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

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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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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.

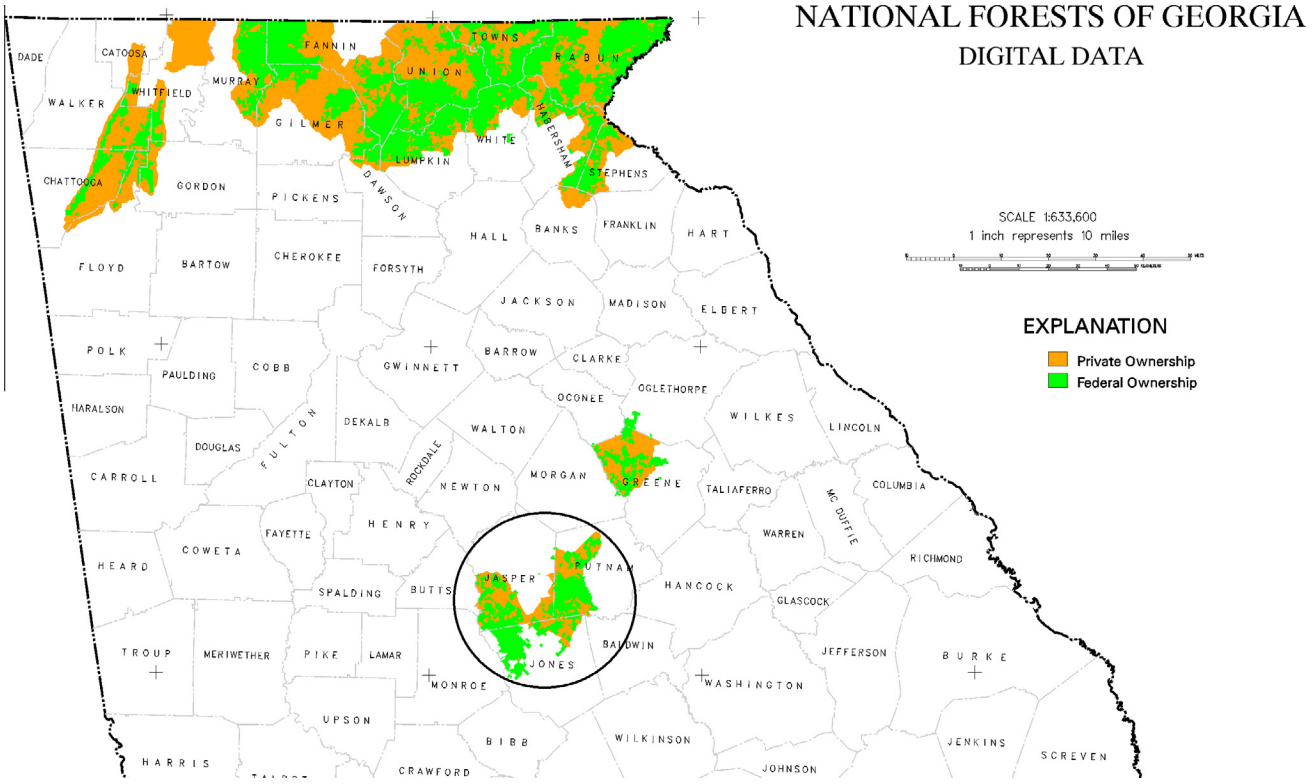

Fig. 1. Location of the southern portion of the Oconee National Forest (circled) in the state of Georgia where the study was conducted (courtesy of the U.S. Geological Survey).