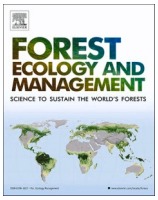
Forest Ecology and Management 572 (2024) 122310

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Response of understory vegetation to long-term occupancy by introduced *Pinus* species in temperate deciduous hardwood forests

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ARTICLE INFO

Keywords:
Edaphic gradients
Litter
Pine plantations
Regeneration
Soil chemistry
Species composition

ABSTRACT

In many temperate regions of the world, conifer species have been planted to stabilize soils and promote site recovery on former hardwood sites that were cleared for agriculture. In many areas of eastern North America, these conifer plantings consisted of introduced (non-native) *Pinus* species planted on abandoned agricultural land once dominated by mesophytic hardwood species. These plantings constitute a shift in overstory composition away from native hardwood species with nutrient-rich litter that decomposes more quickly towards *Pinus* species with recalcitrant litter that may alter soil chemistry and nutrient availability. To examine how edaphic conditions associated with long-term introduced *Pinus* species occupancy are related to forest regeneration and herbaceous-layer diversity and composition, we sampled a total of 97 plots in planted *Pinus echinata* and *Pinus strobus* stands and naturally regenerated hardwood stands growing on two ecological landtype phases (ELTPs) of southern Indiana, USA forests, *Fagus-Acer saccharum/Arisaema* Mesic Ridges, and *Acer saccharinum/Boehmeria* Bottomlands. We collected vegetation data and analyzed soil samples to examine herbaceous-layer species distribution across gradients using non-metric multidimensional scaling (NMS) ordination. Two-way ANOVA was used to examine differences in individual species and species functional groups across stand types (*P. echinata*, *P. strobus*, and native hardwoods) and ELTPs. Our results show that differences in soil chemistry resulting from *Pinus* spp. occupancy were associated with differences in 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 exchange capacity, cation content, and soil aluminum concentration. Hardwood sites had significantly greater herbaceous-layer cover (139.6 ± 8.0 %) than *P. echinata* (48.5 ± 6.2 %) or *P. strobus* sites (81.7 ± 7.7 %), as well as greater herbaceous-layer species richness and diversity (mean species richness was 46.9 ± 2.1 on hardwood stands vs. 33.3 ± 1.6 and 36.4 ± 2.0 on *P. echinata* and *P. strobus* stands, respectively). *Pinus echinata* stands contained a greater density of woody regeneration, including *Quercus* spp. (201 ± 48 saplings ha^{-1}) and *Fagus grandifolia* stems (415 ± 82 saplings ha^{-1}), both of which occurred in greater density than *Acer saccharum* (163 ± 93 saplings ha^{-1}) and *A. rubrum* (70 ± 64 saplings ha^{-1}). Our results suggest that pine occupancy has created divergent successional trajectories in comparison to hardwood stands. These differing trajectories may offer both challenges and opportunities for restoration efforts. For example, the greater abundance of *Quercus* reproduction under *P. echinata* on ridges, combined with less productive soils, may allow *Quercus* stems to be promoted into the canopy with less competition from mesophytic competitors.

1. Introduction

Worldwide, planted forests cover 294 million hectares (FAO, 2022). *Pinus* is the predominant genus in planted forests, globally comprising approximately 35 % of total plantation area (West, 2014). Many of these planted forests consist of large plantations grown to produce wood for

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https://doi.org/10.1016/j.foreco.2024.122310
Received 16 July 2024; Received in revised form 17 September 2024; Accepted 19 September 2024
Available online 28 September 2024

industrial use, principally the production of building materials or pulp for paper, and comprise major commercial enterprises (West, 2014). For example, by the end of the 20th century, production pine plantations occupied nearly 13 million hectares in the southern United States (Fox et al., 2007), with a rate of conversion of hardwood forests to pine plantations of 0.45 % annually (Wear and Greis, 2002). However, while *Pinus* species are frequently planted for economic production, the genus has also been planted throughout the world in afforestation efforts on lands degraded by historic land use. For example, the genus has been planted to aid recovery of land degraded by intensive agriculture in eastern China (Zhao et al., 2021), northwestern Spain (Rigueiro-Rodríguez et al., 2012), and southcentral Chile (Toro and Gessel, 1999).

In the eastern United States during the early to mid-20th century, federal and state agencies planted extensive tracts of *Pinus* species on newly acquired public lands in an effort to curb erosion and regrow forests 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 into more recent decades with planting by the USDA Forest Service and state conservation agencies. *Pinus echinata* (shortleaf pine), *Pinus strobus* (white pine), and *Pinus resinosa* (red pine) were planted across large portions of the Central Hardwood Region (Sieber and Munson, 1992), and were generally introduced outside their native ranges. In Indiana, Ohio, and Illinois, around 58,107 ha of these non-native *Pinus* plantations persist today (USDA Forest Service, 2013).

Dominance by *Pinus* spp. is associated with low nutrient content in soils. Due to its slow rate of decomposition, *Pinus* litter accumulates on the forest floor, resulting in diminished nutrient release into the mineral soil and slower organic matter cycling (Binkley and Valentine, 1991; Prescott and Vesterdal, 2021). A review of 700 studies comparing conifers and hardwoods by Barbier et al. (2008) found that conifer and hardwood stands differ in understory composition through complex interactions of the light environment, moisture availability, nutrients dynamics, and litter inputs. Conifer dominance in forests may lower soil pH, buffering capacity, exchangeable bases, base saturation, and nutrient availability through inputs of litter (Berg and McClaugherty, 2008). These soil characteristics, combined with the allelopathic nature of coniferous litter, are frequently associated with lower plant species diversity in *Pinus* stands (Barbier et al., 2008; Berg and McClaugherty, 2008).

Herbaceous-layer communities are directly affected by litter characteristics, which differ between *Pinus* and hardwood forests (Barbier et al., 2008; Yu and Sun, 2013). The accumulation of *Pinus* litter alters moisture and temperature conditions and may act as a physical barrier to germination and establishment (Barbier et al., 2008; Facelli and Pickett, 1991a; Loydi et al., 2013). Facelli and Pickett (1991a), (1991b) found that annual and perennial herbs are often more affected by litter depth than graminoids. Additionally, a 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.

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 matter 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, which may be limited due to large seed size and limited availability of dispersers, and the ability of these species to tolerate degraded soil conditions (Flinn and Marks, 2007). Once established, populations of these mature forest species expand slowly, often through clonal growth (Holmes and Matlack, 2018). 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, including *Pinus* species to abandoned agricultural sites alters the composition and diversity of recovering forests that would otherwise develop on these old fields.

Because of the wide distribution of pine plantations occupying former agricultural fields on public lands in the eastern US, managers have considered strategies to convert these stands back to native hardwoods. The success of conversion will depend, in part, on the lasting impact *Pinus* species have had on soil and vegetation communities. In addition, though the long-term occupancy of *Pinus* monocultures has been studied with regard to soil quality (Auten, 1945; Billings, 1938; Sauer et al., 2007), and artificial regeneration (Lesko and Jacobs, 2018; Lesko et al., 2024), long-term effects on the herbaceous layer are not as well understood (Barbier et al., 2008). To better understand these long-term impacts, we examined the influence of four decades of *Pinus* spp. dominance on herbaceous and woody species distribution across underlying gradients of stand conditions and soil chemistry. Specifically, we compared the plant species composition of *P. echinata* and *P. strobus* plantations to that of hardwood stands that naturally regenerated after land abandonment on two land types: mesic ridges and bottoms. In this study, we addressed the following questions:

1. How has *Pinus* species occupancy influenced the composition and diversity of herbaceous-layer species on bottoms and ridges? We hypothesize that composition in *Pinus* stands will distinctly differ from hardwood stands due to the long-term influence of *Pinus* occupancy. We further hypothesize that composition differences will be more pronounced in *Pinus* stands on ridges than in bottoms because of the lower soil buffering capacity of less productive ridge soils (Van Kley et al., 1994; Zhalnin and Parker, 2009).
2. How has *Pinus* species occupancy influenced the woody regeneration-layer on bottoms and ridges? We hypothesize that *Pinus* stands on ridges will have greater abundance of woody regeneration, and woody species composition in the regeneration layer that has shifted away from mesic species, such as *A. saccharum*, towards species more tolerant of nutrient-poor conditions, such as those in the family Fagaceae. The long-term occupancy of pine on more xeric ridges will result in soil conditions (lower pH, reduced cation availability, etc.) that favor the reproduction of Fagaceae.

2. Methods

2.1. Study sites

Sample sites were chosen within the Tell City Unit of the Hoosier National Forest, southern Indiana, USA within the Crawford Upland Subsection as defined by Homoya et al. (1984). In ArcMAP v10.1, we selected study sites based upon Ecological Landtype Phase (ELTP), which is a land classification unit delineated by several variables including dominant vegetation, indicator species, soil type, elevation, slope, and slope aspect (Van Kley et al., 1994). Because ELTP 40 (*Fagus-Acer saccharum/Arisaema* Mesic Ridges), and ELTP 62 (*Acer saccharum/Boehmeria* Bottomlands) were the most common ELTPs in our study region, and because *Pinus* plantations were largely planted in bottoms and on ridges, we confined our sampling to these two ELTPs. To limit variability of soil across potential plots, we used the USDA NRCS Soil Survey Geographic Database (SSURGO) to confirm that sites had similar soils. Soils on ELTP 40 were mostly silt loam over sandstone parent with an argillic horizon of silt loam or silty clay between 20 cm and 68 cm (Van Kley et al., 1994), with an average A horizon depth of 4.7 ± 0.8 cm and average pH of 5.5 ± 1.1. ELTP 62 consists of silt loam alluvium over 2 m thick with a poorly differentiated A horizon thickness of 10 cm and average pH of 6.8 ± 0.2 (Van Kley et al., 1994). The two most common soil series mapped within sites on mesic ridges and bottoms were Apalona (fine-silty, mixed, active, mesic Oxyaquic Fragiudalfs) and Wellston (fine-silty, mixed, active, mesic Ultic Hapludalfs; USDA NRCS, 2013).

Across both ELTPs, we selected three vegetation types for sampling: *P. echinata*-dominated plantations, *P. strobus*-dominated plantations, and naturally regenerated hardwood forests. These pine species are non-native to this region, but were widely planted during the early to mid-20th century and many mature stands persist today. Digitized aerial photographs from the 1940s were overlain in ArcMAP to ensure that chosen sites were previously utilized for agriculture. To reduce edge effects, we 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 coordinates of plot centers were randomly selected in ArcMAP. Lastly, sites that experienced secondary disturbances such as logging, windstorms, or fire were rejected. In total, we sampled 43 ridge *P. echinata* stands, 25 ridge *P. strobus* stands, seven ridge hardwood stands, nine bottom *P. echinata* stands, seven bottom *P. strobus* stands, and 13 bottom hardwood stands. According to Forest Service records, these sample sites comprised all suitable sample sites of our three stand types within the study area.

We determined the age of each stand sampled to ensure that *Pinus* and hardwood sites were of a comparable age by collecting cores from 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). Average stand age was between 25 and 40 years, because most of the plantations in the Hoosier National Forest were created after the 1940s.

2.2. Field sampling

Vegetation was sampled from May 13 to August 15, 2013, using a nested plot design (Jenkins and Parker, 1998; 1999; Van Kley and Parker, 1993). From a common center, we established a nested 0.01 ha circular plot (r = 5.6 m) within a larger 0.05 ha circular plot (r = 12.6 m). Within the 0.01 ha plot, we tallied all woody saplings (> 1 m height, < 3 cm DBH) by species and measured DBH and recorded the species of all stems 3–9.9 cm DBH. Within the 0.05 ha plot, we recorded the DBH and species of all living and dead stems ≥ 10 cm DBH. Four 4 m^2 quadrats (2 m x 2 m) were placed 5.6 m from plot center in cardinal directions. Within each quadrat, we 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. Because of overlapping among plants, summed totals for all species could exceed 100 % cover in a quadrat. Herbaceous-layer species that occurred within the 0.05 ha 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. Species nomenclature follows the USDA PLANTS Database (USDA NRCS, 2023). On each plot, we collected five soil cores to a depth of 10 cm and combined cores into a single sample. A minimum of 400 g per sample was collected per site. 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 5 and July 30 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.

2.3. Sample processing

A subsample of each soil sample was placed into a vial with BBs and shaken with a paint shaker for approximately four hours until homogenized. Total soil C and N (%; Nelson and Sommers, 1982) were determined from these samples using an ECS 4010 CHNSO Analyzer (Costech Analytical Technologies, Inc.) at the Forest Ecology, Silviculture, and Soils Laboratory at Purdue University. The remainder of each soil sample was sent to Brookside Laboratories, Inc. (New Bremen, OH) and analyzed for pH (1:1 in water; McLean, 1982), organic matter (%; loss on ignition; Schulte and Hopkins, 1996), and cation exchange capacity (CEC; $cmol_c$ kg^{-1} 100 g^{-1}; Ross, 1995). In addition, 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}) concentration were determined with Mehlich III extraction (Mehlich, 1984). Resulting concentrations used then used to calculate percent base saturation of Ca, Mg, Na, and K.

Canopy photographs were organized in ImageJ software (Schneider et al., 2012) 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 (Walter, 2008) to yield canopy openness (percent of photo not occupied by tree canopy).

2.4. Data preparation and analysis

We calculated total basal area of dead trees and basal area of living trees (stems ≥3 cm DBH) by species (m^2 ha^{-1}). We also calculated overstory density and sapling (stems ≥ 1 m height; <3 cm DBH) density as stems ha^{-1} by species. Seedling (woody stems < 1 m) density was calculated as stems per 100 m^2 by species. For each plot, percent cover was averaged over four the quadrats by species. For each species, we calculated relative cover (cover of a species/total cover of all species), relative seedling density and relative sapling density by plot (relative density = density of stems of a species/total density of all species). Using percent cover of herbaceous-layer species, we calculated richness (S) and Shannon diversity (H') using PC-ORD Version 5.1 (McCune et al., 2002).

To investigate compositional differences between ELTPs and across stand types, we 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. Prior to analysis, cover data were square root transformed (Field et al., 1982) and a zero-adjustment was performed (Clarke et al., 2006). We 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. The final number of axes was determined by evaluating stress and adding axes until the addition of the next axis resulted in little reduction in the overall stress of the ordination. Correlations of the main matrix with environmental variables (listed in Table 2) were calculated with Pearson's r and vectors of maximum absolute value were plotted on ordination axes for any correlation ≥0.4.

By summing percent cover and relative cover values, we combined individual herbaceous-layer species into the following functional groups: graminoids (grasses and sedges), native herbs (perennial herbs and ferns), non-native herbs, annuals and biennials, native shrubs, non-native shrubs, native vines, non-native vines, and trees (canopy and subcanopy species combined). For seedlings and saplings, we combined density and relative density data for woody species into the following functional groups: native shrubs, non-native shrubs, sub-canopy trees, and canopy trees. Additionally, *Acer saccharum*, *A. negundo*, *A. rubrum*, *Quercus* spp., *Fraxinus* spp., and *Fagus grandifolia* were analyzed as individual species or genera for both seedling and sapling layers. Lists of common species in each functional group are provided in Appendix A.

We 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 cover and density of species and functional groups. This included analyzing variables by stand type (hardwood, *P. echinata*, or *P. strobus*), ELTP (mesic ridges or bottoms), and examining their interaction terms. 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). We used logit and square root transformations on species functional groups as needed to improve normality and equalize variances. Dead basal area, being particularly problematic, was centered, absolute value transformed, and square root transformed to better fit assumptions of normality and constant variance. Non-transformed data are presented for ease of interpretation. When ANOVA revealed significant differences, we used the Tukey multiple comparisons test for post-hoc comparisons ($\alpha = 0.05$).

3. Results

3.1. Overstory structure and composition

Overstory basal area (BA) was greater in *P. echinata* and *P. strobus* stands than naturally regenerated hardwood sites, averaging 45.3 ± 1.6 and 46.6 ± 2.0 vs. 28.5 ± 2.0 m^2 ha^{-1} respectively (Table 1). Basal area did not differ by ELTP. Basal area of dead trees (DBA) was significantly greater in *P. strobus* sites than *P. echinata* or hardwood sites, with an average of 4.3 ± 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 stands. Understory light availability as measured by canopy openness did not vary with ELTP, but was significantly greater in *P. strobus* stands than hardwood or *P. echinata* stands.

Pinus echinata comprised 74 % and 77 % of standing live basal area in bottom and ridge *P. echinata* stands, respectively. Liriodendron *tulipifera* comprised 6 % of basal area in *P. echinata* bottom stands and 7 % in *P. echinata* ridge stands. *Acer saccharum* comprised 6 % of basal area in *P. echinata* bottom stands, while *A. rubrum* comprised 6 % of basal area in *P. echinata* ridge stands. *P. strobus* comprised 83 % of the standing live basal area in *P. strobus* stands on both bottoms and ridges. *A. rubrum* and *Prunus serotina* both comprised 5 % of the basal area of *P. strobus* stands in bottoms. *L. tulipifera* comprised 7 % of basal area in *P. strobus* stands on ridges, while *P. serotina* comprised 3 % of basal area. Dominant overstory species in hardwood bottom stands included *L. tulipifera* (28 % of basal area), *Platanus occidentalis* (15 % of basal area), *A. saccharum* (11 % of basal area) and *P. serotina* (9 % of basal area). Hardwood stands on ridges were heavily dominated by *L. tulipifera* (65 % of basal area).

3.2. Herbaceous-layer species ordination

The herbaceous-layer NMS ordination had a final stress of 17.15, instability of <0.0001, and a three-dimensional solution. Each axis accounted for 35.0 %, 28.0 %, and 15.6 % of variation, respectively, which comprised 78.6 % of the total variation. Axis 1 was strongly correlated with Al concentration (r = 0.506), Na saturation (r = 0.433), CEC (r = −0.426), and Ca concentration (r = −0.399), while Axis 2 was correlated with BA (r = 0.591), litter depth (r = 0.566), stand age (r = 0.461), Al concentration (r = 0.487), and Fe concentration (r = −0.454; Table 2). Axis 3 was correlated with basal area (-0.351), litter depth (-0.329), Zn concentration (r = 0.369) and Ca concentration (r = 0.331; Table 2). Plots were generally separated by stand type and ELTP. Both *P. echinata* and *P. strobus* stands were associated with greater overstory basal area (BA), litter depth, stand age, and percent saturation of Na and concentration of Al, while hardwood sites were associated with increased Ca, Zn, Fe concentrations and greater cation exchange capacity (CEC). Ridge sites were associated with greater BA, litter depth, and Al concentration, whereas bottoms were associated with greater soil nutrient concentration of Ca, Fe, and Zn (Fig. 1).

Functional groups displayed associations with stand type and ELTP and were distributed across both stand and edaphic gradients (Fig. 1). Annuals/biennials, graminoids (grasses/sedges), and non-native species were associated with hardwood and bottom sites and with greater values of Ca, Zn, and CEC and lower values of Al, basal area, and litter depth. Cover of tree seedlings, particularly *Quercus* spp., was associated with *Pinus* ridge plots, and with increasing basal area, litter depth, and Al concentration. Overall, more functional groups were associated with hardwood than with *Pinus* plots, and with bottoms than with ridge plots (Fig. 1).

Table 2
Pearson's correlation coefficients between herbaceous-layer NMS ordination axes scores and environmental variables.

Variable	Axis 1	Axis 2	Axis 3
Overstory basal area	0.266	0.591	−0.351
Overstory density	−0.007	0.389	−0.159
Stand age	0.244	0.461	−0.027
Sapling density	0.334	−0.078	0.151
Canopy openness (%)	0.045	−0.294	−0.148
Litter depth	0.317	0.566	−0.329
pH	−0.034	−0.135	0.240
Cation exchange capacity ($cmol_c$ kg^{-1})	−0.426	−0.285	0.242
Total C (%)	−0.115	−0.180	0.213
Total N (%)	−0.196	−0.358	0.238
OM (%)	−0.211	−0.137	0.082
Al (mg kg^{-1})	0.506	0.487	−0.290
B (mg kg^{-1})	−0.273	−0.235	0.240
Ca (mg kg^{-1})	−0.399	−0.384	0.331
Fe (mg kg^{-1})	−0.203	−0.454	0.155
K (mg kg^{-1})	−0.017	−0.044	0.197
Mg (mg kg^{-1})	−0.239	−0.138	0.253
Na (mg kg^{-1})	−0.014	−0.029	−0.110
P (mg kg^{-1})	−0.270	−0.310	0.132
S (mg kg^{-1})	0.389	0.200	−0.154
Zn (mg kg^{-1})	−0.318	−0.419	0.369
Ca saturation (%)	−0.111	−0.202	0.192
K saturation (%)	0.379	0.296	−0.053
Mg saturation (%)	0.150	0.099	0.129
Na saturation (%)	0.433	0.320	−0.259

3.3. Herbaceous-layer species diversity and cover

Hardwood stands had greater herbaceous-layer species richness and diversity than *Pinus* stands (Table 3). Mean species richness was 46.9 ± 2.1 on hardwood plots vs. 33.3 ± 1.6 and 36.4 ± 2.0 on *P. echinata* and *P. strobus* plots, respectively. Species diversity was significantly greater in hardwood stands (2.5 ± 0.1) than either *Pinus* stand type (2.2 ± 0.1 in *P. echinata* stands and 2.1 ± 0.1 in *P. strobus* stands). Bottoms had

Table 1
Overstory basal area, dead basal area, and canopy openness (mean ± S.E.) for stand type, ELTP, and their interactions. Means with different superscripts were significantly different according to a Tukey multiple comparisons test ($p < 0.05$). *Factors or interaction significantly different ($p < 0.05$). Non-transformed data are presented for ease of interpretation. N = 52 *Pinus echinata, 31 P. strobus,* 20 hardwood, 75 ridge, and 28 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hardwood	Ridge	Bottom	Stand Type F-value	ELTP F-value	Stand Type X ELTP F-value
Basal area (m^2 ha^{-1})	45.3 ± 1.6^a	46.6 ± 2.0^a	28.5 ± 2.0^b	41.2 ± 1.3	39.0 ± 1.7	25.57*	1.03	5.09*
Dead basal area (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 (%)	6 ± 1^a	10 ± 1^b	7 ± 1^a	7 ± 1	7 ± 1	11.61*	0.01	2.49

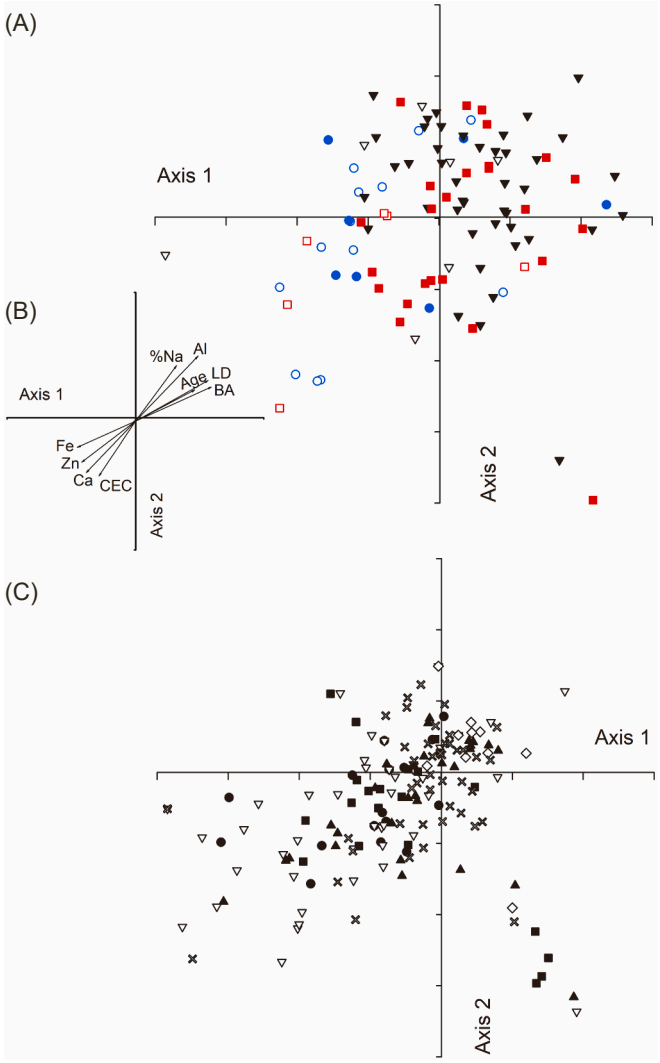

Fig. 1. Non-metric multidimensional scaling (NMS) ordination of herbaceous-layer species cover: (A) Sample plots classified by stand type (*P. echinata*, *P. strobus*, and hardwood) and ELTP (bottom and ridge). (B) Environmental vector correlations with ordination axis scores; vectors with r ≥0.4 are shown. %Na = Na soil saturation,Al = Al concentration, Age = stand age, BA = basal area, Ca = calcium concentration, Fe = Fe concentration, LD = Litter depth, CEC = Cation exchange capacity, Zn = zinc concentration. (C) Functional groups; species were grouped into functional group after analysis. Non-native species includes both herbaceous and woody species.

greater species richness (41.9 ± 1.8) than ridges (35.8 ± 1.3; Table 3).

Mean herbaceous-layer cover (total summed for all species) was significantly greater on hardwood (139.6 ± 8.0 %) than *P. echinata* (48.5 ± 6.2 %) or *P. strobus* plots (81.7 ± 7.7 %; Table 3). A significant interaction between ELTP and stand type revealed that cover on hardwood plots was significantly greater than that on *P. echinata* and *P. strobus* plots on ridges and cover on hardwood and *P. strobus* plots was significantly greater than that on *P. echinata* plots in bottoms. Also, total cover was greater in *P. strobus* plots in bottoms than on ridges.

Annual/biennials, graminoids, perennials herbs and non-native herbs all showed significantly greater cover in hardwood stands than in *Pinus* stands (Fig. 2; Table 3). Annuals/biennials exhibited greater cover in hardwood stands vs. *Pinus* stands (Table 3). Non-native herb cover was significantly greater on hardwood and *P. strobus* plots (5.0 ± 1.6 % for both stand types) than on *P. echinata* plots (0.1 ± 0.1 %) and greater on bottom plots (4.8 ± 1.4) than on ridge plots (2.4 ± 1.1). Tree species cover was greater on ridges than bottoms, but did not differ with stand type. While the cover of native shrubs did not differ across stand types or ELTPs, the cover of non-native shrubs was significantly greater on hardwood plots than on *Pinus* plots. The cover of native vines was greater on hardwood plots than in either *Pinus* stand type, and was greater on ridges than in bottoms. As indicated by a significant interaction, the differences among stand types only occurred on ridges.

Relative cover on ridge plots was heavily dominated by native vines and tree seedlings, regardless of stand type (Fig. 2). Bottoms exhibited less relative cover of native vines. *P. echinata* and *P. strobus* stands in bottoms contained greater relative cover of non-native vines. *P. strobus* plots in bottoms also contained the greatest relative cover of non-native herbs. Hardwood plots in bottom were dominated by native perennial herbs and graminoids.

3.4. Seedling and sapling density and relative density

The total density (stems per 100 m^2) of seedlings did not differ among stand types, but was significantly greater on ridges than bottoms (228 ± 16 stems 100 m^{-2} vs. 129 ± 21 stems 100 m^{-2}; Table 4). *A. negundo* seedling density was significantly greater in hardwood and *P. strobus* plots than in *P. echinata* plots, and significantly greater in bottoms than on ridges. We observed a significant interaction between ELTP and stand type; differences in *A. negundo* among stand types were only significant in bottoms. *A. rubrum* seedling density did not differ with stand type, but was significantly greater on ridges than in bottoms (31 ± 6 stems 100 m^{-2} vs. 8 ± 7 stems 100 m^{-2}). Differences in *A. rubrum* seedling density among site types were only significant on ridges. *A. saccharum* seedling density was significantly greater in *P. echinata* and hardwood plots than in *P. strobus* plots. Differences in *A. saccharum* density across stand types were only significant on ridges. Seedling density of *Fraxinus* species was significantly greater on ridges with ridges exhibiting over twice the density of bottoms (58 ± 10 vs. 21

Table 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 ($p < 0.05$). Non-transformed data are presented for ease of interpretation. N=52 *Pinus echinata, 31 P. strobus,* 20 hardwood, 75 ridge, and 28 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hardwood	Bottom	Ridge	Stand Type F	ELTP F	ELTP X Stand Type F
Annuals/Biennials	0.1 ± 0.1^a	0.1 ± 0.1^a	1.4 ± 0.2^b	0.4 ± 0.1	0.4 ± 0.1	15.3*	1.8	1.1
Graminoids	1.9 ± 1.7^a	2.0 ± 2.0^a	17.5 ± 2.2^b	9.7 ± 1.9^a	4.5 ± 1.4^b	13.5*	8.4*	0.7
Perennial herbs	6.1 ± 2.4^a	11.8 ± 3.0^a	35.7 ± 3.0^b	25.8 ± 2.6^a	10.1 ± 2.0^b	20.3*	15.6*	2.7
Non-native herbs	0.1 ± 0.1^a	5.0 ± 1.6^b	5.0 ± 1.6^b	4.8 ± 1.4^a	2.4 ± 1.1^b	9.0*	6.1*	0.6
Trees	9.6 ± 2.5	19.9 ± 3.1	17.7 ± 3.2	13.2 ± 2.7^a	18.3 ± 2.1^b	2.8	5.8*	1.4
Native shrubs	3.6 ± 1.8	11.2 ± 2.2	11.9 ± 2.3	10.0 ± 2.0	7.8 ± 1.5	2.8	3.1	0.2
Non-native shrubs	1.8 ± 1.8^a	8.4 ± 2.3^a	14.0 ±2.4^b	11.2 ± 2.0	4.9 ± 1.5	16.8*	0.7	1.2
Native vines	15.3 ± 3.3^a	16.6 ± 4.1^a	28.4 ± 4.2^b	9.2 ± 3.6^a	31.0 ± 2.7^b	5.6*	26.2*	9.4*
Non-native vines	6.1 ± 1.3	6.8 ± 1.6	6.4 ± 1.6	8.1 ± 1.4	4.8 ± 1.1	2.9	1.1	2.8
Total cover (all species)	48.5 ± 6.2^a	81.7 ± 7.7^b	139.6 ± 8.0^c	93.4 ± 6.7	86.5 ± 5.1	33.5*	1.2	3.1*
Species richness (S)	33.3 ± 1.6^a	36.4 ± 2.0^a	46.9 ± 2.1^b	41.9 ± 1.8^a	35.8 ± 1.3^b	13.8*	7.6*	2.2
Shannon diversity (H′)	2.2 ± 0.1^a	2.1 ± 0.1^a	2.5 ± 0.1^b	2.2 ± 0.1	2.4 ± 0.1	5.3*	3.7	2.5

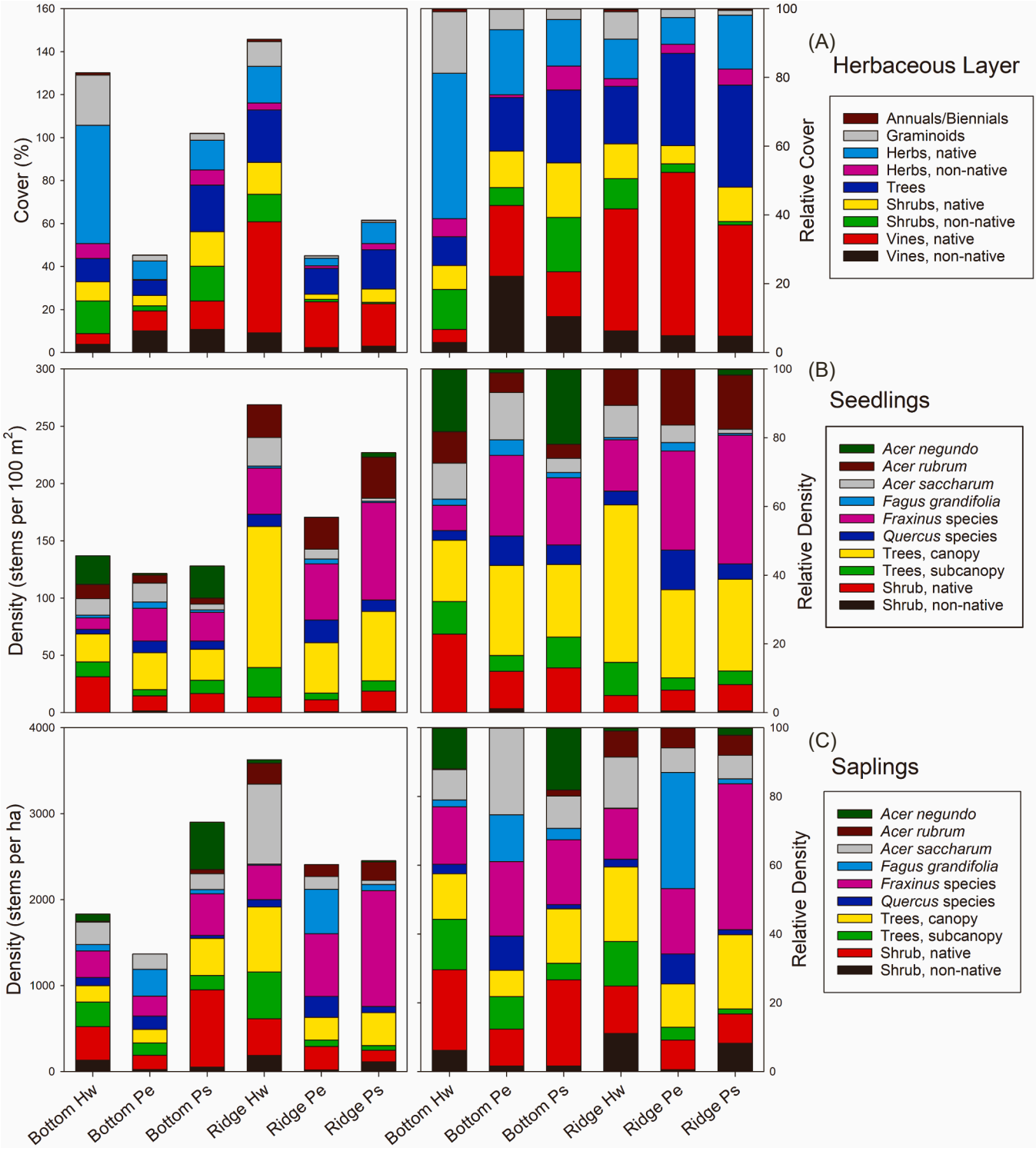

Fig. 2. (A) Herbaceous layer functional group cover and relative cover. (B) Seedling species and functional group density and relative density. (C) Sapling species density and relative density. Hw = hardwood, Pe = *P. echinata*, Ps = *P. strobus*).

± 13 stems 100 m^{-2}). Density of *Quercus* seedlings was significantly greater on *P. echinata* plots than hardwood plots. The density of canopy tree species did not differ among stand types, but was greater on ridges than in bottoms. Exhibited by a significant interaction, hardwood plots had greater densities of canopy tree seedlings than either *Pinus* stand type on ridges, but density did not differ by stand type in bottoms.

Ridge hardwood stands exhibited the greatest relative seedling density of canopy tree species, but this functional group exhibited high relative density across all stand types and ELTPs (Fig. 2). The two *Pinus* stand types on ridges had the greatest relative densities of *Fraxinus* species seedlings. Ridge plots, regardless of stand type, had the greatest relative densities of *A. rubrum* seedlings. *A. negundo* exhibited its greatest relative density on hardwood and *P. strobus* plots located within bottoms. *A. saccharum* relative seedling density was greatest in *P. echinata* stands located within bottoms. The relative density of *Quercus* seedlings was greatest in *P. echinata* stands on both ridges and

Table 4
Species and 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=52 *Pinus echinata,* 31 *P. strobus,* 20 hardwood, 75 ridge, and 28 bottom sites.

Variable	*P. echinata*	*P. strobus*	Hardwood	Bottom	Ridge	Stand Type F	ELTP F	Stand Type X ELTP
A. negundo	1 ± 3^{a}	16 ± 4^{b}	13 ± 4^{b}	18 ± 3^{a}	1 ± 2^{b}	10.5*	29.8*	5.7*
A. rubrum	17 ± 7	20 ± 8	21 ± 9	8 ± 7^{a}	31 ± 6^{b}	0.01	9.9*	0.1
A. saccharum	13 ± 3^{a}	4 ± 4^{b}	20 ± 4^{a}	12 ± 3	12 ± 3	4.8*	0.5	3.2*
F. grandifolia	5 ± 1	2 ± 2	2 ± 2	3 ± 2	2 ± 1	1.2	0.2	0.01
Fraxinus species	39 ± 12	55 ± 15	25 ± 15	21 ± 13^{a}	58 ± 10^{b}	1.6	8.8*	1.8
Quercus species	15 ± 3^{a}	9 ± 3^{ab}	7 ± 4^{b}	7 ± 3	13 ± 2	3.81*	3.1	0.6
Trees, canopy	38 ± 7	44 ± 9	74 ± 9	28 ± 7^{a}	76 ± 6^{b}	2.2	25.2*	5.7*
Trees, subcanopy	6 ± 3	10 ± 3	19 ± 4	10 ± 3	14 ± 2	2.5	0.2	0.6
Shrubs, native	12 ± 5	17 ± 6	22 ± 6	20 ± 5	14 ± 4	0.9	1.9	0.2
Shrubs, non-native	1 ± 1	1 ± 1	<1	1 ± 1	<1	0.8	0.04	0.4
Total density (all species)	145 ± 26	180 ± 32	210 ± 35	129 ± 21^{a}	228 ± 16^{b}	2.2	14.1*	1.3

bottoms.

Differences in the density of saplings by species and functional groups were evident for both stand types and ELTPs (Fig. 2; Table 5). *A. negundo* sapling density was significantly greater in hardwood and *P. strobus* stands than *P. echinata* stands, and significantly greater in bottoms than on ridges. A significant interaction indicatd that differences in the density of *A. negundo* across stand types were only significant in bottom plots. Sapling density of *A. rubrum* did not differ across stand types, but densities were significantly greater on ridges than in bottoms (198 ± 53 vs. 19 ± 70 stems ha^{-1}, respectively, a 10x difference). Hardwood stands contained a significantly greater density of *A. saccharum* saplings than either *Pinus* stand type. However, this difference was only significant on ridges. The density of *Quercus* saplings was significantly greater in *P. echinata* stands than in *P. strobus* stands (201 ± 64 vs. 53 ± 80 stems ha^{-1}). *F. grandifolia* sapling density was significantly greater in *P. echinata* stands than either *P. strobus* or hardwood stands. The density of subcanopy tree sapling was significantly greater in hardwood stands than in either *Pinus* stand type, while the density of non-native shrubs was significantly greater in hardwood stands than in *P. echinata* stands.

Fraxinus species dominated the composition of *P. strobus* stands on ridges, where their relative sapling density was over two times that of other canopy trees, the next most dominant functional group (Fig. 2). *P. echinata* stands on ridges were dominated by *F. grandifolia* saplings, a species that had its next greatest relative density in *P. echinata* stands in bottoms. *P. echinata* stands in bottoms had the greatest relative density of *A. saccharum* saplings, while *P. strobus* stands in bottoms had the greatest relative sapling density of *A. negundo* of any stand type. The relative density of *Quercus* species saplings was greatest in *P. echinata* stands, with near equal relative density on both ridges and in bottoms.

4. Discussion

4.1. Composition differences among stand type

As we hypothesized, long-term occupancy by *Pinus* species resulted in discernable differences in composition and soil chemistry compared to naturally regenerated hardwood stands. In our study, *Pinus* stands were associated with thicker litter layers, lower CEC, reduced soil Ca concentration, and increased Al concentration. Likely as a result of these conditions, *Pinus* stands had lower herbaceous-layer species richness, diversity, and cover compared to hardwood stands. In other studies, lower species diversity in *Pinus* stands has been attributed to the acidifying effect of recalcitrant litter, which reduces soil fertility and favors a limited suite of tolerant species (Landeweert et al., 2001; Krzyszowska et al., 1996). *Pinus* litter also acts as a mechanical barrier to the successful germination and establishment of many species of forest herbs (Berg and McClaugherty, 2003; Read, 1991; Barbier et al., 2008, Loydi et al., 2013). In our study, canopy openness was greater in *P. strobus* stands due to the mortality of overstory trees, however, this greater availability of light was not correlated with greater herbaceous-layer species richness, diversity, or cover. Hardwood plots were associated with greater availability of cations, thinner litter layers, and lower concentration of Al. Hardwood species, including *L. tulipifera*, *A. saccharum*, and *C. florida*, produce nutrient rich litter, which increases decomposition rate, soil base saturation and buffering capacity, and therefore soil fertility (Kalisz, 1986; Finzi et al., 1998; Jenkins et al., 2007; Holzmueller et al., 2007).

Pinus stands, on average, contained fewer functional groups and had overall lower coverage of functional groups in the herbaceous-layer, whereas hardwood stands possessed greater cover of a greater number

Table 5
Species and 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=52 *Pinus echinata, 31 P. strobus,* 20 hardwood, 75 ridge, and 28 bottom sites.

Variables	*P. echinata*	*P. strobus*	Hardwood	Bottom	Ridge	Stand Type F	ELTP F	Stand Type X ELTP
A. negundo	$<1^{a}$	283 ± 47^{b}	64 ± 49^{b}	212 ± 41^{a}	20 ± 31^{b}	11.3*	13.8*	10.8*
A. rubrum	70 ± 64	131 ± 80	125 ± 82	19 ± 70^{a}	198 ± 53^{b}	0.2	4.2*	0.1
A. saccharum	163 ± 93^{a}	116 ± 116^{a}	595 ± 119^{b}	208 ± 101	375 ± 77	5.3*	1.7	3.6*
Quercus	201 ± 48^{a}	53 ± 60^{b}	89 ± 62^{ab}	94 ± 52	135 ± 40	3.3*	0.6	0.1
Fraxinus	480 ± 250	916 ± 311	354 ± 320	341 ± 271	825 ± 207	1.2	1.1	0.2
F. grandifolia	415 ± 82^{a}	61 ± 101^{b}	46 ± 104^{b}	146 ± 88	202 ± 67	9.7*	0.8	2.1
Shrubs, native	218 ± 121	518 ± 150	410 ± 155	486 ± 131	278 ± 100	1.3	1.6	2.8
Shrubs, nonnative	20 ± 33^{a}	81 ± 41^{ab}	158 ± 43^{b}	68 ± 36	105 ± 27	3.8*	0.1	0.2
Trees, canopy	209 ± 73	409 ± 90	475 ± 93	260 ± 79^{a}	468 ± 60^{b}	2.9	4.4*	3.1
Trees, subcanopy	112 ± 47^{a}	111 ± 58^{a}	414 ± 60^{b}	199 ± 51	226 ± 39	4.9*	0.1	2.6
Total density (all species)	1887 ± 517	2676 ± 648	2729 ± 698	2032 ± 423	2829 ± 322	1.2	2.3	1.4

of functional groups. Annuals/biennials, perennial herbs, and invasive species all had greater cover on hardwood sites. 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 (Read, 1991; Berg and McClaugherty, 2003). Research also suggests that these herbaceous-layer groups are particularly sensitive to deep litter layers (Facelli and Pickett, 1991a, 1991b), such as those associated with *Pinus* species.

As we hypothesized, we observed a greater density of woody stems in *Pinus* stands, including *Fraxinus* spp. and *Acer rubrum*, two widely dispersed species that tolerant a wide range of site conditions. In addition, *Quercus* spp. and *F. grandifolia* were larger components of the seedling and sapling layers of *P. echinata* stands compared to other stand types. *Q. rubra* and *F. grandifolia* have been shown to have an affinity for acidic soil conditions compared to *Acer* species and *F. americana* (Finzi et al., 1998; Bigelow and Canham, 2002). Site occupancy by *F. grandifolia* and *Q. rubra* is associated with recalcitrant litter that results in a higher C:N ratio than sites occupied by *A. saccharum* and *F. americana* (Finzi et al., 1998a). Comparatively, soil cation levels, N mineralization rates (Washburn and Arthur, 2003) and pH are lower, while C content is higher (Knoepp et al., 2000), under *Pinus* species than under *Quercus* species or *F. grandifolia.* Therefore, soil conditions under planted *Pinus* species may favor the establishment of *Quercus* species and *F. grandifolia* seedlings relative to *Acer* species. The successful reproduction and persistence of *Quercus* species has been problematic in *Quercus*-dominated forests across the Central Hardwood Region (Jenkins and Parker, 1998; Dey, 2014).

4.2. Composition differences between ELTPs

Functional group cover and density differed between bottoms and ridges. Regardless of stand type, we observed greater density and cover of woody species on ridges, but a greater cover of herbaceous species in bottoms. Herbaceous plants compete well under low light conditions in forests and may have a competitive effect on the establishment and persistence of advance regeneration (George and Bazzaz, 2003; Gilliam, 2007; Royo and Carson, 2008). In addition, herbaceous species can provide protective cover that increases seed and seedling predation of woody species (Royo and Carson, 2008). On ridges, woody seedlings were likely predominant due to the reduced moisture and nutrient availability, which is correlated with increased dominance of woody seedlings (Graves et al., 2006). Bottoms had greater cover of non-native herbs, but functional groups comprised of woody non-native species did not differ between ELTPs. Non-native herbs were likely favored by the same stand and soil characteristics that favored native herbs.

The degree to which *Pinus* plantations affect soil chemistry depends upon the buffering capacity of the soil (Tanikawa et al., 2014). In our ordination analysis, species composition on bottom sites was correlated with greater CEC and cation concentrations than ridge sites, regardless of stand type, suggesting that bottoms have greater buffering capacity than ridges and will display less pronounced effects of long-term *Pinus* occupancy. In our ordination, the species composition of *Pinus* stands on ridges was more strongly related to soil conditions associated with lower productivity, including low CEC, low concentration of Ca, and high concentration of Al, than the composition of *Pinus* stand in bottoms. This supports our hypothesis that plots in *Pinus* stands on ridges would exhibit the greatest effects of long-term pine occupancy compared to plots in hardwood stands or *Pinus* stands in bottoms.

4.3. Implications for management

Prior to the 1800s, the area that became the Hoosier National Forest was dominated by *Quercus-Carya* forests (Lindsey et al., 1965). Forest harvesting via large openings has led to the regeneration and dominance of *L. tulipifera* (Jenkins and Parker, 1998; Morrissey et al., 2008), while selective harvesting via small openings has driven the dominance of *Acer saccharum* (Jenkins and Parker, 1998). The ascension of *L. tulipifera* represents a divergence in successional trajectory away from the historic dominance of *Quercus* species (Swaim et al., 2018), while the increased importance of *A. saccharum* represents accelerated succession towards late-successional shade-tolerant species (Abrams and Scott, 1989). Our 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 we 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 lower availability of cations. As a consequence, this stand type contained less 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.* Conversely, hardwood sites contained greater cover of herbaceous perennials, and greater herbaceous layer species diversity, but also greater cover of non-native herbs and vines.

Differences in browsing intensity by white-tailed deer could contribute to differences in seedling abundance between bottom and ridge sites. However, within southern Indiana, multiple *Quercus* species are highly selected by deer, but *F. grandifolia* is highly avoided (Sample et al., 2023), suggesting that selective browsing would be unlikely to increase the abundance of both species at the same site. In addition, topography has been found to be a non-significant contributor to browse intensity within localized areas (Kniowski and Ford, 2018a).

Because the regeneration of *Quercus* species on productive sites has been highly problematic throughout the eastern United States (Johnson et al., 2009), the edaphically driven promotion of *Quercus* advance regeneration by *Pinus* occupancy could serve 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 establishment of *Quercus* spp. where advanced regeneration is present (Johnson et al., 2009).

Integrating climate change into silvicultural decision making is vital to enhancing the ecological integrity and resiliency of forests. Climate-smart forestry practices can be utilized to mitigate the effects of climate change by creating compositional and structural conditions that may be less vulnerable and better adapted to future conditions (Nagel et al., 2017; Phillips et al., 2020). Expected climate change impacts for southern Indiana include warmer and wetter springs and hotter and drier summers (Phillips et al., 2020). The uptick in the frequency and severity of summertime drought events is expected to create additional physiological stress in forest trees. Furthermore, the hotter and drier conditions are expected to increase the frequency of fire, while the warmer winters may increase the frequency and severity of ice storms (Hamlet et al., 2020; Phillips et al., 2020). The environmental habitat specificity and disturbance adaptations of *P. echinata* and many upland *Quercus* spp. may favor their persistence in the climate conditions of southern Indiana (Iverson et al., 2019). *P. echinata* is native south of this region and may experience a northward range shift under climate change (Iverson et al., 2019). The ample cone production of current *P. echinata* plantations combined with the existence of advanced regeneration of *Quercus* spp. may offer a unique opportunity to utilize silvicultural systems to regenerate mixed-wood stands that will be better adapted to future climate conditions.

Funding

This project was funded by the USDA Forest Service and the Department of Forestry and Natural Resources at Purdue University.

CRediT authorship contribution statement

John M. Kabrick: Writing – review & editing, Methodology, Investigation. **Christopher D. Thornton:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition. **J. Travis Swaim:** Writing – review & editing, Investigation. **Michael Jenkins:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Patrick J. Duffy:** Writing – original draft, Investigation, Formal analysis. **Douglass F. Jacobs:** Writing – review & editing, Resources, Methodology, Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgements

We thank Rob Quackenbush, Michelle McKee, and Samuel Tourtellot for assistance with fieldwork. We also thank Brad Graham, Michael Mashtare, and Madeline Freiburger for help with various components of this project. Jennifer Spitznagle and Janis Gosewehr provided valuable administrative assistance. This project was funded by the Department of Forestry and Natural Resources at Purdue University and the USDA Forest Service.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122310.

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