

Agricultural land-use history causes persistent loss of plant phylogenetic diversity

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Abstract. Intensive land use activities, such as agriculture, are a leading cause of biodiversity loss and can have lasting impacts on ecological systems. Yet, few studies have investigated how land-use legacies impact phylogenetic diversity (the total amount of evolutionary history in a community) or how restoration activities might mitigate legacy effects on biodiversity. We studied ground-layer plant communities in 27 pairs of Remnant (no agricultural history) and Post-agricultural (agriculture abandoned >60 yr ago) longleaf pine savannas, half of which we restored by thinning trees to reinstate open savanna conditions. We found that agricultural history had no impact on species richness, but did alter community composition and reduce phylogenetic diversity by 566 million years/1,000 m². This loss of phylogenetic diversity in post-agricultural savannas was due to, in part, a reduction in the average evolutionary distance between pairs of closely related species, that is, increased phylogenetic clustering. Habitat restoration increased species richness by 27% and phylogenetic diversity by 914 million years but did not eliminate the effects of agricultural land use on community composition and phylogenetic structure. These results demonstrate the persistence of agricultural legacies, even in the face of intensive restoration efforts, and the importance of considering biodiversity broadly when evaluating human impacts on ecosystems.

Key words: *biodiversity conservation; community ecology; community phylogenetics; longleaf pine savanna; restoration ecology.*

INTRODUCTION

Human land use is the leading cause of biodiversity loss globally with few terrestrial ecosystems unaffected by habitat conversion, fragmentation, or other degrading human influences (Sanderson et al. 2002, Foley et al. 2005, Haddad et al. 2015, Newbold et al. 2015). As a consequence, biodiversity conservation is increasingly dependent on our understanding of how past and present land-use activities shape ecosystems (Foster et al. 2003, Cramer et al. 2008, Frishkoff et al. 2014) and, how we can best recover biodiversity in degraded habitats through ecosystem restoration (Brudvig 2011, Suding 2011, Newbold et al. 2015). Yet mitigating the legacies of past human land use represents a major challenge to restoration success (Suding et al. 2004).

This comes despite substantial opportunities for conducting restoration on ecosystems formerly impacted by human land uses (Flinn and Vellend 2005). The abandonment of agricultural and other intensive land-use practices is increasingly common, leading to a global footprint of post-agricultural lands 3.7 times the area of France (235 million ha; Ramankutty and Foley 1999), which would make it the 12th largest country in the

world. Unfortunately, abandoned agricultural lands often have altered biodiversity—particularly of plants—for centuries or even millennia following agricultural abandonment (Dupouey et al. 2002, Flinn and Vellend 2005, Hermy and Verheyen 2007). It is not clear whether, and over what time frames, biodiversity will recover following intensive land use (Flinn and Vellend 2005), and in many cases, active restoration interventions appear necessary (Suding 2011). Determining how to restore post-agricultural ecosystems requires carefully conducted studies—ideally experiments—that quantify biodiversity impacts.

Understanding the impacts of land use and restoration on biodiversity is further challenged by the narrow way that biodiversity has been typically defined in these fields, often by simple metrics such as species richness (Brudvig 2011, Newbold et al. 2015). Intensive land use often decreases species richness (Newbold et al. 2015) and many restoration practices focus on increasing richness. Measures of community composition capture more information than richness because they incorporate species identities and their co-occurrences. Comparing community compositions among sites can further quantify the impacts of land use history and restoration on biodiversity. And in general, increasing land use intensity tends to drive community composition further from that of relatively pristine sites (Brudvig et al. 2014). However, little

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is known about how land use and restoration shape phylogenetically informed measures of biodiversity, which capture aspects of richness, composition, and evolutionary relatedness among species. As a measure of the total amount of evolutionary history represented by the species in a community (i.e., sum of phylogenetic branch lengths), phylogenetic diversity holds potential for informing and assessing success in conservation (Faith 1992, Forest et al. 2007, Isaac et al. 2007, Frishkoff et al. 2014, Hipp et al. 2015). Communities with greater phylogenetic diversity capture a greater breadth of the tree of life (Faith 1992, Isaac et al. 2007), and plant communities with high phylogenetic diversity can support enhanced ecosystem functioning (Maherali and Klironomos 2007, Flynn et al. 2011, Cadotte 2013) and support greater diversity in higher trophic levels (Dinnage et al. 2012, Lind et al. 2015). While agricultural land-use intensification has been shown to decrease bird phylogenetic diversity (Frishkoff et al. 2014) and disturbance and land-use intensity shape plant phylogenetic structure (Knapp et al. 2008, Dinnage 2009, Egorov et al. 2014), the subsequent recovery of phylogenetic diversity after these land-use activities cease remains poorly understood because little consideration has been paid to how land-use legacies and active restoration shape phylogenetic measures of biodiversity.

We employed a unique landscape-scale experiment to evaluate how land-use history and active restoration independently and jointly affect multiple measures of plant biodiversity, including species richness, composition, and phylogenetic diversity. Our study system, longleaf pine savannas, are a biodiversity hotspot with high endemism and species diversity, particularly of ground-layer plants (Noss et al. 2014). This system is also of high conservation concern, because only 3% of the original range remains, making active restoration efforts a priority (Frost 2006). Our experiment includes areas that were tilled and cultivated for agriculture, but which were abandoned from agriculture >60 yr ago and then subsequently managed as pine plantations (hereafter called Post-agricultural sites), and remnants of longleaf pine savanna with no history of agriculture (hereafter called Remnant sites) (Brudvig et al. 2013). To test how land-use history impacts plant biodiversity, we studied ground-layer vascular plant communities in adjacent Post-agricultural and Remnant savannas, within 126 1-ha plots, at 27 locations (Fig. 1). To test how active restoration affects plant biodiversity and how restoration interacts with land-use history, we conducted overstory tree restoration thinning to reinstate the open-canopy conditions indicative of longleaf pine savanna in half of our Post-agricultural and Remnant plots (Jose et al. 2006). We quantified plant community composition and species richness across all treatments and using a phylogeny of all 339 plant species in the system, we calculated multiple phylogenetic based measures of biodiversity. We predicted that Post-agricultural areas would have distinct community composition, decreased species richness and phylogenetic

diversity, and greater phylogenetic clustering compared to Remnant savannas (Frishkoff et al. 2014, Li et al. 2015). We also predicted that restoration would increase species richness (Hiers et al. 2007, Veldman et al. 2014) and, if this was due to promotion of species typical of remnants, that phylogenetic diversity and compositional similarity to remnants would also increase.

METHODS

We conducted our research at 27 sites supporting longleaf pine savanna at the Savannah River Site (SRS), a National Environmental Research Park in South Carolina (33.20° N, 81.40° W), each with adjacent areas of post-agricultural pine plantation and remnant savanna. The Post-agricultural areas were in tillage agriculture until 1951, when agriculture was abandoned and longleaf and loblolly pine plantations were established. Remnant sites support no known history of agriculture and were mature savannas in 1951, based on aerial photography (Brudvig et al. 2013). Prior to this study, all sites showed evidence of fire suppression, including hardwood tree encroachment and canopy closure in remnant sites. At each site, we established a total of four to ten (depending on the size of the remnant) 1-ha (100 m × 100 m) research plots located on both sides of the land-use boundary (Fig. 1). This resulted in a total of 126 plots, but for statistical purposes we averaged across replicate treatment combinations within a site resulting in 108 data points in our analyses. For further details about establishment criteria and the pre-restoration conditions, see Brudvig et al. (2013).

To reinstate open-canopy conditions indicative of longleaf pine savannas in our region, we conducted restoration thinning treatments within half the experimental plots in 2011. Canopy tree thinning is a common restoration practice in this system when tree densities are high due to fire suppression or plantation forestry (Jose et al. 2006) because tree size and density have strong negative impacts on understory plant species richness caused by above- and belowground competition and increased leaf litter and duff (Harrington et al. 2003, Hiers et al. 2007, Veldman et al. 2013, 2014). Thinning was implemented in a randomized 2 × 2 split-plot design, resulting in each site supporting four treatment combinations of overstory tree thinning and agricultural history (Fig. 1). The overstory was mechanically thinned to 10 longleaf pine trees per hectare, with cut trees removed from each site.

In each 1-ha plot we established one 100-m long vegetation sampling transect perpendicular to the land-use boundary (Fig. 1). Each transect contained ten contiguous 10 × 10 m subplots and, within each 10 × 10 m subplot, a nested 1 × 1 m subplot. In 2012, 2013, and 2014, we recorded the presence of all ground-layer vascular plant species within each 10 × 10 m and 1 × 1 m subplot. For the rest of the paper, we focus on data from 2014 because we had greater taxonomic resolution that year and because previous years showed very similar results (Appendix S1: Fig. S6). Individuals that could not

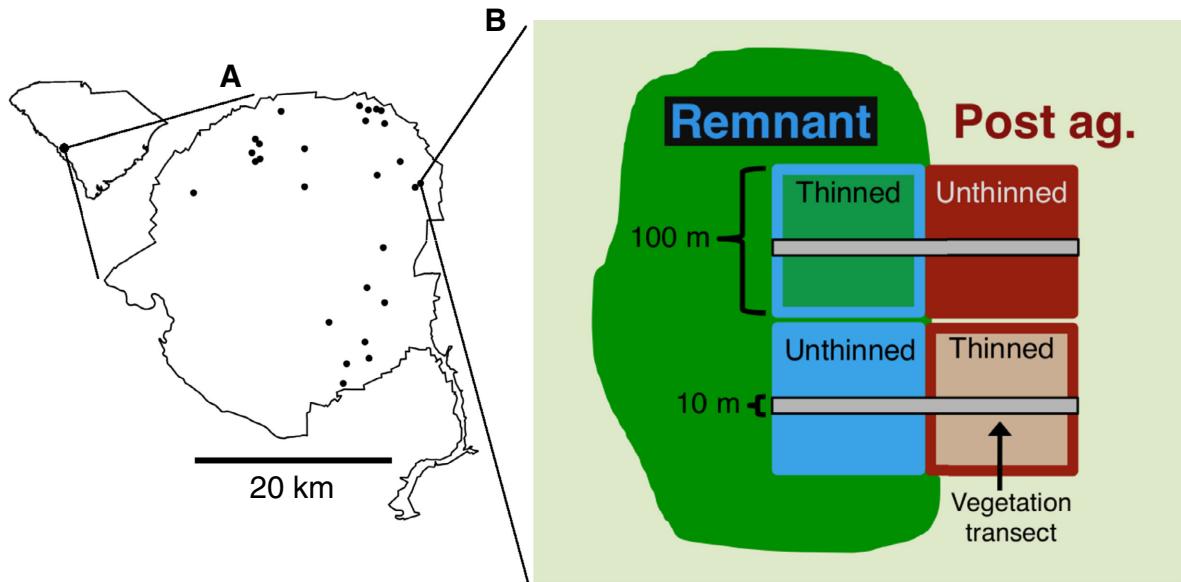


FIG. 1. Maps of study area and diagram of experimental treatments. (A) Locations of 27 experimental sites (closed circles) at the Savanna River Site in South Carolina, each with Post-agricultural and adjacent Remnant savanna. (B) Diagram of an individual experimental site with four 1-ha plots, each with a 1,000 m² vegetation transect. Thinned plots had all but 10 pine trees removed in 2011 to restore savanna structure, whereas Unthinned plots were not manipulated.

be reliably identified to species or could not be distinguished from a congener were recorded as an unknown species in the known genus; this was the case for 18 of the 339 tips in the phylogeny (5.3%). Families were assigned to each genus following APGIII conventions using the Taxonomic Name Resolution Service (Boyle et al. 2013).

We constructed a phylogenetic tree of all species observed in the study using Phylomatic version 3 (Webb et al. 2008) with a dated molecular tree of >32,000 species as the backbone (Zanne et al. 2014). This technique provides high resolution for relationships among families and most genera, and for where data were available, also at the species level. When resolution for our taxa was not present in the Zanne et al. (2014) phylogeny, Phylomatic incorporated our species as polytomies at the lowest level that data were available (Appendix S1: Fig. S4).

All analyses and diversity calculations were done using R version 3.2.2. Using community data from the sampling transects and our dated phylogeny, we calculated three phylogenetic diversity metrics for each transect: (1) phylogenetic diversity, (2) standardized phylogenetic diversity, and (3) mean pairwise distance (MPD). These metrics are complementary because they measure different aspects of evolutionary diversity within communities. Phylogenetic diversity, also known as Faith's phylogenetic diversity, is the sum of phylogenetic branch lengths for all species in a community (Faith 1992). Because it is a summation, phylogenetic diversity is highly positively correlated with species richness (in our data set $r = 0.957$, $N = 108$, $P < 0.001$). To explore changes in phylogenetic measures of diversity that are independent of species richness, we looked at two measures of

phylogenetic structure that measure if species within communities are more closely related (clustered) or more distantly related (even) than expected compared to a null model (Webb et al. 2002). Standardized phylogenetic diversity is Faith's phylogenetic diversity after accounting for the effects of species richness. MPD is the mean evolutionary distance between all pairs of species in a community. It is most sensitive to community changes deep in the phylogeny, whereas standardized phylogenetic diversity is more sensitive to changes at the tips of the phylogeny (Mazel et al. 2015). Thus, comparing results among these metrics can inform whether differences in diversity among communities are driven by changes in co-occurrences of closely related species, mostly within clades (standardized phylogenetic diversity), or distantly related species, mostly among clades (MPD effect size).

Standardized phylogenetic diversity was calculated as the differences between phylogenetic diversity and expected phylogenetic diversity, given our phylogeny and the observed species richness for each sample. We standardized phylogenetic diversity in this way for three reasons: (1) to explore changes in phylogenetic diversity that were independent of species richness, (2) to produce a metric with the same units as phylogenetic diversity (millions of years) for ease of interpretation, and (3) because it had a nearly 1:1 relationship ($r > 0.999$, $N = 108$, $P < 0.001$) with the standardized effect size calculation used in other studies (Mazel et al. 2015). We determined expected phylogenetic diversity using the "pdmoments" function in the PhyloMeasures package (Tsirogianis and Sandel 2015). For MPD we calculated a standardized effect size to remove any possible effects of species richness, calculated

as: (observed value—expected value)/standard deviation of the expected value. Some other studies report net relatedness index (NRI) which is simply MPD effect size multiplied by -1 (Webb et al. 2002). To calculate MPD we used the “mpd.query” function in the PhyloMeasures package (Tsirogianis and Sandel 2015). We also calculated MNTD effect size because it is commonly used in other studies; however, we only include it in the supplemental materials because it was strongly correlated with standardized phylogenetic diversity (Mazel et al. 2015).

We calculated a number of species-level metrics to better understand how differences among species influence phylogenetic diversity differences among habitat types. We conducted a point-biserial correlation coefficient indicator analyses using the “strassoc” function with an alpha value of 0.05 (De Cáceres and Legendre 2009). This assigns a single value (analogous to a correlation coefficient) to each species based on its association with Remnant and Post-agricultural areas along with a 95% confidence interval. Species with values not overlapping zero were either Remnant or Post-agricultural “indicator species.” We conducted this analysis on communities within Unthinned plots, to focus on land-use history without effects of restoration. To consider the phylogenetic uniqueness of indicator species, we determined species evolutionary distinctiveness from our phylogeny of all species found in our study using the “evol.distinct” function based on fair proportions. Evolutionary distinctiveness is a measure of the amount of unique evolutionary history added by each species (Isaac et al. 2007). This species-level metric can help clarify if differences in community phylogenetic diversity are influenced by the evolutionary uniqueness of individual species while community metrics also include aspects of community composition. We then compared

the average difference in evolutionary distinctiveness between Remnant and Post-agricultural indicator species using a t -test.

To test how land-use history and restoration impacted univariate measures of biodiversity, we fit a nested ANOVA using the “aov” function. The “aov” model formula syntax was: $y \sim \text{restoration} \times \text{land use} + \text{error}$ (site/land use/restoration) where “restoration” and “land use” are two level categorical predictors and “site” is a 27 level categorical predictor with one level for each of our independent replicates. These models were fit for each response variable and spatial scale (1, 100, 1,000 m²) separately. We tested effects of our treatments on multivariate plant community composition with a perMANOVA using the “adonis” function in the vegan package (Oksanen et al. 2015). Ideally, site would be included as a blocking factor; however, because the “adonis” function cannot perform a two-level split plot analyses, we instead included site-by-treatment interactions as main effects to account for unexplained variation and to provide the proper degrees of freedom (matching those with the nested ANOVA models) for F -tests. Finally, we visualized results of the perMANOVA using a constrained analysis of principal components (CAP) with a Jaccard dissimilarity matrix and four-level categorical predictor (land use by restoration). This was implemented with the “capscale” function in the vegan package (Oksanen et al. 2015).

RESULTS

Effects of land-use history on biodiversity

Agricultural land-use history reduced phylogenetic diversity, and this was a result of changes in species

TABLE 1. Effects of land-use history (remnant vs. post-agricultural) and restoration (thinned vs. unthinned) and their interactive effect (land-use \times rest.) on multiple measures of plant biodiversity at 1,000 m² scale. Composition results are from a perMANOVA and species richness, phylogenetic diversity, and standardized phylogenetic diversity results are from nested ANOVAs. Bold values have $P < 0.05$.

	df	F	P	r^2
Composition				
Land-use	1, 26	20.33	<0.001	0.10
Restoration	1, 52	14.83	<0.001	0.07
Land-use \times rest.	1, 52	2.07	0.02	0.01
Species richness				
Land-use	1, 26	2.70	0.11	0.09
Restoration	1, 52	64.25	<0.001	0.55
Land-use \times rest.	1, 52	0.06	0.81	<0.01
Phylogenetic diversity				
Land-use	1, 26	8.12	0.01	0.24
Restoration	1, 52	43.91	<0.001	0.46
Land-use \times rest.	1, 52	<0.01	0.98	<0.001
Standardized phylogenetic diversity				
Land-use	1, 26	32.18	<0.001	0.55
Restoration	1, 52	30.91	<0.001	0.37
Land-use \times rest.	1, 52	0.85	0.36	0.02

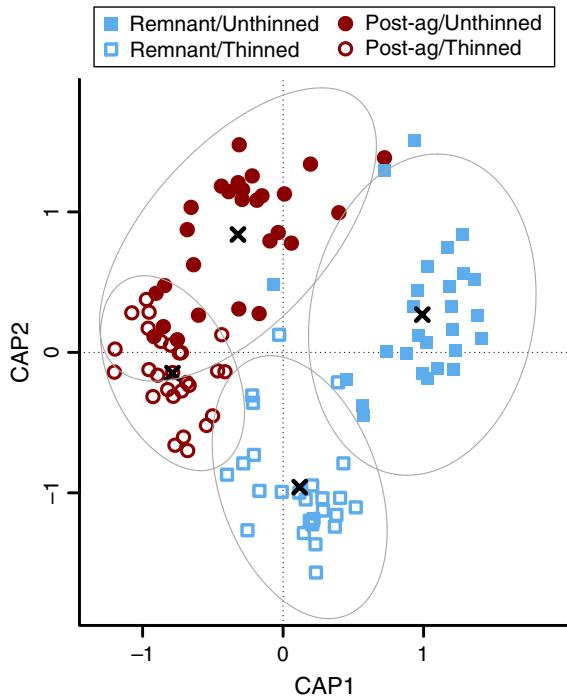


FIG. 2. Plant communities among land-use types and restoration treatments had distinct compositions. Each dot represents the composition of one plot, based on constrained analysis of principal coordinates (CAP) ordination and presence/absence plant community data collected from 1,000 m² transects. X's represent the centroid of each group and the ovals show 95% confidence intervals.

richness, community composition, and phylogenetic clustering. Plant community composition in 1,000 m² plots was distinct between Remnant and Post-agricultural sites, and land-use history explained 10% of the total compositional variation in a multivariate ANOVA (Table 1, Fig. 2). Post-agricultural sites supported an

average of 6.4 fewer species per 1,000 m², although this difference was not significant (Table 1, Fig. 3A). Together these changes resulted in the loss of 566 million years of evolutionary history per 1,000 m² in Post-agricultural savannas (Fig. 3B), which is an 8.9% reduction in total phylogenetic diversity (Table 1). This change in phylogenetic diversity is equivalent to losing, on average, 12 species, as determined using the slope of a linear model between species richness and phylogenetic diversity. Standardized phylogenetic diversity, a measure of phylogenetic structure, was reduced by 255 million years/1,000 m² in Post-agricultural sites compared to Remnant sites, with this difference explaining 55% of the variation in standardized phylogenetic diversity in a nested ANOVA (Table 1, Fig. 3C). The effects of land-use history on standardized phylogenetic diversity were only present at the largest spatial scale (1,000 m²; Appendix S1: Tables S1–S3, Fig. S2). MPD effect size, which is more affected by community changes among between distantly related species than standardized phylogenetic diversity, was not affected by land-use history (Appendix S1: Fig. S2). Finally, we found that Remnant indicator species had 23% higher evolutionary distinctiveness than Post-agricultural indicator species ($t_{83.5} = 1.99$, $P = 0.05$; Appendix S1: Fig. S5).

Effects of restoration thinning on biodiversity

Restoration thinning altered understory plant community composition, increased species richness, but decreased standardized phylogenetic diversity. Community composition differed between Thinned and Unthinned savannas and this effect of restoration explained 7% of the variation in composition in our model (Table 1, Fig. 2). Restoration explained 55% of the variation in species richness in an ANOVA, with Thinned plots supporting an average of 21.4 more species, or 27% more species richness per 1,000 m² than Unthinned plots

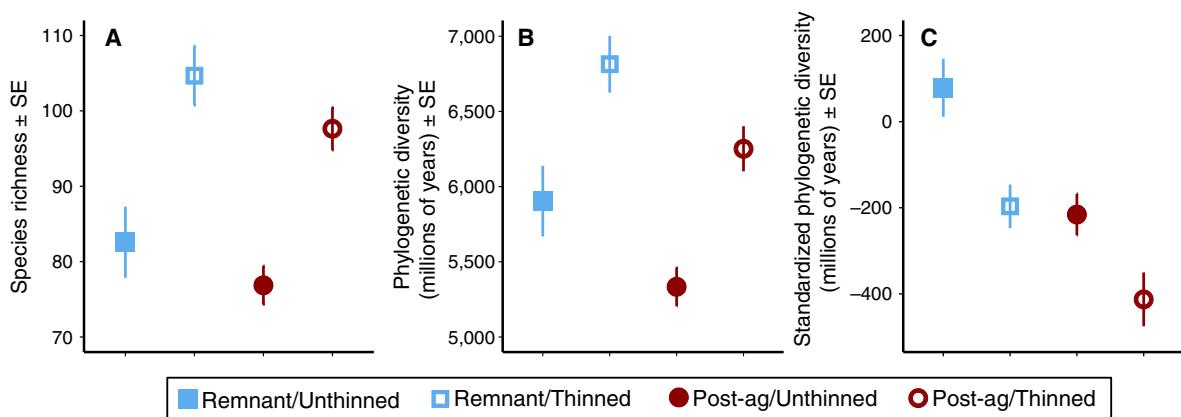


FIG. 3. Effects of agricultural land-use history and restoration thinning on three measures of plant biodiversity: (A) species richness, (B) phylogenetic diversity and (C) species richness-corrected phylogenetic diversity (standardized phylogenetic diversity). Data shown are from our largest spatial scale plots (1,000 m²). Restoration thinning increased both species richness and phylogenetic diversity and Post-agricultural sites have decreased phylogenetic diversity and standardized phylogenetic diversity. Each data point shows the mean of 27 replicates with standard error bars.

(Table 1, Fig. 3A). The effects of restoration on species richness and phylogenetic diversity were consistent across spatial sampling scales (Appendix S1: Tables S1–S3, Fig. S1). The increase in species richness with restoration led to a 16%, or 914 million year, increase in phylogenetic diversity per 1,000 m² (Table 1, Fig. 3B). Despite the increase in species richness and total phylogenetic diversity, thinning decreased standardized phylogenetic diversity by 236 million years (Table 1, Fig. 3C).

DISCUSSION

Understanding how human activities impact biodiversity—and the prospects for its restoration—will be critical to conservation success in an era of unprecedented ecosystem transformation by humans (Foley et al. 2005, Suding 2011, Newbold et al. 2015). Phylogenetic diversity, as a measure of biodiversity that integrates richness and evolutionary history, can inform the conservation value of communities and may also be an important predictor of ecological and ecosystem processes (Cadotte et al. 2012, Dinnage et al. 2012, Srivastava et al. 2012). Using a landscape-scale experiment, we show that agricultural land-use legacies and contemporary restoration shape phylogenetic diversity of ground-layer plant communities within the imperiled longleaf pine ecosystem. We found a persistent (>60 yr) legacy of agricultural history, which altered community composition and resulted in 566 million years loss of phylogenetic diversity per 1,000 m². This legacy effect is comparable to the 855 million years of bird evolutionary history that was lost from tropical forest due to present-day intensive monoculture agriculture (Frishkoff et al. 2014). Restoration through overstory tree thinning increased phylogenetic diversity by 914 million years/1,000 m², due to a large increase in species richness, but at the same time also decreased standardized phylogenetic diversity (which is independent of species richness). These findings illustrate how some aspects of biodiversity (richness) may be rapidly restored, yet others (phylogenetic structure, composition) can remain persistently altered by past human land-use actions even in the face of intensive restoration activities.

Land-use legacies on phylogenetic diversity

Our study provides clear evidence that agricultural land-use legacies reduce phylogenetic diversity, relative to in Remnants. This change was driven primarily by alterations to species composition and phylogenetic structure. Post-agricultural communities were composed of species that were more closely related to one another, relative to the species in remnants, and these changes have persisted for over half a century following agricultural abandonment. Our experiment provides a strong level of control for resolving these agricultural legacies because our paired-plot design controls for confounding factors associated with past land use, such as the

widespread tendencies to farm on more productive soils (Brudvig et al. 2013). Thus, the lasting effects of land use on biodiversity were due to local changes in environmental conditions or species interactions that have resulted from past land-use activities (e.g., Brudvig et al. 2013, Hahn and Orrock 2015). The recovery of biodiversity in post-agricultural or otherwise degraded ecosystems should, in theory, benefit from the dispersal of sensitive species from nearby undisturbed areas. The persistent signatures of land-use on multiple aspect of biodiversity, despite post-agricultural sites being immediately adjacent to undisturbed remnant sites, demonstrates the fine spatial scale over which land-use legacies shape biodiversity and the need for active management to recover lost biodiversity in degraded landscapes.

Phylogenetic structure can be altered through multiple non-mutually exclusive biological processes (Webb et al. 2002, Vamوسي et al. 2009, Li et al. 2015) making it difficult or impossible to infer the mechanisms driving phylogenetic patterns from the patterns alone (Mayfield and Levine 2010). However, we suggest three possible explanations for increased clustering in Post-agricultural sites: (1) Clades containing several closely related species were abundant in Post-agricultural sites, such as the genera *Cyperus*, *Paspalum*, *Desmodium*, and, *Lespedeza* (Appendix S1: Fig. S4). Co-occurrence of these species would tend to increase phylogenetic clustering because of the short evolutionary branch lengths between them and this should be especially true for metrics sensitive to changes at the tips of the phylogeny, like standardized phylogenetic diversity. (2) Post-agricultural sites are younger, resulting in less time for community assembly to play out. Over long time periods, the process of community assembly in Remnants could eliminate closely related species through competition or facilitate the colonization of more distantly related species due to environmental modifications as the community develops (Li et al. 2015). (3) Rare and common species may be more closely related in Post-agricultural sites, relative to rare and common species in Remnant sites. We found increased phylogenetic clustering in Post-agricultural sites only at the largest spatial scales where rare species are more likely to be sampled, but we did not see this pattern in Remnant sites (Appendix S1: Fig. S2), which suggests that the accumulation of rare species is important in driving the changes we see across treatments. This reinforces the importance of considering the scale-dependent effects of anthropogenic biodiversity drivers (Powell et al. 2013). Ultimately, while our work clearly shows that land-use history influences phylogenetic measures of biodiversity, strong inference into the ecological processes underlying this pattern will require further experiments testing how phylogenetic relatedness might influence processes such as dispersal, competition, and plant-consumer interactions (Vamوسي et al. 2009, Mayfield and Levine 2010, Li et al. 2015).

Restoring biodiversity in post-agricultural landscapes

Restoration had dramatic effects on multiple aspects of biodiversity in both Post-agricultural and Remnant savannas, but it did not mitigate the effects of land-use history on community composition and phylogenetic clustering. Reducing tree density in savannas decreases above- and belowground competition between trees and ground-layer vegetation, resulting in colonization of new species and increased fine scale species richness (Harrington et al. 2003, Veldman et al. 2013). This influx of new species resulted in unique communities in Thinned savannas (Fig. 2) and it increased species richness by 27% (Fig. 3A). Yet, because these newly establishing species in Thinned/Post-agricultural savannas were not Remnant indicator species, thinning did not cause a convergence in community composition between Remnant and Post-agricultural savannas like we predicted. Also unexpectedly, thinning caused communities to have less phylogenetic diversity than expected given their species richness (Fig. 3C) in both Remnant and Post-agricultural plots. This suggests that thinning benefited species that were, on average, closely related to species already present and thus did not function to alleviate the lost phylogenetic diversity in Post-agricultural savannas.

Active restoration of ecosystems degraded by past human land use is an increasingly important tool for conservation (Suding et al. 2004) and a broader focus on multiple aspects of biodiversity, including phylogenetic diversity, is likely to give greater insight into management decisions (Brudvig 2011, Hipp et al. 2015). For example, our results suggest that restoration practices, such as sowing the seeds of Remnant species—particularly those that are phylogenetically unique from existing species—may be required to restore community composition and phylogenetic diversity in post-agricultural longleaf pine ecosystems. Developing restoration strategies tailored to specific degraded conditions will be critical for recovering biodiversity across complex landscapes (Suding et al. 2004, Brudvig et al. 2014). Our work points to historical agricultural land use as key driver of habitat degradation, meriting careful attention as we hone such restoration approaches.

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AUTHORSHIP

LAB designed the study and conducted the research, NET analyzed the data, NET wrote the first draft of the paper, and LAB made revision.

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