ABSTRACT

MOYLETT, HEATHER MARGARET CAMPBELL. The Impact of Prescribed Burning on Native Bee Communities (Hymenoptera: Apoidea: Anthophila) in Longleaf pine (*Pinus palustris* Mill.) Savannas in the North Carolina Sandhills. (Under the direction of Clyde E. Sorenson.)

Longleaf pine (*Pinus palustris* Mill.) savannas are diverse fire-dependent ecosystems, containing great species richness representing large numbers of rare and endemic plant and wildlife species. This ecosystem has been threatened by exploitation of the pines and fire suppression. Restoration and conservation efforts have been focused primarily on successfully reintroducing fire, and the reestablishment of flora and vertebrate fauna. The impact of fire on invertebrate warrants attention because of the high proportional diversity they represent and the significant functional roles they serve. Native bees (Hymenoptera: Apoidea: Anthophila) provide the majority of pollination services in longleaf savannas, and are essential to the endurance of longleaf savannas.

The present study had two main objectives; conduct an ecological study to describe the response of the native bee community to prescribed burning on a three year burn rotation and to conduct a thorough survey of the bee fauna to provide an updated inventory for the region. The study was conducted on the Walthour-Moss Foundation in Moore County, one mile north of Southern Pines, a site of historical interest due to extensive surveys by Dr. T. B. Mitchell.

Of the 106 bee species collected during the ecological study, 82 species were collected from sites that were burned the same year as sampling, 72 species from one year post-fire sites, 67 species from the two years post- fire sites, and 40 species from our control sites. Individual abundance and estimated species richness (Chao 1) were significantly higher in sites burned the same year of sampling and one year post-fire than in the control sites. Diversity (Simpson’s diversity index) was not found to be different between the burned and unburned sites. An analysis of five bee functional groups found that wood-nesting and ground- nesting bees had a greater relative abundance in unburned areas, sand and floral specialist relative abundance was highest in sites burned the same year as sampling, while nest parasites were found to be most abundant in one year post-fire sites. This

suggests that the bee community is at its greatest diversity within the year of the burn and one year post-fire.

In total, 2,936 bees were collected during the survey representing 137 described species in 34 genera and six families. Halictidae had the greatest number of individuals and species represented. Our results were compared to three previous surveys that were conducted in Sandhills/longleaf pine habitat that extends through southeastern United States. The surveys were conducted in the Carolina Sandhills National Wildlife Refuge (CSNWR) in South Carolina, in southern Louisiana where the survey results were combined with the species list from a survey conducted by Charles D. Michener (1947) in Mississippi, and in the University of Florida Ordway-Swisher Biological Station (OSBS) in Florida. The Foundation's bee fauna was most similar to that found in the CSNWR survey, with 79 species in common. Less overlap occurred with 62 species in common with the southern Louisiana and Mississippi survey and 39 species in common with the OSBS survey. These surveys provide a comprehensive representation of the bee fauna present in the Sandhill/longleaf pine habitat, but additional surveys are required in the Sandhills of Georgia. These measures, combined with the complete digitization of the Mitchell collection housed at the NC State Insect Museum, Raleigh, North Carolina (NCSU), will provide an exhaustive treatment of the bee diversity of the Sandhill/longleaf pine habitat that can be used to inform future land management decisions and conservation efforts.

The Impact of Prescribed Burning on Native Bee Communities (Hymenoptera: Apoidea: Anthophila) in Longleaf Pine (*Pinus palustris* Mill.) Savannas in the North Carolina Sandhills

by
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DEDICATION

To my father, William L. Campbell.

BIOGRAPHY

Heather Moylett was born in Greensboro, NC and grew up playing outdoors. This is where her love for the environment and interest in biology started. She completed her B.S. in Fisheries and Wildlife Biology from NC State University in 2005. Immediately after graduation she moved to New York City and worked as an Urban Park Ranger for the NYC Parks Department. After two years, Heather became the scientific assistant to the Curator of Bees at the American Museum of Natural History, Dr. Jerome Rozen. It is here that she discovered and cultivated her love of bees.

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Introduction

Fire is a major disturbance that impacts both species-assemblages and habitat structure, making the ecosystems that evolved under its influence unique (Hobbs and Huenneke 1992, Waldrop et al. 1992). Longleaf pine savannas are highly diverse fire-dependent ecosystems, containing great species richness representing large numbers of rare and endemic plant and wildlife species (Frost 1993, Walker 1993, Van Lear et al. 2005). The loss of the longleaf pine savanna ecosystem has spurred substantial interest in restoring this habitat. Restoration and conservation efforts have been focused primarily on successfully reintroducing fire, and on the reestablishment of flora and vertebrate fauna (Peet and Allard 1993, Noss et al. 1995, Costa and DeLotelle 2006, Frost 2006, Campbell et al. 2008, Outcalt 2008). The impact of fire on invertebrate assemblages deserves special consideration because of the high proportional diversity they represent and the important functional roles they serve in their respective habitats (Ferrenberg et al. 2006). Native bees provide the majority of pollination services in longleaf savannas, and they are essential to the endurance of the longleaf savanna ecosystem (Proctor et al. 1997, Moisset and Buchmann 2011). Within the last decade three surveys and one study were conducted seeking to characterize the native bee diversity in longleaf pine savannas; one survey was conducted in the Carolina Sandhills National Wildlife Refuge (CSNWR) in South Carolina (Droege, unpublished data from 2006-2009 survey), another in the University of Florida Ordway-Swisher Biological Station (OSBS) in Putnam County, Florida (Hall and Ascher 2014). The third, in southern Louisiana, was conducted in tandem with a study comparing the diversity of bees in wet low-land longleaf pine savannas to that of dry upland longleaf pine savannas (Bartholomew and

Prowell 2006). However, the impact of fire and fire periodicity on native bee diversity and community composition was not investigated in any of these works. In an effort to better inform land management decisions and conservation efforts, we must investigate how changes across ecological gradients, caused by human mediated disturbance, influence community composition. In this study we seek to identify how native bee communities in the longleaf pine savannas in the Sandhills are impacted by prescribed burning, and if there is any significant effect of time within the 3-year burn rotation.

Longleaf pine (*Pinus paustris* Mill.) savannas comprise an endangered ecosystem (Noss, LaRoe III, and Scott 1995; Means and Grow 1985) that, prior to European settlement, covered nearly 37 million hectares of the southeastern United States (Boyer 1990, Frost 1993). Over the past two centuries much of the longleaf pine was harvested for timber, turpentine and the naval stores industry (Wahlenberg 1946, Frost 1993) or razed to make way for agriculture, leaving only 1.3 million hectares of fragmented forest remaining (Engstrom et al. 1996). Exclusion of fire in the longleaf pine savanna also became common practice beginning in the 1850s; citing soil degradation, malformation of trees, and endangerment important forest industries (turpentine production and pulp wood) as support. Prescribed burning was utilized by private land owners but it did not become an accepted silvicultural practice until the 1960's and was not introduced as a management tool for the conservation of nongame species until the early 1970s (Johnson and Hale 2002).

A wealth of research has emerged in the past 20 years seeking to illuminate the relationship between invertebrates and fire (Rieske-Kinney 1995, Hanula and Wade 2003, Potts et al. 2003, Moretti et al. 2004, 2006, Coleman and Rieske 2006, Joern and Laws 2013). The outcomes of these studies are varied depending on the time of year the fire is initiated and what successional stage and ecological niche the invertebrate occupies. In longleaf ecosystems, the majority of research has focused on the role of invertebrates as a food source (Hanula and Engstrom 2000, Horn and Hanula 2002, Armitage and Ober 2012) or the efficacy of fire in controlling pestiferous invertebrates (Rieske-Kinney 1995, Sullivan et al. 2003, Campbell et al. 2008). Folkerts et al. (1993) conservatively estimated that there are 4,000 to 5,000 species characteristic to longleaf pine savannas and of that 10% are endemic to the ecosystem. Arthropod herbivores, detritivores, and pollinators play important roles in the function of the community and disturbance, including fire and forestry practices, likely have a major impact on the diversity and abundance of these groups (Folkerts et al. 1993). Hanula and Wade (2003) explored the impact of dormant-season burns at different fire frequencies on ground-dwelling invertebrates in longleaf pine stands for over 40 years in Osceola National Forest in Florida. They found that the response to fire was species specific. In order to use fire as an effective management tool a greater understanding of its impact on the present invertebrate communities is needed.

Bees (Hymenoptera: Apoidea: Anthophila) are a highly diverse group with over 19,500 described species represented world-wide and, of that number, 3,600 species are known to occur in the United States and Canada (Ascher and Pickering 2010). There is a growing concern for the status of North American bees due to observed population declines, including a recent report naming 37 eastern North American species that have not been collected or seen in over 20 years (National Academy of Sciences 2007, Colla et al. 2012). Historically, very few North American bee populations have been monitored; only a limited number of quantitative studies on native populations have been completed, leaving ecologists with insufficient baseline data with which to compare current population trends (National Academy of Sciences 2007, Colla et al. 2012). There are also relatively few studies that investigate how changes in land-use shape bee communities (Goulson et al. 2008). The majority of studies have been general, mainly focusing on pollinators as a group (Pitts-Singer et al. 2002, Campbell et al. 2007). Bees are attracted to areas based on the availability of pollen and nectar, but a species' success is influenced by disturbance (fire, agriculture, residential and commercial development), habitat structure, and availability of nesting resources (Potts *et al*. 2003, 2005, Prowell and Bartholomew 2006, Cane *et al*. 2007, Williams and Kremen 2007, Grundel *et al*. 2010).

Winfree *et al*. (2007) examined how human disturbance affects bee communities in forested ecosystems. They found that bee abundance and species richness decreased with increasing forest cover but increased in agricultural fields and areas of urban and suburban development. Of the 130 species collected, 18 showed a positive association with extensive canopy cover. The results suggest that, within a certain threshold, anthropogenic land use may be compatible with the conservation of many bee species. This is an unexpected outcome, as similar investigations suggest a negative relationship between human land use and bee abundance and species richness (examples given by author, Kremen *et al*. 2002, 2004). The threshold at which disturbance precipitated by human land use benefits bees is unknown, and it may be that in previous studies the level of anthropogenic disturbance was outside of this undefined threshold. The ecosystem evaluated in a study may also influence the outcome (Winfree et al. 2007). Kremen *et al*. (2002, 2004) worked within the Mediterranean scrub of California, while Winfree *et al*. (2007) worked in the Pinelands of southern New Jersey. It may be that bee species that exist in the more forested eastern United States are accustomed to utilizing disturbed areas and are now able to take advantage of those created through human-mediated disturbance (Winfree et al. 2007). The dissimilarity in species richness may also be due to different species occupying different successional stages in a disturbed landscape resulting in higher total richness than that found in less disturbed landscapes. This is supported by looking at different types of disturbance.

Moretti et al. (2009) compared taxonomic response and functional group response of bee communities to fire in two different climate regions, the Mediterranean scrub in Israel and the temperate chestnut forest in southern Switzerland. Functional groups are composed of species with similar ecological behaviors and/ or morphologies (e.g. body size). The results of the study found that the species diversity and composition in both climates shifted related to post-fire age, while there was greater stability observed in functional group representation when exposed to fire in the Mediterranean region then in the more temperate chestnut forests. Functional group stability is achieved by replacement of functionally similar species (i.e., functional redundancy) which dominate under different environmental conditions in the heterogeneous landscapes of the region. Analyzing functional group response provides researchers with the ability to identify the mechanisms that link species composition to disturbance, thereby adding increased clarity when making land management and conservation decisions (Moretti et al. 2009). The patchy distribution of different successional types is a shared trait in longleaf pine savannas and Mediterranean scrub regions (Noss et al. 1995).. While there are many characteristics that are recognized as important in bee autecology, we selected five groups that had been used for comparison in previous studies (Williams et al. 2001, 2010, Potts et al. 2003, Bartholomew et al. 2006, Winfree et al. 2007, Moretti et al. 2009, Hall and Ascher 2014) and may be most sensitive to the presence or absence of fire. The specific functional groups we chose for our study were based on nesting and floral preference: bees that require wood or pithy stems for nesting, species that excavate nests in soil, sand specialists, nest parasites, and floral specialists (oligoleges).

In our study we combine species composition response and functional group response in order to evaluate how the bee community in the longleaf pine savannas of the North Carolina Sandhills is impacted by fire. We expect that this will provide a clearer and more accurate assessment of how the community responds as a whole. We predict that: (1) areas that are burned on a three year rotation will support greater bee diversity; (2) and the greatest diversity will be in the first two years post-fire; (3) the relative species abundance of all functional groups will be higher in areas burned on a three year rotation, with the exception of wood nesting bees, which will be highest in the areas that have not burned in 50 years or more; and (4) bee diversity will be positively correlated with floral diversity and negatively correlated with ground and canopy cover

Methods

Site description

My study took place on the Walthour-Moss Foundation (Figure 1) property one mile north of Southern Pines in Moore County, NC. The Walthour-Moss Foundation, from here on referred to as the Foundation, has preserved over 1620 hectares of primarily upland pine savannas; longleaf pine is the dominant tree in most stands on the property. The Foundation is used primarily for equestrian purposes (trail riding, fox hunts, and jumping events) and places a high emphasis on aesthetics and maintenance of utility for these purposes. The property is made up of small parcels of land that have been assembled over the past 40 years through donations and land acquisitions, including a large donation from the NC DOT of 73 hectares in 2005. As the steward of this distinct ecosystem, the foundation has made a concerted effort to introduce a 3 year burn rotation, approximating the natural rate of fire disturbance (Frost 1993, 2006), to nearly 90% of the property. Historically the burn units have been approximately 28 hectares or less in extent; recently, they have switched to burn units of 81-121 hectares, which are more consistent with current forestry standards. With the exception of a few parcels, the majority (85-90%) of the Foundation is maintained on this 3 year burn rotation. Burns are typically initiated during the winter months, during the dormant season. This timing was chosen because it is typically easier to control fire in cooler months, and vertebrate wildlife is less likely to be active at that time (Knapp et al. 2009). In 2013, the Foundation began working with the Nature Conservancy to implement growing-season burns. Burning during the growing season is more in line with the historical fire season and reduces the stem density of understory hardwoods and the incidence of fungal infections such as brown spot needle blight (*Scirrhia acicula*) more effectively than burns initiated at other times of year. Numerous grass species, flowering forbs, shrubs, and herbaceous species also flower more vigorously when burned in late spring or early summer (Knapp et al. 2009). While it is of great interest to identify how growing-season burns impact the bee community, we did not include areas burned during the growing season as they did not exist at the start of the 2012 field season.

Unburned Foundation areas are characterized by a dense midstory of turkey oak (*Quercus laevis*) or bluejack oak (*Q. incana*) and a canopy of longleaf pine, Virginia pine, loblolly pine, or a combination. Density of trees, and thus, canopy cover, is higher in the unburned plots. Shading and dense leaf litter in these areas makes the herbaceous understory sparse. The burned areas are open longleaf pine stands with scattered turkey oak and wiregrass in the understory. In some of the burned plots, old dogwoods (*Cornus florida*) persist from historic locations of home sites. In addition to burning, some sites on the foundation are raked for pine straw, and in areas where fire has been absent for extended periods, herbicides are used to reduce fuel load in preparation for future burns. Soil survey information (Soil Survey Staff 2009) indicates that all of the study plots are characterized by well-drained, sandy soils. The two series represented on the property were Candor (sandy) and Vaucluse (loamy sand), both common in the Sandhills. In this study we selected sites that had only been burned during the dormant season and received no raking or herbicide.

Sampling and specimen curation

To test how fire periodicity affects bee communities, I surveyed bees at 16 sites situated within the Foundation. The sites were chosen based on their fire history; burned in the same year of survey (0B), burned one year previously (1B), burned two years previously (2B), and no history of burn in the past 50 years (C). The sites that had not been burned served as the control. Four replicates of each treatment type were represented within the 16 sites. Within each site, bees were surveyed along an 80 meter transect using bee bowls. Five sets of three 178 mL plastic soufflé cups (triplets) were placed along each transect, with one cup painted fluorescent blue, one fluorescent yellow and the other left white as described in the "The Very Handy Manual" (Droege 2012) . The triplets were placed perpendicular across each transect at 20m intervals, while cups within triplets were spaced 5 m apart. In addition to bee bowls, sweep nets were used to capture bees foraging on flowers. Sweep netting was done opportunistically during each sampling trip in 2013 and not specific to any particular burn history so the resultant data will not be included in our analyses, but will be reported in a forthcoming publication.

The colors used to paint the cups have been tested and found to be most attractive to the majority of bee species present in eastern North America (Droege, unpubl. data and Grundel *et al*. 2011). Each cup was filled with a mix of water and Dawn® dish soap (Procter & Gamble, Cincinnati, Ohio, USA), decreasing the surface tension of the water, so that as bees landed they drowned in the liquid. Bowls were set out in the morning and collected in the early evening, averaging 7-9 hours of exposure each sampling date. Sampling was conducted approximately every two weeks (average 13.3 days) from April 15 to October 15 in 2012 for a total of 13 sampling dates. In 2013, bees were collected at the same frequency from April 13 to September 28, for a total of 11 sampling dates. On each sampling trip the number of flowering stems and flowering species within 5 m on either side of each transect was also recorded. Additional site indices, including percent ground cover, percent woody debris, and percent canopy cover were taken twice a year, in March and July. Percent ground cover and woody debris was measured using a 1 m^2 frame divided into sixteenths; six measurements were taken at each transect and averaged. Percent canopy cover was measured with a spherical densitometer using the methods described by Lemmon (1956) at 3 points along each transect and averaged. I recorded basal area for each transect once a year using a basal area factor 10 prism (BAF 10) using the methods described by Hovind and Rieck (1970).

After each sampling date the specimens were pinned, labelled, identified, and databased. To make my determinations I relied heavily upon Discover Life's bee species guides (available at discoverlife.org; Perlmutter 2010) and cross-checked the determinations with the bee reference collection housed in the North Carolina State University (NCSU) Insect Museum. When I was unable to identify a specimen, or was unsure of my determination, the specimens were shipped to experienced taxonomists for confirmation. The taxonomists I consulted for this project were Dr. John S. Ascher of the National University of Singapore and the American Museum of Natural History, Dr. Jason Gibbs of Michigan State University (formerly Cornell University), and Dr. Sam Droege of the United States Geological Service Patuxent Wildlife Research Center. Once identified, the specimen was given a barcode label and its metadata was entered into the NCSU Insect Museum's database (specimen data available at: http://specimens.insectmuseum.org/). The specimens are deposited in NSCU Insect Museum, Raleigh, North Carolina.

Analysis

Bee community structure: abundance, richness, diversity, and functional groups

The effect of treatment and sampling date on the bee communities was investigated by observing differences in total bee abundance (the number of individual bees captured per transect per sample), estimated species richness (the estimated number of species based on abundance data, Chao1), and Simpson's Diversity Index. The estimated species richness is the sum of the observed number of species and the quotient $a^2/2b$, where a and b equal the number of singletons (one individual in a sample) and doubletons (two individuals in a sample), respectively (Gotelli and Colwell 2011). The Chao 1 estimator is useful for biodiversity studies, like ours, with abundance data that have a large number of rare species because the estimator adds a correction factor to observed species density (raw number of observed species) based on the number of rare species in a sample (Chao 1984, Gotelli and

Colwell 2011). Simpson's diversity index calculates the probability that two individuals selected at random from a sample will not belong to the same species. Simpson's diversity index was selected because of the mathematical simplicity of the formula which produces values that fall between 0 and 1 (diversity increasing as value approaches 1), allowing for improved clarity when drawing inferences. Values of estimated species richness and the Simpson's diversity index were calculated for each transect per sampling date and year using the Vegan package (Oksanen et al. 2013) in R statistical software system, version 3.0.1 (R Development Core Team).

The effects of the treatment and sampling date/year on the response variables were analyzed using generalized linear mixed models using a complete randomized, repeated measures design. In order to standardize the dataset we removed the first sample taken in 2012 because one of the control transects was not sampled. Treatment was the fixed effect and the variation between transects was the random effect. Because the transects were sampled repeatedly throughout each season and over two years, sampling date was used as the repeated measure for each year and year was used as the repeated measure for pooled data. The error was modelled on a Poisson distribution for the analysis of total bee abundance, while for the statistically derived measures, estimated species richness and Simpson's diversity index, the error term was modelled on a normal distribution. Analyses were conducted using the lme4 package (Bates et al. 2014) in R statistical software system, version 3.0.1 (R Development Core Team).

To account for how bee abundance may influence species richness we rarefied our samples. Rarefaction curves were calculated using sample-based abundance data; repeated samples for each transect were pooled by treatment and separated by sample year (i.e. 2012, n=11 samples per transect, 4 transects per treatment; 2013, n=11 samples per transect, 4 transects per treatment), and then pooled by treatment over both sampling years (i.e. n=24 samples per transect, 4 transects per treatment). An additional pooled rarefaction curve was generated using a secondary treatment factor, burn sequence, over both sampling years (i.e. n=24 samples per transect, 4 transects per burn sequence). Burn sequence captures the successional changes in transects from 2012 to 2013; the transects burned in 2012 shift to 1 year since burned transects in 2013 (1S), transects burned in 2011 shift from 1 year since burned in 2012 to 2 years since burned in 2013 (2S), transects burned in 2010 shift from 2 years since burned in 2012 to burned year of survey in 2013 (0S), and the control transects remain constant. Values were averaged over replicate treatment transects and the mean accumulated number of species were plotted against the mean number of individuals. Because sample-based rarefaction depends on spatial distribution of individuals and placement of samples, the rarefaction curves were calculated with EstimateS software, 9.1.0 (Colwell 2013), using Monte Carlo re-sampling.

Five functional groups were identified as potentially sensitive to prescribed burning based on nesting preference and floral resource fidelity: bees that require wood or pithy stems for nesting, excavate nests in soil, sand specialists, nest parasites, and floral specialists (for a list of species included in each functional group, see Appendix A). Information on floral and nesting or habitat specialization was compiled from published literature and expert experience (Sam Droege and John Ascher, unpublished data; discoverlife.org). Obligate wood nesting species are defined as bees that nest in logs and pithy stems. Ground nesting species are defined as bees that excavate nests in the ground; species that opportunistically nest in cavities in the ground were excluded. Sand nesting species are specialized ground nesting bees that require sandy soils. Nest parasites, include cleptoparasites and social parasites, steal or feed upon the food stores of their host species, effectively starving or killing the host's progeny. Floral specialists (oligolectic) are defined as bees that collect pollen from one plant family or only a few genera. Floral specialists (oligolectic) are defined as bees that collect pollen from one plant family, genus, or a single species. Floral resource availability dictates the suitability of an area for oligolectic species and the presence or recent absence of one of these species can be illustrative of the flora present or the impacts landscape changes have had in a given area (Roulston and Goodell 2011). These groups were identified as potentially sensitive because the availability of the nesting and floral resources are impacted by regular burning. The availability of woody debris is reduced, possibly limiting obligate wood-nesting bees, while the area of bare ground is increased which has been shown to benefit ground-nesting bees (Potts et al. 2005). Finally, rank frequency curves were constructed for the 10 most common bee species for the different treatment levels using frequency data pooled over both sampling years.

Relative species abundance of the functional groups was used to examine their response to burning (i.e., scaled to the abundance of all bees). The relative species abundance data for each transect was summed across samples for each year, eliminating the effect of sample date. The counts of individuals belonging to each functional group were summed by transect and divided by the total number of individuals recorded for the same transect. Because the data are proportional, a general linear model with a binomial distribution for the error term was used to investigate the effect of burning on each functional group.

Bee community composition

Differences in the composition of species among transects was investigated for 2012, 2013, and pooled by treatment. Dissimilarity among transects in terms of their species composition was investigated using non-metric multidimensional scaling (NMS; PC-ORD version 6, McCune and Mefford 2011) based on the Sorenson (Bray-Curtis) distance measure. The effects of fire and sample date or year were determined using a two-way factorial design permutational multivariate analysis of variance (PerMANOVA) using the same distance measure that was used for the NMS analysis. Pearson and Kendall Correlations analyses were conducted to investigate correlations between environmental variables measured throughout the two year study and the community composition by fitting habitat vectors to ordinations of species. Analyses were conducted using PC-ORD ver 6 (McCune and Mefford 2011).

Results

Over the 2012 and 2013 seasons 2,146 bees were collected, representing 106 species and 29 genera (12 Apidae, 7 Megachilidae, 7 Halictidae, and three Andrenidae. In 2012; 52, 47, 47, and 28 species were collected from transects burned in 2012 (0B), transects burned in 2011 (1B), transects burned in 2010 (2B) and the control transects which have not been burned in the past 50 years or longer, respectively. In 2013, the trend is very similar to that of 2012 with 53, 48, 46, and 28 species collected from transects burned in in 2013 (0B), transects burned in 2012 (1B), transects burned in 2011 (2B) and the control, respectively. The number of individuals collected for each treatment increased in 2013, with the exception of transects that had been burned the year before the survey (1B). The number of individuals captured in the 1B transects decreased in 2013 but the number of species captured remained the same (Table 1).

Bee community structure: abundance, richness, diversity, and functional groups

Total bee abundance across both sampling years was significantly affected by burning (X^2= 13.59, P< 0.0035) and sample year (X^2= 4.67, P< 0.031) but not by an interaction between these two factors (X^2= 2.39, P< 0.495). On average, the bee abundance was higher in burned sites versus unburned sites and abundance was higher in all treatments in 2013 with the exception of the 1 year post-fire (1B) transects (Table 2a, Figure 2a). Total bee abundance was significantly higher in sites burned the same year as the samples were collected (0B) and significantly lower in unburned sites (C). The sites where one or two years had elapsed since burning showed a minor decrease in bee abundance compared to the sites burned the same year as study (Table 2a). Estimated species richness was significantly affected by burning (F= 5.705, P< 0.0162) but was not affected by sample year (F= 0.043, P< 0.838) or the interaction between the two factors (F= 0.441, P< 0.519). The estimated species richness for each treatment level remained nearly constant across sampling years, with estimated species richness being highest in sites that were burned the year of the study (0B), and the lowest in the unburned sites (C) (Table 2b, Figure 2b). As observed with bee abundance, estimated species richness decreased significantly in unburned sites and experienced a minor decrease in sites burned one and two years since previous (Table 2). The bee diversity (Simpson's diversity index, Figure 2c) was not significantly affected by burning (F= 1.462, P< 0.233), sampling year (F= 0.007, P< 0.933) or the interaction between the two (F= 1.494, P< 0.222). Bee diversity was highest in sites burned the same year as the study and decreased as time since burn increased. The rarefaction curves consistently show that the sites that were burned are more similar to one another in number of species per individuals than the control sites that had not been burned (Figures 3a, b, c). Rarefaction curves indicate that for both sample years, fewer species were collected than were predicted to have occurred in the areas sampled.

The two species that were most abundant across all treatment levels were *Lasioglossum* (*Dialictus*) *reticulatum* (Crawford) and *Augochlorella aurata* (Smith) (Fig 4). *Lasioglossum* (*D.*) *reticulatum* (Robertson) was the most common species in burned sites, followed by *A. aurata* (Figures 4 a, b, c). In unburned (Figure 4d) sites *A. aurata* was the most common species followed by *L.* (*D.*) *reticulatum*. The sand specialist, *Lasioglossum* (*Dialictus*) *apopkense* (Robertson), falls as the third or fourth most common species in burned sites and *Ceratina (Zadontomerus) calcarata* Robertson *or C(Z.) dupla* Say, stem nesting species that are not easily differentiated based on female morphology and often grouped together in publications (Hall and Ascher 2010, 2011, 2014), is the third most common species in unburned sites. Mean rank frequency curves (pooled over both sampling years) show that in the sites burned in the same year as the study, the top five ranked species had higher average frequencies than in all other treatment levels (Figure 4a). The most common genus represented across all treatment levels was *Lasioglossum* (*Dialictus*) (Figure 4).

Based on the proportion of species for each functional group, for all samples combined, the bee community was comprised of 12.3% wood nesting species, 55.7% ground nesting species, 14.2% sand specialists, 14.2% nest parasites, and 15.1% floral specialist species (see Appendix A for species allocations). The relative species abundance of the functional groups was not significantly affected by burning; however there were some interesting patterns observed that may be useful for comparison. The relative species abundance of wood nesting bees was found to be lowest in the sites burned the same year of sample (0B) and highest in the control sites, which have not been burned in over 50 years (Table 3a; Figure 5a). This outcome is in line with our hypothesis that this functional group would be most abundant in control sites. However, sites where one year had elapsed had the second highest relative species abundance for wood nesting bees. The relative species abundance of ground nesting bees was lowest in sites where one year had elapsed since burning (1B), and was highest in sites burned two years previous (2B) and the unburned sites (C) (Table 3b; Figure 5b). The relative species abundance of sand specialists was highest in sites burned the same year as sample (0B), and gradually decreased as each year elapsed with the control sites supporting the lowest relative species abundance (Table 3c; Figure 5c). We had anticipated that ground nesting bees and sand specialists, which are only specialized ground nesting bees, would have a similar pattern with the relative species abundance being highest in the recently burned sites (0B, 1B) and lowest in the unburned sites (C). However, only sand specialists met this expectation, suggesting that ground nesting bees that do not show a preference for sandy soils may require different conditions that are available in sites with the longest interval between burns. Parasitic bee relative species abundance was the highest in sites burned same year as sampling (0B) and lowest in the sites burned two years previous to sampling. Interestingly, the control sites had the second largest proportion of parasitic species (Table 3d; Figure

5d). The abundance of parasitic bees is dependent on the abundance of their respective hosts. The relative frequency of floral specialists was highest in sites burned the same year of sampling (0B) and lowest in the sites two years previous (2B). The unburned sites (C) supported an unexpectedly high relative species abundance of floral specialists (Table 3e; Figure 5e).

Bee community composition

In total, nearly 24% (25 of 106) of species collected occurred in both burned and unburned sites, 66% (70 of 106) of the species occurred only in the burned sites, and nearly 4% (4 of 106) of the species occurred only sites that had not been burned. Of the species that were collected only in burned sites, 41% (29 of 70) were collected in all burn levels, 18% (13 of 70) were collected only in sites burned the same year as the study (0B), 18% for sites burned one year previous to the study (1B), and 10% (7 of 70) of the species were collected only from sites burned two years prior to survey (2B). The number of unique species was higher in burned sites compared to unburned sites. When comparing the number of unique species recorded at different burn levels, the more recent burns (0B and 1B) have the same number while the number of unique species in the sites that went the longest since being burned (2B) was 50% lower than the other burn treatments.

The composition of bee communities across both years was significantly different based on treatment (pseudo-F= 2.65, P= 0.0002) and sample year (pseudo-F= 4.03, P= 0.0004), but was not affected by an interaction between treatment and sample year (pseudo-F= 0.89, P= 0.62). The composition of the bee community was significantly affected by burning in 2012 (pseudo-F=1.713, P=0.0328) and 2013 (pseudo-F=1.879, P=0.0202), as well.

The ordination analysis of the bee community showed that the sites that had been burned on a 3 year rotation were more similar to one another than to the sites that had not been burned in more than 50 years. Three statistics are used to support the validity of NMS ordination. “Stress”, a measure of goodness of fit, assesses the incongruity between the rank order of distances in the data, and the rank order of distances in the ordination (McCune and Mefford 2011). “Instability” represents how much the stress value varies with each additional run; low instability values increase the confidence in the stress value. The NMS will select the most appropriate dimensionality of the final graphical solution where additional dimensions will not decrease the stress value. For the Sorenson (Bray-Curtis) ordination for data pooled over sample years, the stress was 12.237, the instability was 0, and the cumulative proportion of variance explained by three axes was 0.863 (Figure 6a shows the two axes explaining the most variance). The pooled data ordination plot shows that the burned sites are clustered and overlap indicating that they are more similar to one another. The unburned sites are spread further apart and mostly separate from the burned sites. However, there is some overlap of the unburned sites with the sites that had not been burned in at least one year, representing some similarity between those sites. Variation in bee community composition was associated with the variation in some environmental indices; specifically, basal area and the percent of canopy cover are correlated with unburned sites.

For the ordination for 2012, the stress was 15.434, the instability was 0, and the cumulative proportion of variance explained by two axes 0.844 (Figure 6b). The ordination plot shows a pattern similar to that observed for the data pooled over sample year with the sites burned on a three year rotation appearing more similar to one another, however, here there is no overlap of unburned and burned sites. The number of environmental indices associated with variation in the bee community composition of 2012 increased. For 2012, flowering species diversity and average flower abundance by transect is correlated with the burned sites, while basal area, percent ground cover, and percent canopy cover are correlated with the unburned sites.

Discussion

Bee community structure: abundance, richness, diversity, and functional groups

Total bee abundance was greater in the sites that were burned compared to the unburned sites. This corresponds with the findings of Winfree et al. (2007) where disturbed areas supported a greater abundance than more densely forested areas. However, where abundance is higher in all other treatments, we observe a distinct decrease in the one year post-fire sites in 2013 (Fig. 3a) offering a possible explanation as to why abundance is the only response variable year has a significant effect on. Despite this abrupt decline in abundance, species density in the one year post-fire sites (1B) was comparable for both years (Table 1). Estimated species richness was highest in the most recently burned sites (0B, 1B) and lowest in the unburned sites. As expected abundance, estimated species richness, and diversity begin to decline as more time elapses since the last burn. This pattern suggests that the sites are beginning to move through successional stages as the time since the last burn increases. In the absence of fire, the shrub layer and opportunistic hard wood saplings begin to flourish, out competing other plants, limiting the herbaceous understory, and increasing canopy cover (Frost 1993). Unfortunately, there are no areas on the Foundation that are burned at longer intervals so we are unable to determine at what interval the bee community begins to resemble that present in our control sites.

The decline in abundance in sites one year since burn (1B) in 2013 and the absence of a significant treatment effect on diversity was unexpected and we believe our sampling methods may be partly responsible. Specimens for this study were collected only in bee bowls because the sweeping method employed in 2012 was ineffective for sampling bees and more appropriate for arthropod sampling in agricultural fields. Additionally, the bowls were not elevated for improved visibility as vegetation became denser throughout the growing season. Bee bowls are very effective at attracting bees, but have been found to only capture about 70% of species present, typically those species that are more abundant and generalist foragers (Grundel et al. 2011). The rarefaction curves generated (Figure 3) never reached an asymptote; while this is not uncommon in invertebrate studies, this does indicate that our sample did not provide a complete inventory of the present bee community (Gotelli and Colwell 2011). Reliance on bee bowls may bias how bee families and species are represented in a survey. Members of Halictidae, when compared to other bee families, are more likely to be captured in bee bowls (Roulston et al. 2007, Grundel et al. 2011), particularly species in the genus *Lasioglossum* (*Dialictus*) (Figure 4) (Cane et al. 2000) because the majority are ground-nesting, generalists. The two most common species reported in our rank frequency curves, *Lasioglossum* (*Dialictus*) *reticulatum* and *Augochlorella aurata* are primitively eusocial, ground-nesting, generalists In our study, Halictidae comprised 43.4% (46 species) of the species and 83% (1,782 individuals) of the individuals collected, and 9 of the 10 most frequently captured species for each treatment belonged to this family (Figure 4). *Lasioglossum* (*Dialictus*) represented 65% (30 species) of the species and 70.5% (1,256 individuals) of the individuals belonging to Halictidae collected during this study. Bee bowl trapping and sweep netting are complementary, but species capture rates have been found to be higher for netting than for bowls (Grundel et al. 2011) because the collector is able to capture bees that would and would not be found in bee bowls. We believe species density records could have been higher in our study if sweep netting had been incorporated into our sampling method.

The functional groups we investigated were not significantly affected by the presence or absence of fire in this ecosystem. However, if the savanna was allowed to move through succession and become a dense forest this would likely not be the case for most functional groups. A longleaf pine savanna is burned 81-121 hectares at a time, thereby creating a heterogeneous landscape with parcels at different stages of succession constantly and provides the opportunity for functional stability. In comparing the taxonomic response and functional groups response we see that fire and fire periodicity are influential at the species level but functional groups are slower to respond. While we found that there was no significant treatment effect for any of the functional groups but there were obvious trends present in the data that may provide perspective and allow for comparison between treatment levels.

We anticipated that there would be greater abundance of wood-nesting bees in the control sites due to the increased availability of fallen logs, a preferred nesting site for *Augochlora pura* (Say), and pithy stems, utilized by a number of wood-nesting species including *Ceratina (Zadontomerus) calcarata or C. (Z.) dupla* (Figure 5a). While our expectations were met we found that the difference in the percentage of woody debris available was negligible between treatments, with the highest percentage found in sites burned one year previous to sampling (38.8% of ground with woody debris present) and the lowest being the unburned sites (33.7% of ground with woody debris present).

We had anticipated that the abundance of ground nesting bees would be lowest in the control sites because of the amount ground cover, canopy cover, and cooler and damp microclimate. Sphecoid wasps, a paraphyletic sister group to bees, have ground nesting lineages that are closely associated with xeric regions (Michener 2007). Sixty-four percent of bees are ground nesters (Cane 1991, Michener 2007) and nest site selection for these species is predicated on many factors including, bee size, annual precipitation and temperature, and soil moisture and texture. This expectation was not met despite the control sites having the greatest about of ground (98.6%) and canopy cover (82.6%) of any of the other treatment levels. This could also be an artifact of the control sites being of a smaller size compared to the swaths that are burned on the Foundation, meaning they are perhaps too closely situated to burned sites for representative species of the different functional groups to be excluded. Bees are capable of flying great distances while foraging. *Nomia melanderi* Cockerell and *Bombus* spp. have been seen foraging up to 1.5 km or more from their nests (Cane and Neff 2011). Another possibility is that ground nesting bees that next less than 5 cm below the surface may experience mortality in the areas most recently burned reducing the representation of the group (Cane and Neff 2011). The representation of sand specialists on the Foundation was exactly as we had anticipated (Figure 5c), with the greatest relative species abundance in the sites burned the same year as sampling and decreasing as each year post-fire passes. Sand specialists and ground-nesting bees do not follow the same trend because sand specialists are a specialized type of ground-nesting bee that requires open, sandy soils. The soil characteristics required by ground-nesting bees, in general, are variable and not correlated among species, making it difficult to predict preferences based on bee species' familial or tribal affiliation (Cane 1991).

The proportion of parasitic bee species I found in this study falls short of the proportion of parasitic bees present in North America and in North Carolina (Mitchell 1960, 1962). It has been estimated that nearly 20% of all North American bee species are nest parasites (O'Toole and Raw 2004). However, because the Sandhills habitat is so specific, we do not feel that the nest parasites are underrepresented. Cleptoparasitic bees have been recently recognized as possible indicators of diversity for bee communities (Sheffield et al. 2013). Sheffield et al. (2013) argue that cleptoparasites fulfill the role of an apex predator in a bee community and just like the apex predator; cleptoparasites depend on the presence and abundance of their host for survival. So their diversity and abundance relative to all bees is indicative of the status of the bee community. If parasites are truly indicators of bee community health, we could assert that the bee community we identified is thriving and because the greatest relative species abundance is found in sites burned one year previous, suggests that one year after the burn is when the bee community is at its most stable. However, we do so hesitantly. Hall and Ascher (2014) warn that care should be taken in interpreting these data when relying heavily on bee bowls because low numbers may be an artifact of biased sampling. As previously discussed, bee bowls were used consistently throughout our survey while sweep netting was only employed in 2013. In spite of this, we found species density was relatively high for cleptoparasites with 15% of the overall species density comprised of nest parasites. The low abundance of the cleptoparasitic species is likely due in part to the cryptic and specialist nature of cleptoparasites (Michener 2007) and the specific habitat of the longleaf pine savanna.

All parasitic species collected were cleptoparasites with the exception of one; *Lasioglossum* (*Dialictus*) *lionotum* (Sandhouse) is a social parasite of *L.* (*D.*) *imitatum* (Smith). The social parasite, *L.* (*D.*) *lionotum*, collected during our survey was not reported in the other regional surveys, but its host, *L.* (*D.*) *imitatum* was collected in the CSNWR and the Louisiana/Mississippi surveys. *Lasioglossum* (*D.*) *imitatum* is a primitively eusocial ground-nesting bee with workers that forage regularly. Once a female *L.* (*D.*) *lionotum* successfully establishes herself as the queen within the nest of *L.* (*D.*) *imitatum* she no longer needs to forage making *L.* (*D.*) *lionotum* less likely to be captured in bowls or by sweep net.

The emergence and life span of oligolectic species coincides with the flowering period of their respective host, making them highly seasonal, typically solitary, and, often, less abundant than generalist species (O'Toole and Raw 2004). In our study, 10 oligoleges were collected in the spring and 7 were collected in the fall. Oligolectic species exclusively forage on one species or a group of related species for pollen but may be seen foraging nectar from flowers outside of this group (O'Toole and Raw 2004), offering a possible explanation for captures in bowls or on a species outside of the expected host range. *Perdita* (*Perdita*) *halictoides* Smith was collected in a bowl but two species within the host genus, *Physalis*, are present on the Foundation, including a rare sandhills endemic, *Physalis lanceolata* Michaux (Sorrie 2011).Three *Lasioglossum* (*Dialictus*) *ceanothi* (Mitchell), a rare species specific to *Ceanothus* (Rhamnaceae) (Gibbs 2011), were collected. Unfortunately all were female as the male of this species has not yet been described (Gibbs 2011).

The four additional *Perdita* species collected were specific to Asteraceae and collected only in the fall, when large numbers of asters bloom, demonstrating the close relationship between oligolege phenology and that of their respective host plants. Oligolecty is thought to be a rare specialization in savannas because, unlike deserts, there is a constant and shifting floral resource. Greater polylecty is proposed as the case for pollinators in general in longleaf pine savannas (Folkerts et al. 1993).

Bee community composition

The distance between many of the burned sites is shorter, on average, so we would expect greater similarity. The unburned sites have received no active management in over 50 years. This situation creates an interesting dynamic, where not only are the unburned sites not similar to the burned sites, they are not similar to one another. In the absence of management, the sites have begun to transition through different successional stages; one unburned site was dominated by loblolly pine, another dominated by oak, while the others were in the softwood to hardwood transition. The species are mainly clustered within the burned sites, which is no surprise when 66% of the species collected were found only in burned sites and 24% of overall species collected were found in all sites. Only 4% of the species collected were found solely in unburned sites, two species are of interest; *Lasioglossum* (*Dialictus*) *cressoni* is a wood nesting species, *Perdita* (*Perdita*) *halictoides* is an oligolectic, ground nesting bee that provisions with *Physalis* spp. pollen only. *Physalis lanceolata* (Sandhills Ground-cherry) is an endemic to the Sandhills and is the only *Physalis* spp. reported to be present on the Foundation. Ten percent of the species collected from burn sites were found solely in the two year post-fire (2B) sites. However, if we include all the species collected on the Foundation we find that the bees collected only on these sites make up 6% of the total species density. The bees collected solely on the sites burned the same year as sampling (0B) and one year previous (1B) each represent 12% of the total species density.

The correlations between some environmental indices and the variation in bee species composition support the hypothesis that prescribed burning is a major factor that causes post-fire changes in community composition. In 2012, this is clearly illustrated with flower abundance and flower species density correlated with the burned sites, while basal area, percent canopy cover, and percent ground cover are correlated with the unburned sites. Flower species richness (density and abundance included here) and canopy cover have been shown to be influential in how the bee community is composed (Moretti et al. 2009, Grundel et al. 2010). The results of this study indicate that a 3 year burn rotation can alter the composition of the bee community in the longleaf pine savanna.

Conclusion

Where fire occurs it has an immediate catastrophic effect on a habitat but recovery is rapid, especially in fire-adapted ecosystems. Potts et al. (2003) observed that the diversity of flowering plants and bees in the semi-arid Mediterranean scrub region of Israel peaked in the first two years following fire and declined steadily over the next 50 years. A similar burst of bee diversity, as well as abundance, following prescribed burning was also observed in the black oak savanna of Indiana (Grundel et al. 2010) and the Blue Ridge Mountains of North Carolina (Campbell et al. 2007). In our study, we find this same trend. Overall diversity was highest in the sites that were burned the same year as sampling, and those burned one year previous to sampling, and begin to decline in the sites burned two years previous to sampling.

The Sandhills region extends from North Carolina, through South Carolina, into Georgia, with isolated pockets of similar habitat found scattered across northern Florida. It is important to study how disturbance influences the bee community in the eastern Sandhills/longleaf pine savanna to provide perspective on species turnover and resource availability, in order to fully understand how best to manage this unique and threatened habitat. Bees are keystone species, but there are still relatively few studies that investigate how changes in land-use and management shape bee communities in North America, especially the southeastern U.S. Our study seeks to address both of these deficits and provide pertinent information for prescribing actionable conservation programs for native bees as well as continued work in longleaf pine savannas. Our study is just one of the many needed to help complete our understanding of North American bee fauna.

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Table 1

Number of individuals and species captured in each treatment level for each sampling year and pooled. The number of species collected in each treatment for each year is comparable. More individuals were collected in 2013 at all treatment levels with the exception of 1B.

	2012		2013		Pooled	
	Individuals	*Species*	*Individuals*	*Species*	*Individuals*	*Species*
0B	301	52	428	53	729	82
1B	290	47	252	44	572	72
2B	251	47	357	43	608	67
Control	181	28	227	29	408	40

Table 2
Type-III sums of squares for the effect of burning and sample year on a) bee abundance, b) estimated species richness, and c) bee diversity (Simpson's index) of pooled data across sampling years.

Individual Abundance	Estimate	Std. Error	Z value	Pr(>|Z|)	
(Intercept)	1.502	0.1583	9.486	< 2e-16	***
Treatment (1B)	-0. 1076	0.226	-0.476	0.634	
Treatment (2B)	-0. 2878	0.2276	-1.265	0.2059	
Treatment (C)	-0.8148	0.2361	-3.452	0.000557	***
Year 2013	0.4834	0.2237	2.160	0.030754	*

Species Richness (Chao 1)	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	7.5672	1.1543	6.555	1.55e-07	***
Treatment (1B)	-1.1650	0.9154	-1.273	0.218282	
Treatment (2B)	-1.7901	0.9154	-1.956	0.065192	
Treatment (C)	-4.6948	1.0186	-4.609	0.000154	***
Year 2013	-0.1317	1.4151	-0.093	0.92672	

Simpson's Diversity Index	Estimate	Std. Error	t value	Pr(>|t|)	
(Intercept)	0.744145	0.025065	29.688	<2e-16	***
Treatment (1B)	-0.013689	0.031335	-0.437	0.6627	
Treatment (2B)	-0.043542	0.031335	-1.390	0.1662	
Treatment (C)	-0.063932	0.033222	-1.924	0.0668	.
Year 2013	-0.001809	0.021616	-0.084	0.9334	

Table 3
Type-III sums of squares for the effect of burning on the relative frequency of a) wood nesting bees, b) ground nesting bees, c) sand specialists, d) parasitic bees, and e) floral specialists, data pooled across sampling years.

Wood nesting species	Estimate	Std. Error	Z value	Pr(>|Z|)
(Intercept)	-3.4441	2.0044	-1.718	0.0857
Treatment (1B)	1.0535	2.1885	0.481	0.6388
Treatment (2B)	0.2519	2.4764	0.102	0.9190
Treatment (C)	1.4593	2.1048	0.693	0.4881
Year 2013	0.3944	1.3134	0.300	0.7639

Ground nesting species	Estimate	Std. Error	Z value	Pr(>|Z|)
(Intercept)	0.52534	0.82138	0.640	0.522
Treatment (1B)	-0.11211	1.03362	-0.108	0.914
Treatment (2B)	0.07115	1.04636	0.068	0.946
Treatment (C)	0.08223	1.04728	0.079	0.937
Year 2013	0.08976	0.73774	0.122	0.903

Sand specialist species	Estimate	Std. Error	Z value	Pr(>|Z|)
(Intercept)	-1.6244	1.0754	-1.511	0.131
Treatment (1B)	-0.2289	1.3053	-0.175	0.861
Treatment (2B)	-0.7398	1.4537	-0.509	0.611
Treatment (C)	-1.3418	1.7237	-0.778	0.436
Year 2013	0.4324	1.0701	0.404	0.686

Parasitic species	Estimate	Std. Error	Z value	Pr(>|Z|)
(Intercept)	-3.7138	2.6001	-1.428	0.153
Treatment (1B)	-0.7925	3.5291	-0.225	0.822
Treatment (2B)	-1.3383	4.2902	-0.312	0.755
Treatment (C)	-0.3788	3.1109	-0.122	0.903
Year 2013	0.5665	2.6461	0.214	0.83

Floral specialist species	Estimate	Std. Error	Z value	Pr(>|Z|)
(Intercept)	-3.6765	2.5078	-1.466	0.143
Treatment (1B)	-0.1876	3.0712	-0.061	0.951
Treatment (2B)	-0.7973	3.6772	-0.217	0.828
Treatment (C)	-0.2956	3.1603	-0.094	0.925
Year 2013	0.3689	2.4074	0.153	0.878

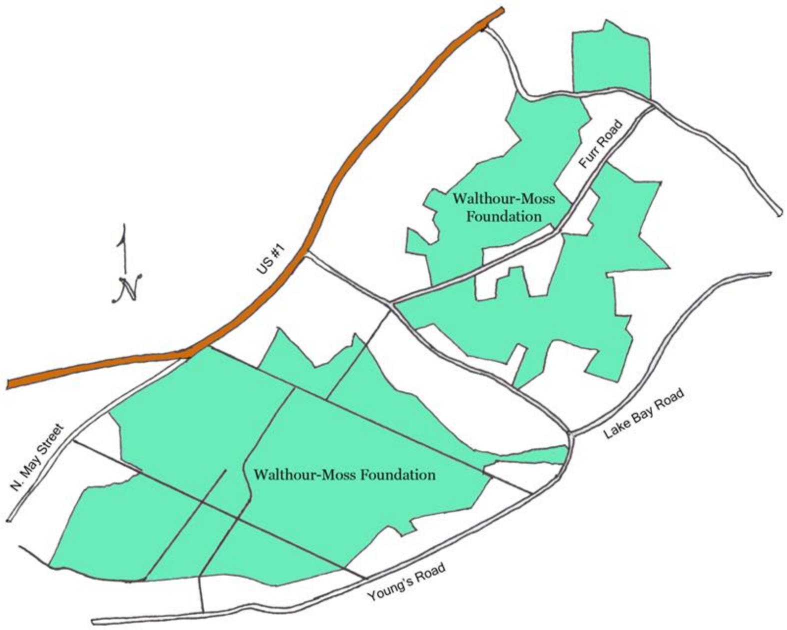


Figure 1 Map of Walthour-Moss Foundation

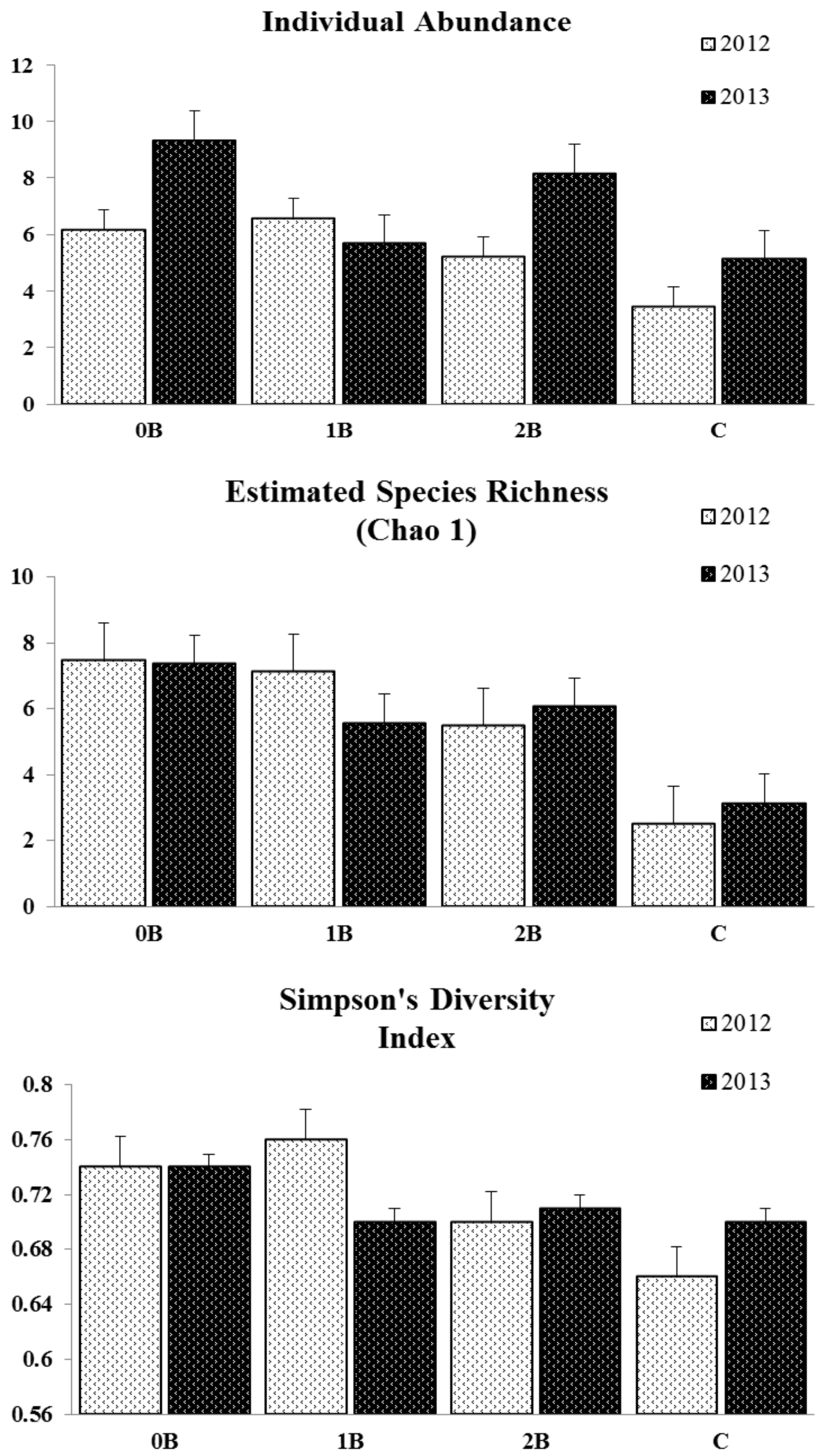


Figure 2 Mean (±1 SE) of a) total bee abundance, b) estimated species richness, and c) Simpson's diversity index of burned (0B, 1B, 2B) and unburned (C) areas for both sampling years .

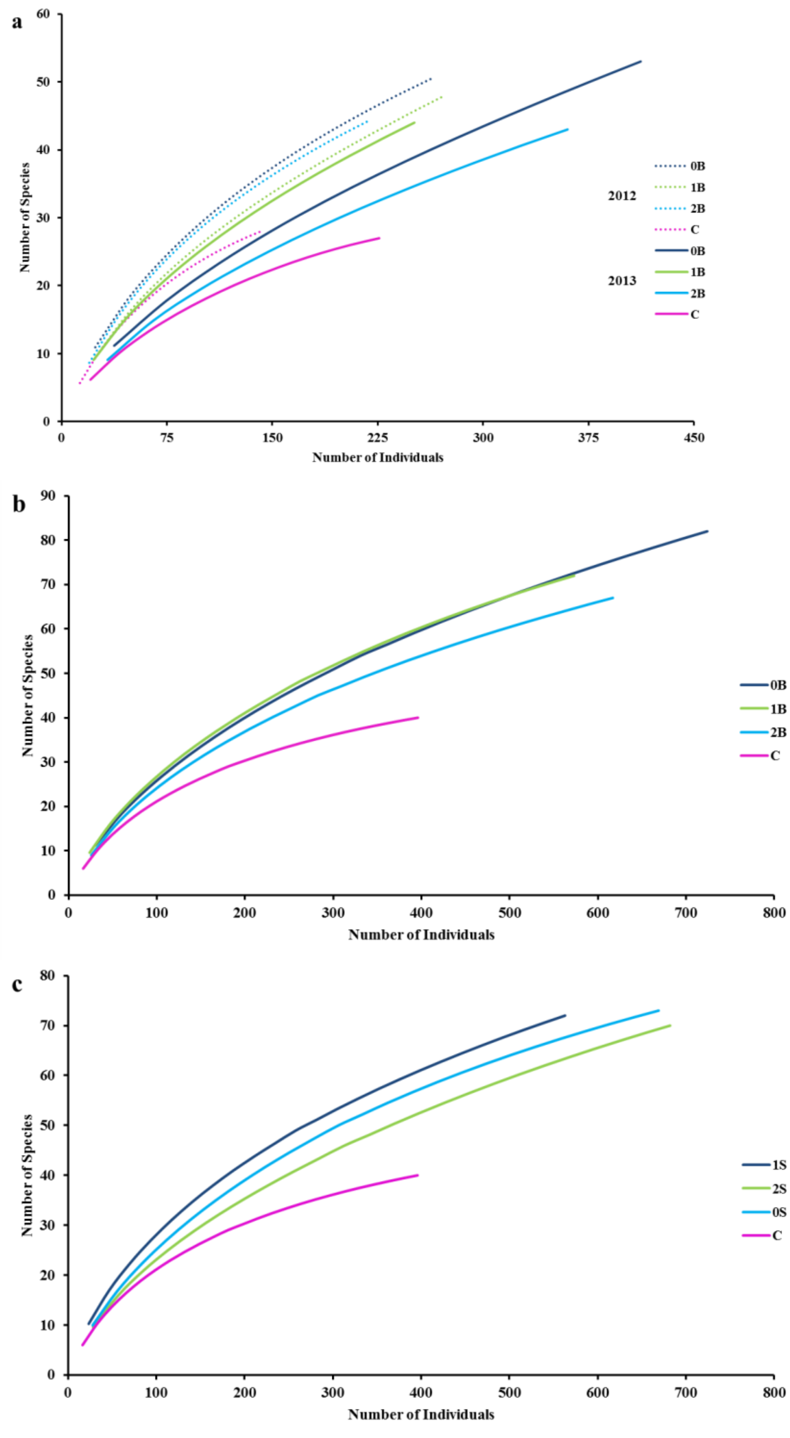
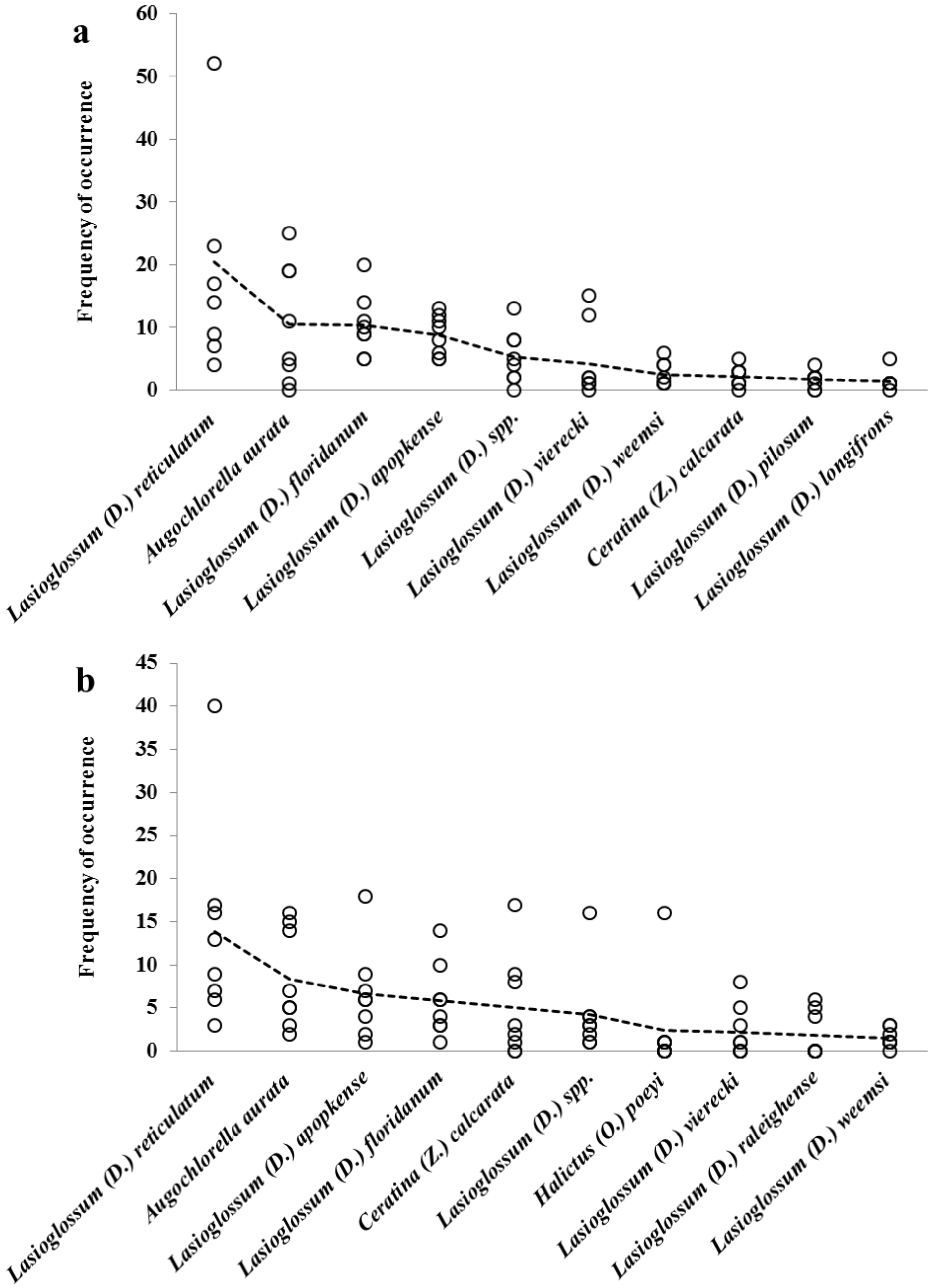
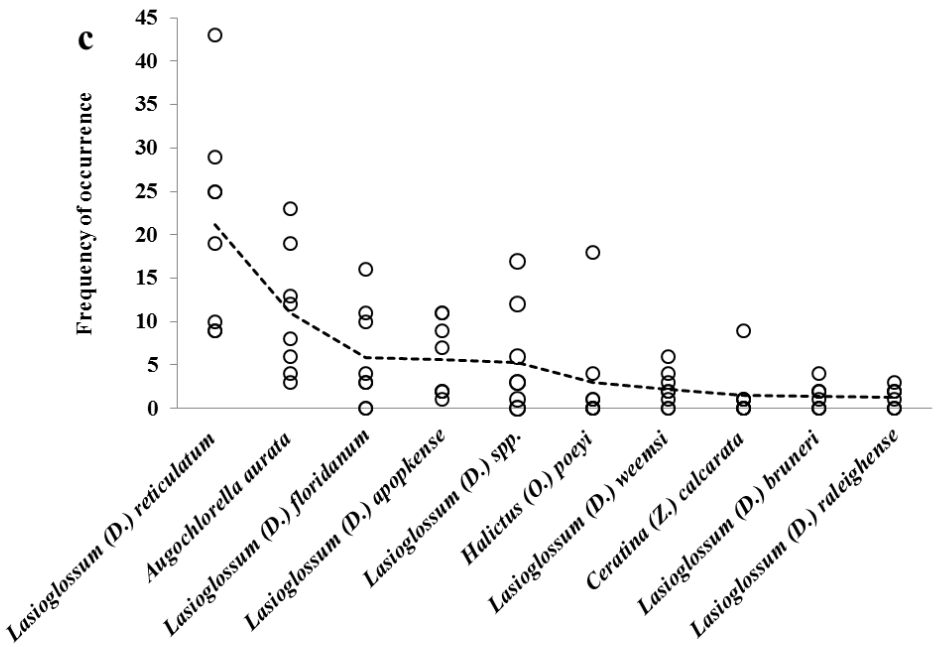


Figure 3 Rarefaction curves of number of bee species captured in burned (0B, 1B, 2B) and unburned (C) transects. a) shows curves for each year at the four treatment levels (n=11 samples per transect), b) shows curves pooled by treatment over years (n= 24 samples per transect), and c) shows curves pooled by burn sequence over years (n= 24 samples per transect).

Figure 4 Rank frequency curves based on 10 most common bee species in areas a) burned year of sampling (0B), b) burned 1 year before sampling (1B), c) burned 2 years before sampling (2B), and d) not burned in >50 years (C). Open circles show the frequency of species on individual transects. Frequency data are pooled over both sampling years.


a
Frequency of occurrence
60
50
40
30
20
10
0
Lasioglossum (D.) reticulatum
Augochlorella aurata
Lasioglossum (D.) floridanum
Lasioglossum (D.) apopkense
Lasioglossum (D.) spp.
Lasioglossum (D.) vierecki
Lasioglossum (D.) weemsi
Ceratina (Z.) calcarata
Lasioglossum (D.) pilosum
Lasioglossum (D.) longifrons
b
Frequency of occurrence
45
40
35
30
25
20
15
10
5
0
Lasioglossum (D.) reticulatum
Augochlorella aurata
Lasioglossum (D.) apopkense
Lasioglossum (D.) floridanum
Ceratina (Z.) calcarata
Lasioglossum (D.) spp.
Halictus (O.) poeyi
Lasioglossum (D.) vierecki
Lasioglossum (D.) raleighense
Lasioglossum (D.) weemsi


c
Frequency of occurrence
45
40
35
30
25
20
15
10
5
0
Lasioglossum (D.) reticulatum
Augochlorella aurata
Lasioglossum (D.) floridanum
Lasioglossum (D.) apopkense
Lasioglossum (D.) spp.
Halictus (O.) poeyi
Lasioglossum (D.) weemsi
Ceratina (Z.) calcarata
Lasioglossum (D.) bruneri
Lasioglossum (D.) raleighense

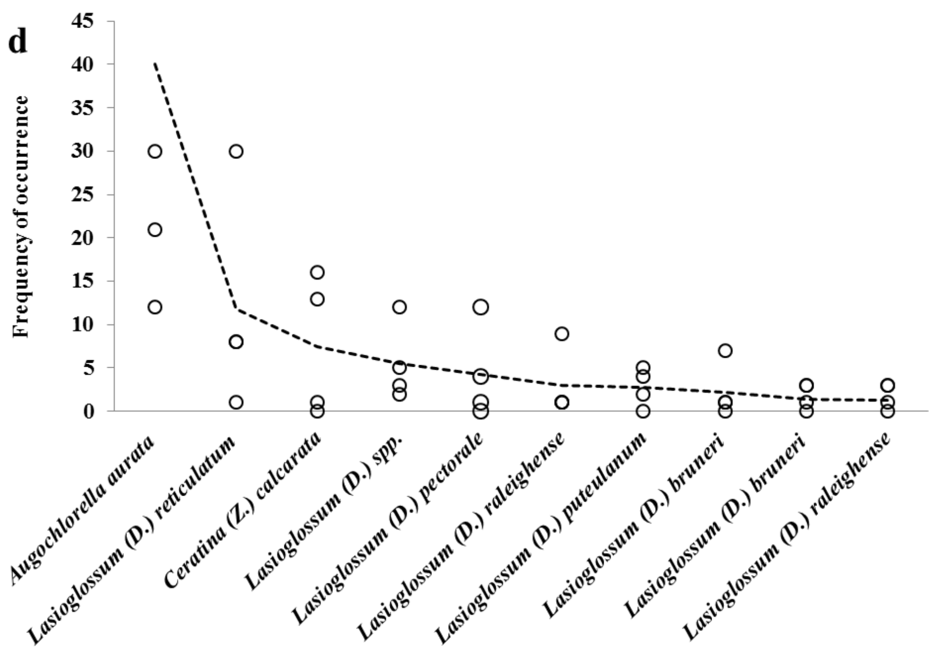
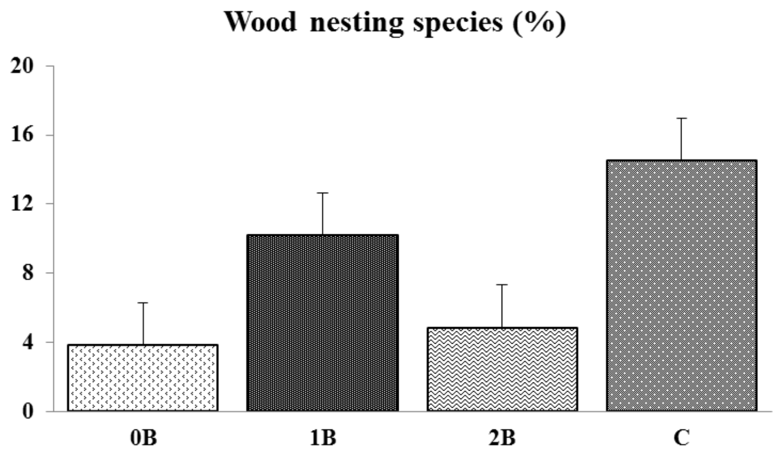
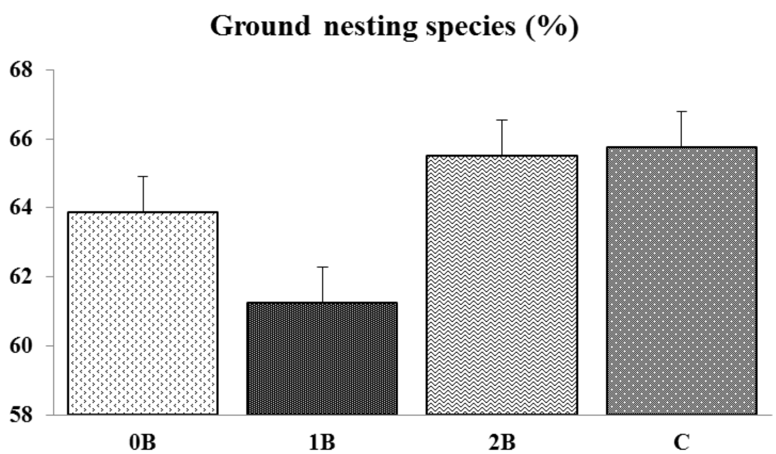
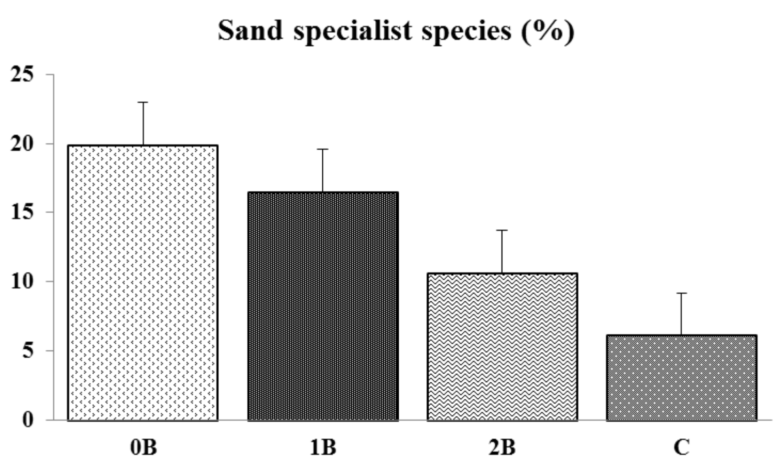
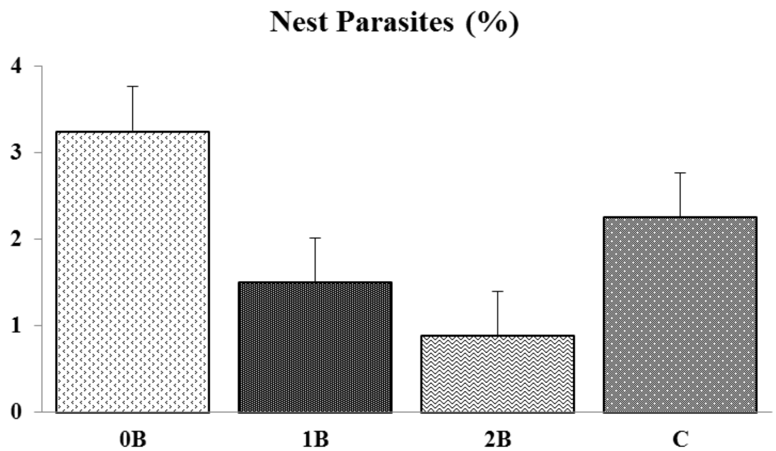

d
Frequency of occurrence
45
40
35
30
25
20
15
10
5
0
Augochlorella aurata
Lasioglossum (D.) reticulatum
Ceratina (Z.) calcarata
Lasioglossum (D.) spp.
Lasioglossum (D.) pectorale
Lasioglossum (D.) raleighense
Lasioglossum (D.) puteulanum
Lasioglossum (D.) bruneri
Lasioglossum (D.) bruneri
Lasioglossum (D.) raleighense

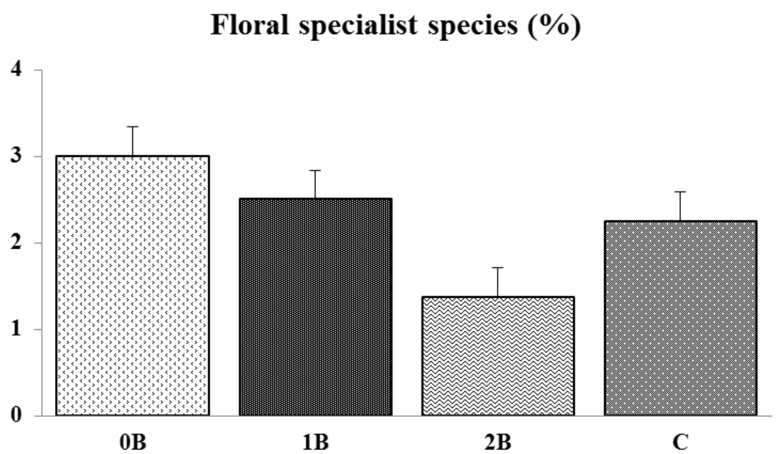
Figure 5 Mean (±1 SE) of a) wood nesting species, b) ground nesting species, c) sand specialist species, d) nest parasites, and e) floral specialist species in burned (0B, 1B, 2B) and unburned (C) areas for both sampling years.


Wood nesting species (%)
20
16
12
8
4
0
0B
1B
2B
C


Ground nesting species (%)
68
66
64
62
60
58
0B
1B
2B
C


Sand specialist species (%)
25
20
15
10
5
0
0B
1B
2B
C


Nest Parasites (%)
4
3
2
1
0
0B
1B
2B
C


Floral specialist species (%)
4
3
2
1
0
0B
1B
2B
C

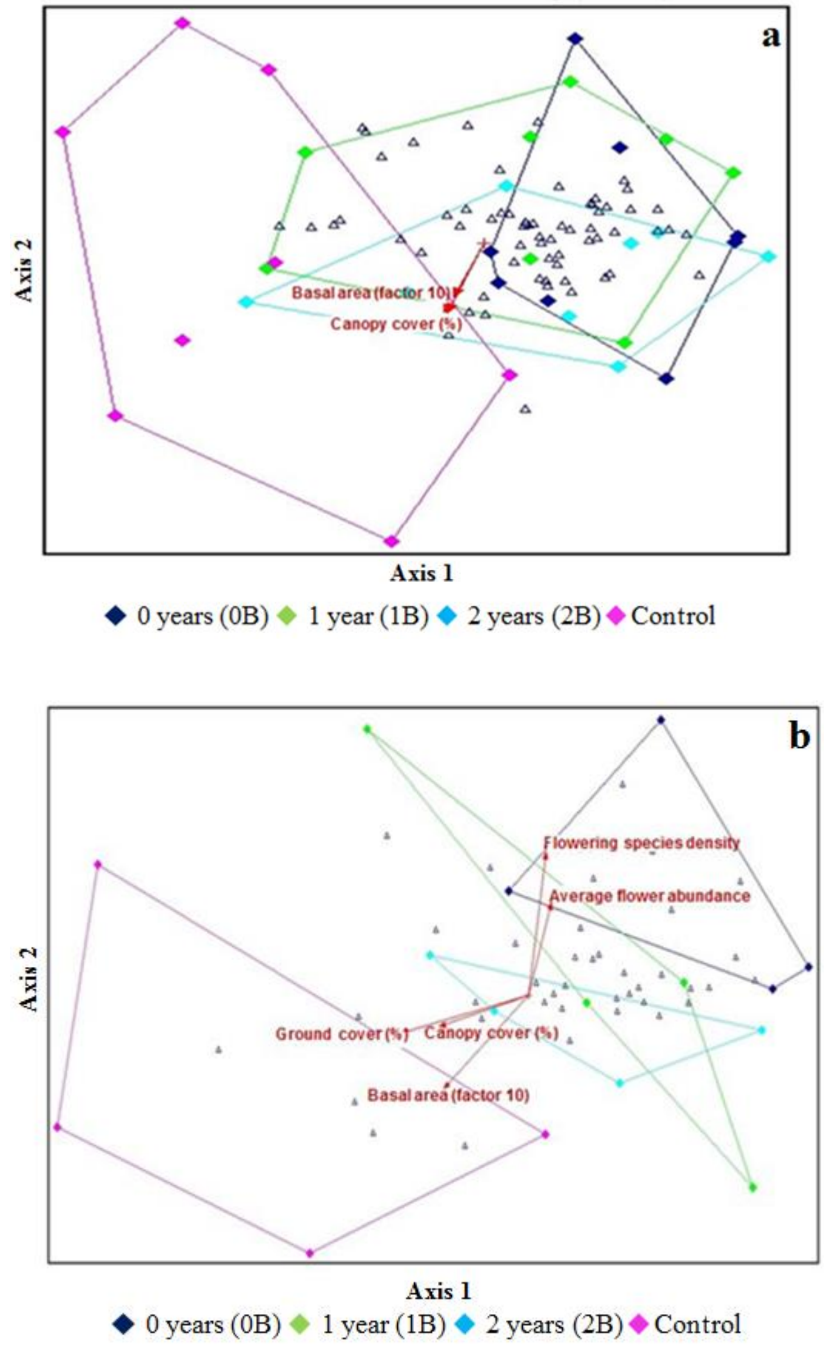


Figure 6 Non-metric multidimensional scaling ordination plots of bee species composition for a) data pooled by sample year (stress = 12.237) and b) and data collected in sampling year 2012 (stress = 15.434). The direction of the vectors indicates the greatest change in the habitat variables and the length shows the strength of the correlations between ordination and habitat variables.

APPENDICES

Appendix A. Native bee species collected on the Walthour-Moss Foundation

Species	Early & late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Ground nester	Sand specialist	Wood nester	Parasite	Host of parasite	Oligolectic	Host of oligolege	Bees collected from
HALICTIDAE																
Agapostemon (Agapostemon) sericeus (Förster, 1771)	27-IV, 13-X	9	3		2			14	*							
Agapostemon (Agapostemon) splendens(Lepeletier, 1841)	26-IV, 28-IX	3	2		4	4		13	*	*						Ss, Sco
Agapostemon (Agapostemon) texanus Cresson, 1872	8-VIII	1						1	*							
Agapostemon (Agapostemon) virescens (Fabricius, 1775)	30-IV, 14-X	18						18	*							
Augochlora (Augochlora) pura (Say, 1837)	13-IV, 26-IV	2						2			*					
Augochlorella aurata (Smith, 1853)	30-IV, 14-X	408	6		30	6		450	*							Cr, Gr, Ha, So, Sd
Augochlorella gratiosa (Smith, 1853)	1-V, 13-X	7	8		1	2		18	*							
Augochloropsis (Paraugochloropsis) metallica (Fabricius, 1793)	27-IV, 28-IX	3			16			19	*							Va, Pan, Ss, Ig, Dt
Augochloropsis (Paraugochloropsis) sumptuosa (Smith, 1853)	6-IV, 25-VII	1			5			6	*	*						Va, Ss, Ca
Halictus (Nealictus) parallelus Say, 1837	31-V, 25-VII	2			1	3		6	*							Ca, Es
Halictus (Odontalictus) poeyi Lepeletier, 1841	14-V, 14-X	42	7		17			66	*							Ca, Es, Pa, Sco, Van
Lasioglossum (Dialictus) apopkense(Robertson,1892)	30-III, 14-X	185	2	1	5			193	*	*						Gr, Rco, Rg
Lasioglossum (Dialictus) batya Gibbs, 2011	16-VI, 14-X	3						3								
Lasioglossum (Dialictus) bruneri (Crawford, 1902)	16-IV, 16-IX	31	2		2	3		38	*							
Lasioglossum (Dialictus) callidum (Sandhouse, 1924)	13-IV, 14-X	15	2		1			18								
Lasioglossum (Dialictus) ceanothi (Mitchell, 1960)	2-VIII, 3-VIII	2			1			3						*	*Ceanothus*	
Lasioglossum (Evylaeus) cinctipes (Provancher, 1888)	18-V, 29-VI	1	2					3	*							
Lasioglossum (Dialictus) coreopsis (Robertson, 1902)	6-IV, 15-IX	8			3	1		12	*							Es, Ld
Lasioglossum (Dialictus) cressonii (Robertson, 1890)	2-VIII	1						1			*					
Lasioglossum (Dialictus) floridanum (Robertson, 1892)	30-III, 13-X	204	1		4	1		210								Ld, Pas, Sco
Lasioglossum (Dialictus) foveolatum (Robertson, 1902)	18-V	1						1								
Lasioglossum (Lasioglossum) fuscipenne (Smith, 1853)	6-IV, 1-VI	2						2	*							

Appendix A. Native bee species collected on the Walthour-Moss Foundation

Species	Early & late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Ground nester	Sand specialist	Wood nester	Parasite	Host of parasite	Oligolectic	Host of oligolege	Bees collected from
Lasioglossum (*Dialictus*) *gotham* Gibbs, 2011	1-VI	1						1	*							
Lasioglossum (*Dialictus*) *illinoense* (Robertson, 1892)	6-IV, 3-VIII	15		1	1			17	*							Cs
Lasioglossum (*Dialictus*) *imitatum* (Smith, 1853)	1-V, 16-VI	2			1			3	*				*Lasioglossum* (*D.*) *imitatum*			Ss
Lasioglossum (*Dialictus*) *lionotum* (Sandhouse, 1923)	31-V	1						1				*				
Lasioglossum (*Dialictus*) *longifrons* (Baker, 1906)	14-IV, 15-VI	17						17								
Lasioglossum (*Dialictus*) *mitchelli* Gibbs, 2010	31-V, 16-VI	7						7								
Lasioglossum (*Evylaeus*) *nelumbonis* (Robertson, 1890)	26-IV	1						1	*					*	Nymphaeaceae	
Lasioglossum (*Dialictus*) *nymphale* (Smith, 1853)	30-III, 13-X	10			2			12	*	*						Ld
Lasioglossum (*Dialictus*) *oblongum* (Lovell, 1905)	6-IV	1						1			*					
Lasioglossum (*Dialictus*) *pectorale* (Smith, 1853)	13-IV, 2-VIII	28			3			31	*							Pan
Lasioglossum (*Dialictus*) *pilosum* (Smith, 1853)	26-IV, 14-X	42						42	*	*						
Lasioglossum puteulanum/isgulare	6-IV, 14-X	17						17								
Lasioglossum (*Dialictus*) *puteulanum* Gibbs, 2009	31-V, 13-X	3						3								
Lasioglossum (*Dialictus*) *raleighense* (Crawford, 1932)	6-IV, 14-X	43			4			47								
Lasioglossum (*Dialictus*) *reticulatum* (Robertson, 1892)	30-III, 14-X	489	1	61	20		3	574	*							Bc, Gr, Rco
Lasioglossum (*Dialictus*) *smilacinae* (Robertson, 1899)	6-IV, 15-VI	8			1			9								
Lasioglossum (*Evylaeus*) *sopinci* (Crawford, 1932)	6-IV, 1-VI	3						3	*	*						
Lasioglossum (*Dialictus*) *subviridatum* (Cockerell, 1938)	30-IV, 14-VI	6						6			*					
Lasioglossum (*Dialictus*) *tegulare* (Robertson, 1890)	15-IV, 3-VIII	6			1			7	*							
Lasioglossum (*Dialictus*) *timothyi* Gibbs, 2010	31-V	1						1								
Lasioglossum (*Dialictus*) *trigeminum* Gibbs, 2011	16-IV, 14-X	18		6	7	1		32								
Lasioglossum (*Evylaeus*) *truncatum* (Robertson, 1901)	1-VI	1			2			3	*							Ig
Lasioglossum (*Dialictus*) *vierecki* (Crawford, 1904)	6-IV, 15-IX	66			18			84	*	*						Es, Gr, Pas, Rg
Lasioglossum (*Dialictus*) *weemsi* (Mitchell, 1960)	6-IV, 14-X	58		4	7			69								Gr, Ss

Appendix A. Native bee species collected on the Walthour-Moss Foundation

Species	Early & late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Ground nester	Sand specialist	Wood nester	Parasite	Host of parasite	Oligolectic	Host of oligolege	Bees collected from
Sphecodes atlantis Mitchell, 1956	15-IV	1						1	*			*	*Lasioglossum* (*Dialictus*)			
Sphecodes brachycephalus Mitchell, 1956	1-V, 13-V	2	1					3	*			*				
Sphecodes mandibularis Cresson, 1872	30-III	1						1	*			*				
ANDRENIDAE																
Andrena (*Scrapteropsis*) *atlantica* Mitchell, 1960	16-IV, 1-VI		1		1	1		3	*							Ig
Andrena (*Holandrena*) *cressonii* Robertson, 1891	13-V	1						1	*							
Andrena (*Callandrena s.l.*) *krigiana* Robertson, 1901	13-IV, 14-IV		5					5	*					*	*Krigia*	
Andrena (*Micrandrena*) *melanochroa* Cockerell, 1898	13-V	1						1	*					*	Rosaceae	
Andrena (*Scrapteropsis*) *morrisonella* Viereck, 1917	13-V, 1-VI	2			2			4	*					*	Ranunculaceae	Ig
Panurginus potentillae (Crawford, 1916)	30-III, 14-IV	2						2	*					*	Potentilleae, esp. *Potentilla*	
Perdita (*Hexaperdita*) *bishoppi* Cockerell, 1906	1-IX, 2-IX	1	2					3	*	*				*	Asteraceae	
Perdita (*Perdita*) *consobrina* Timberlake, 1928	24-VIII, 6-IX	5	4	1	4	2		16	*	*				*	Asteraceae	Pp
Perdita (*Hexaperdita*) *georgica* Timberlake, 1928	6-IX, 28-IX	1			2			3	*	*				*	Asteraceae	Pp
Perdita (*Perdita*) *gerardiae* Crawford, 1932	24-VIII, 15-IX	6			1			7	*	*				*	*Agalinis*	Pp
APIDAE																
Anthophora (*Melea*) *abrupta* Say, 1837	30-III, 14-V	2	4		3	4		13	*							Ld, Rcu
Bombus (*Pyrobombus*) *bimaculatus* Cresson, 1863	14-IV, 28-IX	2			14	3		19								Va, Ig, Ss, Gr, Ca
Bombus (*Separatobombus*) *griseocollis* (DeGeer, 1773)	31-V, 14-X	4			8			12								Ca
Bombus (*Pyrobombus*) *impatiens* Cresson, 1863	18-V, 14-X	7			15	2		24								Ca, Ig
Bombus (*Pyrobombus*) *vagans* Smith, 1854	18-V, 1-VI	3						3								
Ceratina (*Zadontomerus*) *calcarata* Robertson, 1900 or *C*(*Z.*) *dupla* Say, 1837	30-III, 14-V	53	61		5	3		122			*					
Epeolus erigeronis Mitchell, 1962	1-VI		1					1	*			*	*Colletes* spp.			
Habropoda laboriosa (Fabricius, 1804)	30-III, 1-V		2		9	2		13	*					*	*Vaccinium*	Va
Melecta (*Melecta*) *pacifica* Cresson, 1878	30-III	1						1	*			*	*Anthophora* spp.			
Melissodes (*Melissodes*) *bimaculata* (Lepeletier, 1825)	24-VII		1					1	*							

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Species	Early & late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Ground nester	Sand specialist	Wood nester	Parasite	Host of parasite	Oligolectic	Host of oligolege	Bees collected from
Melissodes (Melissodes) communis Cresson, 1878	1-VI	1						1	*							
Melissodes (Melissodes) comptoides Robertson, 1898	9-VIII, 1IX	2	1					3	*							
Melissodes (Eumelissodes) dentiventris Smith, 1854	13-X, 14-X	2	1					3	*					*	Asteraceae, esp. Astereae	
Melitoma taurea (Say, 1837)	1-VI	1						1	*					*	*Ipomoea*	
Nomada australis Mitchell, 1962	13-IV, 26-IV	1	1					2	*			*	*Agapostemon* spp.			
Nomada fragariae Mitchell, 1962	6-IV, 14-V	1	2			1		4	*			*	*Andrena* spp.			
Nomada luteola Olivier, 1811	26-IV, 13-V	3	2		1			6	*			*	*Andrena* spp.			Va
Nomada parva Robertson, 1900	16-IV, 18-V	6	2		2	1		11	*			*	*Andrena* spp.			
Ptilothrix bombiformis (Cresson, 1878)	16-VI		1					1	*					*	*Hibiscus*	
Svastra (Epimelissodes) atripes (Cresson, 1872)	8-VIII, 28-IX	1	2		1			4	*					*	*Chamaecrista* & *Senna*	Sca
Xylocopa (Xylocopoides) virginica (Linnaeus, 1771)	16-IV, 28-IX	2			6	4		12								Sca, Va
MEGACHILIDAE																
Anthidiellum (Loyolanthidium) notatum (Latreille, 1809)	29-VI, 5-IX	2			8	7		17								Gr, Es, Pas, Lb
Coelioxys (Boreocoelioxys) sayi Robertson, 1897	5-IX, 14-X	2	1		1	2		6				*	*Megachile brevis* and *M. mendica*			Lb
Heriades (Neotrypetes) carinatus Cresson, 1864	14-V, 14-VI	1			4			5								Ig, Es
Hoplitis (Alcidamea) pilosifrons (Cresson, 1864)	14-IV, 18-V	2	4			2		8			*					Ld
Hoplitis (Alcidamea) producta (Cresson, 1864)	14-IV, 26-IV	1	5					6			*					
Hoplitis (Alcidamea) truncata (Cresson, 1878)	30-III, 15-VI	1	3		4	2		10			*					Bc, Tv, Nc
Megachile (Xanthosarus) addenda Cresson, 1878	1-V, 31-V	4						4	*	*						
Megachile (Litomegachile) brevis Say, 1837	15-IV, 16-VI	3	1			1		5								
Megachile (Chelostomoides) exilis Cresson, 1872	19-VII		1					1								
Megachile (Chelostomoides) georgica Cresson, 1878	31-V, 14 X	23	13		23	13		72								Bc, Gr, Lb, Pas
Megachile (Megachiloides) integrella Mitchell, 1926	30-VI	1						1								
Megachile (Litomegachile) mendica Cresson, 1878	16-IV, 14-X	6	1		1	8		16	*							Ld
Megachile (Leptorachis) petulans Cresson, 1878	31-V, 14-VIII	3	2		1	1		7								Ss

Appendix A. Native bee species collected on the Walthour-Moss Foundation

Species	Early & late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Ground nester	Sand specialist	Wood nester	Parasite	Host of parasite	Oligolectic	Host of oligolege	Bees collected from
Megachile (Litomegachile) brevis Mitchell, 1937	1-V, 19-VII	7						7								
Megachile(Megachiloides) rubi Mitchell, 1924	15-IV, 15-VI	1	3			6		10	*	*						
Megachile (Litomegachile) texana Cresson, 1878	18-V, 15-IX	15	2		1	6		24								Gr
Osmia (Melanosmia) atriventris Cresson, 1864	13-IV		5					5			*					
Osmia (Helicosmia) caerulescens (Linnaeus, 1758)	6-IV		1					1								
Osmia (Melanosmia) collinsiae Robertson, 1905	6-IV, 13-IV	1	1					2								
Osmia (Helicosmia) georgica Cresson, 1878	30-III, 14-V	4	7		2			13			*			*	Asteraceae	Pan
Osmia (Melanosmia) inspergens Lovell *and* Cockerell, 1907	6-IV, 30-IV	4	12		2			18								Va
Osmia (Osmia) lignaria Say, 1837	13-IV		1					1								
Osmia (Melanosmia) pumila Cresson, 1864	6-IV, 27-IV	3	2					5			*					
Osmia (Melanosmia) sandhouseae Mitchell, 1927	6-IV, 31-V	17	15		4			36								Va
Stelis (Heterostelis) australis Cresson, 1878	8-VIII, 23-VIII	1			1			2				*	*Trachusa* spp.			Van
Stelis (Stelis) labiata (Provancher, 1888)	27-IV, 13-V	1	1					2				*	*Hoplitis* spp.			
Stelis (Stelis) lateralis Cresson, 1864	26-IV, 1-VI	1	1					2				*	*Hoplitis* spp.			
Totals		2017	216	75	286	114	12	2720								

Appendix B. Plants bees were collected from (Abbreviations used in App. 1). All plants were growing wild.

	Species	Common Name	Families	Season
Rco	*Rhus copallinum* L.	winged sumac	Anacardiaceae	mid-Aug - mid-Sept
Rg	*Rhus glabra* L.	smooth sumac	Anacardiaceae	late May - early June
Ig	*Ilex glabra* (L.) Gray	gallberry	Aquifoliaceae	late-April - mid-May
Aa	*Ageratina aromatica* (L.) Spach	small-leaved white snakeroot	Asteraceae	late Aug - Oct
Cr	*Cirsium repandum* Michx.	sandhill thistle	Asteraceae	mid-May - July
Es	*Erigeron strigosus* Muhl. ex Willd.	slender daisy-fleabane	Asteraceae	May - Oct
Ha	*Helianthus atrorubens* L.	purpledisk sunflower	Asteraceae	late July - Oct
Pan	*Packera anonyma* (A. Wood) W.A. Weber & A. Löve	Small's ragwort	Asteraceae	May - early June
Pas	*Pityopsis aspera* (Shuttleworth ex Small) Small	sticky golden-aster	Asteraceae	late July - Oct
Pp	*Pityopsis pinifolia* (Elliot) Nuttall	sandhills golden-aster	Asteraceae	late June - Sept
Sco	*Silphium compositum* Michaux var. *compositum*	rosinweed	Asteraceae	early June - mid Sept
So	*Solidago* spp.	goldenrod	Asteraceae	Aug - Oct
Sd	*Symphyotrichum dumosum* (L.) Nesom var. *dumosum*	rice-button aster	Asteraceae	mid-Aug - Oct
Va	*Vernonia angustifolia* Michaux var. *angustifolia*	slender ironweed	Asteraceae	late June - early Sept
Oh	*Opuntia humifusa* (Rafinesque) Rafinesque	prickly pear	Cactaceae	late May - mid-June
Ss	*Stipulicida setacea* Michaux	wire-plant	Caryophyllaceae	May - Aug
Ca	*Clethra alnifolia* L.	Coastal sweetpepperbush	Clethraceae	mid-June - July
Gd	*Gaylussacia dumosa* (Andr.) Torr. & Gray	dwarf huckleberry	Ericaceae	mid-March - early May
Va	*Vaccinium* spp.	blueberry	Ericaceae	mid-March - early May
Bc	*Baptisia cinerea* (Raf.)Fernald & B.G.Schub.	wild indigo	Fabaceae	May - mid-June
Cs	*Crotalaria spectabilis* Roth	rattlebox, showy rattlepod	Fabaceae	July - Sept
Gr	*Galactia regularis* (L.)Britton & al.	eastern milkpea	Fabaceae	early June - Aug
Tv	*Tephrosia virginiana* (L.) Persoon	goat's rue	Fabaceae	May - June
Lb	*Lespedeza bicolor* Turcz.	bush clover	Fabaceae	mid-June - Sept
Lv	*Lespedeza virginica* (L.)Britton	slender bush-clover	Fabaceae	July - Sept
Ld	*Lupinus diffusus* Nuttall	sandhill lupine	Fabaceae	late March - early May
Sca	*Seymeria cassioides* (J.F. Gmelin) Blake	senna seymeria	Orobanchaceae	Aug - mid-Oct
Pi	*Passiflora incarnata* L.	passion flower, maypops	Passifloraceae	May - Aug
Nc	*Nuttallanthus canadensis* (L.) D.A. Sutton	common toadflax	Plantaginaceae	mid-March - early May
Rcu	*Rubus cuneifolius* Pursh	sand blackberry	Rosaceae	late April - late May
Dt	*Diodella teres* (Walter) Small	poorjoe weed	Rubiaceae	June - Nov

The bee fauna (Hymenoptera: Apoidea: Anthophila) of the Sandhills at the Walthour-Moss Foundation in North Carolina

Introduction

There are over 19,500 described species of bees (Hymenoptera: Apoidea: Anthophila) world-wide and, of that number, 3,600 species are known to occur in the United States and Canada (Ascher and Pickering 2010). There is a growing concern for the status of North American bees due to observed population declines, including a recent report naming 37 eastern North American species that have not been collected or seen in over 20 years (National Academy of Sciences 2007, Colla et al. 2012). Historically, very few North American bee populations have been monitored; only a limited number of quantitative studies on native populations have been completed, leaving ecologists with insufficient baseline data with which to compare current population trends (National Academy of Sciences 2007, Colla et al. 2012). The southeastern United States is cited as one of the more under-sampled areas over the past 20 years (Colla et al. 2012, Hall and Ascher 2014). However, North Carolina remains one of the more thoroughly sampled areas for the region due to the efforts of Dr. Theodore B. Mitchell. Dr. Mitchell was a bee taxonomist and faculty member in the Entomology department at NC State University from 1926–1961. Throughout his career, Dr. Mitchell collected regularly, amassing one of the largest bee collections in the southeastern US, now housed in the NC State Insect Museum (NCSU). The majority of the bees were collected from North Carolina, especially from the Southern Pines area in the Sandhills region (Mitchell 1960, 1962). The Sandhills is a special geographic and physiographic area that was once the coastline, but now marks the boundary between the piedmont and the coastal plain (Sorrie 2011). The sampling of the native bee fauna in North Carolina has been limited over the past 50 years. In an effort to provide updated species records and to improve our current understanding of bee diversity in the Sandhills and southeastern U.S., we completed a two-year survey of the native bees in the Sandhills of North Carolina. This survey was conducted as a part of an ecological study looking at how prescribed burning impacts native bee communities.

The Walthour-Moss Foundation is a privately managed preserve located in the Sandhills, one mile north of Southern Pines, North Carolina, and is dominated by longleaf pine (*Pinus palustris* Mill.)

savannas. Longleaf pine savannas are an endangered ecosystem (Noss, LaRoe III, and Scott 1995; Means and Grow 1985) that, prior to European settlement, covered nearly 37 million hectares of the southeastern United States (Boyer 1990, Frost 1993). Over the past two centuries much of the longleaf pine was harvested for timber, turpentine and the naval stores industry (Wahlenberg 1946, Frost 1993) or razed to make way for agriculture, leaving only 1.3 million hectares of fragmented forest remaining (Engstrom et al. 1996). Exclusion of fire in the longleaf pine savanna also became common practice beginning in the 1850s; citing possible soil degradation, malformation of trees, and endangerment of important forest industries (turpentine production and pulp wood) as support. Prescribed burning was utilized by private land owners but it did not become an accepted silvicultural practice until the 1960s and was not introduced as a management tool for the conservation of non-game species until the early 1970s (Johnson and Hale 2002).

Fire is a major disturbance that impacts both species assemblages and habitat structure, making the ecosystems that evolved under its influence unique (Hobbs and Huenneke 1992, Waldrop et al. 1992). The longleaf pine ecosystem is shaped and maintained by fire (Frost 1993, Outcalt 2000, Aschenbach et al. 2010), creating highly diverse ecosystems that contain great species richness characterized by large numbers of rare and endemic plant and wildlife species (Frost 1993, Walker 1993). The health and constancy of the longleaf pine savanna ecosystem is also dependent on the services of pollinators, the majority of which are bees. Bees act as keystone species in many environments and are the most abundant and efficient pollinators of flowering plants worldwide (Proctor et al. 1997, Moisset and Buchmann 2011). Bees are attracted to sites based on the availability of pollen and nectar, but a species' success is influenced by disturbance (e.g., fire, agriculture, residential and commercial development), habitat structure, and availability of nesting resources (Potts *et al*. 2003, 2005, Prowell and Bartholomew 2006, Cane *et al*. 2007, Williams and Kremen 2007, Grundel *et al*. 2010). Longleaf pine savannas managed on a regular burn rotation provide a dynamic environment with various successional stages and unique communities interspersed throughout the greater ecosystem (Van Lear et al. 2005).

Longleaf pine savannas support a distinctive bee fauna with specific life histories. Over the past decade three systematic surveys were conducted in an effort to characterize the biodiversity, one in the Carolina Sandhills National Wildlife Refuge (CSNWR) in South Carolina (Droege, unpublished data from 2006-2009 survey), another in southern Louisiana where the survey results complemented a species list from a survey conducted by Charles D. Michener (1947) of bees in longleaf pine savannas in Mississippi (Bartholomew et al. 2006), and, most recently, in the University of Florida Ordway-Swisher Biological Station (OSBS) in Putnam County, Florida (Hall and Ascher 2014). The surveys conducted in South Carolina, Mississippi, and southern Louisiana added a significant number of new species records to their respective state's species lists. This is due to the bee fauna being historically under-sampled for these states, emphasizing the importance of these types of systematic surveys. In South Carolina, Sam Droege reported that the bee species list for CSNWR would include 200 species with nearly 100 representing new South Carolina state records. The 2014 survey of bees in longleaf pine savannas of OSBS did not establish many new state records, as this was accomplished in previously published surveys conducted in southern Florida (Pascarella et al. 1999, Deyrup et al. 2002, and discussion in Hall and Ascher 2010, 2011). The survey conducted at OSBS represents the under-sampled bee fauna of north-central Florida. The authors found that the bee fauna was different from that of southern Florida and shared sand specialist species with those found in the Sandhills of North Carolina, including a new state record, the Sandhill endemic *Colletes howardi* Swenk, which had previously only been described from Southern Pines, NC. Each survey considered specific functional groups within the respective bee communities. Sand specialists were identified for each survey, while floral specialists and cleptoparasites were discussed only in the southern Louisiana, Mississippi, and Florida surveys. Sand specialist bees, including many Sandhill endemics, are ground nesting bees that require sandy soils. Floral specialists (oligolectic) are defined as bees that collect pollen from one plant family or only a few genera. Cleptoparasitic bees lay their eggs in the brood cells of another, typically closely related species, rather than foraging for nectar and pollen themselves. Cleptoparasitic bees are often host specific. It has been estimated that nearly 20% of all North American bee species are cleptoparasites (O'Toole and Raw 2004). Documenting the presence and abundance of species belonging to these groups is important to understanding the longleaf pine savanna habitat, and may help to illuminate possible shifts with in the ecosystem.

Thanks to T.B Mitchell's considerable collecting, the North Carolina state bee species list is comprehensive, with 528 described bee species reported (Ascher and Pickering 2010). Due to Mitchell's efforts we do not anticipate establishing new state records. Instead, it is our goal to describe the bee species richness and abundance, as well as describe the functional groups represented within this special habitat, thereby providing an updated record of the bee fauna, and their floral associations. This work will contribute to the comprehensive study of bees within longleaf pine savannas in the southeastern U.S.

Methods

Site description

My study took place on the Walthour-Moss Foundation, one mile north of Southern Pines in Moore County, NC. The Walthour-Moss Foundation, from here on referred to as the Foundation, has preserved over 1620 hectares of primarily upland pine savannas; longleaf pine is the dominant tree in most stands on the property. The Foundation is used primarily for equestrian purposes (trail riding, fox hunts, and jumping events) and places a high emphasis on aesthetics and the maintenance of utility for these purposes. The property is made up of many small parcels of land that have been assembled over the past 40 years through donations and land acquisitions, including a large donation of 73 hectares from the NC DOT in 2005. As stewards of this endangered ecosystem, the foundation has made a concerted effort to introduce a 3 year burn rotation, approximating the natural rate of fire disturbance (Frost 1993, 2006), to as much of the acquired acreage as is possible. Historically, the burn units have been approximately 28 acres or less in extent; recently, they have switched to burn units of 81-121 hectares, which are more consistent with current forestry standards. With the exception of a few parcels, 85-90% of the foundation is maintained on this 3-year burn rotation. Prescribed fires are typically initiated during the winter months (January through March), in what is termed a “dormant season” burn. This method was chosen because it is typically easier to control fire in cooler months and wildlife is less likely to be active at that time (Knapp et al. 2009). In 2013, the Foundation began working with the Nature Conservancy to implement growing-season burns. Burning during the growing season is comparable to the historical fire season and is more effective in reducing stem density of understory hardwoods and the incidence of fungal infections such as brown spot needle blight (*Scirrhia acicola* (Dearn.) Siggers) than burns initiated at other times of year. Numerous grass species, flowering forbs, shrubs, and herbaceous species also flower more vigorously when burned in late-spring or early-summer (Knapp et al. 2009).

Unburned Foundation areas are characterized by a dense midstory of turkey oak (*Quercus laevis* Walter) and/or bluejack oak (*Q. incana* Roxb.) and a canopy of longleaf pine, Virginia pine (*Pinus virginiana* Mill.), loblolly pine (*Pinus taeda* L.) or a combination. Density of the trees, and thus, canopy cover and shade, is higher in these plots. Also, leaf litter in these areas is abundant, making the herbaceous understory sparse. The burned areas are open longleaf pine stands with scattered turkey oak and wiregrass in the understory. In addition to burning, some sites on the foundation are raked to harvest accumulating pine straw, and in areas where fire has been absent, the managers are applying herbicides to reduce fuel load in preparation for future burns. Soil survey information (Soil Survey Staff 2009) indicates that all of the study plots are characterized by well-drained, sandy soils. The two soil series represented on the property are Candor (sandy) and Vaucluse (loamy sand), both common in the Sandhills.

Sampling and specimen curation

The majority of the bees were collected using bee bowls placed along 16 separate 80 meter transects sited throughout the Foundation. The sites were chosen based on their fire history, with four treatments: burned in the same year of survey (0B), burned one year previously (1B), burned two years previously (2B), and no history of burn in the past 50 years (C). The observed differences in bee abundance, diversity, species richness and community composition between the different burn histories are discussed elsewhere. Four replicates of each treatment type were represented within the 16 sites. Five sets of three 178 mL plastic soufflé cups were placed along each transect, with one painted fluorescent blue, one fluorescent yellow and the other left white. The sets of three bowls were placed perpendicular across each transect at 20m intervals, while bowls within each set were spaced 5 m apart.

The colors used to paint the cups have been tested and found to be most attractive to the majority of bee species present in eastern North America (Droege 2012). Each cup was filled with a mix of water and Dawn® dish soap (Procter & Gamble, Cincinnati, Ohio, USA), decreasing the surface tension, so that as bees landed they drowned in the liquid. Bowls were set out in the morning and collected in the early evening, averaging 7-9 hours of exposure on each sampling date. In addition to bee bowls, sweep nets were used to capture bees foraging on flowers. Sweep netting was done opportunistically during each sampling trip in 2013 and not specific to any particular burn history. The species of flowering plant individual bees were collected from were recorded. Specimen collection was undertaken approximately every two weeks (average 13.3 days) from April 15 to October 15 in 2012 for a total of 13 sampling dates. In 2013, bees were collected at the same frequency from April 13 to September 28, for a total of 11 sampling dates.

After each sampling date, the specimens were pinned, labelled, identified, and databased. To make my determinations I relied heavily upon Discover Life's bee species guides (available at discoverlife.org; Perlmutter 2010) and cross-checked the determinations with the bee reference collection housed in the NC State Insect Museum. When I was unable to identify a specimen, or was unsure of my determination, the specimens were shipped to experienced taxonomists for confirmation. The taxonomists I consulted for this project were Dr. John S. Ascher of the National University of Singapore and the American Museum of Natural History, Dr. Jason Gibbs of Michigan State University, and Dr. Sam Droege of the United States Geological Service Patuxent Wildlife Research Center. Once identified, the specimen was given a barcode label and its metadata was entered into the NC State Insect Museum's database (specimen data available at http://specimens.insectmuseum.org/). The specimens are deposited in the NC State Insect Museum, Raleigh, North Carolina. Specimen data is available on the NCSU Insect Museum's website at http://insectmuseum.org/.

Analysis

Basic statistics were generated in order to describe the bee biodiversity. To account for how bee abundance may influence bee diversity, individual-based rarefaction was used to calculate standardized species richness (expected number of species for a given number of individuals (Gotelli and Colwell 2001) for each sampling year and pooled across years. Because rarefaction gives a conservative estimate of species richness for a given area we also calculated an extrapolated estimate of the total number of bee species expected for each sampling year and across sampling years using the Chao 1 estimator (Chao 1984). Estimated species richness (Chao 1) is the sum of the observed number of species and the quotient $a^2/2b$, where a and b equal the number of singletons (one individual in a sample) and doubletons (two individuals in a sample), respectively (Gotelli and Colwell 2010) account for the number of rare species represented in a sample. The Chao 1 estimator is useful for biodiversity studies with abundance data that have a large number of rare species because the estimator adds a correction factor to observed species density (raw number of observed species) based on the number of rare species in a sample (Chao 1984, Gotelli and Colwell 2010). Rarefaction curves were used to investigate sampling adequacy and were calculated for each year (n=12 samples per year) and pooled across years (n=24 total samples). Standardized species richness, estimated species richness, and rarefaction curves were calculated for each sampling year and across sampling years using the vegan package (Oksanen et al. 2013) in R statistical software system, version 3.0.1 (R Development Core Team). Finally, rank frequency curves were constructed for the 10 most common bee species for the different treatment levels using frequency data for each year and pooled over both sampling years.

Functional groups have recently been found to play a primary role in determining what mechanisms connect changes in species composition to changes in habitats (Hooper et al. 2005, Díaz et al. 2007, Kremen et al. 2007, Moretti et al. 2009, Sheffield et al. 2013). We identified three functional groups that exhibit life histories that may provide insight into bee communities of the longleaf pine savannas: sand specialists, floral specialists, and cleptoparasites (Table 1). Information on floral, nesting or habitat specialization was compiled from published literature and expert experience (S. Droege and J.S. Ascher, personal communication; discoverlife.org, Robertson 1929, Packer 2007). Sand nesting species are specialized, ground-nesting bees that prefer sandy soils. For our survey we include all ground nesting species that show a preference for, or are most abundant in, xeric and sandy areas. Floral specialists (oligolectic) are defined as bees that collect pollen from one plant family, genus, or a single species. Floral resource availability dictates the suitability of an area for oligolectic species and the presence or recent absence of one of these species can be illustrative of the flora present or the impacts landscape changes have had in a given area (Roulston and Goodell 2011). The proportional abundance of individuals and species of each functional group (i.e., scaled to the abundance of all bees) is reported to illustrate how each group is represented in the survey area.

Results

Over the 2012 and 2013 seasons, 2,936 bees were collected representing 137 described species in 34 genera and six families (Table 1). About 84% of the bees were collected in bowls and 16% in nets. Sixty (44%) species were captured in bowls and nets, 51 (37%) species were captured only in bowls, and 26 (19%) species only with nets. Of the bees collected 85% were female, 13% were male, and 2% remained unsexed. The numbers and proportions of species and bees in each family were as follows: Colletidae - 7 species (5.10%), 12 bees (.41%); Melittidae - 1 species (.72%), 4 bees (.14%); Halictidae - 53 species (38.68%), 2267 bees (77.21%); Andrenidae - 14 species (10.21%), 63 bees (2.15%); Megachilidae - 37 species (27%), 355 bees (12.1%); Apidae - 23 species (16.80%), 266 bees (9.06%). Halictidae was the family with the greatest number of individuals and of species represented.

In 2012, 1,294 bees were collected representing 101 species. There was an increase in abundance and species density in 2013 with 1,642 bees collected representing 107 species. Species rarefaction and the Chao 1 richness estimators were used to assess the species richness for both years and across sampling years (Table 3). Rarefied species richness corrects for the effect abundance has on species richness, by standardizing the data set by the lowest number of individuals captured for any given sample (Gotelli and Colwell 2001). Individual-based rarefaction was calculated for our survey using the abundance data from 2012 so the rarefied species richness remains the same as the species density for 2012 but drops to 100.36 and 109.31 for 2013 and the pooled data, respectively. The estimated species richness (Chao 1) for 2013, 125.47, is lower than that of 2012, 145, despite a greater number of individuals and species collected for that year. This difference highlights the variation in the number of rare species between years. There were 33 singletons and 11 doubletons collected in 2012 and 27 singletons and 18 doubletons collected in 2013. Rarefaction curves indicate that for both sample years, fewer species were collected than were predicted to have occurred in these areas. However, repeated sampling over the two years resulted in a greater proportion of the species pool for a given sample being detected (Figure 2).

Eight out of the ten most frequently captured species (Fig 3) species belonged to Halictidae: *Lasioglossum* (*Dialictus*) *reticulatum* (Robertson) (575 individuals), *Augochlorella aurata* (Smith) (450), *L.* (*D.*) *floridanum* (Robertson) (214), *L.* (*D.*) *apopkense* (Robertson) (193), *L.* (*D.*) *vierecki* (Crawford) (85), *L.* (*D.*) *weemsi* (Mitchell) (71), *Halictus poeyi* Lepeletier (64), and *L.* (*D.*) *raleighense* (Crawford) (45). The two most common species, *L.* (*Dialictus*) *reticulatum* and *A. aurata* are primitively eusocial, meaning the colony is founded by a single queen that acts as a solitary bee until her daughters emerge and become workers. Primitively eusocial colonies break down when reproductive females are produced making them temporary, unlike highly eusocial colonies that are usually permanent (Michener 2007). This level of sociality combined with low flower fidelity enables these species' respective populations to reach higher levels than other species. *Lasioglossum* (*D.*) *apopkense* and *L.* (*D.*) *vierecki* are common ground nesting bees that have a preference for sandy soils, explaining their abundance in regions like the Sandhills (Sheffield et al. 2013). The fifth most common bee collected during our survey was *Ceratina* (*Zadontomerus*) *calcarata* Robertson or *C* (*Z.*) *dupla* Say. While females cannot be confidently separated between the two species, nearly 50% of the specimens collected were male and identified as *C.* (*Z.*) *calcarata* based on morphology. Bees in the genus *Ceratina* are small carpenter bees that nest in pithy stems (Michener 2007). These bees were collected most often in areas of the Foundation that had not been burned in over 50 years.

The three functional groups combined represent 36.5% of the species (50 species) and 16% of the individuals (474 individuals) collected during our survey on the Foundation (Table 4). The numbers and proportions of species and bees in each functional group were as follows: Sand specialists - 16 species (11.7%), 404 specimens (13.8%); floral specialists - 21 species (15.33%), 92 specimens (3.13%); and cleptoparasites - 20 species (14.6%), 55 specimens (1.87%). The comparison between the proportions of individuals to species for each functional group is interesting. Sand specialists made up the greatest proportion of individuals but lowest proportion of species, indicating that the species collected were represented in higher numbers of individuals. The opposite is true for floral specialist and cleptoparasitic species that had a high proportion of rare species represented (Figure 4).

Discussion

The Sandhills region extends from North Carolina, through South Carolina, into Georgia, with isolated pockets of similar habitat found scattered across northern Florida. The geographic span of the Sandhills appears botanically similar, with an overstory of longleaf pine and understory of wiregrasses (*Arisitida stricta* Michaux var. *stricta* and *A. stricta* Michaux var. *beyrichiana* (Trin. & Rupr.) D.B. Ward), but floral differences exist based on the geographic location, differences in climate, seasonality, soils, and fragmentation. It is important to have a systematic survey of the bees of the eastern Sandhills/longleaf pine savanna to provide perspective on species turnover, in order to fully understand how best to manage this unique and endangered habitat. Here I draw comparisons between this and the other three regional surveys. No attempt at replicating sampling methods or standardizing data for statistical analyses has been made, though all surveys used bee bowls for collecting. Of the bees collected in the different surveys, the bee fauna we identified was most similar to that found in the CSNWR survey, with 79 species in common (S. Droege, unpublished data). Less overlap occurred with increasing distance and decreasing latitude, relative to our study site, with 62 species in common with the southern Louisiana and Mississippi (Bartholomew et al. 2006) survey and 39 species in common with the OSBS (Hall and Ascher 2014) survey.

As anticipated, due to Mitchell's comprehensive and long-term sampling of the Sandhills, no new state records were established during this survey. However, the sampling methods employed may also be partly responsible. We relied heavily on bee bowls, while we conducted extensive sweep netting in only one year of the survey (2013). The bowls were not elevated for improved visibility as vegetation became denser throughout the growing season. Bee bowls are very effective at attracting bees, but have been found to only capture about 70% of species present, typically those species that are more abundant and generalist foragers (Grundel et al. 2011). The rarefaction curves generated (Figure 2) never reach an asymptote; while this is not uncommon in invertebrate studies, this does indicate that our sample did not provide a complete inventory of the present bee community (Gotelli and Colwell 2010). Reliance on bee bowls may bias how bee families and species are represented in a survey. Members of Halictidae, when compared to other bee families, are more likely to be captured in bee bowls (Roulston et al. 2007, Grundel et al. 2011), particularly species in the genus *Lasioglossum* (*Dialictus*) (Cane et al. 2000) because the majority are ground-nesting, generalist foragers. In my survey, Halictidae comprised 39% of the species and 77% of the individuals collected, and 8 of the 10 most frequently captured species belonged to this family (Figure 3). *Lasioglossum* (*Dialictus*) represented 52% (28 species) of the species and 64% (1,443 individuals) of the individuals belonging to Halictidae collected during this survey. Bee bowl trapping and sweep netting are complementary but species capture rates have been found to be higher for netting than for bowls (Grundel et al. 2011). In my survey, only 20% of the species collected were captured exclusively by net. I believe this to be an artifact of using a sweep net for a single year of the survey. Increased sampling with sweep nets would likely result in increased species density on the Foundation as it would provide greater opportunity to capture less abundant, more specialized species that are less likely to be captured by bowls.

Host plants and oligoleges

The bees collected using sweep nets were collected while foraging on flowering plants. We captured 486 individuals, representing 85 species. Of the bees species collected by sweep netting, 55% were collected in the spring, 15% were collected in the fall, and 30% were collected in the spring and fall. The trend is reflected in the seasonal changes in the floral resources available on the Foundation; 35% of plant species surveyed flowered in the spring, 6% flowered in the summer, 16% flowered in the fall, 30% flowered in the spring and fall, and 13% flowered in the summer and fall.

The two most abundant plant families we collected bees from are Asteraceae (35% of the species) in the fall and Fabaceae (23% of the species) in the spring. The flowering species that were most abundant were *Vaccinium* spp. (Ericaceae) and *Ilex glabra* (L.) A. Gray (Aquifoliaceae) in the spring, *Clethra alnifolia* L. (Clethraeae), *Galactia regularis* (L.) Britton et al. (Fabaceae), and *Stipulicida setacea* Michx. (Caryophyllaceae) in the summer, and *Solidago* spp. and *Pityopsis aspera* (Shuttlw. ex Small) Small (Asteraceae) in the fall. Of the 85 species collected foraging on flowers, 16% were collected from *Vaccinium* spp., 12% from *G. regularis*, 11% from *I. glabra*, and 10% from *C.*

alnifolia. In Table 1, the plants in bold indicate floral associations with bee species found during our survey that have not been previously reported in Mitchell (1960, 1962) and Hurd (1979).

Oligolectic bees were represented in this survey by 91 individuals of 21 species, comprising only 3.13% of the total number of individuals but 15.33% of the total number of species (Table 4, Figure 4). The emergence and life span of oligolectic species coincides with the flowering period of their respective host making them highly seasonal, typically solitary, and, often, less abundant than generalist species (O'Toole and Raw 2004). In our survey, 13 oligoleges were collected in the spring, 7 were collected in the fall, and only 1 species (*Perdita* (*Alloperdita*) *bradleyi* (Viereck) was collected in the spring and fall. All oligoleges were either collected from their known floral host plant or in bee bowls with the exception of *Perdita* (*Perdita*) *gerardiae* Crawford which was not collected from its known floral host plant, *Agalinis*, but from *Pityopsis pinifolia* (Elliott) Nutt. Oligolectic species exclusively forage on one species or a group of related species for pollen but may be seen foraging nectar from flowers outside of this group (O'Toole and Raw 2004), offering a possible explanation for captures in bowls or on a species outside of the expected host range. *Perdita* (*Perdita*) *halictoides* Smith was collected in a bowl but two species within the host genus, *Physalis*, are present on the Foundation, including a rare sandhills endemic, *Physalis lanceolata* Michaux (Sorrie 2011).Three *Lasioglossum* (*Dialictus*) *ceanothi* (Mitchell), a rare species specific to *Ceanothus* (Rhamnaceae) (Gibbs 2011), were collected. All were female, which is unfortunate as the male of this species has not yet been described (Gibbs 2011). The four additional *Perdita* species collected were specific to Asteraceae and collected only in the fall, demonstrating the close relationship between oligolege phenology and that of their respective host plants.

In our survey oligolectic abundance was low but the species made up 15% of the species present in the community. This agrees with the trend established by the previous surveys with oligoleges representing 12%, 14%, and 17% of the species present in the communities in CSNWR, Louisiana/Mississippi, and OSBS respectively. *Andrena* (*Callandrena* s.l.) *krigiana* Robertson, associated with *Krigia virginica* (L.) Willd. (LaBerge, 1967), was reported from every survey at low abundances. *Lithurgus* (*Lithurgopsis*) *gibbosus* Smith, oligolectic on *Opuntia* (Cactaceae) was collected in our study, CSNWR, and OSBS, but not from the Louisiana/Mississippi surveys. *Lasioglossum* (*Dialictus*) *ceanothi* (Mitchell) was only collected in our study giving further credence to its status as a rare species. Oligolecty is thought to be a rare specialization in savannas because, unlike deserts, there is a constant and shifting floral resource. Greater polylecty is proposed as the case for pollinators in general in longleaf pine savannas (Folkerts et al. 1993).

Sand specialists

Sphecoid wasps, a polyphyletic assemblage of specialized predators and nest provisioners, from which Anthophila arose, have ground nesting lineages that are closely associated with xeric regions (Michener 2007). It is postulated that bees arose from these sphecid wasp lineages and radiated out from the xeric regions (O'Toole and Raw 2004, Michener 2007) of their origin, providing a logical argument for why bee diversity is higher in xeric environments with sandy soils than more humid and tropical regions (Michener 1979). Nesting in the ground is the most common nesting location for bee species (Cane 1991, Michener 2007) and nest site selection is predicated on many factors including, bee size, annual precipitation and temperature, and soil moisture and texture. Soil texture has been found to be very important in defining ideal nest location (Cane 1991).

Ground-nesting, sand specialist bees were the most abundant functional group on the Foundation, represented in this survey by 404 individuals and 16 species and comprising 13.76% of the total number of individuals and 11.7% of the total number of species (Table 4, Figure 4). This outcome was expected due to the xeric habitat characteristics of the Sandhills, and mirrors the proportion of sand specialist bees found in the CSNWR (14%), OSBS (18%), and Louisiana/Mississippi (11%) surveys.

The sand specialists *Lasioglossum* (*Dialictus*) *apopkense* (Robertson) and *L.* (*D*) *vierecki* (Crawford) were the 4th and 6th most frequently collected species during our survey (Figure 3). Both species are generalist foragers and primitively eusocial, which enables them to have greater abundance in ideal habitats. *Agapostemon splendens* (Lepeletier) is considered to be the most common species of *Agapostemon* in the southeastern U.S. and nests almost exclusively in sandy soils, in aggregations or alone (Roberts 1972). Only 13 individuals were collected from the Foundation during our survey, while 17 were collected from Louisiana/Mississippi, 39 from CSNWR, and 63 from OSBS. *Agapostemon* (*A.*) *sericeus* (Förster) and *A.* (*A.*) *virescens* (Fabricius) were equally, if not more, abundant with 14 and 18 individuals collected, respectively. *Augochloropsis* (*Paraugochloropsis*) *sumptuosa* (Smith), another rare sand specialist, was collected in three of the four surveys, with the exception of the survey in Louisiana and Mississippi. In our survey we captured 6 individuals; only one was collected at the CSNWR, but 304 individuals were recovered at OSBS. The number of individuals collected from OSBS suggests that the commonness of *A.* (*P.*) *sumptuosa* in Florida Sandhills should be revisited.

Cleptoparasites

Cleptoparasites were represented in this survey by 55 individuals of 20 species, comprising 1.87% of the total number of individuals and 14.6% of the total number of species (Table 4, Figure 4). The proportion of cleptoparasitic bee species present on the Foundation falls short of the proportion of cleptoparasitc bees present in North America and in North Carolina (Mitchell 1960, 1962) but because the Sandhills habitat is so specific we do not feel that the cleptoparasites are underrepresented. Similar proportions of cleptoparasites were reported for the other surveys, with 9% in CSNWR, 13% in OSBS, and 11% in Louisiana/Mississippi, supporting this assertion.

Based on the argument presented by Sheffield et al. (2013), in which cleptoparasites are identified as indicators of bee community health, we could assert that the bee community present at our study site is thriving. Hall and Ascher (2014) warn that care should be taken in interpreting this data when relying heavily on bee bowls because low numbers may be an artifact of biased sampling. As previously discussed, bee bowls were used consistently throughout our survey while sweep netting was only employed in 2013. In spite of this, we found species density was relatively high for cleptoparasites in bee bowls and sweep nets, with 45% of the cleptoparasitic species captured only in bee bowls, 30% captured only in sweep nets, and 25% captured by both sampling methods. The low abundance of the cleptoparasitic species collected in our study is likely due in part to the cryptic and specialist nature of cleptoparasites (Michener 2007).

All parasitic species collected were cleptoparasites with the exception of one; *Lasioglossum* (*Dialictus*) *lionotum* (Sandhouse) is a social parasite of *L.* (*D.*) *imitatum* (Smith). A social parasite enters a host nest, dominates or kills the host nest's main reproductive female, and exploits the host nest's workers to rear her offspring. This behavior has evolved repeatedly among Halictidae (Wcislo 1997). Cleptoparasites differ in that the female lays her eggs in the constructed or finished cell of the host bee and then leaves. Cleptoparasitic larvae develop rapidly, typically hatch before the host larvae, and then dispatch the host eggs/larvae using their elongate mandibles or by outcompeting host larvae for nest provisions (Michener 2007). The social parasite, *L.* (*D.*) *lionotum*, collected during our survey was not reported in the other surveys, but its host, *L.* (*D.*) *imitatum* was collected in the CSNWR and the Louisiana/Mississippi surveys. *Lasioglossum* (*D.*) *imitatum* is a primitively eusocial ground-nesting bee with workers that forage regularly. Once a female *L.* (*D.*) *lionotum* successfully establishes herself as the queen within the nest of *L.* (*D.*) *imitatum* she no longer needs to forage making *L.* (*D.*) *lionotum* less likely to be captured in bowls or by sweep net.

Conclusion

In our two year survey we captured 137 species, representing 26% of the total species recorded for North Carolina, in a 1620 hectare area. Despite our underutilization of sweep netting, we were able to provide a representative sample of the oligolectic and parasitic species present on the Foundation. Unfortunately, we were unable to collect *Colletes howardi*, described by Dr. Mitchell from the Sandhills of North Carolina. Prior to 2013, the type location was the only location from which it was known; it was recently collected at OSBS (Hall and Ascher 2014), but the extent of its range and abundance still remains poorly documented, leaving its conservation status uncertain. The bee diversity described in the CSNWR, Louisiana/Mississippi, and OSBS surveys illustrate how similar the bee communities are, but how differences in flora affect differences in communities.

The four surveys combined provide a more complete representation of the distinctive bee fauna that is supported by the Sandhill/longleaf pine habitat. However, there is still a need for additional surveys in the Sandhills of southern South Carolina and Georgia. Additionally, the complete digitization of the Mitchell collection will allow for direct comparisons between the bee abundance and species density present in the North Carolina Sandhills in the 1970s and that of today. Through these exhaustive measures we will be provided a more thorough treatment of the bee diversity supported in the Sandhill/longleaf pine habitat that extends through the southeastern U. S. can that be used to inform land management decisions and conservation efforts in the future.

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Table 1 Native bees collected on the Walthour-Moss Foundation

Species	Early and late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Sand specialist	Oligolege and host	Parasite	Bees collected from
COLLETIDAE												
Colletes distinctus Cresson, 1868	30-IV				1			1				
Colletes kincaidii Cockerell, 1898	28-IX				1			1				So
Colletes nudus Robertson, 1898	14-VIII				1			1				
Colletes thoracicus Smith, 1853	30-III, 27-IV				2			2				Pan, Va
Hylaeus (Prosopis) affinis (Smith, 1853)	28-IX				1			1				
Hylaeus (Paraprosopis) floridanus (Robertson, 1893)	30-III, 28-IX				3	2		5				Lb, So
Hylaeus (Paraprosopis) georgicus (Cockerell, 1898)	28-IX				1			1				So
MELITTIDAE												
Melitta americana (Smith, 1853)	26-IV, 12-V				3	1		4		Ericaceae		Va
HALICTIDAE												
Agapostemon (Agapostemon) sericeus (Förster, 1771)	27-IV, 13-X	9	3		2			14				
Agapostemon (Agapostemon) splendens (Lepeletier, 1841)	26-IV, 28-IX	3	2		4	4		13	*			Ss, Sco
Agapostemon (Agapostemon) texanus Cresson, 1872	8-VIII	1						1				
Agapostemon (Agapostemon) virescens (Fabricius, 1775)	30-IV, 14-X	18						18				
Augochlora (Augochlora) pura (Say, 1837)	13-IV, 26-IV	2						2				
Augochlorella aurata (Smith, 1853)	30-IV, 14-X	408	6		30	6		450				Cr, Gr, Ha, So, Sd
Augochlorella gratiosa (Smith, 1853)	1-V, 13-X	7	8		1	2		18				
Augochloropsis (Paraugochloropsis) metallica (Fabricius, 1793)	27-IV, 28-IX	3			16			19				Va, Pan, Ss, Ig, Dt
Augochloropsis (Paraugochloropsis) sumptuosa (Smith, 1853)	6-IV, 25-VII	1			5			6	*			Va, Ss, Ca
Halictus (Nealictus) parallelus Say, 1837	31-V, 25-VII	2			1	3		6				Ca, Es
Halictus (Odontalictus) poeyi Lepeletier, 1841	14-V, 14-X	42	7		17			66				Ca, Es, Pa, Sco, Va
Halictus (Protohalictus) rubicundus (Christ, 1791)	2-VI				1			1				Ig
Lasioglossum (Dialictus) apopkense (Robertson, 1892)	30-III, 14-X	185	2	1	5			193	*			Gr, Rc, Rg
Lasioglossum (Dialictus) batya Gibbs, 2011	16-VI, 14-X	3						3				
Lasioglossum (Dialictus) bruneri (Crawford, 1902)	16-IV, 16-IX	31	2		2	3		38				

Table 1 Continued

Species	Early and late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Sand specialist	Oligolege and host	Parasite	Bees collected from
Lasioglossum (Dialictus) callidum (Sandhouse, 1924)	13-IV, 14-X	15	2		1			18				
Lasioglossum (Dialictus) ceanothi (Mitchell, 1960)	2-VIII, 3-VIII	2			1			3		*Ceanothus*		
Lasioglossum (Evylaeus) cinctipes (Provancher, 1888)	18-V, 29-VI	1	2					3				
Lasioglossum (Dialictus) coreopsis (Robertson, 1902)	6-IV, 15-IX	8			3	1		12				Es, Ld
Lasioglossum (Dialictus) cressonii (Robertson, 1890)	2-VIII	1						1				
Lasioglossum (Dialictus) floridanum (Robertson, 1892)	30-III, 13-X	204	1		4	1		210				Ld, Pa, Sco
Lasioglossum (Dialictus) foveolatum (Robertson, 1902)	18-V	1						1				
Lasioglossum (Lasioglossum) fuscipenne (Smith, 1853)	6-IV, 1-VI	2						2				
Lasioglossum (Dialictus) gotham Gibbs, 2011	1-VI	1						1				
Lasioglossum (Dialictus) illinoense (Robertson, 1892)	6-IV, 3-VIII	15		1	1			17				Cs
Lasioglossum (Dialictus) imitatum (Smith, 1853)	1-V, 16-VI	2			1			3				Ss
Lasioglossum (Dialictus) lionotum (Sandhouse, 1923)	31-V	1						1			*	
Lasioglossum (Dialictus) longifrons (Baker, 1906)	14-IV, 15-VI	17						17				
Lasioglossum (Dialictus) Mitchelli Gibbs, 2010	31-V, 16-VI	7						7				
Lasioglossum (Evylaeus) nelumbonis (Robertson, 1890)	26-IV	1						1		Nymphaeaceae		
Lasioglossum (Dialictus) nymphale (Smith, 1853)	30-III, 13-X	10			2			12	*			Ld
Lasioglossum (Dialictus) oblongum (Lovell, 1905)	6-IV	1						1				
Lasioglossum (Dialictus) pectorale (Smith, 1853)	13-IV, 2-VIII	28			3			31				Pan
Lasioglossum (Dialictus) pilosum (Smith, 1853)	26-IV, 14-X	42						42	*			
Lasioglossum puteulanum/tegulare	6-IV, 14-X	17						17				
Lasioglossum (Dialictus) puteulanum Gibbs, 2009	31-V, 13-X	3						3				
Lasioglossum (Dialictus) raleighense (Crawford, 1932)	6-IV, 14-X	43			4			47				
Lasioglossum (Dialictus) reticulatum (Robertson, 1892)	30-III, 14-X	489	1	61	20		3	574				Bc, Gr, Rco
Lasioglossum (Dialictus) smilacinae (Robertson, 1899)	6-IV, 15-VI	8			1			9				
Lasioglossum (Evylaeus) sopinci (Crawford, 1932)	6-IV, 1-VI	3						3	*			

Table 1 Continued

Species	Early and late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Sand specialist	Oligolege and host	Parasite	Bees collected from
Lasioglossum sp.	6-IV, 14-X	140	9	2	11	7		169				Pas, Pp, Rco, Ss
Lasioglossum (*Dialictus*) *subviridatum* (Cockerell, 1938)	30-IV, 14-VI	6						6				
Lasioglossum (*Dialictus*) *tegulare* (Robertson, 1890)	15-IV, 3-VIII	6			1			7				
Lasioglossum (*Dialictus*) *timothyi* Gibbs, 2010	31-V	1						1				
Lasioglossum (*Dialictus*) *trigeminum* Gibbs, 2011	16-IV, 14-X	18		6	7	1		32				
Lasioglossum (*Evylaeus*) *truncatum* (Robertson, 1901)	1-VI	1			2			3				Ig
Lasioglossum (*Dialictus*) *vierecki* (Crawford, 1904)	6-IV, 15-IX	66			18			84	*			Es, Gr, Pas, Rco, Rg
Lasioglossum (*Dialictus*) *weemsi* (Mitchell, 1960)	6-IV, 14-X	58		4	7			69				Gr, Ss
Sphecodes atlantis Mitchell, 1956	15-IV	1						1			*	
Sphecodes brachycephalus Mitchell, 1956	1-V, 13-V	2	1					3			*	
Sphecodes heraclei Robertson, 1897	1-V				1			1			*	
Sphecodes mandibularis Cresson, 1872	30-III	1						1			*	
Sphecodes minor Robertson, 1898	14-IV				1			1			*	
Sphecodes sp.	13-IV, 14-IV		5					5			*	
ANDRENIDAE												
Andrena (*Scrapteropsis*) *atlantica* Mitchell, 1960	16-IV, 1-VI		1		1	1		3				Ig
Andrena (*Holandrena*) *cressonii* Robertson, 1891	13-V	1						1				
Andrena (*Melandrena*) *hilaris* Smith, 1853	30-III, 27-IV				8	3		11				Va, Gd
Andrena (*Callandrena s.l.*) *krigiana* Robertson, 1901	13-IV, 14-IV		5					5		*Krigia*		
Andrena (*Micrandrena*) *melanochroa* Cockerell, 1898	13-V	1						1		Rosaceae		
Andrena (*Scrapteropsis*) *morrisonella* Viereck, 1917	13-V, 1-VI	2			2			4		Ranunculaceae		Ig
Andrena sp.	30-III, 27-IV					3		3				Va
Panurginus potentillae (Crawford, 1916)	30-III, 14-IV	2						2		Potentilleae, esp. *Potentilla*		
Perdita (*Hexaperdita*) *bishoppi* Cockerell, 1906	1-IX, 2-IX	1	2					3	*	Asteraceae		
Perdita (*Alloperdita*) *bradleyi* Viereck, 1907	30-IV, 6-IX				1	2		3	*			Pp
Perdita (*Perdita*) *consobrina* Timberlake, 1928	24-VIII, 6-IX	5	4	1	4	2		16	*	Asteraceae		Pp
Perdita (*Hexaperdita*) *georgica* Timberlake, 1928	6-IX, 28-IX	1			2			3	*	Asteraceae		Pp

Table 1 Continued

Species	Early and late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Sand specialist	Oligolege and host	Parasite	Bees collected from
Perdita (Perdita) gerardiae Crawford, 1932	24-VIII, 15-IX	6			1			7	*	*Agalinis*		Pp
Perdita (Perdita) halictoides Smith, 1853	31-V			1				1	*	*Physalis*		
APIDAE												
Anthophora (Melea) abrupta Say, 1837	30-III, 14-V	2	4		3	4		13				Ld, Rc
Bombus (Pyrobombus) bimaculatus Cresson, 1863	14-IV, 28-IX	2			14	3		19				Va, Ig, Ss, Gr, Ca
Bombus (Separatobombus) griseocollis (DeGeer, 1773)	31-V, 14-X	4			8			12				Ca
Bombus (Pyrobombus) impatiens Cresson, 1863	18-V, 14-X	7			15	2		24				Ca, Ig
Bombus sp.	28-IX				1			1				
Bombus (Pyrobombus) vagans Smith, 1854	18-V, 1-VI	3						3				
Ceratina (Zadontomerus) calcarata Robertson, 1900 *or C.(Z.) dupla* Say, 1837	30-III, 14-V	53	61		5	3		122				
Epeolus erigeronis Mitchell, 1962	1-VI		1					1			*	
Habropoda laboriosa (Fabricius, 1804)	30-III, 1-V		2		9	2		13		*Vaccinium*		Va
Melecta (Melecta) pacifica Cresson, 1878	30-III	1						1			*	
Melissodes (Melissodes) bimaculata (Lepeletier, 1825)	24-VII		1					1				
Melissodes (Melissodes) communis Cresson, 1878	1-VI	1						1				
Melissodes (Melissodes) comptoides Robertson, 1898	9-VIII, 1IX	2	1					3				
Melissodes (Eumelissodes) dentiventris Smith, 1854	13-X, 14-X	2	1					3		Asteraceae, esp. Astereae		
Melitoma taurea (Say, 1837)	1-VI	1						1		*Ipomoea*		
Nomada australis Mitchell, 1962	13-IV, 26-IV	1	1					2			*	
Nomada fragariae Mitchell, 1962	6-IV, 14-V	1	2			1		4			*	
Nomada luteola Olivier, 1811	26-IV, 13-V	3	2		1			6			*	Va
Nomada parva Robertson, 1900	16-IV, 18-V	6	2		2	1		11			*	
Nomada rubicunda Olivier, 1811	26-IV, 27-IV				3			3	*		*	Nc, Va
Nomada sp.	13-IV, 26-IV	2	2					4			*	
Nomia (Acunomia) maneei Cockerell, 1910	8-VIII				1			1				Gr
Ptilothrix bombiformis (Cresson, 1878)	16-VI		1					1		*Hibiscus*		

Table 1 Continued

Species	Early and late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Sand specialist	Oligolege and host	Parasite	Bees collected from
Svastra (Epimelissodes) atripes (Cresson, 1872)	8-VIII, 28-IX	1	2		1			4		*Chamaecrista & Senna*		Sca
Xylocopa (Xylocopoides) virginica (Linnaeus, 1771)	16-IV, 28-IX	2			6	4		12				Sc, Va
MEGACHILIDAE												
Anthidiellum (Loyolanthidium) notatum (Latreille, 1809)	29-VI, 5-IX	2			8	7		17				Gr, Es, Pas, Lb
Coelioxys (Glyptocoelioxys) germana Cresson, 1878	9-VIII				1			1			*	Ca
Coelioxys (Coelioxys) immaculata Cockerell, 1912	30-III, 1-V				2			2			*	Rco
Coelioxys (Boreocoelioxys) sayi Robertson, 1897	5-IX, 14-X	2	1		1	2		6			*	Lb
Heriades (Neotrypetes) carinatus Cresson, 1864	14-V, 14-VI	1			4			5				Ig, Es
Heriades (Neotrypetes) leavitti Crawford, 1913	14-V				1	1		2				Pan
Hoplitis (Alcidamea) pilosifrons (Cresson, 1864)	14-IV, 18-V	2	4			2		8				Ld
Hoplitis (Alcidamea) producta (Cresson, 1864)	14-IV, 26-IV	1	5					6				
Hoplitis (Alcidamea) truncata (Cresson, 1878)	30-III, 15-VI	1	3		4	2		10				Bc, Tv, Nc
Lithurgus (Lithurgopsis) gibbosus Smith, 1853	1-VI				1			1		Cactaceae		Oh
Megachile (Xanthosarus) addenda Cresson, 1878	1-V, 31-V	4						4	*			
Megachile (Litomegachile) brevis Say, 1837	15-IV, 16-VI	3	1			1		5				
Megachile (Chelostomoides) exilis Cresson, 1872	19-VII		1					1				
Megachile (Chelostomoides) georgica Cresson, 1878	31-V, 14 X	23	13		23	13		72				Bc, Gr, Lb, Pas
Megachile (Megachiloides) integrella Mitchell, 1926	30-VI	1						1				
Megachile (Litomegachile) mendica Cresson, 1878	16-IV, 14-X	6	1		1	8		16				Ld
Megachile (Xanthosarus) mucida Cresson, 1878	15-VI					1		1				Ld
Megachile (Leptorachis) petulans Cresson, 1878	31-V, 14-VIII	3	2		1	1		7				Ss
Megachile brevis pseudobrevis	1-V, 19-VII	7						7				
Megachile(Megachiloides) rubi Mitchell, 1924	15-IV, 15-VI	1	3			6		10	*			
Megachile sp.	14-V, 6-IX	3	2	1	1	22	9	38				Aa, Ca, Dt, Gr, Ig, Lb, Lv, Pan, Pi, Pas, Pp, Rco, Sca, Sco, Ss, Rg

Table 1 Continued

Species	Early and late dates of collection	Bowls - Females	Bowls - Males	Bowls - not sexed	Netted - Females	Netted - Males	Netted - not sexed	Totals	Sand specialist	Oligolege and host	Parasite	Bees collected from
Megachile (Litomegachile) texana Cresson, 1878	18-V, 15-IX	15	2		1	6		24				Gr
Osmia (Melanosmia) atriventris Cresson, 1864	13-IV		5					5				
Osmia (Helicosmia) caerulescens (Linnaeus, 1758)	6-IV		1					1				
Osmia (Melanosmia) collinsiae Robertson, 1905	6-IV, 13-IV	1	1					2				
Osmia (Osmia) cornifrons (Radoszkowski, 1887)	14-IV				1			1				
Osmia (Helicosmia) georgica Cresson, 1878	30-III, 14-V	4	7		2			13		Asteraceae		Pa
Osmia (Melanosmia) inspergens Lovell *and* Cockerell, 1907	6-IV, 30-IV	4	12		2			18				Va
Osmia (Osmia) lignaria Say, 1837	13-IV		1					1				
Osmia (Melanosmia) pumila Cresson, 1864	6-IV, 27-IV	3	2					5				
Osmia (Melanosmia) sandhouseae Mitchell, 1927	6-IV, 31-V	17	15		4			36				Va
Osmia sp.	6-IV, 31-V	5	11		1			17				
Osmia (Melanosmia) virga Sandhouse, 1939	30-III, 26-IV				2			2		Ericaceae		Va
Stelis (Heterostelis) australis Cresson, 1878	8-VIII, 23-VIII	1			1			2			*	Van
Stelis (Stelis) labiata (Provancher, 1888)	27-IV, 13-V	1	1					2			*	
Stelis (Stelis) lateralis Cresson, 1864	26-IV, 1-VI	1	1					2			*	
Stelis (Dolichostelis) louisae Cockerell, 1911	14-IV, 24-VII				4			4			*	Bc, Ca
Totals		2162	241	78	340	134	12	2967				

Table 2. Plants bees were collected from (Abbreviations used in Table 1). All plants were growing wild.

	Species	Common Name	Families	Season
Rco	*Rhus copallinum* L.	winged sumac	Anacardiaceae	mid-Aug - mid-Sept
Rg	*Rhus glabra* L.	smooth sumac	Anacardiaceae	late May - early June
Ig	*Ilex glabra* (L.) Gray	gallberry	Aquifoliaceae	late-April - mid-May
Aa	*Ageratina aromatica* (L.) Spach	small-leaved white snakeroot	Asteraceae	late Aug - Oct
Cr	*Cirsium repandum* Michx.	sandhill thistle	Asteraceae	mid-May - July
Es	*Erigeron strigosus* Muhl. ex Willd.	slender daisy-fleabane	Asteraceae	May - Oct
Ha	*Helianthus atrorubens* L.	purpledisk sunflower	Asteraceae	late July - Oct
Pan	*Packera anonyma* (A. Wood) W.A. Weber & A. Löve	Small's ragwort	Asteraceae	May - early June
Pas	*Pityopsis aspera* (Shuttleworth ex Small) Small	sticky golden-aster	Asteraceae	late July - Oct
Pp	*Pityopsis pinifolia* (Elliot) Nuttall	sandhills golden-aster	Asteraceae	late June - Sept
Sco	*Silphium compositum* Michaux var. *compositum*	rosinweed	Asteraceae	early June - mid Sept
So	*Solidago* spp.	goldenrod	Asteraceae	Aug - Oct
Sd	*Symphyotrichum dumosum* (L.) Nesom var. *dumosum*	rice-button aster	Asteraceae	mid-Aug - Oct
Va	*Vernonia angustifolia* Michaux var. *angustifolia*	slender ironweed	Asteraceae	late June - early Sept
Oh	*Opuntia humifusa* (Rafinesque) Rafinesque	prickly pear	Cactaceae	late May - mid-June
Ss	*Stipulicida setacea* Michaux	wire-plant	Caryophyllaceae	May - Aug
Ca	*Clethra alnifolia* L.	Coastal sweetpepperbush	Clethraceae	mid-June - July
Gd	*Gaylussacia dumosa* (Andr.) Torr. & Gray	dwarf huckleberry	Ericaceae	mid-March - early May
Va	*Vaccinium* spp.	blueberry	Ericaceae	mid-March - early May
Bc	*Baptisia cinerea* (Raf.)Fernald & B.G.Schub.	wild indigo	Fabaceae	May - mid-June
Cs	*Crotalaria spectabilis* Roth	rattlebox, showy rattlepod	Fabaceae	July - Sept
Gr	*Galactia regularis* (L.)Britton & al.	eastern milkpea	Fabaceae	early June - Aug
Tv	*Tephrosia virginiana* (L.) Persoon	goat's rue	Fabaceae	May - June
Lb	*Lespedeza bicolor* Turcz.	bush clover	Fabaceae	mid-June - Sept
Lv	*Lespedeza virginica* (L.)Britton	slender bush-clover	Fabaceae	July - Sept
Ld	*Lupinus diffusus* Nuttall	sandhill lupine	Fabaceae	late March - early May
Sca	*Seymeria cassioides* (J.F. Gmelin) Blake	senna seymeria	Orobanchaceae	Aug - mid-Oct
Pi	*Passiflora incarnata* L.	passion flower, maypops	Passifloraceae	May - Aug
Nc	*Nuttallanthus canadensis* (L.) D.A. Sutton	common toadflax	Plantaginaceae	mid-March - early May
Rcu	*Rubus cuneifolius* Pursh	sand blackberry	Rosaceae	late April - late May
Dt	*Diodella teres* (Walter) Small	poorjoe weed	Rubiaceae	June - Nov

Table 3. Number of individuals, species captured (species density), rarefied species richness, and estimated species richness (Chao 1) for each sampling year and pooled across both sampling years.

	2012	**2013**	**Pooled**
Individual abundance	1294	1642	2936
Species density	101	107	137
Rarefied species richness	101	100.36	109.31
Estimated species richness (Chao 1)	145 ± 23.86	125.47 ± 10.19	182.77 ± 23.79

Table 4. Number of individuals, species captured (species density), and proportion of individuals and species present in the overall community for each functional group by sampling year and pooled across both years.

	Sand specialist	Floral specialist	Parasitic species
Individual abundance	404	92	55
Species density	16	21	20
Abundance (%)	13.8	3.13	1.87
Species (%)	11.7	15.33	14.6

Figure 2 Map of Walthour-Moss Foundation

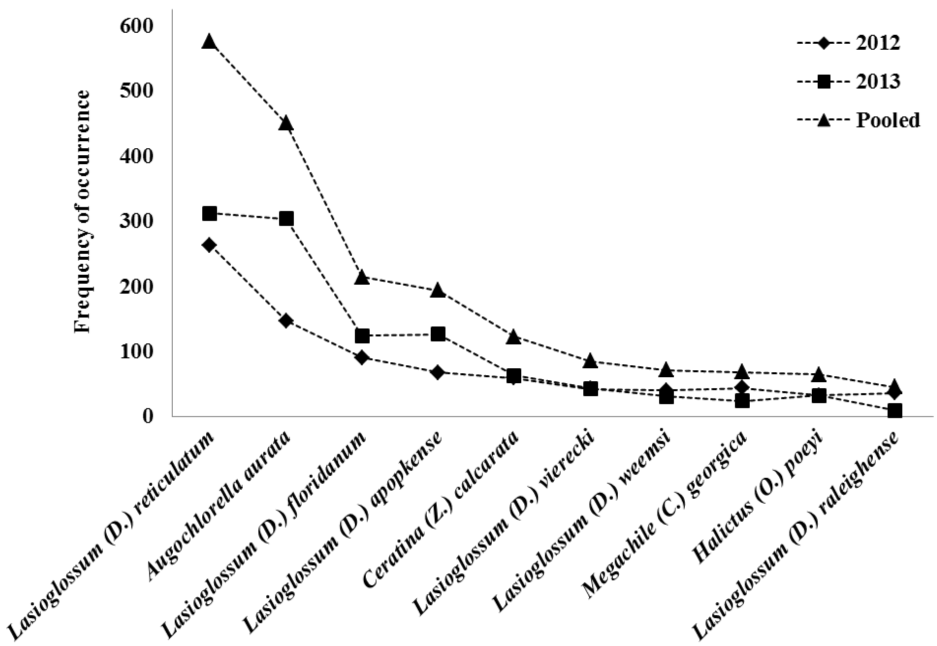

Figure 2 Rank frequencies based on the 10 most common bee species for 2012, 2013, and across both sampling years.

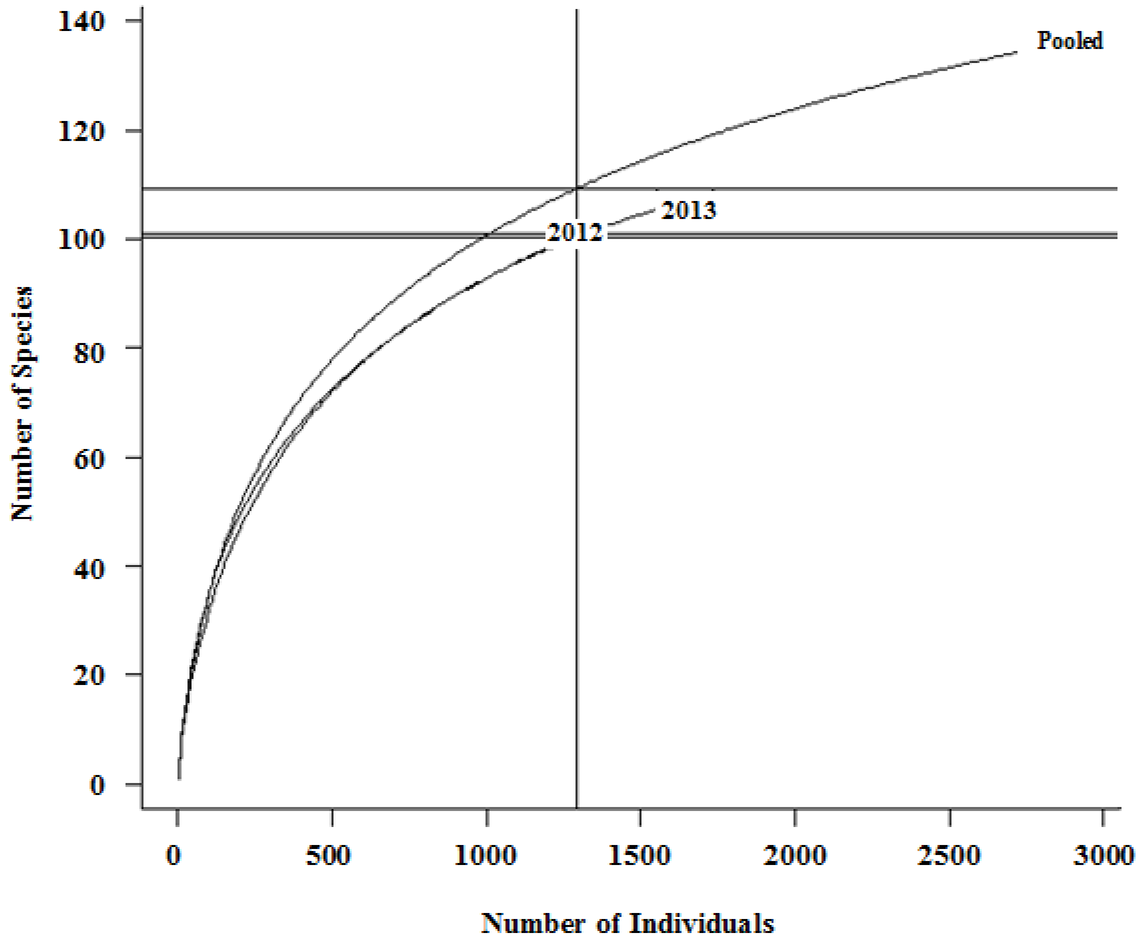

Figure 3 Rarefaction curves of number of bee species captured in 2012, 2013, and pooled across both sampling years.

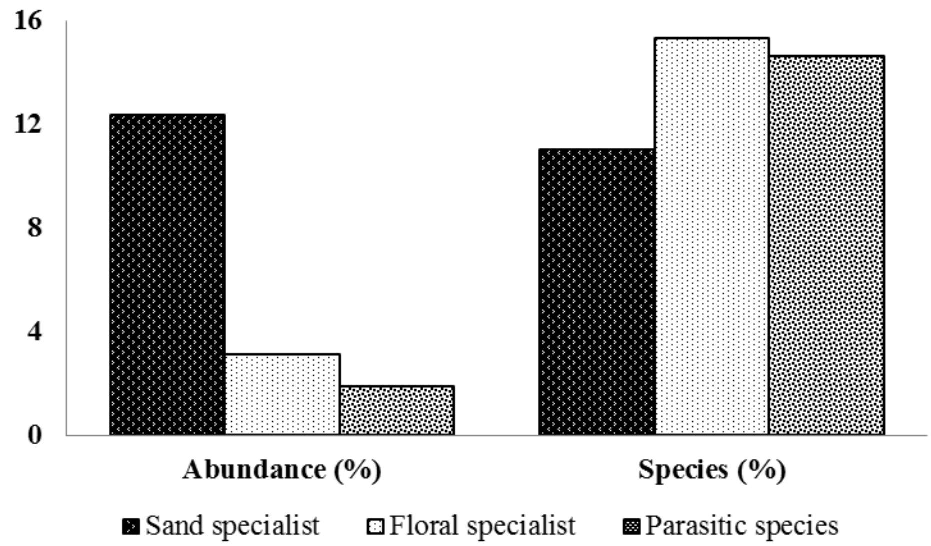

Figure 4 Proportion of functional groups by individual abundance and species density.