Fall 2014

Vegetation And Soil Characteristics Of Pine Plantations And Naturally Regenerated Hardwood Forests On The Hoosier National Forest

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Graduate School Form 30
(Updated 11/20/2014)

PURDUE UNIVERSITY
GRADUATE SCHOOL
Thesis/Dissertation Acceptance

This is to certify that the thesis/dissertation prepared

By Patrick James Duffy

Entitled

Vegetation and Soil Characteristics of Pine Plantations and Naturally Regenerated Hardwood Forests on the Hoosier National Forest

For the degree of Master of Science

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Head of the Department Graduate Program Date

VEGETATION AND SOIL CHARACTERISTICS OF PINE PLANTATIONS AND NATURALLY REGENERATED HARDWOOD FORESTS ON THE HOOSIER NATIONAL FOREST

A Thesis

Submitted to the Faculty

of

Purdue University

by

Patrick James Duffy

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

December 2014

Purdue University

West Lafayette, Indiana

To my parents, for illustrating the value of determination and perseverance,
and to my wife, without whom I would miss the forest for the trees.

ACNKOWLEDGEMENTS

I would like to thank a few exceptional people, whose work ethic and expertise were invaluable throughout my tenure at Purdue. I thank my committee: Dr. Michael Jenkins, Dr. Douglass Jacobs, and Dr. John Kabrick for their expertise, helpfulness, patience, and constant guidance throughout my thesis. I thank those who aided in data collection including: Michael Jenkins, Chris Thornton, Rob Quackenbush, Michelle McKee, and Samuel Tourtellot. I thank Brad Graham and Michael Mashtare for their knowledge, and Madeline Freiburger for her help in sample processing. I thank Jennifer Spitznagle and Janis Gosewehr for being an exceptional help in administrative tasks. Finally, I thank the Department of Forestry and Natural Resources at Purdue University, the Hardwood Tree Improvement and Regeneration Center, and the United States Forest Service, without whose funding and interest I would not have had this opportunity.

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ABSTRACT

Duffy, Patrick James M.S., Purdue University, December 2014. Vegetation and soil characteristics of pine plantations and naturally regenerated hardwood forests on the Hoosier National Forest. Major Professor: Michael Jenkins.

During the 1930s there was widespread erosion on farmland and subsequent land abandonment. As a result, *Pinus strobus* L. (white pine), *P. resinosa* Aiton (red pine), and *P. echinata* Mill. (shortleaf pine) were planted in the Midwest to prevent erosion and rehabilitate sites. These species were selected due to their wide availability at the time. Currently, it is the goal of the U.S. Forest Service to provide a more natural and sustainable landscape, in part by removing these non-native *Pinus* stands and by replacing them with native hardwood species. The ultimate success of hardwood restoration depends, in part, on the lasting influence of *Pinus* stands on the soil where they were planted. This is worthy of concern because species of the family Pinaceae have a noted impact on nutrient availability, organic matter cycling, soil acidity, and soil buffering capacity compared to mesophytic hardwood species.

This study investigates the impact that *Pinus* plantations have had on soil and vegetation communities compared to hardwood stands. I sampled old-field sites on mesic ridges and bottoms in the Hoosier National Forest that were planted to *P. echinata* and *P. strobus*, or naturally regenerated to mixed hardwood species. I measured overstory and understory vegetation, including saplings, seedlings

and herbaceous-layer species. I measured environmental variables including soil, litter depth, and canopy openness. Soils were sampled and analyzed for macronutrients, micronutrients, pH, organic matter, exchange capacity, and Al. I used Non-metric multidimensional scaling (NMS) ordination and two-way ANOVA with Tukey multiple comparisons post hoc tests ($\alpha = 0.05$) to statistically analyze data.Species composition under *Pinus* stands was distinctly different from that of hardwood stands. *Pinus* stands had lower concentrations of organic matter (OM; -21%), total carbon (TC; -29%), total nitrogen (TN; -30%), manganese (Mn; -37%), calcium (Ca; -24%), Zinc (Zn; -13%), and boron (B; -24%). *Pinus* stands had 2-5 times greater litter depth and 17% greater concentrations of Al compared to naturally regenerated hardwoods. As a result, *Pinus* stands displayed lower herbaceous-layer cover, species richness, and diversity. Hardwood stands contained a greater number of plant functional groups and had greater cover of graminoids, perennials, invasive species, and other mesophytic woody species including *Acer saccharum* Marshall (sugar maple), *Lindera benzoin* L. (spicebush) and *Cornus florida* L. (flowering dogwood). Herbaceous functional groups were more dominant on bottoms, while seedlings and saplings were more dominant on ridges. Ridge hardwood stands contained more mesophytic woody species, whereas ridge *P. echinata* stands contained a greater density of understory *Quercus* spp. and *Fagus grandifolia* Ehrh. (American beech).

Soil fertility proved to be a driving factor in understory communities in my study. Infertile soil with deep litter hosted lower plant cover, but a greater density of *Quercus* spp., whereas more nutrient rich soils hosted mesophytic species. Bottomland soil was better buffered, allowing *Acer* spp. to ascend to the overstory with *Pinus*. The result was that, in bottoms, *Pinus* did not have as large an impact on soil or vegetation communities, resulting in greater similarity to hardwood stands.

CHAPTER 1 INTRODUCTION AND LITERATURE REVIEW

1.1 Setting and Historical Context

Land cover in Indiana was once dominated by hardwood forest. Two glacial events (Illinoian and Wisconsin) defined most of the landscape of northern Indiana, leaving relatively flat topography and productive soils derived from glacial parent material (Welch et al. 2001). In southern Indiana, glacial melt water formed rivers and carved valleys within the sedimentary bedrock, resulting in largely bedrock-derived soils. In sum, Indiana is generally comprised of the northern Norman Upland and southern Crawford Upland subsections, which are divided by the Mitchel Plain (Homoya et al. 1984). The Norman Upland has narrow ridges and steep valleys, whereas the Crawford Upland contains broad ridges and valleys, which provide suitable sites for agriculture and contain caves, springs, and mineral deposits which became economically important around 1818 (Sieber and Munson 1992). Both subsections were divided into four management units that comprise the Hoosier National Forest. The Norman Upland contains the Pleasant Run Unit, while the larger Crawford Upland contains the Lost River Unit, Patoka River Unit, and the Tell City Unit.

With human occupation, anthropogenic disturbance shaped the structure and composition of forest communities. Evidence of Native American tribes has been dated to well over 12,000 years before present, beginning with nomadic hunters and gatherers. Through time, Native Americans altered the landscape through cultivation and the use of fires for hunting, berry production, land clearing for agriculture, and

for the creation of fire breaks (William 2000; Stewart 2002; Johnson et al. 2009). European settlers later cleared land for the production of corn and beans, and later cash crops such as tobacco, as well as for building materials and fuel. The severity of this land alteration increased as small family farms spread across the landscape (Sieber and Munson 1992).

As the population grew, the demand for wood products increased, and most forests were cleared by the early 1900s (Carman 2013). This was followed by unsustainable farming practices, resulting in severely eroded soil, and the bankruptcy of property owners, many of whom abandoned their land during the Great Depression. With this increase in available land, the Week's Act of 1911 and its expansion: the Clarke-McNary Act of 1924 became influential in shaping national forest property. The Adolph Leopold land surveys of 1931 documented land degradation (Sieber and Munson 1992), ultimately resulting in the purchase of largely post agricultural lands, which became the Hoosier National Forest (HNF) in 1951 (Jenkins and Parker 2001).

During the 1930s, the Civilian Conservation Corps (CCC) and the Works Progress Administration (WPA) started planting *Pinus* species in many areas of degraded and abandoned farmland across much of the United States (Parker and Ruffner 2004). The most commonly planted species in Indiana were *Pinus strobus* L. (white pine), *P. resinosa* Aiton (red pine), and *P. echinata* Mill. (shortleaf pine; Otis 1986; Sieber and Munson 1992), due to their wide availability as nursery stock (Dumroese et al. 2005). This planting strategy has continued into the 1970s, as is evidenced by the fact that *Pinus* stands in the HNF post date the CCC and WPA. At greater than 40 years old, most of these stands are available for harvest. However, the predominance of hardwood saw mills in the Midwest reflects a lack of market demand for the estimated 58,107 hectares of *Pinus* in Indiana, Ohio, and Illinois (USDA Forest Service 2013). Net present value, which is the sum potential monetary gain over a given time period discounted to the present, could be improved if native hardwoods were grown

instead, in order to reflect market demands. Furthermore, without direct management these stands have the potential to succeed to dominance by currently low value species such as *Rosa multiflora* Thunb. (multiflora rose), *Fraxinus* spp. L. (ash), *Acer rubrum* L. (red maple), and *Acer negundo* L. (boxelder). Higher value species such as *Quercus* spp. (oaks) and *Juglans* spp. L. (walnut) can provide greater economic quality to these forests. Ecological quality is being considered in conversion as well.

Ecological quality, in terms of species richness and diversity, spatial heterogeneity, ecological resilience, and functional space, can be reduced in conifer monocultures. There is evidence that planted conifer monocultures have reduced vertical and horizontal heterogeneity compared to natural growth. Habitat heterogeneity is a prime determiner of functional diversity as well (Lindenmayer and Hobbs 2004). As a consequence, high quality food sources and shelter may be limited. Therefore, lower faunal diversity is expected in conifer plantations (Lindenmayer and Hobbs 2004; McGrath et al. 2004; Bielecki et al. 2006; Oxbrough et al. 2012; Paritsis and Aizen 2008). As species differ in their response to various abiotic risks and pathogens, stands with greater numbers of species spread risk, and as one species may die out through insect pests, fungal pathogens, wind, or fire, more resistant species may fill in gaps, thereby maintaining forest structure. Therefore, mixed stands are more resistant to disturbance and are more resilient afterward (Jactel et al. 2009). Non-native conifer monocultures are generally more susceptible to risk from insect pathogens (Jactel and Brockerhoff 2007), as mixed stands of genetically distinct individuals spread the risk from herbivory by creating a mosaic of host and non-host trees, where the distance between host trees acts as a buffer from infection. This trend is particularly notable for specialist pests (Jactel and Brockerhoff 2007). Many conifers are also at greater risk for wind damage, partly because they keep their leaves in winter when most storm damage occurs (Schütz et al. 2006). In addition, conifer species often contain higher concentrations of resins and oils in needles and bark, and are consequently more flammable. This

increases the likelihood of fire, as well as fire intensity, and thus the likelihood of damage and tree mortality. Thus, *Pinus* monocultures are generally at a greater risk to fire damage (Gonzalez et al. 2006). Lastly, in a meta-analysis, Piotto (2008) found that stands with a number of dominant overstory species produce greater diameter growth over monocultures, improving net present value. Thus, conversion to mixed hardwood stands may decrease risk, increase spatial heterogeneity and functional groups, increase biodiversity, improve stand value, and generally improve ecological value (Lindenmayer and Hobbs 2004). Currently, it is the goal of the U.S. Forest Service to provide a more natural and sustainable landscape, in part by removing these non-native *Pinus* stands and by replacing them with mixed hardwood species. The ultimate success of restoration efforts depends, in part, on the lasting influence of *Pinus* stands on the soil where they were planted.

1.2 Impacts of Agriculture on Soil

Through tillage, soil organic matter (SOM) aggregates, mineral aggregates and roots are disturbed and displaced (Six et al. 1999). This comes partly from the physical perturbation of the soil, and partly from erosion of both SOM and small particles when fields are dormant (McLauchlan 2006). Decomposition requires aeration, so the rate of SOM loss is highly correlated with the concentration of O_2. Since O_2 diffuses into soil slowly, tillage increases the rate of decomposition of organic matter (Six et al. 1999). Humus decomposes into a variety of compound types including enzymes, nutrients, and organic acids. Organic acids play a role in pH, complexation or chelation, and the release of nutrients into the soil (Sposito 2008). For example, oxalic acid, HOOC-COOH, dissociates at varying pH to yield one or two moles of H^+ per liter ($^-$OOC-COOH or $^-$OOC-COO$^-$), allowing complexation or chelation at one or two sites per molecule, respectively. In doing so, it may complex Fe^{3+}, Al^{3+}, Mg^{2+}, and other metals while simultaneously lowering soil pH. Similarly, humic and fulvic acids from humus

dissociate in solution at varying levels of pH, releasing H^+ and balancing their charge through complexation. In addition, organic matter structure is highly variable and largely amorphous and contains varying carboxylic and phenolic groups. These groups dissociate H^+ to produce negatively charged, hydrophilic sites to bind hydrophilic compounds like nutrient cations, while also containing lipophilic sites to bind hydrophobic compounds. For this reason, humus binds a large proportion of soil nutrients, from 1 to 9 $mol_c\ kg^{-1}$ whereas average mineral soil in a typical Alfisol contains 0.15 $mol_c\ kg^{-1}$. These amorphous molecules form colloidal structures, which are non-crystalline aggregations, which aid soil nutrient retention (Sposito 2008). Tillage breaks aggregates apart, allowing for the disruption and loss of SOM (Six et al. 1999).

The principal factors controlling soil acidity are the quantity of acids present, the strength of acids, and the degree of dissociation of acids (Binkley et al. 1989). The presence of acids are driven by $CO_{2\ (g)}$ input, Acid deposition of S and N sources from fertilizers and acid rain (Helyar and Porter 1989; Sposito 2008), humus dissociation and decomposition as discussed above, proton biocycling principally in the rhizosphere, and reactions with Al and Fe hydroxyl groups in mineral soil (Sposito 2008). Thus in addition to tillage altering humus decomposition, ammonium fertilizers are important in increasing acidification (Tarkalson et al. 2006; Helyar and Porter 1989).

As soil acidifies, the concentration of protons is great enough to remove large quantities of cations, allowing eluviation from surface soil. These nutrient cations are released from the surface of clay minerals, in the interlayers of clay minerals, and on the broken edges of minerals. The rate at which inter-layer minerals desorb in the presence of H^+ at low pH is complex, and directly related to their hydrolysis constant and enthalpy of hydration. The hydrolysis constant describes how likely an ion is to incite hydrolysis, which is the breaking apart of water, usually resulting in the complexation of that metal with OH^-. The enthalpy of hydration describes the amount of energy necessary for that metal to bind with

water, and so the greater the absolute value, the less likely that metal is to bind with water. The practical significance is that exchangeable cations between clay minerals with high enthalpies of hydration will hold the structure of that mineral, a good example of which being calcium. This is also partly because Ca has a small hydrated radius and keeps clay interlayers from expanding (Sposito 2008). At low pH, proton attack occurs, and cations which occupy the interlayer may be replaced by H^+, which compromises the clay structure, and at the same time attacks clay aggregates, dispersing clays into smaller particle sizes and effectively reducing the presence of clay in the surface soil over time (Sposito 2008).

Al and Si are found primarily in the crystal lattices of phyllosilicate minerals (clay minerals), and through isomorphic substitution, smaller concentrations of Mg, and Fe are held in the structure of many phyllosilicates. Minerals dissolve at low pH, releasing these species into solution. As Fe and Al are released from crystalline mineral structures, the species released depend on pH. For Al, the minimum amount of dissolution occurs around pH five. Below that, Al(III) is the principal species released, and $Al(OH)^{2+}$, $Al(OH)_2{}^+$, and $Al(OH)_3$ become more dominant in that order with increasing pH (Sposito 2008). The majority of Al-toxicity comes from the adsorption of $Al^{3+}{}_{(aq)}$ to root sites. In addition, as Al incites hydrolysis and binds with hydroxyl groups, it releases H^+, which is why Al plays a strong role in soil acidification, is considered an acid cation, and is of concern to plant health at lower soil pH (Wright 1989; Sposito 2008).

The result is that with tillage and decreased pH, clay and organic aggregates are disturbed and can be displaced, nutrient cations can be released and leached, Al can be released from clays, and the resulting surface soil can have larger average grain size.

Therefore, at low pH nutrient availability is diminished and soil texture may increase, and because most of the water holding capacity and cation exchange capacity in soil comes from humus and phyllosilicates, nutrient holding capacity and moisture retention can be reduced (Helyar and Porter 1989).

Tillage also affects soil carbon, and soil carbon is indicative of soil health (Kasel and Bennett 2007). Soil carbon includes humus, which provides a source of nutrients and serves as a component of soil structure. Soil carbon includes carboxyl groups, which provide adsorption sites and microbial substrate, the latter being necessary to sustain microbial populations. Soil carbon includes enzymes and amino acids, which are directly used to sustain life. Lastly, soil carbon includes earthworms and other soil fauna that affect porosity, soil permeability, and decomposition (Kasel and Bennett 2007; Karlen et al. 1994).

Tillage allows soil organic carbon (SOC) to be exposed to a greater oxygen concentration, allowing for accelerated oxidation and resulting in increased decomposition and loss of soil organic matter. SOC is also lost through erosion (McLauchlan 2006). Diminished SOC corresponds to diminished substrate for microorganisms as well, further hindering microbial capacity. Soil microbes are instrumental to soil function through nitrogen fixation, methane oxidation, and decomposition (Borken et al. 2003; Kasel and Bennett 2007). Therefore, diminished SOC is analogous to diminished soil health (Kasel and Bennett 2007). Intensive agriculture also causes the loss of available nitrogen (N) and phosphorous (P) through increased decomposition, increased erosion, decreased plant input rates as plants are harvested, and increased uptake of P by leguminous plants (McLauchlan 2006).

The severity of agricultural soil degradation in the Midwest was exacerbated during the Dust Bowl Era by non-fallow farming practices, the effects of which were most severe in drought years (Hurt 1981). Auten (1945) and Billings (1938) suggested that within decades of planting *Pinus* on old-field sites, soil quality, aeration and growing capacity may improve. Billings (1938) shows that over the first 12 years after planting *P. echinata* on an old-field Piedmont soil, a prevalent, nutrient-poor tillage layer dissipated to yield a thicker A horizon, likely due to litter build up and root growth. Over time, the various O, A, and B horizons became thicker, and nutrient availability increased. Additionally, species composition shifted from shallow rooting herbaceous species to more deeply rooting hardwood species over time. The success of *Pinus* on these poor quality sites likely results from their tolerance to nutrient-poor conditions. However, literature suggests that the long-term impact of *Pinus* on these sites may not be beneficial for the regeneration of native hardwoods.

1.3 Impacts of Conifers on Soil

The long-term impact of conifers on soil frequently involves nutrient loss and soil acidification through litter and root inputs. These impacts are the result of slower decomposition and litter buildup on the forest floor (Berg and McClaugherty 2003; Stendahl et al. 2010), differing concentrations of nutrients and chemical compounds within litter, and lower soil pH from litter and ectomycorrhizal leachates (Hizal et al. 2013; Berg and McClaugherty 2003; Yin et al. 2014).

The biomolecules released from litter vary by species, and litter from *Pinus* spp. contains low concentrations of labile organic substances and nutrients, such as sugars, water soluble nutrients and phenolic acids, but contains larger proportions of large molecular weight compounds, such as cellulose, hemicellulose and lignin. Labile compounds are readily lost from litter, whereas high molecular weight compounds decompose slowly. As they decompose, they

release intermediary, labile compounds. Lignin releases phenolic acids, which can be allelopathic. As these compounds decompose, they leave increasingly recalcitrant fractions, and as a result, late stage decomposition features high lignin and N concentrations. Nitrogen inhibits the enzyme ligninase, which aids in the decomposition of lignin, and so high leaf N concentrations correspond to high remaining lignin concentrations. High variability in litter decomposition by species has been observed due to variation in initial N concentrations. In the uncommon case where conifer litter has very low N concentrations (<0.0036%), lignified tissue may decompose more readily. Along with N, the enzyme Manganese Peroxidase (MnP) is affective to the decomposition of lignin. However, its solubility increases with decreasing pH (Berg and McClaugherty 2003), so its availability may be limited as pH diminishes. Therefore, litter in conifer stands decomposes more slowly than broadleaf litter in part because of decreased Mn concentrations where acid soil is found and because of N and lignin concentrations within litter (Berg and McClaugherty 2003). In addition, as litter decomposes, the amount of surface area increases, thereby increasing microbial degradation. Because coniferous litter resists decay, its surface area increases more slowly, further retarding decomposition (Kuiters and Sarink 1986).

This delayed decomposition affects the temporal release of phenols, which have been found to be allelopathic (Berg and McClaugherty 2003). These readily soluble organic acids are leached from both deciduous and coniferous litter, both in early stage decomposition and as an intermediary product of lignin decomposition (Berg and McClaugherty 2003). However, deciduous litter inputs peak between October and January, after litterfall when plants are dormant. Due to slower decomposition and greater litter persistence, coniferous litter releases phenols during the growing season, resulting in the potential inhibition of ground layer growth (Blaschke 1981).

In addition to high lignin concentrations, coniferous litter generally releases nutrients into soil more slowly compared to broadleaf trees (Berg and McClaugherty 2003; Pritchett 1979; Binkley and Valentine 1991; Yin et al. 2014). In particular, Northup et al. (1995) show that the high polyphenol content in conifer litter corresponds to a shift in the form of nitrogen released, and thus its availability and mobilization. Nitrogen is generally released in organic forms through proteins and amino acids, as well as mineral forms in ammonium (NH_4^+), or nitrate (NO_3^-). Ammonium is the major source of biologically available N for most species, and NO_3^- is the most readily leached form (Vitousek and Matson 1985). Organic N often forms protein-tannin complexes, which are recalcitrant aggregations of hydrophobic organics to polyphenols. As such, the concentration of organic N increases with polyphenol content in litter, whereas mineral forms of N decrease. In addition, N mineralization is limited in acid soil and in cold climates, where organic N provides increasing fractions of total soil N. Conifers form ectomycorrhizal (ECM) associations. ECM are found in habitats limited by mineral N availability. First, that they are found in habitats with an average pH below 5 (Read 1991), and in species with relatively high polyphenol leaf content, which is associated with a dominance of N in proteins and limited mineral N (Northup et al. 1995, Smith and Read 2010; Yin et al. 2014). Evidence suggests that many species of ECM can directly utilize these protein sources as well as amino acids. In a comparison of amino acid uptake in *Pinus*, *Picea*, and *Fagus*, Wallenda and Read (1999) illustrated that the affinity for common organic N sources is high in ECM fungal species. ECM can utilize organic N directly by enzymes such as carboxypeptidase, which breaks N apart from these proteins (Northup et al. 1995).

That ECM and ericoid mycorrhizae (EM) readily utilize organic N has been well studied (Smith and Read 2010). However, recent evidence suggests that vesicular arbuscular mycorrhizae (AM) may readily utilize complex organic sources for N, although there is no direct evidence of saprotrophy in AM fungi (Smith and Read 2010). One hypothesis suggests that hyphae readily grow

towards organic N rich patches and utilize that source while it decomposes (Leigh et al. 2009). Whether they directly increase proteolytic activity, or improve the activity of saprotrophic fungi, ECM and EM outcompete AM for organic N sources (Smith and Read 2010). In a study comparing amino acid uptake in AM to ECM with *A. saccharum*, *Quercus*, and *Tsuga canadensis*, Gallet-Budynek et al. (2009) showed that both functional types take up amino acids directly. AM formed with species of higher labile litter content and improved mineral N availability, where ECM formed with species of recalcitrant litter and soil enriched in organic material, as literature suggests. 70% of N in ECM came from organic N, compared to 20% for AM. Nave et al. (2013) showed that ECM were more common in mineral N limited sites, which transitioned to AM dominated sites as mineral N increased, and that *Quercus*, in association with ECM, were superior competitors for N. While there is evidence that AM compete well for both organic and mineral N, there is greater support in the literature for the concept that ECM utilize complex organic N directly, but direct evidence of this is also somewhat limited (Smith and Read 2010). There is still a lack of direct evidence to elucidate the competitive difference of ECM and AM for organic N sources (Smith and Read 2010; Näsholm et al. 2009; Uibopuu 2013), partly from a lack of field studies comparing them directly (Yin et al. 2014). However, Yin et al. (2014) show that ECM exudates and enzymatic activity have a strong impact on nutrient cycling, especially from organic sources, and nutrient acquisition in stands with recalcitrant litter and slow decomposition.

Relatively low pH has been observed in conifer stands, and comes from the release of strong aliphatic acids: oxalic, malic, citric, and formic acid during litter decomposition (Pohlman and McColl 1988) and from ectomycorrhizal leachates (Helyar and Porter 1989; Landeweert et al. 2001). Soil acidity, as measured by pH, is determined by acid concentration, degree of acid dissociation (which correlates negatively to base saturation), and the strength of acids present (Binkley et al. 1989). pH will be lower with a high concentration of organic acids, low base saturation, and with strong organic acids, where a low acid dissociation

constant (pKa) corresponds to high acid strength. When aliphatic organic acids dissociate, they complex or chelate metals and lower soil pH (Helyar and Porter 1989; Landeweer et al. 2001). Oxalic, formic, citric, and malic acid are also strong acids (pKa = 1.23, 3.76, 3.08, 3.40; Zhang et al. 2009), thus having a strong impact on soil pH. Pohlman and McColl (1988) found that 60-80% of litter extracts of *Pinus ponderosa* Lawson & C. Lawson (ponderosa pine), *Calocedrus* Kurz (incense cedar), and *Pseudotsuga menziesii* (Mirb.) Franco (douglas-fir) were made of oxalic, mallic, gallic, and protocatechuic acid, with oxalic acid dominating *Pinus* litter. Other studies have found relatively high concentrations of oxalic, formic, acetic, and citric acid in *Pinus banksiana* Lamb. (jack pine), *Pinus rigida* Mill. (pitch pine), *Pinus lambertiana* Douglas (sugar pine), *Pinus radiata* D. Don (Monterey pine), *Picea rubens* Sarg. (red spruce), *P. strobus*, and *Tsuga canadensis* (L.) Carrière (eastern hemlock; Smith 1969; Krzyszowska et al. 1996). Fox and Comerford (1990) showed that this suite of aliphatic organic acids is common for many other *Pinus* species, including *Pinus elliotii* Engelm. (slash pine), *Pinus taeda* L. (loblolly pine), and *Pinus palustris* Mill. (longleaf pine).

Polyphenolic compounds and organic acids released from conifer litter (Pollman and McColl 1988) and ectomycorrhizae (Hue et al. 1986; van Hees et al. 2005) dissolve sesquioxides of Fe and Al through chelation. These acids include freely released aliphatic acids, including oxalic, malic, and citric acid, and polyphenolic compounds such as tannin and phenols (Pohlman and McColl 1988; Muir et al. 1964). In describing podsolization, De Coninck (1980) found that metal-organic complexes formed with Si, Al, and Fe translocated through the soil profile in solution. In cold climates, this eluviation of sesquioxides, combined with slow decomposition and nutrient-poor litter, results in podsolization: the formation of a soil with low concentrations of nutrients in surface horizons, a corresponding low pH and a high degree of surficial leeching. Where climate is milder, such as in Ohio, Indiana, and Illinois, a high degree of leaching is unlikely, and so conifers are likely to have a lesser impact on soil.

The increase in soil acidity from the release of organic acids increases the solubility of nutrients, and reduces the integrity of silicate minerals (Sauer et al. 2007), as well as organic and clay aggregates and structures (Sposito 2008). Soluble nutrients are eluviated and a disruption in clay and humus aggregates facilitates sandier textured soil through the loss of smaller particles and reduced total exchange capacity (TEC). The reduction in TEC occurs because organic matter and clay mineral surfaces hold the majority of exchange capacity. This results in a soil with reduced nutrient availability, reduced water holding capacity, diminished buffering capacity, and potential Al-toxicity (Pritchett 1979).

Al(III) becomes increasingly available below a pH of five, and as the principle Al species that adsorbs to roots, it corresponds to increased Al-toxicity (Wright 1989; Sposito 2008). The rhizosphere responds to increased Al-toxicity through organic acids and plays a large role in soil acidification and nutrient transport. When ectomycorrhizae (ECM) release their organic acids, Al(III) and Fe(III) are complexed or chelated. There is evidence that ECM will respond to Al concentration by releasing increased concentrations of oxalic acid, which complexes Al and keeps it from root surfaces (Zheng et al. 1998). Thus, ECM associations are of a competitive advantage in environments where pH is low through higher tolerance to Al(III) as they release greater concentrations of Al(III) into the soil environment and away from the rhizosphere. The dissociation of these organic acids lowers soil pH as well (Sposito 2008). Consequently, ECM lower nutrient availability and remove trivalent metals to some degree. Since members of the family Pinaceae are known to form ECM associations (Pritchett 1979), it follows that conifers lower pH through litter and that they form ECM associations, which lower soil pH as a self-replacing competitive strategy.

Conifers form ECM, which strongly change the soil environment, increasing the availability of nutrients, and increasing access to complex organic N and P sources. They inhabit sites with slow nutrient cycling, with recalcitrant leaf litter and lower average pH (Read 1991; Smith and Read 2010; Yin et al. 2014). Many

hardwood and herbaceous species, on the other hand, form vesicular arbuscular mycorrhizal (AM) associations. Hyphae of AM more rapidly acquire mineral nutrients, which are quickly cycled in leaf litter, as associated species have highly labile litter content. As bases, like Ca, are cycled more quickly, and because exudates do not strongly alter soil acidity like ECM, this promotes higher pH and allows for more robust microbial populations, and increases the availability of mineral nutrients, including N. Therefore, P becomes the most limiting nutrient therein, and evidence suggests that AM are superior competitors for mineral P compared to ECM (Read 1991; Smith and Read 2010; Yin et al. 2014).

The association of ECM with conifers is partly why conifers are better able to tolerate extreme soil conditions. However, the degree to which conifers change the soil environment depends upon the inherent buffering capacity of the soil. Buffering capacity is largely determined by cation exchange capacity, which is determined largely by the amount of humus and phyllosilicate minerals, and to a lesser degree by hydroxides and carbonates. Sodalite, cancrinite, nahcolite, calcite, and other carbonates react in solution with pH to dissociate their metal cation and to bind H^+.

$$CaCO_{3(s)} + H^+ = HCO_3^{-}{}_{(aq)} + Ca^{2+}{}_{(aq)}$$

Soil will be increasingly buffered against pH change with greater concentrations of carbonates, hydroxides, humus, and phyllosilicates (Sposito 2008). The two land types studied here were mesic ridges and bottoms, and were defined by Ecological Land Type Phases (ELTP; Zhalnin 2004). The two ELTPs differ, in part, by parent material, soil texture, and topographic position, so it is reasonable to expect a notable difference in buffering capacity between ELTP 13, mesic ridges, and ELTP 42, bottoms. Though both tend to be silt loam soils, bottoms contain two meters of silt alluvium, whereas mesic ridges average silt loam to clay loam up to 68 cm, with sandstone parent material beneath. Lastly, mesic ridges and bottoms differ in average pH, 5.5 vs. 6.8 (Zhalnin 2004), implying that

bottoms are better buffered. Thus, water and nutrient rich alluvial materials transported to bottoms should provide an added source of exchangeable bases, phyllosilicates, and organic matter from surrounding sources, which should provide added buffering capacity in bottoms.

Bottomland soils also have a greater water input rate from upland and upstream sources, and as a consequence have the potential to have standing water for a greater proportion of the year. Gases like O_2 and CO_2 diffuse into inundated soil far more slowly than dry soil, and over time soil O_2 is depleted and CO_2 accumulates through respiration. As O_2 is the greatest electron acceptor, O_2 depletion correlates to an increase in available electrons, and an inevitable reduction of NO_3^-, SO_4^{2-}, Fe^{3+}, Mn^{4+}, and CO_2 as they take up electrons. These redox sensitive species (N, S, Fe, Mn, C, and O) are released from minerals such as goethite (FeOOH) and replaced by H^+. This is partly responsible for the superior buffering capacity of bottomland soils (Sposito 2008).

$$MnOOH_{(s)} + 3H^+_{(aq)} + e^- = Mn^{2+}_{(aq)} + 2H_2O_{(l)}$$

$$FeOOH_{(s)} + 3H^+_{(aq)} + e^- = Fe^{2+}_{(aq)} + 2H_2O_{(l)}$$

As a redox sensitive species, Fe is reduced and leached quickly in soils and so certain bacteria, fungi, and grasses have developed siderophores to complex Fe(III; Sposito 2008). Siderophores are biomolecules which complex Fe(III), and thus lower its redox potential so that it remains in soil more readily. Without this complexation, Fe(III) is reduced to Fe(II), which is soluble and quickly leaches from surface soil. In addition, these organic compounds complex other trivalent metals such as Al(III) and divalent nutrient cations, potentially lowering metal toxicity to microbes and retaining some soil nutrients (Sposito 2008).

1.4 The Herbaceous Layer in Forested Ecosystems

Improving ecological quality in forest ecosystems is partly a matter of improving ecosystem function, which refers to ecological processes that control energy, nutrient, and organic matter fluctuation throughout the environment (Cardinale et al. 2012). To that end, biodiversity and the range of functional traits in an ecosystem need to be considered. Biodiversity is the variety of life, including variation in genes, species, and functional traits, and can be measured through taxonomic or functional diversity. Functional traits include morphological, physiological, phenological, and behavioral traits which can be measured individually and directly influence performance (Cardinale et al. 2012).

Therefore, functional diversity is a measure of the range, distribution, and abundance of functional traits in a given ecosystem, whereas taxonomic diversity is a measure of the range, distribution, and abundance of species in a given ecosystem. A distinct difference between the two measures is that while taxonomic diversity does not always directly relate to ecosystem function, functional diversity does (Cardinale et al. 2012).

In a review of two decades of research, Cardinale et al. (2012) showed that biodiversity and ecosystem stability are positively correlated, where stability refers to the resistance to change in ecosystem functions and services. Furthermore, diverse communities are more productive because of a variety of functional traits, rather than a variety of species (Cardinale et al. 2012). For these reasons, this study investigates taxonomic diversity as well as the variety of functional groups in the southern Hoosier National Forest. The herbaceous layer in forested communities plays an important role in biodiversity, regeneration, and nutrient cycling (Gilliam 2007). This stratum typically contains the largest number of species within forest ecosystems, and thus overall plant species diversity is largely a function of herbaceous-layer diversity (Yu and Sun 2013). Vegetation communities are increasingly threatened by fragmentation, species invasions, and environmental degradation. Since species in the herbaceous layer are more

prone to extirpation than those of other forest strata (Gilliam 2007), the herbaceous layer is a critical element in efforts to conserve biodiversity. Rare plants, in particular, have specific habitat requirements, so they can serve as indicators of biodiversity loss in response to changing disturbance regimes (Gilliam 2007). In addition, herbaceous communities influence advance regeneration through competition with seedlings. Because seedlings have to grow through the shade of the herbaceous and shrub layers, a denser layer may reduce the ability of woody plants to regenerate, and may reduce advance regeneration (Gilliam 2014; Gilliam and Roberts 2003).

The herbaceous layer also contributes to soil quality by influencing the cycling of nutrients. Herbaceous litter concentrations of N, P, Mg, and K are generally much greater than in woody plants and decompose several times faster. Thus, through nutrient uptake and litter decomposition, the herb layer rapidly cycles nutrients, decreasing nutrient leaching (Gilliam 2007). The most notable example is in that spring ephemerals may act as a vernal dam, effectively making nutrients more available for later season seedlings, and facilitating healthy forest soil (Muller 1978; Muller 2003; Gilliam 2007).

The composition of the herbaceous community is most directly related to the availability of light, moisture, and soil nutrients, and forms a strong linkage with forest overstories (Jenkins and Parker 1999; 2000; 2001; Lipscomb and Nilson 1990; Yu and Sun 2013; Gilliam and Roberts 2003; Gilliam 2007; 2014). The term linkage refers here to a relationship wherein the dynamics of the overstory significantly affect those of the understory. Specifically, that preexisting forest structure influences microclimate and microtopography, which influences moisture, light, and nutrient levels, which drive herbaceous species diversity, richness, and evenness (Gilliam et al. 1995). Disturbance changes the existing forest structure, altering these three factors through the distribution of living trees, standing dead wood, and coarse woody debris. For these reasons, this study investigates herbaceous-layer communities.

Conifers frequently have lower herbaceous-layer diversity (Barbier et al. 2008). This is a consequence of overstory linkage, and relates to the fact that conifer plantations have low overstory species richness. This should also correlate to low woody species diversity where seed sources may be limited (Gilliam 2014, Gilliam 2007). As a consequence of plantation, vertical and horizontal heterogeneity is reduced, which results in reduced functional diversity as well (Lindenmayer and Hobbs 2004). This results in reduced shelter and food availability, and can result in lower faunal diversity (Lindenmayer and Hobbs 2004). Additionally, there is evidence to suggest that conifers frequently lower soil pH, buffering capacity, exchangeable bases, or nutrient availability and have greater litter depth and allelopathic litter, all of which can lower species diversity or change functional group distributions in *Pinus* stands (Barbier et al. 2008; Blaschke 1981; Berg and McClaugherty 2003).

Litter quality directly affects herbaceous-layer species (Gilliam 2014), and litter depth alters light availability and quality, acts as a mechanical barrier to establishment and germination, and affects moisture and temperature (Barbier et al. 2008, Facelli and Pickett 1991a; Loydi et al. 2013). Species vary in their response to litter depth, yet it is agreed that deep litter (>500 g m^2) acts as an effective mechanical barrier for most species, although this provides a competitive opportunity for a select few (Barbier et al. 2008; Loydi et al. 2013; Sydes and Grime 1981). In a meta-analysis of litter on understory diversity, Xiong and Nilsson (1999) showed similar results, suggesting that litter depth affects species richness more than biomass, showing that community composition is strongly affected by litter depth, and relates to litter quality. Facelli and Pickett (1991a; b) provide evidence that graminoids are less sensitive to litter than annual and perennial herbs, and that tree litter may be more inhibiting than herbaceous litter. Additionally, in a recent meta-analysis, Loydi et al. (2013) show that increased litter depth also may increase soil moisture availability, which can aid seedling establishment in dry sites. There is evidence that larger seed size, such as that of *Juglans* spp. also correlates to a greater ability to germinate in

thick litter because of greater energy reserves (Loydi et al. 2013). Meers et al. (2010) suggest that *Pinus* litter and ectomycorrhizae have a negative effect on herbaceous layer diversity as well. Other studies show that *Pinus* spp., *Quercus* spp., and *Fagus* spp. all appear to lower understory diversity and reduce soil fertility to a degree (Barbier et al. 2008). It is logical to conclude that they may be reasonable habitat companions due to having similar strategies for leaf nutrient retention (recalcitrant litter) and mycorrhizal relationships.

It appears Quercus regeneration is occasionally high in conifer plantations, which is partly reflected in that their acorns have mild moisture requirements for germination and medium litter depth may provide better moisture conditions on dry ridges. However, *Quercus* regeneration appears to be highly dependent upon seed bank and propagule supply from past land use (Navarro-González et al. 2013). The fact that these trends are difficult to predict is reflective of the fact that there is a complex interaction between soil acidification, nutrient availability, litter depth, light transmittance, throughfall, and interspecific understory competition. Gilliam (2014) suggests that herbaceous species often outcompete seedlings for nutrients and increase nutrient cycling because of labile litter content. Therefore, they can have a direct negative impact on advance regeneration (Gilliam 2007). Where they are affected by litter depth, they may decrease in abundance and provide a competitive opportunity for a more tolerant,woody species.

1.5 Study Objectives

The primary objective of this thesis was to determine how the long-term presence of non-native *Pinus* species affected soil chemistry and influenced the composition and diversity of herbaceous-layer plant communities. This was done by comparing *P. echinata* plantations, *P. strobus* plantations, and naturally regenerated hardwood forest sites on mesic ridges and bottoms. In Chapter 2, we investigate differences in soil chemistry of the A horizon (top 10 cm of mineral

soil) between *Pinus* and hardwood sites by analyzing samples for concentrations of total C (%), total N (%), P (mg kg^{-1}), Ca (mg kg^{-1}), Mg (mg kg^{-1}), Zn (mg kg^{-1}), B (mg kg^{-1}), and Al (mg kg^{-1}). In addition, we also determined litter depth (cm), pH, C/N ratio, total exchange capacity (meq 100 g^{-1}), and organic matter (%). Chapter 3 examines the difference in herbaceous and seedling species composition and diversity across stand types in response to soil chemistry and site characteristics, including non-metric multidimensional scaling (NMS) ordination and indicator species analysis.

I hypothesize that *Pinus* stands will have lower pH and nutrient status, with greater litter depth and Al. This will be more evident in ridges than bottoms due to the difference in buffering capacity afforded by topographic position and soil type. I further hypothesize that differences in soil conditions between *Pinus* and hardwood stands will be correlated to differences in herbaceous-layer diversity and composition. Finally, I hypothesize that the regeneration density of mesophytic tree species, such as *A. saccharum*, will be lower on *Pinus* sites, while the density of *Quercus* spp. regeneration will be greater.

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CHAPTER 2 RESPONSE OF SOIL CHEMISTRY TO LONG-TERM OCCUPANCY BY NON-NATIVE *PINUS* SPECIES

2.1 Abstract

Species of the family Pinaceae have a distinct impact on nutrient availability, organic matter cycling, soil acidity, and soil buffering capacity compared to many hardwoods. This is the result of slow litter decomposition and litter accumulation, differing concentrations of recalcitrant and labile compounds in litter, and low soil pH from litter and ectomycorrhizal (ECM) leachates. A slower rate of nutrient cycling can result, and acidification corresponds to increased nutrient leaching and a release of Al into the soil solution. The degree to which *Pinus* stands affect soil chemistry, however, depends on the initial buffering capacity of the soil. *Pinus* spp. in my study were planted on old-fields where soil erosion and degradation should yield low buffering capacity. Consequently, decades of *Pinus* occupancy may have a lasting impact on soils. Currently in the Midwestern United States, managers are converting stands to native hardwood mixtures. However, the suite of appropriate silvicultural actions and the success of these conversions will depend on the lasting influence of *Pinus* on soil and vegetation communities. To investigate these long-term impacts, I compared the soil chemistry and species composition of *Pinus echinata* and *P. strobus* plantations in southern Indiana to those of nearby naturally regenerated hardwood stands. To assess potential differences resulting from topographic position, *Pinus* plantations and hardwood stands were examined on both mesic ridges and bottoms. On average, soils in *Pinus* plantations had lower concentrations

of organic matter (OM; -21%), total carbon (TC; -29%), total nitrogen (TN; -30%), manganese (Mn; -37%), calcium (Ca; -24%), zinc (Zn; -13%), and boron (B; -24%). *Pinus* stands had 2-5 times greater litter depth and 17% greater concentrations of Al compared to naturally regenerated hardwoods. The difference between *Pinus* and hardwood stands was greater on ridges than bottoms, as bottom *Pinus* appeared to have minimal impact on soil chemistry. This was likely due to superior buffering capacity in bottom soils, and the presence of codominant *Acer* spp. in *Pinus* overstories.

2.2 Introduction

In the Midwest, *Pinus echinata* Mill. (shortleaf pine) and *Pinus strobus* L. (white pine) were planted on eroded, abandoned old-fields (Otis 1986; Sieber and Munson 1992). These plantations may not be as ecologically valuable as native hardwood mixtures as a result of lower functional heterogeneity, and lower average diversity (Barbier et al. 2008; Facelli and Pickett 1991a; Loydi et al. 2013; Lindenmayer and Hobbs 2004; Bielecki et al. 2006). Thus, land managers are seeking favorable conversion strategies for the regeneration of native hardwoods. The success of conversion will depend, however, upon the lasting impact of *Pinus* stands on soil chemistry and productivity.

Species of the family Pinaceae impact nutrient availability, organic matter cycling, soil acidity, and soil buffering capacity in ways explicitly different from mesophytic hardwoods. This is the result of slow litter decomposition and the resulting accumulation of litter (Berg and McClaugherty 2003; Stendahl et al. 2010; Finzi et al. 1998) that contains high concentrations of recalcitrant compounds (Berg and McClaugherty 2003; Read 1991; Finzi et al. 1998; Kuiters and Sarink 1986; Pohlman and McColl 1988). Under such conditions, soil pH is typically low because of acid inputs from decomposing litter and ectomycorrhizal leachates

(Hizal et al. 2013; Berg and McClaugherty 2003; Binkley and Valentine 1991; Read 1991; van Hees et al. 2005). *Pinus* litter is generally nutrient-poor and degrades slowly, resulting in diminished nutrient input into mineral soil (Berg and McClaugherty 2003; Pritchett 1979; Binkley and Valentine 1991). Furthermore, a greater proportion of nutrients may be in organic rather than mineral form, which are not as readily absorbed by roots (Smith and Read 2010).

Conversely, the herbaceous and woody species found in this study, including *Acer* spp. L. (maple) and *Liriodendron tulipifera* L. (tuliptree), commonly have more rapidly decomposing litter and vesicular-arbuscular mycorrhizal (VAM) associations. Through rapid decomposition and cycling of nutrients like Ca, in association with VAM, these species may promote improved base saturation and buffering in soil, higher pH, and increased nutrient mineralization through larger bacterial populations (Kalisz 1986; McClaugherty et al. 1985; Berg and McClaugherty 2003; Finzi et al. 1998; Jenkins et al. 2007; Holzmueller et al. 2007; Gilliam 2014; Read 1991; Smith and Read 2010). Therefore, conifers and hardwoods have distinctly different effects on soil chemistry that serve to replicate soil conditions in which they are superior competitors.

Conifers naturally occur on infertile, dry, and/or acid soils, which is partly why they were used to afforest highly eroded old-fields in the Midwest (Auten 1946; Billings 1938). Native conifer soil is typically lower in pH, exchangeable bases, base saturation, organic matter, and exchange capacity compared to adjacent hardwoods (Brown and Curtis 1952; Pohlman and McColl 1988; Ste-Marie and Pare 1999). This is the result of both the natural soil conditions on which they best compete, and the soil chemical change incurred by conifers. However, the degree to which conifers change soil conditions depends on the soil's initial buffering capacity.

In poorly buffered, low pH soils, such as in the Piedmont soils of the Carolinas, conifers naturally cause low pH, infertile soil conditions (Binkley et al. 1989; Richter et al. 1994; Binkley and Sollins 1990; Pallant and Riha 1999; Binkley and Valentine 1988). Conversely, well-buffered soils show much less change associated with conifers (Hizal et al. 2013; Rolfe and Boggess 1973; France et al 1989).

The geology of southern Indiana is largely comprised of sandstone bedrock underlying silt loam soils of the Wellston and Apalona series (Table 2.1). These soils typically have lower buffering capacity when compared to the glacial till-dominated soils in northern Indiana (Zhalnin 2004; Homoya et al. 1984). Furthermore, ridges typically have lower buffering capacity than bottoms (Sposito 2008). Bottoms in southern Indiana receive greater inputs of silt loam alluvium from glacial meltwater and receive greater annual inputs of water and aqueous nutrients. In addition to this improved input of nutrients, the greater moisture content of bottom soils compared to ridges likely leads to greater rates of reduction in soils as well. In reduction, redox sensitive species (N, S, Fe, Mn, C, and O) are released from minerals such as goethite (FeOOH) and replaced by H^+.

$$FeOOH_{(s)} + 3H^+_{(aq)} + e^- = Fe^{2+}_{(aq)} + 2H_2O_{(l)}$$

All of these factors improve buffering capacity in bottoms (Zhalnin 2004; Sposito 2008). Therefore, *Pinus* plantations may have a more lasting impact on soil chemistry on ridges, but less of an impact on bottoms.

The impact of *Pinus* spp. on soils has been well studied in their natural setting (Sauer et al. 2007; Smith and Read 2010; Read 1991). However, less is known about soil impacts in plantations, where *Picea abies* (L.) Karst. (Norway spruce) has received extensive study (Bergh et al. 1999; Binkley and Valentine 1991; Herault et al. 2005; Humphrey 2005) compared to members of the genus *Pinus.* In southern Indiana both *P. echinata* and *P. strobus* are non-native species

(Lawson 1990; Wendel and Smith 1990) that were planted on former hardwood sites outside of their native ranges. Little is known about how long-term site occupancy by these species has affected soils in forests without a native conifer species. In addition, regardless of nativity, difference in soil chemistry between monocultures and diverse stands is not yet fully understood (Barbier et al. 2008).

To investigate the long-term impacts of *Pinus* plantations on soils and vegetation communities, I studied *P. echinata* and *P. strobus* plantations and compared them to naturally regenerated hardwood stands in old-fields on mesic ridges and bottoms in southern Indiana. I sampled vegetation communities and soil chemistry on 113 plots. In this study I address the following hypotheses:

1) The occupancy of *Pinus* on these bedrock-derived soils will show discernable impacts on soil chemistry. Soils under *Pinus* stands will have lower pH and reduced nutrient availability, as well as greater litter depths and Al concentrations compared to adjacent naturally regenerated hardwood stands.
2) The effect of *Pinus* spp. on soil chemistry will differ between ridges and bottoms. Because bottoms have more highly buffered soil, the effects of *Pinus* spp. on soil chemistry will be less pronounced. As such, the differences in soil chemistry between *Pinus* and hardwood sites should be more pronounced on ridges than in bottoms.

2.3 Methods

2.3.1 Study Sites

Sample sites were chosen within the Tell City Unit of the Hoosier National Forest within the Crawford Upland Subsection (CUP) as defined by Homoya et al. (1984). In ArcMAP v10.1, I used Ecological Landtype Phase (ELTP) to select sample sites, which is a land classification delineated by several variables including dominant vegetation, indicator species, soil type, elevation, slope, and slope aspect (Van Kley 1993). Because ELTP 13 *Fagus-Acer saccharum/Arisaema* Mesic Ridges, and ELTP 42 *Acer saccharinum/Boehmeria* Bottomlands were the most common ELTPs in our study region, and because both contained an abundance of *Pinus* plantations, we confined our sampling to these two. To limit variability of soil across potential plots, I used Natural Resource Conservation Service (NRCS) soil series data to assure that sites had similar soil types. While NRCS data show that there are many specific soil groups found within each ELTP, most of these soils only differ slightly. Soils on ELTP 13 tend to be silt loam over sandstone parent with an argillic horizon of silt loam or silty clay between 20 and 68 cm (NRCS 2013), with an average A horizon depth of 4.7 ± 0.8 cm and an average pH of 5.5 ± 1.1. ELTP 42 consists of silt loam alluvium over 2 m thick with a poorly differentiated A horizon estimated at 10 cm and an average pH of 6.8 ± 0.2 (Zhalnin 2004). The two most common NRCS soil series found within sites on mesic ridges and bottoms were Apalona silt loam and Wellston silt loam (Table 2.1). Both have average pH values between 3.5-7.3 and average CEC below 20 meq per 100 g (NRCS 2013). Other soil series found within sites contained similar values for pH, CEC, and soil type.

Across mesic ridges and bottoms, I selected three vegetation types for sampling: *Pinus echinata* Mill. (shortleaf pine) plantations, *Pinus strobus* L. (white pine) plantations, and naturally regenerated hardwood sites. Hardwoods that had regenerated naturally after agricultural abandonment included *Platanus occidentalis* L. (American sycamore), *Liriodendron tulipifera* L. (tuliptree), *Juniperus virginiana* L. (eastern redcedar), *Juglans nigra* L. (black walnut), *Acer negundo* L. (boxelder), *A. rubrum* L. (red maple), and *A. saccharum.* Digitized aerial photographs from the 1940s were overlain in ArcMAP to ensure that chosen sites were previously utilized for agriculture. To reduce edge effects, I used a 20 m buffer from roads, and a 40 m buffer between adjacent stand types to minimize the influence of surrounding litter types. Within these buffered delineations, the final sample coordinates were randomly selected in ArcMAP. Lastly, sites that experienced secondary disturbances such as logging, windstorms, or fire after agricultural abandonment were rejected. At all sites, I recorded GPS coordinates and marked plot locations with rebar and witness tree tags.

I determined the age of each stand sampled to ensure that *Pinus* and hardwood sites were of a comparable age. While stand age data were collected by the USDA Forest Service by coring various representative trees within a defined stand, the resulting polygons represented by these ages were often quite large. Therefore, in order to more accurately represent overstory age on sampled plots, I cored three dominant trees at 30 cm above the ground using an increment borer. The average age of these three trees was used to estimate stand age (Jenkins and Parker 1999; 2000). By using only sites that were historically used for agriculture, we limited stand age to a maximum of 70 years, due to the fact that land was largely abandoned in the 1930s and 1940s (Welch et al. 2001). The average age was between 25 and 40 years, because most of the plantations in the Hoosier National Forest occurred later than the 1940s.

2.3.2 Field Sampling Design

Due to the fact that soils vary across each ELTP, and because past agricultural use altered A horizon thickness through increased erosion (Welch et al. 2001), I collected soil samples at 0-10 cm and 10-20 cm using an impact driven soil corer. Sampling at these depths allowed me to capture the zone of herbaceous-layer rooting. All soil sampling was conducted in cardinal directions, 5.6 m from plot center. A minimum of 400 g per sample was collected per site. For the 0-10 cm sample, five cores were taken and put into separate bags, and for 10-20 cm depth, five cores were combined into one sample because of a lack of funding for laboratory analysis. I also collected litter from three 25 cm^2 quadrats located 5.6 m west, north, and east of plot center. In total, 585 soil samples and 351 litter samples were collected (Figure 2.1).

2.3.3 Laboratory Analysis

Soil samples were air dried on paper plates for three to five days. Samples were then crushed with a mortar and passed through a 2 mm sieve to separate mineral and non-mineral material. Coarse grained material volume was then measured using volumetric displacement. The soil sample volume was calculated by subtracting the volume of coarse fragments from the total volume of the sample. Bulk density (D_b) was then calculated by taking the mass of dry soil over the corrected core volume. Litter samples were dried at 70^oC for 48 hours or until constant mass (Amacher et al. 2003). Non-litter material was then separated and weighed, while litter was passed through a Wiley mill to reduce particle size. A subsample of each ground sample was then placed into a vial with BBs and shaken with a paint shaker for approximately four hours until homogenized. Within the Forest Ecology, Silviculture, and Soils Laboratory at Purdue University, total carbon (TC%) and nitrogen (TN%) were estimated using an ECS CosTech 4010 Elemental Analyzer. A horizon soil samples were sent to

Brookside Laboratories, Inc. (New Bremen, OH) to analyze pH_{water}, organic matter (%), total exchange capacity (TEC; meq 100 g $^{-1}$), estimated nitrogen release, S (ppm), P (mg kg^{-1}), Ca (mg kg^{-1}), Mg (mg kg^{-1}), K (mg kg^{-1}), Na (mg kg^{-1}), B (mg kg^{-1}), Fe (mg kg^{-1}), Mn (mg kg^{-1}), Cu (mg kg^{-1}), Zn (mg kg^{-1}), and Al (mg kg^{-1}) were measured by Mehlich III Extraction, and percent Ca, Mg, Na, and K for base saturation (Nelson and Sommers 1996; McLean 1982; Schulte and Hopkins 1996; Ross 1995; Mehlich 1984; Bray and Kurtz 1945).

2.3.4 Sampling Design and Data Analysis

In total, I sampled 44 ridge *P. echinata* sites, 26 ridge *P. strobus* sites, 7 ridge hardwood sites, 9 bottom *P. echinata* sites, 7 bottom *P. strobus* sites, and 13 bottom hardwood sites, resulting in an unbalanced experimental design. These sample sites comprised all suitable sample sites within the study area.

I used two-way Analysis of Variance (ANOVA) with categorical variables stand type and ELTP to more closely examine explanatory variables that were correlated with ordination axes, including functional groups ($r^2 > 0.2$; Chapter 3). This included analyzing variables by stand type (*P. echinata*, *P. strobus*, or hardwood), ELTP (mesic ridges or bottoms), and their interaction term. The interaction compared individual types, for example: ridge *P. echinata* vs. ridge hardwood, ridge *P. strobus* vs. bottomland *P. strobus*, etc. Assumptions of normality and constant variance were assessed with plots of studentized residuals versus fitted values (Neter et al. 1996). We also used residual plots to screen potential outliers (Neter et al. 1996). I used a square root transformation for litter depth, Ca, B, Zn, and canopy openness. For Fe, I removed an extreme outlier and log transformed. Non-transformed data are presented for ease of interpretation. Dead basal area, being particularly problematic, was centered, absolute value transformed, and square root transformed in order to better fit assumptions of normality and constant variance. When ANOVA revealed

significant differences, I used the Tukey multiple comparisons test for post hoc comparisons (α = 0.05). If assumptions were violated after transformation, I used a Kruskal-Wallis ANOVA on Ranks with Dunn's Multiple Comparisons (α = 0.05). Because A horizon pH, organic matter (%), and total exchange capacity should have a large influence on exchangeable cations and Al-toxicity, I regressed these against the dependent variables exchangeable cations and Al. As with ANOVA, I inspected residuals and transformed data as needed.

2.4 Results

pH, OM (%), TC (%), TN (%), B (mg kg^{-1}), Mn (mg kg^{-1}), Ca (mg kg^{-1}), and Zn (mg kg^{-1}) in the top 10 cm of soil were all greater in hardwoods than *Pinus* stands. Both A and B horizon pH were lower in *Pinus* than hardwood stands ($F = 2.9, 9.8$, $p = 0.06, <0.001$). B horizon pH was significantly lower than A horizon pH as well (Mann-Whitney Ranked Sum Test; $U = 140.5$, $p<0.001$). Mean A horizon pH was 5.5 ± 0.1 in *Pinus* stands and 5.9 ± 0.1 in hardwood stands, while mean B horizon pH was 4.2 ± 0.09 in *Pinus* stands and 4.56 ± 0.08 in hardwood stands. B horizon pH was lowest in ridge *P. echinata* stands with a mean of 4.0 ± 0.05. Organic matter was greater in ridge hardwoods than ridge *Pinus* stands. Organic matter (%) ranged from 2.4 to 5.6, with a mean of 3.6 ± 0.1 in ridge *Pinus* and 4.6 ± 0.2 in ridge hardwood stands, with a significant interaction term ($F = 8.2$, $p<0.001$). Total carbon (%) differed significantly between stand types through their interaction term as well. Percent total carbon was greater on ridge hardwood than on ridge *Pinus* sites, averaging 1.7 ± 0.1 on *Pinus* and 2.3 ± 0.1 on hardwood sites ($F = 6.6$, $p = 0.002$). Total nitrogen (%) was analogous to total carbon, with a mean of 0.1 ± 0.01 and 0.2 ± 0.01 on ridge *Pinus* and ridge hardwood sites, respectively ($F = 4.0$, $p = 0.02$; Figure 2.2; Table 2.2).

Litter depth (cm) showed the opposite trend, and was greater in *Pinus*, following the trend *P. echinata*>*P. strobus*>hardwood ($F = 15.7$, $p<0.001$). Mean litter depth was 19.0 ± 2.0 in *P. echinata*, 14.1 ± 2.5 in *P. strobus*, and 5.6 ± 2.6 in hardwoods stands. Litter mass (g m^{-2}) was significantly greater in *Pinus* than hardwood stands (*P. echinata*>*P. strobus*>hardwood), with means of 823.9 ± 67.5, 592.4 ± 83.7, and 287.1 ± 86.3, respectively. Litter carbon to nitrogen ratio (LC:LN) in bottoms was significantly greater in *Pinus* than in hardwood stands (LC:LN = 40.3 ± 1.9 for *P. echinata*, 35.6 ± 2.4 for *P. strobus*, and 27.9 ± 1.6 for hardwoods; $F = 9.3$, $p<0.001$). Concentrations of B ($F = 7.9$, $p = 0.002$), Ca ($F = 4.3$, $p = 0.02$), and Zn ($F = 14.1$, $p<0.001$) were all greater in hardwood than in *Pinus* stands. For Mn, the interaction term was significant ($F = 4.6$, $p = 0.01$), and soils on ridge hardwood sites contained more Mn than *Pinus* stands (Figure 2.2; Table 2.2). Bottomland sites showed fewer trends, due in part to the small number of suitable sites available. In bottoms, soil concentrations of Fe ($F = 4.2$, $p = 0.02$), Zn ($F = 14.1$, $p<0.001$), Ca ($F = 4.3$, $p = 0.02$), and B ($F = 7.9$, $p<0.001$) were greater in hardwood stands than *P. echinata* stands, with a significant interaction term for Fe ($F = 4.3$, $p = 0.02$). TEC ($F = 12.3$, $p<0.001$), P ($F = 5.7$, $p = 0.02$), Na ($F = 6.8$, $p = 0.01$), and Zn ($F = 7.2$, $p = 0.01$) were greater in bottoms than ridges. TEC ranged from 4.2 to 22.7, with a mean of 8.8 ± 0.4 on ridges, and 11.2 ± 0.6 on bottoms (Table 2.2).

Soil Al concentrations (mg kg^{-1}) were significantly greater on ridges than on bottoms. Soil N concentrations were significantly greater in *Pinus* stands than hardwood stands, and the interaction term was significant ($F = 5.4$, $p = 0.01$). With a significant interaction term, Al was greater in bottom *P. strobus* than bottom hardwood stands ($F = 5.4$, $p = 0.006$; Figure 2.2; Table 2.2).

2.5 Discussion

The results of my study show that decades of *Pinus* occupancy have resulted in changes to soil chemistry. Overall, *Pinus* stands had thicker litter layers and greater litter mass, less soil organic matter, and reduced nutrient concentrations compared to hardwood sites. Specifically, total N and total C were lower in *Pinus* than in hardwood stands, but Al content was greater. The soil differences observed between *Pinus* and hardwood stands partly resulted from the slow decomposition and resulting buildup of litter on the forest floor (Berg and McClaugherty 2003; Stendahl et al. 2010). Litter from *Pinus* spp. contains low concentrations of labile compounds, such as sugars, water soluble nutrients and phenolic acids, but contains larger proportions of large molecular weight compounds, such as cellulose, hemicellulose and lignin. Labile compounds are readily lost from litter, whereas high molecular weight compounds decompose slowly. This accumulation of high molecular weight compounds results in the accumulation of a thick litter layer in *Pinus* forests (Berg and McClaugherty 2003). In my study, I observed litter depths in *Pinus* stands 2-5 times greater than those in hardwood stands. This recalcitrance of *Pinus* litter resulted in lower organic matter content in the surface soil of *Pinus* stands, which contributed to reduced TC, TN, and micronutrient content likely due to reduced mineralization. Additionally, the accumulation of litter mass in conifer forests alters moisture and temperature conditions, and may act as a mechanical barrier to germination and seedling establishment (Barbier et al. 2008, Facelli and Pickett 1991a; Loydi et al. 2013). Loydi et al. (2013) found that a litter mass of >500 g per m^2 significantly reduced the ability of plants to germinate. However, it appears that deep litter afforded a competitive opportunity for species that tolerate such litter conditions by producing large seeds, such as *Quercus* spp. In my study, the deep litter layer I observed in *Pinus* stands (mean > 500 g per m^2) may have contributed to the greater regeneration of *Quercus* spp. there (Chapter 3).

The Al concentrations in *Pinus* stands suggest that more Al was released from silicate minerals and sorption sites, thus increasing the possibility of Al-toxicity in this stand type (Wright 1989). Overall, ridge soils contained higher concentrations of Al than bottom soils. Increased soil Al content may have contributed to the greater density of *Quercus* spp. and *F. grandifolia* stems observed in *P. echinata* sites (Chapter 3). Seedlings of both of these genera/species have been shown to be resistant to higher levels of soil Al than the majority of their competitors (McCormick and Steiner 1978; Schaedle et al. 1989).

Many studies suggest that soil acidity should be affected by agricultural use. Old-fields experience soil degradation in several ways, including the loss of soil organic matter and small particles through tillage and erosion (McLauchlan 2006), which reduces buffering capacity (Sposito 2008). In addition, old-fields may be acidified by ammonium fertilizer input (Tarkalson et al. 2006). Therefore, old-field sites may have lower CEC and OM, and be more susceptible to pH change than uncultivated fields. In my study, the fact that OM and TEC were relatively low across all stand types suggests that past agricultural use may have decreased the amount of humus in the soil. *Pinus* stands are slow to replenish this material, as is evident in the deep litter depth and low OM, TC, and TN in *Pinus* stands compared to hardwoods. However, base saturation in this study was high, averaging around 70% across all sites. This suggests that both hardwood stands and conifer plantations in this study are somewhat well buffered against pH change. This is particularly true in bottoms, which we expected to be better buffered. This is supported by higher TEC, and greater concentrations of certain nutrients including Na and Zn, that I observed in bottoms compared to ridges. Furthermore, Fe showed a trend only in bottoms, and because Fe is a redox sensitive species, it is reasonable to conclude that Fe was reduced and made soluble, allowing for leaching or uptake. Through this reduction, soil buffering was improved (Sposito 2008). Lastly, ELTP data suggest that, due to its land position, bottoms should receive greater nutrient inputs in

solution from runoff, improving soil fertility and buffering capacity (Zhalnin 2004). Conversely, though base saturation was high in ridges, ridge sites were less well buffered and did, in fact, show distinct differences between *Pinus* and hardwood stands.

This study showed diminished pH and nutrient status in *Pinus* plantations. Furthermore, that the B horizon pH was significantly lower than A horizon pH may signify that some leaching is occurring at moderate depth. Native conifer forests typically have lower pH and buffering capacity than adjacent hardwood forests (Brown and Curtis 1952; Pohlman and McColl 1988; Ste-Marie and Pare 1999), which is largely a consequence of low nutrient concentrations in litter and strong acids released from litter and ectomycorrhizae (Hizal et al. 2013; Berg and McClaugherty 2003; Binkley and Valentine 1991; Read 1991; van Hees et al. 2005). However, the degree to which conifers alter soil conditions depends upon the initial buffering capacity of the soil. Binkley et al. (1989) and Richter et al. (1994) studied old-field conifer plantations in the Carolinas on sand to sandy loam Piedmont soils, which had minimal initial base saturation, organic matter percentage, and/or CEC, contributing to low buffering capacity. As a consequence, conifer soils remained poorly buffered with diminished pH averaging 4.14-4.97. On 20 year-old *Pinus taeda* L. (loblolly pine) plantations on old-fields, Binkley et al. (1989) showed that pH was diminished due to low base saturation, which was largely a consequence of elevated acid strength. Binkley and Sollins (1990) showed that the strength of acids and base saturation determined pH change in *Alnus-Pinus* stands, with a mean pH of 4.6-5.1, and corresponding low base saturation (0.09-0.34%). Conifer stands had lower OM, and texture increased to loam soils. Pallant and Riha (1999) observed surface soil pH that ranged from 3.4 to 3.6 under planted *P. resinosa* in south-central New York and Binkley and Valentine (1989) observed a mean pH of 4.2 under planted *P. strobus* in south-central Connecticut.

In a study conducted in southern Illinois, a region with native forest composition and history similar to my study area, Rolfe and Boggess (1973) found pH values under 35 year-old *P. echinata* plantations that were similar to those I observed in my study (pH ≈ 5). However, the pH values observed under *P. echinata* by Rolfe and Boggess (1973) did not differ from those observed in adjacent hardwood stands. Interestingly, Rolfe and Boggess (1973) observed little difference between surface soil (0 - 8 cm) and subsurface (8 -15 cm) pH under *P. echinata*, while in my study pH values under *Pinus* spp. were significantly lower in 10-20 cm depth vs. 0-10 cm, ranging between 4.04 and 4.25. Although pH values did not differ, Rolfe and Boggess (1973) did observe lower concentrations of bases and less OM in *P. echinata* stands than in hardwood stands. These studies illustrate that the degree to which conifers affect soil pH depends on the initial buffering capacity of the soil, as well as the strength of acids released from litter and roots. These studies also show that conifers frequently lower concentrations of exchangeable bases, base saturation, OM, and CEC, thus lowering buffering capacity. However, conifers do not always alter pH concordantly, and further study is necessary to thoroughly understand the phenolic compounds released from individual species' litter and their impacts on soil chemistry (Berg and McClaugherty 2003).

While the differences we observed between *Pinus* and hardwood stands were largely driven by decades of site occupancy by *Pinus* species, the hardwood species that established after land abandonment also affected soil conditions and augmented the contrast with *Pinus* stands. In my study, hardwood overstories were dominated by *L. tulipifera,* and understories were dominated by *A. saccharum* and *L. benzoin*, with *C. florida* as a common associate (Chapter 3). *Liriodendron tulipifera* foliage has been shown to produce litter with high concentrations of P, Ca, and Mg relative to other species (Chandler 1941; Jenkins et al. 2007), including *Quercus* spp. which likely dominated the forests in my study area prior to clearing for agriculture (Jenkins and Parker 1998; Morrissey et al. 2008). According to Kalisz (1986), *L. tulipifera* contributes to

improved soil nutrient availability following old-field succession. Base saturation, especially with Ca, increases because *L. tulipifera* roots accumulate nutrients and keep nutrient cycling near the surface, promoting nutrient rich humus. *A. saccharum* and *L. benzoin* litter decays rapidly and contains high concentrations of N and water soluble compounds, especially Ca (Chandler 1941; Jenkins et al. 2007). Similarly, *C. florida* foliage accumulates Ca and produces rapidly decomposing litter, which promotes nutrient rich soil (Thomas 1969; Jenkins et al. 2007) through more rapid mineralization (Holzmueller et al. 2007).

In my study, differences between stand types were less pronounced in bottoms compared to ridges. Soils on bottoms were better buffered than those on ridges, as is evidenced by increased TEC and nutrient availability resulting from upland sources of alluvium (Zhalnin 2004). This may have allowed *Acer* species to establish and recruit in the subcanopy and canopy of *P. echinata* and *P. strobus* stands. This may have further reduced the impacts of litter and root inputs from *Pinus* species (Schuster and Dukes 2014; Read 1991). Additionally, unlike hardwood stands on ridges, hardwood stands in bottoms contained large components of *P. occidentalis*, *J. nigra*, *Acer* spp. and *B. nigra*, in addition to *L. tulipifera* (Chapter 3). While *L. tulipifera* and *A. saccharum* litter has been shown to increase soil cation levels, these other species likely have mixed effects on soil chemistry (Henry 1934; Reinsvold and Reeves 1986; Meiners 2014; Al Naib and Rice 1971; Leroy and Marks 2006; Willis 2000).

2.6 Conclusions

Decades of occupancy by *Pinus* species in plantations have altered soil chemistry in southern Indiana forests relative to soils in areas that underwent natural succession to hardwoods. In *Pinus* stands, I observed thicker litter layers, less soil organic matter, and reduced cation concentrations than hardwood sites.

In addition, total N and total C were lower in *Pinus* than in hardwood stands, but Al content was higher. Changes that I observed, compared to other conifer studies, suggest that the degree to which *Pinus* spp. affect soil chemistry depends upon the initial buffering capacity of the soil, the species planted, and the length of *Pinus* residence time. In addition to the effects of *Pinus* species, the differences between stand types I observed were also likely augmented by the mix of species in developing stands on hardwood sites. *L. tulipifera*, *A. saccharum*, and other native species that were dominant or common on my hardwood sites have been shown to ameliorate soil nutrient content and may have contributed to site recovery.

Pinus and hardwood stands in bottoms were more similar than pine and hardwood stands on ridges because of increased soil buffering capacity and the intermixing of *Acer* species and *Pinus species* in the overstory, which in combination likely reduced the cumulative effects of litter inputs from *Pinus* species.

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2.8 Figures

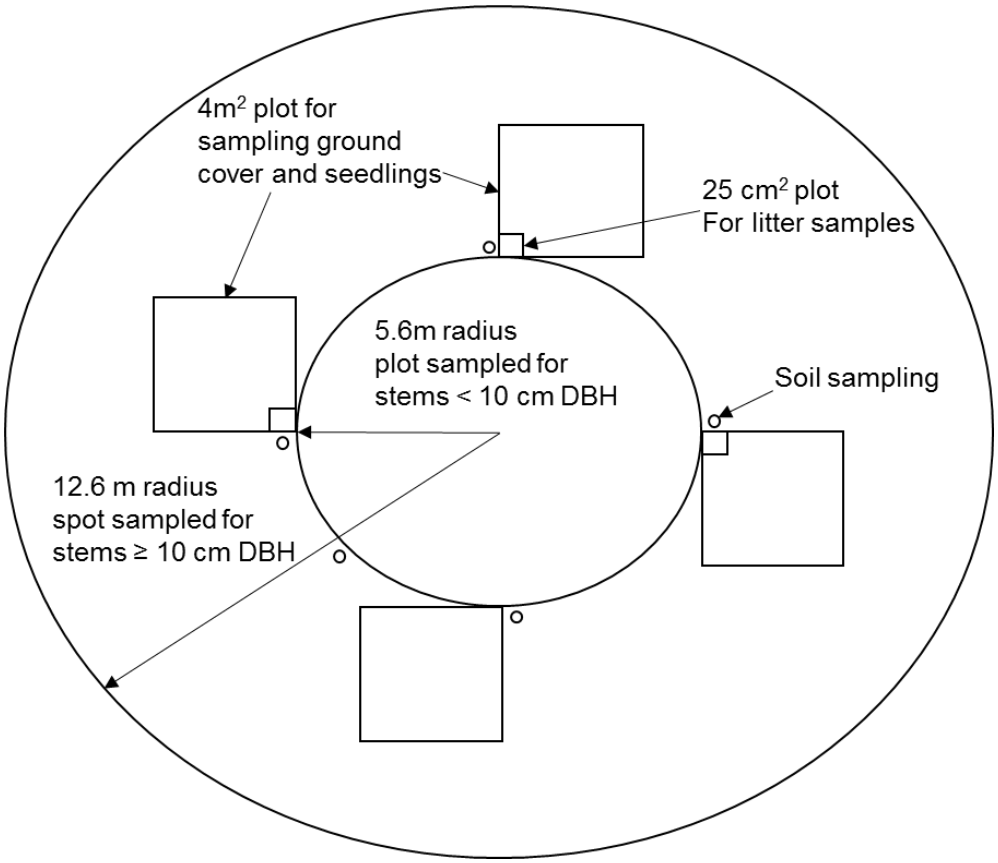

Figure 2.1 Nested plot sampling design, 0.01 ha plot within a 0.05 ha plot.

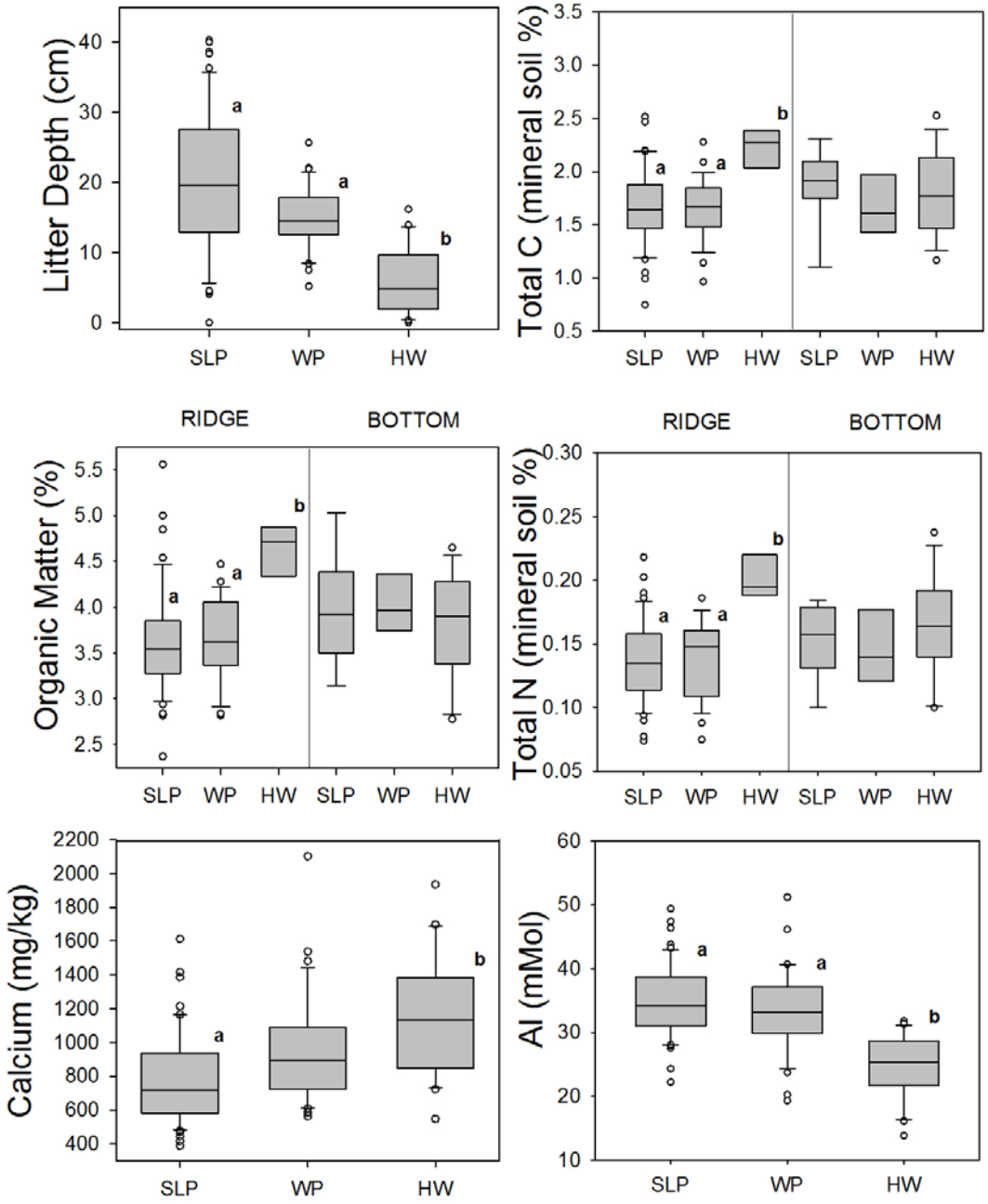

Figure 2.2 Litter depth and soil variables are listed by stand type and ELTP for 0-10 cm depth. Letters represent significant differences in values ($p < 0.05$). SLP = *Pinus echinata*, WP = *P. strobus*, and HW = hardwood.

2.9 Tables

Table 2.1 Soil series listed by stand type and ELTP. The two most common series were Apalona and Wellston Silt Loams.

Stand Type	Soil Series
Ridge *Pinus echinata*	Apalona Silt Loam
Ridge *Pinus echinata*	Wellston Silt Loam
Ridge *Pinus echinata*	Adyeville-Tipsaw-Ebal Complex
Ridge *Pinus echinata*	Hosmer Silt Loam
Ridge *Pinus echinata*	Ebal-Duechers_kitterman Complex
Ridge *Pinus strobus*	Apalona Silt Loam
Ridge *Pinus strobus*	Wellston Silt Loam
Ridge *Pinus strobus*	Adyeville-Tipsaw-Ebal Complex
Ridge *Pinus strobus*	Adyeville-Wellston-Duechars Silt Loams
Ridge *Pinus strobus*	Adyeville Silt Loam
Ridge *Pinus strobus*	Ebal-Duechers_kitterman Complex
Ridge *Pinus strobus*	Tipsaw-Adyeville Complex
Ridge Hardwood	Apalona Silt Loam
Ridge Hardwood	Wellston Silt Loam
Ridge Hardwood	Adyeville-Tipsaw-Ebal Complex
Ridge Hardwood	Tipsaw-Adyeville Complex
Bottom *Pinus echinata*	Apalona Silt Loam
Bottom *Pinus echinata*	Gatchel Silt Loam
Bottom *Pinus echinata*	Adyeville-Tipsaw-Ebal Complex
Bottom *Pinus echinata*	Gatchel Loam
Bottom *Pinus strobus*	Adyeville Silt Loam
Bottom *Pinus strobus*	Adyeville-Tipsaw-Ebal Complex
Bottom *Pinus strobus*	Tipsaw-Adyeville Complex
Bottom *Pinus strobus*	Ebal-Duechers_kitterman Complex
Bottom Hardwood	Wellston Silt Loam
Bottom Hardwood	Apalona Silt Loam
Bottom Hardwood	Adyeville-Tipsaw-Ebal Complex
Bottom Hardwood	Markland Silty Clay Loam
Bottom Hardwood	Ebal-Duechers_kitterman Complex
Bottom Hardwood	Haymond Silt Loam
Bottom Hardwood	Gatchel Silt Loam
Bottom Hardwood	Tipsaw-Adyeville Complex
Bottom Hardwood	Cuba Silt Loam
Bottom Hardwood	Adyeville-Wellston-Duechars Silt Loams

Table 2.2 Soil variables for stand type, ELTP, and their interaction (mean ± S.E.). Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). F values are listed on the right. *Factors or interaction significantly different ($p < 0.05$). Non-transformed data are presented for ease of interpretation. Samples are from 0-10 cm depth. N=53 *Pinus echinata, 33 P. strobus,* 20 Hardwood, 77 ridge, and 29 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hardwood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
A horizon pH (**ridge only**)	5.53 ± 0.06^{a}	5.66 ± 0.07^{ab}	5.86 ± 0.14^{b}	5.68 ± 0.06^{b}	5.49 ± 0.07^{b}	2.89	4.19*	1.70
B horizon pH	4.20 ± 0.08^{a}	4.20 ± 0.10^{a}	4.56 ± 0.11^{b}	4.27 ± 0.05	4.33 ± 0.06	9.83*	0.54	1.03
TEC (meq 100 g^{-1})	9.15 ± 0.68	10.21 ± 0.85	10.56 ± 0.91	8.75 ± 0.42^{a}	11.19 ± 0.55^{b}	1.69	12.30*	0.14
Organic Matter % (**ridge only**)	3.65 ± 0.08^{a}	3.63 ± 0.11^{a}	4.66 ± 0.20^{b}	3.98 ± 0.08	3.96 ± 0.11	4.13*	0.03	8.21*
Litter Depth (cm)	18.97 ± 1.96^{a}	14.10 ± 2.45^{a}	5.56 ± 2.64^{b}	13.99 ± 1.22	11.76 ± 1.60	15.70*	1.23	0.34
Litter Mass (g m^{-2})	824 ± 68^{a}	592 ± 83^{a}	287 ± 86^{b}	638 ± 56	498 ± 73	12.10*	2.32	1.78
Litter C:N Ratio (**bottom only**)	40.30 ± 1.94^{a}	35.64 ± 2.38^{a}	27.89 ± 1.62^{b}	36.37 ± 0.88	34.61 ± 1.16	9.30*	1.46	4.06*
Total Nitrogen % (**ridge only**)	0.14 ± 0.01^{a}	0.14 ± 0.01^{a}	0.20 ± 0.01^{b}	0.16 ± 0.01	0.16 ± 0.01	0.31	9.63	3.99*
Total Carbon % (**ridge only**)	1.65 ± 0.05^{a}	1.65 ± 0.07^{a}	2.32 ± 0.13^{b}	1.87 ± 0.05	1.78 ± 0.07	6.14*	1.11	6.57*
Calcium (mg kg^{-1})	855.3 ± 73.0^{a}	945.1 ± 91.3^{ab}	1118.0 ± 98.4^{b}	900.6 ± 45.5	1045.0 ± 59.6	4.33*	3.71	1.32
Sodium (%)	0.82 ± 0.05^{a}	0.77 ± 0.06^{ab}	0.66 ± 0.07^{b}	0.81 ± 0.03^{a}	0.68 ± 0.04^{b}	3.56*	6.80*	0.66
Boron (mg kg^{-1})	0.29 ± 0.02^{a}	0.29 ± 0.03^{a}	0.38 ± 0.03^{b}	0.32 ± 0.01	0.31 ± 0.02	7.85*	0.07	0.99

Variable	*P. echinata*	*P. strobus*	Hardwood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
Iron (mg kg^{-1}) (**bottom only**)	155.0 ± 13.5[a]	181.0 ± 16.6[ab]	225.0 ± 11.3[b]	146.0 ± 6.2	187.0 ± 8.1	4.16*	16.40*	4.32*
Manganese (mg kg^{-1}) (**ridge only**)	158.3 ± 11.4[a]	151.4 ± 15.0[a]	250.3 ± 28.3[b]	186.7 ± 11.3	182.3 ± 14.9	1.26	0.06	4.63*
Zinc (mg kg^{-1})	1.7 ± 0.1[a]	1.9 ± 0.2[b]	2.0 ± 0.2[b]	1.8 ± 0.1[a]	2.2 ± 0.1[b]	14.10*	7.16*	2.16
Phosphorus (mg kg^{-1})	71.3 ± 5.1[a]	79.8 ± 6.4[a]	87.3 ± 6.8[b]	83.2 ± 3.2	75.7 ± 4.1	3.44*	2.11	2.42
Aluminum (mg kg^{-1})	863.3 ± 30.7[a]	842.2 ± 38.5[a]	712.6 ± 41.4[b]	861.0 ± 19.1[a]	750.5 ± 25.1[b]	8.58*	12.40*	5.43*
Bulk Density (Mg m^{-3}) (**ridge only)**	1.01 ± 0.02[a]	1.07 ± 0.02[a]	0.87 ± 0.04[b]	0.98 ± 0.02	1.07 ± 0.02	5.73*	9.30*	3.12*

TEC = total exchange capacity

CHAPTER 3 RESPONSE OF UNDERSTORY COMMUNITIES TO LONG-TERM OCCUPANCY BY NON-NATIVE *PINUS* SPECIES

3.1 Abstract

During the early to mid-20th century, conifer species were planted widely on abandoned farmland in the eastern United States to stabilize soils and promote site recovery. In many areas, non-native *Pinus* species were planted on sites that were dominated by mesic hardwood species prior to clearing. Therefore, these plantings constitute a shift in overstory composition towards species with recalcitrant litter that may decrease soil pH and nutrient availability. They also constitute a shift away from endemic species with more nutrient rich litter that decomposes more quickly. These plantations provide an excellent opportunity to examine soil and environmental conditions associated with long-term occupancy by *Pinus* species as they influence the diversity, composition, and resilience of herbaceous-layer communities. In this study, I compared herbaceous-layer composition in *Pinus echinata* and *Pinus strobus* plantations to that of naturally regenerated hardwood stands in the Tell City Unit of the Hoosier National Forest. Sample plots were distributed between two ecological landtype phases (ELTPs), ELTP 13, *Fagus-Acer saccharum/Arisaema* Mesic Ridges, and ELTP 42, *Acer saccharinum/Boehmeria* Bottomlands. Site measurements and chemical analysis of soil samples were used to examine species distribution across gradients using non-metric multidimensional scaling (NMS) ordination. Two-way ANOVA was used to examine differences in species functional

groups across stand types and ELTP. My results show that changes in soil chemistry resulting from *Pinus* spp. occupancy have altered the composition and distribution of herbaceous-layer species in ordination space. Species across stand types and ELTPs were distributed across dominant gradients related to litter depth, cation content, and soil aluminum concentration. Hardwood sites were associated with greater herbaceous-layer cover, particularly in bottoms. *Pinus echinata* stands contained a greater density of understory *Quercus* spp. and *Fagus grandifolia* stems, particularly in ridges. My results suggest that pine occupancy has created divergent successional trajectories in comparison to hardwood stands. These differing trajectories may offer unique challenges and opportunities for restoration efforts. For example, *Pinus*-*Quercus* associations may provide a means to restore native *Quercus* communities to parts of this landscape.

3.2 Introduction

The composition of plant communities is largely determined by interspecific competition for light, moisture, and soil nutrients (Gilliam 2014; Aerts 1999; Grace 2012). As such, species differ in their strategies for nutrient acquisition and allocation based on habitat types. Within species, traits that favor dominance in a nutrient-rich environment by maximizing tree growth often correspond to limited growth or survival on nutrient-poor sites where competition is present (Aerts 1999). Species that allocate resources to acquiring nutrients through prolific root growth or by retaining nutrients to minimize loss have an advantage in nutrient-poor soil. These strategies for acquiring nutrients depend, in part, on characteristics of mycorrhizal associates, which are influenced by soil type (Read 1991).

For example, conifers frequently compete and persist in nutrient-poor soils through nutrient retention in recalcitrant litter and through ectomycorrhizal associations, which allow persistence in nutrient limited, low pH soils (Aerts 1999; Smith and Read 2010).

Dominance by *Pinus* spp. facilitates low nutrient conditions in soils. *Pinus* litter contains high recalcitrant fractions, whereas hardwood litter typically contains greater labile fractions. Low *Pinus* labile content corresponds to forest floor accumulation and diminished nutrient release into mineral soil as well as slower organic matter cycling (Berg and McClaugherty 2008; Pritchett and Fisher 1979; Binkley and Valentine 1991). A review of 700 studies comparing conifers and hardwoods by Barbier et al. (2008) found that conifer and hardwood overstories differ in understory composition through complex interactions of the light environment, moisture availability, nutrients dynamics, and litter inputs. There is evidence to suggest that conifer dominance in forests may lower soil pH, buffering capacity, exchangeable bases, base saturation, organic matter, and nutrient availability through inputs of litter. Additionally, that litter affects germination and moisture retention. These soil characteristics, combined with the allelopathic nature of coniferous litter, frequently lower plant species diversity or change plant functional group distributions in *Pinus* stands (Barbier et al. 2008; Blaschke 1981; Berg and McClaugherty 2003).

Herbaceous-layer communities are directly affected by litter quality and composition differs between *Pinus* and hardwood forests (Gilliam 2014). The accumulation of *Pinus* litter alters moisture and temperature conditions, and may act as a mechanical barrier to germination and establishment (Barbier et al. 2008, Facelli and Pickett 1991a; Loydi et al. 2013). Facelli and Pickett (1991a and b) found that annual and perennial herbs are often more impacted by litter depth than graminoids, and that woody litter may be more inhibiting than herbaceous litter. Additionally, a recent meta-analysis by Loydi et al. (2013) found that increased litter depth can increase soil moisture availability, which can

aid in the establishment of woody seedlings. The accumulation of recalcitrant litter may favor the germination of large-seed species in particular, such as those in the genus *Quercus* due to their greater energy reserves. Evidence also suggests that *Fagus* spp., and *Quercus* spp. are similar to *Pinus* spp. with regard to litter nutrient retention, ectomycorrhizal associations, and subsequent lower herbaceous-layer diversity (Barbier et al. 2008; Read 1991). Herbaceous species compete with seedlings for light, and have a direct impact on advance regeneration. Through rapid nutrient uptake and cycling, they also generally have a positive impact on nutrient availability (Gilliam 2007; Gilliam 2014). Graminoids and woody species may make up a greater proportion of the composition of conifer monocultures, whereas non-graminoid herbaceous species are typically associated with more fertile soil conditions (Facelli and Pickett 1991a; Loydi et al. 2013).

Long-term agriculture on former forest sites results in a loss of biological legacies, such as rhizomes and the native seed bank, and the alteration of soil physical and chemical properties, such as reduced A-horizon depth, organic mater content and cation availability (Jenkins and Parker 2000, Flinn and Marks 2007). As a result, the recovery of vegetation communities on abandoned agricultural sites is often dependent upon the dispersal ability of species from surrounding communities and the ability of these species to tolerate degraded soil conditions (Flinn and Velland 2005; Flinn and Marks 2007). While the typically slow progression from old-field to secondary forest has been widely studied (e.g., Bazzaz 1975, Inouye et al. 1987; Myster and Pickett 1994), less is known about how the introduction of non-native conifers to abandoned agricultural sites alters the composition and diversity of recovering forests that would otherwise develop on these old-fields.

During the early to mid-20th century, federal agencies in the U.S. planted trees on newly acquired public lands in an effort to curb erosion and regrow forestland on abandoned farmland. These replanting efforts began with the Civilian

Conservation Corps and Works Progress Administration in the 1930s (Parker and Ruffner 2004), and continued with the USDA Forest Service and state conservation agencies more recently. *Pinus echinata* Mill. (shortleaf pine), *Pinus strobus* L. (white pine), and *Pinus resinosa* Aiton. (red pine) were planted across large portions of the Central Hardwoods Region (Otis 1986, Sieber and Munson 1992). In Indiana, Ohio, and Illinois, around 58,107 hectares of these non-native *Pinus* spp. persist today (USDA Forest Service, 2013). In these states, there is very limited and sporadic economic value to these stands, and research suggests that they may not be as ecologically desirable as mixed stands of native hardwoods (Barbier et al. 2008, Facelli and Pickett 1991a; Loydi et al. 2013; Lindenmayer and Hobbs 2004). For this reason, managers have begun exploring strategies to convert these stands to native hardwoods. The success of conversion will depend in part on the lasting impact *Pinus* species have had on soil and vegetation communities where planted. In addition, though the long-term occupancy of *Pinus* monocultures has been studied with regard to soil quality, the long-term impact on the herbaceous-layer is not as well understood (Auten 1945; Billings 1938; Sauer et al. 2007; Barbier et al. 2008). Therefore, this study offers an excellent opportunity to examine the compositional trajectory of understory communities as influenced by four decades of *Pinus* spp. dominance and the resulting alterations to soil chemistry. Such an examination provides valuable insight into the resiliency of forest ecosystems in the face of long-term changes to the edaphic environment.

To examine the long-term impacts of *Pinus* establishment, I compared the plant species composition of *P. echinata* and *P. strobus* plantations to that of hardwood stands that naturally regenerated after land abandonment. I did so on two soil types: mesic ridges and bottoms. In this study, I address the following hypotheses:

1) The soil conditions associated with long-term *Pinus* occupancy will result in pronounced differences in species composition between *Pinus* and hardwood forests.
2) Shifts in understory composition will be more pronounced on ridges than in bottoms because of their difference in soil buffering capacity and overstory composition.
3) On ridges, *Pinus* site litter conditions in particular will have favored the establishment of woody species over herbaceous species, and will have shifted the composition of woody regeneration away from mesic species such as *A. saccharum* and towards species more tolerant of nutrient-poor conditions, such as those in the family Fagaceae.

3.3 Methods

3.3.1 Study Sites

Sample sites were chosen within the Tell City Unit of the Hoosier National Forest within the Crawford Upland Subsection (CUP) as defined by Homoya et al. (1984). In ArcMAP v10.1, I selected study sites based upon Ecological Landtype Phase (ELTP), which is a land classification delineated by several variables including dominant vegetation, indicator species, soil type, elevation, slope, and slope aspect (Van Kley 1993). Because ELTP 13 *Fagus-Acer saccharum*/*Arisaema* Mesic Ridges, and ELTP 42 *Acer saccharinum/Boehmeria* Bottomlands were the most common ELTPs in our study region, and because both contained an abundance of *Pinus* plantations, we confined our sampling to these two types. To limit variability of soil across potential plots, I used Natural Resource Conservation Service (NRCS) soil series data to ensure that sites had similar soil types. While NRCS data show that there are many specific soil groups found within each ELTP, most of these soils only differ slightly. Soils on

ELTP 13 tend to be silt loam over sandstone parent with an argillic horizon of silt loam or silty clay between 20 cm and 68 cm (NRCS 2013), with an average A horizon depth of 4.7 ± 0.8 cm and average pH of 5.5 ± 1.1. ELTP 42 consists of silt loam alluvium over 2 m thick with a poorly-differentiated A horizon estimated at 10 cm and average pH of 6.8 ± 0.2 (Zhalnin 2004). The two most common NRCS soil series found within sites on mesic ridges and bottoms were Apalona silt loam and Wellston silt loam (Table 3.1). Both have average pH values between 3.5-7.3 and average CEC below 20 meq per 100 g (NRCS 2013). Other soil series found within sites contained similar values for pH, CEC, and soil type.

Across mesic ridges and bottoms, I selected three vegetation types for sampling: *P. echinata*-dominated plantations, *P. strobus*-dominated plantations, and naturally regenerated hardwood forests. Hardwood species that regenerated naturally after agricultural abandonment included *Platanus occidentalis* L. (American sycamore), *Liriodendron tulipifera* L. (tuliptree)*, Juniperus virginiana* L. (eastern redcedar), *Juglans nigra* L. (black walnut), *Acer negundo* L. (boxelder), *A. rubrum* L. (red maple), and *A. saccharum.* Digitized aerial photographs from the 1940s were overlain in ArcMAP to ensure that chosen sites were previously utilized for agriculture. To reduce edge effects, I used a 20 m buffer around roads, and a 40 m buffer between adjacent stand types to minimize the influence of surrounding vegetation types. Within these buffered delineations, the final sample coordinates were randomly selected in ArcMAP. Lastly, sites that experienced secondary disturbances such as logging, windstorms, or fire after agricultural abandonment were rejected. At all sites, I recorded GPS coordinates and marked plot locations with rebar and witness tree tags. In total, I sampled 44 ridge *P. echinata* sites, 26 ridge *P. strobus* sites, 7 ridge hardwood sites, 9 bottom *P. echinata* sites, 7 bottom *P. strobus* sites, and 13 bottom hardwood sites. These sample sites comprised all suitable sample sites within the study area.

I determined the age of each stand sampled to ensure that *Pinus* and hardwood sites were of a comparable age. While stand age data were collected by the USDA Forest Service by coring various representative trees within a defined stand, the resulting polygons represented by these ages were often quite large. Therefore, in order to more accurately represent overstory age on sampled plots, I cored three dominant trees at 30 cm above the ground using an increment borer. The average age of these three trees was used to estimate stand age (Jenkins and Parker 1999; 2000). By using only sites that were historically used for agriculture, we limited stand age to a maximum of 70 years, due to the fact that land was largely abandoned in the 1930s and 1940s (Welch et al. 2001). The average age was between 25 and 40 years, because most of the plantations in the Hoosier National Forest occurred later than the 1940s.

3.3.2 Field Sampling Design

Vegetation was sampled from May 13 to August 15, 2013 using a nested plot design (Jenkins and Parker 1998; 1999; 2000; 2001; Van Kley 1993). From a common center, I established a 0.01 ha circular plot (r = 5.6 m) within a 0.05 ha circular plot (r = 12.6 m). Within the 0.01 ha plot, I tallied all woody saplings (> 1 m height, < 3 cm DBH) by species and measured DBH and recorded the species of all stems greater than 3 cm DBH. Within the 0.05 ha plot, I recorded the DBH and species of all stems ≥ 10 cm DBH. A 4 m^2 quadrat was placed 5.6 m from plot center in each cardinal direction, resulting in a total of four quadrats. Within each quadrat, I tallied seedlings (woody stems < 1 m tall) by species and estimated the percent cover of herbaceous-layer species, which included the cover of woody species below 1 m, and could exceed 100% cover.

Herbaceous-layer species that occurred on the plot but were not found in the quadrats were given a cover value equal to half that of the lowest species cover recorded in the quadrats (Figure 3.1). Species nomenclature follows the USDA PLANTS Database (NRCS 2014). Canopy openness was measured using a Nikon EOS 20D camera with 10 MP, mounted with an 8 mm fisheye lens. Pictures were taken between June 5th and July 30th to keep data within range of peak leaf out (Constabel and Lieffers 1996). At each site, the camera was mounted on a tripod at 1 m above the ground, and leveled. Four photos were taken, one in each cardinal direction 5.6 m from plot center, with the camera facing north.

Due to the fact that soils vary across each ELTP, and because past agricultural use alters the A horizon thickness through increased erosion (Welch et al. 2001), I collected soil samples at 0-10 cm and 10-20 cm using an impact driven soil corer. Sampling at these depths allowed me to capture the zone of herbaceous-layer rooting. All soil sampling was conducted adjacent to the 4 m^2 quadrats. A minimum of 400 g per sample was collected per site. For the 0-10 cm sample, five cores were taken and put into separate bags, and for 10-20 cm depth, five cores were combined into one sample because of a lack of funding for laboratory analysis. I also collected litter from three 25 cm^2 quadrats located 5.6 m west, north, and east of plot center. In total, 585 soil samples and 351 litter samples were collected. Soils were analyzed for organic matter (%), total exchange capacity (TEC; meq 100 g^{-1}), pH, total C (TC; %), total N (TN; %), P (mg kg^{-1}), Ca (mg kg^{-1}), Mg (mg kg^{-1}), Zn (mg kg^{-1}), B (mg kg^{-1}), and Al (mg kg^{-1}); see chapter 2 for full description of soil chemical analyses.

Canopy photographs were organized in ImageJ software by defining north, east, and west coordinates for batch processing. A first image was separated into the blue color spectrum, displayed in grey scale, and given a threshold of Minimum to limit the allowed range of wavelengths of light. This first image layout was used with a batch processing macros.ijm file to run all 351 images. To avoid

skewed readings, images which displayed sunflecks were removed, resulting in a total of one to four images per site, with an average of three per site. Those images were then analyzed in CIMES-fisheye software (Jean-Michel Walter 2009) to yield canopy openness, gap fraction, and canopy closure.

3.3.4 Sampling Design and Data Analysis

I calculated total basal area (TBA), living basal area (LBA), and dead basal area (DBA) as m^2 ha^{-1}. I also calculated overstory density and sapling density as stems ha^{-1}. Seedling density was calculated as stems per 100 m^2 by species. Percent cover was averaged over four plots by species. Using percent cover of herbaceous-layer species, I calculated richness (S), Shannon-Weiner diversity (H'), and Evenness using PC-ORD Version 5.1 (McCune et al. 2002).

To investigate compositional differences between ELTPs and stand types within the Hoosier National Forest, I used non-metric multidimensional scaling (NMS) ordination with PC-ORD version 5.1 (McCune et al. 2002). NMS is appropriate for non-normally distributed datasets such as with species percent cover, partly by avoiding assumptions of linear relationships among variables. An arcsine square root transformation was used on the herbaceous-layer species data to improve normality and decrease the effect of scarcity/rarity within the matrix. I used the Sorenson (Bray-Curtis) distance measure on Autopilot mode, on the Slow and Thorough setting with default settings of a 0.00001 stability criterion, 50 real runs, and 50 randomized runs of 500 iterations for each dimensionality (from one to six), using a random number starting point to find the appropriate dimensionality. Then, 250 real and 250 randomized runs were conducted for the ordination. Correlations of the main matrix with environmental variables were calculated with Pearson's r and vectors of maximum absolute value were plotted on ordination axes for any correlation greater than 0.2.

Indicator species analysis was conducted using the herbaceous-layer main matrix with 4999 runs of a Monte Carlo test. Additionally, I created dominance tables for overstory, sapling, and herbaceous-layer species. By summing percent cover values, I combined individual herbaceous species into the following functional groups: graminoids, sedges, perennials, annuals, biennials, and invasive ground cover. Similarly, I combined woody species into the following functional groups: native shrubs, invasive shrubs, native vines, invasive vines, sub canopy trees, and other species. Additionally, *Acer saccharum*, *A. negundo*, *A. rubrum*, *Quercus* spp., *Fraxinus* spp., *Fagus grandifolia* Ehrh. (American beech), were analyzed as individual species or genera. I analyzed the sapling layer for *A. saccharum, A. negundo*, *A. rubrum*, *Quercus* spp., *Fraxinus* spp., shrubs, *F. grandifolia*, sub canopy trees, and other species.

The most common species in the annuals/biennials group were largely *Sanicula canadensis* L. (black snakeroot) and *Impatiens capensis* Meerb. (spotted touch-me-not) and the most common species in the perennials group were *Packera aurea* (L.) Á. Löve & D. Löve (heart-leaved golden ragwort), *Lycopodium* spp. (clubmoss), moss, and *Ageratina altissima* (L.) R.M. King & H. Rob. (white snakeroot). Invasives consisted mostly of *Rosa multiflora* Thunb. (multiflora rose), *Lonicera japonica* Thunb. (Japanese honeysuckle), and *Microstegium vimineum* (Trin.) A. Camus (Japanese stiltgrass). Shrubs consisted largely of *Lindera benzoin* (L.) Blume (spicebush), *Smilax* spp. (greenbrier), and *Rubus* spp. (blackberry). Native vines were largely *Toxicodendron radicans* (L.) Kuntze (poison-ivy), and *Parthenocissus quinquefolia* (L.) Planch. (Virginia creeper; Appendix C). Subcanopy trees consisted of *Amelanchier* spp. (serviceberry), *Aralia spinosa* L. (devil's walkingstick), *Asimina triloba* (L.) Dunal (pawpaw), *Carpinus caroliniana* Walter (musclewood), *Cercis canadensis* L. (redbud), *Cornus florida* L. (flowering dogwood), *Morus rubra* L. (red mulberry), *Ostrya virginiana* (Mill.) K. Koch (ironwood), *Rhus* spp. (sumac), and *Salix* spp. (willow). Finally, the other tree species group of the seedling and sapling layers included *Aesculus glabra* Willd. (Ohio buckeye), *Celtis occidentalis* L. (hackberry),

Diospyros virginiana L. (persimmon), *Juglans nigra*, *Juniperus virginiana* L. (red cedar), *Liquidambar styraciflua* L. (sweetgum), *Prunus serotina* Ehrh. (black cherry), *Sassafras albidum* (Nutt.) Nees (sassafras), *L. tulipifera*, and *Pinus* spp. The most common woody herbaceous-layer species, excluding tree seedlings, were *T. radicans*, *P. quinquefolia*, *L. benzoin*, *L. japonica*, and *R. multiflora.*

I used two-way Analysis of Variance (ANOVA) with stand type and ELTP as categorical variables to more closely examine explanatory variables that were correlated with ordination axes, including functional groups. This included analyzing variables by stand type (*P. echinata*, *P. strobus*, or hardwood), ELTP (mesic ridges or bottoms), and examining their interaction terms. The interaction compared individual types, for example: ridge *P. echinata* vs. ridge hardwood, ridge *P. strobus* vs. bottomland *P. strobus*, etc. Assumptions of normality and constant variance were assessed with plots of studentized residuals versus fitted values (Neter et al. 1996). We also used residual plots to screen potential outliers (Neter et al. 1996). I used an arcsine square root transformation on species functional groups. I used square root transformations on litter depth, Ca, Zn, B, and Mn. Lastly, I removed an extreme outlier for Fe, and log transformed. Non-transformed data are presented for ease of interpretation. Dead basal area, being particularly problematic, was centered, absolute value transformed, and square root transformed in order to better fit assumptions of normality and constant variance. When ANOVA revealed significant differences, I used the Tukey multiple comparisons test for post hoc comparisons ($\alpha = 0.05$). Where transformations could not improve assumptions, I used Kruskal-Wallis ANOVA on Ranks with Dunn's Multiple Comparisons post hoc test ($\alpha = 0.05$).

3.4 Results

3.4.1 Species Distribution Across Environmental Gradients

The NMS ordination had a final stress of 17.56, instability of <0.0001, and a three-dimensional solution. Each axis accounted for 12.9%, 30.0%, and 35.6% of variation respectively, which totaled 78.5% of the total variation. Sites were well divided by stand type and ELTP. Both *P. echinata* and *P. strobus* stands were associated with increased TBA, litter depth, and Al, while hardwood sites were associated with increased Ca, Zn, and TEC. Ridge sites were associated with high values of TBA, litter depth, and Al, whereas bottoms were associated with high soil nutrient content (Figure 3.2). Axis three was correlated with litter depth (r^2 = 0.296), Al (r^2 = 0.40), Zn (r^2 = 0.24), Ca (r^2 = 0.28), and TEC (r^2 = 0.23), while axis two was largely associated with TBA (r^2 = 0.22), litter depth (r^2 = 0.17), and Fe (r^2 = 0.12). In effect, litter depth, TBA, Na, and Al increased with ridge sites and with *P. echinata*, while soil nutrients, TEC, Ca, and Zn increased with bottoms and hardwood sites (Figure 3.2).

Functional groups displayed clear associations with stand type and ELTP and were distributed across both stand and edaphic variables (Figure 3.2). Annuals, biennials, graminoids, and invasives were associated with hardwood and bottom sites and with greater values of Ca, Zn, and TEC and lower values of Al, TBA, and litter depth. Cover of seedlings, particularly *Quercus* spp., *F. grandifolia*, and *A. rubrum* trended with *Pinus* ridge sites, and with increasing values of TBA, litter depth, and Al. Overall, more functional groups were associated with hardwood than with *Pinus* sites, and with bottoms than with ridges (Figure 3.2).

3.4.2 Soil Conditions

pH, OM (%), TC (%), TN (%), B (mg kg^{-1}), Mn (mg kg^{-1}), Ca (mg kg^{-1}), and Zn (mg kg^{-1}) of the top 10 cm of soil were all greater in hardwood than in *Pinus* stands (max p = 0.04). Additionally, fewer trends were observed in bottoms between *Pinus* and hardwood sites because of a limited number of suitable sites, higher buffering capacity, and a difference in vegetation composition. Soil Fe, Zn, Ca, and B were greater in hardwood bottoms than *P. echinata* bottoms. TEC, P, Na, and Zn were greater in bottoms than ridges. Lastly, soil Al (mg kg^{-1}) was significantly greater on ridges than on bottoms and was significantly greater in *Pinus* stands than hardwoods. On bottom sites, Al was greater in *P. strobus* than hardwoods (Chapter 2).

3.4.3 Stand Structure and Composition

Total basal area (TBA) was greater in *Pinus* plantations than naturally regenerated sites, averaging 45.0 ± 2.3 and 26.7 ± 2.8 $m^2\,ha^{-1}$ respectively ($F = 25.6$, $p < 0.001$). However, basal area of dead trees (DBA) was significantly greater in *P. strobus* sites than *P. echinata* or hardwood sites, with an average of 2.4 ± 0.7 $m^2\,ha^{-1}$ in *P. strobus*, 1.8 ± 0.6 $m^2\,ha^{-1}$ in *P. echinata*, and 1.4 ± 0.8 $m^2\,ha^{-1}$ in hardwood ($F = 8.9$, $p<0.001$). Understory light availability as measured by canopy openness did not vary with TBA or ELTP. It differed only with DBA, which was only greater in *P. strobus* sites than *P. echinata* or hardwood sites ($F = 11.6$, $p < 0.001$; Table 3.2).

Hardwood sites had greater species richness ($F = 10.8$, $p < 0.001$) and Shannon-Weiner diversity ($F = 5.3$, $p = 0.007$) than *Pinus* sites. Species richness averaged 35 ± 2.4 on *Pinus* vs. 46 ± 2.9 on hardwood sites, and diversity averaged 2.2 ± 0.1 on *Pinus* sites vs. 2.6 ± 0.2 on hardwood sites. Not surprisingly, average herbaceous-layer percent cover was greater in hardwood sites than *Pinus*,

averaging 66.2 ± 9.0 and 142 ± 11.0 for *Pinus* and hardwoods respectively (F = 42.9, p<0.001; Table 3.2). Graminoids, perennials, annuals, biennials, sedges, native shrubs, invasive shrubs, and native vines all showed greater average cover in hardwoods than in *Pinus* stands. Biennials exhibited greater values in bottom hardwood vs. *Pinus*, showing a significant interaction term. Invasive shrub cover was greater in hardwood than in *P. echinata* stands. Mean percent cover for graminoids was 1.7 ± 2.9 and 16.4 ± 3.5 on *Pinus* and hardwood sites, respectively (F = 12.7, p <0.001). Perennials averaged 7.5 ± 4.4 on *Pinus* sites and 29.4 ± 5.3 on hardwood sites (F = 12.68, p <0.001). Lastly, native vines averaged 19.3 ± 3.2 and 50.9 ± 6.9 on ridge *Pinus* vs. ridge hardwood with a significant interaction term (F = 7.16, p = 0.001; Table 3.3; Figure 3.3).

Acer saccharum, subcanopy trees, and other tree seedlings had greater density in hardwood than in *Pinus* stands. For saplings, *A. saccharum*, subcanopy trees, other tree species, and invasive shrubs had higher stem density in hardwoods than *Pinus* stands. Average seedling density (stems per 100 m^2) for *A. saccharum* was 4.0 ± 5.3 and 19.7 ± 5.7 in *P. strobus* and hardwood sites respectively (F = 3.9, p = 0.023). Subcanopy tree seedlings averaged 8.1 ± 4.3 in *Pinus* and 20.6 ± 5.1 in hardwood stands (F = 4.8, p = 0.01). Other tree seedlings averaged 27.5 ± 4.3 and 52.7 ± 9.1 for ridge *Pinus* stands and ridge hardwoods respectively, with a significant interaction term at α = 0.1 (F = 2.99, p = 0.06; Table 3.4; Figure 3.3). Average sapling stem density (stems ha^{-1}) for *A. saccharum* was 98.4 ± 89.7 and 928.6 ± 192.4 in ridge *Pinus* and ridge hardwood sites respectively, with a significant interaction term (F = 3.6, p = 0.032). Subcanopy tree saplings averaged 111.6 ± 69.8 in *Pinus* and 413.8 ± 83.5 in hardwood stands (F = 9.3, p<0.001). Other tree saplings averaged 176.5 ± 49.6 and 500.0 ± 106.3 in ridge *Pinus* vs. ridge hardwood stands with a significant interaction term at α = 0.1 (F = 3.0, p = 0.05). Lastly, for invasives shrubs, sapling density averaged 49.5 ± 49.7 and 147.3 ± 59.6 in *Pinus* stands vs. hardwoods, respectively (F = 2.9, p = 0.06; Table 3.5; Figure 3.3).

Bottoms had greater species richness than ridges (F = 10.0, p = 0.002), averaging 42 ± 1.8 and 35 ± 1.4, respectively (Table 1). Bottoms had greater percent cover of invasive shrub species, invasive groundcover species, perennials, biennials, and sedges. Invasive shrub percent cover averaged 4.6 ± 1.6 in bottoms and 11.2 ± 2.0 on ridges (F = 6.7, p = 0.01). Invasive groundcover averaged 7.0 ± 1.6 and 12.9 ± 2.0 in bottom and ridge sites, respectively (F = 5.3, p = 0.02). Perennials averaged 9.5 ± 2.4 and 20.0 ± 3.2 (F = 6.8, p = 0.01) and biennials averaged 0.6 ± 0.4 and 2.0 ± 0.5 (F = 5.5, p = 0.02; Table 2). In addition, *A. negundo* seedlings and saplings had higher stem density in bottoms than ridges (Table 3.3; Figure 3.3).

Conversely, total seedling density was higher on ridges than bottoms, averaging 200.5 ± 111.0 and 130.1 ± 118.5 stems per 100 m^2 respectively (F = 14.1, p<0.001). For seedlings and saplings, *A. rubrum*, *Quercus* spp., *Fraxinus* spp., and other tree species were generally greater on ridges than bottoms. For seedlings (stems per 100 m^2), mean *A. rubrum* density was 29.8 ± 5.4 on ridges and 8.2 ± 7.1 on bottoms (F = 5.8, p = 0.02). Mean *Quercus* spp. density was 13.2 ± 2.3 on ridges and 7.2 ± 3.0 on bottoms (F = 2.5, p = 0.09). Mean *Fraxinus* spp. density was 58.8 ± 9.6 on ridges and 21.2 ± 12.6 on bottoms (F = 5.6, p = 0.02). Lastly, density of other tree species was 35.9 ± 3.7 on ridges and 8.2 ± 4.8 on bottoms (F = 21.2, p<0.001; Table 3.4; Figure 3.3). Mean sapling density (stems per hectare) for *A. rubrum* was 198.1 ± 53.0 on ridges and 19.2 ± 69.5 on bottoms (F = 4.2, p = 0.04). Mean density for *Quercus* spp. was 134.7 ± 39.9 on ridges and 93.7 ± 52.3 on bottoms (F = 2.1, p = 0.12). Lastly, mean other tree density was 284.3 ± 42.6 on ridges and 67.0 ± 55.8 on bottoms (F = 9.6, p = 0.003; Table 3.5; Figure 3.3). Lastly, native vine percent cover was greater on ridges than bottoms with an average of 29.8 ± 2.8 and 8.6 ± 3.6 respectively (F = 21.5, p<0.001; Table 3.3; Figure 3.3). Mean *Quercus* spp. and *F. grandifolia* densities were greater on *P. echinata* sites than hardwoods for both seedlings (stems per 100 m^2) and saplings (stems per ha). Mean *Quercus* spp. seedling density was 15.7 ± 3.6 for *P. echinata* and 7.3 ± 4.9 for hardwood, with a

significant interaction term at α = 0.1 (F = 2.5, p = 0.09). Mean *F. grandifolia* seedling density was 4.9 ± 1.9 on *P. echinata* and 2.1 ± 2.6 on hardwood, though it was not significant (F = 1.3, p = 0.28; Table 3.4; Figure 3.3). For saplings, mean *Quercus* spp. density was 201.1 ± 64.0 on *P. echinata* and 89.0 ± 86.4 on hardwoods, though it was not significant (F = 2.1, p = 0.12), and mean *F. grandifolia* sapling density was 414.9 ± 108.0 on *P. echinata* and 45.6 ± 106.1 on hardwoods (F = 5.5, p = 0.01; Table 3.5; Figure 3.3). Ridge hardwoods were dominated by *L. benzoin* and *A. saccharum*.

Bottomland *P. echinata* sites were somewhat dominated by *A. saccharum*, *F. grandifolia*, and *Fraxinus* spp. saplings, bottomland *P. strobus* were dominated by *L. benzoin*, *A. negundo*, and *Fraxinus* spp., and bottomland hardwoods by a wider mix of saplings (Table 3.4; Table 3.5; Appendix C; Figure 3.3).

3.4.4 Indicator Species Analysis

Not surprisingly, the overstory of *P. echinata* and *P. strobus* ridge stand types were almost exclusively dominated by *P. echinata* and *P. strobus* respectively, while hardwood sites were dominated by L. *tulipifera* (Table 3.4). Overstory indicator species analysis showed similar trends. For ridge *P. echinata* sites, *P. echinata* (IV = 56.3, p = 0.0002) and *A. rubrum* (IV = 31.5, p = 0.02) were indicators. For ridge *P. strobus* sites, *P. strobus* was an indicator (IV = 48.3, p = 0.0002). For ridge hardwood sites, *L. tulipifera* (IV = 38.3, p = 0.01), *Ulmus rubra* Muhl. (red elm; IV = 29.4, p = 0.02), and *J. nigra* (IV = 27.8, p = 0.02) were the overstory indicators. For bottom *P. echinata* sites, *A. saccharum* (IV = 37.2, p = 0.004), and *O. virginiana* (IV = 19.1, p = 0.049) were indicators. For bottom *P. strobus* sites, *A. negundo* (IV = 28.3, p = 0.01) and *Gleditsia triacanthos* L. (honeylocust; IV = 16.7, p = 0.048) were indicators. Lastly for bottom hardwoods, *P. occidentalis* (IV = 45.2, p = 0.001) and *Betula nigra* L. (river birch; IV = 18.2, p = 0.03) were indicators. In terms of saplings, for ridge *P. echinata* sites, *F.*

grandifolia (IV = 42, p = 0.01) and *Q. velutina* (IV = 27, p = 0.04) were indicators. For bottom *P. strobus*, *A. negundo* (IV = 22.5, p = 0.01), *U. rubra* (IV = 35.1, p = 0.004), and *D. virginiana* (IV = 38.7, p = 0.03) were indicators. Lastly, for bottomland hardwoods, *P. occidentalis* was an indicator (IV = 18.2, p = 0.03; Table 3.6).

Indicator species in the herbaceous stratum varied between stand types and ELTPs. There were no significant indicators for ridge *P. echinata* sites, and *Asplenium platyneuron* (L.) Britton, Sterns & Poggenb. (ebony spleenwort) was the only indicator for ridge *P. strobus* (IV = 29.2, p = 0.049). However, ridge hardwood sites had 13 indicators including the woody species: *A. saccharum* (IV = 54, p = 0.01), *U. rubra* (IV = 53.5, p = 0.01), *L. styraciflua* (IV = 46.8, p = 0.02), and *C. occidentalis* (IV = 45.1, p = 0.03), and the herbaceous species: *Helianthus annuus* L. (common sunflower; IV = 42.3, p<0.001) and *Eupatorium purpureum* L. (spotted joe pye weed; IV = 41.7, p = 0.02). Bottomland *P. echinata* had nine indicators, including *Monarda fistulosa* L. (beebalm; IV = 40, p = 0.002), and *Vibernum* spp. (IV = 29.6, p = 0.047). Bottomland *P. strobus* had seven indicators, including *A. negundo* (IV = 50.1, p = 0.01), and *M. vimineum* (IV = 40.2, p = 0.01), an invasive grass species. Lastly, bottomland hardwood sites had 19 indicators including *P. aurea* (IV = 76.7, p<0.001), *S. canadensis* (IV = 62.1, p = 0.002), *Verbesina alternifolia* (L.) Britton ex Kearney (wingstem; IV = 58.2, p<0.001), *Asarum canadense* L. (wild ginger; IV = 53.2, p<0.001), *Laportea canadensis* (L.) Weddell (wood nettle; IV = 58.2, p<0.001), and *I. capensis* (IV = 47.0, p = 0.002; Table 3.6).

3.5 Discussion

3.5.1 Community Divergence by Stand Type

In my study, soil conditions resulting from *Pinus* occupancy directly impacted the composition of herbaceous-layer communities and the distribution of species across edaphic gradients. Greater litter depths likely contributed to slower nutrient cycling, as was evident in the reduced organic matter and macronutrient availability in surface soil. This was a result of recalcitrant litter, which on average breaks down more slowly than hardwood litter (Berg and McClaugherty 2003). Soils in *Pinus* stands had slightly lower pH, lower concentrations of Ca, and higher concentrations of Al (Chapter 2). Likely as a result of this lower soil fertility, *Pinus* stands had lower Shannon-Wiener diversity, species richness, and percent cover when compared to hardwood sites. Literature suggests that lower species diversity in *Pinus* stands is common due to the acidifying effect of litter and mycorrhizal leachates of aliphatic organic acids, which lowers soil fertility (Pohlman and McColl 1988; Helyar and Porter 1989; Landeweert et al. 2001; Smith 1969; Krzyszowska et al. 1996; Fox and Comerford 1990) and favors a limited suite of species tolerant of such conditions. Research has also shown that *Pinus* litter acts as a mechanical barrier to the successful germination and establishment of many species, including annuals, biennials, and many perennial herbs (Meers et al. 2010; Berg and McClaugherty 2003; Read 1991; Barbier et al. 2008, Facelli and Pickett 1991a; Loydi et al. 2013; Blaschke 1981). In the ordination, greater litter depth and high Al concentrations, and low cation availability were most strongly associated with *P. echinata* plots, while *P. strobus* plots were associated with intermediate values of these variables. There is some evidence to suggest that *P. strobus* may have more intermediate litter depths compared to many other species in Pinaceae and Fagaceae (Barbier et al. 2008). In my study, understory richness, diversity, and cover were also intermediate in *P. strobus* stands compared to *P. echinata* and hardwood stands, suggesting that that understory communities were affected by litter depth and soil

fertility directly. In addition, canopy openness was greater in *P. strobus* stands, yet this greater availability of light did not correlate to increased cover or species diversity. Conversely, hardwood plots were associated with high availability of cations, reduced litter depths, and low levels of Al. In addition to the absence of *Pinus* spp., these improved soil conditions are likely a result of the occupancy of *L. tulipifera*, *A. saccharum*, and other species such as *C. florida*, who rapidly cycle calcium and other nutrients, improving soil base saturation and buffering capacity, and therefore soil fertility (Kalisz 1986; McClaugherty et al. 1985; Berg and McClaugherty 2003; Finzi et al. 1998; Jenkins et al. 2007; Holzmueller et al. 2007).

Pinus sites, on average, contained fewer functional groups and had overall lower coverage of functional groups, whereas hardwoods possessed greater coverage of a greater number of groups. Annuals, biennials, perennial herbs, and invasive species were all more common on hardwood sites, likely as a consequence of improved soil fertility. The species in these functional groups have more rapid litter decomposition compared to conifers and form arbuscular mycorrhizal (AM) associations, which facilitate rapid uptake of cations, increase pH, and often improve buffering capacity, all of which contribute to active microbial communities (Berg and McClaugherty 2003; Aerts 1999; Read 1991; Smith and Read 2010). Research also suggests that these herbaceous groups are particularly sensitive to deep litter layers (Facelli and Pickett 1991 a and b), such as those associated with *Pinus* species.

In *Pinus* stands, I observed a greater density of woody stems, such as *Fraxinus* spp. and *Acer rubrum*, which are widespread generalist species that display tolerance of a wide range of soil conditions. In addition, *Quercus* spp. and *F. grandifolia* were more common on *P. echinata* sites than other stand types. Evidence suggests that *Quercus* may establish well in deep litter because of large seeds with large energy reserves (Loydi et al. 2013). Additionally, members of Fagaceae have slow nutrient cycling and litter decomposition, and form

ectomycorrhizal associates (Read 1991; Smith and Read 2010), which facilitate soil acidification through organic acid leachates; a strategy that increases uptake of limited nutrients and minimizes Al-toxicity (Read 1991; Smith and Read 2010; Van Hees et al. 2005; Zheng et al. 1998).

3.5.2 Community Divergence by ELTP

I observed marked differences in the soil chemistry of ridges and bottoms, which in turn influenced species distributions. Within ELTPs, I observed more defined differences in soils between *Pinus* and hardwood stands on ridges than on bottoms. The more nutrient-rich and well buffered soil in bottoms allowed *Acer* spp. to persist and advance into the canopy within *P. echinata* and *P. strobus* stands over the past 40 years. Because *Pinus* and *Acer* species differ in terms of litter residence time, cation concentration, and mycorrhizal associates, their influence on soil should also differ (Berg and McClaugherty 2003; McClaugherty et al. 1985**;** Read 1991). Additionally, with greater moisture availability in bottoms compared to ridges (Zhalnin et al. 2004), nutrient cycling may have been more rapid. This was evident in that litter depth and macronutrient availability did not differ greatly between stand types within bottoms compared to stand types on ridges, suggesting that moisture content contributed to greater similarity in decomposition rates between stand types.

Liriodendron tulipifera dominated hardwood stands on ridges and this species has been shown to have positive effects on decomposition rates and nutrient availability (Kalisz 1986). On bottoms, *L. tulipifera* was codominant with *J. virginiana, P. occidentalis*, and *J. nigra*. These species vary in litter decomposition rates and mycorrhizal types (Henry 1934; Reinsvold and Reeves 1986; Meiners 2014; Leroy and Marks 2006), and in the case of *J. nigra* and *P. occidentalis*, produce allelopathic compounds (Meiners 2014; Willis 2000; Al Naib and Rice 1971). Consequently, their accumulated effects on soil chemistry are

likely more variable, and there is little evidence to suggest that these species would promote understory diversity (Henry 1934; Reinsvold and Reeves 1986; Al Naib and Rice 1971; Leroy and Marks 2006; Willis 2000). The potential buffering from change of soils in bottoms driven by *Pinus* spp. is supported by earlier studies. Research has shown that *Pinus*, and other acidifying species such as ericaceous shrubs, have more pronounced impacts on soils that are poorly buffered (Grant, 1978; Binkley et al. 1989; Richter et al. 1994; Binkley and Valentine 1991; Binkley and Sollins 1990; Hizal et al. 2013; Rolfe and Boggess 1973).

Functional group distributions were clearly different due to soil differences between ridges and bottoms. Bottoms had greater mean cover across functional groups than ridges, including annuals, biennials, and perennials, as well as greater cover of *Acer* species, likely as a result of reduced interference from deep litter layers (Facelli and Pickett 1991 a and b) and greater soil fertility. The cover of invasive species was greatest in bottom *P. strobus* and bottom hardwood stands. However, bottom *P. strobus* stands had the lowest canopy cover due to the dieback and mortality of mature *P. strobus* trees, which may have contributed some to the greater total plant cover and greater cover of invasive species.

Regardless of stand type, I observed greater density and cover of woody species on ridges, but a greater cover of herbaceous species in bottoms. Herbaceous plants compete well for nutrients in the herbaceous layer and may have a negative impact on the establishment and persistence of advance regeneration (Gilliam 2007). On ridges, where herbaceous groups were likely inhibited by thick litter and low nutrient availability, woody plants exhibited greater importance.

3.5.3 Potential for Restoration

Prior to the 1800s, the Hoosier National Forest was dominated by *Quercus-Carya* forests. Forest harvesting via large openings has led to the regeneration and dominance of *L. tulipifera,* while selective harvesting via small openings has driven the dominance of *Acer saccharum* (Jenkins and Parker 1998). The ascension of *L. tulipifera* represents a clear divergence in successional trajectory (Zhalnin 2004), while the increased importance of *A. saccharum* represents accelerated succession towards late-successional shade-tolerant species (Abrams and Scott 1989). My study has shown that the establishment of *Pinus* plantations decades ago has led to another very pronounced divergence in successional trajectory. In the hardwood stands I sampled, the increased importance of mesophytic species, such as *L. tulipifera* and *A. saccharum*, has come at the expense of masting species in the genera *Quercus* and *Carya*. Soils on *P. echinata* ridges, and to a lesser degree *P. echinata* bottoms, contained thick litter layers, high concentrations of Al, and low availability of cations. As a consequence, this stand type contained low cover of herbaceous species and mesophytic woody seedlings. However, site occupancy by *P. echinata* has also led to increased cover and density of *Quercus* spp. and *Fagus grandifolia.* Because the regeneration of *Quercus* species on productive sites has been highly problematic throughout the *Quercus-Carya* forest (Johnson et al. 2009), this edaphically driven promotion of *Quercus* advance regeneration should be explored as a restoration opportunity for managers. Given the appropriate silvicultural strategies, it is likely that the use of shelterwoods and low intensity burning treatments on these sites may allow for the successful regeneration of *Quercus* spp. where advanced regeneration is present (Johnson et al. 2009).

3.6 Conclusion

Pinus stands had a clear impact on soil chemistry in my study (Chapter 2), which showed a direct impact on the composition and distribution of understory communities. Where mesophytic hardwoods dominated, soil fertility was greater, and species richness and cover of herbaceous species groups were greater. *Pinus* stands displayed lower herbaceous species diversity and total cover, but greater density and importance of understory *Quercus* spp. stems. These differences between *Pinus* and hardwoods were less pronounced in bottoms. This is likely due, in part, to the large component of *Acer* spp. that established in the overstory, intermixed with *Pinus* species in bottoms. These *Acer* spp. contributed to litter inputs and likely reduced the effects of *Pinus* species on soil chemistry. In addition, hardwood stands in bottoms contained a mix of canopy species with varying effects on soil chemistry.

Overstory species composition strongly affected soil conditions (Chapter 2), which in turn strongly influenced species distributions. This reflects an ecological feedback loop in which both *Pinus* and mesophytic species are superior competitors in specific soil conditions, and have competitive strategies that replicate those soil conditions.

3.7 References

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3.8 Figures

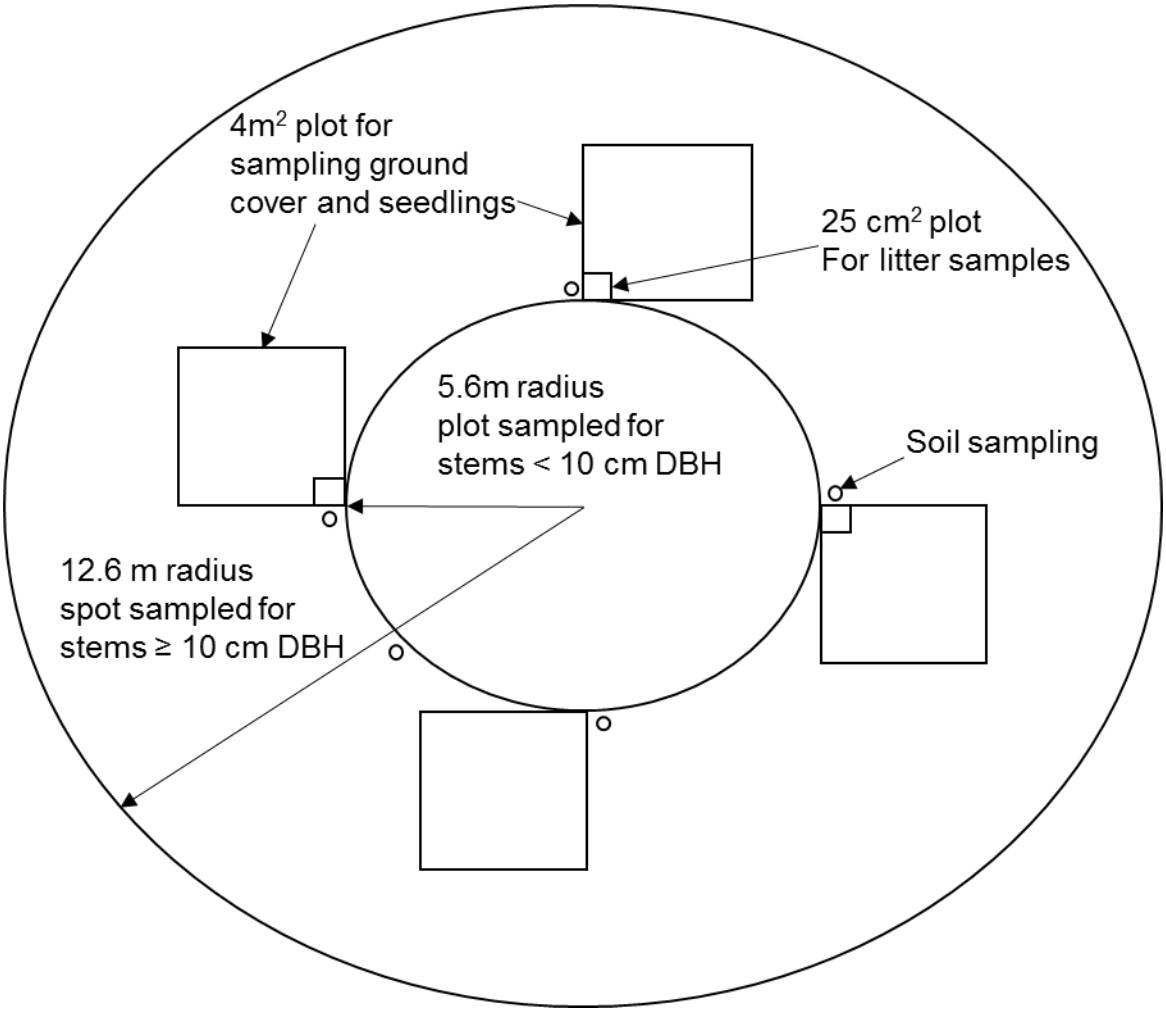

Figure 3.1 Nested plot sampling design, 0.01 ha plot within a 0.05 ha plot.

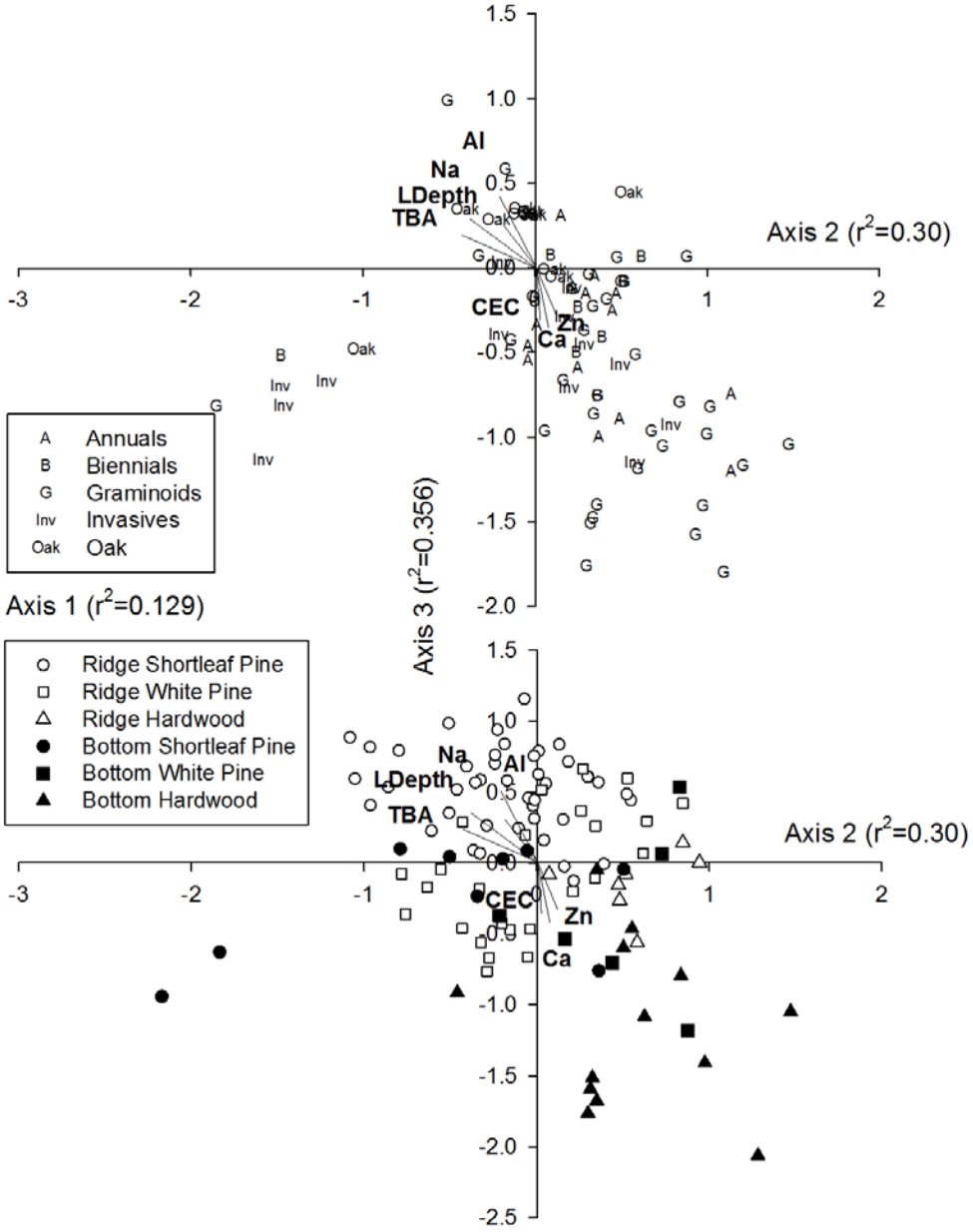

Figure 3.2 Non-metric multidimensional scaling (NMS) ordination reveals trends by herbaceous-layer functional groups (top) as well as by stand type and Ecological Land Type Phase (ELTP; bottom). Several functional groups are omitted for clarity of presentation (sedges, perennials, and native shrubs), though they show a similar trend. TBA = Total Basal Area (m^2 ha^{-1}), LDepth = Litter Depth (cm).

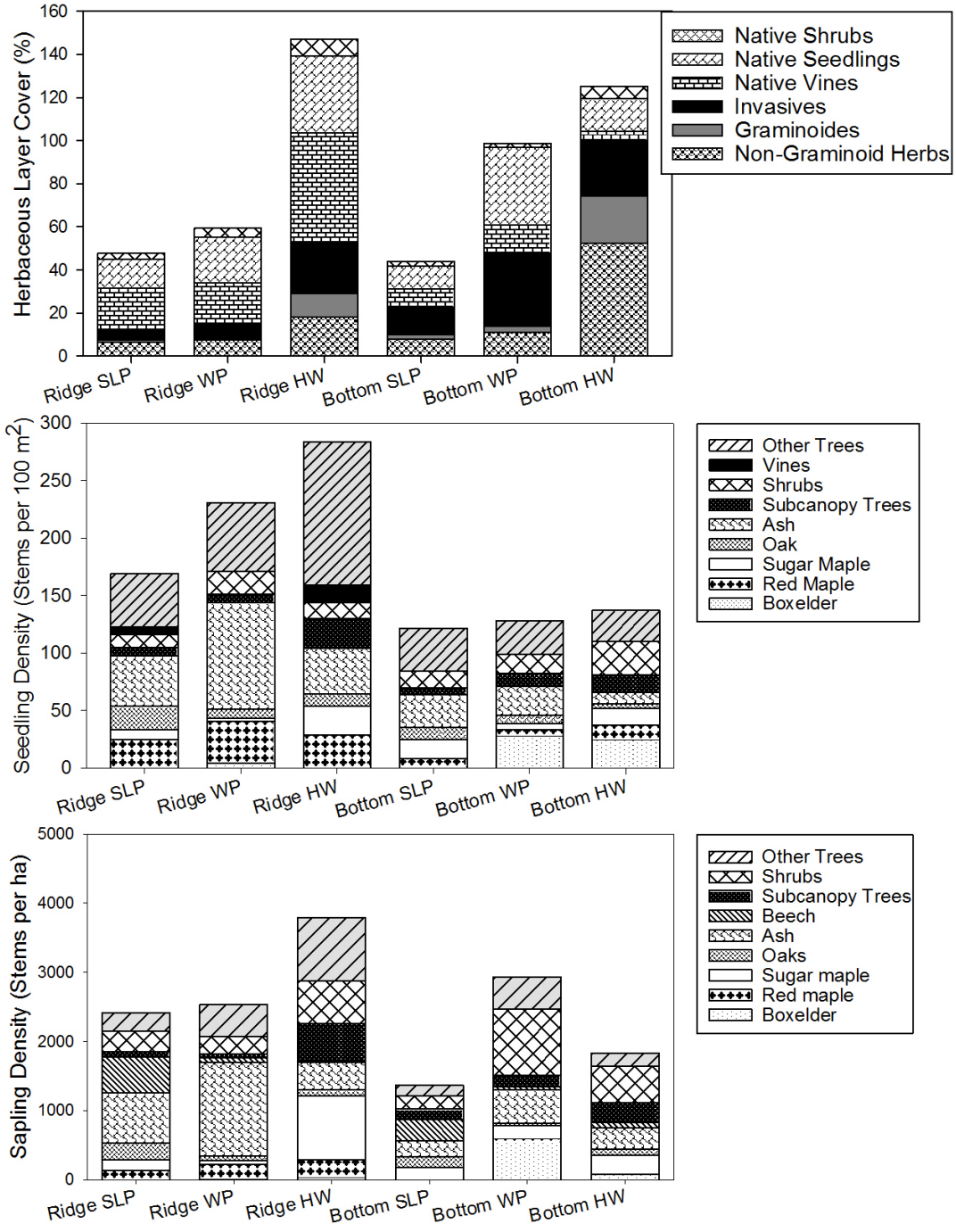

Figure 3.3 Mean percent cover and mean density of herbaceous layer functional groups (top), seedling groups (middle), and sapling groups (bottom). SLP = *P. echinata*, WP = *P. strobus*, HW = hardwood.

3.9 Tables

Table 3.1 Soil series listed by stand type and ELTP. The two most common series were Apalona and Wellston Silt Loams.

Stand Type	Soil Series
Ridge *Pinus echinata*	Apalona Silt Loam
Ridge *Pinus echinata*	Wellston Silt Loam
Ridge *Pinus echinata*	Adyeville-Tipsaw-Ebal Complex
Ridge *Pinus echinata*	Hosmer Silt Loam
Ridge *Pinus echinata*	Ebal-Duechers_kitterman Complex
Ridge *Pinus strobus*	Apalona Silt Loam
Ridge *Pinus strobus*	Wellston Silt Loam
Ridge *Pinus strobus*	Adyeville-Tipsaw-Ebal Complex
Ridge *Pinus strobus*	Adyeville-Wellston-Duechars Silt Loams
Ridge *Pinus strobus*	Adyeville Silt Loam
Ridge *Pinus strobus*	Ebal-Duechers_kitterman Complex
Ridge *Pinus strobus*	Tipsaw-Adyeville Complex
Ridge Hardwood	Apalona Silt Loam
Ridge Hardwood	Wellston Silt Loam
Ridge Hardwood	Adyeville-Tipsaw-Ebal Complex
Ridge Hardwood	Tipsaw-Adyeville Complex
Bottom *Pinus echinata*	Apalona Silt Loam
Bottom *Pinus echinata*	Gatchel Silt Loam
Bottom *Pinus echinata*	Adyeville-Tipsaw-Ebal Complex
Bottom *Pinus echinata*	Gatchel Loam
Bottom *Pinus strobus*	Adyeville Silt Loam
Bottom *Pinus strobus*	Adyeville-Tipsaw-Ebal Complex
Bottom *Pinus strobus*	Tipsaw-Adyeville Complex
Bottom *Pinus strobus*	Ebal-Duechers_kitterman Complex
Bottom Hardwood	Wellston Silt Loam
Bottom Hardwood	Apalona Silt Loam
Bottom Hardwood	Adyeville-Tipsaw-Ebal Complex
Bottom Hardwood	Markland Silty Clay Loam
Bottom Hardwood	Ebal-Duechers_kitterman Complex
Bottom Hardwood	Haymond Silt Loam
Bottom Hardwood	Gatchel Silt Loam
Bottom Hardwood	Tipsaw-Adyeville Complex
Bottom Hardwood	Cuba Silt Loam
Bottom Hardwood	Adyeville-Wellston-Duechars Silt Loams

Table 3.2 Species richness, diversity, and stand variables for stand type, ELTP, and their interaction (mean ± S.E.). Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). F values are listed on the right. *Factors or interaction significantly different ($p < 0.05$). Non-transformed data are presented for ease of interpretation. N=53 *Pinus echinata, 33 P. strobus,* 20 Hardwood, 77 ridge, and 29 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hardwood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
Species Richness (S)	33.7 ± 2.2^{a}	36.6 ± 2.7^{a}	45.9 ± 2.9^{b}	35.2 ± 1.4^{a}	42.3 ± 1.8^{b}	10.77*	10.02*	2.01
Species Diversity (H')	2.2 ± 0.1^{a}	2.1 ± 0.2^{a}	2.6 ± 0.2^{b}	2.2 ± 0.1	2.4 ± 0.1	5.30*	3.70	2.64
Total Basal Area (m^2 ha^{-1})	45 ± 2^{a}	47 ± 3^{a}	28 ± 3^{b}	41 ± 1	39 ± 2	25.57*	1.03	5.09*
Seedling Density (stems per 100 m^2)	145 ± 26	180 ± 32	210 ± 35	228 ± 16^{a}	129 ± 21^{b}	2.20	14.07*	1.30
Sapling Density (stems ha^{-1})	1887 ± 517	2676 ± 648	2729 ± 698	2829 ± 322	2032 ± 423	1.21	2.25	1.38
Standing Dead Wood (m^2 ha^{-1})	1.8 ± 0.6^{a}	4.3 ± 0.7^{b}	1.4 ± 0.8^{a}	2.4 ± 0.4	2.6 ± 0.5	8.89*	0.18	1.06
Canopy Openness (%)	0.06 ± 0.01^{a}	0.10 ± 0.01^{b}	0.07 ± 0.01^{a}	0.07 ± 0.00	0.07 ± 0.01	11.61*	0.01	2.49

Table 3.3 Functional groups (mean ± S.E.) based upon herbaceous-layer cover (%) by stand type, ELTP, and their interaction. Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). F values are listed on the right. *Factors or interaction significantly different ($p < 0.05$; **$p < 0.1$). Non-transformed data are presented for ease of interpretation. N=53 *Pinus echinata,* 33 *P. strobus,* 20 Hardwood, 77 ridge, and 29 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hard wood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
Native Shrubs	2.54 ± 1.05[a]	3.06 ± 1.31[a]	6.87 ± 1.42[b]	4.98 ± 0.65	3.33 ± 0.86	6.15*	2.35	0.26
Native Vines (**ridge only**)	19.30 ± 2.80[a]	19.20 ± 3.67[a]	50.90 ± 6.93[b]	29.80 ± 2.78[a]	8.57 ± 3.64[b]	3.25*	21.53*	7.16*
Invasive Shrubs	1.77 ± 2.49[a]	8.38 ± 3.12[a]	13.65 ± 3.36[b]	4.63 ± 1.55[a]	11.20 ± 2.03[b]	7.91*	6.66*	3.05
Invasive Groundcover	6.93 ± 2.49	11.88 ± 3.12	11.05 ± 3.36	7.00 ± 1.55[a]	12.90 ± 2.03[b]	1.66	5.30*	1.89
Graminoids	1.45 ± 2.60[a]	1.90 ± 3.25[a]	16.35 ± 3.50[b]	4.17 ± 1.62	8.98 ± 2.12	12.68*	3.26	1.42
Perennials	6.57 ± 3.89[a]	8.36 ± 4.87[a]	29.35 ± 5.25[b]	9.54 ± 2.42[a]	20.00 ± 3.18[b]	12.68*	6.84*	4.13*
Annuals	0.05 ± 0.17[a]	0.13 ± 0.21[a]	0.89 ± 0.23[b]	0.26 ± 0.10	0.45 ± 0.14	9.35*	1.16	1.25
Biennials (**bottom only**)	0.40 ± 0.76[a]	0.23 ± 0.95[a]	5.24 ± 0.64[b]	0.61 ± 0.35[a]	1.96 ± 0.46[b]	9.29*	5.52*	6.36*
Sedges	0.43 ± 0.48[a]	0.17 ± 0.60[a]	2.01 ± 0.65[b]	0.36 ± 0.30[a]	1.37 ± 0.39[b]	4.95*	4.23*	1.51
Sum Percent Cover	49.20 ± 0.08[a]	83.10 ± 0.11[a]	141.95 ± 0.11[b]	88.20 ± 0.05	94.60 ± 0.07	43.07*	0.57	3.96*

Table 3.4 Functional groups (mean ± S.E.) based upon seedling density (stems per 100 m^2) by stand type, ELTP, and their interaction. Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). F values are listed on the right. *Factors or interaction significantly different ($p < 0.05$; **$p < 0.1$). Non-transformed data are presented for ease of interpretation. N=53 *Pinus echinata,* 33 *P. strobus,* 20 Hardwood, 77 ridge, and 29 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hard wood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
A. negundo (**bottom only**)	1.4 ± 5.3^a	28.1 ± 6.5^b	25.0 ± 4.4^b	1.4 ± 2.4^a	18.2 ± 3.2^b	6.30*	17.95*	4.48*
A. rubrum	15.7 ± 8.7	20.9 ± 10.9	20.5 ± 11.7	29.8 ± 5.4^a	8.2 ± 7.1^b	0.16	5.88*	0.28
A. saccharum	12.6 ± 4.2	4.0 ± 5.3	19.7 ± 5.7	12.1 ± 2.6	12.1 ± 3.4	3.90*	0.00	1.68
*Quercus**	15.7 ± 3.6^a	7.7 ± 4.5^a	7.3 ± 4.9^b	13.2 ± 2.3^a	7.2 ± 3.0	2.52**	2.62	0.63
Fraxinus	36.0 ± 15.5	58.8 ± 19.4	25.1 ± 20.8	58.8 ± 9.6^a	21.2 ± 12.6^b	1.39	5.60*	1.01
Subcanopy Trees	6.6 ± 3.8^a	9.6 ± 4.7	20.6 ± 5.1^b	13.7 ± 2.4	10.8 ± 3.1	4.79*	0.57	0.99
Shrubs	13.0 ± 5.9	18.1 ± 7.3	21.1 ± 7.9	14.7 ± 3.7	20.0 ± 4.8	0.70	0.77	0.70
F. grandifolia	4.9 ± 1.9	1.5 ± 2.4	2.1 ± 2.6	2.3 ± 1.2	3.4 ± 1.6	1.28	0.26	0.01
Other tree species	14.6 ± 5.9	23.0 ± 7.3	28.5 ± 7.9	35.9 ± 3.7^a	8.2 ± 4.8^b	2.00	21.20*	2.99

Table 3.5 Functional groups (mean ± S.E.) based upon sapling density (stems per hectare) by stand type, ELTP, and their interaction. Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). F values are listed on the right. *Factors or interaction significantly different ($p < 0.05$; **$p < 0.1$). Non-transformed data are presented for ease of interpretation. N=53 *Pinus echinata,* 33 *P. strobus,* 20 Hardwood, 77 ridge, and 29 bottom sites.

Variables	*P. echinata*	*P. strobus*	Hard wood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
A. negundo (**bottom only**)	0.0 ± 69.1^{a}	550.0 ± 84.6^{b}	84.6 ± 57.5^{ab}	19.6 ± 31.4^{a}	211.5 ± 41.1^{b}	11.30*	13.77*	10.84*
A. rubrum	69.8 ± 85.1	131.0 ± 106.5	125.3 ± 114.7	198.1 ± 53.0^{a}	19.2 ± 69.5^{b}	0.23	4.19*	0.11
A. saccharum (***ridge only***)	148.8 ± 77.6^{a}	48.0 ± 101.8^{a}	928.6 ± 192.4^{b}	375.1 ± 77.0	207.6 ± 101.1	5.25*	1.74	3.55*
Quercus	201.1 ± 64.0	52.7 ± 80.1	89.0 ± 86.4	134.7 ± 39.9	93.7 ± 52.3	2.14	0.39	0.20
Fraxinus	479.5 ± 332.0	915.7 ± 425.6	353.9 ± 447.8	824.5 ± 206.8	341.5 ± 271.3	0.91	2.01	0.38
F. grandifolia	414.9 ± 108.0^{a}	61.0 ± 135.2^{b}	45.6 ± 145.7^{b}	201.6 ± 67.3	146.1 ± 88.3	5.49**	0.25	0.58
Shrubs	238.7 ± 169.1	599.0 ± 211.7	568.7 ± 228.0	383.6 ± 105.3	554.0 ± 138.2	2.06	0.96	2.27
Subcanopy Trees	111.8 ± 62.0^{a}	111.4 ± 77.6^{a}	413.8 ± 83.5^{b}	226.0 ± 38.6	198.6 ± 50.6	9.33*	0.19	3.03
Invasive Shrubs*	18.1 ± 44.2^{a}	81.0 ± 55.3^{a}	147.3 ± 59.6^{b}	99.1 ± 27.5	65.1 ± 36.1	2.89**	0.56	0.26
Other Hardwoods (**ridge only**)	120.9 ± 42.9^{a}	232.0 ± 56.2^{ab}	500.0 ± 106.3^{b}	284.3 ± 42.6	67.0 ± 55.8	3.04	9.59*	3.14*

Table 3.6 Indicator Species for overstory, sapling, and herbaceous-layer strata. IV = importance value. SLP = *P. echinata*, WP = *P. strobus*, HW = hardwood.

Overstory	Stand Type	IV	P value	Mean	S.Dev
Pinus echinata	Ridge-SLP	56.3	0.0002	17.6	4.25
Acer rubrum	Ridge-SLP	31.5	0.0234	19.7	4.74
Pinus strobus	Ridge-WP	48.3	0.0002	15.1	5.22
L. tulipifera	Ridge-HW	38.3	0.0048	20.9	4.93
Ulmus rubra	Ridge-HW	29.4	0.0166	11.2	6.08
Juglans nigra	Ridge-HW	27.8	0.0154	9.8	5.81
Acer saccharum	Bottom-SLP	37.2	0.0038	17.7	5.28
Ostrya virginiana	Bottom-SLP	19.1	0.0494	8.5	5.26
Acer negundo	Bottom-WP	28.3	0.009	9.3	5.46
Gleditsia triacanthos	Bottom-WP	16.7	0.0478	5.7	4.36
Platanus occidentalis	Bottom-HW	45.2	0.0012	11.4	6.15
Betula nigra	Bottom-HW	18.2	0.0252	6.7	4.69
Sapling	Stand Type	IV	P value	Mean	S.Dev
Fagus grandifolia	Ridge-SLP	42	0.0052	19.5	5.83
Quercus velutina	Ridge-SLP	27	0.0404	14.9	5.53
Acer negundo	Bottom-WP	38.7	0.0056	11	6.25
Ulmus rubra	Bottom-WP	35.1	0.0042	9.2	5.6
Diospyros virginiana	Bottom-WP	22.5	0.0308	8.5	5.28
Platanus occidentalis	Bottom-HW	18.2	0.0276	7.2	4.2
Herbaceous Layer	Stand Type	IV	P value	Mean	S.Dev
Asplenium platynueron	Ridge-WP	29.2	0.0498	16.5	6.4
Acer saccharum	Ridge-HW	54	0.0064	25.2	8.03
Ulmus rubra	Ridge-HW	53.5	0.0128	23.6	9.83
Nyssa sylvatica	Ridge-HW	46.8	0.0194	19.9	9.55
Celtis occidentalis	Ridge-HW	45.1	0.0278	21.3	9.3
Toxicodendron radicans	Ridge-HW	44.5	0.0002	24.5	3.82
Parthenocissus quinquefolia	Ridge-HW	43.5	0.0182	28.1	5.77
Helianthus annuus	Ridge-HW	42.3	0.0008	8.1	5.43
Eupatorium purpureum	Ridge-HW	41.7	0.0214	16.8	8.51
Ranunculus recurvatus	Ridge-HW	28.1	0.0266	9.7	6.25
Lichen	Ridge-HW	27.7	0.0342	15.9	5.24
Juglans cinerea	Ridge-HW	25.8	0.0184	8.2	5.21
Desmodium glutinosum	Ridge-HW	25.1	0.022	9	5.38
Cretaegus spp.	Ridge-HW	24.7	0.0154	7.6	4.56

Stand Type	IV	P value	Mean S.Dev	Stand Type	IV
Monarda fistulosa	Bottom-SLP	40	0.0018	8.7	5.37
Heuchera spp.	Bottom-SLP	33.3	0.0002	7.6	4.43
Vibernum acerifolium	Bottom-SLP	29.6	0.047	15.1	7.09
Actaea pachypoda	Bottom-SLP	26.8	0.0186	9.3	5.69
Polygonatum biflorum	Bottom-SLP	25.4	0.0292	10.4	5.98
Vibernum rufidulum	Bottom-SLP	22	0.0242	7.4	5.34
Sanicula acalypha	Bottom-SLP	21.7	0.0228	7.7	4.71
Leucanthemum vulgare	Bottom-SLP	18	0.047	8	4.88
Lonicera maackii	Bottom-SLP	17.7	0.0466	8.1	5.21
Acer negundo	Bottom-WP	50.1	0.0046	16.5	7.64
Cornus florida	Bottom-WP	40.3	0.0418	20.5	9.04
Microstegium vimineum	Bottom-WP	40.2	0.0116	16.1	6.99
Fraxinus pennsylvanica	Bottom-WP	39.9	0.0154	16.8	7.6
Mitella diphylla	Bottom-WP	25.4	0.0394	10	6.29
Panicum lanuginosum var implicatum	Bottom-WP	25.3	0.0178	7.9	4.84
Collinsonia canadensis	Bottom-WP	16.6	0.0404	6.7	5
Packera aurea	Bottom-HW	76.7	0.0002	16.9	7.77
Sanicula canadensis	Bottom-HW	62.1	0.002	25.8	8.75
Verbesina alternifolia	Bottom-HW	58.2	0.0004	12.2	6.88
Asarum canadense	Bottom-HW	53.2	0.0004	11.3	6.52
Laportea canadensis	Bottom-HW	47.7	0.0004	10.2	6.07
Impatiens capensis	Bottom-HW	47.6	0.0018	12.9	6.78
Clematis virginiana	Bottom-HW	31.4	0.0314	14.1	6.99
Boehmeria cylindrica	Bottom-HW	30.6	0.0338	13.8	7.17
Elymus virginicus	Bottom-HW	29.8	0.013	8.6	5.62
Apios americana	Bottom-HW	29.7	0.0074	9.4	5.49
Aster sp 1	Bottom-HW	29.3	0.0272	10.5	6.49
Cryptotaenia canadensis	Bottom-HW	26.1	0.0376	11.4	6.46
Diarrhena americana	Bottom-HW	25.9	0.0344	11.3	6.08
Cephalanthus occidentalis	Bottom-HW	23.1	0.017	7.6	4.41
Osmorhiza longistylis	Bottom-HW	23.1	0.0184	7.6	4.76
Glechoma hederacea	Bottom-HW	22.8	0.0424	10.1	6.25
Hypericum punctatum	Bottom-HW	22.3	0.0298	8.1	5.02
Euonymus americanus	Bottom-HW	15.4	0.0294	7.3	4.36
Aster sp 3	Bottom-HW	15.4	0.0282	7.2	4.26

CHAPTER 4 CONCLUSIONS AND MANAGEMENT IMPLICATIONS

4.1 Conclusions

In my study, *Pinus* stands contained lower nutrient availability, greater litter depth, and greater Al content compared to hardwood stands. This corresponded to lower species richness, diversity, and functional richness in *Pinus* stands. Specifically, whereas mesophytic functional groups dominated hardwood stands with greater soil fertility, more tolerant *Fraxinus, A. rubrum, Quercus,* and *Fagus* species dominated *Pinus* sites. This is supported by the fact that while light availability was greater in *P. strobus* stands, species richness, diversity, and cover generally were not. Additionally, this is supported in that *P. strobus* stands contain intermediate values for both edaphic variables and understory cover values.

I predicted that *Pinus* stands would show discernable differences in soil chemistry in terms of nutrient availability, litter depth, and Al. *Pinus* stands had lower soil pH, OM (%), TC (%), TN (%), B (mg kg^{-1}), Mn (mg kg-1), Ca (mg kg^{-1}), and Zn (mg kg^{-1}) and greater litter depth and Al (mg kg^{-1}). Measures of soil fertility followed the general order *Pinus echinata* < *P. strobus* < hardwood stands. In my study, I observed litter depths in *Pinus* stands 2-5 times greater than those in hardwood stands. This recalcitrance of *Pinus* litter resulted in lower organic matter content in the surface soil of *Pinus* stands, which contributed to reduced TC, TN, and micronutrient content likely due to reduced decomposition rates (Table 2.1).

I also predicted that differences in soil conditions would cause compositional differences between *Pinus* and hardwood stands. Species diversity, distribution, cover, and composition of understory species did differ. Across all stand types, hardwood stands displayed the greatest species richness, Shannon-Weiner diversity, and total cover of herbaceous-layer species while *P. echinata* stands displayed the lowest (Table 3.2). Overall, herbaceous-layer species displayed clear distributions across edaphic gradients related to *Pinus* species occupancy.

Additionally, I predicted that *Pinus* species on ridge sites would inhibit the establishment of herbaceous species, largely from litter acting as a mechanical barrier, and that drier ridge sites would favor woody plants. Cover of seedlings, particularly *Quercus* spp., *F. grandifolia*, and *A. rubrum* were in fact associated with *Pinus* ridge sites, greater litter depth, and greater concentrations of Al (Figure 3.2 & Figure 3.3).

I further predicted that differences between stand types would be more pronounced on ridges, due to the greater buffering capacity of soils in bottoms. I observed greater differences in soil variables between stand types on ridges, whereas bottoms did not show as many distinct differences. Soils in bottoms were better buffered through higher moisture availability and cation exchange capacity from adjacent alluvium. Also, the overstory of *Pinus* stands in bottoms contained a large component of *Acer* species, which likely reduced the effects of recalcitrant *Pinus* litter. I also observed differences in soil chemistry between hardwood stands on ridges and bottoms. Bottom hardwood stands contained a mix of overstory species, whereas hardwood overstories on ridges were dominated by *Liriodendron tulipifera*; a species whose litter has been shown to ameliorate soil conditions. The mix of species in bottoms, which included *J. virginiana, P. occidentalis*, and *J. nigra* in addition to *L. tulipifera*, may have less pronounced ameliorating impacts on soil (Appendix C). However, there was a notably greater cover of herbaceous species in bottoms, likely as a result of greater moisture availability and reduced litter depth (Figure 3.3; Table 2.2). On

ridges, I observed greater density and cover of woody species than in bottoms. Mesophytic woody species, including *A. saccharum, C. florida, L. benzoin,* and *R. multiflora* were common in ridge hardwood stands, while *Quercus* spp. and *Fagus grandifolia* were more common in ridge *P. echinata* stands (Figure 3.3; Table 3.4; Table 3.5). Species in Pinaceae and Fagaceae tolerate low soil fertility in similar ways. *Quercus* also show high tolerance for soil Al, which was higher in *Pinus* plantation soils. Therefore, there is potential for regenerating *Quercus* in *Pinus* ridges, given the appropriate suite of silvicultural treatments.

4.2 Management Implications

In considering which suite of silvicultural options is most appropriate for establishing hardwood stands on former pine sites, it is necessary to identify management goals. Generally, managers are interested in improving their forests' net present value (NPV), and improving biodiversity in concert with protecting threatened species. There is virtually no market for the estimated 58,107 ha of *Pinus* stands that occur in Indiana, Ohio, and Illinois (USFS 2013). Therefore, managers should largely focus on biodiversity when identifying management goals in these stands. Plantations show lower average diversity because of lower average structural heterogeneity (Lindenmayer and Hobbs 2004). They may host fewer macroinvertebrates, birds, and small mammals as a result (Lindenmayer and Hobbs 2004). *Pinus* plantations have shown this trend in particular, and can show reduced plant diversity partly as a result of deep, allelopathic litter (McGrath et al. 2004; Bielecki et al. 2006; Oxbrough et al. 2012; Paritsis and Aizen 2008; Loydi et al. 2013; Blasche 1981). However, there is evidence that *Pinus* plantings can provide some winter cover for some animal species to a limited age (Parker 1986). Additionally, in the case of the fragmented landscape of Indiana, Ohio, and Illinois, these plantations surrounded by remnant native vegetation may provide some degree of heterogeneity at the landscape scale (Lindenmayer and Hobbs 2004).

Therefore, large-scale conversion should only be performed where there is evidence of ecological benefit, and potential future economic value, such as converting these stands to *Quercus* species.

In my study, *Pinus echinata* sites contained 230 ± 314 sapling stems per hectare and 1910 ± 1687 seedling stems per hectare of advance regeneration of *Quercus* species. Compared to the other stand types I studied, this result suggests that *P. echinata* stands on ridges could provide an important opportunity for the restoration of *Quercus*-dominated stands. Johnson et al. (2009) estimate that, in the xeric Missouri Ozarks, 988 to 1482 stems per hectare of 3-6 feet is adequate advance regeneration for maintaining *Quercus* species following clearcut harvestings. This suggests that techniques to promote height growth of oak and reduce the density of competing mesophytic species may be necessary for successful conversion to *Quercus*-dominated forests. The literature suggests that shelterwood/burning treatments may be more effective in promoting the growth and persistence of small-stature *Quercus* regeneration (Johnson et al. 2009; Brose et al 1999). Under this system, repeated burning is used in conjunction with overstory removal to promote *Quercus* growth and dominance in the understory prior to release via reductions in overstory density. Additionally, due to limited propagule supply and advance regeneration, natural regeneration may be augmented with *Quercus* underplantings.

Unlike the moderate success of *Quercus* under *Pinus echinata*, *P. strobus* stands show a large degree of top-kill and a large proportion or *Fraxinus*, *A. rubrum*, and invasives. The data reported on *P. strobus* reflects a small portion of the sites visited because most sites contained a noteworthy dieoff of overstory *P. strobus* and were rejected as study sites. This implies that, given no management, most of the overstory will die off within a century, which will provide a mixed age class structure, a large degree of coarse woody debris, and large spatial heterogeneity. This may aid in providing functional space for various fauna, and improve functional diversity (Lindenmayer and Hobbs 2004; McCarthy and Bailey 1994;

Lohr et al. 2002). Given that there is a small proportion of *P. strobus* stands at less than 1% of total HNF forest cover, and that these stands occupy added winter cover in a mosaic of native hardwood vegetation, no management may be the best option.

4.3 Future Directions

My study has provided important information about the effects of decades of occupancy of *Pinus* species on forest communities. My results demonstrated that *Pinus* occupancy is associated with reductions in soil fertility and nutrient availability. However, the mechanisms that drive these changes in edaphic conditions are poorly understood. To better understand the impacts of conifers on soils, native herbaceous species, and woody regeneration, studies need to focus on factors that create these impacts, such as litter recalcitrance, mycorrhizal relations, and their associated acid exudates in conjunction with plant community distributions and abundances. In addition, my study considered light availability during the summer growing season, showing no differences between *Pinus* and hardwood species. However, it is possible that *Pinus* stands have ecologically relevant light limitation during the early spring, which may affect the vernal flora. Based upon these limitations in my study, future research should focus on the mechanisms driving differences in competitive success, tolerance, and ecosystem function, rather than the species themselves.

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APPENDICES

Appendix A Study Variables

All variables listed for stand type, ELTP, and their interaction (mean ± S.E.). Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). F values are listed on the right. *Factors or interaction significantly different ($p < 0.05$; **$p < 0.1$). Non-transformed data are presented for ease of interpretation. SLP = *P. echinata*, WP = *P. strobus*, HW = hardwood. In total, I sampled 44 ridge *P. echinata* sites, 26 ridge *P. strobus* sites, 7 ridge hardwood sites, 9 bottom *P. echinata* sites, 7 bottom *P. strobus* sites, and 13 bottom hardwood sites.

Variable	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW	Ridge	Bottom
Species Richness (S)	27.3 ± 1.4^{a}	35.0 ± 1.8^{a}	43.3 ± 3.4^{b}	40.1 ± 3.0^{a}	38.2 ± 3.6^{a}	48.5 ± 2.5^{b}	35.2 ± 1.4^{a}	42.3 ± 1.8^{b}
Species Diversity (H')	1.9 ± 0.1^{a}	2.1 ± 0.1^{a}	2.5 ± 0.2^{b}	2.5 ± 0.2^{a}	2.1 ± 0.2^{a}	2.7 ± 0.1^{b}	2.2 ± 0.1	2.4 ± 0.1
Understory evenness	0.58 ± 0.02	0.60 ± 0.03	0.67 ± 0.05	0.67 ± 0.04	0.59 ± 0.05	0.68 ± 0.04	0.62 ± 0.02	0.65 ± 0.03
Total Basal Area ($m^2\ ha^{-1}$)	45 ± 1^{a}	44 ± 1^{a}	35 ± 3^{b}	46 ± 3^{a}	49 ± 3^{a}	22 ± 2^{c}	41 ± 1	39 ± 2
Standing Dead Wood ($m^2\ ha^{-1}$)	1.3 ± 0.4^{a}	3.9 ± 0.5^{b}	1.9 ± 0.9^{a}	2.2 ± 0.8^{a}	4.6 ± 1^{b}	0.9 ± 0.6^{a}	2.4 ± 0.4	2.6 ± 0.5
Seedling Density (stems per 100 m^2)	169 ± 16	232 ± 21	284 ± 40	122 ± 35	128 ± 43	137 ± 29	228 ± 16^{a}	129 ± 21^{b}

Variable	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW	Ridge	Bottom
Sapling Density (stems ha^{-1})	2409 ± 325	2452 ± 426	3628 ± 805	1366 ± 710	2900 ± 870	1830 ± 591	2829 ± 322	2032 ± 423
Stand Age	59.4 ± 1.7^{a}	39.0 ± 2.2^{c}	47.1 ± 4.2^{b}	59.6 ± 3.7^{a}	36.0 ± 4.5^{c}	48.9 ± 3.1^{b}	47.8 ± 1.7	48.2 ± 2.2
Litter C:N Ratio	37.60 ± 0.89	36.45 ± 1.16	35.06 ± 2.20	40.30 ± 1.94^{a}	35.64 ± 2.38^{a}	27.89 ± 1.62^{b}	36.37 ± 0.88	34.61 ± 1.16
Litter Depth (cm)	21.00 ± 1.23^{a}	15.35 ± 1.61^{a}	5.61 ± 3.04^{b}	16.94 ± 2.68^{a}	12.85 ± 3.28^{a}	5.50 ± 2.23^{b}	13.99 ± 1.22	11.76 ± 1.60
Litter Mass (g m^{-2})	970 ± 56^{a}	709 ± 73^{a}	233 ± 139^{b}	677 ± 122^{a}	475 ± 150^{a}	340 ± 102^{b}	638 ± 56	498 ± 73
TEC (meq 100 g^{-1})	7.84 ± 0.42	9.26 ± 0.56	9.16 ± 1.05	10.46 ± 0.93	11.16 ± 1.14	11.95 ± 0.77	8.75 ± 0.42^{a}	11.19 ± 0.55^{b}
Organic Matter (%)	3.65 ± 0.08^{a}	3.63 ± 0.11^{a}	4.66 ± 0.20^{b}	3.97 ± 0.18	4.07 ± 0.22	3.83 ± 0.15	3.98 ± 0.08	3.96 ± 0.11
A horizon pH	5.53 ± 0.06^{a}	5.66 ± 0.07^{ab}	5.86 ± 0.14^{b}	5.54 ± 0.12	5.28 ± 0.15	5.64 ± 0.10	5.68 ± 0.06^{a}	5.49 ± 0.07^{b}
B horizon pH	4.04 ± 0.05^{a}	4.23 ± 0.06^{a}	4.56 ± 0.12^{b}	4.25 ± 0.11^{a}	4.19 ± 0.13^{a}	4.56 ± 0.09^{b}	4.27 ± 0.05	4.33 ± 0.06
Total Nitrogen (%)	0.14 ± 0.01^{a}	0.14 ± 0.01^{a}	0.20 ± 0.01^{b}	0.15 ± 0.01^{a}	0.15 ± 0.01^{a}	0.17 ± 0.01^{a}	0.16 ± 0.01	0.16 ± 0.01
Total Carbon (%)	1.65 ± 0.05^{a}	1.65 ± 0.07^{a}	2.32 ± 0.13^{b}	1.88 ± 0.12	1.68 ± 0.14	1.79 ± 0.10	1.87 ± 0.05	1.78 ± 0.07
Bray Phosphorus (mg kg^{-1})	1.29 ± 0.41	2.27 ± 0.54	1.54 ± 1.02	1.83 ± 0.90	3.71 ± 1.10	4.39 ± 0.75	1.70 ± 0.41^{a}	3.31 ± 0.54^{b}
Sulphur (ppm)	11.84 ± 0.28	10.64 ± 0.36	10.71 ± 0.69	10.33 ± 0.60	11.67 ± 0.74	10.00 ± 0.50	11.06 ± 0.27	10.67 ± 0.36

Variable	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW	Ridge	Bottom
Calcium (mg kg^{-1})	752.1 ± 46.1^{a}	961.2 ± 60.1^{ab}	988.4 ± 113.5^{b}	958.4 ± 100.1^{a}	929.0 ± 122.6^{ab}	1247.5 ± 83.3^{b}	900.6 ± 45.5	1045.0 ± 59.6
Sodium (%)	0.92 ± 0.03^{a}	0.81 ± 0.04^{ab}	0.71 ± 0.08^{b}	0.71 ± 0.07^{a}	0.73 ± 0.08^{ab}	0.60 ± 0.06^{b}	0.81 ± 0.03^{a}	0.68 ± 0.04^{b}
Boron (mg kg^{-1})	0.27 ± 0.01^{a}	0.29 ± 0.02^{a}	0.40 ± 0.03^{b}	0.30 ± 0.03^{a}	0.28 ± 0.04^{a}	0.36 ± 0.02^{b}	0.32 ± 0.01	0.31 ± 0.02
Iron (mg kg^{-1})	146.1 ± 6.2^{a}	146.7 ± 8.1^{ab}	145.4 ± 15.4^{a}	155.0 ± 13.5^{a}	181.0 ± 16.6^{ab}	225.4 ± 11.3^{b}	146.1 ± 6.2	187.1 ± 8.1
Manganese (mg kg^{-1})	158.3 ± 11.4^{a}	151.4 ± 15.0^{a}	250.3 ± 28.3^{b}	188.9 ± 24.9^{ab}	195.8 ± 30.5^{ab}	162.1 ± 20.7^{a}	186.7 ± 11.3	182.3 ± 14.9
Zinc (mg kg^{-1})	1.71 ± 0.07^{a}	1.57 ± 0.10^{a}	2.24 ± 0.18^{b}	1.71 ± 0.16^{a}	2.12 ± 0.20^{b}	1.67 ± 0.14^{b}	1.84 ± 0.07^{a}	2.17 ± 0.10^{b}
Magnesium (%)	13.10 ± 0.59	13.61 ± 0.78	14.73 ± 1.47	12.68 ± 1.29	12.62 ± 1.58	11.82 ± 1.08	13.82 ± 0.59	12.37 ± 0.77
Copper (mg kg^{-1})	2.67 ± 0.20	2.89 ± 0.27	2.04 ± 0.51	2.46 ± 0.45	3.02 ± 0.55	3.10 ± 0.37	2.53 ± 0.20	2.86 ± 0.27
Potassium (mg kg^{-1})	74.77 ± 3.18	76.20 ± 4.20	98.71 ± 7.87	67.78 ± 6.94	83.33 ± 8.51	75.92 ± 5.78	83.23 ± 3.15	75.68 ± 4.14
Aluminum (mg kg^{-1})	969 ± 19^{a}	82 ± 25^{b}	788 ± 48^{c}	757 ± 42^{ab}	857 ± 52^{a}	637 ± 35^{b}	861 ± 19^{a}	750 ± 25^{b}
Canopy Openness (%)	0.07 ± 0.00^{a}	0.09 ± 0.01^{b}	0.06 ± 0.01^{a}	0.05 ± 0.01^{a}	0.10 ± 0.01^{b}	0.07 ± 0.01^{a}	0.07 ± 0.00	0.07 ± 0.01
Bulk Density (g cm^{-3})	1.01 ± 0.02^{a}	1.07 ± 0.02^{a}	0.87 ± 0.04^{b}	1.05 ± 0.04	1.10 ± 0.05	1.05 ± 0.03^{a}	0.98 ± 0.02	1.07 ± 0.02
Base Saturation (%)	70.73 ± 1.54	74.67 ± 2.02	78.56 ± 3.82	70.87 ± 3.37	64.18 ± 4.13	72.69 ± 2.80	74.66 ± 1.53^{a}	69.25 ± 2.01^{b}

TEC= Total Exchange Capacity

Appendix B Complete List of Species

All species listed. Species codes correspond to functional groups (P = perennials, A = annuals, B = biennials). "+" represents the stand type(s) where a species was found at least once.
SLP = *P. echinata*, WP = *P. strobus*, HW = hardwood.

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
P1	Achillea millefolium			+			
P2	Actaea pachypoda				+	+	+
P3	Ageratina altissima	+	+	+	+	+	+
P4	Agrimonia gryposepala		+	+	+	+	+
P5	Agrimonia rostellata	+	+	+		+	+
P6	Allium canadense var canadense	+					+
P7	Allium tricoccum				+		+
P8	Amphicarpaea bracteata	+	+	+	+	+	+
P9	Anemonella thalictroides				+		+
P10	Antennaria parlinii			+			
P11	Apios americana				+		+
P12	Arisaema dracontium		+	+	+	+	+
P13	Arisaema triphyllum	+	+	+	+	+	+
P14	Aristolochia serpentaria	+	+	+	+	+	+
P15	Arnoglossum plantagineum					+	+
P16	Asarum canadense				+	+	+
P17	Asclepias syriaca		+	+	+		
P18	Asplenium platynueron	+	+	+	+	+	+
P19	Aster drummondii		+				
P20	Aster prenanthoides					+	+
P21	Aster sp	+	+	+	+		
P22	Aster sp #1			+		+	+
P23	Aster sp #2						+
P24	Aster sp #3						+
P25	Aster umbellatus		+		+		

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
P26	Boehmeria cylindrica		+	+	+	+	+
P27	Chamerion angustifolium		+			+	+
P28	Cicuta maculata					+	+
P29	Circaea lutetiana	+	+		+	+	+
P30	Collinsonia canadensis	+				+	
P31	Coronilla varia			+		+	
P32	Cryptotaenia canadensis	+	+		+		+
P33	Cunila origanoides						+
P34	Desmodium cuspidatum var cuspidatum			+			
P35	Desmodium glutinosum		+	+			+
P36	Desmodium nudiflorum	+	+	+	+	+	+
P37	Desmodium paniculatum			+	+		
P38	Desmodium rotundifolium	+					
P39	Eupatorium perfoliatum						+
P40	Eupatorium purpureum	+	+	+	+	+	+
P41	Eupatorium sp						+
P42	Eutrochium maculatum	+	+		+		+
P43	Frasera caroliniensis		+		+		
P44	Galium obtusum		+	+	+		+
P45	Galium aparine	+	+	+	+	+	+
P46	Galium circaezens	+	+	+	+	+	+
P47	Galium concinnum	+	+	+	+		
P48	Galium pilosum	+	+				
P49	Galium sp		+		+		+
P50	Galium triflorum						+
P51	Geranium maculatum		+				
P52	Geum canadense	+	+	+	+	+	+
P53	Goodyera pubescens	+	+	+	+		
P54	Hackelia virginiana		+				
P55	Helianthus microcephalus						+
P56	Helianthus annuus			+			+
P57	Herb sp # 1	+					
P58	Herb sp # 2		+				

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
P59	Herb sp # 3		+				
P60	Herb sp # 4	+					
P61	Houstonia caerulea	+					
P62	Houstonia purpurea		+				
P63	Heuchera sp				+		
P64	Hydrastis canadensis				+		+
P65	Hydrophyllum sp						+
P66	Isopyrum biternatum						+
P67	Laportea canadensis				+		+
P68	Lespedeza cuneata	+	+	+	+	+	
P69	Lespedeza reptans			+			
P70	Lespedeza virginica						+
P71	Leucanthemum vulgare		+		+	+	
P72	Lichen	+	+	+	+	+	+
P73	Lycopodium dendroideum	+	+	+	+		+
P74	Lysimachia ciliata	+	+				
P75	Lysimachia nummularia	+	+			+	+
P76	Maianthemum racemosum	+			+		
P77	Melilotus officinalis		+				
P78	Menispermum canadense	+	+	+	+		+
P79	Mitella diphylla		+	+	+	+	+
P80	Monarda fistulosa	+	+		+		
P81	Moss	+	+	+	+	+	+
P82	Osmorhiza claytonii	+	+	+	+		+
P83	Oxalis illinoensis						+
P84	Oxalis stricta	+	+	+	+	+	+
P85	Oxalis viola	+	+				
P86	Osmorhiza longistylis						+
P87	Packera aurea	+	+	+	+	+	+
P88	Panax quinquefolius		+		+		
P89	Phryma leptostachya	+	+	+	+		+
P90	Phytolacca americana		+			+	
P91	Podophyllum peltatum	+	+	+	+		+
P92	Polygonatum biflorum	+	+		+		
P93	Polygonum virginianum		+		+	+	+

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
P94	Polemonium reptans				+	+	+
P95	Prenanthes altissima		+		+		
P96	Pycnanthemum tenuifolium	+	+	+			+
P97	Ranunculus hispidus			+			+
P98	Ranunculus recurvatus	+	+	+			
P99	Ranunculus sp			+			
P100	Rudbeckia hirta						+
P101	Ruellia sp					+	+
P102	Ruellia strepens						+
P103	Salvia lyrata		+		+	+	+
P104	Sanguinaria canadensis						+
P105	Sanicula odorata		+				
P106	Scutellaria incana				+	+	+
P107	Stachys officinalis			+			
P108	Staphylea trifolia						+
P109	Stellaria pubera						+
P110	Symphyotrichum turbinellum					+	
P111	Taraxacum officinale	+	+	+			
P112	Teucrium canadense						+
P113	Urtica dioica	+	+				
P114	Verbena urticifolia	+		+	+		
P115	Verbesina alternifolia		+		+	+	+
P116	Viola palmata				+		+
P117	Viola sororia	+	+	+	+	+	+
P118	Viola striata		+	+	+		+
P119	Viola triloba	+	+	+			
P120	Zizea aurea			+			+
A1	Ambrosia artemisiifolia			+			+
A2	Brassica rapa			+			
A3	Chamaecrista fasciculata	+	+	+			+
A4	Commelina communis	+					
A5	Conyza canadensis			+	+		+
A6	Datura stramonium		+			+	
A7	Erigeron annuus	+	+			+	
A8	Erigeron philadelphicus		+	+	+		
A9	Impatiens capensis	+	+	+	+		+

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
A10	Ipomoea sp			+			+
A11	Lactuca biennis	+	+			+	+
A12	Lobelia inflata						+
A13	Pilea pumila		+				
A14	Portulaca oleracea	+					
B1	Barbarea vulgaris		+				
B2	Cirsium sp		+	+			
B3	Cirsium vulgare				+		
B4	Cynoglossum officinale	+	+	+			
B5	Cynoglossum virginianum	+	+		+	+	+
B6	Oenothera biennis			+			
B7	Sanicula acalypha	+			+		
B8	Sanicula canadensis	+	+	+	+	+	+
F1	Dryopteris sp				+	+	+
F2	Polystichum acrostichoides	+	+	+	+	+	+
F3	Botrychium dissectum					+	+
F4	Botrychium virginianum	+	+	+	+	+	+
F5	Cystopteris protrusa	+					+
F6	Onoclea sensibilis	+	+		+		+
F7	Polypodium virginianum		+	+	+	+	+
G1	Brachyelytrum erectum	+	+		+		+
G2	Chasmanthium latifolium					+	+
G3	Cinna sp						+
G4	Danthonia spicata	+	+	+			
G5	Diarrhena americana	+	+	+	+	+	+
G6	Dichanthelium clandestinum		+				+
G7	Elymus hystrix			+	+	+	+
G8	Elymus virginicus			+			+
G9	Eragrostis sp				+		
G10	Erianthus alopecuroides		+	+			
G11	Festuca subverticillata						+
G12	Juncus sp						+
G13	Luzula multiflora	+					
G14	Luzula sp #1						+
G15	Luzula sp #2						+
G16	Panicum boscii	+	+	+	+	+	+

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
G17	Panicum commutatum	+	+	+	+	+	+
G18	Panicum dichotomum	+	+	+			+
G19	Panicum lanuginosum var implicatum				+	+	+
G20	Panicum polyanthes			+			+
G21	Panicum sp			+	+		
G22	Panicum sp #1	+	+	+	+	+	+
G23	Panicum sp #10		+	+	+	+	
G24	Panicum sp #11						+
G25	Panicum sp #12	+					
G26	Panicum sp #2		+	+			+
G27	Panicum sp #4	+					
G28	Panicum sp #5			+			
G29	Panicum sp #6			+			+
G30	Panicum sp #7	+					
G31	Panicum sp #8		+	+	+		+
G32	Panicum sp #9	+					
G33	Panicum villosissimum		+	+			
G34	Solidago flexicaulis					+	+
G35	Solidago sp		+			+	+
G36	Scirpus atrovirens						+
S1	Carex blanda	+					
S2	Carex digitellus	+					
S3	Carex grayi						+
S4	Carex hirsutella	+	+	+	+		+
S5	Carex scleria	+					
S6	Carex sp		+	+	+		
S7	Carex sp #1	+		+		+	+
S8	Carex sp #2		+	+	+		+
S9	Carex sp #3	+					
S10	Carex sp #4	+	+				+
S11	Carex sp #5	+					
S12	Carex sp #6	+	+	+	+		+
S13	Cyperus psuedovegetus				+		+
IH1	Alliaria officinalis				+		+
IH2	Microstegium vimineum	+	+	+	+	+	+
IH3	Polygonum cuspidatum	+	+		+		+
NV1	Toxicodendron radicans	+	+	+	+	+	+

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
NV2	Parthenocissus quinquefolia	+	+	+	+	+	+
NV3	Clematis virginiana	+	+	+	+	+	+
NV4	Vitis aestevalis	+	+	+	+		+
NV5	Vitis labrusca	+	+		+	+	+
NV6	Dioscorea quaternata	+	+	+	+	+	+
IV1	Campsis radicans	+	+	+	+	+	+
IV2	Celastrus orbiculatus		+	+	+	+	
IV3	Lonicera japonica	+	+	+	+	+	+
IV4	Glechoma hederacea		+		+	+	+
IS	Bambusa sp				+		
IS2	Berberis thunbergii				+		+
IS3	Elaeagnus umbellata	+	+	+	+		+
IS4	Lonicera mackii	+			+		+
IS5	Rosa multiflora	+	+	+	+	+	+
IS6	Euonymus americanus						+
NS1	Cephalanthus occidentalis						+
NS2	Hammamelis virginiana						+
NS3	Hypericum prolificum		+				
NS4	Hypericum punctatum	+					+
NS5	Hypericum purpureum		+				
NS6	Juniperus communis var. depressa			+			
NS7	Ligustrum obstusifolium	+		+			+
NS8	Ligustrum vulgare			+			
NS9	Potentilla simplex	+	+	+	+		+
NS10	Rosa carolina	+	+	+			+
NS11	Rosa setigera						+
NS12	Rubus allegheniensis	+		+		+	
NS13	Rubus hispidus		+		+	+	
NS14	Rubus occidentalis	+	+	+	+	+	+
NS15	Rubus sp #1	+	+	+	+	+	+
NS16	Rubus sp #2	+	+			+	+
NS17	Rubus strigosus		+				+
NS18	Sambucus canadensis	+	+		+		+
NS19	Smilax bona-nox	+			+		
NS20	Smilax glauca	+	+	+	+	+	+
NS21	Smilax rotundifolia	+	+	+	+	+	+
NS22	Smilax tamnoides	+	+		+		+

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
NS23	Vaccinium pallidum	+			+		+
NS24	Vibernum acerifolium	+	+		+		+
NS25	Vibernum dentatum	+	+			+	+
NS26	Vibernum prunifolium	+		+			
NS27	Vibernum rufidulum	+			+		
NS28	Symphoricarpos orbiculatus	+	+		+	+	+
T1	Acer negundo	+	+	+	+	+	+
T2	Acer rubrum	+	+	+	+	+	+
T3	Acer saccharum	+	+	+	+	+	+
T4	Aesculus glabra			+		+	+
T5	Amelanchier arborea	+			+		+
T6	Aralia spinosa		+				+
T7	Asimina triloba	+		+	+		+
T8	Celtis occidentalis	+	+	+	+	+	+
T9	Cercis canadensis	+	+	+	+	+	+
T10	Cornus florida	+	+	+	+	+	+
T11	Cornus racemosa						+
T12	Cornus stolonifera				+		+
T13	Carpinus caroliniana	+	+		+		+
T14	Carya cordiformis	+	+	+	+	+	+
T15	Carya glabra	+	+		+		+
T16	Carya ovata	+	+	+	+	+	+
T17	Carya tomentosa	+	+	+	+	+	+
T18	Corylus americana	+				+	+
T19	Cretaegous sp			+	+		
T20	Fagus grandifolia	+	+	+	+	+	+
T21	Fraxinus americana	+	+	+	+		
T22	Fraxinus pennsylvanica	+	+	+	+	+	+
T23	Juglans cinerea	+	+	+			
T24	Juniperus virginiana	+	+	+	+		+
T25	Lindera benzoin	+	+	+	+	+	+
T26	Liquidambar styraciflua	+	+	+			+
T27	Liriodendron tulipifera	+	+	+	+	+	+
T28	Morus rubra	+	+				
T29	Nyssa sylvatica	+	+	+	+		+
T30	Pinus echinata	+	+				
T31	Pinus strobus	+	+				
T32	Pinus virginiana	+					

Spp. Code	Species	Ridge SLP	Ridge WP	Ridge HW	Bottom SLP	Bottom WP	Bottom HW
T33	Platanus occidentalis		+		+		+
T34	Prunus serotina	+	+	+	+	+	+
T35	Prunus virginiana		+				
T36	Rhus copallinum		+	+			
T37	Robinia psuedoaccacia		+				
T38	Salix nigra						+
T39	Sassafras albidum	+	+	+	+	+	+
T40	Ulmus alata	+	+		+		+
T41	Ulmus americana	+	+	+	+		+
T42	Ulmus rubra	+	+	+	+	+	+
T43	Diospyros virginiana	+	+	+		+	
T44	Ostrya virginiana	+	+		+		+
O1	Quercus alba	+	+	+	+	+	+
O2	Quercus coccinea	+					
O3	Quercus imbricaria	+	+		+	+	+
O4	Quercus marilandica	+					
O5	Quercus montana	+		+	+		+
O6	Quercus muehlenbergii	+	+		+	+	+
O7	Quercus prinus	+	+		+		
O8	Quercus rubra	+	+	+	+	+	+
O9	Quercus stellata	+			+		
O10	Quercus velutina	+	+	+	+	+	+

Appendix C Density and Percent Cover of Common Species

Density (mean stems per ha ± 1 S.E.) of common overstory species by stand type and ELTP. SLP = *P. echinata*, WP = *P. strobus*, HW = hardwood.

Species	Ridge			Bottom		
	SLP	WP	HW	SLP	WP	HW
Pinus echinata	34.1 ± 9.2	0.1 ± 0.3	0.8 ± 2.4	32.6 ± 7.3	0.0 ± 0.0	0.4 ± 1.2
Pinus strobus	0.7 ± 3.4	36.7 ± 10.6	1.6 ± 3.4	0.3 ± 0.7	41.0 ± 15.9	1.0 ± 3.2
Liriodendron tulipifera	2.9 ± 4.5	2.9 ± 3.8	17.3 ± 9.8	2.7 ± 3.6	0.9 ± 1.1	7.3 ± 7.8
Acer rubrum	2.5 ± 2.4	0.7 ± 1.5	0.1 ± 0.1	0.9 ± 1.2	1.0 ± 1.1	1.7 ± 2.5
Acer saccharum	1.4 ± 2.3	0.0 ± 0.1	1.4 ± 1.5	2.2 ± 2.4	0.0 ± 0.1	2.1 ± 4.3
Prunus serotina	0.2 ± 0.5	1.1 ± 2.3	1.8 ± 2.6	0.5 ± 0.7	2.4 ± 2.7	1.2 ± 1.8
Platanus occidentalis	0.0 ± 0.2	0.0 ± 0.0	2.4 ± 5.8	0.6 ± 1.7	1.4 ± 2.3	3.5 ± 4.0
Juniperus virginiana	0.3 ± 0.7	0.4 ± 1.0	0.3 ± 0.5	1.8 ± 2.8	0.4 ± 0.9	1.2 ± 2.5
Fraxinus americana	0.4 ± 1.0	0.6 ± 1.1	0.1 ± 0.2	0.3 ± 0.5	0.1 ± 0.2	0.5 ± 1.0
Ulmus americana	0.2 ± 0.6	0.0 ± 0.1	1.1 ± 2.3	0.8 ± 1.6	0.0 ± 0.0	0.3 ± 0.5
Sassafras albidum	0.3 ± 0.5	0.4 ± 1.5	0.1 ± 0.2	0.1 ± 0.1	0.0 ± 0.0	0.4 ± 1.0
Fraxinus pennsylvanica	0.0 ± 0.0	0.0 ± 0.0	1.3 ± 2.8	0.0 ± 0.0	0.7 ± 1.3	0.5 ± 1.2
Nyssa sylvatica	0.1 ± 0.4	0.2 ± 0.7	0.7 ± 2.1	0.0 ± 0.1	0.0 ± 0.0	0.1 ± 0.1
Diospyros virginiana	0.2 ± 0.5	0.2 ± 0.5	0.0 ± 0.1	0.4 ± 0.4	0.2 ± 0.4	0.1 ± 0.2
Liquidambar styraciflua	0.3 ± 1	0.2 ± 0.9	0.0 ± 0.0	0.6 ± 1.3	0.0 ± 0.0	0.0 ± 0.0
Quercus alba	0.0 ± 0.0	0.1 ± 0.7	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Species	Ridge			Bottom		
	SLP	WP	HW	SLP	WP	HW
Juglans nigra	0.0 ± 0.2	0.0 ± 0.0	0.6 ± 1.1	0.0 ± 0.0	0.0 ± 0.0	0.6 ± 1.2
Cornus florida	0.1 ± 0.2	0.0 ± 0.0	0.4 ± 0.4	0.1 ± 0.1	0.0 ± 0.0	0.2 ± 0.5
Ulmus rubra	0.0 ± 0.2	0.1 ± 0.3	0.5 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.1
Fagus grandifolia	0.1 ± 0.3	0.0 ± 0.0	0.0 ± 0.1	0.2 ± 0.2	0.0 ± 0.1	0.0 ± 0.0
Acer negundo	0.0 ± 0.0	0.0 ± 0.1	0.5 ± 1.3	0.0 ± 0.0	0.4 ± 0.5	0.1 ± 0.2
Quercus velutina	0.0 ± 0.1	0.2 ± 0.8	0.0 ± 0.1	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0

Density (mean stems per ha ± 1 S.E.) of common sapling species by stand type and ELTP. SLP = *P. echinata*, WP = *P. strobus*, HW = hardwood.

Species	Ridge			Bottom		
	SLP	WP	HW	SLP	WP	HW
Fraxinus americana	293 ± 608	872 ± 1376	211 ± 476	263 ± 590	33 ± 82	273 ± 452
Fraxinus pennsylvanica	391 ± 1506	504 ± 1242	33 ± 100	138 ± 256	333 ± 631	145 ± 221
Fagus grandifolia	518 ± 620	72 ± 137	56 ± 133	288 ± 503	50 ± 84	55 ± 151
Lindera benzoin	266 ± 792	184 ± 434	500 ± 545	63 ± 74	583 ± 1141	236 ± 559
Acer saccharum	114 ± 202	48 ± 82	633 ± 1486	375 ± 570	183 ± 325	382 ± 634
Acer rubrum	120 ± 315	212 ± 514	78 ± 199	88 ± 173	50 ± 84	100 ± 332
Sassafras albidum	91 ± 226	112 ± 224	133 ± 364	0 ± 0	67 ± 163	9 ± 30
Quercus velutina	139 ± 178	52 ± 142	67 ± 100	25 ± 71	0 ± 0	9 ± 30
Acer negundo	0 ± 0	20 ± 41	44 ± 133	0 ± 0	533 ± 862	91 ± 192
Prunus serotina	9 ± 36	96 ± 246	111 ± 203	0 ± 0	33 ± 82	9 ± 30
Quercus alba	66 ± 112	16 ± 62	67 ± 166	13 ± 35	0 ± 0	9 ± 30
Liriodendron tulipifera	18 ± 79	76 ± 161	44 ± 73	0 ± 0	0 ± 0	73 ± 179
Cornus florida	9 ± 36	32 ± 75	111 ± 209	0 ± 0	100 ± 245	64 ± 150
Elaeagnus umbellata	5 ± 30	88 ± 219	11 ± 33	25 ± 71	17 ± 41	64 ± 180
Cercis canadensis	9 ± 47	16 ± 80	256 ± 522	0 ± 0	0 ± 0	9 ± 30

Species		Ridge			Bottom	
	SLP	WP	HW	SLP	WP	HW
Rosa Multiflora	9 ± 60	32 ± 160	144 ± 288	0 ± 0	0 ± 0	64 ± 211
Ostrya virginiana	36 ± 81	4 ± 20	89 ± 203	50 ± 107	0 ± 0	0 ± 0
Carpinus caroliniana	16 ± 78	0 ± 0	11 ± 33	38 ± 74	50 ± 122	127 ± 390
Nyssa sylvatica	20 ± 55	28 ± 121	100 ± 229	0 ± 0	0 ± 0	18 ± 60
Ulmus alata	16 ± 91	20 ± 82	67 ± 200	50 ± 141	0 ± 0	0 ± 0

Percent cover (mean ± S.E.) of common herbaceous-layer species by functional group in three stand types.

Species/ groups		Ridge			Bottom	
	SLP	WP	HW	SLP	WP	HW
ANNUALS/ BIENNIALS						
Sanicula canadensis	0.11 ± 0.00	0.65 ± 0.01	0.48 ± 0.01	0.36 ± 0.01	0.15 ± 0.00	4.53 ± 0.06
Impatiens capensis	0.01 ± 0.00	0.08 ± 0.00	0.13 ± 0.00	0.02 ± 0.00	0.00 ± 0.00	0.80 ± 0.01
Cynoglossum virginianum	0.01 ± 0.00	0.06 ± 0.00	0.00 ± 0.00	0.01 ± 0.00	0.08 ± 0.00	0.71 ± 0.02
PERENNIALS						
Packera aurea	0.01 ± 0.00	0.09 ± 0.00	0.44 ± 0.01	0.01 ± 0.00	1.17 ± 0.02	16.60 ± 0.21
Lycopodium dendroideum	4.50 ± 0.17	0.00 ± 0.00	0.11 ± 0.00	2.11 ± 0.06	0.00 ± 0.00	0.40 ± 0.02
Moss spp.	0.41 ± 0.00	1.59 ± 0.04	2.88 ± 0.04	0.78 ± 0.01	0.97 ± 0.01	1.51 ± 0.02
Ageratina altissima	0.06 ± 0.00	2.11 ± 0.04	1.54 ± 0.03	0.28 ± 0.00	1.51 ± 0.02	1.80 ± 0.01
Asarum canadense	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.03 ± 0.00	0.02 ± 0.00	3.91 ± 0.07
FERNS						
Polystichum acrostichoides	2.01 ± 0.0374	3.06 ± 0.11	4.38 ± 0.06	4.06 ± 0.05	1.98 ± 0.02	3.57 ± 0.04
Onoclea sensibilis	0.00 ± 0.00	0.01 ± 0.00	0.00 ± 0.00	0.03 ± 0.00	0.00 ± 0.00	2.58 ± 0.09

Species/ groups		Ridge			Bottom	
	SLP	WP	HW	SLP	WP	HW
GRAMINOIDS						
Panicum boscii	0.08 ± 0.00	0.27 ± 0.01	1.11 ± 0.02	0.72 ± 0.02	0.01 ± 0.00	5.54 ± 0.14
Panicum commutatum	0.72 ± 0.03	0.11 ± 0.00	0.36 ± 0.01	0.30 ± 0.01	1.44 ± 0.03	2.05 ± 0.05
Diarrhena americana	0.00 ± 0.00	0.05 ± 0.00	1.63 ± 0.04	0.01 ± 0.00	0.21 ± 0.00	3.91 ± 0.08
INVASIVES						
Rosa multiflora	1.08 ± 0.03	0.46 ± 0.01	11.94 ± 0.10	2.09 ± 0.05	16.08 ± 0.26	14.35 ± 0.21
Lonicera japonica	2.21 ± 0.03	2.92 ± 0.07	9.04 ± 0.09	10.05 ± 0.10	10.56 ± 0.16	3.74 ± 0.05
Microstegium vimineum	0.47 ± 0.03	2.79 ± 0.08	2.39 ± 0.04	0.29 ± 0.01	7.03 ± 0.11	4.80 ± 0.09
Polygonum cuspidatum	0.67 ± 0.04	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.10 ± 0.00
SHRUBS						
Lindera benzoin	1.48 ± 0.05	3.11 ± 0.08	11.25 ± 0.21	3.38 ± 0.06	14.5 ± 0.22	4.25 ± 0.06
Smilax rotundifolia	1.24 ± 0.02	0.11 ± 0.00	1.30 ± 0.02	0.32 ± 0.01	0.08 ± 0.00	0.37 ± 0.01
Rubus sp.	0.29 ± 0.01	0.81 ± 0.02	1.94 ± 0.05	0.74 ± 0.02	1.04 ± 0.02	2.20 ± 0.04
Smilax glauca	0.61 ± 0.01	0.24 ± 0.01	2.26 ± 0.05	0.38 ± 0.00	0.15 ± 0.00	0.23 ± 0.01
Symphoricarpos orbiculatus	0.22 ± 0.01	1.71 ± 0.04	0.00 ± 0.00	0.26 ± 0.01	0.05 ± 0.00	1.20 ± 0.02
Potentilla simplex	0.07 ± 0.00	0.68 ± 0.01	0.01 ± 0.00	0.06 ± 0.00	0.00 ± 0.00	0.60 ± 0.01

Species/ groups		Ridge			Bottom	
	SLP	WP	HW	SLP	WP	HW
VINES						
Toxicodendron radicans	17.21 ± 0.15	13.37 ± 0.17	37.77 ± 0.34	6.86 ± 0.12	8.25 ± 0.09	1.73 ± 0.02
Parthenocissus quinquefolia	1.89 ± 0.03	5.49 ± 0.06	11.09 ± 0.13	1.57 ± 0.01	4.67 ± 0.08	0.92 ± 0.01
Clematis virginiana	0.02 ± 0.00	0.21 ± 0.01	1.64 ± 0.04	0.02 ± 0.00	0.09 ± 0.00	1.36 ± 0.02
TREES						
Fraxinus americana	3.44 ± 0.07	5.34 ± 0.07	4.32 ± 0.04	1.99 ± 0.03	0.00 ± 0.00	0.00 ± 0.00
Fraxinus pennsylvanica	1.08 ± 0.03	5.84 ± 0.17	0.66 ± 0.02	0.72 ± 0.01	8.27 ± 0.13	1.10 ± 0.03
Acer rubrum	0.67 ± 0.01	1.83 ± 0.03	1.32 ± 0.02	0.10 ± 0.00	0.31 ± 0.00	1.38 ± 0.04
Acer saccharum	0.65 ± 0.02	0.13 ± 0.00	3.13 ± 0.05	0.56 ± 0.01	0.27 ± 0.00	1.13 ± 0.02
Fagus grandifolia	1.80 ± 0.03	0.13 ± 0.00	0.20 ± 0.01	1.16 ± 0.02	1.44 ± 0.01	0.23 ± 0.01
Sassafras albidum	0.71 ± 0.01	0.76 ± 0.01	1.00 ± 0.02	0.02 ± 0.00	0.05 ± 0.001	0.04 ± 0.00
Quercus velutina	0.91 ± 1.14	0.36 ± 0.49	0.66 ± 1.30	0.09 ± 0.12	0.06 ± 0.10	0.10 ± 0.28
Prunus serotina	0.22 ± 0.00	0.71 ± 0.01	1.71 ± 0.01	0.21 ± 0.00	1.54 ± 0.03	0.11 ± 0.00
Cornus florida	0.16 ± 0.00	0.38 ± 0.01	0.16 ± 0.00	0.06 ± 0.00	4.22 ± 0.07	0.25 ± 0.01
Carya cordiformis	0.49 ± 0.01	0.32 ± 0.01	0.20 ± 0.00	0.37 ± 0.00	0.30 ± 0.00	0.72 ± 0.02
Ulmus rubra	0.14 ± 0.00	0.27 ± 0.01	3.30 ± 0.06	0.10 ± 0.00	0.35 ± 0.01	0.30 ± 0.01
Cercis canadensis	0.31 ± 0.01	0.10 ± 0.00	2.07 ± 0.04	0.01 ± 0.00	0.79 ± 0.02	0.27 ± 0.01

Species/ groups		Ridge			Bottom	
	SLP	WP	HW	SLP	WP	HW
Nyssa sylvatica	0.19 ± 0.00	0.13 ± 0.00	2.47 ± 0.06	0.08 ± 0.00	0.00 ± 0.00	0.14 ± 0.00
Celtis occidentalis	0.05 ± 0.00	0.31 ± 0.01	1.84 ± 0.03	0.08 ± 0.00	0.01 ± 0.00	0.06 ± 0.00
Acer negundo	0.00 ± 0.00	0.22 ± 0.01	0.01 ± 0.00	0.04 ± 0.00	2.94 ± 0.03	1.66 ± 0.04

Appendix D Selected Site Pictures

Figure 1: *Pinus echinata* ridge site.

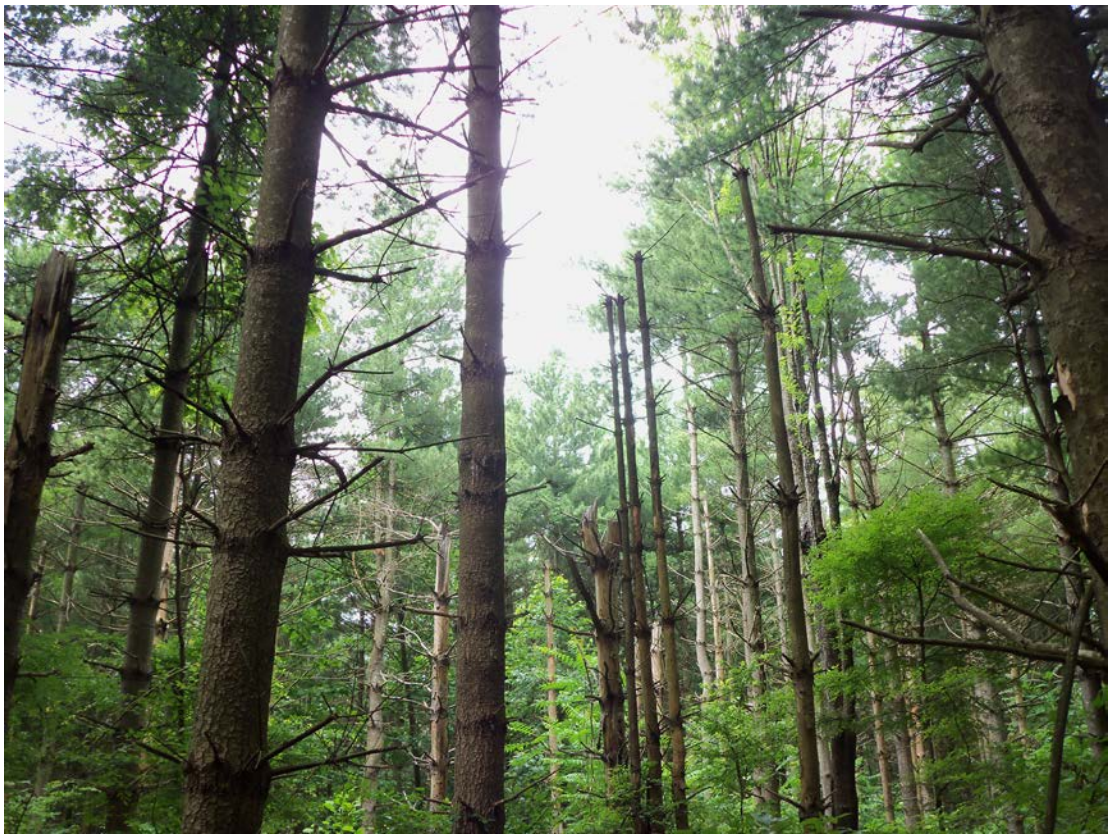

Figure 2: Adjacent to *Pinus strobus* ridge site illustrating a large degree of adjacent dieoff.

Figure 3: Hardwood ridge site dominated by *Liriodendron tulipifera*.

Figure 4: *Pinus echinata* bottom site.

Figure 5: *Pinus strobus* bottom site.

Figure 6: Hardwood bottom site.