NATIVE BEES IN MANAGED PINE FORESTS: IMPACTS OF STAND-LEVEL HABITAT CHARACTERISTICS AND TRAPPING METHOD COMPARISONS

by

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(Under the Direction of Kamal J.K. Gandhi)

ABSTRACT

Native bees (Hymenoptera) are crucial pollinators of forest plants, and yet, they have been rarely studied in managed pine forests in the southeastern U.S. I determined which stand ages and forest structure attributes best supported native bees, and further compared two trap-types. I sampled bees in four stand age classes of managed loblolly pine (*P. taeda* L.) forests using pan and blue vane traps for two years. Greater numbers of native bees were caught in early establishment stands, and greater species and functional diversity in early establishment and mature thinned stands. Canopy openness, percent of flowering plants, least decayed woody debris, snags, and litter depth were important factors driving bee communities. Although, blue vane traps caught more bees and distinct groups of species than pan traps, both traps caught similar species diversity. Overall, my results identified critical forest elements that may assist in conserving native bees in managed pine forests.

INDEX WORDS: Blue van traps, Forest management, Forest structure, Managed pine, Native bees, Pan traps, Passive trapping, Pollinators, Wild bees

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CHAPTER 1

INTRODUCTION AND LITERTURE REVIEW

Importance of Insect Pollinators

Insect pollinators are a crucial component to all ecosystems, providing over $15 billion in pollination services annually in the U.S. (Calderone, 2012). Thirty-five percent of global crop production relies on insect pollinators to some extent (Klein et al., 2007, Calderone, 2012). Insect pollinators also enhance biodiversity and are critical to plant species survival (Tepedino, 1979). Bees are globally recognized as the most important pollinators (Tepedino, 1979, Steinhauer et al., 2014). They depend exclusively on pollen and nectar from flowers for their entire life cycle, and collecting it leads to pollination as a by-product (Tepedino, 1979). Bees possess specialized adaptations for acquiring and transporting pollen and nectar to their brood. These physical adaptations include corbiculae, or pollen baskets, found on their hind legs, and elongated mouthparts used to acquire nectar (Faegri and van der Pijl, 1979). Many bees also have behavioral adaptations to collect pollen, and flowers adapted to attract bees as well (Faegri and van der Pijl, 1979).

The most well-known bee species in the world is the European honeybee (*Apis mellifera* L.). Most bee research has focused on honeybees due to their agricultural importance (Winfree et al., 2007b). However, there are over 4,000 species of native bees in the U.S. that are also important pollinators (Moisset and Buchmann, 2011). In many instances, wild, native bees are more efficient pollinators than honeybees (Garibaldi et al., 2013). Native bees are more effective at pollinating commercially valuable crops such a blueberry (*Vaccinium* sect. *Cyanococus),* cranberry (*Vaccinium* subg. *Oxycoccus*), eggplant (*Solanum melongena* L.), pumpkin (*Cucurbita* spp), tomato (*Solanum lycopersicum* L.), and watermelon [*Citrullus lanatus* (Thunb.) Matsum. & Nakai] (Moisset and Buchmann, 2011). Also, native bees increase crop production compared to honeybees alone (Greenleaf and Kremen, 2006, Winfree et al., 2008, Garibaldi et al., 2013). Relying on multiple bee species for pollination rather than honeybees alone can create "biological insurance" against future honeybee decline, as native bees will continue pollinating crops even in absence of honeybees (Winfree et al., 2007b).

Unfortunately, there is evidence to suggest wild and domesticated pollinators are in decline due to a variety of factors including habitat degradation, disease, climate change, and pesticide use (Potts et al., 2010, Vanbergen, 2013). Some bumble bee species (*Bombus* spp.) are declining in Asia, Europe, and North America (Williams and Osborne, 2009). Using repeated biodiversity inventories of historically sampled areas and museum specimen data in Illinois, half of all historically present bumble bee species were found to have experienced local extirpation or declines during 1900-2007, with most declines occurring between 1940 and 1960 coinciding with agriculture intensification in the state (Grixti et al., 2009). Many declining bumble bee species in the U.S. had a high presence of pathogens and reduced genetic diversity (Cameron et al., 2011). In the Northeast U.S., the *Bombus* genus declined by 30% in 140 years (Bartomeus et al., 2013). Additionally, bumble bees in Europe and North America had constricted ranges, as they did not move north after losing their southern ranges due to warming (Kerr et al., 2015). This indicates that in both these regions, climate change may limit bumble bee habitat.

Other native bee species are in decline in addition to bumble bees. Over a 120-year period, there was a net loss of 46% of plant-pollinator interactions and half of native bees species went locally extinct in an Illinois, U.S. temperate forest (Burkle et al., 2013). Declines of native bees have been observed in Britain and the Netherlands when compared to pre-1980 records (Biesmeijer et al., 2006). In the U.S., it was modeled that from 2008 to 2013 there was a 23% decline in abundance of wild bees across all land area potentially due to habitat loss in cropland (Koh et al., 2016). Additionally, climate change might play a significant role in bee declines. Increased precipitation decreased spring bee abundance and increased temperature decreased fall bee abundance in a study in Delaware, Maryland, and Washington, DC, U.S. (Kammerer et al., 2021). If climate change leads to increased temperature and precipitation, this could be detrimental for native bees in this region.

However, there is some debate as to whether all native bees are declining. Overall, native pollinators show mixed responses to environmental change and additional monitoring may be needed to determine if native bees are declining (Ghazoul, 2005, Holden, 2006). Especially in North America, there may be inadequate documentation of widespread insect (Crossley et al., 2020) and pollinator declines (Cane and Tepedino, 2001). Local scale extinctions or declines do not mean that there are also larger scale declines (Bartomeus and Winfree, 2013). Marked decline in bee species was not observed between 1916 and 1970 in a diverse habitat in Illinois (Marlin and LaBerge, 2001). In the Northeast U.S., there was no significant decline in non-*Bombus* bees species over a 140-year period (Bartomeus et al., 2013). Although there were shifts in community composition, only three species out of 187 analyzed declined significantly (Bartomeus et al., 2013). Additionally, orchid bees (Tribe Euglossini) in Panama showed no change in species richness from 1979 to 2000 (Roubik, 2001). Overall, there is not enough evidence to determine if all bee species are declining. Hence, it is imperative to develop a better understanding to the challenges for bee communities, since bees provide important ecosystem services. More baseline data are needed to establish long-term studies to adequately assess potential bee decline in North America.

Native Bees and Forested Habitats

Forests are important natural resources that cover over 310 million hectares or 34% of the land area of the U.S. (Oswalt and Smith, 2014). Forest products generate $200 billion in sales in the U.S. (Oswalt and Smith, 2014). In the Southeast, 86% of forest land is privately owned, and about three out of every four of these hectares is owned by individuals or organizations who have commercially harvested their timber (Butler and Wear, 2013). The Southeast holds approximately 40% of 210 million hectares of timberland in the county and is known as the "woodbasket" of the U.S. (Oswalt and Smith, 2014). The Southeast has about 80 million hectares of managed private forest (Butler and Wear, 2013). In Georgia, there are 9.9 million hectares of forest, accounting for about 66% of the total land area (Lambert, 2020). Of this land, 84% is classified as nonindustrial private forest, and 5% is owned solely by forest industry (Lambert, 2020). Loblolly pine (*Pinus* taeda L.) is the most common tree making up these forests as 39% of all live trees on the landscape and 32% of standing volume (Lambert, 2020). Hence, most of Georgia is forested, and most of this forest is privately owned and made up of loblolly pine, making this a pervasive land cover type in the state.

Pine trees are not pollinated by bees and so a relevant question is - how do native bees contribute to the overall pine forest ecosystems? Bees are important for pollinating native plants (Kremen et al., 2007, Ollerton et al., 2011). Having a greater diversity of bees contributes to a greater diversity of native plants (Fontaine et al., 2006). Bee diversity also contributes to increased native plant reproduction in the form of higher seed production (Frund et al., 2013). Additionally, a loss of phylogenetic diversity from pollinator communities can cause a decline in pollination services (Grab et al., 2019). Bees declining in a temperate forest in Illinois led to decreased interactions with plants, which could lead to a loss of redundancy in pollination systems and an increased vulnerability to environmental stressors (Burkle et al., 2013). In Britain and the Netherlands, declining bees also caused declines in the plants they pollinated when compared to plants not pollinated by these bees (Biesmeijer et al., 2006). Many native plants present in forests would be negatively affected by not having a robust native bee community, which would overall be a detriment to the ecosystem processes, if not economic values.

Forests are important for bees, providing many resources such as pollen, nectar, and nesting materials (e.g. woody debris, mud, and bare ground) (Roulston and Goodell, 2011). Additionally, forests may act as pollinator reservoirs for adjacent habitats (Hanula et al., 2016), increasing ecosystem services from bees nearby. Farms closer to natural areas had more native bees contributing to pollination services (Klein et al., 2007). Proximity to forests may improve pollination in agriculture even when honeybees are present. Agricultural fields located further from forests have lower native pollinator species richness, flower visitation rate, and fruit set (Garibaldi et al., 2011).

Although nearby forests promote native bees in agricultural fields, bees also may prefer more open canopy forests over dense forest cover. In patchy areas with both fragmented forests and anthropogenic landscapes, bee abundance and species richness were greater in agricultural fields and developed areas than in extensive forest (Winfree et al., 2007a). Wild bee abundance and diversity were positively related to early successional habitat with bees preferring forest openings over mature forest patches within hardwood forests (Proctor et al., 2012, Taki et al., 2013, Roberts et al., 2017, Mullally et al., 2019). Bee abundance and diversity were highest in areas where the most trees were removed from the canopy in hardwood forests in New York, U.S. (Romey et al., 2007). Native bee diversity was reduced in forests with dense trees and high canopy cover in mixed pine and hardwood forests in New England, U.S. (Odanaka and Rehan, 2020). Bee species richness increased with clearcut size in managed boreal forests in Sweden (Rubene et al., 2015). There were higher abundance and species richness of bees in clearcut areas, and as tree cover increased, bee abundance and richness decreased in managed pine forests in the Southeast U.S. (Miljanic et al., 2019). Thinned plots had higher bee abundance and diversity in longleaf pine (*Pinus palustris* Mill) forests in South Carolina, U.S. (Breland et al., 2018, Odanaka et al., 2020). In Georgia, U.S., a higher diversity of bees was also found in clearcuts than in mature pine and hardwood forests (Fortuin and Gandhi, 2021). Bee abundance was higher in restored pine savannas when compared to nearby closed canopy plantations and managed forests in Florida, U.S. (Dixon et al., 2022). Native bees had the highest abundance and species richness in cleared forests and mature pine forests with an open canopy and an herbaceous understory in southeastern U.S. pine forests (Hanula et al., 2015). These conditions can be generated by forest management practices, such as thinning and gap creation and can benefit pollinators in multiple forest types (Taki et al., 2013, Hanula et al., 2015, Hanula et al., 2016). Open conditions can lead to increased floral resources from increased light reaching the understory. Floral resources are also very important for bees (Roulston and Goodell, 2011), as bees rely on them to survive for their entire life cycle (Tepedino, 1979). Increased floral resources has been found to increase bee diversity in many forests (Romey et al., 2007, Rubene et al., 2015, Gelles et al., 2022), thus prompting a positive response from wild bees in these open canopy conditions.

In addition to forest canopy openness, other structural characteristics such as coarse woody debris and bare ground present in forests may benefit bees. Woody debris is an important nesting resource for certain bees (Roulston and Goodell, 2011). Removing woody debris reduced bee diversity in southeastern pine plantations (Loy et al., 2020). Increased woody debris increased bee diversity in pine dominated forests in Colorado, U.S. (Gelles et al., 2022). In addition to woody debris, bare ground is also an important nesting resource. Ground nesting bees rely on bare non-compacted soil (Roulston and Goodell, 2011), and increased bare ground increased abundance and diversity of wild bees in South Carolina longleaf pine forests (Odanaka et al., 2020). Additionally, sites with more frequent prescribed fire and consequently more bare ground had increased abundance of native ground nesting bees (Ulyshen et al., 2021).

Sampling Methods for Native Bees in Forests

Two commonly used passive sampling methods for bees are colored pan traps and blue vane traps. Pan traps consist of colored plastic bowls or pans (96 to 355 mL) filled with water and a small amount of dish soap to break the surface tension. Vane traps consist of a 1.9 L collecting jar that can also be filled with soapy water, a screw top funnel, and two interconnecting ultraviolet semitransparent polypropylene vanes on the top. Both trap types use color as their sole visual bee attractant, mimicking flowers. Flowers attract pollinators with specialized traits (Faegri and van der Pijl, 1979), and color is an important floral characteristic to draw in bees (Kevan, 1972). For pan traps, blue, yellow, and white are reliable colors for effectively sampling bees (Campbell and Hanula, 2007, Geroff et al., 2014), while red pans are not effective for sampling Hymenoptera (Campbell and Hanula, 2007). For vane traps, blue vanes are significantly more effective than yellow vanes for sampling bees (Geroff et al., 2014, Hall, 2018).

Pan traps are one of the most used sampling methods for bees in a variety of areas. Across Europe in both agricultural and semi-natural landscapes, pan traps were found to be the most efficient, cost effective, and unbiased when compared to five other survey methods including transect walks and trap nests (Westphal et al., 2008). Active sampling methods such as transect walks can have collector bias. Collector skill level, microhabitat knowledge, and preference for larger or more colorful bees can cause bias (Nielsen et al., 2011). Elevated pan traps caught higher bee abundance and species richness, while malaise traps were virtually ineffective in an Illinois hardwood forest (McCravy and Ruholl, 2017). Additionally, pan traps were more effective than malaise traps for catching bees in southeastern U.S. forests (Campbell and Hanula, 2007).

Blue vane traps have not been in use as long as pan traps but are effective for sampling bees in open and dense areas (Hall, 2018). Blue vane traps were more effective than pan traps, capturing a higher species richness of bees in orchards (Joshi et al., 2015). Bee abundance and species richness were higher in blue vane traps compared to pan traps and aerial netting in prairie habitats (Rhoades et al., 2017). However, using pan and blue vane traps simultaneously may be a more effective method than using either alone. Blue vane and pan traps can collect distinct bee communities in the same area (Rhoades et al., 2017). Pan traps catch more rare bee species relative to the blue vane traps (Joshi et al., 2015). Additionally, pan traps catch more small bees (Roulston et al., 2011), while blue vane traps catch larger bodied bees, such as *Bombus* spp. and *Melissodes* spp. (Geroff et al., 2014).

Goals and Objectives of the Thesis

Chapter 2: Stand Age Class Affects Communities of Native Bees in managed Pine Forests

Native bee research has largely occurred in agricultural systems, and native bee communities in forested systems are understudied. There is also a documented lack of research on pollinators in managed pine forests specifically (Rivers et al., 2018). Consequently, there are few detailed studies of the relationship between native bee populations and communities at different age classes in managed forests. The southeastern U.S. is especially critical for discerning this relationship because many forests in the southeastern U.S. are managed for multiple purposes, namely timber production (Wear and Greis, 2002). Hence, I examined how attributes of forest structure and composition within stands relate to characteristics of native bee communities, by comparing different age classes of loblolly pine before and after thinning and canopy closure. Discerning the relationship between pollinator populations and communities and forest structure will inform managers on what factors will help preserve pollinators in these areas. This increased knowledge about bee communities in managed pine forests will lead to integrated economic and conservation efforts and solutions that can benefit both the pollinators and stakeholders.

The goal was to determine which attributes of forest age, structure, and composition best support native bees. Bee communities are assessed by: 1) abundance, which is the number of bees caught; 2) species diversity, which is measured by the raw species richness and rarefied species richness; 3) functional diversity, which measured by the evenness and dispersion of different functional groups.; and 4) differences in species composition using multivariate approaches.

The first objective was to compare communities of native bees among four stand age classes by answering the following questions: how does forest age class affect bee abundance and diversity? The second objective was to assess the effects of stand-level structure and composition on bee communities by answering the following question: which elements of stand structure and composition are important factors for bee community abundance, diversity, and functional diversity? Stand composition metrics included tree species, tree basal area, tree density, tree height, percent understory plant cover, and understory plant species diversity. Stand structure metrics included percentage of canopy openness, woody debris cover, litter cover and depth, and bare ground.

Chapter 3: Pan and Blue Vane Traps Sample Different Communities of Native Bees in Managed Pine Forests in the Southeastern U.S.

A standardized sampling protocol is needed to accurately assess native bee populations and communities in managed southeastern U.S. pine forests because of the limited research. Little work has been done to assess the effectiveness of common trapping methods for bees in forests in the region. Sampling for bees in these forests presents unique challenges not encountered in other commonly sampled landscapes (i.e., prairies). Forests contain overstory and sometimes complex mid and understories with a mix of woody shrubs and herbaceous plants that can make active sampling such as sweep netting a challenge (Campbell and Hanula, 2007). Additionally, sampling in multiple age classes of forest can make standardizing protocol of active sampling difficult or impossible as vegetation structure and flower species present for sweep netting or targeted flower sampling varies among different forest ages (Roulston et al., 2011). Hence, I compared the effectiveness of two commonly used passive bee sampling methods including colored pan and blue vane traps.

The goal of this project was to compare two passive trapping methods, colored pan and blue vane traps in for capturing native bees in managed southern pine forests. The metrics used for comparison were bee abundance, species diversity, functional diversity, and species composition. I answered the following specific questions: 1) do the two trap types collect different bee abundance and diversity; 2) are any species associated with a particular trap type; and 3) do certain trap types catch bees of a particular size, sociality or seasonality?

Forests in this region are especially important from an economic standpoint, as many are managed for timber production (Wear and Greis, 2002). It is, therefore, important to know how different aspects of forest structure and composition affect bees to guide future management decisions for pollinator protection. A better understanding of the advantages and disadvantages of each trap type is also important for future research and monitoring purposes in forests. Preserving ecologically important pollinators while successfully managing these economically important forests for multiple management are the goals.

CHAPTER 2

STAND AGE CLASS AFFECTS COMMUNITIES OF NATIVE BEES IN MANAGED PINE FORESTS[1]

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[1] Favorito, C.M., Barnes, B.F., Briggs, E.L., Fortuin, C.C., Greene, D.U., Larsen-Gray, A.L., Martin, J.A., McCarty, E, and Gandhi, K.J.K. To be submitted to Forest Ecology and Management.

Abstract

Native bees provide critical pollination services to both crops and to native plants in forests. Unfortunately, there is some evidence to suggest that native bees are declining due to factors such as habitat loss, disease, pesticide use, and climate change. Privately-owned and managed loblolly pine (*Pinus taeda* L.) forests cover a large area in the southeastern U.S. and could be important for native bees. However, there is little research on native bees in this forest-type, and hence, we examined forest structure and composition attributes that best supported native bees. Our research objectives were to compare native bee communities among different stand age classes of working loblolly pine forests and to test the effects of stand-level structure and composition on native bee communities. We sampled bees and forest attributes in four stand age classes [0-3 years (early establishment), 4-7 years (pre-thinned with a closing canopy), 8-13 years (pre-thinned with a closed canopy), and 14-20 years (post-thinned)] of privately-owned pine managed forests in the Upper Coastal Plain region of Georgia. Results from 5,933 bees and 88 species indicated that native bees were ~80-367% more abundant in early establishment stands, and more diverse in early establishment and post-thinned stands. Functional dispersion, a measure of beta diversity, was also greater in early establishment and post-thinned stands. Canopy openness, percent of plants flowering, and percent cover of minimally decayed woody debris were important variables driving the bee community in the early establishment stands, while number of snags and litter layer depth were important variables driving the bee community in the older stands. Overall, native bees appear to benefit from various ages of stands, especially open and mature pine areas, and diverse land cover types embedded within stands. Maintaining open canopy stand types by planting trees at wider spacing and/or thinning as early as possible may conserve and maintain native bee communities in this region.

Introduction

Insect pollinators are highly valuable in all agricultural and forested ecosystems. From an economic standpoint, insect pollinators provide over $15 billion in pollination services in the United States annually, and, on a global scale, 35% of all crops rely on insect pollinators to some extent (Klein et al., 2007, Calderone, 2012). Bees (Hymenoptera: Anthophila) are the most efficient and effective insect pollinators because they rely on floral resources for their entire life cycle, so they possess specialized adaptations for pollination (Faegri and van der Pijl, 1979, Tepedino, 1979, Steinhauer et al., 2014). Although the introduced European honeybee (*Apis mellifera* L.) is one of the most well-known bee species, there are over 4,000 native bee species in North America that are important pollinators, sometimes even more effective than honeybees (Moisset and Buchmann, 2011, Garibaldi et al., 2013). Unfortunately, some bee species may be declining due to factors such as habitat degradation, disease, climate change, and pesticide use (Potts et al., 2010, Vanbergen, 2013, Steinhauer et al., 2014). However, there is debate whether this is true for all species in all environments, especially in North America (Cane and Tepedino, 2001, Ghazoul, 2005, Bartomeus et al., 2013). Small-scale extinctions or declines do not necessarily indicate large-scale declines, and many species' populations have remained stable (Marlin and LaBerge, 2001, Bartomeus et al., 2013, Bartomeus and Winfree, 2013). Overall, more information is needed to determine if North American bees are declining in various forest-types and under natural and anthropogenic disturbances.

In addition to providing economic benefit via crop pollination, bees also are important in natural systems, including forests, where they pollinate many native plants and improve plant species survival (Tepedino, 1979, Kremen et al., 2007, Ollerton et al., 2011). Forests are extensive in the Southeast U.S., particularly in Georgia where they make up 66% of the total land area (Lambert, 2020). Previous research on native bees in forest ecosystems shows that bees prefer more open canopy areas. Within hardwood forests, wild bees were more abundant and diverse in forest openings than in mature forest patches (Romey et al., 2007, Proctor et al., 2012, Taki et al., 2013, Roberts et al., 2017, Mullally et al., 2019, Odanaka and Rehan, 2020). In pine (*Pinus* spp.) forests, there was higher bee abundance and species richness in clearcuts (Hanula et al., 2015, Miljanic et al., 2019, Fortuin and Gandhi, 2021), and in areas that were thinned or had a more open canopy (Breland et al., 2018, Odanaka et al., 2020, Dixon et al., 2022). Clearcuts and thinned forests allow greater light into the understory and more floral resources to grow with a positive effect on bee diversity (Romey et al., 2007, Rubene et al., 2015, Gelles et al., 2022). Bees are also positively associated with nesting resources, such as woody debris and bare ground (Odanaka et al., 2020, Fortuin and Gandhi, 2021, Ulyshen et al., 2021, Gelles et al., 2022), indicating that a combination of structural characteristics may be most beneficials to bees.

The majority of Georgia forests are privately owned and consist of loblolly pine (*P. taeda* L.) (Lambert, 2020). These privately owned forests that span approximately 80,000 ha in the Southeast are potentially important for native bees, but there has been limited research into pollinators in any managed conifer forests in North America (Butler and Wear, 2013, Rivers et al., 2018). One study compared native bee communities in various growth stages of pines and hardwoods in the Georgia Piedmont using only pan traps (Hanula et al., 2015). However, the present study differs as it was conducted in the Upper Coastal Plain, included more and sequential age classes of pines, and used both pan traps and blue vane traps. As the area of planted pine is expected to increase 20-72% within the next 50 years in the Southeast, there is a general need for greater research in these intensively managed pine ecosystems (Butler and Wear, 2013).

Hence, the goal of our two-year study was to determine which attributes of forest age, structure, and composition best support native bees. We had two research objectives as follows: 1) to compare communities of native bees among four stand age classes spanning from clearcut, through canopy closure, and after thinning; and 2) to assess the effects of stand-level structure and composition on bee communities by measuring various structural characteristics within these stands. Results from this study may provide insight into management activities that can benefit both native bees and their economically important forests.

Methods

Study Sites

Study sites were managed loblolly pine forests located in the Southeastern Plains Ecoregion of Georgia. While stands were dominated by loblolly pine, there was a hardwood component in the stands, primarily sweetgum (*Liquidambar styraciflua* L.), southern red oak (*Quercus falcata* Michx.), and water oak (*Quercus nigra* L.). Soils in these areas are classified as sandy loam, loamy sand, and sand Ultisols (Soil Survey Staff, 2021). Average annual precipitation was 148.3 ± 1.3 cm for all sites with a range of 124.5 - 177.0 cm (PRISM Climate Group, 2020). Average annual temperature was 19.2 ± 0.04 °C with a range of 18.7 - 20.1°C (PRISM Climate Group, 2020). Average elevation of the sites is 78.7 ± 1.4 m with a range of 57.9 - 103.9 m (PRISM Climate Group, 2020).

Pine stands >2 ha were selected in each of the following stand age classes: 1) 0-3 years (recently established); 2) 4-7 years (pre-thinned, closing canopy); 3) 8-13 years (pre-thinned, closed canopy); and 4) 14-20 years (post-thinned, open canopy) (Table 2.1). These categories were chosen to represent varying levels of stand structure particularly canopy openings.

Sampling was conducted during the summers of 2020 and 2021, and different stands were used each year. There were four randomized complete blocks that had one stand from each of the four stand age classes for a total of 16 stands sampled per year and 32 stands during the two-year study (four blocks x four stand age classes x two years). Blocks were located >1 km apart to ensure independent sampling. Three 10 m radius plots were established at each stand. Plots were separated by >50 m from each other and were located >15 m from roads. There was a total of 96 plots during the two-year study (16 stands x three plots per stand x two years).

Stand Attributes

Stand measurements were conducted in August 2020 and 2021 in each plot. Data collected included overstory tree species and their diameter at breast height (DBH) from which we calculated basal area and tree density/ha. Additionally, the number of standing dead trees (or snags) and their decay class (1-5) were recorded (USDA Forest Service FIA, 2016). The heights (m) of five randomly selected trees per plot were measured using a digital clinometer. The percent canopy openness was measured using a spherical densiometer in four cardinal directions at the plot center. Also, within each plot, four 1 m^2 quadrats were established approximately 5 m from the center in each cardinal direction. Within these quadrats the percent of understory plant cover, woody debris cover, litter cover, and bare ground were visually estimated. The depth of the litter (cm) was also measured and the decay class of the woody debris and the percent of the flowering plants were also noted. Understory plant species were identified along with the number of stems of each plant species (to provide a measure of plant density) in one-third of the plots (one per stand) in September 2021 (Weakely, 2020).

Native Bee Sampling

Pan and blue vane traps were used to sample the bee community because these traps may sample different species in the same area (Rhoades et al., 2017). Pan traps are effective for sampling bees in forests in this region (Campbell and Hanula, 2007) and tend to catch more rare bee species relative to the blue vane traps (Joshi et al., 2015). Pan traps were arranged in clusters that consisted of a blue, white, and yellow 118 mL plastic cup (Solo brand) filled with water and a small amount of odorless dish detergent to break the surface tension. The color and height of traps mimics flowers and attracts pollinators. Each cup was held at a height of ~ 0.5 m off the ground on a wire plant prop. A pan trap cluster was used at each of the plots. The pan traps were set ~5 m away from the center of the plot at approximately a 120° angle from one another. Traps were set for 6-7 consecutive days per month, emptying and resetting after 3-4 days, during June-September 2020 and May-September 2021.

Blue vane traps capture a greater abundance and diversity of native bees than pan traps (Joshi et al., 2015, Gibbs et al., 2017, Rhoades et al., 2017) and are effective for sampling bees in open and wooded areas (Hall, 2018). Each blue vane trap (SpringStar, Inc.) consists of a 1.9 L collecting jar with a screw top funnel and two interconnecting ultraviolet semitransparent blue polypropylene vanes on the top. Bees are attracted to the blue color, fly into the funnel, and become trapped in the jar, which had the same water and detergent mixture as the pan traps. These traps were hung from a pole ~1.5 m off the ground. One trap was placed in the center of each plot with three pan traps surrounding it. These traps were deployed and operated concurrently with the pan traps.

All trap catches were collected, water drained, and insects stored in the freezer until they were sorted and identified. After sorting, bees were washed with dish soap and water, dried in a small clothes dryer, and pinned. Bees were identified to species using the Discover Life online key (Ascher and Pickering, 2020) and with some both identified and confirmed by Sam Droege, United States Geological Survey. The representative specimens of each taxon identified were deposited at the Georgia Museum of Natural History, University of Georgia, Athens.

Each bee species was assigned to functional groups for nesting, sociality, diet, size, and peak season using literature and reference sources (Mitchell, 1960, Michener, 2007, Gibbs, 2011, Williams et al., 2014, Wilson and Messinger, 2015, Ascher and Pickering, 2020, Fortuin and Gandhi, 2021, Messinger and Wilson, 2021).

- Nesting: Species were assigned to one of five categories:
    1. Cavity: nesting in deadwood or pithy stems (not decayed) by excavating or using those already excavated.
    2. Litter: nesting in leaf litter, the organic layer of soil or piles of wood usually not excavating the nests themselves.
    3. Softwood: nesting in decaying wood.
    4. Occupied: cleptoparasitic bees that lay their eggs in the nests of other species.
    5. Soil: nesting in the soil by excavating nests.
- Sociality: Species were classified as social or solitary. Species were considered social if there was any cooperation within a colony. Species were considered solitary if one queen makes her own nest even if the species nests together in the same area.
- Diet: Species were classified as specialist or generalist. Specialists usually forage on only a specific plant family or genus while generalists forage on a variety of plants.
- Size: Species were classified as small, medium, or large based on published lengths. Small was 3.5-9 mm, medium was 9.5-15 mm, and large was 15.5-22 mm.

- Peak season: Species were classified as early-season if they are most active February - April, mid-season if they are most active May - July late-season if they are most active August - October. Peak seasons were established using both references and collected data from the study.

Statistical Analyses

Individual stand was the unit of replication in the study. Bee catches were aggregated for all traps in a stand over the entire trapping season for each year. Bee abundance was standardized to account for differences in sampling effort as the 2021 sampling season was one month longer than the 2020 sampling season (due to Covid-19 travel constraints in 2020). For each stand, the raw number of bees caught for the entire year was divided by the number of trapping days in that year and then multiplied by 30 (to indicate bee captures/month). All analyses were conducted in R [version 4.1.3, (R Core Team, 2022)] and significance of tests was evaluated at the $\alpha = 0.05$ level.

The normality of residuals for bee catch/month data was tested using the Shapiro-Wilks test. The catch data were not normally distributed, so it was square root-transformed. A one-way Analysis of Variance (ANOVA) test was used to determine if monthly bee catches varied among the four stand age classes using the aov function in R. The stand age class was the fixed effect with the block as a random effect. The ANOVA was followed by Tukey's post-hoc test to determine which groups were significantly different from each other.

Seven species [*Ceratina floridana* Mitchell, *Lasioglossum floridanum* (Robertson), *L. nymphale* (Smith), *L. puteulanum* Gibbs/*tegulare* (Robertson), and *Melissodes bimaculatus* (Lepeletier)] represented >5% of the total bee catches. The catches of each species were first standardized the same way as described above. For all seven of these species, residuals were found to not be normally distributed using the Shapiro-Wilks test. Hence, *C. floridana, L. floridanum, L. nymphale, L. puteuelanum/tegulare,* and *M. bimaculatus* catch data were square root-transformed. One-way ANOVAs were performed on the transformed data to compare catches of each bee species among stand age classes, and Tukey's post-hoc tests were used for pairwise comparisons. Stand age class was the fixed effect and block was a random effect in the models. The catch data for *L. retinaculum* and *M. communis* were analyzed using Kruskal-Wallis tests because the residuals could not be normalized using a transformation. Significant models were followed by the Dunn test with the Bonferroni p adjustment for multiple comparisons.

Bee diversity among stand age classes was evaluated using species richness and rarefied species richness using individual-based rarefaction (R package "vegan") (Oksanen et al., 2020). Species richness and rarefied species richness were both used as measures of alpha diversity, or the mean diversity of species at a given site (Whittaker, 1972). Rarefaction used the smallest sample size, or the smallest number of individual bees captured on a stand. Species richness and rarefied species richness were analyzed with a one-way ANOVA using the aov function followed by Tukey's post-hoc tests to determine how both richness metrics varied among stand age classes. The normality of residuals for both were verified using the Shapiro-Wilks test. For both the models, the stand age class was a fixed effect.

Canonical correspondence analysis (CCA) was used to determine which stand attributes explained a significant amount of the variance in the native bee species distribution among sites. CCA is a combination of regression and ordination methods used to assess the influence of environmental variables on species distribution. The response variable is a site by species matrix, and the predictor variables are the stand attributes. Species catches were square-root transformed to reduce the influence of large catches, and then the transformed data were divided by the number of trapping days. The CCA axes were constrained by the environmental variables (stand attributes). There were 16 explanatory variables: tree basal area (m^2/ha), tree density (trees/ha), tree height (m), number of snags, snags average decay class, percent cover of woody debris in decay class 1-5, and percentage of understory plant cover, understory plants flowering, canopy openness, litter cover, and bare ground, and litter depth (cm). Variance Inflation Factors (VIFs) were also computed to check for redundancy in the predictor variables. VIFs <10 were treated as acceptable. Three explanatory variables (basal area, percent litter cover, and tree height) had to be dropped to achieve all VIFs to be less than 10, i.e., to remove redundant variables. The significance of the overall CCA and each stand attribute explanatory variable was tested to determine if the CCA explains more variance than would be expected by chance.

Indicator species analyses were used to determine if any species were associated with a particular stand age class. The R package “indispecies” and the multi-level pattern analysis (“multiplatt”) function were used (De Cacers and Legendre, 2009). The “multiplatt” function assesses the association between species distribution and combinations of groups of sites. The groups of sites looked at were the stand age classes (and combinations of stand age classes). The species-site group association function used was the indicator value index (“Ind.val.g”) (Dufrene and Legendre, 1997). A permutation test with 9,999 permutations was used to test the significance of the associations. Only species with >20 individuals were used for these analyses.

Functional group diversity was assessed using the metrics functional dispersion and functional evenness. Functional dispersion (FDis) relates to the variability in functional group composition. It is measured by the spread of individual species in a multivariate space defined by their traits, by measuring the distance each species is to the centroid, which is weighted by each species’ relative abundance (Laliberte and Legendre, 2010). Functional dispersion is also a measure of beta diversity or the ratio between local and regional species diversity across sites (Whittaker, 1972, Anderson et al., 2006). Functional evenness (FEve) describes how evenly functional traits of species are distributed in multivariate space (Villeger et al., 2010). These metrics were computed using the “FD” package in R using Distance Based Functional Diversity Indices (“dbFD” function) (Laliberte et al., 2014). The bee functional traits were nesting, sociality, diet, season, and size class. First a species-species distance matrix was generated and then used to perform a Principal Coordinates Analysis (PCoA). Resulting FEve and FDis values were compared among age classes using Kruskal-Wallis tests as residuals were found to not be normally distributed using Shapiro-Wilks tests. Significant results were followed by the Dunn test for multiple comparisons with a Bonferroni p adjustment.

Regressions were used to assess whether there was a significant linear relationship between two bee community variables (2021 bee rarefied species richness and 2021 bee catches per month) and three understory plant community variables (understory plant species richness, numbers of plant stems, and percent plant cover in quadrats) in 2021. The number of understory plant stems were counted in each quadrat to serve as a measure of plant density. The percentage of understory plant cover including grasses in the quadrats served as a measure of understory plant cover. Six linear models were run using the lm function in R:

1) Understory plant species richness was regressed with 2021 bee rarefied richness.
2) Understory plant species richness was regressed with 2021 bee catches.
3) The number of plant stems was regressed with 2021 bee rarefied richness.
4) The number of plant stems was regressed with 2021 bee catches.
5) The percentage of plant cover in the quadrats was regressed with 2021 bee rarefied richness

6) The percentage of plant cover in the quadrats was regressed to 2021 bee catches.

The same six models were all conducted again with catches and species richness just for bees caught in September 2021 because plant species information was only collected that month.

Results

A total of 5,933 individual bees from 88 species were collected over the 2-year study period in all traps. European honeybees (55 individuals) were removed before analyses, as they are not native. Sixty-six individuals from the genera *Ceratina, Melissodes, Lasioglossum, Svastra,* and *Triepeolus* could only be identified to the genus-level (Table 2.2). Seven species of bees were common, making up >5% of all trap catches. They were *C. floridana* (657 individuals; 11.18% of total), *L. reticulatum* (642 individuals; 10.92% of total), *M. communis* (452 individuals; 7.69% of total), *L. floridanum* (377 individuals; 6.41% of total), *L. nymphale* (349 individuals; 5.94% of total), *L. puteulanum/tegulare* (332 individuals; 5.65% of total), and *M. bimaculatus* (330 individuals; 5.61% of total).

Total mean bee catches ranged from ~70 bees/month in the 8-13-year stand age class to ~330 bees/month in the 0-3-year stand age class. Bee catches were different among stand age classes [$F_{(3,25)} = 12.047$, $p < 0.001$] (Figure 2.1). Bee catches were ~80-367% greater in the 0-3-year stand age class than all the other stand age classes ($p < 0.001$ – 0.0.34). There were also ~159% more bees captured in the 4-7-year stand age class than the 8-13-year stand age class ($p = 0.034$).

At the species-level, trap catches of *C. floridana* were different among age classes [$F_{(3,25)} = 5.377$, $p = 0.005$]. The 4-7-year-old forests had more *C. floridan*a caught than rest of the age classes ($p = 0.007$-0.039) (Figure 2.2A). The catches of *L. floridanum* were different among stand age classes [$F_{(3,25)} = 9.267$, $p = 0.002$] where more *L. floridanum* were caught in the 0-3-year stand age class than rest of the age classes (p <0.001-0.006) (Figure 2.2B). The catches of *Melissodes communis* differed among age classes [$\chi^2_{(3)} = 18.168$, $p = 0.004$]. The 0-3-year stand age class had more *M. communis* caught than the 8-13-year stand age class ($p = 0.001$) (Figure 2.2C). The catches of *Melissodes bimaculatus* differed among stand age classes [$F_{(3,25)} = 3.699$, $p = 0.025$], and there was also a significant effect of the block [$F_{(3,25)} = 4.574$, $p = 0.011$]. More *M. bimaculatus* were caught in the 0-3-year than the 8-13-year stand age class ($p = 0.018$) (Figure 2.2D). The catches of *L. nymphale* were different among stand age classes [$F_{(3,25)} = 8.29$, $p = 0.0005$] with greater catches in the 0-3-year old than the other three age classes (p = 0.004 - 0.010) (Figure 2.2E). The catches of *L. reticulatum* and *L. puteulanum/tegulare* were not different among stand age classes (p = 0.091-0.915).

Bee species richness was different among stand age classes [$F_{(3,28)} = 11.42$, $p < 0.001$] (Figure 2.3A). The 0-3-year-old forests had higher species richness than the 4-7- ($p = 0.02$) and 8-13-year ($p < 0.001$) old forests. Also, the 14-20-year-old had the higher species richness than the 8-13-year-old forest ($p = 0.006$). The rarefied species richness was also different among stand age classes [$F_{(3,28)} = 4.977$, $p = 0.007$](Figure 2.3B). The rarefied species richness was higher in the 14-20-year forests when compared to the 4-7 ($p = 0.039$) and 8-13 ($p = 0.036$) year old forests.

Canonical correspondence analysis showed that eight stand attributes tested explained 57% of the variation in the bee species composition. Stand attributes differed in how they affected the species composition [$F_{(13,18)} = 1.85$, $p = 0.001$]. Significant variables included percent canopy openness ($p = 0.003$), percent cover by woody debris class 1 ($p = 0.050$), percent plants flowering ($p = 0.043$), litter depth ($p = 0.014$), and number of snags ($p = 0.049$) (Figure

2.4). On the CCA ordination plot for sites, stands in the 0-3-year-old forests were associated with higher canopy openness, percent understory plants flowering, and woody debris in decay class 1 (least decayed), and lower litter depth and number of snags. Stands in the other age classes were associated with lower canopy openness, percent understory plants flowering, and woody debris in decay class 1, and higher litter depth and number of snags (Figure 2.4A). On the CCA ordination plot for species, most of the species overlapped in the central area. However, some soil-nesting species from the genera *Lasioglossum* and *Melissodes* were associated with greater canopy openness. Additionally, some species from the genus *Ceratina* that are cavity/deadwood nesters were associated with greater snags (Figure 2.4B).

Overall, there were 14 indicator species and of these 13 were soil nesting, one was cavity nesting, eight were solitary, six were social, 12 were generalist, and two were specialist. Also, seven species were small, six were medium, and one was large. One was active in early season, 10 in mid-season, and three in late season (Table 2.3). There were five species associated only with the 0-3-year stand age class, and all of these were soil nesting species. Additionally, a total of seven other species were associated with the 0-3-year stand age class along with the 14-20-year stand age class (1 species) and the 14-20 and 4-7-year (6 species). Two species were associated with the 4-7, 8-13, and 14-20-year stand age classes. Of these one was soil nesting, and the other was cavity nesting. Our second most captured species *L. floridanum*, was associated with the first, second, and fourth age classes and is also soil nesting. No species were found to be associated with any other single age class aside from the 0-3-year stand age class.

Functional dispersion was different among stand age classes [$\chi^2_{(3)} = 14.91$, $p = 0.002$] (Figure 2.5A). It was greater in the 0-3-year stand age class than in the 4-7-year ($p = 0.049$) and 8-13-year stand age classes ($p = 0.010$). Additionally, functional dispersion was greater in the

14-20-year stand age class than the 8-13-year (p = 0.036). A greater functional dispersion indicates greater beta diversity in that stand age class. Functional evenness was not different among age classes [$\chi^2_{(3)} = 4.69$, p = 0.196] (Figure 2.5B) indicating that different functional groups were evenly distributed among forest ages.

Linear models indicated that 2021 bee catches, and rarefied richness were not related to plant species richness and plant stems (p = 0.228 - 0.896). However, there was a positive relationship between bee catches and rarefied richness and percent plant cover (p = 0.018 and 0.038, respectively) (Figure 2.6 A-B). Interestingly, there were no linear relationships between September only bee richness or catches with any of the plant variables (p = 0.242 - 0.762).

Discussion

In two years, we caught 5,933 bee adults represented by 88 species indicating a rich community of native bees in these working pine forests in the southeastern U.S. The major trends observed in our study were as follows: 1) native bees were most numerous in the early establishment stands (0-3 years); 2) native bees had the greatest alpha and beta diversity in the early establishment and post-thinned stands (0-3 years and 14-20 years); 3) different stand attributes drove the bee communities in the early establishment stands and the older stands; 4) a group of species of bees were trapped primarily in the early establishment stands and another group was using both the early establishment and the older stands. Hence, native bee abundance, species richness and diversity, and composition differed across the four stand age classes of pine forests.

Native bee catches were greatest in the 0-3-year-old stands, and species richness of native bees was greater in the 0-3 and the 14-20-year-old stands. In contrast, the lowest bee catches, and species richness was in the 8-13-year-old stands. The other age classes tended to have more open canopies than the 8-13-year-old stands. The average canopy openness for the 0-3-, 4-7-, and 14-20-year-old stands was ~56% open versus the 8-13-year-old stands which had ~15% canopy openness. More open canopy conditions allow more light availability to the understory plants, and hence, a greater potential for floral resources (Romey et al., 2007, Lettow et al., 2014, Gelles et al., 2022). In addition, there were increased nesting resources in these age classes, such as increased bare ground and woody debris. In evidence, the average bare ground percentage was ~15% in the 0-3-, 4-7-, and 14-20-year-old stands and only ~4% in the 8-13-year stands where it was mainly covered by pine needle litter. The average woody debris cover was ~16% for the 8-13-year-old stands and ~21% for the others. Similar to our study, many previous studies have found a greater abundance and species richness of bees in clearcut areas (Proctor et al., 2012, Hanula et al., 2015, Rubene et al., 2015, Roberts et al., 2017, Miljanic et al., 2019, Mullally et al., 2019, Odanaka et al., 2020, Fortuin and Gandhi, 2021) and also older thinned forests (Hanula et al., 2015, Breland et al., 2018, Odanaka et al., 2020, Odanaka and Rehan, 2020). While results are consistent with these studies, we also had greater catches and species richness in the 4-7-year stand age class. Other studies often leave out the “middle” successional stages of forests (Odanaka and Rehan, 2020) that haven’t yet reached canopy closure, so these 4-7 year old stands may have more similar conditions to the 0-3-year stands. Hence, managed loblolly pine forests from clearcut to canopy closure (~age 7) and after thinning (~age 14) are important for maintaining native bees.

Functional dispersion was greater in the 0-3 and 14-20-year stand age classes. High functional dispersion indicated that these stand age classes have a greater beta diversity. Greater functional dispersion in early establishment stands contrasts with other studies, however these other studies compared clearcuts to other non-managed forest types that may have different forest structures with more resources for bees (Loy et al., 2020, Fortuin and Gandhi, 2021). Functional evenness was not different among age classes, suggesting that age classes did not support different functional groups. Similar functional evenness across stand ages could be explained by the variation among habitats in the older stands (4-7, 8-13, and 14-20 years) as they were all interspersed in the ordination plot indicating that these habitats shared similar characteristics and hence, bee community composition.

Ceratina floridana was the most common species caught with the most individuals being caught in the 4-7-year-old forests. This species is cavity nesting and nests in deadwood or pithy stems (Wilson and Messinger, 2015), which were more abundant in older verses early establishment stands. Another study in this region found another species of *Ceratina* to be associated with older forests rather than early establishment stands (Fortuin and Gandhi, 2021). *Lasioglossum floridanum*, *L. nymphale, Melissodes communis*, and *M. bimaculatus* all had the most individuals caught in the 0-3-year age class. All these species are soil nesting, and previous studies in the region have found that clearcuts or more open canopy forests favor soil nesting groups (Fortuin and Gandhi, 2021, Ulyshen et al., 2021).

There were five indicator bee species for the 0-3-year age class only, along with seven other indicator species for a combination of stand age classes. All of these 12 species are soil nesting bees. As mentioned previously, clearcuts favor soil nesting groups (Fortuin and Gandhi, 2021), likely due to a higher presence of bare soil used for nesting. There were no other indicator species for any other single age class besides the 0-3-year old forests. Hence, there is a distinct community of bees present in the 0-3-year stand age class that likely utilizes these stand ages for both foraging and nesting. Having distinct community of bees in the early establishment stands is consistent with the ordination results, as all the 0-3-stand age classes had unique species composition. However, there were also a group of soil nesting bee species that utilized both the 0-3-year stand age class and one or more of the older stand age classes. These soil nesting bees likely nest in areas of bare soil either in the clearcuts or open areas of the forest and then may forage or utilize other resources in the forest. Most of the species in this group are either medium or large sized, so foraging and nesting in different areas is possible, as foraging distances in wild bees are determined by body size (Gathmann and Tscharntke, 2002, Greenleaf et al., 2007). Only one indicator species was cavity nesting species (*Ceratina calcarata* Robertson), and it was associated with the 4-7-, 8-13, and 14–20-year age classes, which would have more available snags and downed wood for cavity nesting. Overall, there was bee community utilizing only the 0-3-year (clearcut/recently established) stand age class and another bee community utilizing a combination of the clearcut and other older stands. Although the 0-3-year stand age class had the highest number of catches of bees and high species richness, the other stands were also important for certain bee species.

Eight stand attributes explained 57% of the variation in the bee community. The stand attributes that affected the bee species distribution were canopy openness, percent cover by woody debris class 1, percentage of plants flowering, litter depth, and number of snags. Ordination analyses indicated that the 0-3-year stand age classes clustered close to the canopy openness, percent plants flowering, and woody debris class 1 (least decayed). The litter depth and the number of snags were also significant for some of the 4-7-, 8-13-, and 14-20-year-old stands. Within these forested stand age classes, different variables may be driving the bee community's response, and therefore, retention of these features may be critical to maintenance of bee communities over long-term. Greater abundance and diversity of bees with increasing canopy openness (Romey et al., 2007, Nielsen et al., 2011, Hanula et al., 2015, Odanaka et al., 2020), greater floral resources (Nielsen et al., 2011, Rubene et al., 2015, Ulyshen et al., 2021), and more woody debris in clearcuts (Nielsen et al., 2011, Loy et al., 2020, Gelles et al., 2022) have been previously documented.

As expected, there was a positive relationship between 2021 bee catches and rarefied richness and understory plant cover (Romey et al., 2007, Rubene et al., 2015). Since the R^2 values ranged from 0.273 to 0.337, this relationship is weak likely because plant cover data was only collected towards the end of the season (August), so plants present only in spring or early summer may have been missed. Late-season plant species data may explain why we did not find a relationship between bee catches and rarefied richness and plant species richness, although the identity of the plant species may be critical. Future work on native bee habitats in forests in this region may aim to collect plant data throughout the season for a more complete picture.

Conclusions

Overall, managed loblolly pine forest stands with more open canopy conditions supported native bee communities. Both alpha and beta diversity were greater in early establishment and mature thinned stands, and pre-thinned, closing canopy also supported high bee numbers and greater numbers of species than pre-thinned, closed canopy stands. Although there was a distinct bee community present in recently established stands, other species utilized both early establishment and older stands in this region. A mosaic of habitats spanning a variety of age classes would be beneficial to maintaining native bees in this region. Many bee species require a variety of floral and nesting resources present in both forest and open areas, so having multiple stand types close together may benefit them (Gathmann and Tscharntke, 2002, Roulston and Goodell, 2011). Thinning and/or wider spacing of trees at planting for a more open canopy in these forests may further benefit these bees. Future studies on native bees in conifer-dominated forests may focus on the landscape configuration and density of various age classes, thinning scenarios at different basal areas, and shortening the presence of dense closed-canopy stands to create more favorable conditions for bees for their long-term conservation in managed pine ecosystems.

Tables

Table 2.1: Mean (± SE) stand attributes of 0-3, 4-7, 8-13, and 14-20 years old, Southeastern Plains ecoregion, Georgia.

Age Class	**0-3 years**	**4-7 years**	**8-13 years**	**14-20 years**
Mean Canopy Openness (%)	100 ± 0	34.303 ± 5.038	16.401 ± 2.483	32.036 ± 2.915
Mean Height of Pines (m)	2.925 ± 0.224*	5.817 ± 0.327	10.013 ± 0.388	13.322 ± 0.452
Mean Age of Pines	1.625 ± 0.232	5.5 ± 0.255	10 ± 0.313	16.75 ± 0.451
Mean Tree Density (trees/ha)	889.146 ± 101.73*	1126.819 ± 89.376	1198.875 ± 68.091	681.714 ± 60.039
Mean Pine Density (trees/ha)	880.657 ± 104.13*	1106.127 ± 84.157	1119.39 ± 61.957	575.61 ± 48.996
Mean Hardwood Density (trees/ha)	8.489 ± 4.879*	120.692 ± 33.24	79.485 ± 37.059	106.103 ± 25.395
Mean Tree Basal Area (m^2/ha)	1.169 ± 0.174*	10.628 ± 1.051	27.045 ± 4.049	21.417 ± 1.174
Mean Pine Basal Area (m^2/ha)	1.157 ± 0.175*	10.497 ± 1.051	26.858 ± 4.057	20.881 ± 1.12
Mean Hardwood Basal Area (m^2/ha)	0.012 ± 0.007*	0.131 ± 0.031	0.188 ± 0.061	0.53 ± 0.137

*For the 0-3 year age class, some trees were too small to measure and those are omitted in averages.

Table 2.2: Number of native bee species in each stand age class in managed loblolly pine forests in Southeastern Plains ecoregion, Georgia.

HYMENOPTERA FAMILY	HYMENOPTERA SPECIES	STAND AGE CLASS (YEARS)				SPECIES TOTAL
		0-3	4-7	8-13	14-20	
Andrenidae	*Perdita bishopp*i Cockerell	2	0	0	2	4
Andrenidae	*Perdita boltoniae* Robertson	0	0	0	8	8
Andrenidae	*Perdita nubila* Timberlake	1	0	0	1	2
Andrenidae	*Perdita sp*	0	1	0	0	1
Apidae	*Bombus bimaculatus* Cresson	2	2	3	1	8
Apidae	*Bombus griseocolis* (De Geer)	1	0	0	2	3
Apidae	*Bombus impatiens* Cresson	52	45	23	47	167
Apidae	*Bombus pensylvanicus* (De Geer)	87	59	25	64	235
Apidae	*Ceratina calcarata* Robertson	7	25	72	28	132
Apidae	*Ceratina cockerelli* H.S. Smith	0	1	0	0	1
Apidae	*Ceratina dupla* Say	5	6	1	2	14
Apidae	*Ceratina floridana* Mitchell	42	485	71	59	657
Apidae	*Ceratina floridana* Mitchell / *dupla* Say	2	32	0	4	38
Apidae	*Ceratina floridana* Mitchell / *strenua* Smith	8	47	5	5	65
Apidae	*Ceratina sp*	0	10	1	2	13
Apidae	*Ceratina strenua* Smith	0	1	1	2	4
Apidae	*Melissodes bimaculatus* (Lepeletier)	177	63	9	81	330
Apidae	*Melissodes boltoniae* Robertson	6	3	0	5	14
Apidae	*Melissodes communis* Cresson	324	55	19	54	452
Apidae	*Melissodes comptoides* Robertson	49	6	0	11	66
Apidae	*Melissodes denticulatus* Smith	1	0	0	0	1
Apidae	*Melissodes dentiventris* Smith	1	0	0	1	2
Apidae	*Melissodes mitchelli* LaBerge	0	1	0	0	1
Apidae	*Melissodes sp*	3	0	0	0	3
Apidae	*Melissodes tepaneca* Cresson	73	2	2	4	81
Apidae	*Melitoma taurea* (Say)	61	21	7	90	179
Apidae	*Peponapis pruinosa* (Say)	5	1	0	2	8
Apidae	*Ptilothrix bombiformis* (Cresson)	66	30	0	35	131
Apidae	*Svastra aegis* (LaBerge)	1	0	0	0	1
Apidae	*Svastra atripes* (Cresson)	199	49	0	34	282
Apidae	*Svastra obliqua* (Say)	182	10	1	8	201
Apidae	*Svastra sp*	1	0	0	0	1
Apidae	*Triepeolus Cressonii* (Robertson)	0	0	0	1	1
Apidae	*Triepeolus sp*	0	0	0	1	1
Apidae	*Xylocopa micans* Lepeletier	0	1	0	0	1
Apidae	*Xylocopa virginica* (Linnaeus)	3	0	0	0	3
Colletidae	*Colletes brevicornis* Robertson	1	0	0	0	1
Colletidae	*Hylaeus affinis* (Smith) / *modestus* Say	0	0	0	1	1
Halictidae	*Agapostemon splendens* (Lepeletier)	26	3	0	5	34
Halictidae	*Agapostemon virescens* (Fabricius)	1	0	0	0	1
Halictidae	*Augochlora pura* (Say)	4	8	13	11	36
Halictidae	*Augochlorella aurata* (Smith)	5	49	30	45	129
Halictidae	*Augochloropsis metallica fulgida* (Smith)	0	0	1	2	3
Halictidae	*Halictus parallelus* Say	4	0	0	1	5

Halictidae	*Halictus poeyi* Lepeletier	75	11	10	12	108
Halictidae	*Lasioglossum admirandum* (Sandhouse)	1	0	0	1	2
Halictidae	*Lasioglossum apopkense* (Robertson)	14	5	0	4	23
Halictidae	*Lasioglossum callidum* (Sandhouse)	6	2	0	1	9
Halictidae	*Lasiogolssum callidum* (Sandhouse) / *trigeminum* Gibbs	0	0	0	1	1
Halictidae	*Lasioglossum coreopsis* (Robertson)	2	0	0	2	4
Halictidae	*Lasioglossum creberrimum* (Smith)	1	0	0	0	1
Halictidae	*Lasioglossum floridanum* (Robertson)	265	53	15	44	377
Halictidae	*Lasioglossum foxii* (Robertson)	0	4	6	1	11
Halictidae	*Lasioglossum hitchensi* Gibbs	4	7	3	3	17
Halictidae	*Lasioglossum illinoense* (Robertson)	5	0	1	2	8
Halictidae	*Lasioglossum imitatum* (Smith)	10	9	3	0	22
Halictidae	*Lasioglossum leucocomus* (Lovell)	12	0	0	0	12
Halictidae	*Lasioglossum leviense* (Mitchell)	5	4	3	2	14
Halictidae	*Lasioglossum longifrons* (Baker)	117	2	0	1	120
Halictidae	*Lasioglossum lustrans* (Cockerell)	5	0	0	0	5
Halictidae	*Lasioglossum nymphale* (Smith)	280	30	4	35	349
Halictidae	*Lasioglossum pectoral* (Smith)	44	84	64	71	263
Halictidae	*Lasioglossum pilosum* (Smith)	57	0	0	0	57
Halictidae	*Lasioglossum platyparium* (Robertson)	1	0	0	0	1
Halictidae	*Lasioglossum puteulanum* Gibbs / *tegulare* (Robertson)	107	75	35	115	332
Halictidae	*Lasioglossum raleighense* (Crawford)	0	1	0	2	3
Halictidae	*Lasioglossum reticulatum* (Robertson)	207	205	139	91	642
Halictidae	*Lasioglossum smilacinae* (Robertson)	0	1	0	0	1
Halictidae	*Lasioglossum spp*	25	8	7	7	47
Halictidae	*Lasioglossum trigeminum* Gibbs	14	2	1	0	17
Halictidae	*Lasioglossum vierecki* (Crawford)	4	2	0	0	6
Halictidae	*Lasioglossum weemsi* (Mitchell)	15	14	6	9	44
Halictidae	*Sphecodes mandibularis* Cresson	0	0	4	0	4
Megachilidae	*Ashmeadiella floridana* (Robertson)	1	0	0	0	1
Megachilidae	*Hoplitis pilosifrons* (Cresson)	3	0	0	0	3
Megachilidae	*Hoplitis producta* (Cresson)	0	2	0	0	2
Megachilidae	*Lithurgopsis gibbosa* (Smith)	0	0	0	1	1
Megachilidae	*Megachile albitarsis* Cresson	0	0	0	2	2
Megachilidae	*Megachile georgica* Cresson	3	0	0	6	9
Megachilidae	*Megachile integra* Cresson	1	0	0	0	1
Megachilidae	*Megachile mendica* Cresson	2	0	1	0	3
Megachilidae	*Megachile petulans* Cresson	1	0	0	0	1
Megachilidae	*Megachile sculpturalis* Smith	2	0	0	0	2
Megachilidae	*Megachile texana* Cresson	8	1	0	1	10
Megachilidae	*Osmia atriventris* Cresson	0	1	0	0	1
Megachilidae	*Osmia inspergens* Lovell and Cockerell	0	0	1	0	1
Megachilidae	*Osmia sandhouseae* Mitchell	7	6	0	7	20
STAND AGE CLASS TOTAL		**2706**	**1545**	**587**	**1040**	**5878**
TOTAL NUMBER OF SPECIES		**69**	**57**	**34**	**58**	**87**

Table 2.3: Bee species with functional traits that were indicator species in four stand age classes in managed loblolly pine forests in Southeastern Plains ecoregion, Georgia.

AGE CLASS	BEE SPECIES	P-VALUE[a]	NESTING[b]	SOCIALITY	DIET	SPECIALIST PLANT FAMILY	SIZE	SEASON[c]
0-3	*Lasioglossum longifrons*	0.0001	Soil	Social	Generalist	NA	small	Early
0-3	*Svastra obliqua*	0.0002	Soil	Solitary	Specialist	Asteraceae	med	Late
0-3	*Halictus poeyi*	0.029	Soil	Social	Generalist	NA	small	Mid
0-3	*Agapostemon splendens*	0.022	Soil	Solitary	Generalist	NA	med	Mid
0-3	*Lasioglossum pilosum*	0.048	Soil	Social	Generalist	NA	small	Mid
0-3 + 14-20	*Melissodes comptoides*	0.0053	Soil	Solitary	Generalist	NA	med	Late
0-3 + 4-7 + 14-20	*Lasioglossum floridanum*	0.012	Soil	Social	Generalist	NA	small	Mid
0-3 + 4-7 + 14-20	*Melissodes communis*	0.001	Soil	Solitary	Generalist	NA	med	Mid
0-3 + 4-7 + 14-20	*Melissodes bimaculatus*	0.048	Soil	Solitary	Generalist	NA	med	Mid
0-3 + 4-7 + 14-20	*Svastra atripes*	0.0028	Soil	Solitary	Generalist	NA	large	Late
0-3 + 4-7 + 14-20	*Ptilothrix bombiformis*	0.0064	Soil	Solitary	Specialist	Convolvulaceae	med	Mid
0-3 + 4-7 + 14-20	*Lasioglossum apopkense*	0.022	Soil	Social	Generalist	NA	small	Mid
4-7 + 8-13 + 14-20	*Augochlorella aurata*	0.017	Soil	Social	Generalist	NA	small	Mid
4-7 + 8-13 + 14-20	*Ceratina calcarata*	0.017	Cavity	Solitary	Generalist	NA	small	Mid

[a] P-value for permutation test to determine if taxon is an indicator species.

[b] Nesting refers to the primary substrate the bee species uses for nesting. Soil-nesting species nest in bare soil. Cavity nesting bees nest in deadwood.

Figures

Figure 2.1: Native bee catches per month for each stand age class. Circles represent means and bars represent standard errors. Different letters represent significant differences among stand age classes (Tukey's HSD).

Figure 2.2: Catches per month of five of the seven most common native bee species for each stand age class: *Ceratina floridana* (A), *Lasioglossum floridanum* (B), *Melissodes communis* (C), *Melissodes bimaculatus* (D), and *Lasioglossum nymphale* (E). Circles indicate means, and bars indicate standard errors. Different letters represent significant differences among stand age classes (Tukey's HSD [A, B, D, E] and Dunn's test [C]).

Figure 2.3: Mean bee species richness (A) and mean rarefied species richness (B) for each stand age class with standard error bars. Different letters represent significant differences using Tukey's HSD.

Figure 2.4: Canonical correspondence analysis of species composition for sites (A) and species (B) to determine which stand attributes explain a significant amount of the variance in native bee species distribution. Stand attributes (tree density (trees/ha), number of snags, snags average decay class, percent cover of woody debris in decay class 1-5, percent understory plant cover, percent understory plants flowering, percent canopy openness, litter depth (cm), and percent bare ground) explained 57% of the variation in bee species composition [$F_{(13,18)} = 1.85$, $p = 0.001$]. Significant habitat characteristics are marked with *.

Figure 2.5: Functional dispersion (A) and functional evenness (B) among stand age classes. Circles represent means and bars represent stand errors. Different letters represent significant differences among stand age classes (A; Dunn's test).

Figure 2.6: Linear regressions of 2021 bee rarefied richness (A), and 2021 bee catches (B) and percent plant cover.

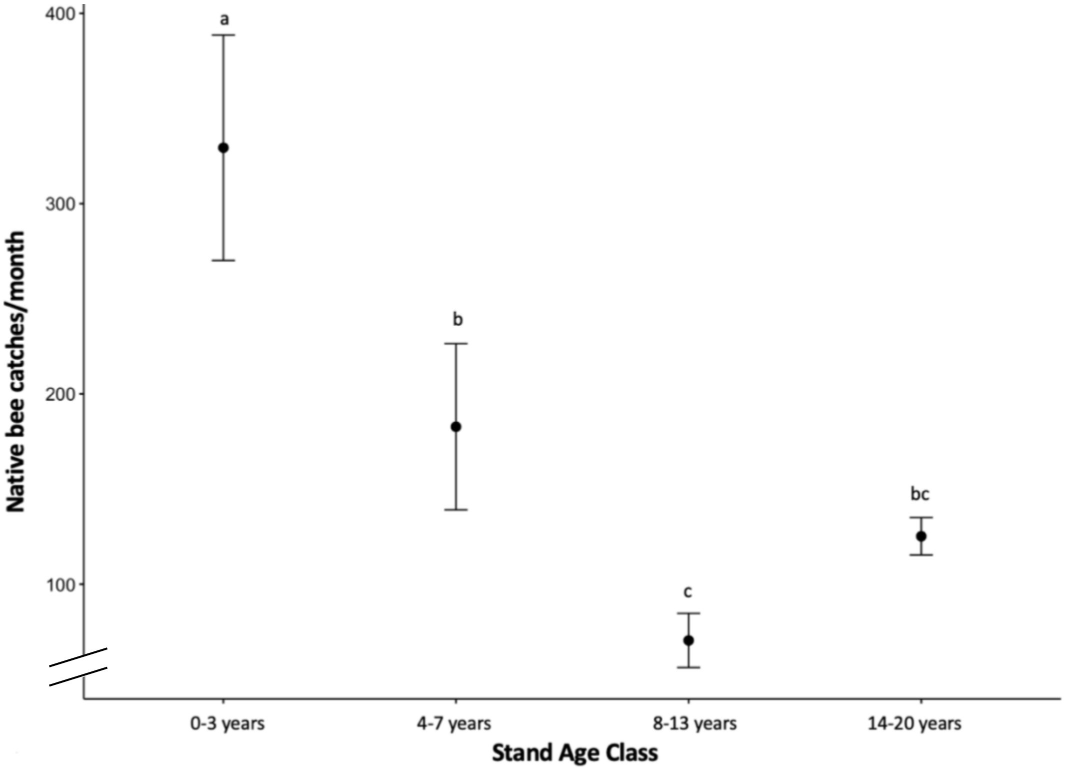
400
300
200
100
a
b
c
bc
Native bee catches/month
0-3 years
4-7 years
8-13 years
14-20 years
Stand Age Class

Figure 2.1

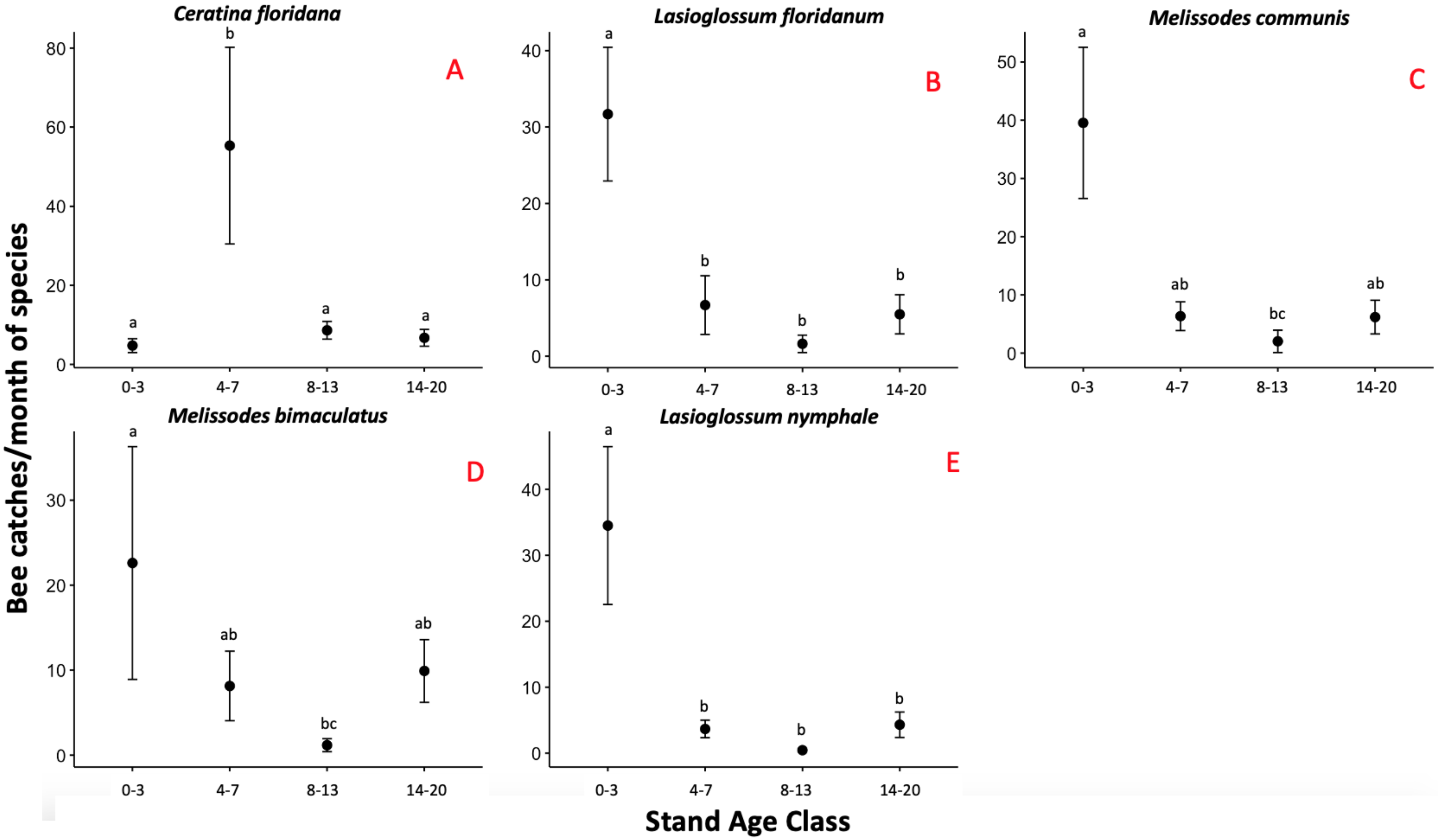
Ceratina floridana
A
Lasioglossum floridanum
B
Melissodes communis
C
Melissodes bimaculatus
D
Lasioglossum nymphale
E
Bee catches/month of species
Stand Age Class
0-3
4-7
8-13
14-20
a
b
ab
bc
0
10
20
30
40
50
60
80

Figure 2.2

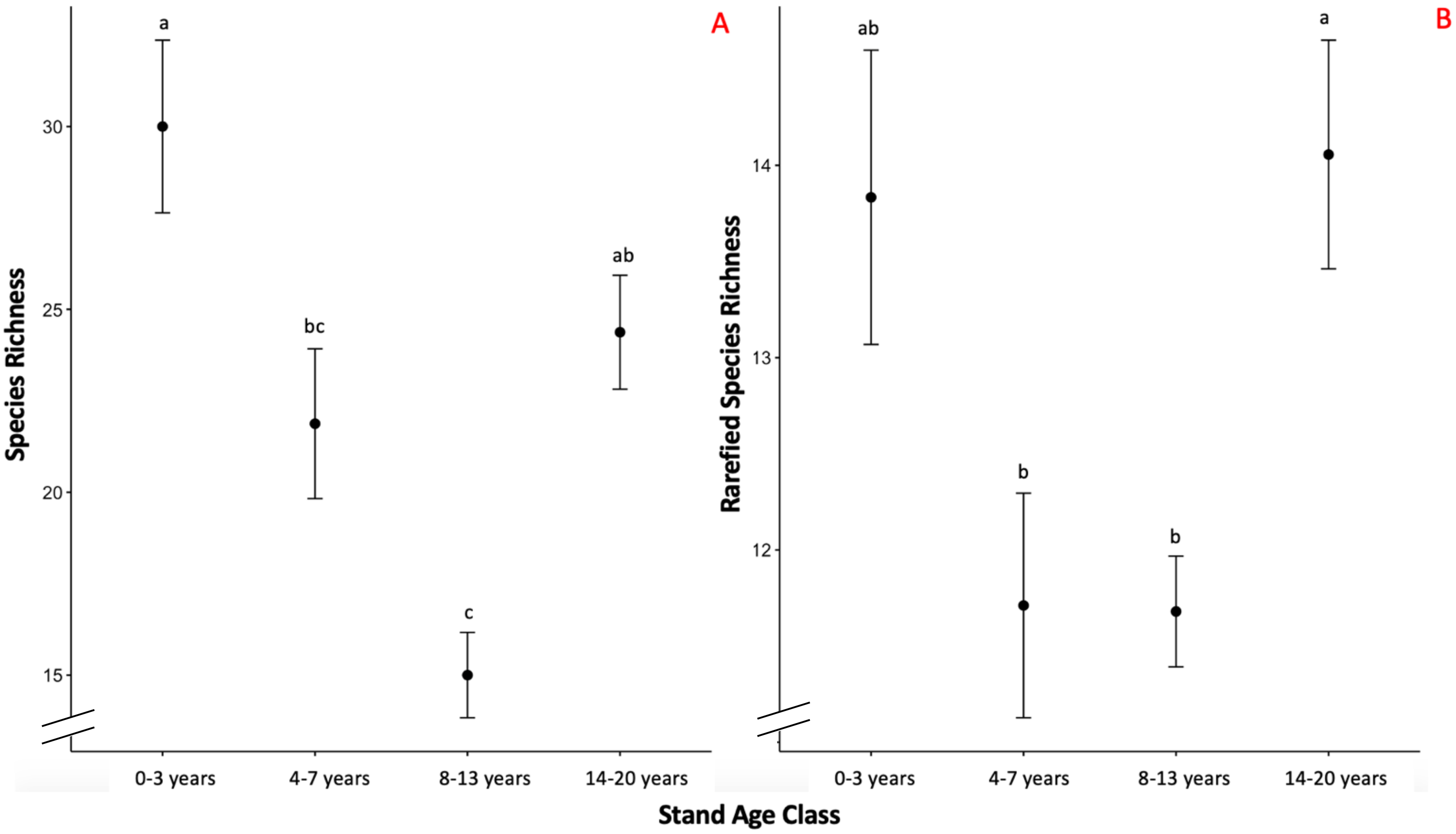
A
B
Species Richness
Rarefied Species Richness
30
25
20
15
14
13
12
a
bc
c
ab
ab
b
b
a
0-3 years
4-7 years
8-13 years
14-20 years
Stand Age Class

Figure 2.3

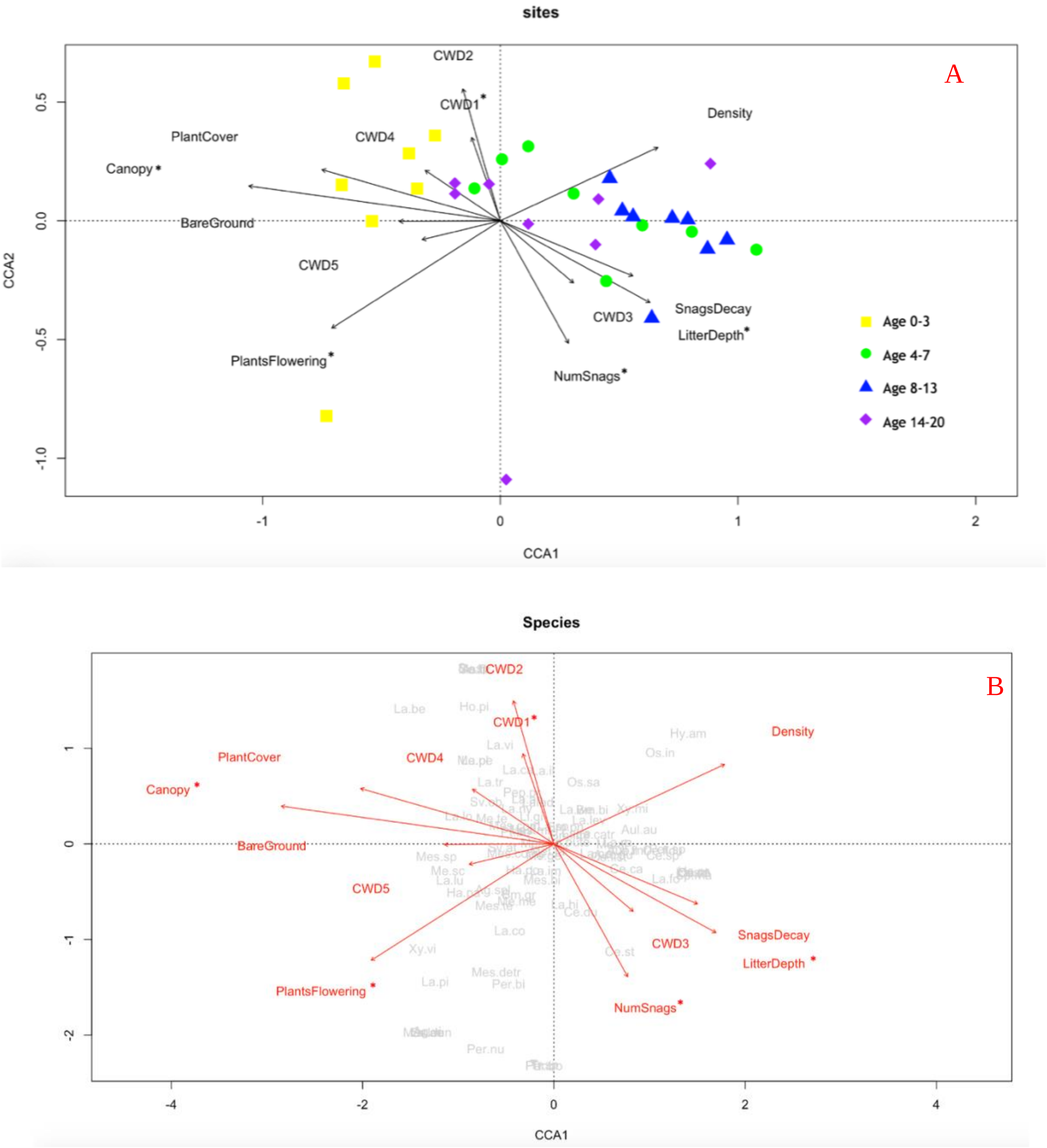
sites
A
CWD2
CWD1*
Density
PlantCover
CWD4
Canopy*
BareGround
CWD5
CWD3
SnagsDecay
LitterDepth*
PlantsFlowering*
NumSnags*
Age 0-3
Age 4-7
Age 8-13
Age 14-20
CCA2
0.5
0.0
-0.5
-1.0
-1
0
1
2
CCA1
Species
B
CWD2
La.be
Ho.pi
CWD1*
Hy.am
Density
Os.in
La.vi
PlantCover
CWD4
Me.pe
Canopy*
La.tr
Os.sa
Sv.ob
La.ny
La.bi
Xy.mi
La.lo
Me.te
La.le
Aul.au
La.catr
BareGround
Mes.sp
Sv.at
Ce.sp
Me.sc
La.lu
Ce.ca
Ha.im
Mes.bi
La.fo
CWD5
Ag.sp
Em.gr
Mes.te
La.hi
Ce.du
La.co
SnagsDecay
Xy.vi
Ce.st
CWD3
LitterDepth*
Mes.detr
La.pi
Per.bi
PlantsFlowering*
NumSnags*
Per.nu
1
0
-1
-2
-4
-2
0
2
4
CCA1

Figure 2.4

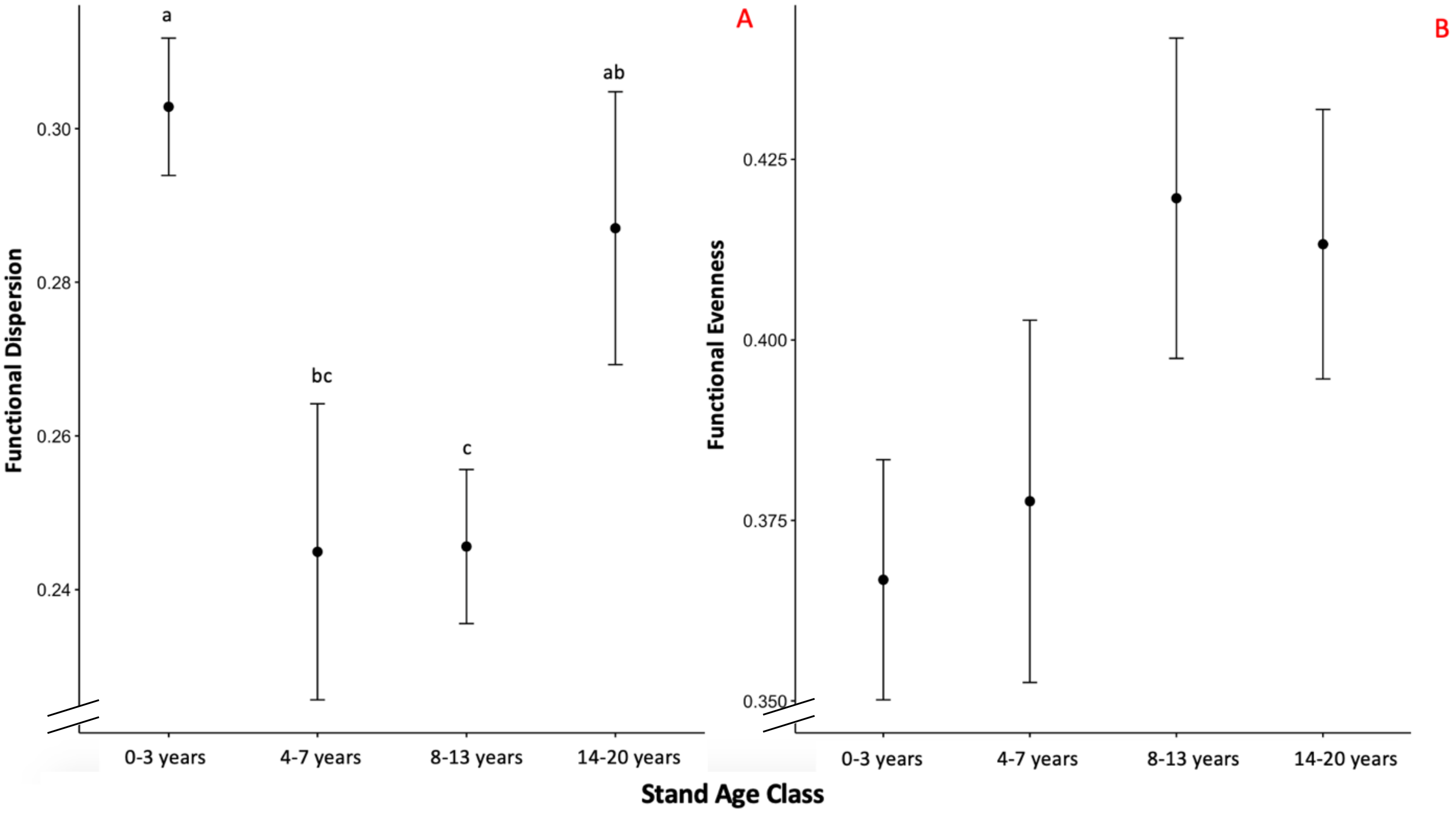
A
B
Functional Dispersion
0.30
0.28
0.26
0.24
a
bc
c
ab
Functional Evenness
0.425
0.400
0.375
0.350
0-3 years
4-7 years
8-13 years
14-20 years
0-3 years
4-7 years
8-13 years
14-20 years
Stand Age Class

Figure 2.5

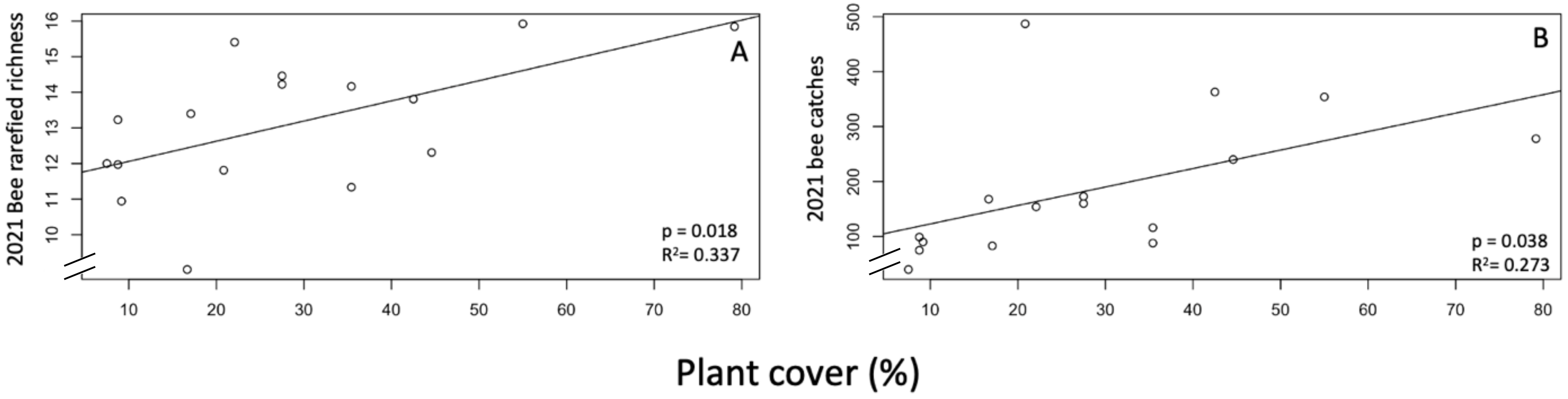
2021 Bee rarefied richness
16
15
14
13
12
11
10
A
p = 0.018
R²= 0.337
2021 bee catches
500
400
300
200
100
B
p = 0.038
R²= 0.273
10
20
30
40
50
60
70
80
Plant cover (%)

Figure 2.6

CHAPTER 3

PAN AND BLUE VANE TRAPS SAMPLE DIFFERENT COMMUNITIES OF NATIVE BEES IN PINE FORESTS IN THE SOUTHEASTERN U.S.[2]

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[2] Favorito, C.M., Barnes, B.F., Briggs, E.L., Fortuin, C.C., Greene, D.U., Larsen-Gray, A.L., and K.J.K. Gandhi. To be submitted to Environmental Entomology.

Abstract

Native bees are crucial pollinators for both economically important crops and ecologically important forest plants. Managed loblolly pine forests are an extensive land cover in the Southeast U.S., but native bees in these areas are largely understudied. Effective methods for sampling native bees in these areas need to be evaluated. The goal of this study was to compare the effectiveness of two common trapping methods, pan traps and blue vane traps, which have yet to be compared in pine forests. Both trap types captured similar species diversity in this environment. Blue vane traps captured greater numbers of bees than pan traps. Blue vane traps also caught greater functional diversity of bees. Ordination and indicator species analyses revealed that these two trap types captured largely distinct groups of species. These results indicate that using both trap types concurrently is the best method to discover as much of the bee community as possible, especially when active methods such as aerial or sweep netting are not feasible in dense forests or forests with little to no understory vegetation.

Introduction

The Southeast holds approximately 80 million hectares of managed private forest, making this a large potential habitat for native bees (Butler and Wear, 2013). Native bees are critical for pollinating plants in these forests, and for providing pollination services to nearby commercial crops (Klein et al., 2007, Kremen et al., 2007, Garibaldi et al., 2011, Moisset and Buchmann, 2011, Ollerton et al., 2011). A greater diversity of native bees leads to a more diverse plant community in forests (Fontaine et al., 2006). Additionally, pollination by native bees increases plant seed production (Frund et al., 2013). In general, native bees in conifer forests are understudied (Rivers et al., 2018), so there is a need to determine effective sampling methods for these bees in this type of habitat.

There are many potential passive and active methods for sampling native bees. Many of these methods have been tested and compared in agricultural and grassland settings (Joshi et al., 2015, Rhoades et al., 2017), but few have been tested in forests. Pan traps (sometimes called bowl traps or bee bowls) are colored plastic cups or bowls usually ranging in size from about 96-355 mL. They are typically filled with water and odorless dish detergent to break the surface tension. Pan traps are commonly used because they are efficient and cost effective (Westphal et al., 2008). They are more effective than malaise traps in forest environments for capturing native bees (Campbell and Hanula, 2007, McCravy and Ruholl, 2017). Vane traps (yellow or blue vane traps) use two interconnecting ultraviolet semitransparent vanes on the top attached to a screw top funnel and a collecting jar. The collecting jar is usually a standard 1.9 L size and can be filled with soapy water or used dry. Blue vane traps are effective for sampling bees in both open and wooded habitats (Hall, 2018). Blue vane traps can capture a greater abundance and species richness of bees when compared to pan traps, but using both trap types can be beneficial as they can detect different bee communities in the same area (Joshi et al., 2015, Rhoades et al., 2017). The bees are attracted to both types of traps by their colors, as they are colored to mimic flower color that is attractive to bees (Kevan, 1972). Specific trap colors that reliably catch native bees are blue, yellow, and white for pan traps and blue for vane traps (Campbell and Hanula, 2007, Geroff et al., 2014, Hall, 2018). Pan traps catch more rare and smaller bodied bees, while blue vane traps catch larger bodied bees (Roulston et al., 2011, Geroff et al., 2014, Joshi et al., 2015).

Pine forests can have complex structures that can vary with the age of the forest, making active sampling for bees challenging. Active sampling in forests can often be more difficult than sampling in other habitats, such as prairies or row crop fields. Dense under- or mid- stories can make walking transects in these habitats for sweep netting difficult or impossible (Campbell and Hanula, 2007). Forest structure also varies with age, so standardizing protocols among stand age classes may not be possible, leading to problems with experimental design. For example, some stand ages may not possess flowering understory plants for targeted flower sampling or even any herbaceous vegetation for sweep netting (Roulston et al., 2011). Additionally, other active sampling methods, such as transect walks, can be subject to collector bias based on the collector’s skill level, potential microhabitat knowledge, and preference for larger or more colorful bees (Nielsen et al., 2011).

Considering the importance of vast conifer forests as repositories of native bee diversity, we aimed to evaluate the effectiveness of two commonly used trapping methods, pan traps and blue vane traps, in managed pine (*Pinus* spp.) stands in the Southeast U.S. Our objectives were to compare the native bee abundance and diversity for each of the traps, to determine if any native bee species were associated with a particular trap type, and to compare the functional diversity present in each trap type.

Methods

Study Sites

Study sites were loblolly pine (*Pinus taeda* L.) privately-owned managed forests in the southeastern Plains ecoregion of Georgia, U.S. Soils are classified as sandy loam, loamy sand, and sand Ultisols (Soil Survey Staff, 2021). The mean annual precipitation was 148.3 ± 1.3 cm for all sites with ranging from 124.5 - 177.0 cm (PRISM Climate Group, 2020). The mean annual temperature was 19.2 ± 0.04 °C ranging from 18.7 - 20.1°C (PRISM Climate Group, 2020). The mean elevation was 78.7 ± 1.4 m ranging from 57.9 - 103.9 m (PRISM Climate Group, 2020). Pine stands >2 ha from one of four stand age classes were selected. These were 0-3 years (early establishment), 4-7 years (pre-thinned, closing canopy), 8-13 years (pre-thinned, closed canopy), and 14-20 years (post-thinned, open canopy). On some of the sites there was a small hardwood component of mainly sweetgum (*Liquidambar styraciflua* L.), southern red oak (*Quercus falcata* Michx.), and water oak (*Quercus nigra* L.). Different stands were sampled in 2020 and 2021. A randomized complete block design was used with four blocks and 16 total stands per year. Blocks were >1 km apart to ensure independent samples. On each stand, three 10 m radius plots were established that were >50 m from each other and >15 m from any road. A total of 48 plots were sampled each year with 96 total plots for the study.

Bee Sampling

On each of the 96 plots, one blue vane trap (SpringStar, Inc.) and three colored pan traps were deployed. Pan traps were blue, yellow, and white 118 mL plastic cups (Solo brand) filled with water and odorless dish detergent (Figure 3.1). Each pan trap was placed on a wire plant prop stake approximately 0.5 m off the ground. The pan traps were placed approximately 5 m from the center of the plot at 120° angles from one another. These traps were set for 6-7 consecutive days per month from June-September 2020 and May-September 2021. Traps were emptied and reset after 3-4 days during the trapping periods.

Blue vane traps consisted of a 1.9 L yellow collecting jar with a screw top funnel and two interconnecting ultraviolet semitransparent blue polypropylene vanes on top (Figure 3.2). The jar was filled with a small amount of the same water and dish detergent mixture as the pan traps. Bees are attracted to the color, fly into the funnel, and become trapped in the jar. Blue vane traps were hung from a pole approximately 1.5 m off the ground in the center of each plot. They were all set concurrently with the pan traps.

Trap catches (bees and bycatch) were collected after each trapping period. The water was strained, and the specimens were stored in the freezer until they could be sorted and identified. Bees were prepared for identification by being washed with dish soap and water, dried and fluffed in a small clothes dryer, and pinned. Bees were identified to species using references (Michener, 2007, Ascher and Pickering, 2020) and by Sam Droege, United States Geological Survey. Specimens identified by lab members were also confirmed by S. Droege. The bee collection is deposited at the Georgia Museum of Natural History, University of Georgia, Athens.

Bee species were sorted into functional groups based on sociality, diet, size, and peak season using published literature and references (Mitchell, 1960, Michener, 2007, Gibbs, 2011, Williams et al., 2014, Wilson and Messinger, 2015, Ascher and Pickering, 2020, Fortuin and Gandhi, 2021, Messinger and Wilson, 2021).

- Sociality: All bee species were considered solitary or social. All species that have nests with individual queens, even if they nest in aggregate were classified as solitary. Species were classified as social if there is any level of cooperation within a colony.
- Diet: Bee species were sorted into specialist (oligolectic) and generalist (monolectic) groups. Oligolectic bees forage on a specific family or genus of plants, while monolectic bees forage on a wide variety of plants.
- Size: Bees species were sorted into size class based on lengths found in references. Small was 3.5- 9 mm, 9.5-15 mm was medium, and 15.5-22 mm was large.
- Peak season: Bee peak activity season was found using references and collected data. Species that are most active February-April were early season, May-July were mid-season, and August-October were late season.

Statistical Analyses

All the bees caught over the trapping season were combined for each stand and trap type (pan or blue vane). As there were differences in sampling effort for 2020 and 2021, the bee catch data were standardized by bee captures/month by dividing the total bees caught by the number of trapping days and multiplying by 30 (reflecting captures per month). Analyses were run in R (version 4.1.3) (R Core Team, 2022), and tests were considered significant at the $\alpha = 0.05$ level.

A two-way Analysis of Variance (ANOVA) was used to compare the standardized catches of bees caught in each trap-type including age class as a fixed effect, as well as the interaction of trap type and age class. Standardized catch data had non-normal residuals using the Shapiro-Wilks test, so they were transformed with a Box-Cox transformation. The ANOVA was run using the aov function and followed with Tukey’s post-hoc test.

Bee diversity between trap-types was evaluated using rarefied species richness via individual-based rarefaction to account for differences in sampling effort. The rarefied species richness for each replicate and trap type was estimated using the “rarefy” function in the R package “vegan” (Oksanen et al., 2020). The sample used was the smallest number of individual bees collected for one stand and trap type. The rarefied species richness was compared between trap types using a two-way ANOVA with trap type as the fixed effect, age class as a random effect, and the interaction of trap type and age class via the aov function and Tukey’s post-hoc test. The normality of residuals was tested using the Shapiro-Wilks test.

Indicator species analysis was used to compare the species associations between the trap types. Species with >20 individuals caught were included in this analysis. The multi-level pattern analysis (“multiplatt”) function was used in the R package “indispecies” with the indicator value index (“Ind.val.g”) as the species site association function (Dufrene and Legendre, 1997, De Cacers and Legendre, 2009). The function used a permutation test with 9,999 permutations to test if the associations were significant.

The diversity of functional groups of bees was evaluated between trap types by using two metrics, functional evenness and functional dispersion. Functional evenness (Feve) measures how evenly functional traits are distributed between groups (Villeger et al., 2010). Functional dispersion (Fdisp) is a metric that takes the distance of each species from the centroid in trait space and weights it by the species’ relative abundance (Laliberte and Legendre, 2010). Fdisp can also be considered a measure of beta diversity, or the variability of species distributions among different sampling units (Anderson et al., 2006). Feve and Fdisp were computed using the Distance-Based Functional Diversity Indices function (“dbFD”) in the “FD” package in R (Laliberte et al., 2014). A species-species distance matrix was generated and then a Principal

Coordinates Analysis (PCoA) was performed. The traits used to compute the metrics were sociality, diet, size class, and peak season. Then, a two-sample t-test was run on each of the metrics (Feve and Fdisp) to compare them between trap types. Equal variances between samples were verified using the “var.test” function. Additionally, the dominant functional traits for each stand age class and trap type were found using the Community-Weighted Mean (“CWM”) function.

Non-metric multidimensional scaling (NMDS) was used to plot species distributions between trap types. This ordination was run using the “metaMDS” function in the R package “vegan” (Oksanen et al., 2020). The function measures the distances between points in ordination space, running several times to find the best configuration before it reaches the best solution for the data. NMDS was run in two dimensions. Before running the analysis, data were square root transformed to lessen the influence of large counts and then divided by the number of days the traps were out to account for differences in sampling effort between the years of the study. Convex hulls were added to show the different trap types on the ordination plot.

Results

Over the two-year study 5,933 individual bees from 88 species were caught in all traps. Fifty-five *Apis mellifera* L. individuals were removed from the analyses. Blue vane traps caught 3,501 individuals from 66 species and pan traps caught 2,377 individuals from 73 species. The average (±SE) species richness caught per stand by blue vane traps was 16.844 (± 1.044) species and for pan traps was 14.313 (± 1.050) species. Sixty-six individuals could not be identified to species and were identified to the genus level (Table 3.1).

Standardized bee catches were different between trap types [$F_{1,56} = 10.552$, $p = 0.002$] with blue vane traps capturing ~47% more adult bees (Figure 3.3). Stand age class was also significant in this model [$F_{3, 56} = 23.039$, $p < 0.001$]. The 0–3-year stand age class had a greater catch than all other stand age classes (p ranged from <0.001 to 0.002). The 8–13-year stand age class also had a lower catch of bees than the 4-7- and 14-20-year stand age classes (p ranged from <0.001 to 0.003). The interaction effect of trap type*age class was not significant ($p = 0.736$).

Rarefied species richness was not different between trap types ($p = 0.551$). Stand age class was significant [$F_{3,56} = 3.307$, $p = 0.027$] (Figure 3.5). The 14-20-year stand age class had a greater rarefied species richness than the 4-7-year stand age class ($p = 0.044$). The interaction effect of trap type*age class was not significant ($p = 0.833$).

Indicator species analysis showed 11 species associated with blue vane traps and five species associated with pan traps. No species were associated with both the traps. Species associated with blue vane traps were mostly medium or large sized (except for three *Ceratina* species), while all the species associated with pan traps were smaller in size (Table 3.2).

Functional evenness was different between trap types ($t_{62} = 4.113$, $p < 0.001$). Blue vane traps had higher functional evenness than pan traps (Figure 3.4). Functional dispersion was also different between trap types ($t_{62} = 3.183$, $p = 0.002$), and blue vane traps also had higher functional dispersion than pan traps (Figure 3.5). Dominant traits reported from community-weighted means show that for all stand age classes most bees caught in blue vane traps were solitary and most bees caught in pan traps were social. Also, the dominant bee size class for all pan traps was small. For blue vane traps, the 0-3-year and 14-20-year stand age classes had mostly medium-sized bees while the 4-7 and 8-13-year stand age classes had mostly smaller-sized bees (Table 3.3).

NMDS reached a solution in two dimensions with a stress of 0.184. The ordination plot showed the convex hulls for each trap type having an area of overlap, but with distinct species clouds surrounding them (Figure 3.6). Smaller species such as those from the genus *Lasioglossum* surrounded the pan trap hull, while more medium- to larger-sized species such as those from the genera *Bombus* and *Melissodes* surrounded the blue vane trap hull. Smaller bees from the genus *Ceratina* also surrounded the blue vane trap hull, and this was consistent with the indicator species results.

Discussion

Blue vane traps caught ~47% more native bees than pan traps in our study in pine-dominated stands, and these results are consistent with previous studies in orchard and prairie habitats (Joshi et al., 2015, Rhoades et al., 2017). Since there was no interaction effect of trap type x age class, these traps do not catch more bees in certain stand age classes. In contrast, there was no difference in rarefied species richness between the trap types, so one trap type did not catch a higher diversity of bees than the other. Previous studies have found that blue vane traps had a greater diversity of bees (Joshi et al., 2015, Rhoades et al., 2017), however they did not sample in pine forests, indicating habitat-specific responses to trap-types.

There were 11 indicator species for blue vane traps and five for pan traps. No species were associated with both trap types, indicating that these trap types captured unique communities. Indicator species for blue vane traps were mostly solitary and medium- or large-sized. Previous studies have documented medium to large sized bees in blue vane traps (Stephen and Rao, 2005, Kimoto et al., 2012, Geroff et al., 2014). Of the 235 total *Bombus pensylvanicus* (De Geer) individuals in our study, 231 were collected in blue vane traps. This species may be added to the Endangered Species List, so blue vane traps could be important for monitoring for it in the future, especially in pine forest habitat. There were three small sized species associated with blue vane traps, all from the genus *Ceratina*. A study comparing pan and blue vane traps in apple orchards documented *Ceratina* species to be associated with blue vane traps (Joshi et al., 2015). Because *Ceratina* spp. nest in deadwood or pithy stems, they are more common in forested areas, which have a greater presence of these resources. Blue vane traps may catch more *Ceratina* in forested areas because they are larger and may be easier to see than pan traps.

Community-weighted means reported the dominant traits for each trap type and stand age class. For blue vane traps, most species were solitary, and for pan traps most species were social, as consistent with the indicator species results. This size relationship could be due to larger bees being able to escape the pan traps (Roulston et al., 2011). For pan traps for all stand age classes, the dominant bee size was small, also consistent with the indicator species results. For blue vane traps, the 0-3- and 14-20-year stand age classes had a dominant bee size of medium, consistent with the indicator species results, and the 4-7 and 8-13-year stand age classes had a dominant size of small. The 4-7 and 8-13-year stand age classes may have had a dominant size of small due to the presence of *Ceratina* spp. that nest in deadwood or pithy stems, and these stand age classes have a greater presence of these resources than the others.

Functional evenness and dispersion were greater in the blue vane traps than in the pan traps in these pine forests. The blue vane traps caught species with a more even distribution of functional traits and captured a higher beta diversity than the pan traps. Similar functional dispersion was observed between pan and blue vane traps in a tall grass prairie study (McCravy et al., 2019).

Results from the NMDS showed the convex hulls for each trap type having an area of overlap, but with distinct species surrounding each of them. The ordination results were consistent with the indicator species and community-weighted mean dominant traits results. For pan traps, there were many small species surrounding the pan trap hull, such as those from the genera *Lasioglossum* and *Perdita*. The blue vane trap hull had more medium-to-large sized species, such as those from the genera *Bombus* and *Melissodes* (and *Ceratina* – a smaller bee species). These genera have also been commonly caught previously in blue vane traps (Geroff et al., 2014). Overall, pan and blue vane traps had some overlap in their species distributions, but largely captured different groups of species.

There are some critiques of these trapping methods. Pan traps captured fewer or different bee species than aerial netting in the same area and are biased toward small bee species (Cane et al., 2000, Roulston et al., 2011, Gibbs et al., 2017). Blue vane traps can also be biased to catch more common and large species, in contrast to rare and smaller species (Geroff et al., 2014, Joshi et al., 2015). However, active methods, such as aerial netting, sweep netting, and observational transect walks can be very difficult or impossible in certain forest types. Some stand age classes have no understory flowering plants to target for netting, and some stand age classes have very dense understory vegetation making walking a transect not feasible (Campbell and Hanula, 2007, Roulston et al., 2011). Hence, we wanted to compare two of the most feasible trapping methods for use in forest environments.

Conclusions

In managed pine forests in the Southeast U.S., blue vane traps captured greater numbers of native bees than pan trees, however similar bee diversity was found in both the trap-types. Functional diversity was greater in blue vane traps suggesting that they capture different bee communities with blue vane traps catching generally larger bodied, solitary bees and pan traps catching smaller bodied social bees. Hence, when sampling for bees in a managed pine forest environment, we recommend using both trap types simultaneously to capture the greatest portion of the bee community as is possible, especially when active bee capture methods are not practical.

Tables

Table 3.1: Counts of bees caught in each trap type by species in managed loblolly pine forests in Southeastern Plains ecoregion, Georgia.

NATIVE BEE SPECIES	**BLUE VANE TRAP**	**PAN TRAP**	**TOTALS**
Ceratina floridana Mitchell	573	84	657
Lasioglossum reticulatum (Robertson)	154	488	642
Melissodes communis Cresson	396	56	452
Lasioglossum floridanum (Robertson)	77	300	377
Lasioglossum nymphale (Smith)	142	207	349
Lasioglossum puteulanum Gibbs / *tegulare* (Robertson)	65	267	332
Melissodes bimaculatus (Lepeletier)	290	40	330
Svastra atripes (Cresson)	244	38	282
Lasioglossum pectorale (Smith)	133	130	263
Bombus pensylvanicus (De Geer)	231	4	235
Svastra obliqua (Say)	149	52	201
Melitoma taurea (Say)	171	8	179
Bombus impatiens Cresson	145	22	167
Ceratina calcarata Robertson	107	25	132
Ptilothrix bombiformis (Cresson)	127	4	131
Augochlorella aurata (Smith)	58	71	129
Lasioglossum longifrons (Baker)	3	117	120
Halictus poeyi Lepeletier	19	89	108
Melissodes tepaneca Cresson	57	24	81
Melissodes comptoides Robertson	56	10	66
Ceratina floridana Mitchell / *strenua* Smith	61	4	65
Lasioglossum pilosum (Smith)	25	32	57
Lasioglossum spp	11	36	47
Lasioglossum weemsi (Mitchell)	4	40	44
Ceratina floridana Mitchell / *dupla* Say	34	4	38
Augochlora pura (Say)	19	17	36
Agapostemon splendens (Lepeletier)	10	24	34
Lasioglossum apopkense (Robertson)	2	21	23
Lasioglossum imitatum (Smith)	10	12	22
Osmia sandhouseae Mitchell	16	4	20
Lasioglossum hitchensi Gibbs	5	12	17
Lasioglossum trigeminum Gibbs	2	15	17
Ceratina dupla Say	13	1	14

Lasioglossum leviense (Mitchell)	2	12	14
Melissodes boltoniae Robertson	5	9	14
Ceratina spp	10	3	13
Lasioglossum leucocomus (Lovell)	4	8	12
Lasioglossum foxii (Robertson)	2	9	11
Megachile texana Cresson	8	2	10
Lasioglossum callidum (Sandhouse)	2	7	9
Megachile georgica Cresson	4	5	9
Bombus bimaculatus Cresson	8	0	8
Lasioglossum illinoense (Robertson)	2	6	8
Peponapis pruinosa (Say)	7	1	8
Perdita boltoniae Robertson	6	2	8
Lasioglossum vierecki (Crawford)	0	6	6
Halictus parallelus Say	4	1	5
Lasioglossum lustrans (Cockerell)	0	5	5
Ceratina strenua Smith	1	3	4
Lasioglossum coreopsis (Robertson)	0	4	4
Perdita bishoppi Cockerell	1	3	4
Sphecodes mandibularis Cresson	0	4	4
Augochloropsis metallica fulgida (Smith)	0	3	3
Bombus griseocolis (De Geer)	2	1	3
Hoplitis pilosifrons (Cresson)	2	1	3
Lasioglossum raleighense (Crawford)	0	3	3
Megachile mendica Cresson	3	0	3
Melissodes spp	2	1	3
Xylocopa virginica (Linneaus)	3	0	3
Hoplitis producta (Cresson)	0	2	2
Lasioglossum admirandum (Sandhouse)	1	1	2
Megachile albitarsis Cresson	0	2	2
Megachile sculpturalis Smith	2	0	2
Melissodes dentiventris Smith	1	1	2
Perdita nubila Timberlake	0	2	2
Agapostemon virescens (Fabricius)	0	1	1
Ashmeadiella floridana (Robertson)	1	0	1
Ceratina cockerelli h.s. Smith	1	0	1
Colletes brevicornis Robertson	0	1	1
Hylaeus affinis (Smith) / *modestus* Say	0	1	1
Lasioglossum callidum (Sandhouse) / *trigeminum* Gibbs	1	0	1
Lasioglossum creberrimum (Smith)	0	1	1
Lasioglossum platyparium (Robertson)	0	1	1

Lasioglossum smilacinae (Robertson)	0	1	1
Lithurgopsis gibbosa (Smith)	0	1	1
Megachile integra Cresson	1	0	1
Megachile petulans Cresson	1	0	1
Melissodes denticulatus Smith	1	0	1
Melissodes mitchelli LaBerge	0	1	1
Osmia atriventris Cresson	1	0	1
Osmia inspergens Lovell and Cockerell	1	0	1
Perdita sp	0	1	1
Svastra aegis (LaBerge)	1	0	1
Svastra sp	1	0	1
Triepeolus cressonii (Robertson)	0	1	1
Triepeolus sp	0	1	1
Xylocopa micans Lepeletier	0	1	1
Total individuals	3,501	2,377	5,878
Total species	66	73	87*

*some species were caught in both trap types

Table 3.2: Indicator bee species list with functional groups in managed loblolly pine forests in Southeastern Plains ecoregion, Georgia.

TRAP	SPECIES	P-VALUE^{a}	SOCIALITY	DIET	SIZE	SEASON^{b}
Blue Vane	*Bombus pensylvanicus*	0.001	Social	Generalist	Large	Mid
Blue Vane	*Bombus impatiens*	0.001	Social	Generalist	Medium	Mid
Blue Vane	*Ceratina floridana*	0.001	Solitary	Generalist	Small	Mid
Blue Vane	*Melitoma taurea*	0.001	Solitary	Specialist	Medium	Mid
Blue Vane	*Melissodes communis*	0.009	Solitary	Generalist	Medium	Mid
Blue Vane	*Melissodes bimaculatus*	0.0034	Solitary	Generalist	Medium	Mid
Blue Vane	*Ceratina calcarata*	0.0013	Solitary	Generalist	Small	Mid
Blue Vane	*Ceratina floridana/ strenua*	0.003	Solitary	Generalist	Small	Mid
Blue Vane	*Svastra atripes*	0.0088	Solitary	Generalist	Large	Late
Blue Vane	*Ptilothrix bombiformis*	0.001	Solitary	Specialist	Medium	Mid
Blue Vane	*Melissodes comptoides*	0.027	Solitary	Generalist	Medium	Late
Pan	*Lasioglossum floridanum*	0.007	Social	Generalist	Small	Mid
Pan	*Lasioglossum weemsi*	0.001	Social	Generalist	Small	Mid
Pan	*Halictus poeyi*	0.014	Social	Generalist	Small	Mid
Pan	*Lasioglossum apopkense*	0.002	Social	Generalist	Small	Mid
Pan	*Lasioglossum longifrons*	0.009	Social	Generalist	Small	Early

[a] P-value for permutation test to determine if taxon is an indicator species.

[b] Season refers to the peak season the species is active. Early is February to April, mid is May to July, late is August to October.

Table 3.3: Community weighted means of dominant functional groups by trap type and age class in managed loblolly pine forests in Southeastern Plains ecoregion, Georgia.

TRAP TYPE	AGE CLASS	SOCIALITY	DIET	SIZE CLASS	PEAK SEASON
Blue Vane	0-3	Solitary	Generalist	Medium	Mid
Blue Vane	4-7	Solitary	Generalist	Small	Mid
Blue Vane	8-13	Solitary	Generalist	Small	Mid
Blue Vane	14-20	Solitary	Generalist	Medium	Mid
Pan	0-3	Social	Generalist	Small	Mid
Pan	4-7	Social	Generalist	Small	Mid
Pan	8-13	Social	Generalist	Small	Mid
Pan	14-20	Social	Generalist	Small	Mid

Figures

Figure 3.1: An example of pan traps (blue, yellow, white) that were used in the study to capture bees on wire plant props.

Figure 3.2: An example of a blue vane trap that were used in the study to capture bees.

Figure 3.3: Bee catches/month for each trap type in Georgia. Circles represent means and bars are standard errors. Different letters represent significant differences between trap types (Tukey’s HSD).

Figure 3.4: Functional evenness by trap type in Georgia. Circles represent means and bars represent standard errors. Different letters represent significant differences between trap trypes (Tukey’s HSD).

Figure 3.5: Functional dispersion by trap type in Georgia. Circles represent means and bars represent standard errors. Different letters represent significant differences between trap types (Tukey’s HSD).

Figure 3.6: Non-metric multidimensional scaling showing species distributions and trap types for sampling bees in Georgia.

Figure 3.1

Figure 3.2

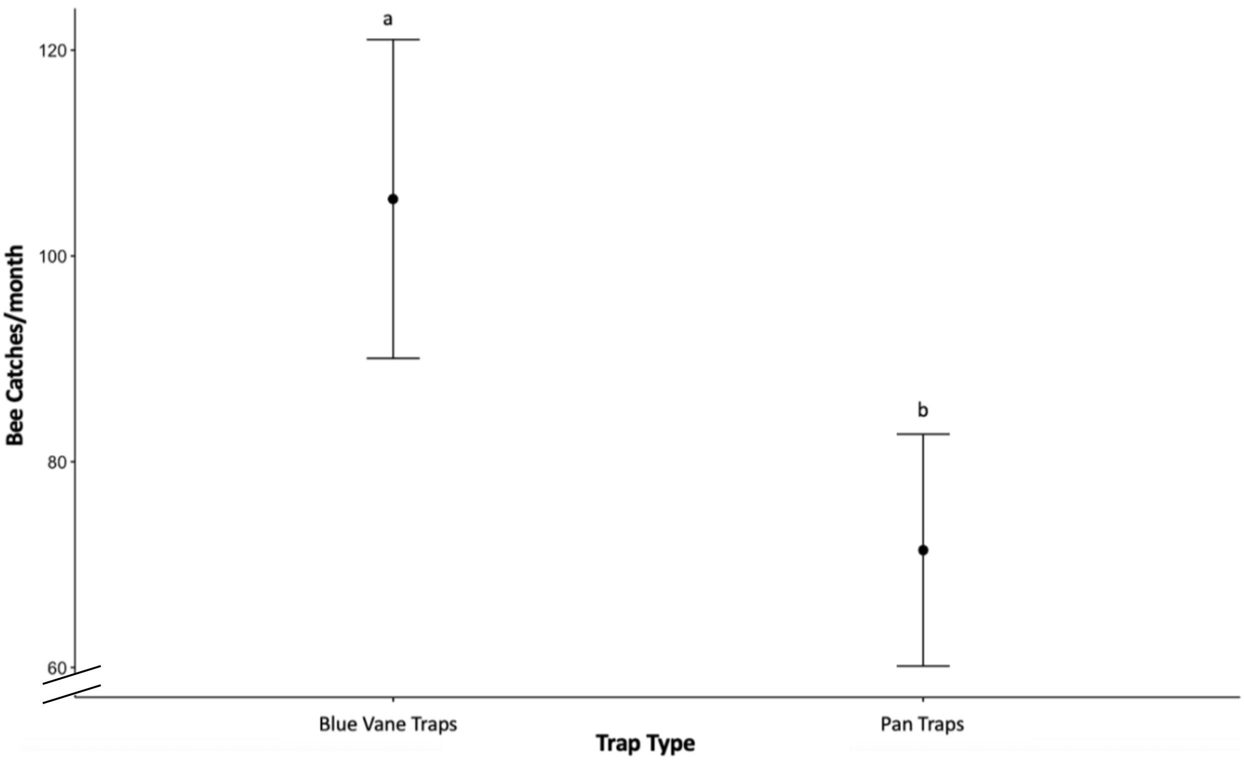
a
b
120
100
80
60
Bee Catches/month
Blue Vane Traps
Pan Traps
Trap Type

Figure 3.3

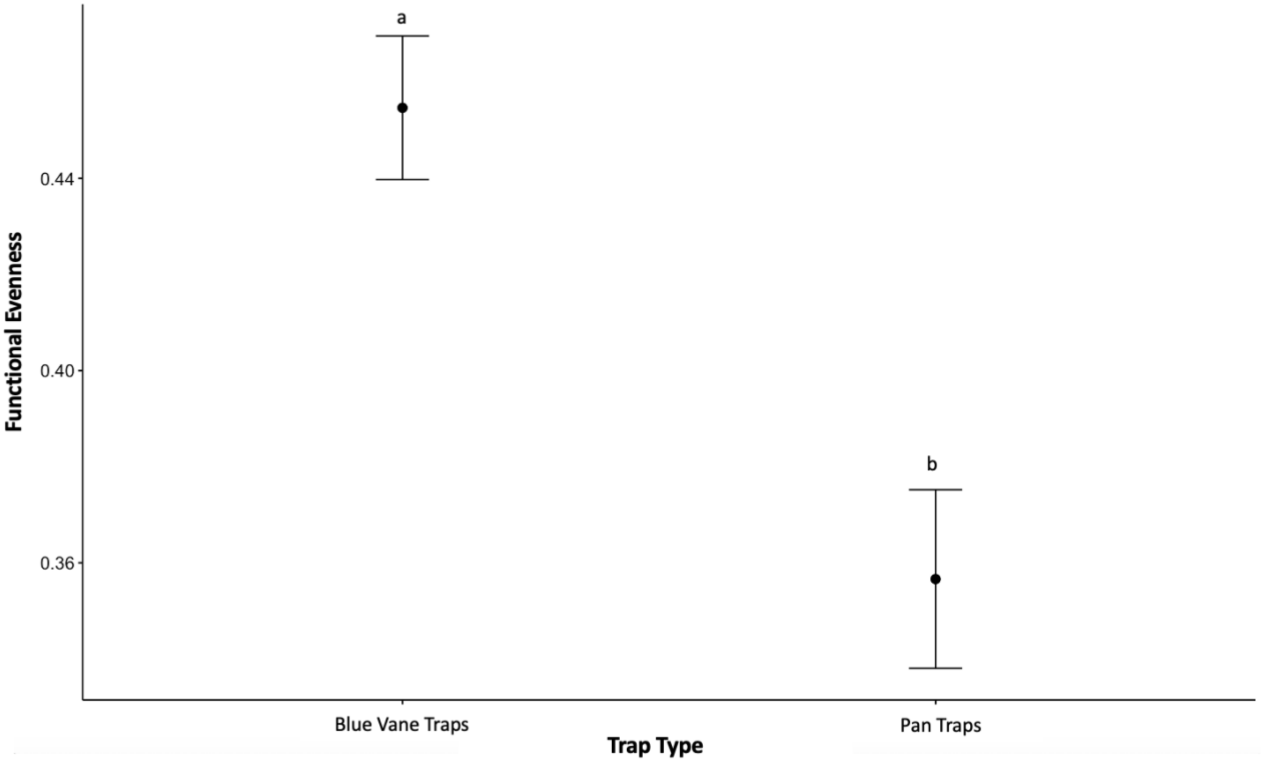
a
b
0.44
0.40
0.36
Functional Evenness
Blue Vane Traps
Pan Traps
Trap Type

Figure 3.4

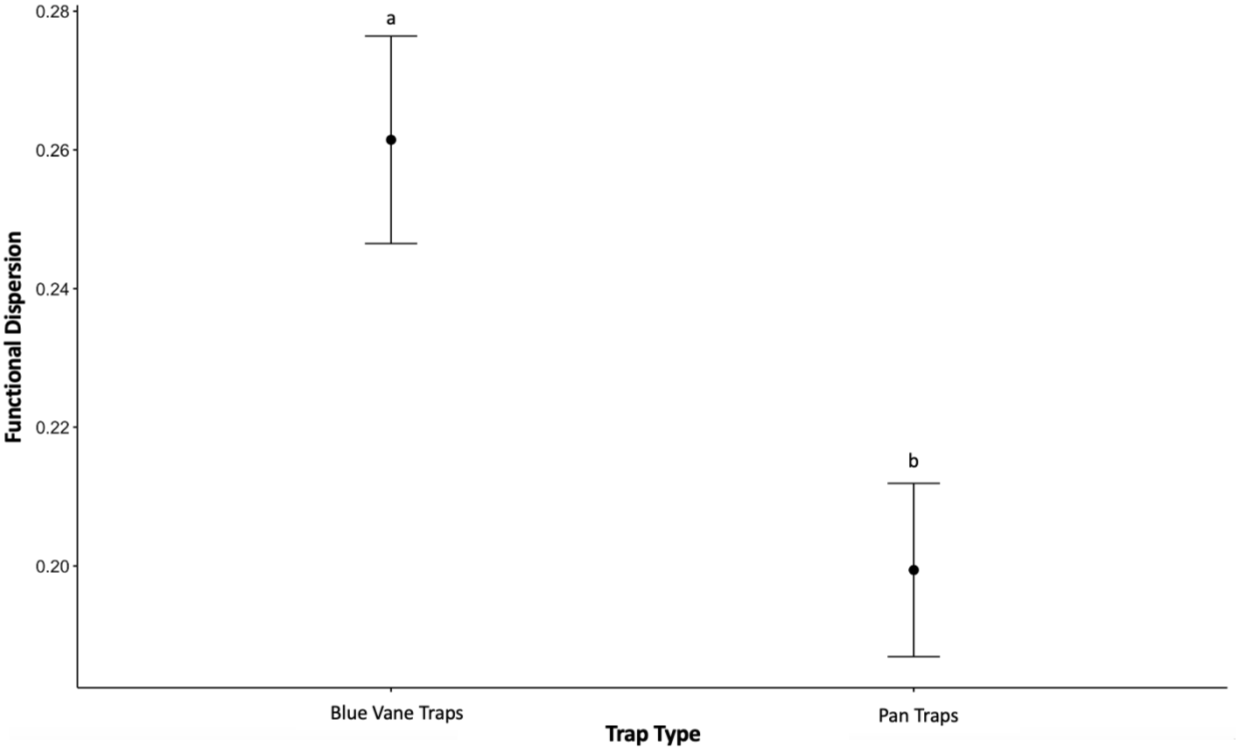
0.28
0.26
0.24
0.22
0.20
Functional Dispersion
a
b
Blue Vane Traps
Pan Traps
Trap Type

Figure 3.5

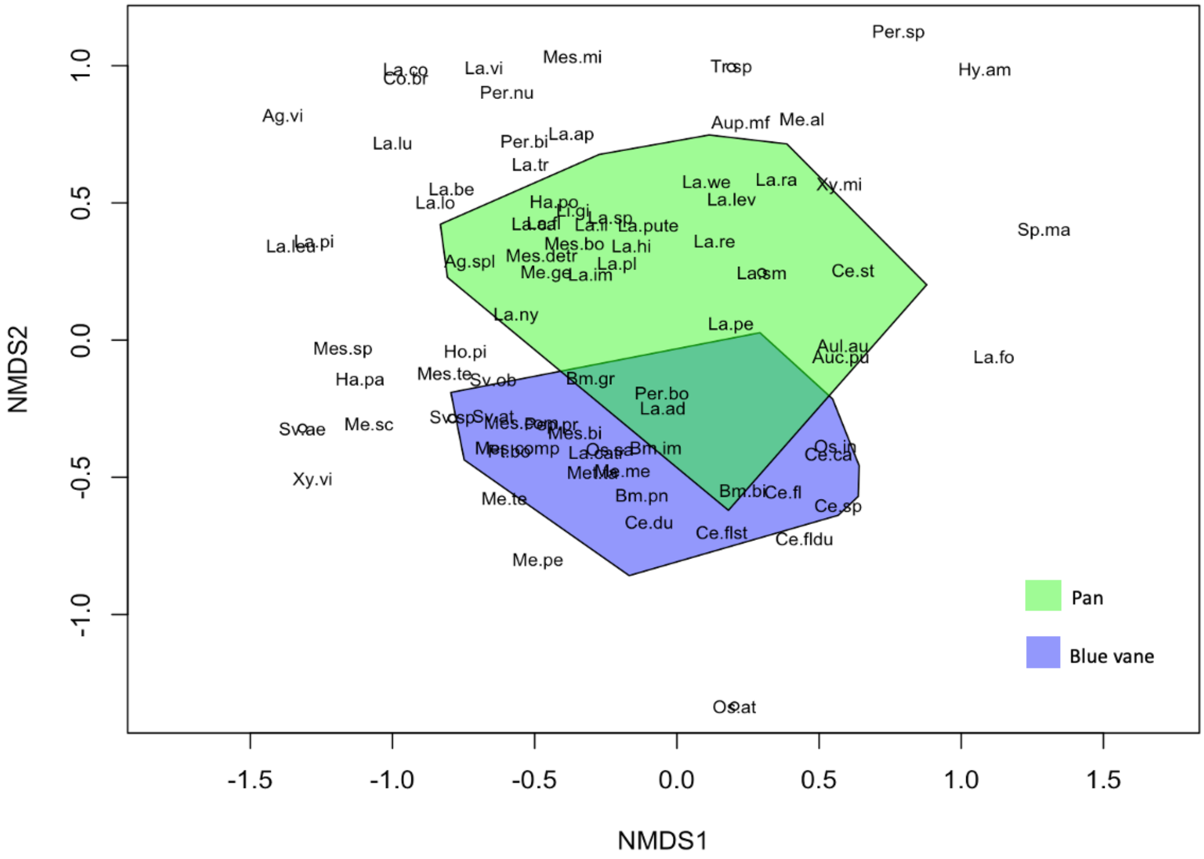
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-1.0
-1.5
1.5
Per.sp
Hy.am
La.co
Co.bi
La.vi
Mes.mi
Tr.sp
Per.nu
Ag.vi
Aup.mf
Me.al
La.lu
Per.bi
La.ap
La.tr
La.we
La.ra
Xy.mi
La.be
La.lo
Ha.po
La.lev
Li.gi
La.sp
La.ca
La.al
La.fl
La.pute
Sp.ma
La.leu
La.pi
Mes.bo
La.hi
La.re
Ag.spl
Mes.detr
La.pl
Me.ge
La.im
La.sm
Ce.st
La.ny
La.pe
Mes.sp
Ho.pi
Aul.au
Auc.pu
La.fo
Ha.pa
Mes.te
Sv.ob
Bm.gr
Per.bo
La.ad
Sv.ae
Me.sc
Sv.sp
Sv.at
Mes.pe
Per.pr
Mes.bi
Mes.comp
Pt.bo
La.ca
Os.sa
Bm.im
Os.in
Ce.ca
Me.fl
Me.me
Xy.vi
Me.te
Bm.pn
Bm.bi
Ce.fl
Ce.sp
Ce.du
Ce.flst
Ce.fldu
Me.pe
🟩 Pan
🟦 Blue vane
Os.at

Figure 3.6

CHAPTER 4

CONCLUSIONS AND FUTURE DIRECTIONS

The main goal of my two-year project was to better understand the responses of native bees in variously aged managed loblolly pine (*Pinus taeda* L.) forests, along with assessing the efficacy of trap-types for sampling their populations and communities. The first research objective was to determine which attributes of forest age, structure, and composition best support native bees. I compared numbers of individual bees, species richness, rarefied species richness, and functional diversity among four stand age classes. Stand-level habitat characteristics were also measured and analyzed with ordination to determine drivers of bee communities in these forests. These included tree species, tree basal area, tree density, tree height, percent understory plant cover, understory plant species diversity, percentage of canopy openness, woody debris cover, litter cover and depth, and bare ground. Native bees were sampled in privately-owned managed loblolly pine forests using pan and blue vane traps for two years (2020-2021). Results from 5,933 bees and 88 species indicated that the most important habitats for native bees in these forests were the recently established (0-3 years old), the pre-thinned open canopy (4-7 years old), and post-thinned (14-20 years old) stands which all included an open canopy. These stands overall had more bees, and greater alpha and beta diversity than the pre-thinned closed canopy (8-13 years old) stands. Different habitat variables appear to be driving bee communities in the 0-3-year-old stands than the other stands. The 0-3-year-old stands appear to have unique species composition. Canopy openness, minimally decayed woody debris, and plants flowering were important forest attributes affecting bee communities in the 0-3-year-old stands, while numbers of snags and litter depth were important in other forested stands.

Due to the limited work in general on native bees in managed southeastern pine forests, fewer studies have assessed the efficacy of trapping methods in these areas. My research objective was to compare the effectiveness of two commonly used traps for bees - pan traps and blue vane traps. Over the two-year study period, blue vane traps captured a greater number of bees than pan traps as well as a greater functional diversity. Both trap types caught a similar species diversity. The two trap types also caught mostly different groups of species, with blue vane traps generally catching larger mostly solitary bees and pan traps catching mostly smaller social bees. This study is one of the few to compare pan traps and blue vane traps (Geroff et al., 2014, Joshi et al., 2015, McCravy and Ruholl, 2017, Rhoades et al., 2017), and the first to do so in managed southeastern pine forests.

Management Recommendations

Based on the results of these studies, managed loblolly pine forests in the Southeast support a robust and diverse native bee community, including *Bombus pensylvanicus* (De Geer), a species currently being considered for the Endangered Species List. Having a variety of forest stages, from clearcut to mature thinned stands would benefit native bees in this region, as different groups of species utilized varying open and/or forested habitats. Many native bee species require floral and nesting resources present in both open and forested areas, so having multiple stages relatively close together may provide a benefit (Gathmann and Tscharntke, 2002, Roulston and Goodell, 2011). The lowest numbers of bees, as well as the lowest alpha and beta diversity, were in closed canopy stands, so measures such as thinning and planting at a wider spacing could also benefit native bees.

Pan and blue vane traps captured largely distinct groups of native bee species, so using both trap types concurrently would be best to capture as much of the community as possible. In some forested stands, active sampling methods. such as aerial or sweep netting, transect walks, or targeted flower observations, may either be very difficult or impossible due to stand conditions or it may be impossible to standardize sampling procedures among stands.

Directions for Future Research

Future studies about native bees in pine forests could be conducted at the landscape instead of the stand level. Different densities and configurations of age classes could impact bees. For example, a clearcut stand is surrounded only by dense forests could host a different community than a clearcut surrounded by less dense stands. Increasing early successional habitat within 2 km of a site increased soil-nesting bee species richness and increasing the size of the clearcut further increased the species richness in boreal forests in Sweden (Rubene et al., 2015). Increasing landscape heterogeneity especially in poor habitats such as cornfields was important for wild bee communities in the Southeast U.S. (Miljanic et al., 2019). Future work in the Southeast could include sequential age class of managed pine forests across larger spatial scales, since this land-use type is so widespread and economically important in this region. The percentages of different age classes of managed pine forests present across the Southeast is currently unknown and likely often changes as stands are harvested and trees grow. Future studies could also include thinning at different basal areas and ages in order to test the impacts on of the length that stands are in the closed canopy stage and how this impacts native bees, as this study demonstrated this stage is least beneficial to them. Overall, my study enhances the current knowledge about native bees and their distributions and habitat associations in managed pine forests, which may assist in their long-term conservation efforts.

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