EVALUATING THE ROLE OF HERBICIDE USE TO CONSERVE WILD BEES IN WORKING LOBLOLLY PINE FORESTS

by

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

ABSTRACT

Working loblolly pine (*Pinus taeda* L.) forests rely on herbicides to remove understory plants and promote forest productivity, yet there has been limited research on herbicide effects on wild bees. During 2022-2023, I conducted a study in loblolly pine stands in the Piedmont region of Georgia. Stands of two stages (early post-establishment or thinned mid-rotation) underwent imazapyr application through either: 1) broadcast chemical site preparation (early post-establishment only); 2) broadcast chemical site preparation + banded herbaceous weed control (early post-establishment only); 3) broadcast woody release (midrotation only); or 4) control with no herbicide. I sampled bees with blue, yellow, and white pan traps and blue vane traps, and recorded stand basal area, understory floral resources, and canopy openness. Wild bee catches were similar among treatments for both stages and sampling years. While plant richness and cover were higher in untreated midrotation stands during both sampling years, herbicide treated stands had 29-46% higher bee richness in both years. My results indicate that herbicide treated stands may support pollinators through greater habitat heterogeneity, particularly through maintaining open habitat conditions that benefit soil nesting bees.

INDEX WORDS: Blue vane traps, forest management, herbicides, managed pine, native bees, pan traps, pollinators, understory plants, wild bees

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DEDICATION

To my parents, who have provided unwavering love and support for my scientific endeavors, even when it involves bringing thousands of bee specimens inside the house.

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INTRODUCTION AND LITERTURE REVIEW[1]

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1.1 Introduction

The southern United States is often referred to as the “wood-basket” of the world, largely due to its abundance of working pine forests (*Pinus* spp.) (Wear and Greis 2013). Loblolly pine (*P. taeda* L.) is a commonly planted species, along with shortleaf (*P. echinata* Mill.), longleaf (*P. palustris* Mill.), and slash (*P. elliottii* Engelm.) pines (Wear and Greis 2013). Working pine forests are a significant economic and ecological resource. In 2011, southern forest industries generated more than $250 billion in revenue, provided over a million jobs, and supplied almost $54 billion in income to local communities (Henderson et al. 2015). Pine forests also sequester carbon, offer wildlife habitat, prevent soil erosion, and protect water quality (Elliot et al. 1996; Lichter et al. 2008; Jones et al. 2009b; Shah et al. 2022). As such, southern forests are a regional and national treasure.

Demand for timber products is growing and the amount of pine acreage in the southern U.S. is expected to increase > 60% by 2040 (Wear and Gries 2002). Forest landowners rely on sustainable management practices such as site preparation, fertilization, thinning, herbicides, and prescribed fire to improve stand health and maintain or increase growth rates (Zhao et al. 2016). While prescribed fire effectively removes understory vegetation, there are many social, logistic, and safety constraints that preclude burning near highly populated areas (Provencher et al. 2001). Herbicides mimic natural fire disturbance by reducing hardwoods, promoting herbaceous cover, and preventing forest homogenization (Menges and Gordon 2010). In cases where prescribed fire is unfeasible or not preferred, land managers can rely on chemical use to control competing vegetation and meet forest management objectives (Wigley et al. 2002; Guynn et al. 2004). Planted pine productivity can increase dramatically as a result of varying herbicide application methods (e.g. chemical site preparation, herbaceous weed control, and midrotation woody release), with growth gains of 100% or more in some studies (Stewart 1987; Glover et al. 1989; Miller et al. 1991; Glover and Zutter 1993; Haywood 1994; Wagner et al. 2006; Zhao et al. 2008).

Chemical applications have a long history in forestry settings. Herbicides became particularly widespread in the 1960s and 1970s, when 2,4,5-T was used to reduce hardwood competition in planted pines (Fox et al. 2007). While 2,4,5-T was inexpensive and highly effective, there were concerns about its toxicity to non-target organisms and its registration for forestry use was canceled in 1979 (Fox et al. 2007). In the following years, alternative forest herbicides were developed with less potential for environmental harm (e.g., low mammalian/fish toxicity, rapid site degradation, and minimal off-site movement) (Neary et al. 1993; Fox et al. 2007). These new chemicals (including glyphosate, hexazinone, imazapyr, metsulfuron methyl, sulfometuron methyl, and triclopyr) were cost-effective and easy to apply, making them attractive alternatives to traditional vegetation control methods (Guynn et al. 2004; Fox et al. 2007). These products allowed for more frequent use and expansion of chemical applications in planted pine stands.

Herbicides are generally applied a maximum of 3-4 times (in many stands only 1-2 times) over the life of a southern working pine stand managed for sawtimber (~25-30 year rotations). Applications are typically on: 1) recently clearcut stands for site preparation before planting to reduce woody vegetation such as trees, shrubs, and vines; 2) newly planted seedlings (1-2 years) to reduce competition from herbaceous (grass or broadleaf weeds) vegetation; 3) juvenile (2-4 years) stands to control woody competitors not controlled during site preparation; and 4) midrotation (10-18 years) stands often in conjunction with thinning to reduce stocking of competing hardwood trees (Shepard et al. 2004; Fox et al. 2007; Cunningham 2008). In the

Coastal Plain region, herbicides are also used to clear forest understories and prepare stands for pine straw raking operations (Moorhead and Dickens 2015; Dickens et al. 2020b).

Many forest landowners attempt to optimize working forest management to protect and promote biodiversity. In 2017, approximately 38.6 million hectares of forestland were certified with at least one sustainable forestry certification system in the U.S., with roughly 39% of those certified hectares occuring in southern states (Alvarez 2018). These voluntary programs (e.g., American Tree Farm System, Forest Stewardship Council, and Sustainable Forestry Initiative) assure consumers that wood products are produced sustainably with minimal impacts on sensitive plant and animal species (Alvarez 2018). Current forest management guidelines recommend herbicides to improve forest productivity, facilitate regeneration, and restore ecological function (Society of American Foresters 2019). Given the objective of sustainable forest management to conserve biodiversity, it is important to understand how these chemical applications influence biological communities in working pine forests.

Of the roughly 2.16 million species described worldwide, flowering plants and insects constitute approximately 17% and 49% of global biodiversity respectively (IUCN Red List 2022). The North American Coastal Plain has been described as a global biodiversity hot-spot, in large part due to its 1,500 endemic plant species (Noss et al. 2015). Understory plant species are a small portion of forest biomass, but they contribute significantly to biodiversity, structure, and function, provide important ecological services, and support the long-term sustainability of working pine stands (Gilliam 2007; Jeffries et al. 2010). Multiple studies have concluded that there are few lasting effects of chemical application on plant communities (Miller et al. 1999; Boateng et al. 2000; Miller and Miller 2004), but floristic responses to herbicides are not universal, and can vary depending on climatic, edaphic, and geographic factors, especially if forests are subject to region-specific management practices.

Over one million insect species have been described worldwide—approximately 100,000 of which are found in North America (Stork 2018). Unfortunately, some terrestrial insect populations are experiencing global declines, with the orders Coleoptera, Hymenoptera, and Lepidoptera most at risk of future extinctions (Sánchez-Bayo and Wyckhuys 2019). These declines are likely related to anthropogenic threats such as habitat loss and change, pesticide exposure, invasive species, and climate change (Sánchez-Bayo and Wyckhuys 2019). Although insects are the most taxonomically diverse group in forest ecosystems, little is known about the non-target impacts of herbicides on their populations in southern forests (Wilson 1987; Guiseppe et al. 2006). Most research concerning forest herbicides and wildlife has been conducted on terrestrial vertebrates such as birds, mammals, and amphibians (Guiseppe et al. 2006). In comparison, insects are severely underrepresented in the field of wildlife science, with <1% of peer-reviewed publications including invertebrates as focal taxa (Grodsky et al. 2015). This knowledge gap is especially concerning since arthropod biodiversity is often positively correlated with surrounding plant phylogenetic diversity (Dinnage et al. 2012).

1.2 Response of Understory Plant and Insect Communities to Herbicides

Chemical Site Preparation

Selective herbicides are often applied via broadcast application to recently harvested stands to reduce competing vegetation and prepare for crop tree establishment (Lowery and Gjerstad 1991; Fox et al. 2007). Short-term negative effects of chemical site preparation (CSP) on herbaceous cover and species richness are well-documented (e.g., Blake et al., 1987; Miller et al., 1999; Lane et al., 2011), but multiple studies reported that herbaceous plants recover relatively quickly (<5 years) after initial herbicide exposure (Miller et al. 1999; Keyser et al. 2003; Jones et al. 2010; Addington et al. 2012; Cipollini et al. 2012; Knapp et al. 2014). By disturbing existing plant communities, CSP encourages high species turnover and promotes a greater expression of early successional herbaceous plants that may benefit disturbance adapted wildlife (Jones et al. 2012).

Soil properties can influence vegetation responses to CSP. Wilkins et al. (1993) evaluated changes in understory plant communities following increasing rates of hexazinone application (1.7, 3.4, and 6.8 kg/ha) along an edaphic gradient (xeric sandhill, mesic flatwood, and hydric hammock soils). Herbaceous species richness and diversity declined in the xeric sandhill, did not vary in the mesic flatwoods, and increased in the hydric hammock soil types. Hexazinone, a photosynthesis inhibitor, has application rates that are dependent on soil texture and organic matter content—sandier textured soils require less hexazinone to obtain adequate vegetation control than those with more clay and/or organic matter (Tu et al. 2001). In hydric hammock soil types, large quantities of hexazinone would be needed to offer any control of woody or herbaceous species. Hence, understory plant communities may have differential responses to CSP depending on abiotic factors.

Forest insect responses to CSP are likely taxa-specific and linked to changes in habitat conditions. Epigeal species, or those which inhabit the soil-litter surface, may be especially sensitive to CSP applications. Ants are dominant organisms in terms of abundance, biomass, and species diversity (~1,000 species in North America) in forest ecosystems (Gullan and Cranston 2000; Fisher and Cover 2007). These ubiquitous insects are dependent on understory plants for foraging and nesting resources and may be directly impacted by CSP applications (Hölldobler and Wilson 1990; Guiseppe et al. 2006). One study conducted in Malaysia tested the direct toxicity of glyphosate, triclopyr, and clethodim herbicides on the soil-dwelling ant species *Odontomachus simillimus* (Smith) (Zanuri & Khalik 2014). Although researchers did find an increase in ant mortality with increased herbicide exposure, mortality remained low when herbicides were applied within their permitted use concentrations. Lough (2003) evaluated the effects of glyphosate CSP on the abundance and diversity of ants in clearcut conifer stands over two years. In both young (3-5 years since clearcut) and mid-aged (10-15 years since clearcut) naturally regenerated stands, ant abundance was higher in chemically prepared sites with no difference in species diversity. Ant abundance was positively correlated with softwood stem density, indicating that CSP may affect forest ants by improving nesting sites (e.g., increased plant debris and greater soil exposure) or altering foraging habitat availability (Lough 2003; Guiseppe et al. 2006).

Carabid beetles are another common epigeal taxa in southern forests (Ward 1997; Iglay et al. 2012). With over 2,000 species described in North America, these highly diverse insects fulfill important roles as predators (and sometimes herbivores) in forest ecosystems and are sensitive to changes in ground-level habitat characteristics (Ciegler 2000; Riddick 2008; Iglay et al. 2012). Unlike many forest insect taxa, carabid responses to some forest management practices are well-studied, with most research evaluating the effects of prescribed fire or clearcut harvests on beetle assemblages (e.g., Niemela et al., 1993; Gandhi et al., 2001; Hanula et al., 2009). However, considerably less research has been conducted on carabid responses to forest herbicides (e.g., Ward, 1997; Duchesne et al., 1999; Iglay et al., 2012; Trager et al., 2013). Laboratory studies have identified negative physiological and behavioral effects of direct herbicide exposure on carabid beetles, but given the dispersal ability of these insects and the infrequent nature of herbicide treatments (one CSP application every ~25-30 years for stands managed for sawtimber), prolonged exposure to forest herbicides is unlikely (Kegel 1989; Brust 1990; Shepard et al. 2004; Iglay et al. 2012). Iglay et al. (2012) reported community and species-specific effects of imazapyr application on carabids in midrotation loblolly pine forests, with some beetle species exhibiting reduced abundance in treated stands. In contrast, Trager et al. (2013) found increased carabid abundance in northern hardwood stands the year following herbicide application and no differences in beetle species richness between control and herbicide treated plots. Carabid beetle assemblages likely shifted after chemical application, with herbicide treated stands supporting more open-habitat specialists tolerant of stand disturbances (Trager et al. 2013).

Herbaceous Weed Control

Land managers often apply herbicides one to two years after planting to temporarily suppress herbaceous weeds and reduce competition for soil moisture, nutrients, and growing space for newly planted seedlings (Lauer et al. 1993; Shepard et al. 2004). Multiple studies concluded that forb cover, species richness, and diversity recover relatively quickly from these applications (<10 years) or even exceed pretreatment diversity levels over time (e.g., Keyser et al. 2003; Lane et al. 2011; Marsh et al. 2012). However, application type can impact understory vegetation responses to herbaceous weed control (HWC) (Fig. 1). Marsh et al. (2012) reported decreased herbaceous cover of northern bobwhite (*Colinus virginianus* L.) forage plants in broadcast treated plots in comparison to a banded application in the first year following herbicide treatment. Similarly, Jones et al. (2010) noted that relative to banded application, broadcast spray reduced herbaceous cover in treatment years. Broadcast spray, which is applied non-selectively by air via helicopter or from the ground by skidder application, will affect a larger portion of the plant community than a more conservative banded application where herbicides are sprayed selectively in 1-1.5 m bands centered on crop trees (Miller and Miller 2004; Shepard et al. 2004; Dickens et al. 2020a). Banded applications may increase overall plant diversity over time by increasing wildlife habitat heterogeneity and creating multiple seral stages applications within a single stand (Miller and Miller 2004).

Forest insect responses to HWC are poorly studied and likely vary by taxa, chemical formulations, and application methods. Herbivorous insects consume leaf tissue and plant sap from phloem or xylem and HWC may indirectly impact their biology by altering the nutritional quality of host plants (Guiseppe et al. 2006). Hemipteran sap-sucking insects (e.g., aphids, leafhoppers, and scales) are biodiverse (~100,000 species globally) and commonly found in temperate forest ecosystems, but there has been little research on the effects of herbicides on their populations (Baker 1972; Stork 2018). Hemipteran abundance was similar between control and HWC treated sites in subtropical rainforest remnants (Nakamura et al. 2008) and southern loblolly pine stands (Iglay 2007). In contrast, glyphosate treatments reduced Hemipteran abundance in a northeastern conifer forest, while triclopyr had no effect on insect captures in the same study (Ward 1997). This discrepancy may stem from the selectivity of the two chemicals—unlike broad spectrum glyphosate, triclopyr has minimal effects on grasses, which could provide beneficial foraging resources for Hemipteran insects (Wigley et al. 2002).

Butterflies and moths are important pollinators, with over 140,000 flower-visiting species worldwide (Ollerton 2017). Many forest lepidopterans rely on herbaceous vegetation to complete their life-cycle, with caterpillars feeding on host plant material and adults consuming nectar from flowers (Chew and Robbins 1984). These insects may be exposed to HWC through both direct contact (spray drift/residues) or ingestion of plant material (Russell and Schultz 2010). Russel & Schultz (2010) assessed the direct effect of sethoxydim and fluazifop-*p*-butyl herbicides (two grass control herbicides that are labeled for HWC in southern pines) on the larval development of two butterfly species, the Puget blue (*Icaricia icarioides blackmorei* W. Barnes and McDunnough) and the cabbage white (*Pieris rapae* L.). Caterpillars and host plants were sprayed with the maximum labeled application rates recommended for spot spray for the two herbicides, with or without the addition of a soy-based nonionic surfactant in the spray solution. Cabbage white caterpillars experienced reduced survival, wing size, and pupal weights after both herbicide treatments, while the Puget blue exhibited reduced development time from the date of treatment to eclosure.

There may be two mechanisms by which herbicides reduce insect pupal weights: 1) herbicides may lower the amounts of sugar, nitrogen, and protein available in plant material, and 2) herbicide residues may have a repellent effect on larvae that stops or reduces feeding rates (Russell and Schultz 2010). Hence, land managers could reduce adverse effects on developing lepidopterans by applying herbicides in the late summer or early fall when larvae have entered diapause (Russell and Schultz 2010). This is when most herbicides are applied in southern forests—except for early spring HWC applications at the start of the first or second growing season when competition from herbaceous plants for soil moisture can be extreme for young planted pines (Shepard et al. 2004). Surfactants may also contribute to herbicide toxicity. These adjuvants are added to reduce the surface tension and spread of herbicide across plant tissues, or improve penetration of herbicides into plant tissue, but are not subject to the same toxicity testing requirements as active herbicidal ingredients (Tu et al. 2001; Tatum 2004). A lepidopteran twig miner species (*Leucoptera spartifoliella* Hübner) exhibited increased mortality after direct exposure of a silicone-based surfactant (Affeld et al. 2004). Surfactants may harm insects by damaging their protective waxy cuticle, which is important for gas exchange and water retention (Affeld et al. 2004). Yet, little is known about the effects of nonionic and methylated seed oil surfactants, the most common surfactants used in forestry foliar herbicide sprays, on herbivorous insect physiology and behavior (Tu et al. 2001).

Other studies have assessed the indirect effects of HWC on the Nantucket pine tip moth (*Rhyacionia frustrana* Comstock), a common lepidopteran pest in young regenerating southern pine stands (Ross et al. 1990, 2005; Nowak et al. 2003). Ross et al. (1990) observed an initial increase in tip moth damage in the first two years after HWC, but by the third growing season, damage rates were equal between treated and untreated stands. In a similar study, there were no differences in tip moth infestation rates between herbicide treated and untreated plots (Ross et al. 2005). In contrast, Nowak et al. (2003) found reduced tip moth pupal weights in herbicide treated plots, along with greater population fluctuations in comparison to untreated control sites. Decreased pupal weights may be associated with increased resin production. By removing competing vegetation and increasing tree vigor, HWC may help bolster pine defenses against lepidopteran pest species (Nowak et al. 2003).

Woody Release Treatments

Release treatments are used to control woody vegetation in early stand establishment (<10 years old) while growth rates are at their greatest if chemical site preparation is inadequate and in older midrotation stands after thinning to remove competing hardwood trees, and maintain or improve stand growth rates (Haywood 1995; Quicke et al. 1996; Shepard et al. 2004; Zapata-Curatas et al. 2021). Herbaceous plant diversity can recover quickly (even within 2-3 years) from woody release with no residual changes from pre-treatment conditions in both juvenile (e.g., Boyd et al., 1995; Brockway et al., 1998; Freeman and Jose, 2009) and midrotation (e.g., Harrington and Edwards, 1999; Harrington, 2011; Iglay et al., 2014) stands. Woody plant species richness and diversity has been shown to decrease after release treatments, but this reduction is expected given the nature of these applications (Brockway et al. 1998; Miller et al. 2003). Herbicides formulated for hardwood control may have fewer impacts on herbaceous plants in established pine stands. Triclopyr is commonly applied for spot or broadcast control of woody plants but does not impact most graminoid species (Wigley et al. 2002).

Herbaceous cover is similarly quick to rebound following woody release treatments, with some studies even reporting slight increases in herbaceous cover over time (Welch et al. 2004; Jones et al. 2009a; Outcalt and Brockway 2010; Harrington 2011; Turner et al. 2020). With a reduction in competitive woody species, forest stands are more open with increased understory light availability—conditions that support diverse plant and pollinator communities (Hanula et al. 2015). Cain (1999) observed reductions in herbaceous plant cover following an early post-stand establishment release treatment, but this study is likely an outlier since intensive herbicides were applied continuously over a 4-5 year period, which is not representative of typical southern pine silvicultural practices. As southern pine stands mature, herbaceous cover will naturally decline over time without regular canopy disturbances (e.g., additional thinning, prescribed fire, tree mortality, and natural disturbances). Campbell et al. (2015) reported decreases in herbaceous cover in partially or fully closed canopy stands, primarily as a result of reduced understory light availability. Hence, woody control is likely most impactful on understory plant communities in early post-establishment stands prior to canopy closure or in older, midrotation stands after thinning (Jones et al. 2012).

Release treatments may have more lasting effects on understory plant species composition in southern forests. Boyd et al. (1995) noted residual changes in overstory, shrub, and herbaceous layer species composition seven years after woody release in early post-establishment pine stands. American persimmon (*Diospyros virginiana* L.), water oak (*Quercus nigra* L.), and blueberries (*Vaccinium* spp.) decreased in abundance, while sawtooth blackberry (*Rubus argutus* Link) and legumes became more dominant. In midrotation pine stands, Oswald et al. (2009) found that shrubs such as American beautyberry (*Callicarpa americana* L.) and yaupon holly (*Ilex vomitoria* Ait.) were reduced two years after hardwood release, while abundance of Virginia creeper (*Parthenocissus quinquefolia* L.), ground-cherry (*Physalis* spp.), and green indigo (*Baptisia sphaerocarpa* Nutt.) increased in herbicide treated plots. By removing woody vegetation, release treatments increase species turnover and promote early successional and disturbance adapted plant species (Jeffries et al. 2010; Jones et al. 2012).

Herbicides such as glyphosate and imazapyr are broad spectrum and impact a wide range of plant species, while other chemicals target specific plant taxa (Wigley et al. 2002). Metsulfuron is highly effective at suppressing blackberry (*Rubus* spp.) cover as well as some woody and grass species, whereas broad spectrum imazapyr does not control blackberries or legumes and is favorable for many wildlife management goals (Wigley et al. 2002; Miller and Miller 2004; Iglay et al. 2010a). Glyphosate poorly controls some woody species such as hickory (*Carya* spp.) and dogwood (*Cornus florida* L.) and some waxy, thick-leaf cuticle shrub species such as gallberry [*Ilex glabra* (L.) Gray], fetterbush [*Lyonia lucida* (Lam.) K. Koch], and saw palmetto [*Serenoa repens* (Bartram) Small] (Shiver et al. 1991). Some broadleaf weeds and grasses are naturally resistant or have developed resistance to glyphosate such as field horsetail (*Equisetum arvense* L.), morning-glories (*Ipomoea* spp.), yellow nutsedge (*Cyperus esculentus*

L.), horseweed or mare's tail (*Conyza canadensis* L.), Palmer amaranth (*Amaranthus palmeri* S. Wats.), and dayflower species (*Commelina* spp.) (Boerboom and Owen 2006). Sethoxydim and clethodim reduce graminoid cover with few effects on surrounding broadleaf weeds, while triclopyr has little impact on grass and sedge abundance (Wigley et al. 2002). Land managers should consider the potential effects of different chemicals on specific plant taxa before application since these long-term compositional shifts will undoubtably impact wildlife resource availability.

Herbaceous plant responses to release treatment may vary with labeled herbicide application rates. Brockway et al. (1998) applied two rates of liquid hexazinone (1.1 and 2.2 kg/ha) to early post-establishment longleaf pine stands. While both application rates removed competing woody vegetation, the 2.2 kg/ha treatment was most effective at increasing wiregrass (*Aristida stricta* Michx.) cover. In general, the application rates represented in the reviewed studies are likely too low to cause significant adverse effects on herbaceous plant communities. Since forest herbicides are expensive to produce and apply, land managers are incentivized to use the lowest labeled application rates of the product as possible to control competing vegetation. According to a 1999 survey of timber companies by the National Council for Air and Stream Improvement (NCASI), average herbicide application rates are typically far lower than the highest rates allowed by product labels (Shepard et al. 2004).

Release treatments have the potential to influence forest insect communities by altering understory floral resource availability. Wild bees provide essential pollination services in natural environments and contribute to forest ecosystem function through assisting in plant regeneration, enhancing biodiversity (~4,000 species in North America), and creating habitat for other species through their nesting behavior (Kearns et al. 1998; Morato and Martins 2006; Michener 2007;

Neuschulz et al. 2016). Direct herbicide exposure has been shown to negatively impact wild bees through both increased mortality and sub-lethal impairment of reproductive and foraging behavior (Abraham et al. 2018; Belsky and Joshi 2020; Araújo et al. 2021; Graffigna et al. 2021). However, direct exposure is likely a rare occurrence in working forests, since herbicides are applied sparingly (usually <3 applications per stand rotation) and the uptake or drying of herbicides occurs quickly (<24-hour restricted entry intervals for many products) (Shepard et al. 2004; Tatum 2004; Lambert et al. 2020).

Little research exists on the indirect effects of woody vegetation control on wild bee populations. Bried and Dillon (2012) found no differences in bee species richness between control plots and those that received a combined woody release and mowing treatment in pitch pine (*Pinus rigida* Mill.) scrub oak barrens. In southern forests, pine stands with open canopies and little shrub cover support the most abundant and species rich wild bee communities (Hanula et al. 2015). By removing dense shrub cover and midstory hardwoods, woody release treatments increase understory light levels and may improve floral resource availability for pollinating insects (Miller and Wigley 2004). Future research may also address how woody vegetation control impacts nesting resources for wild bee species—30% of which rely on woody debris (e.g., decaying wood, pithy stems, and abandoned wood-boring beetle holes) to complete their lifecycle (Bloom et al. 2022).

1.3 Goals and Objectives of the Thesis

Chapter 2: Forest Herbicide Treatments Support Wild Bee Populations and Communities in Working Loblolly Pine (*Pinus taeda* L.) Stands

The use of pesticides with regard to pollinator conservation has come under heightened scrutiny in recent years, yet limited research has been conducted on the indirect effects of herbicide application on wild bee communities in forested ecosystems (Bried and Dillon 2012; Iwasaki and Hogendoorn 2021). This knowledge gap is especially concerning since working pine forests, which are an important economic and ecological resource across the southern United States, rely on herbicide application to manage understory plant cover and maintain or increase forest productivity (Miller & Wigley, 2004; Moore et al., 2013). Wild bee communities in these systems may be negatively impacted by commonly used herbicide application methods, and as a result, their critical pollination services may be limited.

To conserve pollinators in working forests, we completed a multi-year study to evaluate the indirect effects of herbicides on wild bee communities. Results from this project will allow us to determine how wild bee species, as mediated through their interactions with understory plant communities, respond to different herbicide application methods in early and mid-rotation loblolly pine stands. The overall goal of this research was to identify herbicide application methods that both increase yields in working loblolly pine forests and conserve wild bee communities and their vital pollination services.

Our first objective was to evaluate the indirect effects of herbicide use on wild bee populations and communities over a two-year period. We assessed bee communities by multiple metrics including: 1) abundance, or the number of bees captured in sampling traps; 2) species diversity, which was measured by raw species richness and rarefied species richness; 3) functional diversity, or the evenness and dispersion of different bee functional groups; and 4) species composition, which was assessed with multivariate analyses. Our second objective was to assess changes in understory plant communities as a result of forest herbicide use with direct links to wild bee responses. Understory plant community metrics included: 1) percent understory plant cover; and 2) understory plant species richness.

Chapter 3: Understory Plant Community Responses Following Imazapyr Herbicide Application in Georgia Loblolly Pine Forests

Modern forest management relies on herbicide application to control competing vegetation and promote forest productivity in managed pine stands (Wagner et al. 2004). Since understory plants provide essential foraging resources for native pollinators and other wildlife, it is important to understand the potential impacts of herbicide use on their abundance and community structure (Hanula and Horn 2011; Ulappa et al. 2020). Herbicide use may benefit flower-visiting insects by removing dense woody shrub cover, which often stunts understory herbaceous plant growth and limits available floral resources (Freeman and Jose 2009; Hanula and Horn 2011). Conversely, herbicide application may cause long-term impacts to the abundance and species composition of understory plant communities—possibly by reducing total understory plant cover and triggering unprecedented changes to the surrounding forest ecosystem (Strong and Sidhu 2005; Ulappa et al. 2020).

The goal of our research was to understand the effects of different imazapyr herbicide application methods on understory plant communities in working loblolly pine forests. We assessed changes in the understory plant communities using various metrics including: 1) total percent understory plant cover; 2) percent cover per plant species; 3) species diversity; and 4) species composition. By sampling stands for two consecutive years, we tracked changes in understory plant communities over time. It is critical that we understand the potential timeline of herbicide impacts on understory plants to ensure that land managers are employing forest management practices that are sustainable for years to come.

While multiple studies have found that the impacts of forest herbicides on understory plant communities are generally short-lived (subsiding after less than a decade), it is important to assess if this pattern persists in southern loblolly pine plantations (Keyser et al. 2003; Freeman and Jose 2009; Peter and Harrington 2018). If the impacts of herbicides do persist long-term in these forests, ecosystem services may be limited, since understory plants are vital to the success of threatened pollinator species, in addition to other wildlife such as ungulates and small mammals (Carey and Harrington 2001; Proctor et al. 2012; Ulappa et al. 2020). By understanding the effects of different herbicide application methods on understory plant communities over time, land managers can create forest management plans that preserve biodiversity and ecosystem function, while also promoting forest productivity and economic growth.

CHAPTER 2

FOREST HERBICIDE TREATMENTS SUPPORT WILD BEE POPULATIONS AND COMMUNITIES IN WORKING LOBLOLLY PINE (*Pinus taeda* L.) STANDS[2]

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2.1 Abstract

Working loblolly pine (*Pinus taeda* L.) forests rely on herbicides to remove understory plants and promote forest productivity, yet there has been limited research on herbicide effects on wild bees. The objectives of our study were to: 1) evaluate the indirect effects of different herbicide application methods on wild bees over a two-year period; and 2) determine linkages between changes in understory plants and wild bee responses. In 2022-2023, we sampled loblolly pine stands in the Piedmont region of Georgia. Stands of two stages (early post-establishment or thinned midrotation) underwent imazapyr application through either: 1) broadcast chemical site preparation (early post-establishment only); 2) broadcast chemical site preparation + banded herbaceous weed control (early post-establishment only); 3) broadcast woody release (midrotation only); or 4) control with no herbicide. We sampled bees with pan and blue vane traps, and also recorded stand basal area, understory floral resources, and canopy openness. We captured 7,975 bees from 114 species, indicating a rich bee community in these stands. Total wild bee catches, functional dispersion, and functional evenness were similar among treatments for both stages and sampling years. Early post-establishment rarefied bee species richness was positively correlated with understory plant cover in the second sampling year, but all early post-establishment treatments had similar bee richness. Bare ground cover signifcantly explained bee species composition and six soil-nesting indicator species were associated with early post-establishment treatments. In midrotation stands, bee catches and rarified species richness were negatively correlated with understory plant richness in the first and second sampling years, respectively. Midrotation treated stands had 29-46% greater bee richness than controls in both years. These stands were also associated with a greater number of snags, wood decay, and bare ground cover than untreated stands. Overall, our results indicate that there

were minimal impacts of herbicide applications on wild bees in early post-establishment stands, and that midrotation hardwood release herbicide treatments supported species rich pollinator communities.

2.2 Introduction

Wild bees (Hymenoptera: Apoidea) provide essential pollination services in both forested and agricultural environments. Over 20,000 species of bees have been described globally, with approximately 4,000 species found in North America alone (Michener 2007). These diverse insects contribute significantly to ecosystem functioning through assisting in plant regeneration, enhancing local plant biodiversity, and creating habitat for other species through their nesting behavior (Kearns et al. 1998; Morato and Martins 2006; Neuschulz et al. 2016). Unfortunately, there is evidence that some wild bee populations are declining, in part due to anthropogenic stressors such as pesticide exposure, habitat loss and change, introduced diseases, and climate change (Potts et al. 2010). In comparison to domesticated European honeybees (*Apis mellifera* L.), wild bees are more efficient pollinators of many crop plants indigenous to the Americas, including blueberries and cranberries (*Vaccinium* spp.), pumpkins and squashes (*Cucurbita* spp.), and nightshades such as tomatoes (*Solanum lycopersicum* L.) and eggplants (*S. melongens* L.) (Moisset and Buchmann 2011). Hence, wild bee population declines may harm agricultural yields, in addition to other negative impacts on the integrity and functioning of forested ecosystems (Garibaldi et al. 2013).

Forested ecosystems are important repositories for wild bees and provide both forage (e.g., pollen and nectar) and nesting (e.g., mud, leaves, and resin) resources (Winfree et al. 2007; Roulston and Goodell 2011). Forests may be particularly important for obligate wood-nesting species, or those that must nest in deadwood or tree cavities (Michener 2007). In a pine-oak heath ecosystem, wood-nesting bee species were associated with extensive forest cover on a local scale (Winfree et al. 2007). In Californian agricultural fields, crop pollination services were positively correlated with proximity to forests, suggesting that wild bee populations likely rely on forest ecosystems for some critical resources (Kremen et al. 2004). Despite the potential value of forest ecosystems in supporting pollinator biodiversity, few studies have assessed wild bee communities in these habitats (Rivers et al. 2018).

The southern United States is often referred to as the “wood-basket” of the world on account of its ~39 million ha of working pine (*Pinus* spp.) forests (Wear and Greis 2013). In addition to other silvicultural practices, herbicides are often applied to these working pine stands to remove competing vegetation and improve site productivity (Miller and Wigley 2004). The U.S. Environmental Protection Agency has registered over a dozen different herbicide formulations for use in forest management and other vegetation control practices (USEPA 2023). Applications of these herbicides typically occur on: 1) recently clearcut stands for site preparation before planting to reduce woody vegetation such as trees, shrubs, and vines; 2) newly planted seedlings (1-2 years) to reduce competition from herbaceous vegetation; 3) juvenile (2-4 years) stands to control woody competitors not controlled during site preparation; and 4) midrotation (10-18 years) stands in conjunction with thinning to reduce competing hardwood trees (Shepard et al. 2004; Fox et al. 2007; Cunningham 2008). Planted pine productivity can increase dramatically (sometimes growth gains of > 100%) as a result of herbicide treatments (Stewart 1987; Glover et al. 1989; Miller et al. 1991; Glover and Zutter 1993; Haywood 1994; Wagner et al. 2006; Zhao et al. 2008).

Multiple studies have reported few lasting effects of herbicide applications on understory plant communities (Miller et al. 1999; Boateng et al. 2000; Miller and Miller 2004). However, the potential effects of herbicides on pollinator communities, which rely on flowering plants for both food and nesting resources, are less clearly understood (Neill and Puettmann 2013; Fortuin and Gandhi 2021). In planted pine forests, early establishment and thinned, midrotation stands with open canopies and little shrub cover support the most abundant and species rich wild bee communities (e.g., Hanula et al. 2015; Odanaka et al. 2020; Fortuin and Gandhi 2021; Favorito et al. 2023). By reducing woody shrub cover and midstory hardwoods, herbicides may increase understory light levels and improve floral resource availability for pollinating insects (Miller and Wigley 2004). Further, herbicides may also impact wild bees by altering nesting habitat, since 30% of species rely on woody debris (e.g., decaying wood, pithy stems, and abandoned wood-boring beetle holes) to complete their life-cycles (Bloom et al. 2022).

Direct herbicide exposure has been shown to negatively impact wild bees through both increased mortality and sub-lethal impairment of reproductive and foraging behavior (Abraham et al. 2018; Belsky and Joshi 2020; Araújo et al. 2021; Graffigna et al. 2021). However, limited research has been conducted on the indirect effects of herbicides on wild bees on a population or community scale, and the studies that have been completed have largely taken place in agricultural environments (Pardo et al. 2020; McDougall et al. 2021). Bried & Dillon (2012) found no differences in bee species richness between control plots and those that received a combined woody release and mowing treatment in pitch pine (*P. rigida* Mill.) scrub oak barrens. However, the mechanisms by which forest herbicides can impact wild bees—whether they stem from changes in floral resources or nesting habitat availability—are poorly understood.

Hence, the goal of our study was to assess how herbicide applications influence wild bees in both early establishment and midrotation planted pine forests in the southern U.S. Our research objectives were to: 1) evaluate the indirect effects of herbicide treatments on wild bee populations and communities over a two-year period; and 2) determine linkages between changes in understory plant communities and wild bee responses. This study will provide critical information on how herbicides may be used to increase site productivity and meet forest management objectives in working pine stands, while also conserving wild bees and their vital pollination services.

2.3 Methods

Study Sites & Herbicide Treatments

The study was conducted in privately owned loblolly pine (*P. taeda* L.) stands in the Piedmont ecoregion of Georgia (approximately 33°20’ N, 83°4’ W), where the herbicide imazapyr is commonly used to control competing vegetation (Dickens et al. 2020a). Stands were dominated by loblolly pine trees and saplings, with a minor hardwood component composed of sweetgum (*Liquidambar styraciflua* L.), winged elm (*Ulmus alata* Michx.), and red maple (*Acer rubrum* L.). In 2020, the average annual temperature for all stands was 18 ± 0.08 °C, the average annual precipitation was 167.4 ± 1.70 cm, and the average elevation was 151.15 ± 5.09 m (PRISM Climate Group 2020). Common soils in this area included sandy loam, clay loam, and loamy sands in the Ultisol soil order (NRCS 2022).

Planted loblolly pine stands belonging to two successional stages received the following imazapyr (N = 20, four stands per treatment):

1) Early post-establishment stands (0-2 years old)

    a. control with no herbicide
    b. chemical site preparation (aerial broadcast spray)
    c. chemical site preparation (aerial broadcast spray) + first-year herbaceous weed control (banded application)
2) Midrotation, thinned (20 years old)
    a. control with no woody release
    b. woody release (broadcast spray)

Early post-establishment and thinned midrotation stands were chosen since herbicides are most often applied to these stand stages, and their relatively open canopies will likely support large pollinator populations (Hanula et al. 2015; Mathis et al. 2021). Early post-establishment chemical site preparation (CSP) and midrotation woody release broadcast herbicide treatments were applied in the summer and early fall of 2020, and the early post-establishment herbaceous weed control (HWC) banded application occurred in the spring of 2021. Since this study occurred in operational timber stands, all three herbicide application treatments (control, broadcast, and banded) were not tested in each stand stage. Specifically, banded herbicide applications are not a standard forest management practice in midrotation stands (land managers instead use either ground or aerial broadcast applications).

All study stands were > 5 ha in size and located > 1 km apart to minimize sample dependence. Larger stands were preferred since wild bee species richness has been shown to increase with habitat patch size, possibly as a result of increased floral diversity and microhabitat availability in larger habitat patches (Steffan-Dewenter 2003; Steffan-Dewenter et al. 2006; Lázaro et al. 2020). Additionally, all selected stands were fire excluded and the early post-establishment stands did not receive mechanical site preparation. Midrotation stands received either a chemical or mechanical site preparation treatment.

We conducted the study over the summers of 2022 and 2023. The same stands were used for both years, except for the early post-establishment control treatment stands, which were replaced since two-year-old early post-establishment stands without chemical site preparation or herbaceous weed control treatments are not an operational reality. Within each stand, we established three 10 m radius circular sampling plots. These three plots were located ≥ 50 m from the stand edge to avoid unforeseen edge effects and ≥ 50 m from the nearest sampling station to minimize dependency between plots. In total, we established 120 sampling plots during the two-year study (20 stands x 3 plots per stand x 2 years).

Stand Attributes

We recorded stand attributes for each sampling plot in the middle of the sampling season (June/July) in 2022 and 2023. Data collected included the number of logs (> 10 cm DBH) and snags (> 5 cm DBH) and their decay class (1-5) and the percent canopy openness at the plot center (Mills and MacDonald 2004; Woodall and Monleon 2007). For midrotation stands, we recorded all tree species present and their diameter at breast (DBH) within a 10 m radius of the plot center, which was used to calculate basal area (Table 2.1). Additionally, we recorded the heights of the five loblolly pine trees located closest to each sampling plot. Canopy openness and tree height were estimated using a spherical densiometer and clinometer respectively.

Within each circular sampling plot, we also established four 1 m^2 quadrats located approximately 5 m from the plot center in the four cardinal directions. Within each quadrat, we visually estimated the percent of understory plant cover, dead vegetation, litter fall, bare ground, and woody debris. We also measured the litter depth (cm), number of hollow stems/twigs, and decay class (1-5) of woody debris. Understory plant species and their percent dominance were recorded (Weakley 2022); however, all graminoid species were grouped as “grasses” since they can be difficult to identify to species level and are typically pollinated by abiotic factors (Wiegmann and Waller 2006).

Wild Bee Sampling

We sampled wild bees in each circular sampling plot for two growing seasons following herbicide application using three colored pan traps (blue, white, and yellow) and blue vane traps (Campbell and Hanula 2007; Favorito et al. 2023). Each pan trap was placed at the edge of the sampling plot (~5 m from the center) at an approximately 120° angle from each other (Figure 2.1). The pan traps consist of ~4 oz plastic bowls that were placed together in clusters to attract flower visitors. The bowls were filled with a mixture of one part propylene glycol and three parts water and a small amount of odorless dish soap to break the surface tension. To mimic surrounding floral resources in the stand, the pan traps were elevated ~0.5 m off the ground using a plant wire stake.

Blue vane traps, which capture large-bodied pollinators, were also deployed alongside the pan traps in both the understory and midstory (Gibbs et al. 2017). The vane traps (SpringStar, Inc.) consist of a 1.9 L yellow collecting jar which is connected to two interlocked ultraviolet semitransparent blue polypropylene vanes using a screw top funnel. Floral visitors mistake the colorful blue vanes for flowers, enter the funnel, and are trapped in the collecting jar which is filled with the same propylene glycol and soapy water mixture used in the pan traps. One understory blue vane trap was placed in the center of each sampling plot and raised ~1.5 m off the ground using a garden stake. An additional midstory blue vane trap was elevated ~8-10 m off the ground in the nearest suitable loblolly pine tree to each sampling plot to capture bees higher in the canopy.

Both the blue, yellow, and white pan traps and the blue vane traps were deployed for one week per month during May – September in 2022 and 2023, with the traps emptied and redeployed after three days. We collected all trap catches, drained the liquid, and stored the insects in the freezer until they could be sorted to separate any captured wild bees from the other insect bycatch. To prepare the wild bees for pinning and identification, we washed all specimens with water and dish soap and dried them using a small clothes dryer (Panda Appliances Co Ltd, model PAN725SF; Nanjing, China). After the wild bees had been processed and pinned, we identified them to species level using taxonomic keys including Gibbs (2010), Gibbs (2011), and Discover Life online keys (Ascher and Pickering 2020). Sam Droege (United States Geological Survey) and Elsa Youngsteadt (North Carolina State University) also assisted with species identifications.

After identification, we assigned each wild bee species to functional groups according to their body length, sociality, preferred diet, flight season, and preferred nesting substrate (Mitchell 1960; Michener 2007; Gibbs 2011; Williams et al. 2014; Wilson and Messinger 2015; Ascher and Pickering 2020; Fortuin and Gandhi 2021; Messinger and Wilson 2021; Favorito et al. 2023):

- Body Length: Species were classified as either small (3.5-9 mm), medium (9.5-15 mm), or large (15.5-22 mm) based on the length from their head to abdomen.
- Sociality: Species were classified as either social or solitary. Bees were considered social if they form colonies with cooperation between multiple adult

females. Species were considered solitary if adult females independently create and provision their own nests, without help from other individuals.

- Diet: Species were classified as oligolectic or polylectic. Oligolectic species are specialists that forage on specific plant taxa (often a single plant family or genus), while polylectic species are generalists that visit a variety of plant species.
- Flight Season: Species were designated as early-season (most active February – April), mid-season (most active May – June), or late-season (August – October). We determined peak flight season through published literature and our study data.
- Nesting Substrate: Species were assigned to one of six preferred nesting substrate categories.
    1. Soil: Species that excavate soil to create nests in the ground.
    2. Pre-existing Cavities: Species that nest in pre-existing cavities, including abandoned rodent burrows and anthropogenic structures.
    3. Deadwood: Species that nest in undecayed deadwood or pithy stems. These species may or may not actively excavate their nests.
    4. Softwood: Species that excavate nests in decaying wood.
    5. Litter: Species that nest in dead plant material on the ground, including leaf litter, wood piles, and the organic soil layer. These species typically do not actively excavate their nests.
    6. Occupied: Cleptoparasitic species that lay their eggs in the nests of other bee species.

Statistical Analyses

We conducted all analyses in R [version 4.1.3, (R Core Team 2022)] with a significance level of $\alpha = 0.05$. The unit of replication was the individual stand and bee catches were aggregated for all traps in a stand over the entire trapping season for each sampling year (N = 20). Catches from different trap types, colors, and heights were grouped for our analyses. We tested the normality of residuals for the total bee catches using the Shapiro-Wilks test and all catch data were normally distributed. One-way Analysis of Variance (ANOVA) tests and two-sample t-tests were used to determine if total bee catches varied among the herbicide treatments respectively, in the early post-establishment and midrotation stand stages. We also used two-sample t-tests to determine if total bee catches differed by vane trap height (understory vs. midstory) in midrotation stands. ANOVAs were followed by Tukey's post-hoc tests to determine which groups significantly differed from one another.

Four species [*Bombus impatiens* (Cresson), *Lasioglossum floridanum* (Robertson), *Melissodes bimaculatus* (Lepeletier), and *M. communis* (Cresson)] represented > 5% of the total bee catches. We used one-way ANOVAs and two-sample t-tests to determine if total bee catches of these common species varied among the different herbicide treatments. Shapiro-Wilks tests indicated that the residuals of *L. floridanum*, *M. bimaculatus*, and *M. communis* were not normally distributed for some combinations of stand stage and study year. These catch data were square root-transformed and one-way ANOVAs were reperformed on the transformed data. Residuals that could not be normalized using a transformation were analyzed using the non-parametric Kruskal-Wallis test. Any significant models were followed by the Dunn test with the Bonferroni p adjustment for multiple comparisons.

We evaluated bee diversity among herbicide treatments using two measures of alpha diversity: 1) species richness, and 2) rarefied species richness using individual-based rarefaction (R package “vegan”) (Whittaker 1972; Oksanen et al. 2020). Rarefaction was applied to the lowest bee catch sample size, or the lowest number of bees captured at an individual stand. We analyzed both species richness and rarefied species richness using one-way ANOVAs, two-sample t-tests, and Tukey’s post-hoc tests to determine if bee diversity metrics varied among stand stages and sample years. All residuals were tested using the Shapiro-Wilk test, and residuals that could not be normalized using a square root transformation were analyzed with the Kruskal-Wallis test, and if significant, were analyzed with the Dunn test with Bonferroni *p* adjustments for multiple comparisons.

We used canonical correspondence analysis (CCA) to determine which habitat characteristics explained a significant amount of variance in bee species composition among herbicide treated stands (R package “vegan”). CCA combines regression and ordination methods to assess the influence of environmental variables on species composition, using a site by species matrix as the response variable and stand attributes as predictor variables. We first used a square-root function to transform bee species catches to reduce the influence of large captures. The CCA axes were then constrained by the habitat characteristics measured for their stand stage. Early post-establishment variables included percent understory plant cover, dead vegetation, bare ground, woody debris, and litter, litter depth (cm), coarse woody debris decay, and the number of snags, logs, and hollow stems. Midrotation analyses included three additional variables: tree basal area (m^2/ha), tree density (trees/ha), and total tree height (m). We used variance inflation factors (VIFs) to check for redundancy in the predictor variables, with VIFs <10 treated as acceptable (Vittinghoff et al. 2012). Two early post-establishment variables (percent litter cover and litter depth) and five midrotation variables (tree basal area, tree height, and percent cover of litter, woody debris, and dead vegetation) were dropped to achieve predictor variable VIFs <10. We then tested the significance of the two overall CCAs and each explanatory habitat characteristic to determine if the models explained more variance than would be expected by chance.

Indicator species analyses were used to determine if any bee species were associated with a particular herbicide treatment in each stand stage or with understory or midstory vane traps in midrotation stands. Only species with > 20 individuals were included in these analyses. We used the R package “indispecies” and the multi-level pattern analysis (“multiplatt”) function, which measures the association between species distribution and groups of sites (DeCacers and Legendre 2009). We also used the indicator value index (“Ind.val.g”) species-site group association function and tested the significance of the associations with a permutation test with 9,999 permutations (Dufrene and Legendre 1997).

We assessed functional group diversity with two metrics: 1) functional dispersion, and 2) functional evenness. Functional dispersion (FDis) is a measure of variability in functional group composition, and is considered an equivalent of beta diversity, or the ratio of local and regional species diversity across sites (Whittaker 1972; Anderson et al. 2006). We assessed functional dispersion by measuring the spread of individual species in a multivariate space defined by their traits, or the distance of each species from the centroid, which is then weighted by the relative abundance of each species (Laliberte and Legendre 2010). In contrast, functional evenness (FEve) is a measure of how evenly species functional traits are distributed in multivariate space (Villeger et al. 2010). We calculated these metrics with the “FD” package in R, using the Distance Based Functional Diversity Indices (“dbFD” function) (Laliberte et al. 2014). We classified each bee species under five functional trait categories: 1) nesting substrate; 2) sociality; 3) diet breadth; 4) flight season; and 5) size class. We generated a species-species distance matrix and conducted a Principal Coordinates Analysis (PCoA). We then compared the resulting FEve and FDis values among herbicide treatments for each stand stage using one-way ANOVAs and two-sample t-tests. Shapiro-Wilks tests were used to test all residuals. Non-normal residuals were analyzed using the Kruskal-Wallis test, followed by the Dunn test with Bonferroni adjustments for multiple comparisons.

We used Ordinary Least Squares (OLS) regressions to assess whether there were significant linear relationships between bee community variables (catches and rarefied species richness) and understory plant community variables (species richness and average percent cover) at the plot level in 2022 and 2023. Four separate linear models were run using the lm function with default settings in R for each stand stage and sampling year: 1) understory plant species richness was regressed with bee catches; 2) understory plant species richness was regressed with bee rarefied richness; 3) percent plant cover was regressed with bee catches; and 4) percent plant cover was regressed with bee rarefied richness.

2.4 Results

We captured 7,975 individual bees from 114 species during 2022-2023. Non-native, domestic European honeybees (*Apis mellifera* L.) (112 individuals) were excluded from analyses. Ninety-four individuals from the genera *Andrena*, *Ceratina*, *Colletes*, *Lasioglossum*, *Megachile*, and *Melissodes* could only be identified to the genus-level due to specimen damage (Table 2.2). Four species of bees were common, making up > 5% of all trap catches: 1) *L. floridanum* (1164 individuals; 14.39% of total); 2) *M. bimaculatus* (726 individuals; 8.98% of total); 3) *B. impatiens* (641 individuals; 7.93% of total); and 4) *M. communis* (620 individuals; 7.67% of total).

Total bee catches were similar among treatments for both stand development stages and sampling years ($p = 0.264-0.704$). Catches of these common species were also not different among herbicide treatments in either stand development stage ($p = 0.116-0.967$). Early post-establishment stands had similar bee species richness and rarified species richness among treatments for both sampling years ($p = 0.06-0.996$). However, midrotation woody release broadcast treated stands had 46% [$t_{(6)} = 2.84$, $p = 0.03$] and 29% [$t_{6)} = 3.02$, $p = 0.023$] higher bee richness than controls in 2022 and 2023, respectively (Figures 2.2A-B). Midrotation rarified species richness was similar among treatments for both sampling years ($p = 0.053-0.067$). Bee catches were 74% greater in understory blue vane traps [$t_{(14)} = -4.39$, $p < 0.001$] and indicator species analysis did not identify any species associated with traps at the midstory level.

In early post-establishment stands, CCA analysis indicated seven habitat variables explained 36% [$F_{(7,16)} = 1.26$, $p = 0.023$] of the variation in bee species composition (first axis eigenvalue = 0.134; second axis eigenvalue = 0.09). Only one attribute, percent cover of bare ground, was significant [$F_{(1,16)} = 1.81$, $p = 0.014$] (Figure 2.3A). Overall, control stands were more similar to each other with increasing variability in herbicide treated stands. Most bee species overlapped in the central area of the ordination plot, but some soil-nesting bees in the genus *Lasioglossum*, as well as the specialist ground-nesting megachilid, *Trachusa dorsalis* (Lepeletier), were associated with greater bare ground cover in the broadcast CSP + banded HWC treated stands (Figure 2.3B).

For midrotation stands, CCA analysis showed that nine habitat variables explained 65% [$F_{(9,6)} = 1.23$, $p = 0.046$] of the variation in bee species composition (first axis eigenvalue =

0.231; second axis eigenvalue = 0.196) (Figure 2.4A). However, no specific habitat attributes were significant (p = 0.201-0.734). Midrotation treated stands were associated with a greater number of snags, coarse woody debris decay, and bare ground cover than control stands. Again, most bee species overlapped in the central area of the ordination plot, but the species composition of control and woody release broadcast stands were quite distinct, with certain species associated with their preferred nesting materials. For example, the soil-nesting andrenid, *Panurginus polytrichus* (Cockerell), was associated with bare ground cover, the deadwood-nesting halictid, *Lasioglossum coeruleum* (Robertson), with increased tree density and number of logs, and *Ceratina floridana* (Mitchell), a small-bodied deadwood-nester, with a greater number of snags (Figure 2.4B).

Indicator species analysis identified 19 bee species that were associated with particular herbicide treatments (Table 2.3). Of those species, most were soil-nesting (16 species), with only two deadwood-nesting and one litter-nesting species. Thirteen species were social, six were solitary, and most species were small-bodied, with only three medium and two large species. Two bees had a narrow diet breadth, specializing on Asteraceae and Cucurbitaceae. Most bees (17 species) were mid-season fliers, with only two late-season species. There were six bees species associated with all three early post-establishment treatments, all of which were soil-nesting. *B. griseocollis* (De Geer), a social litter-nesting species, was associated with the two non-control early post-establishment herbicide treatments. *L. floridanum* and *C. dupla* (Say), were associated solely with the early post-establishment broadcast CSP + banded HWC treatment. *Ceratina calcarata* (Robertson), a deadwood-nesting species, was associated with both midrotation herbicide treatments. Functional dispersion, and thus beta diversity, was similar among herbicide treatments in early post-establishment [$\chi^2_{(2)} = 4.52$, p = 0.105] and midrotation

[$t_{(7)}$ = 0.184, p = 0.859] stands. Functional evenness was also similar in early post-establishment [$F_{(2,21)}$ = 8.17, p = 0.455] and midrotation [$t_{(7)}$ = 0.550, p = 0.600] stands, suggesting that functional trait diversity was evenly distributed between the herbicide treatments in each stand stage.

Linear models indicated that there were no relationships between bee catches/rarefied species richness and plant cover/species richness in early post-establishment stands in the first sampling year (p = 0.207-0.761). However, in the second sampling year, early post-establishment bee rarified species richness was positively correlated (p = 0.05, R^2 = 0.109) with understory plant cover (Figure 2.5A). All other second-year early post-establishment linear models were non-significant (p = 0.331-0.725). In midrotation stands, bee catches were surprisingly negatively correlated (p = 0.012, R^2 = 0.254) with understory plant richness in the first sampling year (Figure 2.5B). Similarly, midrotation bee rarified species richness was negatively correlated (p = 0.041, R^2 = 0.177) with understory plant richness in the second sampling year (Figure 2.5C). All other midrotation linear models were non-significant (p = 0.113-0.979).

2.5 Discussion

Our first research objective was to evaluate the indirect effects of imazapyr herbicide treatments on wild bees in working loblolly pine forests. In both early post-establishment and midrotation stand stages, herbicide treated stands supported abundant and species rich wild bee communities similar to their untreated counterparts. Total bee catches, species richness, rarefied species richness, functional dispersion, and functional evenness were all similar between broadcast CSP, broadcast CSP + banded HWC, and control early post-establishment stands.

However, in the midrotation stands, bee species richness was greater in broadcast woody release treated stands for both study years. Our results are consistent with Bried & Dillon (2012), which found no significant differences in bee species richness between control plots and those that received a combined hardwood release and mowing treatment in pitch pine (*P. rigida* Mill.) scrub oak barrens.

Our second research objective was to determine linkages between changes in understory plant communities and wild bee responses. As expected, there was a positive relationship between early post-establishment bee rarified species richness and understory plant cover in the second sampling year. Previous research has observed greater bee abundance and diversity with increasing floral resources (Nielsen et al. 2011; Rubene et al. 2015; Ulyshen et al. 2021; Favorito et al. 2023), and the early successional understory plant communities in our study likely provided beneficial pollen and nectar resources for wild bees. However, in midrotation stands, total bee catches and rarified bee species richness were negatively correlated with understory plant richness in the first and second sampling year, respectively. While these results may seem counterintuitive, it is important to note that in addition to floral resources, wild bees require appropriate nest sites to complete their life cycle (Michener 2007). Availability of nesting substrates and building materials can predict bee community composition and may act as a limiting factor in bee diversity (Potts et al. 2005; Hudewenz and Klein 2013). Midrotation control stands were associated with greater understory plant cover than herbicide treated stands, but they may have lacked suitable nesting material or access to nesting sites for the vast majority (~75%) of all bee species that excavate nests in bare soil (Antoine and Forrest 2021).

Habitat characteristics in early post-establishment stands were highly variable within each herbicide treatment. While control stands were more similar to each other than treated stands, all three treatments had a large degree of overlap in their associated stand characteristics (e.g., understory plant, dead vegetation, and woody debris cover). These similarities may help explain the lack of differences found in the wild bee communities at each treatment type. Of the seven habitat variables in early post-establishment stands used for CCA analysis, only bare ground cover significantly explained bee species composition, and the six indicator species associated with all three early post-establishment treatments were soil-nesting bees. Our results are consistent with previous studies in southern working forests that found that clearcuts and other early post-establishment conditions greatly favor soil-nesting bee species (Fortuin and Gandhi 2021; Favorito et al. 2023). Bare ground cover varied widely within each early post-establishment treatment, but our results indicate that herbicide application did not significantly reduce bee catches or diversity metrics in comparison to untreated controls. In fact, broadcast CSP + banded HWC herbicide treated stands supported multiple rare specialist ground-nesting bees including *T. dorsalis* and *Melissodes mitchelli* (LaBerge).

Herbicide treatments directly shaped understory habitat conditions in midrotation stands. Control stands were dominated by herbaceous and woody vegetation, while imazapyr treated stands were associated with greater amounts of snags, coarse woody debris decay, and bare ground cover. These differences in habitat characteristics likely drove patterns in the wild bee community. Broadcast woody release treated stands had ~30% greater average percent bare ground cover than control stands. While total bee catches were similar between treated and untreated midrotation stands, species richness was higher in herbicide treated stands for both study years. Although midrotation CCA analysis did not identify bare ground cover as a significant explanatory variable, this greater species richness may stem from the presence of ground-nesting bees such as *Halictus poeyi* (Lepeletier) and *L. floridanum* which were absent in control stands. Four indicator species, all of which are soil-nesting halictids, were associated with each early post-establishment treatment and midrotation broadcast woody release stands, but not midrotation control stands. While previous research has identified thinning as an effective management tool to improve pollinator diversity in closed-canopy pine forests (e.g., Favorito et al. 2023), our results indicate that hardwood release herbicide treatments may provide additional benefits to ground-nesting wild bee communities through removing understory plant cover and improving nesting habitat conditions through increases in bare mineral soil exposure.

Interestingly, the number of hollow stems was not a significant explanatory variable in either early post-establishment or midrotation stands. We intended for this variable inform about the available nesting material for cavity- and deadwood-nesting species (especially those in the genera *Ceratina* and *Hylaeus*) that create nests in pithy stems of dead vegetation. However, the majority of hollow stems included in our analyses originated from dogfennel [*Eupatorium capillifolium* (Lam.) Small] plants, which may not be a preferred nesting material for stem-nesting bee communities at our stands. Future research on wild bees in working forests may aim to sample a wider variety of hollow stems (particularly from broadleaf weed species) to better gauge nesting resource availability for cavity- and deadwood-nesting species in planted forest stands.

3.6 Conclusions

Wild bee communities in herbicide treated loblolly pine stands had similar total catches, catches of common bee species, species richness, and functional diversity as those in untreated controls. In the second sampling year, understory plant cover was positively correlated with rarified bee species richness in early post-establishment stands, whereas midrotation stands showed a negative relationship between understory plant and rarified bee species richness. Our results indicate that midrotation woody release broadcast herbicide treatments may support soil-nesting bees by removing understory vegetation and increasing available nesting habitat. In addition to increasing pine forest productivity and stand health, herbicides may also provide critical ecological benefits by improving wild bee habitat conditions. It remains to be seen whether low intensity prescribed burns (which also control understory vegetation) may provide similar ecological benefits for pollinators alone or in combination with herbicides in these stands. Future studies on wild bee communities in working pine forests may investigate how other common management practices, including fertilization, pine straw raking, thinning, and prescribed fire, alter wild bee foraging resources, nesting habitat availability, and overall responses to forest herbicide applications.

2.7 Acknowledgements

We are grateful for the funding provided by the D.B. Warnell School of Forestry and Natural Resources (University of Georgia), Society of American Foresters (Mollie Beattie Visiting Scholars Program), and Weyerhaeuser Company. Sam Droege (USGS Patuxent Wildlife Research Center) and Elsa Youngsteadt (North Carolina State University) provided invaluable help with bee identifications. Laboratory and field assistance was also provided by Joshua Barbosa, Sarah Carnes, and Whit Bolado.

Table 2.1: Mean (+ SE) stand attributes of sampled midrotation loblolly pine (*Pinus taeda* L.) forests of the Georgia Piedmont in 2023.

Herbicide Treatment	**Control**	**Broadcast Spray**
Mean Canopy Openness (%)	30.02 ± 2.32	28.61 ± 1.45
Mean Height of Pines (m)	16.82 ± 0.19	16.58 ± 0.41
Mean Age of Pines (years)	21 ± 0	21 ± 0
Mean DBH of Pines (cm)	23.55 ± 0.75	24.63 ± 0.70
Mean Time Since Thinning (years)	4.5 ± 0.29	4.63 ± 0.38
Mean Tree Density (trees/ha)	615.40 ± 60.49*	525.21 ± 42.11*
Mean Pine Density (trees/ha)	464.20 ± 47.25*	442.98 ± 24.61*
Mean Hardwood Density (trees/ha)	145.89 ± 40.80*	79.58 ± 33.13*
Mean Tree Basal Area (m^2/ha)	22.69 ± 1.62*	24.12 ± 1.58*
Mean Pine Basal Area (m^2/ha)	21.63 ± 1.54*	23.44 ± 1.54*
Mean Hardwood Basal Area (m^2/ha)	0.03 ± 0.01*	0.02 ± 0.01*

*Trees <5 cm DBH were not measured and omitted in averages.

Table 2.2: Number of wild bee species in herbicide treated loblolly pine (*Pinus taeda* L.) forests of the Georgia Piedmont.

		HERBICIDE TREATMENT[b]					
FAMILY	**SPECIES[a]**	**EE CONTROL**	**EE BROAD**	**EE BROAD + BANDED**	**MR CONTROL**	**MR BROAD**	**SPECIES TOTAL**
Andrenidae	*Andrena alleghaniensis* Viereck	1	0	0	0	0	1
Andrenidae	*Andrena gardineri* Cockerell	0	0	0	0	1	1
Andrenidae	*Andrena macra* Mitchell	1	0	0	0	0	1
Andrenidae	*Andrena perplexa* Smith	0	0	2	0	0	2
Andrenidae	*Andrena personata* Robertson	0	1	0	0	0	1
Andrenidae	*Andrena* sp.	0	1	0	0	0	1
Andrenidae	*Calliopsis andreniformis* Smith	0	0	0	0	1	1
Andrenidae	*Panurginus polytrichus* Cockerell	2	1	1	3	1	8
Andrenidae	*Perdita bishoppi* Cockerell	0	0	2	0	0	2
Andrenidae	*Perdita boltoniae* Robertson	0	1	0	0	0	1
Apidae	*Anthophora abrupta* Say	2	3	3	11	11	30
Apidae	*Bombus bimaculatus* Cresson	121	45	52	44	75	337
Apidae	*Bombus fraternus* Smith	5	7	5	0	0	17
Apidae	*Bombus griseocollis* De Geer	17	26	25	3	3	74
Apidae	*Bombus impatiens* Cresson	137	140	92	134	138	641
Apidae	*Bombus pensylvanicus* De Geer	33	51	56	45	19	204
Apidae	*Ceratina calcarata* Robertson	3	3	1	37	60	104
Apidae	*Ceratina cockerelli* H.S. Smith	4	2	4	0	0	10
Apidae	*Ceratina dupla* Say	0	3	15	0	2	20
Apidae	*Ceratina floridana* Mitchell	2	2	1	1	5	11
Apidae	*Ceratina* spp.	2	0	1	0	17	20
Apidae	*Ceratina strenua* Smith	30	20	49	107	120	326
Apidae	*Eucera atriventris* Smith	2	0	2	11	0	15
Apidae	*Eucera dubitata* Cresson	2	1	0	1	0	4
Apidae	*Eucera hamata* Bradley	3	5	3	0	0	11
Apidae	*Eucera (Peponapis) pruinosa* Say	8	13	8	0	0	29
Apidae	*Eucera rosae* Robertson	4	3	4	1	1	13
Apidae	*Holcopasites calliopsidis* Linsley	1	0	0	0	0	1
Apidae	*Melecta pacifica* Cresson	0	0	0	1	0	1
Apidae	*Melissodes bimaculatus* Lepeletier	132	164	162	179	89	726
Apidae	*Melissodes communis* Cresson	231	187	167	9	26	620
Apidae	*Melissodes comptoides* Robertson	94	81	57	29	71	332
Apidae	*Melissodes mitchelli* LaBerge	0	0	5	0	0	5
Apidae	*Melissodes* spp.	1	1	0	0	0	2
Apidae	*Melissodes tepaneca* Cresson	32	51	54	0	3	140
Apidae	*Melitoma taurea* Say	8	30	1	2	9	50
Apidae	*Ptilothrix bombiformis* Cresson	3	4	2	6	1	16
Apidae	*Svastra aegis* LaBerge	0	1	0	1	0	2
Apidae	*Svastra atripes* Cresson	30	36	40	0	5	111
Apidae	*Svastra obliqua* Say	30	131	80	1	0	242
Apidae	*Svastra petulca* Cresson	1	0	0	0	0	1
Apidae	*Triepeolus lunatus* Say	2	0	0	0	0	2
Apidae	*Xylocopa micans* Lepeletier	2	2	2	0	1	7
Apidae	*Xylocopa virginica* L.	4	8	9	4	0	25
Colletidae	*Colletes brevicornis* Robertson	4	1	0	0	0	5
Colletidae	*Colletes* sp.	0	0	0	0	1	1
Colletidae	*Colletes thoracicus* Smith	0	0	0	0	1	1
Colletidae	*Hylaeus affinis* Smith / *modestus* Say	0	0	3	2	0	5

Colletidae	*Hylaeus modestus* Say	0	1	0	0	0	1
Colletidae	*Hylaeus ornatus* Mitchell	0	0	1	0	0	1
Halictidae	*Agapostemon splendens* Lepeletier	3	0	7	0	0	10
Halictidae	*Agapostemon virescens* Fabricius	1	4	0	0	0	5
Halictidae	*Augochlora pura* Say	9	21	18	42	22	112
Halictidae	*Augochlorella aurata* Smith	3	4	0	16	7	30
Halictidae	*Augochloropsis viridula* Smith	0	1	1	0	0	2
Halictidae	*Halictus parallelus* Say	2	3	14	0	0	19
Halictidae	*Halictus poeyi* Lepeletier	56	90	173	0	51	370
Halictidae	*Halictus rubicundus* Christ	2	0	4	0	0	6
Halictidae	*Lasioglossum apocyni* Mitchell	0	1	0	0	0	1
Halictidae	*Lasioglossum apopkense* Robertson	5	6	17	0	0	28
Halictidae	*Lasioglossum bruneri* Crawford	33	41	60	26	25	185
Halictidae	*Lasioglossum callidum* Sandhouse	33	10	50	1	1	95
Halictidae	*Lasioglossum coeruleum* Robertson	0	0	0	4	0	4
Halictidae	*Lasioglossum coreopsis* Robertson	29	43	61	2	3	138
Halictidae	*Lasioglossum disparile* Cresson	1	3	4	0	0	8
Halictidae	*Lasioglossum floridanum* Robertson	24	16	1022	0	102	1164
Halictidae	*Lasioglossum hitchensi* Gibbs	11	30	40	0	3	84
Halictidae	*Lasioglossum illinoense* Robertson	13	16	47	1	5	82
Halictidae	*Lasioglossum imitatum* Smith	63	86	105	1	8	263
Halictidae	*Lasioglossum leucocomus* Lovell	2	3	7	0	0	12
Halictidae	*Lasioglossum leucocomus* Lovell / *pilosum* Smith	0	3	4	0	0	7
Halictidae	*Lasioglossum leviense* Mitchell	2	17	15	0	2	36
Halictidae	*Lasioglossum longifrons* Baker	83	52	62	0	0	197
Halictidae	*Lasioglossum lustrans* Cockerell	1	2	2	0	0	5
Halictidae	*Lasioglossum nymphale* Smith	1	0	38	0	0	39
Halictidae	*Lasioglossum oblongum* Lovell	0	0	0	0	1	1
Halictidae	*Lasioglossum pectorale* Smith	3	8	4	0	8	23
Halictidae	*Lasioglossum pilosum* Smith	12	64	108	0	0	184
Halictidae	*Lasioglossum platyparium* Robertson	0	2	1	0	0	3
Halictidae	*Lasioglossum pruinosum* Robertson	1	1	3	0	0	5
Halictidae	*Lasioglossum puteulanum* Gibbs / *tegulare* Robertson	56	53	61	7	20	197
Halictidae	*Lasioglossum raleighense* Crawford	0	1	0	1	3	5
Halictidae	*Lasioglossum reticulatum* Robertson	0	0	11	0	0	11
Halictidae	*Lasioglossum* spp.	10	22	28	2	4	66
Halictidae	*Lasioglossum trigeminum* Gibbs	21	6	32	0	1	60
Halictidae	*Lasioglossum vierecki* Crawford	0	0	2	0	0	2
Halictidae	*Lasioglossum weemsi* Mitchell	1	0	1	0	1	3
Halictidae	*Lasioglossum zephyrus* Smith	1	2	4	0	1	8
Halictidae	*Nomia maneei* Cockerell	0	1	0	0	0	1
Halictidae	*Nomia nortoni* Cresson	0	1	5	0	0	6
Halictidae	*Sphecodes atlantis* Mitchell / *cressonii* Robertson	0	2	0	0	0	2
Megachilidae	*Coelioxys mexicanus* Cresson	1	0	0	0	0	1
Megachilidae	*Coelioxys modestus* Smith	0	0	0	1	0	1
Megachilidae	*Coelioxys sayi* Robertson	0	0	1	0	0	1
Megachilidae	*Heriades leavitti* Crawford / *variolosa* Cresson	11	11	4	0	1	27

Megachilidae	*Hoplitis pilosifrons* Cresson	8	6	6	0	0	20
Megachilidae	*Hoplitis producta* Cresson	1	3	1	0	0	5
Megachilidae	*Lithurgopsis gibbosa* Smith	0	0	2	0	0	2
Megachilidae	*Megachile addenda* Cresson	0	0	1	0	0	1
Megachilidae	*Megachile albitarsis* Cresson	1	2	0	0	0	3
Megachilidae	*Megachile pseudobrevis* Mitchell	2	2	0	0	0	4
Megachilidae	*Megachile brevis* Say / *pseudobrevis* Mitchell	1	1	2	0	0	4
Megachilidae	*Megachile campanulae* Robertson	0	0	0	0	2	2
Megachilidae	*Megachile georgica* Cresson	2	5	0	2	0	7
Megachilidae	*Megachile mendica* Cresson	10	5	5	1	5	26
Megachilidae	*Megachile mucida* Cresson / *gemula* Cresson	1	0	0	0	0	1
Megachilidae	*Megachile petulans* Cresson	3	6	3	1	1	14
Megachilidae	**Megachile sculpturalis* Smith	0	6	1	0	0	7
Megachilidae	*Megachile* spp.	2	1	0	0	1	4
Megachilidae	*Megachile texana* Cresson	1	2	4	0	0	7
Megachilidae	*Osmia atriventris* Cresson	0	0	4	1	0	5
Megachilidae	*Osmia chalybea* Smith	1	0	1	0	2	4
Megachilidae	*Osmia georgica* Cresson	0	2	0	1	1	4
Megachilidae	*Osmia inspergens* Lovell & Cockerell	0	1	0	0	0	1
Megachilidae	*Osmia sandhouseae* Mitchell	51	40	33	13	14	151
Megachilidae	*Stelis diversicolor* Crawford	1	0	0	0	1	2
Megachilidae	*Stelis lateralis* Cresson	1	0	0	0	0	1
Megachilidae	*Trachusa dorsalis* Lepeletier	1	0	1	0	0	2
Megachilidae	*Trachusa ridingsii* Cresson	0	0	1	0	0	1
	Herbicide treatment total	**1535**	**1732**	**2992**	**753**	**959**	**7975**
	Total number of species	**77**	**75**	**79**	**39**	**48**	**114**

[a] Non-native species are marked with an asterisk (*).

[b] KEY: EE = early post-establishment
MR = midrotation
BROAD = broadcast spray
BANDED = banded application

Table 2.3: Indicator bee species and their functional traits in herbicide treated loblolly pine (*Pinus taeda* L.) forests of the Georgia Piedmont.

Treatment(s)[a]	Bee Species	*P*-Value[b]	Nesting[c]	Sociality	Diet	Specialist Plant Family	Size	Season
EE Control **EE Broad** **EE Broad + Band**	*Lasioglossum callidum*	0.008	Soil	Social	Generalist		Small	Mid
	Lasioglossum longifrons	<0.001	Soil	Social	Generalist		Small	Mid
	Lasioglossum trigeminum	0.011	Soil	Social	Generalist		Small	Mid
	Melissodes tepaneca	<0.001	Soil	Solitary	Generalist		Med	Mid
	Svastra atripes	0.007	Soil	Solitary	Generalist		Large	Late
	Svastra obliqua	<0.001	Soil	Solitary	Specialist	Asteraceae	Med	Late
EE Broad **EE Broad + Band**	*Bombus griseocollis*	0.041	Litter	Social	Generalist		Large	Mid
	Eucera (Peponapis) pruinosa	0.007	Soil	Solitary	Specialist	Cucurbitaceae	Med	Mid
	Lasioglossum apopkense	0.004	Soil	Social	Generalist		Small	Mid
	Lasioglossum leviense	<0.001	Soil	Social	Generalist		Small	Mid
	Lasioglossum pilosum	0.003	Soil	Social	Generalist		Small	Mid
EE Broad + Band	*Ceratina dupla*	0.006	Deadwood	Solitary	Generalist		Small	Mid
	Lasioglossum floridanum	0.038	Soil	Social	Generalist		Small	Mid
EE Broad **MR Broad** **MR Control**	*Augochlorella aurata*	0.017	Soil	Social	Generalist		Small	Mid

EE Control **EE Broad** **EE Broad + Band** **MR Broad**	*Halictus poeyi*	<0.001	Soil	Social	Generalist	Small	Mid
	Lasioglossum illinoense	0.041	Soil	Social	Generalist	Small	Mid
	Lasioglossum imitatum	0.016	Soil	Social	Generalist	Small	Mid
	Lasioglossum puteulanum/tegulare	0.028	Soil	Social	Generalist	Small	Mid
MR Broad **MR Control**	*Ceratina calcarata*	<0.001	Deadwood	Solitary	Generalist	Small	Mid

[a] Key: EE = early post-establishment
MR = midrotation
BROAD = broadcast spray
BANDED = banded application

[b] P-value for permutation test to determine if taxon is an indicator species.

[c] Refers to the primary nesting substrate for the bee species:
Deadwood = species that nest in undecayed deadwood or pithy stems
Litter = species that nest in dead plant material on the ground, including leaf litter, wood piles, and the organic soil layer
Soil = species that excavate soil to create nests in the ground

Figures

Figure 2.1: Example of blue vane traps and blue, white, and yellow pan traps used to capture bees in herbicide treated loblolly pine (*Pinus taeda* L.) forests of the Georgia Piedmont.

Figure 2.2: Mean bee species richness (A, B) for midrotation herbicide treatments in 2022 and 2023 with standard error bars. Different letters represent significant differences in means.

Figure 2.3: Canonical correspondence analysis (CCA) of species composition for early post-establishment stands (A) and bee species (B). Understory habitat characteristics (percent understory plant cover, dead vegetation, bare ground, and woody debris, CWD decay, and the number of logs and hollow stems) explained 36% of the variation in bee species composition [$F_{(7,16)} = 1.26$, $p = 0.023$]. Significant variables are marked with *.

Figure 2.4: Canonical correspondence analysis (CCA) of species composition for midrotation stands (A) and bee species (B). Understory habitat characteristics (percent understory plant cover, bare ground, canopy openness, tree density, CWD decay, litter depth, and the number of logs, snags, and hollow stems) explained 65% of the variation in bee species composition [$F_{(9,6)} = 1.23$, $p = 0.046$].

Figure 2.5: Linear regressions of 2023 rarefied bee richness and early post-establishment plant cover (A), 2022 bee catches and midrotation plant richness (B), and 2023 rarefied bee richness and midrotation plant richness (C).

Figure 2.1

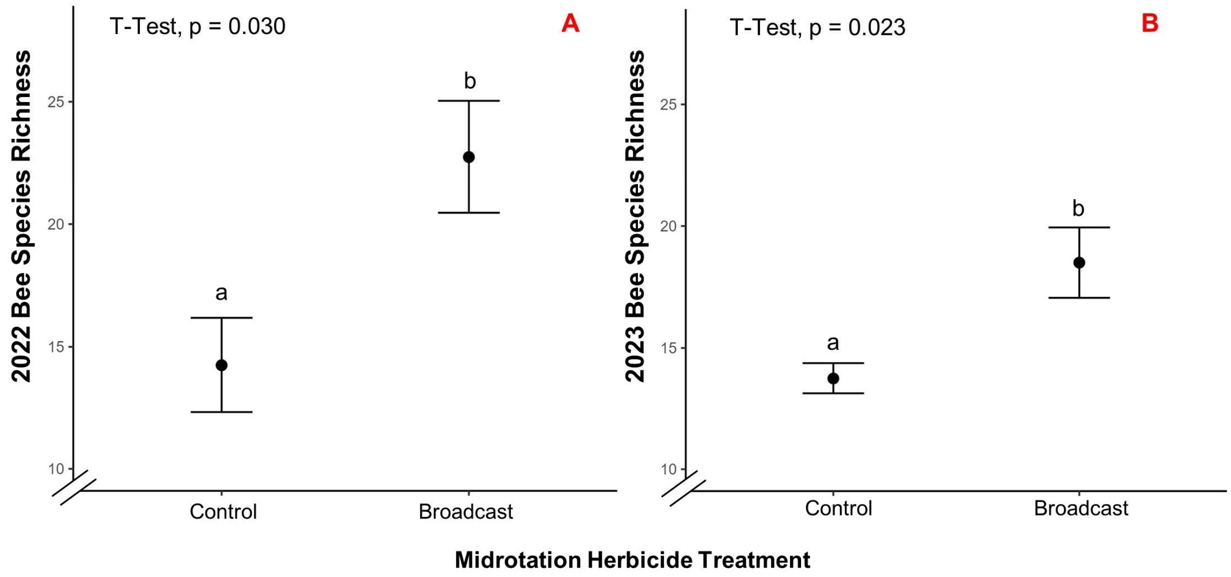
T-Test, p = 0.030
A
2022 Bee Species Richness
25
20
15
10
a
b
Control
Broadcast
T-Test, p = 0.023
B
2023 Bee Species Richness
25
20
15
10
a
b
Control
Broadcast
Midrotation Herbicide Treatment

Figure 2.2

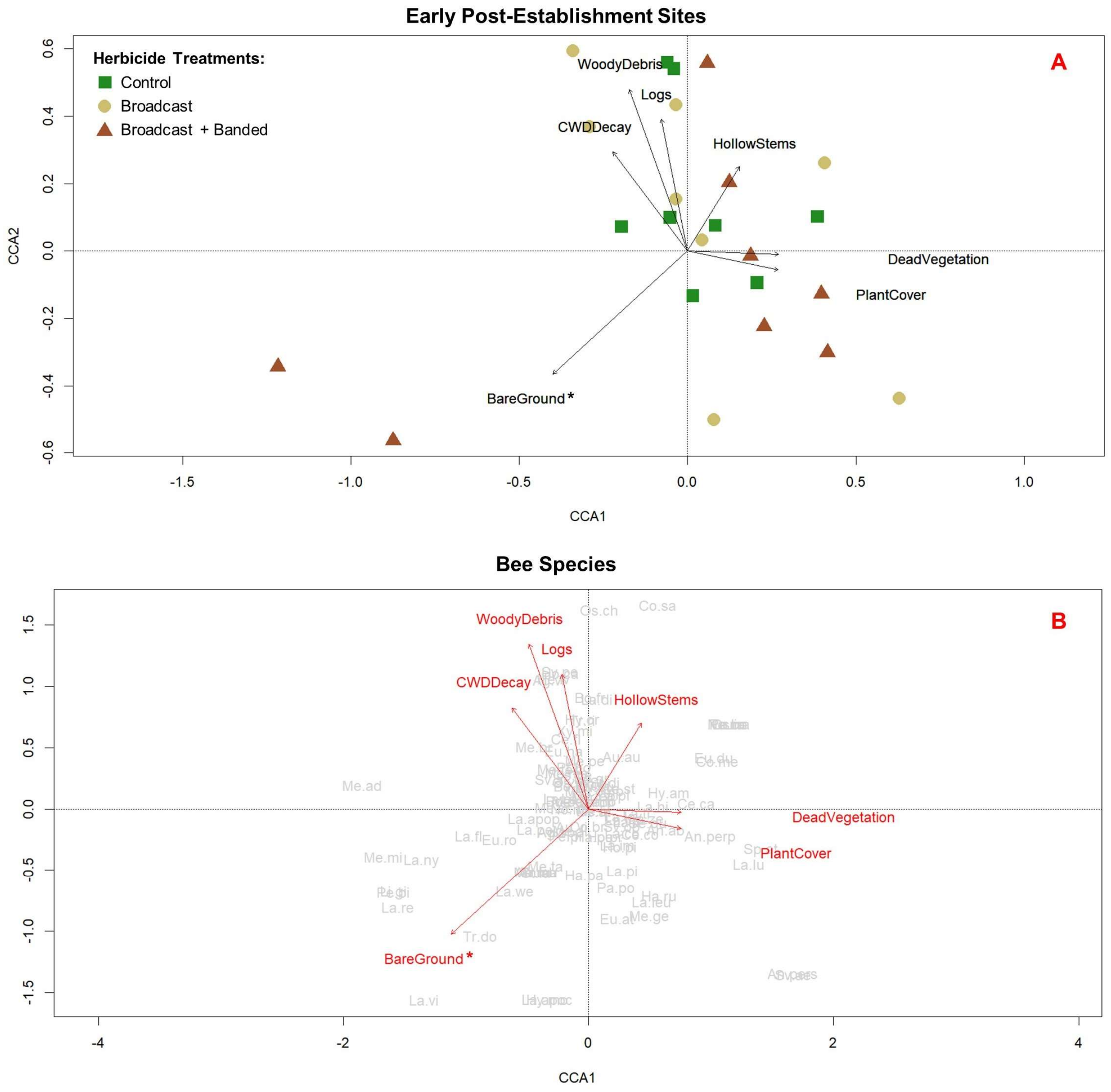
Early Post-Establishment Sites
Herbicide Treatments:
🟩 Control
● Broadcast
▲ Broadcast + Banded
A
WoodyDebris
Logs
CWDDecay
HollowStems
DeadVegetation
PlantCover
BareGround*
CCA2
CCA1
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-1.5
-1.0
-0.5
0.0
0.5
1.0
Bee Species
B
WoodyDebris
Logs
CWDDecay
HollowStems
DeadVegetation
PlantCover
BareGround*
Gs.ch
Co.sa
Hy.or
Me.ad
Au.au
Eu.du
Co.me
Hy.am
Ce.ca
La.apop
La.fl
Eu.ro
An.perp
La.lu
Me.mi
La.ny
Ha.ba
La.pi
La.we
Pa.po
Ha.ru
La.re
Eu.at
Me.ge
Tr.do
La.vi
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
-4
-2
0
2
4
CCA1

Figure 2.3

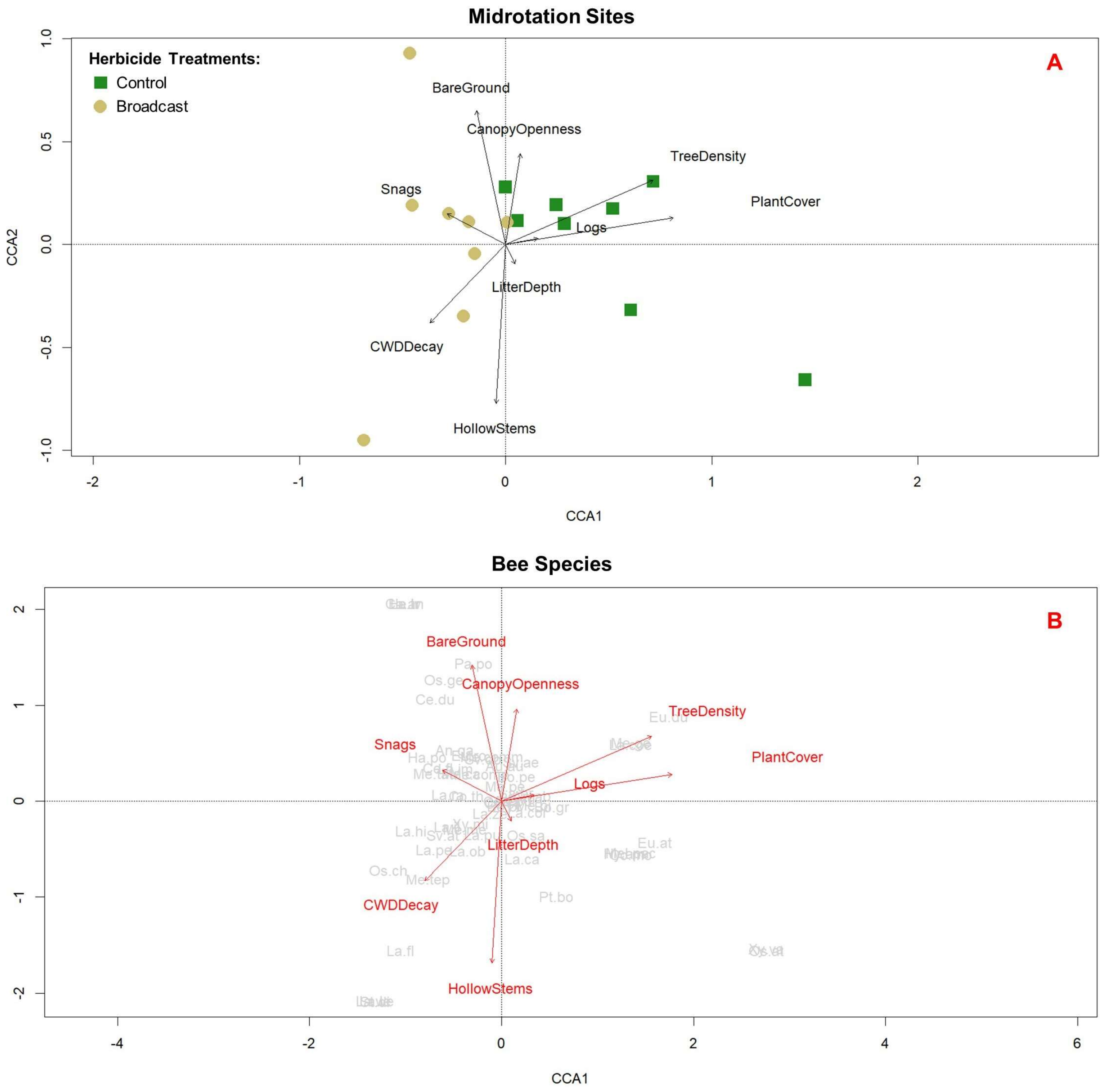
Midrotation Sites
A
Herbicide Treatments:
🟩 Control
● Broadcast
BareGround
CanopyOpenness
TreeDensity
PlantCover
Snags
Logs
LitterDepth
CWDDecay
HollowStems
CCA2
1.0
0.5
0.0
-0.5
-1.0
-2
-1
0
1
2
CCA1
Bee Species
B
BareGround
CanopyOpenness
TreeDensity
PlantCover
Snags
Logs
LitterDepth
CWDDecay
HollowStems
Pa.po
Os.ge
Ce.du
Eu.du
Ha.po
La.hi
La.pe
La.ob
Os.ch
La.fl
Pt.bo
Eu.at
La.ca
Os.sa
2
1
0
-1
-2
-4
-2
0
2
4
6
CCA1

Figure 2.4

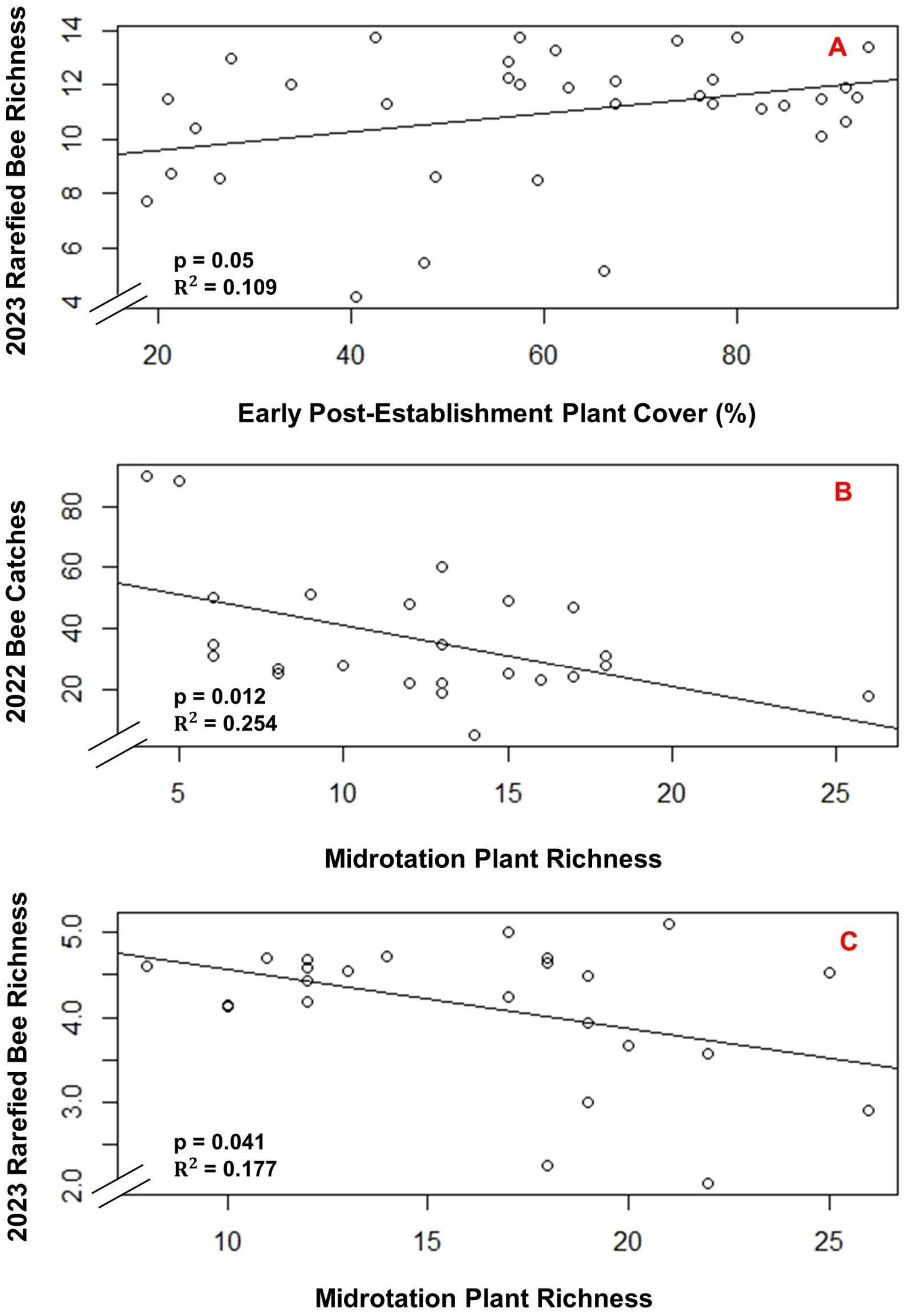
A
2023 Rarefied Bee Richness
4
6
8
10
12
14
20
40
60
80
Early Post-Establishment Plant Cover (%)
p = 0.05
R^2 = 0.109
B
2022 Bee Catches
20
40
60
80
5
10
15
20
25
Midrotation Plant Richness
p = 0.012
R^2 = 0.254
C
2023 Rarefied Bee Richness
2.0
3.0
4.0
5.0
10
15
20
25
Midrotation Plant Richness
p = 0.041
R^2 = 0.177

Figure 2.5

CHAPTER 3

UNDERSTORY PLANT COMMUNITY RESPONSES FOLLOWING IMAZAPYR HERBICIDE APPLCIATION IN GEORGIA LOBLOLLY PINE FORESTS[3]

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3.1 Abstract

Working pine (*Pinus* spp.) forests rely on herbicides to reduce competing vegetation and promote stand productivity, but there is still uncertainty regarding the potential impacts of chemical applications on herbaceous biodiversity and overall forest sustainability. Our research objective was to assess the direct effects of different imazapyr herbicide treatments on understory plant communities in loblolly pine forests of the Georgia Piedmont. Stands of two stages (early post-establishment or thinned mid-rotation) received imazapyr application through either: 1) broadcast chemical site preparation (early post-establishment only); 2) broadcast chemical site preparation + banded herbaceous weed control (early post-establishment only); 3) broadcast woody release (midrotation only); or 4) control with no herbicide. We sampled understory vegetation during 2022 and 2023 in each stand using twelve 1 m^2 quadrats (240 quadrats for each year of the study). Within each quadrat, we visually estimated the percent of total understory plant cover, identified all non-graminoid understory plant species, and recorded the number of individuals for each species and their percent dominance. We identified 112 native and 18 introduced understory plant species over the course of the study. Early post-establishment plant communities showed significant recovery from the first to second sampling year. Plant species richness increased 36% in the broadcast chemical site preparation and 65% in the broadcast chemical site preparation + banded herbaceous weed control treatments, but control stands had 20-22% greater diversity and 21% greater species evenness than the broadcast chemical site preparation + banded herbaceous weed control stands. In the midrotation stand development stage, herbicide treated stands were dominated by early successional plant species and had a 59% increase in species richness over two sampling years, but total plant cover remained stable. Our results indicate that early post-establishment plant communities can recover

quickly (<2 years) following herbicide treatments, and that midrotation broadcast woody release herbicide applications can shift understory plant communities to favor disturbance-adapted, imazapyr-tolerant species.

3.2 Introduction

Working pine (*Pinus* spp.) forests of the southern United States are a significant ecological and economic resource. In addition to sequestering carbon, providing wildlife habitat, and protecting water quality (Lichter et al. 2008; Jones et al. 2009b; Shah et al. 2022), these forests supply approximately 15% of global wood fiber and are expected to grow > 60% in acreage by 2040 (Wear and Gries 2002; Siry et al. 2006). To meet the rising demand for timber products, southern forest landowners rely on various herbicide application methods (e.g., chemical site preparation, herbaceous weed control, and woody release treatments) to control competing vegetation and improve planted pine productivity (Wagner et al. 2004). Herbicides can be very effective at increasing growth rates in working forest systems, with growth gains of 100% or more reported in some studies (Stewart 1987; Glover et al. 1989; Miller et al. 1991; Glover and Zutter 1993; Haywood 1994; Wagner et al. 2006; Zhao et al. 2008).

Given the objective of sustainable forest management to protect and promote biodiversity, it is important to understand how herbicide applications influence herbaceous plant communities in southern working forests. Understory plant species constitute a small portion of total forest biomass, but they contribute significantly to forest biodiversity, structure, and function, provide critical ecological services and resources for wildlife (e.g., forage and cover), and support the long-term sustainability of working pine forests (Gilliam 2007; Jeffries et al. 2010). Multiple studies have found that there are few lasting effects of chemical application on herbaceous plants (e.g., Boateng et al., 2000; Miller et al., 1999; Miller and Miller, 2004), but floristic responses to herbicides are not universal across climatic, edaphic, and geographic gradients. Hence, it is important to assess if this pattern persists in southern planted loblolly pine (*P. taeda* L.) stands that are widely managed in this region. If the effects of herbicides do persist long-term on understory plant communities in working forests, ecosystem services may be limited, since herbaceous plants provide essential foraging resources for native pollinators and other ecologically important wildlife including ungulates and small mammals (Carey and Harrington 2001; Hanula and Horn 2011; Proctor et al. 2012; Ulappa et al. 2020; Briggs et al. 2024).

Effects of chemical treatment on understory plant structure and composition may vary with stand development stage and application type. By removing hardwood trees and other competing woody vegetation, woody release treatments in midrotation stands can promote the establishment of early successional herbaceous plants and may increase overall site diversity (Jones et al. 2012). In contrast, herbaceous weed control treatments in newly planted pine stands directly target understory plant communities and may temporarily suppress herbaceous layer biodiversity (Lauer et al. 1993; Shepard et al. 2004). Previous studies have reported that forb cover, richness, and diversity can return to pretreatment levels within five years of the initial herbicide application (e.g., Keyser et al., 2003; Lane et al., 2011; Marsh et al., 2012). However, additional research is needed to assess how variables such as application method (e.g., broadcast spray or banded application), site characteristics (e.g., soil texture, precipitation patterns, and organic matter content), and existing plant community structure influence floristic responses to herbicides and overall understory plant recovery.

Our research objective was to assess the direct effects of different imazapyr herbicide treatments on understory plant communities in early post-establishment and midrotation working loblolly pine forests of the Georgia Piedmont. We measured changes in understory plant communities over a two-year period using various metrics including total percent understory plant cover, percent cover per plant species, and species richness, diversity, and composition. By understanding the impacts of herbicide application on understory plants over time, land managers can create sustainable forest management plans that preserve biodiversity and ecosystem function while also improving stand productivity to meet global woody supply needs.

3.3 Methods

Study Sites & Herbicide Treatments

We conducted the study in privately owned planted loblolly pine stands in the Piedmont physiographic region of Georgia, where forest managers often use the herbicide imazapyr to control competing vegetation (Dickens et al. 2020a). Midrotation stands were primarily composed of loblolly pine trees and saplings, with some scattered hardwoods including sweetgum (*Liquidambar styraciflua* L.), winged elm (*Ulmus alata* Michx.), and red maple (*Acer rubrum* L.). In 2020, the average annual temperature for all stands was 18 ± 0.08 °C, the average annual precipitation was 167.4 ± 1.70 cm, and the average elevation was 151.15 ± 5.09 m (PRISM Climate Group 2020). In this region, common soils include sandy loam, clay loam, and loamy sand Ultisols (NRCS 2022).

Planted loblolly pine stands of two successional stages received the following imazapyr treatments (N = 20, four stands per treatment):

1) Early post-establishment stands (0-2 years old)

   a. control with no herbicide
   b. chemical site preparation (aerial broadcast spray)
   c. chemical site preparation (aerial broadcast spray) + first-year herbaceous weed control (banded application)
2) Midrotation, thinned (20 years old)
   a. control with no woody release
   b. woody release (broadcast spray)

We chose the early post-establishment and thinned midrotation stands since herbicides are most often applied to these successional stages (Wagner et al. 2004; Dickens et al. 2020a). Early post-establishment chemical site preparation and midrotation woody release broadcast herbicide treatments were applied in the summer and early fall of 2020, and the early post-establishment herbaceous weed control banded application occurred in the spring of 2021. All three herbicide application treatments (control, broadcast, and banded) were not tested in each stand stage. Specifically, banded herbicide applications are not a standard forest management practice in midrotation stands (land managers instead use either ground or aerial broadcast applications). The stands were > 5 ha in size and located > 1 km apart. All selected stands were fire excluded and the early post-establishment stands did not receive mechanical site preparation. Midrotation stands received either a chemical or mechanical site preparation treatment.

The study was conducted during the summers of 2022 and 2023. All stands, except for the early post-establishment control stands, were sampled in both years. The early post-establishment control stands were replaced in the second year of sampling since 2-year-old stands without chemical site preparation or herbaceous weed control treatments are not an operational reality for many forest landowners. We established three 10 m radius circular sampling plots within each stand. The sampling plots were located ≥ 50 m from the stand edge to avoid unforeseen edge effects and ≥ 50 m from the nearest sampling station to minimize dependency between plots. Overall, we established 120 sampling plots (20 stands x 3 plots per stand x 2 years).

Understory Plant Sampling

Understory plant sampling occurred in June and July of 2022 and 2023. We established four 1 m^2 quadrats within each circular sampling plot (for a total of 12 quadrats per stand and 240 quadrats for each year of the study), located ~5 m from the plot center in the four cardinal directions. Within each of the quadrats, we visually estimated the percent of total understory plant cover, identified all understory plant species, and recorded the number of individuals for each species and their percent dominance (Weakley 2022). We classified all species as either native or non-native and assigned them to one of five functional groups (ferns, forbs, graminoids, vines, or woody plants) according to their growth form and life history characteristics (USDA 2008). However, all graminoid species were grouped as "grasses" for this study. Since this research was completed as part of a larger study on the impacts of herbicides on pollinator communities, it was not logistically feasible to identify every graminoid species, especially since grasses, sedges, and rushes are typically pollinated by abiotic factors (Wiegmann and Waller 2006).

Statistical Analyses

We conducted all analyses in R [version 4.1.3, (R Core Team 2022)] with a significance level of $\alpha = 0.05$ and the unit of replication was the individual stand, with percent total understory plant cover averaged for all quadrats at a stand. Analyses were performed separately for the two stand ages. We used Analysis of Variance (ANOVA) tests and two-sample t-tests to assess if mean understory plant species richness and mean total plant cover varied between the early post-establishment and midrotation herbicide treatments in the first and second sampling year. We also used a two-way ANOVA to determine if sampling year influenced understory plant species richness and total plant cover to early post-establishment herbicide treatments. Our two explanatory variables (herbicide treatment and sampling year) interacted significantly, so we instead used paired sample t-tests to assess changes in plant richness and cover over time in each herbicide treatment and stand stage. Early post-establishment control stands were not included in these change over time analyses since they were replaced in the second sampling year. We also used one-way ANOVAs and two-sample t-tests to determine if mean forb, vine, graminoid, and woody plant cover varied between the early post-establishment and midrotation herbicide treatments after the second sampling year (two years following chemical application). ANOVAs were followed by Tukey's post-hoc tests to determine which groups significantly differed from one another. We tested the normality of all residuals using the Shapiro-Wilk test, and residuals that could not be normalized using a square root transformation were analyzed using either the non-parametric Wilcoxon Rank Sum or Kruskal-Wallis tests. Any significant Kruskal-Wallis models were followed by the Dunn test with Bonferroni *p* adjustments for multiple comparisons.

We characterized understory plant diversity among herbicide treatments by calculating two diversity indices commonly used in community ecology: 1) the Shannon-Weiner index (H'), and 2) Simpson's diversity index (D). The Shannon-Weiner index ranges from 0 (no diversity) to ~5 (highest diversity) and estimates the uncertainty associated with predicting the species of a randomly selected individual from a given community (Shannon 1948). The Simpson diversity index ranges from 0 (no diversity) to 1 (theoretical maximum diversity), and measures the probability that two individuals randomly selected from a given community will be different species (Simpson 1949). We calculated both indices using the number of individuals of each plant species counted within the quadrats. We also calculated Pielou's evenness index (*J*), which measures the evenness in the pattern of relative species abundances within a community (Pielou 1966). ANOVAs, two-sample t-tests, and Tukey's post-hoc tests were used to determine if plant diversity metrics varied among herbicide treatments in each stand stage. All residuals were tested using the Shapiro-Wilk test, and residuals that could not be normalized using a square root transformation were analyzed with either the Wilcoxon Rank Sum or Kruskal-Wallis tests. Significant Kruskal-Wallis models were followed by the Dunn test with the Bonferroni p adjustment for multiple comparisons.

Indicator species analyses were used to determine if any plant species were associated with a particular herbicide treatment. We used the R package "indispecies" and the multi-level pattern analysis ("multiplatt") function, which measures the association between species distribution and groups of sites (DeCacers and Legendre 2009). Only plant species with > 20 individuals were included in these analyses. We also used the indicator value index ("Ind.val.g") species-site group association function and tested the significance of the associations with a permutation test with 9,999 permutations (Dufrene and Legendre 1997). To better visualize differences in the understory plant communities at our stands, we used non-metric multidimensional scaling (NMDS) to plot plant species distributions between the herbicide treatments in the early post-establishment and midrotation stand stages. We conducted the ordination in two dimensions using the "metaMDS" function in the R package "vegan" (Oksanen et al. 2020). Data were square root transformed before analyses to lessen the influence of large counts. Convex hulls highlight the different herbicide treatments in each ordination plot.

3.4 Results

We identified 112 native and 18 introduced plant species across all stands in 2022 and 2023, including two ferns, 68 forbs, 26 vines, and 34 woody plants (Table 3.1). In early post-establishment stands, plant species richness was 25% lower in the broadcast chemical site preparation (CSP) and 48% lower in the broadcast CSP + banded herbaceous weed control (HWC) treatments than in control stands [$F_{(2,9)} = 43.44$, $p < 0.001$] in the first sampling year (Figure 3.1). Total plant cover was similar among treatments ($p = 0.854$). Plant species richness was similar ($p = 0.744$) among treatments in the second sampling year, while broadcast CSP and broadcast CSP + banded HWC stands had 59% and 65% greater total plant cover than control stands [$F_{(2,9)} = 8.61$, $p = 0.008$], respectively. Sampling year significantly influenced the responses of plant species richness [$F_{(2,18)} = 4.62$, $p = 0.024$] and total plant cover [$F_{(2,18)} = 4.35$, $p = 0.029$] to herbicide treatments. Early post-establishment plant communities showed significant recovery from the first to second sampling year. Plant species richness increased 36% in the broadcast CSP [$t_{(3)} = -4.39$, $p = 0.022$] and 65% in the broadcast CSP + banded HWC [$t_{(3)} = -5.98$, $p = 0.009$] treatments over two years, and broadcast CSP + banded HWC stands exhibited a 54% increase in total plant cover [$t_{(3)} = -3.26$, $p = 0.047$].

There were no differences in forb, vine, graminoid, or woody plant cover between treatments in the second sampling year ($p = 0.149$-0.707), but forb and graminoid cover did trend higher in broadcast and broadcast + banded stands. Woody plant cover was low across all treatments. Shannon-Weiner diversity index indicated that broadcast CSP + banded HWC stands had 22-42% lower total plant species diversity than control stands in 2022 [$F_{(2,9)} = 10.27$, p = 0.005] and 2023 [$F_{(2,9)} = 5.89$, p = 0.023] (Table 3.2). Simpson's diversity index had similar results, with broadcast CSP + banded HWC stands having 20-25% lower total plant species diversity than control stands in 2022 [$F_{(2,9)} = 5.48$, p = 0.028] and 2023 [$F_{(2,9)} = 11.33$, p = 0.003]. While Pielou's evenness index was similar among treatments in the first sampling year (p = 0.0501), broadcast CSP + banded HWC stands had 21% and 15% lower species evenness [$F_{(2,9)} = 9.79$, $p < 0.001$] than control and broadcast CSP treated stands in the second year, respectively.

In midrotation stands, plant species richness [$t_{(6)} = -3.42$, p = 0.014] and total plant cover [$t_{(6)} = -7.51$, $p < 0.001$] were 61% and 125% lower in herbicide treated stands than control stands in the first sampling year, respectively (Figure 3.2). Results in the second sampling year were similar, with 46% lower plant species richness [$t_{(6)} = -3.83$, p = 0.008] and 77% lower total plant cover [$t_{(6)} = -5.54$, p = 0.001] in the broadcast woody release treatment than in control stands. Herbicide treated stands displayed a 59% increase in species richness [$t_{(3)} = -9$, p = 0.003] from the first to second sampling year, while total plant cover remained stable (74% increase, p = 0.058). Midrotation control treatments did not have any changes in plant species richness or total plant cover over two years (p = 0.079-0.553). Woody plant cover was 103% lower in herbicide treated stands [$t_{(6)} = -3.88$, p = 0.008] in the second sampling year. Forb, vine, and graminoid cover did not differ between treatments but did trend higher in untreated stands (p = 0.125-0.200). All diversity indices were similar between the midrotation herbicide treatments during the study (p = 0.256-0.766).

Indicator species analysis identified 18 plant species that were associated with particular herbicide treatments (Table 3.3). The indicator species consisted of nine forbs, six vines, and three woody plants. Asteraceae was the most common family (six species), followed by Fabaceae with three species. Two forbs, horseweed (*Conyza canadensis* L.) and orangegrass (*Hypericum gentianoides* L. B.S.P.), were associated with all three early post-establishment treatments. One hardwood tree species (*Acer rubrum* L.) and one non-native forb (*Trifolium dubium* Sibth.), were solely associated with midrotation control stands, while one herbaceous (*Desmodium marilandicum* L. DC.) and one woody (*Gelsemium sempervirens* L. J.St-Hil.) vine species were associated with both midrotation treatments.

The early post-establishment NMDS analysis reached a solution in two dimensions with a stress of 0.180 and the ordination revealed no overlap between control and herbicide treated stands (Figure 3.3). Untreated stands contained early successional disturbance-adapted species such as American burnweed (*Erechtites hieraciifolius* L. Raf.), common ragweed (*Ambrosia artemisiifolia* L.), and three-seeded mercury (*Acalypha gracilens* Gray). Broadcast CSP and broadcast CSP + banded HWC stands were largely overlapping with a few distinct species surrounding each treatment hull. Species associated with both herbicide treatments included St. Andrew’s cross (*Hypericum hypericoides* L. Crantz), horseweed, and woody species such as eastern redbud (*Cercis canadensis* L.) and black cherry (*Prunus serotina* Ehrh.).

The midrotation NMDS analysis reached a solution in two dimensions with a stress of 0.176 and the ordination plot revealed a small section of overlap with otherwise unique species clouds surrounding the control and broadcast woody release treatments (Figure 3.4). Herbicide treated stands contained early successional specialists including American burnweed and three-seeded mercury, as well as sawtooth blackberry (*Rubus argutus* Link.), which is typically tolerant of broad spectrum imazapyr application (Wigley et al. 2002). Untreated stands were associated with woody species such as pignut hickory (*Carya glabra* Miller), sweetgum

(*Liquidambar styraciflua* L.), and willow oak (*Quercus phellos* L.), and herbaceous forbs including trailing bush-clover (*Lespedeza procumbens* Michx.) and vines such as invasive Japanese honeysuckle (*Lonicera japonica* Thunb.).

3.5 Discussion

In two years, our study identified 130 understory plant species across all stand stages and herbicide treatment classes. While early post-establishment herbicide treated stands initially had lower plant species richness than untreated controls, broadcast CSP and broadcast CSP + banded HWC stands showed significant increases in plant species richness and total cover during the study. Herbicide treated stands even possessed greater total plant cover than untreated control stands in the second sampling year. These results are consistent with previous research that observed a quick recovery of plant communities following herbaceous weed control treatments, often within two years of herbicide application (e.g., Keyser et al., 2003; Lane et al., 2011; Miller and Chamberlain, 2008). Chemical application type has been shown to impact understory vegetation responses to herbaceous weed control, with non-selective broadcast sprays typically affecting a larger portion of the herbaceous plant community than more conservative banded applications centered on crop trees (e.g., Jones et al., 2010; Marsh et al., 2012).

Unfortunately, our study did not include a mechanical site preparation + banded HWC treatment—instead, all herbicide treated stands were chemically prepared with a broadcast imazapyr application. Plant species richness was higher in broadcast CSP stands than broadcast CSP + banded HWC stands in the first sampling year. However, vegetative communities in the two herbicide treatments were similar by the second year, with no differences in plant richness, total cover, or diversity. Ordination plots for the broadcast CSP and broadcast CSP + banded

HWC plant communities were also overlapping, with patches of distinct species surrounding each treatment hull. While the additional banded HWC application may have further suppressed the understory plant community initially, understory vegetation recovered quickly with significant increases in plant species richness and total cover over time.

Our early post-establishment control stands were recently clearcut, not yet planted stands with high levels of soil disturbance from harvest operations. Broadcast CSP and broadcast CSP + banded HWC stands had higher total plant cover than control stands in the second sampling year, but diversity indices indicated that control stands had higher total plant species diversity than broadcast CSP + banded HWC stands during the study. Ordination plots revealed that this diversity likely stems from an abundance of early successional plant species that thrive in recently disturbed, open areas (e.g., American burnweed, common ragweed, and three-seeded mercury). These pioneer species may provide important floral resources for beneficial insects, particularly those belonging to the plant families Asteraceae and Fabaceae, which are highly attractive to pollinators and contain many important host plants of threatened, specialized bees (Kuppler et al. 2023). Unfortunately, we cannot discuss changes in untreated plant communities over time since our control stands were replaced in the second sampling year due to logistical constraints associated with operational working forests.

As expected, midrotation control stands had greater plant species richness and total plant cover than herbicide treated stands during the study. However, understory plant species richness did increase in the broadcast woody release treatment from the first to second sampling year, which is consistent with previous research on the recovery of herbaceous vegetation following midrotation hardwood release (e.g., Harrington, 2011; Harrington and Edwards, 1999; Iglay et al., 2014). Woody plant cover was also higher in control stands, indicating that the woody release treatments were effective at removing competing hardwood trees and woody shrubs. By reducing competitive woody species, these treatments open forest stands and increase understory light availability—conditions that support diverse herbaceous plant communities.

Species diversity indices and evenness were similar between the midrotation herbicide treated and control stands, but the woody release treatments had noticeable effects on understory plant species composition. Imazapyr herbicide formulations target a broad spectrum of plant taxa but are known to poorly control important wildlife forage species including blackberries and legumes (Wigley et al. 2002; Iglay et al. 2010a). Herbicide treated stands in our study contained many early successional specialist plants, including herbicide-resistant sawtooth blackberry. Boyd et al. (1995) found similar changes in plant species composition following combination of imazapyr, glyphosate, and hexazinone woody release treatments in early post-establishment pine stands. Woody species such as American persimmon (*Diospyros virginiana* L.), water oak (*Quercus nigra* L.), and blueberries (*Vaccinium* spp.) were reduced, while sawtooth blackberry and legumes became more dominant. As evidenced by our study and previous research in southern pine stands (e.g., Jones and Chamberlain, 2004; Jose et al., 2010; Oswald et al., 2009), woody release treatments can increase species turnover and promote disturbance adapted plant species (Jeffries et al. 2010; Jones et al. 2012). Woody release applications may also be useful for land managers without the ability to complete prescribed burns who still wish to promote herbaceous cover and create early successional habitat conditions to meet specific wildlife management objectives (Wigley et al. 2002; Guynn et al. 2004).

3.6 Conclusions

Understory plant communities in working loblolly pine stands showed significant recovery following chemical site preparation, herbaceous weed control, and woody release herbicide treatments over our two-year study. Plant species richness in both early post-establishment and midrotation herbicide treated stands increased from the first to second sampling year. Our results indicated that early post-establishment plant communities can recover quickly (<2 years) following herbicide treatments, and that midrotation woody release herbicide applications can shift understory plant communities to favor disturbance-adapted, imazapyr-tolerant species. Future studies on understory plant communities in working pine forests may investigate how other application types (i.e., banded-only treatments), different herbicides and tank mixtures, and existing plant community structure may influence vegetation responses to forest herbicide applications.

3.7 Acknowledgements

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Table 3.1: Average percent cover (± SE) of understory plant species in herbicide treated early establishment and midrotation working loblolly pine (*Pinus taeda* L.) stands in the Piedmont of Georgia, 2022–2023.

Plant Species[a]	EE Control	EE Broadcast	EE Broadcast + Banded	MR Control	MR Broadcast
Ferns					
Asplenium platyneuron (L.) B.S.P.				0.02 (0.02)	0.01 (0.01)
Botrypus virginianus (L.) Michx.				0.01 (0.01)	
Forbs					
Acalypha gracilens (Gray)	0.20 (0.05)		0.01 (0.01)	0.02 (0.02)	0.02 (0.01)
Ambrosia artemisiifolia (L.)	0.16 (0.09)	0.01 (0.01)	0.01 (0.01)	0.03 (0.02)	0.08 (0.05)
Chamaecrista fasciculata (Michx.) Greene		0.01 (0.01)			0.04 (0.04)
Chimaphila maculata (L.)				0.02 (0.02)	
Cirsium horridulum (Michx.)	0.31 (0.31)				0.03 (0.03)
*_Cirsium vulgare_ (Savi)	0.16 (0.12)	2.20 (0.69)	0.57 (0.26)	0.14 (0.10)	0.36 (0.27)
Clinopodium georgianum (Harper)	0.02 (0.02)			0.21 (0.09)	
Cnidoscolus urens (L.) Arthur			0.10 (0.06)		
Conyza canadensis (L.) Cronq.	0.74 (0.22)	2.64 (0.49)	1.60 (0.41)	0.09 (0.06)	0.01 (0.01)
Diodia virginiana (L.)	0.02 (0.02)	0.91 (0.54)	0.82 (0.23)		
Elephantopus tomentosus (L.)	0.01 (0.01)			0.16 (0.16)	
Erechtites hieraciifolius (L.) Raf.	2.60 (0.80)	0.01 (0.01)	0.08 (0.04)	0.81 (0.33)	3.56 (0.99)
Erigeron strigosus (Muhl)		0.02 (0.02)			0.09 (0.06)
Eupatorium capillifolium (Lam.) Small	4.24 (0.84)	2.02 (0.53)	1.09 (0.30)	2.07 (0.77)	0.29 (0.09)
Eupatorium compositifolium (Walter)		0.17 (0.12)	0.10 (0.06)		
Eupatorium hyssopifolium (L.)	0.09 (0.06)	0.03 (0.03)		0.49 (0.12)	0.09 (0.07)
Eupatorium serotinum (Michx.)	1.81 (0.52)	0.90 (0.37)	0.23 (0.15)	0.21 (0.11)	0.27 (0.09)
Euphorbia corollata (L.)				0.03 (0.02)	
*_Fatoua villosa_ (Thunberg) Nakai				0.01 (0.01)	
Galium pilosum (Aiton)	0.01 (0.01)	0.01 (0.01)		0.01 (0.01)	0.05 (0.05)
Gamochaeta purpurea (L.) Cabrera	0.95 (0.20)	0.58 (0.11)	0.22 (0.06)	0.20 (0.06)	0.30 (0.12)
Geranium carolinianum (L.)	0.02 (0.01)	0.03 (0.02)	0.04 (0.03)		
Helenium amarum (Raf.) H. Rock		3.68 (1.24)		0.16 (0.16)	
Helianthus angustifolius (L.)				0.07 (0.05)	
Hypericum gentianoides (L.) B.S.P.	0.29 (0.10)	0.55 (0.19)	0.07 (0.03)	0.01 (0.01)	
Hypericum hypericoides (L.) Crantz	0.01 (0.01)	0.27 (0.21)	0.18 (0.11)	0.25 (0.16)	0.03 (0.03)
Hypericum mutilum (L.)				0.04 (0.04)	
*_Hypochaeris chillensis_ (Kunth) Britton	0.06 (0.05)	0.18 (0.12)	0.02 (0.02)	0.08 (0.06)	
Krigia cespitosa (Raf.) K.L. Chambers	0.01 (0.01)	0.01 (0.01)	0.39 (0.26)		
Lactuca graminifolia (Michx.)			0.01 (0.01)		
Lechea mucronate (Raf.)			0.01 (0.01)		
*_Lespedeza cuneata_ (Dum.Cours.) G.Don	0.15 (0.05)	0.28 (0.13)	1.24 (0.40)	0.27 (0.08)	0.18 (0.06)
Lespedeza hirta (L.) Hornem.			0.05 (0.05)		
Lespedeza procumbens (Michx.)	0.94 (0.28)	3.85 (1.03)	0.59 (0.25)	4.28 (0.77)	0.54 (0.21)

Lespedeza repens (L.) W.P.C.Barton		0.78 (0.27)			
Lespedeza violacea (L.) Pers.		0.08 (0.05)			
Lespedeza virginica (L.) Britton		0.19 (0.12)	0.04 (0.03)	0.08 (0.05)	0.05 (0.04)
Mimosa microphylla (Dryand.)	0.02 (0.02)		0.04 (0.04)		
Oenothera laciniata (Hill)		0.02 (0.02)			
Oxalis stricta (L.)	0.51 (0.10)	0.25 (0.07)	0.18 (0.05)	0.18 (0.05)	0.05 (0.03)
Packera anonyma (Wood)	0.05 (0.03)	0.23 (0.13)	0.36 (0.15)	0.29 (0.15)	0.13 (0.08)
Physalis heterophylla (Nees)		0.04 (0.04)			
Phytolacca americana (L.)	0.09 (0.05)		0.05 (0.04)	0.22 (0.21)	
Plantago aristata (Michx.)	0.14 (0.05)	5.84 (1.36)	14.58 (1.89)	0.01 (0.01)	
Pluchea camphorata (L.) DC.	0.05 (0.05)				
Polypremum procumbens (L.)	0.25 (0.10)	0.20 (0.12)	1.02 (0.43)		
Potentilla simplex (Dana)	0.55 (0.18)	0.11 (0.06)		1.52 (0.34)	
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt	0.05 (0.05)	0.11 (0.07)	0.02 (0.01)	0.07 (0.04)	0.01 (0.01)
Pycnanthemum pycnanthemoides (Leavenworth) Fernald				0.03 (0.03)	
Ruellia caroliniensis (J.F.Gmel.) Steud.		0.04 (0.04)			
**Rumex acetosella* (L.)	0.13 (0.08)	0.04 (0.03)	0.16 (0.08)		
Salvia lyrata (L.)				0.11 (0.08)	
Sanicula canadensis (L.)				0.04 (0.04)	0.03 (0.03)
Scoparia dulcis (L.)	0.03 (0.03)				
**Senna obtusifolia* (L.) Irwin & Barneby	0.05 (0.02)		0.08 (0.04)		
Smallanthus uvedalia (L.) Mack.	0.02 (0.02)				
Solanum carolinense (L.)	0.25 (0.16)	0.35 (0.19)	0.02 (0.02)	0.02 (0.02)	
Solidago altissima (L.)	0.15 (0.07)			0.23 (0.13)	0.25 (0.21)
Tragia urticifolia (Michx.)				0.03 (0.03)	
Trichostema dichotomum (L.)	0.25 (0.16)		0.01 (0.01)	0.01 (0.01)	0.02 (0.02)
**Trifolium arvense* (L.)			0.03 (0.03)		
**Trifolium dubium* (Sibth.)	0.02 (0.02)		0.04 (0.04)	0.51 (0.21)	
**Trifolium repens* (L.)	0.07 (0.05)				
**Trifolium vesiculosum* (Savi)			0.04 (0.04)		
**Verbena rigida* (Spreng.)		1.75 (0.46)	2.65 (0.77)	0.03 (0.03)	0.08 (0.06)
Verbesina occidentalis (L.) Walter		0.52 (0.32)			0.03 (0.03)
Viola sororia (Willd.)	0.03 (0.02)			0.02 (0.01)	0.05 (0.04)
**Wahlenbergia marginata* (Thunb.) DC.	0.10 (0.06)	0.67 (0.22)	0.09 (0.04)	0.03 (0.02)	0.11 (0.06)
Graminoids	15.92 (1.80)	25.57 (2.13)	25.55 (2.47)	22.30 (2.13)	6.08 (0.90)
Vines					
Ampelopsis arborea (Wunderlin)	0.02 (0.02)				
Berchemia scandens (Hill) K. Koch	0.05 (0.05)				
**Calystegia sepium* (L.) R.Br.	0.01 (0.01)				
Campsis radicans (L.) Bureau	0.03 (0.02)	0.09 (0.06)	0.02 (0.02)	0.22 (0.09)	0.17 (0.08)
Clitoria mariana (L.)	0.01 (0.01)	0.72 (0.26)	0.03 (0.03)	0.85 (0.18)	0.19 (0.11)
Cocculus carolinus (L.) DC.	0.03 (0.02)			0.01 (0.01)	0.19 (0.12)
Desmodium marilandicum (L.) DC.				1.27 (0.32)	0.77 (0.29)
Desmodium rotundifolium (DC.)		0.01 (0.01)		0.02 (0.02)	
Galactia regularis (L.) B.S.P.		0.03 (0.03)			
Gelsemium sempervirens (L.) J.St-Hil.	0.14 (0.05)	0.05 (0.04)	0.02 (0.01)	1.20 (0.28)	0.46 (0.12)

Gonolobus suberosus (L.) R.Br.						0.06 (0.05)
Jacquemontia tamnifolia (L.) Griseb.	0.01 (0.01)	0.25 (0.10)				
**Lonicera japonica* (Thunb.)	0.75 (0.22)	0.16 (0.09)	0.21 (0.11)		3.16 (0.70)	0.53 (0.33)
Parthenocissus quinquefolia (L.) Planch.	0.40 (0.19)				0.44 (0.13)	0.10 (0.04)
Passiflora incarnata (L.)	0.01 (0.01)	0.02 (0.02)	0.10 (0.10)			
Rubus argutus (Link.)	5.82 (1.18)	4.18 (0.79)	2.80 (0.71)		3.68 (0.57)	3.18 (0.66)
Rubus cuneifolius (Pursh)					0.33 (0.19)	
Rubus trivalis (Michx.)	0.56 (0.21)	0.30 (0.14)	1.76 (0.48)		0.21 (0.15)	1.69 (0.73)
Smilax bona-nox (L.)	0.73 (0.23)	0.16 (0.09)	0.40 (0.20)		1.21 (0.25)	0.96 (0.26)
Smilax glauca (Walter)	0.32 (0.08)	0.02 (0.01)	0.27 (0.09)		0.32 (0.12)	0.23 (0.07)
Smilax rotundifolia (L.)						0.01 (0.01)
Strophostyles umbellata (Muhl. ex Willd.) Britt.	0.30 (0.14)	0.55 (0.27)	0.10 (0.05)		0.02 (0.02)	
Tephrosia spicata (Walter) Torr. & Gray	0.01 (0.01)		0.08 (0.06)		0.10 (0.08)	
Toxicodendron pubescens (Mill.)			0.03 (0.03)			
Toxicodendron radicans (L.) Kuntze	0.01 (0.01)				0.09 (0.04)	
Vitis rotundifolia (Michx.)	5.74 (1.30)	1.05 (0.46)	0.16 (0.12)		4.26 (1.50)	0.19 (0.10)
Woody						
Acer rubrum (L.)	0.01 (0.01)				0.35 (0.10)	0.01 (0.01)
**Albizia julibrissin* (Durazz.)					0.06 (0.02)	0.10 (0.05)
Amelanchier arborea (F.Michx.) Fernald					0.10 (0.10)	
Aralia spinosa (L.)	0.16 (0.16)					
Baccharis halimifolia (L.)		0.20 (0.16)	1.09 (0.52)		0.23 (0.12)	0.02 (0.02)
Callicarpa americana (L.)	2.60 (0.86)	0.19 (0.16)	0.10 (0.10)		0.68 (0.33)	0.66 (0.52)
Carya glabra (Miller)		0.05 (0.05)			0.32 (0.22)	
Carya illinoinensis (Wangenh.) K.Koch					0.02 (0.02)	
Celtis tenuifolia (Nutt.)	0.01 (0.01)				0.04 (0.04)	0.03 (0.03)
Cercis canadensis (L.)	0.05 (0.02)	0.43 (0.13)	0.89 (0.50)		0.43 (0.13)	0.19 (0.09)
Crataegus sp.	0.04 (0.03)				0.15 (0.09)	
Diospyros virginiana (L.)	0.05 (0.03)		0.07 (0.07)		0.47 (0.31)	0.05 (0.04)
Fraxinus americana (L.)					0.02 (0.02)	
Gleditsia triacanthos (L.)						0.04 (0.04)
Ilex vomitoria (Sol. ex Aiton)					0.03 (0.03)	
Juniperus virginiana (L.)					0.16 (0.16)	
**Ligustrum sinense* (Lour.)					0.13 (0.09)	
Liquidambar styraciflua (L.)	2.58 (1.12)	1.04 (0.62)	0.14 (0.11)		0.86 (0.43)	0.63 (0.38)
Liriodendron tulipifera (L.)			0.01 (0.01)		0.01 (0.01)	
Nyssa sylvatica (Marshall)					0.01 (0.01)	
**Paulownia tomentosa* (Thunb.) Steud.	0.73 (0.73)					
Platanus occidentalis (L.)					0.07 (0.07)	
Prunus serotina (Ehrh.)		0.04 (0.04)	0.01 (0.01)		0.06 (0.05)	0.02 (0.01)
**Pyrus calleryana* (Decne.)		0.10 (0.10)			0.03 (0.03)	
Quercus alba (L.)	0.52 (0.43)					
Quercus falcata (Michx.)	0.06 (0.05)		0.16 (0.16)		0.13 (0.06)	0.05 (0.03)
Quercus nigra (L.)			0.31 (0.31)			
Quercus phellos (L.)			0.02 (0.02)		0.10 (0.06)	0.03 (0.02)
Quercus rubra (L.)	0.02 (0.01)				0.16 (0.08)	0.05 (0.04)

Rhus copallinum (L.)	0.24 (0.09)	0.13 (0.11)	0.07 (0.05)	0.40 (0.27)	0.10 (0.07)
Ulmus alata (Michx.)	0.19 (0.09)	0.74 (0.30)	0.15 (0.09)	1.29 (0.29)	0.28 (0.10)
Vaccinium arboreum (Marshall)	0.21 (0.21)	0.04 (0.04)		0.31 (0.23)	
Vaccinium elliottii (Chapm.)				0.51 (0.33)	0.10 (0.10)
Vaccinium stamineum (L.)			0.26 (0.21)	0.26 (0.19)	
Total Number of Species	**75**	**62**	**64**	**89**	**58**

Actual means (SE) are presented. EE = early post-establishment, MR = midrotation.

[a] Non-native species are marked with an asterisk (*).

Table 3.2: Shannon-Weiner (*H′*) and Simpson (*D*) plant species diversity and Pielou's evenness index (*J*) of herbicide treated early post-establishment loblolly pine (*Pinus taeda* L.) forests of the Georgia Piedmont.

Index	**Year**	**EE Control[1]**	**EE Broadcast[1]**	**EE Broadcast + Banded[1]**	***P*-value (α = 0.05)**
H′	2022	2.49 (0.11) A	2.12 (0.10) AB	1.63 (0.18) B	0.005
	2023	2.33 (0.04) A	2.17 (0.06) AB	1.86 (0.16) B	0.023
D	2022	0.87 (0.02) A	0.81 (0.02) AB	0.68 (0.06) B	0.028
	2023	0.84 (0.01) A	0.77 (0.02) AB	0.69 (0.03) B	0.003
J	2022	0.75 (0.03)	0.69 (0.03)	0.57 (0.06)	0.050
	2023	0.68 (0.01) A	0.64 (0.01) A	0.55 (0.03) B	0.006

[1] Actual means (± SE) are presented. Within rows, means followed by the same uppercase letter did not significantly differ (α = 0.05). EE = early post-establishment.

Table 3.3: Indicator plant species in herbicide treated loblolly pine (*Pinus taeda* L.) forests of the Georgia Piedmont.

Treatment(s)[a]	**Plant Species**[b]	***P*-Value**[c]	**Family**	**Functional Group**
EE Control **EE Broad** **EE Broad + Band**	*Conyza canadensis*	<0.001	Asteraceae	Forb
	Hypericum gentianoides	0.038	Asteraceae	Forb
EE Broad	**Cirsium vulgare*	0.031	Asteraceae	Forb
EE Broad **EE Broad + Band**	*Diodia virginiana*	0.042	Rubiaceae	Forb
	Plantago aristata	0.001	Plantaginaceae	Forb
EE Broad + Band	*Krigia cespitosa*	<0.001	Asteraceae	Forb
EE Control **MR Control**	*Pontentilla simplex*	0.031	Rosaceae	Forb
EE Broad **MR Control**	*Clitoria mariana*	0.005	Fabaceae	Vine
EE Control **EE Broad** **MR Control**	*Vitis rotundifolia*	0.009	Vitaceae	Vine
EE Broad **EE Broad + Band** **MR Control**	*Baccharis halimifolia*	0.013	Asteraceae	Woody
MR Control	*Acer rubrum*	0.001	Sapindaceae	Woody
	**Trifolium dubium*	0.002	Fabaceae	Forb
EE Control **MR Control** **MR Broad**	*Erechtites hieraciifolius*	0.008	Asteraceae	Forb
	**Lonicera japonica*	0.027	Caprifoliaceae	Vine
	Parthenocissus quinquefolia	0.039	Vitaceae	Vine
MR Control **MR Broad**	*Desmodium marilandicum*	<0.001	Fabaceae	Vine
	Gelsemium sempervirens	0.017	Gelsemiaceae	Vine

[a] Key: EE = early post-establishment

MR = midrotation
Broad = broadcast spray
Banded = banded application

[b] Non-native species are marked with an asterisk (*).

[c] P-value for permutation test to determine if taxon is an indicator species.

Figures

Figure 3.1: Mean understory plant species richness in 2022 (A) and mean total understory plant cover in 2023 (B) in early post-establishment herbicide treated loblolly pine (*Pinus taeda* L.) stands in the Georgia Piedmont. Change in mean understory plant species richness over time in early post-establishment broadcast CSP (C) and broadcast CSP + banded HWC (D) stands. Change in mean total understory plant cover over time in early post-establishment broadcast CSP + banded HWC (E) stands. Different letters represent significant differences in means. Error bars represent standard errors.

Figure 3.2: Mean understory plant species richness (A, B) and mean total understory plant cover (C, D) in midrotation herbicide treated loblolly pine (*Pinus taeda* L.) stands in the Georgia Piedmont in 2022 and 2023. Change in mean understory plant species richness over time in the midrotation broadcast woody release treatment (E). Mean woody plant cover (F) in midrotation stands two years following herbicide treatments. Different letters represent significant differences in means. Error bars represent standard errors.

Figure 3.3: Non-metric multidimensional scaling showing plant species distributions for early post-establishment herbicide treated loblolly pine (*Pinus taeda* L.) stands in the Georgia Piedmont.

Figure 3.4: Non-metric multidimensional scaling showing plant species distributions for midrotation herbicide treated loblolly pine (*Pinus taeda* L.) stands in the Georgia Piedmont.

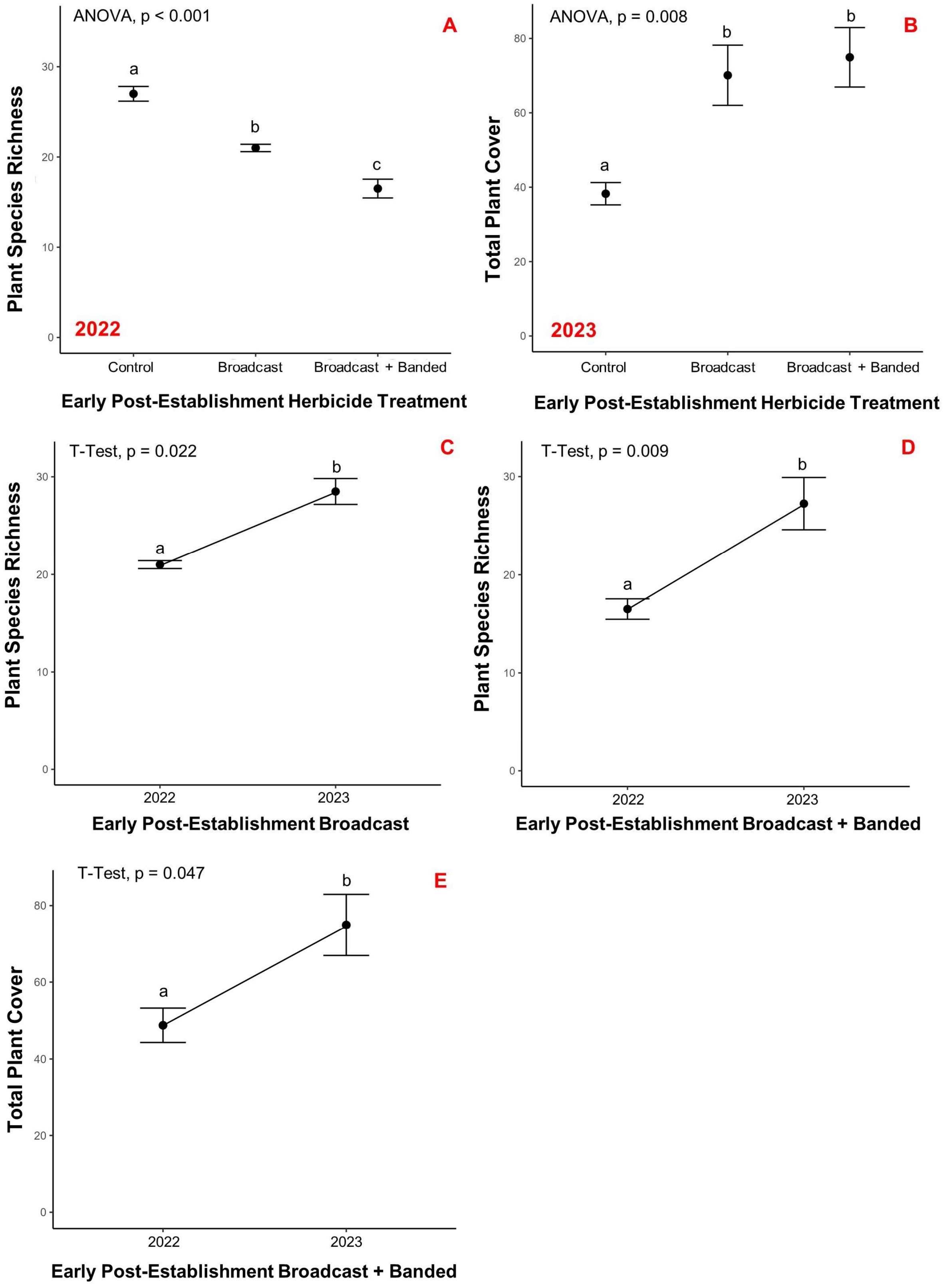

ANOVA, p < 0.001
A
Plant Species Richness
0
10
20
30
a
b
c
2022
Control
Broadcast
Broadcast + Banded
Early Post-Establishment Herbicide Treatment
ANOVA, p = 0.008
B
Total Plant Cover
0
20
40
60
80
a
b
b
2023
Control
Broadcast
Broadcast + Banded
Early Post-Establishment Herbicide Treatment
T-Test, p = 0.022
C
Plant Species Richness
0
10
20
30
a
b
2022
2023
Early Post-Establishment Broadcast
T-Test, p = 0.009
D
Plant Species Richness
0
10
20
30
a
b
2022
2023
Early Post-Establishment Broadcast + Banded
T-Test, p = 0.047
E
Total Plant Cover
0
20
40
60
80
a
b
2022
2023
Early Post-Establishment Broadcast + Banded

Figure 3.1

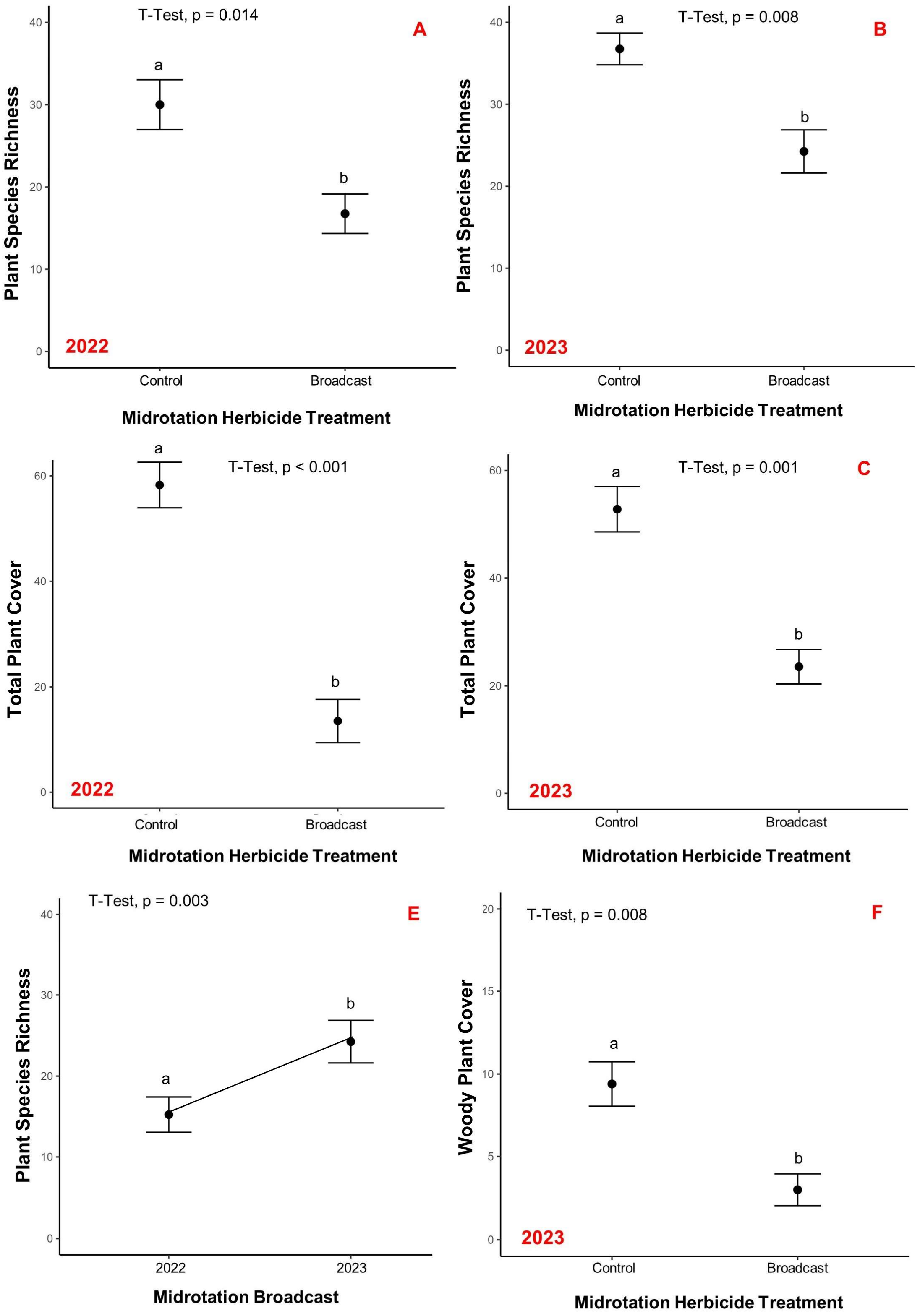
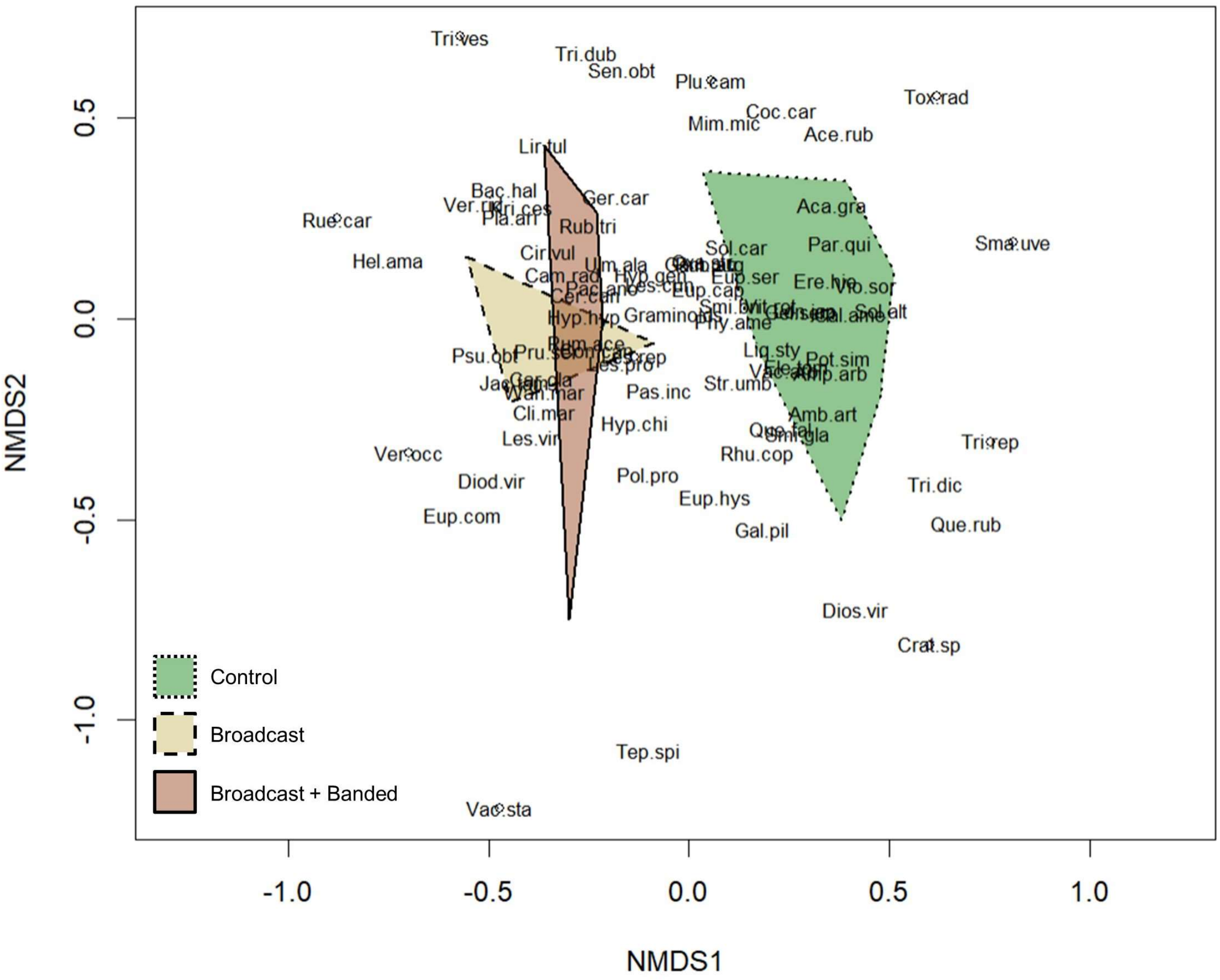

T-Test, p = 0.014
A
a
b
Plant Species Richness
40
30
20
10
0
2022
Control
Broadcast
Midrotation Herbicide Treatment
a
T-Test, p = 0.008
B
b
Plant Species Richness
40
30
20
10
0
2023
Control
Broadcast
Midrotation Herbicide Treatment
a
T-Test, p < 0.001
b
Total Plant Cover
60
40
20
0
2022
Control
Broadcast
Midrotation Herbicide Treatment
a
T-Test, p = 0.001
C
b
Total Plant Cover
60
40
20
0
2023
Control
Broadcast
Midrotation Herbicide Treatment
T-Test, p = 0.003
E
b
a
Plant Species Richness
40
30
20
10
0
2022
2023
Midrotation Broadcast
T-Test, p = 0.008
F
a
b
Woody Plant Cover
20
15
10
5
0
2023
Control
Broadcast
Midrotation Herbicide Treatment

Figure 3.2



Early Post-Establishment Herbicide Treatment

Figure 3.3

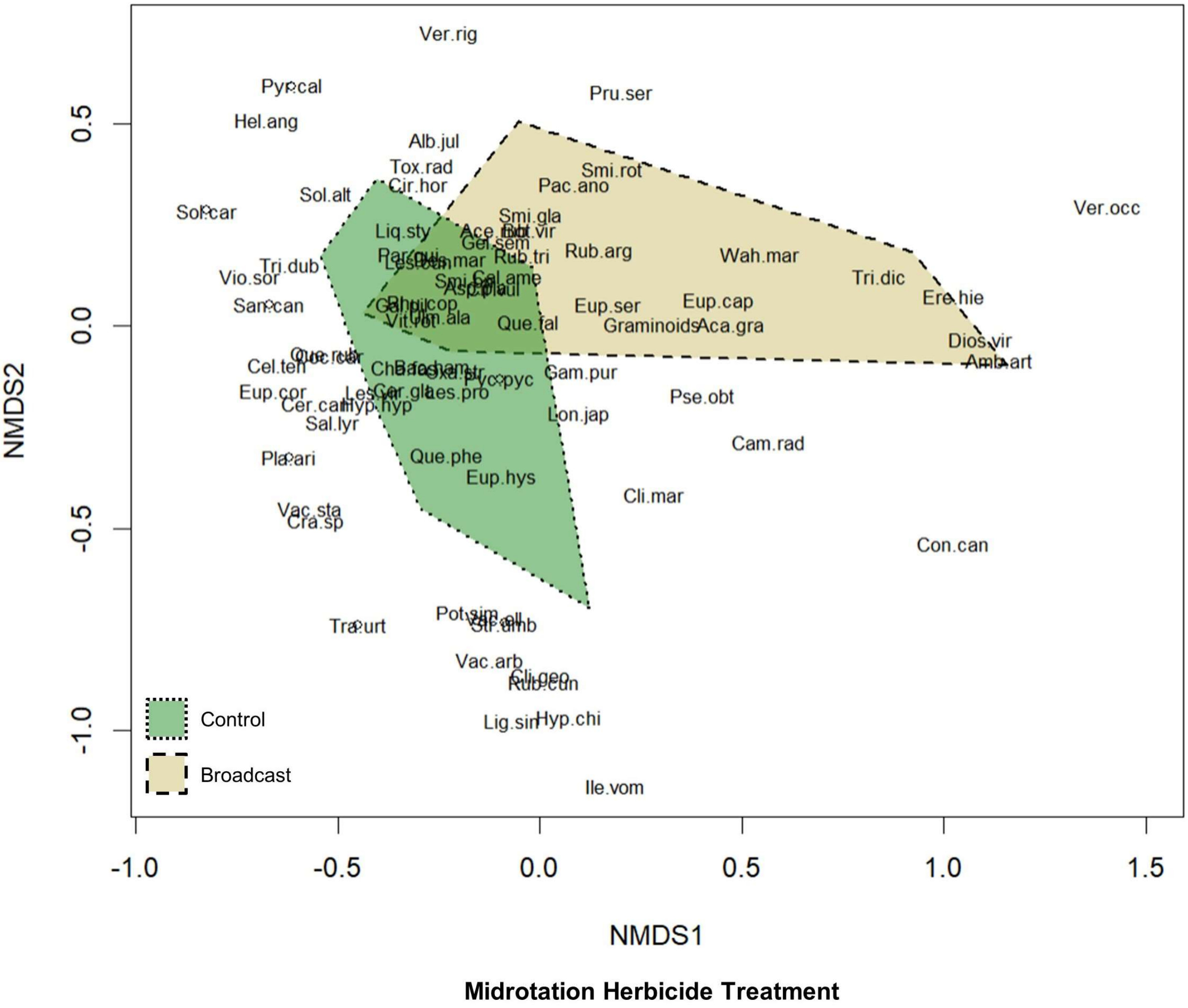

Ver.rig
Pyr.cal
Pru.ser
Hel.ang
Alb.jul
Tox.rad
Smi.rot
Sol.alt
Cir.hor
Pac.ano
Sol.car
Ver.occ
Smi.gla
Liq.sty
Ace.rub
Bot.vir
Gel.sem
Rub.arg
Wah.mar
Tri.dub
Les.cun
Rub.tri
Vio.sor
Smi.bon
Cal.ame
Tri.dic
Asp.plaul
Ere.hie
Eup.ser
Eup.cap
San.can
Vit.rot
Ulm.ala
Rhu.cop
Que.fal
Graminoids
Aca.gra
Dios.vir
Que.rub
Cel.ten
Amb.art
Gam.pur
Pyc.pyc
Eup.cor
Cer.gla
Des.pro
Pse.obt
Cer.can
Hyp.hyp
Lon.jap
Sal.lyr
Cam.rad
Pla.ari
Que.phe
Eup.hys
Cli.mar
Vac.sta
Cra.sp
Con.can
Pot.sim
Str.umb
Tra.urt
Vac.arb
Cli.geo
Rub.cun
Lig.sin
Hyp.chi
Ile.vom
NMDS2
NMDS1
0.5
0.0
-0.5
-1.0
1.5
Control
Broadcast
Midrotation Herbicide Treatment

Figure 3.4

CHAPTER 4

CONCLUSIONS AND FUTURE DIRECTIONS

The main goal of this two-year research study was to determine how different imazapyr herbicide applications impact wild bee and understory plant communities in southern working loblolly pine (*Pinus taeda* L.) forests. Pollinators were sampled using blue vane and blue, white, and yellow pan traps in herbicide treated early post-establishment and midrotation loblolly pine stands of the Georgia Piedmont. Stand-level habitat characteristics were also measured, including tree species, basal area, total height, understory plant metrics (total cover, species richness, and diversity), percent canopy openness, and other fine-scale variables such as the amount of woody decay, bare ground cover, and depth of the litter layer. Results from this study suggest that both early post-establishment and midrotation herbicide treated stands can support abundant and species rich wild bee communities similar to their untreated counterparts. There were no differences in total bee catches, species richness, rarefied species richness, functional dispersion, and functional evenness between control, broadcast, and broadcast + banded early post-establishment stands. However, in midrotation stands, broadcast treated stands had greater bee species richness and different species composition than control stands. Midrotation bee community composition appears to be driven by nesting habitat availability, particularly the increased amount of bare ground cover found in broadcast herbicide treated stands, which likely supports more abundant and diverse soil-nesting bee communities.

Another objective of this study was to determine how understory plant communities in working loblolly pine stands respond to different operational herbicide treatments over time.

Plant species richness in both early post-establishment and midrotation herbicide treated stands increased during the study. Our results indicate that early post-establishment plant communities can recover quickly (<2 years) following herbaceous weed control treatments. Further, midrotation broadcast woody release applications can increase species turnover and shift understory plant communities to favor disturbance-adapted, herbicide-tolerant species. Overall, this work contributes to the growing body of knowledge on the indirect effects of herbicides on understory plant community composition and biodiversity (e.g., Boateng et al., 2000; Iglay et al., 2014; Lane et al., 2011; Miller et al., 1999), and it is the first study to examine wild bee responses to herbicides in southern working pine forests.

4.1 Management Recommendations

According to the results of this study, imazapyr herbicide treatments applied to working early post-establishment and midrotation loblolly pine forests support abundant and species rich wild bee communities. Understory vegetation also recovered quickly following herbicide exposure, with many stands exhibiting significant increases in total understory herbaceous cover and plant species richness over time. While this study did not assess differences in broadcast-only vs. banded-only herbaceous weed control treatments, previous research suggests that the method of chemical application can impact understory plant responses to herbicide exposure (e.g., Campbell et al., 2015; Jones et al., 2010; Marsh et al., 2012). Non-selective broadcast sprays affect a larger portion of the understory plant community than banded applications where herbicides are sprayed selectively in bands centered on crop trees (Miller and Miller 2004; Shepard et al. 2004; Dickens et al. 2020a). Wild bee communities, which rely on understory plants for both floral and nesting resources, may also be further impacted by broadcast sprays.

It’s best if land managers avoid repeated, non-selective broadcast sprays when possible, since banded applications can result in similarly stocked stands and stand productivity as broadcast treatments, while also maximizing herbaceous vegetation in recently planted early post-establishment stands (Lauer et al. 1993; Lane et al. 2011; Campbell et al. 2015).

Land managers could instead use the investment associated with broadcast herbaceous weed control to apply midrotation release treatments (if hardwood basal area creates a need for this type of application), where herbicides can be used to remove competing woody vegetation and enhance understory biodiversity (Lauer et al. 1993; Oswald et al. 2009; Iglay et al. 2010b, 2014; Harrington 2011; Jones et al. 2012). Densely planted, closed-canopy pine stands typically do not support robust pollinator communities (e.g., Favorito et al., 2023; Odanaka et al., 2020). Hence, woody release treatments in conjunction with sound pine thinning operations may be useful for land managers who wish to increase understory light and promote herbaceous plant species, enhance bare ground cover and attract soil-nesting bees, and create early successional habitat conditions to meet other specific wildlife management objectives (Wigley et al. 2002; Guynn et al. 2004). These measures will help ensure the continued survival of the many sensitive bee species that frequent southern working pine forests, including *Bombus penslyvanicus* (De Geer), which is currently under consideration for listing under the U.S. Endangered Species Act (Tyler 2021).

4.2 Directions for Future Research

Very little research has been conducted on the indirect effects of forest herbicide applications on wild bee communities (e.g., Bried and Dillon, 2012). Future studies on pollinators in working forests may investigate how other common management practices, including fertilization, thinning, and prescribed fire, alter wild bee foraging resources, nesting habitat availability, and overall responses to herbicide treatments. Given the limitations of this study, further research may assess how other herbicide application types (i.e., banded-only treatments), different chemical formulations, tank mixtures, and application rates, and specific site characteristics (e.g., soil texture, pH, organic matter and drainage, weather patterns, and existing plant community structure) can influence native pollinator and vegetation communities in working forests. Specifically, researchers could evaluate how historical land use practices impact future plant communities and their recovery from herbicide applications (Franklin et al. 2016). Old-field sites, where pine forests have been naturally or artificially regenerated on abandoned agricultural land, may require fewer or less intense herbicide treatments depending on prior land use (e.g., intensely managed agricultural row crop fields versus pastures) in comparison to unplowed stands that have been forested for several decades (Hedman et al. 2000; Ostertag and Robertson 2007; Brudvig et al. 2014).

Differences in vegetative structure and composition stemming from historical land use practices could in turn influence pollinator communities, which rely on specific forage (e.g., pollen and nectar) and nesting (e.g., deadwood, leaves, and resin) resources to complete their lifecycle (Winfree et al. 2007; Roulston and Goodell 2011). There is also a paucity of long-term studies (> 10 years) assessing the responses of wild bee and understory plant communities to herbicide treatments in working pine forests. This knowledge gap is especially concerning since long-term studies are necessary to detect and assess how critical ecosystem functions (e.g., primary productivity, nutrient cycling, and decomposition) important for maintaining forest biodiversity are impacted by repeated chemical applications. These advances in knowledge would help improve modern forest management to better support pollinator health and diversity and ensure sustainable working forests for years to come.

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