UNDERSTORY RESPONSE TO SHELTERWOOD AND BURN TREATMENTS IN A DRY *QUERCUS* FOREST IN INDIANA

by

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ABBREVIATIONS

ANOVA	Analysis of Variance
BA	Basal Area
CWD	Coarse Woody Debris
DBH	Diameter at Breast Height
FWD	Fine Woody Debris
HNF	Hoosier National Forest
NMDS	Non-metric Multidimensional Scaling
PERMANOVA	Permutational Multivariate Analysis of Variance
SD	Standard Deviation
SI	Site Index
TSI	Terrain Shape Index
USDA	United States Department of Agriculture

ABSTRACT

Alterations to the historic fire regime have contributed to widespread regeneration failure in *Quercus* L. (oak) forests of the eastern United States. Composition has shifted from *Quercus* and other fire-adapted species to dominance by mesophytic species. While land managers often focus efforts on restoring *Quercus* regeneration, the herbaceous layer experiences reduced cover and diversity of herb and graminoid species resulting from the increased woody stem density in fire-suppressed forests. Declining abundance of *Quercus* species and diversity in the herbaceous layer reduce the overall habitat quality and ecosystem functions provided by the forest. A combination of overstory harvests and prescribed burning are often conducted to restore the plant community in *Quercus* forests affected by mesophication. Initiated in 2010, our study on the Hoosier National Forest in Indiana conducted shelterwood and midstory (mechanical, chemical, or none) harvests followed by prescribed burning on a less productive site, while leaving a more productive site unburned. Our objective was to evaluate the survival and competitive response of *Quercus* spp. within the regeneration layer and whether diversity and cover increased in the herbaceous layer following treatments. Using nested circular plots, we measured seedling survival and resprout response, in addition to regeneration density before and after treatments. We measured the percent cover of herbaceous-layer species within quadrats and calculated species richness, evenness, and diversity. Using multiple mixed-effects models, ANOVA, and NMDS ordination, we evaluated woody species regeneration and herbaceous-layer composition before and after treatments. Post-treatment, monitored *Quercus* spp. seedlings at the burned site displayed greater survival (> 94%) and resprouting (> 92% of monitored stems), which exceeded most competing species, including *Acer* spp. (~ 59% survival and resprouting) and *Fraxinus americana* (72% survival and resprouting). *Q. alba* seedling (< 3.8 cm DBH) densities doubled after burning; it was one of the most abundant species (9,864 stems ha^{-1}) at the burned site. NMDS ordination indicated a clear shift in regeneration species composition with the burn driving a shift away from mesophytic species towards greater importance of *Quercus* species. Additionally, our burned site had significantly increased herbaceous-layer richness, Shannon diversity index, and total cover compared to pre-treatment. Percent cover increased across all plant functional groups within the herbaceous layer, with trees/shrubs exhibiting the greatest increase. Herbaceous-layer composition at the burned site significantly shifted toward greater importance of graminoids and herbs post-

treatment. Post-treatment, the unburned site contained fewer, and less competitive, *Quercus* seedlings compared to non-*Quercus* competitors and displayed no significant compositional shifts in seedling species composition post-harvest. Our unburned site exhibited significant, but minor, increases in herbaceous-layer richness, evenness, diversity, and total cover. Herbaceous-layer composition at the unburned site was significantly different post-treatment, shifting towards greater importance of vines, trees/shrubs, and herbs. The more-productive unburned site would likely require multiple burns to produce adequate competitive *Quercus* seedlings to perpetuate dominance in the developing stand. Burning would also likely result in greater increases in herbaceous-layer diversity compared to harvesting alone. Conversely, the shelterwood, followed by a single burn, on the less productive site had a more substantial effect on the herbaceous layer, and likely produced an adequate density of *Quercus* reproduction to ensure future dominance by the genus.

CHAPTER 1. INTRODUCTION

Quercus-Carya (oak-hickory) forests are a dominant forest type in eastern North America and have high ecological and economical value. *Quercus* L. trees play an important role in the ecosystem by providing carbon storage, nutrient cycling, water filtration, and wildlife habitat (Fralish, 2004; Johnson et al., 2019; Kimmins, 2004). Members of *Quercus* are classified as foundation species because of their historical dominance and critical role in forest structure and mast production (Fralish, 2004; Hanberry and Nowacki, 2016). A variety of wildlife species rely on *Quercus* as a food source, including insects, birds, such as *Aix sponsa* L. (Wood Duck), and mammals, such as *Odocoileus virginianus* Zimmerman (white tailed deer) and *Ursus americanus* L. (black bear; Brose et al., 2014; Fralish, 2004). In addition to their ecological services, *Quercus* trees have high timber value, with 25% of growing stock volume in the eastern United States consisting of *Quercus* species (Johnson et al., 2019). The lumber is used for a variety of purposes such as furniture, cabinets, whiskey barrels, flooring, and railroad ties (Brose et al., 2014). The high ecological and economic importance of *Quercus* forests encourages greater interest in the management and restoration of these systems.

While overstories in *Quercus*-dominated forests offer great ecological value to the forest, the herbaceous layer is the most species-rich stratum, providing many ecological services (Fralish, 2004; Gilliam, 2007; Hanberry et al., 2020; Whigham, 2004). The herbaceous layer serves as habitat and a food source to a diversity of species, including insects, songbirds, and small mammals (Fralish, 2004; Hanberry et al., 2020). Despite comprising a small portion of the aboveground biomass, herbaceous plants provide significant inputs of litter and nutrients in proportion to their mass (Gilliam, 2007; Welch et al., 2007). Herbaceous litter has high nutrient concentrations and decomposes rapidly, providing a quick release of nutrients annually (Welch et al., 2007). Intact herbaceous layers also reduce nutrient loss and soil erosion from the system (Fralish, 2004; Gilliam, 2007; Peterson and Rolfe, 1982).

Historically, *Quercus* forests were more open, with a dense, diverse herbaceous layer and a limited midstory layer beneath a widely spaced overstory (Hanberry et al., 2020; Hanberry and Abrams, 2018). Prior to European settlement, Native Americans applied fire to the landscape, resulting in periodic, low intensity surface fires that maintained these open forests (Brose et al., 2001; Dey, 2002; Hanberry et al., 2020; Parker and Ruffner, 2004). *Quercus* species benefited from periodic fire that increased light availability, reduced litter layers, and killed competing species in the regeneration layer (Arthur et al., 2012; Brose et al., 2014, 2001; Johnson et al., 2019). Mature *Quercus* trees have a greater ability to survive fire compared to co-occurring genera, with their thick bark and members of the subgenus *Leucobalanus* (white oak group) superior ability to compartmentalize fire wounds and reduce decay (Abrams, 1996; Brose et al., 2014; Smith, 2015). *Quercus* seedlings have several fire adaptations including preferential root development, hypogeal germination, buried bud banks, and prolific resprouting (Abrams, 1996; Brose et al., 2014; Johnson et al., 2019). With large temporal variations in the historic fire interval, *Quercus* reproduction are not top-killed by subsequent fire as they grow into larger size classes during fire-free periods (Dey, 2014; Guyette et al., 2002).

During European settlement, the frequency of forest disturbances increased as demand for lumber, fuel, and agricultural land by a growing population increased the harvesting, burning, and clearing of forests (Abrams, 1992; Dey, 2014; Guyette et al., 2003, 2002; Johnson et al., 2019). The landscape was more prone to wildfires due to slash from logging and increased human ignition sources such as steam engines during the Industrial Revolution (Brose et al., 2001; Dey, 2002). Fire often became more frequent and more severe, reducing the length of fire-free intervals and preventing *Quercus* spp. reproduction from recruiting into the overstory. Fire largely disappeared from much of the eastern forest with the initiation of the fire suppression era in the early-mid 1900s. This long fire-free period initially permitted the development of *Quercus*-dominated forests (Brose et al., 2001; Dey, 2014). However, other factors contributed to the dominance of *Quercus* spp., including the loss of the once-dominant *Castanea dentata* (Marshall) Borkh. (American chestnut) to *Cryphonectria parasitica* (Murrill) Barr (chestnut blight; (Johnson et al., 2019). In addition, overhunting in the 1800s and early 1900s reduced the populations of deer and other wildlife species that fed on acorns or browsed *Quercus* reproduction, further promoting *Quercus* abundance (Dey, 2014; Ellsworth and McComb, 2003). With extensive land use changes, European settlers created more open environments such as forest clearings, which further favored *Quercus* spp. when they were allowed to succeed to forest after abandonment (Dey, 2014).

With the continued suppression of fire, *Quercus*-dominated forests became overstocked and densely shaded (Brose et al., 2001; Hanberry et al., 2014c), contributing to the contemporary regeneration failure of *Quercus* species by promoting "mesophication", the shift from xerophytic and pyrophilic species like *Quercus* to mesophytic species, in particular, *Acer rubrum* L. (red maple) and *Acer saccharum* Marshall (sugar maple; Alexander et al., 2021; Brose et al., 2013; Nowacki and Abrams, 2008; Thomas-Van Gundy and Nowacki, 2013). Mesophytic species prefer moist conditions and are typically shade-tolerant and fire-sensitive. The increased importance of shade-tolerant species in *Quercus* forests lowers the probability of fire due to increased shade and moisture, and less flammable leaf litter (Alexander et al., 2021; Alexander and Arthur, 2014; Kreye et al., 2018; Nowacki and Abrams, 2008; Varner et al., 2016). *Quercus* leaves provide more optimal fuel because they are thicker, contain more phenolics and lignin, pack loosely, dry more effectively, and decompose more slowly (Nowacki and Abrams, 2008) than the leaves of mesophytic hardwoods such as *Acer* spp. the leaves of which are thinner, contain less lignin, decompose quickly, and flatten onto the forest floor, trapping moisture (Nowacki and Abrams, 2008; Varner et al., 2016).

Numerous studies have documented the shifting composition of eastern *Quercus* forests towards dominance by mesophytic species including *Fagus grandifolia* Ehrh. (American beech), *Acer rubrum*, *Liriodendron tulipifera* L. (tulip-poplar), and *Prunus serotina* Ehrh. (black cherry) particularly on more mesic sies (Abrams and Downs, 1990; Aldrich et al., 2005; Fei et al., 2011; Hanberry, 2019; Palus et al., 2018). However, xeric sites also undergo mesophication, but at a much slower rate than mesic sites (Abrams, 1992; Olson et al., 2014) and the more shade-tolerant species that outcompete *Quercus* spp. are influenced by the limited moisture availability, in which *Quercus* spp. are more competitive (Abrams, 1996; Johnson et al., 2019; Lorimer, 1992). An example of this occurs in the Missouri Ozarks such that *Quercus* spp. may be replaced by other more shade-tolerant members of the genus *Quercus* (Olson et al., 2014). Although changes in composition may be less drastic on xeric sites, efforts should be made to restore *Quercus* regeneration on these xeric forests as they are also ecologically and economically important. Not only is *Quercus* regeneration negatively impacted by mesophication, but the herbaceous layer also undergoes a compositional shift (Hanberry and Abrams, 2018) towards reduced species diversity, reduced cover of forbs and grasses, coupled with increased abundance and cover of shade-tolerant shrubs and woody vines (Davison and Forman, 1982; Fralish, 2004; Hanberry and Abrams, 2018).

The oak-fire hypothesis states that (1) periodic fire has been an important historic disturbance; (2) *Quercus* have multiple adaptations to fire; (3) lack of fire on the landscape contributes to the failure of *Quercus* regeneration; and (4) the reintroduction of fire will promote *Quercus* regeneration (Abrams, 1992; Brose et al., 2001, 2013; Lorimer, 1992; McEwan et al., 2011;

Nowacki and Abrams, 2008). This hypothesis is widely accepted by managers, resulting in the increased use of prescribed burning to restore *Quercus* regeneration in the eastern United States Repeated burning has yielded varying results in regenerating *Quercus* species, depending on site productivity, harvest history, and fire intensity (Alexander et al., 2008; Blankenship and Arthur, 2006; Brose et al., 2013, 2014; Green et al., 2010; Hutchinson et al., 2005). The combined use of prescribed burning with silvicultural treatments generally yielded a more positive response by *Quercus* seedlings (Brose, 2010; Brose et al., 2014; Iverson et al., 2008; Vander Yacht et al., 2019). In addition, several studies have observed a more positive response by *Quercus* seedlings to fire application on xeric sites compared to mesic sites (Burton et al., 2010; Hutchinson et al., 2005a; Iverson et al., 2008). The treatments used to restore *Quercus* also benefit the herbaceous layer, with combined harvesting and burning often increasing diversity, richness, and cover more than harvest or burning alone (Kinkead, 2013; Lettow et al., 2014; Phillips et al., 2007).

Forests on xeric sites may offer a more cost-effective option for the restoration of *Quercus* forests because they typically require fewer burns to successfully regenerate *Quercus* species due to their lower suitability for many mesophytic species. Because the silvicultural and burn treatments used to restore *Quercus* often benefit the herbaceous layer, it is important to monitor both the regeneration and herbaceous layer during *Quercus* forest restoration. Our long-term study was initiated in 2010 on the Hoosier National Forest in southern Indiana within two *Quercus*-dominated sites, a less productive, xeric site, and a more productive, mesic site. Between 2012 and 2015, both sites received an establishment cut of a shelterwood system and midstory treatments (chemical, mechanical, or none). In April of 2019, a prescribed burn was conducted on the xeric site, but the mesic site was not burned. Chapter 2 examines how the regeneration layer of the two sites responded to these treatments, and whether a single burn following overstory harvest produced adequate and competitive *Quercus* seedlings on the more xeric site. Research questions addressed in Chapter 2 include: (1) How does the regeneration layer respond to overstory manipulation and midstory treatment within two sites with similar overstory composition but different site productivity? (2) How does the response of the regeneration layer differ with midstory treatments (mechanical, herbicide, vs. none)? (3) Does the combination of a single burn with overstory manipulation and midstory treatment on a less productive, more xeric site lead to more successful *Quercus* regeneration without the need for repeated burns? Chapter 3 examines how the herbaceous layer responded to silvicultural treatments at both sites, and additional burn treatment at the less productive site. Research questions addressed in Chapter 3 include: (1) How does the herbaceous layer respond to overstory and midstory treatments within two sites with similar overstory composition but different burn treatments and site productivity? (2) Does the response of the herbaceous layer differ with midstory treatment (mechanical, herbicide, vs. none)?

CHAPTER 2. REGENERATION RESPONSE TO SHELTERWOOD-BURN TREATMENTS IN A DRY *QUERCUS* FOREST

Alterations to the historic fire regime have contributed to widespread regeneration failure in *Quercus* L. (oak) forests of the eastern United States. Composition has shifted from *Quercus* and other fire-adapted tree species (i.e. *Carya* spp.) to dominance by mesophytic species. Our long-term study was initiated in 2010 on the Hoosier National Forest in southern Indiana to study how *Quercus* regeneration responded to shelterwood and midstory treatments on a less-productive burned site and a more-productive unburned site. Our objective was to evaluate whether a single burn produced adequate competitive *Quercus* seedlings following harvest treatments on the less productive site and evaluate the competitive status of *Quercus* seedlings on the more productive site following harvests. Using nested circular plots, we measured seedling survival, height, and resprout response of individual seedlings, in addition to regeneration density pre- and post-treatments. Multiple mixed-effects models and NMDS ordination were used to evaluate post-treatment response in 2020 and 2021. Among post-treatments on the burned site, monitored *Quercus* spp. seedlings had greater survival (> 94%) and resprout response (> 92%) than most competing species, including *Acer* spp. (~ 59% survival and resprouting) and *Fraxinus americana* (72% survival and resprouting). *Q. alba* seedling (< 3.8 cm DBH) densities doubled after burning and was also one of the most abundant species (9,864 stems ha^{-1}) in these strata at the burned site. NMDS ordination indicated a clear shift in seedling-species composition with the burn driving a shift away from mesophytic species towards greater importance of *Quercus* species. Among harvest treatments, the unburned site contained fewer, and less competitive, *Quercus* seedlings compared to non-*Quercus* competitors and displayed no discernable pattern in compositional shifts in species composition post-harvest. The more-productive unburned site would likely require multiple burns to produce adequate competitive *Quercus* seedlings to encourage dominance in the future canopy, while a single burn on the less productive site has likely produced adequate density of *Quercus* reproduction to ensure future dominance by the genus.

2.1 Introduction

Quercus L. (oak) species have played a crucial role in human culture for thousands of years as we relied on them for food, fuel, and lumber. They are also a foundation species in forests of the eastern United States, producing critical mast for multiple wildlife species in addition to providing diverse forest structure (Dickson, 2004; Fralish, 2004; Hanberry and Nowacki, 2016). However, *Quercus* forests of eastern North America are in decline due to a multitude of factors, one of which is a lack of competitive regeneration (Johnson et al., 2019; Lorimer, 1992). Human alterations to the historic fire regime have been a major contributor to *Quercus* regeneration failure throughout the eastern forest. Prior to European settlement, Native Americans used periodic, low-intensity fires to manage and maintain the forest landscape to suit their needs (Brose et al., 2001; Parker and Ruffner, 2004). This regime resulted in more open forests, woodlands, and savannas (Hanberry et al., 2014a, 2014b), and favored the accumulation of large, competitive advance reproduction of *Quercus* species in forest understories (Johnson et al., 2019). *Quercus* reproduction has several adaptations to fire, such as hypogeal germination, preferential root development, and prolific sprouting (Abrams, 1996; Brose et al., 2014, 2001). Mature trees have thick bark and, compared to co-occurring genera, greater ability to compartmentalize fire wounds by members of the subgenus *Leucobalanus* (white oak group), thus reducing stem decay (Abrams, 1996; Brose et al., 2014, 2001; Smith, 2015). While repeated burning favored *Quercus*, competing species were vulnerable to fire-induced mortality due to thinner bark, epigeal germination, and preferential carbon allocation to shoot development (Brose et al., 2014). Historic fire return intervals varied temporally, and occasional longer fire-free periods allowed *Quercus* regeneration to grow large enough to not be top-killed by subsequent burns (Dey, 2014; Guyette et al., 2002).

Growing populations and high demand for resources with European settlement had shifted disturbance from the historic fire regime to intense logging, burning, and land clearing (Abrams, 1992; Dey, 2002; Guyette et al., 2003, 2002; Johnson et al., 2019). The increased frequency of burning resulting from these land practices reduced the occurrence of fire-free intervals critical to the recruitment of *Quercus* stems into the canopy. An increase in wildfires in the eastern United States prompted the initiation of the fire-suppression era in the early to mid-1900s (Brose et al., 2001; Dey, 2002). *Quercus* species initially benefited from the prolonged fire-free period and open environments created by extensive land clearings, allowing the genus to become dominant in the overstory of many forests (Brose et al., 2001; Dey, 2014). Additionally, the loss of the once-dominant *Castanea dentata* (Marshall) Borkh (American chestnut) and overhunting of many wildlife species that fed on *Quercus* contributed to the dominance of *Quercus* species during this time period (Dey, 2014; Ellsworth and McComb, 2003; Johnson et al., 2019). However, continued fire suppression contributed to the decline of *Quercus* forests through a lack of competitive *Quercus* regeneration (Brose et al., 2001; Lorimer, 1992).

Decades of fire suppression resulted in densely shaded and overstocked *Quercus* forests (Brose et al., 2001; Hanberry et al., 2014c), driving the process of "mesophication", a compositional shift from xerophytic and pyrophilic species like *Quercus* toward dominance by mesophytic species, such as *Acer* L. species (Alexander et al., 2021; Nowacki and Abrams, 2008; Thomas-Van Gundy and Nowacki, 2013). Mesophytic species thrive in moist conditions and are typically fire-sensitive and shade-tolerant, while many *Quercus* species are shade-intolerant and typically found on more xeric sites (Johnson et al., 2019). Several studies have documented this shift in dominance towards mesophytic species in eastern forests (Abrams and Downs, 1990; Aldrich et al., 2005; Fei et al., 2011; Hanberry, 2019; Palus et al., 2018), with mesic sites changing more rapidly than xeric sites (Abrams, 1992; Olson et al., 2014). The forest conditions become unfavorable to fire as shade and humidity increase, and mesophytic leaf litter is less flammable than *Quercus* leaves (Alexander et al., 2021; Alexander and Arthur, 2014; Kreye et al., 2018; Nowacki and Abrams, 2008; Varner et al., 2016).

According to the oak-fire hypothesis, (1) fire has historically been a crucial disturbance in *Quercus* forests of eastern North America; (2) *Quercus* spp. have multiple adaptations to fire; (3) fire suppression is a major reason for the *Quercus* regeneration decline; and (4) the reintroduction of fire will encourage *Quercus* reproduction (Abrams, 1992; Brose et al., 2013, 2001; Lorimer, 1992; McEwan et al., 2011; Nowacki and Abrams, 2008). With the acceptance of this hypothesis, there has been increased use of prescribed fire to restore *Quercus* regeneration in *Quercus-Carya* (oak-hickory) forests. The application of prescribed fire can be beneficial by increasing light to the understory by killing fire-sensitive mesophytic species in the midstory and understory, creating growing space for larger *Quercus* spp. that survive the fire and smaller stems that re-sprout after being top-killed (Brose et al., 2001). Fire also reduces leaf litter depth, which allows better root penetration by germinants, provides short-term nutrient release, and kills competing seeds and seedlings (Arthur et al., 2012; Brose et al., 2014, 2001). The application of multiple fires results in generally positive effects on *Quercus* regeneration with a few negative effects across multiple studies (Blankenship and Arthur, 2006; Brose et al., 2013, 2014; Hutchinson et al., 2005a).

Research has highlighted the benefits of repeated burning, including the promotion of acorn germination and the improved establishment of seedlings under conditions of reduced litter depth, reduced interspecific competition, and increased light availability (Brose et al., 2013; Dey, 2014). Due to the high abundance of rapid growing mesophytic competitors, repeated burning may be more necessary on more productive *Quercus* sites. However, fewer burns on drier, less productive sites may be sufficient to suppress non-*Quercus* competitors, due to the reduced growth rates on these sites. Meta-analyses have shown varying results of the application of two or more prescribed burns to a mature *Quercus* forest, ranging from mostly neutral to positive results on *Quercus* regeneration, depending on harvest history, site productivity, or season of burn (Brose et al., 2014, 2013). Two burns following a thinning yielded increased *Quercus* densities on intermediate and xeric sites, while mesic sites continued to have lower densities, particularly in the larger size classes (Iverson et al., 2008). The application of a single fire in several studies yielded neutral to negative results in *Quercus* seedling competitiveness over time when applied in mature *Quercus* stands (Brose et al., 2014). A single burn following a shelterwood reduced competitors while improving *Quercus* regeneration, depending on fire intensity on a more productive site (Brose, 2010; Brose and Van Lear, 1998). Multiple studies have found *Quercus* seedlings respond more positively to fire application on xeric sites than mesic sites (Burton et al., 2010; Hutchinson et al., 2005a; Iverson et al., 2008). The survival and response of *Quercus* seedlings to a fire varies with site productivity and fire intensity. A large proportion of the *Quercus* regeneration research has focused on how multiple fires can help establish *Quercus* on more productive sites. Despite the prevalence of xeric *Quercus* forests in the eastern United States, there have been fewer studies on the effects of single burns on less productive *Quercus* forests. With a slower mesophication process on drier sites, fewer burns may be needed to maintain *Quercus* dominance, requiring less effort and cost by land managers. When combined with silvicultural treatments, a single fire on these less productive sites could promote adequate *Quercus* regeneration to ensure dominance in the developing stand. Conversely, more mesic sites will often require multiple burns even in combination with harvesting.

Research has shown mixed, but limited, success establishing *Quercus* reproduction using prescribed fire in the absence of overstory manipulation, however, a combination of prescribed fire and silvicultural techniques to reduce overstory and midstory density have also been implemented with positive results depending on the site (Brose, 2010; Brose et al., 2014; Iverson et al., 2008; Vander Yacht et al., 2019). An example is the shelterwood-burn technique proposed by (Brose et al., 1999a) which employs an initial shelterwood cut to increase light and stimulate root growth of current *Quercus* regeneration, germinate seeds of competing species, and allow the remaining canopy trees to provide enough leaf litter to carry a subsequent prescribed fire. Accordingly, approximately 40 to 60% of the original stand basal area remains after the first cut, leaving mostly dominant and codominant *Quercus* trees. The initial shelterwood cut provides a more optimal environment for *Quercus* regeneration by increasing light on the forest floor, while also providing partial shade and protection from extreme temperatures and wind effects, and suppressing regeneration of aggressive shade-intolerant species such as *Liriodendron tulipifera* (Dey, 2014; Johnson et al., 2019). After the initial cut, there is a 3-to-5-year period for *Quercus* regeneration to respond to the release and advance root development before a prescribed fire is applied to the site, with repeated fires as needed. Overstory trees are retained on the site or harvested after *Quercus* regeneration is at a desirable stocking density (Brose et al., 1999a). While the shelterwood-burn method has been used on more productive (more mesic) sites, our study examined how *Quercus* regeneration responds to its application on a less productive (more xeric) site after a single prescribed burn.

Midstory treatments are often implemented in addition to overstory harvests to further increase light and reduce competition in the midstory layer. Schlesinger et al. (1993) suggests that on average sites (SI_{50} 17-20 m) conducting an overstory harvest may be sufficient without the need for understory/midstory removal, but more productive sites ($SI_{50} \geq 21$ m) may need a midstory treatment to reduce competition. Midstory treatments in *Quercus*-dominated forests have been shown to increase growth of *Quercus* seedlings compared to areas without midstory removal (Craig et al., 2014). The application of midstory treatments in conjunction with overstory removal may increase *Quercus* seedling growing conditions and reduce competition (Loftis, 1990).

Since xeric sites undergo slower mesophication, and *Quercus* seedlings are physiologically adapted to low-moisture conditions, less time and effort may be needed to successfully regenerate *Quercus* species, allowing the establishment of reproduction following a single prescribed fire following a harvest that increases light availability. We investigated whether one burn produced adequate *Quercus* regeneration after a shelterwood cut in a xeric *Quercus*-dominated forest. This study aimed to evaluate the response of *Quercus* regeneration to the application of an overstory harvest and three midstory treatments at two sites: (1) a less productive dry site where a single burn followed silvicultural treatments and (2) a more productive and mesic site where silvicultural treatments were not followed by burning. The midstory treatments at both sites consisted of mechanical cutting, herbicide application, or no midstory removal.

We evaluated the survival, resprout response, growth, abundance, and competitiveness of *Quercus* seedlings compared to competing mesophytic species. Research questions addressed in this study were:

(1) How does the regeneration layer respond to overstory manipulation and midstory treatment within two sites with similar overstory composition but different site productivity? We predicted that *Quercus* seedlings would have higher survival, growth, and abundance compared to mesophytic species on the burned site, due to *Quercus* spp. ability to survive fire and resprout afterward and physiological advantage of the genus on dry sites. We predicted that *Quercus* seedlings would be at a less competitive advantage compared to mesophytic competitors at the unburned site, due to the site having more moisture and productive soils and no burns to reduce competition of mesophytic species.

(2a) How does the response of the regeneration layer differ with midstory treatments (mechanical, herbicide, vs. none) between two sites with similar overstory composition but different site productivity? We predicted that seedlings would display greater growth and abundance in the chemical/mechanical treatments versus no midstory removal due to increased light to the regeneration layer at both sites.

(2b) Does mechanical midstory treatment result in more sprouting than herbicide? If so, what effect does it have on the abundance and growth of *Quercus* regeneration? We also predicted that *Quercus* spp. would have less growth and lower abundance in mechanical versus chemical midstory treatments due to lower resource availability following vigorous resprouting after mechanical treatment.

(3) Does the combination of a single burn with overstory manipulation and midstory treatment on a less productive, more xeric site lead to more successful *Quercus* regeneration without the need for repeated burns? We predicted that one burn following the silvicultural treatments would produce competitive *Quercus* seedlings because the single burn would adequately reduce competing mesophytic species.

2.2 Methods

2.2.1 Study Sites

We collected data on the Hoosier National Forest (HNF), which is located across nine counties of southern Indiana. The forest falls within the Central Hardwood Region of North America and the Crawford Upland Section of Indiana (Homoya et al., 1985; Parker and Ruffner, 2004; Van Kley et al., 1995). *Quercus-Carya* is the dominant forest type within the Section, with *Fagus-Acer* (beech-maple) forest also occurring (Homoya et al., 1985; Johnson et al., 2019; Parker and Ruffner, 2004). *Quercus* L. and *Carya* Nutt. (hickory) species are commonly found together on drier sites, while on more mesic sites *Quercus* species may be mixed with other hardwood species (Johnson et al., 2019). Stand records indicate that 69% of the stands in the HNF were established between 1800 and 1940 (Parker and Ruffner, 2004). Old-growth *Quercus* forests are rare within the Region and the few remaining remnants developed during periods of frequent low-intensity fire (Parker and Ruffner, 2004). Across the Region, fire suppression has driven a shift to greater dominance of mesophytic species such as *Acer saccharum* and *Fagus grandifolia* in the midstory (Parker and Ruffner, 2004). The soils of the HNF are mainly sandstone derived, with a few shale or limestone outcrops, and are largely comprised of silt loams or fine sandy loams and occasionally silty clay loams (Van Kley et al., 1995).

Our plots on the HNF are within two study sites located approximately 35 km northeast of Tell City, Indiana: Jeffries and Sixty-six (Figure 1). Both sites reside in the northeast corner of Perry County approximately 5 km north of the Ohio River and the Indiana-Kentucky state line. The sites are dominated by *Q. alba* L. (white oak) and *Q. stellata* Wangenh. (post oak) on dry slopes with some areas of *F. grandifolia* and *Acer saccharum* on mesic slopes and ridges. Each site has eight units subjected to different combinations of silvicultural treatments. The total study area at Jeffries is 28.9 ha and 26.4 ha at Sixty-six. Sixty-six is a more productive site with a site index$_{50}$ (SI_{50}) of 24.4 m for *Q. alba*, while Jeffries is less productive with an average SI_{50} of 17.6 m for *Q. alba* (Carmean, 1972; Thornton, n.d.).

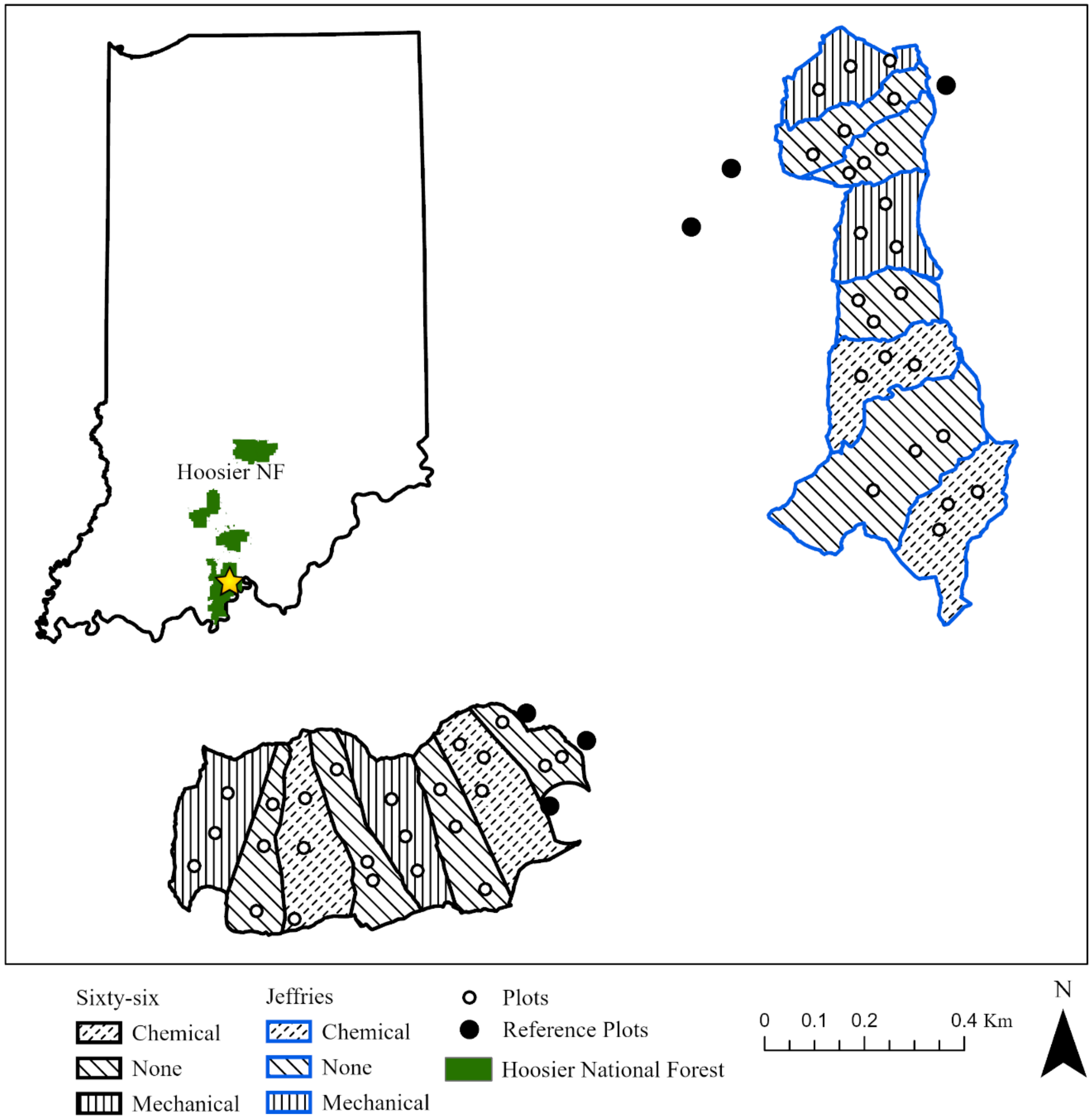


Figure 1. Jeffries (blue) and Sixty-six (black) study sites in the Hoosier National Forest, Indiana (star). Chemical = shelterwood with chemical midstory removal, none = shelterwood without midstory removal, mechanical = shelterwood with mechanical midstory removal.

2.2.2 Experimental Treatments

Overstory treatments

Both Jeffries and Sixty-six received alternating overstory treatments, with four initial shelterwood cuts and four commercial thinning units per site. The shelterwood treatments generally followed the shelterwood-burn method described by Brose et al. (1999a) with an initial cut that preferentially removed competing species, such as *A. saccharum*, *L. tulipifera*, and *F. grandifolia*, and poor-quality trees, while leaving mainly dominant and codominant *Quercus* and *Carya* trees in the overstory (Thornton, n.d.). At Jeffries, the shelterwood units ranged in size from 2.8 to 4.1 ha with a total treatment area of 13.7 ha, and the basal area was reduced from an average of 23.9 to 11.0 m^2 ha^{-1} (Appendix A, Table A.1). The four shelterwood units at Sixty-six ranged in size from 3.7 to 4.1 ha with a total treatment area of 15.7 ha and basal area was reduced from an average of 27.8 to 14.1 m^2 ha^{-1} (Appendix A, Table A.2).

A thinning from below was performed within the other four units at Jeffries, which reduced the basal area from an average of 25.3 to 13.6 m^2 ha^{-1} (Appendix A, Table A.1) in units that ranged from 2.2 to 8.1 ha with a total treatment area of 15.2 ha. At Sixty-six, the thinning units ranged in size from 1.9 to 3.1 ha with a total area of 10.7 ha; the basal area was reduced from an average of 25.1 to 15.5 m^2 ha^{-1} (Appendix A, Table A.2). All overstory harvests at Jeffries were conducted between May 2012 and October 2015, while Sixty-six harvests were completed between November 2011 and October 2012. Each site included unharvested reference areas outside of the eight harvest units. Because we found no statistical differences (t-test, $p > 0.05$) in post-harvest basal areas between shelterwood and thinning treatments, overstory harvests at both sites were pooled and hereafter referred to as initial shelterwood cuts.

Midstory Treatments

At both sites, the shelterwood units received non-commercial (midstory) treatments of non-*Quercus* species in conjunction with the overstory removal (Appendix A, Tables A.1, A.2). Two units received a mechanical treatment in which all non-merchantable stems > 2.54 cm diameter at breast height (DBH) were cut with chainsaws without herbicide treatment and the other two units received herbicide treatment of stems > 2.54 cm and up to 17.8 cm DBH. The cut stump or girdled midstory trees were treated with Pathway herbicide (10.2% picloram + 39.6% 2,4-D) or a comparable mixture diluted to 50% using a chainsaw and chemical spray bottle. Midstory treatments were completed in the spring of 2015 at Jeffries and spring of 2013 at Sixty-six by contractors (Turman Creek Tree Farms, 2013). Thinned units did not receive a midstory treatment at either site.

Prescribed Burn

Continuing to follow the shelterwood-burn method (Brose et al., 1999a), the USDA Forest Service conducted a prescribed burn using aerial ignition and drip torches at Jeffries on April 16, 2019 (Figure 2a). The fire was applied 4-5 years after the original harvests and burned a total of 301 ha, including the study site. The fire burned with air temperatures between 23.3-29.4 ºC, relative humidity at 28-35%, and winds ranging 3-11 km hr^{-1} with gusts up to 14 km hr^{-1} (Harriss, 2019). Flame lengths ranged 25.4-35.6 cm, flame heights ranged 12.7-20.3 cm, and rate of spread ranged 10.1-40.2 m hr^{-1} with a head fire flame height of 61.0-91.4 cm and flame length of 1.2 m (Harriss, 2019).

a. b.

Figure 2. (a.) Prescribed burn conducted by the USDA Forest Service on April 16, 2019, and **(b.)** charring postburn at Jeffries. Pictures courtesy of the USDA Forest Service.

2.2.3 Plot Design

In 2010 three permanent 0.047 ha plots were established in each unit across all treatments and in each reference area for a total of 54 plots across both study sites. The plots were randomly stratified across a topographic gradient and were positioned at least one tree height from stand borders to ensure a buffer from edge effects. Each sample plot (Figure 3) consisted of a single 0.047 ha overstory plot (12.6 m radius), a single 0.016 ha concentric midstory subplot (8 m radius), a single 40.5 m^2 regeneration subplot (3.6 m radius; 6 m from plot center at 45°), twelve 1-m^2 circular vegetation quadrats (along 12 m transects at 3, 6, 9, and 12 m from main plot center at 135, 225, and 315°), and four fuel transects (12.6 m in length; oriented from the overstory plot center at 0, 90, 180, and 270°). In 2010, all overstory (≥ 11.4 cm DBH) and midstory (≥ 3.81 cm DBH and < 11.4 cm DBH) trees within their corresponding plots were tagged. Within each regeneration subplot, an average of 38 (ranging from 19 to 59) seedlings (< 3.8 cm DBH) of varying species and height classes were tagged for continued monitoring.

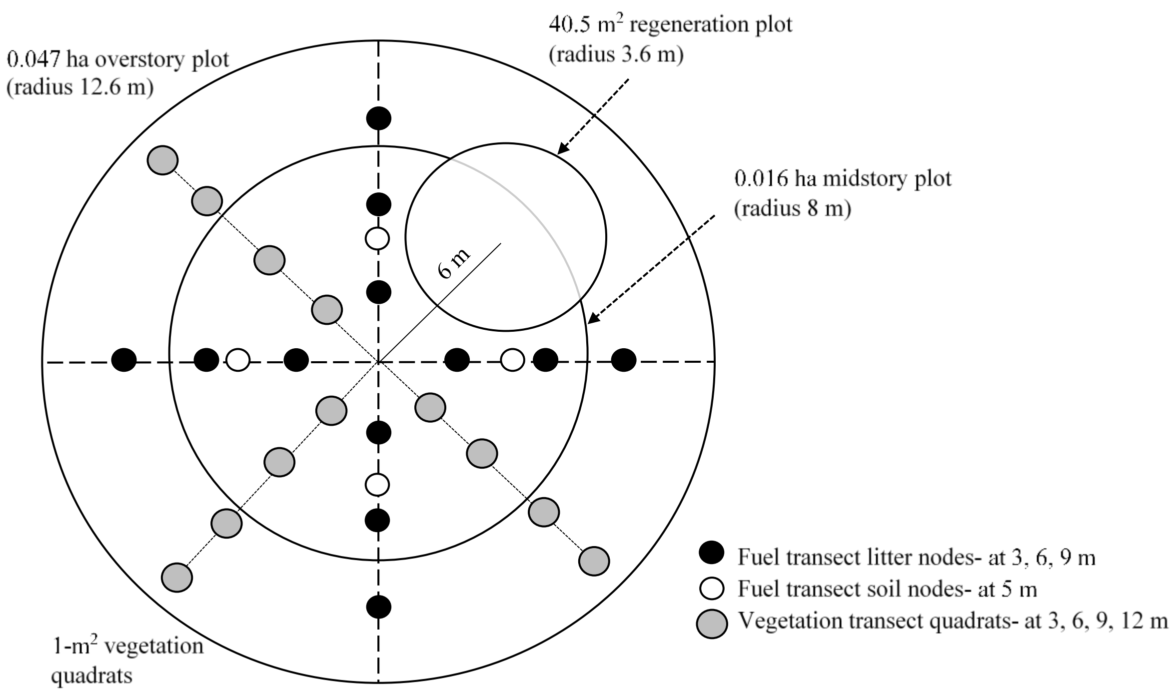


Figure 3. Nested design of overstory, midstory, and regeneration plots, and vegetation and fuel transects.

2.2.4 Field Measurements

Pretreatment data were collected for the overstory and regeneration layer before treatments in 2010. Site factor data were also collected and included percent slope, aspect, and terrain shape index (TSI). TSI is the measured slope gradient from plot center to plot boundary in 45º increments, with 8 measurements total (McNab, 1989). Data were also collected during and after treatments in the years 2012, 2013, 2014, 2015, and 2018.

Fire Effects

At the Jeffries site, we measured fire temperatures during the April 2019 burn and char heights directly after to quantify fire intensity and severity. We placed stakes with aluminum paint tags approximately 12.6 m from the main plot center in all cardinal directions (0, 90, 180, 270º) and one at the plot center with two paint tags on each stake. One tag was approximately 30.5 cm off the ground and the other at the litter surface, at approximately 0 cm. Six dots of heat-activated Tempilaq paint with activation temperatures of 79.4, 121.1, 162.8, 204.4, 315.6, and 426.7 ºC were applied to each tag. Tags would melt at 661.1 ºC. After the burn was conducted, the tags were evaluated for fire temperature based on the temperature reaction of the paint dots. In addition, we buried one HOBO Temp datalogger approximately 10 cm deep at each plot center prior to the burn to record the temperature every three seconds during the burn. Char height, the maximum height of the bark burned from the fire (cm), was measured on trees of varying species and DBH on each Jeffries overstory plot after the burn, ranging from 9 to 21 trees per plot (Figure 2b).

Paint tag data showed that maximum fire temperatures at ground level (~ 0 cm) ranged from below 79.4 ºC and above 661.1 ºC with average temperatures ranging from 248.9 to 426.7 ºC. Temperatures at the greater height of about 30.5 cm ranged from below 79.4 ºC and greater than 426.7 ºC with average temperatures, ranging from 76.7 to 315.6 ºC. Mean char heights averaged 37.24 cm, ranging from 7.6 to 93.9 cm. Paint tag temperatures and char heights did not significantly differ across treatment areas (ANOVA, $p > 0.05$). Due to the length of time the HOBO devices were in the ground, many of them did not collect consistent data. However, we had at least one working HOBO device from each treatment unit, except unit 8. The maximum temperatures recorded ranged from 84 to 546.9 ºC with an average of 206.7 ºC. Those that reached temperatures above 100 ºC (eight devices), attained temperatures above 100 ºC for an average of 61 seconds, ranging from 42 to 105 consecutive seconds.

Overstory and Midstory

In the summer of 2020, we measured the DBH of tagged live trees and snags ≥ 11.4 cm DBH within the 0.047 ha circular plots (Figure 3) in each treatment unit. We measured tagged live midstory trees ≥ 3.81 cm DBH and < 11.4 cm DBH within a concentric 0.016 ha circular subplot. We tagged, measured DBH, and identified species of all ingrowth trees (trees that grew into a larger size class) in the overstory and midstory classes. We also recorded the survival status (alive/dead) of midstory and overstory trees. The survival status of tagged overstory and midstory trees was reassessed in the summer of 2021 at the Jeffries site. All measurements were to the nearest 0.254 cm. We used a concave, spherical densiometer to estimate canopy cover within the 40.5 m^2 regeneration subplot 3.6 m from the center at each cardinal direction (0º, 90º, 180º, 270º).

Tree Regeneration

Within each plot, we sampled tree regeneration in a 40.5 m^2 circular subplot (Figure 3) during the summer of 2020. We tallied stems by species into five height/diameter classes: (1) < 0.3 m, (2) 0.3-0.6 m, (3) 0.61-0.9 m, (4) 0.91-1.36 m, and (5) ≥ 1.37 m tall and < 3.8 cm DBH. Each stem was tallied regardless if they were resprouts having shared root systems. Species and DBH were recorded for all stems in class 5. Within the same 40.5 m^2 plot, we also assessed each tagged seedling of varying species and size classes (originally tagged in 2010) for survival status, basal diameter (~1.27 cm from the ground, to nearest 0.0254 cm), height (to nearest 0.254 cm), and origin (seed origin, mature stem resprout, or seedling resprout). In addition, the number of resprouts was recorded and the height and basal diameter were taken from the tallest stem. Individually tagged seedlings were remeasured for survival status, height, and basal diameter of the tallest stem, and the number of sprouts in the summer of 2021 at the Jeffries site.

To evaluate competition with our *Quercus* seedlings, we measured the height, basal diameter, species, and the number of sprouts of the tallest seedling within a 2-meter radius around each surviving tagged *Quercus* seedling. The competitive status of surviving tagged *Quercus* seedlings was assessed by measuring the crown light exposure (0-5, Bechtold, 2003) relative to the same cohort of seedlings and percent canopy encroachment within a 45-degree cone (adapted from Frank et al., 2018). The percent canopy encroachment was assessed by visualizing a 45-degree cone 5 m above the apical bud of each seedling and visually estimating the percent woody vegetation occupying the cone. We used cover classes: trace, 0-1, 1-2, 2-5, 5-10, 10-25, 25-50, 50-75, 75-95, and > 95% (Peet et al., 1998).

Fuels

Following the methods of Brown (1974) and Brown et al. (1982), we measured dead and down woody material along four 12.6 m transects at each 0.047 ha overstory plot (Figure 3) for all treatments in the summer of 2020. Fine woody debris (FWD) included 1-hour (< 0.6 cm), 10-hour (0.6-2.53 cm), and 100-hour (2.54 to 7.6 cm) fuels. Coarse woody debris (CWD, 1,000-hour fuel) was downed wood > 7.6 cm in diameter. Using a go-no-go fuel gauge, we identified and tallied the 1- and 10-hour fuels along the first 1.3 m section and tallied the 100-hour fuels along 3.5 m of each fuel transect. We measured the 1,000-hour fuels along the entire length of each 12.6 m transect, recording diameter at point of intersection to nearest 0.1 cm, species if possible, decay class (1-5, Lutes et al., 2006), and position (on the ground vs. above ground). Along each of the fuel transects at points 3.1, 6.1, and 9.1 m (total of 12 measurements for each per plot), we also measured the depth of the litter and duff layers to the nearest 0.254 cm. At those 12 points, the percent cover of leaf litter, duff, and bare ground was visually estimated within a 0.5 m^2 (70.6 x 70.6 cm) frame.

Soil

Along each fuel transect 5 m from the 0.047 ha plot center, we collected surface mineral soil down to 10 cm using a trowel, combining the four subsamples to create a composite sample for each plot. Samples were sealed in plastic bags and stored in a freezer until they were shipped to Brookside Labs in New Bremen, OH for chemical analysis. Brookside Labs analyzed S (ppm), P (ppm), Ca (mg kg^{-1}), Mg (mg kg^{-1}), K (mg kg^{-1}), Na (mg kg^{-1}), B (mg kg^{-1}), Fe (mg kg^{-1}), Mn (mg kg^{-1}), Cu (mg kg^{-1}), Zn (mg kg^{-1}), and Al (mg kg^{-1}) by Mehlich III extraction (Mehlich, 1984). Samples were also analyzed for pH_{water}, total exchange capacity (meq 100 g^{-1}), percent organic matter, estimated nitrogen release (#N ac^{-1}), Bray II P (mg kg^{-1}), NO_3 (ppm), NH_4 (ppm), percent

Ca, Mg, K, Na, H, and other bases (Bray and Kurtz, 1945; Dahnke and Johnson, 1990; McLean, 1982; Ross and Ketterings, 1995; Schulte and Hopkins, 1996). Soil NO_3 and NH_4 were summed for total soil N.

2.2.5 Data Preparation

Summary statistics calculated for each plot included (1) average fire temperature by height (0 or 30.5 cm; ⁰C), (2) average char height (cm), (3) total live basal area (BA, m^2 ha^{-1}), (4) average percent canopy density, (5) regeneration stems (per 100 m^2) by height class, (6) average CWD volume (m^3 ha^{-1}), and (7) average FWD volume (m^3 ha^{-1}). Total live BA was calculated per plot from DBH measurements of tagged overstory, midstory, and ingrowth trees in the plot. We calculated percent canopy density from densiometer-derived canopy cover using the equation: 100 - (#dots * 1.04; Lemmon, 1957). We calculated an average CWD volume from collected CWD fuel measurements and the FWD volume was calculated for each fine fuel class, then totaled together and averaged per plot (Harmon and Sexton, 1996). For analyses investing post-burn effects, the average change in litter and duff depth from 2018 to 2020 was calculated. Aspect was transformed to a linear scale ranging from 0 to 2, with a 0 value facing southwest and 2.0 facing northeast, using the equation (Beers et al., 1966): transformed aspect = cos(45 - aspect) + 1.

Final status was determined for each tagged seedling, assuming that two consecutive surveys of the seedling being dead or missing resulted in classification as a dead seedling. For competitor data, we calculated a height ratio between each tagged *Quercus* seedling and its nearest competitor to evaluate competitive status. Data imputation was conducted for any missing or inaccurate measurements of seedling height and basal diameter based on calculated growth rate from earlier or later data.

Seedling species were grouped into tree species groups (hereafter, species groups) for analysis, based on study focus and abundance. These consisted of *Quercus alba*, *Quercus velutina* Lam., *Quercus rubra* L., Other *Quercus* spp. (*Quercus montana* Willd., *Q. stellata, Q. coccinea* Münchh., *Q. marilandica* Münchh.), *Carya* spp., *Acer saccharum*, *Acer rubrum*, *Fraxinus americana* L., *Sassafras albidum* (Nutt.) Nees, *Ostrya virginiana* (Mill.) K. Koch, Canopy Other, and Subcanopy Other. The Canopy Other tree species group consisted of larger trees (> 12 m tall) such as *Liriodendron tulipifera*, *Prunus serotina*, *Ulmus americana* L., and *Nyssa sylvatica* Marshall. The Subcanopy Other group consisted of shrubs and smaller trees such as *Cercis canadensis* L. and

Cornus florida L. At both sites, *P. serotina* contributed to 34% of the Canopy Other group for tagged seedlings, while *C. canadensis* made up the majority of the Subcanopy Other group, 60% at Jeffries and 54% at Sixty-six. *Prunus serotina* also contributed 18% and 17% of the Canopy Other group in the regeneration data at Jeffries and Sixty-six, while *C. canadensis* made up 25% and 21% of the Subcanopy Other species group at Jeffries and Sixty-six. Nomenclature follows the USDA PLANTS Database (USDA, NRCS, 2022).

2.2.6 Statistical Analysis

Before data analysis, all highly skewed data were log-transformed to improve normality. We also standardized some explanatory variables by dividing by the standard deviation, to minimize differences between variable ranges. Due to the small number of reference plots available, they were removed before data analysis. To evaluate how the regeneration layer responded to and differed between our treatments we fit multiple mixed effects models on survival, resprouting response, height, and seedling density (question 1 and 2). Using R (R Core Team, 2020), we fit binomial models to estimate survival (alive vs. death) since treatment at both sites using the final status of individual seedlings as the response. To test direct fire effects at the Jeffries site, we fit a binomial model on post-burn survival of tagged seedlings from the time period of 2018 to 2021. We also fit another binomial model for overall survival across the entire time frame of the study (2010 - 2021). Binomial models were also fit to estimate individual seedling resprout response (topkilled and resprouted vs. not topkilled and resprouted) after the burn at Jeffries in 2020 and 2021. We fit a Poisson model to estimate the number of resprouts of our tagged seedlings after the burn at Jeffries in 2020 and 2021. For tagged seedlings, linear models were fit to estimate the tallest resprout height post-burn at the Jeffries (2020 and 2021) and seedling height at the Sixty-six (2020). The explanatory variables included in these models were: pretreatment basal diameter, total live BA, average canopy density, fire effects (mean char height, average maximum fire temperature), soil chemical characteristics (pH, total N, P, Al), percent slope, transformed aspect, average FWD and CWD volumes, litter and duff depths, species group, and treatment. We also fit negative binomial models using the MASS package (Venables and Ripley, 2002) to estimate regeneration density at both sites in 2020. A negative binomial model was used because the data were over-dispersed and did not fit a Poisson distribution. The same explanatory variables as above were used except for basal diameter, and with the addition of seedling height class (1-5). Models were produced with a backward stepwise algorithm and chosen based on the lowest AIC, and then all models were tested for goodness-of-fit before interpretation. Wald Chi-square tests were used to determine significant explanatory variables. For post-hoc analysis, Tukey multiple pairs comparison tests were run on significant main effects for all models.

To evaluate the competitive status of our tagged *Quercus* seedlings at both sites (question 3), we fit a linear model to estimate *Quercus*-competitor height ratios in 2021 with *Quercus* species, competitor species, and treatment as explanatory variables. A linear model was also used to estimate canopy cover within the 45-degree cone, in 2021, using the midpoint as the response variable and *Quercus* species and treatment as the explanatory variables. The canopy cover model for Sixty-six included nested unit and plot random effects. A box-cox transformation was used on the height-ratios and canopy midpoint to improve model fit (Box and Cox, 1964). A cumulative model was fit to estimate *Quercus* seedling light class (0-5) in 2021 with *Quercus* species and treatment as explanatory variables using the VGAM package (Yee, 2015; Yee and Wild, 1996). Analysis of Variance (ANOVA) or Wald Chi-square tests determined significant explanatory variables of the models.

Models were tested with the treatment unit and plot as random effects, but preliminary analyses determined that random effects were small and insignificant in most models. Interaction effects were tested in all models, but were either insignificant or did not add much explanatory power to the model, therefore, we used additive models. For all tests, alpha = 0.05.

Using relative seedling density, we ran non-metric multidimensional scaling (NMDS) ordination with the vegan package (Oksanen et al., 2019) using the Bray-Curtis dissimilarity matrix to examine post-treatment compositional shifts in the regeneration layer between the years 2010 and 2020 at both sites. We initially included the data from 2018 in the NMDS, but the stress was lowered by removing it from the analysis. Species with fewer than five occurrences between both years were excluded from the analysis. A maximum of 50 iterations were allowed. The number of axes was determined by stress and a scree plot (McCune and Grace, 2002), with the intention of having stress well below 0.2 (Kruskal, 1964). The envfit function (999 permutations) was used to fit environmental vectors onto the ordination and calculated correlation coefficients for the environmental variables (Tables 4, 6) in relation to the ordination. Only environmental variables with p-values < 0.05 were displayed on the graphs.

We also ran a Permutational Multivariate Analysis of Variance (PERMANOVA, 999 permutations) using the adonis function (Anderson, 2001) to test whether the centroid or dispersion of year or treatment groups are different within the ordination. We tested the homogeneity of dispersion of the groups (functions: betadisper, anova, permutest) before reporting final PERMANOVA results. We also conducted a SIMPER test to perform pairwise comparisons of groups to identify the percentage each species contributed to the differences between treatments or years. For all tests, alpha = 0.05.

2.3 Results

2.3.1 Jeffries Site

Seedling Survival after Fire

In 2020 *Quercus* and *Carya* seedlings averaged over 90% survival after the burn, while *Acer* species survived less than 67% of the time. *Fraxinus americana* and *Ostrya virginiana* also had lower average survival rates than *Quercus* spp. at 70 and 76%, respectively. Survival in 2021 exhibited similar trends (Table 1). Variables significantly influencing survival after the prescribed burn in 2020 were soil pH, species group, canopy density, transformed aspect, and percent slope ($p < 0.05$; Appendix A, Table A.3). Results are presented in odds ratio (OR) of survival vs. death or change in odds %: (OR - 1) * 100. A unit increase in pH decreased the odds of survival by 46% ($p < 0.05$), with all other variables fixed. An increase in one standard deviation (SD = 0.96) of average canopy density increased the odds of survival by 40% ($p < 0.05$). A unit increase in transformed aspect decreased the survival odds by 94% ($p < 0.01$) while an increase in percent slope increased the odds of survival by 17% ($p < 0.001$).

Similar to 2020, the 2021 post-burn survival model identified the significant explanatory variables as soil pH and species group, but also soil total N and average FWD ($p < 0.05$; Appendix A, Table A.3). A unit increase in pH decreased the odds of survival by 60% ($p < 0.01$). An increase in soil N increased survival odds by 13% ($p < 0.05$). An increase in a unit of FWD decreased the odds of survival by 9% ($p < 0.05$). Post-hoc Tukey tests indicated that *Carya* spp., other *Quercus*, *Q. alba*, *Q. rubra,* and *Q. velutina* had greater odds of survival than *A saccharum* by factors of 67.4, 29, 84.3, 47.3, and 20.2, respectively ($p < 0.05$; Table 1). Factor refers to how many times a species group's, or other variables', odds are greater or reduced compared to another. *Q. alba* exhibited greater survival odds post-fire than *F. americana* by a factor of 37.2 ($p < 0.05$).

Table 1. Two-year post-burn survival rates since 2018 (mean and range, %) at Jeffries by species group in 2021 excluding the reference plots. Statistical differences between groups are marked with superscripts according to a post-hoc Tukey test (α = 0.05).

Species Group	Mean	Min	Max	No. Seedlings	
Acer rubrum	66.7	50.0	100.0	19	ab
Acer saccharum	48.8	25.0	100.0	20	a
Canopy other	92.7	50.0	100.0	50	bc
Carya spp.	98.6	75.0	100.0	52	bc
Fraxinus americana	71.5	25.0	100.0	61	ab
Ostrya virginiana	75.6	33.3	100.0	55	ac
Other *Quercus* spp.	94.2	66.7	100.0	29	bc
Quercus alba	98.4	66.7	100.0	51	c
Quercus rubra	100.0	100.0	100.0	34	bc
Quercus velutina	95.3	50.0	100.0	50	bc
Sassafras albidum	81.3	33.3	100.0	17	ac
Subcanopy other	86.4	33.3	100.0	63	bc

Seedling Survival since 2010

In 2020, *Quercus alba* survival rate averaged 57.5%, while other *Quercus* species averaged 70% or above since pretreatment (2010). *Acer* species averaged 33-43% survival, while *F. americana* and *O. virginiana* averaged 44% and 55% survival since 2010, respectively. Similar trends were seen in 2021 (Table 2). Overall, survival rates decreased over time since 2010, with *Q. alba, O. virginiana*, and *F. americana* having greater rates post-burn than *A. saccharum* and *S. albidum* (Figure 4a). This trend was not seen in the shelterwood treatment with mechanical midstory removal in which *O. virginiana* and *A. saccharum* had the higher survival rates post-burn (Figure 4a). Variables significantly affecting overall seedling survival in 2020 include pretreatment basal diameter (log transformed, 2010), total BA, mean char height, total soil N, soil P, species group, and treatment ($p < 0.05$; Appendix A, Table A.3).

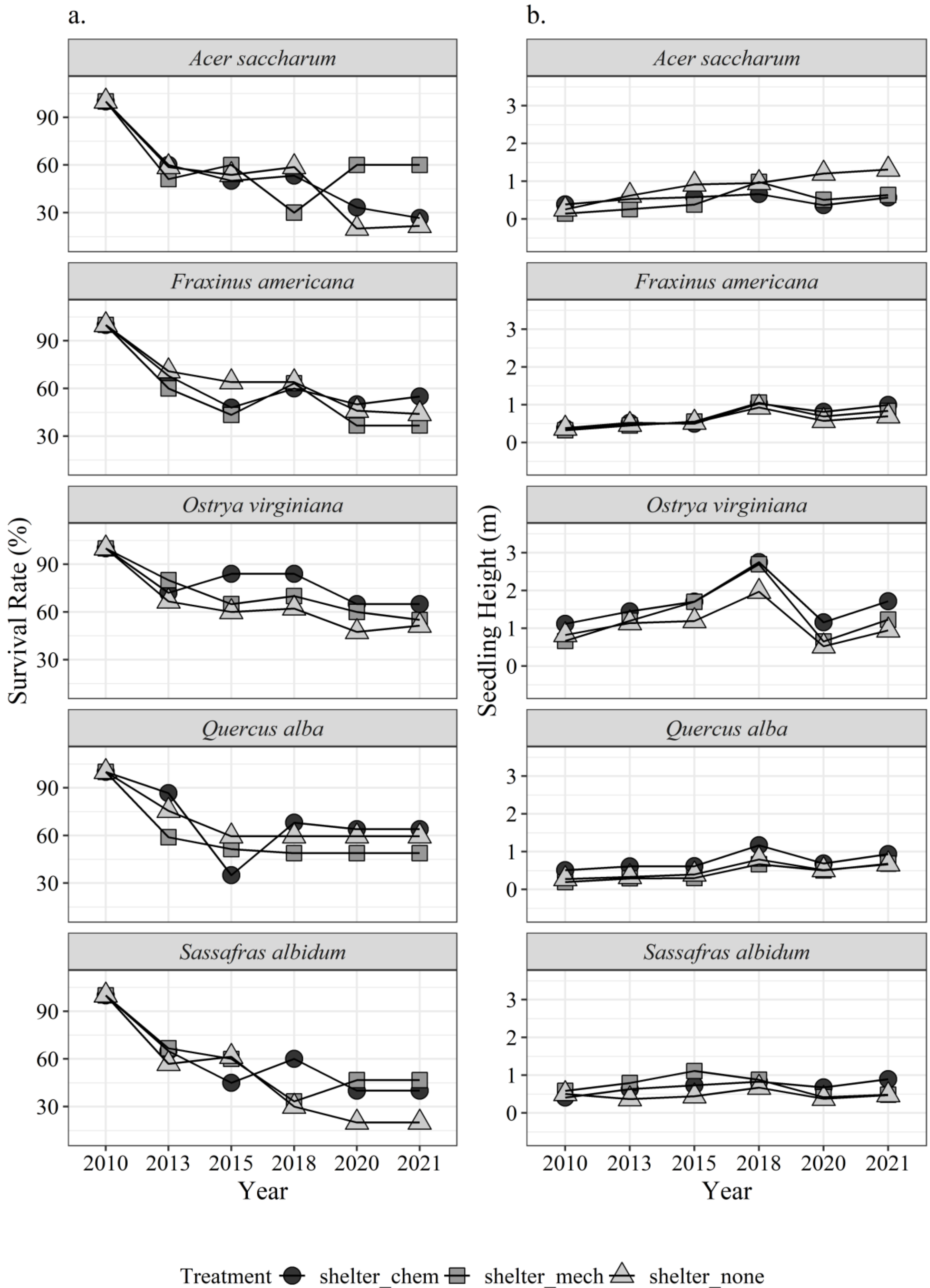
Results are presented in odds ratio or change in odds (%) of survival vs. death. A unit increase in log basal diameter increased the odds of survival by 71% ($p < 0.001$). An increase in total BA reduced the odds of survival by 10.1% ($p < 0.001$), and an increase in mean char height also reduced survival by 26.4% ($p < 0.01$) with all other factors held constant. An increase in soil N or P increased survival odds by 4% or 7.3%, respectively ($p < 0.05$). Seedling survival in 2021 followed similar trends with significant explanatory variables. In 2021, post-hoc tests revealed *Carya* spp. had greater odds of survival than *A. rubrum* by a factor of 4.7 ($p < 0.05$; Table 2). *Carya* spp., other *Quercus* spp., *Q. alba*, *Q. rubra*, and *Q. velutina* exhibited greater survival odds than *A. saccharum* by factors of 12.9, 10.5, 7.3, 9.8, and 10.5, respectively ($p < 0.001$). *F. americana*, *O. virginiana*, and *S. albidum* had reduced odds of survival compared to *Carya* by 76%, 76%, and 90.5%, respectively ($p < 0.01$). *Q. velutina* had greater odds of survival than *F. americana* by a factor of 3.5 and greater odds of survival than *O. virginiana* by a factor of 3.4 ($p < 0.05$). *Sassafras albidum* had decreased odds of survival compared to other *Quercus* spp., *Q. alba*, *Q. rubra*, and *Q. velutina* by 88%, 83%, 87.6%, and 88.5%, respectively ($p < 0.001$; Table 2). The shelterwood without midstory removal treatment had greater survival than those with chemical midstory removal and mechanical removal by a factor of 2.5 and 1.9 ($p < 0.01$).

Table 2. Mean and range of survival rates (%) since 2010 at Jeffries by species group in 2021 excluding the reference plots. Statistical differences between groups are marked with superscripts according to a post-hoc Tukey test (α = 0.05).

Species Group	Mean	Min	Max	No. Seedlings	
Acer rubrum	42.6	25.0	60.0	28	abc
Acer saccharum	29.3	20.0	60.0	30	a
Canopy other	65.8	16.7	100.0	77	cd
Carya spp.	75.7	20.0	100.0	70	d
Fraxinus americana	44.0	20.0	100.0	96	ac
Ostrya virginiana	56.0	20.0	100.0	80	ac
Other *Quercus* spp.	73.6	33.3	100.0	41	cd
Quercus alba	57.5	20.0	100.0	92	cd
Quercus rubra	71.8	40.0	100.0	51	cd
Quercus velutina	73.2	40.0	100.0	67	bd
Sassafras albidum	35.6	20.0	60.0	45	a
Subcanopy other	60.8	18.2	100.0	97	cd

Figure 4. (a.) Survival rate (%) and **(b.)** seedling height (m; mean) of the five most abundant tagged species from 2010 to 2021 at the Jeffries site by treatment. Shelter_chem = shelterwood with chemical midstory removal, shelter_mech = shelterwood with mechanical midstory removal, and shelter_none = shelterwood without midstory removal.

Figure 4 continued



Resprout Response

In 2020, *Quercus* seedlings had an average post-burn resprout rate above 86%, compared to *Acer* species which resprouted at a rate of 67% or lower on average (Figure 5). *F. americana* and *O. virginiana* also had a lower resprout response than *Quercus* spp., with an average rate of 70% each. Resprout rate remained similar in 2021 (Table 3). Resprout response after the burn in 2020 was significantly affected by species group, transformed aspect, and percent slope ($p < 0.05$; Appendix A, Table A.3). Results are presented in odds ratio or change in odds (%) of being topkilled and resprouting vs. not being topkilled and resprouting. An increase in percent slope increased the chance of resprouting by 12% ($p < 0.01$), while an increase in a unit of transformed aspect decreased resprouting odds by 83% ($p < 0.05$). Resprouting response in 2021 was also significantly affected by species group, but soil pH, FWD, and litter depth change were also significant ($p < 0.05$; Appendix A, Table A.3). A unit increase in pH decreased the odds of resprouting by 50% and an increase in total average FWD decreased resprouting odds by 9% ($p < 0.05$). A unit increase in change in litter depth (i.e., reduced litter depth) increased the odds of resprouting by a factor of two ($p < 0.05$). In 2021, post-hoc Tukey tests showed that *Carya* spp., other *Quercus* spp., *Q. alba*, *Q. rubra*, and *Q. velutina* all had greater odds of resprouting than *A. saccharum* by factors of 30.1, 35.8, 111.7, 36.2, and 18, respectively ($p < 0.01$; Table 3). *Quercus alba* also displayed greater resprouting odds than *F. americana* by a factor of 32 ($p < 0.05$).

Table 3. Two-year post-burn resprout rates since 2018 (mean and range, %) at Jeffries by species group in 2021 excluding the reference plots. Statistical differences between groups are marked with superscripts according to a post-hoc Tukey test (α = 0.05).

Species Group	Mean	Min	Max	No. Seedlings	
Acer rubrum	66.7	50.0	100.0	19	ac
Acer saccharum	51.4	25.0	100.0	17	a
Canopy other	93.2	66.7	100.0	48	bc
Carya spp.	95.8	50.0	100.0	52	bc
Fraxinus americana	71.5	25.0	100.0	61	ab
Ostrya virginiana	69.9	33.3	100.0	55	ac
Other *Quercus* spp.	94.2	66.7	100.0	29	bc
Quercus alba	98.4	66.7	100.0	51	c
Quercus rubra	98.2	75.0	100.0	34	bc
Quercus velutina	92.5	25.0	100.0	50	bc
Sassafras albidum	81.3	33.3	100.0	17	ac
Subcanopy other	66.7	50.0	100.0	19	ac

Figure 5. Resprouting *Quercus* seedlings post-burn at Jeffries in May 2020 on Hoosier National Forest, Indiana.

Resprout Count

The average number of *Quercus* resprouts per stem in 2020 was 2.8 (ranging from 1 to 12) compared to *Acer* spp. with 3.3 (ranging from 1 to 7) and *F. americana* with 2.9 (ranging from 1 to 10) resprouts. *Ostrya virginiana* had a greater average number of resprouts with 4, ranging from 1 to 13 per stem. Resprout counts in 2021 followed similar trends but generally had smaller maximum counts (Figure 6a). Resprout count were significantly affected by basal diameter (log, 2018), soil pH, species group, percent slope, and litter depth change ($p < 0.05$; Appendix A, Table A.4). With one unit increase in log basal diameter, the expected number of resprouts increased by a factor of 1.4 ($p < 0.001$), with all other variables fixed. When pH increased by one unit, the expected count of resprouts decreased by a factor of 0.8 ($p < 0.001$). A unit increase in percent slope decreased the expected number of resprouts by a factor of 0.97 ($p < 0.01$). One unit increase in litter depth change (i.e., reduced litter depth) decreased the expected resprout count by a factor of 0.82 ($p < 0.01$). Silvicultural treatments had no significant effect on the number of resprouts in 2020 ($p > 0.05$). Post-hoc Tukey tests indicated *O. virginiana* and Subcanopy Other had a greater number of resprouts than *Carya* spp. by factors of 1.7 and 1.6, respectively ($p < 0.05$). *Quercus rubra* had fewer expected resprouts than *O. virginiana* by a factor of 0.6 ($p < 0.01$), and Subcanopy Other had a greater number of resprouts than *Q. rubra* by a factor of 1.6 ($p < 0.05$).

In 2021, basal diameter (log) and species group remained significant explanatory variables of resprout count, but soil Al, FWD, and treatment were also significant ($p < 0.05$; Appendix A, Table A.4). An increase in standard deviation (SD = 0.97) of soil Al increased the expected resprout count by a factor of 1.1 ($p < 0.001$) with all other variables fixed. With a unit increase in FWD, the expected number of resprouts decreased by a factor of 0.97 ($p < 0.05$). Significant differences between species group and treatment pairs were not detected in 2021 ($p > 0.05$, Figure 6a).

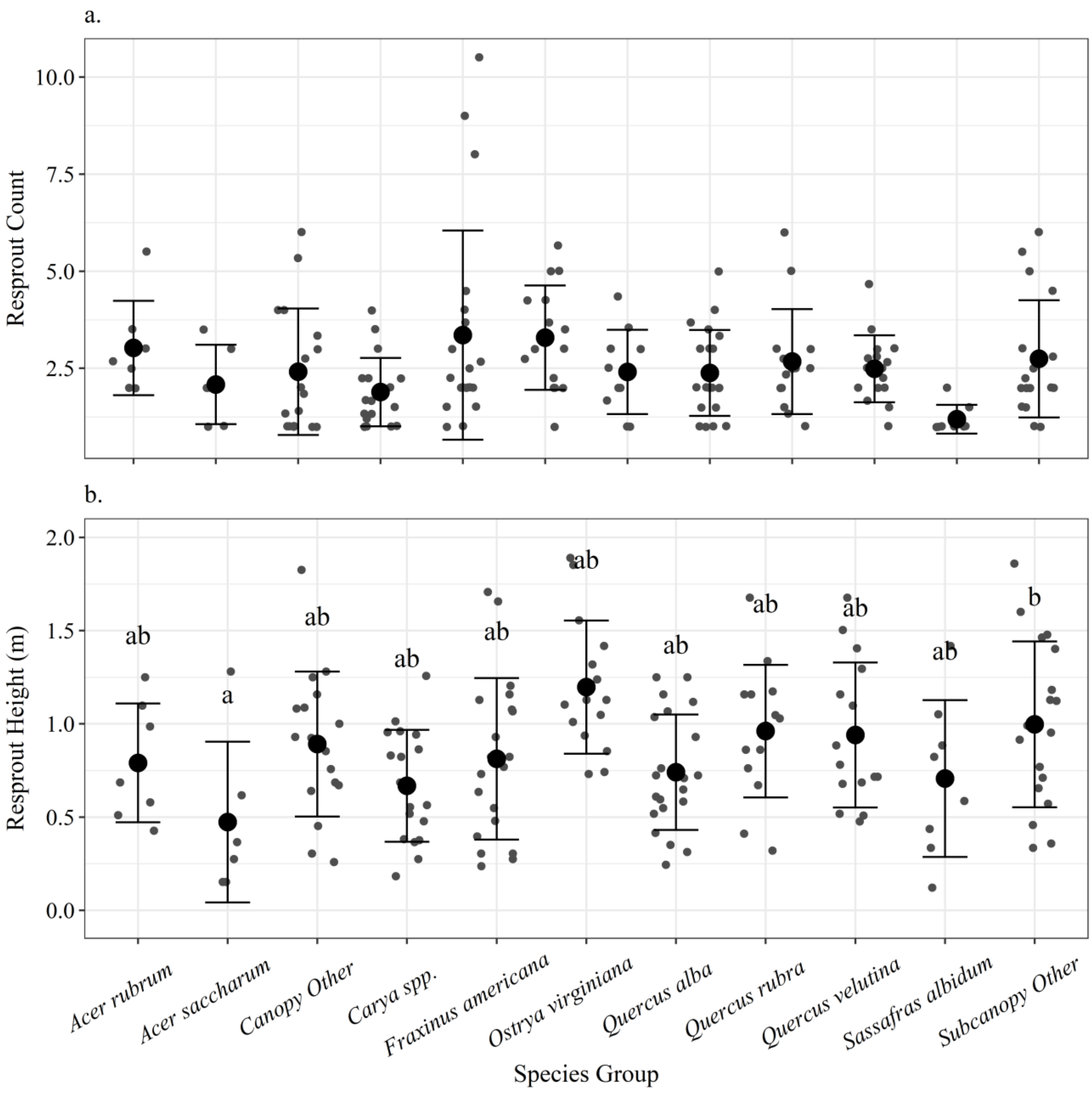


Figure 6. (a.) Resprout count and **(b.)** height (m; mean ± SD) by species groups post-burn at Jeffries in 2021. Superscripts denote significant differences of resprout heights between species groups according to a post-hoc Tukey test (α = 0.05).

Resprout Heights

In 2020, the average height of *Quercus* resprouts was 0.67 m (0.09-1.98) and increased to 0.92 m (0.12-2.74) in 2021. *Acer* spp. and *F. americana* heights averaged 0.53 and 0.66 m and increased to 0.68 and 0.86 m in 2021. *Ostrya virginiana* resprouts averaged 0.62 m (0.09-1.4) in 2020 and increased to 1.2 m (0.3-2.1) in 2021. In 2020, resprout heights were significantly affected by basal diameter (log, 2018), mean char height (standardized), total soil N, species group, and transformed aspect (R^2 = 0.3907, $p < 0.05$; Appendix A, Table A.4). With every unit increase in log basal diameter, there was a 0.46 log m increase in log resprout height ($p < 0.001$). With an increase in one standard deviation of mean char height (SD = 0.78), there was a decrease of 0.1 log m in log resprout height ($p < 0.01$). Log resprout heights increased by 0.02 log m with every increase in soil N and they increased by 0.39 log m with an increase in transformed aspect ($p < 0.05$). Post-hoc Tukey tests indicated that the mean log height of Subcanopy Other was larger than *Carya* spp. by 0.33 log m and was also larger than *O. virginiana* by 0.46 log m ($p < 0.05$). Basal diameter and soil N significantly affected resprout height in 2021, as were total BA (log, 2018) and average canopy density (standardized, 2018; R^2 = 0.4657, $p < 0.05$; App. Table 10). Every increase in log BA decreased log resprout height by 0.28 and every increase in one standard deviation of canopy density (SD = 0.85) decreased log resprout height by 0.1 ($p < 0.01$). Subcanopy Other mean resprout height was 0.68 log m greater than *A. saccharum* ($p < 0.05$) with no differences detected between other species group pairs (Figure 6b). Post-hoc Tukey tests didn’t detect significant differences between treatment groups, but the model showed that the treatments shelterwood with mechanical midstory removal and shelterwood without midstory removal exhibited 0.18 and 0.17 greater log resprout height than shelterwood with chemical midstory removal ($p < 0.05$).

Regeneration Density

Pre-burn, *Q. alba* averaged approximately 4,890 stems ha^{-1} and then doubled to 9,860 stems ha^{-1} post-burn. Comparatively, *F. americana* and *O. virginiana* increased from approximately 8,710 and 3,900 stems ha^{-1} to 11,330 and 6,890 stems ha^{-1} after the burn. In 2020 (post-burn), regeneration density was significantly affected by height class (1-5), species group, mean char height (standardized), total soil N, transformed aspect, FWD in 2018, and treatment ($p < 0.05$; Appendix A, Table A.4). An increase in one standard deviation of char height (SD = 1) decreased the number of seedlings by a factor of 0.87, while an increase in N increased the number of seedlings by a factor of 1.03 ($p < 0.001$). A unit increase in transformed aspect decreased regeneration density by a factor of 0.60 ($p < 0.05$). The density of seedlings also decreased with an increase in FWD by a factor of 0.97 ($p < 0.001$), with all other variables held constant. Post-hoc Tukey tests indicated shelterwood without midstory removal had a greater post-burn abundance of seedlings than shelterwood with chemical midstory removal by a factor of 1.4 ($p < 0.01$; Figure 7). Differences between species groups were detected with *F. americana*, *O. virginiana*, and *Q. alba* having a greater abundance of seedlings than *A. rubrum* by factors of 4.3, 3.2, and 4.7 ($p < 0.001$), respectively (Figure 7). *Quercus rubra* and *Q. velutina* had significantly fewer seedlings than *F. americana* by a factor of 0.46 and 0.37 ($p < 0.001$), respectively. Other *Quercus* species, *Q. rubra*, and *Q. velutina* had significantly fewer seedlings than *O. virginiana* ($p < 0.001$; Figure 7). Across all species groups, there were significantly fewer seedlings in the taller height classes (4 and 5) compared to the shorter classes (classes 1, 2, and 3; $p < 0.001$), and height class 3 had significantly fewer seedlings than classes 1 and 2 (Figure 8). No significant differences were found between height classes 1 and 2, and between classes 4 and 5 (Figure 8).

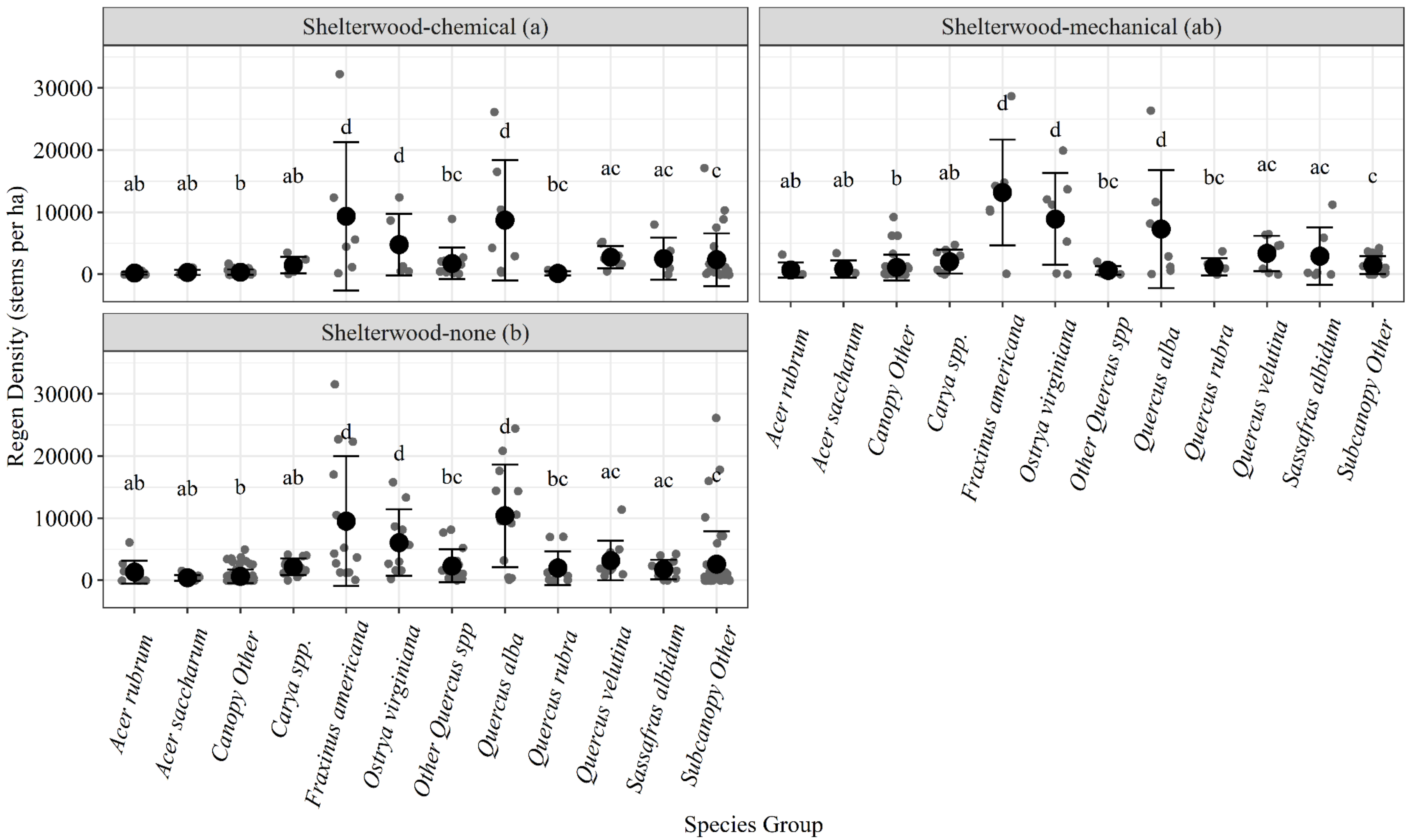


Figure 7. Regeneration density (stems ha^{-1}; mean ± SD) by treatments post-burn at Jeffries in 2020. Superscripts indicate significant differences between species groups and treatment groups according to a post-hoc Tukey test (α = 0.05). Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

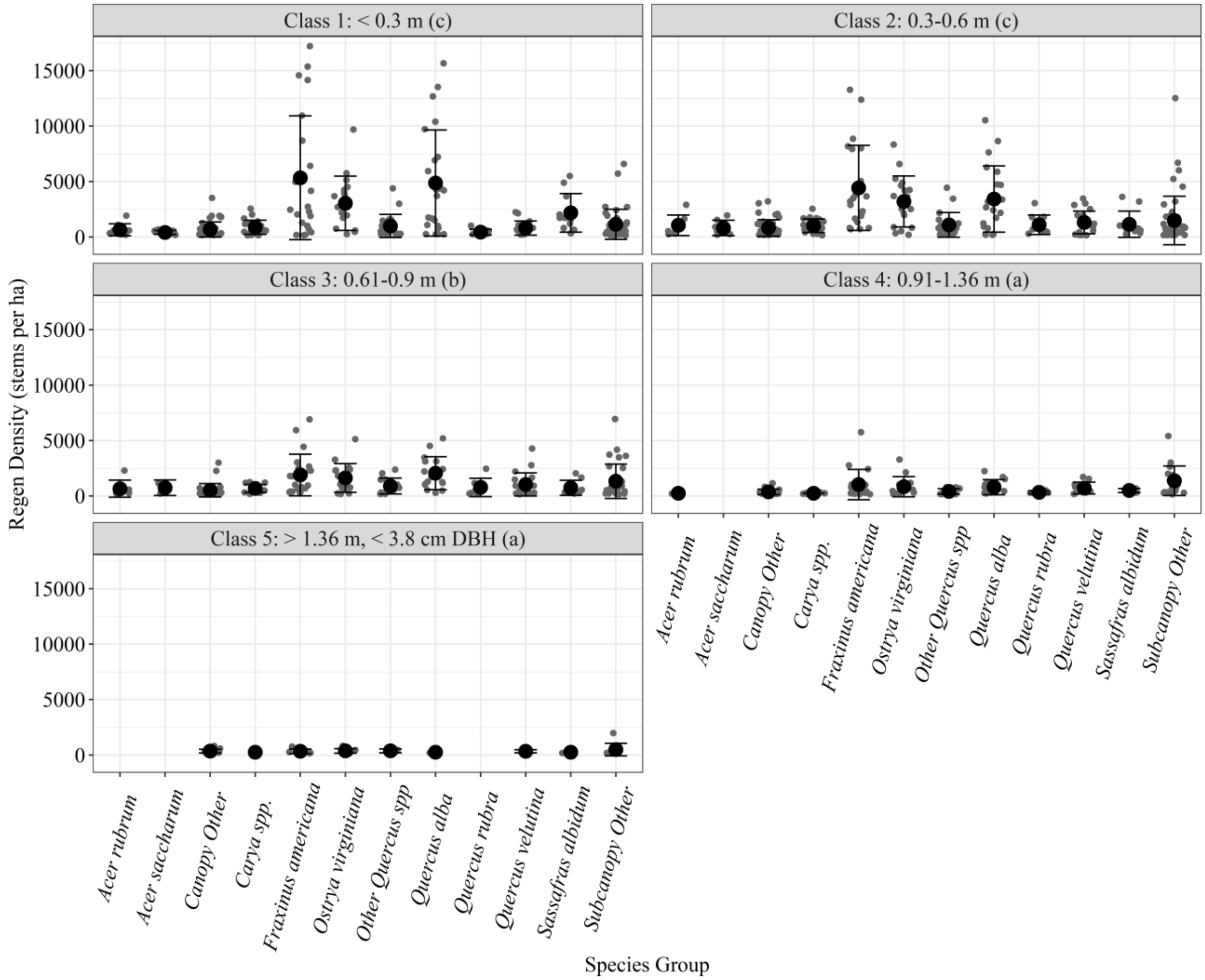


Figure 8. Regeneration density (stems ha^{-1}; mean ± SD) by height class (1-5) at Jeffries in 2020. Superscripts denote significant differences between height classes according to a post-hoc Tukey test (α = 0.05).

NMDS Ordination

The NMDS of the regeneration-layer species composition resulted in a solution with two dimensions and stress of 0.164 after 20 runs (linear R^2 = 0.869). Environmental and stand factors that were significantly correlated with the ordination included post-harvest BA, mean char height, pH, soil organic matter, Al concentration, total N, average canopy density in 2020, and percent slope ($p < 0.05$), with pH (R^2 = 0.56, p = 0.001) and Al (R^2 = 0.59, p = 0.001) exhibiting the strongest correlations (Table 4, Figure 9a). NMDS axis 1 was strongly related to site quality and site characteristics such as pH, Al, total N, organic matter, average canopy density, and BA (Figure

9a). NMDS axis 2 was strongly related to the fire treatment (mean char height) as well as the percent slope (Figure 9a). Relative abundance of *F. americana* and *A. saccharum* was correlated with plots with more productive soils, while several *Quercus* species were correlated with plots containing higher soil Al concentrations (Figure 9a). The fire treatment pushed species composition from *A. saccharum* and *F. americana* to one with a higher relative abundance of *Q. alba* and *Q. velutina* (Figure 9a). Plots from 2010 were associated with a higher relative abundance of *Acer* species and *S. albidum*, while 2020 plots were associated with higher relative abundances of *Q. alba*, *Q. velutina*, and *Carya* spp. (Figure 9b). While there was overlap in the distribution of plots between years 2010 and 2020, there was a clear grouping between the two years (Figure 9b). There was a high degree of overlap between treatment groups, especially with shelterwood with mechanical midstory removal and without midstory removal (Figure 9c). The shelterwood with mechanical midstory removal does not appear to have been conducted across the entire environmental gradient at the site, as the grouping does not span across axis 1 (Figure 9c). Shelterwood without midstory removal was distributed across the environmental gradient represented by axis 1, while shelterwood with chemical midstory removal was distributed across axis 2 towards the portion of the ordination associated with greater mean char height and greater Al concentration (Figure 9c). Between 2010 and 2020, most plots on the right side of the graph exhibited compositional shifts away from *A. rubrum* and *S. albidum* in ordination space and towards greater importance of *Q. stellata* and *Q. alba*, the two most dominant overstory *Quercus* species, along axis 2 (Figure 9d), the axis most strongly associated with increased char height and decreasing percent slope (Figure 9a). However, plots on the left side of the graph displayed smaller compositional shifts in multiple directions, which was associated with *A. saccharum* and *F. americana* and greater soil productivity and residual density of canopy trees (Figure 9d).

The PERMAVONA did not detect significant differences between treatments, but it did detect a significant difference between the years 2010 and 2020 ($p < 0.05$). The SIMPER test indicated that *S. albidum*, *F. americana,* and *Q. alba* were the top three contributors of the differences between the years 2010 and 2020, contributing 17, 16, and 13%, respectively.

Figure 9. NMDS ordination of regeneration-layer species composition at Jeffries in 2010 and 2020: **(a.)** Biplot of regeneration species with significant ($p < 0.05$) environmental factors MeanChar_ht (mean char height), Al_mg.kg (soil Al), Slope (percent slope), BA_2018 (basal area in 2018), Organic.Matter (percent soil organic matter), totalN_ppm (total soil N), pH (soil pH), and AVcanopy.density_2020 (average canopy density in 2020) as vector arrows; **(b.)** Biplot of regeneration plots and species grouped by years 2010 and 2020; **(c.)** Biplot of regeneration plots and species grouped by silvicultural treatments shelter_chem (shelterwood with chemical midstory removal), shelter_mech (shelterwood with mechanical midstory removal), and shelter_none (shelterwood without midstory removal); **(d.)** Successional vector changes of regeneration composition moving from years 2010 to 2020. Species abbreviations: ACRU = *Acer rubrum*, ACSA2 = *Acer saccharinum*, ACSA3 = *Acer saccharum*, AMAR3 = *Amelanchier arborea*, ARSP2 = *Aralia spinosa*, CARYA = *Carya* spp., CECA4 = *Cercis canadensis*, CELTIS = *Celtis* spp., CEOC = *Celtis occidentalis*, COFL2 = *Cornus florida*, CRATA = *Crataegus* spp., DIVI5 = *Diospyros virginiana*, FRAM2 = *Fraxinus americana*, JUNI = *Juglans nigra*, LIBE3 = *Lindera benzoin*, LITU = *Liriodendron tulipifera*, MORU2 = *Morus rubra*, NYSY = *Nyssa sylvatica*, OSVI = *Ostrya virginiana*, PRSE2 = *Prunus serotina*, QUAL = *Quercus alba*, QUCO2 = *Quercus coccinea*, QUERC = *Quercus* spp., QUMA3 = *Quercus marilandica*, QUMO4 = *Quercus montana*, QURU= *Quercus rubra*, QUST = *Quercus stellata*, QUVE = *Quercus velutina*, RHCO = *Rhus copallinum*, RHGL = *Rhus glabra*, SAAL5 = *Sassafras albidum*, ULAL = *Ulmus alata*, ULAM = *Ulmus americana*, ULMUS = *Ulmus* spp., ULRU = *Ulmus rubra*.

Figure 9 continued

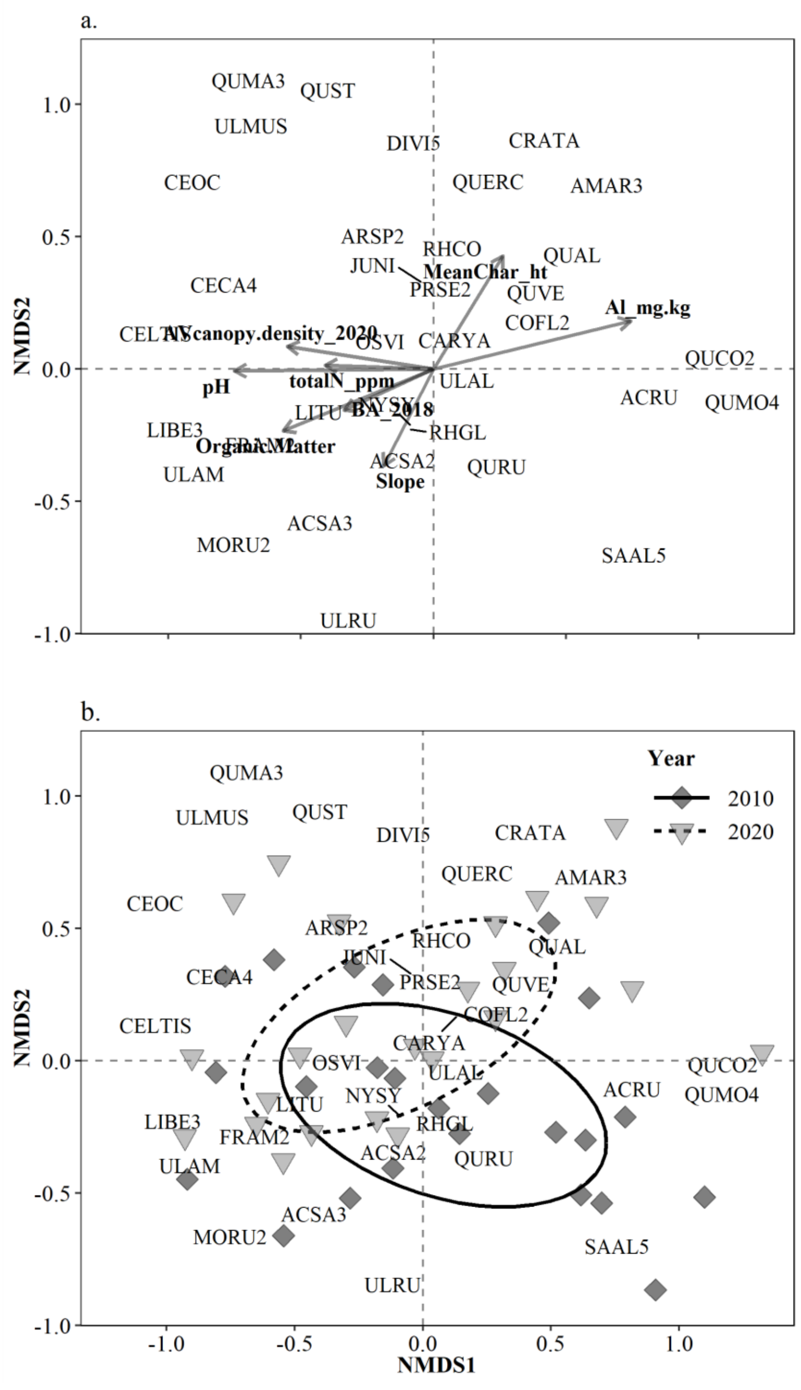
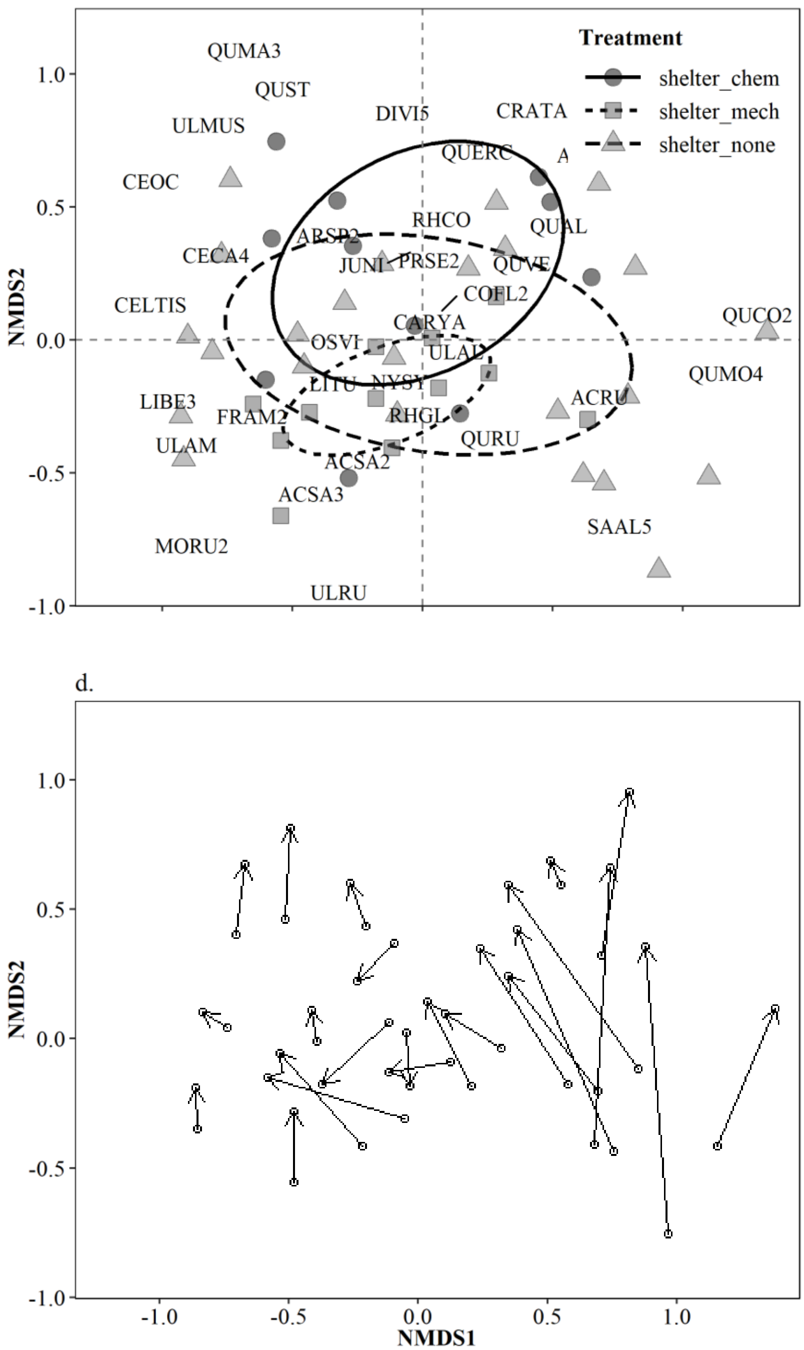


Figure 9 continued

c.



d.

Table 4. Correlation coefficients and p-values (bold: $p < 0.05$) for environmental variables with NMDS ordination of Jeffries regeneration density data.

Environmental Variable	R^2	P-value
BA (2010)	0.086	0.118
BA (2018)	**0.138**	**0.035**
BA (2020)	0.119	0.053
High Mean Temp (30.5 cm)	0.085	0.131
Low Mean Temp (0 cm)	0.060	0.251
Mean Char Height	**0.251**	**0.005**
pH	**0.564**	**0.001**
% Organic Matter	**0.376**	**0.001**
P	0.120	0.057
Al	**0.587**	**0.001**
Total N	**0.167**	**0.014**
Canopy Density (2018)	0.090	0.124
Canopy Density (2020)	**0.312**	**0.002**
Canopy Density (2010)	0.036	0.43
CWD (2018)	0.081	0.156
CWD (2020)	0.078	0.183
FWD (2018)	0.058	0.25
FWD (2020)	0.099	0.079
Litter Depth (2018)	0.011	0.76
Duff Depth (2018)	0.045	0.345
Litter Depth (2020)	0.068	0.209
Duff Depth (2020)	0.029	0.481
Litter Change (2018-2020)	0.115	0.066
Duff Change (2018-2020)	0.037	0.435
Transformed Aspect	0.013	0.753
% Slope	**0.169**	**0.012**
Average TSI	0.030	0.498

Quercus Competitive Status

The most common species competing with *Quercus* seedlings were other *Quercus* species (37% of the time), in particular *Q. alba*. The next most abundant competitor species was *O. virginiana* which competed with *Quercus* spp. 23% of the time across all treatments. The average height ratio between the tagged *Quercus* seedling and its competitor was 0.48, ranging from 0.04 to 3.05. No significant differences were found in these height ratios among treatment groups ($F_{2,145} = 1.645$, $p = 0.197$). The median light class of tagged *Quercus* seedlings was light class 4, meaning four sides of the seedling received sunlight. The light classes were not significantly different across treatments ($p > 0.05$). The probability of a *Quercus* seedling having light class 4 was higher than all other classes across all treatments and *Quercus* spp. with an overall probability of 35.2 %. Light class 5 had the second-highest probability overall at 22.2%. The percent canopy of neighboring seedlings that fell within the projected 45-degree cone above each tagged *Quercus* seedling had an average midpoint of 5.25, ranging from 0.3 to 37.5% across all treatments. The linear model did not detect differences between treatment groups for the percent canopy cover within the 45-degree cone ($F_{2,167} = 0.604$, $p = 0.548$).

2.3.2 Sixty-six Site

Seedling Survival since 2010

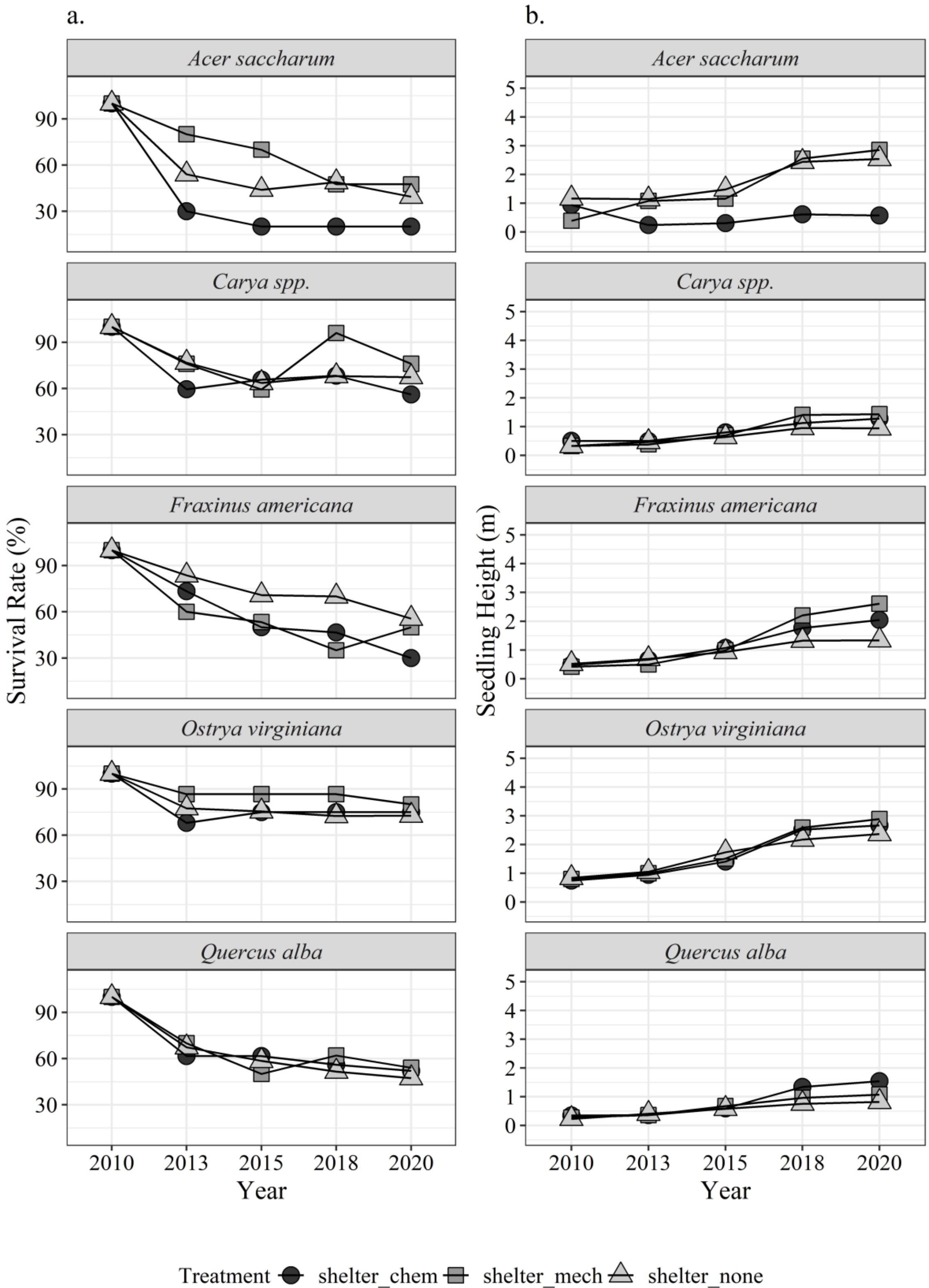
In 2020, *Quercus alba* had an average survival rate since 2010 of 50.2%, while the rates of *Q. rubra and Q. velutina* were higher at 61.8 and 78.5%, respectively (Table 5). *Acer* species averaged approximately 39% survival and *F. americana* averaged 46.9%, while *O. virginiana* averaged 74.4% survival since 2010 (Table 5). Overall, survival rates decreased after 2010 and then recovered after all harvests were complete in 2013 (Figure 10a). *Ostrya virginiana* and *Carya* spp. tended to have the highest survival rates over time, while *A. saccharum* tended to have the lowest, except in the shelterwood with mechanical midstory removal (Figure 10a). Significant explanatory variables of overall seedling survival since treatment were basal diameter (log, 2010), total live BA (2020), total soil N, and species group ($p < 0.05$; Appendix A, Table A.5). Results are reported in odds ratios or change in odds (%) of survival vs. death. A unit increase in log basal diameter increased the odds of survival by 80.2% ($p < 0.001$), while all other variables are held constant. An increase in BA increased the odds of survival by 4.7%, while a unit increase in soil N decreased the odds of survival by 4.1% ($p < 0.01$). Post-hoc Tukey tests indicated that *Carya* spp. had greater odds of survival than *A. rubrum* by a factor of 3.6 ($p < 0.05$, Table 5). *Carya* spp., *O. virginiana*, and *Q. alba* had greater odds of survival than *A. saccharum* by factors of 6.1, 5.1, and 3.5, respectively ($p < 0.05$). *Fraxinus americana*, *Q. velutina*, and *S. albidum* had reduced odds of survival compared to *Carya* spp. by 77.2%, 74%, and 95%, respectively ($p < 0.05$). *Sassafras albidum* had lower odds of survival than *O. virginiana*, *Q. alba*, and *Q. rubra* by 93.6%, 90.7%, and 90.1%, respectively ($p < 0.01$; Table 5). Post-hoc Tukey tests also detected that the shelterwood without midstory removal treatment had 55.5% greater odds of survival than shelterwood with chemical midstory removal ($p < 0.05$).

Table 5. Mean and range of survival rates (%) since 2010 at Sixty-six by species group in 2020 excluding the reference plots. Statistical differences between groups are marked with superscripts according to a post-hoc Tukey test ($\alpha = 0.05$).

Species Group	Mean	Min	Max	No. Seedlings	
Acer rubrum	39.4	20.0	60.0	38	ad
Acer saccharum	39.2	20.0	75.0	53	ab
Canopy other	55.6	8.3	100.0	173	cd
Carya spp.	66.3	33.3	100.0	88	c
Fraxinus americana	46.9	20.0	100.0	73	ae
Ostrya virginiana	74.4	20.0	100.0	84	cd
Other *Quercus* spp.	33.3	33.3	33.3	3	ac
Quercus alba	50.2	20.0	80.0	97	cde
Quercus rubra	61.8	20.0	100.0	52	bcde
Quercus velutina	78.5	33.3	100.0	21	ad
Sassafras albidum	23.3	20.0	33.3	21	a
Subcanopy other	71.1	16.7	100.0	75	cd

Figure 10. (a.) Survival rate (%) and **(b.)** seedling height (m; mean) of the five most abundant tagged species from 2010 to 2021 at the Sixty-six site by treatment. Shelter_chem = shelterwood with chemical midstory removal, shelter_mech = shelterwood with mechanical midstory removal, and shelter_none = shelterwood without midstory removal.

Figure 10 continued



Seedling Heights

Pretreatment (2010) *Quercus* seedlings averaged 0.36 m (0.09-2.3 m) in height, then increased to an average height of 1.35 m (0.09-5.2 m) in 2020. *Acer* spp. averaged 0.5 m tall (0.3-8.2 m) in 2010 and increased to 1.8 m (0.09-9.1 m) in 2020. *Fraxinus americana* and *O. virginiana* averaged 0.5 m (0.08-3.1 m) and 0.8 m (0.12-4.6 m) pretreatment, respectively, increasing to 1.7 m (0.2-3.5 m) and 2.6 m (1.1-4.8 m) in 2020. Seedling heights steadily increased since 2013, with *Q. alba* and *Carya* spp. tending to have lower average heights except in shelterwood with chemical midstory removal in which *A. saccharum* had the lowest average height (Figure 10b). The linear model indicated that tagged seedling heights in 2020 were significantly influenced by basal diameter (log, 2010), soil P, soil total N, species group, and treatment (R^2=0.452, $p < 0.05$; Appendix A, Table A.5). With every unit increase in log basal diameter, there was a 0.56 log m increase in seedling height ($p < 0.001$). Each unit increase in soil P resulted in a 0.03 log m increase in seedling height ($p < 0.05$), while each increase in soil N decreased seedling height by 0.03 log m ($p < 0.001$). Post-hoc Tukey tests indicated *O. virginiana* had a greater average seedling height than *Carya* spp. by 0.65 log m ($p < 0.001$; Figure 11). The average seedling heights of *Quercus alba* and *S. albidum* were shorter than *O. virginiana* by 0.72 and 1.94 log m, respectively ($p < 0.001$). *Sassafras albidum* had a shorter average seedling height than *Q. alba* by 1.2 log m ($p <0.01$), while Subcanopy Other had a greater average seedling height than *Q. alba* by 0.48 log m ($p < 0.05$; Figure 11). Post-hoc Tukey tests also found that shelterwood without midstory removal had shorter seedlings compared to those in the chemical and mechanical midstory removal treatments by 0.54 and 0.63 log m, respectively ($p < 0.001$; Figure 11).

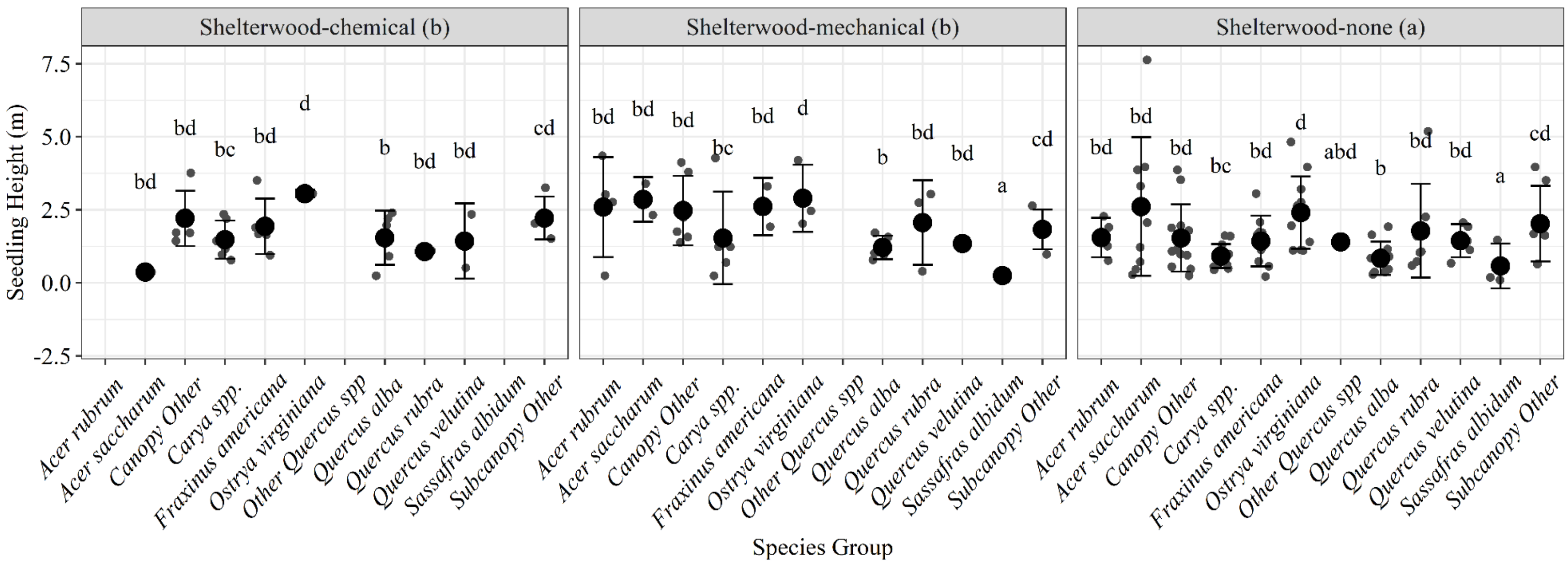


Figure 11. Seedling heights (m; mean ± SD) by treatment at Sixty-six in 2020. Superscripts denote significant differences between species groups and treatments according to a post-hoc Tukey test (α = 0.05). Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

Regeneration Density

Pretreatment (2010) *Q. alba* averaged approximately 4,170 stems ha^{-1} and increased to an average of 5,750 stems ha^{-1} in 2020. *Acer rubrum* started with an average of approximately 1,810 stems ha^{-1} in 2010, then more than doubled to 4,200 stems ha^{-1} in 2020. *Fraxinus americana* and *O. virginiana* increased slightly from an average of 6,450 and 2,020 stems ha^{-1} in 2010 to 7,259 and 3,021 stems ha^{-1} in 2020. In 2020, regeneration density was significantly affected by height class (1-5), BA (2020), soil P, species group, average canopy density (2020), and treatment ($p < 0.05$; Appendix A, Table A.5). An increase in BA increased estimated seedling abundance by a factor of 1.03 ($p < 0.001$). A unit increase in soil P decreased estimated seedling abundance by a factor of 0.97, while a unit increase in canopy density increased the seedling abundance by a factor of 1.02 ($p < 0.01$). Post-hoc Tukey tests revealed that *Carya* spp., Other *Quercus* spp., *Q. rubra*, and *Q. velutina* had lower seedling abundance than *A. rubrum* by factors of 0.57, 0.22, 0.45, and 0.32, respectively ($p < 0.05$; Figure 12). *Fraxinus americana* and *Q. alba* had greater seedling abundance than *A. saccharum* by factors of 2.6 and 2.14, respectively ($p < 0.001$). *Ostrya virginiana*, other *Quercus* spp., *Q. rubra*, and *Q. velutina* had lower seedling abundance than *F. americana* by factors of 0.53, 0.14, 0.29, and 0.2, respectively ($p < 0.001$; Figure 12). Post-hoc Tukey tests also found the shelterwood with mechanical midstory removal and shelterwood without midstory removal treatments had lower seedling abundance than shelterwood with chemical midstory removal by factors of 0.51 and 0.63 ($p < 0.001$; Figure 12). Overall, shorter height classes (1) had significantly greater seedling abundance than taller classes (2, 3, 4, 5), except height class 5 had greater seedling abundance compared to height classes 2, 3, and 4 ($p < 0.05$; Figure 13). However, no significant differences were found between height classes 2 and 4, and between classes 3 and 4.

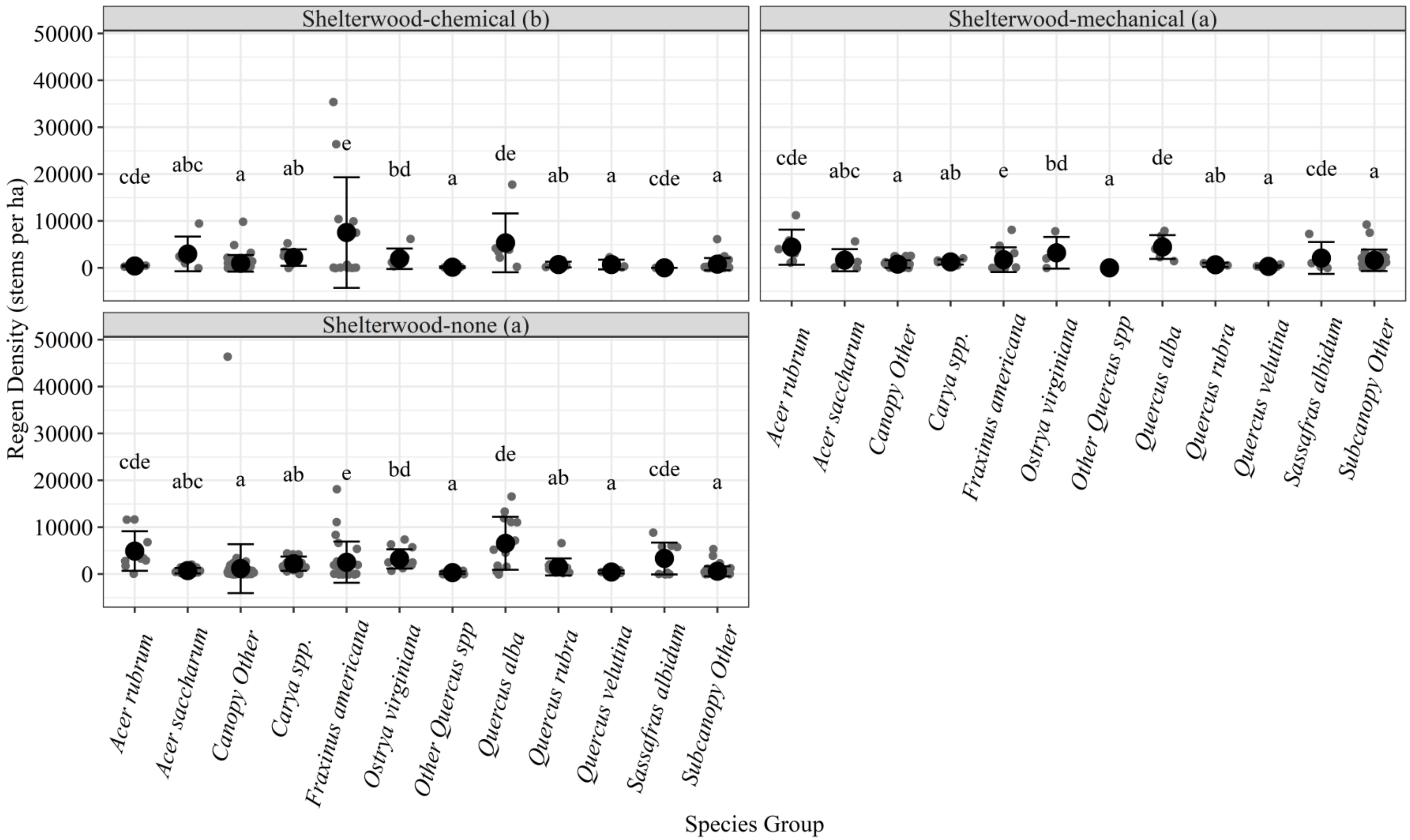


Figure 12. Regeneration density (stems ha^{-1}; mean ± SD) by treatment at Sixty-six in 2020. Superscripts denote significant differences between species group and treatment groups according to a post-hoc Tukey test (α = 0.05). Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

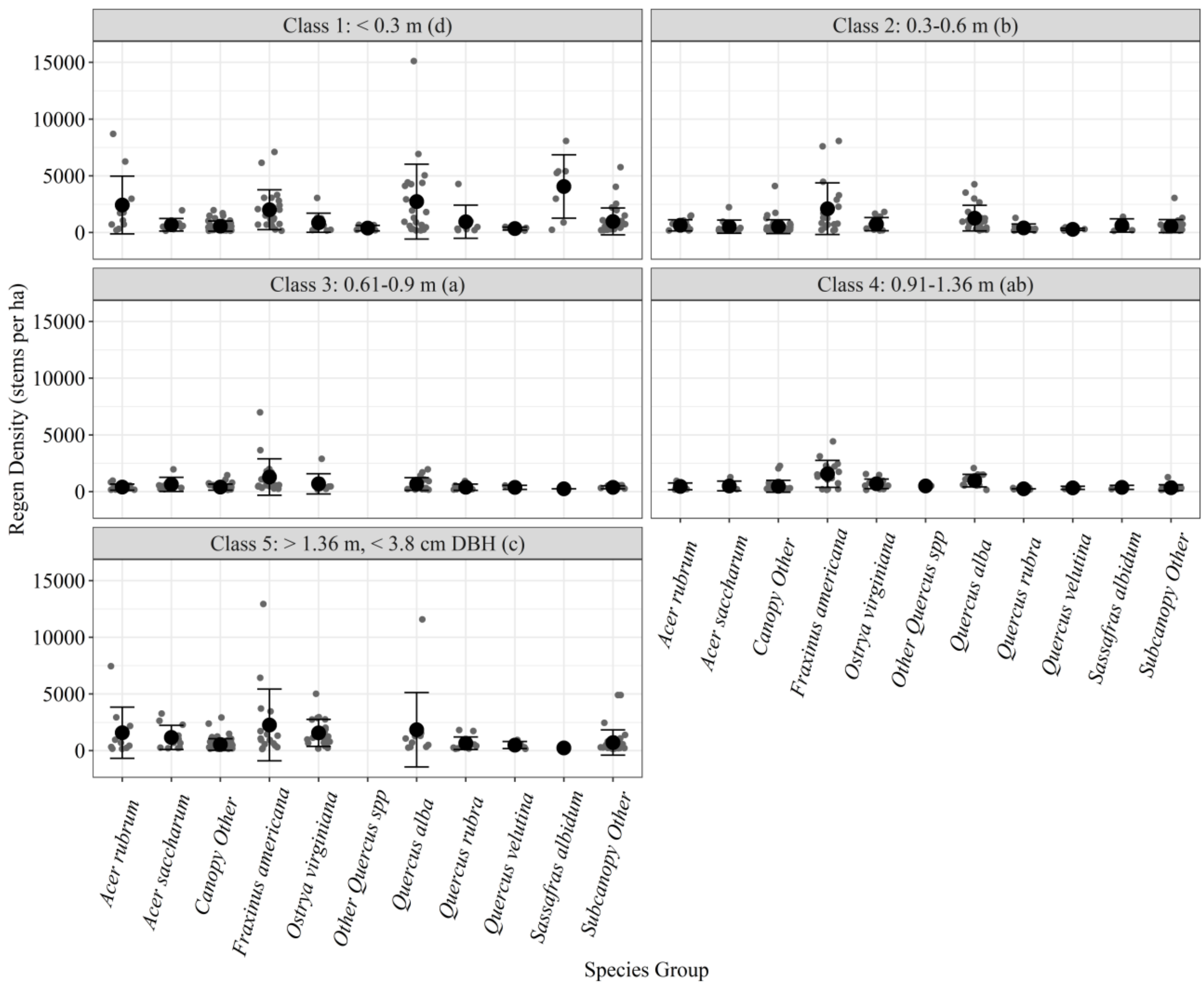


Figure 13. Regeneration densities (stems ha^{-1}; mean ± SD) by height class (1-5) at Sixty-six in 2020. Canopy Other > 40,000 stems ha^{-1} not pictured in height class 1 graph to allow for better differentiation between species groups. Superscripts denote significant differences between height classes according to a post-hoc Tukey test ($\alpha = 0.05$).

NMDS Ordination

The NDMS of the regeneration-layer species composition at Sixty-six resulted in a solution with two dimensions and stress of 0.180 after 20 runs (linear $R^2 = 0.838$). The environmental factors that significantly correlated with the ordination were post-harvest BA, pH, organic matter, Al, transformed aspect, and average TSI, with pH ($R^2 = 0.50$, p = 0.001) and organic matter ($R^2 = 0.45$, p = 0.001; Figure 14a, Table 6) having the strongest correlations. The NMDS axis 1 was strongly related to site quality (Al, pH, organic matter) and average TSI (terrain shape index;

Figure 14a). Transformed aspect and post-harvest BA were strongly related to NMDS axis 2 (Figure 14a). *Ulmus alata* and *C. canadensis* were correlated with plots with higher quality soils, while *A. rubrum* and *Q. velutina* were correlated to plots with higher soil Al content as well as higher average terrain shape index (Figure 14a). *Acer saccharum* and *C. florida* were correlated with plots with a higher basal area (Figure 14a). Plots from 2010 and 2020 had high overlap and showed no clear differentiation (Figure 14b). Shelterwood with mechanical midstory removal and shelterwood without midstory removal treatments had high overlap, while shelterwood with chemical midstory removal showed clear differentiation along axis 1 and was associated with plots with a higher relative abundance of *F. americana* (Figure 14c). Unlike Jeffries following the burn, vector arrows at Sixty-six showed no discernable pattern of composition change from 2010 to 2020 (Figure 14d).

The PERMANOVA detected significant differences between treatments ($p < 0.001$) and years ($p < 0.05$). The SIMPER test indicated that *F. americana, Q. alba*, and *S. albidum*, were the top three contributors of the differences between treatments and years, collectively contributing 39-47% and 43%, respectively.

Figure 14. NMDS ordination of regeneration-layer species composition at Sixty-six in 2010 and 2020: **(a.)** Biplot of regeneration species with significant ($p < 0.05$) environmental factors transaspect (transformed aspect), TSI.AVG (average TSI), Al_mg.kg (soil Al), BA_2020 (basal area in 2020), BA_2018 (basal area in 2018), Organic.Matter (percent soil organic matter), and pH (soil pH) as vector arrows; **(b.)** Biplot of regeneration plots and species grouped by years 2010 and 2020; **(c.)** Biplot of regeneration plots and species grouped by silvicultural treatments shelter_chem (shelterwood with chemical midstory removal), shelter_mech (shelterwood with mechanical midstory removal), and shelter_none (shelterwood without midstory removal); **(d.)** Successional vector changes of regeneration composition moving from years 2010 to 2020. Species abbreviations: ACRU = *Acer rubrum*, ACSA3 = *Acer saccharum*, AMAR3 = *Amelanchier arborea*, ARSP2 = *Aralia spinosa*, CARYA = *Carya* spp., CECA4 = *Cercis canadensis*, CELTIS = *Celtis* spp., CEOC = *Celtis occidentalis*, COFL2 = *Cornus florida*, CRATA = *Crataegus* spp., DIVI5 = *Diospyros virginiana*, FAGR = *Fagus grandifolia*, FRAM2 = *Fraxinus americana*, HAVI4 = *Hamamelis virginiana*, JUNI = *Juglans nigra*, JUVI = *Juniperus virginiana*, LITU = *Liriodendron tulipifera*, MORUS = *Morus* spp., NYSY = *Nyssa sylvatica*, OSVI = *Ostrya virginiana*, PLOC = *Platanus occidentalis*, PRSE2 = *Prunus serotina*, QUAL = *Quercus alba*, QUERC = *Quercus* spp., QURU= *Quercus rubra*, QUST = *Quercus stellata*, QUVE = *Quercus velutina*, RHCO = *Rhus copallinum*, RHGL = *Rhus glabra*, SAAL5 = *Sassafras albidum*, ULAL = *Ulmus alata*, ULAM = *Ulmus americana*, ULRU = *Ulmus rubra.*

Figure 14 continued

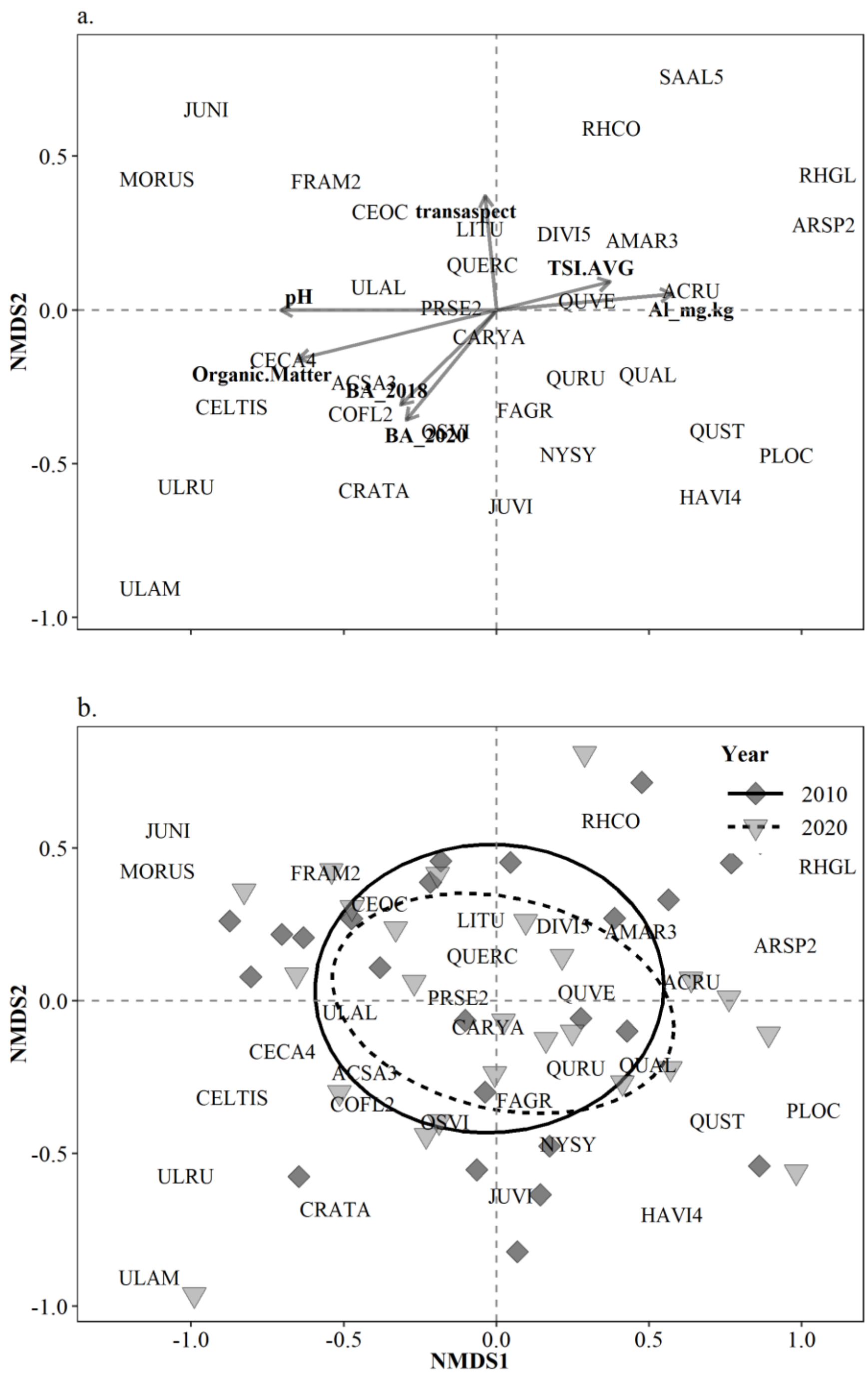


Figure 14 continued

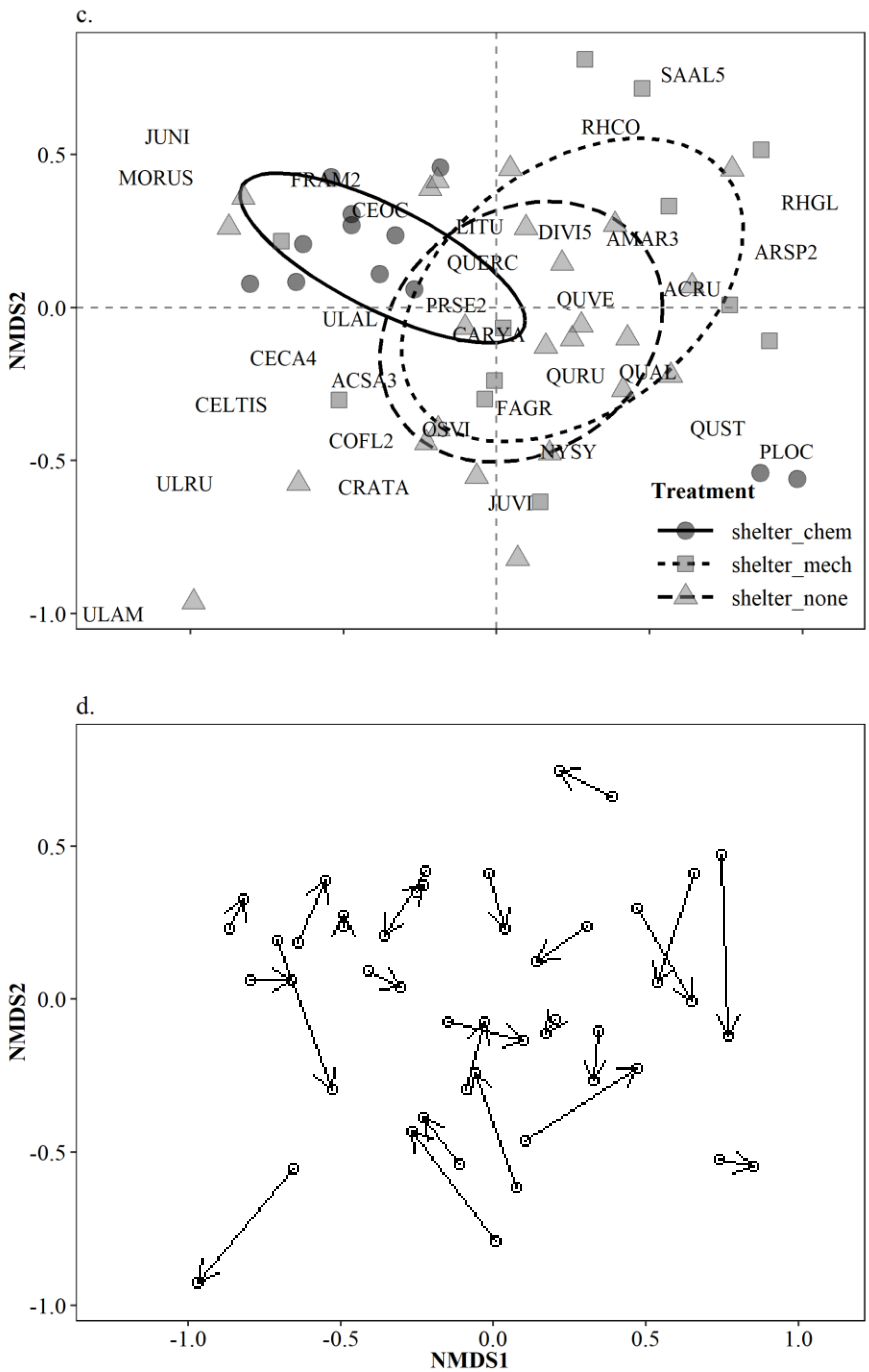


Table 6. Correlation coefficients and p-values (bold: p < 0.05) for environmental variables with NMDS ordination of Sixty-six regeneration density.

Environmental Variable	R^2	P-value
BA (2010)	0.114	0.069
BA (2018)	**0.193**	**0.01**
BA (2020)	**0.215**	**0.007**
pH	**0.500**	**0.001**
% Organic Matter	**0.448**	**0.001**
P	0.033	0.472
Al	**0.334**	**0.001**
Total N	0.028	0.536
Canopy Density (2018)	0.096	0.115
Canopy Density (2020)	0.007	0.844
Canopy Density (2010)	0.032	0.51
Transformed Aspect	**0.140**	**0.035**
% Slope	0.047	0.327
Average TSI	**0.147**	**0.03**

Quercus Competitive Status

Ostrya virginiana was the most common species competing with tagged *Quercus* seedlings, 46% of the time, while *Acer* species were the next most abundant competitor, 15% of the time. The average height ratio between the tagged *Quercus* seedlings and their competitors was 0.35, ranging from 0.03 to 1.0. Height ratios were significant among treatment levels ($F_{2,74} = 4.615$, $p = 0.012$), with shelterwood without midstory removal having lower mean *Quercus*-competitor height ratios compared to shelterwood with chemical midstory removal ($p < 0.05$). The median light class was light class 1 across all treatments, meaning one side of the seedling received sunlight. Light classes were not significantly different across treatments ($p > 0.05$). The probability of *Quercus* seedlings having a light class of 0 was higher than all other light classes with a probability of 42%. Light class 1 had the second-highest probability of occurring with a probability of 17%. The percent canopy of neighboring seedlings that fell within the projected 45-degree cone had an average midpoint of 30.5, ranging from 0.3 to 85.0% across all treatments. Differences were not detected among treatments for percent canopy cover within the 45-degree cone ($p > 0.05$), but there were some random effects in which the plot contributes to variation of the data.

2.4 Discussion

To achieve sufficient *Quercus* regeneration, land managers often combine silvicultural treatments with prescribed burns, with more productive sites typically requiring multiple burns and less productive sites requiring fewer. One of our study's objectives was to assess whether a shelterwood harvest at a less productive site, combined with midstory removals, would achieve competitive *Quercus* regeneration following a single prescribed burn. After a single burn, we generally observed greater survival and resprouting of *Quercus* seedlings compared to competing species (question 1). Shelterwood studies conducted on more productive sites (SI_{50} 23 m in studies vs. 17.6 m at Jeffries) have also observed lower mortality of *Quercus* seedlings compared to competitors following burning (Brose, 2010; Brose and Van Lear, 1998). Generally, *Quercus* species maintained higher survival rates with increasing burn intensity compared to competing species such as *Acer rubrum* and *Liriodendron tulipifera* (Brose, 2010; Brose and Van Lear, 1998). Although *L. tulipifera* was not a main competitor on our site, our results were similar to these studies observing greater *Quercus* seedlings survival post-burn than *Acer* spp. *and F. americana*, the main competitors on our site (Table 1). A meta-analysis conducted by Brose et al. (2013) also found *Quercus* seedlings resprouted at a higher rate than mesophytic species following burning, particularly when seedlings were released from competition. Studies of controlled basal heating or burning on seedlings also found higher resprouting rates in *Quercus* spp., particularly *Q. rubra*, compared to *Acer* spp. (Huddle and Pallardy, 1996; Keyser, 2019). Although *Q. rubra* has often displayed a greater resprout response than *Q alba* following basal heating, we found comparable resprouting rates among species.

Following the shelterwood and burn, *Quercus* seedlings doubled in density and were more abundant than most competitors. In particular, *Q. alba* was one of the most abundant species following the burn (Figure 8). Similar studies observed greater abundance of *Quercus* spp. seedlings compared to *A. rubrum* and *L. tulipifera* seedlings following a shelterwood and higher intensity spring burn (Brose, 2010; Brose et al., 1999b). Brose et al. (1999b) averaged 1,709 *Quercus* stems ha^{-1} for low-medium intensity, 2,385 stems ha^{-1} for medium-high intensity, and 4,160 stems ha^{-1} for their high intensity burns. Our burn, with an average temperature of 195º C

(77-315º C) measured at 30 cm, was most comparable to the low-medium intensity burn observed in Brose et al. (1999b) with temperatures 135-200º C measured at 1 m. Because Brose et al. (1999b) counted all stems originating from one root system as one individual and we counted each stem, we divided our *Quercus* densities by the average number of *Quercus* resprouts (2.8 resprouts per stem) to allow comparison to their densities. In comparison, densities of *Quercus* seedlings ≥ 0.3 m tall at Jeffries averaged 3,522 stems ha^{-1} which are more comparable to the higher intensity burn densities (4,160 stems ha^{-1}) seen in Brose et al. (1999b). Brose et al. (1999b) has shown that a single burn of relatively high intensity following a shelterwood cut can produce a *Quercus*-dominated stand, even on a more productive site. Our results suggest that on a less productive site, a single lower intensity burn following a shelterwood may be sufficient to promote *Quercus* dominance.

At Jeffries, species composition shifts from mesophytic species such as *A. rubrum* and *S. albidum* toward greater importance of *Quercus* spp. were observed in our NMDS (Figure 9d) on plots associated with lower soil productivity (higher Al, lower pH). These plots were influenced to a greater extent from the fire treatment (char height) compared to plots associated with greater soil productivity (greater N, organic matter, and pH) and mesophytic species such as *A. saccharum* and *F. americana*. These more productive plots shift in multiple directions indicating no clear compositional shift and suggesting the fire did not significantly drive these plots toward greater *Quercus* relative density. This is consistent with sites with lower productivity retaining more *Quercus* and shifting more readily away from mesophytic species with the application of fire (Burton et al., 2010; Hutchinson et al., 2005a; Iverson et al., 2008)

Our results found that a single burn following a shelterwood harvest produced *Quercus* seedlings that are more competitive on a more xeric site (question 3). The burn treatment shifted species composition in the regeneration layer toward greater importance of *Quercus* spp. and reduced the abundance of seedlings of competing species at Jeffries. Following the burn, *Quercus* seedlings had a competitive advantage because they had fewer competitors from other species, less impediment from taller neighboring seedlings, and increased *Quercus*-competitor height ratios. While seedlings were abundant at Jeffries, they were generally less than 0.9 m tall, regardless of species. Within the shorter height classes (1-3), *Quercus* spp. comprised an average of 34% compared to 23% for *F. americana*, 6% for *S. albidum*, and 4% for *Acer* spp. (data not shown).

Quercus spp. made up a large proportion of the regeneration layer and have greater or comparable relative abundance compared to competitors.

While our results suggest that *Quercus* seedlings at Jeffries are more competitive with those of other species, differences in metrics used to assess regeneration make comparison to field standards difficult. According to Sander et al. (1976), to achieve adequate *Quercus* regeneration 1,070 stems ha^{-1} (height > 1.37 m) are needed to attain a minimum of 30% BA *Quercus* in the future overstory in the Missouri Ozarks. According to the HNF silvicultural guidelines, approximately 988 competitive *Quercus-Carya* stems per ha are desired by the end of the fifth growing season post-treatment on lower quality sites. Competitive seedlings are defined as being 80% of the height of the nearest competitor. At this stage, we have over 3,500 *Quercus* stems ha^{-1} ($\geq$ 0.3 m) and they have comparable densities to their main competitors across height classes, but it is too soon to compare our results to these metrics. While we do not have sufficient height yet, our results are only two years post-burn and additional years of growth post-fire will likely produce a greater abundance of competitive *Quercus* stems.

Seedling survival, resprout response, and density were influenced by fire severity and the size of seedlings pre-burn. At Jeffries, we observed that taller char heights, associated with greater burn severity, were, in turn, associated with decreased survival odds, resprouting odds, number of resprouts, and seedling density across all species. Our NMDS ordination indicated that char height was associated with higher relative density of many *Quercus* spp., but lower relative density of mesophytic species, such as *Acer saccharum* and *A. rubrum*. We also found larger pre-burn basal diameter was associated with better odds of post-burn survival, greater number of resprouts, and greater resprout and seedling height at both sites. The high root:shoot ratios and buried bud banks resulting from hypogeal germination of *Quercus* spp. (Abrams, 1996; Brose et al., 2014; Brose and Van Lear, 2004; Johnson et al., 2019) likely provided a resprouting advantage after fire not offered by the epigeal germination of competing species (Honkala and Burns, 1990). Several studies also found a correlation between larger pre-burn basal diameter or height and increased survival, resprout density, and resprout height (Alexander et al., 2008; Dey and Hartman, 2005; Keyser, 2019).

Our study also found that edaphic and topographic variables influenced the survival, resprouting, and abundance of seedlings from all species. Typically, less acidic soils are more productive (Fernández and Hoeft, 2009), and should, therefore, have a positive effect on regeneration. We found higher concentrations of soil nutrients (N and P) at Jeffries were associated with greater survival odds, seedling abundance, and resprout height, while less acidic soil were associated with reduced survival odds, resprouting odds, and number of resprouts. The NMDS also found that more productive soils with greater N concentration, organic matter, and pH were associated with greater relative densities of competitors *F. americana*, *O. virginiana*, and *A. saccharum* (Figure 9a), similar to results found by Swaim et al. (2018). However, greater abundance of *Quercus* species seedlings is often associated with lower soil pH (Swaim et al., 2018) and greater soil Al concentration (Cronan et al., 1989; Kabrick et al., 2014). This was reflected in our NMDS ordination with higher relative densities of *Quercus* seedlings correlated with higher concentrations of Al and lower pH (Figure 9a). Taller seedlings were associated with higher concentrations of P at Sixty-six, similar to Jeffries. Contrary to Jeffries, lower seedling abundance was associated with greater P concentrations at Sixty-six and higher soil N levels was associated with shorter seedlings and decreased survival across all species. Additionally, Weigel and Peng (2002) observed greater stump sprouting probabilities of *Quercus* spp. with increasing site productivity (site index) initially following clearcutting, but after 10 years site index was negatively associated with the competitive status of members of the subgenus *Leucobalanus* (white oak group). This suggests that greater soil productivity may initially benefit the competitive status of *Quercus* spp., but with time this benefit decreases.

Topographic factors influenced the species composition and response to treatments at Jeffries as well. Steeper slopes were associated with increased survival and resprouting odds, while east-northeasterly sites displayed decreased survival and resprouting odds and lower seedling abundance. The greater abundance of *Quercus* seedlings we observed at Jeffries likely results from their ability to establish and persist on the drier conditions of southwest-facing slopes could influence these results (Johnson et al., 2019; Kabrick et al., 2014; Swaim et al., 2018). In addition, the xeric conditions of these aspects and steeper slopes are typically associated with greater burn severity (char height), which favor *Quercus* spp. due to their several fire adaptations. Even though we observed greater survival on steeper slopes, our ordination showed a negative correlation between *Quercus* seedling densities and percent slope. This is consistent with other studies that found higher *Quercus* densities on less-steep slopes and lower densities with steeper slopes (Johnson et al., 2019; Walters, 1990). However, percent slope on plots at Jeffries ranged from 0 to 9%. Although we saw a strong shift in species composition of the regeneration layer that was associated with silvicultural and fire treatments, seedlings were still influenced by site and other environmental variables. Because Jeffries is on the lower end of the productivity and moisture gradient associated with *Quercus* dominated forests in southern Indiana, the site was predisposed to favor *Quercus* spp. and disfavor the heavy establishment of mesophytic species. Therefore, less intense, and infrequent fire may be used to favor *Quercus* spp. on these sites, where site conditions may act as a filter to reduce the abundance and vigor of mesophytic competitors.

Generally, *Quercus* seedlings at Sixty-six displayed survival, height, and density responses comparable to most competitors following silvicultural treatments without the addition of fire (question 1). Although many *Quercus* spp. had greater survival over time compared to *Acer* spp. and *Sassafras albidum* (Table 5), survival was comparable for most species. *Quercus* spp. average seedling height was also comparable to most species, but *F. americana*, *Acer.* spp., and *O. virginiana* were typically taller than *Quercus* spp. While *Q. alba* is fairly abundant at Sixty-six, *F. americana* had greater average density and *A. rubrum* and *S. albidum* were comparable in density. In the shorter height classes (1-3), *Quercus* spp., on average, comprised 27% of seedlings, while *F. americana* comprised 21%, *Acer* spp. 11%, and *S. albidum* 15% (data not shown). *Quercus* spp. comprised 18% of seedlings in taller height classes (4-5), while *F americana* comprised 24%, *Acer* spp. 16%, and other canopy species 16% (data not shown). The comparable proportions of seedling densities between species, in addition to the lower *Quercus*-competitor height ratios, increased shading with stand development, and future impediment from neighboring stems suggests that *Quercus* seedlings received high levels of competition at this site. In a shelterwood study on a site of similar productivity to Sixty-six, competitors greatly outnumbered *Quercus* spp. and there was a large reduction in stocked *Quercus* 11 years post-harvest in the absence of fire (Brose, 2010). Numerous studies have shown *Quercus* spp. do not persist in developing stands after harvests on productive stands without subsequent burn treatments (Brose, 2010; Hilt, 1985; Jenkins and Parker, 1998; Swaim et al., 2016). Our results are similar to Brose et al. (1999b), which found that *Quercus* spp. in shelterwood harvests without prescribed burning had lower competitive status than harvests that were burned. Although *Quercus* seedlings on unburned sites were often taller than those on burned sites, competitors were also taller, occurred at greater densities, and were closer to *Quercus* seedlings (Brose et al., 1999b). Our results suggest that shelterwood harvests alone on more productive sites produce less competitive *Quercus* seedlings that will be unable to maintain dominance in developing stands. Literature suggests that burning, either a single higher intensity burn or multiple burns (Brose, 2014, 2010; Brose et al., 1999b), may be needed to favor *Quercus* on this site.

We observed reduced survival, taller seedling heights, and reduced densities in response to differences in midstory treatments. We expected seedlings within the shelterwood without midstory removal to have reduced survival, shorter heights, and lower densities due to increased shading compared to the other treatments (question 2a); however, this was often not the case at Jeffries. Seedlings had greater survival odds across all species without midstory removal compared to both midstory removal treatments at Jeffries. Seedling resprouts were taller without midstory removal and with mechanical removal compared to chemical removal at Jeffries. In addition, seedling density was higher in shelterwood without midstory removal compared to chemical midstory removal at Jeffries (Figure 7). Greater seedling survival and density with shelterwood without midstory removal compared to midstory removals could be attributed to greater shelter provided by the greater residual basal area (Appendix A, Table A.1). Across all species at Sixty-six, seedlings had greater survival odds without midstory removal than following chemical removal, which was supported by our model showing increased survival odds with increased BA. Following our prediction, seedlings were taller in chemical and mechanical removal treatments compared to no midstory removal at Sixty-six. Our results also displayed lower seedling densities with mechanical midstory removal and no midstory removal compared to chemical removal at Sixty-six, which could be explained by the higher midstory BA following mechanical and no midstory removal compared to chemical (Appendix A, Table A.2). Craig et al. (2014) found greater height, growth, and survival of *Quercus* spp. and *A. rubrum* seedlings in a *Quercus*-dominated forest (SI_{50} 19.8 – 21 m) with midstory removal treatments compared to those without, supporting our observation of taller seedlings with midstory removal at Sixty-six. A study in the Missouri Ozarks suggested that *Quercus* seedlings on more productive sites benefit more from the addition of midstory treatments, while overstory harvest alone is sufficient to promote *Quercus* seedlings on less productive sites (Schlesinger et al., 1993). On mesic sites, such as riparian forests, complete midstory removal increased survival and growth of *Quercus* seedlings versus sites with no midstory removal (Lhotka and Loewenstein, 2013, 2009) More research may be needed to determine the long-term effects of midstory removal on more xeric sites, but our results suggest that midstory treatments may be counterproductive on these less productive sites.

We had predicted that mechanical midstory treatments would result in greater sprouting and reduce *Quercus* growth and abundance (question 2b). Mechanical midstory treatments did not appear to cause more sprouting than chemical treatments, only 2% and 3% of midstory trees sprouted following chemical and mechanical treatments at Jeffries, respectively, and 7% and 12% resprouted with chemical and mechanical treatments, respectively, at Sixty-six (data not shown). The slightly taller and more abundant *Quercus alba* seedlings in chemical versus mechanical treatments (Figure 12, 13) could be attributed to the slightly greater sprouting with mechanical treatment at Sixty-six but many other variables influence the regeneration layer including soil, topography, and light availability (Johnson et al., 2019; Kabrick et al., 2014; Kimmins, 2004; Swaim et al., 2018).

Our results emphasize that shelterwood and midstory treatments alone on a more mesic site undergoing mesophication do not produce adequate stems of competitive *Quercus* species to perpetuate *Quercus*-dominated forests. Brose (2010) suggested that medium to high intensity fire following a shelterwood cut could improve the competitive status of *Quercus* for at least a decade on more productive sites, such as Sixty-six. However, more productive sites often benefit from multiple fires to suppress competition and release *Quercus* seedlings (Blankenship and Arthur, 2006; Green et al., 2010), especially when combined with a shelterwood cut. Repeated burning sets back fire-sensitive species while fire-adapted *Quercus* spp., with superior survival and resprouting post-fire (Abrams, 1996; Brose et al., 2014), can become more competitive and dominate the future overstory. Future management at Sixty-six may require multiple prescribed burns, following the initial burn to be conducted in the spring of 2022. Conversely, our study found a shelterwood treatment combined with a single burn on a less productive site had positive effects on *Quercus* regeneration. With the high survival and resprout response of *Quercus* to the fire, in addition to increased abundance, it appears that one burn may be sufficient to promote adequate regeneration on the Jeffries site. The greater tolerance of *Quercus* species to low moisture and nutrient availability (Cronan et al., 1989; Johnson et al., 2019; Kabrick et al., 2014) augments their ability to compete on less productive sites. We recommend that *Quercus* regeneration densities and competitive status be reevaluated in a few years to confirm sufficient densities of competitive seedlings remain to meet desired levels recommended by Sander et al. (1976) and the HNF silvicultural guidelines before final overstory removal at Jeffries.

Successfully regenerating and restoring *Quercus*-dominated forests can be both time-consuming and costly. However, if less productive sites can produce sufficient *Quercus* seedlings with one burn, it is more cost-effective for land managers to restore these less productive sites. While these sites may have lower economic value in terms of timber production, continuing to maintain their *Quercus* dominance is important as these stands provide vital ecological services across the Central Hardwoods Region. Over 70% of the HNF is *Quercus*-*Carya* forest, half of which is dominated by *Q. alba*, *Q. rubra*, and *Carya* spp. (Woodall et al., 2007). As such, the forests of HNF are representative of a large portion of the Central Hardwood Region (Johnson et al., 2019; Woodall et al., 2007). The wide spatial distribution of xeric *Quercus*-dominated forests offers a more efficient management option to maintain this ecologically valuable forest type across the Region.

CHAPTER 3. HERBACEOUS LAYER RESPONSE TO SHELTERWOOD AND BURN TREATMENTS IN A DRY *QUERCUS* FOREST

Quercus L. (oak) forests are undergoing a compositional shift to increased dominance of mesophytic species due to fire suppression and resulting effects of mesophication. While land managers often focus efforts on restoring *Quercus* regeneration, the herbaceous layer is also negatively impacted by the increased woody stem density in fire-suppressed forests. Initiated in 2010, our study on the Hoosier National Forest in Indiana evaluated the response of the herbaceous layer to shelterwood and midstory treatments on a less-productive burned site and a more-productive unburned site. Using ANOVA and NMDS ordination, we evaluated the richness, evenness, diversity, and herbaceous-layer cover changes post-treatment. Following a shelterwood and burn treatment, the less productive site had significantly increased richness, diversity, and total cover compared to pre-treatment. Cover increased across all plant functional groups, with trees/shrubs exhibiting the greatest increase. Herbaceous-layer composition at the burned site significantly shifted toward greater importance of graminoids and herbs post-treatment. Our more productive site had significant, but minor, increases in richness, evenness, diversity, and total cover following a shelterwood harvest without fire. Herbaceous-layer composition at the unburned site was significantly different following harvest treatments, shifting toward greater importance of vines, trees/shrubs, and herbs. Our results suggest that the addition of fire on the more productive site may be needed to improve the herbaceous-layer more noticeably than a shelterwood harvest alone. Conversely, the shelterwood and burn on the less productive site had a more substantial effect on the herbaceous-layer.

3.1 Introduction

Quercus L. (oak) forests in the eastern United States are valuable ecosystems that provide multiple ecological services including water filtration, nutrient cycling, carbon storage, and lumber production (Kimmins, 2004). Members of the genus *Quercus* are also a foundation species as they provide critical mast and diverse forest structure for multiple wildlife species (Dickson, 2004; Fralish, 2004; Hanberry and Nowacki, 2016). In addition to substantial ecological value, *Quercus* forests have great economic importance as they supply valuable timber in the United States (Brose et al., 2014). These critical ecosystems are prevalent throughout the eastern United States and the Central Hardwood Region, but were more abundant and dominant historically (Parker and Ruffner, 2004).

Historically, forests in the eastern United States were more open, and many of these open forests were dominated by *Quercus* species (Hanberry et al., 2020). Underneath a widely-spaced overstory, these forests displayed a dense and diverse herbaceous layer, and a limited midstory layer (Hanberry et al., 2020; Hanberry and Abrams, 2018). These open forests were maintained by periodic, low-intensity fire that created a high light environment, but also prevented a dense midstory from establishing (Hanberry et al., 2020). The many fire adaptations of *Quercus* spp., such as thick bark and compartmentalization of fire wounds, assisted in their ability to persist and survive periodic fires (Abrams, 1996; Brose et al., 2014). The dense herbaceous layer also provided fine fuels to sustain surface fires in this open-forest environment (Hanberry et al., 2020). The herbaceous layer is the most species-rich stratum in the eastern deciduous forest, where it provides habitat for a correspondingly rich diversity of insects, birds, and mammals (Fralish, 2004; Gilliam, 2007; Hanberry et al., 2020; Whigham, 2004).

In addition to its contribution to diversity and habitat, the herbaceous layer contributes to litter inputs and nutrient cycling within the forest (Gilliam, 2007). Although herbaceous plants comprise a small portion of aboveground biomass, their short-lived foliage provides high nutrient inputs that decompose more quickly than tree litter (Gilliam, 2007; Welch et al., 2007). Overstory foliage may contribute much greater biomass to annual litterfall compared to herbaceous litter, but the rapid decomposition, and high nutrient content of the herbaceous litter results in an outsized role in nutrient cycling per unit mass compared to the overstory (Welch et al., 2007). Herbaceous plants can also immobilize nutrients that would have otherwise been lost from the ecosystem, particularly nitrogen and potassium (Fralish, 2004; Peterson and Rolfe, 1982; Whigham, 2004).

Quercus-dominated forests have been heavily impacted by changes to the historic fire regime, particularly fire suppression that began in early-mid 1900s (Brose et al., 2001; Nowacki and Abrams, 2008). Without periodic fire to reduce midstory density, more-open *Quercus* forests became densely shaded and overstocked with succession and stand development (Brose et al., 2001; Hanberry et al., 2014c), a process referred to as “mesophication” (Alexander et al., 2021; Nowacki and Abrams, 2008). This process occurs when there is a compositional shift from xerophytic and pyrophilic species, such as *Quercus* species, to mesophytic species, such as *Acer* *rubrum* L. (red maple) and *A. saccharum* Marshall (sugar maple; Alexander et al., 2021; Brose et al., 2013; Nowacki and Abrams, 2008). This shift in dominance towards mesophytic species has been documented by multiple studies (Abrams and Downs, 1990; Aldrich et al., 2005; Fei et al., 2011; Hanberry, 2019; Palus et al., 2018), with mesic sites shifting more rapidly than xeric sites (Abrams, 1992; Olson et al., 2014). As mesophytic species become more dominant, dense shading results in greater moisture on the forest floor, which, in turn, results in less flammable fuels (Alexander et al., 2021; Nowacki and Abrams, 2008). A large body of research has focused on *Quercus* regeneration failure resulting from mesophication and lack of fire on the landscape (Dey, 2014; Lorimer, 1992; Nowacki and Abrams, 2008), however fewer studies have examined the effects of mesophication on the herbaceous layer (Davison and Forman, 1982; Fralish, 2004).

The increased shade of forests undergoing mesophication (Nowacki and Abrams, 2008) causes a compositional shift in the herbaceous layer (Hanberry and Abrams, 2018). The abundance and cover of shade-tolerant shrubs and vines generally increase, while the diversity, richness, and abundance of forbs and grasses generally decrease, including the loss of rare disturbance-dependent species (Davison and Forman, 1982; Fralish, 2004; Hanberry and Abrams, 2018). The decline in diversity and cover of the herbaceous layer with mesophication has indirect negative effects on other taxa, such as fungi, insects, birds, and mammals, that utilize forest understories as habitat (Fralish, 2004; Hanberry and Abrams, 2018). A loss in herbaceous-layer cover may also result in increased soil erosion and reduced litter and nutrient inputs, as well as increased nutrient loss from the system (Fralish, 2004; Gilliam, 2007).

Restoration efforts in *Quercus* forests have largely focused on restoring *Quercus* regeneration through harvesting and prescribed fire (Brose, 2010; Brose et al., 2013; Dey, 2014), but the herbaceous layer can also benefit from these treatments (Hanberry et al., 2018). The herbaceous-layer response to harvesting can vary depending on forest type, stand age, and harvest intensity (Gilliam, 2007). While some studies have not found significant changes in herbaceous species and cover following harvesting alone (Kinkead, 2013; Phillips et al., 2007), Zenner et al. (2006) found that increases in species richness and cover in the herbaceous layer corresponded with increasing opening size. Numerous studies have also found that harvesting generally increases woody species cover and density, particularly in harvests with larger openings, like clearcuts (Kinkead, 2013; Phillips et al., 2007; Zenner et al., 2006). In addition, several studies have shown increased herbaceous species diversity, richness, and abundance with burning or harvests combined with burning (Bowles et al., 2007; Burton et al., 2010; Holzmueller et al., 2009; Hutchinson et al., 2005b; Kinkead, 2013; Lettow et al., 2014; Phillips et al., 2007; Taft, 2003). Burning reduces litter depth and provides a short-term input of nutrients, which favors herbaceous plant germination (Hutchinson, 2005; Kinkead, 2013) while often reducing woody plant density, particularly shade-tolerant species (Bowles et al., 2007; Hutchinson et al., 2005). Most results indicated a more positive response of herbaceous-layer diversity and cover with combined harvesting and burning treatments versus burning or harvesting alone (Kinkead, 2013; Phillips et al., 2007), which suggests that the herbaceous layer benefits from increased sunlight, decreased litter depths, and reduced competition from woody species. To further increase light to the forest floor, midstory treatments are often implemented in conjunction with overstory removal, particularly on more productive sites (Loftis, 1990; Schlesinger et al., 1993).

Because the herbaceous layer is also negatively impacted by fire suppression and mesophication, when evaluating success of *Quercus* forest restoration, research should also examine the response of all species in the herbaceous layer, not just woody plants. Because the herbaceous layer contains the majority of the plant diversity in forests and plays a critical role in many ecosystem processes, monitoring its responses to restoration efforts is critical to restoring the entire forest ecosystem. We investigated the herbaceous-layer response to silvicultural and burn treatments that aimed to regenerate *Quercus* species in a *Quercus*-dominated forest. This study evaluated the response of the herbaceous layer to an overstory harvest and three midstory treatments at two sites: (1) a more xeric, less productive, site that was burned following harvesting and (2) a more productive, mesic site that was unburned. At both sites, mechanical cutting and herbicide application were implemented as midstory treatments and compared to a no treatment reference.

We evaluated percent cover by species, as well as the species richness, evenness, and diversity of the herbaceous layer before and after treatments. Research questions examined in this study were:

(1) How does the herbaceous layer respond to overstory and midstory treatments within two sites with similar overstory composition but different burn treatments and site productivity? We predicted that the less productive and burned site would have increased herbaceous percent cover, diversity, and richness due to increased light levels and reduced woody competition. We further predicted that the unburned site would have a

slight increase or no change in herbaceous cover and diversity, but increased woody cover without fire to reduce woody species density.

(2) Does the response of the herbaceous layer differ with midstory treatment (mechanical, herbicide, vs. none) between two sites with similar overstory compositions but different site productivity? We predicted mechanical and chemical treatments would exhibit greater herbaceous cover and diversity versus no midstory treatment due to greater light availability in treated midstories at both sites.

3.2 Methods

3.2.1 Study Sites

We conducted our study on the Hoosier National Forest (HNF), which spans nine counties in southern Indiana. The forest falls within the Central Hardwood Region of North America and the Crawford Upland Section of Indiana (Homoya et al., 1985; Parker and Ruffner, 2004; Van Kley et al., 1995). The dominant forest type of the Section is *Quercus-Carya*, with *Fagus-Acer* (beech-maple) forest also occurring (Homoya et al., 1985; Johnson et al., 2019; Parker and Ruffner, 2004). Drier sites are dominated by *Quercus* L. and *Carya* Nutt. (hickory) species, while *Quercus* species may be mixed with other hardwood species on more mesic sites (Johnson et al., 2019). Based on Forest Service records, the majority of stands on the HNF are between 80 – 120 years old (Parker and Ruffner, 2004). Across the Region, midstory composition has shifted to greater dominance of mesophytic species such as *Acer saccharum* and *Fagus grandifolia* Ehrh. (American beech) due to fire suppression (Parker and Ruffner, 2004). The soils of the HNF are mainly sandstone derived, with a few shale or limestone outcrops, and are largely comprised of silt loams or fine sandy loams and occasionally silty clay loams (Van Kley et al., 1995).

Our plots on the HNF are within two study sites, Jeffries and Sixty-six (Figure 1, Chapter 2), located approximately 35 km northeast of Tell City, Indiana. Both sites reside in the northeast corner of Perry County approximately 5 km north of the Ohio River and the Indiana-Kentucky state line. *Quercus alba* L. (white oak) and *Quercus stellata* Wangenh. (post oak) dominate the dry slopes while *F. grandifolia* and *Acer saccharum* are more abundant on mesic slopes and ridges. There are eight units at each site subjected to different combinations of silvicultural treatments.

The total study area at Jeffries is 28.9 ha and 26.4 ha at Sixty-six. Sixty-six is a more productive site with a site index$_{50}$ (SI_{50}) of 24.4 m for *Q. alba*, while Jeffries is less productive with an average SI_{50} of 17.6 m for *Q. alba* (Carmean, 1972; Thornton, n.d.).

3.2.2 Experimental Treatments

Overstory Treatments

Both Jeffries and Sixty-six received alternating overstory treatments; four initial shelterwood cuts and four commercial thinning units per site. The shelterwood treatments generally followed the shelterwood-burn method described by Brose et al. (1999a) with an initial cut that preferentially removed competing species such as *A. saccharum*, *Liriodendron tulipifera* L. (yellow-poplar), and *F. grandifolia*, as well as poor-quality trees, while leaving mainly dominant and codominant *Quercus* and *Carya* trees in the overstory (Thornton, n.d.). At Jeffries, the shelterwood units had a total treatment area of 13.7 ha, ranging in size from 2.8 to 4.1 ha, and the basal area was reduced from an average of 23.9 to 11.0 $m^2 ha^{-1}$ (Appendix A, Table A.1). The four shelterwood units at Sixty-six had a total treatment area of 15.7 ha, ranging in size from 3.7 to 4.1 ha and basal area was reduced from an average of 27.8 to 14.1 $m^2 ha^{-1}$ (Appendix A, Table A.2).

The remaining four units at Jeffries underwent a commercial thinning, which reduced the basal area from an average of 25.3 to 13.6 $m^2 ha^{-1}$ (Appendix A, Table A.1) in units that ranged from 2.2 to 8.1 ha with a total treatment area of 15.2 ha. At Sixty-six, the thinning units ranged in size from 1.9 to 3.1 ha with a total area of 10.7 ha; the basal area was reduced from an average of 25.1 to 15.5 $m^2 ha^{-1}$ (Appendix A, Table A.2). All overstory harvests at Jeffries were conducted between May 2012 and October 2015, while Sixty-six harvests were completed between November 2011 and October 2012. Each site included unharvested reference areas outside of the eight harvest units. Because we found no statistical differences (t-test, $p > 0.05$) in basal areas between shelterwood and thinning treatments, overstory harvests at both sites were pooled and hereafter referred to as initial shelterwood cuts.

Midstory Treatments

At both sites, the shelterwood units received non-commercial (midstory) treatments of non-*Quercus* species in conjunction with the overstory removal (Appendix A, Tables A.1, A.2). Two units received a mechanical treatment in which all non-merchantable stems > 2.54 cm diameter at breast height (DBH) were cut with chainsaws without herbicide treatment and the other two units received herbicide treatment of stems > 2.54 cm and up to 17.8 cm DBH. The cut stump or girdled midstory trees were treated with Pathway herbicide (10.2% picloram + 39.6% 2,4-D) or a comparable mixture diluted to 50% using a chainsaw and chemical spray bottle. Midstory treatments were completed in the spring of 2015 at Jeffries and spring of 2013 at Sixty-six by contractors (Turman Creek Tree Farms, 2013). Thinned units did not receive a midstory treatment at either site.

Prescribed Burn

Continuing to follow the shelterwood-burn method (Brose et al., 1999a), the USDA Forest Service conducted a prescribed burn using aerial ignition and drip torches at Jeffries on April 16, 2019 (Figure 2a, Chapter 2). The fire was applied 4-5 years after the original harvests and burned a total of 301 ha, including the study site. The fire burned with air temperatures between 23.3-29.4 ºC, relative humidity at 28-35%, and winds ranging 3-11 km hr^{-1} with gusts up to 14 km hr^{-1} (Harriss, 2019). Flame lengths ranged 25.4-35.6 cm, flame heights ranged 12.7-20.3 cm, and rate of spread ranged 10.1-40.2 m hr^{-1} with a head fire flame height of 61.0-91.4 cm and flame length of 1.2 m (Harriss, 2019).

3.2.3 Plot Design

In 2010, three permanent 0.047 ha plots were established in each unit across all treatments and in each reference area for a total of 54 plots across both study sites. The plots were randomly stratified across a topographic gradient and were positioned at least one tree height from stand borders to ensure a buffer from edge effects. Each sample plot (Figure 3, Chapter 2) consisted of a single 0.047 ha overstory plot (12.6 m radius), a single 0.016 ha concentric midstory subplot (8 m radius), a single 40.5 m^2 regeneration subplot (3.6 m radius; 6 m from plot center at 45º), twelve 1-m^2 circular vegetation quadrats (along 12 m transects at 3, 6, 9, and 12 m from main plot center at 135, 225, and 315º), and four fuel transects (12.6 m in length; oriented from the overstory plot center at 0, 90, 180, and 270º). In 2010, all overstory and midstory trees within their corresponding plots were tagged.

3.2.4 Field Measurements

Pretreatment data were collected for the overstory and herbaceous-layer before treatments in 2010 and 2011. Site data were also collected and included percent slope, aspect, and terrain shape index (TSI). TSI is the measured slope gradient from plot center to plot boundary in 45º increments, with 8 measurements total (McNab, 1989). Data were also collected during and after treatments in the years 2012, 2013, 2014, 2015, and 2018.

Fire Effects

At the Jeffries site, we measured fire temperatures during the April 2019 burn and char heights directly after to quantify fire intensity and severity. Aluminum tags with dots of heat activated paint were placed at five points within each plot at ground level (~ 0 cm) and approximately 30.5 cm off the ground (see Chapter 2). To measure temperature fluctuations during the burn, we buried a HOBO Temp datalogger approximately 10 cm deep at each plot center before the burn. Char height, the maximum height of the bark burned from the fire (cm), was measured on trees of varying species and DBH on each Jeffries overstory plot after the burn, ranging from 9 to 21 trees per plot (Figure 2b, Chapter 2).

Maximum fire temperatures from paint tags ranged from below 79.4 ºC to above 661.1 ºC with average temperatures ranging from 248.9 to 426.7 ºC. at ground level (~ 0 cm). Temperatures ranged from below 79.4 ºC to greater than 426.7 ºC with average temperatures ranging from 76.7 to 315.6 ºC at 30.5 cm height. Mean char heights averaged 37.2 cm, ranging from 7.6 to 93.9 cm. Paint tag temperatures and char heights did not significantly differ across treatment areas (ANOVA, $p > 0.05$). Due to the length of time the HOBO devices were in the ground, many of them did not collect consistent data. However, we had at least one working HOBO device from each treatment unit, except unit 8. The maximum temperatures recorded ranged from 84 to 546.9 ºC with an average of 206.7 ºC (see Chapter 2).

Overstory and Midstory

In 2020, we measured DBH and status (alive/dead) of all tagged overstory (≥ 11.4 cm DBH) and midstory (≥ 3.81 cm DBH) trees, as well as ingrowth trees (trees that grew into a larger size class) within the overstory and midstory plots (see Chapter 2). In the summer of 2021, the survival status of tagged overstory and midstory trees was reassessed at the Jeffries site. All measurements were to the nearest 0.254 cm. We used a concave, spherical densiometer to estimate canopy cover within the 40.5 m^2 regeneration subplot 3.6 m from the center at each cardinal direction (0º, 90º, 180º, 270º).

Herbaceous Layer

We sampled herbaceous-layer vegetation cover (all vascular plants within 1 m height) during the months of June and July of 2020 within twelve 1-m^2 circular quadrats along three transects within the 0.047 ha plot (Figure 2, Chapter 2). We estimated percent cover of herbaceous and woody vegetation by species in the following cover classes: < 1, 1, 2-5, 6-10, 11-25, 26-50, 51-75, 76-100. All plants were identified to species or genus level. Many grasses were grouped into Poaceae (grass family) due to difficulty of identification, while all *Carex* L. species (sedges) were grouped by genus.

Fuels

Following the methods of Brown (1974) and Brown et al. (1982), we measured dead and down woody material along four 12.6 m transects extending from the center of each 0.047 ha overstory plot (Figure 3, Chapter 2) in the summer of 2020. Using a go-no-go fuel gauge, we tallied fine woody debris (FWD); 1-hour (< 0.6 cm) and 10-hour (0.6–2.53 cm) fuels along 1.3 m, then 100-hour (2.54-7.6 cm) fuels along 3.5 m. Coarse woody debris (CWD) or 1,000-hour fuels (> 7.6 cm) were measured for diameter at point of intersection to nearest 0.1 cm, species if possible, decay class (1-5, Lutes et al., 2006) and position (on ground vs. above ground) along the entire transect of 12.6 m. Along each of the fuel transects at points 3.1, 6.1, and 9.1 m (total of 12 measurements for each per plot), we also measured the depth of the litter and duff layers to the nearest 0.254 cm. At the same points (3.1, 6.1, and 9.1 m), the percent cover of leaf litter, duff, and bare ground was visually estimated within a 0.5 m^2 (70.6 x 70.6 cm) frame, totaling 12 measurements per overstory plot.

Soil

Along each fuel transect 5 m from the 0.047 ha plot center, we collected surface mineral soil down to 10 cm using a trowel, combining the four subsamples to create a composite sample for each plot. Samples were sealed in plastic bags and stored in a freezer until they were shipped to Brookside Labs in New Bremen, OH for chemical analysis. Brookside Labs analyzed P (ppm) and Al (mg kg^{-1}) using Mehlich III extraction (Mehlich, 1984), pH_{water}, total exchange capacity (meq 100 g^{-1}), percent organic matter, Bray II P (mg kg^{-1}), NO_3 (ppm), and NH_4 (ppm; Bray and Kurtz, 1945; Dahnke and Johnson, 1990; McLean, 1982; Ross and Ketterings, 1995; Schulte and Hopkins, 1996). Soil NO_3 and NH_4 were summed for total soil N.

3.2.5 Data Preparation

Summary statistics calculated for each plot included average fire temperature by height (0 or 30.5 cm; ⁰C), average char height (cm), total live basal area (BA, m^2 ha^{-1}), average percent canopy density, average CWD volume (m^3 ha^{-1}), and average FWD volume (m^3 ha^{-1}). Total live BA was calculated per plot from DBH measurements of tagged overstory, midstory, and ingrowth trees in the plot. We calculated percent canopy density from canopy cover using the equation: 100 - (#dots * 1.04; Lemmon, 1957). We calculated an average CWD volume from collected CWD fuel measurements and the FWD volume was calculated for each fine fuel class, then totaled together and averaged per plot (Harmon and Sexton, 1996). For analyses investing post-burn effects, the average change in litter and duff depth from 2018 to 2020 was calculated. Aspect was transformed to a linear scale ranging from 0 to 2, with a 0 value facing southwest and 2.0 facing northeast, using the equation: transformed aspect = cos(45 - aspect) + 1 (Beers et al., 1966).

The herbaceous layer was grouped into four functional groups: non-graminoid herbs, hereafter herbs, (forbs, ferns, and herbaceous vines), graminoids, woody vines, and trees/shrubs. At Jeffries, common herbs included *Cunila origanoides* (L.) Britton (common dittany), *Galium circaezans* Michx. (licorice bedstraw), and *Helianthus divaricatus* L. (woodland sunflower). Common herbs at Sixty-six included *Galium circaezans*, *Sanicula* L. spp. (black snakeroot), and *Aristolochia serpentaria* L. (Virginia snakeroot). Common graminoids at Jeffries and Sixty-six included *Carex* spp, *Dichanthelium* (Hitchc. & Chase) Gould spp. (panic grass), and Poaceae (grasses). Common trees/shrubs at both sites are *Fraxinus americana* L. (white ash), *Carya* spp., *Quercus alba*, and

Ostrya virginiana (Mill.) K. Koch (ironwood). Common vines at both sites include *Smilax rotundifolia* L. (roundleaf greenbrier), *Toxicodendron radicans* (L.) Kuntze (eastern poison ivy), and *Parthenocissus quinquefolia* (L.) Planch (Virginia creeper). Nomenclature follows the USDA PLANTS Database (USDA, NRCS, 2022).

Summary statistics calculated for each plot included average percent cover of herbaceous-layer species (including both herbaceous and woody species), average total percent cover of herbaceous-layer plants, average cover and relative cover by plant functional group, and average species richness, Shannon diversity, and evenness/equitability (McCune and Grace, 2002). We calculated relative cover as a ratio of the sum cover of each functional group divided by the total cover of all functional groups in each quadrat. Shannon diversity index uses the equation: $H' = -\sum_i^S p_i \log p_i$, such that p_i is the proportion of individuals made up of species *i* and S is the number of species or species richness (McCune and Grace, 2002). Evenness or the Shannon equitability index uses the equation: $J = \frac{H\prime}{\log S}$, such that H' is the diversity and S is species richness (McCune and Grace, 2002). Prior to data analysis, log-transformations were performed on highly skewed data to improve normality. We also standardized some explanatory variables by dividing by the standard deviation to minimize differences between variable ranges.

3.2.6 Statistical Analysis

Due to the small number of reference plots available, they were removed prior to data analysis. Using R (R Core Team, 2020), we fit linear models for each response variable: total herbaceous-layer cover, average richness, average diversity, average evenness, and average cover and average relative cover by plant functional groups. Explanatory variables used for the total cover models included total live BA, average canopy density, fire effects (mean char height, average maximum fire temperature), soil chemical characteristics (pH, total N, P, Al), percent slope, transformed aspect, average FWD and CWD volumes, litter and duff depths, functional group, treatment, and year. Total cover models were produced with a backward stepwise algorithm and chosen based on the lowest AIC. All other models for Jeffries, tested fire effects as explanatory variables and were removed if insignificant. Explanatory variables used in remaining models included year, treatment, and plant functional group when applicable. Analysis of variance (ANOVA) tests were used to determine significant explanatory variables. For post-hoc analysis, Tukey multiple pairs comparison tests were run on significant main effects for all models. If data did not meet normality and equal variance assumptions, a Kruskal-Wallis non-parametric test and Dunn's post-hoc test were used instead. All models were tested for goodness-of-fit before interpretation. Models were tested with the treatment unit, plot, and year as random effects, but there were either no or very little random effects and they were removed from the models. All models were tested for interaction effects and additive models were used as the interactions either did not add much explanatory power or they were insignificant. For all tests, alpha = 0.05.

Using average cover (midpoint) of herbaceous species we ran non-metric multidimensional scaling (NMDS) ordination with the vegan package (Oksanen et al., 2019) using the Bray-Curtis dissimilarity matrix to examine compositional shifts in the herbaceous-layer between the years 2011 and 2020 at both sites. To reduce noise, species that only occurred once between both years were excluded from the analysis. The data were also arcsine square root transformed, as recommended by McCune and Grace (2002) prior to ordination. A maximum of 50 iterations were allowed. The number of axes was determined by stress and a scree plot (McCune and Grace, 2002), with the intention of having stress well below 0.2 (Kruskal, 1964). The envfit function (999 permutations) was used to fit environmental vectors onto the ordination and calculated correlation coefficients for the environmental variables (Tables 7, 8) in relation to the ordination. Only environmental variables with p-values < 0.05 were displayed on the graphs.

We also ran a Permutational Multivariate Analysis of Variance (PERMANOVA, 999 permutations) using the adonis function (Anderson, 2001) to test whether the centroid or dispersion of year or treatment groups are different within the ordination. We tested the homogeneity of dispersion of the groups (functions: betadisper, anova, permutest) before reporting final PERMANOVA results. We also conducted an Indicator Species Analysis (De Cáceres et al., 2010; Dufrene and Legendre, 1997) using the indicspecies package (De Cáceres and Legendre, 2009) to detect significant indicator species for treatments and years using the same arcsine transformed cover data used in the NMDS. For all tests, alpha = 0.05.

3.3 Results

3.3.1 Jeffries Site

Species Composition

At Jeffries, across both years we identified a total of 157 herbaceous-layer species with an additional 47 taxa identified to genus and three to family, hereafter referred to as “species”. In 2011 (pre-burn), 101 species were identified, with over 90% of them being native. Across all species, the species with the highest average cover were O*strya virginiana*, *Smilax rotundifolia*, *Sassafras albidum* (Nutt.) Nees (sassafras), *Toxicodendron radicans, Fraxinus americana,* and *Quercus alba.* The herbaceous species with the highest cover included *Verbesina helianthoides* Michx. (gravelweed), *Helianthus divaricatus*, and *Cunila origanoides*. The graminoids with the highest cover included *Carex* spp., *Dichanthelium boscii* (Poir.) Gould & C.A. Clark (Bosc’s panicgrass), and *Elymus hystrix* L. (eastern bottlebrush grass). The trees/shrubs with the highest cover included *O. virginiana, S. albidum,* and *F. americana*. Vines with the highest cover included *S. rotundifolia*, *T. radicans*, and *Parthenocissus quinquefolia.* The most common species, those that occur most often on plots, were *Carex* spp., *Carya* spp., *F. americana, S. rotundifolia, O. virginiana*, and *Q. alba*.

In 2020 (post-burn), 173 species were identified, with over 80% of them being native species. Across all species, the species with the highest average cover were *Rubus allegheniensis* Porter (Allegheny blackberry), *T. radicans*, *Cercis canadensis* L. (eastern redbud), and *F. americana*. The herbaceous species with the highest cover included *Lespedeza violacea* (L.) Pers. (violet lespedeza), *Ageratina altissima* (L.) R.M. King & H. Rob. (white snakeroot), and *Helianthus microcephalus* Torr. & A. Gray (small woodland sunflower). The species with the highest cover in the graminoid group included S*cleria oligantha* Michx. (littlehead nutrush), *Carex* spp. and *Dichanthelium boscii*. Trees/shrubs with the highest cover included *Rubus allegheniensis*, *C. canadensis*, and *O. virginiana*. Vines with the highest cover included *T. radicans*, *S. rotundifolia*, and *P. quinquefolia*. The most common species in 2020 included *Carex* spp., *R. allegheniensis, Eupatorium serotinum* Michx. (late boneset), *T. radicans, Dichanthelium boscii*, *F. americana*, and *S. rotundifolia*. Common non-native species included *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass) and *Lonicera japonica* Thunb. (Japanese honeysuckle). The fire-dependent species *Schizachyrium scoparium* (Michx.) Nash (little bluestem) was present in 2020, but not in 2011; however, it was identified in 2015 (pre-burn) but at a much lower frequency.

Species Richness, Evenness, and Diversity

Average species richness before treatments in 2011 was 7.1 (ranging 3.8-14.5), then increased to 11.6 (ranging 8.8-15.2) in 2020 (Figure 15a). Average species evenness was 0.35 (0.15-0.51) in 2011 and increased to 0.52 (0.44-0.58) in 2020 (Figure 15b). Average Shannon diversity index was 0.68 (0.23-1.19) in 2011 then almost doubled to 1.27 (1.07-1.58) in 2020 following treatments (Figure 15c). Species richness ($F_{1,44}$ = 48.6), evenness ($F_{1,44}$ = 71.5), and diversity ($F_{1,44}$ = 95.9) all had significantly greater values in 2020 compared to 2011 ($p < 0.001$). Richness, evenness, and diversity did not significantly differ between midstory treatments ($p < 0.05$).

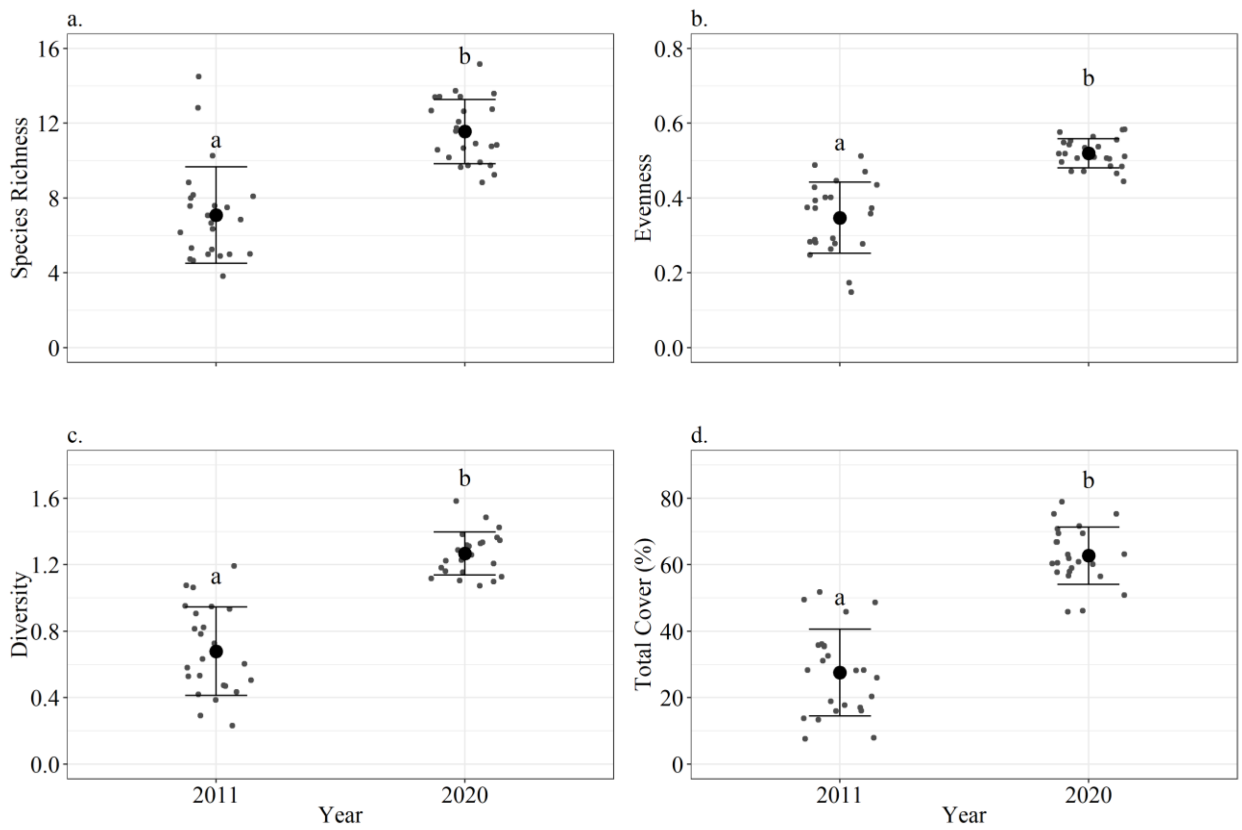


Figure 15. Herbaceous-layer **(a.)** species richness (mean ± SD), **(b.)** evenness (mean ± SD), **(c.)** diversity (mean ± SD), and **(d.).** percent total cover (mean ± SD) at Jeffries in 2011 (pre-treatment) and 2020 (post-treatment). Superscripts denote significant differences between years based on post-hoc Tukey tests (α = 0.05).

Total Herbaceous-layer Cover

Total herbaceous-layer cover averaged 27.6% (ranging 7.6-51.7%) in 2011 then more than doubled to 62.7% (ranging 45.9-78.9%) in 2020 (Figure 15d). Average total herbaceous-layer cover was significantly affected by year, average canopy density (2020, standardized), and average total FWD volume (2018) ($p < 0.05$). An increase in one standard deviation in canopy density (SD = 1) resulted in a significant increase in total cover ($p < 0.05$). An increase in FWD significantly decreased total cover ($p < 0.01$). The total average cover in 2020 was significantly greater than in 2011 ($p < 0.001$). There were no significant differences between midstory treatments ($p > 0.05$).

Cover by Plant Functional Group

At Jeffries average cover by functional group in 2011 was 2.7% for herbs, 2.0% for graminoids, 18.5% for trees/shrubs, and 7.2% for woody vines. Average cover increased in 2020 for all groups to 9.3% for herbs, 7.5% for graminoids, 35.9% for trees/shrubs, and 12.1% for woody vines (Figure 16). Cover was significantly different between functional groups ($F_{3,185} = 83.9$, $p < 0.001$), with trees/shrubs and woody vines having significantly greater cover than herbs and graminoids ($p < 0.001$). Woody vines had significantly lower cover than trees/shrubs ($p < 0.001$). Average cover by functional group was significantly different post-treatment ($F_{1,185} = 96.2$, $p < 0.001$), with 2020 having significantly greater cover than 2011 ($p < 0.001$). No difference was found between midstory treatments ($p > 0.05$).

The average relative cover by functional group in 2011 was 12.5% for herbs, 11.7% for graminoids, 62.5% for trees/shrubs, and 29.1% for woody vines (Figure 17a). In 2020, the average relative cover increased to 15.8% for herbs and 13.4% for graminoids and decreased to 55.3% for trees/shrubs and 19.0% for woody vines (Figure 17b). There was no statistical difference between pre- and post-treatment relative cover and no difference between midstory treatments ($p > 0.05$). Significant differences were found between functional groups ($F_{3,185} = 84.3$, $p < 0.001$), with Tukey post-hoc tests indicating that trees/shrubs and woody vines had greater relative cover than herbs and graminoids ($p < 0.001$). Woody vines had significantly lower relative cover compared to trees/shrubs ($p < 0.001$). No significant differences were detected between herb and graminoid relative cover ($p > 0.05$).

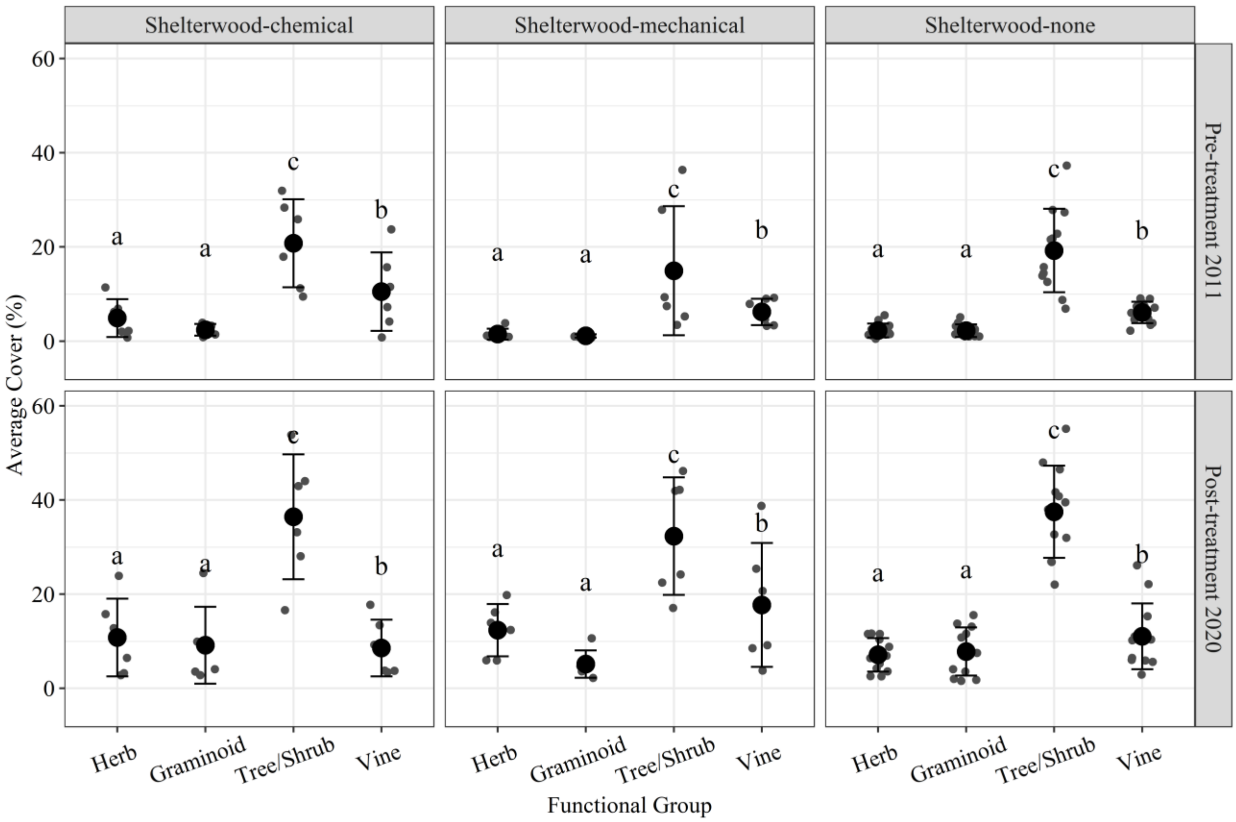


Figure 16. Mean percent cover (± SD) of plant functional groups by treatment in 2011 and 2020 at Jeffries. Superscripts denote significant differences between functional groups according to a post-hoc Tukey test (α = 0.05). Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

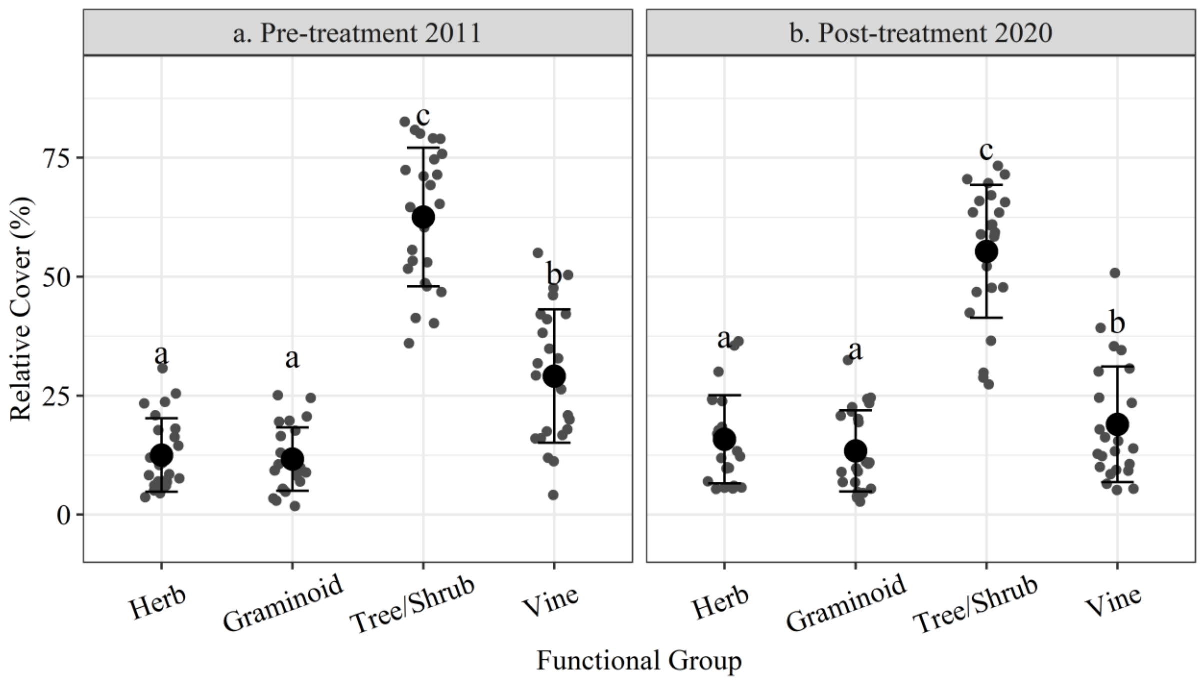


Figure 17. Relative percent cover (mean ± SD) of plant functional groups in **(a.)** 2011 and **(b.)** 2020 at Jeffries. Superscripts denote significant differences between functional groups according to a post-hoc Tukey test (α = 0.05).

NMDS Ordination

The NMDS of the herbaceous-layer species composition resulted in a solution with two dimensions and stress of 0.159 after 20 runs (linear $R^2 = 0.869$). Environmental and stand factors that were significantly correlated with the ordination were pH, soil organic matter, Al concentration, total N, and average canopy density in 2020 ($p < 0.05$), with pH ($R^2 = 0.56$, $p = 0.001$) and Al ($R^2 = 0.57$, $p = 0.001$) exhibiting the strongest correlations (Figure 18a, Table 7). Axis 2 was strongly associated with Al, canopy density, pH, organic matter, and total N (Figure 18a), however, no variables displayed a strong association with axis 1. The abundance of *Quercus* species was strongly associated with plots with higher Al concentrations (Figure 18a). Species such as *T radicans*, *C. canadensis*, *Lespedeza violacea*, and *Sanicula* spp. were associated with plots that had more productive soils and had higher canopy density (Figure 18a). There was clear grouping and separation of years 2011 and 2020 (Figure 18b), with 2011 associated with greater cover of *S. albidum*, *F. americana*, *S. rotundifolia*, *Desmodium* Desv. spp. (ticktrefoil), *Fagus grandifolia*, and *Frasera caroliniensis* Walter (American columbo). The year 2020 was associated with greater cover of Poaceae (grasses), *Carex* spp, *Rubus allegheniensis*, *Aralia spinosa* L. (devil's walkingstick), *Lespedeza* Michx. spp. (lespedeza), *Microstegium vimineum*, and *Dichanthelium* spp. There was a high degree of overlap among treatments with no clear differentiation in ordination space (Figure 18c). Between 2011 and 2020, all plots experienced a compositional shift along axis 1, moving toward greater species richness and greater importance of grasses, sedges, and herbs (Figure 18d). This shift along axis 1 was not associated with any fire or fuel variables. The PERMANOVA revealed no significant differences between midstory treatments, but it did detect a significant difference between the years 2011 and 2020 ($p < 0.05$).

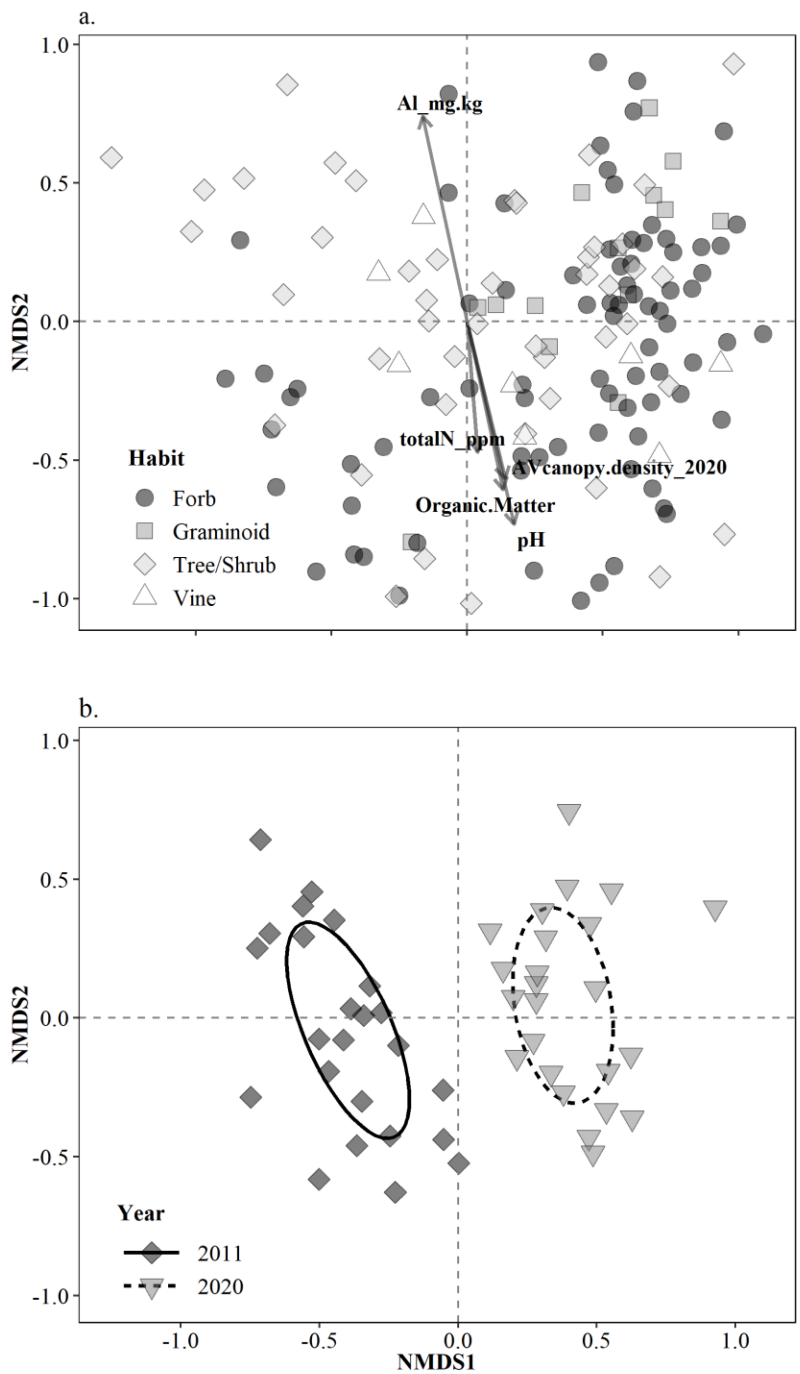


Figure 18. NMDS ordination of herbaceous-layer species composition at Jeffries in 2011 and 2020: **(a.)** Biplot of herbaceous species by plant habit with significant ($p < 0.05$) environmental factors Al_mg.kg (soil Al), Organic.Matter (percent soil organic matter), totalN_ppm (total soil N), pH (soil pH), and AVcanopy.density_2020 (average canopy density in 2020) as vector arrows; **(b.)** Biplot of herbaceous plots grouped by years 2011 and 2020; **(c.)** Biplot of herbaceous plots grouped by silvicultural treatments shelter_chem (shelterwood with chemical midstory removal), shelter_mech (shelterwood with mechanical midstory removal), and shelter_none (shelterwood without midstory removal); **(d.)** Successional vector changes in herbaceous composition between 2011 and 2020. Species list found in Appendix B, Table B.5.

Figure 18 continued

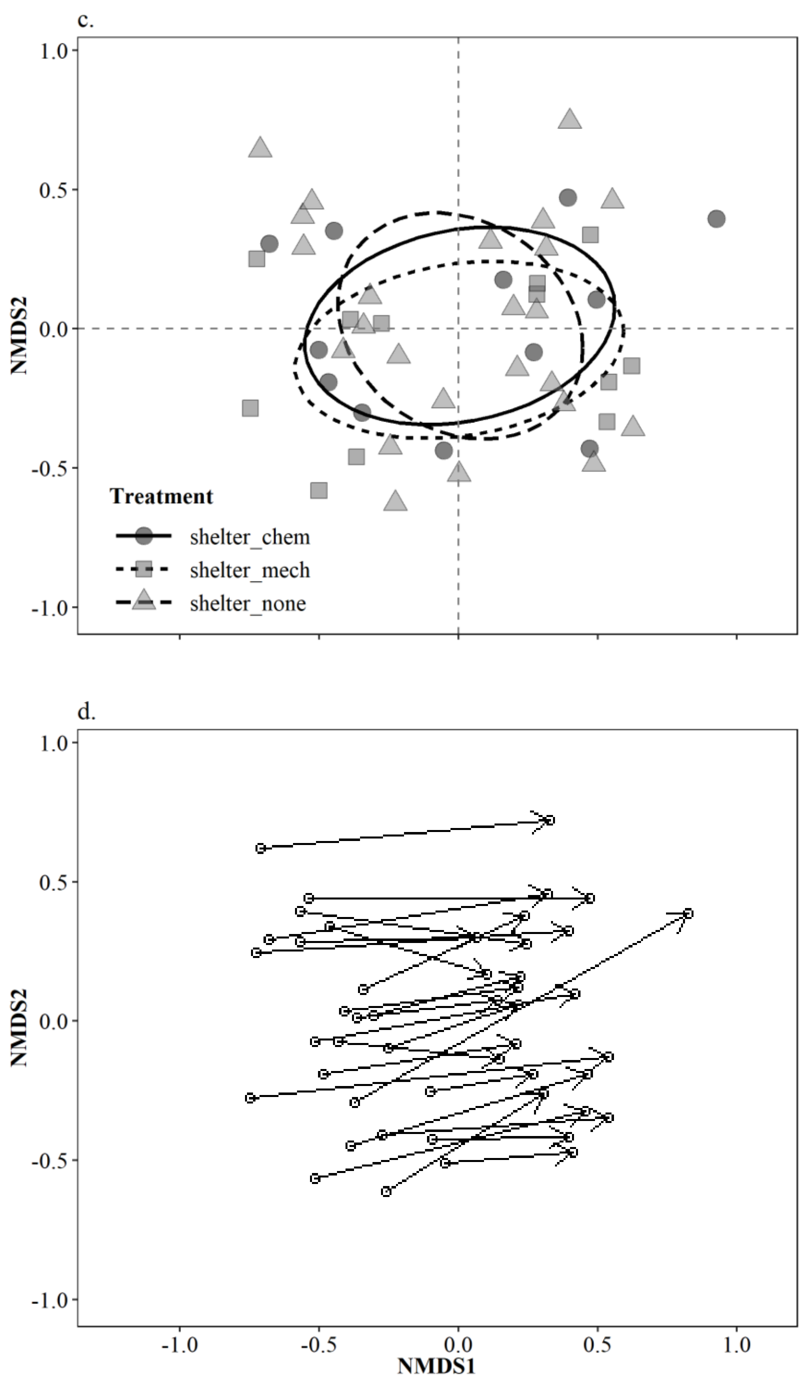


Table 7. Correlation coefficients and p-values (bold: $p < 0.05$) for environmental variables in NMDS ordination of Jeffries herbaceous composition.

Environmental Variable	R^2	**P-value**
BA (2010)	0.063	0.218
BA (2018)	0.118	0.076
BA (2020)	0.098	0.121
High Mean Temp (30.5 cm)	0.020	0.625
Low Mean Temp (0 cm)	0.003	0.932
Mean Char Height	0.116	0.065
pH	**0.563**	**0.001**
% Organic Matter	**0.383**	**0.001**
P	0.033	0.478
Al	**0.573**	**0.001**
Total N	**0.224**	**0.002**
Canopy Density (2018)	0.030	0.514
Canopy Density (2020)	**0.339**	**0.001**
Canopy Density (2010)	0.033	0.462
CWD (2018)	0.083	0.136
CWD (2020)	0.072	0.184
FWD (2018)	0.045	0.372
FWD (2020)	0.018	0.673
Litter Depth (2018)	0.003	0.931
Duff Depth (2018)	0.026	0.556
Litter Depth (2020)	0.019	0.654
Duff Depth (2020)	0.034	0.476
Litter Change (2018-2020)	0.022	0.624
Duff Change (2018-2020)	0.016	0.72
Transformed Aspect	0.097	0.103
% Slope	0.080	0.158
Average TSI	0.011	0.778

Indicator Species Analysis

Indicator species for chemical treatments were *Symphyotrichum undulatum* (L.) G.L. Nesom (wavyleaf aster), *Verbesina* L. spp. (crownbeard), *Quercus velutina* Lam. (black oak), *Quercus stellata*, and *Solidago* L. spp. (goldenrod), for mechanical treatments were *Ageratina altissima* and *Liriodendron tulipifera*, and for no midstory removal *Prenanthes altissima* L. (tall rattlesnakeroot; $p < 0.05$; Appendix B, Table B.1). Indicators of both chemical removal and no midstory removal was *Carex* spp. while *T. radicans* was an indicator species of both mechanical and no midstory removal ($p < 0.05$). There were 11 indicator species in 2011 with the strongest associations with *Polygonatum biflorum* (Walter) Elliott (smooth Solomon's seal), *Vaccinium stamineum* L. (deerberry), and *Desmodium nudiflorum* (L.) DC. (nakedflower ticktrefoil; $p < 0.05$; Appendix B, Table B.2). In 2020 there were 51 indicator species, with the strongest associations with *Rubus allegheniensis*, *Lobelia* L. spp. (lobelia), and *Eupatorium serotinum*, but also included the invasive species *Microstegium vimineum* ($p < 0.05$, Appendix B, Table B.2).

3.3.2 Sixty-six Site

Species Composition

At Sixty-six, a total of 138 herbaceous-layer species were identified between both years, with an additional 34 taxa identified to genus and one to family, hereafter "species." In 2011, 94 species were identified, with over 90% of them being native. Across all species, those with the highest average cover were *F. americana*, *T. radicans*, *O. virginiana*, *Quercus coccinea* Münchh. (scarlet oak), and *S. albidum*. Species with the greatest cover within herbs were *Amphicarpaea bracteata* (L.) Fernald (American hogpeanut), *Verbesina helianthoides*, and *Helianthus divaricatus*. Graminoids with the highest cover included *Carex* spp., *Dichanthelium boscii*, and *Elymus* L. spp. (wildrye). Trees/shrubs with the greatest cover were *F. americana*, *O. virginiana*, and *Q. coccinea*. Vines with the greatest cover were *T. radicans*, *S. rotundifolia*, and *P. quinquefolia*. The most common species were *Carex* spp., *F. americana*, *Carya* spp., *Q. alba*, and *S. rotundifolia*.

In 2020, 152 species were identified, with over 86% of them being native. Across all species, species with the highest average percent cover included *T. radicans, O. virginiana, F. americana, Q. alba*, and *Verbesina* spp. Species with the greatest cover within herbs included *Verbesina* spp., *Solidago* spp., and *Lespedeza* spp. Graminoids with the highest cover were *Microstegium* *vimineum* (a non-native species), *Carex* spp., and *Dichanthelium boscii*. Species with the greatest cover within trees/shrubs included *O. virginiana*, *F. americana*, and *Q. alba*. Vines with the greatest cover were *T. radicans, Lonicera japonica* (a non-native species), and *P. quinquefolia*. The most common species in 2020 were *T. radicans, Carex* spp., *S. rotundifolia*, *P. quinquefolia*, and *R. allegheniensis.*

Species Richness, Evenness, and Diversity

At Sixty-six, average species richness in 2011 was 6.2 (ranging 4.3-10.3), which slightly increased to 7.9 (ranging 4.3-13.6) in 2020 (Figure 19a). In 2011, average evenness was 0.33 (0.17-0.48) and slightly increased to 0.39 (0.22-0.51) in 2020 (Figure 19b). Average Shannon diversity index increased from 0.61 (0.24-1.12) in 2011 to 0.80 (0.37-1.21) in 2020 (Figure 19c). Richness ($F_{1,43} = 9.6$), evenness ($F_{1,43} = 5.6$), and diversity ($F_{1,43} = 9.6$) significantly increased from 2011 to 2020 ($p < 0.05$). No differences in richness, evenness, or diversity were found with differences in midstory treatments ($p > 0.05$).

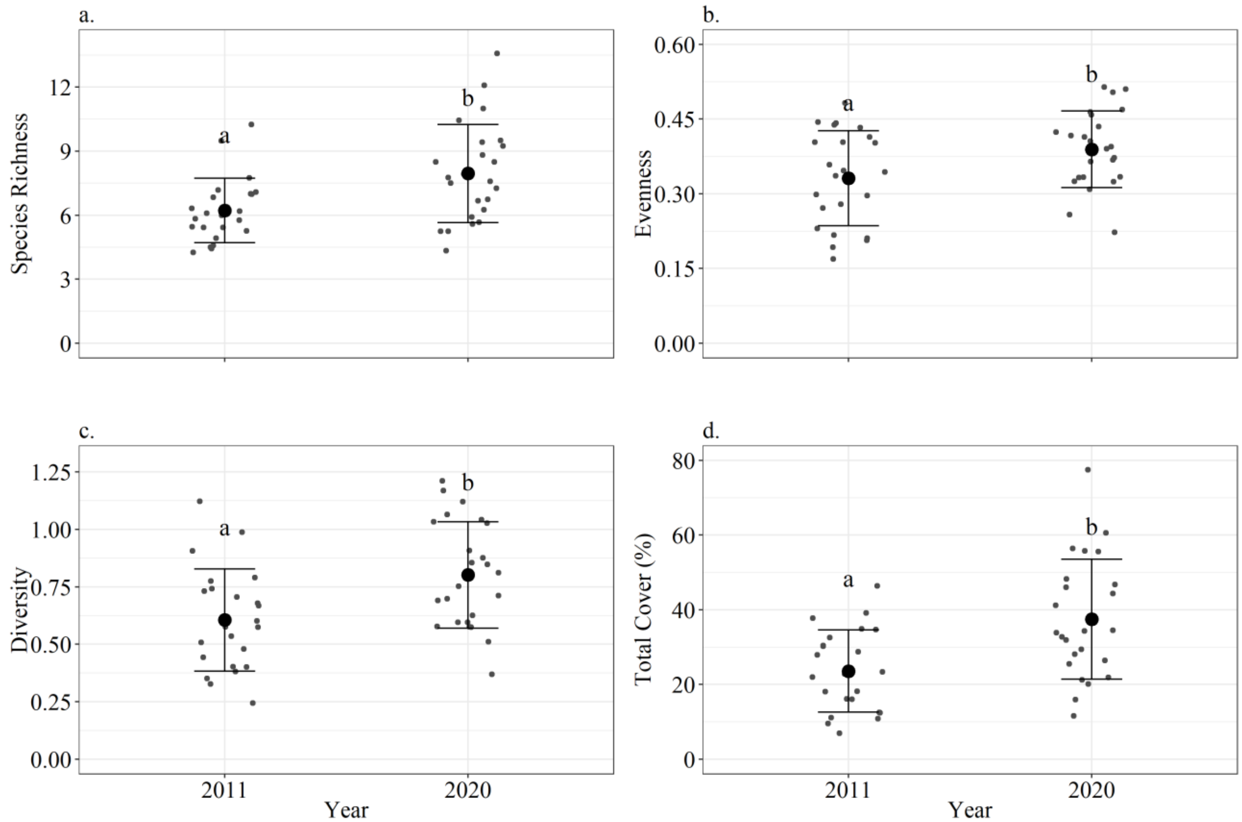


Figure 19. Herbaceous-layer **(a.)** species richness (mean ± SD), **(b.)** evenness (mean ± SD), **(c.)** diversity (mean ± SD), and **(d.).** percent total cover (mean ± SD) at Sixty-six in 2011 (pre-treatment) and 2020 (post-treatment). Superscripts denote significant differences between years based on post-hoc Tukey tests ($\alpha = 0.05$).

Total Herbaceous-layer Cover

Average total cover increased from 23.6% (ranging 6.9-46.4%) in 2011 to 37.5% (ranging 11.6-77.5%) in 2020 (Figure 19d). Average total cover was significantly influenced by year ($F_{1,42} = 16.2$), treatment ($F_{2,42} = 6.4$), and BA (2018; $F_{1,42} = 6.3$; $p < 0.05$). An increase in BA significantly increased total cover ($p < 0.05$). Total cover was significantly lower in mechanical or no midstory removal compared to chemical midstory removal ($p < 0.05$). Post-treatment (2020) had significantly greater total cover than pre-treatment (2011) ($p < 0.001$).

Cover by Plant Functional Group

At Sixty-six, the average cover by functional group in 2011 was 1.7% for herbs, 2.0% for graminoids, 16.0% for trees/shrubs, and 6.3% for woody vines. In 2020, the average cover increased to 4.4% for herbs, 17.8% for trees/shrubs, and 15.8% for woody vines, with no change for graminoids at 1.9% (Figure 20). Cover was significantly different between functional groups ($F_{3,181} = 98.5$, $p < 0.001$), with trees/shrubs and woody vines having significantly greater cover than herbs and graminoids ($p < 0.001$). Woody vines had significantly less cover than trees/shrubs ($p < 0.001$) and no significant differences were detected between herbs and graminoids ($p > 0.05$). Average cover by functional group was significantly different between years ($F_{1,181} = 16.7$, $p < 0.001$), with 2020 having significantly greater cover than 2011 ($p < 0.001$). Average cover was also significantly affected by treatments ($F_{2,181} = 3.6$, $p < 0.05$), with shelterwood with no midstory removal having significantly reduced cover compared to chemical midstory removal ($p < 0.05$).

The average relative cover by functional group in 2011 was 11.4% for herbs, 11.7% for graminoids, 62.0% for trees/shrubs, and 29.6% for woody vines. In 2020, the average relative cover increased to 12.9% for herbs and 38.2% for woody vines, but decreased to 6.6% for graminoids and 51.3% for trees/shrubs (Figure 21). Using a Kruskal-Wallis test due to non-normality and nonequal variance, relative cover by plant functional group was not significantly different between years or midstory treatments ($p > 0.05$). However, relative cover was significantly different between functional groups ($p < 0.0001$), with a Dunn's post-hoc test indicating that trees/shrubs and woody vines had greater relative cover than herbs and graminoids ($p < 0.001$). Woody vines had significantly reduced relative cover compared to trees/shrubs ($p < 0.01$). There were no significant differences between herb and graminoid relative cover ($p > 0.05$)

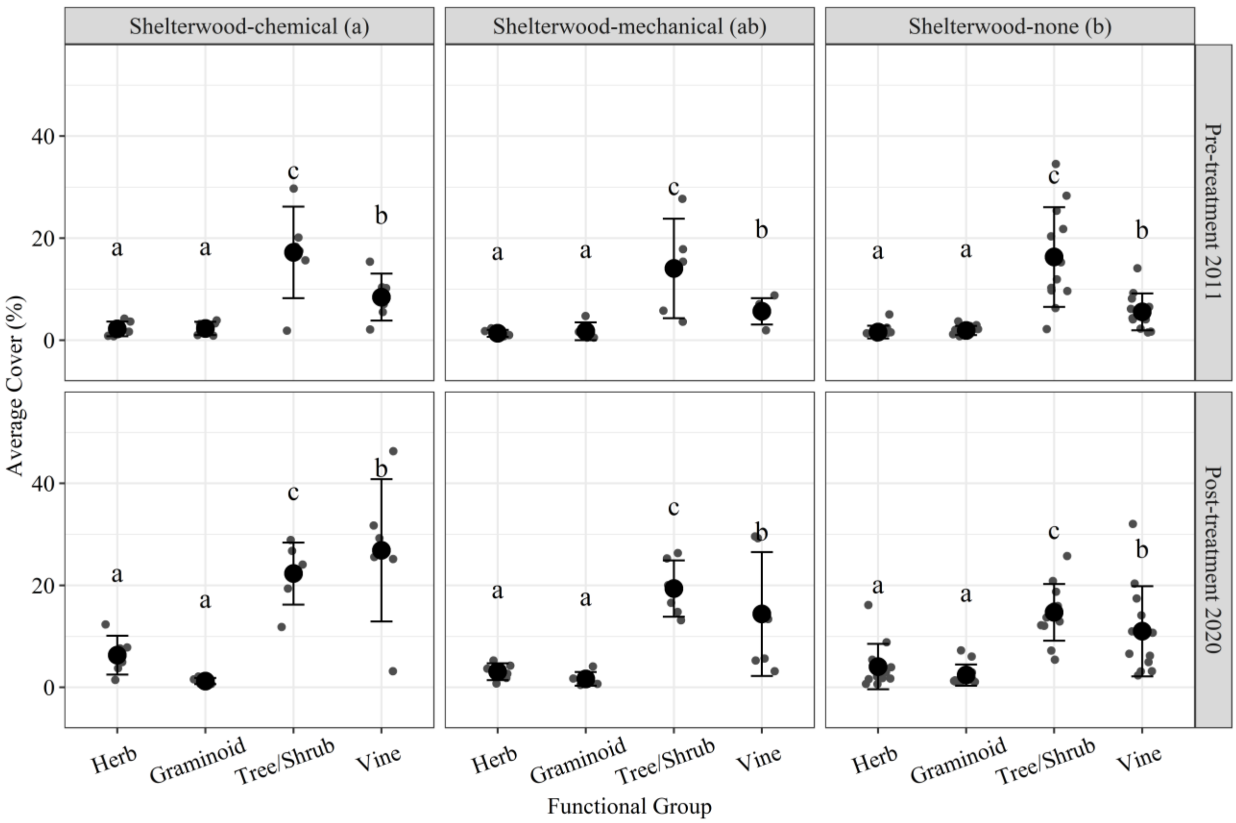


Figure 20. Mean percent cover (± SD) of plant functional groups by treatment in 2011 and 2020 at Sixty-six. Superscripts denote significant differences between functional groups and treatments according to a post-hoc Tukey test (α = 0.05). Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

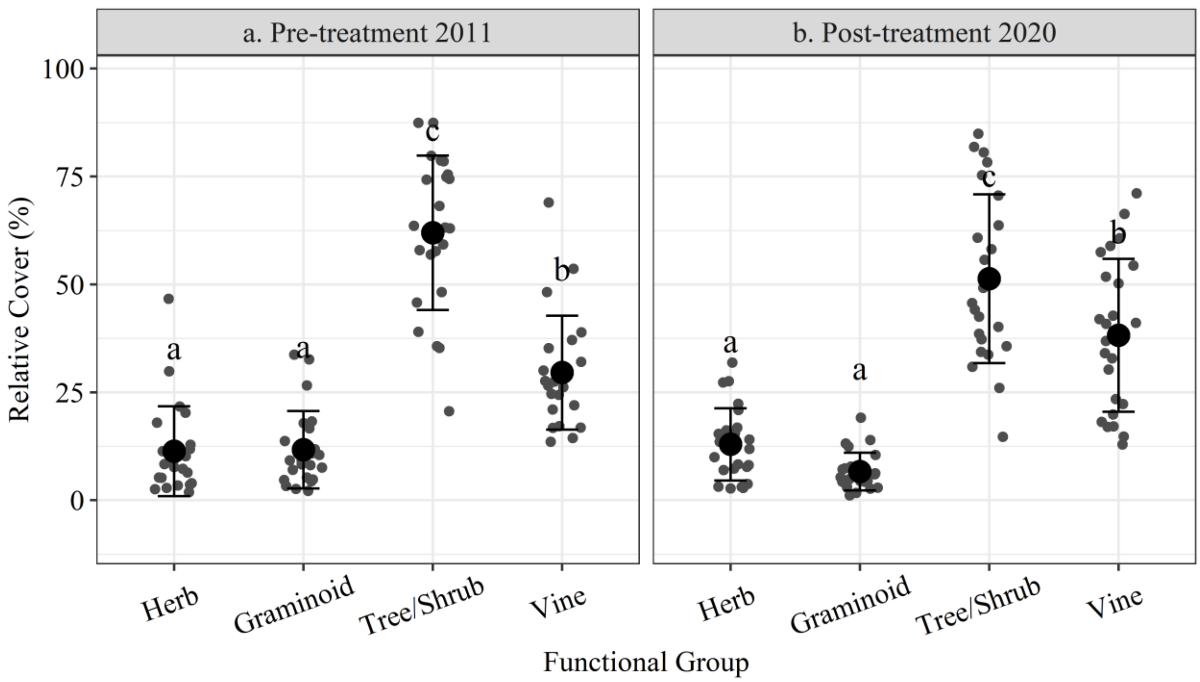


Figure 21. Relative percent cover (mean ± SD) of plant functional groups in **(a.)** 2011 and **(b.)** 2020 at Sixty-six. Superscripts denote significant differences between functional groups according to a post-hoc Dunn's test (α = 0.05).

NMDS Ordination

The NMDS of the herbaceous-layer species composition at Sixty-six resulted in a two-dimension solution with a stress of 0.183 after 20 runs (linear R^2 = 0.836). The environmental factors significantly correlated with the ordination were post-harvest BA, pH, soil organic matter, Al concentration, total N, and percent slope ($p < 0.05$), with pH (R^2 = 0.31, p = 0.001) and organic matter (R^2 = 0.34, p = 0.001) having the strongest correlations (Figure 22a, Table 8). Axis 1 was strongly related to organic matter, post-harvest BA, pH, percent slope, and Al concentration (Figure 22a). Total N appears to be equally related to both axis 1 and 2 (Figure 22a). Sites with higher BA, more productive soils, steeper slopes, and more basic soil are associated with *Lespedeza* spp., Poaceae, *Dichanthelium boscii*, *C. canadensis*, *Phryma leptostachya* L. (American lopseed), *Ruellia carliniensis* (J.F. Gmel.) Steud (Carolina wild petunia), and *Viola* L. spp. (violet; Figure 22a). Plots with higher Al concentration were associated with *Quercus alba*, *Acer rubrum*, *Desmodium nudiflorum*, and *Smilax* L. spp. (greenbrier; Figure 22a). There was clear separation by year (Figure 22b), with 2011 associated with higher cover of *Sassafras albidum*, *Vitis* L. spp. (grape), *Carya* spp., and *Carex* spp. The year 2020 was associated with greater cover of *Dichanthelium* spp., *T. radicans*, *Sanicula* spp., *Cunila origanoides*, *Q. rubra* L. (northern red oak), *Microstegium vimineum*, and *Vaccinium* L. spp. (blueberry). There was high overlap between treatments, with mechanical midstory removal having more separation along axis one and being associated with higher cover of *S. albidum* and *A. rubrum* (Figure 22c). There was a clear compositional shift from 2011 to 2020 along axis 2, shifting to a greater number of species and a greater importance of woody vines, trees/shrubs, and herbs (Figure 22d). The PERMANOVA detected significant differences between treatments ($p < 0.05$) and years (p = 0.001).

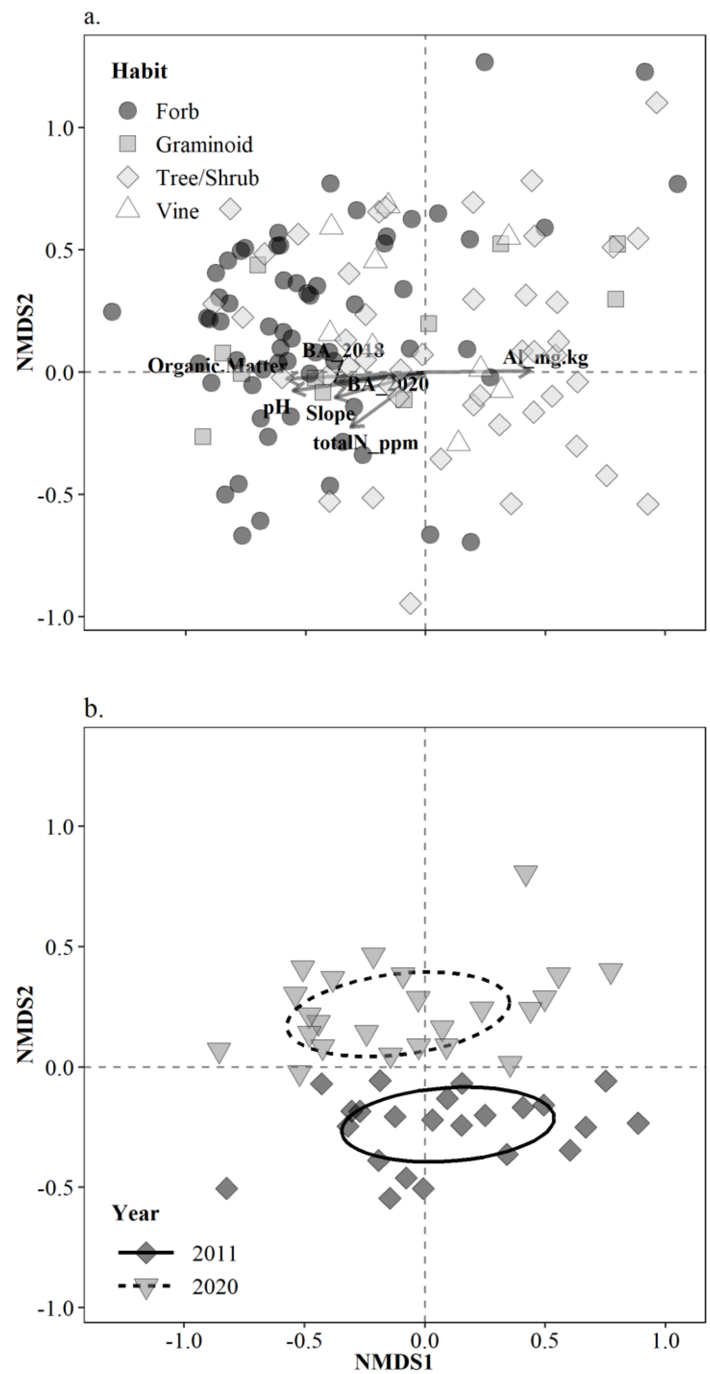


Figure 22. NMDS ordination of herbaceous-layer species composition at Sixty-six in 2011 and 2020: **(a.)** Biplot of herbaceous species by plant habit with significant ($p < 0.05$) environmental factors Al_mg.kg (soil Al), Organic.Matter (percent soil organic matter), totalN_ppm (total soil N), pH (soil pH), Slope (percent slope), and BA_2018 (basal area in 2018) as vector arrows; **(b.)** Biplot of herbaceous plots grouped by years 2011 and 2020; **(c.)** Biplot of herbaceous plots grouped by silvicultural treatments shelter_chem (shelterwood with chemical midstory removal), shelter_mech (shelterwood with mechanical midstory removal), and shelter_none (shelterwood without midstory removal); **(d.)** Successional vector changes of herbaceous composition moving from years 2011 to 2020. Species list found in Appendix B, Table B.5.

Figure 22 continued

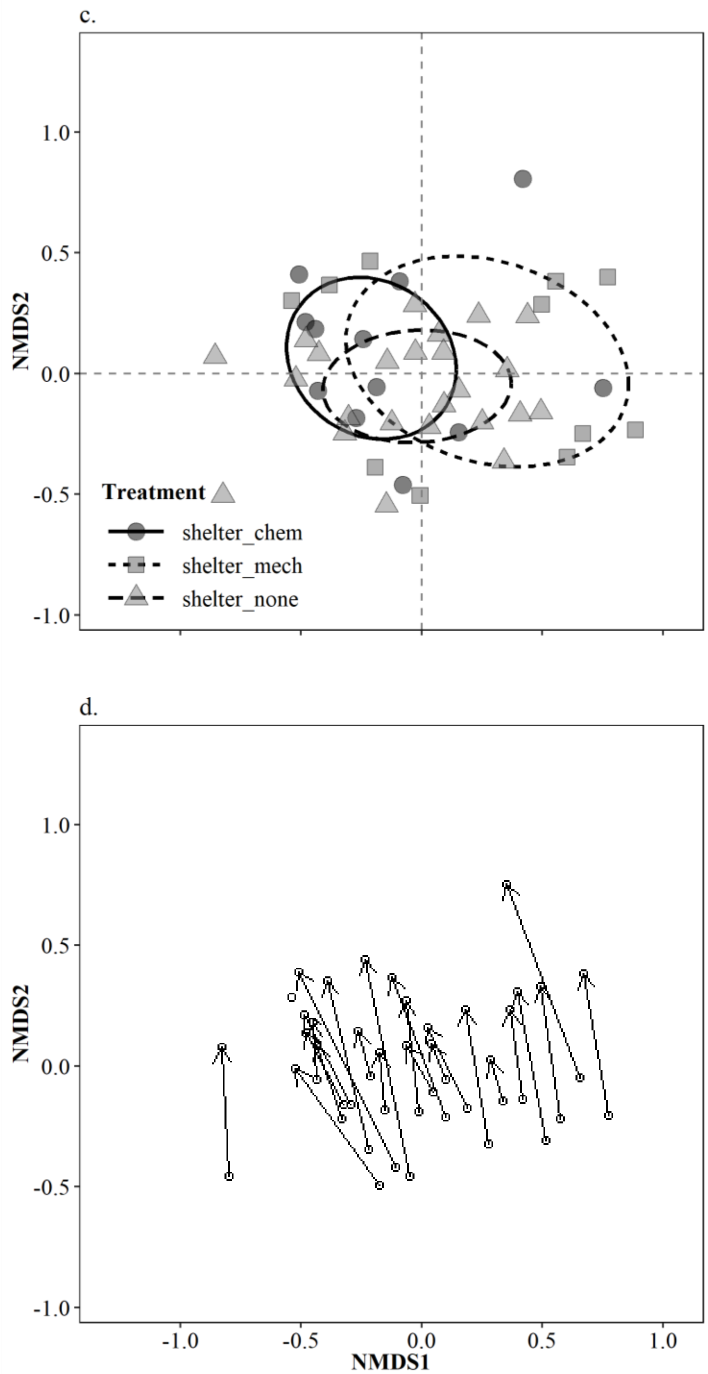


Table 8. Correlation coefficients and p-values (bold: $p < 0.05$) for environmental variables in NMDS ordination of Sixty-six herbaceous composition.

Environmental Variable	R^2	P-value
BA (2010)	0.003	0.943
BA (2018)	**0.147**	**0.035**
BA (2020)	0.130	0.063
pH	**0.309**	**0.001**
% organic matter	**0.338**	**0.001**
P	0.024	0.598
AL	**0.189**	**0.007**
Total N	**0.148**	**0.036**
Canopy Density (2018)	0.023	0.611
Canopy Density (2020)	0.024	0.591
Canopy Density (2010)	0.040	0.418
Transformed Aspect	0.003	0.942
% Slope	**0.155**	**0.03**
Average TSI	0.081	0.143

Indicator Species Analysis

Indicator species for mechanical midstory removal included *Vaccinium pallidum*, *Aralia spinosa*, *A. rubrum*, *Prenanthes altissima*, and *Symphyotrichum* Nees spp. (aster; $p < 0.05$; Appendix B, Table B.3). Indicators of chemical midstory removal included *Agrimonia* L. spp. (agrimony), *Cornus florida* L. (flowering dogwood), *T. radicans*, *F. americana*, and *Passiflora lutea* L. (yellow passionflower), while *C. canadensis* was an indicator of both chemical and no midstory removal ($p < 0.05$; Appendix B, Table B.3). Nine species were indicators for 2011, with *Polygonatum biflorum*, *Vitis* spp., and *Q. coccinea* having the strongest associations ($p < 0.05$; Appendix B, Table B.4). There were 18 indicator species for 2020, with *R. allegheniensis*, *Polygonatum pubescens* (Willd.) Pursh (hairy Solomon’s seal), and *Vitis aestivalis* Michx. (summer grape) having the strongest associations but also included the invasive species *M. vimineum* ($p < 0.05$; Appendix B, Table B.4).

3.4 Discussion

While land managers in the Central Hardwood Forest Region often focus management efforts on establishing and releasing *Quercus* reproduction, the common silvicultural practice of combining harvesting with prescribed burning often improves the herbaceous-layer diversity and cover as well. Our study's objective was to assess the herbaceous-layer response to shelterwood treatments at a less productive, burned site and a more productive, unburned site. Following a shelterwood and single burn, the herbaceous layer increased in richness, evenness, diversity, and total cover at Jeffries (question 1). Average cover for all plant functional groups also increased after treatment, with woody species having a greater average cover and relative cover than herbs and graminoids (Figures 16, 17). Generally, studies examining the combined effects of thinning and burn treatment in *Quercus* forests have also observed increased species richness and increased cover of forbs, graminoids, and woody species following treatment (Kinkead, 2013; Phillips et al., 2007). Phillips et al. (2007) observed greater increases in cover with more time since thinning and burn treatment (up to 4 years) compared to immediately after treatment, while species richness had a rapid increase following treatment then increased more gradually over time. We may see a similar trend at our site with greater time since treatment, as our herb and graminoid cover each increased less than 10% one year following the burn. The large increase in tree/shrub cover we observed suggests that the treatments benefited tree regeneration the most, while also improving herbaceous cover and diversity. Our observed increase in herbaceous plant diversity and cover with harvesting and burning, can in turn, enhance the diversity and abundance of wildlife and insect species that rely on dense, diverse herbaceous-layers. Studies have observed increased abundance and diversity of pollinating insects, correlating with increased herbaceous cover and reduced basal area following harvesting or harvest-burn treatments (Campbell et al., 2007; Proctor et al., 2012). We also observed greater total herbaceous-layer cover, which can contribute to a reduction in soil erosion and additional litter and nutrient inputs (Fralish, 2004; Gilliam, 2007; Welch et al., 2007). Overall, our results suggest that a single burn following a shelterwood cut on a more xeric site significantly improved herbaceous-layer diversity and cover.

The NMDS ordination showed a significant shift in herbaceous-layer species composition post-treatment to one consisting of more graminoids, *Rubus* spp. and various herb species (Figures 18a, 18d). Similar to our results, other studies have observed an increase in *Rubus* spp. abundance and importance following fire (Maginel et al., 2019; Reich et al., 1990). Repeated fire studies found significant changes in herbaceous-layer composition, with increased frequency, abundance, or importance of graminoids, particularly *Carex* spp. and *Dichanthelium* spp. (Hutchinson et al., 2005b; Maginel et al., 2019; Taft, 2003). Hutchinson et al. (2005b) also observed increased frequency of *Viola* spp. and many summer flowering forbs that were significant indicators of burning, such as *Ageratina altissima* (formerly *Eupatorium rugosum*) and *Lespedeza* spp. We observed similar results with increased abundance of *Carex* and *Dichanthelium* spp., and *Viola* spp., *A. altissima*, and *Lespedeza* spp. being significant indicator species of post-treatment composition (Appendix B, Table B.2). Following prescribed burning, a barrens site observed an increase in many transitional woodland species, such as *Eupatorium serotinum* (Anderson et al., 2000), a species that was abundant and a post-burn indicator at Jeffries. The increased light levels produced by the treatments likely benefited many summer flowering herbs and graminoids at our site. An increase in herbs and graminoids may augment the input of fine fuels to better sustain the movement of surface fires in future burns (Hanberry et al., 2020, 2018, 2014b). Additionally, an increased abundance of *Rubus* spp. at the site can provide valuable flowers and fruits for insects and birds (Labbé and King, 2020; McCarty et al., 2002; Proctor et al., 2012).

The post-burn compositional shift at Jeffries was not associated with any of our burn-related variables (char height, fire temperature, fuels) in the ordination. This was unexpected and may suggest that the fire at Jeffries was of sufficient severity to drive similar shifts in composition across all study plots, regardless of char height and other measures of severity. It is also possible that this shift could be correlated with a variable we did not measure. Hutchinson et al. (2005b) also observed a significant, although minor, shift in composition with burning and the compositional variation was explained more by topo-edaphic variables than fire effects. McGee et al. (1995) observed a significant but slight change in herbaceous-layer species composition with burning, but did not find significant differences in forb and graminoid richness between high and low intensity fire areas. Several studies have investigated the effects of fire frequency on the herbaceous-layer (Bowles et al., 2007; Hutchinson et al., 2005b; Maginel et al., 2019), but fewer have examined fire intensity or severity effects. More research may be needed to determine what variables, other than the fuel, fire, and topo-edaphic variables we measured, are associated with the fire-driven compositional shifts.

Following the harvest at Sixty-six, there were slight but significant increases in herbaceous-layer species richness, evenness, diversity, and total cover (question 1). Woody species dominated the site, with few herbs and graminoids present. Studies conducting thinning treatments in *Quercus* forests resulted in large increases in woody cover after harvest (Kinkead, 2013; Phillips et al., 2007). Although we only had a small increase in trees/shrubs cover and a decrease in their relative cover, we did have a larger increase in woody vine average cover and relative cover. Thinning alone may also result in slight increases in forb and graminoid cover in addition to a slight increase in total species richness (Kinkead, 2013; Phillips et al., 2007), similar to our findings. A study of group selection and thinning treatment effects in *Quercus-Carya* forests of the Missouri Ozarks observed increased species richness and groundcover, increased relative cover of woody vines, but reduced relative cover of tree seedlings (Zenner et al., 2006). Group selection and thinning have comparable harvest intensity to shelterwood cuts, and we observed similar results with increased relative cover of woody vines and decreased relative cover of trees/shrubs. Our findings suggest that harvesting alone has less impact on herbaceous species composition relative to the combined effects of harvests and burning, similar to the findings of other studies in similar *Quercus*-dominated systems (Kinkead, 2013; Lettow et al., 2014; Phillips et al., 2007). Our results show that a shelterwood without burning on a more mesic site increased woody species abundance but did not have a substantial impact on herb and graminoid cover or diversity.

We observed no differences in species richness, evenness, and diversity between midstory treatments at both sites (question 2). There was also no difference between treatments in total cover at Jeffries, but there was significantly greater cover with chemical removal compared to mechanical and no midstory removal at Sixty-six. This coincides with chemical midstory removal resulting in the lowest average basal area when compared to mechanical and no removal at Sixty-six (Appendix A, Table A.2), resulting in greater light availability and herbaceous-layer growth. Because light is a limiting factor in the understory, most herbs respond positively to increased light with greater growth and reproduction (Whigham, 2004). Our findings suggest that while midstory treatments may influence the herbaceous-layer growth at a more mesic site, midstory treatments had no significant effect on the herbaceous-layer on our xeric site.

Both sites displayed increased cover of the invasive species *Microstegium vimineum* following treatments and it was also a significant indicator species in 2020. Invasive plants are often introduced to sites via harvesting equipment and the disturbances created by logging make sites susceptible to invasion (Buckley et al., 2003; Marshall and Buckley, 2008). The presence and cover of *M. viminuem* was often higher on skid trails and haul roads on both sites (personal observation). Dense patches of *M. viminuem* have been found to have reduced native species richness and cover over time or compared to uninvaded areas (Adams and Engelhardt, 2009; Brewer et al., 2015). Oswalt et al. (2007) observed reduced hardwood regeneration densities and richness with greater cover of *M vimineum* in Tennessee. This suggests that not only could the invasion and spread of this species negatively impact the herbaceous plant diversity but tree regeneration as well. However, interactions are complex and *M. vimineum* may take advantage of other disturbances, such as deer herbivory which can reinforce invasive species dominance, such as *M. vimineum* (Knight et al., 2009; Webster et al., 2008). *Microstegium vimineum* is often associated with more productive and mesic sites, and fire can promote its invasion, particularly on these mesic sites (Culpepper et al., 2018; Wagner and Fraterrigo, 2015). Areas invaded with *M. vimineum* can also experience increased fire intensity during prescribed burns compared to uninvaded areas and these higher temperatures may inhibit the germination or establishment of native herbs and trees (Emery et al., 2011; Flory et al., 2015). This suggests that Sixty-six should be monitored more intensely for expansion and negative impacts on the forest, especially following prescribed burning. Future management should consider the response of this species to further disturbances on the sites and implement actions to reduce further spread, such as cleaning harvesting equipment between sites.

Our results suggest that shelterwood and midstory treatments alone do not substantially improve the herbaceous-layer diversity or cover on a more mesic site. Although richness, diversity and cover slightly increased after treatment, the herbaceous layer consisted mainly of woody species. With a dense sapling layer and increased shade, herbs and graminoids were sparse at Sixty-six. Several studies have shown greater increases in diversity, richness, and herbaceous cover when harvesting is combined with prescribed burning in *Quercus* forests and savannas (Kinkead, 2013; Lettow et al., 2014; Phillips et al., 2007). Burning reduces litter and duff depth and increases light to the forest floor, allowing increased germination and growth of herbaceous plants (Hutchinson, 2005). Herbaceous-layer diversity and cover will likely respond positively to the burn planned for spring of 2022 at Sixty-six.

The use of harvest and fire to promote *Quercus* regeneration may also have positive effects on the overall forest plant community, including the herbaceous layer. The herbaceous layer can benefit from this treatment combination by reducing litter depth and shading from woody stems. Improving the diversity and abundance of herbaceous plants in the forest can assist in increasing overall biodiversity and ecological function of the forest. With high level of concern about restoring and maintaining *Quercus* forests in the eastern United States, management, and research, often focuses solely on the response of tree regeneration. However, successful restoration of *Quercus*-dominated forests encompasses the restoration of the entire plant community, including the herbaceous layer, which contains a significant portion of the diversity and ecological function of a forest. It is a cost-effective option for land managers to use the same techniques to simultaneously restore *Quercus* regeneration and the herbaceous layer in *Quercus*-dominated forests.

CHAPTER 4. CONCLUSION

A combination of silvicultural treatment and prescribed burning is often utilized to promote *Quercus* regeneration, with multiple burns typically needed on more productive sites and fewer burns on less productive sites. While land managers generally focus management efforts on the regeneration layer, herbaceous species often benefit from these treatments as well. Our primary objective in Chapter 2 was to assess whether a single fire following shelterwood and midstory treatments would produce sufficient *Quercus* regeneration on a less productive site. On our more xeric, burned site, we observed a compositional shift away from mesophytes such as *Acer* species, toward a greater importance of *Quercus* species. *Quercus* seedlings had greater survival than most competing species and were one of the most abundant species on the site. A shelterwood harvest alone on our more mesic site resulted in greater levels of competition with *Quercus* seedlings having survival rates, heights, and densities comparable to their competitors. Our objective in Chapter 3 was to assess how the herbaceous layer responded to silvicultural treatments on a less-productive, burned site and more-productive, unburned site. The shelterwood and burn treatments on our xeric site yielded increased diversity, richness, and cover of the herbaceous layer compared to pre-treatment levels. Although woody species remained high in cover, there was a significant compositional shift toward greater abundance of forbs and graminoids. Conversely, silvicultural treatments had little effect on the herbaceous layer on our more productive site, except for a large increase in vine cover.

Overall, our study suggested that a shelterwood harvest followed by a single burn may produce adequate *Quercus* regeneration to dominate the future overstory of more xeric sites. Although seedlings were still fairly short two years post-burn, with more time they could advance into taller height classes and be more competitive without the need for further burning. The herbaceous layer also benefited from the combined shelterwood-burn treatment, suggesting that even a relatively low intensity burn can significantly increase forb and graminoid cover and richness. Because *Quercus* have greater drought tolerance compared to mesophytic species (Johnson et al., 2019), mesophytic species are disadvantaged on more xeric sites and are not as competitive with *Quercus* as they are on mesic sites. Therefore, fewer and less intense fires may be needed to promote competitive *Quercus* seedlings on xeric sites, as vigor and abundance of mesophytic competitors is reduced due to water and nutrient-limited site conditions. Additionally, midstory treatments were not found to be beneficial to *Quercus* growth or herbaceous-layer diversity and cover and may be unnecessary on less productive sites.

However, our findings indicate that a shelterwood harvest alone on a more mesic site was not sufficient to reduce mesophytic competition and promote *Quercus* regeneration. Without subsequent burning at this site, it is unlikely that *Quercus* species will maintain dominance into the overstory. The herbaceous plant community also displayed less response to harvesting without fire. Future management may require several burns to reduce competition and improve *Quercus* dominance, in addition to further improving herbaceous diversity and cover. Competition is often more intense on mesic sites, and *Quercus* are more suppressed, resulting in the need for more fires on these sites. Also, our study suggested that midstory treatments improved seedling growth and herbaceous cover on mesic sites. Therefore, we recommend midstory treatments in addition to a shelterwood harvest. Our results were not clear on whether mechanical or chemical midstory removal yielded more positive results on woody regeneration and herbaceous-layer composition, as response may be more dependent upon residual BA rather than method. At this time, we suggest implementing any form of midstory removal to further reduce BA and increase light levels on more productive sites.

Quercus-Carya forests have the largest cover of any forest type in the eastern United States and approximately one-quarter of the timberland volume in the eastern United States is *Quercus* species (Johnson et al., 2019). With mesophication occurring in *Quercus*-dominated forests across the eastern United States, there is great interest in restoring *Quercus* regeneration in these highly ecologically and economically valued forests. It can be time-consuming and costly to successfully restore and regenerate *Quercus*-dominated forests. Therefore, maintaining *Quercus*-dominance can be done more easily by focusing efforts on xeric sites that take less effort and time, compared to mesic sites. While mesic sites often need multiple burns to produce competitive *Quercus* reproduction, fewer burns are typically needed at xeric sites to achieve sufficient levels of regeneration. In addition, when monitoring for restoration success, the herbaceous layer response should be considered as well, as it is also negatively impacted by mesophication and constitutes most of the plant species diversity in hardwood forests. Restoring the *Quercus* regeneration and herbaceous layers within *Quercus*-dominated forests will provide valuable wildlife habitat and improve the ecological functions and services provided by eastern hardwood forests.

APPENDIX A. CHAPTER 2 SUPPLEMENTARY MATERIAL

Table A.1. Mean and range of total live basal area ($m^2\ ha^{-1}$) for overstory and midstory in **(a.)** 2010 and **(b.)** 2018 after all harvests were completed at Jeffries.

a. 2010	**Overstory ($m^2\ ha^{-1}$)**			**Midstory ($m^2\ ha^{-1}$)**		
Treatment	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**
Shelterwood-none	25.27	14.70	41.36	0.48	0.05	0.98
Shelterwood-mechanical	27.18	20.47	42.77	0.83	0.59	1.46
Shelterwood-chemical	20.56	15.45	27.97	0.61	0.28	1.27
Reference	29.14	23.29	34.38	0.71	0.58	0.92
b. 2018						
Shelterwood-none	13.60	8.57	20.65	0.37	0.08	0.82
Shelterwood-mechanical	12.98	7.15	20.45	0.06	0.03	0.09
Shelterwood-chemical	8.92	5.23	13.73	0.19	0.17	0.20
Reference	24.99	19.13	30.28	0.87	0.85	0.89

Table A.2. Mean and range of total live basal area ($m^2\ ha^{-1}$) for overstory and midstory in **(a.)** 2010 and **(b.)** 2018 after all harvests were completed at Sixty-six.

a. 2010	**Overstory ($m^2\ ha^{-1}$)**			**Midstory ($m^2\ ha^{-1}$)**		
Treatment	**Mean**	**Min**	**Max**	**Mean**	**Min**	**Max**
Shelterwood-none	25.07	16.07	36.13	0.89	0.29	1.42
Shelterwood-mechanical	29.38	24.26	34.56	0.57	0.28	1.04
Shelterwood-chemical	26.26	18.99	38.50	0.78	0.34	1.80
Reference	25.66	16.69	31.07	0.31	0.10	0.45
b. 2018						
Shelterwood-none	15.52	8.54	22.30	0.67	0.27	1.41
Shelterwood-mechanical	13.99	4.24	22.81	0.60	0.03	1.88
Shelterwood-chemical	14.13	2.04	24.37	0.14	0.03	0.24
Reference	27.35	13.78	35.68	0.48	0.12	0.91

Table A.3. Binomial model summaries with odds ratios and p-values (bold: p <0.05) for survival since fire, survival since 2010, and resprout response in 2020 and 2021 at Jeffries. Reference levels: Species group=*Acer rubrum*, Treatment= Shelterwood-chemical.

	Survival since Fire-2020	**Survival since Fire-2021**	**Survival since 2010-2020**	**Survival since 2010-2021**	**Resprout Response-2020**	**Resprout Response-2021**
Intercept	7.262 p = 0.137	**142.637** **p = 0.005**	1.088 p = 0.915	1.162 p = 0.850	1.346 p = 0.598	**87.684** **p = 0.007**
Mean Char Height (std)			**0.736** **p = 0.004**	**0.764** **p = 0.011**		
Basal diam. (log, 2018)	1.457 p = 0.100				0.890 p = 0.572	0.707 p = 0.116
Basal diam. (log, 2010)			**1.715** **p = 0.000**	**1.721** **p = 0.000**		
Basal Area (2020)			**0.899** **p = 0.000**	**0.895** **p = 0.000**		
Canopy density (std, 2020)	**1.402** **p = 0.033**		1.185 p = 0.058	1.160 p = 0.099		
pH	**0.541** **p = 0.021**	**0.398** **p = 0.003**				**0.498** **p = 0.015**
Total N (ppm)		**1.126** **p = 0.019**	**1.041** **p = 0.021**	**1.043** **p = 0.015**		1.066 p = 0.127
P (mg/kg)		0.918 p = 0.106	**1.073** **p = 0.018**	**1.068** **p = 0.028**		0.930 p = 0.148
CWD (std, 2020)			0.869 p = 0.144	0.854 p = 0.101		
FWD (2018)		**0.908** **p = 0.034**				**0.910** **p = 0.026**

Table A.3 continued

	Survival since Fire-2020	**Survival since Fire-2021**	**Survival since 2010-2020**	**Survival since 2010-2021**	**Resprout Response-2020**	**Resprout Response-2021**
Litter Change (cm, 2018-2020)		1.872 p = 0.072			1.531 p = 0.105	**2.037** **p = 0.026**
Duff depth (cm, 2020)			0.108 p = 0.064	0.119 p = 0.076		
Transformed Aspect	**0.064** **p = 0.006**	0.194 p = 0.116			**0.165** **p = 0.049**	0.257 p = 0.154
% Slope	**1.169** **p = 0.000**	1.089 p = 0.082			**1.115** **p = 0.003**	1.091 p = 0.059
Acer saccharum	0.398 p = 0.185	0.470 p = 0.281	**0.366** **p = 0.044**	**0.368** **p = 0.045**	0.308 p = 0.083	0.344 p = 0.132
Canopy Other	**5.801** **p = 0.014**	**6.438** **p = 0.010**	**2.514** **p = 0.031**	**2.521** **p = 0.030**	3.566 p = 0.051	**4.241** **p = 0.033**
Carya spp.	**27.353** **p = 0.004**	**31.645** **p = 0.002**	**4.775** **p = 0.000**	**4.730** **p = 0.000**	**7.274** **p = 0.006**	**10.378** **p = 0.003**
Fraxinus americana	0.853 p = 0.789	1.063 p = 0.917	1.118 p = 0.792	1.118 p = 0.791	0.935 p = 0.906	1.201 p = 0.758
Ostrya virginiana	1.291 p = 0.691	1.642 p = 0.408	1.239 p = 0.626	1.124 p = 0.790	1.327 p = 0.639	1.538 p = 0.490
Other *Quercus* spp.	**11.914** **p = 0.008**	**13.599** **p = 0.004**	**3.938** **p = 0.005**	**3.857** **p = 0.006**	**9.375** **p = 0.013**	**12.307** **p = 0.006**
Quercus rubra	**17.732** **p = 0.013**	**22.195** **p = 0.007**	**3.642** **p = 0.006**	**3.592** **p = 0.006**	**23.781** **p = 0.006**	**12.471** **p = 0.005**
Quercus velutina	3.918 p = 0.054	**9.479** **p = 0.004**	**3.426** **p = 0.007**	**3.866** **p = 0.003**	3.017 p = 0.085	**6.183** **p = 0.010**
Sassafras albidum	2.310 p = 0.292	1.800 p = 0.454	0.446 p = 0.083	0.445 p = 0.081	1.843 p = 0.433	1.638 p = 0.530

Table A.3 continued

	Survival since Fire-2020	**Survival since Fire-2021**	**Survival since 2010-2020**	**Survival since 2010-2021**	**Resprout Response-2020**	**Resprout Response-2021**
Subcanopy Other	2.624	**3.606**	2.027	2.131	2.291	3.026
	p = 0.131	**p = 0.044**	p = 0.093	p = 0.072	p = 0.167	p = 0.079
Shelterwood-mechanical	1.383	1.599	1.244	1.329	1.708	1.390
	p = 0.411	p = 0.323	p = 0.395	p = 0.270	p = 0.163	p = 0.449
Shelterwood-none	1.280	**2.359**	**2.372**	**2.535**	1.530	1.737
	p = 0.459	**p = 0.035**	**p = 0.002**	**p = 0.001**	p = 0.150	p = 0.153
Num. Obs.	509	509	923	923	509	509
AIC	407.4	404.2	1138.2	1136.3	460.1	454.8
BIC	487.8	493.0	1244.4	1242.5	536.3	547.9
Log.Lik.	-184.706	-181.080	-547.099	-546.144	-212.058	-205.376

Table A.4. Summaries of estimates and p-values (bold: $p < 0.05$) of Poisson resprout density models (2020, 2021), linear resprout height models (2020, 2021, and negative binomial regen density model (2020) at Jeffries. Reference levels: Species group = *Acer rubrum*, Treatment = Shelterwood-chemical, Height Class = 1.

	Resprout Density-2020	**Resprout Density-2021**	**Resprout Heights-2020**	**Resprout Heights-2021**	**Regen Density-2020**
Intercept	**2.284**	0.480	0.634	0.571	**1.341**
	p = 0.000	p = 0.055	p = 0.136	p = 0.110	**p = 0.000**
Mean Char Height (std)			**-0.101**		**-0.145**
			p = 0.005		**p = 0.000**
Basal diam. (log, 2018)	**0.358**	**0.354**	**0.465**	**0.598**	
	p = 0.000	**p = 0.000**	**p = 0.000**	**p = 0.000**	
Basal Area (log, 2018)			-0.143	**-0.282**	
			p = 0.162	**p = 0.002**	
Canopy density (std, 2018)			-0.063	**-0.098**	
			p = 0.118	**p = 0.005**	
pH	**-0.220**		-0.113		
	p = 0.000		p = 0.052		
Al (mg/kg, std)		**0.127**			
		p = 0.000			
Total N (ppm)			**0.015**	**0.013**	**0.028**
			p = 0.021	**p = 0.011**	**p = 0.001**
FWD (2018)		**-0.021**	-0.014		**-0.035**
		p = 0.012	p = 0.095		**p = 0.000**
Litter Change (cm, 2018-2020)	**-0.193**				
	p = 0.001				
Transformed Aspect			**0.385**		**-0.515**
			p = 0.047		**p = 0.028**
% Slope	**-0.028**				-0.018
	p = 0.003				p = 0.100

Table A.4 continued

	Resprout Density-2020	Resprout Density-2021	Resprout Heights-2020	Resprout Heights-2021	Regen Density-2020
Acer saccharum	-0.301 p = 0.295	-0.136 p = 0.636	-0.308 p = 0.166	**-0.499** **p = 0.025**	-0.204 p = 0.496
Canopy Other	-0.137 p = 0.433	-0.178 p = 0.354	0.083 p = 0.603	0.062 p = 0.697	-0.097 p = 0.641
Carya spp.	**-0.572** **p = 0.002**	-0.378 p = 0.050	-0.137 p = 0.377	-0.049 p = 0.754	0.123 p = 0.585
Fraxinus americana	-0.158 p = 0.375	0.044 p = 0.814	-0.070 p = 0.664	-0.079 p = 0.623	**1.448** **p = 0.000**
Ostrya virginiana	-0.050 p = 0.773	-0.002 p = 0.990	-0.260 p = 0.111	0.002 p = 0.993	**1.166** **p = 0.000**
Other *Quercus* spp.	-0.268 p = 0.151	-0.084 p = 0.675	0.024 p = 0.889	-0.023 p = 0.888	0.355 p = 0.111
Quercus rubra	**-0.573** **p = 0.002**	-0.311 p = 0.114	0.037 p = 0.823	-0.059 p = 0.720	0.080 p = 0.760
Quercus velutina	-0.339 p = 0.052	-0.282 p = 0.136	0.074 p = 0.641	-0.001 p = 0.996	**0.451** **p = 0.042**
Sassafras albidum	**-0.677** **p = 0.012**	**-0.711** **p = 0.018**	-0.032 p = 0.870	-0.019 p = 0.924	**0.583** **p = 0.016**
Subcanopy Other	-0.080 p = 0.645	-0.063 p = 0.739	0.196 p = 0.219	0.182 p = 0.251	**0.675** **p = 0.001**
Shelterwood-mechanical	0.133 p = 0.146	**0.190** **p = 0.034**	-0.003 p = 0.976	**0.183** **p = 0.043**	**0.205** **p = 0.041**
Shelterwood-none	0.001 p = 0.986	0.017 p = 0.841	0.087 p = 0.338	**0.168** **p = 0.037**	**0.346** **p = 0.000**
Height Class 2					0.057 p = 0.471

Table A.4 continued

	Resprout Density-2020	**Resprout Density-2021**	**Resprout Heights-2020**	**Resprout Heights-2021**	**Regen Density-2020**
Height Class 3					**-0.362** **p = 0.000**
Height Class 4					**-0.871** **p = 0.000**
Height Class 5					**-1.368** **p = 0.000**
Num. Obs.	403	405	403	405	840
R2			0.391	0.466	
R2 Adj.			0.357	0.442	
AIC	1452.8	1411.1	567.4	573.4	4365.4
BIC	1524.8	1479.2	659.3	649.5	4479.0
Log.Lik.	-708.424	-688.567	-260.676	-267.714	-2158.689
F			11.636	19.843	

Table A.5. Summaries of estimates and p-values (bold: p-value < 0.05) of binomial survival since 2010 model (log odds ratio), linear seedling height model, and negative binomial regeneration density model at Sixty-six in 2020. Reference levels: Species group = *Acer rubrum*, Treatment = Shelterwood-chemical, Height Class = 1.

	Survival Since 2010	**Seedling Heights**	**Regen Density**
Intercept	-0.512 p = 0.263	-0.068 p = 0.931	0.555 p = 0.500
Basal diam. (log, 2010)	**0.589** **p = 0.000**	**0.566** **p = 0.000**	
Basal Area (2020)	**0.046** **p = 0.002**		**0.025** **p = 0.001**
Canopy density (2020)		0.012 p = 0.128	**0.022** **p = 0.004**
Total N (ppm)	**-0.042** **p = 0.006**	**-0.029** **p = 0.001**	
P (mg per kg)		**0.028** **p = 0.022**	**-0.031** **p = 0.009**
Transformed Aspect			-0.274 p = 0.062
Acer saccharum	-0.539 p = 0.214	-0.070 p = 0.769	**-0.514** **p = 0.009**
Canopy Other	**0.847** **p = 0.019**	0.106 p = 0.590	**-0.682** **p = 0.000**
Carya spp.	**1.275** **p = 0.001**	-0.201 p = 0.329	**-0.566** **p = 0.001**
Fraxinus americana	-0.203 p = 0.611	0.076 p = 0.730	**0.445** **p = 0.004**
Ostrya virginiana	**1.089** **p = 0.008**	**0.450** **p = 0.027**	-0.191 p = 0.273

Table A.5 continued

	Survival Since 2010	**Seedling Heights**	**Regen Density**
Other *Quercus* spp.	-0.319 p = 0.791	0.328 p = 0.648	**-1.511** **p = 0.000**
Quercus rubra	0.656 p = 0.120	0.002 p = 0.994	**-0.801** **p = 0.000**
Quercus velutina	-0.071 p = 0.880	0.184 p = 0.484	**-1.147** **p = 0.000**
Sassafras albidum	**-1.660** **p = 0.004**	**-1.491** **p = 0.000**	0.302 p = 0.226
Subcanopy Other	**1.223** **p = 0.002**	0.210 p = 0.318	**-0.689** **p = 0.000**
Shelterwood-mechanical	0.233 p = 0.267	0.097 p = 0.391	**-0.667** **p = 0.000**
Shelterwood-none	**0.442** **p = 0.016**	**-0.536** **p = 0.000**	**-0.464** **p = 0.000**
Height Class 2			**-0.635** **p = 0.000**
Height Class 3			**-0.996** **p = 0.000**
Height Class 4			**-0.820** **p = 0.000**
Height Class 5			**-0.360** **p = 0.000**

Table A.5 continued

	Survival Since 2010	**Seedling Heights**	**Regen Density**
Num. Obs.	950	426	844
R2		0.452	
R2 Adj.		0.429	
AIC	1167.4	915.1	3903.2
BIC	1249.9	992.2	4012.2

APPENDIX B. CHAPTER 3 SUPPLEMENTARY MATERIAL

Table B.1. Point biserial correlation coefficients and p-values for significant indicator species for treatments at Jeffries. Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

Species	r_{pb}	P-value
Shelterwood-chemical		
Symphyotrichum undulatum	0.382	0.025
Verbesina spp.	0.381	0.039
Quercus velutina	0.379	0.042
Quercus stellata	0.376	0.027
Solidago spp.	0.374	0.034
Shelterwood-mechanical		
Ageratina altissima	0.424	0.011
Liriodendron tulipifera	0.424	0.004
Shelterwood-none		
Prenanthes altissima	0.357	0.032
Shelterwood-chemical + Shelterwood-none		
Carex spp.	0.377	0.034
Shelterwood-mechanical + Shelterwood-none		
Toxicodendron radicans	0.384	0.023

Table B.2. Point biserial correlation coefficients and p-values for significant indicator species for each year at Jeffries.

Species	r_{pb}	P-value
2011		
Polygonatum biflorum	0.556	0.001
Vaccinium stamineum	0.510	0.001
Desmodium nudiflorum	0.460	0.001
Acer saccharum	0.418	0.001
Aristolochia serpentaria	0.396	0.011
Vaccinium pallidum	0.394	0.006
Acalypha virginica	0.390	0.003
Sassafras albidum	0.347	0.021
Diospyros virginiana	0.340	0.013
Rubus spp.	0.318	0.024
2020		
Rubus allegheniensis	0.886	0.001
Lobelia spp.	0.769	0.001
Eupatorium serotinum	0.703	0.001
Lespedeza spp.	0.683	0.001
Vitis aestivalis	0.659	0.001
Rhus copallinum	0.652	0.001
Dichanthelium dichotomum	0.627	0.001
Oxalis stricta	0.593	0.001
Solidago canadensis	0.583	0.001
Viola triloba	0.550	0.001
Ageratina altissima	0.532	0.001
Schizachyrium scoparium	0.515	0.001
Symphyotrichum spp.	0.515	0.001
Dichanthelium spp.	0.491	0.001
Erigeron annuus	0.489	0.001
Potentilla simplex	0.483	0.001
Solanum carolinense	0.464	0.001
Dichanthelium boscii	0.464	0.003
Carex spp.	0.462	0.002
Gnaphalium spp.	0.455	0.001
Vaccinium spp.	0.451	0.002
Houstonia purpurea	0.450	0.001

Table B.2 continued

Species	**r_{pb}**	**P-value**
2020		
Viola spp.	0.450	0.005
Scleria oligantha	0.429	0.001
Krigia virginica	0.425	0.005
Rubus occidentalis	0.407	0.005
Conyza canadensis	0.406	0.007
Aralia spinosa	0.400	0.002
Lespedeza procumbens	0.381	0.004
Hypericum spp.	0.372	0.021
Geum spp.	0.358	0.022
Polygonatum pubescens	0.357	0.022
Parthenocissus quinquefolia	0.352	0.020
Toxicodendron radicans	0.347	0.020
Rhus glabra	0.346	0.020
Amphicarpaea bracteata	0.346	0.015
Ulmus spp.	0.345	0.021
Bidens frondosa	0.341	0.004
Symphyotrichum undulatum	0.337	0.010
Cercis canadensis	0.337	0.021
Vitis vulpina	0.334	0.026
Dichanthelium acuminatum var. *fasciculatum*	0.331	0.024
Apocynum cannabinum	0.330	0.035
Dichanthelium commutatum	0.330	0.030
Polystichum acrostichoides	0.327	0.034
Quercus rubra	0.327	0.029
Prunus serotina	0.324	0.023
Helianthus microcephalus	0.316	0.006
Prenanthes altissima	0.315	0.021
Cirsium discolor	0.300	0.025
Galium circaezans	0.295	0.050
Microstegium vimineum	0.290	0.011
Liriodendron tulipifera	0.286	0.044

Table B.3. Point biserial correlation coefficients and p-values for significant indicator species for treatments at Sixty-six. Shelterwood-chemical = shelterwood with chemical midstory removal, Shelterwood-mechanical = shelterwood with mechanical midstory removal, and Shelterwood-none = shelterwood without midstory removal.

Species	r_{pb}	P-value
Shelterwood-chemical		
Agrimonia spp.	0.479	0.005
Cornus florida	0.422	0.016
Toxicodendron radicans	0.420	0.011
Fraxinus americana	0.415	0.022
Passiflora lutea	0.391	0.027
Shelterwood-mechanical		
Vaccinium pallidum	0.464	0.003
Aralia spinosa	0.415	0.011
Acer rubrum	0.394	0.038
Prenanthes altissima	0.384	0.016
Symphyotrichum spp.	0.375	0.023
Shelterwood-chemical + Shelterwood-none		
Cercis canadensis	0.369	0.045

Table B.4. Point biserial correlation coefficients and p-values for significant indicator species for each year at Sixty-six.

Species	r_{pb}	P-value
2011		
Polygonatum biflorum	0.743	0.001
Vitis spp.	0.485	0.002
Quercus coccinea	0.457	0.004
Sassafras albidum	0.440	0.002
Rubus flagellaris	0.428	0.003
Ulmus rubra	0.368	0.009
Erechtites hieraciifolius	0.343	0.014
Vaccinium pallidum	0.321	0.021
Viburnum prunifolium	0.282	0.048
2020		
Rubus allegheniensis	0.668	0.001
Polygonatum pubescens	0.612	0.001
Vitis aestivalis	0.509	0.001
Toxicodendron radicans	0.452	0.001
Lobelia spp.	0.440	0.006
Ulmus americana	0.430	0.002
Ageratina altissima	0.418	0.001
Viola triloba	0.396	0.010
Parthenocissus quinquefolia	0.380	0.009
Symphyotrichum shortii	0.373	0.008
Ruellia spp.	0.353	0.015
Rubus occidentalis	0.352	0.004
Acalypha spp.	0.341	0.046
Vitis vulpina	0.327	0.046
Aralia spinosa	0.321	0.023
Liriodendron tulipifera	0.303	0.049
Microstegium vimineum	0.268	0.050
Lespedeza hirta	0.256	0.046

Table B.5. Species codes, scientific names, and functional groups of plants at Jeffries and Sixty-six (* = introduced species).

Species Code	Scientific Name	Functional Group
ACALY	*Acalypha* spp.	Herb
ACRU	*Acer rubrum*	Tree/Shrub
ACSA3	*Acer saccharum*	Tree/Shrub
ACVI	*Acalypha virginica*	Herb
AGAL5	*Ageratina altissima*	Herb
AGRIM	*Agrimonia* spp.	Herb
AMAR2	*Ambrosia artemisiifolia*	Herb
AMAR3	*Amelanchier arborea*	Tree/Shrub
AMBR2	*Amphicarpaea bracteata*	Herb
AMELA	*Amelanchier* spp.	Tree/Shrub
ANGE	*Andropogon gerardii*	Graminoid
ANPA9	*Antennaria parlinii*	Herb
ANPL	*Antennaria plantaginifolia*	Herb
ANVE	*Angelica venenosa*	Herb
APCA	*Apocynum cannabinum*	Herb
AQCA	*Aquilegia canadensis*	Herb
ARSE3	*Aristolochia serpentaria*	Herb
ARSP2	*Aralia spinosa*	Tree/Shrub
ARTR	*Arisaema triphyllum*	Herb
ASCLE	*Asclepias* spp.	Herb
ASPL	*Asplenium platyneuron*	Herb
ASQU	*Asclepias quadrifolia*	Herb
ASTR	*Asimina triloba*	Tree/Shrub
BIBI7	*Bidens bipinnata*	Herb
BIFR	*Bidens frondosa*	Herb
BOVI	*Botrychium virginianum*	Herb
BROMU	*Bromus* spp.	Graminoid
BRPA4 *	*Broussonetia papyrifera*	Tree/Shrub
BRPU6	*Bromus pubescens*	Graminoid
CACA18	*Carpinus carliniana*	Tree/Shrub
CAREX	*Carex* spp.	Graminoid
CARYA	*Carya* spp.	Tree/Shrub
CEAM	*Ceanothus americanus*	Tree/Shrub

Table B.5 continued

Species Code	Scientific Name	Functional Group
CECA4	*Cercis canadensis*	Tree/Shrub
CELTI	*Celtis* spp.	Tree/Shrub
CEOC	*Celtis occidentalis*	Tree/Shrub
CESC	*Celastrus scandens*	Vine
CHAMA17	*Chamaecrista* spp.	Herb
CIDI	*Cirsium discolor*	Herb
COAM	*Conopholis americana*	Herb
COAR4 *	*Convolvulus arvensis*	Herb
COCA5	*Conyza canadensis*	Herb
COCO3 *	*Commelina communis*	Herb
COFL2	*Cornus florida*	Tree/Shrub
CRATA	*Crataegus* spp.	Tree/Shrub
CUOR	*Cunila origanoides*	Herb
CYPERACEAE		Graminoid
CYPR4	*Cystopteris protrusa*	Herb
CYVI	*Cynoglossum virginianum*	Herb
DECA8	*Desmodium canescens*	Herb
DEGL4	*Desmodium glabellum*	Herb
DEGL5	*Desmodium glutinosum*	Herb
DENU4	*Desmodium nudiflorum*	Herb
DEPA6	*Desmodium paniculatum*	Herb
DERO3	*Desmodium rotundifolium*	Herb
DESMO	*Desmodium* spp.	Herb
DIACF	*Dichanthelium acuminatum var. fasciculatum*	Graminoid
DIBO2	*Dichanthelium boscii*	Graminoid
DICHA2	*Dichanthelium* spp.	Graminoid
DICO2	*Dichanthelium commutatum*	Graminoid
DIDID	*Dichanthelium dichotomum*	Graminoid
DILI2	*Dichanthelium linearifolium*	Graminoid
DIQU	*Dioscorea quaternata*	Herb
DIVI5	*Diospyros virginiana*	Tree/Shrub
ELCA3	*Elephantopus carlolinianus*	Herb
ELHY	*Elymus hystrix*	Graminoid

Table B.5 continued

Species Code	Scientific Name	Functional Group
ELVI3	*Elymus virginicus*	Graminoid
ELYMU	*Elymus* spp.	Graminoid
ERAN	*Erigeron annuus*	Herb
ERHI12	*Erechtites hieraciifolius*	Herb
ERPH	*Erigeron philadelphicus*	Herb
EUCO10	*Euphorbia corollata*	Herb
EUPAT	*Eupatorium* spp.	Herb
EUPE3	*Eupatorium perfoliatum*	Herb
EUSE2	*Eupatorium serotinum*	Herb
FAGR	*Fagus grandifolia*	Tree/Shrub
FRAM2	*Fraxinus americana*	Tree/Shrub
FRCA2	*Frasera caroliniensis*	Herb
GAAS2	*Galium asprellum*	Herb
GACI2	*Galium circaezans*	Herb
GACO3	*Galium concinnum*	Herb
GATR2	*Galium trifidum*	Herb
GEMA	*Geranium maculatum*	Herb
GEUM	*Geum* spp.	Herb
GEVI4	*Geum virginianum*	Herb
GIST5	*Gillenia stipulata*	Herb
GLTR	*Gleditsia triacanthos*	Tree/Shrub
GNAPH	*Gnaphalium* spp.	Herb
GOPU	*Goodyera pubescens*	Herb
HAVI2	*Hackelia virginiana*	Herb
HAVI4	*Hamamelis virginiana*	Tree/Shrub
HEDI2	*Helianthus divaricatus*	Herb
HELIA3	*Helianthus* spp.	Herb
HEMI3	*Helianthus microcephalus*	Herb
HEST	*Helianthus strumosus*	Herb
HOPUP3	*Houstonia purpurea*	Herb
HYPER	*Hypericum* spp.	Herb
HYPU	*Hypericum punctatum*	Herb
IMCA	*Impatiens capensis*	Herb
IPPA	*Ipomoea pandurata*	Herb

Table B.5 continued

Species Code	Scientific Name	Functional Group
IRIS	*Iris* spp.	Herb
JUCI	*Juglans cinerea*	Tree/Shrub
JUNI	*Juglans nigra*	Tree/Shrub
JUTE	*Juncus tenuis*	Graminoid
JUVI	*Juniperus virginiana*	Tree/Shrub
KRBI	*Krigia biflora*	Herb
KRIGI	*Krigia* spp.	Herb
KRVI	*Krigia virginica*	Herb
LACA	*Lactuca canadensis*	Herb
LACTU	*Lactuca* spp.	Herb
LASE *	*Lactuca serriola*	Herb
LEFR5	*Lespedeza frutescens*	Herb
LEHI2	*Lespedeza hirta*	Herb
LEPR	*Lespedeza procumbens*	Herb
LERE2	*Lespedeza repens*	Herb
LESPE	*Lespedeza* spp.	Herb
LEVI6	*Lespedeza violacea*	Herb
LITU	*Liriodendron tulipifera*	Tree/Shrub
LOBEL	*Lobelia* spp.	Herb
LOIN	*Lobelia inflata*	Herb
LOJA *	*Lonicera japonica*	Vine
LUAL2	*Ludwigia alternifolia*	Herb
LUZUL	*Luzula* spp.	Graminoid
LYLA	*Lysimachia lanceolata*	Herb
LYQU2	*Lysimachia quadrifolia*	Herb
LYSIM	*Lysimachia* spp.	Herb
MARA7	*Maianthemum racemosum*	Herb
MIVI *	*Microstegium vimineum*	Graminoid
MOFI	*Monarda fistulosa*	Herb
MORU2	*Morus rubra*	Tree/Shrub
MORUS	*Morus spp.*	Tree/Shrub
NYSY	*Nyssa sylvatica*	Tree/Shrub
ONSE	*Onoclea sensibilis*	Herb
ORPE	*Orbexilum pedunculatum*	Herb

Table B.5 continued

Species Code	**Scientific Name**	**Functional Group**
OSVI	*Ostrya virginiana*	Tree/Shrub
OXALI	*Oxalis spp.*	Herb
OXST	*Oxalis stricta*	Herb
PALU2	*Passiflora lutea*	Herb
PAQU2	*Parthenocissus quinquefolia*	Vine
PHAM4	*Phytolacca americana*	Herb
PHLE5	*Phryma leptostachya*	Herb
PIEC2	*Pinus echinata*	Tree/Shrub
PIPU2	*Pilea pumila*	Herb
POAC4	*Polystichum acrostichoides*	Herb
POACEAE		Graminoid
POBI2	*Polygonatum biflorum*	Herb
POCA17	*Potentilla canadensis*	Herb
POLYG4	*Polygonum* spp.	Herb
POPE	*Podophyllum peltatum*	Herb
POPE3 *	*Polygonum persicaria*	Herb
POPU4	*Polygonatum pubescens*	Herb
PORE2	*Polemonium reptans*	Herb
POSI2	*Potentilla simplex*	Herb
PRAL3	*Prenanthes altissima*	Herb
PRENA	*Prenanthes* spp.	Herb
PRSE2	*Prunus serotina*	Tree/Shrub
PRTR	*Prenanthes trifoliolata*	Herb
PRVU	*Prunella vulgaris*	Herb
PSEUD43	*Pseudognaphalium spp.*	Herb
PYTE	*Pycanthemum tenuifolium*	Herb
QUAL	*Quercus alba*	Tree/Shrub
QUCO2	*Quercus coccinea*	Tree/Shrub
QUERC	*Quercus* spp.	Tree/Shrub
QUMO4	*Quercus montana*	Tree/Shrub
QUMU	*Quercus muehlenbergii*	Tree/Shrub
QURU	*Quercus rubra*	Tree/Shrub
QUST	*Quercus stellata*	Tree/Shrub
QUVE	*Quercus velutina*	Tree/Shrub

Table B.5 continued

Species Code	Scientific Name	Functional Group
RAHI	*Ranunculus hispidis*	Herb
RARE2	*Ranunculus recurvatus*	Herb
RHCO	*Rhus copallinum*	Tree/Shrub
RHGL	*Rhus glabra*	Tree/Shrub
RHUS	*Rhus* spp.	Tree/Shrub
ROCA4	*Rosa carolina*	Tree/Shrub
ROMU *	*Rosa multiflora*	Tree/Shrub
ROPS	*Robinia pseudoacacia*	Tree/Shrub
ROSA5	*Rosa* spp.	Tree/Shrub
RUAL	*Rubus allegheniensis*	Tree/Shrub
RUBUS	*Rubus* spp.	Tree/Shrub
RUCA4	*Ruellia carliniensis*	Herb
RUELL	*Ruellia* spp.	Herb
RUFL	*Rubus flagellaris*	Tree/Shrub
RUOC	*Rubus occidentalis*	Tree/Shrub
SAAL5	*Sassafras albidum*	Tree/Shrub
SALY2	*Salvia lyrata*	Herb
SAMBU	*Sambucus* spp.	Tree/Shrub
SANIC	*Sanicula* spp.	Herb
SCEL	*Scutellaria elliptica*	Herb
SCELE	*Scutellaria elliptica var. elliptica*	Herb
SCLER2	*Scleria* spp.	Graminoid
SCNE2	*Scutellaria nervosa*	Herb
SCOL2	*Scleria oligantha*	Graminoid
SCSC	*Schizachyrium scoparium*	Graminoid
SCUTE	*Scutellaria* spp.	Herb
SEHE3	*Senna hebecarpa*	Herb
SISYR	*Sisyrinchium* spp.	Herb
SMGL	*Smilax glauca*	Vine
SMRO	*Smilax rotundifolia*	Vine
SOCA3	*Solanum carolinense*	Herb
SOCA4	*Solidago caesia*	Herb
SOCA6	*Solidago canadensis*	Herb
SOHI	*Solidago hispida*	Herb

Table B.5 continued

Species Code	**Scientific Name**	**Functional Group**
SOLAN	*Solanum* spp.	Herb
SOLID	*Solidago* spp.	Herb
SORU2	*Solidago rugosa*	Herb
SOUL2	*Solidago ulmifolia*	Herb
SYMPH4	*Symphyotrichum* spp.	Herb
SYOR	*Symphoricarpos orbiculatus*	Tree/Shrub
SYSH	*Symphyotrichum shortii*	Herb
SYUN	*Symphyotrichum undulatum*	Herb
TARAX	*Taraxacum* spp.	Herb
TORA2	*Toxicodendron radicans*	Vine
TRAU4	*Triosteum aurantiacum*	Herb
ULAL	*Ulmus alata*	Tree/Shrub
ULAM	*Ulmus americana*	Tree/Shrub
ULMUS	*Ulmus* spp.	Tree/Shrub
ULRU	*Ulmus rubra*	Tree/Shrub
UVULA	*Uvularia* spp.	Herb
VAAR	*Vaccinium arboreum*	Tree/Shrub
VACCI	*Vaccinium* spp.	Tree/Shrub
VAPA4	*Vaccinium pallidum*	Tree/Shrub
VAST	*Vaccinium stamineum*	Tree/Shrub
VEAL	*Verbesina alternifolia*	Herb
VEHE	*Verbesina helianthoides*	Herb
VERBE	*Verbena* spp.	Herb
VERBE2	*Verbesina* spp.	Herb
VETH *	*Verbascum thapsus*	Herb
VEUR	*Verbena urticifolia*	Herb
VIAC	*Viburnum acerifolium*	Tree/Shrub
VIAE	*Vitis aestivalis*	Vine
VIBUR	*Viburnum* spp.	Tree/Shrub
VIOLA	*Viola* spp.	Herb

Table B.5 continued

Species Code	Scientific Name	Functional Group
VITR2	*Viola triloba*	Herb
VIPR	*Viburnum prunifolium*	Tree/Shrub
VIPU3	*Viola pubescens*	Herb
VIRU	*Viburnum rufidulum*	Tree/Shrub
VITIS	*Vitis* spp.	Vine
VIVU	*Vitis vulpina*	Vine
ZIAP	*Zizia aptera*	Herb

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