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Approval Sheet

Bee Community Responses in Pine Systems to Future Biofuel Cultivation in Southeastern US.

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Abstract Cover Page

Bee Community Responses in Pine Systems to Future Biofuel Cultivation in Southeastern US.

By

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B.Sc., Saint Louis University, 2012

Advisor: Berry Brosi, Ph.D.

An abstract of

A thesis submitted to the Faculty of the

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Master of Science

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Population Biology, Ecology, and Evolution

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Abstract

Bee Community Responses in Pine Systems to Future Biofuel Cultivation in Southeastern US.

By David Gruenewald

In order to meet projected biofuel demands, pine forests in the Southeastern US are anticipated to be a primary supplier for the cellulosic biomass used for biofuel production, yet there is little understanding how these expected changes in forest management will affect biodiversity in these systems. Due to their agricultural and ecological importance, bees were collected from 40 forest sites across Florida, Georgia, and Alabama. In this study, I focus on measuring the responses of bee communities in the forest management conditions currently in practice compared to the future management conditions expected for biofuel production. Throughout all models, bee abundance, species richness, and community composition were found to be significantly related to the management type and region of sampling while only marginally related to flower communities. This supports previous work that land-use has an impact on bee communities. However, examining the pairwise comparisons of bee abundance and species richness across management types suggests that observed differences in management resides in the age of the forest rather than changes brought on by biofuel production. These results suggest that while management conditions of forests can impact bee diversity, changes in management brought on by biofuel production may not significantly affect bee diversity at the local, short-term scale.

Cover Page

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Bee Community Responses in Pine Systems to Future Biofuel Cultivation in Southeastern US.

1. Introduction

Biofuel production is expected to increase globally over the next decade, yet little work has been done to assess how increased crop production for biofuels will impact biodiversity. In the US, the 2007 Energy Independence and Security Act, administered by the US Department of Energy (DOE), mandates for 136 billion liters of biofuel production by 2022. Last year, the total production of biofuels in the United States was estimated to be 5 billion liters of useable biofuels (EIA, 2014), most of which was derived from corn products. To help meet the high demand for biofuel production, advanced biofuels, such as cellulosic biofuels, will be utilized to account for over half of the mandated goal (approximately 80 billion liters). With the increase in cellulosic biofuel production (Sissine, 2007), pine biomass in the Southeastern U.S. will be a significant contributor for these future objectives (USDA, 2010), despite the current production of cellulosic biofuels being small scale and experimental thus far. The effects of pine expansion for biofuels on biodiversity are unknown. As land use and habitat loss are thought to be the primary driver of biodiversity loss worldwide (Sala et al., 2000), it is imperative to understand the extent to which increased pine production for biofuel use will affect local biodiversity.

Pine forests and plantations in the southeastern United States account for 200 million acres in the Southeast and are managed in a great diversity of ways. With such a large region affected, any changes in management practices due to biofuels may have profound effects. Before European settlement of the Americas, much of the coastal plain of this region existed in longleaf pine (*Pinus palustris*) savannahs, which are now a globally endangered habitat (Lear et al., 2005). Now, approximately 70% of this evergreen tree cover is owned privately or industrially for commercial use in the Southeast. These managed plantations would almost certainly experience dramatic management shifts with the advent of cellulosic biofuel production, especially given DOE mandates. Currently, the majority of harvested wood from the Southeast is used for wood fiber and wood products (Walsh et al., 2003). For the demands of cellulosic biofuels, pine harvests would need to be obtained from either designated new pine plantations or changing current pine management practices. At a local scale, such management changes for biofuel production are likely to include (1) collection of post-harvest woody residues (which in current practice are typically left behind; Allen et al., 2002) and (2) shorter harvest rotations, leading to fewer managed stands with large trees and more frequent harvest disturbance; and (3) higher density plantings (Jones et al., 2009). At a landscape scale, biofuel production may lead to an increase in the area coverage of pine plantations, with unknown conservation implications.

While different management types may be more suited for higher yields, it is uncertain if the most economic management practices correspond with conservation efforts. For instance, the removal of residues may have negative effects on certain taxa, while forest thinning may have positive effects on other taxa. Additionally, increased pine production may lead to a faster turnover of harvesting forests. This will result in higher levels of landscape heterogeneity, potentially benefitting biodiversity levels in the area.

In terms of biofuel impacts on wildlife, one key group to consider is pollinators. Beyond their ecological significance in maintaining wildflower diversity, native pollinators also support local row-crop agriculture in the region (Kremen, 2002). Native pollinators affected by future land use changes for biofuels may impact pollinator-dependent crops such as peanuts and cotton, which are major agricultural exports for the Southeast (SUSTA, 2014). Commercial pine practices do not support rich understory vegetation, potentially disturbing native pollinator populations. However, longleaf pine forests have a very open canopy, allowing for an extremely diverse understory for flowering plant communities (>1,000 flowering plant species; Winfree, 2007). Many of these wildflowers are likely insect pollinated. Of the various taxa of pollinators in the Southeast, bees are of particular interest due to their global decline and relative high diversity in the area.

Due to the agricultural and ecological importance of bees, we need a better understanding of how these future land-use changes may affect bee communities. Bee communities have not been well studied in southeastern pine habitats, either in commercial pine or longleaf pine systems. Some work on pine systems suggests low bee diversity and abundance (Winfree, 2007). The direct effects of pine management on wildflower communities make it particularly interesting to look at how biofuel management may affect bee communities in the Southeast, as bees are highly associated with wildflower communities. In agriculture, pollination services from native bee populations have been shown to help offset the declining populations of commercial bee farmers (Kremen, 2002). Beyond their agricultural and ecological significance, bees are a model system to understand biodiversity changes. Bees are a very useful study group for biodiversity surveys given their very high species richness of over 19,000 described species world-wide (Ascher & Pickering, 2011). However, there is ongoing concern about global declines in native bee species (Biesmeijer et al., 2006; Potts et al., 2010). Due to the possible regional changes in forestry practices, bee communities need to be evaluated across the Southeast.

For this study, I sampled bees in pine forests under different land management practices across Florida, Georgia, and Alabama. I hypothesize that (1) bee diversity, abundance, and community compositions will decrease as the intensity of management increases for local pine forestry practices; and (2) a decrease in bee diversity will correlate with a decline in flower diversity across management types. Correlations between bee and flower diversity must exist beyond how the land management will directly affect flowering plant communities.

2. *Methods*

2.1 *Site Selection and Sample Cycles*

I sampled bees in pine forests in three regions: southern Georgia, northern Florida, and eastern Alabama. The Georgia sites surrounded the Joseph W. Jones Research Center (Baker County), and were sampled during the spring and summer of 2013. The Alabama and Florida sites were sampled in the spring and summer of 2014 and surrounded the town of Greenville, AL (Butler County), and the Tall Timbers Research Station (Leon County, FL), respectively. Within each region, 12 to 14 sites were selected based on management condition. Bees were collected from mid-April to late-July for both years.

Based on potential changes in forest management for biofuels, I first selected sites based on the management conditions in practice. Sampling sites were categorized into 8 distinct management conditions (Table 1): (1a) Clearcut with residues; (1b) Clearcut without residues; (2a) Thinned – managed; (2b) Unthinned – managed; (3a) Young stand; (3b) Old stand; (4) Reference stand [longleaf pine]; and (5) Corn [as an alternative resource for biofuels]. These categories allow for comparisons between the proposed forestry management for biofuels against the current practices for timber production (appropriately grouped in Table 1). Comparisons between these management practices will investigate the potential effects of shorter harvest rotations (old stand vs. young stand), higher density plantings (thinned vs. unthinned), and woody debris collection after normal timber harvesting (clearcut with residues vs. clearcut without residues). For Alabama and Florida, two sites per region were designated for each management condition for a total of 14 sites

Table 1: Management Conditions for Sites

	Plot Type	**Age since planting**
1a)	Clearcut, residues	0 – 5 years
1b)	Clearcut, no residues	0 – 5 years
2a)	Thinned, managed	12 – 15 years
2b)	Unthinned, managed	12 – 15 years
3a)	Young, managed	8 – 12 years
3b)	Old, managed	>15 years
4)	Natural forest (longleaf)	>30 years
5)	Corn	>1 month

each. For Georgia, only 12 sites were sampled, with at least one site for each management condition.

Each site was divided into two separate plots; one each in the interior and at the edge of the tree stand. Bee communities may utilize resources differently at the edge and interior, for instance, since changes in canopy cover may affect wildflower availability. Each plot was 200m x 100m wide, and was surrounded by a minimum of 50m of similar habitat in all directions. The edge plots were exactly 50 m from the edge of the tree stand, bordering non-tree land use (roadways, pastures, or row-crops). Interior plots were placed at each site using ArcGIS to determine the most central position of forest, with a minimum distance of 1,000 meters from any forest edge. To assure that the sites were spatially independent, all sampling sites were separated by at least 2.5 km.

We ran four sampling "cycles" (repeat samples) at each site for each region during the duration of a field season. A cycle consisted of one complete sampling effort of bees for each site (see section 2.2 for more details). A consecutive cycle would begin only after all sites within the region were sampled. Generally, one complete cycle required about one month of sampling effort.

2.2 **Bee Collection & Vegetation Surveys**

We sampled bees for a total of four cycles at each site using two methods together: pan traps and aerial netting, the two most effective bee sampling methods (Westphal et al., 2008). Pan traps are small plastic bowls painted with UV-bright pigments and are filled with a dilute solution of water and a detergent to break surface tension. Bees are attracted to the painted pan traps and drown in the water (Kearns & Inouye, 1993; Westphal et al., 2008). These pan traps were set to the appropriate height of nearby vegetation. We set 15 traps along the middle 100 meters along a transect in the exact center of each plot, alternating with 5 blue, white, and yellow paints. For each pan trap effort, trapping arrays were set before dawn and collected at dawn the following day.

We conducted aerial netting for each site along the full 200 meter transect at the interior and edge plots of the forest. Field team members aerial netted any bees found within 2 meters of either side of the transect. We conducted a single 30-minute aerial netting sampling once in each plot for each cycle, using a stopwatch, with the time used in handling and processing individual specimens excluded. Aerial netting took place between mid-morning and early afternoon, the period of maximum bee activity (Westphal et al., 2008). Specimens caught in nets were destructively sampled using individual ethyl acetate kill jars.

Bee specimens (from both pan traps and aerial netting) were pinned and labeled daily after field work was completed. Bees were then identified to the species level, or lowest possible taxonomic category, with interactive keys from DiscoverLife. Sam Droege, of US Geological Survey, assisted with identifications of several particularly challenging groups (e.g., *Lasioglossum, Megachile,* etc.) while also confirming previous identifications.

Flowering vegetation was recorded during the third and fourth cycle for each field season. All plants currently in bloom growing within 1 meter of either side of a 100 m sampling transect were tallied and identified to species, using reference material from conspecifics outside the sampling transect when necessary.

2.3 **Data Analyses**

2.3.1 Overview

I analyzed changes in bee relative abundance, diversity, and community composition (response variables) in terms of several explanatory variables: management type of each site, region, edge/interior, and blooming plant abundance and richness. I used generalized linear models, including mixed-effects models (GLMs and GLMMs) to analyze bee abundance and species richness in response to the explanatory variables. I then used model selection to identify the most parsimonious yet informative set of models available based on collected data. To help ensure that any observed differences were attributed to the explanatory variables, rather than site proximity, I first assessed spatial autocorrelation in all three response variables. I conducted all analyses using the R statistical programming language (R Core Team, 2013).

In terms of the response variables, I first examined bee relative abundance per cycle. Since abundance is an additive measure, mixed-effects models were used with negative binomial errors (given the discrete response); see section 2.3.3 for more detail. For community composition, I used Bray-Curtis pairwise dissimilarity, since my sampling effort was perfectly balanced and to maximize the use of abundance data (in contrast to Jaccard dissimilarity, which operates using presence-absence data). I analyzed differences in community composition using matrix permutation tests (‘adonis’ function in the ‘vegan’ package for R) (Oksanen et al., 2013).

In contrast to abundance and community composition, I examined several different metrics of bee diversity. It has been demonstrated that diversity has several components and because species richness is a non-additive measure (given species overlap between samples). Specifically, I assessed: (1) relative bee species richness per sampling cycle; (2) accumulation of species within a site over all sampling cycles; (3) final accumulated richness after all sampling cycles; (4) the Shannon-Wiener diversity index, which takes into account both species richness and evenness (“SWDI” hereafter; calculated on final accumulated richness after all sampling cycles); and (5) the Chao1 species richness estimator, which estimates how many species may be in a site given the distribution of rare species (Chao, 1987). For diversity responses 1 and 2, I used mixed-effects models (section 2.3.3) due to repeated measures in a site; responses 3-5 were aggregate measures for each site and thus I used linear (responses 4 and 5) or generalized linear models (response 3, with quasi-Poisson errors due to its discrete nature) to analyze these outcomes. Residuals were examined for model validation to meet all assumptions of the linear models (responses 4 and 5).

2.3.2 Spatial autocorrelation

I used Moran's *I*, calculated in the 'ape' package for R to test for spatial autocorrelation in bee abundance and richness (Paradis et al., 2004). To assess spatial autocorrelation in community composition, I used Mantel tests on pairwise Bray-Curtis dissimilarity using the 'vegan' package for R (Oksanen et al., 2013; Faith et al., 1987). I calculated both Moran's *I* and the Mantel tests for all three regions combined as well as for each region separately.

2.3.3 Mixed-effects models

Because within-site subsamples do not represent independent samples for the purposes of statistical tests, I used a mixed-effects model approach for those responses that utilized data from multiple subsamples within sites. This includes analyses of bee abundance and the first two aforementioned metrics of bee diversity (raw species richness per cycle, and species richness accumulation by cycle). For all three of these responses, I specifically ran generalized linear mixed-effects models with negative binomial errors, given the discrete nature of the responses, which were all overdispersed relative to a straight Poisson distribution. I used site as a random effect to control for repeated measures in all of these analyses, and additionally used region as a fixed effect, since it had only three levels (five levels is considered a bare minimum for incorporation as a random effect; Bolker et al., 2009). As opposed to the analysis of a per-cycle species richness, the analysis of species richness aggregated by cycle included an interaction between each fixed effect and cycle, to see how each fixed effect (e.g. forest management) impacted the accumulation of species in that site over time.

2.3.4 Model Selection and Post-Hoc Tests

I used a model selection approach for the analyses of bee abundance and diversity because of the relatively large number of explanatory variables (5) in each analysis, so that I could determine the best set of models, balancing parsimony with explanatory power. I used an

Aikake's Information Criterion (hereafter AIC) model selection approach throughout so that I could compare non-nested models (Burnham & Anderson, 2002). I did not take an AIC approach with the adonis tests of community composition, because these matrix permutation tests do not generate an AIC or other information-criteria based measure. Instead, I ran a full model (with all explanatory variables), as well as a model with just management type, and I report on the significance of the different effects.

For the AIC analyses, after the best set of model was selected, I ran Tukey's post-hoc tests (using the 'glht' function in the 'multcomp' package; Hothorn et al., 2008) on the explanatory variables to determine differences between levels of categorical fixed effects remaining in each model. For example, I was interested to determine which management practices differed from one another in terms of bee abundance and diversity. Because *p*-values are likely to be inflated by model selection procedures, I considered the post-hoc tests a means to quantify observable differences, but not fully support significance (Burnham & Anderson, 2002).

2.3.5 Community Composition

To assess how community composition of bees is related to the model, I performed an adonis test using the Bray-Curtis dissimilarity index (utilizing the 'vegan' package in R; Oksanen et al., 2013). I performed two separate adonis tests, first using the full model with all explanatory variables and next only examining management type. Since adonis does not generate AIC or other information criteria measures needed for model selection, I report on the p-values of each effect in a full model.

3. Results

3.1 Overview

A total of 3,912 individual bees from 99 different species were collected for analysis. In 2013 in Georgia, 1,882 bees were collected from 61 species. The Florida region had the highest raw species richness with 71 bee species from the 1,399 individuals collected. Finally, 631 individuals were collected from Alabama representing 50 species. The most abundant bee genus for all regions was *Lasioglossum*, comprising roughly 65% of all specimen collected (Table 2). A rank abundance curve is presented in Fig. 1A. There was high variability in bee abundance and species richness between sites, with one site recorded with only one specimen in contrast with the 476 individuals from our most abundant site. The average number of bees collected per site was 97.8 individuals. The species accumulation curve (Fig. 1B) shows a trend of flattening; however, the lack of a plateau in the curve indicates that there are likely additional bee species that were not sampled.

Table 2: The overall abundance (total counts) by genus for the three sampled regions

	Genus Abundances																															
Region	Lasioglossum	Melissodes	Augochlorella	Bombus	Apis	Megachile	Ceratina	Agapostemon	Augochloropsis	Halictus	Melitoma	Ptilothrix	Xylocopa	Perdita	Cemolobus	Svastra	Colletes	Hoplitis	Osmia	Andrena	Augochlorellla	Eucera	Lithurgopsis	Centris	Heiades	Hylaeus	Melitta	Peponapis	Sphecodes	Triepeolus	Xenoglossa	**Grand Total**
AL	431	27	1	56	10	19	16	10	3	12	0	20	11	0	0	8	4	2	1	0	0	0	0	0	0	0	0	0	0	0	0	**631**
FL	791	34	272	31	74	46	38	24	36	15	2	4	5	0	5	0	1	0	3	2	4	4	3	1	0	1	0	0	1	1	1	**1399**
GA	1326	372	6	20	5	19	5	23	18	19	32	2	1	13	7	1	2	5	1	2	0	0	0	0	1	0	1	1	0	0	0	**1882**
Grand Total	**2548**	**433**	**279**	**107**	**89**	**84**	**59**	**57**	**57**	**46**	**34**	**26**	**17**	**13**	**12**	**9**	**7**	**7**	**5**	**4**	**4**	**4**	**3**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**3912**

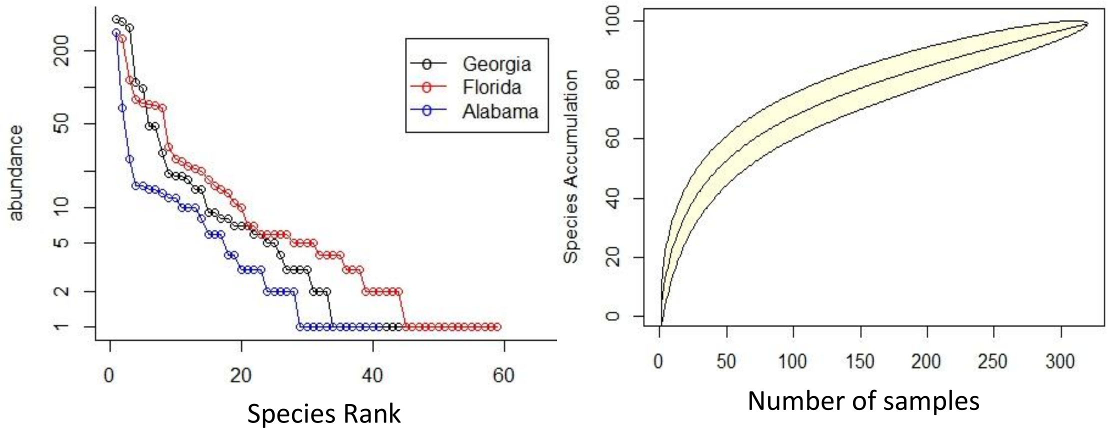

Fig. 1 – (A) Rank abundance curve of species for each region; (B) Species Accumulation Curve calculated by randomizing each sampling effort (80 plots × 4 cycles = 320) 1,000 times without replacement. Confidence Intervals are shown in yellow.

3.2 Spatial autocorrelation

For all regions combined, bee abundances and species richness were found to have significant spatial autocorrelation (Abundance: *Moran's I = 0.193, p-value = 0.04 ; Richness: Moran's I = 0.251, p-value = 0.02*). I then assessed spatial autocorrelation for each region separately. There was no significant spatial autocorrelation for bee abundances in either Alabama or Georgia *(Moran's I [AL] = -0.0769 , p-value = 0.91; Moran's I [GA] = -0.105, p-value = 0.87)*. However, bee abundance in Florida was still found to have spatial autocorrelation *(Moran's I = 0.514, p-value < 0.01)*. However, species richness was not found to be spatially autocorrelated for any of the three regions *(Moran's I [AL] = 0.260, p-value = 0.19; Moran's I [FL] = -0.064, p-value = 0.95; Moran's I [GA] = -0.080, p-value = 0.92).*

Similarly, I found significant spatial autocorrelation in community composition, measured as Bray-Curtis dissimilarity, when considering all regions together (Mantel r = 0.391, p-value < 0.001). Examining each region separately, community composition no longer displayed significant spatial autocorrelation between sites *(Mantel r [AL] = 0.034, p-value = 0.27; Mantel r [FL] = 0.044, p-value = 0.19; Mantel r [GA] = 0.13, p-value = 0.12).*

Because sampling sites were clustered within regions, the pairwise distances between sites across regions were orders of magnitude greater than distances between sites within the same region. The spatial autocorrelation observed with abundance, richness, and community composition all appear to be driven by regional variation rather than local variation. When considering regions separately, the only test to show significant spatial dependence was bee abundance in Florida. Because I performed three separate tests for autocorrelation for the three regions, the odds of finding at least one spurious significant result is nearly 50%. Therefore, for subsequent analyses, I assumed that sites were spatially independent samples.

3.3 Bee Abundances and Species Richness

Based on AIC values calculated for each possible combination of explanatory variables, bee abundance and richness was strongly related to region and management type (Table 3) out of a total of 30 possible models. With 8 possible models containing both management and region as a fixed effect, all 8 models ranked the highest in model selection compared to all other possible combinations (Table 3). This was true for relative abundances, raw species richness, and aggregated species richness. A major increase in AIC (and thus a less useful model) was observed if management was not included as a fixed effect and an even larger increase in AIC was observed if region was removed as a fixed effect (Table 3). This same trend occurred for all GLMMs. When considering sampling efforts throughout time, flower richness and flower abundance was marginally related to relative abundance, species richness, and aggregated species richness. Overall, whether the plot was located near the edge or interior of the site was minimally related to abundance and richness.

Pooling the species richness across all cycles, along with Shannon-Weiner Diversity Index (SWDI) and Chao1 Estimator, presented similar results. Due to the nature of linear models, the residuals of SWDI and Chao1 Estimator models were inspected and met all linear model assumptions. Management and region were consistently found to explain the most variance in diversity between sites. Flower abundance became a stronger explanatory variable for these diversity responses, but still to a lesser degree than management and region. Edge and interior remained a less suitable explanatory variable to the highest ranked models (Table 4).

Table 3. Example of AIC model selection for relative abundance. All fixed effect within each model are marked with "●".

	Fixed Effects for Abundance										
Model Rank	**Management**	**Region**	**Edge/Interior**	**Flower Abundance**	**Flower Richness**	**logLik**	**AIC**	**dLogLik**	**dAIC**	**df**	**weight**
1	●	●				-1015.0	2054.1	29.9	0.0	12	0.326
2	●	●			●	-1014.6	2055.2	30.4	1.1	13	0.184
3	●	●	●			-1014.9	2055.8	30.1	1.7	13	0.138
4	●	●		●		-1015.0	2056.1	29.9	2.0	13	0.121
5	●	●	●		●	-1014.5	2056.9	30.5	2.8	14	0.079
6	●	●		●	●	-1014.6	2057.1	30.4	3.0	14	0.071
7	●	●	●	●		-1014.9	2057.8	30.1	3.7	14	0.051
8	●	●	●	●	●	-1014.4	2058.8	30.6	4.7	15	0.030
9		●			●	-1032.7	2077.3	12.3	23.2	6	<0.001
10		●		●	●	-1032.1	2078.2	12.9	24.1	7	<0.001
…	…	…	…	…	…						
30	●		●	●	●	-1038.4	2102.8	6.6	48.7	13	<0.001

3.4 Management Condition Effects

Because management condition is of key concern to this study and it continuously appeared in the highest ranked models for all diversity metrics, Tukey's HSD was used to make pairwise comparisons to help quantify where differences in management type reside (Fig. 2). While all pairwise comparisons were considered, differences between current and future biofuel management practices (e.g. clearcut with residues vs. clearcut without residues) are of most importance for biofuel expansion.

Table 4. Summary of explanatory variables found in selected best models for each response variable. The components of the highest ranked model (according to AIC) are marked with "●", while the second ranked model is marked with "○".

		Explanatory Variables				
Response Variable:	**Model Type**	**Management**	**Region**	**Edge/Interior**	**Flower Abundance**	**Flower Richness**
Relative Abundance	GLMM	●○	●○			○
Raw Species Richness	GLMM	●○	●○			●
Aggregated Species Richness	GLMM	●○	●○			○
Pooled Species Richness	GLM	●○	●○		●○	○
SWDI	LM	●○	●○	○	●○	
Chao1 Estimator	LM	●	●○			○

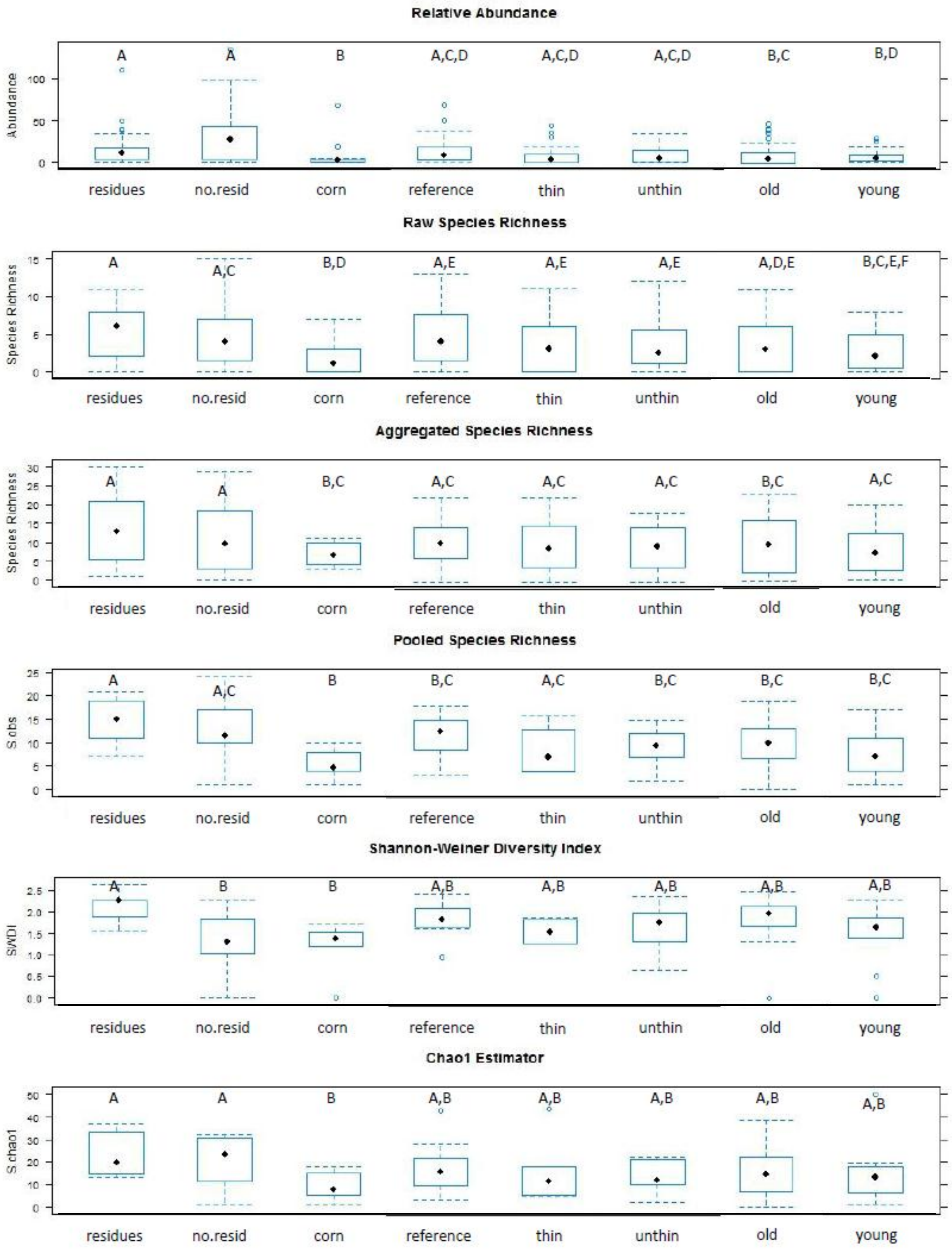

Fig. 2 – Bee diversity responses to different management types. Differences between management types are marked with letters to denote like groups.

3.5 Community Composition

Adonis tests using Bray-Curtis dissimilarity index on the full model show management and region significantly contribute to community composition (Table 5). None of the other tested variables show significant effects on community composition. Performing an adonis test with management as the sole explanatory factor supports that management type is affecting bee community compositions *(R^2 = 0.228, p-value = 0.006).* Community compositions based on bee tribes across management types can be found in Fig. 3.

Table 5. Adonis results for full model of community simmilarity

	Df	SumsOfSqs	MeanSqs	F.Model	R^2	Pr(>F)	
mgmt	11	0.0619246	0.0056295	2.83447	0.227985	0.001	***
region	2	0.0768456	0.0384228	19.34593	0.282918	0.001	***
edg.int	1	0.0017684	0.0017684	0.89038	0.006511	0.427	
flower.rich	1	0.0035647	0.0035647	1.79485	0.013124	0.092	.
flower.abund	1	0.0023905	0.0023905	1.20362	0.008801	0.263	
Residuals	63	0.1251238	0.0019861		0.460661		
Total	79	0.2716176			1.000000		

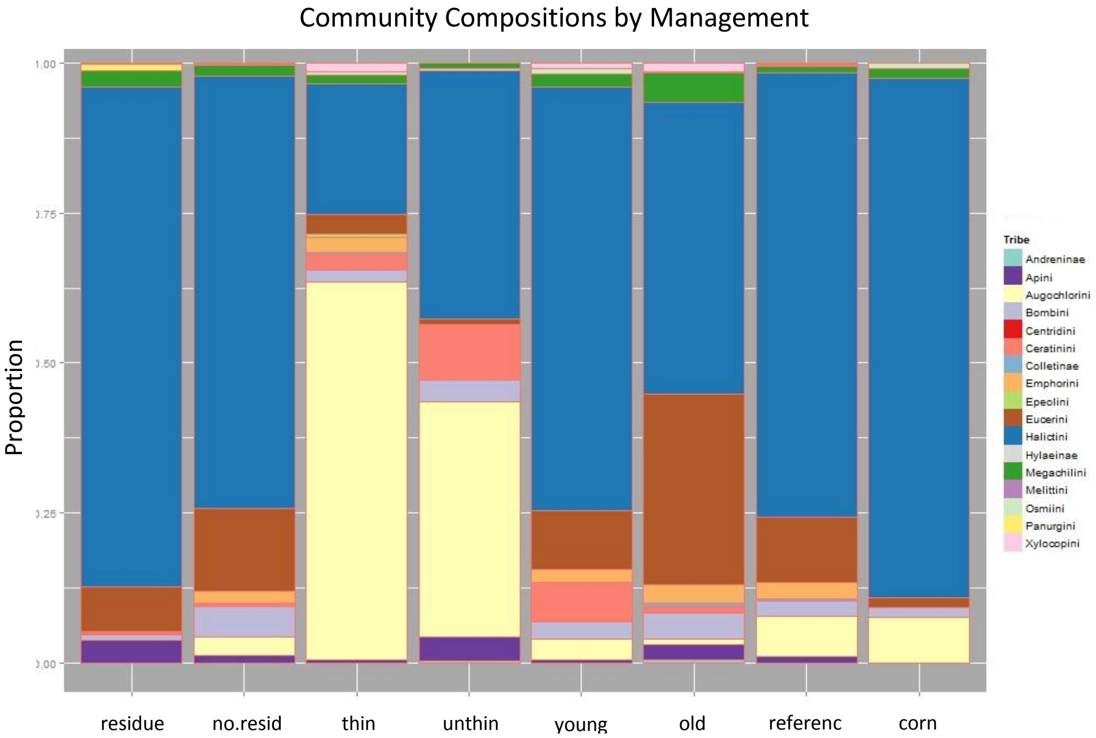

Fig. 3 – Community composition of bee tribes across different management types. For the sake of visibility, this figure uses bee tribes, the taxonomic level between genus and subfamily, rather than species (17 tribes vs. 99 species). All analyses on community composition utilized species data for a more refined comparison.

4. Discussion

Bee abundance, richness, and community composition are all affected by both forest management and region in the Southeastern US. With model selection for all of the response variables, management and region were consistently found to be explanatory variables in the highest ranked models. Flower richness and abundance were found to contribute to bee diversity and composition, but to a lesser degree than either region or management. The effect of interior versus edge sampling was not found to significantly contribute to bee diversity or composition. The consistency of the results across the three regions (Georgia, Alabama, and Florida) gives us additional confidence in our findings as a reliable foundation for management decisions.

These results support previous work showing that bee diversity can be significantly impacted by land use (Sutherland et al., 2006; Winfree et al., 2009). While there has not been direct work in this region, land-use intensity has been found to affect bee abundance and richness in other areas (Klein et al., 2002). Management and anthropogenic disturbances have generally affected bee abundance and bee richness negatively, yet these effects on bee populations are of little magnitude if disturbance intensity is moderate (Winfree et al., 2009). Management type may have shown significant effects in this pine system. However, the management intensity is not always the main driver for changes in bee diversity. Certain management types were consistently observed to have significant differences in all response variables, such as clearcuts compared to corn. However, some differences attributed to management appear to be dependent on the diversity response considered, as the diversity index selected may influence the measured response of a system (Nagendra, 2002; Bock et al., 2007).

Most pairwise differences observed between management conditions were related to the age since planting, rather than direct differences in management practice (Fig. 2). Throughout all models, both types of clearcut sites were found to have significantly higher species abundance and richness. Previous studies have suggested a relatively low bee diversity and abundance within pine systems (Winfree, 2007), so clearcut sites (with the least amount of forest cover compared to other sampled sites) may be expected to have higher bee diversity and abundance. There were occasional differences in bee diversity observed between younger and older pine stands, yet this was largely dependent on the type of diversity response tested. Finally, there were rarely differences in bee diversity between the managed pine stands and the unmanaged, reference stands. This rejects our initial hypothesis that increasing the intensity of management in pine systems will decrease bee diversity. While management type did affect bee diversity, the intensity of the management did not seem to indicate any directionality.

Pairwise comparisons of the management types that we examined suggest that future biofuel cultivation in southern pine plantations may not have a direct impact on bee abundances or richness at the local scale, relative to current forestry practices (Fig. 2). Throughout all models, there were no differences between the three management contrasts we examined (two types each of clearcuts, thinning practices, and stand age/rotation time). All observed differences in management conditions resided between these groups rather than within. Comparing the current management practices to the future management practices for biofuel production (residue harvesting, thinning, and shorter rotations), these findings suggest that bee communities will not be affected at the local scale by management changes due to biofuels. However, changes to management conditions across all pine plantations, or the designation of additional land to pine systems for biofuels, may alter landscape heterogeneity and thus possibly affect bee diversity (Benton et al., 2003; Bennett & Ford, 1997). At the same time, it should be noted that corn sites, the current main source of biomass for biofuels and bioethanol (EIA, 2014), consistently contained the lowest bee diversity. Thus, a switch to pine-based biofuel feedstocks, relative to corn-based, may have positive impacts on bee communities, at least at local scales and over short time periods.

Flower abundance and flower richness had a smaller effect than management and region throughout all models. Flower abundance and richness did not have a large contribution to bee diversity across management types, despite previous work suggesting the high association of bee diversity with wildflower diversity (Potts et al., 2003; Cariveau et al., 2013). Variation in bee diversity explained by wildflower diversity may be overshadowed by the effects of management and region within these models. This is particularly the case because we saw no consistent relationship between management type and blooming plant diversity and abundance. Furthermore, only two cycles of wildflower sampling per site may have been insufficient to adequately represent local flowering communities. This could be highlighted by the temporal variability often observed in plant-pollinator communities (Ebeling et al., 2008).

Beyond the differences on bee abundance and species richness, management type was found to also significantly impact the bee community composition. The bee tribe Halictini (*Halictus, Lasioglossum,* etc.) accounted for the majority of specimens collected throughout all sites except the thinned and unthinned management condition. For these two management conditions, the bee tribe Augochlorini (*Augochlorella*, *Augochloropsis*) was found to represent the majority. Land use has been shown to affect community compositions for both bees and flowering plants in grassland systems (Batary et al., 2010), yet these results do not indicate a potential driver for community shifts. These results suggest that community compositions rebound back to a Halictini dominant system with increased years since planting after the thinning process.

A deeper understanding of the impacts of biofuel cultivation on bees could be supported by further investigations into landscape features and spatial scaling. This work focused on local-scale impacts, but landscape-level factors (such as landscape heterogeneity) could be important drivers of change in bee communities (Brosi, 2009; Kennedy et al., 2013). For example, increasing the extent of pine plantation cover at landscape scales may decrease, or increase, bee diversity and abundance. Future work should include explicit consideration of the spatial scale of such different landscape patterns, as this can be a key factor in shaping biological communities (Levin, 1992; Chase & Leibold, 2002). Another consideration is inclusion of additional land use /

land cover types, such as pastures, which would be particularly helpful for assessing the effects of alternative land uses (and conversion from different land use types to pine forests). This would be particularly helpful in informing future models on the responses of bee communities to potential future area increases for pine plantations (Potts et al., 2010).

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