Large ecosystem-scale effects of restoration fail to mitigate impacts of land-use legacies in longleaf pine savannas

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Ecological restoration is a global priority, with potential to reverse biodiversity declines and promote ecosystem functioning. Yet, successful restoration is challenged by lingering legacies of past land-use activities, which are pervasive on lands available for restoration. Although legacies can persist for centuries following cessation of human land uses such as agriculture, we currently lack understanding of how land-use legacies affect entire ecosystems, how they influence restoration outcomes, or whether restoration can mitigate legacy effects. Using a large-scale experiment, we evaluated how restoration by tree thinning and land-use legacies from prior cultivation and subsequent conversion to pine plantations affect fire-suppressed longleaf pine savannas. We evaluated 45 ecological properties across four categories: 1) abiotic attributes, 2) organism abundances, 3) species diversity, and 4) species interactions. The effects of restoration and land-use legacies were pervasive, shaping all categories of properties, with restoration effects roughly twice the magnitude of legacy effects. Restoration effects were of comparable magnitude in savannas with and without a history of intensive human land use; however, restoration did not mitigate numerous legacy effects present prior to restoration. As a result, savannas with a history of intensive human land use supported altered properties, especially related to soils, even after restoration. The signature of past human land-use activities can be remarkably persistent in the face of intensive restoration, influencing the outcome of restoration across diverse ecological properties. Understanding and mitigating land-use legacies will maximize the potential to restore degraded ecosystems.

ecological restoration | land-use legacy | longleaf pine | restoration ecology

In the face of historic extinction rates and declines to ecosystem functioning (1–3), ecological restoration has emerged as a global priority (4, 5). In turn, large commitments to restoration have been pledged, such as the Bonn Challenge, a global effort to reforest 350 million ha by 2030 (5–7), and 2021 to 2030 has been termed by the United Nations General Assembly "The Decade on Ecosystem Restoration" (8). Yet, restoration is a developing field, with extensive practical and conceptual challenges that must be overcome for these ambitious goals to be met (9, 10).

One such major challenge to restoration is presented by land-use legacies (11), where the altered characteristics of ecosystems persist after cessation of human land uses, such as agriculture and forestry (12–16). Land-use legacies may affect restoration success through soils that have been modified by agriculture (e.g., refs. 12 and 17), or due to slow natural reestablishment of plant species following human land-use abandonment (18, 19). Land-use legacies are potentially far-reaching, with an estimated 10 to 44 million square kilometers of the terrestrial biosphere currently recovering from human land uses abandoned since 1700 (20), an area ∼4.5 times larger than the United States.

The study of land-use legacies is challenging for several reasons (21), and novel research is needed to meet these challenges. First, the initial selection of land for human use is not random, leading to the potential for land-use legacies to be confounded with the environmental conditions that were amenable for human land-use conversion. For example, forests on level, productive soils are more likely to be converted to farm fields than areas with poor soils or sloped topography (22). Once farming is abandoned, these lands may have different environmental conditions from lands that were never farmed, either due to the farming itself or because of initial site-selection bias. Thus, studies on the effects of land-use legacies must carefully control for land-use decision making. Second, land-use legacies can persist for variable amounts of time, leading to uncertainty about when recovery

Significance

The restoration of degraded ecosystems is a global priority, yet successful restoration is challenged by the lingering degrading impacts of human land-use activities, like agriculture. Using a large-scale experiment within the longleaf pine ecosystem, we evaluate how 45 abiotic and biotic ecological properties are affected by legacies of past farming and conversion to pine plantations, as well as contemporary restoration activities to reinstate savanna conditions. Restoration had large and beneficial effects on this ecosystem regardless of land-use history, but a suite of conditions remained persistently altered by land-use legacies even after restoration. Ongoing advances to ecosystem restoration should target persistent legacy effects, to maximize the conservation potential of ecosystems recovering from intensive human use.

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will occur without active restoration interventions. In some cases, land-use legacies last for centuries or even millennia (e.g., refs. 12, 17, 23, 24), whereas in other cases ecological properties may recover over the course of decades (e.g., refs. 25 and 26). This variation may be caused by climate, ecosystem type, soil type, intensity of the original land use, or the identity of the property under study (15). A third challenge is that land-use legacies, as well as restoration, influence entire ecosystems, yet studies of these effects typically focus on one or a few properties of the ecological system—often plants or soils (14, 27, 28). Yet, it is likely that various ecological properties—including abiotic attributes, biodiversity, interactions among species, and others—will recover at different rates following disturbance and during restoration (9, 29). Thus, to comprehensively interpret land-use legacies and guide restoration practices, studies are needed that evaluate recovery across diverse ecological properties.

Despite the likely need for active restoration to overcome some land-use legacies, it remains unclear to what extent current restoration practices counteract land-use legacies. In some cases, restoration activities can, at least in part, ameliorate land-use legacies (e.g., refs. 25 and 30). Yet, in other cases legacies persist even in the face of intensive restoration activities and, in fact, land-use legacies can influence restoration outcomes by altering the biotic or abiotic template onto which restoration operates (e.g., ref. 31). The reasons for this variation remain unclear but—as with land-use legacies themselves—may relate to differences among studies in the ecological property under investigation. Experiments are needed that apply restoration manipulations to areas with different land-use histories, followed by assessments spanning diverse ecological properties, to understand how these historical and contemporary human influences interact.

We overcame these challenges through a synthesis of land-use legacy effects within a large-scale restoration experiment. Our experiment spans 27 replicate blocks and controls for potential biases resulting from past land-use decisions by pairing adjacent 1 ha plots with or without a history of crop cultivation (Fig. 1; ref. 32). Plots with a cultivation history were farmed for corn and cotton before agriculture was abandoned in 1951; the fields were subsequently reforested with native pine trees (33). Plots without a cultivation history support naturally regenerated native pines with a prominent native hardwood tree component due to history of fire suppression (32). We randomly applied restoration treatments to half of the plots in our study, thereby avoiding site selection issues, which can bias restoration studies (34).

Our study took place within the longleaf pine ecosystem, which is a component of the North American Coastal Plain biodiversity hotspot (35). Longleaf pine ecosystems are in need of restoration

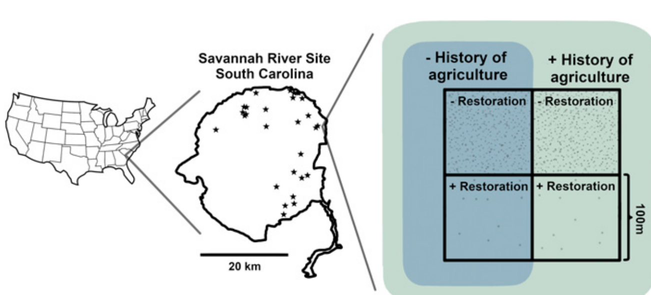

Fig. 1. Map of the large-scale experiment at the Savannah River Site in South Carolina, where the effects of land-use legacies and restoration were measured. Plots were 1 ha (100 × 100 m), grouped into 27 blocks, and were located within longleaf pine patches either with or without a history of agriculture and subsequent pine plantation land use. Half of the plots received an experimental restoration tree-thinning treatment and half were unrestored controls.

because habitat loss and degradation resulting from widespread fire suppression, agricultural legacies, and conversion to plantation forests have left an estimated 3% of historical range intact [i.e., maintained by fire and undisturbed by recent histories of intensive human land use such as agriculture or plantation conversion (36)]. Most former longleaf pine savannas are presently high-density pine plantations or fire-suppressed, hardwood-encroached woodlands and restoration efforts often seek to reestablish historical savanna conditions over the course of years to decades through tree clearing and reinstatement of a frequent surface-fire regime (36). Prior to our study, all plots in our experiment were fire suppressed. The major goals of restoration in this and other fire-suppressed savanna ecosystems (37) are to reinstate open-canopy conditions, which promotes a high density and diversity of native species and various species interactions, such as pollination (36). Our restoration treatment involved clearing trees within half of the plots to produce savanna conditions and leaving trees at high density in the remaining plots; we also conducted prescribed fire management across all plots.

We considered responses of 45 ecological properties, spanning four broad categories: abiotic conditions, the abundance of organisms, the diversity of species, and interactions among species. We asked three questions:

1) What are the legacies of intensive human land use? To address this question, we compared plots with and without a history of agriculture and subsequent pine planting, which had not undergone restoration (Fig. 2). We hypothesized that agricultural legacies would affect soil attributes, including through compaction, reduced organic matter, elevated phosphorus, and altered pH (15), and that the history of pine planting would influence aspects of ecosystem structure including through canopy closure and leaf-litter accumulation (32). Together, the combination of these land-use legacy effects would suppress the abundance and diversity of plants and other taxa and thereby alter various species interactions (14, 27).

2a) What is the response to restoration?

2b) Do land-use legacies alter the outcome of restoration? To address these questions, we compared plots that had received the restoration tree-thinning treatment to plots that had not received restoration (Fig. 2). We then considered whether the outcome of 6 y of restoration differed for plots with and without a history of agriculture/plantation forestry. We hypothesized that restoration would influence numerous abiotic and biotic attributes, by reducing canopy closure and leaf-litter accumulation; these changes would increase the abundance and diversity of plants and other taxa by reinstating the open savanna conditions to which longleaf pine species are adapted (38, 39). We further hypothesized that restoration would alter species interactions by increasing the abundance and diversity of plants, arthropods, and small mammals. We expected that many of these effects of restoration would be of similar magnitude for plots with and without agricultural histories because this treatment reinstated open savanna conditions regardless of land-use history (Fig. 2).

3) Does restoration ameliorate land-use legacies? To address this question, we evaluated whether agricultural legacies present prior to restoration (i.e., those identified in question 1) were no longer evident after restoration (Fig. 2). We hypothesized that, by reinstating open savanna conditions, restoration would ameliorate land-use legacy effects related to above-ground ecosystem structure (e.g., canopy closure and leaf-litter accumulation) and the abundance and diversity of mobile taxa (e.g., bees and small mammals) but not others that change slowly, such as soil variables and the diversity and abundance of less-mobile taxa such as plants and soil microbes (40, 41). Thus, we expected for restoration to more

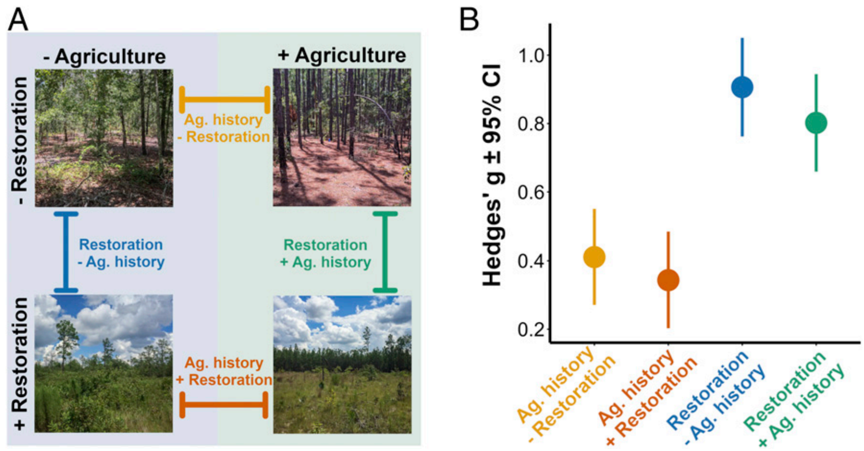

Fig. 2. Agricultural/plantation land-use legacies and restoration influenced 45 ecological properties in longleaf pine savannas. (*A*) The four experimental treatments include plots without (–) and with (+) restoration and plots without (–) and with (+) agricultural/plantation history. The colored bars show four comparisons made among treatments, which correspond to matching colored points in the graph on the right. (*B*) The effects of restoration (Restoration – Ag. history, Restoration + Ag. history; blue and green points) were roughly twice the magnitude of land-use legacy effects (Ag. history – Restoration; orange point). There was no evidence that agricultural/plantation history alters the outcome of restoration (no difference between Restoration – Ag. history and Restoration + Ag. history; blue versus green points) nor that restoration ameliorated legacy effects present in unrestored plots (no difference between Ag. history – Restoration and Ag. history + Restoration; red versus orange points). We consider Hedges' g values of 0.2 small-, 0.5 medium-, and above 0.8 large-magnitude effects.

clearly ameliorate those legacy effects tied to plantation forestry, than those associated with agricultural history.

Results

Question 1: What are the legacies of intensive human land use? Legacies of agriculture and plantation forestry collectively affected the 45 ecological properties of longleaf pine savannas (Hedges' g values of 0.41; Fig. 2), and this effect was statistically significant and of small (Hedges' g values of 0.2) to medium (Hedges' g values of 0.5) magnitude across all four categories of properties (Fig. 3 and *SI Appendix*, Table S2). Compared to unrestored (fire suppressed, hardwood encroached) plots with no history of crop cultivation, unrestored postagricultural/plantation plots had more open canopies and more compacted soils, with elevated soil phosphorus (P) and reduced soil water-holding capacity (*SI Appendix*, Fig. S1 and Table S4). Postagricultural/plantation plots additionally supported greater abundance of grasshoppers and sown plants and greater diversity of live-trapped rodents, soil bacteria, and sown plants (*SI Appendix*, Fig. S1 and Table S4).

Question 2: What is the response to restoration, and do land-use legacies alter the outcome of restoration? Across all measured attributes, restoration had statistically significant and large (Hedges' g values >0.8) effects (Fig. 2 and *SI Appendix*, Table S2). These effects were not different in plots with and without a history of agricultural/plantation land use (Fig. 2 and *SI Appendix*, Table S3). These patterns were evident across all four categories of properties, as there were large effects of restoration for abiotic attributes, individual abundance, and species diversity and medium effects of restoration on species interactions (Fig. 3 and *SI Appendix*, Table S2).

Numerous individual attributes underpinned the effects of restoration thinning and these effects were remarkably consistent between plots with and without a history of agriculture/plantation land use (*SI Appendix*, Fig. S1 and Table S4). In plots with and without a history of agriculture/plantation, restoration increased the following: 1) the abundance of grasshoppers, some rodents, sown plants, fire ants, pyramid ants, bees, and floral cover, 2) the diversity of naturally occurring plants, grasshoppers, live-trapped rodents, soil fungus, sown plants, and bees, and 3) rates of granivory for two plant species (*SI Appendix*, Fig. S1 and Table S4). In plots with and without a history of agriculture/plantation, restoration increased temperature and light availability, reduced litter cover and litter and duff depth, and reduced canopy closure; it also reduced the area that fire burned within plots and the abundance of one rodent species. Only two attributes showed restoration responses in one plot type. Restoration increased abundance of cotton rats in plots without a history of agriculture/plantation only and restoration increased granivory of one seed species (*Vernonia angustifolia*) in postagricultural/plantation plots only.

Question 3: Does restoration ameliorate land-use legacies? We found little evidence that restoration completely ameliorated land-use legacies (*SI Appendix*, Table S3). Following restoration, agricultural/plantation legacies were of similar magnitude (Hedges' g: 0.34 as in unrestored plots (Hedges' g: 0.41) and were still significant for all categories of properties except organism abundance. For organism abundance, the effect of agricultural/plantation history on abundance was reduced by 59% by restoration (Fig. 3 and *SI Appendix*, Table S2), though the amelioration of this land-use legacy by restoration was only of marginal significance ($P = 0.10$; *SI Appendix*, Table S3). Correspondingly, effects of agricultural/plantation history on the abundance of grasshoppers and sown plants, which were present in unrestored plots, were no longer present after restoration (*SI Appendix*, Fig. S1 and Table S4). Similarly, legacy effects on the richness of soil bacteria and richness of sown plants, as well as canopy closure, were mitigated by restoration (*SI Appendix*, Fig. S1 and Table S4). Conversely, legacy effects on live-trapped rodent richness as well as a suite of soil variables were not mitigated by restoration (*SI Appendix*, Fig. S1 and Table S4). Additionally, granivory on one species (*Quercus nigra*), which did not show legacy effects in unrestored plots, was greater in plots without a history of agriculture/plantation after restoration (*SI Appendix*, Fig. S1 and Table S4).

Discussion

Our analysis of 45 ecological properties reveals that prior human land-use activities have long-lasting influences on restoration outcomes within longleaf pine savannas. Legacies of agriculture and plantation forestry were pervasive, spanning abiotic attributes

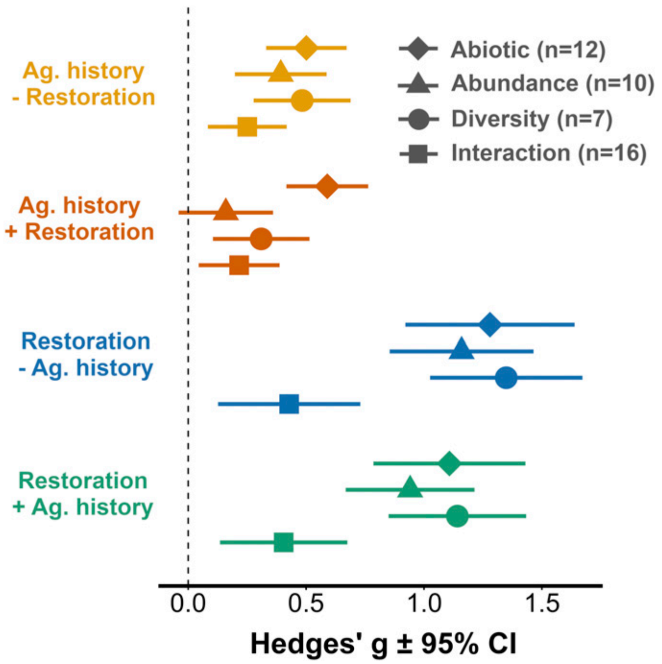

Fig. 3. Effects of land-use legacies and restoration on four major categories of ecological properties within longleaf pine savannas: abiotic conditions, abundance of organisms, diversity of species, and species interactions (n refers to the number of properties measured within each category). The colors of the points correspond with the contrasts illustrated in Fig. 2*A*. The majority of categories were influenced by agricultural/plantation legacies and restoration, with effects typically of greater magnitude for restoration (Restoration – Ag. history, Restoration + Ag. history; blue and green points) than for agricultural/plantation legacies (Ag. history – Restoration; orange points). There was little evidence that agricultural/plantation history alters the outcome of restoration (no difference between Restoration – Ag. history and Restoration + Ag. history; blue versus green points) nor that restoration ameliorated legacy effects present in unrestored plots (no difference between Ag. history – Restoration and Ag. history + Restoration; red versus orange points). We consider Hedges' g values of 0.2 small-, 0.5 medium-, and above 0.8 large-magnitude effects.

of the ecosystem, the abundance of individual organisms, the diversity of species inhabiting savannas, and interactions between species. Restoration by tree thinning to reinstate historical open-canopy savanna conditions had large effects on each of these types of attributes, with restoration effects roughly twice the magnitude of legacy effects. Although this difference in magnitude is undoubtedly related to the specific land-use history and restoration intervention in our experiment, we can be highly confident in these relationships because we experimentally manipulated restoration and controlled for factors that may bias land-use legacy studies. Yet, although the effects of restoration were of similar magnitude in plots with and without histories of intensive human land-use activities, restoration did not ameliorate many legacy effects, especially those associated with past agricultural use. As a result, the signature of historical agricultural land use is remarkably persistent even after abandonment of cropping and intensive restoration activities. Given the pervasive influences of agricultural conversion, tree planting, and fire suppression for savanna ecosystems around the world (37), our findings may have wide-reaching implications.

Pervasive legacy effects were evident over half a century following agricultural abandonment and reforestation. Although the strength of this effect varied somewhat with the type of attribute—twice as pronounced for abiotic attributes compared to species interactions—land-use legacies affected all categories of properties we considered. These findings considerably expand on past similar investigations, in which legacies of agriculture and other human land uses have been evaluated across one or a few attributes (e.g., refs. 12 and 24). By considering 45 ecological properties, we illustrate how agriculture and plantation conversion so fully alter ecosystems that, even six decades after farm abandonment, attributes ranging from foundational soil properties to higher trophic interactions remain disrupted. As a result, reforested former agricultural lands can bear the sorts of pronounced and pervasive effects that characterize ecosystems under active human land use (42), manifest as legacies that persist for many decades.

Restoration by tree thinning had large and rapid (evident within 6 y) impacts on canopy structure, with cascading influence on numerous other components of the ecosystem, largely aboveground. Tree thinning reduced canopy cover from an average of 69% to <7%, which in turn increased near-ground temperatures and light availability and reduced O-horizon (leaf-litter and duff) accumulation. These changes corresponded with increases in plant diversity and abundance, likely due to O-horizon reduction (38, 39) and associated opening of recruitment microsites, as well as increased flower and seed production (40). Restoration also increased the abundance and diversity of arthropods and some rodents, likely due to favorable changes to structure, temperature, and plant resources (26, 43, 44). Restoration also resulted in elevated rates of at least one trophic interaction: granivory (note that two squirrel species also declined, likely due to reduction in tree density; ref. 45). Importantly, as we hypothesized, many of these effects are indicative of progress toward successful longleaf pine savanna restoration. Although we lack high-quality reference sites to serve as benchmarks in our study landscape, this progress is based on key longleaf pine savanna–restoration attributes, including reinstatement of open canopy conditions, reductions to O-horizon accumulation, and promotion of abundant and diverse flora and fauna (36).

Our study provides several key findings about restoring longleaf pine savannas affected by land-use legacies. First, the effects of canopy restoration were of remarkably similar magnitude for plots with and without a history of agriculture and plantation forestry (Fig. 2). Second, restoration successfully mitigated several plantation-related legacy effects, including canopy closure and altered abundances of plants and grasshoppers. Third, however, many of the legacy effects that we observed prior to restoration persisted following canopy restoration (Figs. 2 and 3), especially those most clearly resulting from agricultural land-use history (e.g., soil attributes). As a consequence, our results illustrate both the promise of restoring longleaf pine savannas recovering from intensive histories of human land use but also how sites undergoing restoration can remain persistently altered because of agricultural legacies.

We suggest several ways to confront persistent land-use legacies during the restoration of longleaf pine savannas. First, additional restoration strategies, such as manual reintroduction of plant species (40, 46) or direct manipulation of soils or soil biota (47), may be coupled with canopy thinning and fire management, to mitigate specific land-use legacies. Yet, certain legacy effects, especially those associated with major disturbances like agriculture, may require substantial time to diminish as ecosystems recover during restoration (48), and it is important to note that our study evaluated responses for up to 6 y following restoration. This may or may not pose challenges to restoration success. For example, despite persistent soil legacies in postagricultural longleaf pine savannas (*SI Appendix*, Fig. S1), plant reintroductions perform similarly within sites with and without agricultural histories (46), with success improved by tree thinning (40). Thus, by coupling multiple approaches (e.g., tree thinning and plant reintroduction), practitioners may meet goals despite persistent legacies.

Understanding how restoration actions affect ecosystems and why these outcomes vary among restoration efforts is of increasing importance as we enter the Decade on Ecosystem Restoration (5, 9, 10). Here, we show how restoration had rapid, sweeping impacts on nearly all aspects of an ecosystem, resulting in changes that were evident within 6 y and were typically twice the magnitude of those caused by land-use legacies. These changes were evident in savannas with and without histories of intensive human land use and helped to meet specific restoration goals for this ecosystem. At the same time, a number of land-use legacies persisted nearly unchanged during restoration. Further refinement of restoration strategies to mitigate persistent land-use legacies will maximize the potential presented by land-use abandonment, to promote native biodiversity and ecosystem recovery. Habitat restoration provides great potential to promote native biodiversity and ecosystem functioning on lands with a history of intensive human land use (16, 20).

Materials and Methods

This research took place within a large-scale experiment at the Department of Energy Savannah River Site (SRS), a National Environmental Research Park managed by the US Department of Agriculture Forest Service in South Carolina (33.20°N, 81.40°W) (Fig. 1). The sandy uplands at SRS historically supported open canopy longleaf pine savannas, which were largely converted to corn, cotton, and other crops between 1865 and 1950 (33). Following forest clearance, soils were plowed and regularly tilled or hoed for crop production, with both organic and inorganic fertilizer applications (33). All agriculture was abandoned in 1951 when the US government acquired SRS and these fields were subsequently converted to plantations of longleaf (*Pinus palustris*), loblolly (*P. taeda*), and slash pine (*P. elliotii*).

The experiment included 126 1 ha (100 × 100 m) plots grouped into 27 blocks (Fig. 1) (32). Each block was centered around the boundary between a longleaf pine savanna with no known history of agriculture and a former agricultural field supporting a mature pine plantation (*P. palustris* where possible). We determined land-use history using historical aerial photography and confirmed no differences in soil types on plots with and without agricultural history (32). Blocks included at least 4 and as many as 10 plots, depending on the sizes of areas with and without agricultural history, with half of the plots located within the savanna lacking agricultural history and half of the plots within the postagricultural pine plantation (Fig. 1). Due to a history of fire suppression, all plots supported closed canopy woodland at the onset of the experiment (32). To restore open canopy conditions, we randomly assigned a restoration thinning treatment in 2011 to half of the plots with and half of the plots without agricultural history, using logging equipment to remove trees from plots (Figs. 1 and 2). The thinning treatment reduced tree density from an average of 650 trees/ha (32) to 10 trees/ha (31). One or more prescribed surface fires were subsequently conducted within each block (*SI Appendix*, Table S4). In sum, this resulted in a 2 × 2 factorial manipulation of agricultural/plantation history and restoration thinning (Figs. 1 and 2).

Between 2012 and 2017 we quantified abiotic conditions, the abundance of individuals, the diversity of species, and species interactions within the experimental plots (*SI Appendix*, Table S1). Abiotic variables included temperature and light, the percentage of ground covered by leaf litter, depth of the O horizon (leaf litter and duff), percent canopy closure (which influences understory light availability), soil water-holding capacity, the percentage of ground area burned during prescribed fires, soil compaction, percent soil moisture, soil pH, soil organic matter, and soil phosphorus. Abundance variables included the summed captures of three rodent species using live traps, the number of observations of three individual rodent species using remote trail cameras, counts of grasshoppers, the total number of individuals established from seed addition of 12 herbaceous understory plants, numbers of fire ant (*Solenopsis invicta*) mounds, numbers of pyramid ant (*Dorymyrmex bureni*) mounds, counts of bees, and floral cover. Species diversity variables included the richness of grasshoppers, rodents, soil bacteria, soil fungi, bees, vascular plants naturally occurring in plots, and the richness of 12 herbaceous understory plants added through seed addition. Measures of species interactions included rates of herbivory on four understory herbs, rates of pollination to sentinel black mustard (*Brassica nigra*) plants, the effects of root competition on four understory herbs, and rates of seed removal, as a measure of granivory, on the seeds of six understory herbs and one tree species (*Quercus nigra*). We excluded any data collected within 10 m of the land-use boundary, to avoid potential influence of edge effects. Additional methodological details are available in *SI Appendix*, Table S1.

We used meta-analysis techniques to evaluate responses of the 45 response variables to land-use history and restoration. We first calculated standardized effect sizes, using absolute values of the difference between treatments because directionality does not have a consistent interpretation across the variables we measured. This allowed us to focus on the magnitude of responses across variables, though we do consider directionality during interpretation of individual variable responses.

To calculate standardized effect sizes, we first averaged subsamples to get a single value for each of the four treatment combinations (plot types) within each block (Fig. 1), providing 7 to 27 replicates per variable (*SI Appendix*, Table S1). We did this because some variables had multiple measurements per plot, and some blocks had multiple replicate plots of each treatment combination. We then calculated the mean and SD across blocks for each variable in each of the four treatment combinations: unrestored post-agricultural/plantation, unrestored non-post-agricultural, restored post-agricultural/plantation, restored non-post-agricultural (Fig. 2). We used these values to calculate Hedges' g, a measure of standardized effect size, for the differences between each pair of treatment combinations by using the escalc function in the metafor package in R (49). For example, to quantify how restoration affects the ecological properties within postagricultural/plantation areas ("Restoration + Ag. history") we calculated the effect size of the difference between unrestored postagricultural/plantation plots and restored postagricultural/plantation plots. This was repeated for each treatment combination, resulting in four total effect sizes: the effect of agricultural and plantation history in unrestored plots (Ag. history – Restoration), the effect of agricultural and plantation history in restored plots (Ag. history + Restoration), the effect of restoration in postagricultural/plantation plots (Restoration + Ag. history), and the effect of restoration in plots without agricultural/plantation history (Restoration – Ag. history) (Fig. 2).

We next fit meta-analysis models with the rma function in the metafor package to statistically test our four questions, using the effect sizes, variances, and sample size we obtained from the above Hedges' g calculations. The models included "dataset" (*SI Appendix*, Table S1) as a random effect to account for potential nonindependence of variables collected from the same project. We then ran post hoc tests using the glht function in the multcomp package (50) to obtain *P* values for the contrasts among each of the four effect sizes. To test question 1 (what is the legacy of intensive human land use?), we considered model results for the Ag. history – Restoration effect size. To test question 2a (what is the response to restoration?), we considered model results for both the Restoration + Ag. history and Restoration – Ag. history effect sizes. To test question 2b (do land-use legacies alter the outcome of restoration?), we considered post hoc tests between Restoration + Ag. history and Restoration – Ag. history effect sizes. To test question 3 (does restoration ameliorate land-use legacies?), we considered post hoc tests between Ag. history – Restoration and Ag. history + Restoration effect sizes (Fig. 2).

We fit these models in three different ways depending on the question to be answered. First, we fit models for each of our four effect sizes with no moderator variables to test if the overall effect sizes, across all 45 variables, deviated significantly from zero (see "Overall effect" on *SI Appendix*, Table S2). Next, we fit models to test if response variable category (abiotic, abundance, diversity, interactions) affected the magnitude of effect sizes by including category as a moderator variable (Fig. 3). Finally, to test if the magnitude of responses varied among effect-size types, we fit a model that had all the data and the four-level effect-size types (Ag. history – Restoration, Ag. history + Restoration, Restoration + Ag. history, and Restoration – Ag. history) as a moderator variable (Fig. 2).

When reporting effect sizes using Hedges' g, we consider values of 0.2 small-, 0.5 medium-, and above 0.8 large-magnitude effects (51). We also consider the statistical significance of each effect as determined by our models and, where appropriate, the percent difference between comparison groups as ([Group 1 – Group 2]/Group 2) × 100.

Data Availability. The data and code used in this paper's analyses are publicly available through Dryad (https://doi.org/10.5061/dryad.crjdfn339) (52).

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