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Response of Soil Chemistry to Long-Term Occupancy by Introduced *Pinus* Species in Hardwood Forests

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Abstract

Conifers have been widely planted to stabilize soils and promote site recovery on former hardwood sites that were cleared for agriculture. Decades of confer occupancy may have lasting effects on nutrient availability, organic matter cycling, soil acidity, and soil buffering capacity. In many areas of eastern North America, conifer plantings consisted of non-native *Pinus* species planted on abandoned agricultural land that was once mesophytic hardwood forest. To investigate the long-term effect of *Pinus* occupancy on former hardwood soils, we compared the soil chemistry of *P. echinata* and *P. strobus* plantations planted on bedrock soils 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, mineral soils in *Pinus* plantations had lower pH and less organic matter (-21%), total carbon (-29%), total nitrogen (-30%), manganese (-37%), calcium (-24%), zinc (-13%), and boron (- 24%) compared to hardwood stands. *Pinus* stands also had 2–5 times greater O-horizon depth and 17% greater concentrations of aluminum compared to naturally regenerated hardwood stands. The difference between *Pinus* and hardwood stands was greater on ridges than bottoms, as *Pinus* trees planted in bottoms appeared to have had less impact on soil chemistry. This was likely due to greater buffering capacity in bottom soils and litter from codominant hardwood trees that had advanced into the overstory.

Keywords Aluminum · Buffering capacity · Cations · O-horizon · Litter · Soil acidity · PH · Plantations · Afforestation · Reforestation

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Introduction

Worldwide, *Pinus* species comprise approximately 35% of total plantation area, with the production of wood for building materials and pulp serving as the major planting objective (West 2014). However, the genus has also been planted throughout the world to rehabilitate former forestland degraded by historic land use including agriculture (Toro and Gessel 1999; Rigueiro-Rodriguez et al. 2012; Zhao et al. 2021; Duffy et al. 2024). For example, in the Midwest Region of the United States, *Pinus* species were planted extensively on eroded, abandoned old-fields during the early-mid twentieth century (Otis 1986; Sieber and Munson 1992; Jenkins 2013). Because *Pinus* species naturally occur on infertile, dry, and/or acid soils, and were widely available in nurseries, they were used to afforest highly eroded old fields with degraded soils in the Midwest (Billings 1938; Auten 1945). In the present day, these plantations have less ecological value than native hardwood stands due to lower functional heterogeneity and lower species diversity (Facelli and Pickett 1991; Barbier et al. 2008; Loydi et al. 2013). Thus, many forest managers are seeking strategies to convert pine plantation to native hardwoods. However, the lasting impact of *Pinus* stands on soil chemistry and productivity may be a critical factor in determining the best strategy for conversion. Over the past decades, managers in eastern forests have focused considerable effort on the regeneration of *Quercus* species in forests that have succeeded towards mesophytic late-seral species (Abrams 2003; Dey 2014). Advance regeneration of *Quercus* is more abundant on less productive soils (Fei and Steiner 2008; Kabrick et al. 2014), and management efforts may more efficiently promote *Quercus* reproduction on these less-productive sites (Rademacher et al. 2025). If long-term occupancy by *Pinus* species produces lasting effects on soil structure and chemistry, former *Pinus* sites may offer an opportunity to regenerate *Quercus* species with less intensive management (Duffy et al. 2024). However, studies of how *Pinus* occupancy affects soils on former hardwood sites are lacking.

Pinus species and other conifers influence nutrient availability, organic matter cycling, soil acidity, and soil buffering capacity as a result of slower litter decomposition and the resulting accumulation of thick O-horizon layers on the forest floor (Finzi et al. 1998; Berg and McClaugherty 2003; Stendahl et al. 2010) that contain high concentrations of recalcitrant compounds (Pohlman and McColl 1988; Finzi et al. 1998; Berg and McClaugherty 2003). Under such conditions, soil pH is typically low because of acid inputs from decomposing litter and ectomycorrhizal leachates (Binkley and Valentine 1991; Berg and McClaugherty 2003; Hizal et al. 2013). *Pinus* litter is generally nutrient-poor and degrades slowly, resulting in diminished nutrient input into mineral soil (Binkley and Valentine 1991; Berg and McClaugherty 2003). 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 typically found in hardwood forests have more nutrient-rich and rapidly decomposing litter. Through rapid decomposition and cycling of cations such as Ca, these species promote

improved base saturation and buffering in soil, higher pH, and increased nutrient mineralization through larger bacterial populations (Kalisz 1986; Read 1991; Finzi et al. 1998; Berg and McClaugherty 2003; Holzmueller et al. 2007; Smith and Read 2010). Therefore, conifers and hardwoods have distinctly different effects on soil chemistry that serve to replicate soil conditions under which they are superior competitors. 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).

Geologic and edaphic characteristics influence the response of soils to long-term residency of *Pinus* species within a region. In poorly buffered soils with inherently low soil pH, conifers contribute to low pH and less fertile soil conditions (Binkley and Valentine 1988; Binkley et al. 1989; Richter et al. 1994). Conversely, well-buffered soils may exhibit less response to inputs of conifer litter over time (Rolfe and Boggess 1973; Hizal et al. 2013). At the local scale, ridges typically have thinner soils with a greater volume of coarse fragments, and a lower cation exchange capacity (CEC), and consequently lower buffering capacity than bottoms (Zhalnin 2004). Therefore, *Pinus* plantations may have a more lasting impact on soil chemistry on ridges than in bottoms.

Although the effects of *Pinus* species on soils have been well studied in their native setting (Read 1991; Sauer et al. 2007; Smith and Read 2010), less is known about their effects on former hardwood sites where *Pinus* species are not native. In southern Indiana two *Pinus* species outside of their native range, *P. echinata* and *P. strobus* (Lawson 1990), were planted on former hardwood sites starting in the 1930s after the abandonment of long-term agricultural land (Jenkins 2013). The substate of southern Indiana is largely comprised of sandstone bedrock underlying silt loam soils (USDA Nrcs 2025) that typically have lower buffering capacity when compared to glacial till-derived soils to the north (Homoya et al. 1984; Zhalnin 2004). To investigate the long-term impacts of *Pinus* plantations on these soils, we 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. We sampled the O-horizon and soil on 113 plots to 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 O-horizon depths and Al concentrations compared to adjacent naturally regenerated hardwood stands.
2) The effect of *Pinus* species on soil chemistry will differ between ridges and bottoms. Because bottoms have more highly buffered soil, the effects of *Pinus* species on soil chemistry will be less pronounced. As such, the differences in soil chemistry between *Pinus* and hardwood sites will be more pronounced on ridges than in bottoms.

Methods

Study Sites

Sample sites were located within the Tell City Unit of the Hoosier National Forest within the Crawford Upland Subsection as defined by Homoya et al. (1984). In ArcMAP v10.1, we used the Ecological Classification System for the Hoosier National Forest (Van Kley et al. 1994) to select plot locations. Ecological Landtype Phase (ELTP), which is based on dominant vegetation, herbaceous-layer indicator species, soil type, elevation, slope, and aspect, was identified for each prospective plot location. Because ELTP 13 *Fagus-Acer saccharum/Arisaema* Mesic Ridges (hereafter ridges), and ELTP 42 *Acer saccharinum/Boehmeria* Bottomlands (hereafter bottoms) were the two most common ELTPs in our study region, and because both contained an abundance of *Pinus* plantations, we confined our sampling to these two ELTPs. To limit variability of soil across potential plots, we used Natural Resource Conservation Service (NRCS) soil series data to assure that sites had similar soil types. Although NRCS data show that there are many specific soil groups found within each ELTP, most of these soils only differ slightly. Soils on ridges commonly have a loess cap over sandstone residuum with a silt loam surface and an underlying argillic horizon of silt loam or silty clay between 20 and 68 cm (USDA Nrcs 2025), with an average A horizon depth of 4.7 ± 0.8 cm and an average pH of 5.5 ± 1.1. Bottoms consist 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 1). Both have average pH values between 3.5–7.3 and average CEC below 20 meq per 100 g (Nrcs 2025). Other soil series found within sites contained similar values for pH and CEC and similar soil types.

Across ridges and bottoms, we selected three stand types for sampling: *Pinus echinata* (shortleaf pine) plantations, *Pinus strobus* (white pine) plantations, and naturally regenerated hardwood stands. Hardwood species in naturally regenerated stands included *Platanus occidentalis* (American sycamore), *Liriodendron tulipifera* (tuliptree), *Juniperus virginiana* (eastern redcedar), *Juglans nigra* (black walnut), *Acer negundo* (boxelder), *A. rubrum* (red maple), and *A. saccharum* (sugar maple). Overstory basal area was greater in *P. echinata* and *P. strobus* stands than hardwood stands ($p < 0.05$; 45.3 ± 2.0 and 46.6 ± 2.0 vs. 28.5 ± 2.0 m^2 ha^{-1}, respectively; Duffy et al. 2024).

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 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. In total, we

Table 1 Soil series underlaying sample plots listed by ELTP (bottoms and ridges) and stand type (*P. echinata*, *P. strobus*, and hardwood). Soil series were obtained from the Web Soil Survey of the USDA NRCS (http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx)

Soil Series	Bottom			Ridge		
	P. echinata	*P. strobus*	Hardwood	*P. echinata*	*P. strobus*	Hardwood
Adyeville Silt Loam		X			X	
Adyeville-Tipsaw-Ebal Complex	X	X	X	X	X	X
Adyeville-Wellston-Duechars Silt Loam			X		X	
Apalona Silt Loam	X		X	X	X	X
Cuba Silt Loam			X			
Ebal-Duechers-Kitterman Complex		X	X	X	X	
Gatchel Silt Loam	X	X	X			
Haymond Silt Loam			X			
Hosmer Silt Loam				X		
Markland Silty Clay Loam			X			
Tipsaw-Adyeville Complex		X	X		X	X
Wellston Silt Loam			X	X	X	X

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.

We determined the age of each stand sampled to ensure that *Pinus* and hardwood sites were of a comparable age. Although 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, to more accurately represent overstory age of sampled plots, we 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 approximately 75 years, because land was largely abandoned in the 1930s and 1940s (Welch et al. 2001).

Field Sampling Design

Because soils varied across each ELTP, and because past agricultural use altered A horizon thickness through increased erosion (Welch et al. 2001), we collected soil samples at 0–10 cm (hereafter A-horizon) and 10–20 cm (hereafter B-horizon) increments using an impact-driven soil corer. Sampling at these depths allowed us to capture the zone of herbaceous-layer rooting and the zone of potential leaching. 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 both the A- and B-horizon samples, all four cores were combined into one sample to reduce the cost of laboratory analysis. We also collected O-horizon samples (leaves, small twigs, and seeds down to the mineral soil) from three 25 cm^2 quadrats located 5.6 m west, north, and east of plot center, cutting around the frame after removing larger sticks and non-organic material. O-horizon depth was measured to the nearest cm within each quadrat prior to sampling. In total, 585 soil samples and 351 O-horizon samples were collected.

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 (Db) was then calculated by taking the mass of dry soil over the corrected core volume. O-horizon samples were dried at 70 °C for 48 h or until constant mass (Amacher et al. 2003). Non-leaf litter material was then separated and weighed, while leaf litter and duff were 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, organic matter (%), CEC ($cmol_c\ kg^{-1}$) was measured by the ammonium acetate method, and 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 (Bray and Kurtz 1945; McLean 1982; Mehlich 1984; Ross 1995; Nelson and Sommers 1996; Schulte and Hopkins 1996). B-horizon samples were only tested for pH.

Data Analysis

We used two-way Analysis of Variance (ANOVA) with categorical variables stand type (*P. echinata*, *P. strobus*, and hardwood) and ELTP (ridges and bottoms) to test for differences in stand and soil variables ($\alpha = 0.05$). Stand variables were O-horizon depth (cm), O-horizon mass (g m^{-2}), litter C:N ratio and stand age. Soil variables were pH, organic matter (%), CEC (meq 100 g^{-1}), 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}), Al (mg kg-^{1}), total C (C, %) and total N (N, %). 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 a square root transformation for O-horizon depth, Ca, B, and Zn. For Fe, we removed an extreme outlier

and log transformed. Non-transformed data are presented for ease of interpretation. Soil pH was normally distributed and was analyzed as pH rather than as hydrogen ion concentration. When ANOVA revealed significant differences, we used the Tukey multiple comparisons test for post hoc comparisons ($\alpha = 0.05$).

Results

O-horizon depth was significantly greater in *Pinus* stands, following the trend *P. echinata* > *P. strobus* > hardwood ($p < 0.001$; Table 2, Fig. 1). Mean O-horizon depth was 19.0 ± 2.0 cm in *P. echinata*, 14.1 ± 2.5 cm in *P. strobus*, and 5.6 ± 2.6 cm in hardwood stands. O-horizon mass was significantly greater in *Pinus* than hardwood stands (*P. echinata* > *P. strobus* > hardwood), with means of 823.9 ± 67.5 g m^{-2}, 592.4 ± 83.7 g m^{-2}, and 287.1 ± 86.3 g m^{-2}, respectively. As shown by the significant interaction between stand type and ELTP, litter C:N ratio in bottoms was significantly greater in *Pinus* than in hardwood stands (40.3 ± 1.9 for *P. echinata*, 35.6 ± 2.4 for *P. strobus*, and 27.9 ± 1.6 for hardwoods; $p < 0.001$). Stand age differed among stand types ($p < 0.001$) with *P. echinata* stands displaying significantly greater age than both *P. strobus* and hardwood stands. Hardwood stands were also significantly older than *P. strobus* stands. Stand ages did not differ by ELTP ($p = 0.910$).

Within the A-horizon (top 10 cm of soil), pH, OM, TC, TN, B, Mn, Ca, and Zn were all greater in hardwoods than *Pinus* stands (Table 2). A horizon pH was lower in *P. echinata* (5.53 ± 0.06) stands than hardwood stands (5.86 ± 0.14; $p = 0.04$). B horizon pH was significantly lower in *P. echinata* and *P. strobus* stands than hardwood stands ($p < 0.001$). As reflected by its significant interaction term, organic matter was significantly greater in ridge hardwood stands than ridge *Pinus* stands (Fig. 1; $p < 0.001$). In addition, hardwood stands on ridges had significantly greater organic matter than hardwood stands in bottoms ($p = 0.002$). Total C differed significantly between stand types with a significant interaction term (Fig. 1; Table 2). Carbon was greater in ridge hardwood than in ridge *Pinus* stands, averaging $1.65 \pm 0.07\%$ on *Pinus* and $2.32 \pm 0.13\%$ on hardwood sites ($p = 0.002$). Total N was analogous to total carbon. The significant interaction term indicated that N was significantly greater in hardwood stands than *Pinus* stands on ridges ($p = 0.02$; Fig. 1; Table 2). Concentrations of B ($p = 0.002$), Ca ($p = 0.02$), and Zn ($p < 0.001$) were all greater in hardwood than in *Pinus* stands Fig. 1; Table 2). For Mn, the interaction term was significant ($p = 0.01$), and soils in ridge hardwood stands contained more Mn than *Pinus* stands on ridges (Table 2). In bottoms, soil concentrations of Fe ($p = 0.02$), Zn ($p < 0.001$), Ca ($p = 0.02$), and B ($p < 0.001$) were greater in hardwood stands than *P. echinata* stands, with a significant interaction term for Fe ($p = 0.02$). CEC ($p < 0.001$), P ($p = 0.02$), Na ($p = 0.01$), and Zn ($p = 0.01$) were greater in bottoms than on ridges. CEC ranged from 4.2 to 22.7, with a mean of 8.75 ± 0.42 on ridges, and 11.19 ± 0.55 on bottoms (Table 2). Bulk density was significantly greater in *P. strobus* stands than hardwood stands, and greater in bottoms than on ridges. Based upon a significant interaction, the difference among stand types was significant only on ridges.

Table 2 Stand and 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. A-horizon samples were from 0–10 cm depth and B-horizon samples were from 10-20 cm. N = 53 *Pinus echinata, 33 P. strobus,* 20 hardwood, 77 ridge, and 29 bottom sites. CEC = cation exchange capacity

Variable	*P. echinata*	*P. strobus*	Hardwood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
Stand								
O-Horizon Depth (cm)	19.0 ± 2.0^{a}	14.1 ± 2.5^{a}	5.6 ± 2.6^{b}	14.0 ± 1.2	11.8 ± 1.0	15.70*	1.23	0.34
O- Horizon Mass (g m^{-2})	823.9 ± 67.5^{a}	592.4 ± 83.7^{a}	287.1 ± 86.3^{b}	637.7 ± 55.7	497.9 ± 73.1	12.10*	2.32	1.78
Litter C:N Ratio	40.3 ± 1.9^{a}	35.6 ± 2.4^{a}	27.9 ± 1.6^{b}	36.4 ± 0.9	34.6 ± 1.2	9.30*	1.46	4.06*
Stand Age	59.4 ± 2.0^{a}	36.4 ± 2.5^{b}	48.0 ± 2.5^{c}	47.8 ± 1.7	48.1 ± 2.2	0.01	25.87*	0.93^{a}
Soil								
Bulk Density (Mg m^{-3})	1.03 ± 0.02^{ab}	1.08 ± 0.02^{a}	0.96 ± 0.03^{b}	0.98 ± 0.02^{a}	1.07 ± 0.02^{b}	5.73*	9.30*	3.12*
A horizon pH	5.53 ± 0.06^{a}	5.66 ± 0.07^{ab}	5.86 ± 0.14^{b}	5.68 ± 0.06^{a}	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
Organic Matter (%)	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*
Total Carbon (%)	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*
Total Nitrogen (%)	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*
CEC (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
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
Magnesium (mg kg^{-1})	135.7 ± 11.0	164.4 ± 13.4	164.9 ± 15.7	143.0 ± 9.3	167.0 ± 13.3	1.47	0.30	0.96
Phosphorus (mg kg^{-1})	6.9 ± 0.4	7.9 ± 0.6	8.0 ± 0.6	6.3 ± 0.4^{a}	8.9 ± 0.5^{b}	1.22	14.94	2.34
Potassium (mg kg^{-1})	71.3 ± 5.1^{a}	79.8 ± 6.4^{ab}	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*
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
Iron (mg kg^{-1})	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})	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*
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

Table 2 (continued)

Variable	*P. echinata*	*P. strobus*	Hardwood	Ridge	Bottom	Stand Type	ELTP	Stand Type X ELTP
Sulphur (ppm)	11.1 ± 0.3	11.2 ± 0.4	10.4 ± 0.4	11.1 ± 0.3	10.7 ± 0.4	1.16	0.77	2.88
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

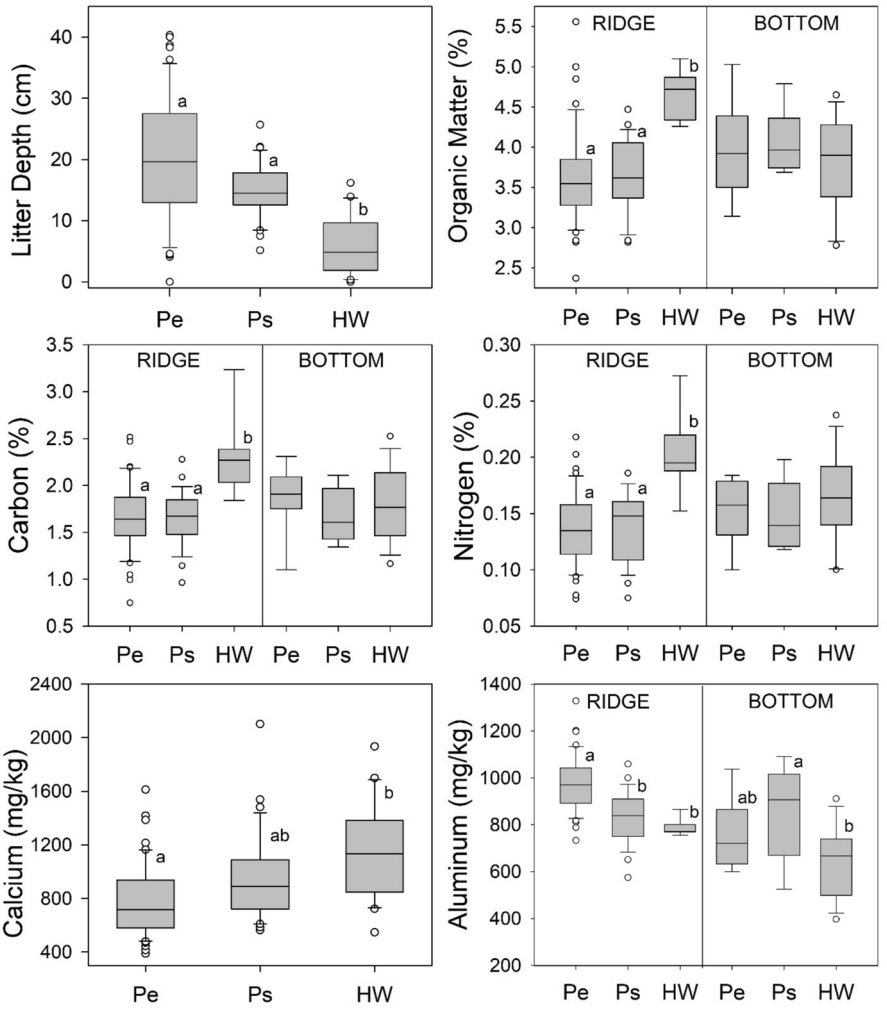

Fig. 1 O-horizon depth and selected soil variables listed by stand type and ELTP for 0- 10 cm depth. Letters represent significant differences in values ($p < 0.05$). Pe = *Pinus echinata*, Ps = *P. strobus*, and HW = hardwood. Split figures represent variables with a significant interaction between factors

Soil Al concentrations (mg kg^{-1}) were significantly greater on ridges than in bottoms (Fig. 1; Table 2). As indicated by a significant interaction term, Al was greater in ridge *P. echinata* stands than in ridge *P. strobus* ($p < 0.001$) and hardwood stands ($p = 0.002$). Al concentrations were also greater in bottom *P. strobus* stands than bottom hardwood stands ($p = 0.002$).

Discussion

In support of our first hypothesis, our study found that decades of *Pinus* occupancy have resulted in changes to soil physical and chemical properties. Overall, *Pinus* stands had thicker O-horizon layers and greater O-horizon mass, less soil organic matter, and reduced nutrient concentrations compared to hardwood sites. Specifically, total N and 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). In our study, we observed O-horizon depths in *Pinus* stands 2–5 times greater than those in hardwood stands. This recalcitrant *Pinus* O-horizon resulted in lower organic matter content in the surface soil of *Pinus* stands, which reduced TC, TN, and micronutrient content, likely due to reduced mineralization. Additionally, the accumulation of O-horizon mass in conifer forests alters moisture and temperature conditions, and may act as a mechanical barrier to germination and establishment of species with low seed weights (Facelli and Pickett 1991; Barbier et al. 2008; Loydi et al. 2013). Conversely, deep O-horizon layers favor the emergence and growth of seedlings of species that produce large seeds, such as *Quercus* spp. (Kostel-Hughes et al. 2005). Across the plots sampled in this study, Duffy et al. (2024) observed a greater density of *Quercus* saplings than *Acer* saplings in *P. echinata* stands compared to hardwood stands, suggesting that conditions under pine trees favored the establishment of *Quercus* reproduction. In addition to microclimate conditions provided by the O-horizon, *Quercus* advanced reproduction has been shown to be positively associated with soil acidity (Kabrick et al. 2014), suggesting that multiple soil characteristics associated with *Pinus* species occupancy favor the regeneration of the genus. Consequently, former *Pinus* plantings may offer an opportunity for managers to more easily establish *Quercus* reproduction in developing stands, particularly on ridges where the genus was historically dominant (Swaim et al. 2018).

We observed greater concentrations of soil Al in *Pinus* stands than in hardwood stands and on ridges than in bottoms. The greatest Al concentrations were found in *P. echinata* stands on ridges where increased acidification under *P. echinata* interacted with reduced buffering capacity in ridge soils to increase the release of Al from silicate minerals and sorption sites (Wright 1989). Increased soil Al content may have contributed to the greater density of *Quercus* spp. and *F. grandifolia* stems observed in *P. echinata* sites across our study plots (Duffy et al. 2024). Seedlings of both of these genera/species have been shown to be more tolerant of 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 is 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). Therefore, old-field sites may have lower CEC and organic matter and may be more susceptible to pH change than

uncultivated fields. In our study, the fact that organic matter and CEC were relatively low across all stand types suggests that past agricultural use may have decreased the amount of organic matter in the soil. *Pinus* stands were slow to replenish organic matter, as is evident in the deep O-horizon and low C and N levels in *Pinus* stands compared to hardwoods.

Our study found lower A and B-horizon pH in *Pinus* stands than in hardwood stands. 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 (Binkley and Valentine 1991; Berg and McClaugherty 2003; Hizal et al. 2013). However, the degree to which planted conifers alter soil conditions depends upon the initial buffering capacity of the soil. Binkley et al. (1989) and Richter et al. (1994) found low pH (4.14–4.97) in conifer plantations on sandy Piedmont soils with low buffering capacity. In a study conducted in southern Illinois, a region with native forest composition and history similar to our study area, Rolfe and Boggess (1973) found pH values under 35 year-old *P. echinata* plantations that were similar to those we observed in our study (pH $\approx$ 5). However, the pH values observed under *P. echinata* by Rolfe and Boggess (1973) did not differ from those observed in adjacent hardwood stands, suggesting greater buffering capacity in the underlying soil compared to our study site. In a study conducted on glaciated soils in east-central Indiana, Lesko et al. (2024) found pH values ranging from 4.25–4.57 in samples taken to 20 cm, which were comparable to what we observed in our B-horizon samples taken at 10–20 cm.

Pinus species in southern Indiana and across the eastern US were planted on degraded agricultural land to accelerate site recovery by stabilizing soil to prevent further erosion (Sieber and Munson 1994). Without planting, research has found that the establishment of native hardwood species on these sites may take a decade or more (Peroni 1994; Jenkins and Parker 2000). However, across the variables we analyzed, we observed more productive soils in hardwood stands than in *Pinus* stands, suggesting that gains in recovery from *Pinus* plantings were overcome, with time, in naturally regenerated stands despite the time lag required for native hardwood species to establish.

The greater productivity of hardwood soils in our study was a product of the native hardwood species that established after abandonment of degraded agricultural land. Foliage of *Liriodendron tulipifera*, the dominant species in our hardwood stands on both ELTPs (Duffy et al. 2024), 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 our study area prior to clearing for agriculture (Jenkins and Parker 1998; Morrissey et al. 2008; Swaim et al. 2018). *Liriodendron tulipifera* contributes to improved soil nutrient availability following old-field succession (Kalisz 1986). Base saturation, especially with Ca, increases because *L. tulipifera* roots accumulate nutrients and keep nutrient cycling near the surface, promoting nutrient rich humus. Litter from two other common native species, *A. saccharum* and *L. benzoin*, decays rapidly and contains high concentrations of N and water-soluble compounds, especially Ca

(Chandler 1941; Jenkins et al. 2007). Similarly, foliage of *Cornus florida,* a common understory species in bottom *P. strobus* stands in our study (Duffy 2014), accumulates Ca and other cations 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 support of our second hypothesis, we observed differences in soil variables in response to *Pinus* occupancy between ELTPs with more pronounced differences on ridges compared to bottoms. Soils on bottoms were better buffered than those on ridges, as is evidenced by greater CEC and nutrient availability resulting from upland sources of alluvium (Zhalnin 2004). These conditions may have allowed hardwood species to establish on the site and recruit into the subcanopy and canopy of *P. echinata* and *P. strobus* stands. *Liriodendron tulipifera* and *A. saccharum* each comprised 6% of the living basal area in bottom *P. echinata* stands (Duffy et al. 2024). *Acer rubrum* and *Prunus serotina* each comprised 5% of the basal area of *P. strobus* stands in bottoms. The establishment of hardwood stems in *Pinus* stands may have further reduced the impacts of litter and root inputs from *Pinus* species (Read 1991; Schuster and Dukes 2014). Additionally, hardwood stands in bottoms also contained the greatest species richness of subcanopy and canopy trees across our six stand types. (Duffy 2014). Although *L. tulipifera* and *A. saccharum* litter has been shown to increase soil cation levels, these other species may have mixed effects on the productivity of soils in *Pinus* stands (Reinsvold and Reeves 1986; Willis 2000; Leroy and Marks 2006; Williams et al. 2013).

Our study quantified differences in soil chemistry following long-term occupancy by *Pinus* species and identified differences in the O-horizon that influence acidity and nutrient inputs among stand types. However, our study did not consider the biomass or annual production of fine roots. Below ground inputs constitute a major component of annual productivity in hardwood forests, Newman et al. (2006) estimated that 54% of total net primary productivity was allocated belowground over a two-year period in Kentucky forests. Below ground turnover may have been an important input of nutrients in our study. Research has shown that annual production of fine roots differs between forest types with greater annual production in hardwood stands compared to conifer stands (Park et al. 2008; Wang et al. 2020). Consequently, how belowground inputs have contributed to soil chemistry differences between *Pinus* and hardwood stands is a potential area of future study in hardwood forests.

Conclusions

Decades of occupancy by *Pinus* species in plantations have altered soil physical and chemical properties in southern Indiana forests relative to soils in areas that underwent natural succession to hardwoods. In *Pinus* stands, we observed thicker O-horizon layers, less soil organic matter, and lower cation concentrations than in hardwood stands. In addition, total N and total C were lower in *Pinus* than in hardwood stands, but Al content was higher. Changes that we observed, compared to other conifer studies, suggest that the degree to which *Pinus* species 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 we 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 hardwood sites have been shown to increase soil nutrient content and may have contributed to site recovery. *Pinus* and hardwood stands in bottoms were more similar than *Pinus* and hardwood stands on ridges because of increased soil buffering capacity and the intermixing of hardwood 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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Data Availability Data will be made available upon request.

Declarations

Ethics Approval None to declare.

Consent to Participate Not applicable.

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