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The effects of forest age and management on bee communities of production forests in the southern United States

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The effects of forest age and management on bee communities of production forests in the
southern United States

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Master of Science
in
Biology

by

Robinson Sudan

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Abstract

Processes structuring bee communities in agricultural landscapes are well-documented compared to those in other anthropogenic landscapes, like production forests. Forests across the temperate zone have historically been under-sampled, in part due to the perception that they provide little habitat to support diverse bee communities. While research suggests that early successional habitats support high levels of bee species richness and abundance, little empirical evidence exists to support the notion that forests, in turn, do not. To understand the relationship between forest successional age and major elements of the bee community, I sampled bees in a southern production pine forest in Hancock County, MS across 2012 and 2013. I found that while bee abundance declines with successional age, species richness does not. Combining this work with other recent research, I propose a generalized framework for understanding the role of disturbance and forest structure in structuring bee communities of southern forests.

Keywords: bees; Apoidea; Hymenoptera; pine forest; community ecology; biodiversity

Introduction

The role of anthropogenic landscapes in biodiversity conservation has become a major topic of research (Jules and Shahani 2003, Bennett et al. 2006). This trend is particularly noticeable for species like bees, which provide important ecosystem services to human communities (Hannon and Sisk 2009, Winfree 2010, Mandelik et al. 2012). Bees are required for pollination of a majority of plant species in both natural and agricultural ecosystems through their activities as pollinators (Klein et al. 2007), yet recent research shows that many bee populations are in decline and/or are threatened with extinction (Potts et al. 2010, Nieto et al. 2014). Globally, habitat loss is a major factor contributing to these declines (Brown and Paxton 2005) and to biodiversity loss in general (Dirzo and Raven 2003, Foley et al. 2005). With conversion of land to agriculture projected to continue (Godfray et al. 2010), research aimed at maintaining native bees within these agricultural landscapes is important for their long-term conservation. In areas where agricultural production dominates, research has led to the development of best management practices (BMPs) for promoting native bees and other pollinators and has contributed to our understanding of processes that drive local abundance and diversity patterns on and around these working lands (Williams and Kremen 2007, Öckinger and Smith 2007, Lonsdorf et al. 2009). However, future bee conservation efforts will require more than a pollination services-based argument (Kleijn et al. 2015).

In contrast to the attention devoted to native bees in agriculture, much less attention has been devoted to other human-dominated areas, like production forests. While research has been ongoing, significant knowledge gaps exist in our understanding of bees' responses to

those ecological processes which presumably drive local diversity patterns in forests (Campbell et al. 2007, Hanula et al. 2015). This lack of information can create uncertainties for conservation and land managers in non-agricultural regions that are dominated by production forests. Here, well-documented ecological processes observed on agricultural landscapes may not be driving bee diversity patterns in the same way. To develop comprehensive recommendations for pollinator conservation on anthropogenic landscapes, research needs to be expanded to include other major land uses beyond agriculture.

Much of the southeastern US is dominated geographically by forestry (Miller et al. 2009) with 46% of the region classified as forest and 86% of forests in timber production (Oswalt et al. 2014). In Mississippi alone, 62% of the state is classified as forest, and the ubiquity of production forestry there can also be understood economically; in 2001, industry output of forestry and related value-added products exceeded \$18.5 billion, and the industry generated over \$1.3 billion in tax revenue (Munn and Tilley 2001). Yet despite the economic and geographic importance of forestry and recent evidence that historical changes leading to current forest conditions have gradually made southeastern forests less favorable for bees (Hanula et al. 2015), extensive surveys of bees on production forests have been non-existent and their potential for providing bee habitat remains unexplored.

These forests do not represent the original forest conditions, however. With removal of fire as the primary disturbance regime and changes in edaphic conditions from European settlement-era agricultural land clearing and subsequent abandonment, species

composition of overstory pines has shifted from fire-tolerant longleaf pine (*Pinus palustris*) to fast-growing, fire-intolerant species like loblolly (*Pinus taeda*) and slash pine (*Pinus elliotii*) (Carroll et al. 2002). In addition, fire suppression has replaced the open, herbaceous understories with dense, shrubby understories (Mitchell et al. 2006), a condition shown to support fewer bees and lower species richness than the historical conditions (Hanula et al. 2015).

Several studies in the temperate zone have found that increasing forest cover has a negative relationship with bee diversity and that decreasing floral richness and abundance likely drive this pattern (Campbell et al. 2007, Winfree et al. 2007a). Other studies have shown a positive relationship between shrub removal and pollinator abundance and diversity (Rudolph and Ely 2000, Hanula and Horn 2011). Hanula et al. (2015) examined elements of forest structure and showed that the bee community of cleared forests and those of open, mature pine forests were similar and were also highest in numbers of bees and bee species out of their seven treatments. Likewise, Grundel et al. (2010) observed a negative relationship between number of bees and forest cover while also showing that bee species richness relates positively to plant species richness and abundance of potential nesting resources. Nesting and floral resources have a significant effect on bee community composition (Potts et al. 2005, Murray et al. 2009, Torné-Noguera et al. 2014), and in southeastern production forests, potential bee nesting resources and some important floral resources vary in abundance among stands of different age since clearcutting (Sudan and Santonastaso, unpublished data).

Forest structure in southeastern pine forests clearly influences bee communities (Breland et al. 2015, Hanula et al. 2015). Figure 1 illustrates how these structural changes to forests are directly related to forest age, succession, and disturbance regimes (Grano 1970, Landers et al. 1995, Carroll et al. 2002, Fox et al. 2004, Mitchell et al. 2006, and Miller et al. 2009).

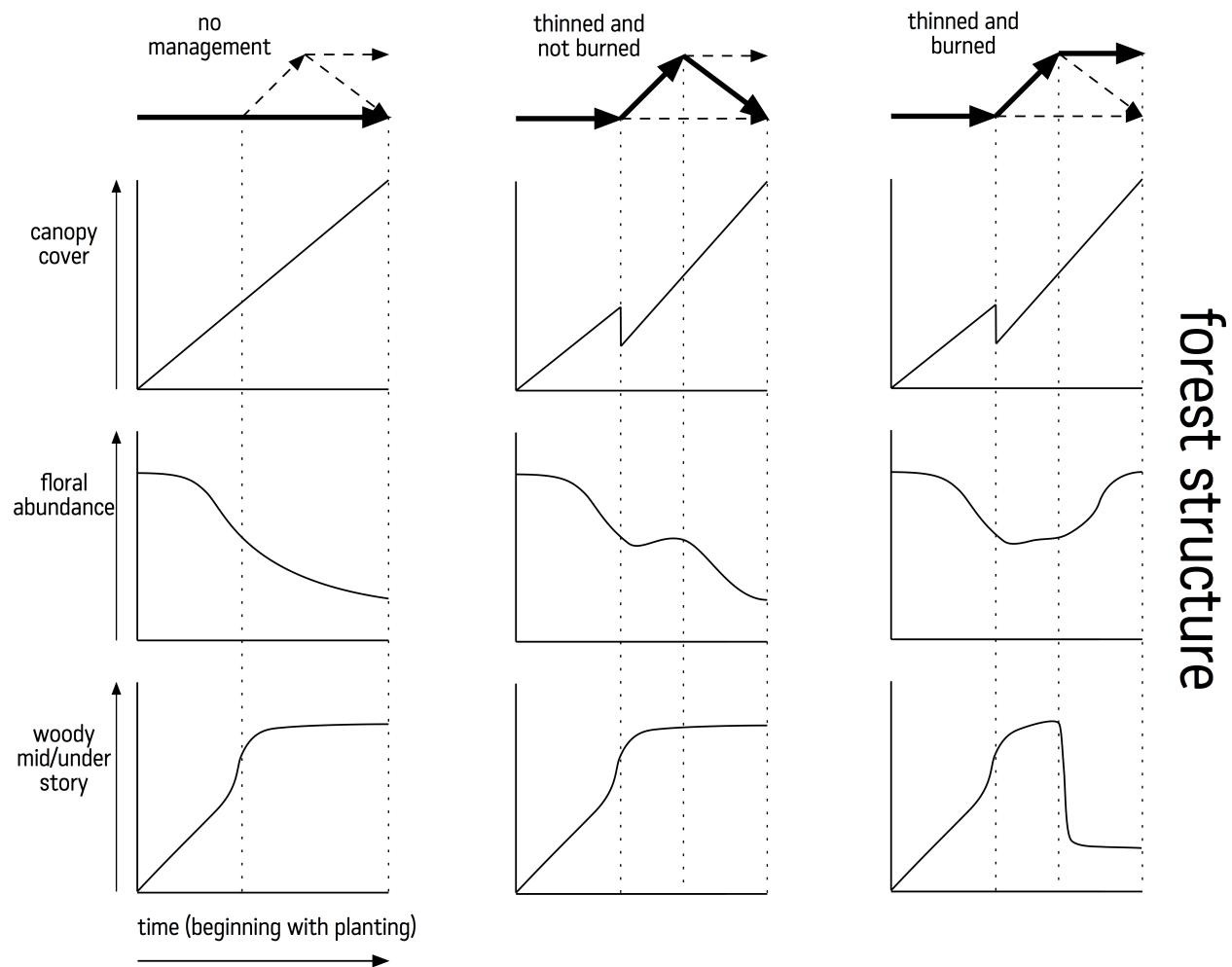


Figure 1) Relationships between elements of forest structure and forest management/disturbance. (Grano et al. 1970, Landers et al. 1995, Carroll et al. 2002, Fox et al. 2004, Mitchell et al. 2006, and Miller et al. 2009). The small diagrams on the top represent specific successional trajectories with dashed lines (representing potential trajectories not taken) extending at points where management activities take place.

For the above forest landscapes where these relationships have been studied, their impacts on bee communities are not entirely straightforward. While we may expect similar trends in the context of production forests, a thorough search of the available literature reveals that these relationships have simply not been examined.

There is wide agreement that production and plantation forests are likely to become an increasingly important part of biodiversity conservation around the globe (Hartley 2002, Carnus et al. 2006, Brockerhoff et al. 2008, Bremer and Farley 2010, Paquette and Messier 2010), and BMPs in the southeastern US have evolved to include measures which promote ecosystem functioning, biodiversity, and conservation at multiple spatial scales (Loehle et al. 2009, Miller et al. 2009). For example, staggering harvest cycles creates a heterogeneous landscape of patches at different successional stages. Additionally, low-lying mixed hardwood stands may remain unlogged for logistical reasons or to provide landscape structural features that further enhance heterogeneity. Production forestry has largely replaced the natural disturbance regime (fire) (Mitchell et al. 2006) and its associated stochasticity with a regular anthropogenic disturbance regime in the form of a roughly 20 year harvest/replanting management cycle (Fox et al. 2004, Miller et al. 2009). However, by maintaining landscape structural complexity, forestry BMPs may produce the same positive effects on bee diversity seen in agricultural systems (e.g. Tscharntke et al. 2005, Winfree et al. 2007b; Winfree et al. 2007a, and Mandelik et al. 2012) and urban and suburban developments (Winfree et al. 2007a) by providing complimentary habitats for nesting and foraging (*sensu* Mandelik et al. 2012; see also Gathmann and Tscharntke 2002, Steffan-Dewenter et al. 2006). However, even a basic understanding of the impacts of forest

management and successional age on bee communities of southeastern production forests is lacking.

In the context of increasing efforts to promote pollinator conservation, this knowledge gap is concerning. While recent research on the effects on bee communities of various forest conditions associated with pine forest restoration have significantly enhanced our understanding of bee communities relative to successional processes across the southeastern US (Bartholomew and Prowell 2006, Hanula et al. 2015, Breland et al. 2015), these studies do not examine these effects in the context of production forestry. However, they do provide an understanding of how the processes and forest conditions associated with the region's historical landscapes shape bee communities. Such knowledge is essential for effective habitat management, and as production forestry is one of the dominant land-uses of the region (Munn and Tilley 2001, Napton et al. 2010, Oswalt and Smith 2014), the ability to compare how bee communities respond to management and succession on these anthropogenic landscapes will greatly expand opportunities for bee conservation across the southeastern US.

Several studies in the temperate zone have found that increasing forest cover has a negative relationship with bee diversity and that decreasing floral richness and abundance likely drive this pattern (Campbell et al. 2007, Winfree et al. 2007a). Hanula et al. (2015) showed that the bee community of cleared forests and pine forests with a combined diverse herbaceous understory and the shrub understory removed were similar and were highest in numbers of bees and bee species out of their seven treatments.

Likewise, Grundel et al. (2010) observed a negative relationship between number of bees and forest cover while also showing that bee species richness relates positively to plant species richness and abundance of potential nesting resources. Nesting and floral resources have a significant effect on bee community composition (Potts et al. 2005, Murray et al. 2009, Torné-Noguera et al. 2014). In southeastern production forests, bee nesting resources and some important floral resources vary in abundance among patches of different age since clearcutting (Sudan and Santonastaso, unpublished data). Although the relationship between forest structure and bee community composition are clearly not straightforward, because of the relationship between bee nesting and floral resource abundance and successional age, bee community would also be expected to vary with successional age in these landscapes

The purpose of this study was to examine the relationship between bee communities and successional age in a production forest. To do this, I tested whether community composition, observed and estimated species richness, species abundance, and evenness varied in response to the age of the sampled patches. I also looked for species associated with different successional stages, as other studies have found bee species associated with forests or woodlands (Winfrey et al. 2007a, Breland 2015). Based on results from previous studies of successional communities and studies finding an influence of forest cover on bee diversity and abundance, I developed these research questions:

- Does bee community composition differ among patches of different successional ages?
- Does bee species richness and abundance decrease in late successional patches?

-Are certain bee species associated with different successional age classes?

Materials and Methods

Study sites

In 2012, 6 study sites were established on a managed pine plantation (Sotera, LLC) in Hancock County, MS. The plantation consists primarily of planted, single-species stands of loblolly, slash, and longleaf pine at varying stages of maturity. Also present on the plantation were naturally occurring mixed hardwood stands which were left as part of best management practices for wildlife. After harvesting by clear-cutting, sites on the Gulf Coastal Plain are sometimes burned but always include some combination of chopping, disking, bedding, subsoiling, and ripping to prepare the site for replanting (Fox et al. 2004, Loehle et al. 2009, Miller et al. 2009). This type of forest management results in a spatially heterogeneous set of well-defined patches with standardized management and extensive site histories.

Two sites were selected for each of 3 age classes, based on age since clear-cut harvest/planting: early succession (0-1 years), mid succession (3-5 years), and late succession (12-20 years), giving us a total of 6 sites. Early successional sites were characterized by newly planted pine saplings with mostly grasses/herbaceous vegetation and some shrubs, likely re-sprouting after clear-cutting and herbicide application during site prep. Mid successional sites were characterized by pines roughly 2-2.5 m in height with grasses more dominant over herbaceous understory and woody understory becoming more developed. Late successional sites were well-developed in terms of a mature

pine canopy as well as a midstory of immature hardwoods and woody understory. Grass and herbaceous vegetation in this age class were both visibly reduced. Sites were adjacent to roads on one side to facilitate access, between 23 and 58 hectares in size and at least 1 km from other sites. Two sites, one in the early successional class and one in the late successional class, were significantly altered by management practices (fire and logging) between sampling years and were replaced by new sites in 2013. The replacement sites were chosen based upon proximity and similarity of age to the 2012 sites.

Sampling protocol

Two 400 m transects were established at each site, at least 200m apart, for a total of 12 transects in the study. Bees were sampled using passive trapping methods for two consecutive years (2012 and 2013). Traps were left at the sites continuously throughout the sampling periods (April to July in 2012 and March to March in 2013-2014) and propylene glycol was used as a killing agent and to preserve specimens between collection events. Sampling periods differed between the two years due to a severe weather event (Hurricane Isaac) in the first year, and sampling protocols were modified for the second year in order to reduce the amount of time spent retrieving samples. In retrospect, consistency in trapping methodology is always preferable when possible, but the constraints imposed by inclement weather, time, and funding challenges made it impossible for us to accomplish this in practice.

In 2012, transects consisted of 5 sampling points, evenly spaced along the transect at 100 m intervals. At each point, 3 plastic cup traps (blue, yellow, and unpainted white) filled with propylene glycol were placed 0.5 m above the ground 5 m from each other. Two vane traps (blue and yellow) were placed on metal poles 1 m above the ground at the middle point (200 m along the transect) of each transect. Samples were collected from April to July, during the peak months of pollinator activity. Because of frequent summer showers and thunderstorms, samples from all sites were retrieved at roughly the same intervals (+/- 2 days), sometimes as short as < 2 weeks between April and July.

The same transects were used for 2013 sampling in the four sites that were sampled in both years. The 2013 sampling protocol was altered to reduce the likelihood of degradation of specimens by dilution of propylene glycol preservative by rainwater.

Three sampling points were established on each transect at 150 m intervals, and used only blue and yellow vane traps instead of three plastic cups. Vane traps were modified with clear plastic hoods to prevent them from filling with rainwater, which also reduced the total number of field visits required to collect samples. With the addition of the plastic hoods, trap effectiveness was not expected to decrease from traps filling with water, and so samples were collected only 2 or 3 times between March, 2013 and March 2014. Sampled bees were washed, dried, and identified to species.

Data and statistical analysis

All analyses were conducted in R (R Core Team 2015). After pooling sampled bees by transect, I then used non-metric multidimensional scaling (NMDS) to determine if

communities from transects of the same Age Classes (early successional, mid successional, late successional) were similar. Following NMDS, I examined the relative frequencies of bee tribes and the influence of Age (years since clear-cut harvest/planting) on five elements of the bee community (community composition, species abundance, observed species richness, estimated species richness, and evenness). I used log transformed Site Age as a continuous variable in all analyses instead of Age Class.

Because sites and sampling protocol between years were not identical, I iteratively examined the effect of Study Year in our community composition models by: 1) treating each year separately, 2) combining years and including Study Year and an interaction effect, 3) and combining years and including Study Year but no interaction effect. While the only published data comparing our two trapping methods (pan and vane traps) on measuring bee diversity indicate that pan traps sample a greater number of species with only 20% overlap between their two treatment groups, functional ecological traits like sociality, floral specialization, body size, and nesting habit fail to explain the differences in species associated between trap types (Ptasznik 2015). This researcher also suggests the use of both pan and vane traps (per our 2012 sampling protocol) in order to best represent the species pool of an area. To further assess the potential influence of Study Year on our results, I compared communities between years using two probabilistic similarity indices (adjusted abundance-based Jaccard and Sorensen) available in the R package SpadeR (Chao et al. 2015). Because they are probabilistic, they are more easily interpreted than some traditional indices, which require a contrasting value for comparison (e.g. Bray-Curtis). Finally, the SpadeR package was also used to produce pair-wise comparisons of species

similarity between Age Classes to assist in interpreting results from community composition analyses.

The specific analytical approaches to measuring variation in community composition are as follows. A permutational MANOVA (Anderson 2001) was used to examine the differences in community composition among Age Classes using $\log(\text{Age})$ as the independent variable. Permutational MANOVA was run using the `adonis` function in R package `vegan` (Oksanen et al. 2015). `adonis` calculates coefficients of each predictor variable for each species. The absolute value of a coefficient for any given species indicates the relative influence of that variable on the abundance of the species. To examine the relationship of abundance and observed species richness to Age I used a Poisson generalized linear mixed model with $\log(\text{Age})$ and Study Year as fixed factors and Site as a random factor, and an observation-specific random effect to account for over-dispersion. To inform selection of the appropriate species richness estimators, I examined the relative proportions of rare species using rank abundance. Linear mixed models with $\log(\text{Age})$ and Study Year as fixed factors and Site as a random factor were then used to measure the effect of Age on estimated species richness (Chao estimator 1, ACE estimator; both log transformed), and species evenness (Pielou's index). I used weighted models for estimated species richness to account for the effects of any large confidence intervals for the estimators. To examine the potential for differing responses to Site Age based on nesting guild, I also re-ran the above analyses (excluding ordination with NMDS) for above ground and below ground nesters. Species accumulation curves were generated using `rrarefy` in the R package `vegan` (Oksanen et al. 2015) set at 200 replications.

To identify bee species associated with Age Classes, I used the `multipatt` function in the R package `indicspecies` (De Cáceres and Legendre 2015). The `multipatt` function examines the associations between species and combinations of groups of sites using several association indices, in this case the *point biserial correlation coefficient* (PBCC); the abundance-based counterpart to Pearson's *phi coefficient of association* (De Cáceres and Legendre 2015).

Results

The total number of bees sampled was 4305 with 94 species recorded (Appendix C).

Results of community analyses are divided into two sections: *ordination and community composition*.

Ordination

Ordination using non-metric multidimensional scaling (NMDS) showed a clear difference between late successional and the younger successional stages, early successional and mid successional (Figure 2), along the first NMDS axis. Between the early successional and mid successional groups, there appeared to be no distinct difference based on the results of the ordination. Ordination results also indicate similarities within Study Year.

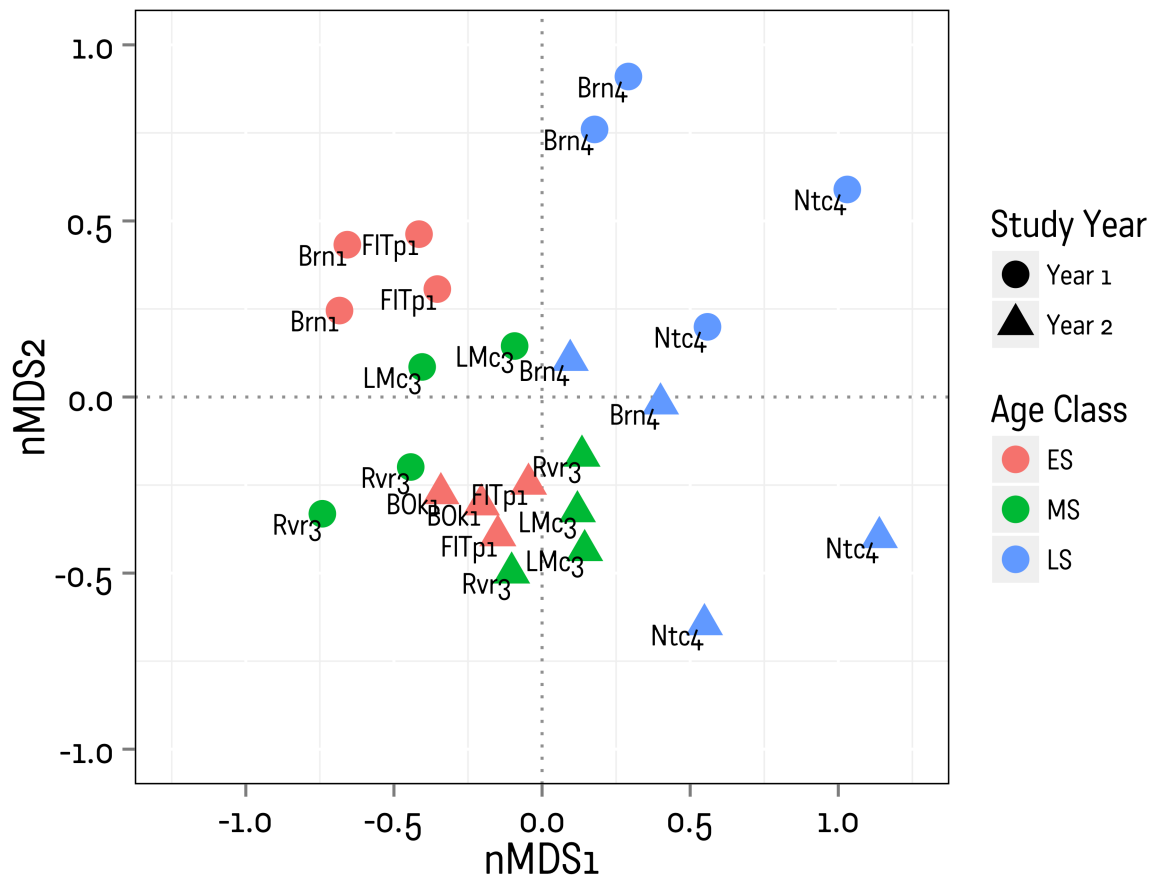


Figure 2-Results of ordination using non-metric multidimensional scaling (NMDS). The stress of the NMDS rotation in two dimensions is (0.185).

Community composition

Results of permutational multivariate analysis of variance showed a significant relationship between Community Composition and both Age and Study Year (Table 1) but only a marginally significant interaction effect (Appendix A). The influence of Study Year was likely due to the slightly different sampling methodologies used between years (Ptasznik 2015).

	DF	Sum of Squares	Mean Squares	F	R²	P-value (F)
log(Age)	1	1.445	1.445	8.147	0.253	0.001*
Study Year	1	0.539	0.539	3.038	0.094	0.008*
Residuals	21	3.724	0.177		0.652	
Total	23	5.708			1	

Table 1-Results of permutational MANOVA using adonis. Formula = Species matrix ~ Age + Study Year. P-values are from a randomization test with 999 permutations.

Figures 3 & 4 show subsamples of 10 species at the lower and upper bounds, respectively, of the `adonis` coefficient for Age.

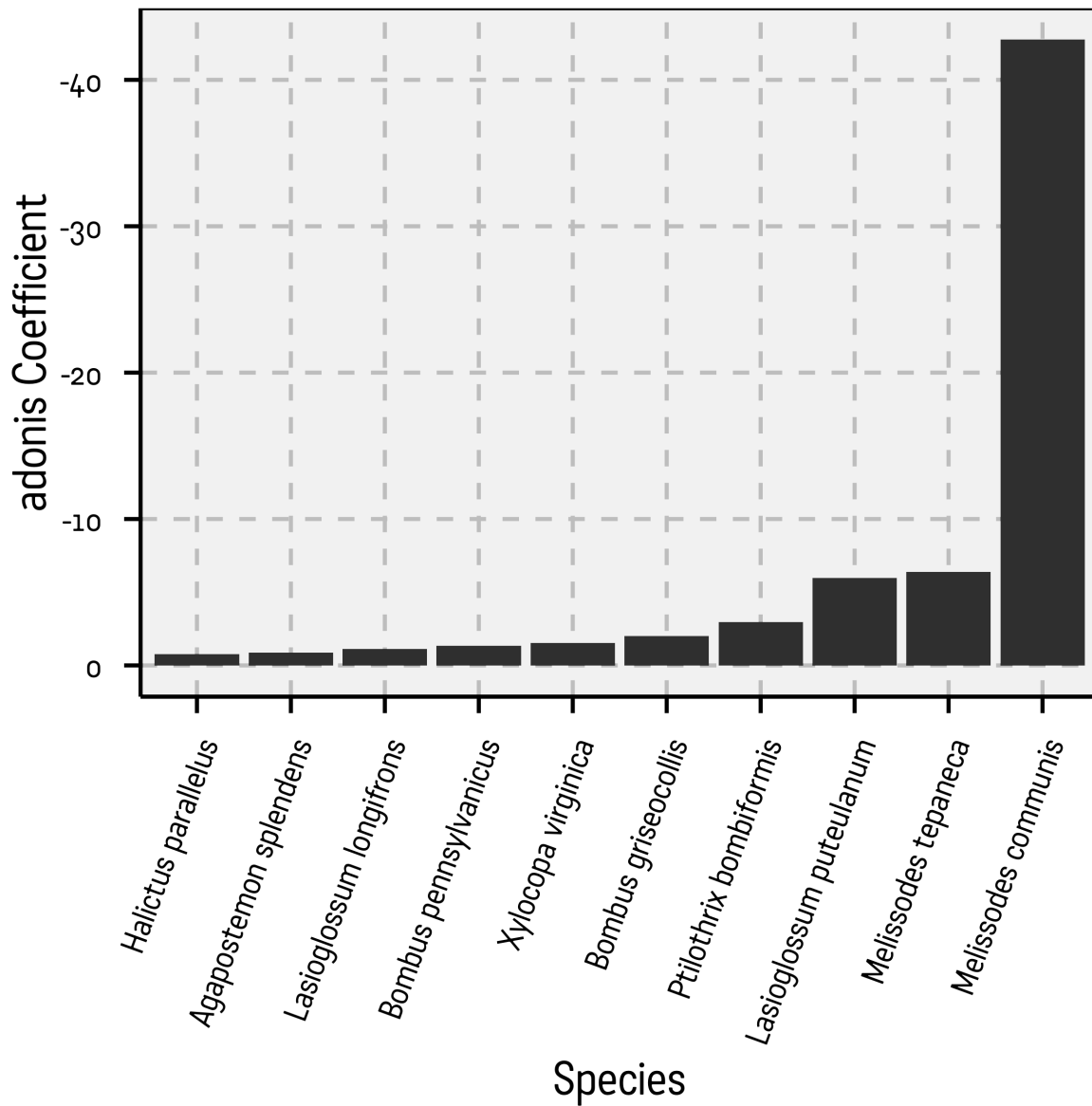


Figure 3) Ten species from the permutational MANOVA with lowest adonis Age coefficient. The negative value of this coefficient for any given species indicates the relative negative influence of Age on the abundance of that species.

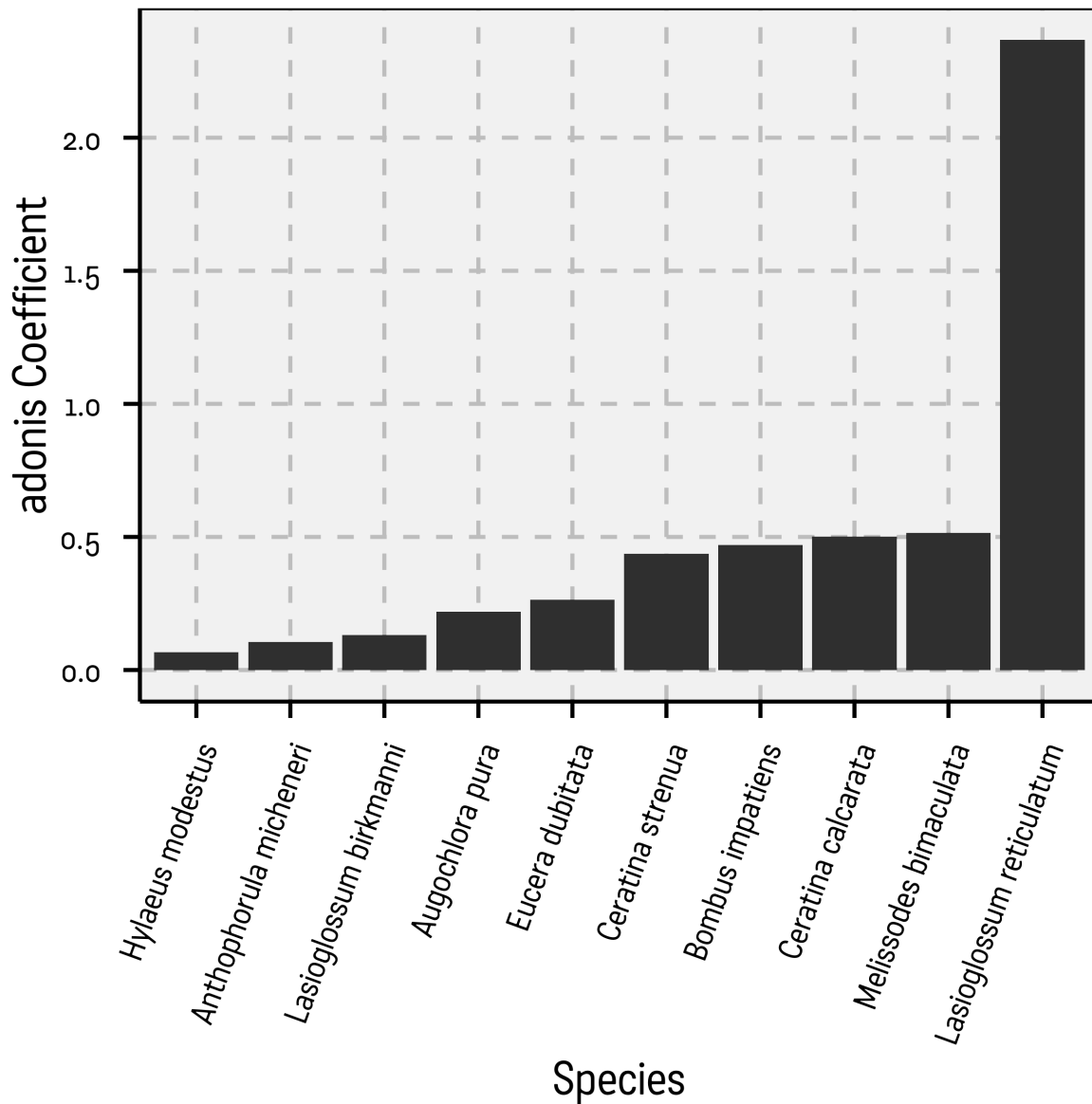


Figure 4) Ten species from the permutational MANOVA with highest adonis Age coefficient. The positive value of this coefficient for any given species indicates the relative positive influence of Age on the abundance of that species.

Results of the `multipatt` analysis (Table 2) show the 11 species significantly associated with an Age Class or a combination of Age Classes.

Age Class	Species	PBCC	p-value
ES	<i>Melissodes communis</i>	0.724	0.002
	<i>Lasioglossum longifrons</i>	0.603	0.004
	<i>Melissodes tepaneca</i>	0.578	0.014
	<i>Lasioglossum apopkense</i>	0.573	0.003
	<i>Agapostemon splendens</i>	0.561	0.019
	<i>Peponapis pruinosa</i>	0.516	0.014
MS	<i>Hoplitis pilosifrons</i>	0.714	0.004
	<i>Ptilothrix bombiformis</i>	0.663	0.001
LS	<i>Lasioglossum reticulatum</i>	0.62	0.002
ES & MS	<i>Bombus griseocolis</i>	0.568	0.009
	<i>Bombus pennsylvanicus</i>	0.465	0.046

Table 2) Results from the multipatt analysis, showing only the significantly associated species. See Appendix * for complete tables with PBCC's (point biserial correlation coefficients) for all species and both years.

Figure 5 shows the relative frequencies of abundant bee tribes from each Age Class (See Appendix B for relative frequency of all tribes).

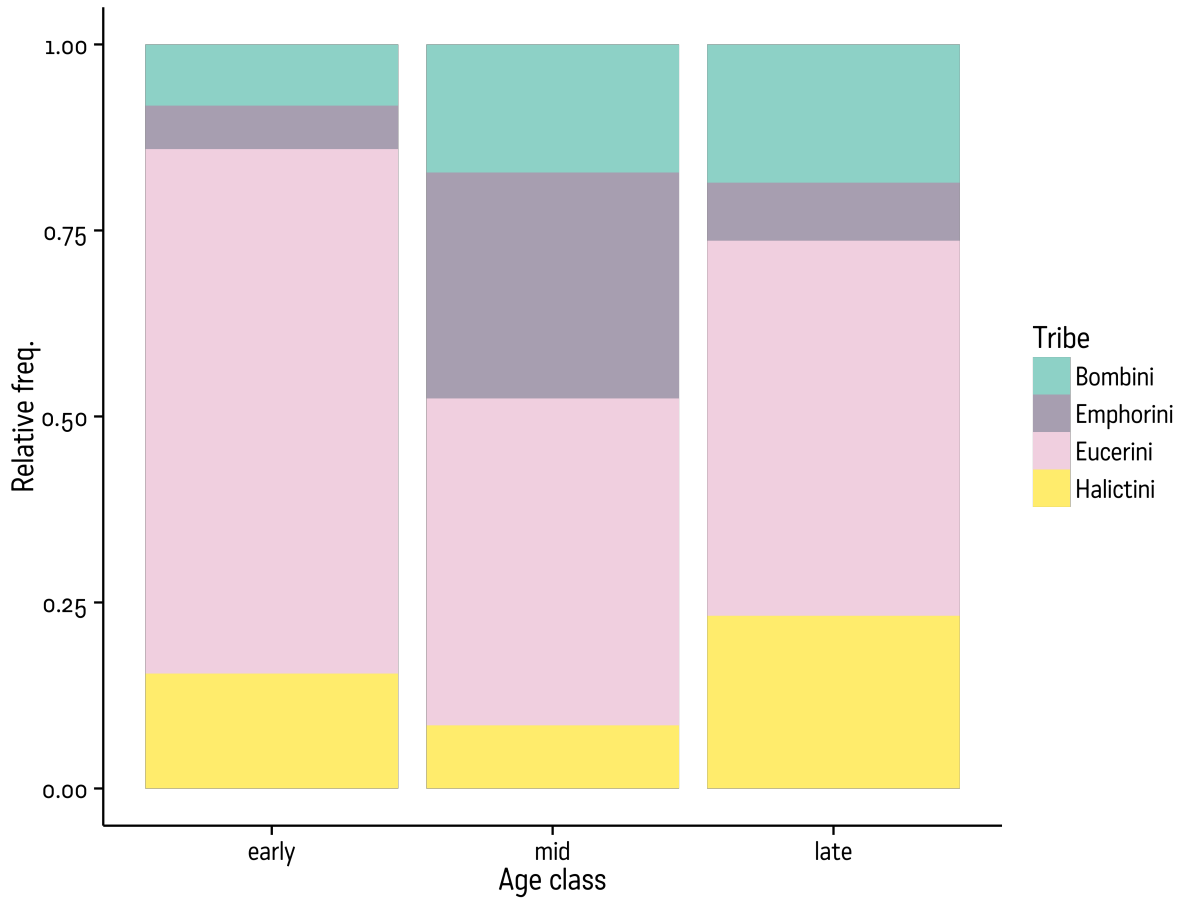


Figure 5) The relative frequencies of abundant bee tribes from each Age Class.

Figure 6 shows the relative frequencies of rare bee tribes from each Age Class.

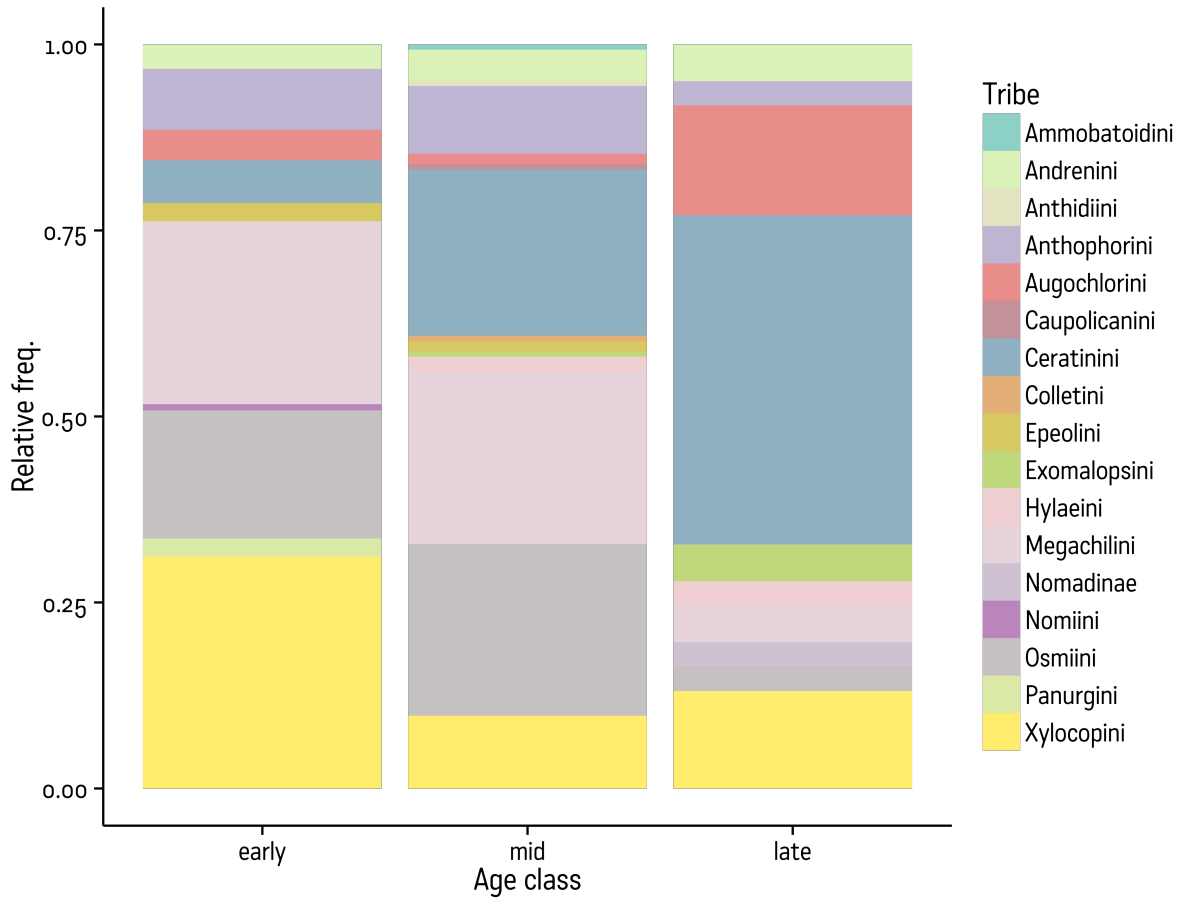


Figure 6) The relative frequencies of rare bee tribes from each Age Class.

For abundance, the interaction between Age and Study Year was non-significant (estimate = 0.08 +/- 0.17, Z = 0.49, P = 0.63) and the interaction was removed from the final model.

As shown in Figure 7, there was a significant decrease in abundance associated with the Age of the transect (estimate = -0.54 +/- 0.14, Z = -3.86, P = < 0.001) but there was no significant difference between Study Years (estimate = 0.29 +/- 0.22, Z = 1.36, P = 0.18).

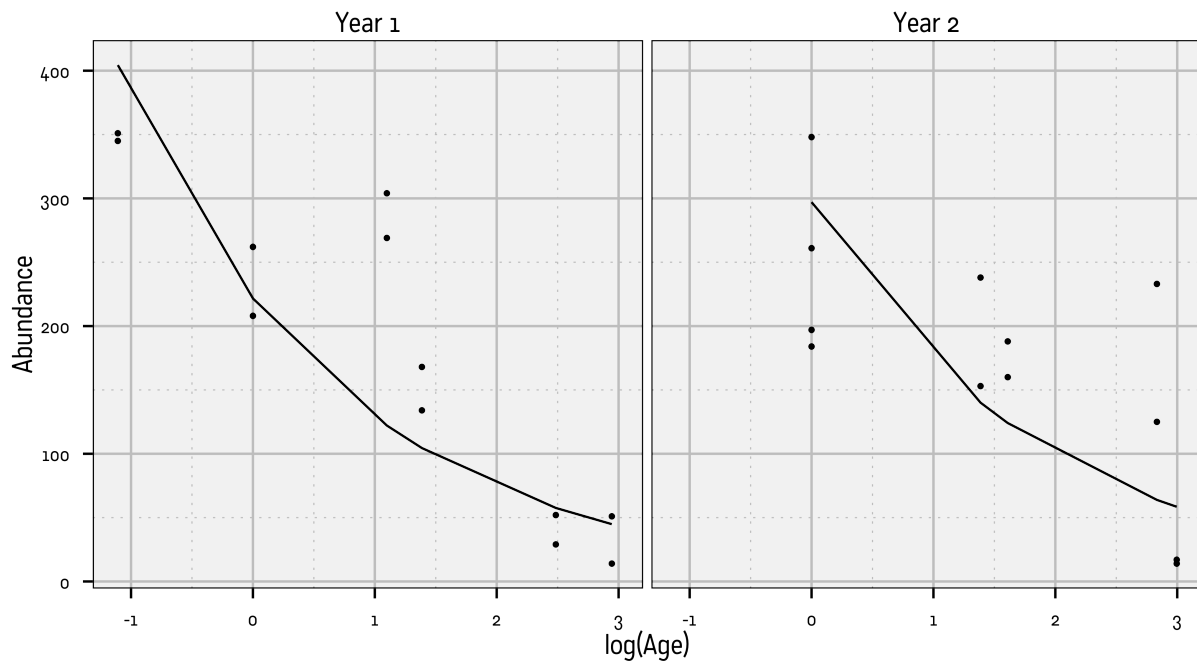


Figure 7) Effect of Age on abundance, shown for both Study Years.

Observed Species Richness in the Year 1 model was significantly influenced by Age (estimate = -0.24 ± 0.08 , $Z = -3.02$, $P = 0.003$), but the effect was absent in the Year 2 model (estimate = -0.12 ± 0.08 , $Z = -1.44$, $P = 0.15$) (all models in Appendix G). In the model that included both years, there was no significant interaction between Age and Study Year (estimate = 0.10 ± 0.08 , $Z = 1.26$, $P = 0.20$), but the effect of Age was significant in this model and the model with both years and no interaction (estimate = -0.19 ± 0.07 , $Z = -2.69$, $P = 0.007$) (Figure 8).

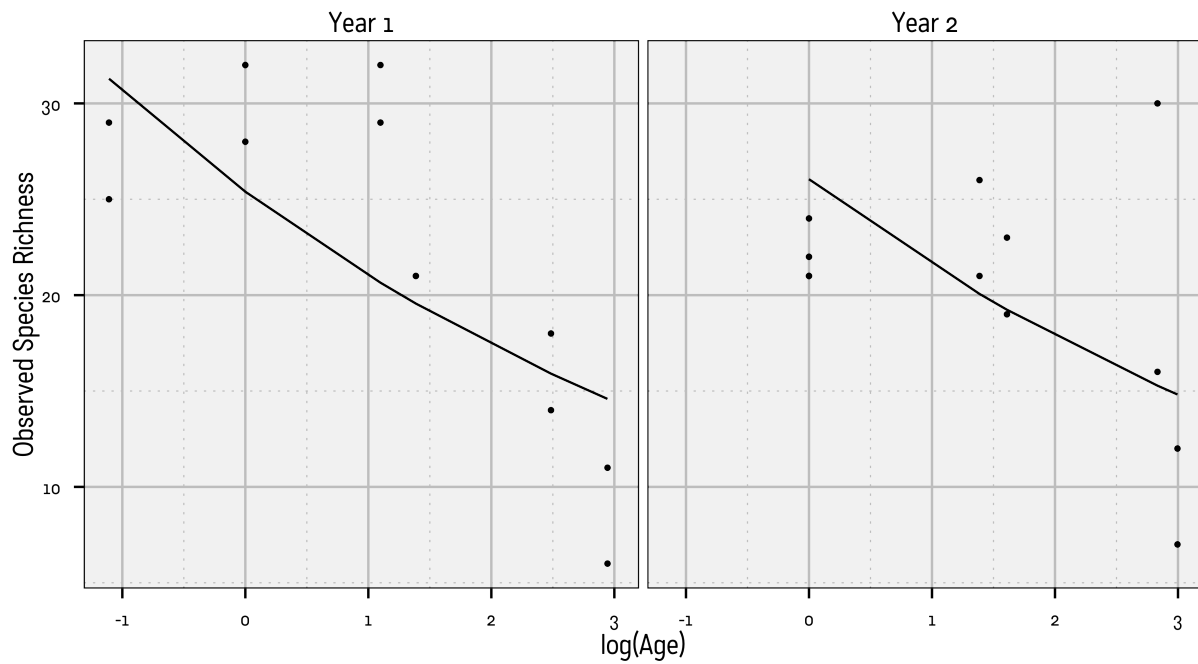


Figure 8) Effect of Age on Observed Species Richness, shown for both Study Years.

For all combinations of models, there was no significant effect of Age or Study Year on either estimator of Species Richness (ACE and Chao 1) (Figure 9), and for the ACE model that included both years without an interaction effect, there was only a marginally significant difference between Study Years (estimate = -0.24 ± 0.13 , $Z = -1.79$, $P = 0.09$).

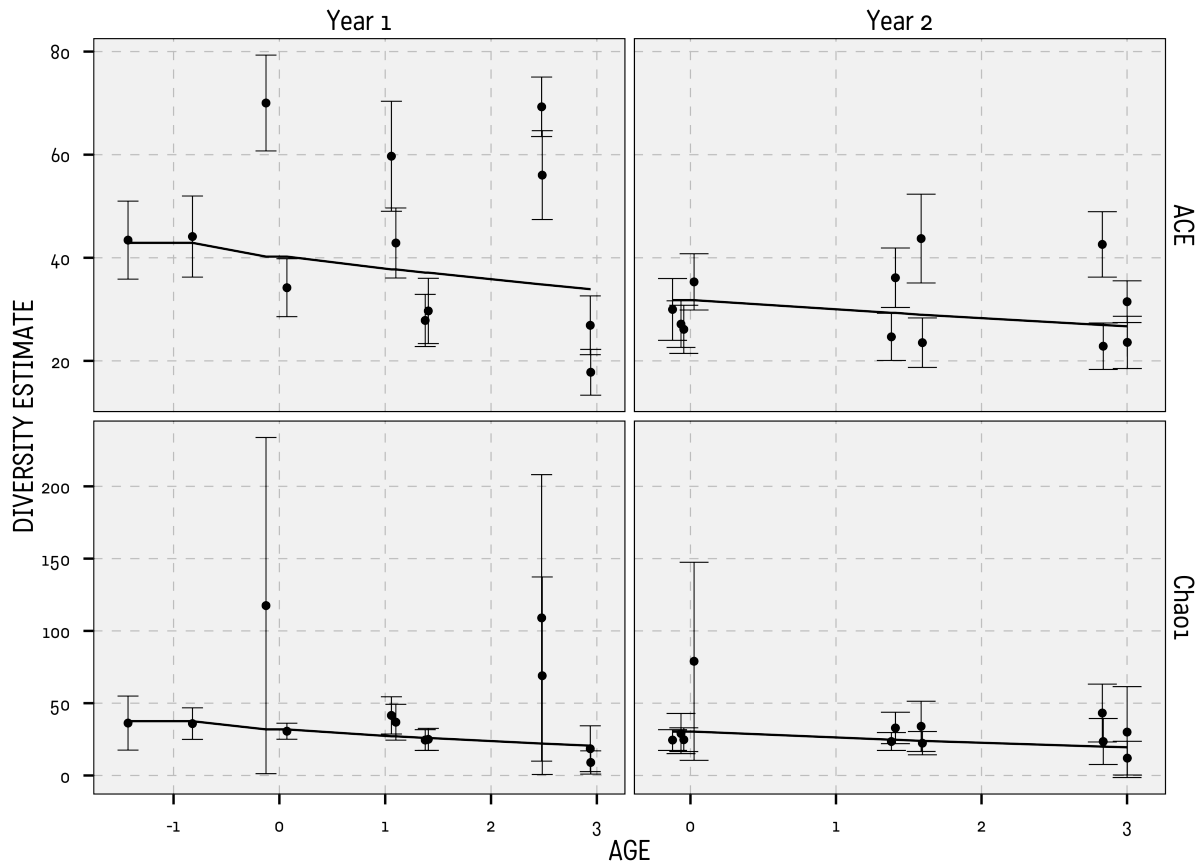


Figure 9) Non-significant effect of Age on Estimated Species Richness (Chao 1 and ACE estimators) for both Study Years.

For Year 1, evenness (Pielou's) showed only a marginally significant increase with Age (estimate = 0.05 +/- 0.02, Z = 2.25, P = 0.09) while Year 2 showed a significant increase (estimate = 0.09 +/- 0.03, Z = 3.32, P = 0.03) (all models in Appendix J). A marginally significant effect for Age (estimate = 0.04 +/- 0.02, Z = 1.96, P = 0.08) as well as for the interaction (estimate = 0.05 +/- 0.03, Z = 1.9, P = 0.07) between Age and Study Year was seen for both years. Removal of the interaction effect resulted in a model with a significant effect of Age (estimate = 0.06 +/- 0.08, Z = 3.5, P = 0.03) and no significant difference between Study Years (estimate = 0.01 +/- 0.03, Z = 0.18, P = 0.9) (Figure 10).

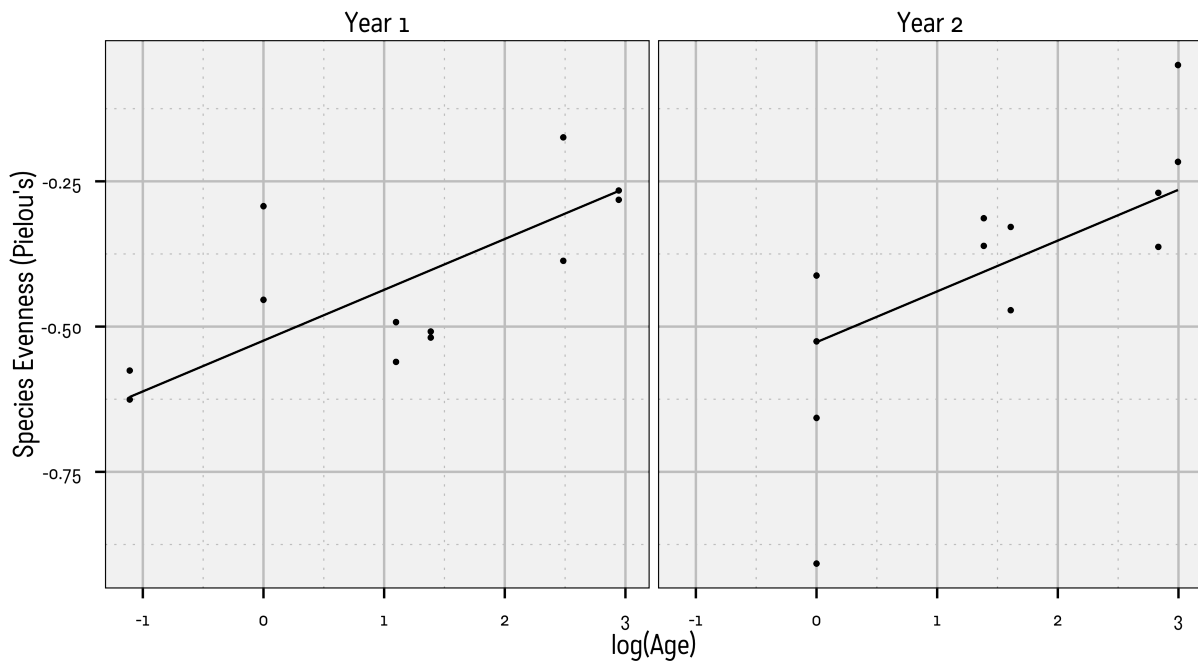


Figure 10) Significant effect of Age on Species Evenness (Peilou's index).

Results from above ground nesting and below ground nesting guilds showed similar patterns to the bee community overall, with the exception of observed species richness (Appendix G) and evenness (Appendix K). In contrast to the overall community, observed species richness for above ground nesting bees showed no significant effect of Age (estimate = -0.09 ± 0.09 , $Z = -1.07$, $P = 0.28$). For the below ground nesting guild, evenness showed no significant effect of Age (estimate = 0.06 ± 0.05 , $Z = 0.97$, $P = 0.36$), however, Study Year (estimate = -0.32 ± 0.12 , $Z = -2.36$, $P = 0.03$) and its interaction with Age (estimate = 0.14 ± 0.07 , $Z = 2.94$, $P = 0.009$) were significant.

Figure 11 shows adjusted abundance-based Jaccard and Sorensen indices of community similarity (Chao et al. 2005) between Study Years. Figure 12 shows several other indices of species overlap (among more than two groups (Chao et al. 2008)) across all Age Classes.

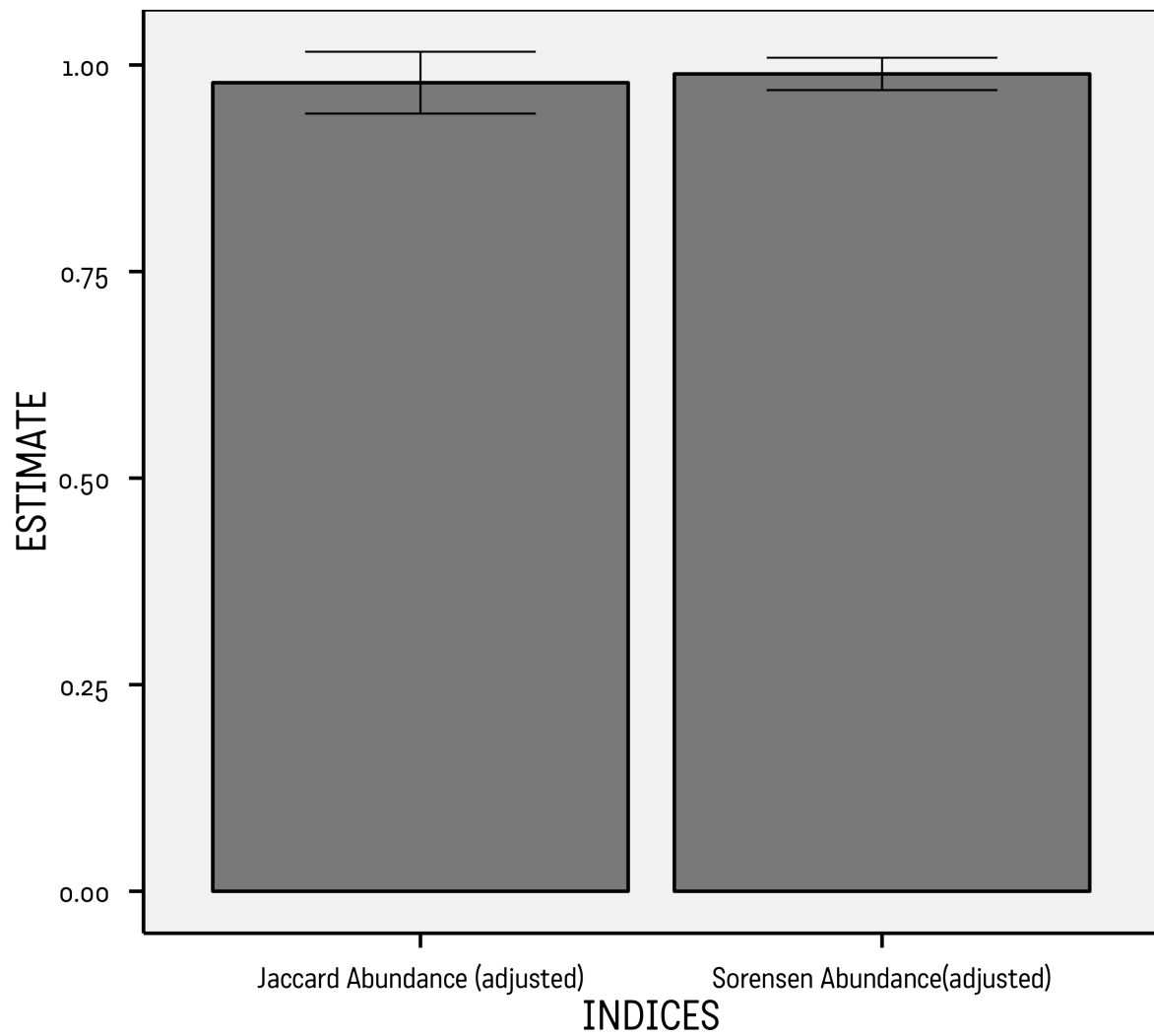


Figure 11) Adjusted abundance-based Jaccard and Sorensen indices of species similarity (Chao et al. 2005, Chao et al. 2006)

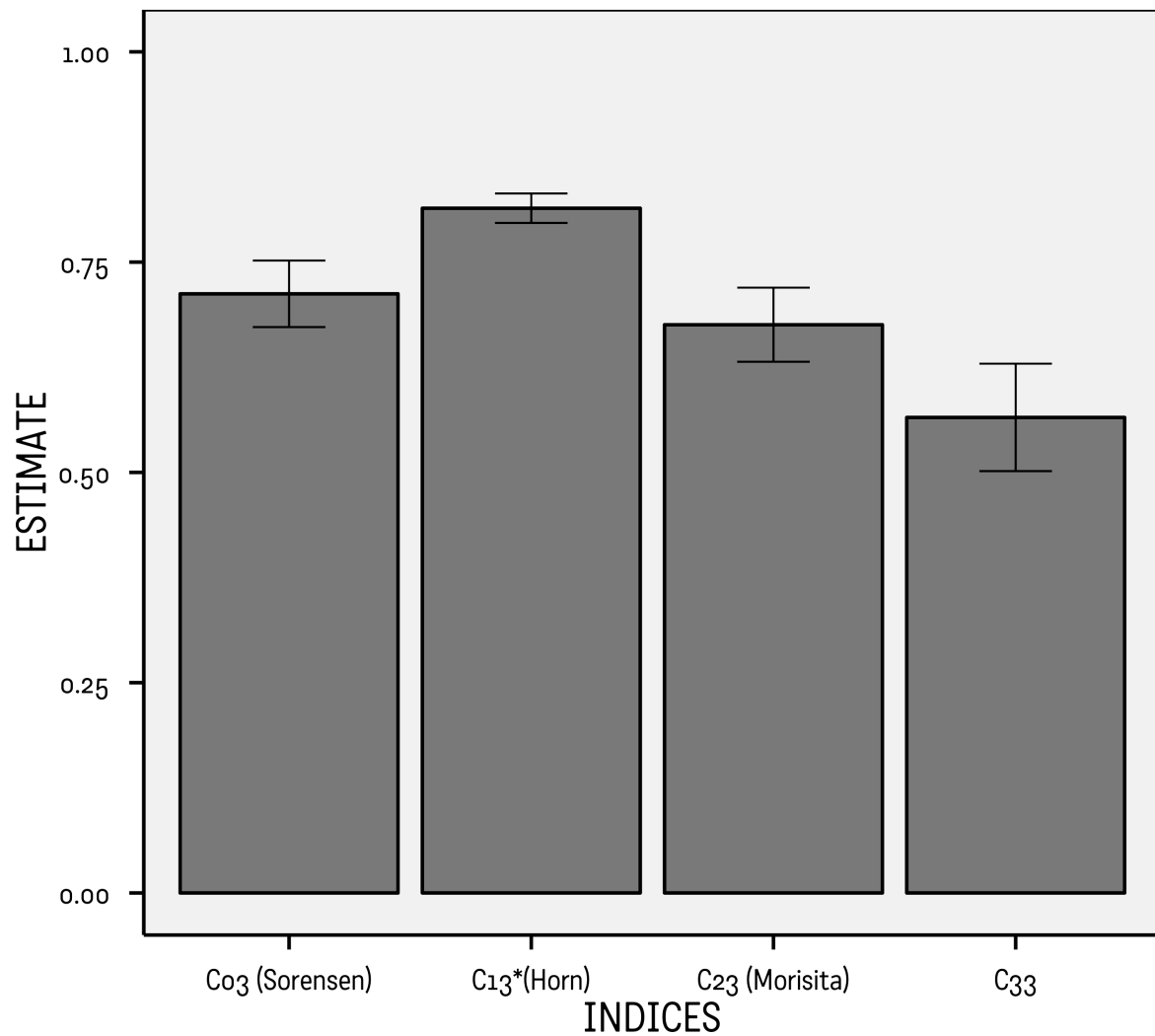


Figure 12) Comparisons of similarity indices (based on Chao et al. 2008) for all Age Classes.

Discussion

According to our contemporary understanding of the relationship between bee communities and temperate forest succession, open, early successional habitat should contain higher species diversity and abundance than older, forested habitat. To our knowledge, only one study has measured this relationship explicitly (see Taki et al. 2013). Our results and those of two recent studies (Campbell et al. 2007 and Hanula et al.

2015) suggest that this understanding is too generalized, particularly when applied to southeastern pine forests, for which ongoing management (i.e. disturbance) both clearly impacts bee community composition (Breland et al. 2015) and is critical in achieving production and conservation objectives (Hartley 2002, Fischer et al. 2006, Lindenmayer et al. 2006, Mitchell et al. 2006).

We show, in accordance with contemporary thinking and therefore somewhat unsurprisingly, that bee community composition, generally, differs among patches of different successional ages. However, our observed and estimated species richness results, which appear to contradict one another at face value, provoke different conclusions specifically about the bee species diversity supported by stands of different ages (Figures 8 and 9, respectively). This has an obvious influence on how the differences I observed in the permutational MANOVA results (Table 1) are to be interpreted. If taken alone, the observed species richness results would suggest that species richness declines significantly as a stand ages. In such a scenario, it could not be excluded from possibly influencing the patterns observed in the permutational MANOVA results. However, observed species richness is highly dependent upon abundance (the number of captured individuals): as more individuals are sampled, observed species richness increases in a non-linear fashion. Since I observed a non-trivial decrease in abundance with increasing stand age (Figure 7), the decrease in observed species richness clearly appears to be an artifact of sampling effort. For this reason, estimated species richness (Chao 1 and ACE estimators; Figure 9) provides a more accurate and meaningful measure of diversity, and I conclude that the species richness of the bee community does not change substantially with Stand Age.

These results contrast with other studies of successional bee communities in that estimated species richness does not decline significantly as the patch moves from recently disturbed (early successional) to forested (late successional). Instead, the only elements influenced by Age were observed species richness (negative), species evenness (positive), and abundance (negative). With respect to abundance, it also appears that a handful of species with high abundances in the early successional stage (Appendix F), a negative association with later successional stages (Figure 3), and a positive association with early and mid successional sites (Table 2) are disproportionately influencing the permutational MANOVA results (Table 1). By excluding these species and others with high abundance across Age Classes, I found that the abundance of the remaining bee community did not decrease significantly with Age (Appendix D; note: the intercepts between years differs significantly), whereas the excluded subset of bee species mirrors the pattern of a significant decrease with Age (Appendix D) seen for the community as a whole (Appendix D and Figure 7). In light of the lack of a significant decline in species richness from early successional to late successional (Figure 9), the observed significant increase in evenness (Figure 10) serves to support this claim. However, indices of species overlap (Figure 12) and pairwise comparisons of species similarity among Age Classes (Figure 13) suggest that there may be some influence of species turnover across Age Classes as well.

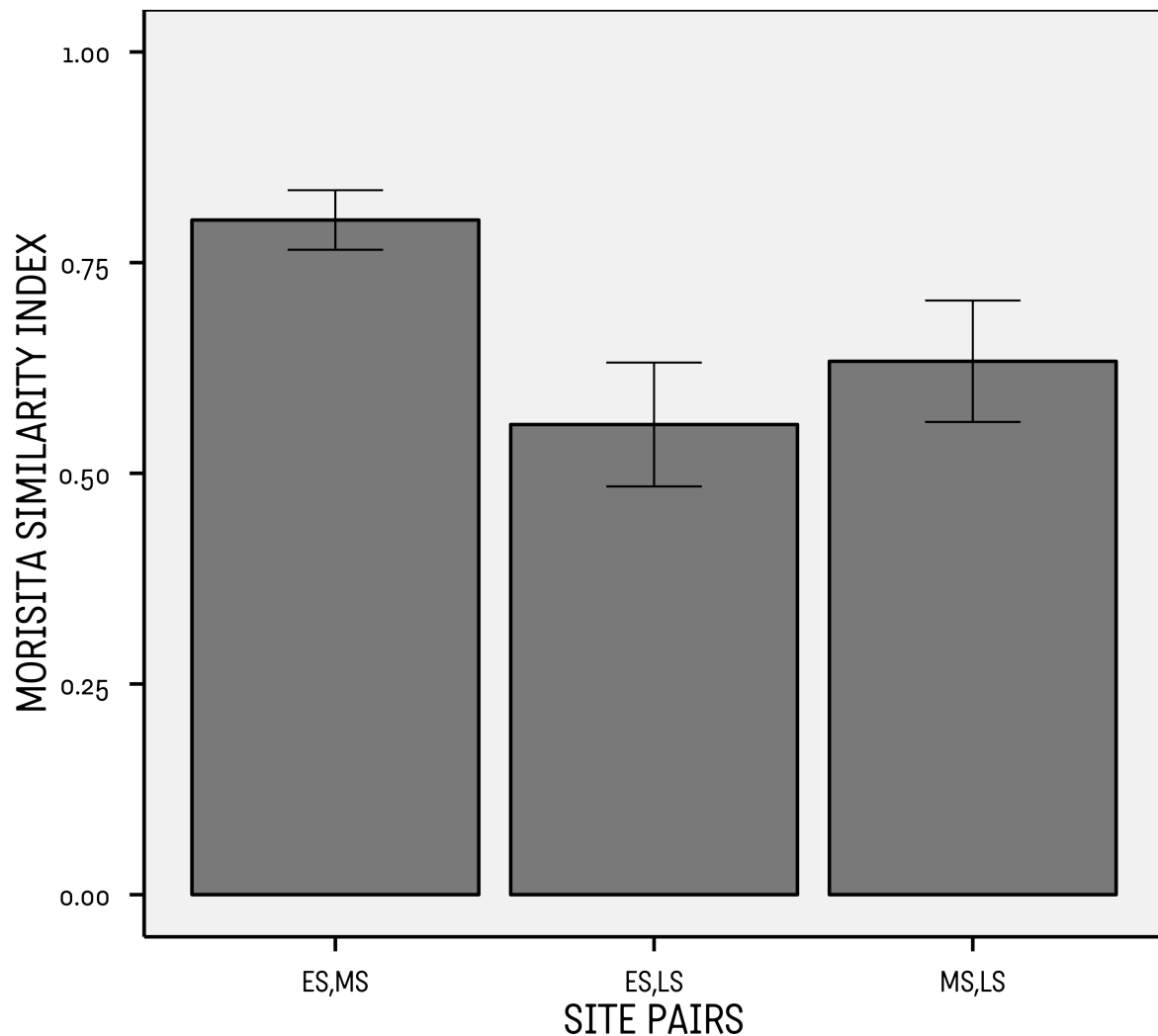


Figure 13) Pairwise comparisons of species similarity between Age Classes using Morisita index (Chao et al. 2008).

The clearest representation of species preferences for particular Age Classes comes from the results of the `multipatt` analysis (Table 2 and Appendix C). Six of the eleven species found to be significantly associated with a particular Age Class belonged to the group of abundant species mentioned above. In contrast, the only species associated with the late successional stage was *Lasioglossum reticulatum*. This species also had the highest `adonis` coefficient for Age; it shows the highest relative increase in abundance with Age of all

species sampled. As this species is not an oligolege, it is unclear what is driving this particular pattern since most members of the subgenus *Dialictus* are ground nesting and not reliant upon woody material for nesting that might be more abundant in late successional sites. In contrast, *Hoplitis pilosifrons*, which excavates nests in pithy stems, was significantly associated with mid successional sites. This is notable given that *Rubus* spp. (a pithy-stemmed group) are significantly more common on this Age Class than on others measured in this study (Sudan and Santonastaso, unpublished data). Other notable results from this analysis indeed show two diet specialists associated with certain Age Classes. *Peponapis pruinosa*, a cucurbit specialist, was associated with early successional sites while the hibiscus specialist, *Ptilothrix bombiformis* was associated with mid successional sites. Data on the distribution of these floral resources across Age Classes in this landscape would help to confirm the reason for this association, but it seems clear that reliance on host plants associated with early and mid successional sites, respectively, plays some role.

A somewhat more problematic result of the permutational MANOVA is the significant difference in community composition observed between Study Years. While this suggests the possibility that the different sampling protocols used between Study Years could be affecting these results, a significant effect of either Study Year or its interaction with Age was absent from all models examining abundance, observed species richness, estimated species richness, and species evenness, with the exception of evenness in below-ground nesting bees (Appendix K). Indeed, Ptasznik (2015) found significant differences in both the number of bees captured and species captured in a comparison of the two trap types

used in our study. However, it is worthwhile to note that there was overlap in trap types used between Study Years; 2012 included a blue and a yellow vane trap at each transect (a third the number used in 2013), in addition to 15 pan traps. It seems possible that the combined effects of all parameters considered in the permutational MANOVA contributed to the significant differences between Study Years. Importantly, though, the other models mentioned above are not only more straightforward in terms of their interpretation, they universally fail to support the idea that Study Year contributed significantly to the overall patterns observed in this study. Finally, even with the concession that trapping rates might differ for different species, a comparison of 2012 and 2013 species assemblages using the adjusted abundance-based Jaccard and Sorensen similarity indices (Chao et al. 2005, Chao et al. 2006) (Figure 11) suggests these communities are overwhelmingly similar in their species composition between years.

Our investigation of abundance and species richness patterns of above and below-ground nesting bee guilds showed few patterns which differed from the community as a whole. For above-ground nesting bees (none of which were particularly abundant; all species in Appendix F are below ground nesting with the exception of *Bombus pennsylvanicus* which also nests below ground), it revealed only that observed species richness did not significantly decline with Age (Appendix G). For below-ground nesting bees, species evenness differed between Study Years and the degree to which it differed seems to have been influenced by Age (Appendix K).

While our findings strongly compliment those of Hanula et al 2015, I show a more generalized relationship of the bee community to stand age in short rotation production forests. In addition, Hanula et al. 2015 measured several environmental variables in seven treatment groups differing in management regimes, age, and structure on sites whose management was governed by a variety of objectives. Our simpler design was dictated by the consistency of management and simpler objectives associated with many production forests. Because these forests are heavily managed for timber productivity and they mature in predictable ways, our variable, Age, provided us with a reliable proxy for several environmental variables, such as canopy openness, woody mid and understory density, and floral abundance, that are known to be influenced by our process of interest for this landscape; succession as it relates to production forestry (Grano et al. 1970, Fox et al. 2004, Mitchell et al. 2006). However, it is likely I would have found similar relationships between the bee community and stand age on our sites had management included longer rotation ages and disturbances associated with thinning and prescribed burning that were used to create some of the forest conditions explored by Hanula et al. (2015).

Despite the differences between our results and those of Hanula et al. (2015), what they do share suggests that certain aspects of forest response to frequent disturbance (clearcutting, thinning, and burning) and forest successional processes in the southeastern US (both human-mediated and “natural”) might serve as mechanistic drivers of bee communities in predictable ways. I think this is particularly germane to conservation when viewed opposite the widespread and oversimplified belief that most bees prefer open habitats to forest (Michener 2000, Winfree et al. 2011, Taki et al. 2013). While our results, as well as

those of Campbell et al. (2007) and Hanula et al. (2015), show that open, early successional sites indeed support high levels of bee abundance and species richness, they also show that forests themselves, and particularly those which are managed (i.e. disturbed) to maintain an open structure (*sensu* Hanula et al. 2015), are not necessarily less species-rich than open sites. Instead, they show a relationship to certain forest structural characteristics related to forestry management-mediated disturbances.

Drawing from our findings and others' results (Campbell et al. 2007, Hanula et al. 2015, and Breland et al. 2015), I propose a generalized framework for understanding the relationships among forestry management activities (human-mediated disturbance), succession, forest structure, and elements of bee communities in southern pine forests. As shown in Figure 1, management activities, which occur throughout the life of a forest, impact the structure of the forest as it matures (Grano 1970, Landers et al. 1995, Carroll et al. 2002, Fox et al. 2004, Mitchell et al. 2006, and Miller et al. 2009). These structural changes in turn result in the composition of bee communities that have been observed in southern pine forests and represented in Figure 14 (Campbell et al. 2007, Hanula and Horn 2007, Breland et al. 2015, Hanula et al. 2015, and our results). Left unmanaged, these stands quickly develop a woody understory and midstory and lose the herbaceous diversity characteristic of recently cleared sites (Figure 1). This unmanaged state is not ideal for forests managed for either production or conservation (Wagner et al. 2004, Wagner 2005, Mitchell et al. 2006). The objectives of production and conservation are often overlapping, with production forests being managed for wildlife habitat and leased to recreational hunters as a supplemental source of income for landowners (Loehle et al.

2009). Similarly, forests managed by government agencies under multiple use objectives can also produce income from the sale of timber and recreational opportunities. Despite differing management objectives, what southern pine forests share in terms of forest structure and response to management activities likely drove the patterns observed in our study and those of others (e.g. Campbell et al. 2007, Breland et al. 2015, and Hanula et al. 2015).

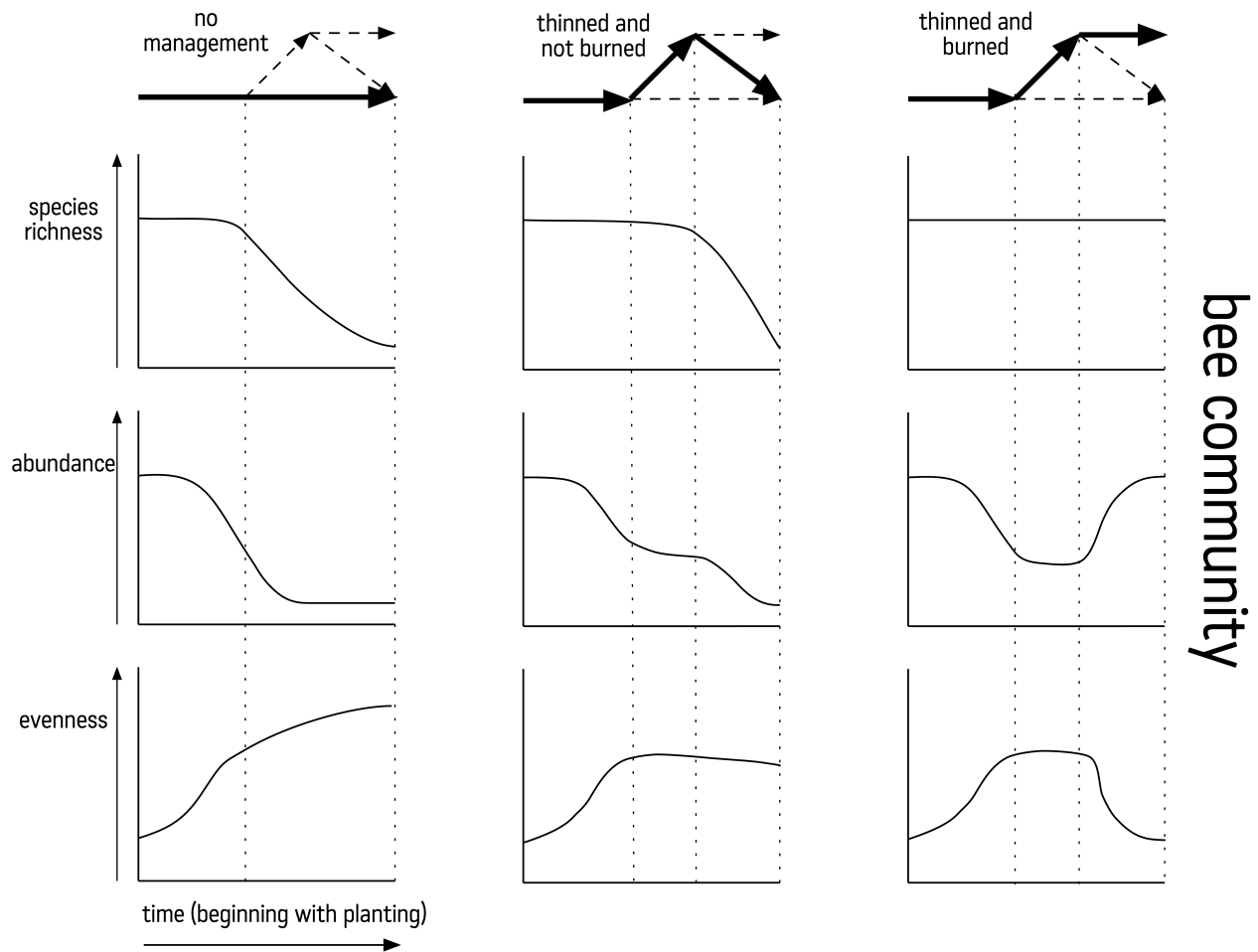


Figure 14) Framework for understanding the influence of various management activities on elements of southeastern pine forest bee communities (Campbell et al. 2007, Breland et al. 2015, Hanula et al. 2015, and our results). The small diagrams on the top represent specific successional trajectories with dashed lines (representing potential trajectories not taken) extending at points where management activities take place.

Conclusions

Much of the recent research on bee communities has focused on agricultural landscapes (see introduction), and this is not surprising because of the important role of wild bees as pollinators of crops (Winfree et al. 2008, Garibaldi et al. 2013). In contrast, the southeastern US has been historically underrepresented in bee surveys (see Colla et al.

2012) and a search of the literature reveals few studies of bee community ecology (but see Bartholomew and Prowell 2006, Breland et al. 2015, Hanula et al. 2015). It is unclear whether this is due to the proportionately depauperate regional species pool, lower percentage of agricultural crops dependent upon pollinators in the region, the perception that extensive forest cover must equate to poor bee habitat, a lack of experts familiar with bee identification, or a combination of the above. What is certain, however, is that the resultant lack of information means that land managers wanting to manage for robust and diverse communities of bees have few resources. More significantly, because of the lack of baseline data, BMPs for bee habitat management in southeastern forests were not developed from extensive studies in these systems and need to be modified with new information as it becomes available.

The ubiquity of pine forests across the southeastern US and the importance of the forestry industry to the economies of southern states suggest that forests could play a critical role in conservation of important pollinators like bees. While our results and a handful of other studies shed some light on the community ecology of bees of southern forests, much remains to be learned. I believe this proposed framework (Figures 1 and 14, combined) will not only provide land managers the tools to make informed decisions for promoting healthy and robust bee communities, but will also serve as a guide for future research. Beyond the specific regional application for management, this framework also explicitly illustrates relationships between forest structure and bee communities, which may be more widely applicable for managed forests of subtropical and temperate zones around the globe. While I recommend caution when attempting to generalize our empirical

results across climates and regions, the framework serves as a blueprint for comparing observed trends from these different places in search of commonalities and potential shared drivers of bee communities in forests.

Despite lacking an explicit spatial component to our work, it has a direct relevance to applied landscape ecology and bee conservation. A simplified characterization of bee habitat suitability for various broadly defined land cover types (e.g. forest, grassland, agricultural, etc.) makes for easily applied tools for conservation (see Lonsdorf et al. 2009). However, I add to a growing body of evidence (e.g. Zurbuchen et al. 2010a, Zurbuchen et al. 2010b, Torné-Noguera et al.) supporting the notion that such characterizations of operational scale (*sensu* Dungan et al. 2002, Lechner et al. 2012) for insects like bees can easily oversimplify their ecological and spatial relationships to land cover types. In our case, this is particularly true for our under-studied region and habitats. Together with Hanula et al. (2015), I specifically show that not all forests, even within the same landscape, are created equal when it comes to their relative ability to support high levels of bee species diversity and abundance. Factors like stand age, forest structure, and management and disturbance history clearly influence habitat suitability. Findings like these should augment our understanding of the operational scale at which bee community dynamics operate within forests. They also highlight how any simplified notion of forests as a generally unsuitable land cover type for bee habitat is an inappropriate characterization.

It seems particularly worthwhile to note finally that future research which consciously avoids confounding land cover type and land use type, and instead combines the

information provided by the two, may help uncover a reasonable substitute for simple acceptance of an easily accessible but operationally mismatched data source.

Instead, more researchers should focus on bees in forested habitats specifically rather than categorically relegating forests to a single, anthropocentrically defined land cover type. The emphasis should be not only on understudied areas and regions, but also on those forests where disturbance regimes have been substantially altered by human land use (as in Barton 2002, Sakulich and Taylor 2007, Hanula et al. 2015) and/or anthropogenic climate change. Understanding the relationships of these changes to the suitability of forests as bee habitat will greatly expand our ability to develop effective conservation efforts into the future.

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Appendices

Appendix A - adonis results for all bees; X= Study Year, *denotes significance; -denotes marginal significance.

adonis results for all models

Year 1

	Df	Sums Of Sqs	Mean Sqs	F Model	R2	Pr(>F)
log(Age)	1	1.137	1.137	6.863	0.407	0.002*
Residuals	10	1.657	0.166		0.593	
Total	11	2.794			1	

Year 2

	Df	Sums Of Sqs	Mean Sqs	F Model	R2	Pr(>F)
log(Age)	1	0.67	0.67	3.838	0.277	0.001*
Residuals	10	1.747	0.175		0.723	
Total	11	2.417			1	

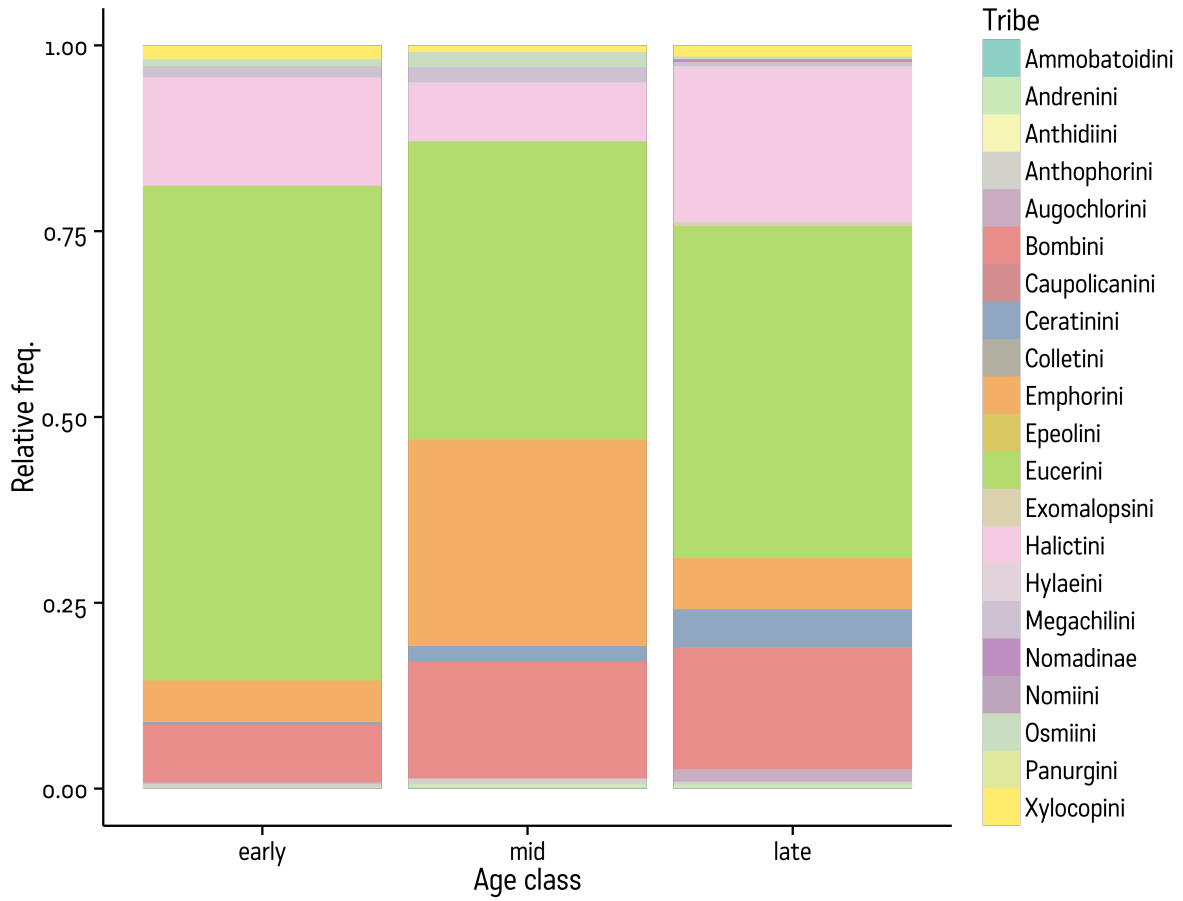
Both years with interaction

	Df	Sums Of Sqs	Mean Sqs	F Model	R2	Pr(>F)
log(Age)	1	1.445	1.445	8.491	0.253	0.001*
X	1	0.539	0.539	3.166	0.094	0.012*
log(Age):X	1	0.321	0.321	1.887	0.056	0.064-
Residuals	20	3.403	0.17		0.596	
Total	23	5.708			1	

Both years no interaction

	Df	Sums Of Sqs	Mean Sqs	F Model	R2	Pr(>F)
log(Age)	1	1.445	1.445	8.147	0.253	0.001*
X	1	0.539	0.539	3.038	0.094	0.008*
Residuals	21	3.724	0.177		0.652	
Total	23	5.708			1	

Appendix B – Relative frequencies of all bee tribes



Appendix C - indicator species analysis (point biserial correlation coefficients)

Species	ES	MS	LS	ES & MS	ES & LS	MS & LS	Species	ES	MS	LS	ES & MS	ES & LS	MS & LS
<i>Agapostemon splendens</i>	0.561	-0.154	-0.407	0.407	0.154	-0.561	<i>Lasioglossum floridanum</i>	-0.213	0.107	0.107	-0.107	-0.107	0.213
<i>Andrena confederata</i>	0.107	-0.213	0.107	-0.107	0.213	-0.107	<i>Lasioglossum hitchensi</i>	-0.147	-0.147	0.295	-0.295	0.147	0.147
<i>Andrena cressonii</i>	0	0	0	0	0	0	<i>Lasioglossum illinoense</i>	0.295	-0.147	-0.147	0.147	0.147	-0.295
<i>Andrena krugiana</i>	-0.147	-0.147	0.295	-0.295	0.147	-0.295	<i>Lasioglossum imitatum</i>	-0.189	0.378	-0.189	0.189	-0.378	0.189
<i>Andrena morrisonella</i>	0.295	-0.147	-0.147	0.147	0.147	-0.295	<i>Lasioglossum leviense</i>	-0.147	-0.147	0.295	-0.295	0.147	0.147
<i>Andrena MS_A</i>	-0.209	0.417	-0.209	0.209	-0.417	0.209	<i>Lasioglossum longifrons</i>	0.603	-0.227	-0.376	0.376	0.227	-0.603
<i>Anthophora abrupta</i>	0.295	-0.147	-0.147	0.147	0.147	-0.295	<i>Lasioglossum pectorale</i>	0.386	-0.245	-0.14	0.14	0.245	-0.386
<i>Anthophora bomboides</i>	0.395	-0.079	-0.316	0.316	0.079	-0.395	<i>Lasioglossum pruinosum</i>	0.295	-0.147	-0.147	0.147	0.147	-0.295
<i>Anthophora micheneri</i>	0.201	0	-0.201	0.201	0	-0.201	<i>Lasioglossum puteolanum</i>	0.393	-0.123	-0.269	0.269	0.123	-0.393
<i>Anthophorula micheneri</i>	-0.25	-0.062	0.312	-0.312	0.062	0.25	<i>Lasioglossum reticulatum</i>	-0.332	-0.288	0.62	-0.62	0.288	0.332
<i>Ashmeadiella floridana</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Lasioglossum sopinci</i>	-0.079	-0.079	0.158	-0.158	0.079	0.079
<i>Augochlora pura</i>	-0.305	-0.174	0.48	-0.48	0.174	0.305	<i>Megachile albitarsis</i>	0.107	0.107	-0.213	0.213	-0.107	-0.107
<i>Augochloropsis metallica</i>	0.279	-0.279	0	0	0.279	-0.279	<i>Megachile brevis</i>	0.235	0.039	-0.274	0.274	-0.039	-0.235
<i>Bombus bimaculatus</i>	0.212	-0.146	-0.066	0.066	0.146	-0.212	<i>Megachile campanulae</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147
<i>Bombus fraternus</i>	0.158	0.016	-0.173	0.173	-0.016	-0.158	<i>Megachile gemula</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147
<i>Bombus griseocollis</i>	0.397	0.171	-0.568	0.568	-0.171	-0.397	<i>Megachile georgica</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Bombus impatiens</i>	-0.331	0.475	-0.144	0.144	-0.475	0.331	<i>Megachile mendica</i>	0.438	-0.147	-0.312	0.312	0.125	-0.438
<i>Bombus pennsylvanicus</i>	0.046	0.419	-0.465	0.465	-0.419	-0.046	<i>Megachile petulans</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Caulopoliana electa</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Megachile pseudobrevis</i>	-0.092	0.34	-0.248	0.248	-0.34	0.092
<i>Ceratina calcarata</i>	-0.375	-0.037	0.412	-0.412	0.037	0.375	<i>Megachile texana</i>	0.149	0.149	-0.297	0.297	-0.149	-0.149
<i>Ceratina cockerelli</i>	0.136	0.238	-0.375	0.375	-0.238	-0.136	<i>Melissodes bimaculata</i>	0.029	-0.241	0.213	-0.213	0.241	-0.029
<i>Ceratina dupla</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Melissodes communis</i>	0.724	-0.074	-0.65	0.65	0.074	-0.724
<i>Ceratina floridana</i>	-0.162	0.42	-0.258	0.258	-0.42	0.162	<i>Melissodes druriella</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Ceratina strenua</i>	-0.391	0.142	0.249	-0.249	-0.142	0.391	<i>Melissodes tepaneca</i>	0.578	-0.221	-0.358	0.358	0.221	-0.578
<i>Colletes speculiferus</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Melitoma taurea</i>	0.109	0.274	-0.383	0.383	-0.274	-0.109
<i>Diadasia afflicta</i>	0.295	-0.147	-0.147	0.147	0.147	-0.295	<i>Nomada A_MS</i>	-0.147	-0.147	0.295	-0.295	0.147	0.147
<i>Dialictus A_MS</i>	0.512	-0.256	-0.256	0.256	0.256	-0.512	<i>Nomada B_MS</i>	-0.147	-0.147	0.295	-0.295	0.147	0.147
<i>Dialictus B_MS</i>	0	0	0	0	0	0	<i>Nomia nortoni</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Dialictus C_MS</i>	0.378	-0.189	-0.189	0.189	-0.189	0.378	<i>Osmia atriventris</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147
<i>Euclera dubitata</i>	-0.147	0.142	0.005	-0.005	-0.142	0.147	<i>Osmia chalybea</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Euclera hamata</i>	0.107	0.107	-0.213	0.213	-0.107	-0.107	<i>Osmia inspergens</i>	0.107	0.107	-0.213	0.213	-0.107	-0.107
<i>Florilegus condignus</i>	0.414	-0.118	-0.296	0.296	0.118	-0.414	<i>Osmia pumila</i>	0.152	0.095	-0.248	0.248	-0.095	-0.152
<i>Habropoda laboriosa</i>	-0.053	0.265	-0.212	0.212	-0.265	0.053	<i>Osmia sandhouseae</i>	0.395	-0.198	-0.198	0.198	-0.395	0.198
<i>Halictus ligatus</i>	0.351	-0.226	-0.125	0.125	0.226	-0.351	<i>Osmia subfasciata</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Halictus parallelus</i>	0.276	0.039	-0.316	0.316	-0.039	-0.276	<i>Panurginus polytrichus</i>	0.403	-0.201	-0.201	0.201	-0.403	0.201
<i>Halictus rubicundus</i>	0.512	-0.256	-0.256	0.256	0.256	-0.512	<i>Peponapis pruinosa</i>	0.516	-0.192	-0.324	0.324	0.192	-0.516
<i>Halcoapostes calliopsidis</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Pilothis bombiformis</i>	-0.226	0.663	-0.437	0.437	-0.663	0.226
<i>Hoplitis pilosifrons</i>	-0.244	0.714	-0.47	0.47	-0.714	0.244	<i>Sphex atlantis</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Hylaeus affinis</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Sphex banksii</i>	-0.213	0.107	0.107	-0.107	-0.213	0.107
<i>Hylaeus confusus</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Stelis diversicolor</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147
<i>Hylaeus modestus</i>	-0.213	-0.213	0.426	-0.426	0.213	-0.213	<i>Svastra atripes</i>	-0.062	0.312	-0.25	0.25	-0.312	0.062
<i>Hylaeus nelumbonis</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147	<i>Svastra obliqua</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147
<i>Lasioglossum apokense</i>	0.573	-0.286	-0.286	0.286	0.286	-0.573	<i>Tripeolus lunatus</i>	0.312	-0.062	-0.25	0.25	0.062	-0.312
<i>Lasioglossum birkmanni</i>	-0.297	0	0.297	-0.297	0	0.297	<i>Tripeolus rugulosus</i>	-0.147	0.295	-0.147	0.147	-0.295	0.147
<i>Lasioglossum callidum</i>	0.226	-0.057	-0.17	0.17	-0.057	-0.226	<i>Xenoglossa strenua</i>	0.295	-0.147	-0.147	0.147	-0.295	0.147
<i>Lasioglossum coreopsis</i>	0.334	-0.042	-0.292	0.292	0.042	-0.334	<i>Xylocopa micans</i>	0.073	0.073	-0.145	0.145	-0.073	-0.073
<i>Lasioglossum creberrimum</i>	0.007	0.337	-0.344	0.344	-0.337	-0.007	<i>Xylocopa virginica</i>	0.329	-0.118	-0.211	0.211	-0.118	-0.329

Point biserial correlation coefficients for each site combination from multipatt

Appendix D – abundance models for all bees, abundant bees, and rare bees; XYear 2 denotes the difference in intercept between Study Years; *denotes significance; -denotes marginal significance.

abundance model for both years and no interaction

	Estimate	Std. Error	z value	Pr...z..
(Intercept)	5.401	0.254	21.256	0
log(Age)	-0.542	0.141	-3.835	0*
XYear 2	0.293	0.216	1.357	0.175

abundance model for abundant bees in both years
without interaction

	Estimate	Std..Error	z.value	Pr...z..
(Intercept)	5.118	0.365	14.026	0
log(Age)	-0.924	0.199	-4.635	0*
XYear 2	0.49	0.351	1.394	0.163

abundance model for rare bees in both years without
interaction

	Estimate	Std..Error	z.value	Pr...z..
(Intercept)	3.718	0.242	15.369	0
log(Age)	-0.106	0.139	-0.767	0.443
XYear 2	0.372	0.173	2.155	0.031*

Appendix E – Rare species list with abundances for Study Years

rare species abundance by Study Year

Species	Year1	Year 2	Species	Year1	Year 2
<i>Andrena confederata</i>	1	1	<i>Lasioglossum creberrimum</i>	11	66
<i>Andrena cressonii</i>	3	0	<i>Lasioglossum floridanum</i>	2	0
<i>Andrena imitatrix</i>	0	1	<i>Lasioglossum hitchensi</i>	0	1
<i>Andrena krigiana</i>	0	1	<i>Lasioglossum illinoense</i>	1	0
<i>Andrena morrisonella</i>	5	0	<i>Lasioglossum imitatum</i>	3	1
<i>Andrena MS_A</i>	1	0	<i>Lasioglossum leviense</i>	1	0
<i>Anthophora abrupta</i>	1	3	<i>Lasioglossum pectorale</i>	7	0
<i>Anthophora bomboides</i>	0	3	<i>Lasioglossum pruinosum</i>	1	0
<i>Anthophorula micheneri</i>	0	4	<i>Lasioglossum reticulatum</i>	67	13
<i>Ashmeadiella floridana</i>	1	0	<i>Lasioglossum sopinci</i>	4	0
<i>Augochlora pura</i>	2	5	<i>Megachile albitarsis</i>	1	1
<i>Augochloropsis metallica</i>	8	1	<i>Megachile brevis</i>	23	1
<i>Bombus bimaculatus</i>	11	30	<i>Megachile campanulae</i>	1	0
<i>Bombus fraternus</i>	3	23	<i>Megachile gemula</i>	1	0
<i>Bombus impatiens</i>	91	145	<i>Megachile georgica</i>	0	1
<i>Caupolicana electa</i>	0	1	<i>Megachile mendica</i>	4	4
<i>Ceratina calcarata</i>	3	17	<i>Megachile petulans</i>	0	1
<i>Ceratina cockerelli</i>	3	8	<i>Megachile pseudobrevis</i>	20	2
<i>Ceratina dupla</i>	2	0	<i>Megachile texana</i>	4	2
<i>Ceratina floridana</i>	6	5	<i>Melissodes bimaculata</i>	77	141
<i>Ceratina strenua</i>	2	20	<i>Melissodes druriella</i>	1	0
<i>Colletes speculiferus</i>	0	1	<i>Melitoma taurea</i>	6	1
<i>Diadasia afflicta</i>	1	0	<i>Nomada A_MS</i>	0	1
<i>Dialictus A_MS</i>	5	0	<i>Nomada B_MS</i>	0	1
<i>Dialictus B_MS</i>	3	0	<i>Nomia nortoni</i>	1	0
<i>Dialictus C_MS</i>	4	0	<i>Osmia atriventris</i>	0	2
<i>Eucera dubitata</i>	5	93	<i>Osmia chalybea</i>	0	1
<i>Eucera hamata</i>	2	0	<i>Osmia inspergens</i>	0	2
<i>Florilegus condignus</i>	3	2	<i>Osmia pumila</i>	2	14
<i>Habropoda laboriosa</i>	0	18	<i>Osmia sandhouseae</i>	4	4
<i>Halictus ligatus</i>	27	9	<i>Osmia subfasciata</i>	0	1
<i>Halictus rubicundus</i>	5	0	<i>Panurginus polytrichus</i>	3	0
<i>Holcopasites calliopsidis</i>	1	0	<i>Peponapis pruinosa</i>	18	4
<i>Hoplitis pilosifrons</i>	7	18	<i>Sphecodes atlantis</i>	2	0
<i>Hylaeus affinis</i>	1	0	<i>Sphecodes banksii</i>	2	0
<i>Hylaeus confusus</i>	1	0	<i>Stelis diversicolor</i>	1	0
<i>Hylaeus modestus</i>	2	0	<i>Svastra atripes</i>	3	1
<i>Hylaeus nelumbonis</i>	0	1	<i>Svastra obliqua</i>	1	0
<i>Lasioglossum apokense</i>	13	1	<i>Triepeolus lunatus</i>	2	2
<i>Lasioglossum birkmanni</i>	2	4	<i>Triepeolus rugulosus</i>	1	0
<i>Lasioglossum callidum</i>	18	3	<i>Xenoglossa strenua</i>	2	0
<i>Lasioglossum coreopsis</i>	1	13	<i>Xylocopa micans</i>	2	3

Species list and abundance of rare bees by Study Year

Appendix F – Abundant species list with abundances for Study Years
abundant species abundance by Study Year

<i>Species</i>	Year 1	Year 2
<i>Agapostemon splendens</i>	14	21
<i>Bombus griseocollis</i>	47	45
<i>Bombus pennsylvanicus</i>	14	99
<i>Halictus parallelus</i>	25	5
<i>Lasioglossum longifrons</i>	18	23
<i>Lasioglossum puteulanum</i>	146	7
<i>Melissodes communis</i>	837	927
<i>Melissodes tepaneca</i>	192	10
<i>Ptilothrix bombiformis</i>	341	254
<i>Xylocopa virginica</i>	30	25

Species list and abundance of abundant bees by Study Year

Appendix G - Observed species richness models for all bees and above ground nesting bees; XYear 2 denotes the difference in intercept between Study Years; *denotes significance; - denotes marginal significance.

observed species richness results for all models

observed species richness for year 1

	Estimate	Std. Error	z value	Pr...z..
(Intercept)	3.298	0.128	25.678	0
log(Age)	-0.235	0.078	-3.021	0.003*

observed species richness for year 2

	Estimate	Std. Error	z value	Pr...z..
(Intercept)	3.152	0.145	21.721	0
log(Age)	-0.115	0.08	-1.435	0.151

observed species richness for both years with interaction

	Estimate	Std. Error	z value	Pr...z..
(Intercept)	3.267	0.119	27.35	0
log(Age)	-0.217	0.072	-3.009	0.003*
XYear 2	-0.107	0.145	-0.734	0.463
int.	0.101	0.08	1.262	0.207

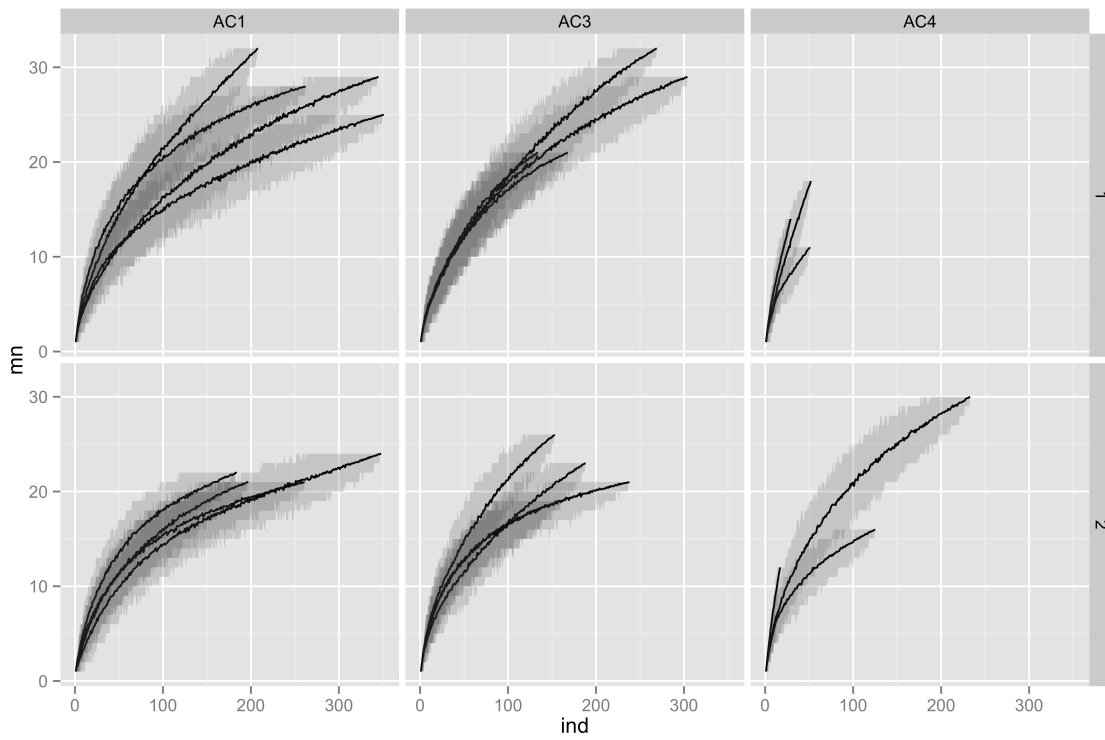
observed species richness for both years without interaction

	Estimate	Std. Error	z value	Pr...z..
(Intercept)	3.235	0.12	26.992	0
log(Age)	-0.188	0.07	-2.678	0.007*
XYear 2	0.025	0.102	0.249	0.803

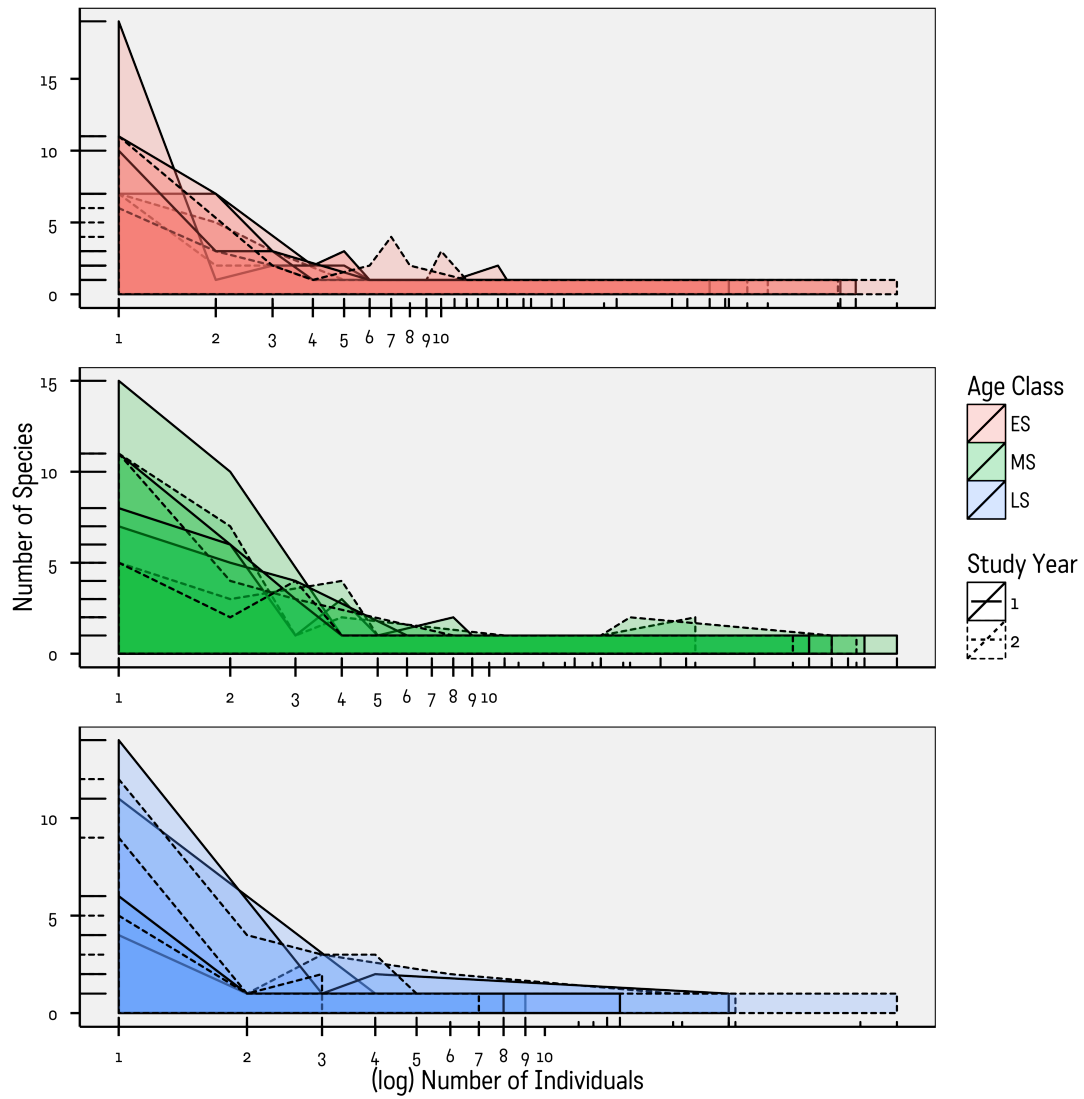
observed species richness for both years (above ground nesting guild)

	Estimate	Std. Error	z value	Pr...z..
(Intercept)	1.675	0.172	9.731	0
log(Age)	-0.094	0.087	-1.072	0.284
XYear 2	0.269	0.181	1.487	0.137

Appendix H – Species accumulation curves by Age Class and Study Year



Appendix I – Rank abundance by Age Class; x axes on logarithmic scale



Appendix J – Species evenness (Pielou’s) for all bees; XYear 2 denotes the difference in intercept between Study Years; *denotes significance; -denotes marginal significance.

results of species evenness model for both years without interaction

	Estimate	Std. Error	df	t value	Pr...t..
(Intercept)	0.593	0.033	7.068	18.203	0
log(Age)	0.058	0.017	3.433	3.507	0.032*
XYear 2	0.006	0.034	19.004	0.175	0.863

Appendix K - Species evenness (Pielou's) for below ground nesting guild; XYear 2 denotes the difference in intercept between Study Years; *denotes significance; -denotes marginal significance.

species evenness results for all years
(below ground nesting guild)

species evenness for year 1

	Estimate	Std. Error	df	t value	Pr...t..
(Intercept)	-0.477	0.058	4	-9.222	0.001
log(Age)	0.081	0.033	4	2.218	0.091-

species evenness for year 2

	Estimate	Std. Error	df	t value	Pr...t..
(Intercept)	-0.774	0.181	4	-6.238	0.003
log(Age)	0.202	0.096	4	2.949	0.042*

species evenness for both years with interaction

	Estimate	Std. Error	df	t value	Pr...t..
(Intercept)	-0.434	0.09	7.978	-6.664	0
log(Age)	0.055	0.054	7.491	0.974	0.36
XYear 2	-0.324	0.124	19.994	-2.357	0.029*
int.	0.138	0.067	18.475	2.942	0.009*

species evenness for both years without interaction

	Estimate	Std. Error	df	t value	Pr...t..
(Intercept)	-0.525	0.079	6.268	-7.937	0
log(Age)	0.132	0.039	3.782	2.438	0.075-
XYear 2	-0.145	0.095	19.011	-0.284	0.78

Appendix L - Results of similarity analysis between Study Years

basic information from Study Year similarity analysis

total number of species	94
# of observed individuals from Year 1	2187
# of observed individuals from Year 2	2118
# of observed species in Year 1	77
# of observed species in Year 2	62
# of observed shared species in both Study Years	45
bootstrap replications for Std. Error estimate	200

Jaccard and Sorensen similairty indices

indices	Estimate	s.e.	shared species est. Year 1	s.e.	shared species est. Year 2	s.e.
Jaccard Abundance (adjusted)	0.9786	0.0191	0.995	0.0163	0.9835	0.0129
Sorensen Abundance (adjusted)	0.9892	0.01	0.995	0.0163	0.9835	0.0129

Appendix M – Results of similarity analysis among Age Classes

basic information from Age Class similarity analysis

number of assemblages	3
total number of species	94
# of observed individuals in ES	2156
# of observed individuals in MS	1614
# of observed individuals in LS	535
# of observed species in ES	65
# of observed species in MS	68
# of observed species in LS	46
# of observed shared species in ES and MS	45
# of observed shared species in ES and LS	33
# of observed shared species in MS and LS	38
# of shared species in all communities	31
bootstrap replications for Std. Error estimate	200

indices of species overlap among all Age Classes

indices	Estimate	s.e.	95%.LCL	95%.UCL
C03 (Sorensen)	0.7122905	0.0201765	0.6727446	0.7518364
C13*(Horn)	0.8140826	0.008928	0.7965837	0.8315815
C23 (Morisita)	0.6755808	0.0224726	0.6302824	0.7187642
C33	0.5653805	0.0325838	0.5064428	0.6307338

pairwise comparisons from multi assemblage similarity analysis using Morisita index

Site Pairs	Estimate	s.e.	95%.LCL	95%.UCL	D.95%.LCL	D.95%.UCL
ES,MS	0.8005826	0.0180388	0.7617989	0.8355091	0.1644909	0.2382011
ES,LS	0.5579076	0.0375264	0.482049	0.6328171	0.3671829	0.517951
MS,LS	0.632949	0.0367564	0.5638257	0.7054405	0.2945595	0.4361743

Vita

The author was born in Houston, Texas. He obtained his Bachelor's degree in Anthropology from the University of Texas at Austin in 2005. He joined the University of New Orleans biological sciences graduate program in 2011 with Dr. Jerome Howard as his major professor.