Forest Ecology and Management 348 (2015) 142–152

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Have changing forests conditions contributed to pollinator decline in the southeastern United States?

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ARTICLE INFO

Article history:
Received 11 December 2014
Received in revised form 27 March 2015
Accepted 31 March 2015
Available online 20 April 2015

Keywords:
Apoidea
Pollinator decline
Forest cover
Native bees
Solitary bees
Forest health

ABSTRACT

Two conservation goals of the early 20th century, extensive reforestation and reduced wildfire through fire exclusion, may have contributed to declining pollinator abundance as forests became denser and shrub covered. To examine how forest structure affects bees we selected 5 stands in each of 7 forest types including: cleared forest; dense young pines; thinned young pines; mature open pine with extensive shrub/sapling cover; mature open pine with extensive herbaceous plant cover and little shrub cover; mature upland hardwood forest; and mature riparian hardwood forest. We sampled bees during the 2008 growing season using pan traps and measured overstory tree density, understory herbaceous plant and shrub diversity and cover, light penetration, and leaf area index. Numbers of bees and numbers of species per plot were highest in cleared forest and in mature pine stands with an herbaceous plant understory. Estimates of asymptotic species richness were highest in mature riparian hardwood forests, cleared forests and open pine forests with an herbaceous plant understory. Bee communities in the cleared forests and in the mature pine with an herbaceous plant understory were grouped together in ordination space which was consistent with perMANOVA results. The best predictor variable for bee species density was total tree basal area which was negatively correlated ($r^2 = 0.58$), while the best model for predicting bee abundance ($r^2 = 0.62$) included canopy openness, plant species density (both positively correlated) and shrub cover (negatively correlated). Our results combined with many others show that thinning forests combined with shrub control provides good bee habitat, is compatible with habitat restoration and management for other species, and the resulting forests will be healthier and less susceptible to old (e.g., southern pine beetle, *Dendroctonus frontalis*) and new (European woodwasp, *Sirex noctilio*) threats.

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1. Introduction

Pollinators are critical components of forest ecosystems where they provide pollination services to many trees, shrubs and herbaceous understory plants. Evidence suggests that pollinators are declining worldwide (e.g., Buchmann and Nabhan, 1996; Kearns et al., 1998; Kremen and Ricketts, 2000; Biesmeijer et al., 2006; National Research Council, 2007; Williams and Osborne, 2009; Potts et al., 2010; Cameron et al., 2011; Bartomeus et al., 2013; Burkle et al., 2013) as a result of changes in land use, fragmentation, agricultural intensification, pesticide use, invasive species, diseases, urbanization, and climate change (Kremen et al., 2002; Steffen-Dewenter et al., 2002; Winfree, 2010; Burkle et al., 2013). How long-term shifts in forest structure may have contributed to pollinator declines has not been considered.

In the past 100 years forests of southeastern North America have undergone dramatic changes. These forests were extensively cleared by logging and experienced repeated wildfires in the late 19th and early 20th century (Ahren, 1929, 1933). Reforestation and wildfire prevention through fire exclusion were conservation priorities implemented in response to perceived forest threats and decline (Lilliard, 1947; Clark, 1984; Williams, 1989; Stanturf et al., 2002; Barnett, 2014).

Despite undergoing extensive alterations in the past century, the amount of land designated as forest has changed little during that period (Conner and Hartsell, 2002; Smith et al., 2009) while forest cover and tree density have increased steadily since the 1930s. Though Wakeley (1930) suggested it would take centuries to replant the forests, the Civilian Conservation Corp planted billions of trees from 1930 to 1942, direct seeding was developed and extensively used (Barnett, 2014), and planting was mechanized resulting in the majority of the land being reforested by the early 1970s. Although the amount of land designated as forest has changed little, forest structure has. Most now have closed

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http://dx.doi.org/10.1016/j.foreco.2015.03.044
0378-1127/Published by Elsevier B.V.

canopies with dense shrub layers beneath, conditions much different from presettlement forests that were composed of a mosaic of open pine and hardwood forests, prairies, and woodland savannas (Carroll et al., 2002). What effect this gradual shift from deforested or lower density forests to dense, closed canopy forests has had on pollinators is unknown but recent studies indicate that forest openings, and forests with open canopies and reduced shrub cover favor pollinators (e.g., Fye, 1972; Rudolph and Ely, 2000; Rudolph et al., 2006a,b; Campbell et al., 2007a,b; Romey et al., 2007; Grundel et al., 2010; Taki et al., 2010; Hanula and Horn, 2011a,b; Schweitzer et al., 2011; Proctor et al., 2012; Hudson et al., 2013).

In this study we examine the relative abundance and diversity of bees to determine how common, present day forest conditions affect them. Bee abundance and community composition were measured in seven forest stand conditions ranging from complete overstory tree removal to mature pine forests with a complex herbaceous plant layer. We measured tree, shrub and herbaceous plant community characteristics, and the amount of light reaching the forest floor in each stand, and used that data to help explain the differences observed in pollinator communities. We discuss our results in the context of past and present land use and how they might be used to improve conservation of pollinators in concert with other forest management goals.

2. Methods and materials

2.1. Study site

The study area was in the southern portion of the Oconee National Forest in the Piedmont of Georgia (Fig. 1). The Oconee National Forest was formed in 1959 out of 38,851 ha of federal land in middle Georgia. Prior to becoming national forest the lands were degraded by extensive cotton farming (http://www.n-georgia.com/forests-history.htm) and almost totally deforested. The forest is typical of the region having been primarily cutover land or abandoned fields when it was formed in 1959. The first 20 years of the forest's existence was characterized by extensive reforestation using primarily loblolly (*Pinus taeda*) and shortleaf pine (*Pinus echinata*). Although typical of the region, the forest differs in that rotation ages are longer and, in the southern portion of the forest, a significant focus of management is to create habitat for the red-cockaded woodpecker, *Picoides borealis*, an endangered species that requires open, mature pine forests with little or no shrub cover or midstory trees (U.S. Fish and Wildlife Service, 2003; Costa and Daniels, 2004). The latter are thought to be structurally similar to those resulting from Native American manipulation of the forests and indicative of the historical pine forests of the region albeit much younger (Carroll et al., 2002). The forest is now predominately loblolly and shortleaf pine ranging in age from newly established to 40–60 year old stands.

During the summer of 2007 the forest experienced an extensive outbreak of southern pine beetle, *Dendroctonus frontalis*, which killed numerous small patches of pine forest. Much of the timber from these areas was salvaged within a short time after death. In 2008, when we conducted our study, these areas represented pine forest with the overstory canopy removed but no site preparation or replanting had occurred. The clearings were 5–10 ha in size. We selected five stands in each of seven forest types (Fig. 2) which included the cleared forest mentioned above plus dense young pines; thinned young pines; mature open pine with extensive sweetgum (*Liquidambar styraciflua* L.) and water oak (*Quercus nigra* L.) saplings; mature open pine with little shrub cover and an herbaceous plant cover composed of vines, tree seedlings, and grass; mature upland hardwood forest consisting primarily of oak and hickory; and mature riparian or bottomland hardwood forest. Except for the cleared forest, stands were >14 ha in size and selected to be as homogenous as possible within forest types. Table 1 provides average stand conditions for the seven forest types.

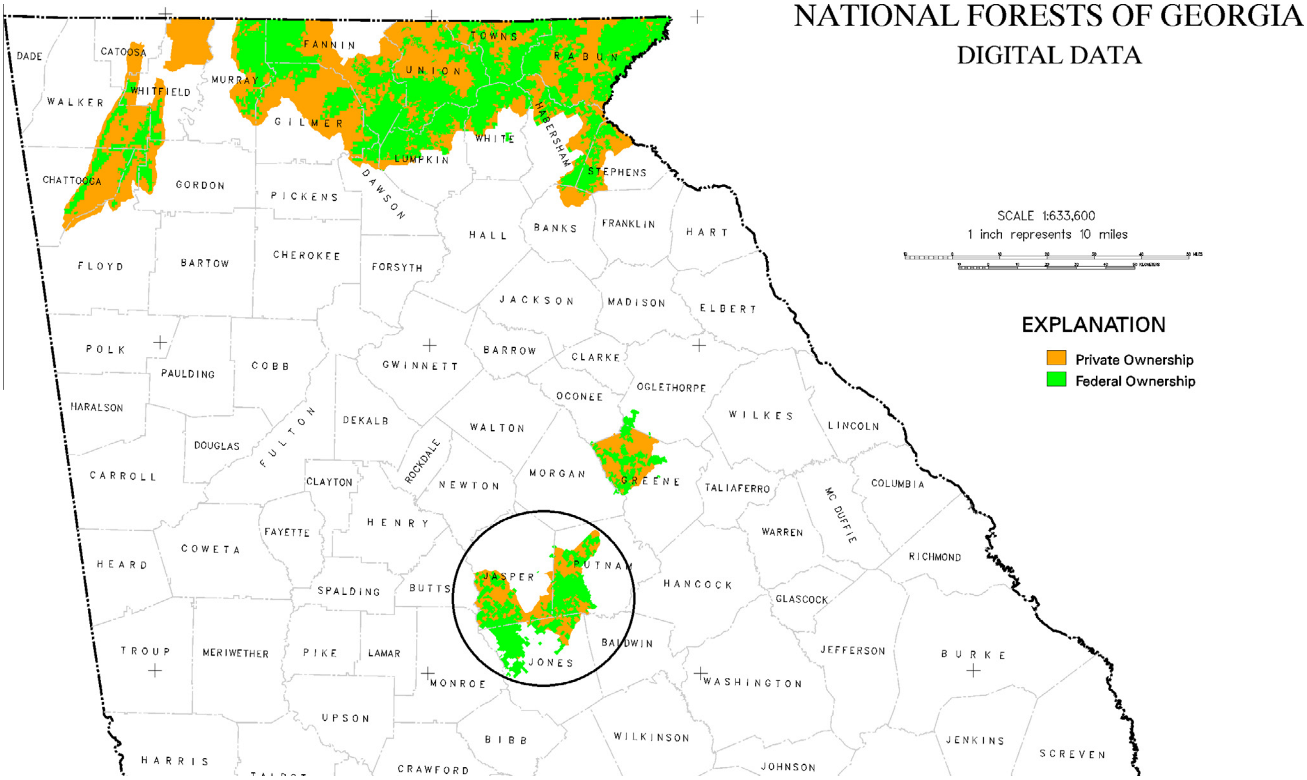

Fig. 1. Location of the southern portion of the Oconee National Forest (circled) in the state of Georgia where the study was conducted (courtesy of the U.S. Geological Survey).

Fig. 2. Examples of forest conditions sampled for pollinators: (A) dense young pine; (B) thinned young pine; (C) mature pine with shrub understory; (D) mature pine with herbaceous understory; (E) mature upland hardwood; (F) mature riparian hardwood; and (G) cleared forest. See Table 1 for average stand measurements.

Table 1
Mean stand attributes (±SE) for forest stands where pollinator abundance and diversity were sampled on the Oconee National Forest, Georgia. Forest conditions are arranged from lowest to highest total tree basal area.

Forest condition	*N*	% Shrub cover	Openness	Leaf area index	% Herb cover	Herb richness	Total basal area (m^2/ha)	Pine basal area (m^2/ha)	Trees >10 cm DBH/ha	DBH (cm)
Cleared forest	5	0.7 ± 0.57	59.3 ± 5.24	0.4 ± 0.11	46.7 ± 3.25	19.2 ± 2.13	3.2 ± 1.19	0.01 ± 0.014	126.0 ± 35.41	14.7 ± 0.54
Mature pine herbaceous	5	7.4 ± 3.70	31.6 ± 4.94	1.1 ± 0.20	79.6 ± 11.10	24 ± 2.57	14.2 ± 1.86	11.8 ± 1.27	170.5 ± 26.69	29.4 ± 1.01
Mature pine shrub	5	25.5 ± 6.82	15.2 ± 1.89	2.1 ± 0.17	87.0 ± 5.96	22.6 ± 2.73	21.7 ± 2.09	15.1 ± 1.10	324.9 ± 27.67	23.7 ± 0.76
Upland hardwood	5	5.3 ± 3.90	12.1 ± 1.01	2.3 ± 0.13	49.1 ± 10.59	14.2 ± 2.89	23.1 ± 2.02	2.1 ± 0.90	348.4 ± 32.84	24.1 ± 0.79
Riparian hardwood	5	15.0 ± 6.45	9.1 ± 0.471	2.6 ± 0.05	72.5 ± 10.96	16.8 ± 1.66	24.6 ± 1.25	1.9 ± 1.31	345.9 ± 21.31	23.6 ± 0.86
Thinned young pine	5	2.5 ± 1.49	14.4 ± 1.41	2.3 ± 0.14	65.4 ± 5.44	19 ± 4.24	26.8 ± 3.0	23.8 ± 3.59	758.6 ± 94.87	19.1 ± 0.27
Dense young pine	5	10.3 ± 6.58	11.1 ± 0.58	2.6 ± 0.09	46.0 ± 4.90	12.8 ± 2.31	30.7 ± 2.54	27.5 ± 2.44	1123.1 ± 88.78	15.2 ± 0.18

2.2. Pollinator sampling

Bees are the most efficient pollinators so we focused on that group. Bees were sampled using pan traps, the most effective way to sample variable forest habitats for direct comparison (Campbell and Hanula, 2007; Westphal et al., 2008; Droege, 2013). Pan traps consisted of blue, white, and yellow Solo® bowls, filled with water containing a small amount of odorless detergent to reduce surface tension, and supported on a wire holder approximately 0.3 m above ground (Campbell and Hanula, 2007). Three traps (one of each color) were placed 5 m apart near the center of each stand and at locations 50 m from the center in each cardinal direction for a total of 5 trapping locations (15 traps) within each stand. Traps were operated four times in 2008 (7–11 April, 12–16 May, 14–18 July and 15–19 September) by placing them in the stands on Monday of each trapping period, revisiting them on Wednesday to refill them if needed, and samples were collected on Friday.

Samples were stored in 70% ethyl alcohol until they could be sorted, processed to facilitate identification (Droege, 2012), pinned, and identified using appropriate keys (Mitchell, 1960, 1962; Gibbs, 2011) and reference collections (Florida State Collection of Arthropods, Gainesville, FL and the Georgia Museum of Natural History, Athens, GA). Specimens of the genus *Lasioglossum* were sent to Jason Gibbs (York University currently Michigan State University) for identification.

2.3. Measuring stand and habitat characteristics

The understory herbaceous plant community and shrub layer was surveyed on all plots in mid-August 2008 using the line-point intercept method (Godínez-Alvarez et al., 2009). Plant and shrub community characteristics were measured along four 30-m long transects radiating from the center of the stand toward the bee trapping locations in each cardinal direction. Sample points were established at 0.6 m intervals so that we sampled 50 points along each transect (200 points per plot). At each point we recorded all herbaceous plant species in contact with the point and all shrub species over the point.

Tree composition and density were also measured in August 2008 on four 0.4 ha subplots at the four bee trapping locations 50 m from the center of the stand in each cardinal direction. At each of the four subplots we identified all trees greater than 10 cm diameter and measured their diameter at 1.5 m height (DBH). Stand basal area, a measure of the amount of the forest area occupied by the cross-sectional area of the tree stems, was calculated from the diameters.

In September 2008 we used a Canon EOS Rebel XTi with a fish-eye lens adaptor mounted on a self-leveling tripod to position the camera 0.5 m above ground and pointing directly up. A photograph was taken at each of the 5 pollinator sampling locations in each stand and average canopy openness and leaf area index was calculated for the stand. Photos were analyzed using WinSCANOPY Version 2006 (Regent Instruments Inc. Quebec City, CA) to determine the percent openness of the canopy, i.e., the amount sky unobstructed by vegetation. The estimate of openness provided by WinSCANOPY takes into account the relative spherical area occupied in elevation rings. Before calculating openness, each photo was adjusted to allow for the greatest contrast between the canopy and the sky. Canopy openness derived from hemispherical photographs provides an accurate and unbiased estimate of within growing-season light availability in pine-woodland systems (Battaglia et al., 2003).

2.4. Statistical analyses

Numbers of bees and number of species captured per plot were analyzed using one-way analysis of variance (PROC GLM; SAS, 2000). We used the Shapiro/Wilk test in PROC UNIVARIATE to test whether the data were normally distributed and the homogeneity of variance (HOV) test in PROC GLM to test residuals. Species data were normally distributed and variance was homogenous but bee abundance data were not. The square root transformation ($\sqrt{x} + 0.5$) corrected the problem so abundance data were transformed prior to analyses. Following analysis of variance, means were separated using the least significant difference (LSD) multiple comparison test.

Sample-based rarefaction curves were calculated using EstimateS 9.1 (Cowell, 2013) for each forest type after summing species captures per plot. Sample-based rarefaction provides estimates of species density, which was our primary interest, but we also rescaled the axis using number of individuals, as recommended by Gotelli and Colwell (2001), to estimate species richness in each forest type. We used the method of MacGregor-Fors and Payton (2013) to calculate 84% confidence intervals for rarefaction curves. Lack of overlap of 84% confidence intervals is equivalent to an α level of 0.05 used in most statistical tests (MacGregor-Fors and Payton, 2013). We also utilized EstimateS to calculate the Chao 2 estimates of overall species richness in each forest type and their 95% confidence intervals. In addition, we used both rarefaction and Chao 2 to estimate the total species richness for the landscape in which we sampled.

Non-metric multidimensional scaling (NMS) ordination analysis of bee abundance in plots was used to examine community differences (PC-ORD; McCune and Mefford, 1999) using the Sorensen (Bray-Curtis) distance measure. The number of axes was set at a maximum of 6 and the number of iterations at 500. Joint plots were used to examine relationships between forest attributes and the bee community ordination scores. Forest attributes included in the analysis were shrub cover, canopy openness, leaf area index, herbaceous plant cover and richness, plant diversity (H′), plot basal area, pine basal area, and tree density. An R^2 of 0.3 was used as the cut-off for vector scaling of joint plots.

Ordination provides a method of visualizing community relatedness among habitats but Anderson (2001) suggests permutation-based nonparametric MANOVA (NPMANOVA) as a method of statistically comparing groupings. We used the NPMANOVA option in PC-ORD to conduct a one-way analysis of differences in bee community composition with forest type as the independent variable and the Sorensen (Bray-Curtis) distance measure. Pairwise comparisons *t*-tests ($\alpha = 0.5$) were used to test the null hypothesis of no difference in bee communities among forest types.

Indicator species analysis based on the method of Dufrêne and Legendre (1997) was utilized to determine which species were indicative or most closely associated with different forest types. The analysis was conducted utilizing PC-ORD software with 5000 permutations.

We were interested in determining which habitat characteristics were associated with higher numbers of bees and greater species densities. We analyzed as dependent variables the number of species caught per plot and the number of bees caught per plot separately utilizing the regression procedure PROC REG in the SAS statistical package (Version 9.3). In the initial analysis we used the variance inflation factor ($\mathrm{VIF} = 1/1 - R_j^2$) to assess whether any independent variables were correlated. A VIF > 10 indicates a high level of correlation, and leaf area index and canopy openness exceeded this limit. Since leaf area index had the highest VIF, and it was estimated from measurements of canopy openness, we removed it and ran the analysis again. This second analysis indicated that no remaining variables exceeded the VIF limit. We then used the forward selection method with a 0.05 significance level for entry into the model. The forward-selection technique calculates *F*-statistics that show how much the variable contributes to the model if it is included. The variable that has the largest *F*-statistic is added to the model first. The *F*-statistics are recalculated for the remaining variables and then the variable with the next highest *F*-statistic is added and the process is continued until no more variables meet the significance level for entry. Variables considered for entry in the model included total basal area, canopy openness, shrub cover, herbaceous plant cover and plant species density.

3. Results

We captured 3848 bees in 128 species. *Augochlorella striata*, *Bombus impatiens*, *Lasioglossum (Dialictus) hitchensi*, *L. (D.) bruneri*, *L. (D.) illinoense*, *L. (D.) imitatum*, *L. (D.) raleighensis*, and *L. (D.) tegulare* were the most common species. Twelve species were indicators of various forest types. The species with the greatest indicator value (IV) were *Melissodes agilis* ($P = 0.001$, IV = 69) and *Ceratina cockerelli* ($P = 0.01$, IV = 60), both indicators of recently cleared pine forest, as were *B. impatiens* ($P = 0.009$, IV = 31), *L. (D.) apopkensis* ($P = 0.008$, IV = 52.3), *L. (D.) coeruleus* ($P = 0.01$, IV = 43), *L. (D.) illinoense* ($P = 0.004$, IV = 55.7), and *L. (D.) tegulare* ($P = 0.0006$, IV = 56). *Andrena personata* ($P = 0.01$, IV = 60) was the only indicator species for mature riparian hardwood forests. *Ceratina calcarata* ($P = 0.05$, IV = 38) was an indicator of open pine forest with a heavy shrub cover, and *L. (D.) hitchensi* ($P = 0.008$, IV = 48) and *L. (D.) raleighensis* ($P = 0.008$, IV = 46) were indicators of mature open pine forest with an herbaceous understory and no shrub cover.

Numbers of bees and number of bee species were highest in cleared forests and in mature pine forests with an herbaceous plant understory (Fig. 3). Other stand types had lower bee abundance and did not differ from one another. Numbers of species were lowest in dense young pine stands which were not significantly different from riparian hardwood forests.

Sample-based rarefaction curves showed similar trends (Fig. 4), i.e., cleared forest and open pine with an herbaceous understory had higher estimated species densities than the other forest types, and dense young pine had the lowest. When the *x*-axis was rescaled to number of individuals to explore rarified species richness, richness appeared to be higher in riparian hardwood forests. Likewise, riparian hardwood forests, cleared forest and mature pine forests with an herbaceous understory had the highest asymptotic species richness estimates (Fig. 5).

Utilizing all 35 sample sites in sample-base rarefaction resulted in a richness estimate of 132 species (119–145; 95% CI) for the entire study area, almost the same number of species captured during the study. The Chao 2 estimate of asymptotic species richness for the study area was 197 species (162–255; 95% CI).

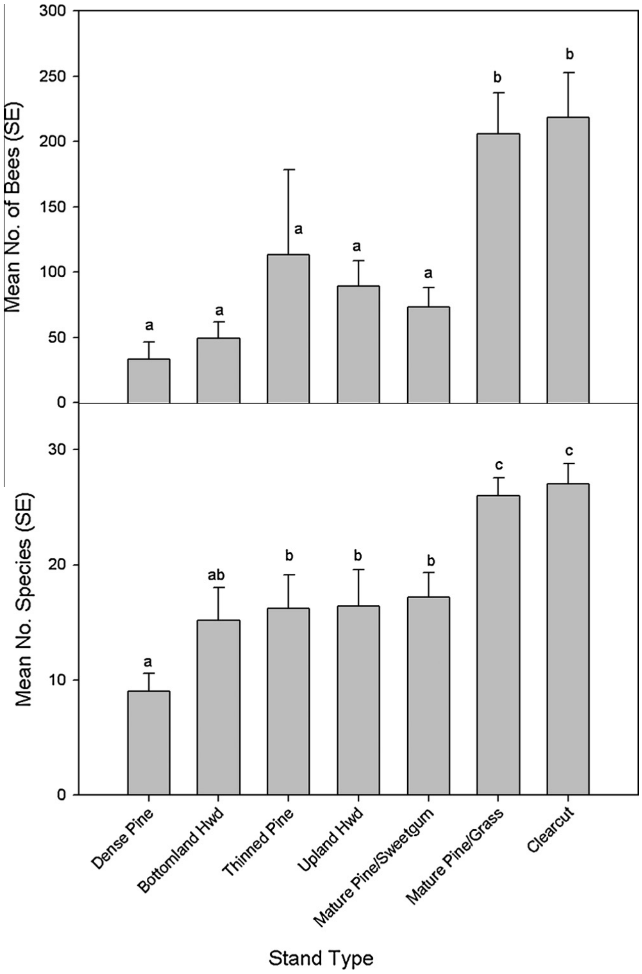

Fig. 3. Mean number of bees and number of species captured in pan traps operated in seven forest conditions on the Oconee National Forest, Georgia. Error bars are standard errors.

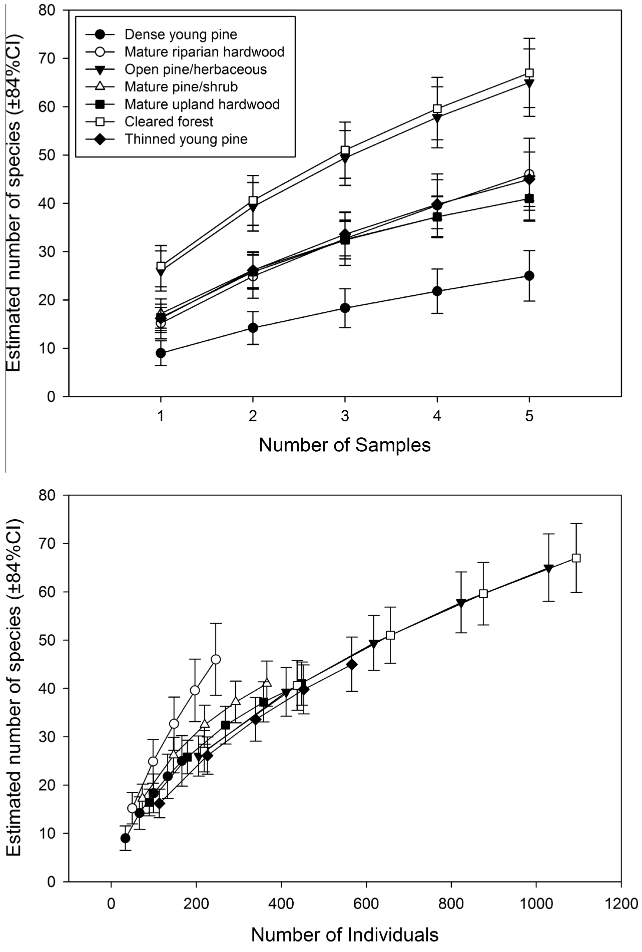

Fig. 4. Sample-based (top) and individual based (bottom) rarefaction curves with 84% confidence intervals (CI) of bees captured in seven forest conditions on the Oconee National Forest, Georgia.

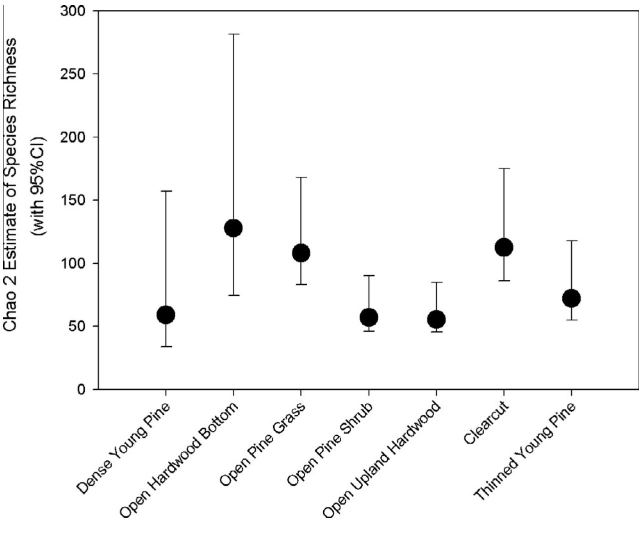

Fig. 5. Chao 2 estimates (±95% CI) of the asymptotic species richness of seven forest conditions in the Oconee National Forest, Georgia.

Bee communities in cleared forest plots differed from communities associated with all other forest stand conditions

Table 2
P-values from a permutation-based nonparametric MANOVA (Anderson, 2001) utilizing the Sorenson (Bray-Curtis) distance measure to evaluate differences in bee communities in seven forest types on the Oconee National Forest, Georgia.

	Dense young pine	Thinned young pine	Mature pine herbaceous	Mature pine shrub	Upland hardwood	Riparian hardwood
Dense young pine						
Thinned young pine	0.17					
Mature pine herbaceous	0.009[a]	0.051				
Mature pine shrub	0.066	0.607	0.01[a]			
Upland hardwood	0.056	0.059	0.007[a]	0.41		
Riparian hardwood	0.025[a]	0.030[a]	0.008[a]	0.063	0.052	
Cleared forest	0.008[a]	0.017[a]	0.33	0.007[a]	0.006[a]	0.009[a]

[a] Denotes forest types in which the bee communities were significantly different from each other $\alpha = 0.05$. Analysis performed using PC-ORD software.

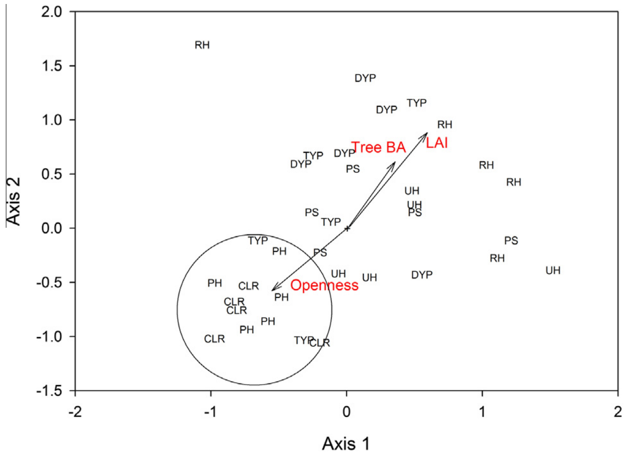

Fig. 6. Non-metric multidimensional ordination of bee communities in seven forest conditions on the Oconee National Forest, Georgia, with joint plots of leaf area index (LAI), tree basal area (BA) and openness that were correlated with axis one or two. Abbreviations are: dense young pine (DYP), cleared forest (CLR), thinned young pine (TYP), mature pine with a shrub understory (PS), mature pine with herbaceous understory (PH), mature upland hardwood (UH), and mature riparian hardwood (RH).

except the mature open pine with an herbaceous understory (Table 2). Likewise, bee communities in the open pine forest with an herbaceous understory differed in composition from those in all other forest stand conditions studied except the cleared forest and thinned young pine. In addition to differing from the cleared forest and mature pine with an herbaceous understory, bee communities of riparian hardwood forests also differed from dense young pine and thinned young pine, but not the mature pine with a shrub understory or the upland hardwood forests.

Non-metric multidimensional scaling recommended a two-dimensional solution with each axis explaining approximately the same variation in the bee data (final stress = 13.8; axis 1, $r^2 = 0.39$; axis 2, $r^2 = 0.43$; cumulative $r^2 = 0.82$). The NMS showed that bee communities in the cleared forests and in the mature pine with an herbaceous understory were grouped together (Fig. 6) which was consistent with NPMANOVA results (Table 2). Included in this grouping were two thinned young pine stands, also consistent with the NPMANOVA results which showed that thinned young pine forests did not differ in bee community composition from open pine forest with an herbaceous understory. Joint plot analysis indicated that forest openness (axis 1, $r^2 = 0.35$; axis 2, $r^2 = 0.41$) was the only factor associated with bee communities in this grouping while leaf area index (axis 1, $r^2 = 0.41$; axis 2, $r^2 = 0.55$) and tree basal area (axis 1, $r^2 = 0.27$; axis 2, $r^2 = 0.38$) were vectors associated with the axes in the opposite direction.

The best model for predicting bee abundance ($F_{3,\ 33} = 17.14$, $P < 0.0001$; $r^2 = 0.62$) included canopy openness (O), herbaceous plant species density (SD) and shrub cover (SC), expressed as: Square root no. of bees = 3.65 + 0.12(O) + 0.23(SD) – 0.01(SC). Canopy openness was included in the model first and it explained 47% of the variance. The addition of plant species density and shrub cover explained an additional 9% and 6%, respectively. The best model for predicting bee species density ($F_{1,\ 33} = 46.28$, $P < 0.0001$; $r^2 = 0.58$) contained one variable, total basal area (BA) and was: No. of species per plot = 30.65–0.061(BA).

4. Discussion

Forests in North America underwent fundamental and rapid changes since European arrival to the continent and these changes have been profound in the Southeastern region. Prior to European arrival Native Americans shaped the ecosystems of this region with frequent fires and land clearing. On the Coastal Plain, longleaf pine was the dominant tree on over 36 million hectares from Virginia to Texas. These forests were open woodlands, with the highest plant species diversity reported on the continent (Westhoff, 1983), that were maintained by frequent burning (Carroll et al., 2002). Forests of the piedmont and mountains were composed of oaks, southern pines, hickories and chestnut, which were the dominant trees almost everywhere because of widespread use of fire by native inhabitants that favored fire tolerant species (Carroll et al., 2002; Hudson, 1976). The trees were larger and more widely spaced than today, even when compared to present day old growth remnants (Fralish et al., 1991). Like the Coastal Plain, most of these forests were open and fire maintained with little shrub cover (Carroll et al., 2002).

The first major change to these ecosystems occurred when diseases introduced by early explorers reduced aboriginal populations and subsequently, their impact on forested ecosystems (Smith, 1987). After their arrival, the initial colonists, their descendants, and subsequent immigrants affected more and more of the land, cutting trees to build homes and ships, to clear fields, to provide fuel, and for export (Ahren, 1929, 1933; Lilliard, 1947; Clark, 1984; Williams, 1989). By the end of World War I, earlier timber harvesting combined with the demands of war left the region extensively deforested (Ahren, 1929, 1933).

Reforestation of the southeastern United States was a major conservation effort of the 20th century that resulted in forests that are now considered the “wood basket of the nation”. These forests provide 58% of the nation’s timber harvest by volume and represent the largest agricultural-style timber-producing region in the world (Wear, 2002). In concert with reforestation a similarly extensive effort to suppress wildfires resulted in almost complete fire exclusion from forests (Carroll et al., 2002; Stanturf et al., 2002) which lead to dense understories of small trees and shrubs (Carroll et al., 2002).

Bee communities in our study were more species rich and had higher overall abundance in mature pine forests with open canopies, little or no midstory trees or shrubs, and an herbaceous understory, conditions typical in frequently burned stands. Removal of the forest canopy resulted in similar bee communities to those of mature, open pine forests. Open bottomland hardwood forest also had high estimated species richness. Although cleared forests had abundant and diverse bee communities, they would quickly progress to the dense young pine stage with the lowest bee species richness and abundance, similar to other stand types with closed canopies or high shrub cover. Keeping these forest openings attractive habitats for bees over a longer period of time would require frequent disturbance by either fire or mowing. Burning would likely be patchy and ineffective, however, without the overstory pines to provide fuels to support fire movement (Mitchell et al., 2009). Conversely, open pine forests with an herbaceous ground cover can be maintained through application of frequent prescribed burns and periodic thinning to provide a stable, long-term habitat for pollinators.

Our results are consistent with other studies of pollinator communities in forested areas, in showing that pollinator communities benefit from open canopies, reduced shrub cover and greater herbaceous plant cover and diversity. These open forest habitats were created or maintained by fire (Grundel et al., 2010; Taylor and Catling, 2011), harvesting or thinning (Fye, 1972; Romey et al., 2007; Taki et al., 2010; Proctor et al., 2012), shrub removal (Hanula and Horn, 2011a,b; Hudson et al., 2013) or a combination (Rudolph and Ely, 2000; Rudolph et al., 2006a,b; Campbell et al., 2007a,b).

The best predictor of bee species density was total basal area of overstory trees which showed a negative correlation so that as basal area increases bee species density decreases. Tree basal area is more closely proportional to leaf area or foliage mass than attributes like tree density or frequency (McCune and Grace, 2002), and it is easy to measure, so it provides a simple method for assessing forest stands as potential habitat for bees. The best model for predicting bee abundance in the study area was more complex and included canopy openness, herbaceous plant species density and shrub cover. Both canopy openness and plant species density exhibited a positive relationship with bee abundance while shrub cover had a negative relationship.

These results were evident when looking at open pine stands with little or no shrub cover which had more bees and more species than similar stands that had a dense shrub layer. Although the shrubby pine stands had slightly higher pine and overall basal areas, in part due to mid-story trees, they had over three times the shrub cover. The low openness or high leaf area index in these stands (Table 1) was due mostly to the shrub layer since the hemispherical camera was positioned below it. Dense shrub layers have been shown to negatively impact herbaceous plant cover and diversity (e.g., Woods, 1993; Baker and Van Lear, 1998; Collier and Vankat, 2002; Gerber et al., 2008; Hudson et al., 2014) and pollinators (McKinney and Goodell, 2010; Hanula and Horn, 2011a,b; Fielder et al., 2012; Hudson et al., 2013).

Reforestation in the southeastern United States in combination with fire exclusion has resulted in large areas of dense forests with high understory shrub cover (Stanturf et al., 2002). This long-term trend and our results suggest that forests of this region have gradually become less favorable for bees. Concern over the fate of pollinators has reached the highest levels of the U.S. government (Obama, 2014). The increasing alarm over declining numbers of pollinators, the high level of interest, and predicted losses of forest land to urbanization (Wear and Greis, 2013) are likely to result in shifts toward pollinator conservation and management in forests.

Fortunately, forest conditions that favor pollinators are also consistent with other forest conservation goals. For example, the mature open pine stands with an herbaceous understory we studied were within the habitat management areas of the red-cockaded woodpecker, so conservation of this endangered species favors pollinators as well. Rudolph et al. (2006a,b) showed similar results for butterflies, including monarchs, *Danaus plexippus*, in red-cockaded woodpecker habitat. Likewise, forest health could benefit from efforts to conserve bees. Currently, large areas of southeastern pine forest are overstocked (Krist et al., 2007; http://www.fs.fed.us/foresthealth/technology/nidrm_spb.shtml) which increases their susceptibility to southern pine beetle attack (Belanger and Malac, 1980; Belanger et al., 1993). Thinning overstocked stands to reduce basal area is promoted as an effective method of reducing risk of attack (Nowak et al., 2008) and it is widely recognized as effective for reducing mortality from bark beetle species in other regions of North America (Fettig et al., 2007). Similarly, dense pine forests in the eastern United States are at risk from the European woodwasp, *Sirex noctilio*. First discovered in North America in 2004 in upstate New York (Hoebeke et al., 2005), *S. noctilio* is a pest of pine worldwide (Carnegie et al., 2006) that favors pines stressed by overcrowding and inadequate water (Morgan and Stewart, 1966). As it spreads southward hazard rating maps show much of the southern United States' pine forests are moderate to high hazard for damage depending on the weight placed on loblolly pine (Chase, 2013). Thinning to reduce tree densities is an effective means of improving tree health and increasing forest resistance to damage by *S. noctilio* (Haugen et al., 1990; Dodds et al., 2010).

Two conservation goals of the early 20th century, extensive reforestation and reduced wildfire through fire exclusion, may have contributed to declining pollinator abundance over time as forests became denser and shrub covered. Our results combined with many others suggest that thinning forests combined with shrub control, by fire or other means, improves bee habitat. Forest structure resulting from these treatments is also compatible with habitat restoration and management for the red-cockaded woodpecker, and should result in stands less susceptible to old (southern pine beetle) and new (European woodwasp) threats.

Acknowledgements

We thank Jason Gibbs for identifying *Lasioglossum* spp., Mike Cody and Chris Crowe for assistance in the field and laboratory, and John Nowak and Kay Kirkman for reviewing earlier drafts of this manuscript. Wenhua Pan, Kim Love-Myers, and Yuan Zhang provided assistance with statistical analyses. Funding for the study was provided by the USDA Forest Service, Southern Research Station's research work unit 4552, Insects, Diseases and Invasive Plants.

Appendix A

See Table A.1.

Table A.1
List of bee species captured during a study on the effects of forest conditions on pollinators in the Piedmont of Georgia, USA during the growing season of 2008.

Species[b]	Treatments[a]							Total
	DYP	RH	PH	PS	UH	CLR	TYP	
Andrenidae								
Andrena bisalicis			1					1
Andrena cressonii	1	2					2	5
Andrena erigeniae		3						3
Andrena gardeneri					1	1		2
Andrena hilaris		1				1		2
Andrena ilicis		8			1		1	10
Andrena imitatrix						1	2	3
Andrena macra	1					3		4
Andrena morrisonella			1		1		1	3
Andrena nasonii		1						1
Andrena nivalis			1					1
Andrena perplexa	1	2			2			5
Andrena personata		6						6
Andrena spiraeana			2			1		3
Andrena violae		15	2	2	3		3	25
Andrena H2296	1							1
Andrena H2306						1		1
Andrena H2310			1					1
Andrena H2313					2			2
Andrena H2383A						1		1
Panurginus polytrichus				1				1
Perdita discreta						3		3
Perdita gerardiae			1		1	1		3
Perdita H2297			1					1
Apidae								
Anthophora abrupta				2	1	1		4
Apis mellifera		1	1		3	5	1	11
Bombus bimaculatus	4	1	1	4	2	3	1	16
Bombus griseocollis			1	1		2	1	5
Bombus impatiens	20	8	55	25	39	85	40	272
Ceratina calcarata		7		30	35		8	80
Ceratina cockerelli						3		3
Ceratina dupla		3	6	4		3	4	20
Ceratina strenua	3		8	49	2		28	90
Epeolus lectoides			1					1
Melissodes agilis			24		3	65	2	94
Melissodes apicata						1		1
Melissodes bimaculata			6	5	2	4	3	20
Melissodes comptoides			2	2		18		22
Melissodes dentiventris				1				1
Melissodes tepaneca			1					1
Melissodes H2378						1		1
Melitoma taurea	1					3		4
Nomada bishoppi		1				1		2
Nomada cressonii				2				2
Nomada dentariae				1				1
Nomada illinoensis		1						1
Nomada lepida			3					3
Nomada luteola	1	1		1	4	2		9
Nomada sayi		1						1
Nomada H2298			2					2
Nomada H2320			1				1	2
Ptilothrix bombiformis			7			1		8
Stelis ater	1							1
Svastra obliqua			1			2		3
Eucera atriventris		1	1				2	4
Eucera dubitata		1	2	2	2	1		8
Xylocopa micans			1			2		3
Xylocopa virginica			4	2		5	3	14
Colletidae								
Colletes inaequalis		2	4	1	1		1	9
Hylaeus illinoisensis		1			3			4
Hylaeus modestus	1	3			1		1	6
Hylaeus sparsus		3						3
Halictidae								
Agapostemon texanus			1					1
Augochlora pura	5	15	4	14	11	4	2	55
Augochlorella gratiosa		4	2	15	24		3	48
Augochlorella aurata	44	85	25	66	145	11	45	421
Augochloropsis metallica		1	1		2	1		5

(*continued on next page*)

Table A.1 (*continued*)

Species[b]	Treatments[a]							Total
	DYP	RH	PH	PS	UH	CLR	TYP	
Halictus ligatus			1	1		4		6
Halictus rubicundus				1	1	3		5
Lasioglossum (Dialictus) apopkense			17			34	1	52
L. (D.) hitchensi			168	5	13	111	52	349
L. (D.) bruneri	56	10	208	39	94	153	130	690
L. (D.) cattellae					4	3		7
L. (D.) coeruleum		4	1		1		2	8
L. (D.) coreopsis			8	1		9	3	21
L. (D.) cressonii							2	2
L. (D.) disparile						1		1
L. (D.) illinoense			63	5	11	112	10	201
L. (D.) imitatum			74	21	5	67	18	185
L. (D.) JG-04	3			2	4	6	1	16
L. (D.) longifrons			2					2
L. (D.) oblongum		2			1			3
L. (D.) pilosum	1		7					8
L. (D.) platyparium			1					1
L. (D.) puteulanum	1		14		1	19	4	39
L. (D.) raleighense	4	1	96	19	4	18	65	207
L. (D.) subviridatum						1		1
L. (D.) tegulare	3		153	14	8	277	40	495
L. (D.) versatum		2	4			6		12
L. (D.) zephyrum						1		1
L. (D.) H2345						4		4
L. (Evyleaus) nelumbonis						1		1
L. (Hemihalictus) lustrans						2		2
L. (H.) macoupinense	7	22	1	7	2		4	43
L. (Lasioglossum) fuscipenne		1					1	2
Sphecodes carolinus		1				1		2
Megachilidae								
Ashmeadiella floridana						1		1
Chelostoma H2342		1					3	4
Hoplitis producta	1	1	1	1	2	1		7
Hoplitis simplex		4						4
Hoplitis truncata			2					2
Megachile frigida			2					2
Megachile latimanus			1					1
Megachile medica			2				1	3
Megachile petulans				2				2
Megachile H2338			1			1		2
Megachile H2340							1	1
Megachile H2344						1		1
Megachile H2346						1		1
Megachile H2348			1					1
Megachile H2358			1					1
Megachile H2364						1		1
Megachile H2371						1		1
Osmia atriventris	3	5	1	6		5	1	21
Osmia chalybea	1		1		4			6
Osmia collinsiae		1	1					2
Osmia cordata			2					2
Osmia distincta				1				1
Osmia georgica		6	12	5	1	3	2	29
Osmia inspergens				1			1	2
Osmia lignaria			2				1	3
Osmia pumila	1	3	6	1	1	1	1	14
Osmia sandhouseae				2				2
Osmia texana		1		2				3
Osmia H2301A		1						1
Osmia H2321	1	1						2
Total	166	246	1029	366	448	1094	499	3848

[a] Treatments are: DYP = dense, young pine; RH = open, riparian hardwood; PH = open mature pine with grass/herbaceous understory; PS = open mature pine with a shrub understory; UH = open upland hardwood; CLR = clearcut; TYP = thinned young pine.

[b] Numbered specimens were unidentified but numbers correspond to the collection at the USDA Southern Forest Sciences Laboratory, Insects, Diseases, and Invasive Plants, Athens, GA.

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