

Pine savanna restoration on agricultural landscapes: The path back to native savanna ecosystem services

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Abstract

Restoration of savanna ecosystems within their historic range is expected to increase provision of ecosystem services to resident human populations. However, the benefits of restoration depend on the degree to which ecosystems and their services can be restored, the rate of restoration of particular services, and tradeoffs in services between restored ecosystems and other common land uses. We use a chronosequence approach to infer multi-decadal changes in ecosystem services under management aimed at restoring fire-dependent pine savannas, including the use of frequent prescribed fire, following abandonment of row-crop agriculture in the southeastern U.S. We compare ecosystem services between restored pine savannas of different ages and reference pine savannas as well as other common land uses (row-crop agriculture, improved pasture, pine plantation, unmanaged forest). Our results suggest that restoring pine savannas results in many improvements to ecosystem services, including increases in plant species richness, perennial grass cover, tree biomass, total ecosystem carbon, soil carbon and C:N, reductions in soil bulk density and predicted erosion and sedimentation, shifts from soil fungal pathogens to fungal symbionts, and changes in soil chemistry toward reference pine savanna conditions. However, the rate of improvement varies widely among services from a few years to decades. Compared to row-crop agriculture and improved pasture, restored savannas have lower erosion, soil bulk density, and soil pathogens and a higher percentage of mycorrhizal fungi and ecosystem carbon storage. Compared to pine plantations and unmanaged forests, restored pine savannas have lower fire-prone fuel loads and higher water yield and bee pollinator abundance. Our results indicate that restoration of pine savanna using frequent fire provides a broad suite of ecosystem services that increase the landscape's overall resilience to climate

change. These results are likely relevant to other savannas dominated by perennial vegetation and maintained with frequent fire.

Keywords

prescribed fire; bee pollinators; old field succession; soil restoration; hydrological modeling; fungal community

1. Introduction

Providing basic needs of human populations while sustaining or restoring naturally functioning ecosystems on which humans depend is a central challenge of natural resources management. The challenge is particularly great in regions historically dominated by old-growth savannas (*sensu* Bond and Parr, 2010; Ratnam et al., 2011; Veldman et al., 2015a) characterized by dominance of perennial C4 grasses, diverse herbaceous plant communities, dependence on frequent fire, and limited tree canopy cover (Bond and Parr, 2010; Veldman et al., 2015a). Such savannas provide a host of ecosystem services (Bengtsson et al., 2019; Zhao et al., 2020), but they have disappeared in most places because of agriculture, fire exclusion, and overgrazing (Bond and Parr, 2010; Carbutt et al., 2011). Most native savannas that remain are unprotected or poorly managed and continue to be lost, increasing the need to restore them when intensive land uses are abandoned (Nerlekar and Veldman, 2020).

Ecosystem restoration is generally thought to increase the number of ecosystem services that sustain societies (Alexander et al., 2016). However, the net benefit of services provided by ecosystem restoration is often limited by the time required for restoration (Dodds et al., 2008), which typically corresponds to direct costs of restoration and the opportunity cost of foregoing more profitable land uses (Alexander et al., 2016; Jessop et al., 2015). Time required for restoring particular aspects of savanna ecosystems vary widely, ranging from less than a year

(e.g., planting dominant plant species) to decades or centuries (e.g., development of plant and microbial communities) (Rohr et al., 2018; Rydgren et al., 2020; Ziter et al., 2017). Full restoration of natural ecosystems is generally unachievable within periods of human study because of financial, political, and ecological constraints (Buisson et al., 2018; Jones et al., 2018; Nerlekar and Veldman, 2020; Rohr et al., 2018). Thus, in addition to understanding benefits provided by remnant native ecosystems, it is important to quantify the benefits of partial restoration that can be accomplished within reasonable management timeframes (Alexander et al., 2016).

Although characteristics of savannas vary greatly worldwide, approaches to their restoration and capacity for restoration to improve ecosystem services show general trends. Restoration typically involves cessation of soil disturbance, removal of non-native plant species, regulation of grazing, reestablishment of historic fire regimes, and dependence on passive dispersal and succession, as needed (Buisson et al., 2018; Diaz-Toribio and Putz, 2017; Fensham et al., 2016; Jones et al., 2018; Redhead et al., 2014; Ren et al., 2016). Planting native plant species also provides some restoration benefits (Cox et al., 2004; Klopff et al., 2017), but its effectiveness tends to be limited (Jones et al., 2018; Ren et al., 2016) because of high costs and limited numbers of species with available and viable seeds (Buisson et al., 2018; Walker and Silletti, 2007). Results of restoration have generally shown increases in plant species richness (Kirkman et al., 2004; Redhead et al., 2014) and overall biodiversity (Barral et al., 2015), transition from forb dominance to grass dominance (Blackburn et al., 2020), shift from annuals to long-lived perennials with less persistent seed banks and lower seed dispersal capability (Clark et al., 2019; Redhead et al., 2014), more abundant and diverse native insect populations (Ulyshen et al., 2020), increases in soil organic matter and C:N (Berg and Hemerik, 2004;

Brudvig et al., 2021; Klopff et al., 2017), decreases in soil nutrients and pH (Berg and Hemerik, 2004; Maharning et al., 2009), and shifts from pathogenic to symbiotic soil fungi and bacteria (Bach et al., 2010; Bauer et al., 2015). These improvements correspond to increased soil carbon sequestration (Deng et al., 2015), robust pollinator communities (Brudvig et al., 2021), reduced soil erosion and sedimentation (Dodds et al., 2008), improved aquifer recharge (Honda and Durigan, 2016), and recovery of imperiled animal species (Cox and Slater, 2007; Greene et al., 2019; Palmer and Sisson, 2017; Wood et al., 2008). Limitations to full restoration to native savannas following intensive soil disturbance also show general trends, including limited seed dispersal, slow clonal reproduction, and non-persistent seed banks of many perennial plant species eliminated by soil disturbance (Buisson et al., 2018; Veldman et al., 2015a), colonization by non-native or off-site species exacerbated by changes in soil nutrient levels (Andrade et al., 2015; Buisson et al., 2018), limited proximity and availability of reference sites (Herrmann et al., 2016), slow recovery of soil microbial communities (Turley et al., 2020), and persistent changes in soil structure (Brudvig et al., 2021).

While ecosystem restoration is expected to increase multiple ecosystem services, intensive land uses for producing specific commodities can provide certain services at equal or higher levels than natural or restored ecosystems (Bullock et al., 2011; Jellinek et al., 2019; Jessop et al., 2015; Power, 2010). For example, afforestation for timber products in areas historically dominated by savannas can increase sequestration of atmospheric carbon at higher levels than historic conditions, though at the cost of native biodiversity (Armstrong and van Hensbergen, 1996; Bond and Parr, 2010; Martin et al., 2014; Joseph W. Veldman et al., 2015) and water yield (Brantley et al., 2018; Farley et al., 2005; Jackson, 2005). Consequently, evaluating the capacity for restored savannas to provide net improvements in ecosystem services

requires consideration of multiple individual services compared among alternate land uses that are locally likely to exist in the absence of restoration (Alexander et al., 2016).

In this study, we use a chronosequence approach to infer multi-decadal changes in multiple ecosystem services during restoration of pine savannas in the North American Coastal Plain (Noss et al., 2014) following abandonment of row-crop agriculture and establishment of a frequent prescribed fire regime. The ecosystem services studied relate to native plant biodiversity, vegetation structure, carbon sequestration, soil nutrients, bee pollinator abundance and diversity, soil fungi functional guilds, soil stability, and hydrological function. We compare each ecosystem service among partially restored pine savannas at different times since abandonment of agriculture, reference (native, never farmed) pine savannas, and other dominant land uses (row-crop agriculture, improved pasture, pine plantation, unmanaged forest) to address the following hypotheses: Ecosystem services provided by restored pine savanna will 1) exceed the level of the initial state of row-crop agriculture, 2) approximate the level of reference pine savanna, and 3) exceed levels of other common land uses over the course of approximately one century. We further interpret the rates of such improvements for their implications to management. Although restored sites in this study are all on former row-crop agricultural land, we consider the results to apply to restoration following other intensive land uses where native vegetation was eliminated and fire was excluded, with the caveat of potential differences in soil disturbance, fertilizer application, and presence of non-native species. We further consider the results to apply broadly to savannas and grassy biomes sharing similar characteristics of C4 grass dominance and high diversity of perennial native plants dependent on frequent surface fires (Bond and Parr, 2010; Nerlekar and Veldman, 2020).

2. Materials and methods

2.1 Study area

We conducted our study within the Red Hills Region of northern Florida and southwestern Georgia, USA (Fig. 1a). The Red Hills Region encompasses approximately 180,000 ha ranging in elevation from about 50-100 m above sea level with mean annual minimum and maximum daily average temperatures of 13.1 °C and 26.2 °C and mean annual precipitation of 1,350 mm (National Climate Data Center 2019, Thomasville, GA, USA). Upland soils are sandy loams and loamy sands in the Ultisol order (Calhoun, 1979). Prior to European colonization, uplands were dominated by pine savannas characterized by an open canopy of mostly longleaf pine (*Pinus palustris* Mill.) and shortleaf pine (*P. echinata* Mill.), with a diverse understory of C4 grasses, forbs, and resprouting woody plants (Ostertag and Robertson, 2007; Van Lear et al., 2005). Fires initiated by lightning or humans occurred mostly at 1-3 year intervals (Frost, 1998; Stambaugh et al., 2011). Such frequent fires are required to maintain native plant species richness (Glitzenstein et al., 2012) and provide habitat to native animal species (Palmer and Sisson, 2017).

Following European colonization in the 1500s, uplands in the region were mostly used for agriculture or frequently burned for cattle grazing (Ackerman, 1976; Paisley, 1989). From the 1880s to the 1930s, most land in the region was purchased for estates to hunt northern bobwhite (*Colinus virginianus* L.). During that period, many agricultural fields were abandoned, burned at mostly two year intervals in late winter or early spring, and allowed to succeed to old-field pine savannas, which we will refer to as “restored” whether or not fully characterizing reference pine savannas that have never been tilled or long-fire excluded (Rother et al., 2020). A slow trend of field abandonment has continued until today. Approximately 140,000 ha of uplands within the region continues to be managed as pine savannas maintained with prescribed fire and selective

timber harvests to maintain basal area within a range of 5-16 m² ha⁻¹, of which approximately 10,000 ha are reference pine savannas (Ambrose, 2001) as described above. Restored pine savannas have passively become dominated by loblolly pine (*P. taeda* L.) and shortleaf pine (Matusick et al., 2020; Robertson et al. 2021) or have been planted in longleaf pine. The herbaceous layer is mostly a subset of plant species found in reference savannas, but has a greater proportion of forbs and shrubs (Ostertag and Robertson, 2007). A significant portion of the region's uplands are also occupied by land uses typical of the southeastern U.S. Coastal Plain, including row-crop agriculture for cotton (*Gossypium hirsutum* L.), peanuts (*Arachis hypogaea* L.), corn (*Zea mays* L.), and soybeans (*Glycine max* (L.) Merr.), commercial pine plantations of mostly loblolly pine for fiber and wood production with little or no prescribed fire, improved pasture of mostly non-native bahiagrass (*Paspalum notatum* Flueggé) for livestock or hay, and unmanaged, closed-canopy pine and broadleaf forests arising from fire exclusion (Kurz, 1944). Wetlands that infrequently carry fire and are mostly dominated by closed-canopy broadleaf forests are not the subject of this study.

2.2 Experimental design

We established study plots in the following upland land cover categories: row-crop agriculture, restored pine savanna where agriculture was abandoned 5-15, 15-30, 30-50, 50-75, or 75-100 years prior, reference pine savanna, improved pasture, pine plantation, and unmanaged forest (further described in Table 1), with 11-15 replicates per category (average of 12.8, 128 plots total). Plots representing each land cover category were distributed approximately evenly among four study areas (Fig. 1b; 2-4 plots per category per area). Study areas were named after large private properties where most plots were established but included other local properties.

We measured plots during the growing season in 2017 in the Tall Timbers and Livingston Place study areas and in 2018 in the Pebble Hill and Avalon areas. We obtained historic aerial photographs from the U.S. Geological Survey EROS Earth Explorer or National Archives covering each area for each decade from the 1930s or 1940s to the present. Photographs were georectified in ArcMap 10.5 (ESRI Inc., Redlands, CA) to interpret time since abandonment of agriculture and determine plot locations. In restored savanna plots, we sampled the largest pine tree with an increment borer to approximate the age of the stand using ring counts to confirm our interpretation of aerial photographs. We chose plot locations that avoided spatial clustering within land cover categories by allowing only one plot within a contiguous area of a given land use, such as a field, pasture, or prescribed burn unit covering at least 5 ha, as confirmed by a test for spatial autocorrelation based on Euclidean distance (Moran's $I = 0.0976$, $P=0.145$).

Descriptions and criteria for land uses studied are presented in Table 1. We field checked restored and reference pine savannas for respective indicator species to confirm their status (Brudvig et al., 2013; Kirkman et al., 2004; Ostertag and Robertson, 2007).

To justify using a chronosequence approach to infer long-term ecosystem change, we considered evidence for the assumption that initial conditions and subsequent changes have been reasonably similar among locations, i.e., the environment is stationary (Cushman, 2010; Damgaard, 2019; Pickett, 1989). In addition to confirming lack of spatial autocorrelation of plots, we selected plot locations within the same soil suborder (Paleudult or Kandiudult great groups; Appendix A, Tables S1, S2) and similar upland topographic positions (ridge tops or upper slopes not exceeding a 5 % gradient). Soil texture measured to 20 cm depth was not significantly different among land use categories (Appendix A, Table S3). Crop rotations and fertilization rates of row-crop sites representing the initial state before pine savanna restoration

have not changed considerably during the past century, mostly involving rotations between nitrogen-fixing legumes (peanuts, soybeans, alfalfa (*Medicago sativa* L.), cowpeas (*Vigna unguiculata* L. (Walp.))) and cotton or corn, application of lime to adjust pH to 5.5-6.5, and addition of N, P, and K fertilizers at similar rates (Bennett, 1921; Mylavarapu et al., 2020). Our assertion that 2-year prescribed fire intervals have been applied to restored and native pine savannas over the past century is based on habitat requirements for northern bobwhite quail for which the properties have been managed (Palmer and Sisson, 2017; Stoddard, 1931), local oral and written history (Crawford and Brueckheimer, 2012; Paisley, 1981; Way, 2011), and local dendrochronological evidence (Rother et al., 2020). Although we did not observe most fires, 2-year interval fires in local reference and restored pine savannas are described elsewhere (Reid et al., 2012; Robertson and Ostertag, 2007).

Invasive non-native species have not yet had a strong influence on restored pine savannas, except for encroachment of *Paspalum notatum* in some areas with recent soil disturbance (Stawowy and Robertson, 2019). The proximity and extent of reference pine savannas providing seed sources has not changed much judging from historic aerial photographs and a more recent regional assessment (Ambrose, 2001), and climate in the region has changed little during the past century (Irizarry-Ortiz et al., 2013).

2.3 Data collection

We collected biomass, tree, and soil data in June-August to correspond to the peak of the growing season when plants were presumed to have seasonal maximum levels of biomass. We identified plants and collected bee pollinators in September-October when the largest portion of plant species were flowering to facilitate plant identification and maximize bee collection. In pine savanna plots which were burned biennially, we took measurements in the second growing

season following the previous fire (approximately 1.5 years post-fire) when plants were at their maximum state of post-fire development before being burned again. Measurements were designed to ultimately provide a single value per plot ($N = 128$) for analysis of each variable of interest, described below.

2.3.1 Herbaceous plants and trees

To estimate variables representing ecosystem services related to the plant community (species richness, perennial grass cover, legume cover), we measured plant species composition and cover in all plots. We identified to species all plants under 2 m tall within a 100 m² area and visually estimated percent cover by assigning one of ten modified Daubenmire (1959) cover classes. In order to estimate herbaceous biomass and dead fuel biomass, we sampled live herbaceous plant biomass, fine litter (dead leaves and herbs and woody material litter <0.6 cm diameter) and coarse litter (woody material 0.6-2.5 cm) by clipping and collecting material to the soil surface within 0.25 m² quadrats at three points systematically located 6 m from the plot center. These three categories of biomass compose the great majority of fuel consumed in the studied community types (Reid et al. 2012). The samples were oven-dried for 24 hours at 70 °C and weighed. In savanna and forested sites, tree biomass was estimated by recording species and measured diameter at breast height (dbh; 1.4 m) for all trees ≥ 2.0 cm dbh within a fixed radius from the plot center. The radius was adjusted in 5 m increments to include at least five trees and ranged from 10-20 m. We then estimated tree biomass using allometric equations for the respective species (Clark et al., 1986; Gonzalez-Benecke et al., 2018; Sabatia et al., 2008; Van Lear et al., 1986).

2.3.2 Bee pollinators

We considered pollinator ecosystem services by measuring bee species richness and abundance. We collected samples in all plots once per week for 5 weeks for the 2017 plots and 6 weeks for the 2018 plots using pan traps (Leong and Thorp, 1999). Three traps (blue, white, and yellow) per plot were placed on wire stands approximately 25 cm above the ground and arrayed in a circle 3 m from the plot center. We filled traps with soapy water and collected them after 3 days. We strained bees and other insects from the water and stored them in 95% ethanol, then later removed, dried, and pin mounted bees with collection data and identified them to the finest taxonomic level possible, typically species. Bee species richness per land cover category was rarefied using EcoSim version 7.0 (Gotelli and Entsminger, 2011) to correct the measurements for variation in bee abundance that may have been attributable to variation in visibility of pan traps in different environments. Rarefaction allowed us to interpolate the bee species richness as if the number of all bees collected per plot location were equal to a standard sample size (45 bees, 5-6 sampling periods combined). Even so, there were not enough bees in the unmanaged plots at Avalon and Livingston Place or the pine plantation at Livingston Place to include in the analysis.

2.3.3 Total Ecosystem carbon

We estimated total ecosystem carbon using measurements of herbaceous plant and tree biomass described above and additional measurements. We estimated live woody biomass per unit area by identifying to species all woody plants under 2 m tall within a 3 m radius from the plot center, measuring stem diameter within 3 cm of the soil surface, and using locally determined allometric equations predicting stem and leaf biomass (Robertson and Ostertag, 2009). To estimate the contribution of dead woody material larger than the fuel size classes, we recorded diameter of surface woody debris >2.5 cm in diameter intersecting 20 m transects in

each cardinal direction from the plot center to calculate wood volume and approximate biomass (Brown, 1974). We sampled soil at 15 locations within 10 m of the plot center using a 2.5 cm diameter soil corer to 20 cm depth. Soil was analyzed by the University of Florida Soil Extension Laboratory to determine total organic carbon. This value was multiplied by two to estimate carbon to 1 m depth (Butnor et al., 2017; Jobbágy and Jackson, 2000; Knops and Bradley, 2009). We also estimated root biomass, assumed to be 30% of above-ground biomass for canopy trees (Cairns et al., 1997) and 100% of above-ground biomass of resprouting woody plants, based on excavations of common resprouting woody plants at 1.5 years post-fire (Robertson unpublished data). We estimated total ecosystem carbon by assuming that biomass was composed of 50% carbon (Vashum and Jayakumar, 2012) and summing carbon measurements per unit area from all the carbon sources measured.

2.3.4 Soil chemistry

The soil samples described above were further analyzed by the same laboratory to determine concentrations of nitrogen, calcium, magnesium, phosphorus, and potassium as well as pH. We also used samples to determine soil texture (% sand, silt, and clay) and measured soil bulk density to convert concentrations to mass per hectare within the depth range sampled. Details of soil collection and analysis are provided in Appendix A, Section S1.

2.3.5 Soil fungi

To characterize the dominance of different fungal functional guilds among land cover categories, we analyzed soil for fungal guild composition. We collected five soil samples at each plot to a depth of 10 cm using a 2 cm diameter soil corer. We combined samples within each plot, placed them in plastic bags, and kept them in a cooler with freezer packs until transferred to a freezer (-18°C). Following homogenization, we shipped overnight a 25 g sub-sample from each

plot to the University of Kansas where samples were kept at -80 °C until analyzed. We assessed the fungal community composition using a standard DNA metabarcoding approach, described in detail in Appendix A Section S2. Briefly, we created amplicon libraries of the ITS2 gene region (Ihrmark et al., 2012), sequenced these on an Illumina MiSeq (San Diego, CA), and processed normalized data through the Qiime2 pipeline using an operational taxonomic unit (OTU) approach (Semenova-Nelson et al., 2019). We categorized soil fungal OTUs by functional guild by matching them to the FUNGuild database (Nguyen et al., 2016) and used only assignments with confidence ranking of probable or highly probable. Overall, 55.2% of OTUs were assignable to a functional guild using FUNGuild and 71.1% of those assigned had confidence rankings of probable or highly probable. We classified the OTUs into 6 functional guilds: plant pathogens, other/unspecified pathogens, saprotrophs, endo/mycorrhizal, endomycorrhizal, and ectomycorrhizal. We calculated the percentage of OTUs found in each guild for each plot. If an OTU was assigned to more than one guild, we counted it as a proportional fraction of one for each guild.

2.3.6 Erosion and hydrological model

To predict runoff, sedimentation, plant transpiration, evapotranspiration, deep percolation, and water yield at the local scale, we used field data collected at plots (see above subsections 2.3.1, 2.3.3, and 2.3.4) as input to the Water Erosion Prediction Project (WEPP version 2012.800; Flanagan and Nearing, 1995) analytical model. Additionally, we estimated tree canopy cover and canopy leaf area index using vertically upward-oriented hemispherical photographs taken at the plot center from 1.0 m above the ground and interpreted using Gap Light Analyzer version 2.0 (Frazer et al., 1999). We estimated leaf area index (LAI) of surface vegetation by taking photographs of the surface vegetation at angle of 57° and interpreting them

using GreenCrop Tracker version 1.0 (Liu and Pattey, 2010). Measurement of field data at the height of the growing season and, where applicable, maximum time since fire provided approximate upper limits on vegetation-related input variables such as maximum standing live biomass, soil surface litter cover, and perennial grass cover. However, WEPP models day-to-day changes in vegetation and hydrological variables in response to recent historic weather patterns in the area, soil physical characteristics, and management actions including biennial prescribed burning of pine savannas, tilling and planting of crop fields, and mowing or grazing of pastures. In addition to field measured data, we used interviews with land managers to obtain information on specific management practices for row-crop and pasture sites used in WEPP modeling. Model parameter meta-data and description of variables used for model input are provided in Appendix A Section S3 and descriptions of predicted variables are provided in WEPP documentation (ars.usda.gov).

2.4 Data analysis

We compared native plant species richness, perennial grass cover, legume cover, herbaceous plant biomass, tree biomass, dead fuel (<2.5 cm thickness) biomass, bee abundance, bee species richness, percentage of each fungal guild, and predicted hydrological and erosion variables among land cover categories and study areas using mixed models ANOVA in SYSTAT version 13 (SYSTAT Software, Inc.) with plot as the unit of replication. Land cover category was a fixed effect, and study area and the interaction between study area and land cover category were random effects. Response variables were log or square root transformed as necessary to meet the normality assumption. Fisher's LSD multiple comparison test was performed following all tests that had an overall significant land cover category effect at $\alpha = 0.05$.

We also performed a non-metric multi-dimensional scaling (NMS) analysis using PC-ORD v. 7 (McCune and Mefford, 2018) to visualize and interpret overall differences among land cover categories with regard to multiple ecosystem service variables measured and relationships among the variables, using plot as the unit of replication. The plotted ordination included vectors indicating the relationships between axes and specific variables. Some variables that were highly correlated with others were excluded for readability but are reported in the results.

3. Results

The 100 m² vegetation plots contained a total of 460 plant species, of which 64 were non-native including four planted crops (Appendix A Table S4). Assuming the chronosequence represents changes in land cover over time, native plant species richness in restored pine savannas rapidly surpassed that of row-crop agriculture, pasture, and unmanaged forest and eventually that of pine plantations as it increased toward, but not equal to, levels of reference pine savannas (Fig. 2A). Percentage of plant species that were perennial increased from 23% in row-crop plots to 64% in 5-15-year-old restored pine savannas to 83% in 75-100-year-old restored pine savannas compared to 88% in reference savannas (data not shown). Perennial grass cover in restored savannas surpassed that of row-crop agriculture, pine plantations, and unmanaged forests by 15-30 years post-agriculture, but it remained lower than reference pine savannas and pastures (Fig. 2B). Legume cover in restored pine savannas was greater than in row crops, pasture, pine plantation, and unmanaged forests by 15-30 years post-agriculture, at which point it was similar to reference pine savannas (Fig. 2C). Herbaceous biomass in row-crop and pasture sites was higher than in restored and reference pine savannas, which in turn had higher values than pine plantations and unmanaged forests, regardless of time post-agriculture (Fig. 2D). Tree biomass in restored pine savannas was generally similar to reference pine savannas,

slightly lower than in pine plantations by the end of the chronosequence, and lower than in unmanaged forests throughout; there were no trees in row crop or pasture plots so they were not included in the analysis (Fig. 2E). Dead fuel biomass was negligible in row crops and pastures, increased upon restoration of pine savannas to levels similar to reference savannas, and was generally lower than in pine plantations and much lower than in unmanaged forests throughout the chronosequence (Fig. 2F).

We trapped a total of 2,793 bees representing 77 species (Appendix A Table S5). Although analysis of bee species composition is beyond the scope of this study, we note that only ten individual bees were the domesticated honey bee (*Apis mellifera* L.), even though hives of this species were kept on most of the studied properties. Bee abundance was much higher in row-crop and pasture plots than in all other land cover categories (Fig. 2G). Bee abundance did not vary with age of restored pine savanna or between restored and reference savannas, but savannas had higher bee abundance than pine plantations and unmanaged forests (Fig. 2G). Bee species richness rarified to 45 bees maximum was similar among most land cover categories except for pine plantation and unmanaged forest types, which respectively had 46% and 71% lower species richness than pine savanna land cover categories averaged together (Fig. 2H).

Total ecosystem carbon in restored savannas increased with time since restoration over the first 30 years of the chronosequence (Fig. 2I). Otherwise it was similar to reference pine savannas and pine plantations, higher than in pastures, and lower than in unmanaged forests (Fig. 2I). Soil carbon changed little from row-crop agriculture to restored pine savannas and was similar to pine plantations during most of the chronosequence, until 75-100 years, when it increased to levels similar to reference pine savannas, pastures, and unmanaged forests (Fig. 2J). Soil nitrogen levels in restored pine savannas did not change notably following abandonment of

agriculture and were similar to reference pine savannas, pine plantations, and unmanaged forests throughout the chronosequence, though it remained lower than in pastures (Fig. 2K). Soil C:N in restored pine savannas gradually increased with time since agriculture toward levels of reference pine savannas, ultimately exceeding levels for pasture and pine plantations but not unmanaged forests (Fig. 2L).

Levels of soil mineral nutrients (calcium, potassium, magnesium, phosphorous) in restored pine savannas generally decreased with time since conversion from row-crop sites toward levels of reference savannas, pine plantations, and unmanaged forests, with most of the change occurring early in the chronosequence (5-30 years post-agriculture; Fig. 3A-D). Levels of mineral nutrients were also lower in restored pine savannas than in pasture during most time periods post-agriculture (Fig. 3A-D). High variation in mineral nutrient levels among study areas, in particular high mineral nutrient levels at Avalon early in the chronosequence, resulted in significant interactions between area and land cover category (Appendix A, Fig. S3). Levels of soil pH showed a pattern similar to mineral nutrients except that pine savannas and pine plantations had higher pH than unmanaged forests (Fig. 3E). Bulk density showed a weak downward trend with time since restoration toward levels of reference savannas and pine plantations, remaining lower than in pastures and higher than in unmanaged forests (Fig. 3F).

Percentage of plant pathogens showed a decreasing trend with time post-agriculture toward levels of reference pine savannas and pine plantations, with lower levels than pastures and higher levels than unmanaged forests throughout the chronosequence (Fig 4A). Percentages of other or unspecified pathogens (Fig. 4B) and saprotrophs (Fig. 4C) did not vary significantly over the chronosequence and was similar to reference savannas and pine plantations throughout, though restored savannas consistently had fewer saprotrophs than pastures and more than

unmanaged forests. Percentage of non-mycorrhizal endophytes varied little over the chronosequence, but it was generally higher in restored savannas than in reference pine savannas and pastures and similar to pine plantations and unmanaged forests (Fig. 4D). Percentage endomycorrhizal fungi showed an approximately inverse pattern to the above mentioned guilds, with lowest values for row-crop and pasture sites and increasing values with age of restored pine savanna toward levels of reference pine savanna, pine plantation, and unmanaged forests (Fig. 4E). Percentage ectomycorrhizal fungi had a similar pattern except that it had higher values in unmanaged forest than in other land cover types (Fig. 4F).

Runoff and sediment yield predicted by WEPP were much higher for row-crop agriculture and slightly higher for pasture than other land cover categories, but otherwise they varied little over the chronosequence or among land uses (Fig. 4G,H). Predicted transpiration increased from row-crop agriculture to younger restored pine savannas, then decreased again toward levels of reference pine savanna, which had lower values than pasture, pine plantation, and unmanaged forest (Fig. 4I). Predicted evapotranspiration showed a similar pattern, except that pasture had lower evapotranspiration than pine savanna (Fig. 4J). Deep percolation showed an inverse pattern to transpiration and evapotranspiration, remaining higher in restored savannas than in pine plantations at most times post-agriculture and in unmanaged forests at all times (Fig. 4K). Total water yield (runoff + deep percolation) showed a similar pattern, except that row-crop agriculture showed higher predicted water yield than all other land cover categories (Fig. 4L). Predicted evapotranspiration, deep percolation, and water yield showed significant interactions between areas and land cover categories, mostly because of high variation among properties in restored pine savannas and pine plantations (Appendix A, Fig. S5).

The NMS analysis including all measured variables relating to ecosystem services shows that plots were clustered according to land cover category though with considerable overlap in some cases (Fig. 5). Vectors for bee species richness and bee abundance were combined, as were plant transpiration and evapotranspiration, because of their high correlation. Row crop and pasture sites were similar in having high herbaceous biomass, mineral nutrient levels, pH, soil nitrogen, bee abundance and species richness, percent fungal pathogens, runoff, and water yield, and low tree biomass, total ecosystem carbon, dead fuel biomass, and percent endomycorrhizal and ectomycorrhizal fungi. Pastures were distinguished from row crops along axis 2 corresponding to their higher perennial grass cover. Pine plantations and unmanaged forests showed opposite trends to the variables listed above, with unmanaged forests representing the greater extreme for tree biomass, ecosystem carbon, dead fuel biomass, and endomycorrhizal and ectomycorrhizal fungi (Fig. 5). Restored and reference pine savannas occupied a central location regarding the above listed variables. They additionally showed a gradient from young to older restored pine savannas to reference pine savannas corresponding to increasing numbers of native plants, soil carbon, and perennial grass cover (Fig. 5).

4. Discussion

Changes in most ecosystem services studied were consistent with our hypothesis that services would increase relative to row crop sites with increasing time since abandonment of agriculture and initiation of pine savanna restoration. Consistent with the goals of restoration, the most notable improvements were in supporting services similar to those provided by reference pine savannas. These changes were generally consistent with those noted in other studies of old-growth grassland and savanna restoration, with citations relating to particular ecosystem services provided below. Improvements in many of the variables associated with ecosystem services were

significant within 5-15 years post-agriculture, especially those relating to development of the plant community, including increases in native plant species richness (Inouye et al., 1987; Redhead et al., 2014), perennial grass cover (Blackburn et al., 2020; Clark et al., 2019; Zhang et al., 2017), and total ecosystem carbon (Wang et al., 2021). There were also decreases in soil plant pathogens and increases in percentage of soil ectomycorrhizal fungi within 15 years, consistent with studies indicating a shift from antagonistic to mutualistic plant-fungal interactions during succession (Bach et al., 2010; Bauer et al., 2015; Maharning et al., 2009; Nara et al., 2003; Zhang et al., 2017). Predicted runoff and sediment yield also decreased rapidly, attributable to soil stabilization by increasing perennial vegetation cover (Schilling et al., 2008; Udawatta et al., 2006; Zhao et al., 2020), despite brief increases between fires and the rapid recovery of resprouting perennial vegetation as modeled by WEPP. Within 30 years, mineral nutrients (Ca, K, Mg, and P) all had decreased significantly (Berg and Hemerik, 2004; Maharning et al., 2009), presumably because of cessation of fertilization and uptake by trees and other perennial plants (Nair et al., 2007) and possibly some loss to lofting of ash during fires (Hough, 1981; Raison et al., 1985). Levels of pH similarly decreased (Barber et al., 2017) corresponding to time since cessation of liming agricultural fields. Percent legume cover also cover increased within 30 years (Blackburn et al., 2020), as did soil C:N (Klopf et al., 2017; Knops and Tilman, 2000; Maharning et al., 2009) reflecting stable levels of soil nitrogen and increasing soil carbon. Over longer periods of time (>50 years), soil C increased relative to initial conditions as in other restored savannas and grasslands (Bach et al., 2010; Barber et al., 2017; Knops and Bradley, 2009; Zhang et al., 2017). This increase may result from fine root turnover of perennial herbaceous plants and less decomposable biomass associated with later successional plant communities (Jones and Donnelly, 2004; Maharning et al., 2009) and possibly reduced

microbial function from repeated prescribed burning (Godwin et al., 2017; Hopkins et al., 2020). Soil bulk density also decreased, presumably as a result of increasing soil aggregation, organic matter accumulation, and root activity (Bach et al., 2010; Brudvig et al., 2021). Percentage of endomycorrhizal fungi increased (Zhang et al., 2017), but slowly, perhaps because of associations with late successional plant species (Koziol and Bever, 2017). While these changes in the ecosystem were in many cases only a step towards complete restoration, their benefits in terms of ecosystem services are considerable, although varying widely in rates of improvement (Buisson et al., 2018; Ren et al., 2016).

Our hypothesis that restoration would eventually provide levels of ecosystem services comparable to those of reference pine savannas was supported for most variables measured, including many aspects of plant community structure, soil chemistry, soil fungal guilds, and hydrological processes. However, there remained limitations on plant species richness and perennial grass cover relative to reference conditions cover even after more than 75 years following abandonment of agriculture. This result is consistent with other studies of savanna plant communities that identify suites of species that rarely recolonize locations where they were eliminated even after several decades (Brudvig et al., 2013; Buisson et al., 2018; Jones et al., 2018; Kirkman et al., 2004; Nerlekar and Veldman, 2020; Ostertag and Robertson, 2007). Percentage of endomycorrhizal fungi and the soil C:N ratio also remained significantly lower than in reference pine savannas. Other studies have similarly have found agricultural legacy effects on soils to persist for decades, attributable to artificial fertilization, erosion of topsoil, loss of organic matter and porous soil structure as a result of tilling, and limits on native plant recolonization that may in turn limit recovery of microbial communities (Bizzari et al., 2015; Brudvig et al., 2013; Zhao et al., 2019; Zhou et al., 2017).

Ecosystem services in addition to those measured in this study but associated with reference pine savannas are also likely to be provided through restoration. Restored savannas are known to provide habitat for several imperiled animal species (Cox and Slater, 2007; Palmer and Sisson, 2017; Wood et al., 2008) and diverse native arthropod communities (Ulyshen et al., 2021; Van Nuland et al., 2013) because of their similarity to reference pine savannas in ecosystem structure and function (Brennan et al., 1998; Cox and Jones, 2009; Hermann et al., 2002). Provision of habitat for northern bobwhite by restored pine savannas supports a hunting culture that has persisted for more than a century and provides the basis for local economies in the southeastern U.S. (Burger et al., 1999). Fuel consumption through frequent, low-severity fires in restored pine savannas (Robertson and Ostertag, 2007) protects timber and soil resources (Hurteau et al., 2008; Varner et al., 2009) and allows for easy containment of wildfires (Boer et al., 2009). Similarities between restored and reference pine savannas in soil total nitrogen levels and cover by nitrogen-fixing legumes suggest that progressive nitrogen loss by volatilization during fires is counterbalanced by nitrogen fixation, as previously indicated (Hendricks and Boring, 1999).

4.1 Comparison of restored pine savannas to other common land uses

Our hypothesis that levels of ecosystem services in restored pine savannas would exceed those of other common land uses was partially but not invariably supported. Land uses focused on producing commodities (row-crop agriculture, improved pasture, commercial pine plantation) showed the highest provisioning services for their target products, as reflected by levels of herbaceous biomass, perennial grass cover, and tree biomass, respectively. However, these land uses provided lower levels of most other ecosystem services. For example, compared to restored pine savannas, row crop agriculture and pasture had higher soil bulk density (Bach et al., 2010), percentage of soil pathogens (Zhang et al., 2017), and predicted erosion and sedimentation (Zhao

et al., 2020), and lower percentages of symbiotic fungi and ecosystem carbon storage (Samuelson et al., 2017). Pine plantations and unmanaged forests had higher evapotranspiration and lower water yield (Brantley et al., 2018), higher fuel loads associated with wildfire risk (Martinson and Omi, 2006), and lower bee pollinator abundance (Breland et al., 2018; Hanula et al., 2015). As in past studies, pine plantations and unmanaged forests provided higher levels of total ecosystem carbon, but at the expense of the herbaceous plant community and associated plant and insect biodiversity (Armstrong and van Hensbergen, 1996; Bond and Parr, 2010; Breland et al. 2018; Martin et al., 2014; Veldman et al., 2015).

4.2 Management and policy implications

Restoring ecosystems and their services to humans depends on establishing foundational ecological processes (Kollmann et al., 2016; Rohr et al., 2018). In old-growth savannas and grasslands, key restoration and management considerations are restoration of historic fire regimes (Bond and Parr, 2010; Mehlman, 1992), management of tree canopy cover (Flake et al., 2021; Platt et al., 2006) and protection from soil disturbance (Brudvig et al., 2013; Nerlekar and Veldman, 2020). Fire can be directly or indirectly connected to all of the improvements in ecosystem services associated with restoration of pine savanna observed in this study. Fires promote an open tree canopy that allows penetration of light that supports of the herbaceous plant community (Flake et al., 2021; Platt et al., 2006). Fire reduces competition and increases plant species richness (Glitzenstein et al., 2012) and favors dominance by perennial grasses (Blackburn et al., 2020; Zhang et al., 2017), which in turn stabilize the soil and reduce water pollution (Schilling et al., 2008; Udawatta et al., 2006). Fire limits fuel loads (Martinson and Omi, 2006) and supports pollinator abundance and species richness (Carbone et al., 2019; Ulyshen et al., 2021). Fire also promotes dominance by pine tree species essential for providing

litter fuels necessary for maintaining the frequent fire regime (Platt et al., 2016). Intensive soil disturbance effectively resets succession in old-growth savannas and grasslands (Fill et al., 2015; Inouye et al., 1987) along with the broad suite of ecosystem services associated with savanna ecosystem development (Zhao et al., 2020). Avoidance of soil disturbance is essential for succession of the plant, microbial, and pollinator communities on which natural fire regimes depend (Fill et al., 2015; Veldman et al. 2015). Restoration of historic grazing intensities is also essential in many savanna and savanna ecosystems (Fuhlendorf et al. 2009), although it was not addressed in this study where only certain pasture sites supported livestock. While more direct methods of restoration such as planting native species and soil rehabilitation provide some improvements (Jones et al., 2018), these are not likely to be successful without restoration of these essential, exogenous ecosystem processes (Kollmann et al., 2016).

Given that most of the desired ecosystem services associated with restoration took decades to develop, our results question the benefit of government programs limited to short-term incentives and cost-share payments for restoration activities (Borgström et al., 2016). Conversely, they underscore the importance of long-term or permanent investments in restoration, such as conservation easements (Rissman et al., 2007). The results also emphasize the importance of supporting private landowners in becoming independent prescribed fire practitioners through training, legislation limiting prescribed fire liability (Sun, 2006), and establishment of landowner associations that pool management resources and expertise (Weir et al., 2016).

Climate change over the next century poses an obvious, and important, caveat to our chronosequence results. Increasing temperatures, wildfires, drought severity, and severe storms predicted in the southeastern U.S. and in many savannas worldwide may affect the trajectory of ecosystem recovery in response to restoration efforts (Dimobe et al., 2018; McNulty et al., 2013;

Scheiter et al., 2015). Even so, ecosystem services provided by restored savannas are likely to be more resilient to climate change than other land uses. Frequent fires may mitigate drought stress effects on trees by reducing competition with fire-sensitive species (Palmquist et al., 2014). Perennial vegetation typical of native savannas is more resilient to wildfires (Andersen et al., 2005; Martinson and Omi, 2006) and can help stabilize soils during increasingly frequent storms (Udawatta et al., 2006). Savannas have less evaporative loss and higher water yield than forested land thus conserving increasingly scarce groundwater (Brantley et al., 2018) and serve as relatively secure repositories for ecosystem carbon (Flanagan et al., 2019; Gonzales-Perez et al., 2004; Samuelson et al., 2017). In this light, restoration of savanna ecosystems should be a high priority for buffering potential effects of climate change.

Despite limits on the potential to fully or rapidly restore grasslands and savannas (Brudvig et al., 2021), we conclude that the long-term prospects for restoring most aspects of native pine savannas and their many ecosystem services is promising. These results provide a strong impetus for restoration through persistent re-establishment of essential ecosystem processes, especially establishment of historically frequent fire regimes, for improving ecosystem and human population resilience in the face of global climate change.

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Appendix A. Supplementary information

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Figure Captions

Fig. 1. (a) Approximate area of the Red Hills Region of northern Florida and southern Georgia and (b) the four replicate study areas within the region

Fig. 2. Variables representing ecosystem services associated with plants, bee pollinators, and carbon and nitrogen. Symbols show the mean value for all research plots within the four study

areas. Level of significance for differences among land cover categories (L), study areas (A), and their interaction (I) are indicated for $P > 0.05$ (*ns*), $P = 0.01-0.05$ (*), $P = 0.005-0.1$ (**), $P < 0.005$ (***). Letters indicate significant differences among land cover categories from multiple comparison tests on the main effect at $\alpha = 0.05$. Values for each study area and additional statistics are in Appendix A Figs. S1, S2, and S3.

Fig. 3 Variables representing ecosystem services associated soil mineral nutrients, pH, and bulk density. Symbols show the mean value for all research plots within the four study areas. Level of significance and differences among land cover categories are indicated as in Fig. 2. Values for each study area and additional statistics are presented Appendix A Fig. S4.

Fig. 4 Variables representing ecosystem services associated with fungal guilds and hydrological and erosion variables predicted by WEPP. Symbols show the mean value measured for all research plots within the four study areas. Level of significance and differences among land cover categories are indicated as in Fig. 2. Values for each study area and additional statistics are presented Appendix A Figs. S5 and S6.

Fig. 5 Results from the NMS analysis where symbols represent plots distributed in the plot according to measurements of all variables associated with ecosystem services. Symbol colors represent land cover categories and symbol shapes represent the study areas. Vectors show the correlation between variables and the axes.

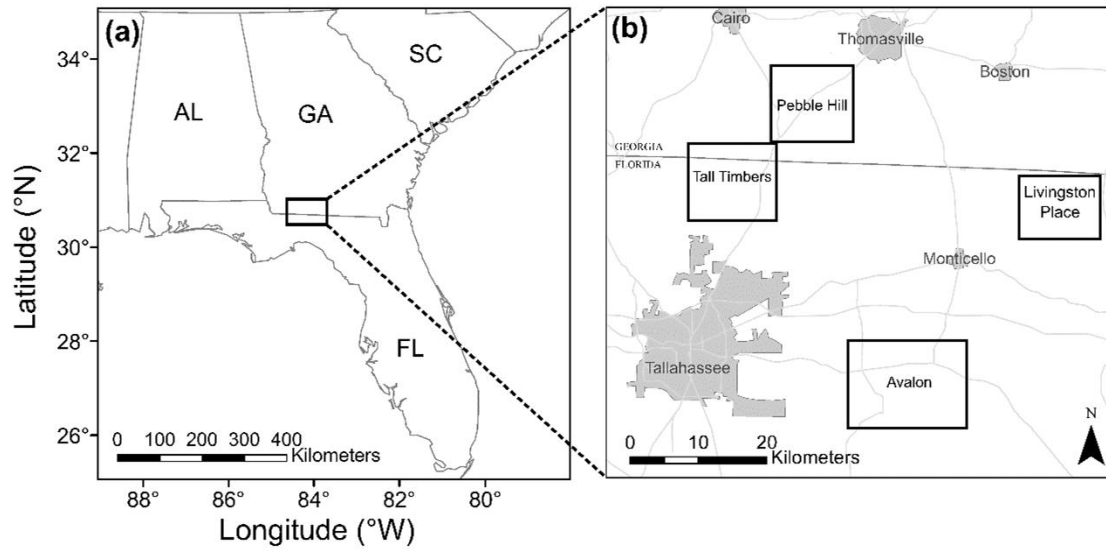


Fig. 1

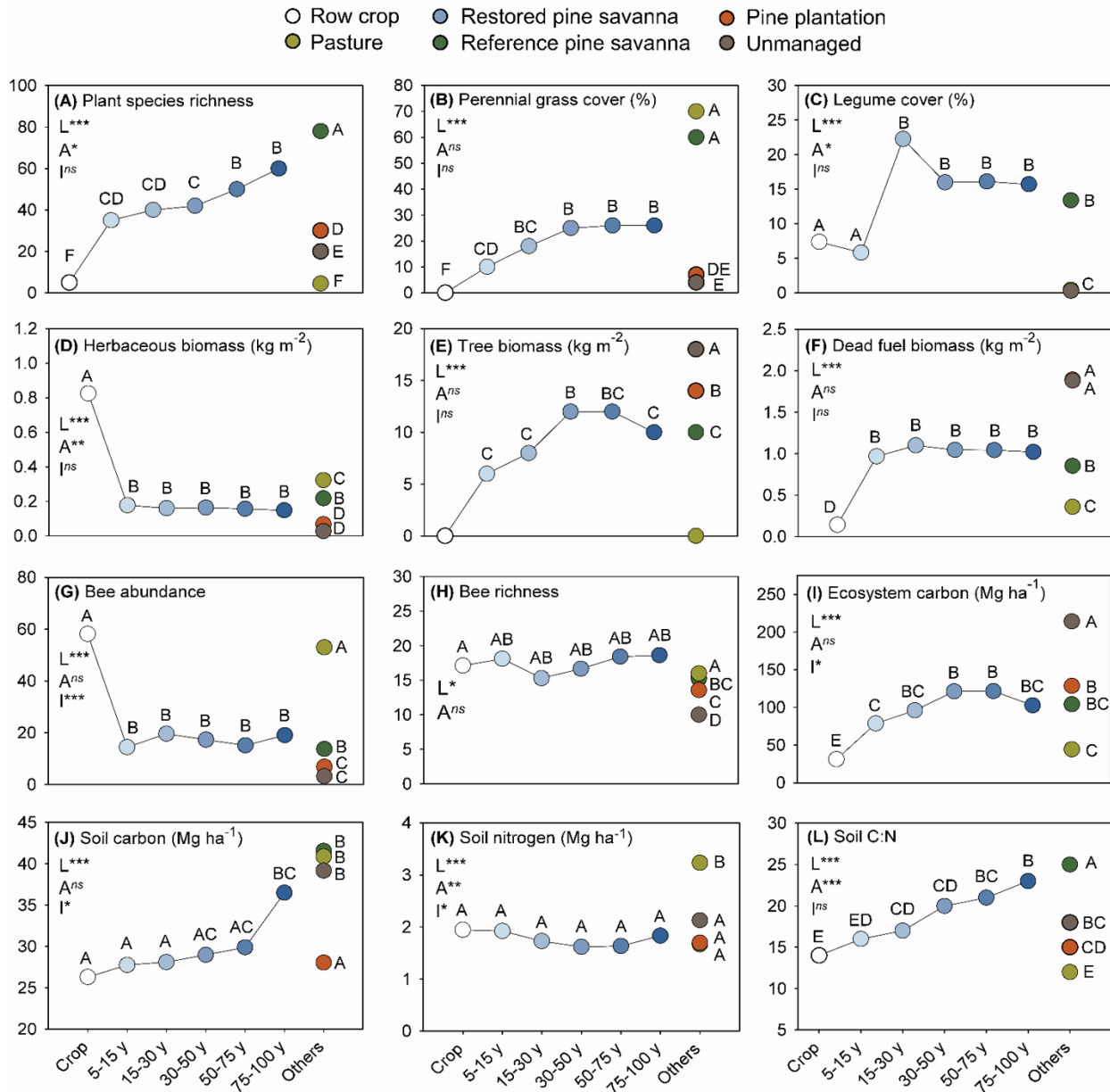


Fig. 2

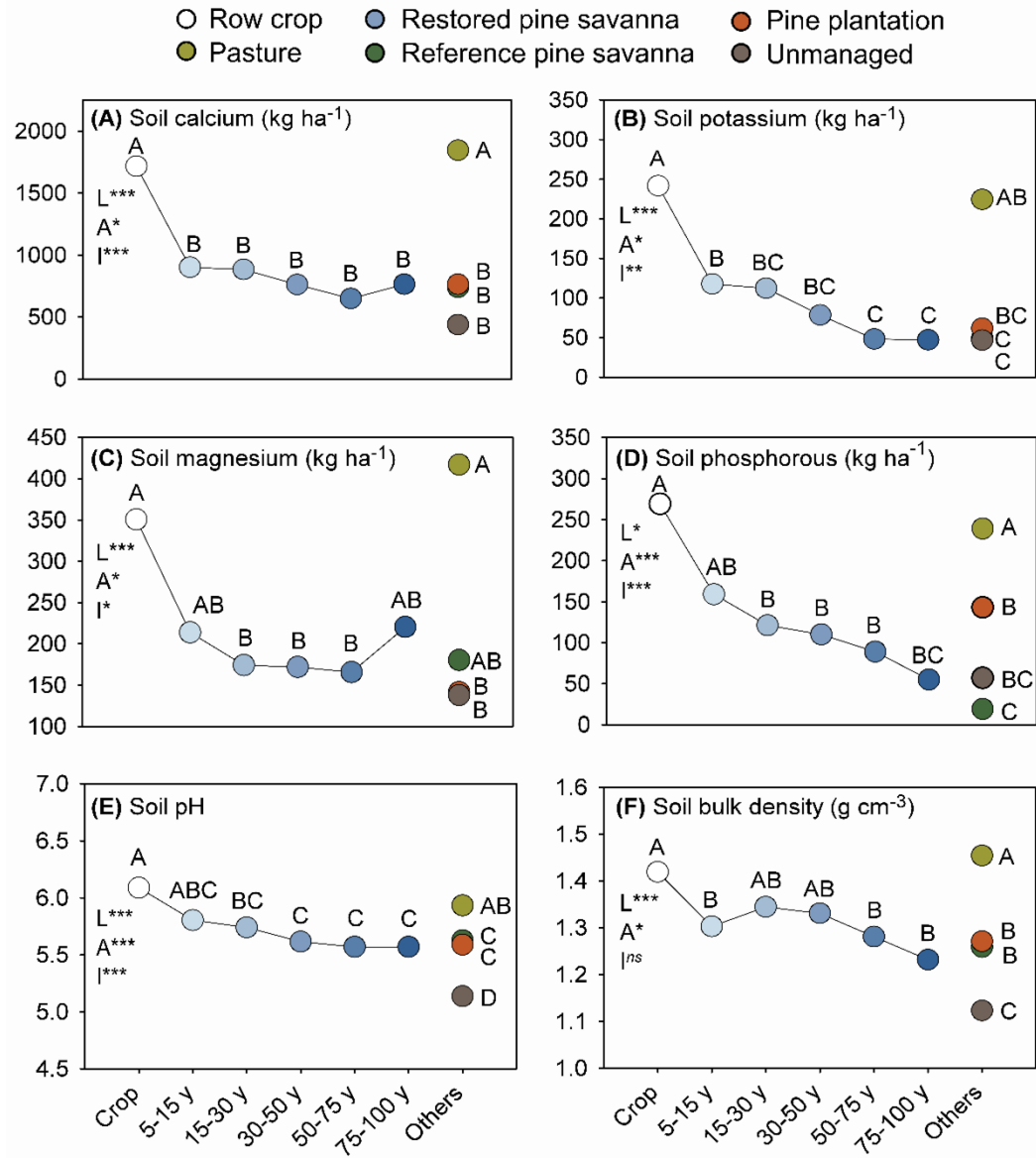


Fig. 3

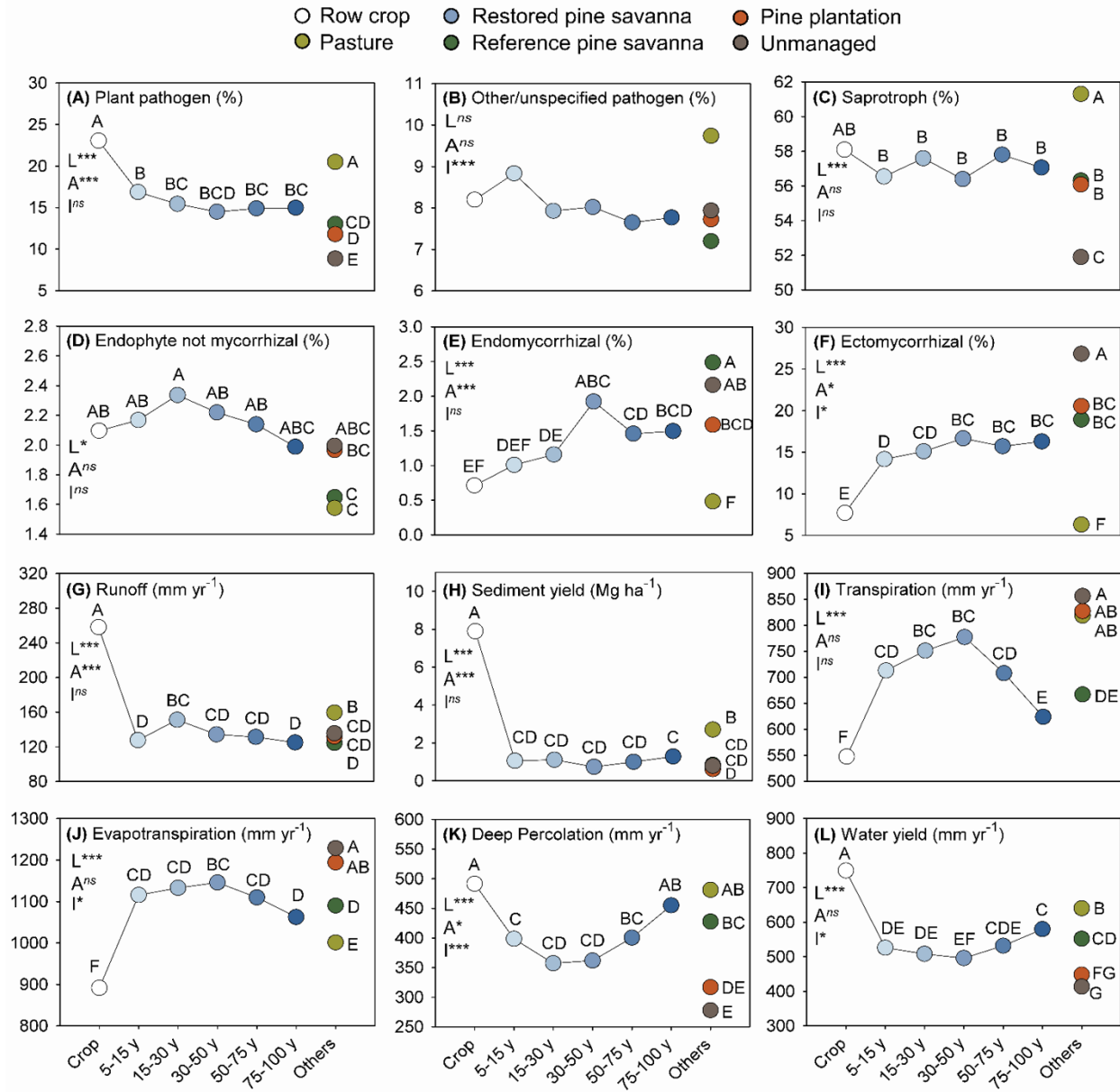


Fig. 4

