RESEARCH ARTICLE

Canopy thinning, not agricultural history, determines early responses of wild bees to longleaf pine savanna restoration

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Longleaf pine savannas are highly threatened, fire-maintained ecosystems unique to the southeastern United States. Fire suppression and conversion to agriculture have strongly affected this ecosystem, altering overstory canopies, understory plant communities, and animal populations. Tree thinning to reinstate open canopies can benefit understory plant diversity, but effects on animal communities are less well understood. Moreover, agricultural land-use legacies can have long-lasting impacts on plant communities, but their effects on animal communities either alone or through interactions with restoration are unclear. Resolving these impacts is important due to the conservation potential of fire-suppressed and post-agricultural longleaf savannas. We evaluated how historical agricultural land use and canopy thinning affect the diversity and abundance of wild bees in longleaf pine savannas. We employed a replicated, large-scale factorial block experiment in South Carolina, where canopy thinning was applied to longleaf pine savannas that were either post-agricultural or remnant (no agricultural history). Bees were sampled using elevated bee bowls. In the second growing season after restoration, thinned plots supported a greater bee abundance and bee community richness. Additionally, restored plots had altered wild bee community composition when compared to unthinned plots, indicating that reduction of canopy cover by the thinning treatment best predicted wild bee diversity and composition. Conversely, we found little evidence for differences between sites with or without historical agricultural land use. Some abundant Lasioglossum species were the most sensitive to habitat changes. Our results highlight how restoration practices that reduce canopy cover in fire-suppressed savannas can have rapid benefits for wild bee communities.

Key words: agricultural legacy, Halictidae, land use, Pinus palustris, pollinators, restoration ecology

Implications for Practice

- Canopy tree thinning to restore longleaf pine savannas rapidly increases wild bee diversity.
- Agricultural history does not affect wild bee communities or alter the effects of canopy tree thinning on wild bee communities.

Introduction

The conversion of natural ecosystems for agricultural production is a leading cause of biodiversity decline and can have lasting effects on ecosystems long after agricultural abandonment (Foster et al. 2003; Newbold et al. 2015). Understanding the effects of these “agricultural legacies” can help us interpret contemporary patterns of biodiversity and is particularly important due to the increase of post-agricultural areas (Foster et al. 2003; Flinn & Vellend 2005; Cramer et al. 2008). Agricultural legacies (the differences between post-agricultural sites and “remnant” sites lacking agricultural history) can persist for decades to millennia in soils, plant communities, and aspects of habitat structure (e.g. Dupouey et al. 2002; McLaughlan 2006; Flinn & Marks 2007; Brudvig et al. 2013). However, the effects of agricultural history on animal communities are less well understood. Given their relative mobility, animals may show similar or dampened responses to agricultural legacies, in comparison to plants, and therefore the response of animals is dependent on the influence of legacies on habitat structure.

Agricultural abandonment also presents opportunities for biodiversity conservation, although these opportunities are accompanied by challenges. First, active restoration may be...
required to reinstate suitable habitat on former agricultural lands (Flinn & Marks 2007; Cramer et al. 2008; Suding 2011). Second, active reintroduction may be necessary for some taxa, even when habitat structure has been restored to former agricultural lands (e.g. Flinn & Vellend 2005; Turley et al. 2017). Third, the potential exists for agricultural history to modify the outcome of restoration activities, such that restoration of post-agricultural areas has a different outcome compared with remnant areas (e.g. Dupouey et al. 2002; Flinn & Vellend 2005; Williams 2011; Turley & Brudvig 2016). Finally, the effects of restoration on animal responses are relatively unknown, in comparison to the effects on plants (Brudvig 2011); with this, it remains unclear how most animal species will respond during efforts to restore post-agricultural lands. Some animal taxa may be less dispersal limited than plants and, therefore, may respond more rapidly to restoration of habitat structure. Here, we evaluate the effects of agricultural legacies and contemporary restoration activities on wild bee communities.

It is important to understand how restoration practices and land-use legacies affect bees, in order to inform broader native bee conservation efforts (Hanula et al. 2016). Bees are the most important insect pollinators of wild plants (Ollerton et al. 2011), but mounting evidence suggests that some bee species are suffering declines (Cameron et al. 2011; Bartomeus et al. 2013; Burkle et al. 2013), while other bee species persist (Colla et al. 2012; Bartomeus et al. 2013). Many more bee species are categorized as data deficient (Bartomeus et al. 2013) requiring additional sampling, taxonomic study, and analyses to determine their status. Loss of bees is of increasing concern due to the possible effects on pollination of crops and native plants (Biesmeijer et al. 2006; Potts et al. 2010). Bee diversity can increase wild plant reproduction (Fruend et al. 2013), so the responses of bee communities should be considered when undertaking ecosystem restoration. However, there is limited understanding of how land-use history affects pollinators, including during restoration, though this knowledge could help inform and shape conservation tactics (Foster et al. 2003).

Longleaf pine (Pinus palustris Mill.) savannas extend from southeastern United States coastal plain from eastern Texas to southeast Virginia. Throughout this range, longleaf pine is a dominant overstory tree in fire-maintained savannas, with high levels of plant diversity and endemism (Noss et al. 2015). The extent of longleaf pine savannas has been reduced by 97% (Frost 2006), making it of critical importance for conservation. Longleaf pine savannas have been negatively affected by resin extraction, harvesting practices, conversion to agriculture, and fire suppression (Frost 1993; Johnson & Hale 2002), which leads to canopy infilling and conversion of open-canopied savannas to closed-canopied woodlands and forests. When longleaf pine savannas transition to a woodland or closed canopy forest, less light reaches the ground, leading to the loss of the herbaceous layer and increases in shrub cover and sustained lower temperatures (Hanula et al. 2016). Differences in temperature affect foraging by bees by inhibiting their ability to thermoregulate and by reducing their foraging resources. Previous studies have shown lower bee abundance and species diversity in closed compared to open canopy forest environments (McKinney & Goodell 2010; Watson et al. 2011; Taki et al. 2013; Hanula et al. 2016). In order to reverse successional changes and reestablish an open canopy with increased sunlight, fire-suppressed agricultural and remnant longleaf pine savannas are managed with selective tree removal and prescribed fires (Jose et al. 2006). These methods simulate the effects of wildfire that originally maintained sparse longleaf pine canopy conditions.

Mechanical removal of invasive shrubs and overstory tree thinning can promote bee population richness and abundance both within and outside longleaf pine savannas (Taki et al. 2010; Hanula & Horn 2011; Fiedler et al. 2012; Proctor et al. 2012; Hanula et al. 2015; Breland et al. 2018). For example, Hudson et al. (2013) showed that the immediate response of pollinators (increasing in abundance and richness) can last up to five years after invasive shrubs were mechanically removed from historically forested areas. Yet, whether the effects of overstory thinning on bees interact with land-use legacies remains unknown. Harrison et al. (2018) found that bee communities in forested habitats differ significantly from agricultural landscapes with forest-associated species being lost from anthropogenic habitats. With this, it is important to consider multiple aspects of bee community response, since restoration may affect the abundance, richness, or community composition of bees (Winfree 2010). Similar responses may result from longleaf pine savanna restoration, given that restoration can increase understory plant richness and diversity, whereas land-use history affects community composition of ground-layer plants (Turley & Brudvig 2016).

Given the potential of land-use legacies and canopy thinning practices to influence bee communities, the goal of this study was to assess the initial response of wild bee communities to restoration of longleaf pine savannas. Specifically, we addressed the following questions:

(1) How do wild bee community composition, abundance, and richness respond to (a) agricultural legacies; (b) restoration by canopy tree thinning; and (c) the interaction between agricultural legacies and restoration?

(2) What environmental factors explain any differences observed in wild bee composition, abundance, and richness?

**Methods**

**Study Sites**

This study was conducted in 2013 at the Department of Energy Savannah River Site (SRS) in South Carolina, a National Environmental Research Park. Historically, the SRS uplands were dominated by longleaf pine savanna that was periodically burned by wildfire and Native Americans (Blake 2005; White 2005; Frost 2006). Between 1865 and 1950, the area was used to grow cotton, corn, and other agriculturally important crops (White 2005).

Our research took place within an experiment that factorially considered agricultural history and restoration thinning of longleaf pine savanna at SRS (Turley & Brudvig 2016). Sites
Figure 1. Map of study sites at the Savannah River Site (SRS) and diagram of experimental design. Left to right: Location of SRS within the state of South Carolina, locations of 12 study sites (blocks) within SRS, and diagram of replicated study site design showing 1 ha plots—sampled for bees using elevated bowl traps. Remnant sites were historically wooded, while post-agriculture sites were farmed until being managed as pine plantations (>60 years). Thinned sites had all trees removed in 2011 except 10 longleaf pines. No trees were removed from unthinned sites.

were separated from each other by approximately 0.8–29.0 km. Each of 12 replicate sites included an area of remnant longleaf pine savanna adjacent to an area of post-agricultural pine plantation. Remnant sites are original stands of longleaf pine savanna with no known history of tillage agriculture and, at the start of our experiment, were dominated in the overstory by hardwoods such as oak and hickory, due to decades of fire suppression (Brudvig et al. 2013). Post-agricultural sites were used as farm-land until 1951 and have since been managed as loblolly pine (*Pinus taeda* L.), slash pine (*Pinus elliottii* Engelm.), or longleaf pine (*Pinus palustris*) plantations (Brudvig et al. 2013).

The experiment follows a block design where at each of 12 sites (blocks), we established four to ten 1 ha plots (100 × 100 m); two to five plots on each side of the historical land use boundary (Fig. 1). This design separates historical land-use actions (farming) from the effects of biased prior decisions made for maximizing agricultural production (Brudvig et al. 2013). Furthermore, the block design controls for differences in collection time and duration, weather conditions, and other environmental factors because these attributes are shared by all plots within a single study site.

To reinstate the historically open-canopied savanna structure, we implemented a restoration thinning treatment in January–March 2012 to half of the of the plots within each block, where all but 10 longleaf pine individual trees were cut down and removed (Fig. 1). Compared to an average of 650 trees/ha in unthinned plots (Brudvig et al. 2013), this constituted a substantial (approximately 98.5%) reduction in tree densities in thinned plots. The result was that each site had four 1 ha plot types: (1) unthinned remnant; (2) thinned remnant; (3) unthinned post-agriculture; and (4) thinned post-agriculture (Figs. 1 & 2). Additionally, although the spatial scale of our plots allowed us to test how pollinator foraging is affected by different habitat types, we acknowledge that pollinators could move between plots because treatment plots within a block are within the flight distance of foraging bees (Greenleaf et al. 2007). Therefore, our study does not allow for us to infer if plots are able to support specific pollinator species.

**Bee Collection**

We collected bees using elevated plastic bowls (96 mL; Solo Brand P325) painted fluorescent blue, fluorescent yellow, or left the original white (Leong & Thorp 1999; Tuell & Isaacs 2009; Droege et al. 2010). Between 24 June and 14 August 2013, we sampled each plot four times by deploying nine bowls (three of each color) arranged in an “X” and spaced 5 m apart within a 20 × 20 m central region of each 100 × 100 m plot. We attached bowls to a stake and elevated them to the height of flowers on the surrounding understory vegetation (typically 0.5–1.0 m) or 0.5 m if no surrounding understory vegetation was present and filled each bowl with a mixture of water and a small amount of unscented Dawn dish soap. We sampled 8–10 plots per day (all plots in 1–2 blocks) by deploying bowls in the morning and retrieved bowls the same evening with total deployment periods ranging from approximately 5–10 hours. All plots within a block were sampled for an identical period during each sampling round. Following collection, bees were stored in 70% ethanol until being pinned and labeled. Specimens were identified by J. Gibbs using published keys (Mitchell 1960, 1962; Coelho 2004; Gibbs 2011; Gibbs et al. 2013).

**Environmental Data**

To explain variation in bee responses to agricultural history and restoration thinning, we collected data from each 1 ha plot in
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Figure 2. Representative photographs of the four thinning and agricultural land-use history treatments applied to longleaf pine savannas at the Savannah River Site, South Carolina.

2013 on biotic and abiotic factors of hypothesized importance for bee nesting and foraging. These included percent canopy cover, percent bare ground, percent sand in the soil [data collected in 2015], percent ground cover by understory vegetation, and plant species richness measures from $10 \times 10$ m plots near each bee sampling array. Full methods for environmental data collection are available in Brudvig et al. (2013).

**Data Analysis**

We performed all statistics in R version 3.2.2 (R Core Team 2015), implemented using RStudio version 0.99.892 (RStudio Team (2015)). We used nonparametric tests for pairwise comparisons due to non-normality of the bee data. Furthermore, to test the effects of restoration treatment on native bee species richness and abundance we performed Wilcoxon rank sum tests. We used the vegan package (Oksanen et al. 2013) to examine community composition, comparing among treatments with canonical analysis of principal coordinates (CAP; Anderson & Willis 2003). Permutational analysis of variance (PERMANOVA) were used to test for treatment and land-use effects on community composition using the “adonis” function in vegan, based on the Morisita-Horn index (Jost et al. 2011). Additionally, we controlled for random block effect by using the “strata” option in the “adonis” function. We also used correlation indices to test for significant associations between individual species and experimental treatments, using the indicspecies package (Cáceres & Legendre 2009).

We tested the effects of biotic and abiotic factors on bee abundance and richness, based on factors expected to be relevant to bee nesting (soil texture and litter depth) and foraging (plant species richness). The environmental variables that we used were canopy cover percentage, the percentage of sand in the soil, bare ground, plant species richness, and percent vegetation. Previous research has shown that increasing canopy cover negatively affects bees, possibly through greater shade and lower understory temperature (McKinney & Goodell 2010; Taki et al. 2010; Hanula et al. 2015; Breland et al. 2018). Bees are affected by temperature, with fewer bees able to fly at lower temperatures (McKinney & Goodell 2010). Therefore, we included canopy cover in our analysis because, while it can influence variables in the understory, canopy cover can independently affect bee foraging activity through lower temperatures. We also tested residuals for overdispersion and tested environmental variables for correlation (no variables correlated at $r > 0.6$; Table S1). We fit mixed effects models with the “lme” function with block as a random effect and environmental variables as fixed effects (Pinheiro et al. 2019). The “dredge” function within the MuMin package was used to choose between competing models by evaluating and selecting the lowest Akaike information criterion with small sample correction (AICc) values (Burnham & Anderson 2002; Bartoń 2014). We selected only the outputs that had values of delta AICc <2 (Table S2) and then excluded any models that contained environmental variables found not to be important for bees, leaving only percent canopy cover, percent bare ground, and percent sand as the significant factors. To determine the contribution of each significant factor to the chosen model, we first calculated the overall variance of the significant factors using the “lme” function. We then calculated the variance for subsets of the chosen model with one factor removed. The $r^2$ values were then each subtracted from the
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Overall variance and the resulting numbers were then multiplied by 100 to obtain the percent contribution of each significant variable.

**Results**

We collected 1,257 bees representing 35 different species (Table S3). Nearly the entirety of the collection, 1,220 specimens, belonged to six genera in the family Halictidae. The halictid genus *Lasioglossum* represented 1,197 specimens. Megachilidae was the next largest family with 22 total specimens in seven different species. In addition, we collected 13 specimens in six species of Apidae and two specimens of one species for Andrenidae.

**Q1:** How do agricultural legacies and restoration affect bee communities?

Tree thinning increased bee abundance in plots by more than 2.4 times ($U = 153; p < 0.0001$) and species richness by more than a third ($U = 287; p = 0.037$; Fig. 3). On average, thinned plots had nearly 61 individuals belonging to more than six species, compared to fewer than 25 individuals of five species in unthinned plots. The average species richness in both thinned and unthinned plots were 6.62 and 5.07, respectively. Land-use history did not have a significant effect on abundance or species richness in plots. Bee community composition was also significantly affected by canopy thinning (PERMANOVA: $F = 12.22$, $df = 1$, $p = 0.001$), but only marginally affected by land-use history ($F = 1.8$, $df = 1$, $p = 0.09$). There was an additional marginal interaction between thinning and land-use history ($F = 2.03$, $df = 1$, $p = 0.08$; Fig. 4). Correlation indices with individual species further supported the significance of tree harvesting on bee communities (Table 1). *Lasioglossum trigeminum* Gibbs was characteristic of thinned remnant plots, *Lasioglossum nymphale* (Smith) and *Lasioglossum vierecki* (Crawford) were characteristic of both thinned post-agriculture-harvest and remnant-harvested plots, and *Lasioglossum apokense* (Robertson) was absent from...
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Figure 4. Canonical analysis of principal components for bee communities in longleaf pine plots with different restoration (thinned vs. unthinned) and landuse histories (remnant vs. post-agricultural). Canopy thinning, but not agricultural landuse history, altered bee species composition, based on canonical analysis of principal coordinates.

unthinned remnant plots. Of the five *Lasioglossum* species that were significant for our correlation indices, four were indicative of thinned plots (Table 1): *L. nymphae*, *Lasioglossum puteulanum* Gibbs, *L. trigeminum*, and *L. apopkense*. Only *Lasioglossum raleighense* (Mitchell) was found to be indicative of unthinned plots.

Q2: What environmental factors explain differences in bee communities among treatments?

Bee abundance was correlated mainly with two environmental variables: percent bare ground and percent canopy cover. We found that the percentage of bare ground was positively correlated with bee abundance ($z = 4.315$, $p < 0.001$) while the percentage of canopy cover ($z = 2.919$, $p < 0.01$) was negatively correlated with bee abundance (Table S2). Percent sand was not correlated with bee abundance, however, the effect was not significant ($z = 1.548$, $p = 0.122$; Table S2). Our second model for variance determined that percent bare ground explained 19.6% of the variance, while canopy cover percentage, which is correlated with bare ground, explained 7.3%. Sand percentage was determined to explain 1.2% of the remaining variance.

Similar to abundance, bee richness was correlated with two environmental variables: bare ground and percent canopy cover. Our initial model showed that bare ground was positively correlated ($z = 3.265$, $p < 0.01$) and percent canopy cover was negatively correlated ($z = 3.187$, $p < 0.01$) and both were significant explanatory variables. We then determined that bare ground explained about 10% while canopy cover explained 4.4% of the overall variance of our model.

Discussion

We evaluated responses of wild bees to the early restoration of longleaf pine savannas by canopy thinning, at plots with or without a history of agriculture. Restoring habitat structure by canopy thinning altered bee community composition and increased the abundance and species richness of wild bees, with some species showing marked responses to treatments. Conversely, we found that a history of agricultural land use had little effect on native bee abundance, species richness, or community composition. These results illustrate how structural restoration can have rapid positive impacts on a bee community across locations, spanning major differences in land-use (agricultural) history.

Prior to restoration, dense canopy conditions and low understory light levels had developed in our system owing to decades of fire suppression (Brudvig et al. 2013). Restoring open canopy conditions by tree thinning had a large positive effect on native bee abundance and richness. Similar effects of canopy density on bees have been observed in forests of northwest Indiana (Grundel et al. 2010). Additionally, biotic and abiotic factors related to tree thinning and removal may be important for native bee diversity (Polatto et al. 2014). The majority of nest-building bees, including the genus *Lasioglossum*, excavate underground burrows (Michener 1974, 2007; Cane 1991), and so availability of bare ground is important for nest site selection (Gregory & Wright 2005; Potts et al. 2005; Hopwood 2008). Removal of canopy trees and invasive shrubs not only generates additional bare ground for these bees but also reverts the forest to early successional stages that provide increased light, warmer temperatures, and increased flowering understory plants (Fye 1972; McGuire et al. 2001; Potts et al. 2003; McKinney & Goodell 2010; Taki et al. 2013). Our results partly reflect these patterns, as canopy thinning increases both plant diversity (Turley & Brudvig 2016) and bee abundance (Table S2); however, we did not find a correlation between plant richness and bee abundance at the plot level in our present study. Thus, although thinning benefits both plants and bees, these responses appear to take place at the scale of landscapes, rather than synchronously at local scales.

Our samples did not include many floral specialist bee species. Yet, despite collecting mainly generalist species, we were still able to detect differences within the wild bee community composition, which demonstrates how strongly the thinning treatment dictates the abundance and richness of the wild bee community. Although we were unable to capture many specialists for our study, we can still infer that the specialist bee community could have similar or larger differences in community composition as a response to the thinning treatment. This is because detecting changes within a generalist community is harder due to their propensity to resist change and that any change within community make-up would affect specialists first before affecting generalist species. A related study at the same site incorporating net collections suggests specialist bees also benefit from canopy thinning (Breland et al. 2018). It should be noted that a great deal of specialist bee species share host plants (e.g. *Helianthus*; Hurd et al. 1980), so plant identity or
functional traits may be more important than plant richness per
se for predicting bee richness.

We found no effect of agricultural land-use history on bee
abundance, richness, or community composition—a surprising
result given that remnant and post-agricultural plots differ
in understory and overstory plant composition (Flinn & Marks
2007; Turley et al. 2017), numerous soil attributes (Flinn
et al. 2002; Flinn & Vellend 2005; Bizzari et al. 2015), and
aspects of ecosystem structure (e.g. litter depth, canopy cover;
Cramer et al. 2008; Williams 2011; Brudvig et al. 2013). Plant
community recovery has been limited by dispersal from rem-
nants to post-agricultural area in this specific system (Turley
et al. 2017) and we suspect that these differences in how plant
and bee communities respond to agricultural history corre-
pond to the relative mobility of these two taxa. Many of the bees
we captured are also generalists, and therefore may actively forage
between post-agricultural and remnant areas. Restoration thin-
ing had some similar impacts on plant and bee communities,
increasing richness and altering community composition which
follows results from other restoration studies (Taki et al. 2013;
Hanula et al. 2015; Turley & Brudvig 2016; Roberts et al. 2017).

Most of the wild bees collected in our study were in the
family Halictidae, particularly Lasioglossum, but this group is
known to favor colored bowl traps (Droege et al. 2010), so we
recognize that our sampling collected only a subset of the bee
community. Lasioglossum is one of the few bee genera that can
be reliably trapped even in highly disturbed systems such as corn
and soybean fields (e.g. Gill & O’Neal 2015; Wheelock et al.
2016). Larger bodied bees or floral specialists, which may be
at greater risk of extirpation (Bartomeus et al. 2013), were not
well represented in our samples partially due to sampling biases
and, perhaps, timing of the collections (Cane 1991; Geroff et al.
2014). Large-bodied species may be more affected by land use,
but they are also able to fly long distances between patches and
so larger experimental plots would be needed to test effects on
these bees. A related study incorporating net collections
across additional sites suggests the patterns observed here are
maintained over multiple years and also apply to a wider range
of bee species (Breland et al. 2018). Although land-use history
did not appear important for bee diversity in this study, it may
play a stronger role in other species with stronger dependencies
on specific floral hosts. Regardless, our results demonstrate
that restoring the savanna condition of longleaf pine sites can
increase bee species richness and abundance.

Restoration and management of fire-suppressed longleaf
pine savanna focuses on reducing the density of trees through
prescribed fire and mechanical thinning, often with a focus on
threatened and endangered species (e.g. red cockaded wood-
pecker) or understory plant communities (Jose et al. 2006).
Our results illustrate how wild bee species richness and
abundance respond favorably to overstory tree thinning. This
effect was rapid, taking place within two years of restoration
thinning and apparent regardless of whether savannas were
remnants or supported agriculture in the past, mirroring the
results found by Griffin et al. (2017) and Fiedler et al. (2012).
Given the wide-ranging importance of promoting pollina-
tors, our work supports the use of overstory tree thinning
to increase the diversity and richness of bees in this biodi-
versity hotspot. The future effects of savanna maintenance
through fire on bee communities will require additional study
as these restorations mature, though bees may respond posi-
tively to fire (Campbell et al. 2007; Taylor & Catling 2011;
Campbell-Moylett 2014).

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Supporting Information
The following information may be found in the online version of this article:

Table S1. Correlation coefficients and p values between modeled environmental variables.
Table S2. Accepted models for both abundance (2a) and richness (2b) that were chosen due to having a delta AICc value less than 3.
Table S3. Bees collected in 2013 using elevated colored bowl traps in longleaf pine restoration experimental plots at the Savannah River Site, South Carolina.

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