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Historical agriculture and contemporary fire frequency alter soil properties in longleaf pine woodlands

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ABSTRACT

Historical agriculture and contemporary disturbances such as fire can each affect soil properties, but the relative impact of their separate and combined effects is poorly understood. We investigated the effects of historical agriculture and contemporary fire frequency on soil properties of longleaf pine woodlands in the Southeastern United States. We sampled 24 pairs of sites from adjacent former agricultural and remnant longleaf pine woodlands based on high ($\geqslant$ four since 1971) and low (< four since 1971) fire frequency. We found no evidence for interactive effects between agricultural history and fire frequency on measured mineral soil properties, yet each disturbance independently affected different aspects of the soil. Effects of past agricultural use were most apparent in the top 15 cm of the mineral soil, with post-agricultural woodlands characterized by increased phosphorus and bulk density, as well as decreased organic matter and soil water holding capacity, compared to remnant woodlands. Some effects of past agricultural use, such as increased phosphorus, were also apparent as deep as 30 cm into the soil profile. However, when expressed as stocks (to account for differences in bulk density) we found that organic matter content was similar among post-agricultural and remnant woodlands. With respect to contemporary fire frequency, less frequently burned sites had thicker O-horizons (litter and duff layers) and showed a trend of greater inorganic nitrogen in mineral soil, relative to frequently burned sites. Overall, our results indicate that agricultural legacies in soils persist 60 years after agricultural abandonment and have impacts that may extend deep into the soil profile. Fire suppression additionally affects soils, resulting in additive effects of historical and contemporary disturbances. Additional research is needed to better determine if and how the combined effects of past and present disturbances will affect ecological systems. These combined and long-lasting impacts of historical and contemporary disturbances may help explain why restoration of native understory vegetation remains challenging.

1. Introduction

Within the last century, abandonment of agricultural lands has increased worldwide (Cramer et al., 2008). In the late 19th century, rapid expansion of agriculture across the United States resulted in the clearance of up to 40% of the nation's forests and woodlands (Houghton and Hackler, 2000). After 1920, forested land increased by 14 million ha as marginal agricultural lands (e.g., low fertility soils), mostly in the Eastern United States, were abandoned and reverted back to forest (Hart, 1968; Houghton and Hackler, 2000). Long after agricultural abandonment, legacies of previous land use on afforested land may linger (Foster et al., 2003; Flinn and Vellend, 2005). Decades after the cessation of agriculture, recovering forests may remain distinct from undisturbed (in recent time) forests in their plant species composition and richness (Hermy and Verheyen, 2007; Veldman et al., 2014) and soil properties (McLauchlan, 2006; Brudvig et al., 2013). With respect to soils, tilling, nutritional amendments, and biomass removal during agricultural activities dramatically alter soil physical and chemical properties (McLauchlan, 2006). Compared to forests without recent agricultural history, soils of post-agricultural forests often contain lower soil organic matter (Flinn and Marks, 2007; Matlack, 2009), increased soil phosphorus (Compton and Boone, 2000; Dupouey et al., 2002; Brudvig et al., 2013), increased pH (Grossmann and Mladenoff, 2008; Matlack, 2009), and greater soil bulk density (Compton et al., 1998; Maloney et al., 2008). In some cases, agricultural legacies in soil properties persist for thousands of

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years (European deciduous forest: Dupouey et al., 2002); in other cases, soil nutrients may recover within two centuries to levels observed in remnant forest never used for agriculture (New England sand plain forest: Compton et al., 1998).

What remains less clear is whether and to what degree these legacies from agriculture interact with contemporary disturbances, such as fire, that also impact soil properties (Foster et al., 2003; Flinn and Vellend, 2005). The effects of fire on soil properties are dependent on intrinsic properties of the burned site as well as properties of the fire itself (Wan et al., 2001; Certini, 2005). Pre-fire site conditions such as fuel load and soil organic matter content can influence fire intensity (i.e., fuel consumption rate) and severity (i.e., degree of change to ecosystem properties), which in turn affect post-fire conditions of soil properties (Neary et al., 2005). For instance, low-intensity surface fires influence soils in the short-term (with recovery to pre-fire levels within 1–5 years) by increasing pH (Certini, 2005) and inorganic, plant-available nitrogen (NO_3 and NH_4) (Wan et al., 2001), and by decreasing soil organic matter and soil carbon (Neary et al., 1999; Certini, 2005). In contrast, high-intensity fires typically result in nitrogen losses due to oxidation (Binkley and Fisher, 2013) and larger releases of inorganic nitrogen due to leaching (Neary et al., 1999; Certini, 2005). Given the lasting effects of historical agriculture on soil and vegetation, the degree to which contemporary fires influence soil properties may be contingent upon the pre-fire condition of the soils as influenced by a site's agricultural history (Duguy et al., 2007). For example, soil carbon losses due to historical agriculture may be exacerbated by additional soil carbon losses due to organic matter combustion from fires. Alternatively, soil carbon losses due to fire may be smaller in post-agricultural sites compared to remnant sites due to larger amounts of fuel (organic matter) in remnant sites (Duguy et al., 2007).

While the impacts of individual disturbances have been widely studied, our understanding of the interactions between multiple disturbances and their cumulative effects on ecosystems remains limited (Turner, 2010). Recent studies examining the interaction between past and present disturbances, specifically agriculture and fire, have found that agricultural history affects the impact of contemporary fire on post-fire recovery of plant community richness and composition (Duguy and Vallejo, 2008; Puerta-Piñero et al., 2012), similarity among plant communities (Mattingly et al., 2015), and soil carbon dynamics (Duguy et al., 2007). More research is needed to better determine if and when the combined effects of past and present disturbances on ecological systems will be additive, synergistic, or offsetting. In this study, we examine the effects of agricultural history and contemporary fire frequency on soils from longleaf pine (*Pinus palustris*) woodlands.

Longleaf pine ecosystems (variably referred to as savannas, woodlands and forests; hereafter woodlands) of the Southeastern US have been greatly impacted by both land-use history and changes to fire regimes. Less than 3% of this habitat remains intact following wood harvesting, turpentining, and clearing for tillage agriculture in the late 19th to early 20th centuries (Frost, 2006). The remaining habitat has been further degraded by changes to its historical fire regime, namely, a long history of fire suppression (Frost, 2006). Similarly, many other fire-maintained ecosystems around the world are also experiencing drastic alterations to their fire regimes (Pausas and Keeley, 2009). In longleaf pine woodlands, a major focus of current restoration efforts is reintroducing historical fire regimes to re-create the open woodlands that support high understory plant diversity and endangered species such as the red cockaded woodpecker (Kirkman et al., 2004; Varner et al., 2005; Gilliam and Platt, 2006). Yet reinstatement of historical fire regimes alone may not always restore fire-suppressed ecosystems (Stephenson, 1999; Varner et al., 2005). Because understory plant richness in longleaf pine woodlands is also strongly linked to variation in soil properties (Kirkman et al., 2001; Brudvig et al., 2013) and because soil properties, in turn, are impacted by agricultural history (McLauchlan, 2006), understanding the interactive effects of previous agriculture and contemporary fire on soils will likely lead to improved management for habitat recovery in longleaf pine woodlands and other fire-maintained ecosystems.

Our study focuses on the influences of historical agriculture and contemporary fire management on soil properties in longleaf pine woodlands. Agricultural fields are typically selected based on soils being suitable for farming (Flinn and Vellend, 2005); thus, comparing properties of soils that differ in agricultural history requires an approach that controls for underlying soil variation. We used a paired-plot design, whereby pairs of post-agricultural and remnant woodlands were immediately adjacent in space and located on the same soil series to avoid potentially confounding issues of past land-use decisions. To date, few studies take this paired-plot approach (but see Brudvig et al., 2013) or account for soil type to understand the effects of agricultural history. In this study, we address the following questions: (1) What is the effect of historical agricultural land use on soil physical and chemical properties 50+ years after agricultural abandonment? (2) Does contemporary fire frequency affect soil properties? (3) Do contemporary fire frequency and historical agriculture have additive, synergistic, or offsetting impacts on soil properties? Based on published work in other sandy-soiled forested ecosystems, we predict soil properties in post-agricultural longleaf woodlands will have less soil carbon and nitrogen, and greater phosphorus and bulk density compared to remnant woodlands, even after 50 years since abandonment (Compton et al., 1998; Maloney et al., 2008). We expect fire frequency to have the greatest effect on soil organic matter and carbon (Neary et al., 1999). If both predictions above hold true, then higher fire frequency will exacerbate the effect of agriculture on some—but not all—soil properties in longleaf pine woodlands.

2. Materials and methods

2.1. Study site

We conducted the study at the Department of Energy's Savannah River Site (SRS), an ~80,000 ha National Environmental Research Park near New Ellenton, South Carolina, United States (Fig. 1). The SRS is located on the border of the Sandhill and Upper Coastal Plain ecoregions and is characterized by a humid subtropical climate (Blake et al., 2005). Of the soil types historically supporting upland longleaf pine woodlands at SRS, the most common soil association is the Blanton–Fuquay–Dolton (47% of SRS area; Kolka et al., 2005). The Blanton series (Loamy, siliceous, semiactive, thermic Grossarenic Paleudults) is the most abundant at SRS, followed by the Fuquay series (Loamy, kaolinitic, thermic Arenic Plinthic Kandiudults) (Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Official Soil Series Descriptions. Available online at http://soils.usda.gov/technical/classification/osd/index.html (Accessed 11 March 2015)). Our work occurred on these two soil series alone. Both the Blanton and Fuquay series are sandy, well-drained, and flat to gently sloping (0–10% grade) soils with low organic matter content (Kolka et al., 2005).

Prior to European settlement, the SRS uplands were longleaf pine woodlands heavily influenced by Native American fire regimes (White, 2005). Historically, these woodlands experienced frequent (every 1–6 years), low intensity surface fires (Frost, 2006). In 1951, SRS was established and the United States Forest Service was contracted to manage existing woodlands and to reforest abandoned farmland and cutover woodlands in the area (Blake, 2005). At the time of government purchase, 38% of the land was in

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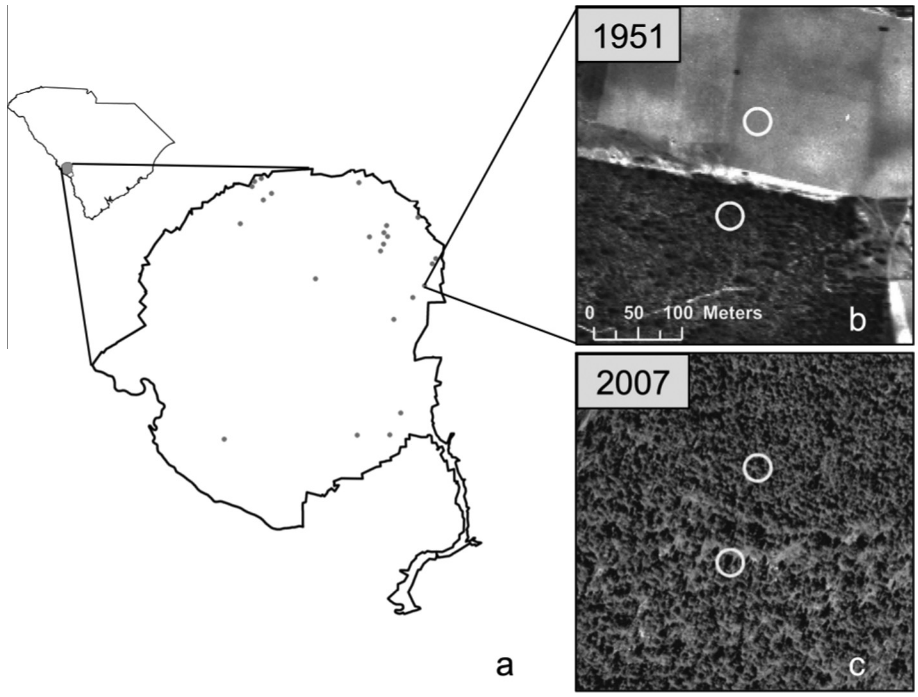

Fig. 1. (a) Location of the Savannah River Site (SRS) in South Carolina, USA, and the locations of the paired longleaf woodlands used in this study (gray dots). To the right, a single pair is illustrated with: (b) an aerial photograph from 1951 showing visible agricultural fields and remnant woodland and (c) a satellite image from 2007 showing contemporary forested woodlands. White circles represent the two sampling locations, which differ in agricultural history but share the same fire frequency since 1971.

agricultural use. By 2001, nearly all of the SRS land had become forested (White, 2005).

2.2. Plot selection

We sampled soils within 24 pairs of woodland stands in a split-plot design, with fire frequency as the whole plot factor (i.e., each woodland in a pair experienced the same fire frequency) and agricultural history as the sub-plot factor. Each pair consisted of two adjacent longleaf pine stands (minimum size = 1 ha), both located on either the Blanton (18 pairs) or Fuquay (6 pairs) soil series but differing in agricultural history (one remnant and one post-agricultural woodland per pair). We visually determined agricultural history from 1951 aerial photographs (Fig. 1b) based on lack of vegetation (indicative of an agricultural field) and tree density (indicative of longleaf pine woodlands) as in Brudvig and Damschen (2011). We then examined satellite photographs of the stands in 2007 to confirm that these areas had not been recently logged and categorized woodlands as either "post-agricultural woodland" or "remnant longleaf woodland". Areas we designated remnant woodland may have been cultivated in the 18th or 19th century, yet they were mature longleaf woodlands as of 1951 and thus had been forested far longer than post-agricultural woodlands. All remnant and post-agricultural woodlands in this study were forested and dominated by a longleaf pine overstory at the time of sampling in 2009. Though compositional differences in overstory trees do exist among sites at SRS, these compositional differences alone have not been found to have a significant effect on soil properties (Brudvig et al., 2013). Soil sampling plots within stands were located a minimum of 25 m from the border between historical agricultural boundaries, but less than 100 m apart from each other to minimize environmental variation unrelated to agricultural history. Each pair of plots was at least 300 m away from any other pair.

We stratified pairs according to their fire history: "high fire frequency" pairs experienced four or more prescribed burns between 1971 and 2009 ($n = 14$, median number of fires = 6, median fire return interval = 7 years), and "low fire frequency" pairs experienced fewer than four prescribed burns in that same time period ($n = 10$, median number of fires = 2, median fire return interval = 13 years). For each pair, fire return interval (FRI) was calculated as the mean number of years between fires beginning with 1971 and ending with the most recent fire. The interval between 1971 and the first recorded fire is likely an underestimate of the true FRI for that time period; however, high and low sites remain distinct with respect to FRI with or without this time interval. All fires on our study sites occurred after 1979, with most fires occurring after 1990. Although some "high fire frequency" stands at the SRS have fire return intervals on the high end of historical estimates (every 1–6 years for this region; Frost, 2006), we designed our sampling to reflect management history and the high and low ends of the frequency continuum at SRS.

2.3. Soil sampling and analysis

We collected soil samples from December 13, 2009 to December 21, 2009. We collected cores from sampling plot locations at eight different points arranged 5 and 15 m in each of the four cardinal directions from a randomly located center point (similar to method described in Latty et al., 2004). At each of the eight sampling points, we measured litter and duff depth and collected mineral soil using a 2.2 cm diameter soil recovery probe at three different depths (0–15 cm, 15–30 cm, 30–45 cm). We combined the soil samples from all eight points to create one composite sample for each depth, within each plot (total $n = 144$). In our statistical analysis, we averaged litter and duff depths across the eight samples in each plot.

Composite soil samples were analyzed by Brookside Laboratories, Inc. (New Knoxville, OH) for phosphorus concentration (Mehlich, 1984), inorganic nitrogen concentration (nitrate (NO_3) and ammonium (NH_4) concentrations combined; Dahnke, 1990), percent carbon (C; Nelson and Sommers, 1996; McGeehan and Naylor, 1988), percent organic matter (OM; Schulte and Hopkins, 1996), total exchange capacity (TEC; Ross, 1995), and pH (McLean, 1982). We determined soil water holding capacity (SWHC) following methods used in Brudvig and Damschen (2011). Using a subsample of soil, we calculated SWHC as the proportional difference in weight between wet soil (dampened to approximately at field capacity) and oven-dry soil (dried at 105 °C for 72 h).

In July 2010, we collected soil from a subset of 16 randomly selected pairs of stands (from the original 24; 10 high fire, 6 low fire) to measure soil bulk density. Near the center point of each stand's December 2009 sampling plots, we used a PVC tube to collect a specific volume (364.97 cm^3) of soil from the top layer. These samples were then air-dried and stored at room temperature. Prior to weighing, samples were oven-dried to constant mass at 60 °C.

2.4. Statistical analyses

All analyses were conducted in R version 3.0.3 (R Core Team, 2014). We investigated individual soil properties with univariate tests, starting with linear mixed-effects models (LME) to assess the effect of agricultural history and fire frequency on soil properties at different depths using the nlme package (Pinheiro et al., 2014). The use of LME allowed us to account for the split-plot design of our study by including woodland pair as a random effect within our models.

For each variable assessed, we began with a full model that included all fixed effects (agricultural history, fire frequency, and their interaction) and the random effect of woodland pairs, with separate models for each soil depth. We chose this approach because our focus was not on how the relationship between disturbances changes with depth (i.e., the interaction) for each variable, but rather in determining if agricultural history and fire frequency affected soil properties at each soil depth. To determine the optimal residual variance structure, we first considered the importance of the random effect of woodland pair, which was removed from the model if inclusion of the effect in the model did not reduce Akaike's Information Criterion (AIC) by >2 (Zuur et al., 2009). For the majority of our models, the inclusion of woodland pair as a random effect did not improve the AIC of the model (likely because our sampling locations were on the same soil type; Table 1) and was removed to avoid over-parameterization (Zuur et al., 2009). Models that did retain woodland pair remained LME models, while models that did not retain woodland pair became simple linear models. Given the spatial clustering of fire treatments across the landscape, we also considered the possibility of spatial autocorrelation among our sites. Inspection of variogram plots of model residuals did not indicate autocorrelation among our sites for any variables assessed (results not shown). After determining the optimal residual variance structure, we assessed the significance of fixed effects in the final model by *F*-tests using marginal (Type III) sum-of-squares due to unbalanced sample size among fire treatment groups (Shaw and Mitchell-Olds, 1993).

We assessed model residuals graphically to determine that residuals met assumptions of normality and homogeneity of variances. Variables were log or inverse transformed as necessary to overcome severe departures from normality. In cases of heterogeneous variance among groups, we included the *varIdent* weights function in the model to estimate variances for each group (Zuur et al., 2009). We based our decisions to include or exclude variance on improvement in AIC by >2, after inclusion of pair as a random effect had already been considered.

Using the analysis approach described above, we assessed soil P concentration, inorganic N concentration, pH, TEC, SWHC, percent OM, and percent C with separate models for each of the three sampling depths. For one sample, the percent C (30–45 cm depth, post-agricultural woodland, high fire frequency) was below the minimum detectable level for total C (<0.20%), and was included in the analysis as 0.1%, the midpoint value between 0 and the minimum detectable level. Qualitatively, results did not differ between a model using the 0.1% value and a model omitting this data point.

We assessed mineral soil bulk density and organic layer (litter and duff) depth at a single sampling depth because they were only measured in the top layer of soil. Due to differences in soil bulk density with agricultural history (see Section 3), we chose to standardize P, inorganic N, C, and OM in the top layer into g m^{-2} (g nutrient m^{-2} = nutrient concentration (mg kg^{-1}) × sampling depth (0.15 m) × soil bulk density (Mg m^{-3})) and also analyzed these four models using the standardized data.

To account for the number of hypothesis tests in this study, we assessed significance of the univariate tests under a controlled false discovery rate (set at 0.05) by adjusting *p*-values with the Benjamini–Hochberg procedure (Pike, 2011). We rounded original *p*-values < 0.001 up to 0.001 for calculating adjustments. We present results for both adjusted and unadjusted *p*-values.

3. Results

There was no significant interaction between agricultural history and fire frequency for any single soil property, though each disturbance affected one or more soil properties (Table 1).

3.1. Agricultural history

Effects of agricultural history were most prominent in the top 0–15 cm of the soil (Table 1, Fig. 2). While phosphorus concentration was greater in the top layer of mineral soil of post-agricultural than in remnant woodlands, percent organic matter, percent carbon, soil water holding capacity, and total exchange capacity were lower in post-agricultural woodlands (Fig. 2). All of these soil properties were positively correlated with percent organic matter (Pearson's correlation coefficient; percent carbon: $r = 0.72$, $p < 0.01$; total exchange capacity: $r = 0.59$, $p < 0.01$; soil water holding capacity: $r = 0.55$, $p < 0.01$). Below 15 cm soil depth, phosphorus continued to show a trend of greater soil concentrations in post-agricultural than remnant woodlands (Fig. 2).

Soil bulk density from 0 to 10 cm was greater in post-agricultural woodlands (1.30 ± 0.03 Mg soil m^{-3}) compared to remnant woodland soils (1.18 ± 0.03 Mg soil m^{-3}; Table 2). After accounting for this difference in bulk density by standardizing soil nutrient concentrations into stocks (g nutrient m^{-2} soil), reanalysis of soil nutrients in the top 0–15 cm showed an effect of agricultural history on phosphorus stock only (Table 2). Phosphorus stocks followed the same pattern as phosphorus concentration, with post-agricultural sites having greater quantities of phosphorus than remnant woodland sites (Fig. 3). For the subset of data used to convert to soil nutrient stocks (i.e., sites where we quantified soil bulk density), results for soil concentrations were qualitatively similar to the full data set.

3.2. Fire frequency

Generally, soil properties were not significantly affected by fire frequency after Benjamini–Hochberg adjustments; however, TEC and inorganic N showed a trend across depths toward greater values in woodlands with low fire frequency (Fig. 4). In particular, inorganic N concentrations in the top 15 cm of soil in low fire frequency woodlands were 50% greater than high fire frequency woodlands. While both litter and duff layers were thinner in woodlands with high fire frequency (Table 3; Fig. 5), mineral soil bulk

Table 1
Results of linear mixed-effects (LME) and linear models of the effects of agricultural history and fire frequency on soil properties. *p*: results of *F*-tests; p_{adj}: adjusted for false discovery rate = 0.05, 63 tests. Bolded values indicate significance at $p < 0.05$.

	Model results								
	Fire			Agricultural history			Fire × agricultural history		
	$F_{1,44}$	p	p_{adj}	$F_{1,44}$	p	p_{adj}	$F_{1,44}$	p	p_{adj}
0–15 cm									
Phosphorus	0.148	0.702	0.922	18.394	**<0.001**	**0.016**	0.187	0.667	0.922
Inorganic nitrogen[a]	6.966	**0.015**	0.079	0.005	0.944	0.975	1.178	0.290	0.710
pH	0.896	0.349	0.758	4.638	**0.037**	0.167	0.006	0.941	0.975
Total exchange capacity[a]	7.577	**0.012**	0.076	17.810	**<0.001**	**0.016**	0.746	0.397	0.834
Soil water holding capacity	3.660	0.062	0.217	10.490	**0.002**	**0.024**	2.135	0.151	0.453
Organic matter (%)	0.154	0.697	0.922	11.268	**0.002**	**0.024**	0.113	0.739	0.922
Carbon (%)	0.338	0.564	0.870	9.278	**0.004**	**0.032**	0.027	0.870	0.962
15–30 cm									
Phosphorus	0.298	0.588	0.875	9.899	**0.003**	**0.027**	0.487	0.489	0.870
Inorganic nitrogen[a]	4.030	0.057	0.217	0.126	0.726	0.922	0.398	0.535	0.870
pH[a]	1.712	0.204	0.584	6.925	**0.015**	0.079	0.009	0.923	0.975
Total exchange capacity	0.360	0.552	0.870	1.133	0.293	0.710	0.535	0.468	0.870
Soil water holding capacity[a]	1.025	0.322	0.751	2.964	0.099	0.328	0.340	0.566	0.870
Organic matter (%)	0.394	0.533	0.870	0.033	0.858	0.962	0.001	0.979	0.995
Carbon (%)	0.125	0.725	0.922	0.042	0.839	0.962	0.466	0.498	0.870
30–45 cm									
Phosphorus	0.283	0.597	0.875	4.160	**0.047**	0.197	0.031	0.860	0.962
Inorganic nitrogen[a]	8.071	**0.010**	0.070	0.050	0.826	0.962	0.963	0.337	0.758
pH	3.699	0.061	0.217	15.728	**<0.001**	**0.016**	0.357	0.553	0.870
Total exchange capacity	12.450	**0.001**	**0.016**	2.550	0.118	0.372	0.000	0.996	0.996
Soil water holding capacity	1.459	0.234	0.614	0.107	0.746	0.922	0.030	0.863	0.962
Organic matter (%)	0.524	0.473	0.870	0.262	0.611	0.875	1.512	0.225	0.614
Carbon (%)	0.019	0.890	0.967	6.222	**0.017**	0.082	0.580	0.450	0.870

[a] Final model included pair as a random effect.

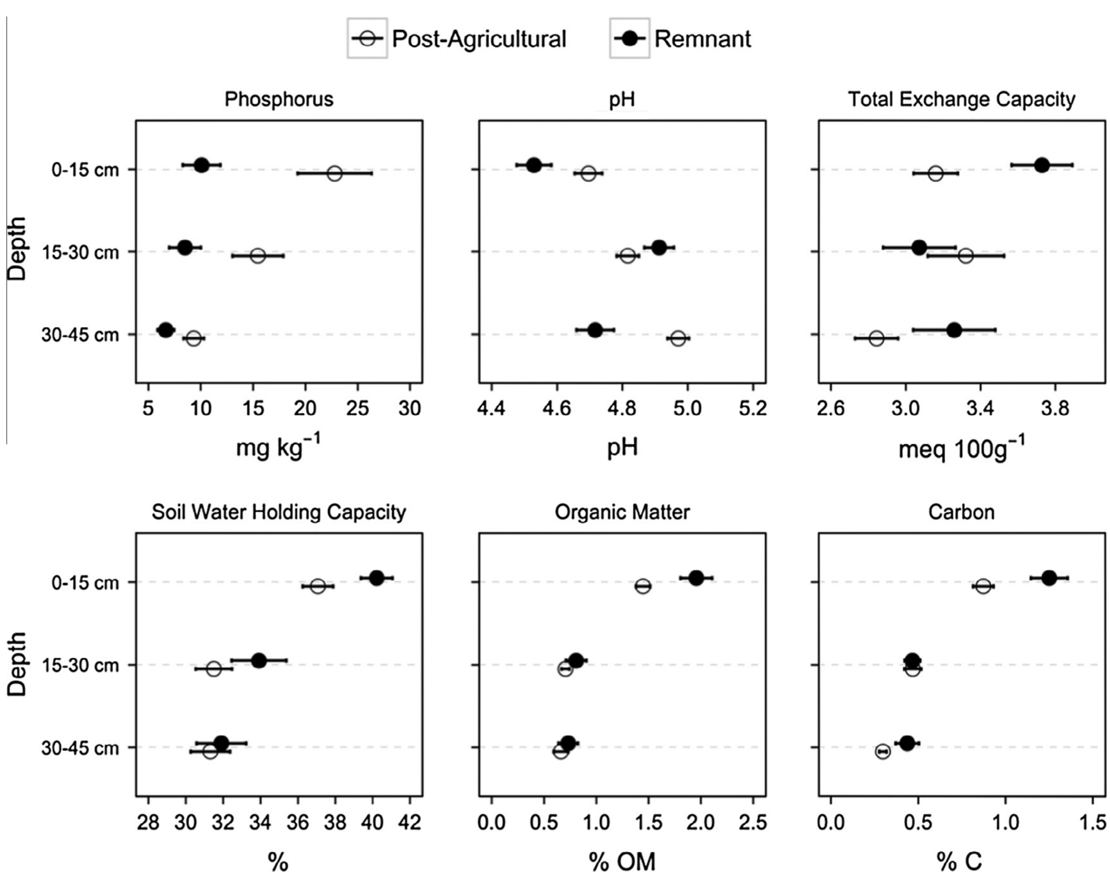

Fig. 2. Mean values (±SE) of soil properties from post-agricultural woodlands and remnant woodlands at three depths below the soil surface.

Table 2
Results of linear mixed-effects (LME) and linear models of the effects of agricultural history and fire frequency on soil properties standardized for bulk density. *p*: results of *F*-tests; p_{adj}: adjusted for false discovery rate = 0.05, 15 tests. Bolded values indicate significance at $p < 0.05$.

Soil properties	Model results								
	Fire			Agricultural history			Fire × agricultural history		
	$F_{1,28}$	p	p_{adj}	$F_{1,28}$	p	p_{adj}	$F_{1,28}$	p	p_{adj}
Bulk density	0.061	0.807	0.822	8.372	**0.007**	**0.035**	0.534	0.471	0.707
Phosphorus	0.285	0.598	0.754	9.559	**0.005**	**0.035**	0.276	0.603	0.754
Inorganic nitrogen	12.449	**0.002**	**0.030**	3.484	0.073	0.252	0.719	0.404	0.707
Organic matter	0.099	0.755	0.822	0.953	0.337	0.707	0.576	0.454	0.707
Carbon	0.788	0.382	0.707	3.204	0.084	0.252	0.051	0.822	0.822

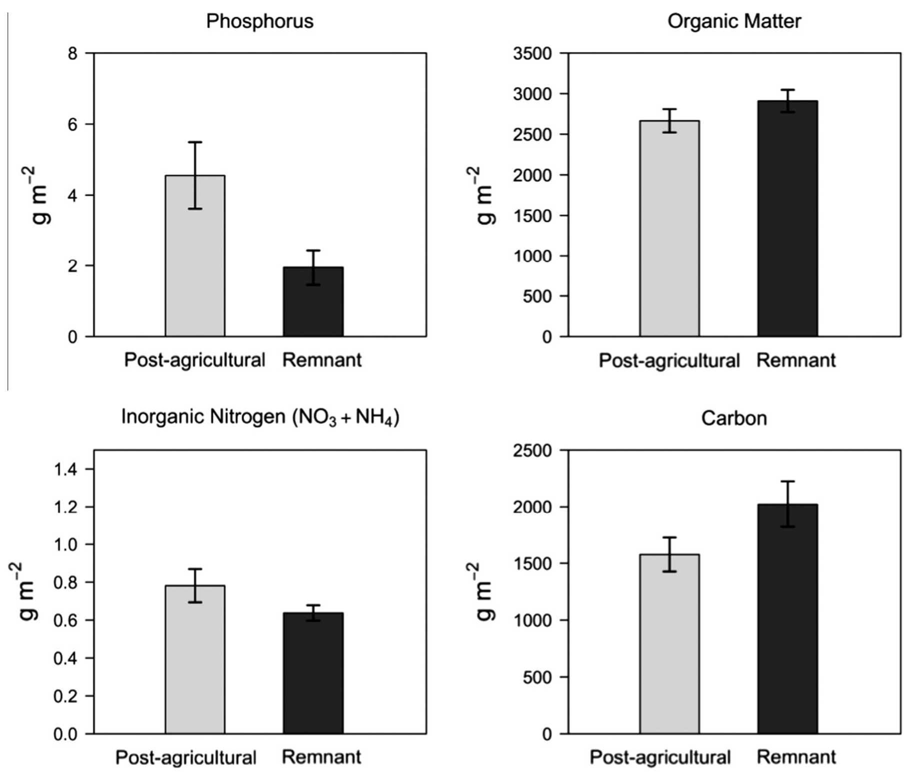

Fig. 3. Mean (±SE) stocks of phosphorus, inorganic nitrogen, organic matter, and carbon content of the top 0–15 cm of soil, standardized using soil bulk density and reported as weight per area.

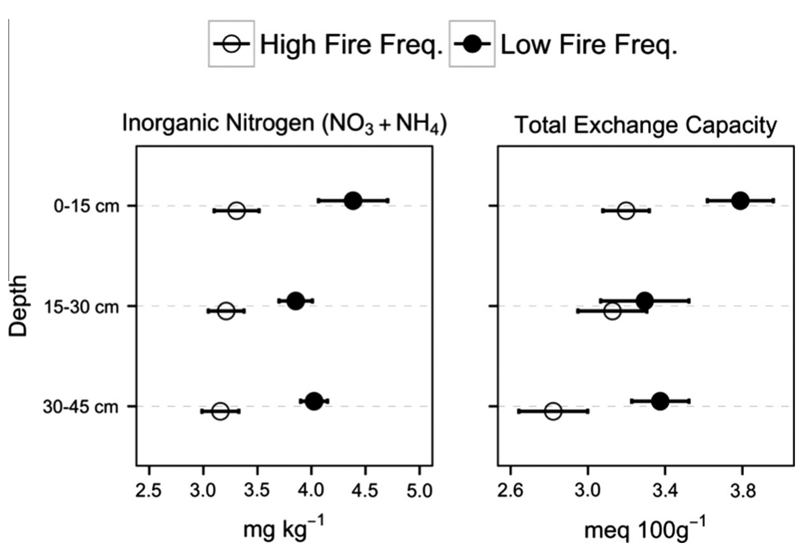

Fig. 4. Mean (±SE) inorganic nitrogen and total exchange capacity at three different depths in soils with different burn frequencies.

Table 3
Results of linear mixed-effects models (LME) of the effects of agricultural history and fire frequency litter and duff depth. p: results of F-tests; p_{adj}: adjusted for false discovery rate = 0.05, 15 tests. Bolded values indicate significance at $p < 0.05$.

Soil properties	Model results								
	Fire			Agricultural history			Fire × agricultural history		
	$F_{1,44}$	p	p_{adj}	$F_{1,44}$	p	p_{adj}	$F_{1,44}$	p	p_{adj}
Litter (cm)	33.625	**<0.001**	**0.003**	0.005	0.944	0.944	0.170	0.682	0.818
Duff (cm)	39.575	**<0.001**	**0.003**	0.208	0.650	0.818	0.790	0.379	0.758

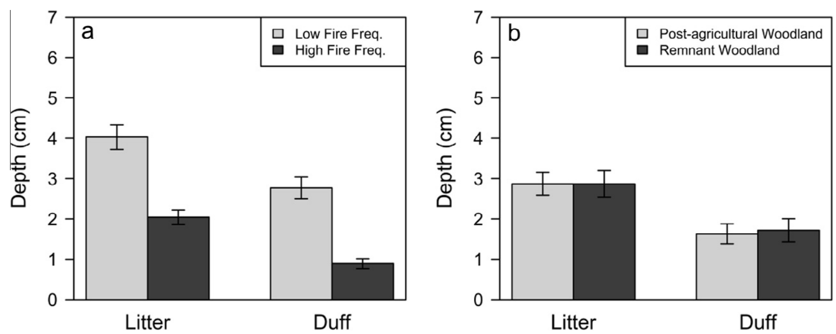

Fig. 5. Mean (±SE) litter and duff measurements separated by treatment type (a. fire frequency; b. agricultural history).

density was not affected by differences in fire frequency (low fire frequency: 1.25 ± 0.04 Mg soil m^{-3}; high fire frequency: 1.24 ± 0.03 Mg soil m^{-3}; Table 2). Similar to the trends observed for concentrations, high fire frequency woodland soils contained reduced inorganic nitrogen stock (low fire frequency: 0.88 ± 0.10 g m^{-2}; high fire frequency: 0.61 ± 0.03 g m^{-2}; Table 2).

4. Discussion

The duration of agricultural legacies in soil properties can vary greatly, persisting for thousands of years (Dupouey et al., 2002) or recovering within several decades (Compton et al., 1998; Maloney et al., 2008). Subsequent disturbance, such as prescribed fire, may affect soil properties differently depending on previous history of agricultural use. In our study, we found no evidence of an interaction between agricultural history and prescribed fire frequency, but both past and present disturbances affected soil properties in distinct ways.

Past agricultural land use affected a greater number of soil properties than did fire frequency. This legacy of agriculture on soils has persisted almost 60 years after afforestation began at the SRS, providing a clear example of how agriculture can impart long-lasting legacies on ecosystems. Many of our results, such as lower percent organic matter in post-agricultural soils, were consistent with other studies from longleaf pine (Markewitz et al., 2002; Brudvig et al., 2013) as well as other types of woodlands with a history of agriculture (Compton and Boone, 2000; Dupouey et al., 2002; McLauchlan, 2006; Grossmann and Mladenoff, 2008; Matlack, 2009). While most studies focus on the upper layer of the soil profile where tilling and most biological activity occurs (but see Koerner et al., 1997; Markewitz et al., 2002), we found a trend of greater phosphorus in post-agricultural woodlands penetrating 30 cm deep into the soil profile. These changes may be a consequence of the soil amendments often applied to agricultural fields (e.g., manure, lime). Changes to soil phosphorus in particular are representative of enduring legacies of historical agriculture (McLauchlan, 2006; MacDonald et al., 2012).

Reduction of organic matter in historically cultivated soils, as observed at SRS and elsewhere, is a product of biomass removal (i.e., forest clearing) and increased decomposition from tilling (McLauchlan, 2006). Importantly, decreased organic matter can affect a host of other soil properties, including those related to nutrient availability (TEC), water retention (SWHC), and soil density (bulk density). For example, organic matter can be the dominant source of cation exchange capacity (and thus micronutrient retention) in acidic sandy soils (e.g., longleaf pine woodlands) (Brady and Weil, 2002) and corresponds with the greater TEC observed in the remnant sites of our study. Organic matter is also a primary source of plant-available (inorganic) nitrogen compounds through mineralization, but results regarding the persistence of nitrogen depletion in post-agricultural soils are inconsistent (Markewitz et al., 2002; Falkengren-Grerup et al., 2006). Since we did not detect an agricultural legacy in soil inorganic nitrogen at SRS, it may be that inorganic nitrogen concentrations in our soils have recovered to the characteristically low levels found in longleaf pine woodlands (Wilson et al., 1999).

Organic matter also increases water retention and thus soil water holding capacities, which play a key role in maintaining water-availability for plants in well-drained sandy soils (Brady and Weil, 2002). As observed in other studies of sandy longleaf pine soils (e.g. Brudvig et al., 2013), we found that remnant woodland soils had both greater amounts of organic matter and greater SWHC. Soil organic matter can also be a major factor in determining soil bulk density (Curtis and Post, 1964). The loss of light-weight, aggregate-forming organic matter combined with the physical long-term effects of tilling, leads to increased bulk density over time in agricultural soils (Brady and Weil, 2002). In our study, greater bulk density persisted over 60 years following agricultural abandonment, and the long duration of soil compaction at SRS is consistent with studies in similar sandy-soiled systems (Compton et al., 1998), including longleaf pine (Maloney et al., 2008; Mattingly and Orrock, 2013).

Increased bulk density in post-agricultural soils may have significant biotic consequences, including decreased soil pore space for water retention, and increased soil strength that makes it difficult for roots to penetrate the soil to access resources (Whalley et al., 1995; Kozlowski, 1999). Though the increase in bulk density

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of post-agricultural soils at SRS (average = 10% increase over remnant woodlands) is below the US Forest Service threshold for mandated remediation (Powers et al., 1998), forest understory species can vary in their sensitivity to increased soil compaction (Small and McCarthy, 2002; Godefroid and Koedam, 2004) and future work might investigate whether this affects plant recruitment on post-agricultural sites.

Bulk density can also influence the interpretation of soil nutrient status if it is not accounted for in nutrient measurements (Compton et al., 1998; Markewitz et al., 2002; Fraterrigo et al., 2005). Comparison of soil nutrient concentrations assumes that soil mass–volume relationships are constant among locations; this assumption does not necessarily hold when comparing remnant and post-agricultural soils (Markewitz et al., 2002). Because agriculture can have a long-lasting effect on soil bulk density (Markewitz et al., 2002; Fraterrigo et al., 2005), quantifying soil nutrient stocks (i.e., g nutrient m^{-2}) offers added insights beyond those afforded by nutrient concentration analyses. For example, soil stocks may provide a more ecologically appropriate measure of the soil nutrient content available to plant root volume (Westman et al., 1985). Interestingly, we found that converting to nutrient stocks by correcting for differences in bulk density provided additional understanding into how agricultural legacies impacted the soils at SRS. While phosphorous stocks remained greater in post-agricultural soils after conversion from concentrations to stocks, accounting for bulk density differences showed that total stocks of organic matter and carbon per hectare did not differ among agricultural histories. In other words, the total weight of organic matter and carbon was similar regardless of agricultural history; organic matter was simply compressed within the greater bulk density of post-agricultural soils. When expressed as stocks, our findings are similar to other studies on sandy soils the Southeastern (Richter et al., 1999; Maloney et al., 2008) and Northeastern US (Compton et al., 1998) where soil OM stocks in post-agricultural forests appear to have recovered to those of nearby remnants. However, we caution that the apparent recovery of nitrogen, carbon, and organic matter stocks to remnant woodland levels at SRS does not necessarily indicate that soils have been restored, as increased bulk density and its potential negative effects on the soil structure (and the consequences for plants) remain.

In comparison to agricultural history, very few soil properties differed between sites with high and low fire frequency after more than 20 years of repeated burning. Because fire frequency did not affect bulk density, the effect of fire on soil nutrient stocks and concentrations was qualitatively similar. Fire frequency did, however, significantly affect the thickness of the forest floor (organic layer). Similarly, other studies have found that fire has the greatest influence on the upper layers of soil, including the organic layer and its nutrient content (Bell and Binkley, 1989; Binkley et al., 1992; Wan et al., 2001; Certini, 2005; Lavoie et al., 2010). When compared to no-burn or burn-suppressed sites, a decrease in the amount of litter is a consistent effect of repeated burning in longleaf and loblolly pine (*Pinus taeda*) woodlands (Binkley et al., 1992; Varner et al., 2005).

In addition to a thicker organic layer, woodlands with low fire frequency showed a consistent trend of greater soil inorganic nitrogen compared to high fire frequency woodlands (up to 50% greater concentration in the top 0–15 cm) that was apparent down to 45 cm depth in the mineral soil. Most studies report few long-term effects of fire deeper than the very top (0–10 cm) layers of mineral soil (Bell and Binkley, 1989; Binkley et al., 1992; Wan et al., 2001; Certini, 2005), including in nutrient-poor longleaf pine (Lavoie et al., 2010, 2014). Stocks of nutrients such as nitrogen in the mineral soil of longleaf and loblolly woodlands may not consistently differ between less frequently (or never) burned and more frequently burned sites, even after > 20 years of repeated burning (McKee, 1982; Binkley et al., 1992; Lavoie et al., 2014). In contrast, nitrogen availability (i.e., inorganic nitrogen from mineralization) may be decreased in the long-term in more frequently burned plots (Bell and Binkley, 1989). Additionally, the SRS has very sandy soils, which may have resulted in the NO_3 component of soil inorganic nitrogen in upper layers migrating to lower parts of the soil profile. Binkley et al. (1992) speculated that observed nitrogen losses in the organic layer due to fire may be transferred to lower levels in the mineral soil. We did not measure nutrient content in the litter and duff (organic) layer, but these layers were thicker in our low fire frequency sites and may have higher nitrogen content compared to high fire frequency sites (Binkley et al., 1992). It is possible that the greater volume of litter and duff in low-fire frequency sites resulted in greater release of inorganic nitrogen via fires or decomposition, leading to greater inorganic nitrogen at all soil depths.

We did not detect an interaction between agricultural history and fire frequency on soil properties in longleaf pine woodlands at SRS, in contrast to studies in other ecosystems. For instance, in Mediterranean scrub forests, fire and agricultural history interact to affect soil properties (Duguy et al., 2007) as well as tree composition and cover (Puerta-Piñero et al., 2012). However, these studies examined the effects of large, stand-replacing fires, in contrast to the relatively low-intensity, frequent prescribed surface fires experienced over in the longleaf pine woodlands at SRS. Our finding that historical and contemporary disturbances exhibit clear, yet distinct, effects on soil properties in longleaf pine woodlands suggests that restoring the fire regime alone may not mitigate the degrading effects of past agricultural use on forest communities.

Soil properties altered by both historical and contemporary disturbances may have important consequences for recovering plant communities, particularly in systems that are a focus of conservation and restoration efforts such as longleaf pine (Walker and Silletti, 2006). Our findings on the effects of agricultural history and fire on soils may, in part, reflect the cumulative effects of plant–soil feedbacks from changes to the recovering plant community following these disturbances. Though disentangling this feedback was beyond the scope of this study, there are several ways in which soil properties may affect the plant community in longleaf pine woodlands. Persistent increases in nutrients such as phosphorus in post-agricultural woodlands might influence natural community assembly via plant–microbe interactions (Johnson, 2009). Because increased phosphorus exacerbates nitrogen-limitation for plants, altering the nutrient environment changes the costs and benefits for fungal and bacterial symbioses (Johnson, 2009; Lau et al., 2012), and may ultimately influence plant community diversity (Collins and Foster, 2009). Additionally, soil moisture is strongly related to understory richness in longleaf pine woodlands (Kirkman et al., 2001; Brudvig et al., 2013), and lower organic matter and soil water holding capacity may thus limit restoration success by intensifying competition from other species for water resources (Walker and Silletti, 2006) and limiting natural seedling recruitment for some species (Iacona et al., 2010). Furthermore, accumulated litter and duff from fire suppression in longleaf pine woodlands and savannas is associated with lower understory species richness, so plant community diversity may benefit from reducing fire-free intervals to minimize litter and duff depth (Hiers et al., 2007; Brudvig et al., 2013; Veldman et al., 2014).

Our work demonstrates the dramatic and lasting effects of agricultural legacies and present-day fire management on soil nutrients and physical properties. Given that variables such as litter depth and soil moisture are important determinants of plant community diversity and productivity in longleaf pine ecosystems (Kirkman et al., 2001; Veldman et al., 2014), our results have implications for ground-layer ecology and management in this system. Indeed, given that soils provide the template upon which plant communities assemble, successful restoration and management require

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understanding how past land use and present management activities influence soil properties. Studies like ours that document the joint impacts of historical and contemporary disturbances on soils provide a foundation for making informed management decisions, which might involve soil nutrient amendments or plant species reintroductions, and are a first step toward increasing and successfully restoring diversity and productivity in degraded landscapes.

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