

Restoration increases bee abundance and richness but not pollination in remnant and post-agricultural woodlands

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Citation: Breland, S., N. E. Turley, J. Gibbs, R. Isaacs, and L. A. Brudvig. 2018. Restoration increases bee abundance and richness but not pollination in remnant and post-agricultural woodlands. *Ecosphere* 9(9):e02435. 10.1002/ecs2.2435

Abstract. Human land use, including agriculture, is a leading contributor to declining biodiversity worldwide and can leave long-lasting legacies on ecosystems after cessation. Ecological restoration is an approach to mitigate these impacts. However, little is known about how animal communities and plant–animal interactions respond to the combined effects of land-use legacies and restoration. We investigated how restoration and agricultural history affect bee (Hymenoptera: Apoidea: Anthophila) communities and pollination function. In 27 paired remnant (no history of agriculture) and post-agricultural longleaf pine (*Pinus palustris* Mill.) woodlands, we established 4–10 1-ha plots (126 total) and experimentally restored half of them, while the other half were left as unrestored controls. Restoration was accomplished through canopy thinning which reinstates open savanna-like conditions. We collected bees in each plot using a combination of bowl trapping and standardized netting transects. Thinning increased bee abundance by 169% and bee richness by 110%, but agricultural land use had no effect on these variables. Bee community composition was affected by restoration and was marginally affected by agricultural history. To measure pollination function, we conducted a sentinel plant experiment in which potted black mustard (*Brassica nigra* L.) plants were placed out in a subset of these sites ($n = 10$) and either bagged to exclude pollinators or left open for pollinator access. Then, we measured fruit and seed set of sentinel plants to compare pollination function among the restoration and land-use history treatments. Seed set and fruit set of sentinel plants were higher in open than bagged plants, indicating that this model system effectively measured pollination, but we found no differences in pollination based on restoration or agricultural history. These results indicate that although pollinator communities may show clear responses to restoration that are largely independent of prior land-use impacts, this does not necessarily translate into differences in pollination function after restoration.

Key words: agricultural history; community ecology; ecological restoration; ecosystem services; land-use legacy; longleaf pine savanna.

Received 19 July 2018; accepted 23 July 2018. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

The transformation of natural ecosystems for intensive land use by humans is a driving force

behind declining biodiversity worldwide (Foley et al. 2005, Newbold et al. 2015). The expansion and intensification of agriculture in recent decades have accelerated these losses (Tilman 1999,

Tscharntke et al. 2005). In addition to the negative impacts of active agriculture on biodiversity, agriculture can leave lasting legacies on ecosystems long after cessation (e.g., Bellemare et al. 2002, Dupouey et al. 2002, Flinn and Vellend 2005). Understanding these legacies will help to guide our efforts to conserve biodiversity through habitat restoration on post-agricultural lands (Suding et al. 2004, Perring et al. 2016).

Post-agricultural ecosystems (where agriculture has been abandoned) are common and present significant opportunities to restore native biodiversity, yet in many cases, active restoration is necessary to realize this potential. For example, as much as 80% of forest cover in areas of Europe and North America is on land with agricultural history (Flinn and Vellend 2005). Numerous ecosystem attributes differ between post-agricultural areas and remnant areas (lacking a history of agriculture), including overstory structure and composition, understory plant diversity and community composition, and soil attributes (Kirkman et al. 1996, Foster et al. 1998, Flinn and Marks 2007, Kuhman et al. 2011, Liiri et al. 2012, Yesilonis et al. 2016). In the face of ongoing agricultural abandonment in some regions of the world (Ramankutty and Foley 1999), development of restoration approaches to mitigate agricultural legacies will be important for the recovery of post-agricultural ecosystems (Flinn and Vellend 2005).

Animal species and communities can be affected by agricultural legacies, though relatively less is known about these impacts compared to those on plants. For example, Bowen et al. (2007) found that some animal species, particularly habitat specialists, are absent or less abundant in forests with a history of agriculture, whereas generalists, including some species not typically found in forests without a history of agriculture, are most abundant in post-agricultural sites. Understanding faunal responses to land-use legacies is important in its own right and also because of the consequences for plant populations through mechanisms such as pollination, seed dispersal (Ferguson et al. 2003, Flinn and Vellend 2005), and herbivory (de la Peña et al. 2016). In a study designed to investigate agricultural legacies in some of the animal communities most closely associated with plants, de la Peña et al. (2016) found that nematode

abundance and composition and above-ground herbivorous invertebrate abundance were all affected by past agricultural land use.

We are not aware of any studies investigating the effects of agricultural legacies on pollinator communities or pollination function. However, since 87.5% of angiosperms are animal-pollinated (Ollerton et al. 2011), land-use legacies on pollinator communities could affect reproduction in a large proportion of plants. Active agricultural land use can have profound effects on pollinator communities and pollination, and these effects often increase with more intense agricultural practices (Tscharntke et al. 2005, Holzschuh et al. 2008, Potts et al. 2010, Kennedy et al. 2013); however, we know little about how long these agricultural legacies persist or if they persist at all once reforestation has occurred.

Restoration activities may help to remediate the impacts of agricultural land use on pollinators and pollination. In many cases, pollinators recover quickly after restoration of degraded ecosystems (Fiedler 2010, Hanula and Horn 2011a, b, Williams 2011, Griffin et al. 2017). However, plant-pollinator networks in restored ecosystems are sometimes less complex than in natural communities (Forup et al. 2008, Williams 2011), suggesting that pollination function may not recover completely. There has been little study of whether agricultural legacies impact pollinators or pollination once restoration activities have been implemented.

To address these issues, we investigated how restoration and agricultural land-use history interact to affect pollinator communities and pollination function. We conducted restoration (tree harvest that we call “restoration thinning”) in sites with one of two types of historical land use: (1) remnant sites, which have no known history of tillage agriculture and (2) post-agricultural sites, which were previously in tillage agriculture that was abandoned approximately 65 yr ago. We asked three questions: (1) Do agricultural legacies continue to affect bee communities and pollination? (2) How does restoration thinning affect bee communities and pollination? (3) Can restoration thinning reverse any effect of agricultural legacies on bee communities and pollination?

Previous work in our experiment has uncovered strong agricultural legacies, including on

numerous soil attributes, litter and duff accumulation, canopy cover, over- and understory plant community composition, and understory plant phylogenetic diversity (but not richness; Brudvig et al. 2013, Turley and Brudvig 2016). The restoration thinning treatment increased plant species richness regardless of land-use history; however, it did not erase the impacts of historical agricultural land use on plant composition and phylogenetic diversity (Turley and Brudvig 2016). Additionally, the thinning treatment resulted in decreased canopy cover and litter, increased temperature and sunlight, and increased flowering in a subset of plants (Brudvig et al. 2013, Hahn and Orrock 2015, Stuhler and Orrock 2016, Turley et al. 2017).

Given the observed effects on the plant community and differences in the abiotic conditions, we predicted that bee community composition would be distinct in remnant and post-agricultural sites and that restoration thinning would increase bee species richness and abundance. Restoration through thinning and the reinstatement of a historical burn regime significantly decreased canopy cover and duff and litter accumulation in remnant and post-agricultural sites, but unrestored remnant sites had higher canopy cover and duff depth than unrestored post-agricultural sites (Brudvig et al. 2013). Because of the differences in plant community before restoration, the interactive effect of land use and restoration on the plant community, and the increase in flowering due to thinning, we expected to see a differential effect of thinning on flowering in remnant and post-agricultural sites. Additionally, we predicted that, with the increase in bee abundance and richness, pollination function would be increased in restored plots.

METHODS

Study site and treatments

Our study took place in longleaf pine (*Pinus palustris* Mill.) woodlands within the Southeastern United States. This ecosystem is of considerable conservation concern because of its high level of endemism and particularly diverse ground cover plant community (Noss et al. 2015). About 97% of the land area once covered by longleaf pine ecosystems has been lost due to fire exclusion, urbanization, and land conversion

for timber production and agriculture (Van Lear et al. 2005). This study was conducted on the Savannah River Site (SRS), an approximately 80,000 hectare National Environmental Research Park located on the upper coastal plain in Aiken and Barnwell Counties, South Carolina. In 1951, the Federal government acquired SRS at a time when 38% of the area was agricultural land (Kilgo and Blake 2005). In subsequent decades, the majority of abandoned cropland was converted to dense closed canopy pine plantations. Intermixed within these post-agricultural areas were remnant woodlands, which were mature forests in 1951 and have no known history of agriculture. Remnant woodlands also had closed canopies and extensive hardwood encroachment due to fire suppression at the time of the study.

We selected 27 sites where post-agricultural woodlands are adjacent to remnant woodlands. At each site, we established between four and ten 1-ha (100 × 100 m) research plots, depending on the size of the remnant, for a total of 126 plots (Fig. 1). To investigate the effects of restoration independently and in conjunction with land-use history, we conducted restoration thinning in half of the experimental plots in 2011. Since pristine longleaf pine savannas are characterized by widely spaced canopy trees and a diverse understory of grasses and forbs (Frost 2006, Peet 2006), canopy thinning is a common restoration technique to reinstate habitat structure and promote native plant diversity (Walker and Silletti 2006). Within a site, half of the post-agricultural and remnant plots were randomly chosen to be mechanically thinned to 10 longleaf pines per hectare, and harvested trees were removed from the sites. The remaining half of the plots received no thinning (referred to as “unthinned”). This resulted in a 2 × 2 split plot design with four restoration and land-use treatment combinations (Fig. 1). This experimental design has the benefit of testing for impacts of land-use history while minimizing the other confounding effects associated with past land-use decisions (e.g., agriculture being focused on more fertile sites; Brudvig et al. 2013). The spatial scale of the plots within each site (adjacent 100 × 100 m plots) allowed us to test how pollinators use the different habitat types for foraging. This contrasts with many pollinator diversity studies in which sites are spatially separated to exceed the foraging

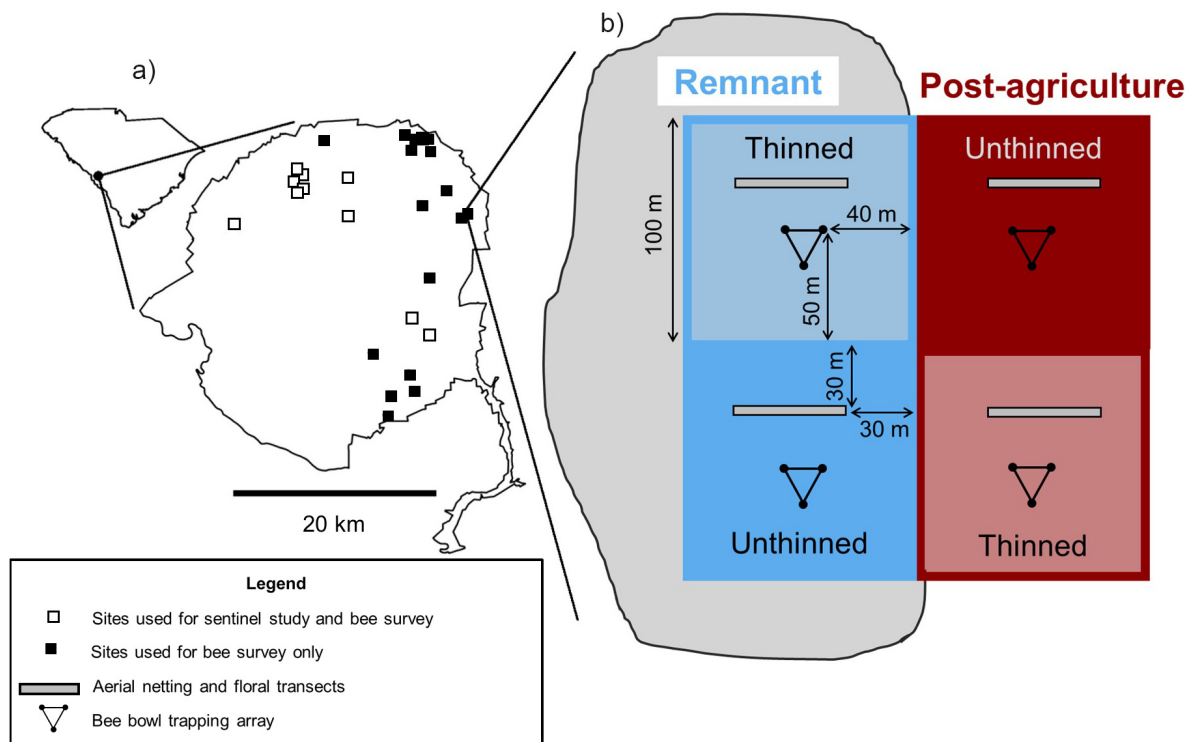


Fig. 1. Map of the study area and experimental design. (a) Research sites were located on the Savannah River Site in South Carolina, USA. The bee survey was conducted in all 27 sites (closed and open squares), and the sentinel plant experiment was conducted in a subset of 10 sites (open squares). (b) Each research site is composed of four 1-ha plots on both sides of the land-use boundary between remnant and post-agricultural areas. Remnant and post-agricultural plots were either thinned (all but 10 trees removed in 2011) or control (no manipulation). Aerial netting, and bee bowl trapping was conducted in each plot and sentinel plants were located at the three points of the bee bowl sampling array.

distance of an individual bee. The typical foraging range of a bee exceeds the size of our plots (Greenleaf et al. 2007, Zurbuchen et al. 2010). We recognize that this scale may not be large enough to infer whether plot types fully support particular pollinator species owing to movement among plot types (e.g., nesting in a thinned plot and foraging in an unthinned plot). As such, we focus on habitat use and note that movement among plots would result in conservative estimates of habitat use in some analyses due to fewer unique species being recovered in particular plot types.

Bee and floral sampling

To compare pollinator communities, we sampled bees across all experimental plots in 2016. We focused on bees as a subset of insect pollinators since bees are generally considered the most

efficient and effective pollinators across a wide variety of ecosystems (Kearns et al. 1998, Michener 2007, Willmer et al. 2017). We surveyed bees with bowl trapping and aerial netting. These two methods are often used in conjunction because they tend to sample complementary subsets of the bee community; bowl trapping captures many small bees, especially from the genus *Lasioglossum*, while aerial netting often captures more large than small bees (Leong and Thorp 1999, Cane et al. 2000, Droege et al. 2010). In each plot, we used nine traps (96-mL plastic cups), three each of white, fluorescent blue, and fluorescent yellow. Since bowls elevated to the level of the flowering vegetation tend to catch more bees (Tuell and Isaacs 2009, Geroff et al. 2014), we constructed bowl sampling platforms which held the bowls approximately one meter

above the ground. Platforms were plastic bucket lids with three holes into which a bowl could be placed, secured on an aluminum conduit pipe that was inserted into the ground. Three platforms were installed in each plot in a 15-m isosceles triangular array located near the center of the each plot (Fig. 1). On sampling days, we placed one white, one blue, and one yellow bowl in each platform and filled them approximately $\frac{3}{4}$ full with a weak solution of Dawn brand dish soap and water. Bees are attracted to these traps, the soap breaks the surface tension of the water, and the bees are captured (Droege 2015). We collected the trapped insects after 24 h by pouring the contents of each trap through a fine mesh sieve and transferring them into Whirl-Pak plastic bags (Nasco, Fort Atkinson, Wisconsin, USA). The insects caught in all nine traps in a plot were pooled together. We then submerged the insects in 95% ethyl alcohol to preserve them until they could be pinned and identified. In one sampling period (fall of 2016), we also placed bee bowls in an identical configuration on the ground for 24 h on a different day than they were collected in the elevated arrays. The blooms of the flowering plants during this time of year were well under 1 m tall so we reasoned that this sampling method might be more effective for the fall. Elevated and ground bowl samples were both included in the analysis.

On sampling days, we also collected bees using aerial netting. We netted all bees found along a 50×4 m transect in each plot (Fig. 1) for 10 min in the morning (between 08:00 and 12:00) and 10 min in the afternoon (between 12:00 and 16:00). Netted bees were killed using ethyl acetate, stored in a freezer, and pinned within 2 weeks of collection. Additionally, along a 50×1 m transect located directly adjacent the bee netting transect (Fig. 1), we estimated the area covered by open flowers.

We conducted bee sampling in all experimental plots three times in 2016: once each between April and May, June and July, and September and October. To avoid the effects of undesirable weather conditions on bee captures (Tuell and Isaacs 2010), we collected bees only on clear to partly cloudy days when the temperature was above 16°C and wind gusts were below 6 m/s. The bees captured in bowl traps and by aerial netting were combined and pooled across all

three sampling rounds for analysis. Bees were identified using published taxonomic revisions (Stephen 1954, Mitchell 1960, 1962, Ribble 1967, LaBerge 1971, Coelho 2004, Gibbs 2011, Rehan and Sheffield 2011, Gibbs et al. 2013, Williams et al. 2014), with names updated following a checklist of valid names for bees (Ascher and Pickering 2016). Specimens are deposited in the J. B. Wallis/R. E. Roughley Museum of Entomology, University of Manitoba.

Pollination experiment

To compare pollination function among the treatment combinations, we conducted a sentinel plant experiment in 2016, at 10 of the 27 sites (Fig. 1). We allowed a model plant, black mustard (*Brassica nigra* L.), to be pollinated in these plots and compared its reproductive output as a proxy for pollination function. Black mustard was chosen for several reasons: (1) It is self-incompatible and benefits from insect pollination (Abrol 2007) so we expected greater reproductive output of plants visited by more pollinators compared to those visited by few or no pollinators; (2) it is visited by a wide range of pollinators (Conner and Neumeier 1995); (3) it does not naturally occur in the study location, so we were able to experimentally control numbers and avoid cross-pollination with natural individuals; and (4) information on the propagation and care of this plant is available and it grows quickly, so we were able to propagate the large numbers of the plants, necessary for our experiment.

We grew black mustard to maturity in a climate-controlled greenhouse. When flowers began to open on the first inflorescence, we tied a string to the main stem of the inflorescence above the uppermost unopen flower, covered the inflorescence with a 25×30 cm pollinator exclusion bag (DelStar Technologies, Middletown, Delaware, USA), and secured the bags at the bottom with a twist tie. Pollinator bags were secured around a wire structure to reduce contact with the inflorescence and to allow room for the stem to elongate. We then transported 15 plants to the field with each plot receiving three trays containing five plants, one tray at each of the three bee bowl stands (Fig. 1). Within a tray, one of the five plants was randomly selected to be left bagged (excluding pollinators), while the bag was removed from the other four plants resulting in 3

bagged plants and 12 open plants per plot. Plant trays were filled with water to prevent water stress. The sentinel plants were left out to be pollinated for approximately 3.75 d, after which we once again covered the inflorescences of all plants with pollinator exclusion bags in the field, returned the plants to a greenhouse, removed the bags, tied a string above the unopen flowers, and replaced the bags. The flowers located in between the two strings were the ones included in the experiment. We continued to tend the plants until the fruits that grew from the experimental flowers reached maturity at which time they were harvested. On each plant, we counted the flowers included in the experiment, fruits which contained seeds at harvest, developed seeds, and clearly underdeveloped seeds, which were either completely flat or severely shriveled.

Data analysis

We averaged the data obtained in the bee and floral survey across replicate treatment combinations at each site resulting in 108 unique data points. We conducted all analyses in R version 3.3.2 (R Development Core Team 2016). To test how bee richness, bee abundance, bee Simpson's diversity, Chao 1 estimated bee species richness, floral cover, and floral species richness were affected by land-use history and restoration, we fit a nested model using the *lme* function in the *nlme* package (Pinheiro et al. 2016). The syntax of the model was $y \sim \text{land use} \times \text{restoration}$, $\text{random} = \sim 1 | \text{site/land use}$, where site is a 27-level categorical variable and "land use" is a two-level categorical variable. We obtained *P*-values using the *anova.lme* function with Type III sums of squares. All models, except for floral cover, met the assumptions of ANOVA, as their residuals were normally distributed and residuals vs. fitted values plots did not show heteroscedasticity. Floral cover values were log transformed ($\log(\text{floral cover} + 1)$) for this model to meet the assumptions of ANOVA. We calculated r^2 values for the fixed effects using a method outlined by Nakagawa and Schielzeth (2013) with the *r2beta* function in the *r2glmm* package (Jaeger 2017). We could not calculate Simpson's diversity for four of our experimental plots because no bees were caught in them, so these were dropped from the model. We calculated Simpson's diversity and Chao 1 estimated species richness for bees using

the *vegan* package (Oksanen et al. 2017). We chose the Chao 1 estimator because it includes abundance in the calculation and accounts for the large number of rare species with a correction factor (Chao 1984). To test the effects of our land-use and restoration treatments on bee community composition, we performed a PERMANOVA using the *adonis* function in the *vegan* package (Oksanen et al. 2017). Since *adonis* does not allow for nested random effects, we fit two models to calculate the treatment of effect of land-use history and restoration separately. The first, for land-use history effects, had the site effect as a fixed predictor ($df = 1, 26$). The second, for restoration effects, had the site $\times$ treatment effect as a fixed predictor ($df = 1, 52$). This structure was used so that the models would have the correct residual degrees of freedom. All models had site as strata or blocks. We plotted an ordination of the bee community using Bray-Curtis distances and a constrained analysis of principal components with a four-level predictor variable consisting of all land-use and restoration treatment combinations. This was calculated with the *capscale* function in *vegan* (Oksanen et al. 2017). To identify species associated with particular treatments, we conducted indicator species analysis using the *multipatt* function in the *indicspecies* package (De Cáceres and Legendre 2009). In indicator species analysis, *A* is the probability that a site belongs to the target site group given that a species is present. *B* is the probability of finding a species in the sites belonging to a site group. Indicator value is calculated using the following formula: $IV = A \times B$ and is equal to one when a species was caught in all replicates of a site type and never caught in any other type of site. *P*-values were calculated using the Monte Carlo method with 999 permutations.

We also tested the effects of land-use history and restoration on fruit and seed set of the sentinel plants. Fruit set was defined as the number of fruits that had matured at the time of harvest and contained at least one seed. We calculated seed set as the number of developed seeds divided by the number of flowers included in the experiment from each plant. We fit a nested model using the *lme* function with the syntax: $y \sim \text{land use} \times \text{restoration} \times \text{bagging treatment}$, $\text{random} = \sim 1 | \text{site/land use/restoration/tray}$, where site is a 10-level categorical variable, land use,

and restoration are both two-level categorical variables, and tray is a three-level categorical variable indicating the three locations within a plot where a plant could be placed. We tested for evidence of land-use history or restoration treatment effects in the interaction term between land use or restoration and bagging treatment, since only the open plants should have experienced differential pollination rates. When two- and three-way interactions were not significant, we explored other treatment effects by dropping the interaction terms from the model. Seed set was log transformed ($\log(\text{developed seeds per flower} + 1)$) for analysis to improve heteroscedasticity in the relationship between the residual and fitted values from the model.

We calculated effect size using the following formula: $(\text{treatment} - \text{control}) / \text{control} \times 100\%$, where controls were unthinned plots and open plants and treatments were thinned plots and bagged plants.

RESULTS

Response of bee and floral communities

Over the course of this study, we collected 1026 bees from 88 species, 31 genera, and all six North American bee families (Appendix S1: Table S1). We captured 406 bees from 69 species in thinned remnant plots, 345 bees from 54 species in thinned post-agricultural plots, 124 bees from 30 species in unthinned remnant plots, and 151 bees from 40 species in unthinned post-agricultural plots.

Restoration thinning increased bee abundance by 169%, bee richness by 110%, and Simpson's diversity by 37% (Table 1, Fig. 2). Thinning also increased floral cover by 699% (Table 1, Fig. 3) and floral richness by 232% (Table 1). Bee community composition was distinct between thinned and unthinned plots, and this restoration effect explained 5% of the compositional variation (Table 1, Fig. 4). Land-use history did not

Table 1. The effects of agricultural land-use history, restoration, and their interaction on measurements of bee diversity in longleaf pine woodlands.

Variable	Effect size	df	F	P	r^2
Bee abundance					
Land-use history	NA	1, 26	1.11	0.30	0.008
Restoration thinning	+169%	1, 52	23.34	<0.001	0.131
Land use $\times$ restoration	NA	1, 52	1.44	0.24	0.009
Bee species richness					
Land-use history	NA	1, 26	0.57	0.46	0.004
Restoration thinning	+110%	1, 52	22.05	<0.001	0.128
Land use $\times$ restoration	NA	1, 52	1.37	0.25	0.009
Bee Simpson's diversity					
Land-use history	NA	1, 26	0.71	0.41	0.006
Restoration thinning	+37%	1, 48	19.04	<0.001	0.125
Land use $\times$ restoration	NA	1, 48	0.54	0.47	0.004
Bee composition					
Land-use history	NA	1, 26	1.70	0.06	0.011
Restoration thinning	NA	1, 52	6.66	<0.001	0.051
Land use $\times$ restoration	NA	1, 52	0.94	0.52	0.007
Floral cover†					
Land-use history	NA	1, 26	0.04	0.84	<0.001
Restoration thinning	+699%	1, 52	49.46	<0.001	0.268
Land use $\times$ restoration	NA	1, 52	4.73	0.03	0.034
Floral species richness					
Land-use history	NA	1, 26	0.98	0.33	0.006
Restoration thinning	+232%	1, 52	80.39	<0.001	0.258
Land use $\times$ restoration	NA	1, 52	2.04	0.16	0.009

Notes: Results for abundance, species richness, and Simpson's diversity are from nested ANOVAs and results for composition are from a PERMANOVA. Values which are significant at $\alpha < 0.05$ are bold. Percent effect size $((\text{treatment} - \text{control}) / \text{control} \times 100\%)$ is included for significant effects except for interactions and bee composition results where effect size cannot be calculated.

† Variable log transformed for analysis to satisfy assumptions of ANOVA.

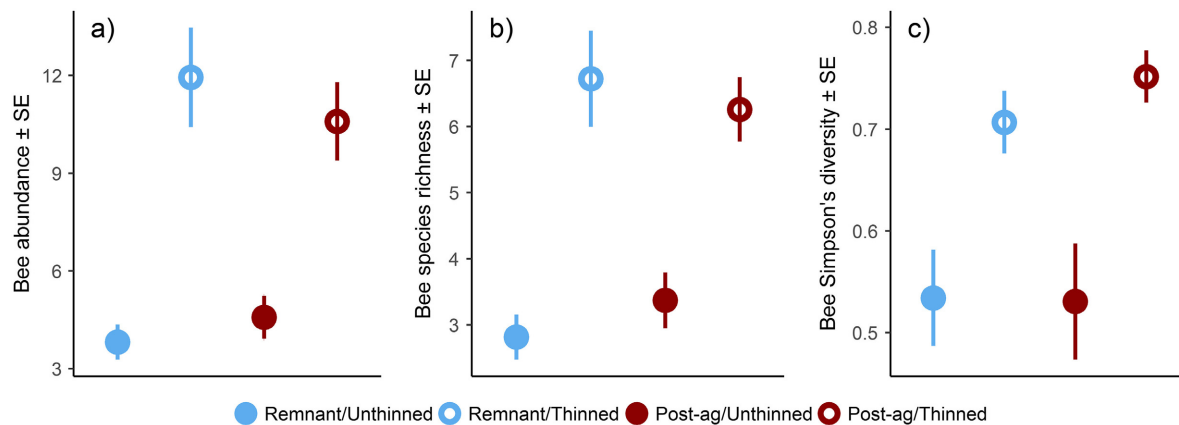


Fig. 2. Restoration thinning increased bee diversity, but land-use history had no effects. Comparison of bee (a) abundance, (b) species richness, and (c) Simpson's diversity among land use and restoration treatment combinations. Each value is the mean of 27 replicate plots $\pm$ standard error.

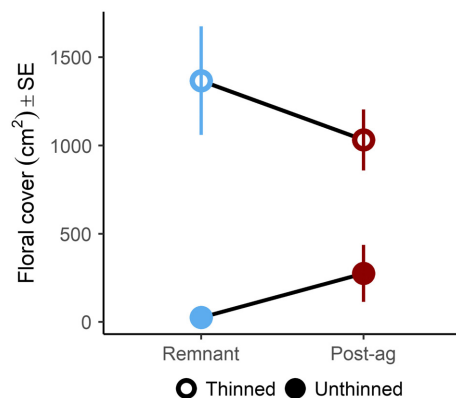


Fig. 3. Restoration thinning greatly increased floral cover. Thinning also had a larger positive effect on floral cover in remnant than in post-agricultural areas. Each value is the mean of 27 replicate plots $\pm$ standard error. For the unthinned remnant data point, the error bars are contained within the diameter of the point.

significantly affect bee abundance, bee species richness, bee Simpson's diversity, floral cover, or floral richness (Table 1, Fig. 2) though there was a marginal effect on composition (Table 1, Fig. 4). The thinning treatment and land-use history had the same effects qualitatively and a very similar effects quantitatively on Chao 1 estimated bee species richness (131% increase with thinning, Appendix S2: Table S1, Fig. S1) as they did on bee species richness; therefore, we focus on bee species richness when discussing these

results. There was a significant interaction between land use and restoration on floral cover (Table 1), such that floral cover increased to a greater degree when remnant plots were thinned (5389%), relative to when post-agricultural plots were thinned (275%; Fig. 3).

Since restoration and land-use history affected bee community composition, we focused on indicator species associated with these treatments separately. Since treatment interactions did not affect composition, we did not investigate indicators for each of the four treatment combinations. Fifteen bee species were associated with either a restoration or land-use treatment (Table 2). There were 12 indicator species of thinned plots, two indicators of unthinned plots, one indicator of post-agricultural plots, and no indicators of remnant plots.

Effects on pollination

Compared to open plants, bagged sentinel plants produced 15% fewer fruits and 33% fewer seeds (Table 3b, Fig. 5), indicating that this was an effective species for assessing pollination. Plants placed in thinned plots produced 10% fewer mature fruits compared to unthinned plots regardless of bagging treatment (Table 3b, Fig. 5b). However, since no interaction terms were significant (Table 3a), neither fruit nor seed set was affected by land-use history or the restoration treatment when bagging was taken into consideration (Fig. 5).

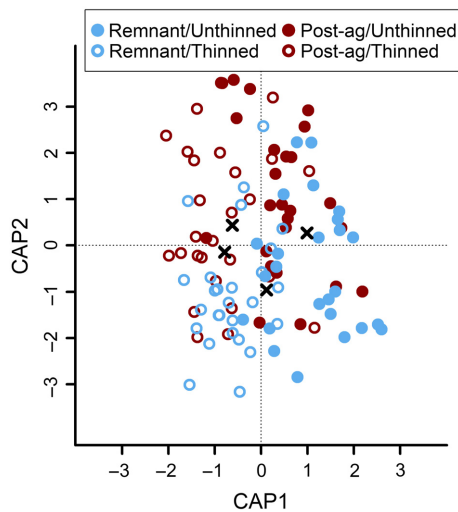


Fig. 4. Restoration thinning had a significant impact on bee community composition, while land-use history had a marginal impact. Constrained analysis of principal coordinates (CAP) ordination of abundance-based bee community data by land use and restoration treatment. Each point represents the community composition of one plot and $\times$'s represent the centroid of each land use/restoration treatment combination.

DISCUSSION

Understanding how land-use legacies affect ecosystems and whether restoration can mitigate legacy effects can facilitate biodiversity conservation at large scales. We investigated the effects of historical agricultural land use and restoration on pollinator communities and pollination within longleaf pine woodlands. Our results reveal that restoration thinning in this system increases bee abundance, richness, and diversity. Unlike for plant communities in our system (Brudvig et al. 2013, Turley and Brudvig 2016), we did not find evidence of an agricultural legacy on the bee community. Furthermore, though we expected that the increase in bee abundance, richness, and diversity in thinned plots would lead to increased pollination, we found no evidence for that in the sentinel plant experiment.

We found that bee communities responded to restoration thinning regardless of historical agricultural land use. This is consistent with findings in other systems where diverse communities of insect pollinators rapidly colonized areas

Table 2. Indicator bee species of (a) thinned, (b) unthinned, (c) post-agricultural, and (d) remnant plots.

Species	A	B	IV	P
a) Thinned				
<i>Lasioglossum apokense</i> (Robertson)	0.86	0.63	0.543	0.001
<i>Megachile mendica</i> Cresson	0.92	0.53	0.498	0.001
<i>Apis mellifera</i> L.	0.88	0.35	0.311	0.002
<i>Lasioglossum imitatum</i> (Smith)	0.86	0.31	0.272	0.012
<i>Megachile georgica</i> Cresson	0.82	0.30	0.242	0.005
<i>Lasioglossum nymphae</i> (Smith)	0.85	0.24	0.204	0.011
<i>Megachile petulans</i> Cresson	0.94	0.20	0.191	0.002
<i>Hoplitis truncata</i> (Cresson)	1.00	0.15	0.148	0.007
<i>Anthidiellum n. notatum</i> (Latreille)	0.93	0.15	0.138	0.026
<i>Megachile texana</i> Cresson	0.90	0.15	0.134	0.026
<i>Lasioglossum trigeminum</i> Gibbs	1.00	0.13	0.130	0.017
<i>Melissodes boltoniae</i> Robertson	1.00	0.11	0.111	0.023
b) Unthinned				
<i>Lasioglossum bruneri</i> (Crawford)	0.76	0.40	0.304	0.010
<i>Lasioglossum raleighense</i> (Mitchell)	0.93	0.16	0.149	0.014
c) Post-agricultural				
<i>Lasioglossum nymphae</i> (Smith)	0.89	0.25	0.222	0.003
d) Remnant				
NA				

Notes: A is the probability that a site belongs to the target site group given that a species is present. B is the probability of finding a species in the sites belonging to a site group. "IV" is the Indicator Value ($IV = A \times B$). Species included in the table are those with $P < 0.05$.

restored by clearing vegetation in the mid- or overstory vegetation (Fiedler 2010, Hanula and Horn 2011a, b, Taylor and Catling 2011, Williams 2011) and where bee richness, diversity, and abundance increase with overstory openness (Grundel et al. 2010, Hanula et al. 2016). Given that canopy openness may be a better predictor of bee responses to restoration than the richness of the flowering plant community, this may explain why we did not detect distinct bee communities in sites with differing land-use history and very distinct plant communities (Brudvig et al. 2013). This is an encouraging result for bee conservation because it suggests that bee communities recover more quickly from past agricultural land use than plants do. This could be because bees are less dispersal limited, which is one factor limiting spread of plants into post-agricultural areas (Turley et al. 2017). However, this pattern could also be caused by a shifting baseline where all bees sensitive to land-use

Table 3. The effects of agricultural land-use history, restoration, bagging, and their interactions on fruit and seed set of black mustard (sentinel) plants, within longleaf pine woodlands.

Variables	Effect size	df	F	P	r ²
a) Full models					
Fruit set (number of mature fruits)					
Land-use history	NA	1, 9	0.36	0.56	0.001
Restoration thinning	NA	1, 18	0.001	0.98	<0.001
Bagging treatment	NA	1, 354	2.96	0.09	0.005
Land use × restoration	NA	1, 18	0.18	0.67	<0.001
Land use × bagging	NA	1, 354	0.003	0.95	<0.001
Restoration × bagging	NA	1, 354	1.69	0.19	0.003
Land use × restoration × bagging	NA	1, 354	1.57	0.21	0.003
Seed set (developed seeds per fruit)†					
Land-use history	NA	1, 9	<0.001	1.00	<0.001
Restoration thinning	NA	1, 18	0.09	0.77	<0.001
Bagging treatment	NA	1, 354	10.70	0.001	0.018
Land use × restoration	NA	1, 18	0.12	0.74	<0.001
Land use × bagging	NA	1, 354	0.63	0.43	0.001
Restoration × bagging	NA	1, 354	0.16	0.69	<0.001
Land use × restoration × bagging	NA	1, 354	0.01	0.91	<0.001
b) Simplified models					
Fruit set (number of mature fruits)					
Land-use history	NA	1, 9	0.28	0.61	0.001
Restoration thinning	−10%	1, 19	5.81	0.03	0.012
Bagging treatment	−15%	1, 357	8.11	0.005	0.015
Seed set (developed seeds per fruit)†					
Land-use history	NA	1, 9	0.85	0.38	0.003
Restoration thinning	NA	1, 19	1.11	0.30	0.003
Bagging treatment	−33%	1, 357	24.21	<0.001	0.041

Note: Values which are significant at $\alpha < 0.05$ are bold, and percent effect size ((treatment−control)/control × 100%) is included for significant effects within the simplified models.

† Variable log transformed for analysis to satisfy assumptions of ANOVA. (a) Interaction effects are not significant in the full model, so (b) they were dropped from the analysis for the simplified models.

changes are absent from the broader landscape. Distinguishing between these alternative interpretations would require pre-agriculture natural history data that in this, and most systems, are not available.

Canopy thinning may have positively affected bee communities in our study through a number of mechanisms. Thinning increased floral abundance and plant richness in this system (Turley and Brudvig 2016), both of which can lead to increased pollinator abundance and richness (Blaauw and Isaacs 2014, Roberts et al. 2017). Thinning also increases light penetration to the understory, promoting warmer dry conditions favored by bees, which increase foraging activity and duration, as well as movement (Linsley 1958). Thinning may also affect nesting site availability in these sites by reducing litter to expose soil. A majority of bees nest in the ground

(Linsley 1958, Michener 2007) and, thus, ground nesting species in our system may have more access to nesting sites in thinned, compared to unthinned plots (Potts et al. 1997). However, the effect of thinning on nesting resources for above-ground nesting bees is less clear since they nest in a variety of materials including stems and cavities, some of which may have increased and others decreased by thinning.

We hypothesize that the land use by restoration interaction effect on floral cover was due to differences in pre-restoration conditions. In this longleaf pine system, unrestored plots have high canopy cover and thick litter and duff accumulation, which together limit flowering of understory plants (Turley et al. 2017). Thinning stimulates flowering by understory plants in both land-use types, but more so in remnant sites (Fig. 3). Because of the hardwood component of

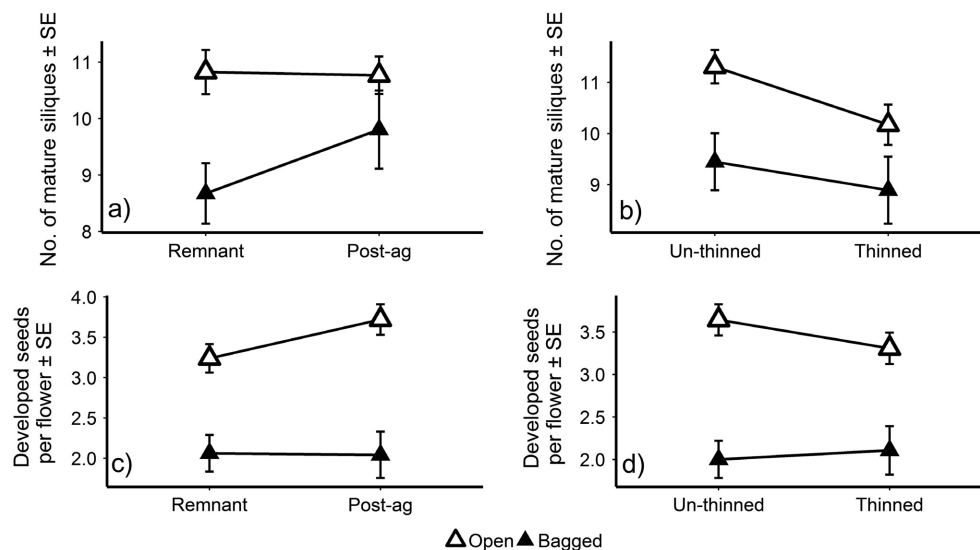


Fig. 5. No evidence that land-use history or restoration thinning affected plant reproductive output. The upper plots show fruit set (number of mature fruits) of bagged and unbagged black mustard plants by (a) land use and (b) thinning treatment. The lower plots show seed set (developed seeds per flower) of bagged and unbagged plants by (c) land use and (d) thinning treatment. Points show mean of 10 replicates $\pm$ standard error.

the unrestored remnant sites, these sites had a thick compact layer of duff (compared to the pine litter in the unrestored post-agricultural plots). That, in conjunction with higher canopy cover in unrestored remnants compared to post-agricultural sites (Brudvig et al. 2013), may explain the relatively larger increase in floral cover with thinning in remnants. Additionally, this effect might relate to compositional differences in the remnant and post-agricultural plant communities (see Turley et al. 2017), if remnant species increase more strongly in flowering following thinning, than do post-agricultural species. It appears, however, that this effect was not large enough to see a similar effect on the bee community or pollination rates.

Bee species associated with individual habitat treatments (indicator species) partially explain the differences in community composition. Thinning had a significant effect on bee community composition, and there were the most indicator species associated with that treatment (12 of thinned, 2 of unthinned; Table 2). Conversely, there was only a weak effect of land-use history on composition and we only found one post-agricultural indicator species (Table 2). The overall low number of indicator bee species suggests

that there is a cosmopolitan group of species that travel between different restoration and land-use treatments and that differences in composition are likely due to shifts in abundance and richness. We note that the indicator species that were associated with thinning were not characterized by a narrow set of functional traits. There were both below- and above-ground nesting bees, and they include species which have a range of foraging distances (Greenleaf et al. 2007, Zurbuchen et al. 2010). These results suggest that thinning does not strongly select for any particular group of bee, but the proximity of our sites may weaken our ability to detect effects of the treatments on this selection. More research is needed to reveal how land use and restoration interact to affect pollinator communities based on species' functional traits. The non-significant difference in composition based on land-use history and lack of indicators of remnant sites are also of note because this is in contrast with the different plant composition based on land use and the high number of plant indicators of remnant sites (Brudvig et al. 2013); again, this may be due to the differential movement capacities of bees and the dispersal-limited understory plant species in this system (Turley et al. 2017).

The results of our sentinel plant study suggest that pollination rates do not differ based on land-use history or canopy thinning in longleaf pine woodlands. Across systems, little is known about how restoration and historical land use affect pollination services and we know of no other comparable studies from longleaf pine or similar systems. Although we saw no treatment effects in this study, we recognize that more research is needed to discover whether access to pollinators is limiting reproduction of understory plants in longleaf pine woodlands.

Our findings are contrary to research that indicates that pollination services are largely determined by the abundance of common bees (Winfree et al. 2015). If this were the case in our sites, we would have expected to detect increased pollination rates in thinned sites, which had far greater bee abundance, compared to unthinned sites. It is possible that the few flowers which are present in the unthinned sites receive adequate pollination from the few pollinators present, and that the we included few enough flowers in our study that this pollination threshold was not met. Another possibility is that pollination rates differ by treatment, but our model system was insensitive to these differences owing to reasons such as the size or proximity of our study plots or visibility of the sentinel flowers to pollinators flying through unthinned plots. We also recognize that, while we only collected bees in this study, other groups of insects can serve as important pollinators (Rader et al. 2016) and these other groups may have also been strongly affected by our treatments. Importantly, more research will be necessary to understand how land-use history and restoration treatments affect pollination of the native understory plants, which comprise the majority of plant species in this system.

Finally, we note that the lower fruit set observed in thinned plots likely does not suggest that overall pollination was lower in these sites, since all of the measures of bee diversity were greater in these areas. The difference was comparable across bagged and open plants, suggesting that it was not connected to pollination. Rather, plant performance may have been affected by desiccation or other reasons in thinned plots, in spite of our attempts to keep plants adequately watered.

CONCLUSIONS

Through a large-scale experiment in a longleaf pine savanna system, we illustrate how restoration by canopy thinning can promote pollinators within woodlands impacted by varying historical conditions. Unlike plants, pollinators colonize newly restored sites regardless of the lasting agricultural legacies that affect many other aspects of the ecosystem. The presence of pollinators does not, however, ensure that all species are experiencing adequate pollination or that pollination function has been restored. More research is needed to reveal whether land-use legacies and restoration practices affect the delivery of pollination services to the diversity of plant species that are a common focus of conservation and restoration efforts.

ACKNOWLEDGMENTS

We thank John Blake, Lindsey Kemmerling, Joe Ledvina, Stephen McCann, John Orrock, Ed Olson, and Emma York for assistance with creating and maintaining this experiment and collecting data. This work was funded by the Department of Agriculture, Forest Service, Savannah River, under Interagency Agreement DE-EM0003622 with Department of Energy, Aiken, SC.

LITERATURE CITED

- Abrol, D. P. 2007. Rapeseed breeding honeybees and rapeseed: a pollinator–plant interaction. *Advances in Botanical Research* 45:337–367.
- Ascher, J. S., and J. Pickering. 2016. Discover life bees species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Draft-45. http://www.discovlife.org/mp/20q?guide=Apoidea_species
- Bellemare, J., G. Motzkin, D. R. Foster, and H. Forest. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *Journal of Biogeography* 29:1401–1420.
- Blaauw, B. R., and R. Isaacs. 2014. Larger patches of diverse floral resources increase insect pollinator density, diversity, and their pollination of native wildflowers. *Basic and Applied Ecology* 15:701–711.
- Bowen, M. E., C. A. McAlpine, A. P. N. House, and G. C. Smith. 2007. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biological Conservation* 140:273–296.

- Brudvig, L. A., E. Grman, C. W. Habeck, J. L. Orrock, and J. A. Ledvina. 2013. Strong legacy of agricultural land use on soils and understory plant communities in longleaf pine woodlands. *Forest Ecology and Management* 310:944–955.
- Cane, J. H., R. L. Minckley, and L. J. Kervin. 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan trapping. *Journal of the Kansas Entomological Society* 73:225–231.
- Chao, A. 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11:265–270.
- Coelho, B. W. T. 2004. A review of the bee genus *Augochlorella* (Hymenoptera: Halictidae: Augochlorini). *Systematic Entomology* 29:282–323.
- Conner, J. K., and R. Neumeier. 1995. Effects of black mustard population size on the taxonomic composition of pollinators. *Oecologia* 104:218–224.
- De Cáceres, M., and P. Legendre. 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574.
- de la Peña, E., L. Baeten, S. Hanne, N. Viaene, N. De Sutter, A. De Schrijver, and K. Verheyen. 2016. Beyond plant-soil feedbacks: mechanisms driving plant community shifts due to land-use legacies in post-agricultural forests. *Functional Ecology* 30:1073–1085.
- Droege, S. 2015. The Very Handy Manual: How to catch and identify bees and manage a collection. [https://www.pwrc.usgs.gov/nativebees/Handy Bee Manual/The Very Handy Manual - 2015.pdf](https://www.pwrc.usgs.gov/nativebees/Handy%20Bee%20Manual/The%20Very%20Handy%20Manual%20-%202015.pdf)
- Droege, S., V. J. Tepedino, G. LeBuhn, W. Link, R. L. Minckley, Q. Chen, and C. Conrad. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. *Insect Conservation and Diversity* 3:15–23.
- Dupouey, J. L., E. Dambrine, J. D. Laffite, and C. Moares. 2002. Irreversible impact of past land use on forest soils and biodiversity. *Ecology* 83:2978–2984.
- Ferguson, B. G., J. Vandermeer, H. Morales, and D. M. Griffith. 2003. Post-agricultural succession in El Petén, Guatemala. *Conservation Biology* 17:818–828.
- Fiedler, A. K. 2010. Restoration of prairie fen plants, insects, and abiotic processes. Dissertation. Michigan State University, East Lansing, Michigan, USA.
- Flinn, K. M., and P. L. Marks. 2007. Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications* 17:452–463.
- Flinn, K. M., and M. Vellend. 2005. Recovery of forest plant communities in post agricultural landscapes. *Frontiers in Ecology and the Environment* 3:243–250.
- Foley, J. A., et al. 2005. Global consequences of land use. *Science* 309:570–574.
- Forup, M. L., K. S. E. Henson, P. G. Craze, and J. Memmott. 2008. The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands. *Journal of Applied Ecology* 45:742–752.
- Foster, D. R., G. Motzkin, and B. Slater. 1998. Land-use history as long-term broad-scale disturbance: regional forest dynamics in Central New England. *Ecosystems* 1:96–119.
- Frost, C. C. 2006. History and future of the longleaf pine ecosystem. Pages 9–42 in S. Jose, E. J. Jokela, and D. L. Miller, editors. *The longleaf pine ecosystem: ecology, silviculture, and restoration*. Springer, New York, New York, USA.
- Geroff, R. K., J. Gibbs, and K. W. McCravy. 2014. Assessing bee (Hymenoptera: Apoidea) diversity of an Illinois restored tallgrass prairie: methodology and conservation considerations. *Journal of Insect Conservation* 18:951–964.
- Gibbs, J. 2011. Revision of the metallic *Lasioglossum* (*Dialictus*) of eastern North America (Hymenoptera: Halictidae: Halictini). *Zootaxa* 3073:1–216.
- Gibbs, J., L. Packer, S. Dumes, and B. N. Danforth. 2013. Revision and reclassification of *Lasioglossum* (*Evyllaesus*), *L.* (*Hemihalictus*) and *L.* (*Sphecodogastra*) in eastern North America (Hymenoptera: Apoidea: Halictidae). *Zootaxa* 3672:1–117.
- Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153:589–596.
- Griffin, S. R., B. Bruninga-Socolar, M. A. Kerr, J. Gibbs, and R. Winfree. 2017. Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. *Restoration Ecology* 25:650–660.
- Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications* 20:1678–1692.
- Hahn, P. G., and J. L. Orrock. 2015. Spatial arrangement of canopy structure and land-use history alter the effect that herbivores have on plant growth. *Ecosphere* 6:1–16.
- Hanula, J. L., and S. Horn. 2011a. Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. *Forest Ecology and Management* 262:674–680.
- Hanula, J. L., and S. Horn. 2011b. Removing an invasive shrub (Chinese privet) increases native bee diversity and abundance in riparian forests of the southeastern United States. *Insect Conservation and Diversity* 4:275–283.
- Hanula, J. L., M. D. Ulyshen, and S. Horn. 2016. Conserving pollinators in North American forests: a review. *Natural Areas Journal* 36:427–439.

- Holzschuh, A., I. Steffan-Dewenter, and T. Tscharnkte. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117:354–361.
- Jaeger, B. 2017. *r2glmm: computes R squared for mixed (multilevel) models*. R package version 0.1.2. <https://github.com/bcjaeger/r2glmm>
- Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* 29:83–112.
- Kennedy, C. M., et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters* 16:584–599.
- Kilgo, J. C., and J. I. Blake. 2005. Ecology and management of a forested landscape: fifty years on the Savannah River Site. Island Press, Washington, D.C., USA.
- Kirkman, L. K., R. F. Lide, G. Wein, and R. R. Sharitz. 1996. Vegetation changes and land-use legacies of depression wetlands of the western coastal plain of South Carolina: 1951–1992. *Wetlands* 16:564–576.
- Kuhman, T. R., S. M. Pearson, and M. G. Turner. 2011. Agricultural land-use history increases non-native plant invasion in a southern Appalachian forest a century after abandonment. *Canadian Journal of Forest Research* 41:920–929.
- LaBerge, W. E. 1971. A revision of the bees of the genus *Andrena* of the Western Hemisphere. Part IV. *Scapteropsis*, *Xiphandrena* and *Rhaphandrena*. *American Entomological Society* 97:441–520.
- Leong, J. M., and R. W. Thorp. 1999. Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. *Ecological Entomology* 24:329–335.
- Liiri, M., M. Häsä, J. Haimi, and H. Setälä. 2012. History of land-use intensity can modify the relationship between functional complexity of the soil fauna and soil ecosystem services: a microcosm study. *Applied Soil Ecology* 55:53–61.
- Linsley, E. G. 1958. The ecology of solitary bees. *Hilgardia* 27:543–599.
- Michener, C. D. 2007. *The bees of the world*. Second edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.
- Mitchell, T. B. 1960. *Bees of the Eastern United States: volume I*. N. C. Agricultural Experimental Station Technical Bulletin 141:1–538.
- Mitchell, T. B. 1962. *Bees of the Eastern United States: volume II*. N. C. Agricultural Experimental Station Technical Bulletin 152:1–557.
- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Newbold, T., et al. 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520:45–50.
- Noss, R. F., W. J. Platt, B. A. Sorrie, A. S. Weakley, D. B. Means, J. Costanza, and R. K. Peet. 2015. How global biodiversity hotspots may go unrecognized: lessons from the North American coastal plain. *Diversity and Distributions* 21:236–244.
- Oksanen, J., et al. 2017. *vegan: community ecology package*. R package version 2.5. <https://cran.r-project.org>, <https://github.com/vegandevs/vegan>
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- Peet, R. K. 2006. Ecological classification of longleaf pine woodlands. Pages 51–94 in S. Jose, E. J. Jokela, and D. L. Miller, editors. *The longleaf pine ecosystem: ecology, silviculture, and restoration*. Springer, New York, New York, USA.
- Perring, M. P., P. De Frenne, L. Baeten, S. L. Maes, L. Depauw, H. Blondeel, M. M. Caron, and K. Verheyen. 2016. Global environmental change effects on ecosystems: the importance of land-use legacies. *Global Change Biology* 22:1361–1371.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2016. *nlme: linear and nonlinear mixed effects models*. R package version 3.1. <https://CRAN.R-project.org/package=nlme>
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25:345–353.
- Potts, S. G., P. Willmer, and E. Biology. 1997. Abiotic and biotic factors influencing nest-site selection by *Halictus rubicundus*, a ground-nesting halictine bee. *Ecological Entomology* 22:319–328.
- R Development Core Team. 2016. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Rader, R., et al. 2016. Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy of Sciences of the United States of America* 113:146–151.
- Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in global land cover: croplands from 1700 to 1992. *Global Biogeochemical Cycles* 13:997–1027.
- Rehan, S. M., and C. S. Sheffield. 2011. Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. *Zootaxa* 50:35–50.
- Ribble, D. W. 1967. The monotypic North American subgenus *Larandrena* of *Andrena* (Hymenoptera: Apoidea). *Bulletin of the University of Nebraska State Museum* 6:27–42.

- Roberts, H. P., D. I. King, and J. Milam. 2017. Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management* 394:111–122.
- Stephen, W. P. 1954. A revision of the bee genus *Colletes* in America North of Mexico. University of Kansas Science Bulletin 36:149–527.
- Stuhler, J. D., and J. L. Orrock. 2016. Historical land use and present-day canopy thinning differentially affect the distribution and abundance of invasive and native ant species. *Biological Invasions* 18: 1813–1825.
- Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19:46–53.
- Taylor, A. N., and P. M. Catling. 2011. Bees and butterflies in burned and unburned alvar woodland: evidence for the importance of postfire succession to insect pollinator diversity in an imperiled ecosystem. *Canadian Field-Naturalist* 125:297–306.
- Tilman, D. 1999. Global environmental impacts of agricultural expansion: the need for sustainable and efficient practices. *Proceedings of the National Academy of Sciences of the United States of America* 96:5995–6000.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity: ecosystem service management. *Ecology Letters* 8:857–874.
- Tuell, J. K., and R. Isaacs. 2009. Elevated pan traps to monitor bees in flowering crop canopies. *Entomologia Experimentalis et Applicata* 131:93–98.
- Tuell, J. K., and R. Isaacs. 2010. Weather during bloom affects pollination and yield of highbush blueberry. *Journal of Economic Entomology* 103: 557–562.
- Turley, N. E., and L. A. Brudvig. 2016. Agricultural land-use history causes persistent loss of plant phylogenetic diversity. *Ecology* 97:2240–2247.
- Turley, N. E., J. L. Orrock, J. A. Ledvina, and L. A. Brudvig. 2017. Dispersal and establishment limitation slows plant community recovery in post-agricultural longleaf pine savannas. *Journal of Applied Ecology* 54:1100–1109.
- Van Lear, D. H., W. D. Carroll, P. R. Kapeluck, and R. Johnson. 2005. History and restoration of the longleaf pine-grassland ecosystem: implications for species at risk. *Forest Ecology and Management* 211:150–165.
- Walker, J. L., and A. M. Silletti. 2006. Restoring the ground layer of longleaf pine ecosystems. Pages 297–325 in S. Jose, E. J. Jokela, and D. L. Miller, editors. *The longleaf pine ecosystem: ecology, silviculture, and restoration*. Springer, New York, New York, USA.
- Williams, N. M. 2011. Restoration of nontarget species: bee communities and pollination function in riparian forests. *Restoration Ecology* 19:450–459.
- Williams, P. H., R. W. Thorp, L. L. Richardson, and S. R. Colla. 2014. *Bumble bees of North America: an identification guide*. Princeton University Press, Princeton, New Jersey, USA.
- Willmer, P. G., H. Cunnold, and G. Ballantyne. 2017. Insights from measuring pollen deposition: quantifying the pre-eminence of bees as flower visitors and effective pollinators. *Arthropod-Plant Interactions* 11:1–15.
- Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* 18:626–635.
- Yesilonis, I., K. Szlavecz, R. Pouyat, D. Whigham, and L. Xia. 2016. Historical land use and stand age effects on forest soil properties in the Mid-Atlantic US. *Forest Ecology and Management* 370:83–92.
- Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging ranges in solitary bees: Only few individuals have the capability to cover long foraging distances. *Biological Conservation* 143:669–676.

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