*Platanus occidentalis* L.
Quercus alba L.	*Oxydendrum arboreum* A.P. DC.	*Sassafras albidum* (Nutt.) Nees	*Rhus copallinum* L.
Quercus coccinea Muenchh.	*Pinus strobus* L.		*Rhus glabra* L.
Quercus montana Willd.			*Viburnum dentatum* L.
Quercus rubra L.			
Quercus velutina Lam.			
Robinia pseudoacacia L.			

2.4 Results

2.4.1 Species Diversity and Richness

The relationships of burn severity with species diversity and richness changed over time since the FTF. For all stems >2 cm (0.79 in) DBH twelve years post-fire, burn severity was positively and significantly related to SHDI ($R^2 = 0.257$, $F_{1, 24} = 9.63$, $p = 0.005$) and richness (OR = 1.161, $p = 0.040$) for all stems > 2 cm (0.79 in) DBH, which was driven by the positive relationship between burn severity and midstory stems ($R^2 = 0.330$, $F_{1, 24} = 13.3$ and $p = 0.001$). Prior to this, there were no significant relationships between burn severity and species diversity and richness. At year six post-fire, burn severity was positive correlated with SHDI ($r_s = 0.393$) and richness ($r_s = 0.621$), though these relationships were not statistically significant. At year one, burn severity displayed a moderately negative correlation with SHDI ($r_s = -0.388$) and species richness ($r_s = -0.350$), but these relationships could not be modeled due to uncorrectable assumption violations.

2.4.2 Stem Density and Basal Area

The relationship between stem density and burn severity also varied by species groupings and size classes twelve years after the FTF. Overall, burn severity was positively related to stem density for all stems >2 cm (0.79 in) DBH ($R^2 = 0.280$, $F_{1, 24} = 10.73$, $p = 0.003$). The non-oak-pine pyrophyte group was the only species group that was related to burn severity for all stems ($r_s = 0.651$, $R^2 = 0.345$, $F_{1, 13} = 8.38$, $p = 0.013$). These stem density trends for all stems >2 cm (0.79 in) were primarily the result of changes in midstory stem density. Increased burn severity yielded increased midstory stem density ($R^2 = 0.293$,

$F_{1, 24}$ = 11.38, p = 0.003), particularly for non-oak-pine pyrophytes (R^2 = 0.392, $F_{1, 13}$ = 10.04, p = 0.007) (Figure 2.2), though oaks had a near-significant relationship as well (R^2 = 0.082, $F_{1, 24}$ = 3.23, p = 0.085). Stem density of canopy trees displayed a negative relationship with burn severity (R^2 = 0.130, $F_{1, 24}$ = 4.74, p = 0.039), primarily among oak species (R^2 = 0.600, $F_{1, 16}$ = 26.51, p < 0.001). Stem density of yellow pine, maple, non-maple mesophytes, and intermediate species' had no relationship with burn severity at either size class.

Twelve years post-fire, basal area of all size classes was influenced by burn severity and varied among species groupings. Total basal area (for all stems > 2 cm (0.79 in) DBH) had a negative relationship with burn severity (R^2 = 0.599, $F_{1, 24}$ = 38.35, p < 0.001). This negative relationship was primarily driven by a significant reduction in oak species basal area (R^2 = 0.502, $F_{1, 24}$ = 26.24, p < 0.001) (Figure 2.3). These basal area trends for all stems >2 cm (0.79 in) were largely the result of changes in canopy basal area, where burn severity was negatively related to canopy basal area (R^2 = 0.662, $F_{1, 24}$ = 50.03, p < 0.001) (Figure 2.4A), particularly in canopy oak species (R^2 = 0.500, $F_{1, 16}$ = 17.98, p < 0.001) (Figure 2.4B). Canopy maples (R^2 = 0.201, $F_{1, 11}$ = 4.02, p = 0.070), yellow pines (R^2 = 0.107, $F_{1, 21}$ = 3.641, p = 0.070), and non-maple mesophytes (R^2 = 0.351, $F_{1, 7}$ = 5.34, p = 0.054) displayed a near-significant negative relationship with burn severity as well. Conversely, among midstory trees there was a positive relationship between basal area and burn severity after twelve years (R^2 = 0.679, $F_{1, 24}$ = 16.22, p < 0.001) (Figure 2.5A). This positive relationship was primarily driven by oaks (R^2 = 0.404, $F_{1, 24}$ = 17.97, p = 0.003) (Figure 2.5C) and non-oak-pine pyrophytes (R^2 = 0.358, $F_{1, 13}$ = 7.26, p = 0.018) (Figure

2.5B). Basal area of yellow pine, maple, intermediate, and non-maple mesophytic species' examined separately were not statistically related to burn severity in any size class.

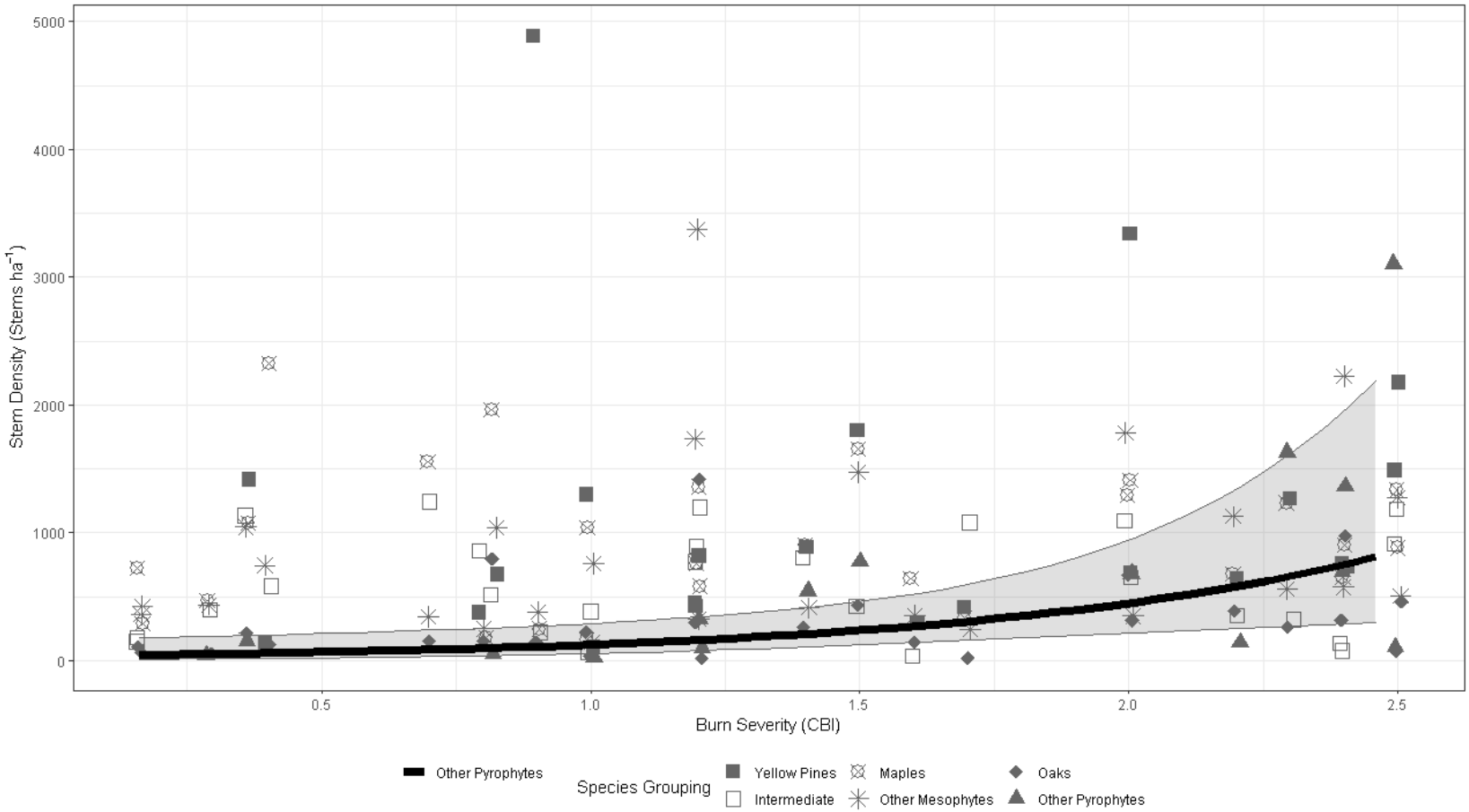

Figure 2.2 Relationship between burn severity, measured as CBI, with midstory (2-10 cm DBH; 0.79-3.94 in DBH) stem density, twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$).

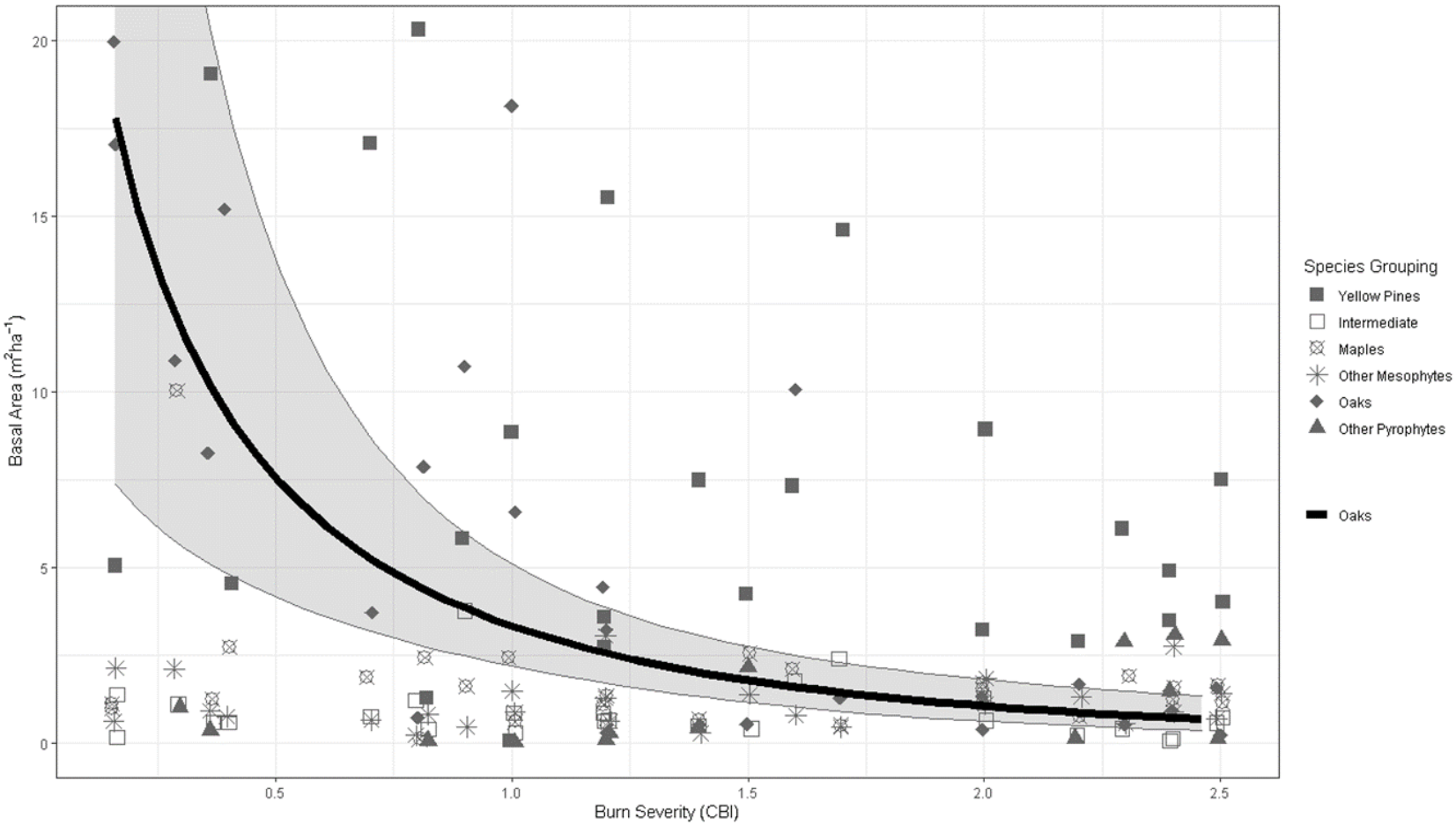

Figure 2.3 Relationship between burn severity, measured as CBI, with basal area of all stems ≥ 2 cm (0.79 in) DBH, twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$).

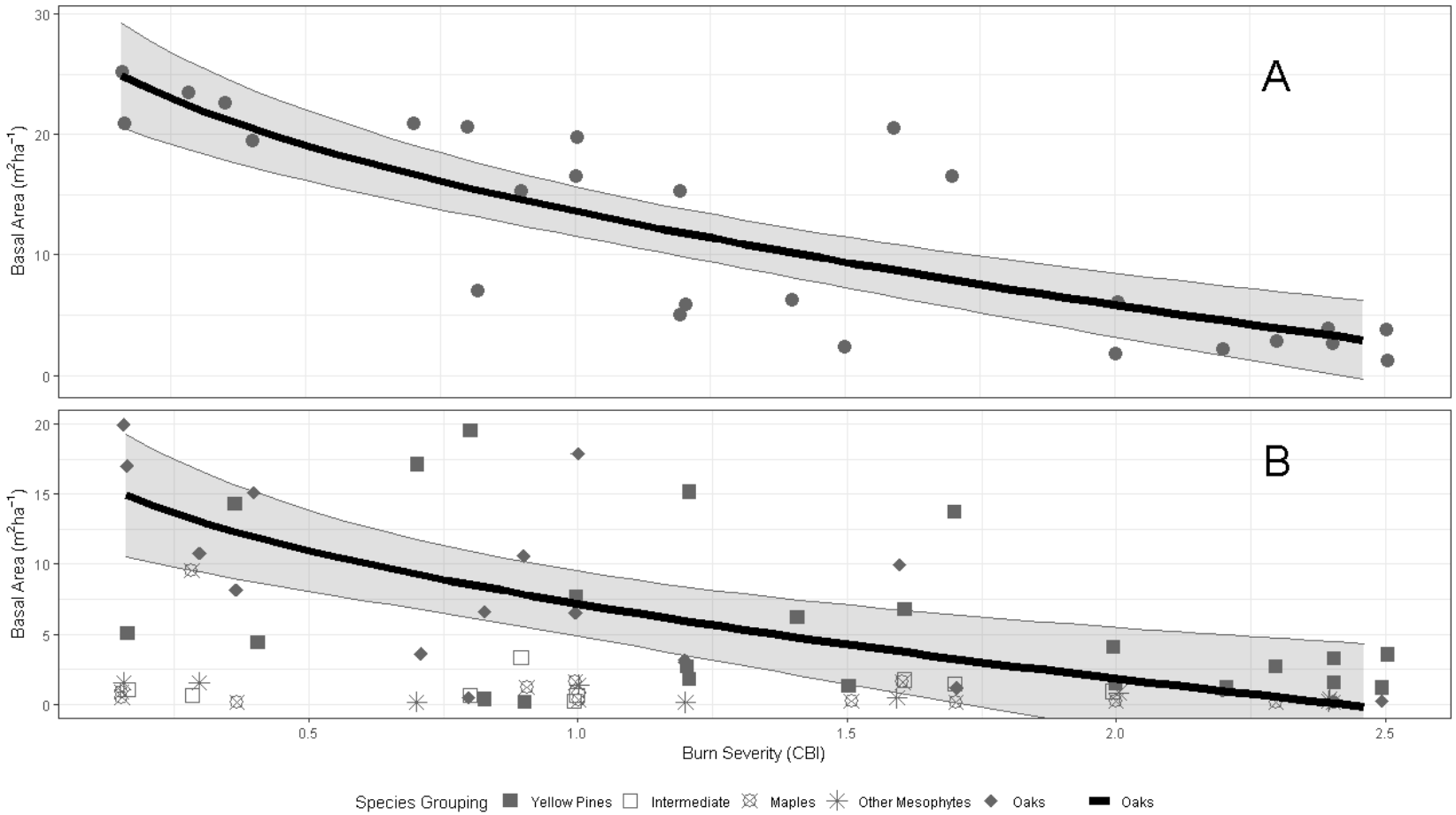

Figure 2.4 Relationship between burn severity, measured as CBI, with basal area of canopy stems (≥ 10 cm (3.94 in) DBH), twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Total canopy basal area per plot (A) and by species groupings (B) are represented. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$).

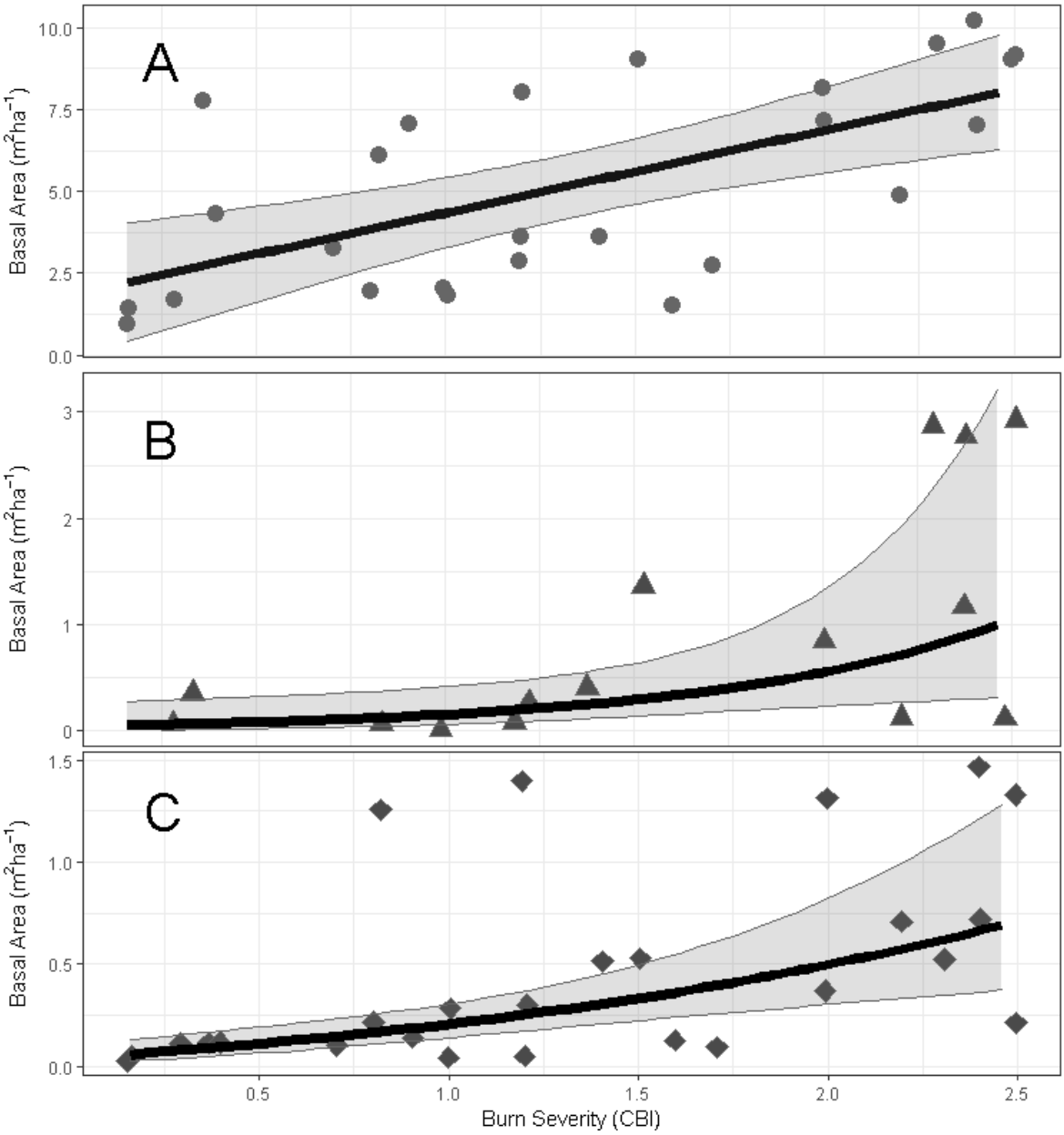

Figure 2.5 Relationship between burn severity, measured as CBI, with midstory (2-10 cm DBH (0.79-3.94 in) DBH) basal area, twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. midstory basal area per plot (**A**) is shown, along with the only significant ($\alpha = 0.05$) species groups: non-oak-pine pyrophytes (**B**), and oak species (**C**).

2.4.3 Importance Values

Twelve years post-fire, there were significant differences between the relative importance values (IV) of different species groupings, which varied among size classes. For all stems > 2 cm (0.79 in) DBH, burn severity was negatively related to oak IV (R^2 = 0.385, $F_{1, 24}$ = 16.65, $p < 0.001$) and positively related to non-oak-pine pyrophyte IV (R^2 = 261, $F_{1, 13}$ = 5.95, p = 0.030). Within the canopy size class, burn severity was negatively related to oak IV (R^2 = 0.241, $F_{1, 16}$ = 6.39, p = 0.022) and positively related to yellow pine IV (R^2 = 0.205, $F_{1, 21}$ = 6.66, p = 0.017) (Figure 2.6). For midstory trees, burn severity was negatively related to mesophytic species' IV (R^2 = 0.273, $F_{1, 24}$ = 10.4, p = 0.004) and positively related to pyrophytic species' IV (R^2 = 0.464, $F_{1, 24}$ = 22.61, $p < 0.001$) (Figure 2.7). Trends for mesophytic species were largely driven by non-maple mesophytes (R^2 = 0.126, $F_{1, 24}$ = 4.62, p = 0.042) (Figure 2.8C) and trends for pyrophytes were driven by non-oak-pine pyrophytes (R^2 = 0.249, $F_{1, 13}$ = 5.65, p = 0.033) (Figure 2.8A).

I also tested whether relationships present between burn severity and relative stem density in 2016 were still present, and whether these relationships varied based on species groupings and across time. At year six, relative stem density of mesophyte species exhibited a near-significant negative relationship with burn severity (R^2 = 0.102, $F_{1, 23}$ = 3.72, p = 0.066) and by year twelve, this negative relationship was statistically significant (R^2 = 0.240, $F_{1, 24}$ = 8.907, $p < 0.001$). This trend was driven by the additive contributions of maple and non-maple mesophytes, as neither were significantly related to burn severity when analyzed separately (R^2 = 0.107, $F_{1, 24}$ = 3.98, p = 0.057 and R^2 = 0.1511, $F_{1, 24}$ = 2.20, p = 0.151, respectively), though maples exhibited a near-significant relationship. In years six and twelve post-fire, pyrophyte relative stem density was significantly positively

related to burn severity ($R^2 = 0.307$, $F_{1, 20} = 10.32$, $p = 0.004$ and $R^2 = 0.360$, $F_{1, 24} = 15.06$, $p < 001$, respectively). In year twelve, this relationship was driven by non-oak-pine pyrophytes ($R^2 = 0.297$, $F_{1, 13} = 6.91$, $p = 0.021$). Species-level relationships of relative stem density at year six were reported by Black et al. (2018).

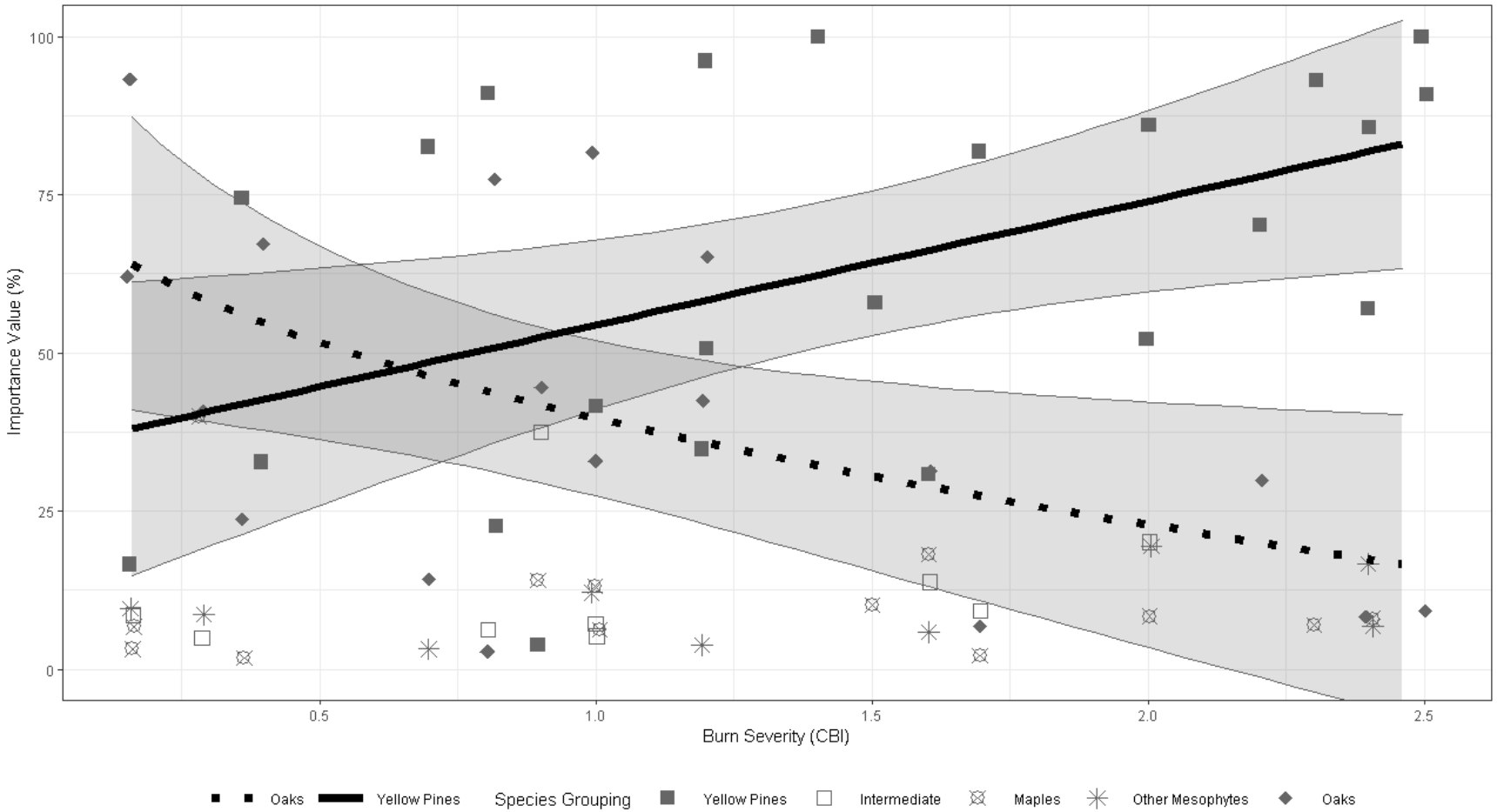

Figure 2.6 Relationship of burn severity, measured as CBI, with canopy (10+ cm (3.94+ in) DBH) species' importance values twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Importance values were calculated as the average of relative stem density and relative basal area. Regression lines are shown only for relationships that are significant ($\alpha = 0.05$).

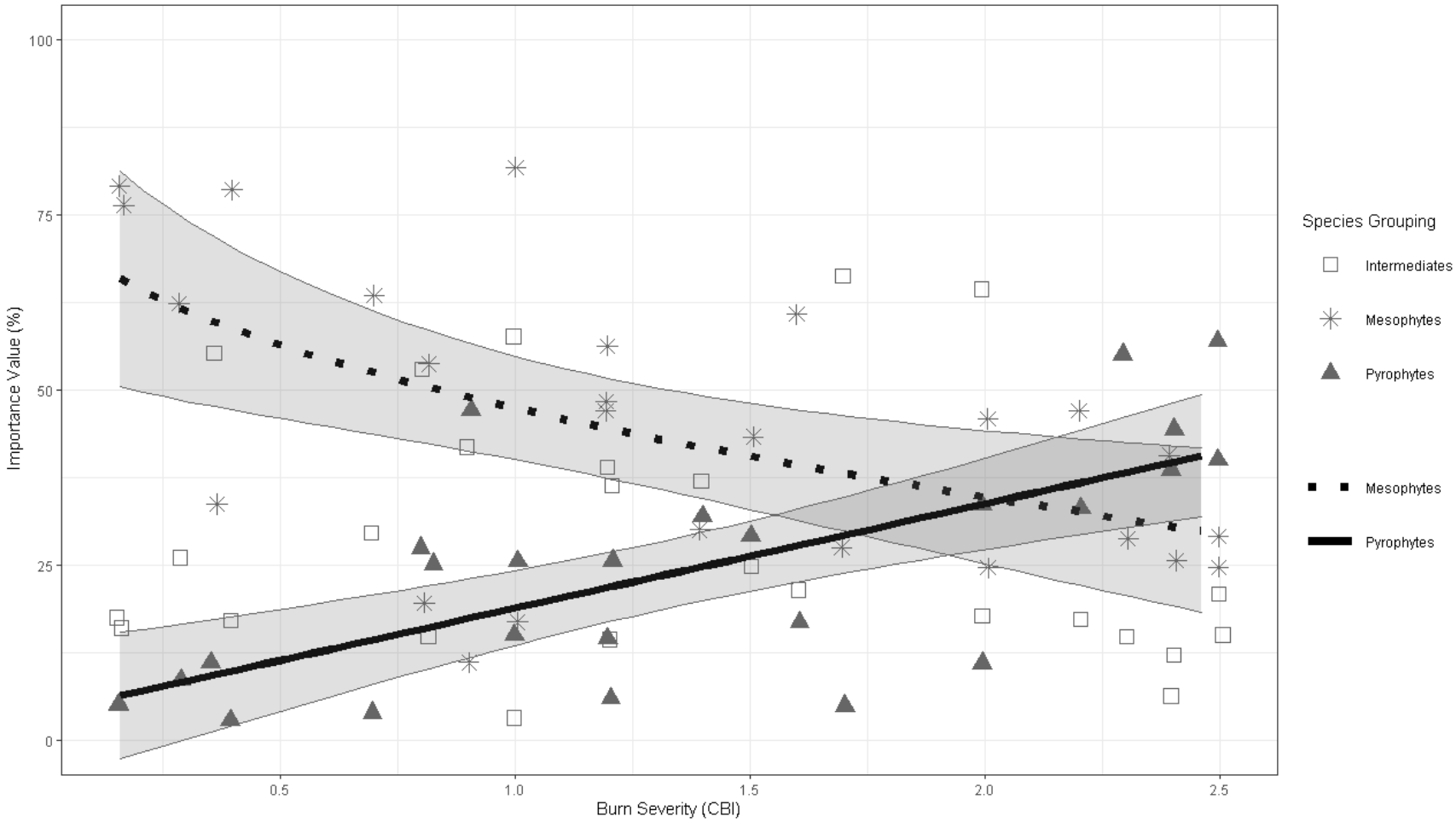

Figure 2.7 Relationship between burn severity, measured as CBI, with midstory (2-10 cm (0.79-3.94 in) DBH) species' importance values twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Importance values were calculated as the average of relative stem density and relative basal area. Species are grouped based on their general fire ecology characteristics and regression lines are shown only for relationships that are significant ($\alpha = 0.05$).

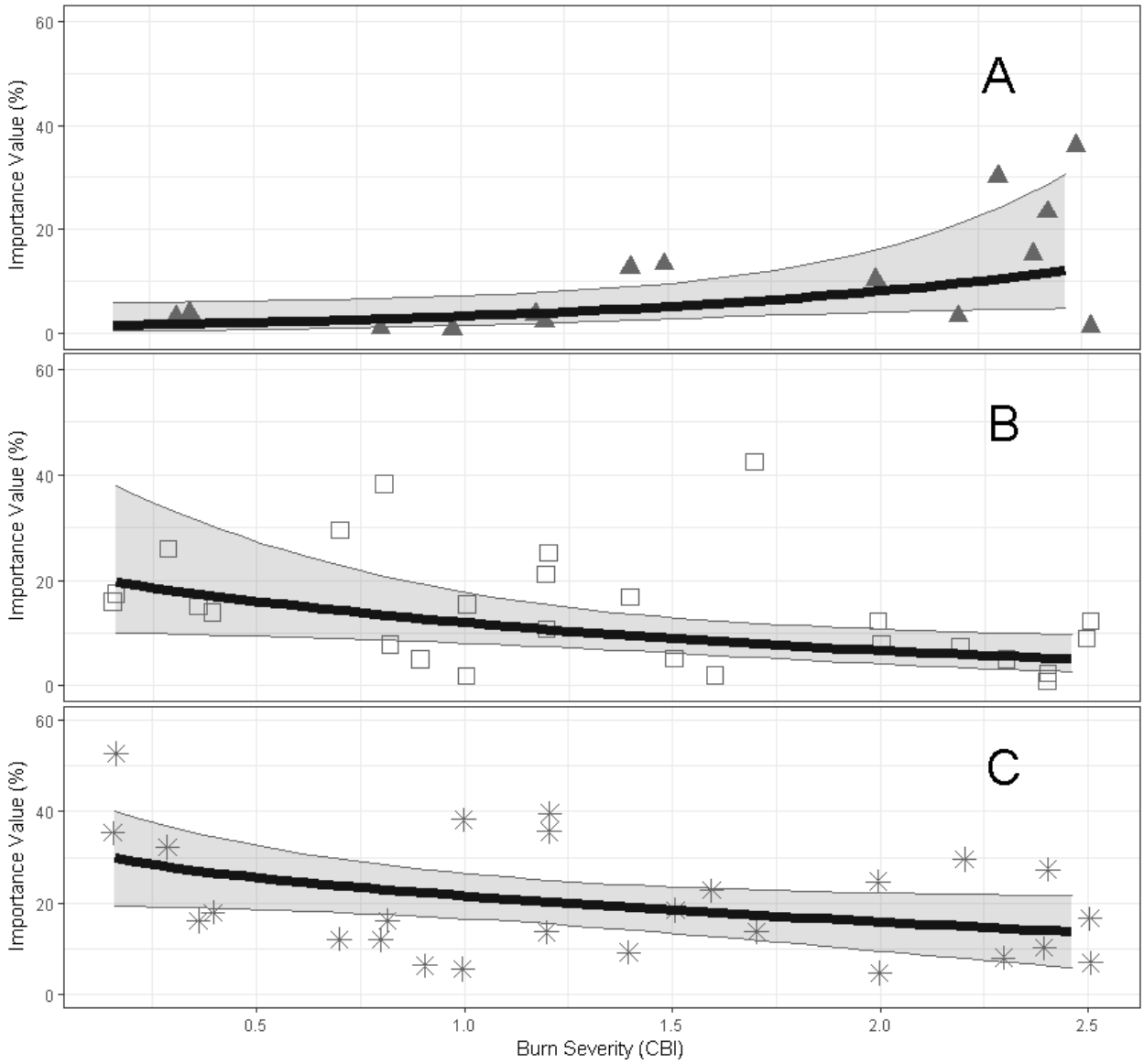

Figure 2.8 Relationship between burn severity, measured as CBI, with midstory (2-10 cm (0.79-3.94 in) DBH) species' importance values twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Importance values were calculated as the average of relative stem density and relative basal area. The only species groupings that are significant ($\alpha = 0.05$) are shown: (**A**) Non-oak-pine Pyrophytes, (**B**) Intermediates, and (**C**) Non-maple mesophytes.

2.4.4 Stem Recruitment

Recruitment of stems into a given size class varied among size classes and across recruitment time. There was a positive relationship between burn severity and midstory pyrophyte stem recruitment between 2011 and 2022 ($R^2 = 0.439$, $F_{1, 23} = 19.80$, $p < 0.001$), particularly for yellow pines ($R^2 = 0.291$, $F_{1, 23} = 10.9$, $p = 0.003$) and non-oak-pine pyrophytes ($R^2 = 0.393$, $F_{1, 23} = 16.52$, $p < 0.001$) (Figure 2.9). Over this time span, burn severity had no influence on the recruitment of mesophytic species ($R^2 = 0.023$, $F_{1, 23} = 0.56$, $p = 0.462$). Conversely, canopy recruitment was positively related to burn severity for intermediate species ($R^2 = 0.144$, $F_{1, 23} = 5.04$, $p = 0.034$) (Figure 2.10). Negative species recruitment in the canopy size class indicated stem mortality, which was observed among mesophytic species in lower severity plots (Figure 2.10). As burn severity increased, there was less mesophytic stem mortality, resulting in a significant positive relationship with burn severity ($R^2 = 0.167$, $F_{1, 23} = 5.81$, $p = 0.024$). Recruitment of pyrophytes into the canopy had no relationship with burn severity, but canopy yellow pines had a near-significant positive relationship ($R^2 = 0.094$, $F_{1, 23} = 3.49$, $p = 0.075$) over twelve years.

Stem recruitment into a given size class between six to twelve years (2016-2022) post-fire also varied among species groups and size classes. Among midstory trees, burn severity was positively related to pyrophyte species recruitment ($R^2 = 0.317$, $F_{1, 23} = 12.12$, $p = 0.002$), particularly for yellow pines ($R^2 = 0.304$, $F_{1, 23} = 11.47$, $p = 0.003$) and non-oak-pine pyrophytes ($R^2 = 0.471$, $F_{1, 23} = 11.68$, $p < 0.001$) (Figure 2.11). For canopy sized trees, the recruitment of all pyrophytes and intermediates was positively related to burn severity ($R^2 = 0.139$, $F_{1, 23} = 4.88$, $p = 0.037$ and $R^2 = 0.378$, $F_{2, 22} = 8.28$, $p = 0.002$, respectively). The relationship among pyrophyte recruitment and burn severity was primarily driven by yellow pines ($R^2 = 0.207$, $F_{1, 23} = 7.25$, $p = 0.013$), but there was a near-significant relationship for oak species as well ($R^2 = 0.151$, $F_{2, 22} =$

3.14, $p = 0.063$). Overall, between post-fire year six and twelve, there was no relationship between burn severity and mesophyte recruitment at any size class.

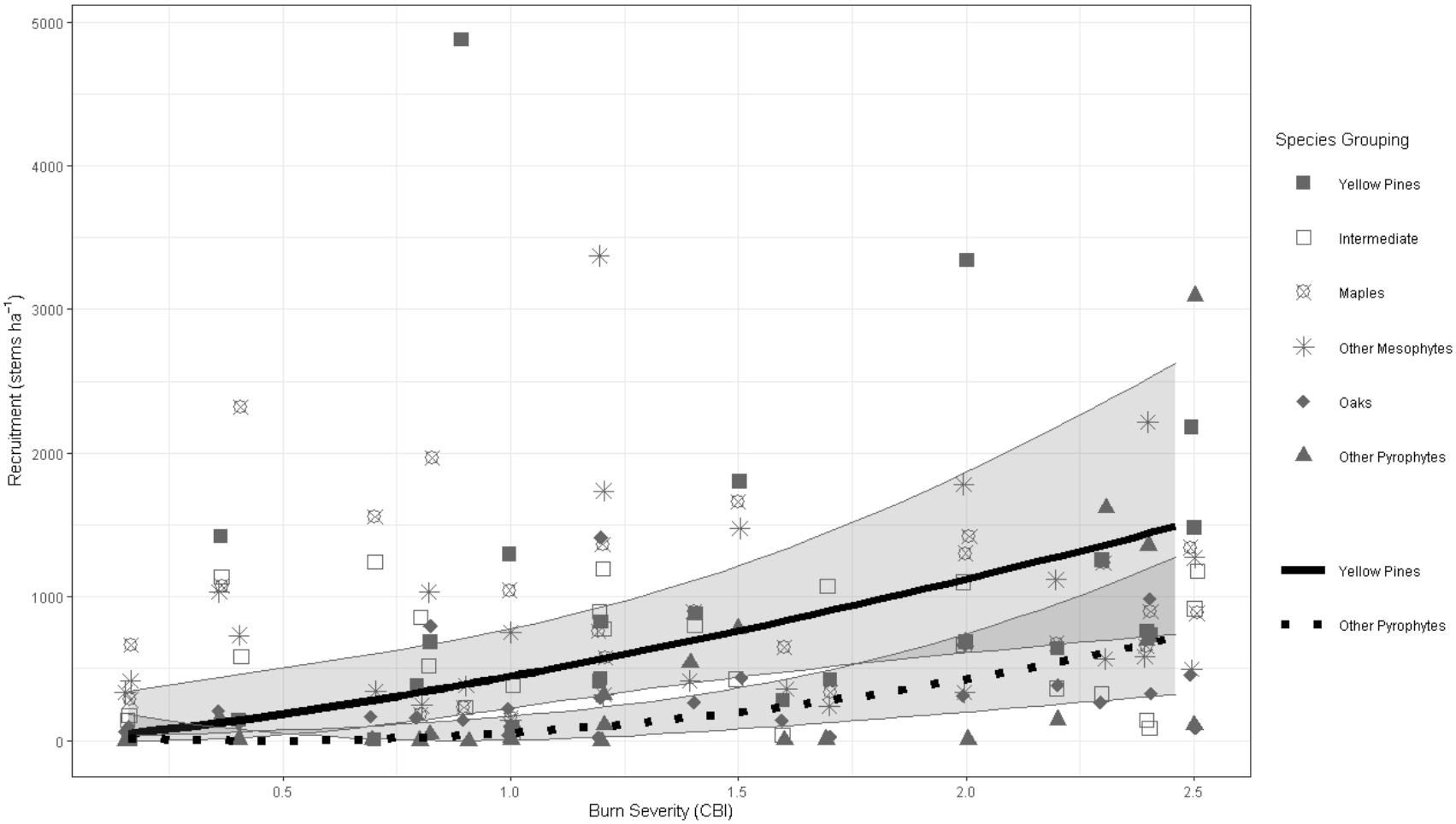

Figure 2.9 Relationship between burn severity, measured as CBI, with midstory (2-10 cm (0.79-3.94 in) DBH) species' recruitment between one and twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Recruitment was calculated as the difference in number of stems between 2022 and 2011. Regression lines are shown only for relationships that are significant (α = 0.05).

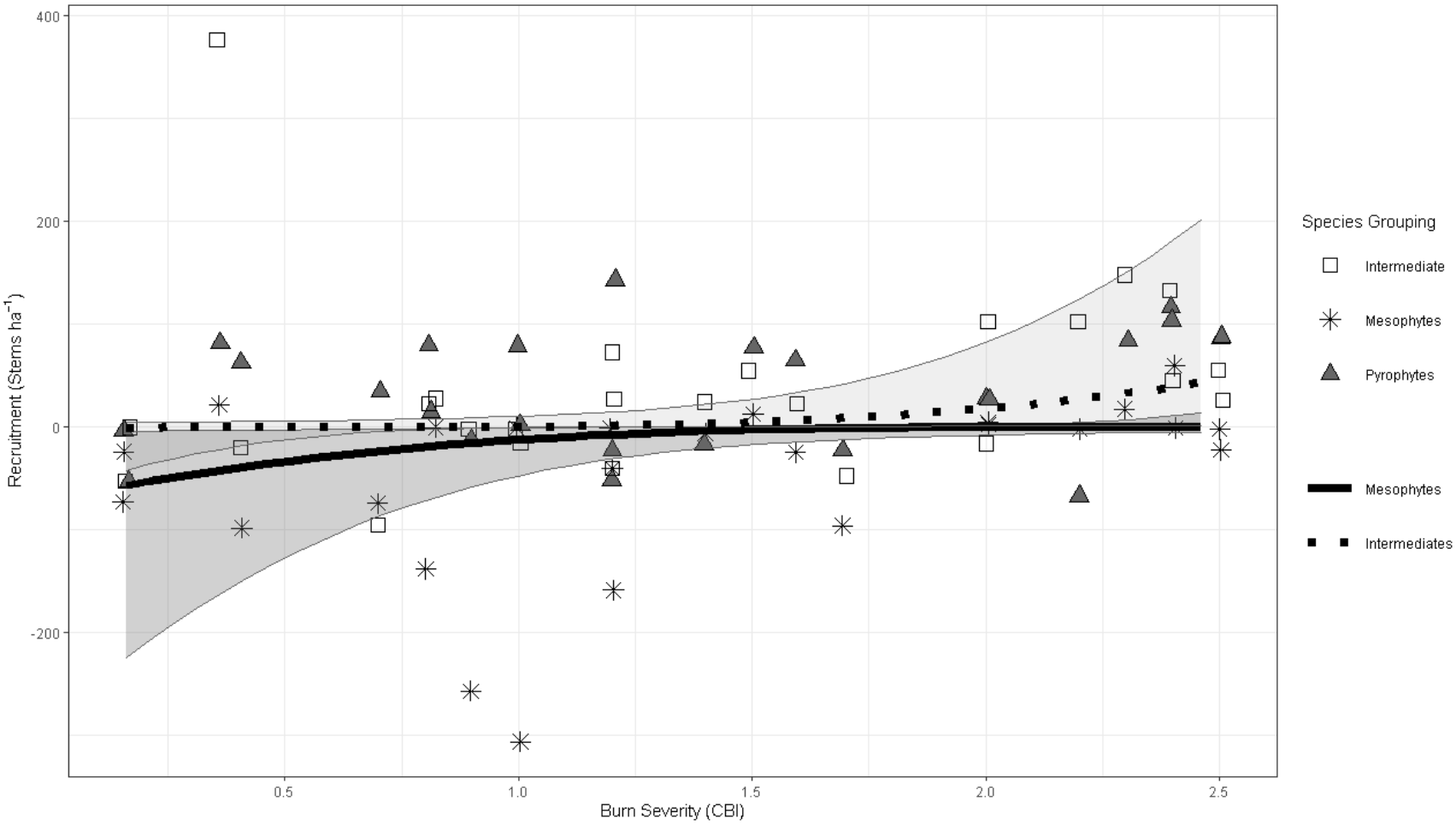

Figure 2.10 Relationship between burn severity, measured as CBI, with canopy (10+ cm (03.94+ in) DBH) species recruitment between one and twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Recruitment was calculated as the difference in number of stems between 2022 and 2011. Regression lines are shown only for relationships that are significant (α = 0.05).

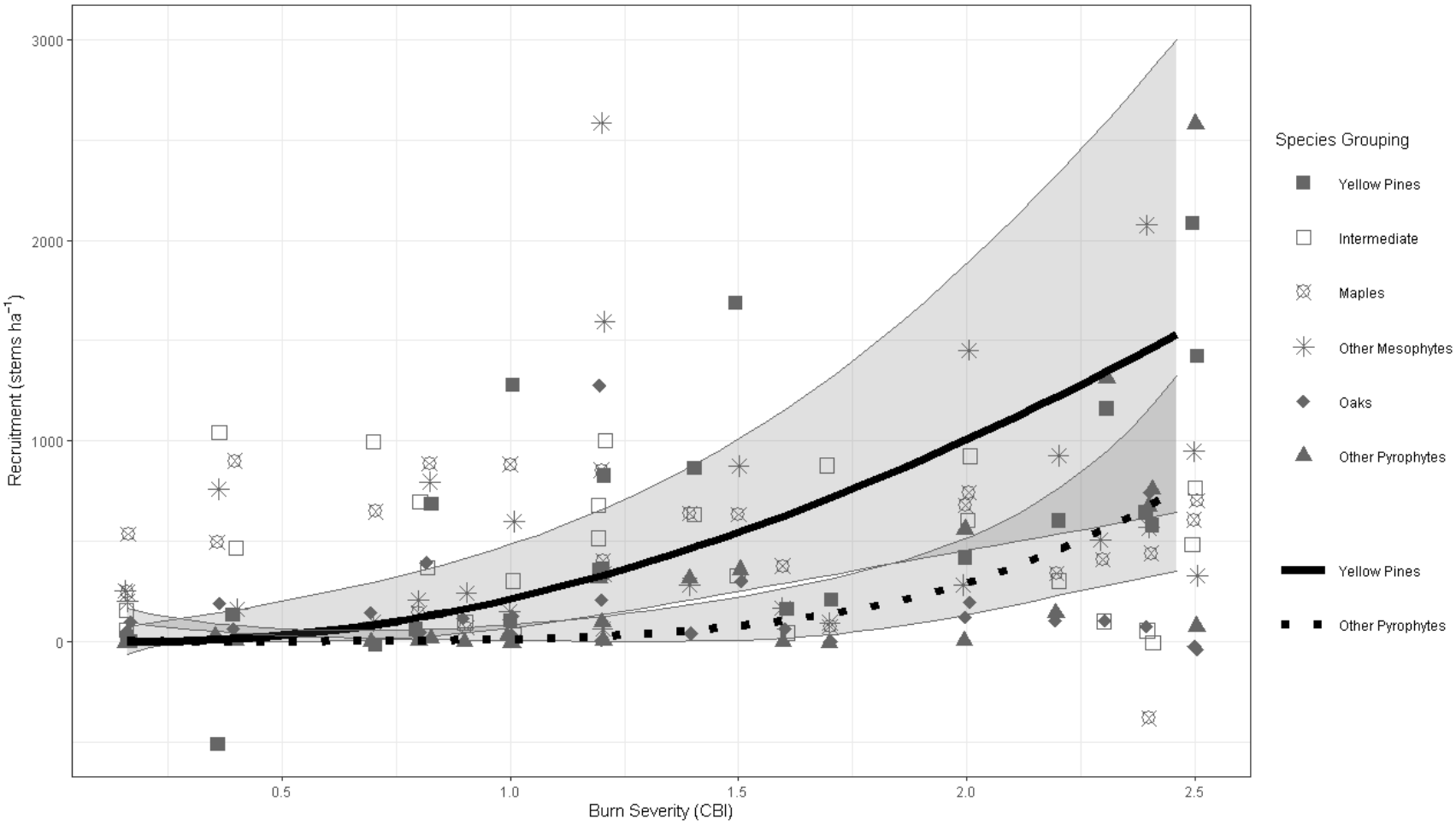

Figure 2.11 Relationship between burn severity, measured as CBI, with midstory (2-10 cm (0.79-3.94 in) DBH) species recruitment between six and twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. Recruitment was calculated as the difference in number of stems between 2022 and 2016. Regression lines are shown only for relationships that are significant (α = 0.05).

2.4.5 Seedlings

For trees <2 cm (0.79 cm) DBH, neither diversity nor overall abundance varied with burn severity after twelve years. Small seedling (<50 cm (19.7 in) height) diversity ($R^2 = 0.014$, $F_{1, 24} = 0.34$, $p = 0.565$), and richness (OR = .978, $p = 0.797$) had no relationship with burn severity, though overall abundance had a near-significant positive relationship ($R^2 = 0.174$, $F_{3, 22} = 2.75$, $p = 0.067$). Small seedlings did vary with burn severity among species groupings, however. The abundance of small seedling pyrophytes was negatively related to burn severity ($R^2 = 0.132$, $F_{1, 24} = 4.816$, $p = 0.038$), which was driven by a decrease in oak small seedlings as burn severity increased ($R^2 = 0.3276$, $F_{1, 19} = 10.74$, $p = 0.004$). Conversely, the abundance of small seedlings of non-maple mesophytes displayed a positive relationship with burn severity ($R^2 = 0.367$, $F_{1, 21} = 13.73$, $p = 0.001$).

Large seedlings (≥50 cm (19.7 in) height) had no relationship with burn severity for overall abundance ($R^2 = 0.012$, $F_{1, 24} = 1.30$, $p = 0.266$), diversity ($R^2 = 0.070$, $F_{1, 24} = 2.89$, $p = 0.102$), or richness (OR = 1.10, $p = 0.346$). Among species groupings, large yellow pine seedlings displayed a negative relationship with burn severity ($R^2 = 0.204$, $F_{1, 17} = 5.60$, $p = 0.030$), and non-maple mesophytes had a near-significant positive relationship with burn severity ($R^2 = 0.085$, $F_{1, 21} = 3.05$, $p = 0.095$).

2.4.6 Non-native Invasive Species

The presence of non-native invasive plant species (NNIP) was strongly related to burn severity twelve years post-burn. For all NNIPs species combined, burn severity was a significant predictor of invasive species presence (OR = 34.58, $p < 0.001$) (Figure 2.12), meaning that for

every increase in CBI of 1.0, there is a 34.58 times increase in the probability of detecting an invasive species. NNIP presence was not related to percent mineral soil at the plot scale (OR = 2.07e-11, p = 0.134). The most prevalent NNIP was Chinese silvergrass (*Miscanthus sinensis* Andersson), which was found on 73.1% of research plots. The other NNIPs were autumn olive (*Elaeagnus umbellata* Thunb.), multiflora rose (*Rosa multiflora* Thunb. ex Murr.), and Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), each of which were found on plots that experienced moderate to high burn severity (CBI ≥ 1.2). I recorded these latter three species only on plots that also had Chinese silvergrass, and each were present on only a single plot.

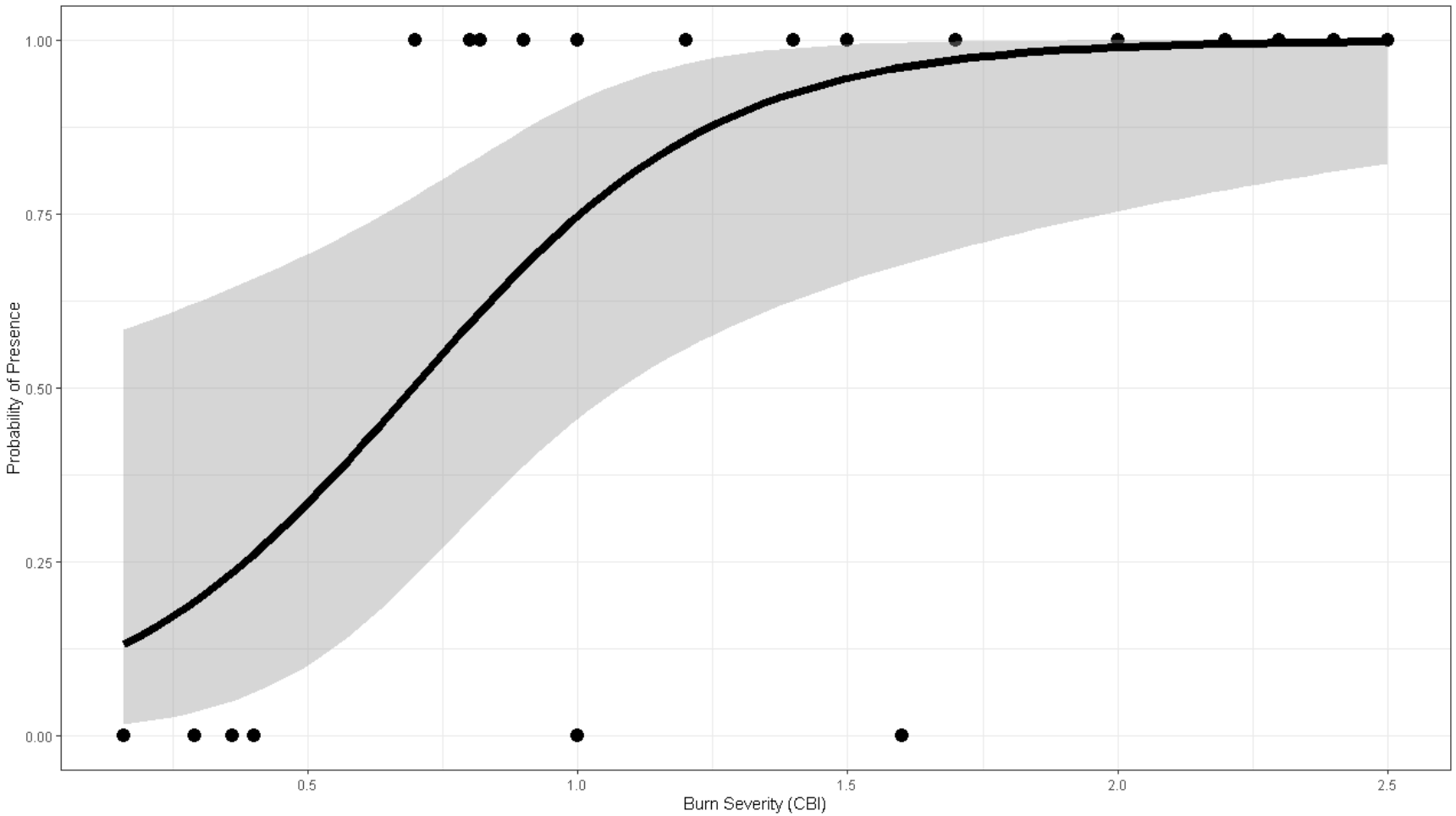

Figure 2.12 Relationship between burn severity, as described by CBI, and the presence/absence of non-native invasive plant (NNIP) species twelve years after a 2010 wildfire on the Cumberland Plateau, Kentucky, USA. The line indicates that burn severity significantly predicts the presence/absence of NNIPs ($\alpha = 0.05$).

2.5 Discussion

My results demonstrate that wildfire continued to have lasting effects on community assemblage and forest structure up to twelve years post-fire, and key among those effects was the increased competitive ability of pyrophytic species relative to the mesophytic competitors that are known to encroach on upland oak-pine ecosystems (Blankenship and Arthur, 2006; Palus et al., 2018). However, my results may indicate that the selective force of increased burn severity favoring pyrophytic species is starting to diminish due to midstory densification, and that to re-stimulate oak species recruitment, a natural disturbance (e.g. wind, ice, etc.), prescribed burning, or targeted management action may need to occur between six and twelve years after a high-severity fire in upland landscape positions. However, this should only be considered if comprehensive NNIP monitoring and eradication measures were successful following the fire and can be implemented subsequent to additional disturbance, as my results highlight how increased burn severity can increase the successful establishment and proliferation of NNIPs.

I hypothesized that species diversity, forest structure, and community assemblage would not vary between or among years (H1), but I found that to be the case only for community assemblage. By year twelve, post-fire regenerating stems had grown into the midstory (2-10 cm (0.79-3.94 in) DBH) size class, which was responsible for nearly all of the yearly variation in structure and diversity. Previous research conducted at this site by Black et al. (2018) found a negative relationship between midstory stem density and burn severity at years one and three, but no relationship at year six; I found positive relationships at year twelve (H2). This indicates that the impact of increased burn severity on reducing midstory stem density may last less than six years post-fire and by year twelve, lower burn severities have the lowest midstory stem densities.

I observed similar variations in species diversity and richness through time, where there were non-significant, yet negative associations between burn severity and species diversity and richness at years one and three, but as time progressed the relationships became positive. The positive relationship between species diversity and richness with burn severity by year twelve is consistent with other studies in the Southern Appalachians (Hagan et al., 2015; Wimberly and Reilly, 2007), and is the result of large increases in resources and colonization opportunities for new species which occur as burn severity increases (Wimberly and Reilly, 2007). The FTF site provided ample colonization opportunities. For example, there was an atypical increase in soil moisture in some of the most severely burned areas—due to a combination of reduced transpiration, the resinous discharge of *Pinus* species, and shallow clay lenses (Claudia Cotton, DBNF Forest Soil Scientist, Winchester, Kentucky, USA, personal communication)—which likely allowed for more mesic species to establish in the early years following the fire than might be observed at other upland sites, resulting in increased diversity and richness. Another explanation for these trends is that by year twelve I may have been observing early post-fire pioneer species, such as sassafrass (*Sassafras albidum* (Nutt.) Nees), black locust (*Robinia pseudoacacia* L., and sumacs (*Rhus* spp.), no longer being regenerated in the moderate to high shade being cast by midstory stems, and now non-pioneer species are regenerating and growing into the midstory size class. This would explain the increased diversity and richness I observed at year twelve, as the early post-fire cohort would still be present along with later-successional regrowth.

I predicted burn severity to be positively related to the recruitment of fire-adapted xeric seedlings and saplings into the midstory size class, as it was in previous data collection years, and I also anticipated midstory xeric stems to be recruited into the canopy size class by year twelve (H3), but these expectations were only partially supported by my results. At year six, Black et al.

(2018) found burn severity to be significantly related to the recruitment of midstory oak and pine stems into the midstory size class. Six years later, increased burn severity is still causing increased numbers of yellow pine stem recruitment, though oak species' recruitment no longer exhibits this relationship. Despite this lack of a relationship for oak species, it should be noted that I did see higher amounts of recruitment at greater burn severities which is an improvement compared to prescribed fire sites where there is a paucity of midstory oak stems. High-severity disturbance is known to be integral to restoring early seral yellow pine communities in areas that have undergone successional changes associated with fire cessation (Barden and Woods, 1976; Saladyga et al., 2022; Vose et al., 1993), but few studies other than Black et al. (2018) have found such clear effects of a single high-severity fire on oak recruitment. The near-significant relationship of oak species recruitment into the midstory at year twelve may indicate that oak seedlings and saplings are being shaded out by the now-dense midstory (Kuddes-Fischer and Arthur, 2002). If so, an additional fire between year six and twelve could restimulate oak midstory recruitment by culling midstory stems and increasing understory light availability (Iverson et al., 2017). While this may negatively impact the oak stems currently in the midstory size class, an additional fire would disproportionately affect competing mesophytic and intermediate species (Arthur et al., 2015) whose juvenile bark is less developed at younger ages compared to oak species (Varner et al., 2016). Returning fire within a six to twelve year fire-free interval would be consistent with historic fire return intervals (FRI) (Lafon et al., 2017), and recent research has directly linked mixed-severity fire at a mean FRI of 7-8 years to oak and pine recruitment (Saladyga et al., 2022). Hagan et al. (2015) observed that seven years following a wildfire, a second burn prompted increases in the relative number of oak stems in xeric oak communities, suggesting that oak species would particularly benefit from an additional burn. Thus, I have reasonable evidence to suggest that

yellow pine species' recruitment into midstory sizes can be stimulated for up to twelve years by higher severity fire, but such a fire can only promote oak species' recruitment for between six and twelve years. Moreover, my results are consistent with Black et al. (2018) that lower-severity fire yields no differences in recruitment between pyrophytic and mesophytic species after twelve years.

Recruitment of pyrophytic species into the canopy size class at year twelve followed a pattern similar to pyrophytic recruitment in the midstory size class at year six, indicating that the post-fire regenerating cohort of pyrophytes observed by Black et al. (2018) are moving into overtopped canopy positions and do so increasingly with burn severity. This may demonstrate that, where high-severity fire occurred, fire can sufficiently alter community assemblages and forest structure in upland ecosystems to a degree that allows for pyrophytic species to maintain canopy dominance. At lower burn severities, canopy recruitment of pyrophytic species between year six and twelve displayed negative recruitment, suggesting that there was some degree of pyrophyte canopy mortality during this time, particularly among oak species. Robbins et al. (2022) simulated landscape-scale fire effects and found old (>100 years) fire-resistant oak trees projected to suffer from delayed mortality following fire events due to fine root growth in organic matter that is consumed by fire (Carpenter et al., 2021). My field observations conform to these model predictions, but only at low levels of burn severity (CBI 0.6 to 1.2), as higher burn severities caused direct stem mortality. Increased burn severity prompted increased canopy recruitment among yellow pine species and oak species displayed a near-significant relationship at year twelve. Since I observed yellow pines that recruited into the midstory at year six and then into the canopy at year twelve, but did not observe the oak species that recruited into the midstory at year six recruit into the canopy by year twelve, there may be competition within the midstory occurring between years six and twelve does not favor oak species. This pattern affirms that restoring and sustaining oak

dominance in eastern U.S. forests requires active, long-term management (Dey, 2014), and to release oaks from competition and prevent them from being permanently overtopped, it is recommended that thinning should occur between ten and twenty years (Zenner et al., 2012). In fact, certain thinning prescriptions, such as crop tree release, have been shown to directly increase the diameter growth and proportion of oak trees that are recruited into dominant and codominant canopy positions (Ward, 2009). Thus, it is likely that targeted management or an additional fire that thins non-oak stems may successfully create conditions that allow for the oaks regenerated by the FTF to become part of the forest canopy.

Mesophytic species' recruitment into midstory size classes and into canopy size classes was expected to be unaffected by burn severity (H4), which my results reflect. At year six, the recruitment of mesophytic competitors was uninfluenced by the effects of burn severity (Black et al., 2018), and this trend remains at year twelve. This is likely due to the generalist nature of the most prevalent mesophytic competitors (i.e. red maple.), where they can thrive on a wide variety of sites with broad ranges of light, moisture, and nutrient availability (Abrams, 1998). Relative to other species groupings, mesophytic competitors exhibited decreased importance and density with increased burn severity at year twelve, which was not the case at year six. In this, at low burn severities, mesophytic species were substantially more important than pyrophytes and intermediates, but as burn severity increased, pyrophytes became more important than mesophytes. The burn severity at which pyrophytes in my study became more important (CBI = ~2.0) is particularly noteworthy, because prescribed fires in this area rarely exceed a CBI of 1.5 (Winkenbach, 2020), and my results provide evidence that the burn severity of prescribed fires is not high enough to alter site conditions in ways that allow for pyrophytic species to outcompete mesophytes. Likewise, these results also indicate that this upland ecosystem has not yet reached

an alternative stable state caused by mesophication and a single higher-severity fire can effectively inhibit or set back the mesophication process. However, mesophication still poses a significant threat to future forest health (Palus et al., 2018), as the process will likely begin to occur again unless additional disturbance or management occurs.

Contrary to my expectation that I would see variation in the species diversity of small (<50 cm height; <19.7 in height) and large seedlings (>50 cm height; >19.7 in height) along my gradient of burn severity (H5), I saw none. However, I did observe variation among species groupings, in that small oak seedling and large yellow pine seedling abundances were negatively related to burn severity. These patterns are likely due to decreases in the amount of sexually mature seed trees in dominant/codominant canopy positions, more seedbank consumption, and more easily predated seeds at higher burn severities, combined with decreased understory light availability caused by midstory shading. In fact, small oak seedling abundance was significantly related to oak canopy basal area. This idea is consistent with oak species' life history traits, wherein it can take scarlet oak, chestnut oak, and black oak approximately twenty years to begin bearing seed (Johnson, 2004; McQuilkin, 2004; Sander, 2004). This suggests that the oak regeneration in high-severity plots I have observed up to year twelve has primarily come from basal sprouting that was prompted by the FTF. Conversely, I may be observing greater amounts of oak small seedling abundances at lower burn severities due to greater amounts of sexually mature canopy oak trees, less predation, and less seedbank consumption by the fire. Large yellow pine seedling abundance had a near-significant relationship with canopy yellow pine basal area ($R^2 = 0.177$, $F_{2, 16} = 2.93$, $p = 0.082$), but this is not surprising considering that the most dominant yellow pine species at the FTF site, pitch pine and Virginia pine, can bear mature seed at three to five years old (Carter and Snow, Jr.,

2004; Little and Garrett, 2004). Overall, this means that I should have observed a moderate amount of pine regeneration and little oak regeneration at year twelve, which I did.

The lack of regenerating seedlings of pyrophytic species with increased burn severity, taken with my assertion that the midstory is now too dense to preferentially recruit pyrophytic oaks, provides additional justification for implementing an additional burn or targeted management action between year six and year twelve. These actions would minimize the competition of future seed trees, stimulate basal sprouting of seedling-sized oak stems, and create a seedbed more conducive to pine seed germination, effectively creating an additional age class of pyrophytic species to develop. Without such actions, I am already observing mesophytic seedlings becoming more abundant where midstories are denser, and this site will likely experience challenges associated with mesophication once again. Up until year twelve, I have reasonable evidence to suggest increased burn severity mitigated or potentially reversed some of the effects of mesophication to a point that additional management could effectively restore upland oak-pine forests. Further, my evidence suggests that over the course of twelve years, low-severity fire has caused few changes in forest structure and species composition, and these areas are continuing to experience mesophication and pyrophytic species' recruitment challenges.

The strong relationship between NNIP presence and burn severity I observed (H6) contradicts the ecosystem benefits stemming from high-severity fire and highlights the obligation land managers have to engage in monitoring and eradication efforts following a fire, especially in high-use areas. Six years post-fire, Black et al. (2018) found only two NNIP species—multiflora rose (*Rosa multiflora* Thunb.) and Chinese silvergrass (*Miscanthus sinensis* Andersson)—occupying a total of 23% of research plots. Six years later, NNIPs were found in 73% of research plots with two additional species present: autumn olive (*Elaeagnus umbellata* Thunb.), and

Japanese stiltgrass (*Microstegium vimeneum* (Trin.) A. Camus). Chinese silvergrass had the greatest recent population expansion, having previously occupied 19% of plots at year six and occupying 73% at year twelve, which can be reasonably attributed to the FTF providing a seed bed and habitat conducive for NNIP establishment (Taylor, 2010), the RRGGA being a high-use area for outdoor recreation, and dense Chinese silvergrass populations lining the roads and highways near the FTF site. What is most concerning about this species' population expansion is the fire hazard it poses, as when it senesces during the fall season, it leaves densely bunched dry standing grasses that reach 1.5 to 3 m (5 to 10 ft) in height (Miller et al., 2010). These bunches are highly flammable and can serve as ladder fuels, carrying fires into the canopy and increasing burn severity (Stewart et al., 2009). Thus, the proliferation of Chinese silvergrass over the FTF burn area poses a major threat to forest health, and a future dormant season fire may inflate burn severity levels to a degree that undermines the compositional and structural benefits observed so far and allows for further establishment and proliferation of NNIPs, potentially resulting in an invasional meltdown scenario (Braga et al., 2018).

To avoid the detrimental effects of NNIPs in post-fire areas, extensive control efforts should be made, and at the FTF site, removal of princess tree (*Paulownia tomentosa* [Thunb.] Siebold & Zucc. Ex. Steud) stems that established immediately after the fire proved successful. In 2011, approximately one year following the FTF, the USDA Forest Service conducted a ground-based survey of areas that were susceptible to NNIP establishment (Claudia Cotton, DBNF Forest Soil Scientist, Winchester, Kentucky, USA, personal communication) that revealed 2,061 princess tree stems had established following the fire (Upadhaya, 2015). Immediately following this survey, these stems were targeted for removal by hand pulling or using a tree pulling device in 2011, 2012, and 2013, and by stem clipping in 2014. By 2016, this method of removal for princess tree

appeared to have been highly effective as no stems were observed in the year six and twelve surveys. While the survey extent in Black et al. (2018) and in my study differed from that of the USDA Forest Service, I can reasonably conclude that the proliferation of princess tree was successfully stifled by these removal efforts. In addition to early monitoring and control methods, these results call attention to the importance of continual monitoring of post-disturbance environments for NNIP establishment, as Chinese silvergrass was not detected in initial surveys, and it is possible that this site could have been safeguarded from this impending threat if it had been detected and controlled early in the invasion process.

2.6 Conclusion

Fire-adapted ecosystems are declining in range and quality due in part to fire exclusion policies facilitating mesophication, and the restoration of these communities is a primary goal of forest management in the southern Appalachians (Dey, 2014). A central issue in restoring these communities is the inability of regenerating oak and pine seedlings and saplings to recruit into larger size classes (Abrams, 2003). My results demonstrate that higher levels of burn severity following a single wildfire can substantially favor pyrophytic pine species recruitment into midstory and canopy positions up to twelve years post-fire, but pryophytic oak species are only favored between six and twelve years (Black et al., 2018). Recruitment of mesophytic competitor species was unresponsive to variation in burn severity, and as time progressed, mesophytic species became less important than pyrophytes at higher levels of burn severity. To further stimulate oak species recruitment and to safeguard the ecosystem benefits of increased burn severity, I recommend that additional management, such as prescribed fire or forest thinning, occur between six and twelve years following a high-severity wildfire. However, following any severe fire and

prior to any additional management actions, comprehensive NNIP monitoring and eradication efforts must be made, as my study indicates that post-fire environments are highly conducive to their establishment and spread, but eradication efforts can sometimes be successful.

Understanding the impacts of wildfire on forest ecosystems in the eastern U.S. is continually becoming more important, as wildfire frequency and size are anticipated to increase from anthropogenic climate change (Lafon and Quiring, 2012). While changes in climate and increased wildfire activity are predicted to favor pyrophytic species like oaks (Iverson et al., 2019), active forest management that is focused on facilitating a more rapid transition to restored oak dominance is needed to avoid degraded forest health, decreased ecosystem services, and undesirable future conditions (Vose and Elliott, 2016). To this end, my study provides evidence that incorporating characteristics of wildfires, such as increased burn severity, combined with other silvicultural tools or natural disturbances may be an effective tool in quickly restoring fire-adapted ecosystems.

CHAPTER 3. MICROCLIMATE CONDITIONS TWELVE YEARS FOLLOWING VARIABLE SEVERITY WILDFIRE IN AN UPLAND OAK-PINE FOREST, KENTUCKY, USA

3.1 Abstract

Forest structure and composition modify topo- and macro-climatic conditions to create understory microclimates that are fundamental in determining the growth and survival of seedlings. Thus, forest structure and composition can play an important role in mitigating the impacts of climate change on future forest communities. Through intentional alteration these forest characteristics, land managers can create microsite growing conditions that are conducive to climate change adaptation strategies. The potential role of utilizing wildfire characteristics to modify microclimate has yet to be studied in eastern U.S. forests. A wildfire within the Daniel Boone National Forest, Kentucky, USA, provided the opportunity to consider how wildfire may alter understory microclimate conditions and how this may impact the success of understory species that are likely to be favored in future climate scenarios. To study this, I took hourly measurements of soil temperature, soil moisture, air temperature, relatively humidity, and photosynthetically active radiation (PAR) over the course of the 2022 growing season at twelve research plots spanning a range of burn severities, from no burn to stand-replacing burn severity. To quantify forest structure and composition, vegetation inventories were taken along with hemispherical photographs that measured leaf area index (LAI) and canopy openness. My results indicate that twelve years after the fire, forest structure was linked to understory microclimate conditions, but was only partially related to burn severity. Particularly, reduction in canopy (10+ cm DBH; 3.94+ in DBH) stem densities had a discernable effect of increasing understory temperatures and vapor pressure deficit (VPD). However,

midstory (2-10 cm DBH; 0.79-3.94 in DBH) regrowth that has occurred over twelve years has largely occluded these effects, and understories are now experiencing lower light conditions, lower temperatures, lower VPD, and greater relative humidity than they likely had in years immediately following the fire. This may already be having an effect on tree regeneration, where oak saplings that were previously more competitive in higher-severity post-burn environments may no longer be. In these areas, reducing midstory stem densities by year twelve post-fire may create microsite conditions that are conducive to oak and pine species growth while also preparing these ecosystems to cope with the destabilizing effects of climate change, as these species are predicted to be better adapted to future climate scenarios in eastern U.S. mixed hardwood forests.

3.2 Introduction

The structure, composition, and geographic distributions of terrestrial ecosystems are currently at risk of being dramatically altered by anthropogenic climate change, directly via average temperature and precipitation changes and indirectly via increases in extreme events, such as droughts, heatwaves, and wildfires (IPCC, 2022). In forest ecosystems, this may result in degraded ecosystem health, reduced biodiversity, decreased resilience to novel stressors, and undesirable future conditions (IPCC, 2022). However, these impacts can potentially be mitigated through forest management aimed at facilitating adaptation to climate change (Janowiak et al., 2014; Spittlehouse and Stewart, 2004). One approach to this is to influence understory microclimate conditions to foster the growth and survival of species in ways that are aligned with future climate scenarios (Muller, 2019). For instance, Muller (2019) found that increased forest thinning intensity caused increased soil moisture

content, and in an area where red pine (*Pinus resinosa*) is facing local species extirpation due to droughts associated with climate change, he recommended canopy stocking levels should be at lower densities to retain soil moisture and create microsite conditions favorable for future red pine regeneration.

By definition, forest microclimates are the near-surface climate conditions that drive biological processes, including air and soil temperature, vapor pressure deficit (VPD), solar radiation, humidity, soil moisture, and wind speed (Chen et al., 1999). While these conditions are largely determined by topo- and macro-climate, forest structure and composition moderate broad-scale climate conditions, where dense amounts of forest cover composed of species with high leaf areas can cast heavy shade that effectively creates understory microclimate conditions that differ from those above the canopy. These microclimates are especially important for seedling and sapling growth and survival (Aussenac, 2000; von Arx et al., 2013). In particular, there is a positive relationship between forest moderating capacity and canopy density (von Arx et al., 2013). In addition to stem density, leaf area index (LAI) (the amount of total leaf area in the canopy) serves as an important metric for describing the elements of forest structure that are relevant for microclimate conditions (Fang et al., 2019). Because of this, lower LAI and canopy densities lead to greater understory light levels (Kovács et al., 2020; Ma et al., 2010), which causes increased air and soil temperatures (Aussenac, 2000; Ma et al., 2010; Morecroft et al., 1998; Wolf et al., 2021), and lower humidity levels (Ma et al., 2010; von Arx et al., 2013). Likewise, decreased density and LAI increases soil moisture through reduced transpiration (von Arx et al., 2013). The degree to which forests modify broad-scale climate conditions varies diurnally and seasonally (von Arx et al., 2013), where the strongest

moderating effects have been observed during mid-day and during summer (Morecroft et al., 1998; Renaud et al., 2011). The seasonality of this moderating capacity may interact with species compositions in ways that determine ecosystem responses and resiliency to extreme climate conditions, such as droughts, severe fire conditions, early growing season frosts, etc. (Davis et al., 2019; von Arx et al., 2013; Wolf et al., 2021). Moderating extreme conditions is particularly important for seedlings and saplings that lack physiological resilience to severe stress (Aussenac, 2000). Thus, changes in forest structure can strongly influence microsite growing conditions in ways that regulate the growth and survival of understory tree species, potentially serving to mitigate or exacerbate the destabilizing effects of changing climate (Muller, 2019).

This has important implications for forest communities currently experiencing regeneration challenges, such as the oak-pine forests of the eastern U.S. Here, due to lack of fire and other disturbances that have historically and pre-historically maintained somewhat open forest canopies, forests have become denser with reduced below canopy wind speed and less understory radiation, causing microclimates to have greater humidity levels, lower vapor pressure deficits, and lower temperatures, in a process known as mesophication (Nowacki and Abrams, 2008). This inhibits the seedlings and saplings of canopy dominant oaks (*Quercus* spp. L.) and pines (*Pinus* spp. L.) from recruiting into larger size classes, as they are adapted to growing in higher-light environments (Abrams, 1992; Nowacki and Abrams, 2008). In their stead, species that are more successful in dense canopy microclimates have become dominant in forest midstories (Abrams, 1992; Fei et al., 2011; Hutchinson et al., 2008), leaving eastern U.S. forests in a transitional state from

fire-maintained oak and pine communities to forests composed of fire-intolerant species (Abrams, 1992).

Despite this unfolding transition, future climate conditions with increases in temperature, drought severity, and wildfire, are predicted to favor oak species (Iverson et al., 2019). However, because oak dominated forests are currently in transition, active forest management that is focused on facilitating a more rapid shift to below-canopy oak dominance is necessary to avoid degraded forest health, decreased ecosystem services, and undesirable future conditions (Vose and Elliott, 2016). Active management that seeks to foster oak regeneration and recruitment typically involves prescribed fire or a combination of thinning and burning (Brose, 2014). However, these treatments are often unsuccessful in opening forest canopies and increasing understory light levels (Chiang et al., 2005) unless intensive management actions occur that involve thinning with multiple burns (Iverson et al., 2017; Refsland and Fraterrigo, 2018). In the future, the utility of these fire management strategies will likely decrease, as prescribed burn windows are becoming shorter with climate change due to hotter and drier conditions that reduce the number of days when weather conditions are within prescribed fire safety parameters (Vose et al., 2021). This, coupled with anticipated increases in wildfire frequency and size (Lafon and Quiring, 2012), have driven researchers and land managers to consider how managing wildfire events and incorporating attributes of wildfire into burning prescriptions may help achieve desired management outcomes (Hiers et al., 2020). Wildfires often exhibit a range of burn severities (Hutchinson et al., 2008) that have the potential to strongly modify forest structure (Black et al., 2018; Saladyga et al., 2022) and alter understory microclimate conditions (Stevens et al., 2015; Wolf et al., 2021). It is theorized that the changes in forest

structure that shift microclimate conditions can last for a minimum of three to five years (Aussenac, 2000; Kovács et al., 2020), but an analysis of longer-term microclimate changes following a wildfire in oak-pine forests of the eastern U.S. has yet to be done.

To study whether variable severity wildfire causes long-term changes in forest structure that alter understory microclimate conditions, I studied a wildfire that occurred in 2010 within the USDA Forest Service Daniel Boone National Forest (DBNF), Kentucky, USA. In particular, my objective was to assess the impacts of the fire on forest structural and microclimate conditions at varying levels of burn severity in the upland oak-pine forest affected by this fire and to consider how this may contribute to the development of silvicultural toolkits for adapting forests to climate change. I hypothesized that: (H1) forest canopy structure, as described by leaf area index (LAI) varies significantly with burn severity, and (H2) forest canopy structure is linked to microclimate variables, particularly air temperature, relative humidity (RH), VPD, photosynthetically active radiation (PAR), and soil moisture.

3.3 Methods

3.3.1 Study Area

The site of this study is the Fish Trap Fire (FTF), a wildfire that burned in fall of 2010 within the Cumberland Plateau physiographic region. The climate of the region is continental, having moderately cold winters and warm, humid summers (Wharton and Barbour, 1973). On average, the annual temperature is 13.1°C (55.6°F) and annual precipitation is 136.47 cm (53.73 in), but summer temperatures reach an average of 23.1°C (73.5°F) and winter temperatures average 2.3°C (36.1°F) (NOAA, 2023). The Fish Trap

Fire and study plots are located within the Red River Gorge Geological Area (RRGGA) of the Daniel Boone National Forest (DBNF).

This study area is characterized by uplands that are highly dissected by streams of the Red River watershed (Braun, 1951). Elevation changes here can be abrupt and elevation ranges from 177 to 439 m (580.7 -1440.3 ft). The ridgetop soils are derived from Pennsylvanian sandstones and conglomerates and shales of the lower Breathitt formation, and are primarily Alticrest and Ramsey soil series (Soil Survey Staff, 2021). Alticrest is a well-drained sandy loam and Ramsey is an excessively drained sandy loam (Soil Survey Staff, 2021). Moreover, the slopes are dominated by Helewacha soil series, consisting of parent material that is coarse loamy colluvium (Soil Survey Staff, 2021). Due to its underlying geology, the RRGGA contains numerous natural sandstone arches, cliffs, rock shelters, and other geologic formations (Braun, 1951). These formations, along with the area's complex topography, provide a myriad of site conditions, microclimatic conditions, and habitat types that produce exceptionally high plant biodiversity, making the forest type here one of the most complex in North America (Braun, 1951; Wharton and Barbour, 1973).

In the RRGGA, the composition of woody vegetation communities ranges from those common to xeric uplands, dominated by scarlet oak (*Q. coccinea* Muenchh.), chestnut oak (*Q. montana* Willd.), black oak (*Q. velutina* Lam.), white oak (*Q. alba* L.) and yellow pines (*P. rigida* Mill., *P. virginiana* Mill., and *P. echinata* Mill.) in the overstory, to mesic cove communities, dominated by eastern hemlock (*Tsuga canadensis* (L.) Carrière), yellow-poplar (*Liriodendron tulipifera* L.), sugar maple (*Acer saccharum* Marshall), eastern white pine (*P. strobus* L.), magnolias (*Magnolia* spp. L.) and hickories

(*Carya* spp. Nutt.) (Wharton and Barbour, 1973). In this study, the focus was on areas that burned in the FTF, which were primarily in xeric communities that have midstories composed of red maple (*Acer rubrum* L.), sourwood (*Oxydendrum arboreum* A.P. DC.), black gum (*Nyssa sylvatica* var. *silvatica*), and sassafras (*Sassafras albidum* (Nutt.) Nees) (Black et al., 2018). Here, the understory shrub community is largely dominated by green briar (*Smilax* spp. L.), mountain-laurel (*Kalmia latifolia* L.) and *Vaccinium* spp. L. (Black et al., 2018).

3.3.2 Fish Trap Fire

The Fish Trap Fire (FTF) was ignited on October 24, 2010 accidentally and burned until November 11, 2010, burning 673.8 ha (1665.0 acre), of which 654 ha (1593.8 acre) was within the DBNF, Kentucky, USA (37°49' N, 83°40' W). In 2011, a fine-scale plot-level assessment of burn severity was conducted using composite burn index (CBI) (Key and Benson, 2006) to quantify the impacts of the fire on site characteristics, such as trees, shrubs, herbs, and substrates (Key and Benson, 2006). The post-hoc use of CBI was determined to be an accurate measure of burn severity (Upadhaya, 2015), with CBI and post-fire differenced normalized burn ratio (ΔNBR) values strongly related ($r = 0.90$, $p = 1.19e\text{-}09$, $F_{1,25} = 87.67$, $R^2 = 0.77$). Additionally, Black et al. (2018) found CBI to have no relationship with Landsat-derived pre-burn normalized differenced vegetation index (NDVI) and topographic wetness index TWI), and concluded that CBI variation was a function of the effects of the fire, rather than pre-fire landscape variability.

The burn severity of the Fish Trap Fire was highly variable, ranging from high-severity stand-replacing fire to unburned areas, which prompted a large range of ecosystem responses. The most severely burned areas occupied <10% of the area burned, experienced nearly 100% loss of vegetation within the year following the fire, and had portions of litter layers that burned down to mineral soil (Black et al., 2018). In locations where there was substantial mortality of large trees, the soil was much wetter for several years following the fire, allowing for the successful establishment of species not commonly found on xeric uplands (David Taylor, DBNF Forest Botanist, Winchester, Kentucky USA, personal communication). This phenomenon was likely due to a combination of factors including a significant reduction in transpiration coupled with shallow bedrock, clay lenses, and the resinous discharge of species such as pitch pine (*P. rigida* Mill) that created hydrophobic soil conditions (Claudia Cotton, DBNF Forest Soil Scientist, Winchester, Kentucky USA, personal communication). Likewise, Black et al. (2018) found stem density, basal area, and understory species richness to be substantially affected by increases in burn severity. Thus, the Fish Trap Fire directly and indirectly modified forest structural and compositional characteristics to varying degrees based on burn severity.

3.3.3 Data Collection

Out of 30 permanent research plots that were established in 2011, twelve were identified as being similar in aspect, elevation, slope, hill shade, and topographic wetness index (TWI) using ArcGIS Pro and field surveys (Figure 3.1). These plots were primarily western-facing aspects (214-292°AZ), with elevations ranging from 329.2 m (1080.1 ft) to 387.9 m (1272.6 ft), slope ranging from 7.5° to 41.8°, early/late growing season hill shade

values ranging from 177.1 to 247.6, middle growing season hill shade values ranging between 229.3 and 249.9, and TWI values ranging from 5.23 to 6.68 (Table 3.1). Since these research plots are similar in landform position and biophysical context, I can reasonably assume that differences in microclimate are not due to these characteristics and are due to other factors. Additionally, these twelve plots had a relatively even distribution of burn severity values (CBI of 0.29 to 2.50) across the range of burn severities of the FTF. These twelve plots were used as a subsample of my 30 permanent research plots to study forest microclimate conditions.

To obtain quantitative metrics that describe the beneath-canopy light environment and growing conditions, I established twelve microclimate stations to collect data on soil moisture, ambient air temperature, relative humidity (RH), and photosynthetically active radiation (PAR). In early April 2022, each microclimate plot had an Onset Hobo H21-USB Micro Station data logger established with two Onset 10-HS Soil Moisture sensors, one Onset Temperature and Relative Humidity sensor, and one Onset PAR sensor attached (Onset Computer, Massachusetts). Onset Solar Radiation Shields (Onset Computer, Massachusetts) were used to protect the temperature and relative humidity sensor and to ensure accurate data collection.

To install these data loggers and sensors, at the center of each circular research plot, a 2 m (6.6 ft) metal post was placed with the Onset Temperature and Relative Humidity and PAR sensors fixed to the pole at 1.5 m (4.9 ft) above the ground. This height was chosen to capture the ambient conditions for sapling-sized trees being recruited into larger size classes. Additionally, at each plot, the two soil moisture sensors were buried in the ground at a depth of 20 cm (7.9 in), at a distance of approximately 4 m (13.1 ft) from the

pole, following the contour of the slope. In the event that establishing these microclimate stations at plot center was not possible, the station was established off-center, but still within the research plot, at the researcher's discretion. These loggers collected data at one-hour time intervals for the length of the growing season, from early April until early November 2022. However, due to equipment malfunction, data collection was less robust beginning in August 2022. This meant that for some variables, data for the fall season could not be analyzed. Data collection was sufficiently complete for analysis of the relationships between forest structure and microclimate for the majority of the growing season.

In addition to these microclimate stations, hemispherical photographs of the forest canopy were captured at each site. During early-September 2022, a Nikon D7000 camera equipped with an 8mm fisheye lens was mounted to a tripod at 1.5 m (4.9 ft) above the ground and two photographs were taken at each of the twelve research plots at plot center. The resulting photos were then analyzed in WinsCANOPY 2016a software ("WinSCANOPY Pro 2016a," 2015) to measure percent canopy cover, canopy gap fraction, LAI, and direct, diffuse, and total understory and overstory solar radiation.

Table 3.1 Landform characteristics of plots selected for microclimate comparison at the FTF study area in the RRGGA of the DBNF, Kentucky

Plot	Burn Severity (CBI)	Elevation (m)	Aspect (degrees)	Slope (degrees)	TWI	Hillshade (Early/Late Growing Season)	Hillshade (Mid Growing Season)
3	2.3	383.2	262	22.1	5.72	212.6	249.9
4	2.5	387.9	286.3	17.8	5.23	192.3	242.7
8	0.36	377.6	255.3	38.3	5.99	222.7	242.2
9	1.2	379.4	272	19.8	5.58	204.9	247.4
10	2.4	384.9	292.2	16.5	5.61	177.1	234
13	1.7	374.8	290.3	25.2	5.95	183.4	236.7
15	0.8	372	226.7	41.8	6.49	247.6	238.2
19	0.4	373.1	281.7	34.7	6.32	186.9	233.7
20	0.7	376.1	288.1	33	6.68	177.4	229.3
21	1	369.3	264.6	15.2	6.33	209.1	249.1
26	1.2	379.6	213.9	11.9	5.51	219.5	245.6
28	0.29	329.2	261.5	7.5	5.58	201.8	243.7
Average		373.9	266.2	23.7	5.9	202.9	241.0
Std. Dev.		14.5	23.9	10.5	0.4	20.1	6.4

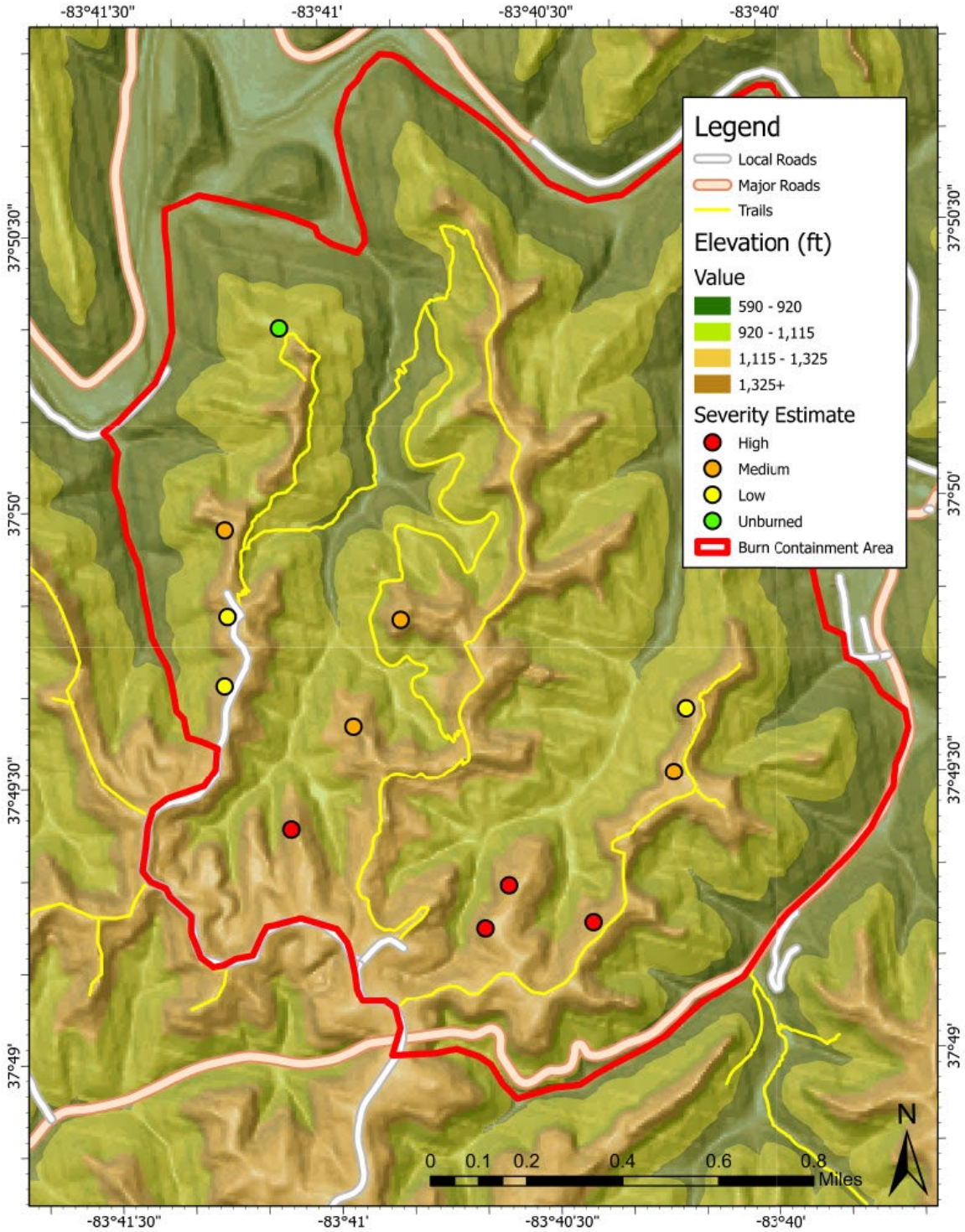

Figure 3.1 Locations of the field plots with microclimate stations at the location of the Fish Trap Fire, a wildfire that burned in 2010 on the Cumberland Platea, Kentucky, USA.

3.4 Statistical Analysis

Linear regression was used to analyze the metrics measured by the hemispherical photograph data. Prior to any regression modeling, violations in model assumptions (linearity, homoscedasticity, independence, and normally distributed residuals) were corrected for using square-root or natural log transformations. I examined the relationship between canopy openness, canopy gap fraction, LAI, and radiation metrics with CBI and forest structural measurements previously measured in Chapter 2, which include basal area and stem density. Linear regression models were created using R (R Core Team, 2023) and for each metric, linear, square-root, and 2nd, 3rd, and 4th degree polynomial models were generated. From these, Aikaikes Information Criteria (AIC) was used to select which model best described the relationship being considered. The resulting best-fit model was then plotted using the ggplot2 and ggpubr packages from R (Kassambara, 2022; R Core Team, 2023; Wickham, 2016).

To examine the hourly data derived from microclimate stations, several calculations were performed to examine trends across the growing season. Using ambient air temperature and relative humidity (RH), vapor pressure deficit (VPD) values were calculated for each hourly observation by taking the difference between saturated (P_{sat}) and effective water pressure of the air (P_{air}), as outlined by Tetens (1930). The calculations for these are:

$$P_{sat} = 0.61078 * \exp(\frac{17.27 * T}{T + 237.3})$$

$$P_{air} = P_{sat} * (\frac{RH}{100})$$

where T is temperature in ˚C and RH is percent relative humidity. VPD, air temperature, RH, PAR, and soil moisture hourly observations were then summarized into maximum and average daily values for each metric.

To analyze how forest structure influences daily trends in microclimate variables, generalized additive mixed-effect models (GAMM) were generated using the *mgcv* package (Wood, 2022) in R (R Core Team, 2023) to conduct a time-series analysis of microclimate response throughout the growing season. In these models, microclimate variables were the response variable, and forest structural measurements of midstory (2-10 cm DBH; 0.79-3.94 in DBH) basal area, canopy (10+ cm DBH; 3.94+ in DBH) basal area, midstory stem density, canopy stem density, and LAI were the predictor variables. I also generated separate models with total basal area and total stem density to consider the interactive effect of midstory and canopy structure. To account for multiple surveys over time, I included plot as a random effect. Further, to remedy statistical assumption violations, the variance structure was fixed to account for heterogeneous variances, and temporal correlation structures were defined using an auto-regressive moving average (ARMA) correlation structure. For each response variable, a global model was generated with all predictor variables and if a given predictor variable was determined to have an insignificant effect on the response via a shrinking basis spline, it was removed from the model for model simplification. Once the simplest model was found, multiple GAMMs were generated with various methods for corrections of assumption violations and with several different numbers of knots used for the basis spline construction. The best model was selected based on an analysis of variance (ANOVA) test, comparing AIC and Bayesian information criterion (BIC), and by visually inspecting diagnostic tests to ensure successful correction for any assumption violations. Then, a Wald test was performed to determine the significance of each predictor variable on

producing a change in the response. Using the *mgcViz* (Fasiolo et al., 2018) and *gratia* (Simpson, 2023) packages in R (R Core Team, 2023), each predictor variable's partial effect was plotted to visualize the effect of a given predictor across the growing season. To consider variation among seasons, I divided my data into spring (April 15 to May 31), summer (June 1 to August 31), and fall (September 1 to October 31) seasons, and applied this process to each.

3.5 Results

3.5.1 Burn Severity and Forest Structure

In Chapter 2, I determined that basal area and stem density measurements were related to burn severity at all 30 research plots. In particular, burn severity was negatively related to total plot basal area, canopy basal area, and canopy stem density, and positively related to total plot stem density, midstory stem density, and midstory basal area. LAI, canopy openness, and canopy gap fraction, which were derived from hemispherical photographs, exhibited no relationship with burn severity. LAI displayed a statistically insignificant relationship with burn severity (R^2 = 0.019, $F_{1, 24}$ = 1.50, p = 0.233), as did canopy openness (R^2 = 0.012, $F_{1, 24}$ = 1.32, p = 0.263) and canopy gap fraction (R^2 = 0.074, $F_{2, 23}$ = 2.01, p = 0.157). LAI was strongly negatively related to canopy openness (R^2 = 0.903, $F_{1, 24}$ = 232.8, p < 0.001) and canopy gap fraction (R^2 = 0.886, $F_{1, 94}$ = 195.3, p < 0.001), which displayed near-perfect negative relationships. Canopy openness and canopy gap fraction displayed a near-perfect positive relationship (R^2 = 0.975, $F_{1, 24}$ = 964.6 p < 0.001). Because of this, canopy openness and canopy gap fraction were omitted from the time-series analysis that was used to compare forest structure to microclimate conditions to avoid collinearity. To ensure LAI was not related to interactions between basal area and stem density measurements, I performed a multiple linear regression on all possible combinations of small

midstory, canopy, and total stem density and basal area, none of which displayed a significant relationship with LAI.

3.5.2 Forest Structure and Microclimate

Temperature

Maximum daily temperature (T_{max}) in the understory varied with forest structural characteristics and across the growing season. Over the course of the entire growing season, the only significant predictors of T_{max} were LAI, midstory basal area, and canopy density. In the spring, the only forest structural measurement that was a significant predictor of T_{max} was canopy stem density (edf = 2.36, $p < 0.001$), where T_{max} was the greatest at stem densities lower than approximately 190 trees ha^{-1} (77 trees ac^{-1}). Greater than this, canopy density did not appear to significantly affect T_{max}. During the summer, LAI (edf = 1.00, $p < 2e\text{-}16$), midstory basal area (edf = 2.37, $p = 0.009$), and canopy density (edf = 1.60, $p = 0.038$) were all significant predictors of T_{max}. The direction of influence of canopy density was largely similar to the springtime pattern (Figure 3.2C). LAI had a negative relationship with maximum daily temperature during summer, where high LAI caused lower T_{max} (Figure 3.2A). The relationship between midstory basal area and T_{max} was parabolic, where T_{max} was greatest where midstory basal area was approximately 5.2 $m^2\ ha^{-1}$ (22.7 $ft^2\ ac^{-1}$) (Figure 3.2B). In fall, forest structure variables had less of an effect on T_{max}, where midstory basal area was the only significant predictor (edf = 2.11, $p = 0.006$). midstory basal area displayed a similar parabolic relationship with T_{max} as it did during the summer. LAI was a near-significant predictor of T_{max} during fall (edf = 1.00, $p = 0.068$) and was negatively associated.

Average daily temperature (T_{avg}) was less related to forest structural measurements compared to T_{max}. LAI was a significant predictor of T_{avg} for the entire growing season; total stem density, total basal area, canopy basal area, midstory basal area, canopy density, and midstory density were not significant predictors. During spring and summer, LAI was negatively related to T_{avg} (edf = 1.00, $p < 0.001$ and edf = 1.00, $p < 0.001$, respectively); during fall the negative relationship was only nearly significant (edf = 1.16, $p = 0.077$).

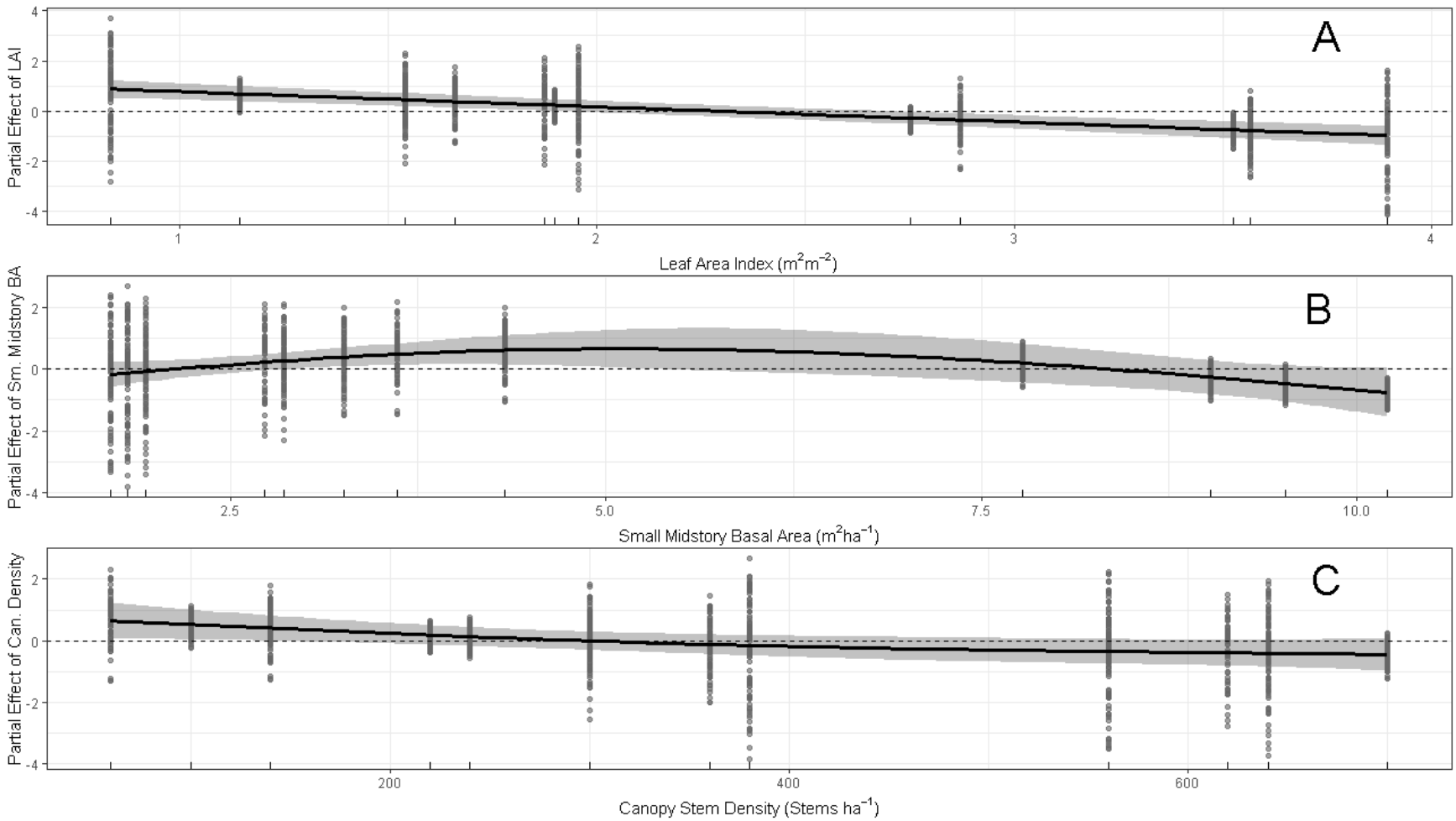

Figure 3.2. The partial effects of leaf area index (**A**), midstory (2-10 cm DBH; 0.79-3.94 in DBH) basal area (BA) (**B**), and canopy (10+ cm DBH; 3.94+ in DBH) stem density (**C**) on maximum daily temperature of the forest understory during summer (June 1 – August 31), twelve years after a 2010 wildfire on the Cumberland Platea, Kentucky, USA. A partial effect of 0 indicates the mean response of the dependent variable, and the shading represents a 95% confidence interval.

Relative Humidity

Maximum daily relative humidity (RH_{max}) varied with LAI, midstory stem density, and canopy stem density after RH_{max} values were transformed using a logit transformation to meet assumption criteria. During each season, canopy stem density was negatively related to RH_{max} ($p < 0.001$ for all seasons). Conversely, in each season LAI was positively related to RH_{max} (Spring: edf = 2.27, $p < 0.001$; Summer: edf = 1.83, $p = 0.004$; Fall: edf = 2.20, $p < 0.001$). During spring, midstory stem density had a parabolic relationship with RH_{max} (edf = 2.69, $p = 0.004$) (Figure 3.3), where increased midstory stem density resulted in decreased RH_{max} until approximately 3800 stems ha^{-1} (1538 stems ac^{-1}), beyond which increased midstory density caused increases in RH_{max}. midstory stem density and RH_{max} had a similar relationship during summer as well (edf = 2.53, $p = 0.017$), but the parabola's minimum was at approximately 5000 stems ha^{-1} (2024 stems ac^{-1}) (Figure 3.3). During fall, this pattern remained, with increased midstory stem density causing decreased RH_{max} until approximately 3800 stems ha^{-1} (1538 stems ac^{-1}), after which the relationship remains relatively constant (edf = 2.820, $p = 0.013$) (Figure 3.3).

Average daily relative humidity (RH_{avg}) was related to leaf area index only; no other forest structure measurement had a significant effect. During the spring, LAI was positively related to RH_{avg} (edf = 1.09, $p = 0.002$), as it was in summer (edf = 1.00, $p < 0.001$) and fall (edf = 1.00, $p = 0.017$).

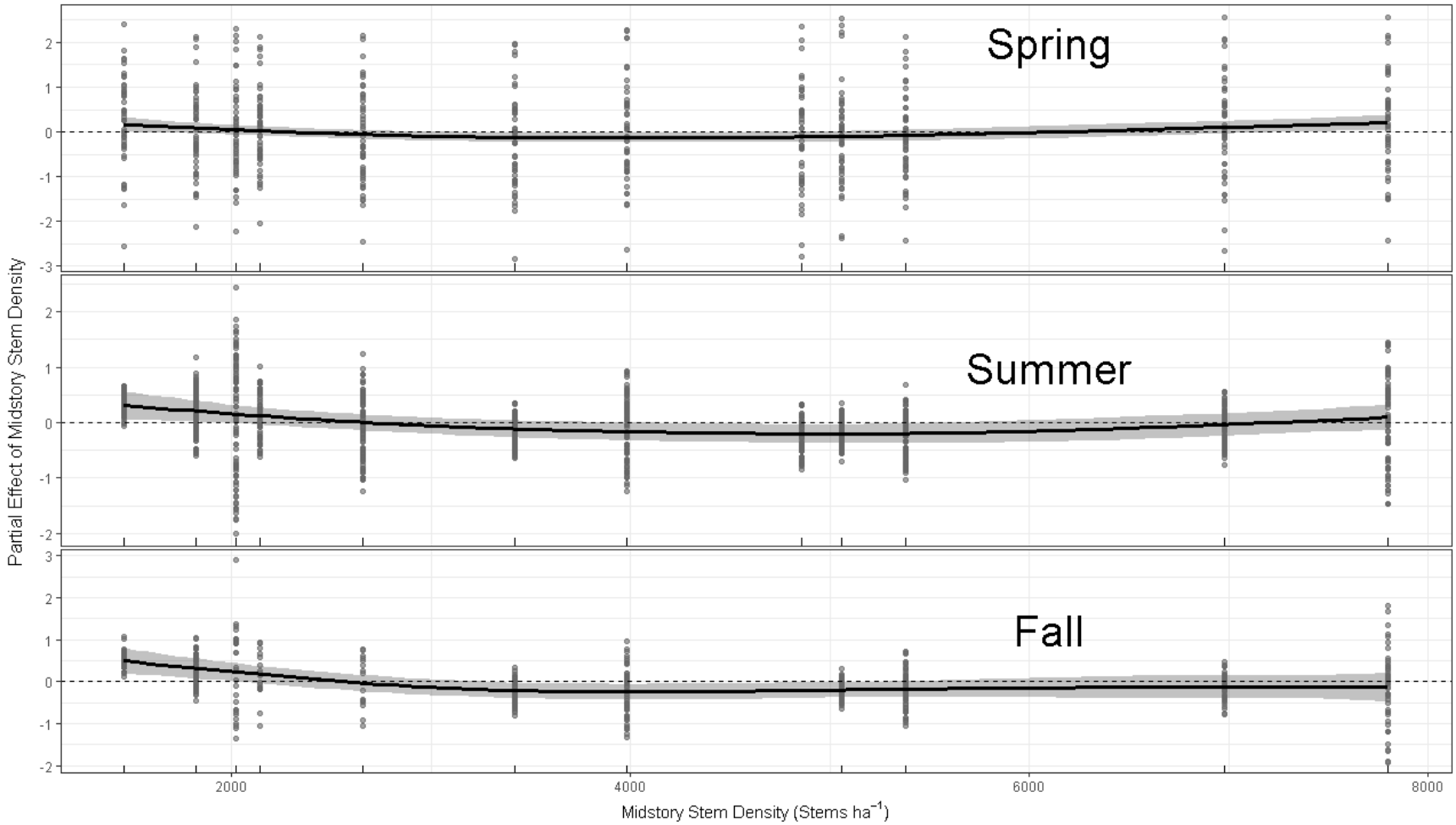

Figure 3.3. The partial effect of midstory (2-10 cm DBH; 0.79-3.94 in DBH) stem density on maximum daily relative humidity of the forest understory during spring (April 15-May 31), summer (June 1-August 31), and fall (September 1-October 31), twelve years after a 2010 wildfire on the Cumberland Platea, Kentucky, USA. A partial effect of 0 indicates the mean response of the dependent variable, and the shading represents a 95% confidence interval.

Vapor Pressure Deficit

Measures of vapor pressure deficit varied with forest structure and across the growing season. LAI, midstory basal area, and canopy stem density were the only significant predictors of maximum daily vapor pressure deficit (VPD_{max}). During the spring, VPD_{max} was only predicted by canopy density (edf = 2.33, p = 0.005), where plots with canopy densities below approximately 200 stems ha^{-1} (80.9 stems ac^{-1}) experienced greater VPD_{max}, and plots with canopy stem densities above approximately 325 ha^{-1} (131.6 stems ac^{-1}) stems experienced lower VPD_{max} (Figure 3.4). During this season, midstory basal area (edf = 1.00, p = 0.625) and LAI (edf = 1.00, p = 0.768) were not related to VPD_{max}. LAI (edf = 1.00, $p < 0.001$) and midstory basal area (edf = 2.54, p = 0.008) were significant predictors of VPD_{max} during the summer, but canopy density was not (edf = 1.00, p = 0.446). midstory basal area displayed a parabolic relationship with VPD_{max} during summer, where VPD_{max} peaks at approximately 5.2 m^2 ha^{-1} (22.7 ft^2 ac^{-1}) (Figure 3.5). LAI was negatively related to VPD_{max} during summer. During the fall, the only significant predictor of VPD_{max} was LAI (edf = 1.87, p = 0.002), which displayed a similarly negative relationship as it did in the summer.

Forest structural measurements had less of an effect on average daily vapor pressure deficit (VPD_{avg}) across the growing season with LAI being the only significant predictor. During spring (edf = 1.65, $p < 0.001$) and summer (edf = 1.52, $p < 0.001$), LAI displayed a negative relationship with VPD_{avg}. During the fall, the relationship between LAI and VPD_{avg} was a near-significant negative relationship (edf = 1.14, p = 0.074).

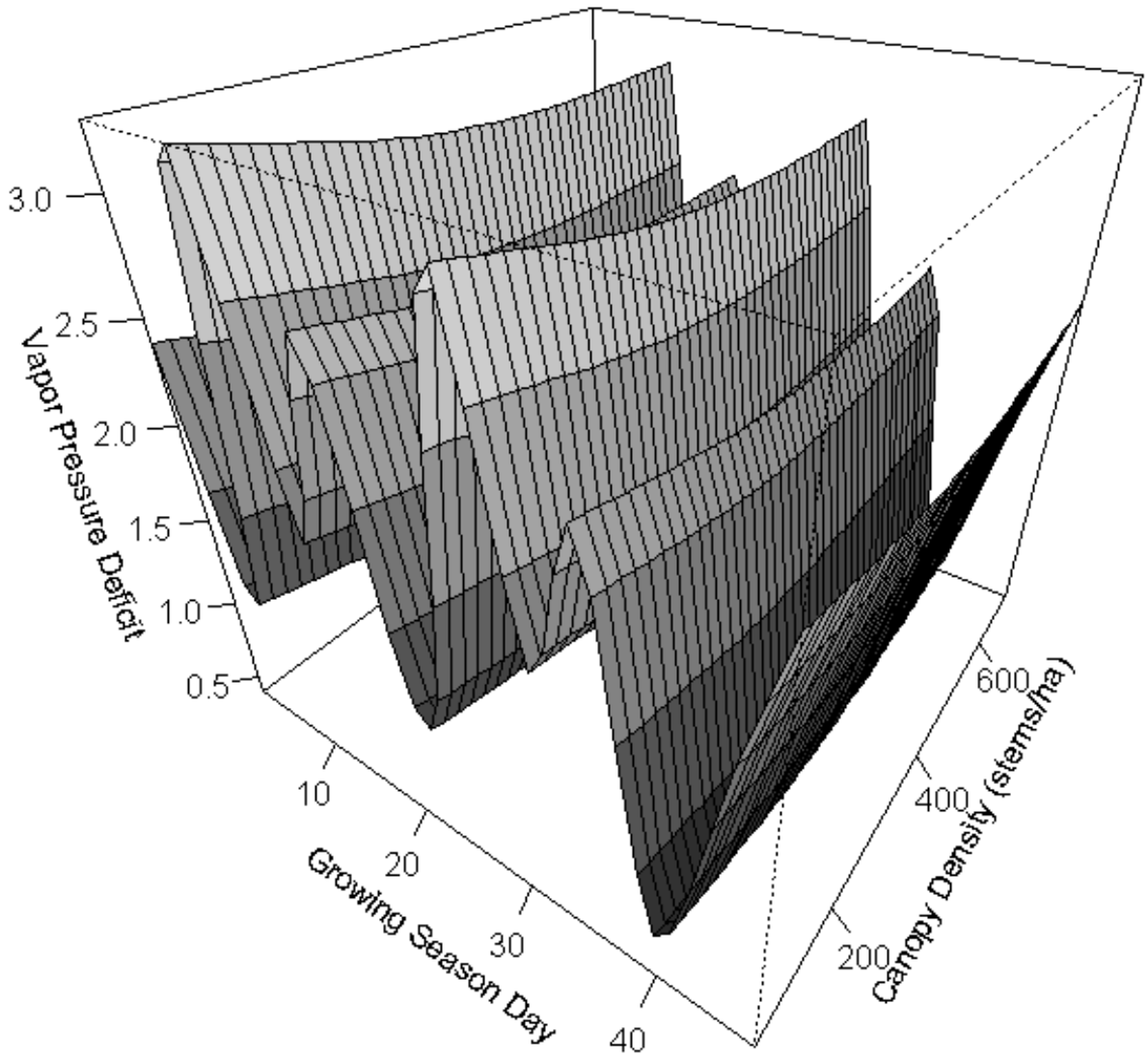

Figure 3.4 The interactive effect of canopy (>10 cm DBH; >3.94 in DBH) stem density and growing season day on maximum daily vapor pressure deficit of the forest understory during spring (April 15- May 31), twelve years after a 2010 wildfire on the Cumberland Platea, Kentucky, USA. Day one of the growing season indicates April 15, 2022.

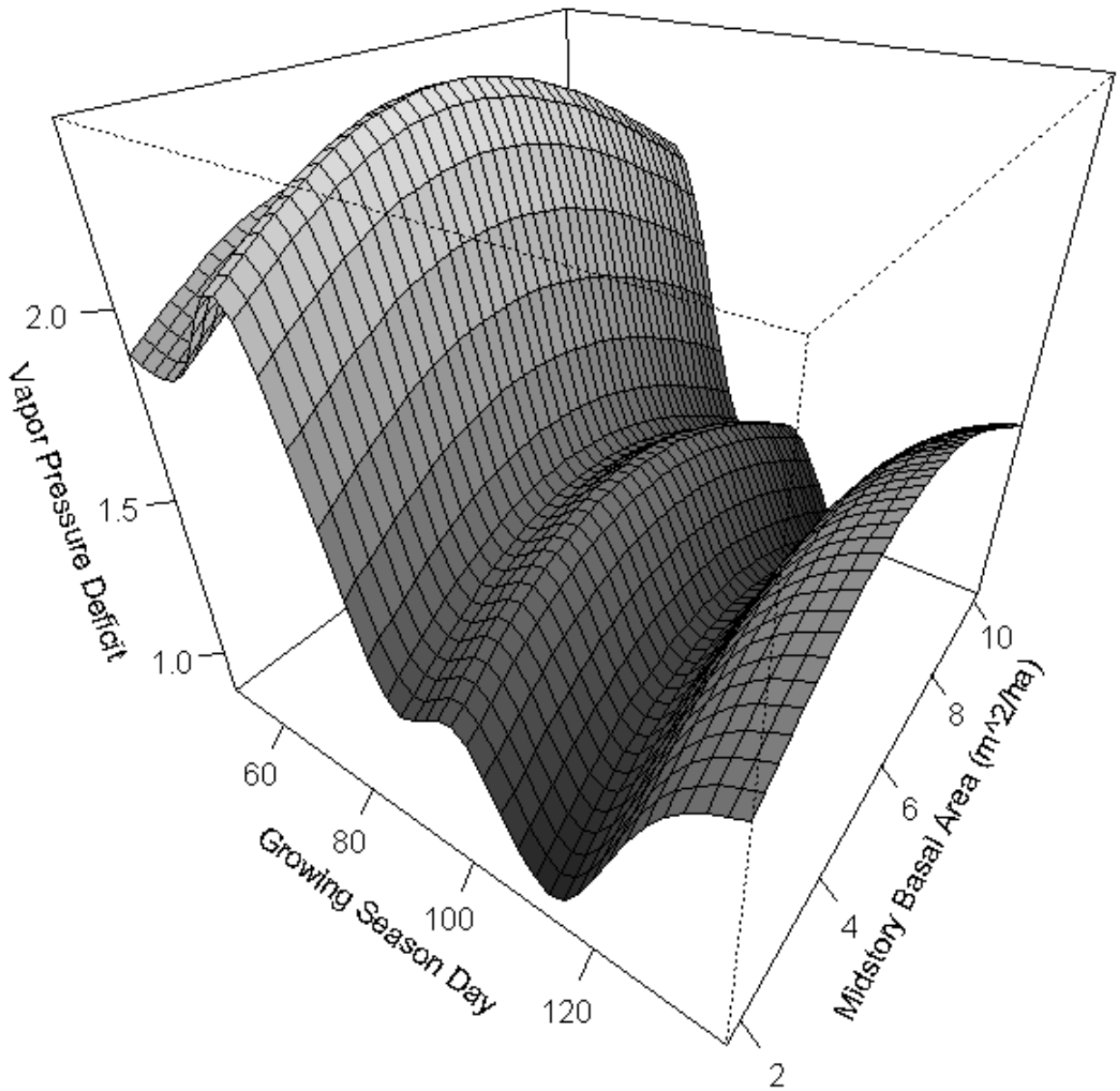

Figure 3.5 The interactive effect of midstory (2-10 cm DBH; 0.79-3.94 in DBH) basal area (BA) and growing season day on maximum daily vapor pressure deficit of the forest understory during summer (June 1-August 31), twelve years after a 2010 wildfire on the Cumberland Platea, Kentucky, USA. Day 60 of the growing season indicates June 14, 2022.

Soil Moisture

Soil moisture varied with forest structure and across the growing season. midstory density, canopy density, and total stem density significantly influenced maximum daily soil moisture (SM_{max}). During spring, total stem density was positively related SM_{max} (edf = 1.58, p = 0.003). This relationship was primarily driven by midstory stem density, which was independently positively related to SM_{max} (edf = 1.55, p = 0.044), whereas canopy density displayed a near-significant negative relationship (edf = 1.00, p = 0.088). During summer, total stem density was positively related to SM_{max} (edf = 1.84, p = 0.002). Likewise, midstory (edf = 1.62, p = 0.047) and canopy (edf = 1.00, p = 0.037) stem density displayed significant relationships with SM_{max} that followed the same pattern as spring. Fall season relationships with SM_{max} could not be modeled due to equipment malfunction.

Average daily soil moisture (SM_{avg}) varied based on forest structural characteristics and across the growing season, with midstory stem density, canopy stem density, and total stem density being the only significant predictors. A model for total stem density could only be generated for the summer season, where there was a positive relationship between total stem density and SM_{avg} (edf = 1.46, p = 0.003). This relationship was primarily the result of midstory stem density, as SM_{avg} was positively related to midstory stem density (edf = 1.50, p = 0.042) and again negatively related to canopy stem density (edf = 1.00, p = 0.031). These relationships were the same during the spring season (edf = 1.60, p = 0.036 and edf = 1.00, p = 0.053, respectively), though spring canopy stem density only exhibited a near-significant relationship. Fall season relationships between forest structure and SM_{avg} could not be modeled due to equipment malfunction.

Photosynthetically Active Radiation

Photosynthetically active radiation (PAR) was related to forest structure throughout the entire growing season, and those relationships varied little among seasons. LAI and total basal area were the only significant predictors of maximum daily PAR (PAR_{max}). For spring, summer, and fall, LAI exhibited a linear negative relationship with PAR_{max} (edf = 1.00, $p < 0.001$ for each season). Total basal area was also significantly related to PAR_{max} during spring (edf = 2.39, p = 0.028), summer (edf = 2.71, p = 0.011), and fall (edf = 1.98, p = 0.034) (Figure 3.6). During spring and summer this relationship was parabolic, where increased basal area caused increased PAR_{max} until approximately 18.0 m^2 ha^{-1} (78.4 ft^2 ac^{-1}), beyond which increased basal area caused decreased PAR_{max}. During fall, the relationship between basal area and PAR_{max} was constant until approximately 18.0 m^2 ha^{-1} (78.4 ft^2 ac^{-1}) and increased basal area after this point caused decreased PAR_{max}.

Average daily PAR (PAR_{avg}) was also related to forest structure in ways that varied throughout the growing season. The only significant predictors of PAR_{avg} were LAI and total basal area. During each season, LAI had a negative linear relationship with PAR_{avg} (edf = 1.00, $p < 0.001$ for all seasons). The relationship between total basal area and PAR_{avg} varied throughout the seasons, where in spring (edf = 2.39, p = 0.030), the relationship was parabolic, similar to that of PAR_{max} with total basal area in spring (Figure 3.7). During summer (edf = 3.36, p = 0.002), the parabolic relationship between PAR_{avg} and total basal area was much more pronounced, with maximum increases in PAR_{avg} occurring at approximately 18.0 m^2 ha^{-1} (78.4 ft^2 ac^{-1}). During fall, the relationship between total basal area and PAR_{avg} was relatively constant until approximately 20.0 m^2 ha^{-1} (87.1 ft^2 ac^{-1}), beyond which PAR_{avg} declines, though this relationship was only near-significant (edf = 1.83, p = 0.063).

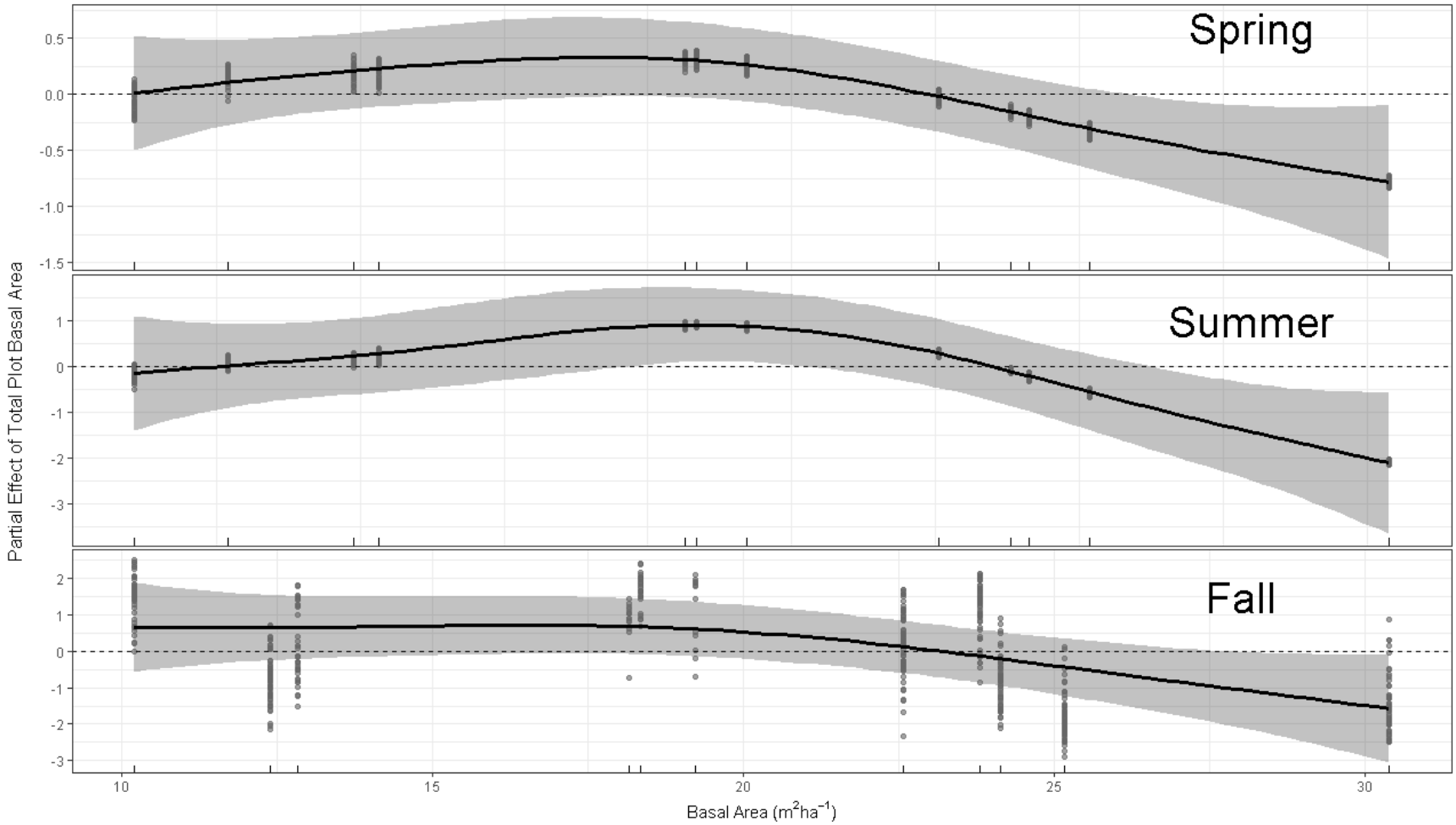

Figure 3.6 The partial effect of basal area of all stems >2 cm (0.79 in) DBH on maximum daily photosynthetically active radiation in the forest understory during spring (April 15- May 31), summer (June 1-August 31), and fall (September 1-October 31), twelve years after a 2010 wildfire on the Cumberland Platea, Kentucky, USA. A partial effect of 0 indicates the mean response of the dependent variable, and the shading represents a 95% confidence interval.

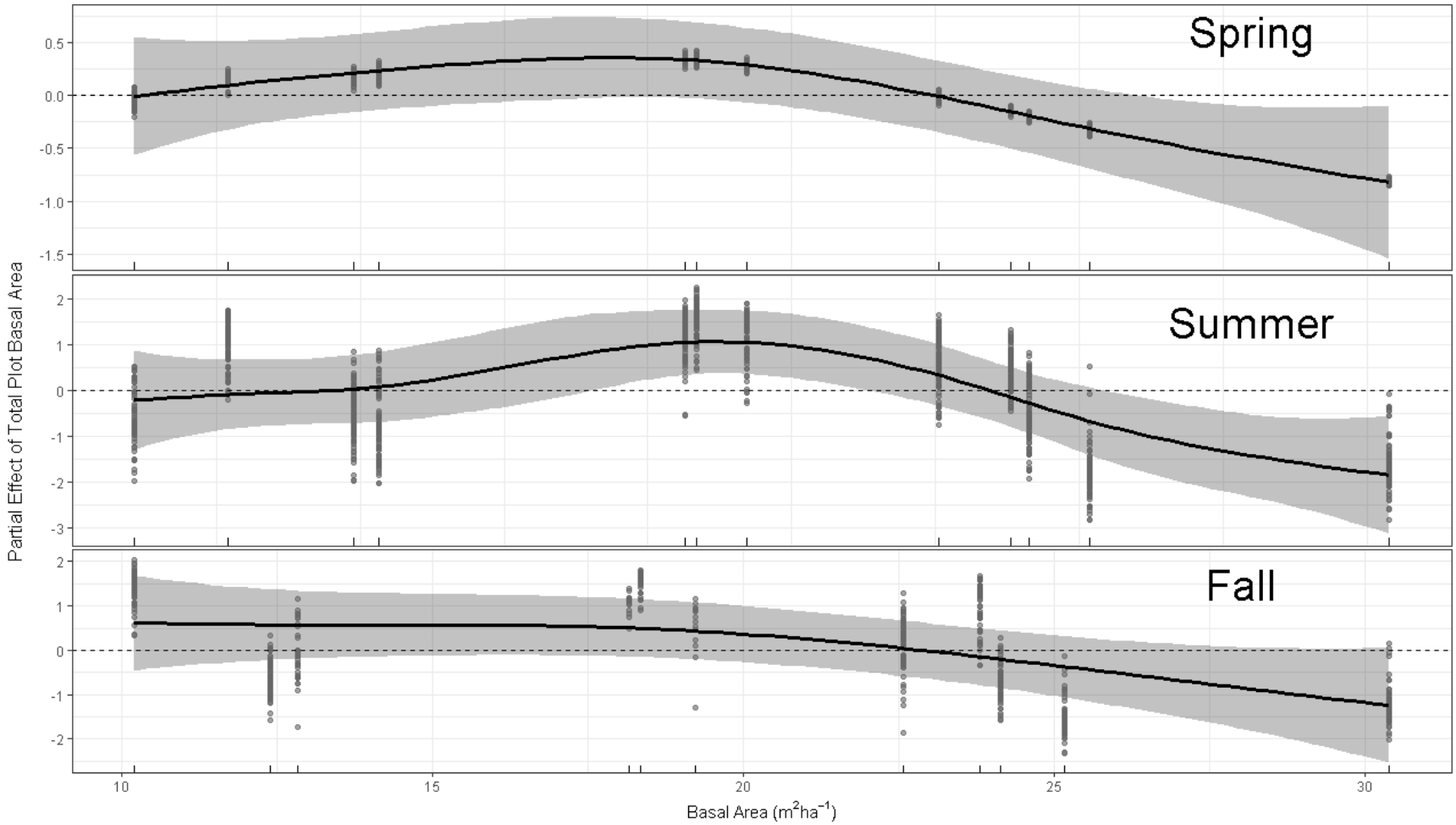

Figure 3.7 The partial effect of basal area of all stems >2 cm (0.79 in) DBH on average daily photosynthetically active radiation in the forest understory during spring (April 15- May 31), summer (June 1-August 31), and fall (September 1-October 31), twelve years after a 2010 wildfire on the Cumberland Platea, Kentucky, USA. A partial effect of 0 indicates the mean response of the dependent variable, and the shading represents a 95% confidence interval.

3.6 Discussion

My results demonstrate that forest understory microclimates in the oak-pine forests of the eastern U.S. can be predicted by forest structural conditions, and that some of these structural conditions are the result of varying levels of burn severity from a wildfire that occurred twelve years prior. Overall, after twelve years, sites that burned at a moderate burn severity (CBI 0.8-1.5) are experiencing the greatest light levels, temperatures, and VPD, and the lowest humidity levels. This is likely because at moderate burn severities, canopy density was reduced enough to increase light availability and temperatures while midstory regrowth has not yet become too dense to shade out the understory. Low-severity fire may have failed to reduce canopy densities and high-severity fire prompted dense midstory regrowth over time, both of which appear to have caused decreased light levels, temperatures, VPD, and increased relative humidity. At sites that experienced moderate burn severities, the current microclimate conditions are more likely to preferentially select for oak and pine species, which are predicted to be more successful throughout the region due to anthropogenic climate change (Iverson et al., 2019). In Chapter 2, I determined that increased burn severity resulted in increased competitive status of pines twelve years following the FTF, but the competitive advantage that oak species experienced for the first six years post-burn (Black et al., 2018) was no longer present. My results here indicate that the mechanism behind this may be that increased midstory basal area and stem density caused decreased temperatures and VPD, and low total basal area causes decreased light levels. This may indicate that to buttress the competitive status of oak species and recruitment into canopy size classes, structural modification of the midstory between years six and twelve following higher severity fire is needed to create microsite conditions conducive to their growth. Otherwise, moderate severity fire may provide the longest-term microclimate conditions that are favorable for oak and pine species.

In Chapter 2, I identified that total, small midstory, and canopy stem density and basal area are related to burn severity twelve years after a wildfire. In this, increased burn severity resulted in decreased total and canopy basal area and canopy stem density, and increased midstory basal area and stem density, and increased total density. These elements of forest structure that are linked to burn severity significantly affect PAR, soil moisture, ambient air temperature, VPD, soil moisture, and relative humidity of forest understory microclimates. This indicates that the effects of wildfire can cause significant variability in microclimate for up to twelve years post-fire. Most studies that analyze the effects of forest disturbances on understory microclimates are concerned with the immediate post-disturbance effects on growing conditions for regenerating seedlings and saplings, but few other studies have sought to understand post-fire microsite conditions after regrowth has occurred during a fire-free period.

I expected LAI to be related to burn severity twelve years following the FTF (H1), however it was not. Further, LAI was not related to any other forest structural measurement that was related to burn severity. In many studies, LAI measurements specifically quantify canopy leaves, but since my hemispherical photographs that quantified LAI were taken at 1.5 m (4.92 ft) above the ground, my measurements of LAI captured the leaf area of small midstory, non-canopy stems as well. Thus, for a seedling or sapling sized tree that is 1.5 m (4.92 ft) tall, the regrowth that has occurred over twelve years following a variable severity wildfire has obfuscated any meaningful concomitant variation in leaf area. This may imply that canopy closure has occurred across the burn area, regardless of burn severity, which would not necessarily have been captured by traditional forest structure measurements. Likewise, this may mean that there is some other fundamental ecosystem characteristic that is causing variation in LAI values, such as in plot-level site productivity or species compositions. If there was variation in site productivity among my

microclimate plots, this would cause regrowth rates and species compositions to respond differently to burn severity over time. While I attempted to control for this in my plot selection by choosing sites that are similar in landform position, it is possible that this could be the case, especially considering my plots had a relatively large range of slope values. Despite this range in slope, however, the range of TWI at these plots was relatively narrow, which indicates there was little variation in water availability and site productivity. Species composition may also influence LAI, as species vary in their branch architecture and leaf morphology (Aussenac, 2000), wherein mesophytic species oftentimes have greater leaf areas (Nowacki and Abrams, 2008). It is also possible that a combination of these factors created variation in my observed LAI values in ways that are not related to burn severity. These factors help explain my conclusions in Chapter 2, where I determined that increasing burn severity no longer promoted the regeneration of shade-intolerant species like oaks, which were being recruited into larger size classes at year 6 (Black et al., 2018), but no longer being recruited into these size classes at year twelve post-burn.

LAI was the forest structure measurement most strongly related to understory microclimate conditions (H2), in that it was significantly related to maximum and average PAR, air temperature, VPD, and RH. LAI is the amount of total leaf area in the entire canopy volume (Fang et al., 2019), which is why it was so closely related to canopy openness in my study. Canopy cover is tightly correlated to understory light levels (Ma et al., 2010), a finding with which my results are in accordance. Generally, my results suggest that as LAI increases and canopies become closed, less light is available in the understory, temperatures decrease, humidity increases, and the atmospheric demand on transpiration (VPD) decreases, which is aligned with findings from similar studies (Davis et al., 2019; Fang et al., 2019; Ma et al., 2010; Planchais and Pontailler, 1997; von Arx et al., 2013). These changes to forest microclimates have strong implications for the growth of

seedlings and saplings and understory plant communities (Muller, 2019; Stevens et al., 2015), and preferentially select for certain species. Increased light availability has been linked to oak, hickory (*Carya* spp.) (Iverson et al., 2017), and pine species (Shelton and Cain, 2000) regeneration and recruitment into larger size classes. VPD decreases can inhibit plants from transpiring (Körner and Challa, 2003) and has been shown to reduce the competitive advantages oak seedlings have over maples in high VPD environments (Parker and Dey, 2008). Since I observed significant variation in LAI that has meaningful effects for the growth and survival of understory species at the FTF plots, but that variation is not linked to burn severity, I can reasonably conclude that after twelve years, the influence of the fire on this aspect of forest structure, and thus on forest microclimates, has diminished over time.

Other measures of forest structure were related to burn severity, indicating that after twelve years, there is some signature of the fire that is influencing understory microclimates. Forest canopy structure was related to ambient air temperature, RH, VPD, and soil moisture (H2), and was particularly important for moderating the maximum daily values of these microclimate measurements. Overall, canopy density was the only canopy structural measurement to affect these microclimate characteristics and my results suggest that there was a canopy density threshold of 200 stems ha^{-1} (81 stems ac^{-1}) needed to affect VPD_{max} and T_{max} (Figure 1; Figure 7). A reduction in stem density below this threshold was necessary to cause any detectable increase in VPD_{max} or T_{max}. Von Arx et al. (2013) found a similar canopy density threshold effect in European temperate forests when analyzing canopy LAI as a measure of density, where they found that sparse canopy (canopy LAI < 4) substantially reduced its capacity to moderate VPD_{max} and T_{max}. My results indicate that in the upland oak-pine forests of the eastern U.S., this threshold may be 200 stems ha^{-1} (81 stems ac^{-1}) and canopy structural modifications intended to increase maximum daily

temperature and VPD may need to reduce canopy density below this amount to have a long-term substantive effect. Canopy density was also negatively related to maximum and average daily soil moisture, which is a well-documented pattern and the result of reduced evapotranspiration and precipitation interception that occurs when canopy densities decrease (Aussenac, 2000; Ma et al., 2010). In Chapter 2, I found that canopy density was negatively related to burn severity twelve years following a wildfire and my results here indicate this relationship can prompt long-term microclimatic changes as well. Similar studies that have quantified the effects of burn severity on immediate post-fire microclimate conditions found similar results that were biologically meaningful for understory tree regeneration (Wolf et al., 2021). Given that Black et al. (2018) found a large increase in pyrophytic species that are typically also heliophytic at the FTF site, it is reasonable to suggest that the canopy structure alterations that were the result of the FTF also had biologically meaningful effects, though I cannot say this definitively.

Small midstory structure was related to ambient air temperature, VPD, soil moisture, and RH, and was important for altering maximum daily values of these variables (H2). Both midstory density and basal area influenced microclimate conditions. The parabolic effect of midstory basal area on RH_{max}, T_{max}, and VPD_{max} may be indicative of an interaction between midstory structure and canopy structure that was caused by burn severity and not able to be detected by my analysis. For instance, in low-severity burn plots that had lower amounts of canopy stem mortality, midstory regrowth would have been lower but T_{max} would still have been substantially moderated by the canopy, yielding low T_{max} values. Conversely, in plots where burn severity was high and canopy densities were greatly reduced, the midstory regrowth over twelve years could intercept incoming solar radiation enough to cause decreased ambient air temperatures (Wolf et al., 2021). However, at medium burn severities, where there was a moderate amount of canopy mortality and some

midstory regrowth, conditions may have remained open enough to cause relatively greater VPD_{max} and T_{max} values twelve years following the fire. This would be consistent with my observation that plots with moderate amounts of total plot basal area, which is primarily influenced by canopy basal area, had the greatest PAR_{max} and PAR_{avg}. It is also possible that in moderate-severity plots where the fire was not severe enough to initially consume or kill canopy stems, delayed mortality of some residual canopy stems (Robbins et al., 2022) created canopy gaps that increased VPD_{max} and T_{max} over time. If this is the case, I would expect midstory regrowth to capitalize on these higher-light conditions within the next few years, which would reduce the PAR, VPD, and temperatures of these moderate-severity burn plots. Such an interaction would also help explain why I saw no influence of total basal area and stem density on VPD_{max} or T_{max}, and why LAI was not related to burn severity nor other structural measurements that were related to burn severity. This may indicate that when considering the long-term microclimate responses to fire events, the midstory regrowth that occurs after twelve years following a fire can reduce the initial changes to forest microclimate that are caused by reductions in forest canopy densities. This lends support to my assertion in Chapter 2 that the midstory size class has grown too dense to create conditions that preferentially select for oak and pine species that thrive in drier, high-light environments.

I observed that understory microclimate conditions were related to forest structure more often during the summer than in the spring or fall, which may indicate that forest structure has a stronger moderating effect during the summer season. To determine this, my study would need to be repeated over several years. Even so, this result is in alignment with other research that has found that the capacity of forest canopies to moderate temperatures and light levels is greatest in summer (Morecroft et al., 1998; Renaud et al., 2011; Renaud and Rebetez, 2009), and during periods of extreme heat (Renaud et al., 2011; Renaud and Rebetez, 2009). Forest composition

plays an important role in these moderating capacities, as Renaud et al. (2011) showed that in stands dominated by beech (*Fagus* spp.), the moderating capacity of the forest was significantly greater than in stands dominated by oak and pine species. This is consistent with the known effects of mesophytic species in eastern U.S. forests, whose high leaf area casts heavier shade than pyrophytic species, and is a key reason why they facilitate mesophication and reduced understory flammability (Nowacki and Abrams, 2008). Taken together, if oak and pine species occupy a greater proportion of forest composition relative to mesophytes, conditions that are conducive to fire (i.e. lower litter moisture, higher temperatures, drier ambient conditions) will be more prevalent throughout the growing season, and particularly in the spring and fall. This may alter burn prescription windows (Hiers et al., 2020) and wildfire occurrences in these seasons, potentially increasing landscape pyrodiversity (Arthur et al., 2021).

3.7 Conclusion

Overall, my results demonstrate that twelve years following a wildfire of varying severity, the reductions in the forest canopy that occurred as burn severity increased are still causing increased temperatures, drier ambient air conditions, and higher light environments. However, the midstory regrowth that has occurred over time has obscured these effects and forest understories are no longer experiencing the open canopy growing conditions, except potentially in locations where there was delayed canopy mortality. Based on the previous results at the FTF site (Black et al., 2018) indicating that shade-intolerant oak and pine species were more successful in regenerating and recruiting into larger class sizes as burn severity increased, it is highly likely that the forest structural modifications that occurred created biologically meaningful changes to understory microclimates that selected for these species. In Chapter 2, I speculated that oak and

pine species were no longer regenerating and oaks were no longer recruiting into larger size classes because of midstory regrowth, and here, the microclimate analysis that I have conducted has affirmed those speculations. Since these species are anticipated to be more successful in future climate scenarios, fostering seedling establishment and development of these species is desirable to avoid degraded ecosystem health and maladapted forest communities in the future. Together with my results in Chapter 2, this research indicates that a high-severity fire should be followed by a midstory removal treatment by year twelve to increase understory light availability, temperatures, and VPD, which would benefit future regenerating pine and oak species and assist these species in recruiting into larger size classes.

APPENDIX 1: A1 Supplemental information for Chapter 2

Table A1-1 Model selection set for the relationship between burn severity (CBI) and Shannon's Diversity Index (SHDI). Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

	Model	AIC
Overall	Linear*	2.8
	Square Root	3
	2nd Quadratic	4.8
	3rd Quadratic	6.7
	4th Quadratic	8.6
Canopy	Linear*	32.9
	Square Root	32.9
	2nd Quadratic	34.8
	3rd Quadratic	36.8
	4th Quadratic	38.7
Small Midstory	Linear	10.3
	Square Root*	10.1
	2nd Quadratic	12.1
	3rd Quadratic	14.1
	4th Quadratic	16.1

Table A1-2 Model selection set for the relationship between burn severity (CBI) and basal area. Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

			Model	AIC
Overall	Plot-Level		Linear	152.4
			Square Root*	151.3
			2nd Quadratic	152.3
			3rd Quadratic	154.1
			4th Quadratic	155.2
	Group Level	Mesophytes	Linear*	56.3
			Square Root	56.1
			2nd Quadratic	56.5
			3rd Quadratic	58.2
			4th Quadratic	60.1
		Pyrophytes	Linear	33.3
			Square Root*	32.3
			2nd Quadratic	33.7
			3rd Quadratic	34.2
			4th Quadratic	34.7
		Intermediates	Linear	82.4
			Square Root*	81.9
			2nd Quadratic	81.9
			3rd Quadratic	83.9
			4th Quadratic	83.6
Canopy	Plot-Level		Linear	160.9
			Square Root*	160.6
			2nd Quadratic	162.3
			3rd Quadratic	164.2
			4th Quadratic	166.2
	Group Level	Mesophytes	Linear	55.4
			Square Root*	55.2
			2nd Quadratic	57.3
			3rd Quadratic	59.1
			4th Quadratic	61
		Pyrophytes	Linear*	61.2
			Square Root	62.5
			2nd Quadratic	63.2
			3rd Quadratic	65.1
			4th Quadratic	65.7
		Intermediates	Linear*	82.4
			Square Root	82.5

			2nd Quadratic	84.4
			3rd Quadratic	85.8
			4th Quadratic	85.5
Midstory	Plot-Level		Linear*	123.6
			Square Root	124.9
			2nd Quadratic	124.3
			3rd Quadratic	124.8
			4th Quadratic	125.6
	Group Level	Mesophytes	Linear*	83.7
			Square Root	83.7
			2nd Quadratic	85.6
			3rd Quadratic	87.2
			4th Quadratic	88.5
		Pyrophytes	Linear	81
			Square Root*	79.7
			2nd Quadratic	82.8
			3rd Quadratic	79.2
			4th Quadratic	80
		Intermediates	Linear	77.2
			Square Root*	76.7
			2nd Quadratic	78.5
			3rd Quadratic	80.5
			4th Quadratic	80.8

Table A1-3 Model selection set for the relationship between burn severity (CBI) and stem density. Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

			Model	AIC
Overall	Plot-Level		Linear*	467.9
			Square Root	467.7
			2nd Quadratic	469.9
			3rd Quadratic	469
			4th Quadratic	470.9
	Group Level	Mesophytes	Linear*	440
			Square Root	439.8
			2nd Quadratic	441.9
			3rd Quadratic	443.7
			4th Quadratic	445.5
		Pyrophytes	Linear*	59.7
			Square Root	60.2
			2nd Quadratic	61.5
			3rd Quadratic	58.4
			4th Quadratic	60.3
		Intermediates	Linear	208.6
			Square Root	207.9
			2nd Quadratic*	207.7
			3rd Quadratic	209.5
			4th Quadratic	210.2
Canopy	Plot-Level		Linear	159.9
			Square Root*	159.7
			2nd Quadratic	161.7
			3rd Quadratic	163.5
			4th Quadratic	164.7
	Group Level	Mesophytes	Linear*	90.3
			Square Root	90.3
			2nd Quadratic	92.3
			3rd Quadratic	94.2
			4th Quadratic	96
		Pyrophytes	Linear	43.9
			Square Root*	42.7
			2nd Quadratic	43.9
			3rd Quadratic	45.4
			4th Quadratic	46.2

		Intermediates	Linear*	148.2
			Square Root	148.1
			2nd Quadratic	150.1
			3rd Quadratic	151.6
			4th Quadratic	150.5
Midstory	Plot-Level		Linear*	469.5
			Square Root	469.4
			2nd Quadratic	471.5
			3rd Quadratic	470.7
			4th Quadratic	472.7
	Group Level	Mesophytes	Linear*	440.9
			Square Root	440.8
			2nd Quadratic	442.8
			3rd Quadratic	444.6
			4th Quadratic	446.4
		Pyrophytes	Linear	74.5
			Square Root*	73.3
			2nd Quadratic	76.2
			3rd Quadratic	71.6
			4th Quadratic	73.6
		Intermediates	Linear	208.2
			Square Root*	20735
			2nd Quadratic	207.3
			3rd Quadratic	209
			4th Quadratic	210

Table A1-4 Model selection set for the relationship between burn severity (CBI) and importance values. Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

		Model	AIC
Overall	Mesophytes	Linear	-32.6
		Square Root*	-32.9
		2nd Quadratic	-31.3
		3rd Quadratic	-31
		4th Quadratic	-29.1
	Pyrophytes	Linear*	-32.3
		Square Root	-32.4
		2nd Quadratic	-31.7
		3rd Quadratic	-31.8
		4th Quadratic	-34.3
	Intermediates	Linear	-17
		Square Root	-17.1
		2nd Quadratic*	-18.7
		3rd Quadratic	-16.9
		4th Quadratic	-17
Canopy	Mesophytes	Linear*	48.7
		Square Root	48.8
		2nd Quadratic	50.6
		3rd Quadratic	52.5
		4th Quadratic	54.4
	Pyrophytes	Linear	-6.5
		Square Root*	-6.6
		2nd Quadratic	-4.7
		3rd Quadratic	-4.8
		4th Quadratic	-11.2
	Intermediates	Linear*	-5.7
		Square Root	-5.6
		2nd Quadratic	-3.7
		3rd Quadratic	-2.9
		4th Quadratic	-8.7
Small Midstory	Mesophytes	Linear	-11.1
		Square Root*	-12.4

		2nd Quadratic	-10.3
		3rd Quadratic	-10.4
		4th Quadratic	-8.7
	Pyrophytes	Linear*	-32.1
		Square Root	-31.1
		2nd Quadratic	-30.8
		3rd Quadratic	-35
		4th Quadratic	-33.2
	Intermediates	Linear	-10.7
		Square Root	-10.3
		2nd Quadratic*	-12.7
		3rd Quadratic	-11
		4th Quadratic	-9.7

Table A1-5 Model selection set for the relationship between burn severity (CBI) and stem recruitment between year six and year twelve. Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

		Model	AIC
Canopy	Mesophytes	Linear	223.4
		Square Root*	223.2
		2nd Quadratic	225.3
		3rd Quadratic	227.1
		4th Quadratic	227.8
	Pyrophytes	Linear	269.3
		Square Root	271.6
		2nd Quadratic*	264.8
		3rd Quadratic	266.8
		4th Quadratic	268.8
	Intermediates	Linear	121.1
		Square Root	121.5
		2nd Quadratic*	123
		3rd Quadratic	124.8
		4th Quadratic	126.6
Small Midstory	Mesophytes	Linear	410
		Square Root*	409.9
		2nd Quadratic	411.9
		3rd Quadratic	416.8
		4th Quadratic	415.8
	Pyrophytes	Linear*	203.9
		Square Root	204.4
		2nd Quadratic	205.6
		3rd Quadratic	201.7
		4th Quadratic	202.8
	Intermediates	Linear	121.8
		Square Root	120.6
		2nd Quadratic*	118
		3rd Quadratic	119.8
		4th Quadratic	121.1

Table A1-6 Model selection set for the relationship between burn severity (CBI) and stem recruitment between year one and year twelve. Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

		Model	AIC
Canopy	Mesophytes	Linear*	126.3
		Square Root	127.3
		2nd Quadratic	127.5
		3rd Quadratic	128.7
		4th Quadratic	129.9
	Pyrophytes	Linear*	276.8
		Square Root	276.9
		2nd Quadratic	278.3
		3rd Quadratic	276.1
		4th Quadratic	277.9
	Intermediates	Linear*	133
		Square Root	133.4
		2nd Quadratic	134.8
		3rd Quadratic	136.6
		4th Quadratic	138.5
Small Midstory	Mesophytes	Linear*	424.9
		Square Root	424.7
		2nd Quadratic	426.8
		3rd Quadratic	428.6
		4th Quadratic	430.3
	Pyrophytes	Linear	72.3
		Square Root*	71.3
		2nd Quadratic	74.2
		3rd Quadratic	69.8
		4th Quadratic	71.8
	Intermediates	Linear	70.2
		Square Root*	69.4
		2nd Quadratic	69.3
		3rd Quadratic	70.4
		4th Quadratic	71

APPENDIX 2: A2 Supplemental information for Chapter 3

Table A2-1 Model selection set for the relationship between burn severity (CBI) and forest structural measurements derived from hemispherical photography. Model selection was based on AIC (Akaike's Information Criterion), visual estimates of model diagnostic tests, and considerations for model simplicity. An asterisk (*) indicates the best model.

	Model	AIC
LAI	Linear	33.5
	Square Root*	32.9
	2nd Quadratic	32.9
	3rd Quadratic	34.9
	4th Quadratic	36.4
Openness	Linear	197.2
	Square Root*	196.6
	2nd Quadratic	196.5
	3rd Quadratic	198.4
	4th Quadratic	199.8
Gap Fraction	Linear	206.6
	Square Root	205.9
	2nd Quadratic*	205.8
	3rd Quadratic	207.6
	4th Quadratic	208.5

Table A2-2 Model selection table for the time analysis of maximum daily temperature using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(Tmax ~ Day + LAI + MidstoryBA + CanopyDensity, random = list (Plot = ~1), method = 'REML', family = gaussian)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	~9	11	3300.3	3347.6	-1639.1
	Null2	11	11	3266.2	3313.6	-1622.1
	Null3	12	11	3071.7	3071.7	-1501.2
	VF1	12	11	3110	3157.4	-1544
	VF2	12	12	3025.9	3077.6	-1500.9
	VF3	12	12	3026.1	3077.8	-1501
	VF4	12	11	3262.8	3310.1	-1620.3
	VF5	12	11	3066.6	3113.9	-1522.3
	COR1	12	12	3068.4	3120.1	-1522.2
	COR2*	12	13	2995.3	3051.3	-1484.7
Summer	Null1	~9	11	4913.3	4967.4	-2445.6
	Null2	10	11	4913.3	4967.4	-2445.6
	Null3	11	11	4905.8	4959.9	-2441.9
	VF1	10	11	5104.6	5158.8	-2541.3
	VF2	10	12	4914	4973.1	-2445
	VF3	10	12	4913.7	4972.8	-2444.9
	VF4	10	11	5257.9	5312.1	-2617.9
	VF5	10	11	5048.7	5102.8	-2513.4
	COR1	10	12	4905.8	4964.8	-2440.9
	COR2*	10	13	4815.7	4879.7	-2394.9
Fall	Null1	~9	11	2618.9	2665	-1298.5
	Null2	10	11	2618.9	2665	-1298.5
	Null3	11	11	2590.4	2636.5	-1284.2
	VF1	11	11	2682.6	2728.7	-1330.3
	VF2	11	12	2592.1	2642.4	-1284
	VF3	11	11	2632.7	2678.8	-1305.3
	VF4	11	11	2705.4	2751.5	-1341.7
	COR1	11	12	2645.9	2696.2	-1311
	COR2*	11	13	2591.6	2646.1	-1282.8

Table A2-3 Model selection table for the time analysis of average daily temperature using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(Tmax ~ Day + LAI, random = list (Plot = ~1), method = 'REML', family = gaussian)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	~9	7	3036.8	3067	-1511.4
	Null2	11	7	2864.7	2894.8	-1425.3
	Null3	13	7	2447	2477.2	-1216.5
	VF1	13	7	2562.4	2592.6	-1274.2
	VF2	13	8	2449	2483.5	-1216.5
	VF3	13	8	2449	2483.5	-1216.5
	VF4	13	7	2504.3	2534.4	-1245.1
	COR1	13	8	2560.9	2595.3	-1272.4
	COR2*	13	9	2368.6	2407.4	-1175.3
Summer	Null1	~9	7	4532.5	4567	-2259.3
	Null2	11	7	4521.2	4555.7	-2253.6
	Null3	13	7	4359.1	4393.6	-2172.6
	VF1	13	7	4579.7	4614.2	-2282.8
	VF2	13	8	4360.9	4400.3	-2172.4
	VF3	13	7	4464	4498.4	-2225
	COR1	12	8	4097.2	4136.6	-2040.6
	COR2*	13	9	3664.2	3708.5	-1823.1
Fall	Null1	~9	7	2498.7	2519.1	-1237.9
	Null2	8	7	2550	2579.3	-1268
	Null3	12	7	2416.2	2445.5	-1201.1
	VF1	12	8	2410	2443.6	-1197
	VF2	12	8	2414.7	2448.2	-1199.3
	VF3	12	7	2445.7	2475.1	-1215.9
	COR1	12	8	2386	2419.5	-1185
	COR2*	12	7	2550	2579.3	-1268

Table A2-4 Model selection table for the time analysis of maximum daily relative humidity using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(RHmax ~ Day + LAI, random = list (Plot = ~1), method = 'REML', family = quasibinomial(link = 'probit'))**

	Model	Knots	df	AIC
Spring	Null1	~9	7	415.7
	Null2	14	7	355.3
	Null3	13	7	388
	COR1	15	8	355.6
	COR2*	14	9	181.5
Summer	Null1	~9	7	358.1
	Null2	13	7	335
	Null3	11	7	310.5
	COR1	11	8	117.8
	COR2*	11	9	22.4
Fall	Null1	~9	7	173.8
	Null2	10	7	173.8
	Null3	11	7	124.8
	COR1	10	8	111.3
	COR2*	10	9	64.5

Table A2-5 Model selection table for the time analysis of maximum daily relative humidity using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(Rhavg ~ Day + LAI + CanopyDensity + MidstoryDensity, random = list (Plot = ~1), method = 'REML', family = quasi)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	12	11	1690		
	Null2	13	11	1665		
	Null3	10	11	1708.1		
	COR1	11	12	1702		
	COR2*	12	13	1566.5		
Summer	Null1	~9	11	2567.7	2621.9	-1272.9
	Null2	8	11	2612	2666.1	-1295
	Null3	12	11	2533.4	2587.6	-1255.7
	VF1	8	11	2756.7	2810.9	-1367.3
	VF2	8	12	2611.6	2670.7	-1293.8
	VF3	8	12	2611.4	2670.4	-1293.7
	VF4	8	11	2990	3044.2	-1484
	COR1*	8	12	2650.7	2709.8	-1313.4
	COR2	8	13	2649.8	2713.7	-1311.9
Fall	Null1	8	11	1316	1362.1	-647
	Null2	12	11	1314	1360.1	-646
	Null3	14	11	1283.1	1329.2	-630.6
	VF1	8	11	1389.2	1435.3	-683.6
	VF2	8	12	1312.8	1363.1	-644.4
	VF3	8	12	1312.6	1362.9	-644.3
	VF4	8	11	1476.5	1522.6	-727.3
	COR1	8	12	1379.4	1429.7	-677.7
	COR2*	8	13	1353.8	1408.3	-664

Table A2-6 Model selection table for the time analysis of maximum vapor pressure deficit using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(VPDmax ~ Day + LAI + MidstoryBA + CanopyDensity, random = list (Plot = ~1), method = 'REML', family = gaussian)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	~9	11	1254.2	1301.6	-616.1
	Null2	11	11	1283.1	1330.4	-630.6
	Null3	12	11	1007.3	1054.7	-492.7
	Null4	13	11	1023.1	1070.4	-500.5
	VF1	13	11	1107.2	1154.6	-542.6
	VF2	13	12	1024.7	1076.3	-500.3
	VF3	13	12	1025	1076.6	-500.5
	VF4	13	11	1061.7	1109	-519.8
	VF5	13	11	1367.6	1415	-672.8
	COR1	13	12	1109.2	1160.9	-542.6
	COR2*	13	13	1062.2	1118.1	-518.1
Summer	Null1	~9	11	1741	1795.2	-859.5
	Null2	10	11	1741	1795.2	-859.5
	Null3	8	11	1853	1907.1	-901.5
	Null4	7	11	1890.7	1944.8	-934.3
	VF1	8	11	2030	2084.1	-1004
	VF2	8	12	1854.6	1913.7	-915.3
	VF3	8	11	2004.5	2058.7	-991.3
	VF4	8	11	2517	2571.1	-1247.5
	COR1	8	12	1880.2	1939.2	-928.1
	COR2*	8	13	1873.2	1937.2	-923.6
Fall	Null1	~9	11	624.6	670.7	-301.3
	Null2	12	11	630.7	676.8	-304.4
	Null3	8	11	695	741	-336.5
	Null4	7	11	690.3	736.4	-334.2
	VF1	7	11	795.2	841.3	-386.6
	VF2	7	12	692.3	742.6	-334.2

VF3	7	12	692.2	742.5	-334.1
VF4	7	11	1003.9	1050	-491
VF5	7	11	729.4	775.4	-353.7
COR1	7	12	765	765	-345.4
COR2*	7	13	690.1	744.6	-332.1

Table A2-7 Model selection table for the time analysis of average vapor pressure deficit using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(SMavg ~ Day + MidstoryDensity+ CanopyDensity, random = list (Plot = ~1), method = 'REML', family = quasibinomial)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	~9	7	527.7	557.9	-256.9
	Null2	8	7	578	608.2	-282
	Null3	13	7	276.6	306.7	-131.2
	VF1	13	7	334.2	364.6	-160.2
	VF2	13	8	278.6	313	-131.2
	VF3	13	8	278.6	313	-131.2
	VF4	13	7	379	409.2	-182.5
	COR1	13	8	380.9	415.4	-182.5
	COR2*	13	9	239.5	278.3	-110.7
Summer	Null1	~9	7	170.9	205.3	-78.4
	Null2	6	7	390	424.6	-188
	Null3	7	7	405.7	440.1	-195.8
	Null4	8	7	344.7	379.1	-165.3
	VF1	8	7	503.4	537.9	-244.7
	VF2	8	8	340.3	379.7	-162.1
	VF3	8	8	338.8	378.2	-161.4
	COR1	8	8	251.6	291	-117.8
	COR2*	8	9	220.2	264.5	-101.1
Fall	Null1	0	7	-152.3	-123	83.2
	Null2	6	7	-439	-14.6	29
	Null3	7	7	-97.3	-68	55.7
	Null4	8	7	-89	-59.7	51.5
	VF1	6	7	-0.8	28.6	7.4
	VF2	6	8	-41.9	-8.4	29
	VF3	6	8	-42.2	-8.7	29.1
	VF4	6	7	45.5	74.8	-15.7
	VF5	6	7	262.6	291.9	-124.3
	COR1	6	8	-145.3	-111.7	80.7
	COR2*	6	9	-168	-130.3	93

Table A2-8 Model selection table for the time analysis of maximum soil water content using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(SMmax ~ Day +TotalDensity, random = list (Plot = ~1), method = 'REML', family = quasibinomial))**

	Model	Knots	df	AIC
Spring	Null1	7	9	-1328.4
	Null2	14	9	-1493.6
	Null3	13	9	-1500
	Null4	12	9	-1487.1
	COR1	12	10	-1497.7
	COR2*	12	11	-1504.6
Summer	Null1	10	9	-897.6
	Null2	12	9	-900.8
	Null3	14	9	-906.2
	Null4	~9	9	-897.6
	COR1	~9	10	-1464.3
	COR2*	~9	11	-1465.6

Table A2-9 Model selection table for the time analysis of average soil water content using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(SMavg ~ Day + MidstoryDensity+ CanopyDensity, random = list (Plot = ~1), method = 'REML', family = quasibinomial)**

	Model	Knots	df	AIC
Spring	Null1	16	9	-2081.3
	Null2	11	9	-2003.5
	Null3	12	9	-2009.4
	Null4	14	9	-2059.6
	COR1	12	10	-2207.5
	COR2*	12	11	-2239.8
Summer	Null1	10	9	-1484.2
	Null2	11	9	-1478
	Null3	12	9	-1471.8
	Null4	13	9	-1485.1
	COR1*	13	11	-2159.8

Table A2-10 Model selection table for the time analysis of maximum photosynthetically active radiation using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(PARmax ~ Day + LAI, random = list (Plot = ~1), method = 'REML', family = gaussian)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	~9	7	1499.3	1529.4	-742.6
	Null2	8	7	1499.9	1530	-742.9
	Null3	14	7	1453.7	1483.9	-719.9
	VF1	14	7	1410.9	1441	-698.4
	VF2	14	8	1412.9	1447.3	-698.4
	VF3	14	8	1410.5	1445	-697.2
	VF4	14	7	1570.5	1600.7	-778.2
	VF5	14	7	1696.3	1726.5	-841.2
	COR1	~9	8	1451.2	1485.7	-717.6
	COR2*	~9	9	1455	1493.7	-718.5
Summer	Null1	12	7	2737.9	2772.4	-1362
	Null2	6	7	2739.2	2773.7	-1362.6
	Null3	8	7	2740	2774.5	-1363
	VF1	6	7	2692.8	2727.3	-1339.4
	VF2	6	8	2688.8	2728.2	-1336.4
	VF3	6	8	2698.3	2737.7	-1341.1
	VF4	8	7	2781.7	2816.2	-1383.9
	VF5	6	7	3096.8	3131.3	-1541.4
	COR1	~9	10	2631.5	2680.8	-1305.8
	COR2*	~9	11	2633.1	2687.3	-1305.6
Fall	Null1	~9	7	1160.4	1189.6	-573.2
	Null2	6	7	1186.3	1215.5	-586.1
	Null3	7	7	1162.7	1192	-574.4
	Null4	8	7	1159.6	1188.9	-572.8
	VF1	~9	7	1175.5	1204.7	-580.7
	VF2	~9	8	1159.8	1193.2	-571.9
	VF3	~9	8	1162	1195.4	-573
	VF4	~9	9	1186.9	1224.5	-584.5
	VF5	~9	7	1230.8	1260.1	-608.4

COR1	~9	9	1140.7	1178.3	-561.3
COR2*	~9	10	1140.8	1182.5	-560.4

Table A2-11 Model selection table for the time analysis of average photosynthetically active radiation using generalized additive mixed effect models. For each season, a several null models were tested using different numbers of knots, then when the optimal amount was found, variance structures were fixed to the model, then temporal autocorrelation corrections were added. Model selection was based off of visual estimates of model diagnostic tests, as well as Akaike's Information Criterion (AIC). An * indicates the best model. **Global Model: gamm(PARmax ~ Day + LAI, random = list (Plot = ~1), method = 'REML', family = gaussian)**

	Model	Knots	df	AIC	BIC	Log Likelihood
Spring	Null1	~9	7	1499.3	1529.4	-742.6
	Null2	8	7	1499.9	1530	-742.9
	Null3	14	7	1453.7	1483.9	-719.9
	VF1	14	7	1410.9	1441	-698.4
	VF2	14	8	1412.9	1447.3	-698.4
	VF3	14	8	1410.5	1445	-697.2
	VF4	14	7	1570.5	1600.7	-778.2
	VF5	14	7	1696.3	1726.5	-841.2
	COR1	~9	8	1451.2	1485.7	-717.6
	COR2*	~9	9	1455	1493.7	-718.5
Summer	Null1	12	7	2737.9	2772.4	-1362
	Null2	6	7	2739.2	2773.7	-1362.6
	Null3	8	7	2740	2774.5	-1363
	VF1	6	7	2692.8	2727.3	-1339.4
	VF2	6	8	2688.8	2728.2	-1336.4
	VF3	6	8	2698.3	2737.7	-1341.1
	VF4	8	7	2781.7	2816.2	-1383.9
	VF5	6	7	3096.8	3131.3	-1541.4
	COR1	~9	10	2631.5	2680.8	-1305.8
	COR2*	~9	11	2633.1	2687.3	-1305.6
Fall	Null1	~9	7	1160.4	1189.6	-573.2
	Null2	6	7	1186.3	1215.5	-586.1
	Null3	7	7	1162.7	1192	-574.4
	Null4	8	7	1159.6	1188.9	-572.8
	VF1	~9	7	1175.5	1204.7	-580.7
	VF2	~9	8	1159.8	1193.2	-571.9
	VF3	~9	8	1162	1195.4	-573

VF4	~9	9	1186.9	1224.5	-584.5
VF5	~9	7	1230.8	1260.1	-608.4
COR1	~9	9	1140.7	1178.3	-561.3
COR2*	~9	10	1140.8	1182.5	-560.4

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VITA

Scott Glenn Culbert was born and raised in Grand Rapids, Michigan. Prior to his time at the University of Kentucky, he earned his B.S. in Environmental Science with a concentration in Natural Resources from Northern Michigan University, where he graduated *magna cum laude* and developed a strong interest in forest and disturbance ecology. Following this, he served as a Peace Corps Volunteer in Senegal, where he helped incorporate agroforestry tree species into agricultural practices. As a graduate student, he was awarded departmental funding to attend the 7th Fire in Eastern Oak Forests Conference to present posters highlighting the research findings that are contained within this thesis. Likewise, the Department of Forestry and Natural Resources graciously awarded Scott their Graduate Student Award of Excellence. After earning his M.S. in Forest and Natural Resource Sciences, he will be working as a Climate Change Resource Assistant with the USDA Forest Service, which will contribute to his overall goal of working to improve society's relationship with the natural world, especially in locations that are experiencing issues that are the result of western intervention and anthropogenic climate change.