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COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Agricultural land-use history does not reduce woodland understory herb establishment

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Abstract

Agricultural land use is a leading cause of habitat degradation, leaving a legacy of ecological impacts long after agriculture has ceased. Yet the mechanisms for legacy effects, such as altered plant community composition, are not well understood. In particular, whether plant community recovery is limited by an inability of populations to establish within post-agricultural areas, owing to altered environmental conditions within these areas, remains poorly known. We evaluated this hypothesis of post-agricultural establishment limitation through a field experiment within longleaf pine woodlands in South Carolina (USA) and a greenhouse experiment using field-collected soils from these sites. In the field, we sowed seeds of 12 understory plant species associated with remnants (no known history of agriculture) into 27 paired remnant and post-agricultural woodlands. We found that post-agricultural woodlands supported higher establishment, resulting in greater species richness of sown species. These results were context dependent, however, with higher establishment in post-agricultural woodlands only when sites were frequently burned, had less leaf litter, or had less sandy soils. In the greenhouse, we found that agricultural history had no impact on plant growth or survival, suggesting that establishment limitation is unlikely driven by differences in soils associated with agricultural history when environmental conditions are not stressful. Rather, the potential for establishment in post-agricultural habitats can be higher than in remnant habitats, with the strength of this effect determined by fire frequency and soil characteristics.

Keywords Agricultural legacy · Establishment limitation · Longleaf pine woodland · Fire · Soil legacy

Introduction

Agriculture covers 40% of the land on Earth, leading to large declines in local biodiversity (Newbold et al. 2015). Moreover, the effect of agriculture on local biodiversity in forests once developed on post-agricultural land can persist long after agriculture has ceased (Foster et al. 2003; Flinn and Vellend 2005). For example, areas with a history of tillage agriculture can have altered plant community composition and reduced plant diversity decades to millennia after agricultural abandonment (Hermy and Verheyen 2007). Globally, the amount of post-agricultural land (where agriculture has been abandoned) covers over 2.35 million km^2, ~ 1.5 times the size of Alaska (Ramankutty and Foley 1999). This presents an opportunity for restoration, but we still know little about the mechanistic causes of post-agricultural land-use legacies on biodiversity, which hinders our ability to restore plant communities on abandoned agricultural lands (Cramer et al. 2008; Suding 2011).

Post-agricultural legacies on plant communities may be caused by dispersal and/or establishment limitation (Flinn and Vellend 2005; Hermy and Verheyen 2007; Standish et al. 2007; Öster et al. 2009). Dispersal limitation results when seeds fail to arrive to post-agricultural areas, either due to poor plant dispersal capacities, or a lack of seed sources (Ehrlén and Eriksson 2000; Turley et al. 2017). Establishment limitation results when individuals arrive to a location

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(e.g., a post-agricultural area), but fail to establish and persist (Crawley 2000; Orrock et al. 2006). The degree to which post-agricultural recovery of plant populations is limited by dispersal and establishment, however, remains unclear, as some studies have found evidence of establishment limitation (Donohue et al. 2000; Graae et al. 2004; Baeten et al. 2009a) while others have found dispersal to be limiting (Verheyen and Hermy 2004; Baeten et al. 2009b). In part, this is due to a lack of experimental tests that disentangle these two processes and compare between post-agricultural woodlands and woodlands with no history of agriculture ('remnant woodlands'; though see Graae et al. 2004; Verheyen and Hermy 2004; Baeten et al. 2009a). We provide such a test through a large-scale seed addition experiment, where we sowed seeds into post-agricultural woodlands and remnant woodlands to compare the degree of establishment limitation within these two habitat types.

Further complicating interpretation of post-agricultural legacies is that establishment limitation, if present, may result from a variety of causes, including competitors, animal consumers (e.g., granivores; Orrock et al. 2006), and shifts in soil physical and chemical properties that may occur as a result of agricultural land use (Henry et al. 2004; Brudvig et al. 2013). Our work considers such mechanisms in two ways. First, we evaluate establishment within our field experiment along several environmental gradients known to be important for patterns of species diversity in our focal longleaf pine ecosystem (fire frequency, leaf litter, and soil characteristics; Kirkman et al. 2001; Brudvig et al. 2014; Veldman et al. 2014). Through this, we consider how these gradients affect establishment and how these gradients may align with (may be causative mechanisms) or interact with agricultural land-use history to affect establishment. For example, fire frequency may be more important for structuring community composition in post-agricultural compared to remnant woodlands in this system (Brudvig and Damschen 2011) and our experiment allows for consideration of whether this operates through differences in plant establishment.

Second, through a greenhouse experiment we provide a focused test of the role of altered soil conditions resulting from agriculture as a mechanism of establishment limitation and, therefore, agricultural legacies to plant communities. Following abandonment, agriculture can have long-lasting effects on soils ('soil legacies'), persisting for decades to thousands of years (Dupouey et al. 2002; McLauchlan 2006). For example, phosphorus is typically more concentrated and organic matter less concentrated in post-agricultural soils than in soils that have not been used for agriculture (Koerner et al. 1997; Compton and Boone 2000; Dupouey et al. 2002; Brudvig et al. 2013; Bizzari et al. 2015). Biotic components (e.g., bacteria and fungi) of the soil are also shaped by land-use history: the microbial communities have been found to differ between remnant and post-agricultural soils (Lee-Cruz et al. 2013; de la Peña et al. 2016). Given that biotic and abiotic components of soil can have strong influences on plant species distributions (Vandegehuchte et al. 2010), soil legacies may alter plant re-establishment in post-agricultural ecosystems.

We studied agricultural legacies in understory plant communities of longleaf pine (*Pinus palustris*) woodlands in the Southeastern United States. Fire-maintained longleaf pine ecosystems are an imperiled biodiversity hotspot, with $<3\%$ of historical area intact (Jose et al. 2006; Noss et al. 2015). Longleaf pine woodlands are broadly altered by a history of agriculture, with post-agricultural areas supporting altered plant community composition relative to remnants for decades or more following agricultural abandonment (Hedman et al. 2000; Brudvig et al. 2013; Veldman et al. 2014). A history of agriculture also affects numerous attributes of soil (i.e., increased P, compaction, decreased N, organic matter, and soil water-holding capacity) in longleaf pine woodlands for decades or more after agricultural abandonment (Brudvig et al. 2013; Mattingly and Orrock 2013; Bizzari et al. 2015). Although agricultural soil legacies may influence the establishment of some exotic species (Mattingly and Orrock 2013), less is known about whether differences in soils in this system contribute to agricultural legacies for plant communities through establishment limitation (i.e., limited re-establishment of longleaf pine woodland species following agricultural abandonment) or whether these and other environmental factors interact with agricultural land-use history to affect plant establishment.

We conducted field and greenhouse experiments to test whether establishment limitations contribute to post-agricultural plant community legacies. To test for post-agricultural establishment limitation, we conducted seed additions in both remnant and post-agricultural longleaf pine woodlands using species indicative of remnants but uncommon in post-agricultural areas. Lower establishment following seed additions into post-agricultural areas compared to remnant areas would provide support for establishment limitation as a cause of agricultural legacies on plant communities. We also tested whether establishment patterns are mediated by environmental factors (e.g., soil properties and burn history) in the field. To investigate soil legacies as a specific mechanism of establishment limitation, we conducted a greenhouse experiment to evaluate whether changes in soil due to agricultural land-use history affects plant establishment and growth.

We specifically evaluated the following questions: (1) Are rates of establishment (richness and abundance of sown species) lower in post-agricultural woodlands compared to remnants? (2) How are rates of establishment altered along environmental gradients and are the influences of these gradients on establishment altered by agricultural land-use history?

Finally, to consider soil legacies as a specific mechanism of agricultural legacies on understory plants, we asked (3) is performance (survival and growth) lower when plants are grown in soils from post-agricultural areas compared to soils from remnant areas?

Materials and methods

Field experiment

To test how agricultural land-use history influences plant establishment in the field, we used a large-scale experiment located at the Savannah River Site (SRS), a National Environmental Research Park in South Carolina (33.20°N, 81.40°W). Within this experiment, each of 27 sites has 1-ha research patches located in remnant longleaf pine woodlands (those with no known history of tillage agriculture) that are immediately adjacent to 1-ha patches in post-agricultural woodlands (tillage abandoned in 1951, > 60 years prior to this experiment; Fig. 1). Due to logging in the nineteenth century and fire suppression over the last century, remnant areas have a closed canopy of hardwood trees (predominantly oak and hickory), but support populations of longleaf pine woodland understory plant species (Brudvig et al. 2013). Post-agricultural areas have a closed canopy of pine trees because they were planted as pine plantations following abandonment from agriculture. This experiment also included a restoration tree-thinning treatment (Turley and Brudvig 2016), but for this study we only consider unthinned plots. While most sites (22 of the 27 sites) have one pair of unthinned research patches of each side of the land-use boundary (as depicted in Fig. 1), some sites could accommodate more than one pair of research patches, including an odd number of patches with thinned remnant paired with unthinned post-agricultural woodland, resulting in a total of 61, 1-ha patches across the 27 sites. Previous work in these experimental plots found over 50 understory plant species that occur primarily only in remnant areas (remnant indicator species) which have largely failed to spread into adjacent post-agricultural areas (Brudvig et al. 2013; Grman et al. 2015; Turley et al. 2017).

To address our first and second research questions, we conducted a seed addition experiment using 12 of these remnant indicator species, all of which were perennials. These included six forbs in the Asteraceae (*Carphephorus bellidifolius*, *Coreopsis major*, *Eupatorium album*, *Silphium compositum*, *Solidago gracillima*, and *Vernonia angustifolia*), one in the Polygonaceae (*Eriogonum tomentosum*), and five grasses in the Poaceae *(Anthaenantia villosa, Aristida beyrichiana, Sorghastrum nutans, Sorghastrum secundum,* and *Sporobolus junceus*). We collected seeds by hand in fall of 2011 from at least three natural populations per species at SRS. We agitated seeds against wire mesh to remove them from seed heads and chaff, but left dispersal structures largely intact. Packets of weighed and counted seeds were created, with an average of 300 seeds per species per packet (range = 106–716, SD 173). In February 2013, we added one packet of seeds of each species by hand into one 1 × 1 m plots within each remnant and post-agricultural patch at each site, so that all 12 species were sown within each 1 × 1 m plot. Sown plots were located 50 m from land-use boundaries (Fig. 1). In fall 2015, near the end of the third growing season after seed additions, we surveyed the middle 0.5 m^2 (0.71 × 0.71 m) of each sown plot to record the presence or absence and abundance (number of individuals) of all sown species.

To address our second research question regarding how environmental conditions might influence establishment, we also collected data on a set of environmental variables that we hypothesized to influence rates of sown species establishment. Fire suppression can negatively affect understory

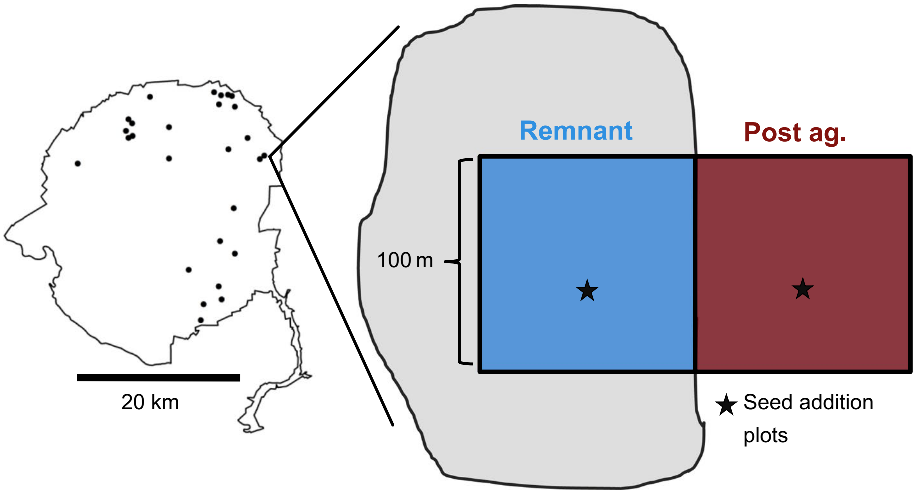


Fig. 1 Locations of the 27 paired remnant and post-agricultural research woodlands (represented by black circles) within the Savannah River Site. At each woodland, seeds of 12 species characteristic of remnant areas were sown into plots to evaluate the effects of agricultural history on plant establishment (represented by stars). A color version of this figure is available online

species diversity in longleaf pine woodlands by increasing tree abundance, canopy cover, and an accumulation of leaf litter and duff (Brockway and Lewis 1997; Hiers et al. 2007; Veldman et al. 2014). We quantified the depth of litter and duff, which we added together as our measure of leaf litter depth, and % canopy cover (with a convex spherical densiometer) above each seed addition plot in 2015. We also compiled fire records and tallied the number of times each plot burned between 1971 (when record keeping was initiated) and 2015. We quantified aspects of soils known to affect patterns of understory diversity and/or be altered by agricultural history in longleaf pine woodlands (Kirkman et al. 2001; Brudvig et al. 2013; Bizzari et al. 2015): soil phosphorus (Bray I method; mg P/kg soil; Bray and Kurtz 1945) and percent sand. Each soil measure was based on one composite soil sample of 1.6-cm wide by 20-cm deep soil cores. A total of 30 cores were collected along two 50 m transects located near the middle of 1-ha plots. Soil analyses followed methods in Brudvig et al. (2013).

Greenhouse experiment

To address our third research question, whether differences between remnant and post-agricultural soils influence growth and survival of seedlings, we conducted a greenhouse experiment with field-collected seeds and soils. In this experiment, we considered how biotic (e.g., the presence of mutualists or pathogens) and abiotic soil factors (e.g., differences in soil phosphorus) might affect plant establishment and performance, by including whole soil (biotic and abiotic factors) and inoculated soil (biotic factors alone) treatments.

We collected soil samples from post-agricultural and remnant woodlands within 10 of the 27 field sites, which we selected based on having the same soil series between pairs of post-agricultural and remnant woodlands. In 2014, we collected ~ 3.6 L of soil from each remnant or post-agricultural plot using the same methods described above except with 30-cm deep soil probes. We also collected seeds from seven species in the Asteraceae plant family that are present at our sites using collecting techniques described above. We focused on Asteraceae because this is among the most diverse and abundant family in our system (Kilgo and Blake 2005) and because this family supports numerous indicator species for remnant and post-agricultural areas (Brudvig et al. 2013). To consider species that might range in responses to remnant and post-agricultural soils, we included remnant indicators (*V. angustifolia, E. album,* and *C. bellidifolius*), post-agricultural indicators (*Eupatorium cuneifolium* and *Eupatorium compositifolium*), and species with no clear association with land-use type (*Liatris tenuifolia* and *Solidago odora*) as determined from Brudvig et al. (2013).

To test how both biotic and abiotic aspects of soil affect plants, we grew each species in whole soils collected from remnants or post-agricultural areas, from each of the ten field sites that we sampled. To isolate effects of biotic soil components, we inoculated batches of 4000 mL of sterile sand/peat moss mixture each with 705 mL (15%) of soil from each of the ten field sites. This approach minimizes abiotic (e.g., nutrients and texture) differences among soils, providing a focused test of the biotic components, which spread throughout the pot following inoculation (Kardol et al. 2007). *Vernonia angustifolia* and *E. album* did not receive the inoculation treatment because of limited germination. For each species and site, there were five replicates of the full soil treatment for both remnant and post-agricultural areas and eight replicates of the inoculated soil treatment for both remnant and post-agricultural areas. For each species, we also included eight sand/peat only controls with no inoculant. The seeds were first germinated in trays filled with sand and then transplanted into 2.5 × 16 cm planting tubes filled with either the full or inoculated soil, from either remnant or post-agricultural soils. We arranged pots into spatial blocks with soil from only one site to reduce risk of contamination. Each site was represented by multiple blocks, one for each replicate, and each species was present in each block. After plants germinated, we added two slow-release fertilizer pellets per planting tube (Osmocote 14-14-14, The Scotts Company, Marysville, OH). We watered the plants daily by hand with a misting nozzle. After ~ 92 days of growth, we harvested, dried, and weighed above- and belowground biomass.

Data analysis

To address our first two questions, we fit generalized linear mixed-effects models with the lmer4 package (Bates et al. 2015) in R version 3.3.2. Models were fit with Poisson error distribution and a log link function because the response variables were counts (number of species and number of individuals) and were left-skewed with a large number of zeros. This resulted in much reduced heteroscedasticity in the relationship between model fitted values and residuals compared to linear models with gaussian error distribution. We developed separate models with one data point per 1-ha patch (61 in total) predicting the number of sown species and the number of sown individuals per seed addition plot, based on land-use history (whether the plot was in a remnant or post-agricultural area) and measured environmental variables. We had control plots with no seed addition as part of the experiment, but only 5 plots out of the 61 contained a single sown species, so we continued the analyses looking at only the seed addition plots. We pooled across species to consider the number of sown individuals, owing to the large number of zeros at the species level.

To test for main effects of land-use history on establishment, we first fit models with only land use as a fixed effect and site as a random effect. To test for effects of environmental variables, we first fit full models that included: land-use history and environmental variables as fixed effects, interactions between each of the environmental variables with land-use history also as fixed effects, and site as a random effect. Environmental variables included in the full models were: soil phosphorous, percent soil sand, number of burns at each site between 1971 and 2015, percent of tree canopy closed, and leaf litter depth. Before fitting the models, we scaled and centered each continuous predictor variable to a mean of 0 and a standard deviation of 1. To determine the best final model, we used the dredge function in the MuMin package (Bartoń 2016), which fits every possible combination of fixed effects and ranks them based on AIC. For the best fit models, we calculated *P* values with a Wald test which is the standard summary output from the glmer function that we used to fit the models (Bates et al. 2015). We calculated R^2 for each factor in the model using the r2beta function in the r2glmm package (Jaeger 2017) using the standardized generalized variance approach. Finally, to visualize the model results, we plotted model predicted values on top of the back-transformed raw data. To limit the influence of extreme data points and to help with data visualization, we removed two outliers from the focal species abundance dataset that had 23 and 41 individuals. Removing these values resulted in the same best fit model and increased *P* values for burns and litter depth × land use factors, but the qualitative results remained unchanged.

To address our third question, we used paired (by field site) *t* tests to compare plant survival and biomass (combined above and below ground) for remnant and post-agricultural pots in the greenhouse experiment, with separate analyses for whole soil and inoculated treatments. Prior to analyses, we averaged replicate pots to get one value per site per treatment combination, thus for all analyses, site was the unit of replication. We calculated the percent effect size for the land-use treatments as (post-agricultural mean − remnant mean)/remnant mean × 100.

Results

Question 1: Effect of land-use history on establishment in the field

There were main effects of land-use history on establishment with more sown species and individuals establishing in post-agricultural plots (Fig. 2). Across all the treatments, an average of 0.80 sown species established in each plot. There were 0.86 (234%) more sown species in post-agricultural plots compared to remnant plots ($z = -3.58$, $P < 0.001$, $R^2 = 0.09$; Fig. 2a). Across all treatments, an average of 2.13 individuals established in each plot, with 2.89 (432%) more individuals in post-agricultural plots ($z = -3.20$, $P = 0.001$, $R^2 = 0.04$; Fig. 2b).

Question 2: Effects of environmental variables on establishment in the field

The establishment of sown species was related to variation in fire frequency and soil conditions across study plots (Tables 1, 2). The richness and abundance of sown species increased with the number of burns (Fig. 3a, b) and this was the largest effect in our models, explaining 8–20% of the variation in establishment. The richness of sown species increased with soil phosphorus, and decreased with soil sandiness, both factors each explaining 6% of variation

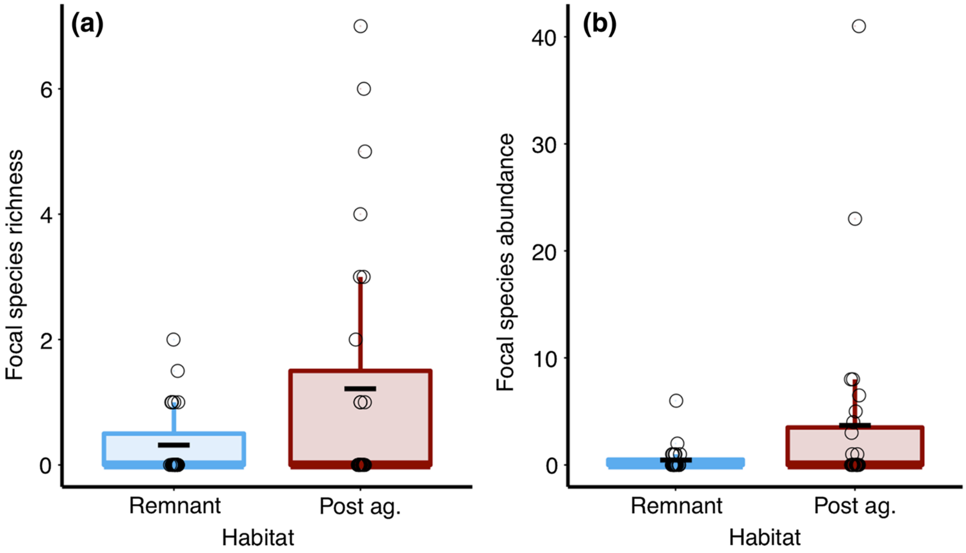


Fig. 2 Results from seed addition plots in the field experiment of **a** the richness of 12 sown species ($P = 0.04$) and **b** the abundance (number) of sown individuals ($P = 0.11$). A color version of this figure is available online

Table 1 Effects of land-use history and environmental factors (% sand, burns and phosphorus) on the richness of sown species

	Estimate	*z* value	*P*	R^2
Land use	0.271	0.485	0.628	0.004
% Sand	− 0.690	− 4.066	< 0.001	0.062
Burns	1.310	4.753	< 0.001	0.201
Phosphorus	0.555	3.970	< 0.001	0.063
Land use X % sand	0.622	2.058	0.040	0.027
Land use X burns	− 0.835	− 1.981	0.048	0.048

Results are from the best fit multiple linear regression model ($n = 61$)

Table 2 Effects of land-use history and environmental factors (% sand, burns and phosphorus) on the abundance (# individuals per plot) of sown species

	Estimate	*z* value	*P*	R^2
Land use	− 0.372	− 0.922	0.356	0.007
% Sand	− 0.617	− 2.213	0.027	0.029
Burns	0.807	1.941	0.052	0.084
Litter depth	− 0.941	− 2.407	0.016	0.075
Land use X % sand	0.919	1.980	0.048	0.038
Land use X litter depth	1.7289	4.044	< 0.001	0.135

Results are from the best fit multiple linear regression model ($n = 61$)

(Fig. 3c, e). Abundance of sown species also decreased with soil sandiness, which explained 3% of the variation (Fig. 3d).

We found evidence that agricultural history altered the roles of environmental factors for the establishment of sown species (Tables 1, 2). The effects of burns and soil sandiness on richness of sown species were stronger in post-agricultural areas than in remnants (Fig. 3a, c). Similarly, soil sandiness also had a larger effect on sown abundance in post-agricultural areas (Fig. 3d). Leaf litter depth had opposing effects with land-use history, with increasing leaf litter depth decreasing abundance in post-agricultural areas but slightly increasing abundance in remnants; this effect explained 13% of the variance (Fig. 3f).

Question 3: Effects of remnant and post-agricultural soils on plant performance

In the greenhouse, we found no consistent differences in the effects of soils from remnant and post-agricultural sites on plant survival or growth. In full soil treatments, averaging across the 7 Asteraceae species, we found no difference in survival ($t = 0.035$, $df = 9$, $P = 0.97$; Fig. 4a) and a trend for greater biomass ($t = 2.00$, $df = 9$, $P = 0.08$; Fig. 4b) in post-agricultural soils, compared to remnant soils. Averaged across all species, full soil treatments had 140% higher biomass ($t = -2.52$, $df = 7.32$, $P = 0.04$) but similar survival ($t = -0.56$, $df = 6.89$, $P = 0.59$) when compared to sand controls, but there were no differences between sand controls and inoculated treatments for biomass ($t = 0.095$, $df = 6.36$, $P = 0.93$) or survival ($t = 0.47$, $df = 6.80$, $P = 0.65$). In inoculated soil treatments, we found no effect of land-use history on survival ($t = -1.51$, $df = 9$, $P = 0.17$; Fig. 4c) or biomass ($t = 0.68$, $df = 9$, $P = 0.51$; Fig. 4d). For one remnant indicator species, *C. bellidifolius*, there was no effect of land use in the full soil treatment ($t < 0.001$, $df = 9$, $P > 0.99$; Fig. 5a), but survival was 21% lower in post-agricultural inoculated soils than in remnant-inoculated soils ($t = -2.70$, $df = 9$, $P = 0.02$; Fig. 5b). All other species were not affected by soil source in either full or inoculated soil treatments.

Discussion

Legacies of agricultural land use on plant communities can be pronounced and long lasting (Dupouey et al. 2002; Flinn and Vellend 2005; Hermy and Verheyen 2007; Brudvig and Damschen 2011; Brudvig et al. 2013, 2014; Bizzari et al. 2015); however, their causes are not well understood, in part because the relative roles of dispersal and establishment limitation remain poorly resolved (Donohue et al. 2000; Graae et al. 2004; Verheyen and Hermy 2004; Baeten et al. 2009a, b, 2015). Through a coupled greenhouse experiment and field experiment that eliminated dispersal limitation, we found evidence that establishment can be higher in post-agricultural woodlands, and that the magnitude of this increase in establishment depends on fire frequency and soil characteristics. In the field, the highest establishment occurred in post-agricultural areas with increased burning frequency and decreased sandiness. In the greenhouse, plants performed similarly when grown with remnant and post-agricultural soils. Together, these lines of evidence suggest that agricultural land-use legacies on plant community diversity and composition are unlikely to be maintained by reduced establishment in post-agricultural areas. Our results do, however, illustrate strong establishment limitation under some environmental conditions—particularly when fire is infrequent and soils are very sandy.

Mechanism behind agricultural land-use legacies

The increased establishment we observed in post-agricultural areas is opposite from what we expected, given that in this and other systems many species fail to recolonize post-agricultural areas (Dupouey et al. 2002; Vellend et al. 2006; Brudvig and Damschen 2011; Brudvig et al. 2013; Freschet et al. 2014), and our field experiment included species that have not colonized these areas in our system. It was, however, congruent with a pattern previously observed for two species (*Solidago nemoralis* and *Seriocarpus tortifolius*)

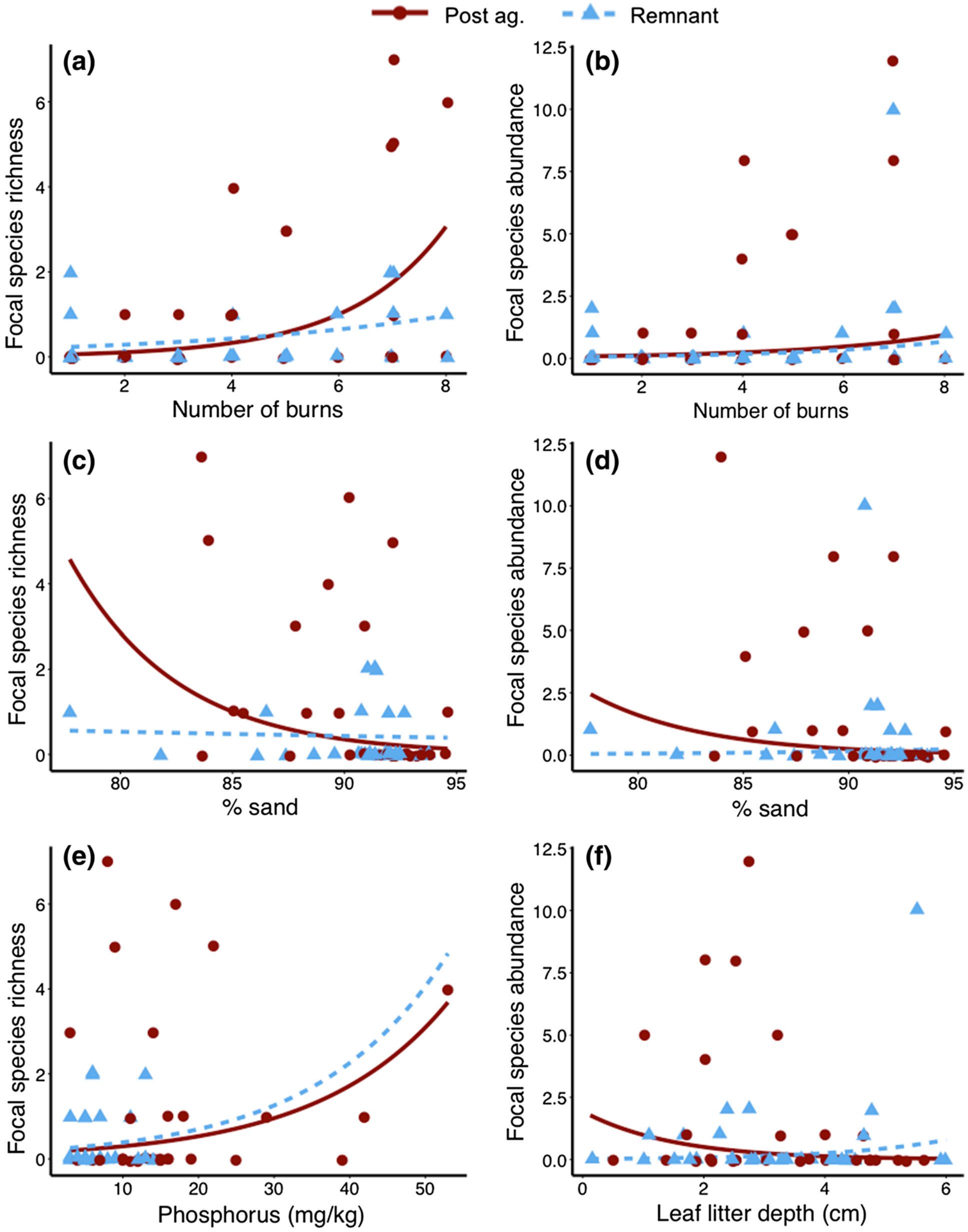


Fig. 3 Relationships between environmental factors (fire frequency and soil attributes) and the richness and abundance of 12 sown longleaf pine understory herbs. **a**, **c**, and **d** The relationships between environmental factors and species richness. **b**, **d**, and **f** The relationships between environmental factors and species abundance. Statistical results are provided in Tables 1 and 2. A color version of this figure is available online

within our system (Hahn and Orrock 2016). There are several possible reasons for this finding.

First, greater establishment in post-agricultural areas could be a result of different overstory conditions, relative to in remnants. In our system, the pine tree-dominated overstory in post-agricultural areas supports lower tree canopy cover, relative to the deciduous hardwood tree-dominated overstory in remnant areas (Brudvig et al. 2013). An increase in canopy cover can reduce understory plant diversity and modify understory community composition in longleaf pine woodlands (Brudvig et al. 2014; Brockway and Lewis 1997; Harrington and Edwards 1999; Hiers et al. 2007; Kirkman et al. 2013), so it follows that rates of establishment may decline with canopy density, particularly an increased density of hardwood trees. Much of these overstory density effects are thought to be mediated through O horizon (litter and duff) accumulation (Hiers et al. 2007; Veldman et al. 2014) and, while the combined depth of litter and duff is similar, remnants support more duff and post-agricultural woodlands more litter in our system (Brudvig et al. 2013). Although our best-fitting models did not contain variables related to canopy cover, bare ground, or litter and duff, we did find that fire frequency was strongly correlated with establishment (Tables 1, 2) but only in post-agricultural areas. Typically, fire mediates overstory and O horizon development in longleaf pine woodlands (Hiers et al. 2007; Veldman et al. 2014) which—coupled with the differences in overstory tree and litter composition between remnants

Fig. 4 Average survival and biomass across seven Asteraceae species grown in the greenhouse in **a**, **b** full soil treatments and **c**, **d** inoculated soil treatments. **a**, **c** Average survival ($P = 0.973$; $P = 0.166$). **b**, **d** Average biomass ($P = 0.076$; $P = 0.512$). A color version of this figure is available online

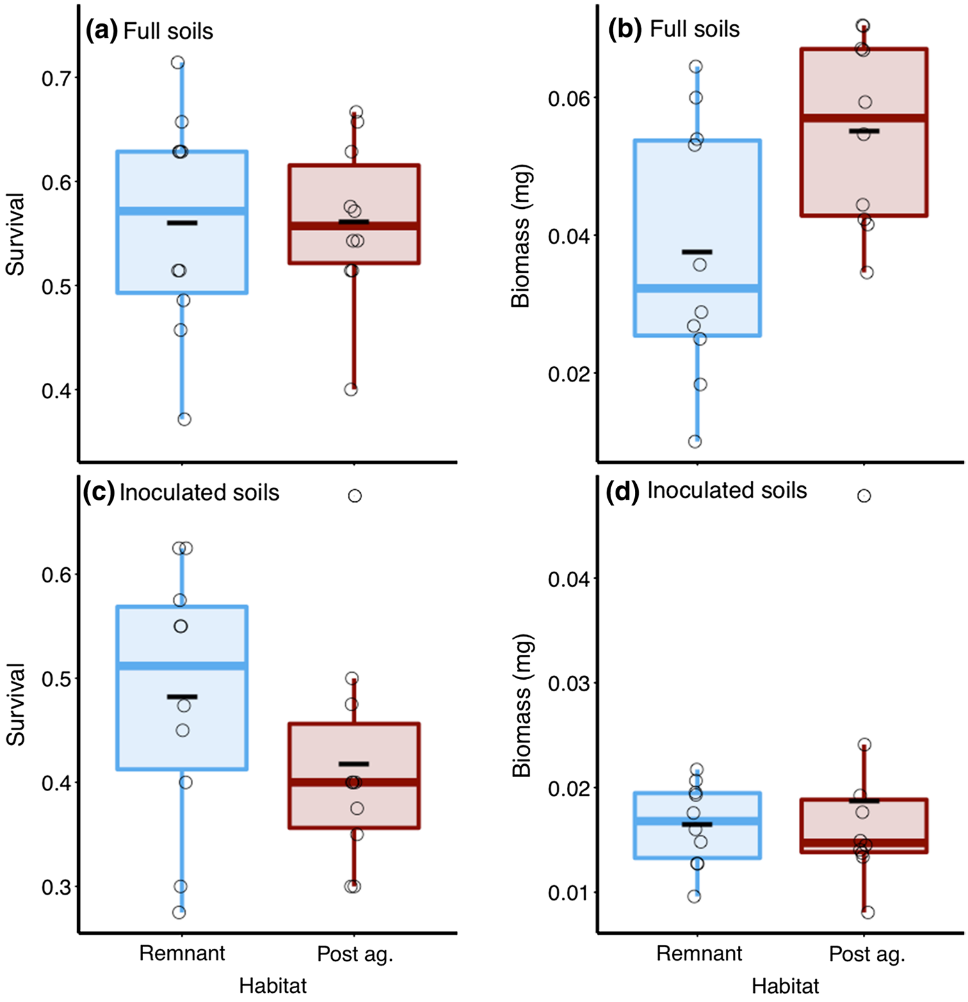
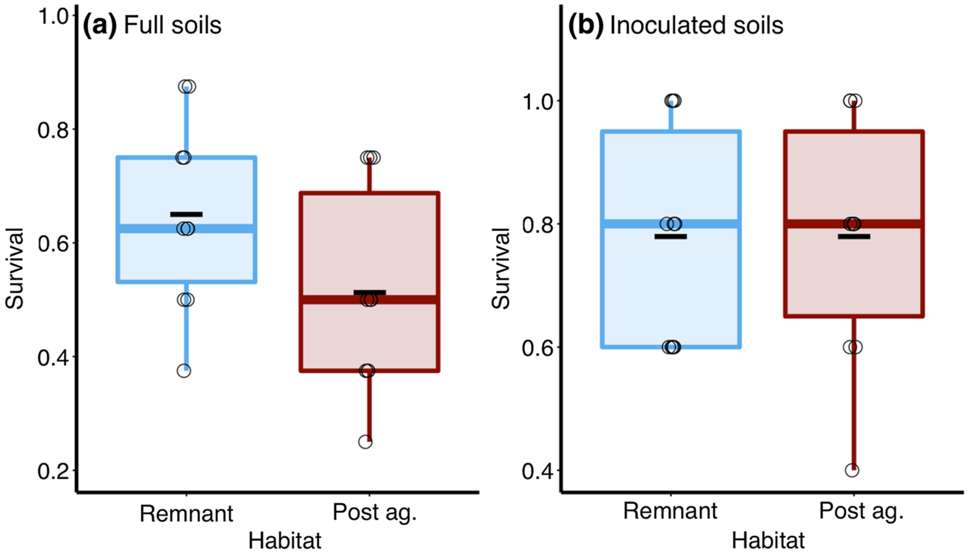


Fig. 5 Average survival for the remnant indicator species *Carphephorus bellidifolius* in **a** the full soil treatments ($P > 0.999$) and **b** the inoculated soil treatments ($P = 0.024$). A color version of this figure is available online



and post-agricultural woodlands (pine vs. hardwood trees)—could in part explain how fire increases establishment in post-agricultural areas.

Second, the increase in post-agricultural establishment could be due to the extra phosphorus in post-agricultural soils from past farming practices (Brudvig et al. 2013).

Other studies suggest that increased phosphorous is a cause of decreased establishment and recruitment over long timescales (Hipps et al. 2005; Stapanian et al. 2016). This effect could relate to the magnitude of that legacy, perhaps resulting in competition with other plants (Endels et al. 2004; Baeten et al. 2009a), although a lack of soil nutrients can also lead to limited recovery in agricultural lands in some systems (Inouye et al. 1994; Fernandes and Sanford 1995; Breen 2015). In our study, the magnitude of the phosphorus legacy was less than in other studies and soil phosphorus was positively correlated with establishment (sown richness), with this pattern at least partly driven by high establishment rates in post-agricultural sites with pronounced phosphorus legacies (right half of Fig. 3e). Thus, it appears that residual fertility from past agricultural use can impact post-agricultural recolonization by increasing establishment in our system and that this effect may contribute to higher establishment in post-agricultural relative to remnant sites.

Third, differences in establishment between post-agricultural and remnant woodlands might also have been due to differences in seed predation, seed death due to pathogens, or seedling death due to herbivory. Past work within our system may shed light on these potential influences on establishment. Red imported fire ants (*Solenopsis invicta*), which can be important granivores in this system, are more abundant in unthinned post-agricultural areas compared to unthinned remnant areas (Stuhler and Orrock 2016a). Seed predation rates do not differ between remnant and post-agricultural woodlands in our system, but predation rate does depend on environmental factors including fire frequency and down woody debris (Stuhler and Orrock 2016b). Together, these results suggest that granivory may not have driven the establishment pattern observed in our study. The effects of herbivory on establishment and survival, on the other hand, can depend on agricultural legacies, and the nature of this relationship varies among species and with ontogenetic stage (Hahn and Orrock 2016). For example, herbivores are relatively more consequential for establishment of *Carphephorus bellidifolius* (a species we also studied) in post-agricultural woodlands, relative to remnants, but the reverse is true for survival (Hahn and Orrock 2016). Thus, depending on the importance of various life stages, herbivore pressure may have contributed to the pattern we observed of increased establishment and survival in post-agricultural longleaf pine woodlands.

Environmental variables impacting establishment

The results of our field experiment also illustrate how agricultural history can alter the roles of environmental gradients for plant establishment. Gradients of fire frequency and soil sandiness are well known to influence the diversity and composition of longleaf pine understory plant communities (e.g., Kirkman et al. 2001; Brudvig et al. 2014; Veldman et al. 2014), so it was unsurprising that rates of establishment increased with fire frequency and decreased with soil sand content (Tables 1, 2). What was surprising was that these effects were only evident in post-agricultural sites, whereas rates of establishment were comparable at points along these gradients in remnants (Fig. 3). There are many possible explanations for this finding and we propose one potential mechanism: different litter-fire dynamics related to variation in overstory tree composition. Owing to the relatively greater flammability of pine vs. oak leaf litter in post-agricultural woodlands (Kreye et al. 2013), fire may open more recruitment microsites in post-agricultural woodlands. This in turn may result in greater rates of establishment from seed, particularly when soil conditions are favorable (e.g., on less sandy sites). Conversely, with less flammable broadleaf litter in habitats never used for agriculture, fire may open few bare soil recruitment microsites, resulting in gradients of fire and soil being relatively less important in remnants. These results provide a potential mechanism (differential rates of establishment from seed) to explain a past finding that understory richness increases with fire frequency in post-agricultural, but not remnant longleaf pine woodlands (Brudvig and Damschen 2011), and begs additional work to understand the interacting impacts of agricultural legacies and prominent environmental gradients.

Impact of soils on establishment

In our greenhouse experiment we found no evidence that soils in post-agricultural areas are limiting plant survival or growth. This was true when considering full soil (abiotic and biotic factors) and inoculated soil treatments (biotic factors only). We recognize two caveats to these results. First, greenhouse conditions were likely less stressful to plants than typical field conditions (e.g., due to daily watering and added fertilizer). Our field results illustrate that the effect of stressful conditions (soil sandiness) may be contingent on agricultural history (Fig. 3c). Given the direction of these field results, we would expect a more stressful greenhouse environment to result in better performance when plants were grown in post-agricultural soils, which would not support the hypothesis that soil conditions mediate an agricultural legacy through establishment limitation. Second, plant performance was typically similar in the inoculation and full soil treatments, compared to sterile sand controls, suggesting that any chemical or biological effects of soils in this system were of limited importance for plant performance (at least under the relatively non-stressful greenhouse conditions). Finally, in spite of these potential limitations, we note that the greenhouse and field results are qualitatively similar. Together, they suggest that agricultural history has not caused a fundamental limitation to establishment in this system.

The one exception to this pattern was *C. bellidifolius*, which had 21% lower survival in post-agricultural-inoculated soils than in remnant-inoculated soils (though not different between whole soil treatments). Previous field-based findings from Hahn and Orrock (2016) found the reverse—that transplants of *C. bellidifolius* had greater survival in post-agricultural woodlands after 1 year, but that survival of *S. tortifolius, S. nemoralis, and S. odora* were not affected by land-use history. Together, our results and those of Hahn and Orrock (2016) suggest species-specific responses to agricultural legacies, though additional work would be needed to evaluate the hypothesis more fully. As a whole, however, our results suggest that soils are not a mediator of post-agricultural legacies on plant communities in our system.

Establishment vs. dispersal limitation

A goal of our study was to understand if plants establish better following seed arrival in remnants or post-agricultural areas and if this can help explain the absence of some plant species in post-agricultural woodlands (Brudvig et al. 2013). We found that establishment of sown species was equal, or when sites were frequently burned or had less sandy soils, even greater in post-agricultural habitats. Yet, it is important to note that establishment was very low overall, with less than 1 of 12 species on average per plot. We can combine this finding with past work from our experiment showing strong dispersal limitation of remnant understory species (Turley et al. 2017; a pattern common across many other systems Turnbull et al. 2000; Clark et al. 2007). It would also be valuable to evaluate community saturation and its relationship with establishment/dispersal in our system. Together, these results suggest that both dispersal and establishment limitation constrain the colonization of remnant understory species into post-agricultural woodlands: seeds rarely arrive and, when they do, rarely establish. However, this does not necessarily imply that colonization should be uniformly low across this landscape. For example, restoration thinning of remnant woodlands greatly increases seed production by remnant understory herbs (Turley et al. 2017) and, as we show here, frequent fire and soil sandiness affect rates of colonization into post-agricultural woodlands. Together, this suggests hotspots of recolonization that may be governed in part by active managements. Importantly, our results show that seed additions were just as effective in post-agricultural areas as remnant areas and even more effective when post-agricultural areas were frequently burned. This suggests that seed additions coupled with burning are management strategies that could, over time, help overcome land-use legacies that have persisted for decades in the absence of active management.

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Author contribution statement LAB, JLO, and NET conceived and designed the experiments. JAL, NET, and CAB performed the experiments. NET analyzed the data. All the authors wrote the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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