



8-2018

ASSESSING BEE COMMUNITY CHARACTERISTICS AND POLLINATION WITHIN GROUP SELECTION OPENINGS IN SOUTHERN APPALACHIA

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I am submitting herewith a thesis written by Hannah Lin Mullally entitled "ASSESSING BEE COMMUNITY CHARACTERISTICS AND POLLINATION WITHIN GROUP SELECTION OPENINGS IN SOUTHERN APPALACHIA." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.

Charles Kwit, Major Professor

We have read this thesis and recommend its acceptance:

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Accepted for the Council:

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Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

ASSESSING BEE COMMUNITY CHARACTERISTICS AND POLLINATION WITHIN
GROUP SELECTION OPENINGS IN SOUTHERN APPALACHIA

A Thesis Presented for the
Master of Science
Degree
The University of Tennessee Knoxville

Hannah Lin Mullally

August 2018

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To my wonderful parents

Mike and Judy Mullally

ACKNOWLEDGEMENTS

I would like to thank my parents for their constant support and encouragement in pursuing my vocation. I thank my friends at the University of Tennessee and around the country who pushed me to grow personally and professionally. My sincere thanks goes to the University of Tennessee Knoxville and the Department of Forestry, Wildlife and Fisheries for the financial support that made this project and my education possible. Dr. Beverly Collins of Western Carolina University has my gratitude for taking me on as a research assistant the summer before my graduate studies began to allow me to get a head start on my field work. For going above and beyond in providing help with statistical analysis, Dr. Jim Fordyce has my thanks. I must thank Dr. David Buckley and Dr. Randy Small for serving on my committee. Their commitment to ensuring the success of this project is more than any student can hope for and I am inspired by their example as dedicated scientists. Of course, I thank all the members of the Kwit lab for their tremendous support, especially Chelsea Miller and Chloe Lash for taking me under their wing as a new graduate student. Finally, I thank my advisor, Dr. Charlie Kwit for believing in me from day one, challenging me to always improve, and encouraging me to set my sights higher than I could have imagined.

ABSTRACT

Bees provide the essential ecosystem service of pollination. Bee communities are often subjected to anthropological activities and in some cases are harmed by these activities. Fortunately, silviculture is a form of anthropological disturbance that can benefit bees and subsequent pollination. While the impacts of intensive silvicultural methods, such as clearcutting, on bees has been well documented, the impacts of lower intensity methods, such as group selection, is less understood. For my first chapter, I investigated bee community characteristics across microsites (center of cut, edge of cut, and closed-canopy forest) in three forest stands subjected to cuts analogous to those associated with low-intensity group selection harvests in the Nantahala National Forest, North Carolina. Bee community dissimilarity, diversity, and indicator species were compared among the three microsites. Results revealed the communities of the center of cut and forest microsites to be dissimilar. Alpha diversity between these two microsites, as measured through a series of diversity measures that progressively down-weighted the importance of rare species, was also significantly different. Communities in edge and forest microsites were dissimilar, and diversity in edge microsites differed significantly from the forest microsite but not the center of cut microsite. Finally, center of cut and forest microsites were characterized by different indicator species, and indicator species for the edge microsites were a subset of the indicator species for center of cut microsites. For my second chapter, I utilized the same forest stands and an additional fourth stand subjected to group selection harvests. I investigated inter- and intra-cut pollen proxy movement as a function of the distance between group selection openings. Results revealed that the distance between openings did not have a significant effect on either inter-cut or intra-cut pollen proxy movement. As the first study to quantify the effects group selection silviculture has on in bee community characteristics in southern Appalachia and the first study to investigate impacts of group

selection on pollination, I have illustrated that incorporating group selection practices in the management of forested landscapes may assist in supporting a wide range of bee community types without significantly impacting the process of pollination.

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INTRODUCTION

Animal-mediated pollination is an essential ecosystem service (Crenna *et al.* 2017). With a majority of angiosperms being pollinated by animals (Ollerton *et al.* 2011), the interaction is a focus of many conservation efforts (Kearns *et al.* 1998). A variety of animals serve as pollinators and move pollen from one conspecific flower to another during their search for food. For successful cross pollination, plant species may rely on a certain species of pollinator or they may be pollinated by a wide variety of animals. However, in terms of flower visitation rates and amount of contributed pollination services, bees as a group are generally considered the most effective pollinators worldwide (Vazquez *et al.* 2005, Winfree *et al.* 2011).

Unfortunately, there is growing evidence that shows bees are in global decline (Biesmeijer *et al.* 2006, Natural Resource Council 2006, Bartomeus 2013). Over the past few decades, bee species richness and overall population numbers have declined (Biesmeijer *et al.* 2006, Potts *et al.* 2010, Burkel *et al.* 2013). Anthropogenic activities have been found to have major impacts on bee communities and subsequent pollination. Some of these activities, such as the intensification of agriculture, have been found to have a negative effect on bees and pollination overall. Intensive agricultural practices such as monocrop plantings with little to no interspersed pollinator habitat have been found to sustain fewer native bees and a less diverse community than agricultural areas which incorporated hedgerows and native bee habitat (Kremen *et al.* 2002, Cranmer *et al.* 2012, Tucker and Rehan 2017).

Silviculture is an anthropogenic activity which also impacts bees and pollination. However, unlike intensive agriculture, silviculture and associated forest management activities have been shown to increase the diversity of bee species (Romey *et al.* 2007, Hanula *et al.* 2015, Rubene *et al.* 2015, Proctor *et al.* 2012, Roberts *et al.* 2017). Silviculture and forest management

activities can create environments which are favorable for many bees. The forest openings created by these activities allow shade-intolerant flowering plants to flourish, and the presence of these plants after forest management activities have been shown to have a positive correlation with bee abundance (Campbell *et al.* 2006, Hanula and Horn 2011, Hanula *et al.* 2015). Areas of bare and open ground created by these activities also provide nesting sites for many ground nesting native bees (Steffan-Dewenter 2002). Although forest management activities such as fire and shrub-removal and intensive silvicultural methods such as clearcutting have consistently been found to yield these increases in bee diversity and abundance, the effects less-intense silvicultural methods, such as group selection, may have on bee communities have been left relatively unstudied.

Successful bee pollination has been shown to have a positive correlation with bee abundance and diversity (Williams and Winfree 2013, Blitzer *et al.* 2016, Crusser *et al.* 2016) which forest management activities can provide. While silviculture and other forest management activities can create environments that promote a more diverse bee community, they also create resource rich areas in the form of flowering plants. Previous research indicates that bees will engage in shorter foraging trips if their nests are in resource rich areas with high pollen availability (Heinrich 1979, Gathmann and Tschardt 2002). These shorter foraging trips will result in pollen movement within a smaller area. Successful pollination may also depend on the amount and connectivity of natural habitat. Fragmentation and removal of natural habitat from agricultural activities have been shown to have a negative correlation with pollination success (Kremen *et al.* 2002, Greenleaf and Kremen 2006). The forest interior around and between silvicultural openings may act as a barrier for pollination between openings since they provide a less than ideal foraging and nesting environment for many species of bees. However, the impacts

of silviculture, specifically the group selection method in the United States, have yet to be studied.

The group selection method is a less intense silvicultural practice as compared to clearcutting. Group selection in a forest stand results in a number of forest openings, surrounded and separated by intact forest. These openings are typically less than five hectares and can be separated by varying distances of intact forest. Even though group selection and other less intense silvicultural methods occur on 61% of the United States' harvest acres (Oswalt and Smith 2014), there has been minimal research on group selection's impact on bee communities and subsequent pollination in the southeastern United States. It is essential to understand the impacts such a widely used method has on bee communities and the process of pollination, particularly in light of global bee declines. Therefore, to understand how group selection silviculture in southern Appalachia affects bee communities and pollination, I examined the effects of different microsites common of forest stands subjected to group selection harvests on bee communities and I assessed the effects of distance between group selection cuts on the movement of a pollen proxy. Based on previous research of the impacts of clearcutting and other silvicultural methods on their impacts to bee communities, I expect bee community characteristics to be significantly different between the microsites created by group selection. I also expect the distance between group selection harvests to significantly impact the rate of pollen movement.

CHAPTER 1
BEE COMMUNITY CHARACTERISTICS ACROSS MICROSITES ASSOCIATED
WITH GROUP SELECTION OPENINGS

This chapter is revised based on a paper submitted by Hannah L. Mullally which is currently in review for acceptance:

Mullally, H.L., D.S. Buckley, J.A. Fordyce, B. Collins, and C. Kwit. Bee community characteristics across microsites associated with group selection openings. *Forest Ecology and Management*. *In review*.

My primary contributions to this paper include (1) development of the study question; (2) identification of the objectives; (3) design and conducting of the field work; (4) gathering and researching literature; (5) processing, analyzing, and interpretation of experimental data; (6) writing the paper.

Abstract

As insect pollinator populations continue to decline due to global change, it is essential to understand the impacts anthropogenic activities have on pollinator communities. Many silvicultural practices are a form of planned disturbance that may have differential effects on pollinator communities, particularly bees. While multiple studies have shown clearcutting is generally beneficial for bees in terms of diversity and abundance, other less-intense silvicultural methods such as group selection are less well understood. In this study, three mixed-mesophytic forest stands (Nantahala National Forest, Graham County, North Carolina, USA) experienced cuts analogous to those associated with low-intensity group selection harvests. We investigated bee community characteristics across microsites (center of cut, edge of cut, and closed-canopy forest) in these forest stands. Bee community dissimilarity, diversity, and indicator species were compared among the three microsites. Results revealed the communities of the center of cut and forest microsites to be dissimilar. Alpha diversity between these two microsites, as measured

through a series of diversity measures that progressively down-weighted the importance of rare species, was also significantly different. Communities in edge and forest microsites were dissimilar, and diversity in edge microsites differed significantly from the forest microsite, but not the center of cut microsite. Finally, center of cut and forest microsites were characterized by different indicator species, and indicator species for the edge microsites were a subset of the indicator species for center of cut microsites. These results suggest that center of cut and forest microsites support differing communities of bees. Incorporating group selection practices in the management of forested landscapes may assist in sustaining a wide range of bee species and different bee community types.

Introduction

Globally, many bee species are experiencing population declines (Bartomeus 2013, Biesmeijer *et al.* 2006). A commonly highlighted concern of these declines is that bees, both native and introduced, greatly contribute to agricultural crop pollination (Gallai *et al.* 2009, Kleijn *et al.* 2015, Potts *et al.* 2010). Although the majority of crop pollination carried out by wild native bee species can be attributed to regionally common species (Kleijn *et al.* 2015), a diverse suite of common and rare species can provide insurance that pollination services will continue as conditions change over time (Burkle *et al.* 2013; Kremen *et al.* 2002; Winfree *et al.* 2007a). Additionally, for natural systems it has been estimated that approximately 87.5% of all flowering plant species on the planet are animal pollinated (Ollerton *et al.* 2011). Because bees are generally considered the most effective pollinators worldwide (Winfree *et al.* 2011; Vazquez *et al.* 2005), they likely contribute to a large portion of this pollination. Intensive agricultural practices such as heavy pesticide application, usage of inorganic fertilizer, and monocrop plantings have been found to sustain fewer native bees and a less diverse community than

organic farms which used minimal pesticides and were near natural bee habitat (Kremen *et al.* 2002, Cranmer *et al.* 2012, Tucker and Rehan 2017). Loss of desirable habitat from agriculture may also contribute to declines as agricultural field size has been found to have a negative correlation with bee diversity (Fahrig *et al.* 2015).

In contrast to large-scale intensive agricultural effects on bee communities, other forms of anthropogenic disturbances, such as some forestry and forest management practices, have been shown to positively effect bees (Romey *et al.* 2007, Hanula *et al.* 2015, Rubene *et al.* 2015, Proctor *et al.* 2012, Roberts *et al.* 2017). Multiple studies have found increases in bee abundance following the creation of 5 ha and larger openings through forest management activities (Romey *et al.* 2007; Winfree *et al.* 2007b, Proctor *et al.* 2012). Large clearcuts measuring several hectares have been found to consistently benefit bees (Romey *et al.* 2007, Hanula *et al.* 2015, Rubene *et al.* 2015). Intensive management in forested areas that have not recently experienced dramatic land cover change may be responsible for such positive patterns. However, the impacts of less-intense reproduction methods, such as group selection, are less well documented (but see Proctor *et al.* 2012, Roberts *et al.* 2017). This represents an important knowledge gap because group selection and other less intense methods occur on 61% of the United States' harvested acres (Oswalt and Smith 2014). These less intense methods are also more publicly acceptable than large-scale clearcutting (Bliss 2000, Gundersen and Frivold 2008).

To address this knowledge gap and investigate whether impacts of group selection cuts on pollinators resemble those of higher intensity clearcutting, we assessed the effects of different microsites (center of cut, edge of cut, and interior forest; hereafter, center of cut, edge, and forest) typical of forest stands experiencing group selection harvests on bee communities in forest stands in the Nantahala National Forest (Graham County, North Carolina, USA). The

objectives of this study were to (1) quantify the degree of dissimilarity in bee communities between center of cut, edge, and forest microsites associated with group selection cuts; (2) compare and contrast bee species diversity among microsites associated with group selection cuts; and (3) identify key species driving bee community differences among microsites.

Methods

Study Sites

This study was conducted in the Nantahala National Forest, Cheoah Ranger District in southwestern North Carolina during the summers of 2016 and 2017 (Fig. 1.1). Sites are mixed-mesophytic forest stands dominated by *Quercus spp.* and *Liriodendron tulipifera* in the overstory and a high abundance of *Rhododendron maximum* in the middlestory and understory. The cuts, which were analogous to group selection cuts, were created by logging contractors in three forest stands during late winter 2016. Each stand contained five 0.4 ha cuts group selection cuts. Unlike most tree harvest situations, felled trees in our study were left on the ground and not removed; while this caused our treatment to be less intensive than typical group selection harvests, areas in the center of cut microsites did experience full canopy removal and hence more open conditions than those prior to the cuts.

Field Methods

Bee communities were sampled in all sites during the summers of 2016 and 2017. In both years, bees were captured and collected from June to mid-July using pan traps. Standard methodology for pan trapping is to use blue, yellow, and white pan traps (Campbell and Hanula 2007), as these colors mimic common floral colors that are associated with floral rewards for

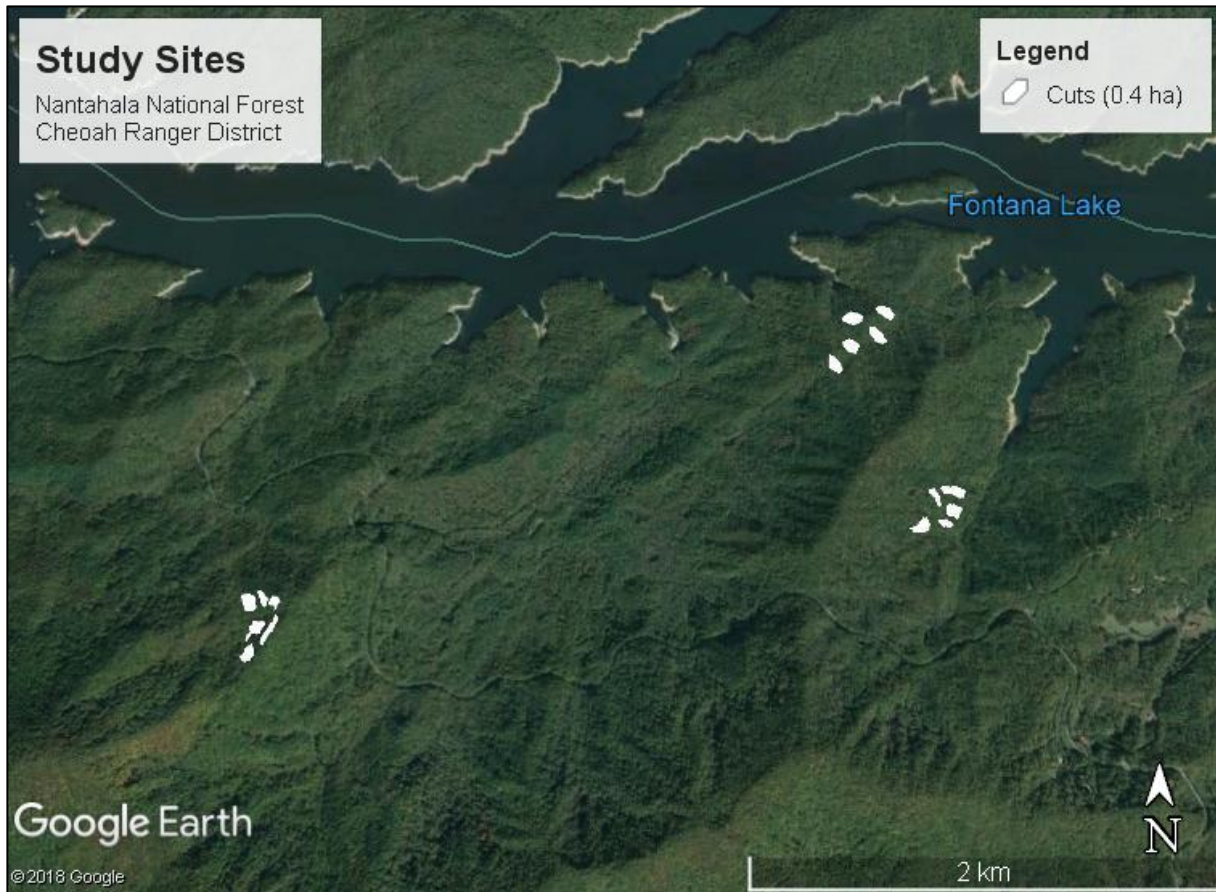


Figure 1.1. Map of study sites in the Nantahala National Forest of western North Carolina (35.4356° N, 83.8191° W). Red areas indicate 0.4 ha forest cuts; clustered cuts ($n=5$) were located in individual forest stands ($n=3$). Bees were collected in June-August of 2016 and 2017.

bees (Leong and Thorp 1999). Small, 2 oz. white plastic cups were painted with blue and yellow paints that also reflect UV light. Pans were elevated 0.5 m above the substrate (Campbell and Hanula 2007) using PVC pipe to make them visible to flying insects.

Pan traps were located along transects spanning two pairs of cut openings at each site. One pan trap of each color was placed along these transects at five points: near the center of both cut openings, on the forest edge of both cuts, and at the midway point between the two cuts within the forest (Fig. 1.2). Edge sampling points were located on the drip line of the canopy. These points of sampling represent the three microsites created by group selection harvests (center of cut, edge, and forest).

Pans were filled with soapy water and left for approximately 48 hours (Campbell and Hanula 2007). Insects caught in the pans were collected, pinned, and organized separately by collection point. Each point was sampled three times per year in mid-June, late June/early July and mid-July using the pan trapping method described above. After pinning, bees were separated from other insects within each collection point group. Bees were identified to the family level and sent to Sabrie Breland at Michigan State University for species identification. Abundances of all bee species collected can be found in the Appendix.

Bee community diversity statistical analysis

All statistical analysis was completed using the statistical software R unless otherwise noted (R Core Team 2017). Species data at each sampling point in time were pooled within years for all analyses. Quantitative Jaccard distances were used to initially determine the amount of dissimilarity in bee communities between microsites (center of cut, edge, and center). R package *vegan* v.2.4.6 (Oksanen *et al.* 2018) was used to build a distance-based redundancy analysis

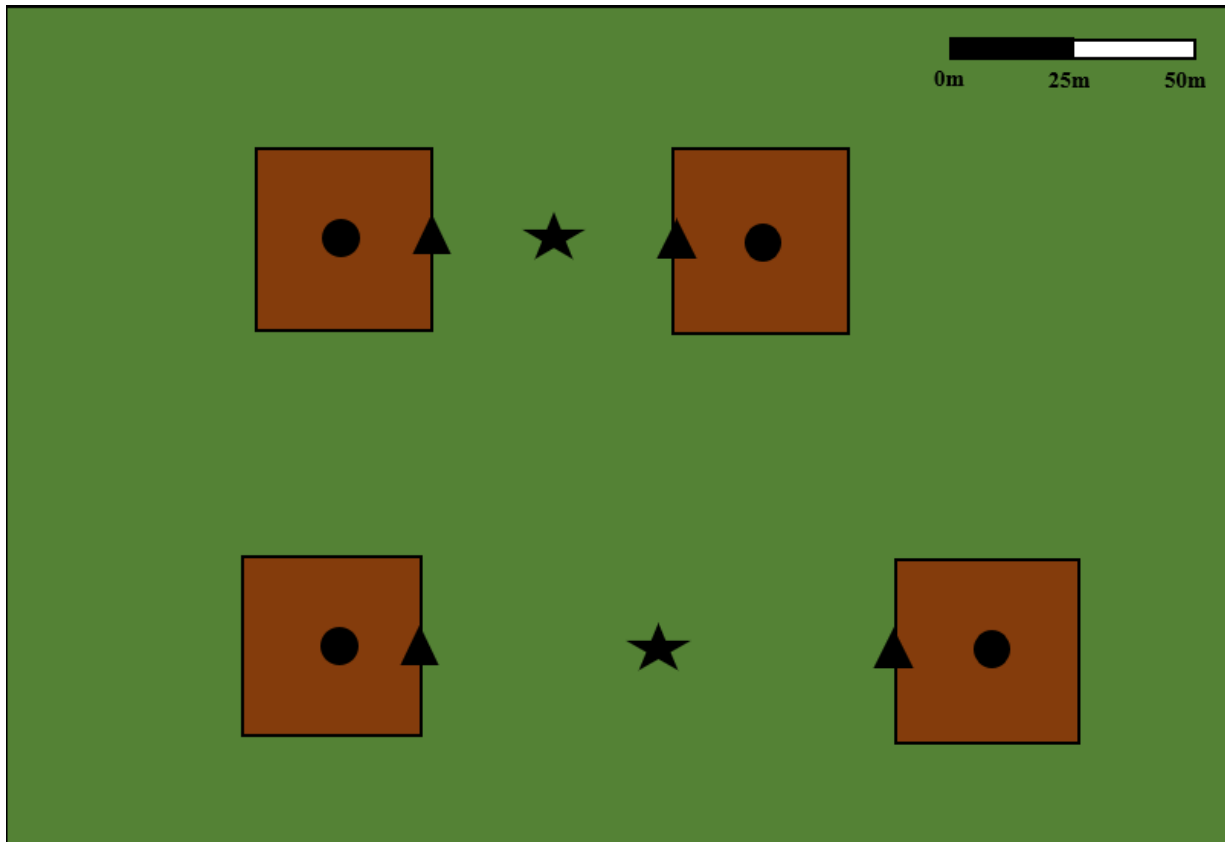


Figure 1.2. Schematic of pan trap sampling. Brown squares represent forest cuts, green represents contiguous forest. Group selection cuts were made 25 m – 200 m apart. Circles represent center of cut sampling points, triangles represent edge sampling points, and stars represent forest sampling points.

(dbRDA) to compare community dissimilarity as a function of microsite. Statistical significance of the model was assessed using 9999 permutations of the data.

Linear mixed effect models were used to analyze α diversity of bee species among microsites. Diversity was calculated as the effective number of species present at a site using Hill numbers (qD) (Jost 2006) across six orders of q in the R package *vegan* v.1.2 (Charney and Record 2012). At $q = 0$, all species present at a site are equally weighted (i.e., richness). At $q = 1$, species are weighted by their relative abundance (analogous to Shannon's entropy). At $q = 2$, rarer species are down-weighted (analogous to Simpson's diversity). Subsequent orders of q continue to down-weight the importance of rare species (Jost 2006). Bee diversity across microsites for each order of q were examined using a linear mixed effects model and the R package *lme4* v.1.1-17 (Bates *et al.* 2015). Model selection was done via backwards stepwise elimination using the R package *lmerTest* v3.0 (Kuznetsova *et al.* 2017) beginning with a model that structured the error term by including random intercepts for stand, year, and transect. The simplest model across all orders of q retained stand and year as random effects and microsite as a fixed effect.

To identify bee species with a particular affinity for each microsite, we used multi-level indicator species analysis (De Cáceres *et al.* 2010) based on point-biserial correlation coefficients, r_g , between habitat and relative abundance (De Cáceres and Legendre 2009). This indicator species analysis technique reflects both habitat specificity and consistency for each species and explores indicator species associated with groups of habitat types. Statistical significance ($\alpha = 0.05$) was determined using 9999 permutations of the data using the R package *indicspec* v.1.7.9 (De Cáceres and Legendre 2009).

Results

We found that microsite did have a significant effect on the dissimilarity of bee communities based on our dbRDA ($F_{2, 187} = 3.29$, $P = 0.001$; Fig. 1.3). Pairwise comparisons among microsites failed to find a difference between cut and edge ($F_{1,157} = 0.496$, $P = 0.218$), but found both cut and edge different from forest microsite ($F_{1,108} = 2.03$, $P < 0.001$ and $F_{1,109} = 1.90$, $P < 0.001$, respectively).

The linear mixed effect models for each diversity order (qD - ${}^{q5}D$) found microsite was significant in explaining diversity. Center of cut and edge microsite had greater diversity compared to forest microsites across all orders of q examined (Fig. 1.4).

Indicator species analysis identified one species significantly associated with center of cut microsites: *Apis mellifera* ($r.g = 0.173$, $P = 0.0433$). One species was significantly associated with forest microsites: *Lasioglossum coeruleum* ($r.g = 0.2$, $P = 0.0084$). One species was associated with the edge microsites, although not significantly at $\alpha = 0.05$: *Ceratina calcarata* ($r.g = 0.158$, $P = 0.0684$). Three species were significantly associated with both cut and edge microsites combined: *Lasioglossum cressonii* ($r.g = 0.293$, $P = 0.0002$), *Lasioglossum bruneri* ($r.g = 0.201$, $P = 0.0089$), and *Lasioglossum sp.7* ($r.g = 0.201$, $P = 0.0096$).

Discussion

Our results illustrate significant differences between the composition of the forest microsite bee community and the bee communities sampled in the center of cut and edge microsites. These findings are similar to those of other studies that documented strong differences between forest bee communities and bee communities of disturbed areas such as

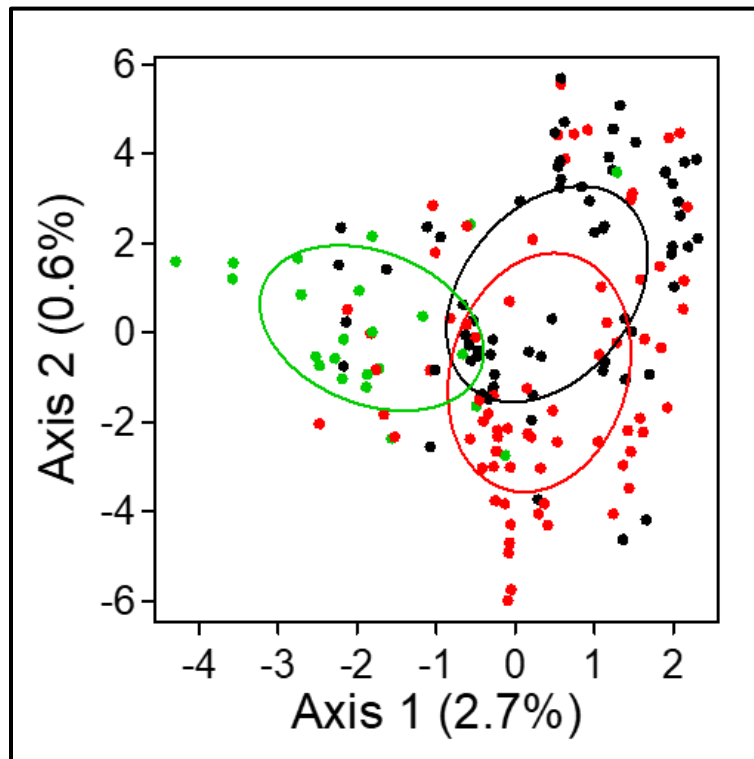


Figure 1.3. Ordination of constrained axes from distance-based RDA among three microsites. Ellipses indicate 1 standard deviation from the centroid. Center of cut, edge, and forest and indicated by black, red and green, respectively.

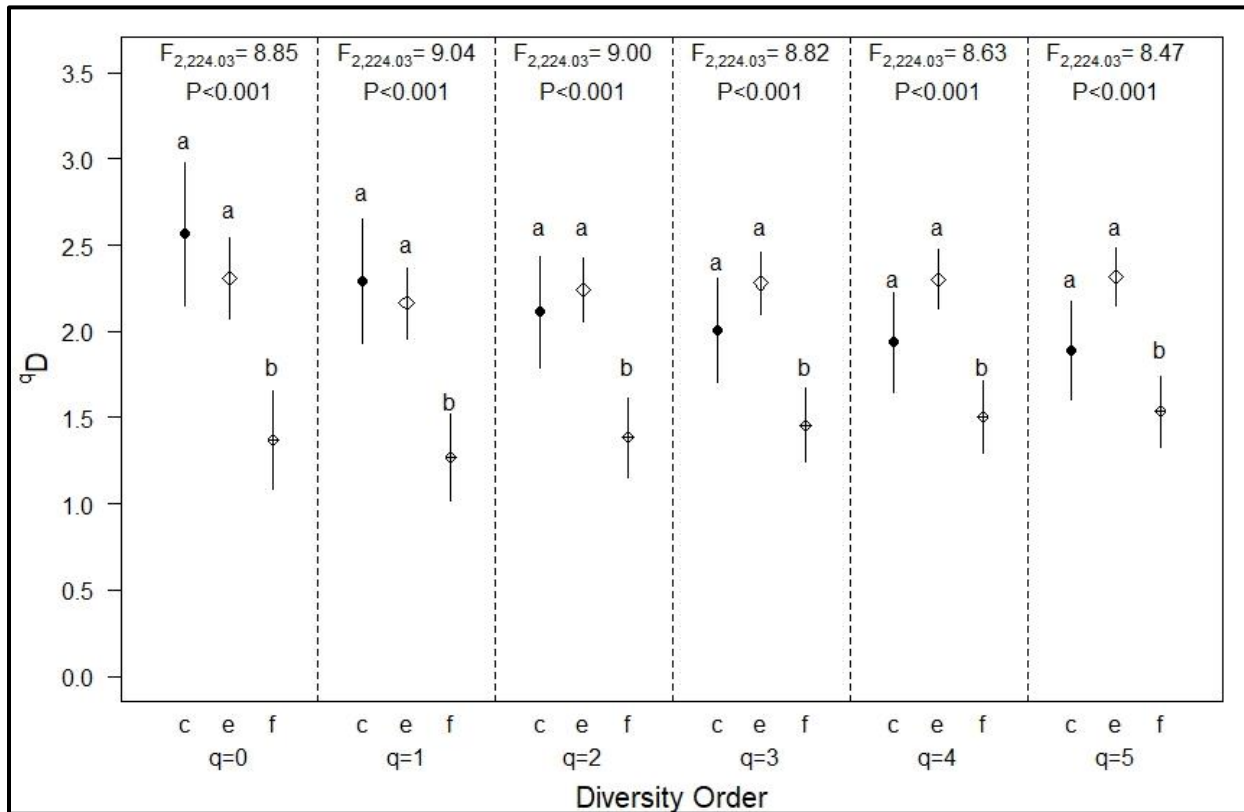


Figure 1.4. Bee diversity of microsite types across six orders of q . c, e, and f indicate center of cut, edge, and forest respectively. The y-axis represents α -diversity as the effective number of species. Symbols represent the mean effective number of species. Closed circles represent center of cut microsite data, open diamonds represent edge microsite data, and crossed circles represent forest microsite data. Bars represent the standard error. Differences in diversity are compared only within the same level of Hill diversity. Different letters at each order of q indicate significantly different diversity (Tukey HSD at $\alpha = 0.05$).

forest fragments, urban environments, and agricultural areas (Botsch *et al.* 2017, Harrison *et al.* 2018).

The significant differences between the center of cut and forest microsites at every level of diversity in our study suggest these microsite types differ in the number or composition of common species (Jost 2006). Rare species between these two microsites also differ. A recent study conducted in New England, USA (Roberts *et al.* 2017) found bees were significantly more diverse in forest openings than the adjacent mature forest. However, Roberts *et al.* (2017) did not find significant differences in bee community composition between forest opening and mature forest. Significantly higher diversity in forest openings than mature forests, as illustrated by our results and the results of Roberts *et al.* (2017) may be explained by enhanced nesting and food resources in these open environments. Many native bees depend on disturbed and open areas for food and nest sites (Steffan-Dewenter 2002). Campbell *et al.* (2006) illustrated that bee abundance was highest in 10 ha forests plots after intensive burning and shrub removal. Similar to burning and shrub removal, silvicultural cutting practices create openings in the forest canopy that result in increased sunlight reaching the bare ground. Bare ground is essential for burrowing bee species that utilize cleared ground to create nests (Vaughan *et al.* 2015) and bee abundance has been shown to be positively correlated with the area of bare ground available (Potts *et al.* 2005, Rodriguez and Kouki 2015). Bare ground and ample sunlight are also beneficial for shade-intolerant guilds of flowering plants, on which bee colonies rely for food and nutrients (e.g. nectar and pollen); indeed, the presence of such plants has been found to have a positive correlation with bee abundance (Campbell *et al.* 2006).

Indicator species analyses of our study coupled with our dbRDA and diversity analyses further support the conclusion that forest and center of cut microsites differ in community

composition. As further evidence of this, no bee species was found to have a significant association with *both* center of cut and forest microsites. It is likely that differences in the predominant indicator species driving the dissimilarity between microsites may be a function of the particular habitat requirements for these species. For example, *Lasioglossum coeruleum*, which was found to be the predominant indicator species of the forest microsites, relies on moist, rotting wood for nesting (Stockhammer 1967, Barrows 1973). A humid forest understory environment would better provide *L. coeruleum* with this habitat requirement than the drier conditions found in the cut and edge microsites. *Apis mellifera* was found to be the predominant indicator species of center of cut microsites. While this species is much more adaptable to a range of environments, they do rely on cavities for nesting (Seeley and Morse 1978). The stumps and slash in the center of cuts of our sites may provide these nesting opportunities. Many other species of *Lasioglossum* such as *L. cressonii* and *L. bruneri* are soil nesters (Miyanaga *et al.* 2017, Michener 2007). Both of these species were found to be indicator species of center of cut and edge microsites. Due to soil disturbance associated with typical group selection cutting, these microsites likely provide the necessary habitat component of dry, warm, bare soil for nest building.

The edge microsites in this study did not differ significantly in diversity on any level of analysis compared to the center of cut microsites. While not statistically significant, edge microsites were found to have greater diversity in diversity analyses which down-weighted the importance of rare species (qD - qD). These results suggest that while the edge and center of cut microsites are similar in diversity, edge microsites may be more diverse with abundant bee species than the center of cut microsites. Edge microsites consistently differed significantly in diversity from the forest microsites on every level of diversity analysis. This is consistent with

our results of the dbRDA analysis which illustrate that edge and center of cut microsites are similar but are dissimilar from the forest microsite. Finally, indicator species analysis of the edge microsites found that the edge microsite alone did not have a species that was significantly associated with it, although one species, *Ceratina calcarata*, was closely associated with the edge microsite. Three species were significantly associated with both edge and center of cut microsites: *Lasioglossum cressonii*, *Lasioglossum bruneri*, and *Lasioglossum sp.7*. These indicator species results, along with the results from the dbRDA and diversity analyses suggest that edge microsites provide an important environment type for bees which is not fully covered by center of cut nor forest microsites.

In this study, the dissimilarity between communities of center of cut and forest microsite types, along with subtle dissimilarities from edge microsites, suggest that a diversity of canopy structures at stand and landscape scales may be important for sustaining a full complement of bees. While timber production, wildlife management, and aesthetics will always have an important influence on the patterns and types of practices implemented, the incorporation of pollinator goals would appear to be feasible. At landscape scales, the inclusion of forest fragments among open agricultural fields promotes bee richness and subsequent pollination services (Schrader *et al* 2017). This is in line with similar research illustrating the potential value for incorporating natural environments among agricultural fields to support crop pollination (Klein *et al.* 2003, Kremen *et al.* 2002, Cranmer *et al.* 2012). Furthermore, the juxtaposition and types of forest management practices may have important implications for native tree species that have more restricted suites of pollinators. For example, bigleaf maple (*Acer macrophyllum*) outcrossing rates in forested settings were lower than expected given the species' dependence on insect pollinators (Iddrisu and Ritland 2004). This indicated a low density of insect pollinators in

the area of study and further highlights the importance of pollinators for forest tree species (Iddrisu and Ritland 2004). Management practices that promote a diversity of bees, such as the group selection method studied, may help address the issue of pollinator limitation related to pollinator decline.

Conclusions

Many practices such as the group selection and shelterwood reproduction methods and thinnings involve the creation of openings of various shapes and sizes. It may be possible to identify subtle changes to these management practices that would benefit pollinators, while still achieving desired effects on timber species. Our study illustrates the differences in bee community, diversity, and indicator species between microsite types created by the group selection method. Center of cut microsites supported a more diverse bee community than forest microsites, however both microsites are needed to support differing bee communities. Additional research is needed on the impact of silvicultural methods that span a gradient from minimal intensity (e.g., single tree selection) to more intensive methods, (e.g., the shelterwood method, thinnings, and other practices) on pollinators to inform and achieve more holistic management of pollinators in forest ecosystems.

CHAPTER 2

INTER-CUT AND INTRA-CUT POLLEN MOVEMENT IN GROUP SELECTION STANDS AS A FUNCTION OF DISTANCE BETWEEN CUTS

Abstract

As insect pollinator populations continue to decline, it is essential to understand the impacts anthropogenic activities have on the pollination abilities of these communities. Silvicultural practices are a form landscape management that can impact the ecosystem service of insect pollination. While multiple studies have investigated the overall foraging patterns of bees, the direct impacts of certain types of silvicultural practices on pollination of forest plants is less understood. Using fluorescent powder as a pollen proxy, I investigated inter- and intra-population insect-mediated movement of pollen between plants in group selection canopy openings in four mixed-mesophytic forest stands in the Nantahala National Forest (Graham County, North Carolina, USA). In particular, inter-cut (i.e., between-cut) movement of the pollen proxy between openings was compared as function of the distance between openings, which ranged from 25 m to 200 m in stands. The probability of intra-cut (i.e., within-cut) pollination was greater than inter-cut pollination in stands. Results also revealed that the distance between openings within a stand did not have a significant effect on pollen proxy movement among openings. These results suggest that the spatial arrangement of group selection cuts in a stand, reflecting the typical distance between openings, do not affect the low frequency of inter-cut insect-mediated pollen movement in forest stands typified by the sizes in our study.

Introduction

Animal-mediated pollination is an essential ecosystem service. Many plants have evolved to rely in part or completely on animal-mediated pollination (Friedman and Barrett 2008, Endress and Doyle 2009, Wragg and Johnson 2011). Globally, it has been estimated that approximately 87.5% of all flowering plant species are animal pollinated in natural systems (Ollerton *et al.* 2011) with bees as the group that contribute the most to this pollination (Winfree

et al. 2011). Humans directly benefit from animal-mediated pollination, particularly the pollination of agricultural crops. Many important crops are reliant on bees for pollination (Westerkamp and Gottsberger 2000, Klein *et al.* 2007). With both natural and agricultural systems relying so heavily on bees and subsequent pollination, it is essential to understand factors that may impact this important ecosystem service that bees provide.

Pollination as a function of distance between intraspecific insect-pollinated plants, apart from Allee effects affiliated with low population numbers, can be influenced by insect species and landscape attributes. In *Bombus* (bumblebee) species alone, there are widely differing observations of foraging distances ranging from a 350 m radius to a 4 km radius around the nest site (Walther-Hellwig and Frankl 2000). In agricultural and grassland study sites, sixteen species of solitary bees were found to vary in their maximum foraging distances, ranging from 150-600 m (Gathmann and Tschardtke 2002).

The distance that bees travel to forage depends on a number of landscape factors and may vary depending on the structure of the surrounding environment (Walther-Hellwig and Frankl 2000). Food resources available in the nest area impact bee foraging distances, and bees have been found to travel farther to forage if their nests are in an area scarce in food resources than if their nests are in resource-rich areas (Heinrich 1979). For example, the foraging trip duration of the polylectic species *Osmia rufa* was shown to decrease as plant species richness increased, possibly due to an increase in pollen availability (Gathmann and Tschardtke 2002). This same study also found that two oligolectic species *Megachile lapponica* and *Chelostoma rapunculi* were less likely to colonize artificial nests that were further away from their respective food plants (Gathmann and Tschardtke 2002). Foraging behavior and bee-mediated pollination can also be affected by anthropogenic activities. In agricultural systems, pollination of crops has

been found to be more successful with greater proximity to and proportion of natural habitat (Kremen *et al.* 2002, Greenleaf and Kremen 2006). In grassland habitat patches fragmented by intensive agriculture, species abundance and richness of flower visiting bees decreased with increasing grassland patch isolation (Steffan-Dewenter and Tschardt 1999). In areas of 19.6 ha, polylectic bee species in tropical forests were less likely to be present in areas of greater forest loss (Lichtenberg *et al.* 2017). This could eventually result in less successful pollination of forest plants within and between forest fragments.

Many silvicultural and forest management activities in temperate forests are planned anthropogenic disturbances that may have significant effects on bee-mediated pollination success in harvested areas. Silvicultural practices have been found to create environments that support higher bee species diversity than closed canopy forest (Romey *et al.* 2007, Hanula *et al.* 2015, Rubene *et al.* 2015, Roberts *et al.* 2017, Mullally *et al.* in review). Furthermore, cut microsites created by group selection harvests have been found to support high bee diversity (Mullally *et al.* in review), which may in turn support successful bee pollination in forest stands. While successful bee pollination has been shown to be positively correlated with bee abundance and diversity (Williams and Winfree 2013, Geib *et al.* 2015, Blitzer *et al.* 2016, Crusser *et al.* 2016), the impacts of group selection silviculture on pollination of regenerating plants between cuts has not yet been investigated. Indeed, animal-mediated pollination of non-crop plants in managed forest systems remains a relatively unexplored area, and it could be posited that pollination among patches created by silvicultural practices would be a function of the distance between such patches. To address this question, I quantified the effects of distance between group selection-sized cuts on inter- and intra-cut pollen movement within four forest stands in the Nantahala National Forest (Graham County, North Carolina, USA).

Methods

Study Sites

This study was conducted in mixed-mesophytic forest stands in the Nantahala National Forest, Cheoah Ranger District in southwestern North Carolina during the summer of 2017. Sites were dominated by *Quercus spp.* and *Liriodendron tulipifera* in the overstory and a high abundance of *Rhododendron maximum* in the middlestory and understory. Three of the group selection cuts studied were created by logging contractors in forest stands during late winter 2016 and a fourth in fall 2016 (Fig. 2.1). Each stand contained five 0.4 ha cuts group selection cuts. Unlike most tree harvest situations, felled trees in this study were left on the ground and not removed; while this caused the treatment to be less intensive than typical group selection harvests, areas in the center of cut microsites did experience full canopy removal and hence more open conditions than prior to the cuts.

Field Methods

To determine if inter-cut pollen movement is affected by the distance between cuts, pollen movement was estimated using fluorescent powder. At each site, one pair of cuts was used. In two stands, the distance between the chosen openings was approximately 25-50 m, and in the other two stands, the distance between the chosen openings was approximately 100-200m. Five potted *Salvia greggii* plants were placed in the centers of the two cuts in each of the four study stands. *S. greggii* is native to Texas (Hatch *et al.* 1990) but was chosen for this study because it flowers in the fall and documented instances of bee-mediated pollination (Frankie *et al.* 2009, Wester and Claben-Bockhoff 2011). Fluorescent powder was deposited on the anthers



Figure 2.1. Map of study sites in the Nantahala National Forest of western North Carolina. Red pins indicate the four stands used in pollen experiments. Experiments took place in August and September 2017.

of four flowers on four of the *S. greggii* plants in each cut using a toothpick (Alder and Irwin 2006). One *S. greggii* plant in each cut patch was not treated with powder to document both intra-cut and inter-cut pollen proxy movement. Blue powder was deposited on plants in one cut and red powder was deposited on plants in the opposite cut (Fig. 2.2). Plants were placed in cut centers in a circular arrangement each approximately 5 m apart, the non-powdered plant was placed in the center of the circular arrangement, and all plants were left for approximately 48 hours. After this period, each powdered flower grouping was collected and placed in individual collection tubes. Remaining flowers were powdered, left for approximately 48 hours, and collected in the same manner. All observations on a given plant across between the two sampling dates were pooled. Flowers were then examined with a dissecting microscope to determine if there was any movement of the pollen proxy.

Statistical Analysis

For inter-cut analysis, fluorescent powder data from each plant was kept separate and pooled across the two collection dates. Data were pooled by date to eliminate the need of including date as a random effect. Data from center flowers were also utilized. The R package lme4 v.1.1-17 (Bates *et al.* 2015) was used to build generalized linear mixed models (GLMMs) with a binomial distribution to test for effect of distance between gaps (i.e., 50 m or 100 m) on the probability of detecting opposing cut fluorescent powder on flowers. In the final GLMM, stand was included as a random variable. Using the R package car v.3.0 (Fox and Weisberg 2011), an ANOVA was performed on the final GLMM to determine if distance between forest openings had a significant effect on the probability of detecting opposing cut fluorescent powder on flowers. All statistical analyses were completed using the statistical language R v. 1.1.414 (R Core Team 2017)

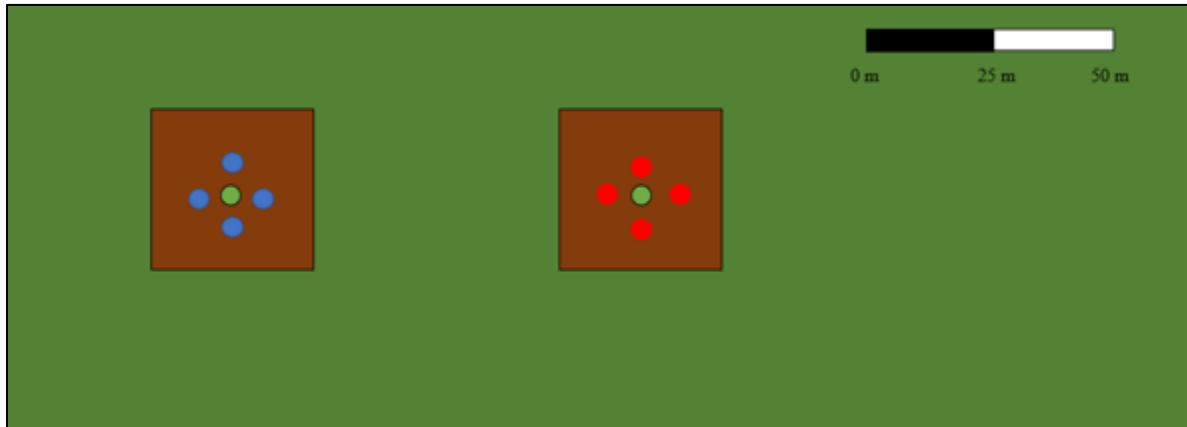


Figure 2.2. Schematic of fluorescent powder sampling of stand using only one pair of cuts separated by 50 m. Brown squares represent forest cuts, green represents contiguous forest. Blue circles represent *S. greggii* plants with blue powder applied, red circles represent *S. greggii* plants with red powder applied, and green circles represent plants with no powder applied to flowers. Circles and the distance between them are not to scale.

Results

From the analysis of the final inter-cut GLMM, the distance between cuts did not have a significant effect on the probability of detecting inter-cut pollen proxy movement ($\chi^2 = 0.002$, $p = 0.96$). On average, one plant out of ten received pollen from the opposite cut. However, all instances of inter-cut pollen movement were found in stands with short distances separating cuts. The rate of inter-cut pollen movement in stands with cuts separated by short distances was 0.2 (Fig. 2.3).

Although there were not enough samples to perform statistical analysis on intra-cut pollen movement ($n = 8$), 50% of the samples were found to have within-in cut pollen movement. Intra-cut pollen movement was equally common in the two distance treatments (Fig. 2.3). Two instances of this intra-cut pollen movement were in stands with short distances between cuts and the other two instances were in stands with long distances between cuts.

Discussion

No significant differences in the rate of inter-cut pollen movement as a function of distance between forest cuts were evident in our study incorporating group selection cuts. Because of the differences in sampling effort between the two pollen proxy movement analyses and because the intra-cut pollen movement data points are also included in the across cut analysis, we cannot compare the results of these two analyses. However, the rate of intra-cut pollen movement (0.5) was higher than the rate of inter-cut pollen movement (0.1). The general lack of inter-cut pollen proxy movement suggests that pollinators are remaining within forest cuts.

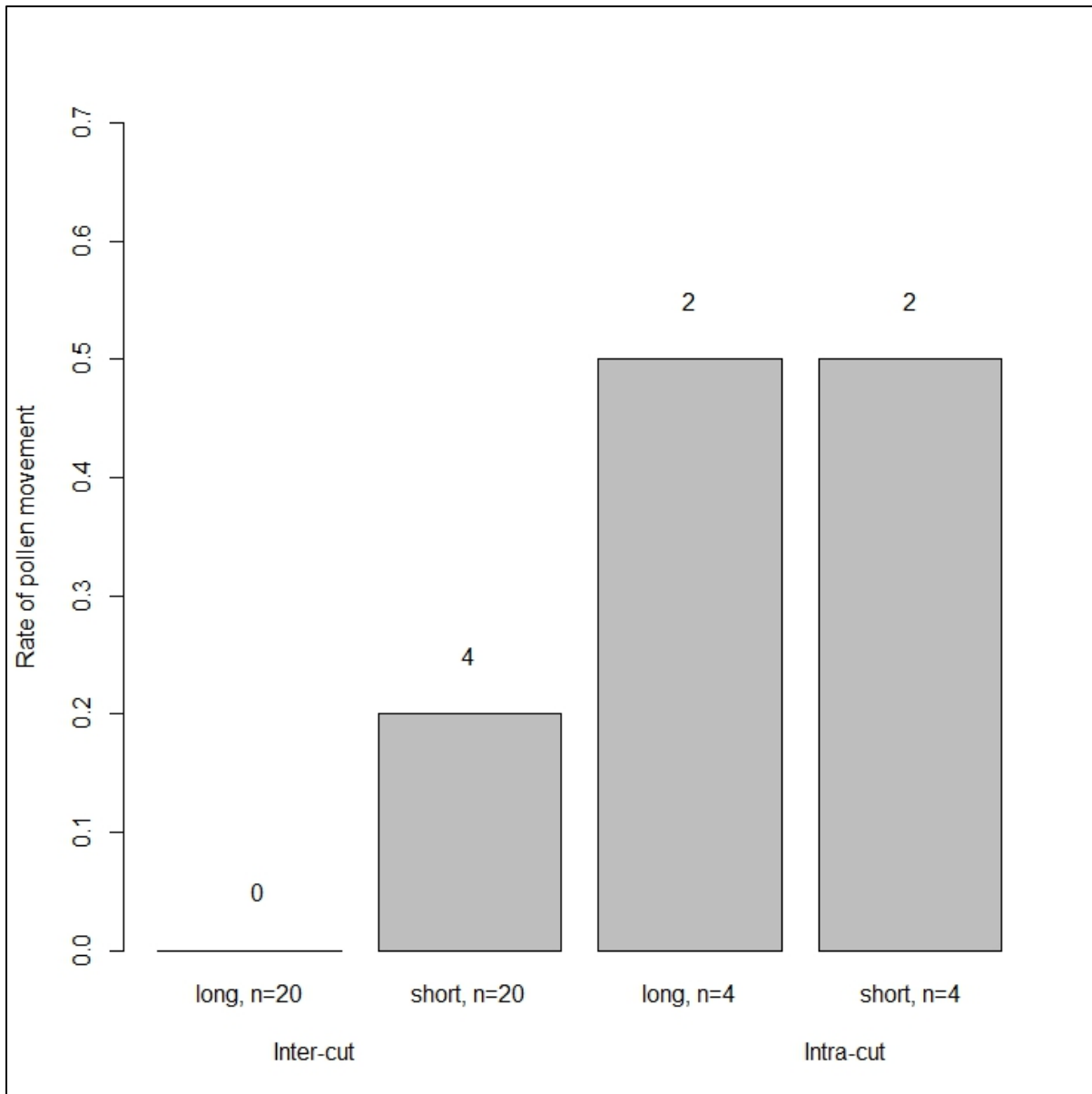


Figure 2.3. Comparison of rates of pollination between distance treatments (long v. short) for inter-cut (n=40) and intra-cut (n=8) samples.

Two main factors could have influenced the results. First, the closed canopy forest separating the cuts may be acting as a barrier to foraging and pollen dispersal for some pollinators. The majority of research regarding barriers to bee movement has focused on agricultural systems (Steffan-Dewenter and Tscharrntke 1999, Walther-Hellwig and Frankl 2000, Kremen *et al.* 2002, Greenleaf and Kremen 2006, Zurbuchen *et al.* 2010, Krewenka *et al.* 2011) and tropical forests experiencing fragmentation (Suni and Brosi 2012, Suni *et al.* 2014, Lichtenberg *et al.* 2017), but the general ideas may apply to forests in southern Appalachia. Species richness and abundance of bees decreased with increasing distances between ideal grassland habitat in Germany, suggesting that there was less movement between isolated grassland patches than between patches in close proximity (Krewenka *et al.* 2011). In grassland habitat fragmented by intensive agriculture, the number of seeds per plant significantly decrease as the distance between grassland habitat fragments increased (Steffan-Dewenter and Tscharrntke 1999). Species abundance and richness of flower visiting bees also decreased with increasing habitat isolation (Steffan-Dewenter and Tscharrntke 1999), which may in turn decrease the rate of successful pollination of plants in habitat patches (Geib *et al.* 2015). Even though certain bees have documented foraging distances that exceed the amount of agricultural separation between habitat, these populations have been found to restrict themselves to shorter foraging distances (Zurbuchen *et al.* 2010). In a tropical forest landscape fragmented by anthropogenic changes (towns, agriculture, etc.) one abundant orchid bee, *Euglossa bombiformis*, was found to have a significant positive correlation with genetic differentiation and distance between forest fragments within years (Suni and Brosi 2012). However, the tropical orchid-bee species, *Euglossa championi*, was found to have low levels of genetic differentiation between forest fragments within years, even in fragments separated by over 80 km (Suni and Brosi 2012, Suni *et al.* 2014).

In this case, fragmentation of desirable habitat caused a significant barrier to movement for one species, but not another. While the intensive agriculture and habitat fragmentation in these studies are much less hospitable than the intact forest in the present study, stretches of forest may be comparable to agricultural fields in that they inhibit ease of foraging for bees between the desirable habitat of forest openings.

A second possibility explaining our result of the lack of a distance effect on inter-cut pollen movement in our group selection harvest system is that the cuts may be providing the necessary resources for pollinators, such that they do not need to move between cuts. A variety of native bees rely on areas of disturbance and openness for food and nesting sites (Steffan-Dewenter 2002) and groups selection sites similar to those utilized in this study can provide this disturbance. My study sites had more bare ground than the forest interior, which is necessary for bee species that burrow into cleared spaces (Vaughan *et al.* 2015). These conditions also create an ideal environment for shade-intolerant species of flowering plants which often provide bees with food. The presence of plants of this guild has been found to be positively correlated with bee abundance (Campbell *et al.* 2006, Hanula and Horn 2011, Hanula *et al.* 2015). A resource rich area such as forest openings may reduce the need for foraging trips outside of the area, resulting in the low level of pollen movement documented in this study.

The results from this study were likely heavily influenced by the small sample size. After pooling the data between the two sampling dates, there were 40 data points for the across-cut portion of the study and eight data points for the within-cut portion. Additionally, there were only four data points which displayed pollen proxy movement between cuts for either treatment. Future research on the subject of pollen movement between and within group selection cuts will need to incorporate a larger sample size to fully capture any effects distance between cuts have

on pollen movement. This study only compared silvicultural cuts that were either 25-50 m apart or 100-200 m apart. These two distance ranges may be too similar to have differing impacts to pollen movement. Group selection cuts within a stand can be made with varying spatial arrangements and ranges of distances between them. This study would be improved by including stands where cuts were much farther apart and stands with even less forest separating cuts.

Conclusions

Group selection silviculture is a form of anthropogenic disturbance that may affect the process of pollination. The results of this study did not yield significant differences in the rate of inter-cut pollen movement as a function of the distance between cuts. The sample size of intra-cut pollen movement was too small to statistically analyze, but the probability of intra-cut pollen movement was higher than the probability of inter-cut pollen movement. The lack of inter-cut pollen proxy movement along with the higher probability of intra-cut pollen proxy movement suggest pollinators are remaining within forest cuts. Intact forest may be functioning as a barrier to movement between cuts. Cuts may also provide nesting and food resources such that the need for bees to move between cuts is decreased. In order to fully appreciate the impacts of group selection silviculture on pollen movement and pollination, future studies should incorporate larger sample sizes and a wider range of distances between cuts to more fully reflect the diversity of group selection cut possibilities.

CONCLUSION

Group selection silviculture impacts bee communities in the southern Appalachian region. Microsites associated with this silvicultural method differ in community composition, diversity, and indicator species. Center of cut and forest microsites were consistently significantly different from each other in these three criteria. Edge microsites are similar to center of cut microsites in the three criteria examined. However, subtle differences between edge and center of cut microsites and the significant differences between the edge and forest microsites suggest that edge microsites provide an important environment type for bees which is not fully covered by center of cut nor forest microsites. While center of cut microsites supported a more diverse bee community than forest microsites, both microsites are necessary to sustain differing bee communities. This study did not find differences in the rate of inter-cut pollen movement as a function of the distance between group selection cuts. However, the probability of intra-cut pollen movement was greater than the probability of inter-cut pollen movement. Intact forest acting as a barrier to movement between group selection cuts or an enhanced environment within cuts may explain general lack of inter-cut pollen proxy movement. A larger sample size and a wider variety of distances between silvicultural cuts should be used in future research. This study is the first to quantify the differences in bee community composition and diversity across microsites created by group selection silviculture in southern Appalachia. It illustrates the potential to integrate management methods which would benefit pollinators while simultaneously achieving the desired effects on important timber species.

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APPENDIX

Appendix. Species abundances in each microsite and total species abundance across all microsities, pooled across stands and dates. Cut and edge microsities had twice as many sampling points as the forest microsite, but the unevenness in sampling was accounted for in statistical analysis.

Species	Abundance			
	Cut	Edge	Forest	Total
<i>Andrena</i> sp.1 2016	2	1	1	4
<i>Andrena</i> sp.1 2017	1	0	0	1
<i>Andrena</i> sp.2 2016	0	1	0	1
<i>Andrena</i> sp.2 2017	5	3	2	10
<i>Andrena</i> sp.3 2016	0	1	0	1
<i>Andrena</i> sp.4 2016	0	1	0	1
<i>Anthophora</i> sp.1	0	1	0	1
<i>Apis mellifera</i>	7	2	0	9
<i>Augochlorerlla aurata</i>	10	12	2	24
<i>Augorchloropsis metallica</i>	1	1	0	2
<i>Augorcholora pura</i>	61	30	32	123
<i>Bombus bimaculatus</i>	3	3	0	6
<i>Bombus impatiens</i>	6	6	2	14
<i>Bombus perplexus</i>	0	0	1	1
<i>Bombus sandersoni</i>	2	0	0	2
<i>Bombus</i> sp. unknown2017	3	8	2	13
<i>Bombus</i> sp.1 2017	0	3	2	5
<i>Ceratina calcarata</i>	1	5	0	6
<i>Ceratina dupla</i>	0	1	0	1
<i>Ceratina strenua</i>	1	0	0	1
<i>Halictus ligatus/poeyi</i>	0	1	0	1
<i>Halictus parallelus</i>	0	0	0	0
<i>Halictus rubicundus</i>	0	1	0	1
<i>Lasioglossum bruneri</i>	61	43	4	108
<i>Lasioglossum callidum</i>	1	0	0	1
<i>Lasioglossum ceanothi</i>	0	1	0	1
<i>Lasioglossum cinctipes</i>	1	0	0	1
<i>Lasioglossum coeruleum</i>	8	9	16	33
<i>Lasioglossum coriaceum</i>	1	0	0	1
<i>Lasioglossum cressonii</i>	145	90	7	242
<i>Lasioglossum foxii</i>	0	1	0	1
<i>Lasioglossum heterognathum</i>	1	0	0	1
<i>Lasioglossum imitatum</i>	3	0	0	3
<i>Lasioglossum smilacinae</i>	1	0	0	1
<i>Lasioglossum</i> sp. unknown 2016	5	4	2	11
<i>Lasioglossum</i> sp. unknown 2017	9	6	2	17

Species	Cut	Forest	Edge	Total
Lasioglossum sp.1 2017	1	1	0	2
Lasioglossum sp.2 2017	1	1	0	2
Lasioglossum sp.3 2017	5	5	3	13
Lasioglossum sp.4 2017	4	5	0	9
Lasioglossum sp.5 2017	3	2	0	5
Lasioglossum sp.6 2017	1	1	0	2
Lasioglossum sp.7 2017	38	35	5	78
Lasioglossum sp.8 2017	11	10	2	23
Lasioglossum sp.9 2017	1	0	0	1
Lasioglossum tegulare	3	1	1	5
Lasioglossum versans	2	1	0	3
Lasioglossum versatum	2	4	0	6
Lasioglossum viridatum	15	17	4	36
Megachile gemula	1	0	0	1
Megachile mendica	2	1	1	4
Melissodes bimaculata	1	0	0	1
Melissodes tepaneca	0	1	0	1
Osmia georgica	0	1	0	1
Peponapis pruinosa	1	0	0	1
Sphecodes sp.1	0	1	0	1

VITA

Hannah Mullally grew up in eastern Nebraska and has always had an interest in nature and conservation. Hannah graduated with a Bachelor of Environmental Science in 2016 from Creighton University where she completed undergraduate research focusing on butterfly pollination in native tallgrass prairies. She continued her research with pollinators at the University of Tennessee, Knoxville to obtain her Master of Science degree in Wildlife and Fisheries. Upon graduating with her M.S., Hannah hopes to work for a non-profit conservation organization where she can use her knowledge of both conservation science and policy. When she isn't working in the lab or studying, Hannah can be found hiking, camping, or volunteering with her favorite community center in Knoxville.