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Research Article

Long-Term Recovery of Selected Indicator Species Following Soil Disturbance and Compaction in an Old-Growth Longleaf Pine (*Pinus palustris*) Woodland

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ABSTRACT

Reference sites with relatively unaltered plant communities are used regularly to establish targets for ecological restoration, yet few are free from anthropogenic disturbances. In this study, we sought to understand the capacity for native community indicators and other plant species to recover from abandoned woods roads and tilled soils within reference sites. We mapped disturbances in a 34 ha portion of the Wade Tract, an old-growth longleaf pine-wiregrass (*Pinus palustris-Aristida stricta*) woodland using GPS and LiDAR and counted stems of 25 native species (20 woody and 5 herbaceous) in plots within disturbances ($n = 32$; disturbed), 3 m adjacent to disturbances ($n = 32$; adjacent), and >5 m from any disturbance ($n = 30$; reference). Ten species were considered indicator species of intact longleaf pine woodlands. We also quantified soil conditions within the disturbed, adjacent, and reference sites. Disturbed sites had more compacted surface soils than adjacent or reference sites and, in a subset of the sites, soil bulk density and soil strength were greater in disturbed than in adjacent. Indicator species were less frequent in disturbed sites than in adjacent or reference sites (except for *Quercus pumila*). Three oaks (*Q. incana*, *Q. margaretta*, and *Q. laevis*) and 3 other woody species (*Rhus copallinum*, *Sassafras albidum*, and *Morella cerifera*) were significantly less common in the disturbed sites than in adjacent or reference sites. The near absence of some oaks and other woody species on disturbed sites warrants including these species as indicators of intact regional ground cover for longleaf pine woodlands. Legacies of small-scale soil disturbances in relatively undisturbed perennial-dominated ground cover flora reveals the potential for cumulative degradation over decades and underscores the need to avoid such disturbances in remnant longleaf pine woodlands.

Index terms: indicator species; native ground cover; oaks; reference conditions; soil disturbance

INTRODUCTION

Intact longleaf pine (*Pinus palustris*) woodlands have distinct plant communities characterized by high species richness in the ground cover, many endemic species, fuels that promote the spread of fire, and perennial plants that resprout after fire. Fire is carried by surface vegetation and pine needles shed by overstory trees that become suspended on bunch grasses and other plants (Mitchell et al. 2006). Combustion and regrowth of ground cover vegetation is critical for nutrient cycling and seed production (Boring et al. 2005) and provides grass-dominated habitat for wildlife (Kirkman and Giencke 2018). Small-scale natural disturbances are common in relatively undisturbed sites and influence soil and plants found in association with disturbances. Tree tip-ups and burrowing and mounding by gopher tortoises (*Gopherus polyphemus*), pocket gophers (*Geomys pinetis*), harvester ants (*Pogonomyrmex badius*), and other animals expose and relocate soil. Also, long-duration combustion of woody fuels can sterilize patches of soil (Hermann 1993; Simkin and Michener 2005).

Given their regular association with high-quality reference sites, the effects of small-scale natural disturbances on vegetation are presumably neutral or beneficial to community stability over time. Potential benefits include aeration and reduction of bulk density of soil, provision of microsites for plant regeneration, and enhanced diversity of plant composition and wildlife habitat over larger areas (Simkin and Michener 2005). Frequency, season, and severity of fire, both natural and anthropogenic, interact with these disturbances to influence ground cover vegetation (Hiers et al. 2007).

Soil disturbance associated with post-Columbian humans may have different and understudied impacts. Common management activities affecting soil include tilling/disking for farming, skid trails, wildlife food plots, and fire breaks that can lead to soil compaction and alter fire behavior. Disking differs from burrowing and mounding in that it homogenizes soil, roots, and mycelial networks over broader areas and penetrates to greater depths. These differences may result in increased soil compaction and reduced root penetration at the bottom of the tilling zone (Hill and Cruse 1985; Grant and Lafond 1993; Lampurlanés and Cantero-Martínez 2003) and loss of soil aggregation and soil organic matter (McVay et al. 2006). Vehicular traffic also directly affects soil compaction (Bigelow et al. 2018) in a manner that has no analogue in natural disturbance regimes.

Longleaf pine communities with low levels of human soil disturbance are rare (Veldman et al. 2015). The Wade Tract (Thomas County, Georgia, USA) is a remnant old-growth stand and the only national natural landmark designated for the longleaf pine ecosystem (Varner and Kush 2004; Gilliam and Platt 2006; Mitchell et al. 2009). The tract has served as a useful reference site for restoration efforts (Walker and Silletti 2006), such as America's Longleaf Restoration Initiative (ALRI 2009), which has a goal of increasing the area of longleaf pine from 1.4 to 3.2 million ha by 2025.

In longleaf pine and other ecosystems with high ground cover diversity, indicator species, which are found regularly in undisturbed locations relative to disturbed locations, serve as important metrics for restoration of the native plant community. While some indicator species are site-specific, others have proven to be robust indicators of relatively undisturbed longleaf pine communities in the eastern portion of the Coastal Plain. The native community indicator species used in this study were *Aristida stricta*, *Dyschoriste oblongifolia*, *Gaylussacia* sp., *Pteridium aquilinum*, *Quercus incana*, *Q. laevis*, *Q. margaretta*, *Q. pumila*, *Tephrosia virginiana*, and *Vaccinium myrsinites* and derived from studies conducted in North Carolina (Brudvig et al. 2014), Georgia (Hedman et al. 2000; Dale et al. 2002; Kirkman et al. 2004; Ostertag and Robertson 2007; Brudvig and Damschen 2011; Brudvig et al. 2013, 2014; Turley et al. 2017), and Florida (Hebb 1971; Schultz and Wilhite 1974; Moore et al. 1982). Presence or absence of these species depends largely on their ability to persist as root stocks or in the seed bank following large- or small-scale disturbance. These species are not as capable of persisting or recolonizing sites following large-scale anthropogenic soil disturbance (White and Walker 1997; Dell et al. 2019). For example, disking for agriculture has lasting effects on soil properties such as soil infiltration rates (Levi et al. 2010) and eliminates native longleaf pine community indicator species for decades, possibly because of limited seed dispersal distances (Kirkman et al. 2004; Ostertag and Robertson 2007; Turley et al. 2017), but their recovery following finer-scale human disturbances such as roads, firebreaks, and wildlife food plots that occur within the Wade Tract and other longleaf pine reference sites remains an open question.

We assessed the hypothesis that soil compaction from two types of anthropogenic soil disturbance, woods roads and "ring-arounds," resulted in fewer native indicator species and woody species in the disturbed areas on the Wade Tract. These disturbances are about 2 m wide. Ring-arounds are lanes harrowed by tractor every few years that circle and protect areas from fire to facilitate pine regeneration and preserve cover for northern bobwhite quail (*Colinus virginianus*; Neel et al. 2010). Woods roads are not disked but instead feature repeated compaction of soils by heavy vehicles. Both types of disturbance occurred >40 y prior to this study. Specifically, we sought to test whether these disturbances (or their edge effects on adjacent ground cover communities) influenced the abundance (i.e., number of stems or clumps) or occurrence of 25 native plant species at the Wade Tract, 20 of which are woody and 10 are widely regarded to be indicators of undisturbed longleaf pine ecosystems.

METHODS

Study Site

Land that became the Wade Tract was first purchased by European settlers 200 y ago following the 1820 land lottery (Tinker 1994). Herbert L. Stoddard Sr., noted wildlife biologist, was hired around 1930 to advise on game and timber management on several hunting estates in the Red Hills region of southwestern Georgia (Way 2011). Stoddard recognized that the stand that became the Wade Tract would be "so valuable for research that none of us living today can foresee all the values the block will have for generations to come" (Stoddard 1961). In 1961 the property was bought by Jeptha H. Wade III to form Arcadia Plantation, and in 1979, the Wade Family placed an 80 ha conservation easement, held by Tall Timbers Research Station, dedicated to research related to old-growth longleaf pine forest ecology. The easement—the first conservation easement established in Georgia—was based, in part, on the map and notes made by Stoddard (Figure 1). Over 535 species of plants have been documented to occur within the easement (R. Carter, pers. comm.). Frequent burning of the area has been uninterrupted since before European settlement (Rother et al. 2020).

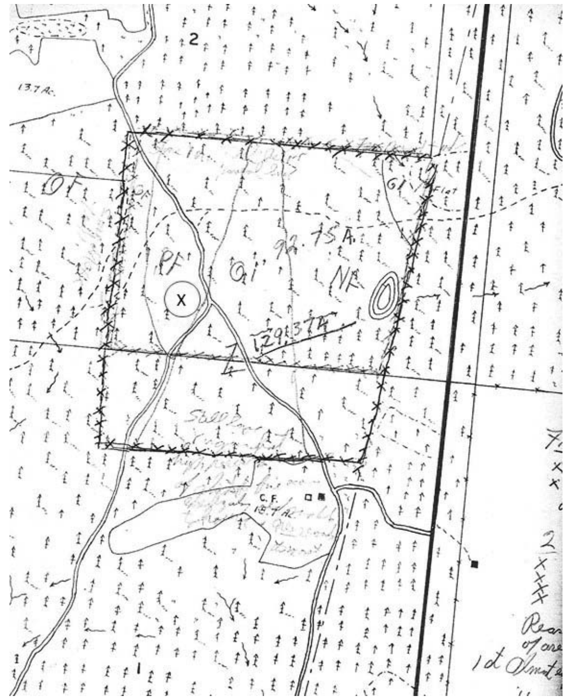

Figure 1.—A sketch by Herbert L. Stoddard Sr. in 1961 of a tract of old-growth longleaf pine on Millpond Plantation. The map is stored in the Tall Timbers Research Station archive. This sketch was the basis for the Wade Tract conservation/research easement. The circled "X" is the same point in Figures 1, 2, and 3.

Despite being considered one of best examples of old-growth longleaf pine woodland (Platt et al. 1988; Landers and Boyer 1999; Varner and Kush 2004), the Wade Tract has small-scale land use legacies that are still evident decades after they occurred. These include historical road and trail networks dating to the 1800s and ring-arounds likely dating to 1935–1978 when many landowners in the Red Hills adopted Stoddard's wildlife management recommendations (Stoddard 1931). In addition to these disturbances, cut tree stumps and box cuts (i.e., exploratory cuts to determine tree soundness) indicate other

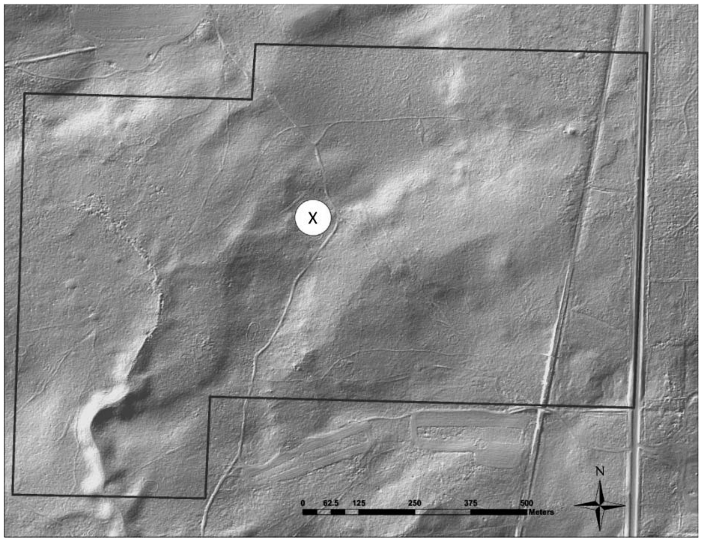

Figure 2a.—A LiDAR scan of the Wade Tract. The entire Wade Tract is indicated by the solid black line.

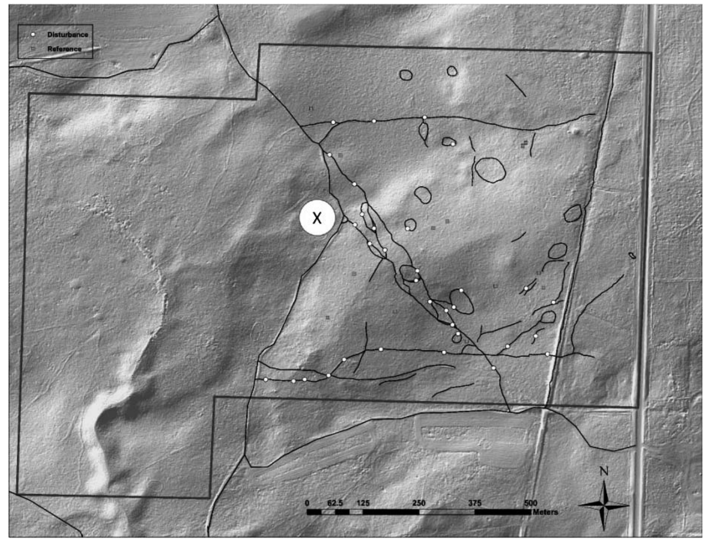

Figure 2b.—Woods roads and ring-arounds in the eastern half of the Wade Tract based on ground-truthing following a fire and the LiDAR scan. The 34 ha study section is to the east of the "X." Sampling sites for disturbed ground (white dots) and undisturbed ground (gray squares) are represented. Note: although nine of the southernmost disturbed and adjacent sampling sites were just south of the Wade Tract boundary, land management practices in Arcadia Plantation outside the boundary were essentially the same as within the easement.

human activities occurred that are no longer permitted on the Wade Tract.

Study Design and Field Methods

We initially mapped ground cover disturbance on the Wade Tract using GPS (Trimble GeoExplorer 3; Sunnydale, California, USA) following a prescribed fire in 2010 (R.T. Engstrom). The Wade Tract is gridded into 1 ha square quadrats marked by metal stakes (Platt et al. 1988). We searched for disturbances by walking along a transect through the middle of the quadrats. When linear disturbances were detected, they were mapped to the end of the disturbance, and the search was resumed through the transects. These data were extended with a survey of ground return topography derived from high-resolution, aerial LiDAR (light detection and ranging) collected using a fixed-wing aircraft with a Leica ALS50 sensor (Leica Geosystems, St. Gallen, Switzerland) in 2018 (Figure 2a). Points were collected at a resolution of 15 returns/m^2 and the data were corrected using sub-meter fixed ground point targets. Vertical accuracy met 10 cm RMSEz 95th percentile requirements. Airborne LiDAR data were classified using the LASclassify and LASground tools in the LAStools LiDAR suite (Isenburg 2014) to create a Digital Elevation Model (DEM).

Based on a 1939 aerial photograph and a 1960 timber map, one braided road network through the Wade Tract (Figures 1, 2a, 2b) was extant at least 80 y ago and could have been created in the 19th century. An approximately decadal sequence of aerial photographs indicates this road was abandoned in the late 1970s shortly before the conservation easement was established (Figures 2b and 3). The ring-arounds were also abandoned at the time the conservation easement was established.

Using the "Create Random Points" tool in ArcMap 10.6 (ESRI, Redlands, California, USA) to generate random points, we selected 32 sampling locations centered in the abandoned roads and ring-arounds (disturbed sites). Data for adjacent sites ($n = 32$) were collected 3 m from the edge of each linear disturbance and alternating the side sampled between consecutive samples. We then established 15 reference sites from random points generated outside a 5 m buffer around mapped disturbances. Each randomly located reference point contained paired sampling sites 3 m apart, mirroring sampling of the disturbed/adjacent sites for a total of 30 reference plots. In ArcMap 10.6, we created GeoPDF files, imported those files into the Avenza application (Avenza Systems, Toronto, Ontario, Canada) on an iPhone, and used those files to navigate to the randomly chosen sampling locations. We

Figure 3.—Ruts of an old woods road through the Wade Tract at least 40 y after the road was abandoned. The road splits suggesting that vehicles had difficulty going uphill on the sandy road. This image was taken on 12 May 2020. This part of the Wade Tract was burned on 5 May.

Table 1.—Summary data for species in reference, adjacent, and disturbed sites at the Wade Tract, Georgia, USA. "Type" indicates whether the species is woody (W) or herbaceous (H), "Freq" is the number of plots in which the species occurred, and "Mean" is the mean number of stems or clumps (i.e., the grasses *Aristida* and *Sporobolus*) in the plots. The species are in order of decreasing frequency on the reference sites. Indicator species from previous literature are noted in bold.

		Reference				Adjacent				Disturbed			
Species	**Type**	**Freq**	**Mean**	**SD**	**Max**	**Freq**	**Mean**	**SD**	**Max**	**Freq**	**Mean**	**SD**	**Max**
Pinus palustris (seedling)	W	30	10.9	8	30	30	11.7	11.8	49	28	14.2	12.8	52
Dyschoriste oblongifolia	H	29				29				28			
Aristida stricta	H	27	8.5	6	17	22	10.7	11.3	36	19	7	8.2	33
Quercus incana	W	25	38.7	36.5	134	13	14.7	28.9	138	2	0.5	2.1	10
Quercus margaretta	W	24	29.3	36.1	152	23	42.8	50.1	172	14	6.1	15.9	82
Rhus copallinum	W	23	2.9	3.3	13	20	3.3	5	24	10	0.6	1	3
***Gaylussacia* sp.** [a]	W	23				22				17			
Vaccinium myrsinites	W	23				20				13			
Pteridium aquilinum	H	19				26				16			
Tephrosia virginiana	H	19				13				13			
Quercus laevis	W	16	8	10.6	37	18	7	10.6	33	1	0.7	3.7	21
Sassafras albidum	W	8	0.7	1.2	4	6	0.9	2.2	8	2	0.1	0.4	2
Sporobolus junceus	H	7	0.2	0.4	1	5	0.2	0.4	1	8	0.4	1.1	6
Diospyros virginiana	W	7	1.5	3.9	15	3	0.2	0.7	4	3	0.1	0.3	1
Quercus pumila	W	6	21	59.8	258	18	46.1	68.4	238	15	15.3	31.4	135
Morella cerifera	W	5	3.5	8.4	30	7	2.3	6.9	36	3	0.4	1.5	6
Quercus marilandica	W	4	1.1	2.9	11	0	0	0	0	1	0.1	0.4	2
Carya tomentosa	W	3	0.1	0.4	2	2	0.2	0.9	5	0	0	0	0
Castanea pumila	W	3	1.5	5.7	29	0	0	0	0	0	0	0	0
Quercus falcata	W	1	0.1	0.4	2	0	0	0	0	0	0	0	0
Vaccinium arboreum	W	1	0.6	3.1	17	1	0	0.2	1	1	0.1	0.5	3
Salix nigra	W	1	0	0.2	1	0	0	0	0	0	0	0	0
Pinus palustris (tree)	W	0	0	0	0	3	0.1	0.4	2	6	0.7	1.8	9
Pinus elliottii (seedling)	W	0	0	0	0	1				0	0	0	0
Quercus nigra	W	0	0	0	0	1	0.2	0.9	5	0	0	0	0
Quercus virginiana	W	0	0	0	0	0	0	0	0	1	0	0.2	1

[a] *Gaylussacia dumosa* and *G. frondosa* are both indicator species and were not distinguished.

established 1 m × 6 m plots that ran parallel with the disturbance and in a random direction with reference sites. Despite >40 y since any active disturbance, each linear feature was easily identified (Figure 3). We sampled 564 m^2 in disturbed ($n = 32$), adjacent ($n = 32$), and reference sites ($n = 30$) for 10 indicator species and 15 additional species (Table 1). We counted tussocks of *A. stricta* and *Sporobolus junceus* and stems of woody species (e.g., *Q. pumila*). We also counted longleaf pine seedlings (stem height <10 cm) and stems >2 cm diameter at breast height. All vegetation samples were collected between 14 March and 5 May 2020. We used Wunderlin and Hansen (2011) for all plant names.

We measured soil strength and soil bulk density at each sampling site to infer relative soil compaction (Batey 2009). Soil strength is quantified based on the force (in Newtons; N) per unit area (cm^2) required for a conical probe to penetrate the soil. We used an Eijkelkamp probe to quantify soil resistance (Eijkelkamp NA, Morrisville, North Carolina, USA; with 100 N/cm^2 soil resistance) and used the inverse as an index of soil resistance. Bulk density represents soil mass per unit volume (Batey 2009). Bulk density was measured by collecting soil samples (4.7 cm diameter) at 3 depths (0–5, 5–15, and 15–30 cm) using an Eijkelkamp soil collection barrel with a removable sleeve and a slide hammer. Samples were dried, weighed, and bulk density calculated as mass of dry soil (g) per unit soil volume (cm^3). Soil strength (N/cm^2) was recorded for each of the above depth increments at 10 locations per site and averaged per site and depth increment prior to analyses. Soil measurements were taken concurrently with vegetation samples, but we also collected additional soil samples for five separate abandoned roads and five abandoned ring-arounds for measurement of soil strength and soil bulk density within fixed depth increments. Measurements were made 5–21 February 2021. At each site, we measured bulk density at the center of the linear feature (ring-around or road) and 3 m adjacent to the disturbance.

Data Analysis

We used permutational multivariate analysis of variance (perMANOVA; Anderson 2001) in PC-Ord (McCune and Mefford 2016) to compare selected plant species presence/absence in disturbed, adjacent, and reference sites. We removed two random pairs of disturbed and adjacent plots because their unbalanced data violated the assumptions used for perMANOVA in PC-Ord. We also used the multilevel pattern analysis *multipatt* function in the *indicspecies* R package (R Core Team 2021) to test for associations among individual species and the different types of sites. The data were converted to presence/absence for species where abundance data were collected. We also applied the *r.g.* function to correct the phi coefficient because disturbed and adjacent sites outnumbered reference sites.

We used the *signassoc* function in the *indicspecies* package in R to test for significant species–vegetation type associations among indicator species. The two-sided test allows each species to be

Table 2.—Species-site associations in reference, adjacent, and disturbed sites with the Wade Tract using the *signassoc* function in the *indicspecies* package as described by Bakker (2008) and Caceres and Legendre (2009). The values listed under each group are *P*-values. Alpha = 0.05. Indicator species from Ostertag and Robertson (2007) are noted in bold.

Species	Type	Reference	Adjacent	Disturbed	Adjusted Alpha
Pinus palustris (seedling)	W	0.21	0.69	0.08	0.22
Dyschoriste oblongifolia	H	0.31	0.39	0.32	0.67
Aristida stricta	H	0.01 [a]	0.49	0.02 [b]	0.03
Quercus incana	W	0.01 [a]	0.58	0.01 [b]	0.03
Quercus margaretta	W	0.08	0.49	0.02 [b]	0.06
Rhus copallinum	W	0.03 [a]	0.49	0.01 [b]	0.03
***Gaylussacia* sp.** [c]	W	0.22	0.84	0.07	0.2
Vaccinium myrsinites	W	0.04 [a]	0.68	0.02 [b]	0.06
Pteridium aquilinum	H	1	0.02 [a]	0.03 [b]	0.06
Tephrosia virginiana	H	0.06	0.12	0.3	0.17
Quercus laevis	W	0.05 [a]	0.02 [a]	0.01 [b]	0.03
Sassafras albidum	W	0.25	1	0.05	0.14
Sporobolus junceus	H	0.93	0.46	0.69	0.84
Diospyros virginiana	W	0.17	0.26	0.33	0.43
Quercus pumila	W	0.01 [b]	0.04 [a]	0.33	0.03
Morella cerifera	W	0.85	0.87	0.41	0.79
Quercus marilandica	W	0.08	0.22	0.29	0.22
Carya tomentosa	W	0.35	0.91	0.32	0.69
Castanea pumila	W	0.18	0.5	0.3	0.45
Quercus falcata	W	0.74	1	1	0.98
Vaccinium arboreum	W	1	1	1	1
Salix nigra	W	0.68	1	1	0.97
Pinus palustris (tree)	W	0.05 [b]	0.61	0.05 [a]	0.14
Pinus elliotii (seedling)	W	1	0.94	1	1
Quercus nigra	W	1	0.73	1	0.98
Quercus virginiana	W	1	1	0.74	0.98

[a] Significantly more likely to be in this plot type than random.
[b] Significantly less likely to be in this plot type than random.
[c] *Gaylussacia dumosa* and *G. frondosa* are both indicator species and were not distinguished.

assigned an expected frequency of occurrence within each vegetation type (Table 2; Bakker 2008, Caceres and Legendre 2009).

Species–site associations were assessed using non-metric multi-dimensional scaling (NMS) in PC-Ord (McCune and Mefford 2016) with Sorensen distance methods. Additionally, vectors representing species abundance and soil resistance measured with a penetrometer ($r^2 > 0.15$) were plotted using bi-plots to assess correlations between these variables and plant species composition identified in the model.

We compared our index of soil resistance among the three different site types using ANOVA. Differences in soil bulk density and soil strength between locations within and outside of abandoned ring-arounds and roads were tested with two-way ANOVAs with location (in, out) and depth increment as fixed factors, interaction term included, using IBM SPSS Statistics 24.0.

RESULTS

The vegetation composition of disturbed, adjacent, and reference sites within the Wade Tract differed significantly ($n = 30$; df = 2; $F = 7.15$; $P = 0.0002$) in the perMANOVA. In pairwise comparisons of vegetation types, disturbed sites differed from adjacent ($P = 0.0002$) and reference sites ($P = 0.0002$). Adjacent sites also differed from reference sites ($P = 0.0008$). NMS showed a clear separation of disturbed plots from the other two plot types (Figure 4), and seven bi-plot vectors correlated with the original ordination space: *Quercus pumila* ($r^2 = 0.475$), *Q. marilandrica* ($r^2 = 0.395$), *P. palustris* seedlings ($r^2 = 0.318$), *Q. incana* ($r^2 = 0.310$), *A. stricta* ($r^2 = 0.213$), *R. copallinum* ($r^2 = 0.165$), and soil resistance ($r^2 = 0.189$). These seven bi-plot vectors highlight all of the measured environmental and species factors that can be associated ($r^2 > 0.15$) with the three axes of the ordination. The lengths of the vectors correlate to the strength of association. Table 1 highlights actual community differences by species between plot types.

Analysis of our focal species found four woody species (*Q. incana*, *Q. laevis*, *Rhus copallinum*, and *Vaccinium arboreum*) and wiregrass (*A. stricta*) that were less likely to occur in disturbed sites and more likely to occur in reference sites. Both *P. aquilinum* and *Q. pumila* were more likely to be found in adjacent sites (Table 2).

Disturbed sites had surface soil that was significantly more resistant to penetration than adjacent or reference sites ($F = 30.8$; df = 2; $P < 0001$). Mean N/depth (in cm) for disturbed sites was 49.1 ($n = 32$; SD = 40.2; range 5 to 150) compared to 8.1 ($n = 32$; SD = 3.73; range 4 to 20) for adjacent and 7.3 ($n = 30$; SD = 3.0; range 3.8 to 15) for reference sites. Abandoned roads and ring-arounds sites had significantly higher soil strength and bulk density (Figure 5) when compared with adjacent sites. Soil strength and bulk density increased significantly with depth of soil. The absences of interaction at different soil depths and

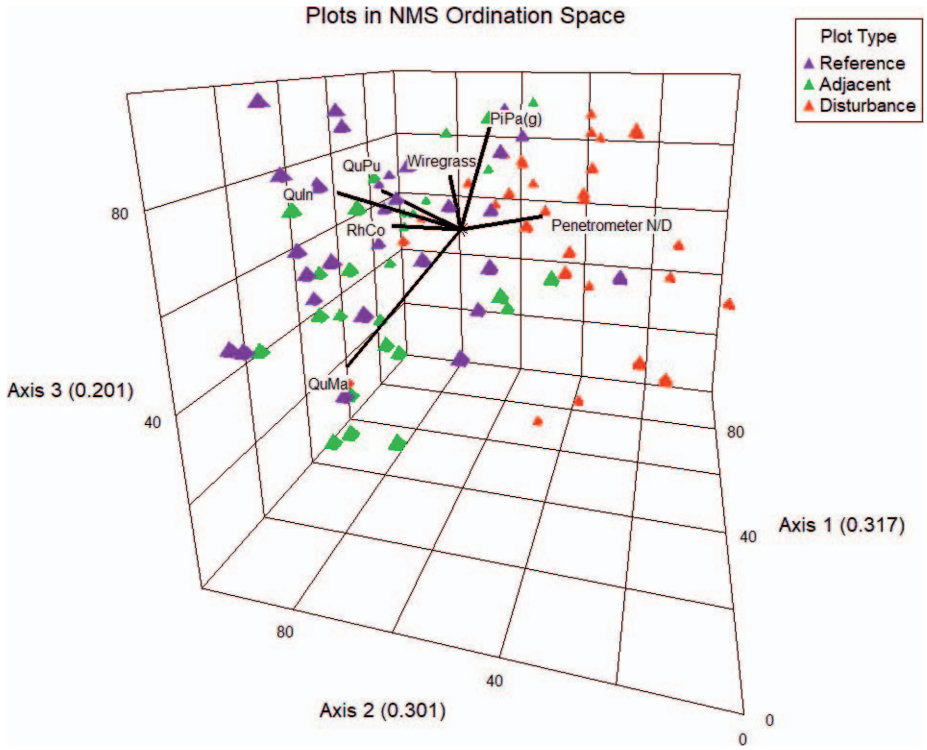

Figure 4.—Non-metric multidimensional scaling (NMS) ordination using Sorensen distance for indicators. Vectors indicating species abundance and soil resistance measured with a penetrometer are scaled to 200% for clarity. The coefficients of determination for the correlations (r^2) between ordination distances and distances in the original analyses by axes are labeled.

difference between disturbed and adjacent sites suggests that the changes were uniform among depth increments (Figure 5).

DISCUSSION

Despite more than 40 y for recovery within the Wade Tract, a reference longleaf pine woodland, the legacy of anthropogenic soil disturbances is still evident in plant species composition of both indicator and woody species. Although disturbed and adjacent sites were only separated by 3 m, changes in plant species composition and soil characteristics were detected. We also found differences between adjacent and reference sites, suggesting adjacent sites were influenced by the nearby linear disturbances.

While all of the indicator species were observed within some disturbed plots, abundance of several pyrophytic oaks (*Q. incana*, *Q. laevis*, and *Q. margaretta*) remained significantly lower in the disturbed areas 40 y after the woods roads and ring-arounds were abandoned. This lack of hardwood recolonization further challenges the prevailing narrative of oak response to disturbance where deciduous hardwoods stem density was not associated with degraded ground cover flora or declines in native fauna (Hiers et al. 2007, 2014). On the other hand, *Dyschoriste oblongifolia*, an herbaceous plant recognized as an indicator species in other studies, was found in equal abundance across all vegetation types. These results suggest this indicator likely recolonized disturbed sites following several decades of recovery. Previous studies identifying *D. oblongifolia* as an indicator species focused on relatively large abandoned agricultural fields, presenting the possibility that this species is capable of recolonizing smaller disturbed areas (Hedman et al. 2000; Kirkman et al. 2004; Ostertag and Robertson 2007; Brudvig and Damschen 2011). *P. aquilinum* and *Q. pumila* were most frequently found in adjacent sites, suggesting these indicator species may fare well in sites with a modest degree of disturbance. While this view is consistent with past studies (Kirkman et al. 2004; Ostertag and Robertson 2007; Brudvig et al. 2014), the underlying mechanisms for this result are unclear.

One of the most surprising results is that many woody species differed dramatically in abundance across the 3 m distance separating disturbed and adjacent sites. The disturbed areas were only 1–3 m wide, but clonal woody species like *Q. margaretta*, *R. copallinum*, *Q. laevis*, and *Q. incana* (Tables 1 and 2) were largely eliminated relative to either reference or adjacent plots. The relatively slow recovery of native oaks and other woody stems within the disturbed area suggests some species like *Q. laevis* or *Q. incana* could be among the most disturbance-sensitive indicators of native ground cover. These results also suggest soil compaction as the mechanism by which disturbances cause lasting species shifts in native hardwoods. While the linear features mapped here were likely to retard the spread of prescribed fires immediately following abandonment, an increase in hardwood stems expected with reduced fire intensity was not observed. Predictably, longleaf pine seedlings were associated with disturbed plots given the conditions required for germination (Croker and Boyer 1975; Boyer 1993; Robertson et al. 2019). The larger longleaf stems associated

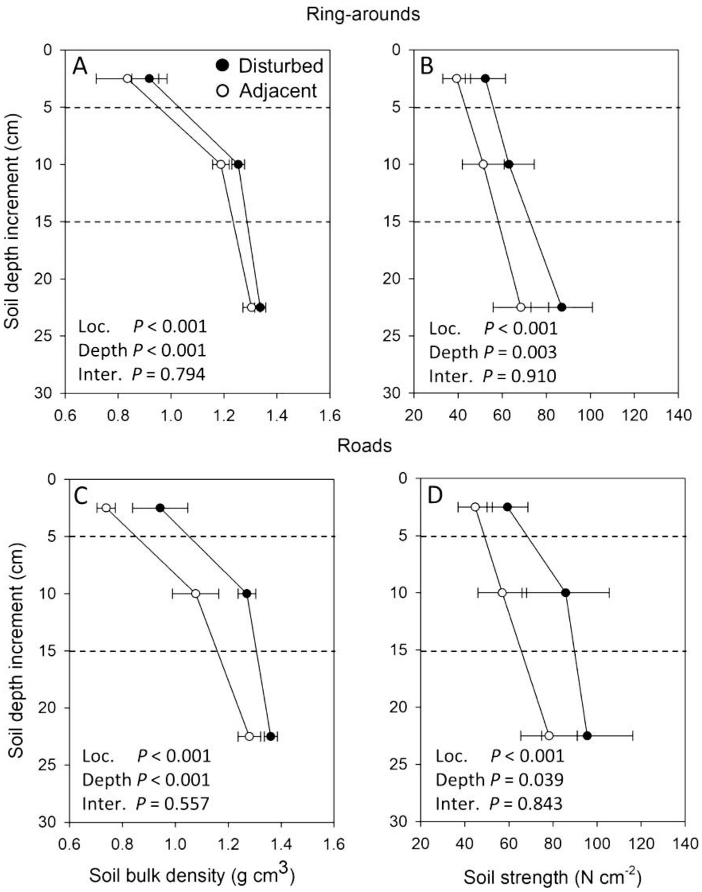

Figure 5.—Soil bulk density and soil strength measured at 0–5 cm, 5–15 cm, and 15–30 cm depth within areas disturbed (solid symbol) and adjacent to areas disturbed (empty symbol) by ring-arounds (A, B) and roads (C, D). Results of two-way ANOVAs testing for effects of location (disturbed vs. adjacent) and depth interval and their interaction effects are presented. Uncertainty bars represent the 95% confidence interval.

with the disturbed plots were from regeneration events after disturbances ceased.

Few reference sites within the range of longleaf pine are without some post-Columbian anthropogenic disturbance, and the Wade Tract, despite its well-documented biodiversity, has a number of linear disturbances (Figure 2b). The persistent soil disturbance in these abandoned features relative to nearby undisturbed sites or the reference matrix may be a key driver limiting recovery of some species, particularly native woody stems. The origin of the roads is unknown, but some of the abandoned roads were likely used for a century or more. Repeated wagon, tractor, and other traffic on the roads crushed mature vegetation and seedlings, eroded soil on slopes, compacted the soil, and created microtopographic features readily visible in LiDAR (Figure 2). Small anthropogenic disturbances that result in soil compaction produced lasting legacies in microtopography and vegetative recovery. For example, DeArmond et al. (2021) summarized evidence that, depending on soil characteristics, skid trails can have detectable effects on soil strength for decades.

Compared to soil disturbance associated with agriculture, ring-arounds and woods roads on the Wade Tract were decidedly small-scale disturbances. Indicator and woody species were less frequent and less abundant in these disturbances. This is likely a result of limitations on establishment related to soil compaction rather than dispersal (Turley et al. 2017). A comparable anthropogenic disturbance to those assessed here is the soil compaction caused by forestry practices, particularly skidder trails. In a review and meta-analysis, Ampoorter et al. (2012) concluded that machine traffic from mechanized tree harvesting caused a decrease in soil pore volume, a loss of pore continuity, and rut formation, which had effects on soil aeration, soil water retention, and hydraulic conductivity. These combined responses can have the effect of reducing elongation and penetration of primary roots, which may reduce the uptake of nutrients and water. Although these effects would be particularly acute on seedlings, they may also affect penetration of rhizomes from the clonal trees studied here. Zenner and Berger (2008) recommended concentrating skidder networks to protect remnant forest patches with species that are sensitive to soil disturbance. We agree with this recommendation for working forests. We also agree with Nerlekar and Veldman (2020) that "old-growth" (undisturbed) grasslands are worthy of conservation. In our study of an old-growth longleaf pine woodland, which has one of the more diverse ground floras in the world, even fine-scale anthropogenic disturbances can result in lasting soil and vegetative legacies.

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LITERATURE CITED

[ALRI] America's Longleaf Restoration Initiative. 2009. Range-Wide Conservation Plan for Longleaf Pine. Regional Working Group for America's Longleaf. <http://www.americaslongleaf.org/media/fqipycuc/conservation_plan.pdf>

Ampoorter, E., A. de Schrijver, L. van Nevel, M. Hermy, and K. Verheyen. 2012. Impact of mechanized harvesting on compaction of sandy and clayey forest soils: Results of a meta-analysis. Annals of Forest Science 69:533–542.

Anderson, M.J. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26:32–46.

Bakker, J.D. 2008. Increasing the utility of Indicator Species Analysis. Journal of Applied Ecology 45:1829–1835.

Batey, T. 2009. Soil compaction and soil management - A review. Soil Use and Management 25:335–345.

Bigelow, S.W., N.A. Jansen, S.B. Jack, and C.L. Staudhammer. 2018. Influence of selection method on skidder-trail soil compaction in longleaf pine forest. Forest Science 64:641–652.

Boring, L.R., J.J. Hendricks, C.A. Wilson, and R.J. Mitchell. 2005. Season of burn and nutrient losses in a longleaf pine ecosystem. International Journal of Wildland Fire 13:443–453.

Boyer, W.D. 1993. Regenerating longleaf pine with natural seeding. Pp. 299–309 *in* S.M. Hermann, ed., Proceedings of the Tall Timbers Fire Ecology Conference No. 18. Tall Timbers Research Station, Tallahassee, FL.

Brudvig, L.A., and E.I. Damschen. 2011. Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34:257–266.

Brudvig, L.A., E. Grman, C.W. Habeck, J.L. Orrock and J.A. Ledvina. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. Forest Ecology and Management 310:944–955.

Brudvig, L.A., J.L. Orrock, E.I. Damschen, C.D. Collins, P.G. Hahn, W.B. Mattingly, J.W. Veldman, and J.L. Walker. 2014. Land-use history and contemporary management inform an ecological reference model for longleaf pine woodland understory plant communities. PLoS ONE 9(1):e8660.

Caceres, M.D., and P. Legendre. 2009. Associations between species and groups of sites: Indices and statistical inference. Ecology 90:3566–3574.

Croker, T.C., Jr., and W.D. Boyer. 1975. Regenerating longleaf pine naturally. Research Paper SO-105. USDA Forest Service, Southern Forest Experiment Station, New Orleans, LA.

Dale, V.H., S.C. Beyeler, and B. Jackson. 2002. Understory vegetation indicators of anthropogenic disturbance in longleaf pine forests at Fort Benning, Georgia, USA. Ecological Indicators 1:155–170.

DeArmond, D., J. Ferraz, and N. Higuchi. 2021. Natural recovery of skid trails: A review. Canadian Journal of Forest Research 51(7)948–961. <https://doi.org/10.1139/cjfr-2020-0419>

Dell, J.E., S.M. Pokswinski, L.A. Richards, J.K. Hiers, B. Williams, J.J. O'Brien, E.L. Loudermilk, A.T. Hudak, and L.A. Dyer. 2019. Maximizing the monitoring of diversity for management activities: Additive partitioning of plant species diversity across a frequently burned ecosystem. Forest Ecology and Management 432:409–414.

Gilliam, F.S., and W.J. Platt. 2006. Conservation and restoration of the *Pinus palustris* ecosystem. Applied Vegetation Science 9:7–10.

Grant, C.A., and G.P. Lafond. 1993. The effects of tillage systems and crop sequences on soil bulk density and penetration resistance on a clay soil in southern Saskatchewan. Canadian Journal of Soil Science 73:223–232.

Hebb, E.A. 1971. Site preparation decreases game food plants in Florida sandhills. Journal of Wildlife Management 35:155–162.

Hedman, C.W., S.L. Grace, and S.E. King. 2000. Vegetation composition and structure of southern coastal plain pine forests: An ecological comparison. Forest Ecology and Management 134:233–247.

Hermann, S.M. 1993. Small-scale disturbances in longleaf pine forests. Pp. 265–274 *in* S.M. Hermann, ed., Proceedings of the Tall Timbers Fire Ecology Conference No. 18. Tall Timbers Research Station, Tallahassee, FL.

Hiers, J.K., J.J. O'Brien, R.E. Will, and R.J. Mitchell. 2007. Forest floor depth mediates understory vigor in xeric *Pinus palustris* ecosystems. Ecological Applications 17:806–881.

Hiers, J.K., J.R. Walters, R.J. Mitchell, J.M. Varner, L.M. Conner, L.A. Blanc, and J. Stowe. 2014. Ecological value of retaining pyrophytic oaks in longleaf pine ecosystems. Journal of Wildlife Management 78:383–393.

Hill, R.L., and R.M. Cruse. 1985. Tillage effects on bulk density and soil strength of two mollisols. Soil Science Society of America Journal 49:1270–1273.

Isenburg, M. 2014. LAStools-efficient LiDAR processing software. Accessed 16 December 2020 from <lastools.org>.

Kirkman, L.K., K.L. Coffey, R.J. Mitchell, and E.B. Moser. 2004. Ground cover recovery patterns and life-history traits: Implications for restoration obstacles and opportunities in a species-rich savanna. Journal of Ecology 92:409–421.

Kirkman, L.K., and L.M. Giencke. 2018. Restoring and managing a diverse ground cover. Pp. 207–232 *in* L.K. Kirkman and S.B. Jack, eds., Ecological Restoration and Management of Longleaf Pine Forests. CRC Press, Boca Raton, FL.

Lampurlanés, J., and C. Cantero-Martínez. 2003. Soil bulk density and penetration resistance under different tillage and crop management systems and their relationship with barley root growth. Agronomy Journal 95:526–536.

Landers, J.L., and W.D. Boyer. 1999. An old-growth definition for upland longleaf and south Florida slash pine forests, woodlands, and savannas. General Technical Report SRS-29. USDA Forest Service, Southern Research Station, Ashville, NC.

Levi, M.R., J.N. Shaw, C.W. Wood, S.M. Hermann, E.A. Carter, and Y. Feng. 2010. Soil properties of southeastern U.S. coastal plain kandiudults. Soil Science Society of America Journal 74:258–271.

McCune, B., and M.J. Mefford. 2016. PC-ORD. Multivariate Analysis of Ecological Data. Version 7. MjM Software Design, Gleneden Beach, OR.

McVay, K.A., J.A. Budde, K. Fabrizzi, M.M. Mikha, C.W. Rice, A.J. Schlegel, D.E. Peterson, K.W. Sweeney, and C. Thompson. 2006. Management effects on soil physical properties in long-term tillage studies in Kansas. Soil Science Society of America Journal 70:434–438.

Mitchell, R., T. Engstrom, R.R. Sharitz, D. De Steven, K. Hiers, R. Cooper, and L.K. Kirkman. 2009. Old forests and endangered woodpeckers: Old-growth in the southern Coastal Plain. Natural Areas Journal 29:301–310.

Mitchell, R.J., J.K. Hiers, J.J. O'Brien, S.B. Jack, and R.T. Engstrom. 2006. Silviculture that sustains: The nexus between silviculture, frequent prescribed fire, and conservation of biodiversity in longleaf pine forests of the southeastern United States. Canadian Journal of Forest Research 36:2724–2736.

Moore, W.H., B.F. Swindel, and W.S. Terry. 1982. Vegetative response to clearcutting and chopping in a north Florida flatwoods forest. Journal of Range Management 35:214–218.

Neel, L., P.S. Sutter, and A.G. Way. 2010. The art of managing longleaf: A personal history of the Stoddard-Neel Approach. University of Georgia Press, Athens.

Nerlekar, A.N., and J.W. Veldman. 2020. High plant diversity and slow assembly of old-growth grasslands. PNAS 117:18550–18556.

Ostertag, T.E., and K.M. Robertson. 2007. A comparison of native versus old-field vegetation in upland pinelands managed with frequent fire, South Georgia, USA. Proceedings of the Tall Timbers Fire Ecology Conference 23:181–191.

Platt, W.J., G.W. Evans, and S.L. Rathbun. 1988. The population dynamics of a long-lived conifer (*Pinus palustris*). American Naturalist 131:491–525.

R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>

Robertson, K.M., W.J. Platt, and C.E. Faires. 2019. Patchy fires promote regeneration of longleaf pine (*Pinus palustris* Mill.) in pine savannas. Forests 10:367.

Rother, M.T., J.M. Huffman, C.H. Guiterman, K.M. Robertson, and N. Jones. 2020. A history of recurrent, low-severity fire without fire exclusion in southeastern pine savannas, USA. Forest Ecology and Management 475:118406.

Schultz, R.P., and L.P. Wilhite. 1974. Changes in a flatwoods site following intensive preparation. Forest Science 20:230–237.

Simkin, S.M., and W.K. Michener. 2005. Faunal soil disturbance regime of a longleaf pine ecosystem. Southeastern Naturalist 4:133–152.

Stoddard, H.L., Sr. 1931. The Bobwhite Quail: Its Habits, Preservation, and Increase. Charles Scribner's Sons, New York.

Stoddard, H.L., Sr. 1961. Unpublished 19 January 1961 letter to J.H. Wade. Tall Timbers Research Station Archives, Tallahassee, FL.

Tinker, N. 1994. History. Pp. 4-1 to 4-68 *in* J.E. Hodges, ed., A Comparative Study of a Portion of the Red Hills Region of Georgia. Thomas College Press, Thomasville, GA.

Turley, N.E., J.L. Orrock, J.A. Ledvina, and L.A. Brudvig. 2017. Dispersal and establishment limitation slows plant community recovery in post-agricultural longleaf pine savannas. Journal of Applied Ecology 54:1100–1109.

Varner, J.M., and J.S. Kush. 2004. Remnant old-growth longleaf pine (*Pinus palustris* Mill.) Savannas and forests of the southeastern USA: Status and threats. Natural Areas Journal 24:141–149.

Veldman, J.W., E. Buisson, G. Durigan, G.W. Fernandes, S. Le Stradic, G. Mahy, D. Negreiros, G.E. Overbeck, R.G. Veldman, N.P. Zaloumis, et al. 2015. Toward an old-growth concept for grasslands, savannas, and woodlands. Frontiers in Ecology and the Environment 13:154–162.

Walker, J.L., and A.M. Silletti. 2006. Restoring the ground layer of longleaf pine ecosystems. Pp. 297–333 *in* S. Jose, E.J. Jokela, and D.L. Miller, eds., The Longleaf Pine Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York.

Way, A.G. 2011. Conserving Southern Longleaf: Herbert Stoddard and the Rise of Ecological Land Management. University of Georgia Press, Athens.

White, P.S., and J.L. Walker. 1997. Approximating nature's variation: Selecting and using reference information in restoration ecology. Restoration Ecology 5:338–349.

Wunderlin, R.P., and B.F. Hansen. 2011. Guide to the Vascular Plants of Florida. 3rd ed. University Press of Florida, Gainesville.

Zenner, E.K., and A.L. Berger. 2008. Influence of skidder traffic and canopy removal intensities on the ground flora in a clearcut-with-reserves northern hardwood stand in Minnesota, USA. Forest Ecology and Management 256:1785–1794.