THE EFFECTS OF FIRE SPATIAL CHARACTERISTICS ON POLLINATORS WITH A FOCUS ON PRESCRIBED FIRES IN THE SOUTHEASTERN UNITED STATES

by

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(Under the Direction of Joseph V. McHugh and Michael D. Ulyshen)

ABSTRACT

Fire is an ecological and evolutionary force on the regulation of species traits, population dynamics, species interactions, and community composition. Reactions to fire disturbances result in adaptations to persist in the habitat, and/or recolonize post-fire. Early research investigated the frequency, seasonality, and severity of fire, but our understanding of how the spatial extent of fire and landscape heterogeneity may impact biodiversity remains underdeveloped. Fire management is structured around conservation objectives and the manipulation of one or more fire characteristics to meet said objectives. Insects are an integral part of these fire disturbed habitats, and their response to fire has gained a lot of recent attention.

Insects are the most biodiverse animal group in the world, and they present many excellent potential bioindicator taxa to assess trends in community composition and dynamics. Insects also possess a wide range of functional diversity and provide critical ecosystem services such as pollination. Insects, and specifically pollinators, have experienced several anthropogenic stressors and disturbances that have led to the concern over the “insect apocalypse.” Conservation research into the optimal habitat conditions to support pollinator communities has been growing over the past few decades. Our goal is to better understand the mechanisms of how pollinators respond to the spatial characteristics of fire.

Results from a meta-analysis suggest that the total area of a fire does not impact pollinators. In loblolly pine forests, we find a negative effect of the internal buffer distance on pollinator communities. However, species richness and diversity remain high in the centers of burns, suggesting the pollinator community is not limited in their ability to recolonize these habitats post-fire. In longleaf pine forests, with even larger internal buffer distances, we find that pollinator diversity is greater in the center than compared to the edge of burns. Our findings suggest that prescribed fire is beneficial to the pollinator communities, and that fire size is not limiting pollinator communities from recolonizing the centers of burns in pine forests of the southeastern United States. Other spatial data such as landscape heterogeneity or pyrodiversity may help us understand the mechanisms behind the effects of fire on pollinators.

INDEX WORDS: Insects, Pollinators, Bees, Butterflies, Fire Ecology, Landscape Ecology, Fire Size, Loblolly Pine, Longleaf Pine, Pyrodiversity

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DEDICATION

I dedicate my dissertation to my partner Matthew and my family for their support. Writing a dissertation is filled with peaks and valleys, and my experience was no different. When the work seemed unconquerable, they provided encouragement and empathy. When I would seemingly enter a fugue state and excitingly ramble about a project or analysis, they would listen (at times begrudgingly). I always felt that I had the help to fight through the work and test the unknown.

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“Never be so polite, you forget your power. Never wield such power, you forget to be polite.” – Marjorie by Taylor Swift.

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CHAPTER 1

INTRODUCTION

Fire is an ecological process that impacts various traits of plants and animals, and humans have been manipulating fire for their purposes for hundreds of thousands of years (Pausas & Keeley 2009, Bowman et al. 2009; Pausas & Ribeiro 2017). Wildland fire science include both wild (naturally, accidentally, or intentionally (arson) ignited) and prescribed fires (intentionally ignited for land management), and most of the research in this field focuses on wildfire behavior and its impacts on the ecosystem (Hiers et al. 2020). Prescribed fire is a tool used to meet land management objectives including increasing biodiversity and habitat quality as well as reducing risks associated with invasive species or fire hazards (Fernandes & Botelho 2003; Agee & Skinner 2005; Xanthopoulos et al. 2006; Fowler & Konopik 2007; Stephens et al. 2012; Ryan et al. 2013; Kalies & Kent 2016; Stephens et al. 2021). Scientists have documented how fire impacts human interests such as property and public health concerns (Bowman et al. 2011) and biotic interactions (Bradstock et al. 2005; Kelly et al. 2014; Bowman et al. 2016). Currently, human management of fire has focused on manipulating one or more of six fire characteristics: fire interval, fire intensity, vertical spread, seasonality, horizontal spread, and fire size (He et al. 2019). The impact prescribed fire has on an ecosystem is determined by intricate interactions between burning conditions (fuels, fire weather, etc.), ignition characteristics, attributes of study organisms, and other moderating effects (historical disturbances, climate, soil, and land use), and how these interactions change over time (O’Brien et al. 2018; Pausas & Keeley 2019; Cochrane & Bowman 2021). Our focus is on how the decisions regarding the human management of fire (prescribed fire primarily) can impact fire behavior and how a habitat or community responds.

Studies on how fire management affects important groups that provide ecosystem services (e.g., insect pollination Ollerton et al. 2011; Klein et al. 2007) have gained a lot of attention as to how these management decisions could impact conservation efforts (NRC 2007; IPBES 2016). Insect pollinator conservation efforts have increased in recent years as their communities have experienced worldwide declines due to landscape-scale changes in land use, habitat fragmentation, agricultural intensification, etc. (Aguilar et al. 2006; Potts et al. 2010; Winfree 2010; Burkle et al. 2013). Forest habitat provides unique floral and nesting resources to pollinators (Mader et al. 2011; Hanula et al. 2016), and the pollinator community found in these forest habitats are often distinct from neighboring habitats (Harrison et al. 2017; Fortuin & Gandhi 2021). These habitats respond with an increase in floral resources which benefit the pollinators following prescribed fires (Huntzinger 2003; Wagner et al. 2003; Waltz and Covington 2004; Campbell et al. 2007; Nyoka 2010; Hanula et al. 2015; Strahan et al. 2015). However, pollinators do not have any known adaptations to survive the direct effects of fire, and they are believed to flee the lethal temperatures of fire and must recolonize the habitat post-fire from the neighboring unburned habitat (Pausas & Parr 2018). While pollinators are known to benefit from fire through the freshly available floral resources (Carbone et al. 2019; Mason et al. 2021), there is a gap in our understanding of how the spatial components of fire may affect pollinators and other conservation concerns (Mason and Lashley 2021).

The purpose of this research is to determine how the spatial components of prescribed fire management decisions (size and shape of fires) impact pollinator communities by creating conditions where they are unable to disperse and recolonize into burned habitats. In the second chapter of this dissertation, we will ask if the total area of a burn unit impacts the pollinator community. The results from the meta-analysis add to previously published positive responses of pollinator communities to fire, but do not detect any response to changes in fire size. In the third chapter, we assess the effect of distance from unburned edge on pollinator communities in loblolly pine forests in the Piedmont region in the southeastern United States. Pollinator abundance, richness, and diversity modestly decline with increasing internal buffer distance. We also suggest alternative interpretations to these results that involve other effects like habitat conditions, historical management choices, and spatial heterogeneity of fire behavior that could impact the response of pollinator communities to fire. In the fourth chapter, we test the spatial characteristics of fire on pollinators in the longleaf pine ecosystem, which has experienced prescribed fires longer than loblolly pine forests. The bee community from large (>500 ha) burn blocks are significantly greater in the centers of the burn units compared to the edge habitat. These three chapters demonstrate continued evidence for the positive effects of prescribed fire on pollinator communities through the increased availability of floral resources post-fire. The negative effects observed were subtle and may indicate that the pollinator community persists within these burned habitats using refugia created by heterogenous fire severity. The comparison between pine forest habitats with different prescribed burn histories along with considerations for the variability of fire behavior and conditions throughout the burn blocks suggest the need for additional research. This field of research is evolving and is complicated by multiple types of data and hypotheses that need focused examination. We believe that this work will add to our understanding of the mechanisms with which the spatial extent of a fire impacts pollinator communities.

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CHAPTER 2

HOW DOES THE SIZE OF FIRE AFFECT POLLINATOR COMMUNITIES?[1]

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Abstract

Fire management objectives intended to address conservation concerns have focused on the vegetation community and overlooked how animals such as pollinators respond. There is a growing interest in understanding how different fire characteristics impact pollinator habitats, but scholarship on the spatial characteristics of fire is underdeveloped. We reviewed available literature and completed a hierarchical meta-analysis to ask how the size of fire impacts pollinator communities. Our results demonstrate continued support of the overall positive benefits of fire for pollinator abundance, richness, and diversity. However, there is no evidence that fire size affects pollinator communities found in the limited available literature. Increased appreciation for the importance of spatial data and advances in the ability to share it may help to better understand this relationship and overcome issues with low sample size. More complex metrics of spatial data and a better understanding of how they can be applied in fire management may provide a better picture for research and help explain how pollinators respond to fire.

Introduction

Fire, along with climate and soils, has influenced the composition and distribution of ecosystems for over 400 million years (Bond et al. 2005; Bowman et al. 2009; Pausas & Keeley 2009) with evolutionary consequences that select for traits that enable species to persist through recurrent fires (Keeley et al. 2011, Keeley et al. 2012; Pausas & Parr 2018). These traits affect *in situ* persistence (Pausas et al. 2004; Keeley et al. 2011) and/or *ex situ* recolonization post-fire (Friend 1993; Niemela 1997; Uys et al. 2006). The evolutionary pressures on species' traits are determined by the fire regime(s) as defined by the combination of six fire characteristics: fire interval, fire intensity, vertical spread, seasonality, horizontal spread, and fire size (He et al. 2019). Each characteristic is placed along a continuum of conditions to define a fire event. While previous reviews have focused on frequency (Darracq et al. 2016), intensity (Cannon et al. 2017), severity (Abella & Springer 2015), or seasonality (Miller et al. 2019) as attributes of fire regimes and their effects on biodiversity or conservation, there is a paucity of data on how the spatial extent of fires impacts biodiversity (Mason & Lashley 2021).

The management of forests using fire in an area of growing research interest for pollinator conservation both nationally and internationally (NRC 2007; IPBES 2016). Forest habitats provide unique floral and nesting resources (Mader et al. 2011; Hanula et al. 2016), and the pollinator community composition is distinct from other types of habitats (Harrison et al. 2017; Fortuin & Gandhi 2021). Changes to forest habitat, land use, agricultural intensification, and other stressors are causing pollinators communities to decline (Aguilar et al. 2006; Potts et al. 2010; Winfree 2010; Burkle et al. 2013; Goulson et al. 2015). Given their ecological (Ollerton et al. 2011) and economic importance (Klein et al. 2007), these declines have led to global assessments of how fires impact pollinators and their habitats (Carbone et al. 2019; Mason et al. 2021). However, there is no clear understanding as to how the spatial extent of fires may impact pollinators.

The lack of apparent adaptations to survive the direct effects of fire suggests that pollinators flee their habitat in response to disturbances by fire and they must recolonize the habitat from unburned edges (Pausas & Parr 2018). The size of a fire would then determine the success of recolonization based on a species dispersal capability. The goal of this study is to address the gap in our understanding of how spatial components of a fire regime impact pollinator communities by completing a meta-analysis of published literature. We hypothesize that pollinator abundance, richness, and diversity will respond positively to fire, but that fire size will have a negative effect as they are believed to recolonize burned habitat from unburned edges. Our expectation is that most studies will have been published in the past ten years as online supplemental materials allow authors to provide more details about experimental design and sizes of burned habitat. The total area of a burn is a simple metric of the spatial characteristics of a fire, and we discuss how more complex forms of spatial data can provide further insight. This growing field of landscape ecology and pollinators (Betts et al. 2019) will help explain how fire impacts pollinator communities.

Methods

We performed a literature search using the online database Web of Knowledge with the following search parameters: publications ranging from Jan 1966 - October 2021 and keyword combinations (fire* OR burn*) AND (pollinat* OR hymenoptera OR lepidoptera). While there are many other types of pollinators, we focused on bees and butterflies as the predominant pollinators as they are (respectively) the most frequent flower visitor and can transport pollen farther than other insect pollinators (Winfree et al. 2011). Ants were not included in the literature search because ant pollination is rare and has the potential to limit pollination (Beattie et al. 1984). The search yielded 2088 articles that were filtered to remove studies that did not focus on insect pollinator taxa as is the focus of this review. Studies measuring impacts of fire on non-nectar/pollen feeding life stages (e.g., lepidopteran larvae) were also not included in the literature search (Carbone et al. 2019). Additional articles included were found in previous publications (Carbone et al. 2019; Winfree et al. 2009).

Further filtration procedures removed articles that did not report fire effects on the abundance, richness, or diversity of an insect pollinator taxon and papers that did not include quantitative data necessary to calculate the effect sizes to be used in the meta-analysis (see below). Additionally, papers that did not report information that could lead to the determination or estimation of the size of fires were not included in this study. The final list of the 19 studies included in this meta-analysis is found in the supplemental materials (Table S4.1). For the burn size category variable, burns less than 20 ha were considered small, burns greater than 20 ha but less than 200 ha were considered medium and burns greater than 200 ha were considered large.

Hedges' d was used as the effect size measure for all studies included in this meta-analysis, and was calculated in one of three ways: (a) using the mean values, sample sizes, and standard deviations from the contrasting treatments (burn vs. control) to calculate the standardized difference (Rosenberg et al. 2013), (b) converting results from Z scores to approximate Hedges' d (Lajeunesse 2013), and (c) using the "esc" package in R to convert results from One-Way ANOVAs and χ^2 statistics to approximate Hedges' d (Lüdecke 2019). Negative values of d imply a decrease in the mean value of the abundance/richness/diversity of pollinators in the burned conditions, and a positive value of d indicates an increase as compared to the un-burned treatment.

Each response variable (abundance, richness, and diversity) was modeled using hierarchical mixed effects meta-analysis models using the inverse-variance-weighted values of Hedges' d (Harrison 2011). Models were fit with fixed effects of burn size category and pollinator taxa (abundance and richness) and random effect to estimate the differences across studies (Borenstein et al. 2009). The models also included a random effect of "paper" as a nesting factor that accounted for the hierarchical structure of the data where multiple effect sizes were calculated from the same paper (Stevens & Taylor 2009; see models in supplemental materials Table S2). Additional steps were taken to assess the Q statistics which describe the variation in effect sizes that can be attributed to differences among categories of each predictor variable (Hedges & Olkin 1985). These analyses were completed in R using the "metafor" package with the restricted maximum likelihood "REML" method (R CoreTeam, 2021, version 4.0.3; Viechtbauer, 2010). Datasets used in the meta-analyses are found in supplemental materials (Tables S4.1).

As with any systematic quantitative review, this study could be affected by publication bias (where studies showing significant results are more likely to be published) and is vulnerable to influential outliers. To date, publication bias (e.g., "trim and fill") and sensitivity analyses for multivariate meta-analytical models are evolving and have not been developed within the ‘metafor’ package in conjunction with the rma.mv() function (Viechtbauer & Cheung 2010; Habeck & Schultz 2015). To test for publication bias we used Egger’s regression test (Egger et al. 1997; Sterne and Egger 2005) by modifying the models to include the inverse standard error of the effect sizes as a moderator. Tests with a significant result at $P \leq 0.10$ (Egger et al. 1997) indicate the presence of publication bias (Sterne & Egger 2005). Effect sizes were considered potential outliers when standardized residual values exceeded 3.0 and were then considered influential if hat values were greater than two times the average hat value or if they had comparatively large Cook’s distance values (Stevens 1984; Viechtbauer & Cheung 2010; Aguinis et al. 2013).

Results

Database, data sets, and diagnostics

We identified 19 studies across four countries that met the selection criteria to be included in the study (Table S2.1). Among these studies, 17, 14, and five studies reported data on abundance, richness, and diversity (respectively) of bees and butterflies, which yielded 49 total effect sizes. The range of average burn size was 0.8 – 400 hectares. The expectation that studies included in this meta-analysis would be more recently published was met given that 68% of studies were published in the last five years (Table S2.1). The Egger’s regression test indicated no presence of publication bias for abundance, richness, or diversity models ($P = 0.545$, 0.651, and 0.669 respectively: Table S2.3). The assessment of potentially influential outliers identified multiple studies (Figure S2.1) that were subsequently removed, and analyses were re-run.

Meta-analysis

Both the original and the post-sensitivity analysis models show a positive effect on the overall weighted-mean effect size of fire on pollinator abundance richness and diversity across all studies, but only significant for richness in the original analysis p-value = 0.0209 (Table S2.4) and for abundance in the sensitivity analysis p-value = 0.0179 (Table S2.6). Individual effect sizes and their confidence intervals are included in the supplemental materials Figures S2.2 and S2.3. The total heterogeneity of effect sizes was not significant for abundance, richness, nor diversity (Table S2.5), and the mixed effects models with the moderator variables (burn size and pollinator) showed no significant effect for both the original and post-sensitivity analyses (Tables S2.4 and S2.6).

Discussion

Our results show that overall, the effect of fire is positive and support previous meta-analyses (Winfree et al. 2009, Carbone et al. 2019, Mason et al. 2021). Bee communities in these ecosystems are found to have higher species richness and abundance in habitats with open canopies and a diverse herbaceous understory that provides floral resources (Hanula et al. 2015). These forests habitat conditions are maintained using prescribed fire (Grundel et al. 2010). Plants and their associated pollinator communities has been shown to respond positively just after the fire occurs and decline slowly over time until another fire event occurs (Potts et al. 2003). Given the broad variability in fire characteristics, it is important to assess the ranges of values for the various metrics that best suit the associated flora and fauna.

However, there seems to be no evidence that fire size affects pollinators. Given the strict selection criteria to be considered for this meta-analysis, the sample size for this meta-analysis is considerably small. Future studies published with more explicit information regarding the size of fires could help to examine this relationship more thoroughly. Researchers are increasingly utilizing options to publish online supplemental materials to share this important level of detail in the experimental design that may have been previously omitted when attempting to publish their findings in space restricted journals. We join other calls to publish studies that more fully address how the spatial components of fire may impact biodiversity (Mason and Lashley 2021).

As research on how the spatial components of fire affect biodiversity continues to develop, the specific components of spatial data used to ask these questions should be considered carefully. The theory as adopted from island biogeography (Simberloff 1974) suggests that as the area of the unburned refugia increases the species richness will increase. If we consider unburned habitat within the landscape of various fire regimes as the islands from island biogeography theory, then can see how the size of the fire refugia and the distance into the burned habitat become relevant for how species recolonize post-fire. However, fire severity within the burn blocks can be heterogenous and provide refugia within the boundary that may allow species to persist and recolonize the burned habitat from within. More complex spatial characteristics of fire such as internal buffer distance (Uys et al. 2006; Watson et al. 2012) can have significant impacts on biodiversity (Hortal et al 2009; Kemp et al. 2016) and provide an explanation as to how pollinator communities respond to fire.

Conclusions

Our intention was to contribute to the assessment of fire characteristics and their impact on the pollinator communities. While we demonstrate that pollinators overall respond to fire positively, as previous literature has done, we do not demonstrate that the total size of burn units has any impact on pollinator communities. Based on these results, recolonization may not be as important as initially thought. There are other types of spatial data that may determine if a species is forced to recolonize or can persist following a fire. We join calls for additional research into the spatial characteristics of fire and how they may impact conservation concerns. Lastly, we recognize the simplistic nature of our question and recommend that more complex pieces of spatial data be used to better understand the mechanisms in which pollinator communities respond to the spatial characteristics of fire.

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CHAPTER 3

RECOLONIZATION OF POLLINATORS FOLLOWING PRESCRIBED BURNS IN LOBLOLLY PINE FORESTS (*PINUS TAEDA*) IN THE SOUTHEASTERN UNITED STATES [2]

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[2] Fair CG, Horn S, Ulyshen MD. To be submitted to *Conservation Biology*

Abstract

Prescribed fire is commonly used to control understory vegetation in managed forests and is especially important in regions adapted to frequent fire. Pollinators generally benefit from this intervention, but it remains unknown how the spatial characteristics of fire affects these organisms. We explored how bee and butterfly communities change with increasing internal buffer distances of burn blocks and how time since burn may affect pollinators. We also compared how nesting habitats and dispersal capabilities may influence the responses of individual taxa. We used colored pan traps to sample bees and butterflies along 500 m transects with increasing internal buffer distances into the centers of burn blocks (222-382 ha) in southeastern U.S. forests. We collected data over two years and used a space-for-time approach to sample during all three years of the burn rotation schedule at the Piedmont National Wildlife Refuge. Response to the interaction of distance and time since fire was inconsistent between subsets of the pollinator communities. Bee richness and diversity significantly declined as distance into the burn blocks increased. Moreover, we found no differences in response among nesting guilds (e.g., soil vs. wood-nesters) or body size classes (large vs. small). Butterflies overall were not sensitive to distance although the large butterfly abundance and richness decreased with increasing internal buffer distances. The loss of species richness and diversity, while concerning, do not confirm loss of plant/pollinator interactions, and this could be an indication that this pollinator community is resilient to fire. These data suggest that the spatial characteristics of fire impacts pollinator communities, and that the mechanisms behind this complex process are species specific.

Introduction

Pollinators provide crucial ecosystem services by pollinating approximately 87% of angiosperm plants (Ollerton et al. 2011), and 35% of global food production comes from plants that depend on pollinators (Klein et al. 2007). Bees and butterflies are the predominant insect pollinators given that (respectively) they are the most frequent flower visitors and can transport pollen farther than other insect pollinators (Winfree et al. 2011). Unfortunately, these important communities are declining due to landscape-scale changes in land use, habitat fragmentation, agricultural intensification, and other stressors (Aguilar et al. 2006; Potts et al. 2010; Winfree 2010; Burkle et al. 2013). Forest habitats provide important floral and nesting resources to these pollinators (Mader et al. 2011; Hanula et al. 2016), and the management of forests with prescribed fires has been a focus of pollinator conservation concern both nationally and internationally (NRC 2007; IPBES 2016). Disturbance by fire has maintained ecosystem function and biological diversity in terrestrial ecosystems for millions of years (Pausas & Keeley 2009). Recent meta-analyses have demonstrated the positive and negative impacts of a wide range of fire characteristics on pollinators (Carbone et al. 2019; Mason et al. 2021; Chapter 2, above). However, our understanding of how spatial factors like fire size affect pollinators remains underdeveloped (Betts et al. 2019; Mason & Lashley 2021), and simple spatial data regarding the total area burned does not provide enough explanation into the pollinators' response (Chapter 2, above).

Pollinators respond indirectly to changes in the floral resources caused by disturbances made by fire. In forests managed with prescribed fire, a tool used to meet land management objectives including increasing biodiversity and habitat quality as well as reducing risks associated with invasive species or fire hazards (Fernandes & Botelho 2003; Agee & Skinner 2005; Xanthopoulos et al. 2006; Fowler & Konopik 2007; Stephens et al. 2012; Ryan et al. 2013; Kalies & Kent 2016; Stephens et al. 2021), pollinators and floral resources increased in abundance, richness, and diversity as canopy openness increased (Huntzinger 2003; Wagner et al. 2003; Waltz and Covington 2004; Campbell et al. 2007; Nyoka 2010; Hanula et al. 2015; Strahan et al. 2015). A complex suite of interactions between the burning conditions (fuels, fire weather, etc.), ignition characteristics, attributes of organisms, and other moderating effects (historical disturbances, climate, soil, and land use) determines how the plant and pollinator communities respond to prescribed fire (O'Brien et al. 2018). The frequency of fire is generally seen as the most significant fire characteristic in these fire-adapted communities (Hiers et al. 2000; Kirkman et al. 2004), and researchers have shown that floral resources and pollinator diversity and abundance decline as time since fire increases (Potts et al. 2003; Breland 2015; Moylett et al. 2020). Life history traits will determine how fire severity impacts particular pollinators. For example, immobile butterfly larvae and pupae at or near soil surface are susceptible to high rates of mortality (Hanula et al. 2016) and benefit from low-severity fires (Hill et al. 2017). Bees that nest in twigs/wood aboveground are exposed to lethal fire temperatures while those that nest at depths >10 cm are protected (Cane & Neff 2011) and benefit from fires of moderate severity (Lazarina et al. 2019). Seasonality of fires has been shown to have a neutral effect on plant-pollinator interactions, and that a variable burn season benefits a variety of native plant species (Hiers et al. 2000). These floral resources are reliant on the disturbance of fire to create these open canopy conditions, and the pollinators are responding indirectly to the fire through the changes in the floral resource community.

Pollinators do not have any apparent adaptations to survive the direct effects of fire but are believed to recolonize post-fire to capitalize on the habitat conditions generated by fire (Pausas & Parr 2018). The spatial scale of fire, specifically increasing internal buffer distances from the edge of a burn, has been shown to negatively impact the recolonization of bird (Watson et al. 2012) and invertebrate communities (Uys et al. 2006). The size and shape of a fire determines the distance that animals must travel to recolonize post-fire, and their success is dependent on their dispersal abilities, as predicted by body size (Gathman & Tscharntke 2002) and wingspan (Sekar 2012) as predictors of bee and butterfly dispersal distances (respectively). Like the vegetation community response to fire over time, this negative effect of distance changes with time since fire and becomes less discernable as pollinators continue to disperse (Watson et al. 2012). Our goal is to determine if the prescribed fire management and resulting sizes of fire negatively impact pollinator communities through limiting their ability to completely recolonize the burned area.

To determine if there was support for this recolonization mechanism for pollinators’ response to prescribed fire, we established transects with increasing internal buffer distances in burn blocks. Burn blocks were burned in different years (hereafter referred to as burn cycles), and the pollinator community was sampled over two years. This space for time approach to the experimental design allowed us to sample 1, 2 and 3 years following a burn. We hypothesized that pollinator (bee and butterfly) abundance, richness, and diversity would decline as interior buffer distance increased. We expect this because pollinators leave a habitat in response to fire, and they recolonize the habitat from the unburned edge inward. However, because flowering plants, which are the food source of pollinators, tend to rapidly increase in abundance immediately after a fire and decline over time, we also expected that evidence of recolonization would become less discernable as time since fire increased.

We also tested three related hypotheses comparing body size, nesting guild, and pollinator taxa. First, smaller species were expected to have a stronger decline than larger species as interior buffer distance increased. This is because smaller species have limited dispersal capabilities compared to larger species. Second, wood-nesting bees were expected to have a stronger decline than soil-nesting species as interior buffer distance increased. This is because the fire would consume potential wood-nesting habitat and limit their dispersal capabilities, but the fire would not limit the soil-nesting habitat. Third, bees were expected to have a stronger decline than butterflies as interior buffer distance increased. Since butterflies are known to transport pollen farther than bees, they wouldn’t be as limited in their dispersal capabilities.

Methods

Study Area

This work took place on the ~14,000 ha Piedmont National Wildlife Refuge (PNWR) located on the southern Piedmont plateau, in Jasper and Jones County, Georgia, USA. The PNWR like much of the surrounding area experienced >100 years of fire suppression (Carroll et al. 2002; Stanturf et al. 2002) and soil erosion/degradation from intensive cotton farming and has since been reforested by the US Fish & Wildlife Service

(USFWS 2010b). The PNWR has both upland pine and pine-hardwood forests with a few grassy fields interspersed. Management at the PNWR is focused on habitat requirements for threatened and endangered species (e.g., red-cockaded woodpecker) which includes timber thinning and regeneration, prescribed fire, and openings management (USFWS 2010a). Prescribed fires are implemented on a two- or three-year rotation to managed red-cockaded woodpecker habitat, with approximately 3,600 ha burned each year (USFWS 2010b).

Experimental Design

In spring 2015, we selected three locations that had paired burn blocks (six total burn blocks) neighboring each other within PNWR. Within each pair of burn blocks, one block burned in 2015, and the other burned in 2016 ("Burn Cycle", hereafter). All six burn blocks had burned every three years for at least a decade prior to when this study began, but were burned less consistently prior (Carl Schmidt, personal communication). Subsequent sampling took place in 2015 and 2016 so that the burn blocks burned in 2015 (Burn Cycle 1) created 0-years and 1-year post burn data, and the burn blocks burned in 2016 (Burn Cycle 2) created 2-years and 0-years post burn data (Fig. 3.1). The burn cycle and sampling year interactions created this space-for-time experimental design that captured data from across the three-year period of the prescribed burn cycle.

The burn blocks ranged from 222-382 ha in size and the burns took place between January and March of each year (Table 3.1). The elevation ranged from 400 to 500 feet above sea level. The slope ranged from 0 to 25 % for all aspects. The ground burns on Jan. 30 and Mar. 15, 2015, and Mar. 1, 2016 were contour fired with drip torches and

ATVs. The aerial burns on Feb. 7, 2015, and Feb. 13 and Mar. 14, 2016 were ignited using PLDO released from a helicopter. The fuel loads in the pine stands were 5.78 tons/acre in the litter and duff, 3.97 tons/acre in the wood debris, and 1.35 tons/acre in the vegetation. The fuel loads in the upland hardwood stands were 5.57 tons/acre in the litter and duff, 5.08 tons/acre in the woody debris, and 1.35 tons/acre in the vegetation. All fuel estimates were made from Brown’s transect run through forest vegetation simulator (Brown 1974). The intended spatial pattern of the fire regime was a checkerboard pattern across the refuge, but the carry over units (burn units that didn’t get completed in the previous year and carry over into the next year) create large burn acreages (Carl Schmidt, personal communication). Additional data describing the weather data, dead fuel variables, and National Fire Danger Rating System indices collected from the nearest weather station are documented for each burn (Table S13-S15). Sampling transects were established in each burn block, beginning at the edge adjacent to the other burn block and extending 500 m toward the block center. 500 m was chosen as the maximum distance because farther internal buffer distances would intersect with neighboring edges and was intended to be sufficient to test the dispersal capabilities of the pollinator communities (Gathman & Tscharntke 2002; Sekar 2012). Because the beginning of each transect was adjacent to the forest not scheduled to be burned in the same year, positions along the transects represent distances from “unburned” habitat (although almost the entire landscape for kilometers in every direction is burned every 2-3 years). Sampling points were placed in a line at 50 m increments (11 per transect and 66 in total) so that each point was at least as far from any other edge of the burn block as it was from the beginning edge of the transect (Fig. 3.1; Table S3.1). Due to the presence of uneven burn block boundaries, the internal buffer distance did not match the distance of the sampling points along the transect. The percentage of the relative buffer distance for each sampling point that fell within the boundary of the burn block was multiplied by the distance along the transect to calculate a normalized internal buffer distance (hereafter “distance”).

Data Collection

Plant data and canopy openness

The understory herbaceous plant community and shrub layer was surveyed at each sampling point in July of each sampling year (Fig. S31.B). The line-point intercept method was used to collect the plant community data (Godinez-Alvarez et al. 2009). We placed four 10 m transects centered at each sampling point in the four cardinal directions (only two transects at 0 m sampling point oriented at 45° and 135° into the burn block), then counted and measured the height of each species every meter along each transect (20 intercept points at 0 m sampling points and 40 intercept points along the rest of the transect). Plant diversity, and the median maximum plant height (hereafter “height”) were recorded by calculating the median of every maximum plant height recorded at every meter along each transect. Additionally, observations of bare ground (as potential bee nesting habitat) were collected using the line-point intercept method, and percent bare ground was calculated by dividing the abundance of bare ground observations by the total number of line-point intercept observations at each sampling point. Photographs of the canopy were taken with a Nikon Stylus TG3 camera with a fish-eye lens adapter mounded on a self-leveling tripod to position the camera 0.9 m above the ground and pointing directly up (Fig. S3.1C). Three photographs were taken at each sampling location in 2015 and 2016 (Fig. S3.1D). We recorded the canopy openness from each photo using the software, WinScanopy Version 2006 (Regent Instruments Inc. Quebec City, CA). The canopy openness value for each sampling point was averaged over the three photographs.

Pollinator sampling

We used colored pan traps to collect pollinator community data. Traps were operated for four-day periods six times in 2015 (Year 1) and seven times in 2016 (Year 2), approximately one month apart during fair weather to optimize pollinator capture. We used blue, white, and yellow colored, 355 ml pan traps (commercially available food bowls: www.partycity.com) elevated approximately 30 cm above ground and filled with water and a few drops of soap to reduce surface tension to maximize trap potential (Campbell & Hanula 2007; Steffan-Dewenter & Westphal 2008; Droege 2013) (Fig S3.1A). Three pan traps were established at each sampling point, one of each color randomly placed with one in the center and one 5 m on each side, perpendicular to the transect direction. At the time of collection, the samples from the three bowls at each sampling point were combined. Samples were taken back to the lab and transferred to 70% ethanol for storage. All bees and butterflies in each sample were mounted and identified to species with a combination of printed (Mitchell 1960; Bouseman & LaBerge 1978; Scott 1986; Gibbs 2011; Gibbs 2013) and online (Ascher 2009) reference materials. Categories of nesting behavior and body size were noted for bee species and wingspan for butterfly species (Table S3.2 and S3.3). Nesting groups included soil, wood, "other" (*Apis melifer, Bombus bimaculatus, B. fraternus, B. griseocollis, B.*

impatiens, and *B. pennsylvanicus*, which are known to nest both in the ground and wood) and rotting wood (Michener 2007). Body size and wingspan group determinations were made with species descriptions and other published literature (small bees: <6 mm, medium bees: ≥6 mm or ≤10 mm and large bees: >10 mm) and (small butterflies: ≤3.4 cm, medium butterflies ≥3.4 cm or ≤4.6 cm and large butterflies: ≥4.6 cm) (Scott 1986; Michener 2007). Pollinator abundance, species richness, and diversity were calculated (Shannon 1948) as indicators of the overall pollinator communities response to prescribed fire (Hanula et al. 2016).

Statistical Analysis

We used R (R Core Team 2014) and lme4 (Bates et al. 2015) to assess several linear mixed effects models to test our hypothesis that bee and butterfly abundance, richness, and diversity decreased with increasing internal buffer distances into burn blocks and the effect of distance interacts with time since fire through the interaction between burn cycle and year. Bee and butterfly abundance, richness, and diversity were subdivided into body size and nesting (bees only) guilds to determine if there was a different response based on relevant natural history characteristics. Additional site-specific data including the herbaceous vegetation, canopy openness, and bare ground were included in the model to account for their impact on the pollinator community. The residuals from each model were assessed for normality and transformed with a natural log or square-root transformation and re-run when necessary. The independent variable distance was centered on zero to allow for model convergence and then back transformed to show predicted counts. A mixed model approach was chosen to effectively control for factors that are relevant to the experimental design but are not the primary focus of the study (Zurr et al. 2009). The effect of interest was distance, and we included the two- and three-way interactions with burn cycle and year as fixed effects to capture the effect of time since fire. Plant diversity was also included in the models as a fixed effect to isolate the pollinator community response to changes in the vegetation community. Other covariates (canopy openness and bare ground (only for bee models)) were included in the models as fixed effects. To account for the nonindependence of samples collected from the same burn block location on different dates, we included random effects of location and sampling point, and to account for nonindependence of samples collected in the same burn cycle in different years, we included random effects of burn cycle and year with year as the subplot factor nested within burn cycle treated as the whole-plot factor. Assumptions of ANCOVA were tested by confirming that covariates were not correlated with the categorical variables (burn cycle and year). For final model selection, non-significant covariates were step wise removed, and nested models (model with non-significant covariates, and model without non-significant covariates) were analyzed with a Chi-Square test to determine if the removal of the non-significant covariate significantly changed the model fit. Hypothesis tests (F tests), using the Kenward-Roger denominator degrees of freedom approximation method, were carried out. To produce figures, final models that resulted in a significant effect of distance, the interaction of distance and year, the interaction of distance and burn cycle, or the interaction of distance, burn cycle, and year were further analyzed with out-of-sample predictions using the *effects* package in R (Fox & Weisberg 2019). Similarly, final models that resulted in a significant effect of burn cycle, year, or the interaction of burn cycle and year were further analyzed with difference in estimated marginal means using *emmeans* package in R (Length 2021). Data that were transformed in models were back transformed in the out-of-sample predictions and estimated marginal mean graphs.

Non-metric multidimensional scaling (NMDS) ordination analyses of plant, bee, and butterfly in plots were used to examine community differences (PC-ORD; McCune & Mefford 1999), and we used the Sorensen (Bray-Curtis) distance measure in these analyses. To focus the signal on consistent response trends, only species where $n \geq 3$ were retained for the analysis. The response matrixes included 84 plant species, 69 bee species, and 36 butterfly species in 132 plots. Variables representing species data were relativized by maximum abundance to reduce the influence of highly abundant species. We used the slow and steady autopilot settings for the NMDS analysis. 2-D ordination plots using the two axes that explained the most variation were made. Joint plots, with an R^2 of 0.1 used as the cut-off for vector scaling, were used to examine the effect of distance, and other variables of interest on plant, bee, and butterfly ordination scores. The values for the three resulting axes were also used as community response variables, in addition to the 20 most abundant bee species in linear modeling as described above.

Results

We collected a total of 11,970 pollinators (124 spp. bees, and 43 spp. butterflies) with 6,854 and 1,916 bees, and 1,689 and 1,466 butterflies in sampling year 1 and 2 (respectively). The soil nesting bees represented most individuals collected (89.3%) followed by wood nesting bees (4.7%) other nesting bees (3.9%) and rotting wood nesting bees (2.1%). The small bees also represented most individuals collected (65.6%)

followed by the medium bees (28.1 %) and large bees (6.3%). The medium butterflies represented most individuals collected (76.0%) followed by small butterflies (18.0%) and large butterflies (6.0%). The relative abundances of each bee and butterfly species collected within each location and year and the total number of individuals collected can be seen in tables S3.2 and S3.3.

Spatial and Temporal Effects of Fire

For the three-way interaction between distance, burn cycle, and year, we found that large bee abundance ($F_{1,57.8}$=8.33; Fig S3.12), abundance of *Melissodes bimaculatus* ($F_{1,57.8}$=4.40; Fig. S3.15), abundance of *L. illinoense* ($F_{1,57.9}$=4.24; Fig S3.20), large bee richness ($F_{1,58.1}$=11.88; Fig S3.2), large bee diversity ($F_{1,58.2}$=9.31; Fig S3.6), small bee diversity ($F_{1,58.1}$=4.81; Fig S2.7), and soil bee diversity ($F_{1,60.4}$=5.41; Fig S3.8) changed in response to increasing internal buffer distance depending on interaction with burn cycle and year. Large bee abundance, richness, and diversity declined as distance increased in burn cycle one and year one, and that decline decreased in burn cycle one and year two in the year following the fire. For burn cycle two and year one, the decline was not discernable from zero, and became negative in year two following the fire. However, individual species and different body size and nesting guilds responded differently to the effect of the interaction between distance, burn cycle, and year. The abundance of *M. bimaculatus* and *L. illinoense* declined as distance increased in burn cycle one and year one, and the decline was not discernable from zero for the other burn cycle and year combinations. Small and soil bee diversity declined as distance increased in burn cycle one and year one, and the decline increased in burn cycle one and year two in the year following the fire. The effect of distance was not significantly different in burn cycle two between year one and year two.

For the two-way interactions between distance and burn cycle, distance and year, and burn cycle and year, we found that the bee community for axis 2 ($F_{1,58.1}$=4.32; Fig S3.20A), and butterfly community composition for axis 2 ($F_{1,57.7}$=6.27; Fig S3.23) changed as internal buffer distance increased depending on the burn cycle. The abundance of *L. imitatum* ($F_{1,58.1}$=6.45; Fig S3.18), abundance of *L. tegulare* ($F_{1,58.2}$=10.01; Fig S3.17A), and the bee community axis 2 ($F_{1,58.1}$=14.94; Fig S3.20B) responded negatively to the effect of distance in year one but not year two. Additionally, total bee richness ($F_{1,2.0}$=32.53; Fig 3.2B), small bee richness ($F_{1,2.0}$=46.84; Fig S3.3B), soil bee richness ($F_{1,2.2}$=26.52; Fig S3.4B), total bee abundance ($F_{1,2.0}$=61.35; Fig S3.11), small bee abundance, ($F_{1,2.0}$=50.34; Fig S3.13), and soil bee abundance ($F_{1,2.0}$=64.71; Fig S3.14) decreased from year one to year two in burn cycle one as time since fire increased, but the decline from year one to year two was less pronounced in burn cycle two. Total bee diversity ($F_{1,2.0}$=37.49; Fig 3.2D), and abundance of *L. tegulare* ($F_{1,2.0}$=42.05; Fig S3.19B) decreased from year one to year two in burn cycle one as time since fire increased and no significant change between years in burn cycle two.

For the main effects, year and distance, we found that the abundance of *L. bruneri* ($F_{1,2.0}$=23.46) was greater in year one compared to year two. The bee community composition for axis 3 ($F_{1,2.0}$=64.53) changed between sampling years. Total bee richness ($F_{1,58.1}$=10.76; Fig. 2.2A), small bee richness ($F_{1,57.4}$=9.44; Fig S3.3A), soil bee richness ($F_{1,59.4}$=6.39; Fig S3.4A), wood-nesting bee richness ($F_{1,58.1}$=5.91; Fig S3.5), total bee diversity ($F_{1,58.2}$=18.98; Fig 3.2C), wood-nesting bee diversity ($F_{1,58.7}$=7.53; Fig S3.9), abundance of *L. raleighense* ($F_{1,58.7}$=8.36; Fig S3.16), abundance of *L. apopkense* ($F_{1,58.1}$=11.11; Fig S3.17), large butterfly richness ($F_{1,57.2}$=6.43; Fig S3.22), and large butterfly abundance ($F_{1,56.4}$=4.48; Fig S3.23) declined as internal buffer distance increased.

Nonmetric multidimensional scaling for the bee community composition recommended a three-dimensional solution with a final stress of 20.98. The R^2 values were 0.220, 0.223 and 0.189 for the three axes respectively. The NMDS ordination using axes 1 and 2 for the bee community data indicated a weak correlation with distance along axis 1, which is opposite the correlation of bee richness, diversity, and the abundance of several bee species (Fig 3.3). Nonmetric multidimensional scaling for the butterfly community composition recommended a three-dimensional solution with a final stress of 23.17. The R^2 values were 0.201, 0.163, and 0.144 for the three axes respectively. The NMDS ordination using axes 1 and 2 for the butterfly community did not demonstrate a strong correlation with distance, but butterfly abundance, richness, and diversity, and abundance of several species were correlated with axis 1 in the opposite direction of plant richness and diversity (Fig S3.25B).

Herbaceous vegetation effects

Overall, we identified a total 116 plant species across our three locations and two years. The number of species per sampling point ranged from four to 28. Plant diversity did not have a significant relationship with distance, but plant height had a positive parabolic relationship where plant height was greatest at the edge and in the center of the burn blocks. Percent Bare ground had a negative parabolic relationship with distance where percent bare ground was lowest at the edge and in the center of the burn blocks (results not included). Nonmetric multidimensional scaling for the plant community composition recommended a three-dimensional solution with a final stress of 23.80. The R^2 values were 0.193, 0.156, and 0.188 for the three axes, respectively. The NMDS ordination using axes one and three for the plant community data did not demonstrate a strong correlation with distance or any of the pollinator data (Fig. S3.25A). Canopy openness ranged from 5.22 to 33.91 among the 66 sampling points. Canopy openness had a significant positive parabolic relationship with distance where canopy openness was greatest at the edge and in the center of the burn blocks (results not included).

The herbaceous vegetation community and other covariates were not significant predictors of overall bee abundance, richness, and diversity, but were significant for subsets of the bee and butterfly data. Plant diversity had a significant negative effect on small bee richness ($F_{1,94.2}$=4.12), soil bee richness ($F_{1,67.8}$=6.32), large bee abundance ($F_{1,98.5}$=4.30), abundance of *M. bimaculatus* ($F_{1,86.8}$=4.70), abundance of *L. bruneri* ($F_{1,111.0}$=4.60), abundance of *L. illinoense* ($F_{1,100.3}$=4.69), abundance of *L. hitchensi* ($F_{1,98.4}$=6.76), total butterfly richness ($F_{1,81.5}$=6.27); large butterfly richness ($F_{1,76.6}$=5.62); total butterfly diversity ($F_{1,84.9}$=5.07), total butterfly abundance ($F_{1,117.0}$=6.71), large butterfly abundance ($F_{1,69.9}$=10.06), small butterfly abundance ($F_{1,96.7}$=4.89), and butterfly community composition for axis 1 ($F_{1,98.2}$=8.19). Plant height had a significant positive effect on abundance of *M. bimaculatus* ($F_{1,92.3}$=4.07), bee community composition for axis 3 ($F_{1,81.9}$=5.63), Large butterfly abundance ($F_{1,84.1}$=5.43). Canopy openness had a significant positive effect on abundance of *L. raleighense* ($F_{1,66.2}$=4.12), abundance of *L. hitchensi* ($F_{1,102.1}$=4.27).

Discussion

This work demonstrates pollinators decline as the internal buffer distances of burn blocks increases and that this effect changes with time since fire. These findings provide support for the idea that pollinators are extirpated from a habitat by fire and that their ability to recolonize post-fire is limited by the size of the fire (that is, dispersal into fire blocks is limited by internal buffer distances; *sensu* Uys et al. 2006; Watson et al. 2012). Since we see a consistent negative response among the different body sizes, nesting guilds, and taxa, we do not observe the expected differences in sensitivity to increasing internal buffer distances. Individual species of the vegetation community have species-specific response to fire (Glitzenstein et al. 1990; Robbins & Myers 1992), which suggests further research into individual species of pollinators that may have specific natural history characteristics and cause them to react more negatively to the spatial characteristics of fire. Similar research on pollinators examines the structure of the plant/pollinator network interactions, which provides a different assessment of the success of the ecosystem service provided by the pollinators (Chacoff et al. 2018). We would expect plant/pollinator networks to remain intact as other networks of interactions have been shown to be promoted by frequent prescribed fires (Dell et al. 2019a). The level of clarity provided by this data could help explain the observed species-specific responses to fire and changes in the floral resource community (pollinators declining as plant diversity increases) caused by fire. Unfortunately, this type of data is not captured with colored pan traps, and made more difficult in forest habitats where focal flowers for observations/netting are sparser (Campbell et al. 2007).

The pollinators response to time since fire is also supported by previous literature where an initial positive response is observed followed be a steady decline over time (Potts et al. 2003; Breland 2015; Moylett et al. 2020). However, there was a considerable amount of inter-annual variation primarily observed in the reduction in bee abundance in year two compared to year one. Initial concerns pointed to the loss of bees as an artifact of repeated sampling in the same locations, but bee communities are shown to be robust to lethal sampling in these monitoring programs (Gezon et al. 2015). Wild bee abundance has been shown to vary in response to fluctuations in temperature and precipitation with resulting reductions to foraging behavior (Blüthgen & Klein 2011). It is possible that capturing additional data could help to isolate the effect of fire size (internal buffer distance) on pollinators.

Furthermore, the pollinator community responded to the different burn cycles differently. This indicates that heterogeneity in the fire characteristics between the burn conditions could be driving the pollinators’ response. While we include relevant fire behavior data known to be crucial to compare patterns between studies (Bonner et al. 2021), there is not sufficient resolution of these data to assess confounding interactions with the internal buffer distances measured in this study. The heterogeneity of fire throughout the burn area has the potential to create refugia from which species can escape the lethal effects of fire and act as sources of *in situ* recolonization within the burn unit as compared to *ex situ* recolonization from outside the burn area (Banks et al. 2010). The presence of these islands of refugia within the burn unit would become the relevant boundaries of recolonization for pollinators.

Lastly, we posit an alternative interpretation to these results. While there is a statistically significant decline in the pollinator abundance, richness, and diversity as the fire size (internal buffer distance) increases, we cannot confirm that the ecosystem service of pollination is limited. While assessing the plant/pollinator networks poses sampling difficulties in these forest habitats, there are many endemic species of flowers in these fire-adapted pine forests (Hardin & White 1989; Barnett 1999; Dell et al. 2019b) that could be individually assessed as to how their associated pollinators respond to the spatial characteristics of fire. If the loss of pollinator abundance, richness, and diversity is due to the loss of species associated with these endemic plant species, then there would be a stronger case for concern. An argument could be made that the pollinator community is robust to disturbance caused by prescribed fire, as over two thirds of the bee species still present at the end of the 500 m transects. The decline in pollinator abundance, richness, and diversity in response to fire in this habitat could be attributed to changes in the habitat conditions and historical management choices. Due to the history of fire suppression, forest habitat in the Piedmont region shifted towards dense hardwood forests with a less open canopy and different floral resources (Carroll et al. 2002; Stanturf et al. 2002). The new habitat conditions would support a different community of pollinators that were not adapted to conditions created by fire (Harrison et al. 2017; Fortuin & Gandhi 2021). As recurrent prescribed fires have increasingly been adopted as a land management strategy (Carroll et al. 2002; Stanturf et al. 2002), the habitat conditions have changed and no longer support specialist species. Over time and continued use of prescribed fires, the pollinator community would return to its original composition of fire-adapted species. This begs the question, does the effect of fire size (internal buffer distance) impact pollinators in habitats where prescribed fire has been in use longer and the pollinator community has stabilized to the habitat conditions created by the fire?

Conclusion

We intentionally stop short of making specific management recommendations as specific local factors (conservation priorities, forest type, land use history, etc.) may affect decisions regarding the spatial characteristics of fire (O'Brien et al. 2018). Our goal is to identify patterns and determine support for the recolonization mechanism where pollinators extirpated by fire return to the habitat inward from neighboring unburned habitat. By focusing on the negative effect of distance on total bee richness and diversity, we find one species of bee is lost every 100 meters farther into a burn unit, and lower bee diversity in the centers of the burn unit compared to the edges. This suggests that pollinators respond to disturbance by fire using the recolonization mechanism. However, we find inconsistent support for our hypothesis as individual functional groups of body size, nesting guild, and pollinator taxa show different responses than overall pollinator abundance, richness, or diversity. This highlights the need for more detailed research on species-specific responses to fire. Overall, these results suggest that the pollinator community is broadly resistant to the disturbances caused by fire, and that changes in the forest structure in response to continued use of prescribed fires create resultant shifts in the pollinator community composition. Given the unanswered questions regarding the limited design and available data provided by this study, we suggest continued tests of the recolonization mechanism by pollinators in response to prescribed fire.

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Table 3.1: Descriptive statistics for the different burn blocks chosen for study at the Piedmont National Wildlife Refuge.

Burn Block	Hectares	Burn Dates	Burn Cycle	2015 Canopy Openness	2016 Canopy Openness
Five points	222.58	10 March 2015	1	12.55 ± (1.48)	19.34 ± (2.14)
Natural rock	347.63	7 February 2015	1	12.32 ± (1.34)	16.55 ± (2.11)
Caney creek	341.96	30 January 2015	1	13.79 ± (1.75)	15.11 ± (1.75)
Five points	250.50	14 March 2016	2	12.29 ± (1.17)	17.89 ± (1.81)
Natural rock	231.08	1 March 2016	2	12.52 ± (1.42)	12.35 ± (1.37)
Caney creek	382.43	13 February 2016	2	16.50 ± (1.98)	10.89 ± (1.70)

Table 3.2: ANOVA results for the effects of distance (Dist), burn cycle (BC), year (Yr), plant diversity (PD), plant height (PH), Canopy Openness (Open), Percent Bare Ground (BG), the interaction of distance and burn cycle, the interaction of distance and year, the interaction of burn cycle and year, and the interaction of distance burn cycle and year on natural log-transformed bee abundance (N), square root-transformed bee richness (S), Shannon’s bee diversity (H’), sqrt-transformed butterfly abundance, sqrt-transformed butterfly richness, and Shannon’s butterfly diversity using Kenward-Roger denominator degrees of freedom approximation method.

	Ln(Bee N)	Sqrt(Bee S)	Bee H’	Sqrt(Butterfly N)	Sqrt(Butterfly S)	Butterfly H’
Dist	$F_{1,58.0}=0.44$	$F_{1,58.1}=10.76^{**}$	$F_{1,58.2}=18.98^{***}$	$F_{1,57.5}=1.05$	$F_{1,57.5}=2.18$	$F_{1,57.4}=2.22$
BC	$F_{1,2.0}=0.53$	$F_{1,2.0}=0.67$	$F_{1,2.0}=0.53$	$F_{1,2.0}=0.71$	$F_{1,2.0}=0.08$	$F_{1,2.0}=0.21$
Yr	$F_{1,2.0}=235.42^{**}$	$F_{1,2.0}=143.01^{**}$	$F_{1,2.0}=8.69$	$F_{1,2.0}=1.32$	$F_{1,1.9}=0.82$	$F_{1,2.0}=0.33$
PD				$F_{1,117.0}=6.71^{*}$	$F_{1,81.5}=6.27^{*}$	$F_{1,84.9}=5.07^{*}$
PH						
Open						
BG						
Dist*BC	$F_{1,58.0}=0.25$	$F_{1,58.1}=0.40$	$F_{1,58.2}=2.05$	$F_{1,58.0}=0.86$	$F_{1,58.0}=0.01$	$F_{1,57.9}=0.26$
Dist*Yr	$F_{1,58.1}=3.05$	$F_{1,58.2}=1.16$	$F_{1,58.2}=0.003$	$F_{1,57.4}=0.70$	$F_{1,57.7}=0.61$	$F_{1,57.8}=0.09$
BC*Yr	$F_{1,2.0}=61.35^{*}$	$F_{1,2.0}=32.53^{*}$	$F_{1,2.0}=37.49^{*}$	$F_{1,2.0}=2.04$	$F_{1,2.0}=2.41$	$F_{1,2.0}=1.68$
Dist*BC*Yr	$F_{1,58.1}=2.41$	$F_{1,58.2}=0.25$	$F_{1,58.2}=1.29$	$F_{1,57.7}=0.20$	$F_{1,57.9}=2.41$	$F_{1,58.0}=1.13$

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, and $^{***}p<0.001$

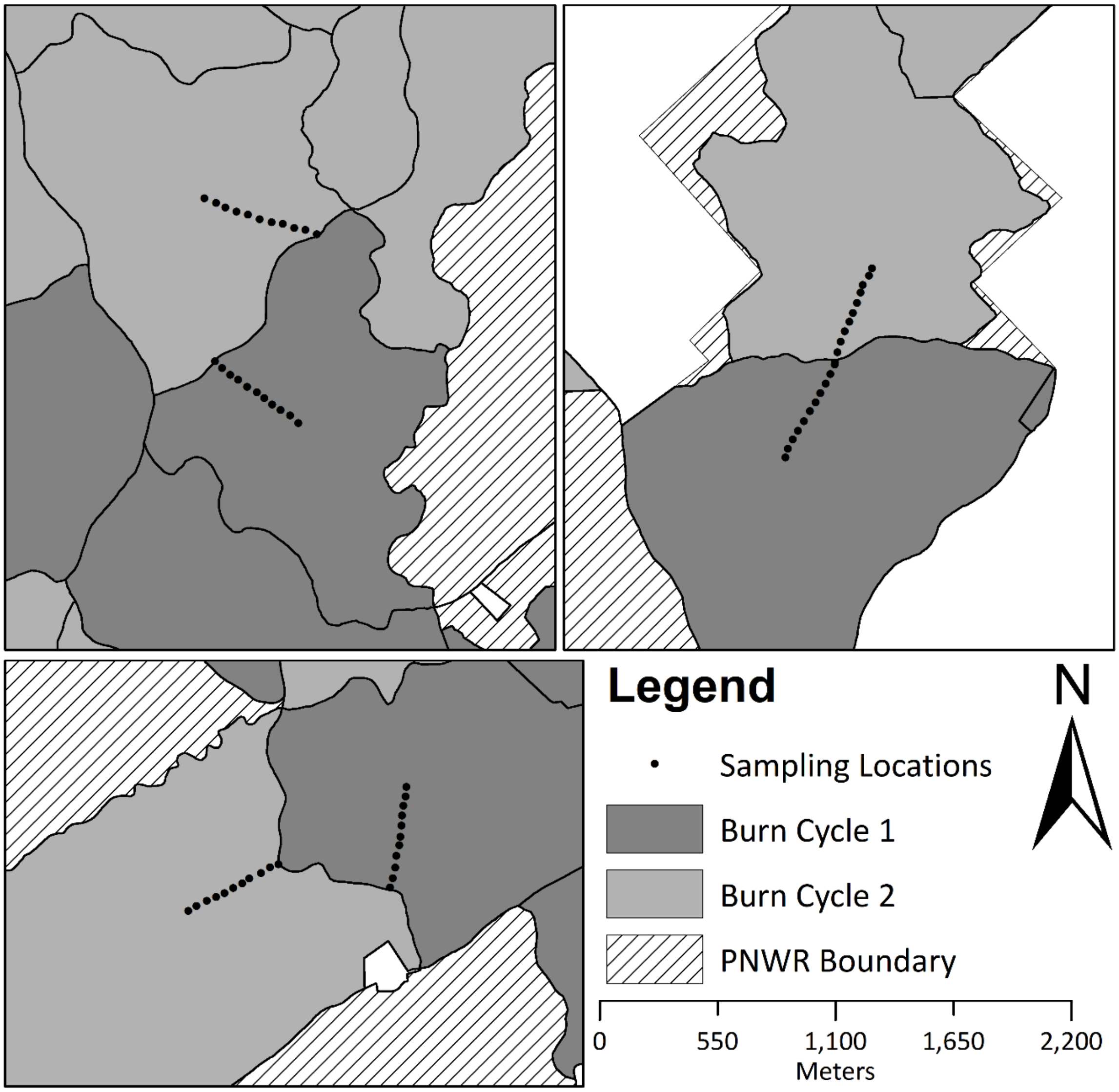

Figure 3.1: Map of sampling points (black circles) at the Piedmont National Wildlife Refuge, Jones Co. GA. Each panel is a different location (top left: Caney Creek, top right: Five Points, bottom: Natural Rock).

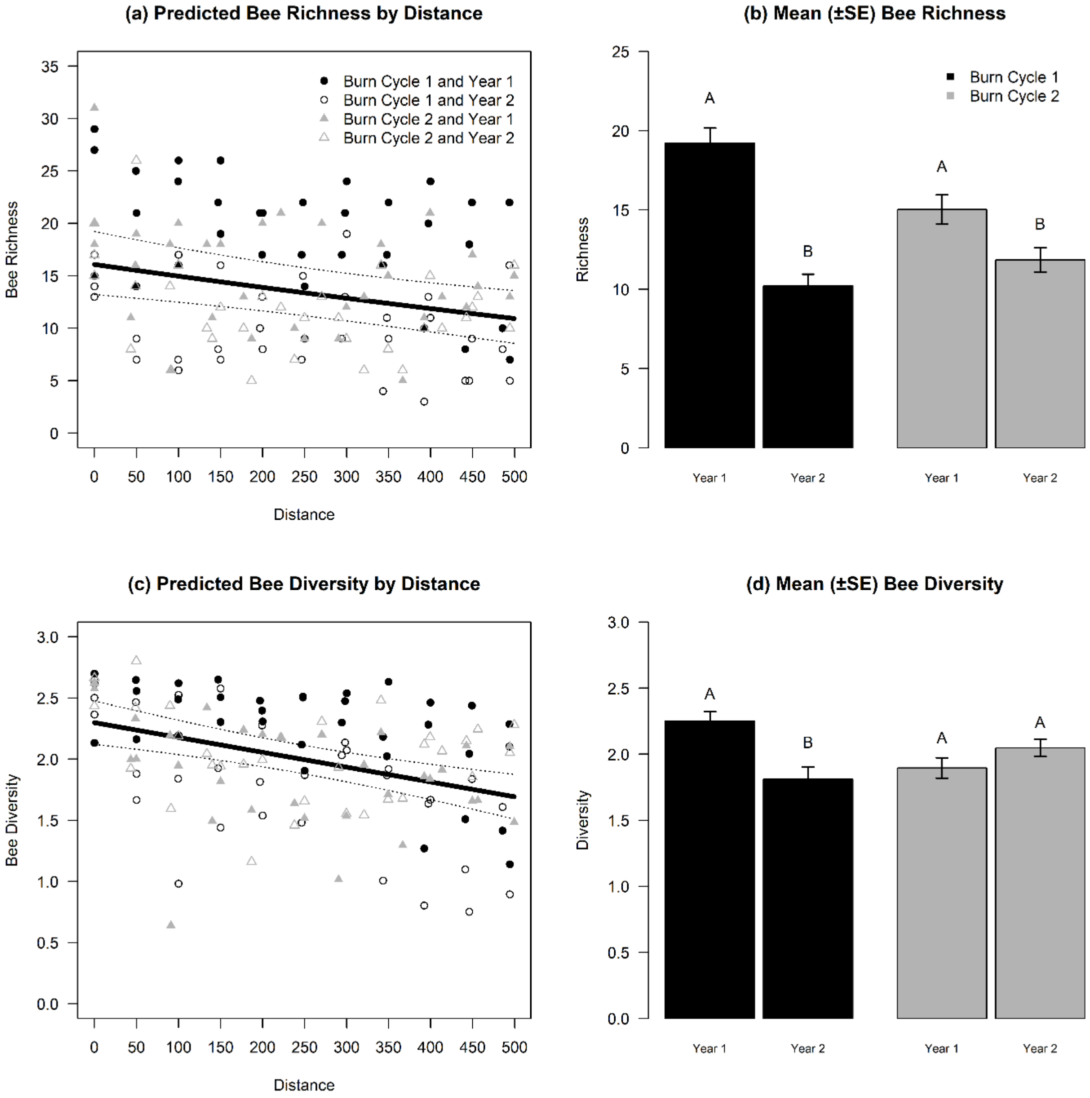

Figure 3.2: Back-transformed predicted bee richness as a function of distance into burn blocks (a), mean (±SE) bee richness for each burn cycle and year (b), predicted Shannon's bee diversity as a function of distance into burn blocks (c), and mean (±SE) bee diversity for each burn cycle and year (d) (*see Table 2*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (circles and triangles).

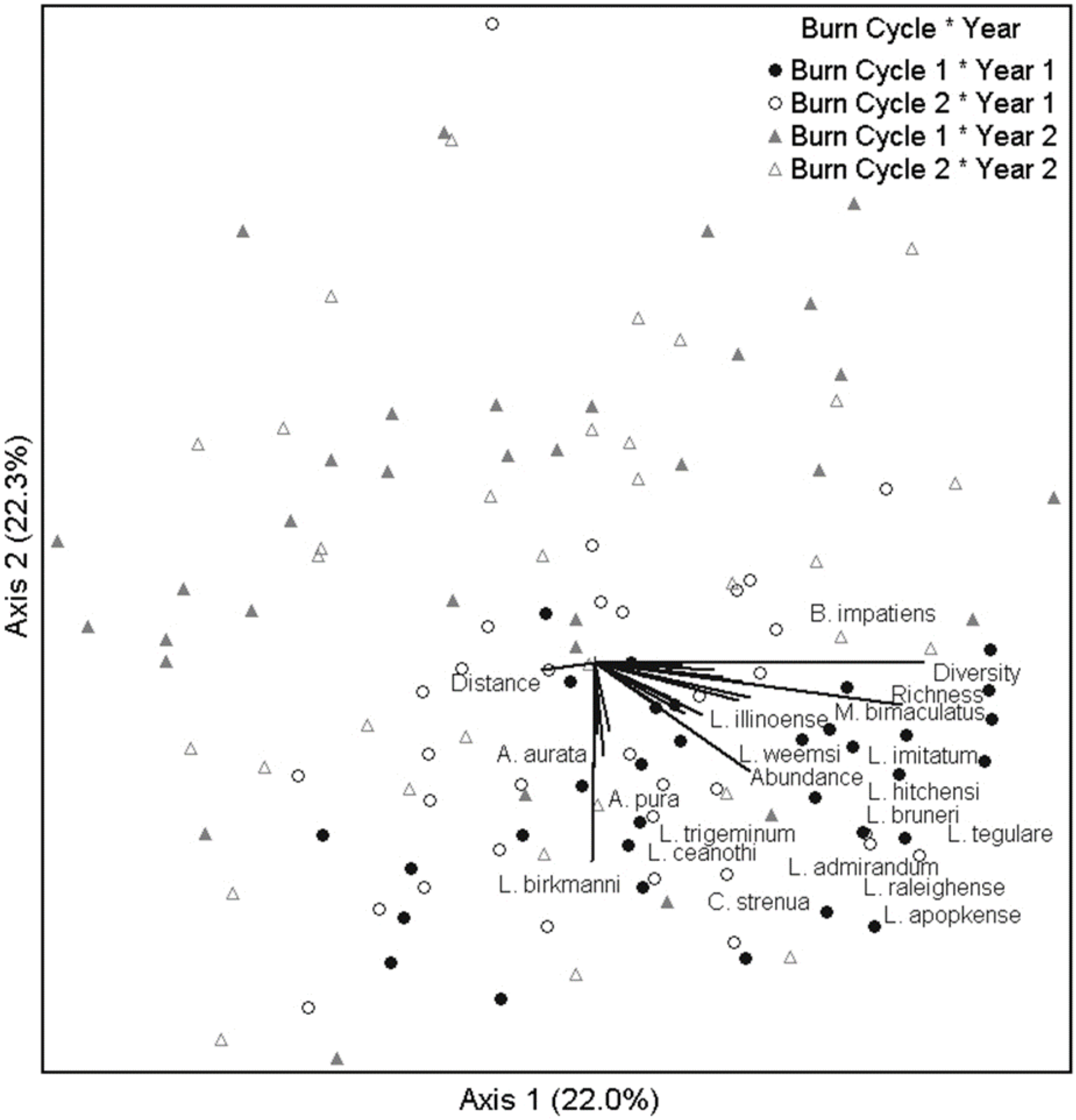

Figure 3.3: Non-metric multidimensional ordination of bee communities observed along a gradient of distance into burn blocks in the Piedmont National Wildlife Refuge, with joint plots of Distance, Bee Abundance, Bee Richness, Shannon's Bee Diversity, and abundance of *Bombus impatiens* (B. impatiens), *Lasioglossum tegulare* (L. tegulare), *L. imitatum*, *L. illinoense*, and *L. hitchensi*.

CHAPTER 4

EFFECTS OF LARGE BURN SIZE ON POLLINATOR COMMUNITIES IN LONGLEAF PINE (*PINUS PALUSTRIS*) IN THE SOUTHERASTERN UNITED STATES[3]

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[3] Fair CG, Hiers JK, Pokswinski SC, Ulyshen MD. To be submitted to *Conservation Biology*

Abstract

The longleaf pine (*Pinus palustris*) ecosystem (LLPE) is managed using frequent low severity prescribed fire to maintain overstory dominance by longleaf pine and maintain herbaceous plant communities in the understory and support fire-dependent fauna. Open forest conditions created by prescribed fire generally benefit flowering plants and their associated pollinators. We compared pollinator communities in the LLPE from the centers to the edges of large burns (>500 ha). Related comparisons between small and large bees and wood- and soil-nesting bees were made. Sampling locations included Eglin Air Force Base and Apalachicola National Forest in Florida, USA. We used color pan traps to sample bee communities. Overall, bee abundance and richness had no significant differences between the center and edge habitats. However, bee diversity, wood-nesting bee abundance, and large bee abundance at Apalachicola National Forest, and wood-nesting bee abundance at Eglin Air Force Base were greater in the center of burn blocks. These data suggest that the size of the burns is not limiting the ability of bees to recolonize following the frequent low-severity fires in the LLPE. Prescribed fire has been more consistently used in this ecosystem and region in the United States as compared to other forest habitats like loblolly pine (*Pinus taeda*). This history of prescribed fire and fire suppression may have changed the composition of pollinator communities in this region. Alternative types of spatial data could help to explain patterns we observe and elucidate the mechanism of how bees and other pollinators respond to disturbances by fire.

Introduction

Given the ecological (Ollerton et al. 2011) and economic (Klein et al. 2007) importance of insect pollinators, and their declining communities (Aguilar et al. 2006; Potts et al. 2010; Winfree 2010; Burkle et al. 2013), questions regarding the conservation of their habitat, including forests such as the longleaf pine (*Pinus palustris*) ecosystem (Mader et al. 2011; Hanula et al. 2016), and the management of forest habitat with prescribed fires, has been a growing concern (NRC 2007; IPBES 2016). The seemingly destructive forces of disturbance by fire have maintained ecosystem function and biological diversity of terrestrial ecosystems for over 400 million years (Pausas & Keeley 2009). Prescribed fire is the intentional ignition of fuels to meet land management objectives including increasing biodiversity and habitat quality as well as reducing risks associated with invasive species or fire hazards (Fernandes & Botelho 2003; Agee & Skinner 2005; Xanthopoulos et al. 2006; Fowler & Konopik 2007; Stephens et al. 2012; Ryan et al. 2013; Kalies & Kent 2016; Stephens et al. 2021). There are many interactions between fire behavior, habitat conditions, and other moderating effects that determine the effects of prescribed fires (O’Brien et al. 2018), and both pollinators and their associated floral resources have varied responses to individual and interacting effects.

Previous studies have shown that both pollinators and the floral resource community increase in abundance, richness, and diversity as canopy openness increases as a result of fire (Huntzinger 2003; Wagner et al. 2003; Waltz and Covington 2004; Campbell et al. 2007; Nyoka 2010; Hanula et al. 2015; Strahan et al. 2015). Research investigating specific fire characteristics including fire frequency (Hiers et al. 2000; Kirkman et al. 2004), time since fire (Potts et al. 2003; Breland 2015; Moylett et al.

2020), fire severity (Cane & Neff 2011; Hanula et al. 2016; Hill et al. 2017; Lazarina et al. 2019), and seasonality (Hiers et al. 2000) have shown optimal ranges of these fire characteristics for plants and their associated pollinators. Recent meta-analyses have assessed the positive and negative responses of pollinators to several of these fire characteristics (Carbone et al. 2019; Mason et al. 2021, Chapter 2, above). Our understanding of the impact spatial factors like fire size has on pollinators is still developing (Betts et al. 2019; Mason & Lashley 2021).

The longleaf pine ecosystem in the southeastern United States provides an opportunity to expand on the results from Chapter 3, above and test this question with even larger burn blocks and a different history of prescribed fire. The longleaf pine ecosystem requires frequent low severity fires to maintain high levels of floral and faunal diversity (Kirkman et al. 2004; Jose et al. 2006; Mitchell et al. 2006; O'Brien et al. 2008; Mitchell et al. 2009), and in the absence of these fires, non-fire dependent broadleaf vegetation will gain a competitive advantage that will cause the canopy to close, extensive habitat degradation, and a loss of plant diversity (Mitchell et al. 2009; Noss et al. 2014). Plants in the longleaf pine ecosystem have evolved traits (resprouting, germination by heat/smoke, etc.) that have allowed them to persist under recurrent fires (Keeley et al. 2011; 2012), and this keeps the overstory tree, the longleaf pine, dominant and the other vegetation primarily as the understory (Boyer 1990; Jose et al. 2006). Other strategies adapted by mobile fauna allow species to leave and avoid the lethal temperatures of fire, and then recolonize a habitat post-fire (Pausas & Parr 2018). The success of recolonization is dependent on the dispersal abilities of species as determined by the size and shape of the fire and predicted by body size (Gathman & Tscharntke

2002), and exposure to lethal temperatures as bees that nest in twigs/wood aboveground are exposed while those that nest in depths >10 cm are protected (Cane & Neff 2011). Prescribed fires in the longleaf pine forests in the southeastern United States can exceed thousands of hectares and allow us to test if the effect of burn size impacts pollinator recolonization at larger scales and with different prescribed fire history than in Chapter 3 of this dissertation.

To determine if recolonization of bees (our focus based on results from Chapter 3 where total bee richness and diversity reacted to distance but not total butterfly abundance, richness, or diversity) in response to prescribed fires in large, burned areas (> 500 ha) is limited, we sampled bee communities in both the edges and centers of burn blocks. We hypothesized that bee abundance, richness, and diversity would be lower in the centers than the edges of the burn blocks. We include data on the floral resource community to isolate the direct response of pollinators to fire. We also tested two related hypotheses comparing body size and nesting guild. First, we expected smaller bees to have lower abundance, richness, and diversity in the centers than in the edges of the burn blocks than larger bees. This is because smaller bees have limited dispersal capabilities compared to larger bees. Second, wood-nesting bees were expected to have lower abundance, richness, and diversity in the centers than in the edges of the burn blocks than soil-nesting bees. This is because the fire would consume potential wood-nesting habitat and limit their dispersal capabilities, but the fire would not limit the soil-nesting habitat.

Methods

Study Area

Sites were selected from burn blocks in Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB) located in the Florida longleaf pine mixed flatwood/sandhill region in Wakulla, Leon, Santa Rosa, and Okaloosa County, Florida, USA (Fig. 4.1). The ANF became a national forest in 1936 and is the largest forest in Florida (230,670 ha), and the current management conditions (including prescribed fires) are directed for conservation of the longleaf pine ecosystem and the rare and endemic species found in this ecosystem (Trager et al. 2018). EAB covers 186,350 ha, and the forests are managed using prescribed fire to maintain optimal longleaf pine habitat and associated animal and plant life (Hudak et al. 2016).

Experimental Design

In winter 2017, we selected five sites each within ANF and EAB that experiences a prescribed fire in 2016 and were large enough to have an inner buffer exceeding 1000 m. The burn blocks ranged from 691-1578 ha in size (Table 4.1). Sampling locations were established in each burn block, with two edge locations 50 m from the edge of the burn block and another location approximately 1000 m into the center of the burn block resulting in 30 total sampling locations (Fig 4.1, Table S4.1).

Data Collection

Pollinator sampling

We used colored pan traps to collect bee community data. Traps were operated for three-day periods six times from ANF and seven times from EAB, during fair weather to optimize pollinator capture. We used blue, white, and yellow colored, 355 ml pan traps (commercially available food bowls: www.partycity.com) elevated approximately 30 cm above ground and filled with water and a few drops of soap to reduce surface tension to maximize trap potential (Campbell & Hanula, 2007; Steffan-Dewenter & Westphal, 2008; Droege, 2013) (Fig. S4.1). At each sampling location, one set of three pan traps (one of each color) was installed 50 m from the edge or in the center of each burn block (sample A), and another set 5 m farther away from the edge or into the center of each burn block (sample B). One of each color pan trap was randomly placed with one in the center and one 5 m on each side, perpendicular to the edge of the burn block. At the time of collection, the three bowls from sample A were consolidated into a single container, and the three bowls from sample B were consolidated into a separate container. This process was repeated for each sampling location. Samples were taken back to the lab and transferred to 70% ethanol and stored. All bees in each sample were identified to species with a combination of printed (Mitchell 1960; Bouseman & LaBerge 1978; Gibbs et al. 2011; and Gibbs 2013) and online (Ascher 2009) reference materials. Categories of nesting behavior and body size were also noted for each taxon (Table S4.2). Nesting groups included soil, wood, "other" (*Apis melifera*, and *Bombus bimaculatus*, which are known to nest in both the ground and wood) and rotting wood (*Augochlora pura*) (Michener 2007). Body size group determinations were made with species descriptions and other published literature (small bees: <6 mm, medium bees: ≥6 mm or ≤10 mm and large bees: >10 mm) (Michener 2007). Bee abundance, species richness, and diversity metrics were calculated (Shannon 1948).

Canopy Openness, Plant, and Soil Type Data

Photographs of the canopy were taken with a Nikon Stylus TG3 camera with a fish-eye lens adapter mounted on a self-leveling tripod to position the camera 0.9 m above ground and pointing directly up. Photographs were taken at the six trap locations at the 30 sampling points in 2017. We recorded the canopy openness value from each photo using the software, WinScanopy Version 2006 (Regent Instruments Inc. Quebec City, CA). The canopy openness value for each point was averaged over the six photos taken at each trap per sampling point.

In September or October of 2017, a 10 m x 10 m square plot was set up to sample understory herbaceous plant community and shrub layer at each sampling location. The point intercept method was used to collect plant abundance data along the perimeter of the 10 m X 10 m square plot with sampling points made every meter (40 total). Plant richness data were collected using 1 m^2 quadrat twice within the 10 m X 10 m square plot. Plant height data were recorded four times along the perimeter of the 10 m X 10 m square plot. Additionally, observations of bare ground (as potential bee nesting habitat) were collected by counting the abundance of bare ground observations from the vegetation sampling methods at each sampling location. These methods were adapted based on methods from the North Carolina Vegetation Survey (Peet et al. 1998) and other related studies in the longleaf pine ecosystem (Provencher et al. 2000; Provencher et al. 2001a; Provencher et al. 2001b).

The percentage of area classified as wetland soil present within 1000 m of each sampling location was calculated using ArcGIS and soils data collected from the region. Soil types were categorized as wetland or non-wetland based on criteria set by the USDA Natural Resources Conservation Service (USDA-NRCS 2010). Soil moisture can be influential in nesting behavior of bees (Michener 2007) and affects fire behavior (O'Brien et al. 2018).

Statistical Analysis

We used R (R Core Team, 2014) and lme4 (Bates et al. 2015) to assess several linear mixed effects to test our hypothesis that bee abundance, richness, and diversity would be lower in the center compared to the edge sampling locations. Data collected over the multiple sampling dates were pooled, and data from ANF and EAB were analyzed separately due to inconsistent sampling between EAB and ANF locations caused by military activity at EAB (data from F-25 and F-7 burn blocks were removed from the analysis). Additional site-specific data including the herbaceous vegetation, canopy openness, bare ground, and wetland were included in the model to account for their impact on the bee community. The residuals from each model were assessed for normality and transformed with a ln or sqrt transformation when necessary. Given the variability in unmeasured site-specific and fire behavior variation, we used a mixed model approach to control for this unmeasured variation (Zurr et al. 2009). The location (edge vs. center) of the sampling location along with other covariates (plant abundance richness and height, canopy openness, percent wetland, and percent bare ground) were included in the model as a fixed effect. To account for the non-independence of the different burn blocks, we included the random effect of burn block. For final model selection, non-significant covariates were step-wise removed, and nested models (model with non-significant covariates, and model without non-significant covariates) were analyzed with a Chi-Square test to determine if the removal of the non-significant covariate significantly changed the model fit. Hypothesis tests (F tests), using the Kenward-Roger denominator degrees of freedom approximation method, were carried out using *lmerTest* (Kuznetsova et al. 2017). Data that were transformed in models were back transformed in the estimated marginal mean graphs.

Non-metric multidimensional scaling (NMDS) ordination analyses of bee abundance in plots was used to examine community differences (PC-ORD; McCune & Mefford 1999), and we used the Sorensen (Bray-Curtis) distance measure in this analysis. To focus the signal on consistent response trends, only species where $n \geq 3$ were retained for the analysis. The response matrixes included 19 bee species in 15 plots from ANF, and 17 bee species in 9 plots from EAB. Variables representing species data were relativized by maximum abundance to reduce the influence of highly abundant species. We used the slow and steady autopilot settings for the NMDS analysis. Additional analyses included a cluster analysis where groupings of sampling locations were assessed using the group average method and the Sorensen (Bray-Curtis) distance measure. Finally, a one-way permutation-based MANOVA procedure was used to evaluate differences in bee community composition and relative abundance between locations for both ANF and EAB sites (PC-ORD; McCune & Mefford 1999). This test requires equal replicates for the grouping variable, so the two edge sites were analyzed separately.

Results

We collected a total of 3,320 (51 spp.) bees with 1,666 (37 spp.) and 1,354 (40 spp.) bees from ANF and EAB (respectively). The relative abundances of each bee species collected within each site and the total number of individuals collected as well as their nesting and body size categories can be seen in Table S4.2.

We found that bee diversity ($F_{1,9.1}$=5.44*; Fig 4.2C), wood bee abundance ($F_{1,7.0}$=11.78*; Fig S4.2), large bee abundance ($F_{1,6.6}$=12.54*; Fig S4.3) at ANF, and wood bee abundance ($F_{1,2.0}$=74.76*; Fig S4.2) at EAB had higher diversity in the center locations than the edge locations. The effect of location was not statistically significant for bee abundance, and richness at ANF and the abundance, richness, and diversity at EAB (Table 4.2; Fig 4.2) nor the remaining nesting and body size guilds (Table S4.3-S4.6; Fig S4.2, S4.3). While most of the results were not statistically significant, they did have the same trend where the abundance, richness, and diversity were all greater in the centers compared to the edges of the burn blocks.

Nonmetric multidimensional scaling (NMDS) for the bee community composition from ANF recommended a one-dimensional solution with a final stress of 32.79. The R2 value for axis one was 0.473. The sample sites from ANF did not show any grouping based on sampling location from the NMDS plot (Fig S4.4). NMDS for the bee community composition from EAB recommended a one-dimensional solution with a final stress of 18.74. The R2 value for axis one was 0.709. The sample sites from EAB did not show any grouping based on sampling location from the NMDS plot (Fig S4.5). Cluster analyses based on sampling location did not indicate possible groupings for both ANF and EAB sites (Figs S4.5 and S4.6). The results from the PerMANOVA test indicate that the effect of location was not significant ($F_{2,14}$=0.80) and ($F_{2,8}$=0.46) for both ANF and EAB sites (respectively) (Table S4.7).

The amount of bare ground had a significant positive effect on bee abundance ($F_{1,4.6}$=12.03*), large bee abundance ($F_{1,5.4}$=16.68**), wood nesting bee richness ($F_{1,9.5}$=5.83*), and wood nesting bee diversity ($F_{1,10.6}$=7.00*) at ANF. The positive response of total and large bee abundance was expected given that most species are soil-nesters (Table S4.2). The positive results from the wood nesting bees could be explained if the abundance of bare ground is also connected to the availability of woody vegetation for nesting habitat. The amount of wetland had a significant negative effect on wood bee abundance at EAB ($F_{1,1.3}$=89.71*), wood nesting bee richness at ANF ($F_{1,9.5}$=5.83*) and large bee diversity at ANF ($F_{1,3.7}$=12.21*).

Discussion

The purpose of this study was to assess the effect of large (>500 ha) burn blocks on pollinator communities as they recolonize a habitat post-burn. We find no support for our hypothesis that the pollinators are less able to reach the centers of these large burn blocks following a fire. While only a portion of the data showed significant differences between the edge and center locations, the trends were consistent in that bee abundance richness and diversity for both large and small, and soil and wood-nesting bees was greater in the center than the edge locations. Alternatively, the assumptions made about the homogeneity of fire behavior across these burn blocks could have obscured the response of the pollinator community to the fire conditions. The effects of fire characteristics can vary greatly especially at fine spatial scales (Hiers et al. 2009), which could allow for low severity conditions to exist heterogeneously throughout the burn block and create refugia for pollinators to recolonize from rather than outside of the entire burn unit. Given the spatial heterogeneity of fire characteristics, it is likely that bees are not completely extirpated from burn blocks and are instead able to find refugia within the burn blocks to use as sources of recolonization (Whelan et al. 2001; Banks et al. 2010). Tests of the “pyrodiversity begets biodiversity” hypothesis (Martin & Sapsis 1992) have shown mixed results based on taxa and context (Jones & Tingley 2021), but it has been shown to be useful to understand pollinator responses to fire (Ponisio 2020; Ulyshen et al., in press). Continued tests of the pyrodiversity hypothesis in a range of habitats and conditions could help develop our understanding of the spatial effects of fire on pollinators.

While the spatial heterogeneity may provide more information for understanding the mechanism behind the pollinators’ response to fire, other site-specific characteristics such as land use history may be more influential (O’Brien et al. 2018). The history of fire in the loblolly pine forests in Chapter 3 is much more recent than the longleaf pine forests in this study. This could explain why we see negative impacts of fire size on pollinators where the community structure in a dense forest habitat (Harrison et al. 2017) is changing to that of a more open pine forest and no effect on the pollinator community where the habitat has long been consistent. Furthermore, fire behavior could impact other components of the pollinator community like phylogenetic heterogeneity (e.g., Harrison et al. 2018) or the plant/pollinator network.

There are obvious concerns with pollinator conservation, and forest habitat management can play a significant role in this endeavor. Prescribed fires as a method of forest management are beneficial to many species in their fire-adapted ecosystems. There is much to learn regarding how different fire characteristics and land use histories impact pollinator communities. More research should be conducted before any land management recommendations that keep pollinator conservation in mind can be made.

While specific management recommendations cannot be made without knowledge of the specific local factors (conservation priorities, forest type, land use history, etc.) that may affect decisions regarding the desired spatial characteristics of a planned fire (O'Brien et al. 2018), our results help to clarify the mechanism by which pollinators respond to the spatial characteristics of fire. These results do not support the recolonization mechanism where pollinators extirpated by fire return to the habitat from neighboring unburned habitat. Instead, we believe that the heterogeneity of fire behavior within the burn blocks may help explain how pollinators respond to prescribed fire. Refugia created by low severity fire within a burn block can allow pollinators to persist following a fire and act as sources for recolonization from within the burn block. Overall, these results suggest that the pollinator community in the LLPE is broadly resistant to the disturbances caused by fire. Future research investigating the pyrodiversity hypothesis (Martin & Sapsis 1992) is needed as are studies examining the recolonization mechanisms used by pollinators in response to prescribed fire.

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Table 4.1: Area of burn blocks chosen for study at the Piedmont National Wildlife Refuge.

Site	Burn Block	Hectares
ANF	233	1369.79
	240	942.94
	243	1051.43
	248	1192.94
	328	1578.19
EAB	F7	1020.39
	F25	782.24
	G8	1241.73
	J13	691.77
	K8	1469.41

Table 4.2. ANOVA results for the effects of location, canopy openness (Openness), percent wetland (% wetland), bare ground (BG), plant abundance (PA), and plant richness (PR) on natural log-transformed bee abundance (N), square root-transformed bee richness (S), and Shannon's bee diversity (H') using Kenward-Roger denominator degrees of freedom approximation method from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB).

	ANF			EAB		
	Ln(Bee N)	Sqrt(Bee S)	Bee H'	Sqrt(Bee N)	Ln(Bee S)	Bee H'
Location	$F_{1,7.9}=0.85$	$F1_{,8.3}=1.40$	$F_{1,9.1}=5.44^{*}$	$F_{1,0.6}=0.20$	$F_{1,2.9}=0.01$	$F_{1,1.1}=0.21$
Openness	$F_{1,4.9}=2.49$			$F_{1,0.7}=0.001$	$F_{1,3.7}=1.64$	$F_{1,1.2}=1.97$
% Wetland				$F_{1,1.0}=0.04$		$F_{1,1.6}=11.64$
BG	$F_{1,4.6}=12.03^{*}$	$F_{1,9.5}=4.53$		$F_{1,0.9}=0.22$	$F_{1,1.9}=0.02$	$F_{1,1.3}=4.96$
PA			$F_{1,10.8}=4.25$	$F_{1,6.4}=0.02$		$F_{1,1.8}=0.50$
PR				$F_{1,1.1}=0.01$		$F_{1,1.5}=0.78$
PH			$F_{1,9.5}=3.87$	$F_{1,1.8}=0.08$	$F_{1,0.9}=0.35$	

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, and $^{***}p<0.001$

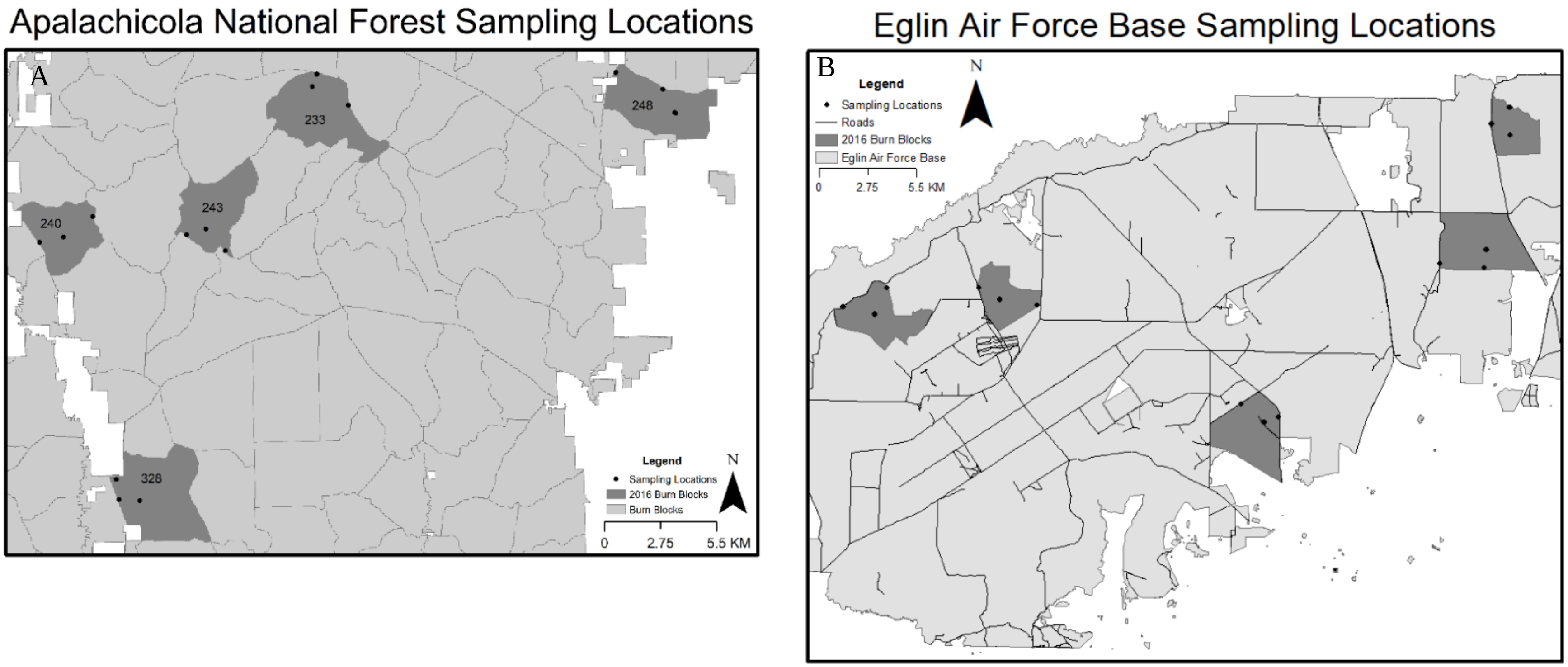

Figure 4.1: Map of sampling locations in the (a) Apalachicola National Forest and (b) Eglin Air Force Base.

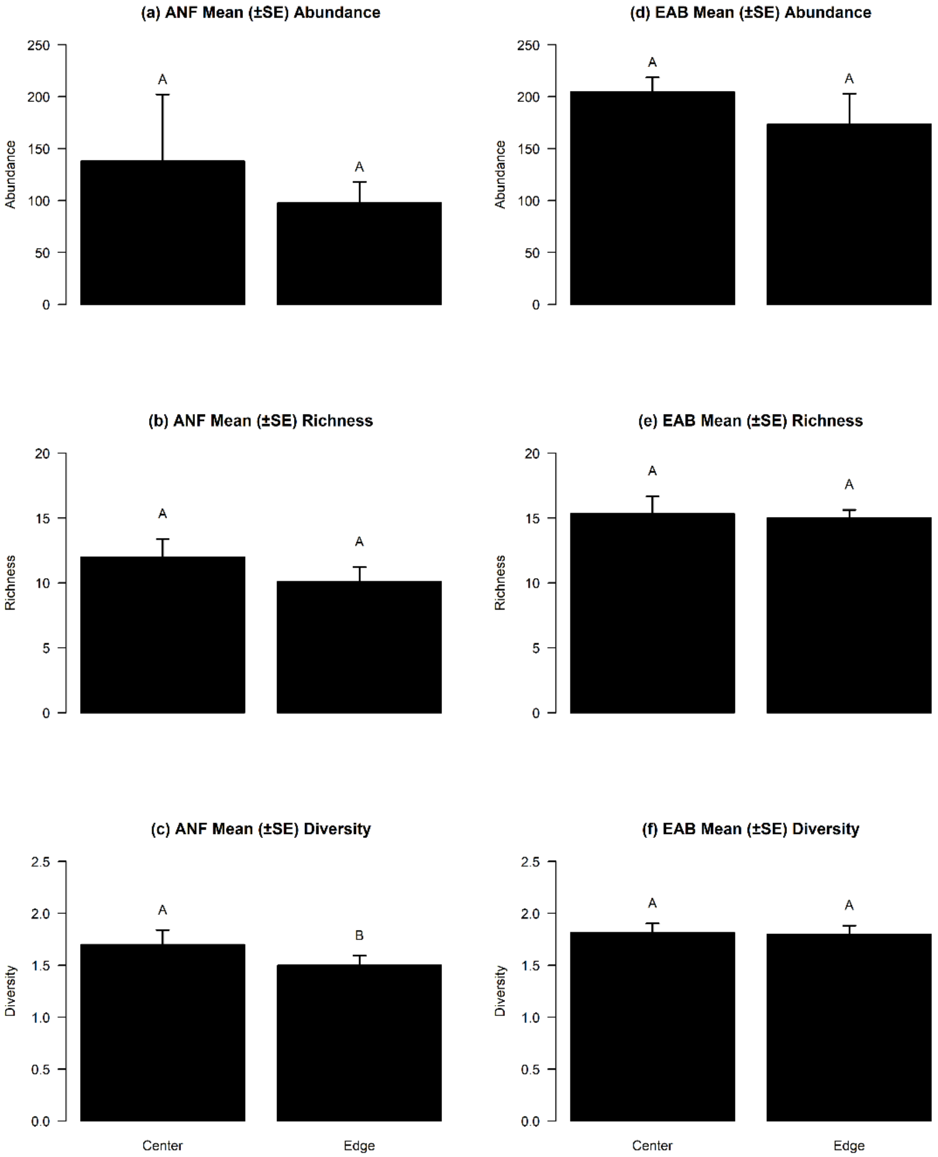

Figure 4.2: Bar graphs of mean (±SE) bee abundance, richness, and diversity collected from the center, and edge locations at Apalachicola National Forest (ANF), and Eglin Air Force Base (EAB).

CHAPTER 5

CONCLUSIONS

Fire is a complex evolutionary and ecological force that has been manipulating biodiversity for hundreds of millions of years (Pausas & Keeley 2009, Bowman et al. 2009), and we are beginning to understand how to manage fire regimes (He et al. 2019, Cochrane & Bowman 2021) to meet the needs of humans (Bowman et al. 2011) and biodiversity conservation (Pausas & Keeley 2019). Insects and specifically pollinators (Ollerton et al. 2011) can serve as useful bioindicator to test these management decisions. While overall effects of fire on pollinators is positive (Carbone et al. 2019; Mason et al. 2021), there is an insufficient amount of research that addresses the spatial extent of fire and its potential impact on biodiversity (Mason and Lashley 2021).

Our contribution to this discussion shows that the variety of ways to describe the impact of spatial extent of a fire on biodiversity (pollinators specifically) can obfuscate the true relationships and mechanisms. Results from our meta-analysis in Chapter 2 demonstrate continued support for the beneficial impacts of fire on pollinator communities, generally. The hypothesis that the total size of fire would impact the response of pollinators to fire was not supported. The size and shape of the fire and potential refugia will determine the distance a species will be able to move to recolonize a habitat (Brotons et al. 2005; Knight & Holt 2005; Watson et al. 2012). Therefore, the size of a fire alone may not fully capture the spatial conditions of a fire, and instead the distance to unburned edge could be more informative (Collins et al. 2017, Watson et al.

2012). We then tested the pollinator recolonization mechanisms in loblolly pine forests in the Piedmont region of the United States in Chapter 3. Distance from unburned edge as measured by increasing internal buffer distance was shown to negatively affect recolonization through declines in pollinator abundance, richness, and diversity. While we observed a loss of one bee species every 100 m into the burn blocks and a reduction of bee diversity as internal buffer distance increased, we do not believe that these losses are as concerning as they initially appear. We were unable to determine if the plant/pollinator networks were impacted by fire size, and we also believe that other effects like habitat conditions, historical management choices, and spatial heterogeneity of fire behavior could further explain the pollinator communities response to fire. We tested the recolonization mechanism in longleaf pine forests where prescribed fires have been used for longer periods of time in Chapter 4. We did not observe any negative effects of fire size on pollinator communities. This suggests that fire history and other spatial characteristics of fire should be investigated further.

Pyrodiversity is defined as the heterogeneity in one or more fire characteristics that produces a resultant change in biological diversity at a particular spatial extent (Martin & Spasis 1992). There have been many tests of the pyrodiversity hypothesis with mixed results and suggestions for improved methods of analysis (Bradstock et al. 2005, Bowman et al. 2016, Kelly et al. 2017, Jones & Tingley 2021). Studies that include this landscape level data are using evolving practices of collecting data and reporting/measuring spatial data. Determining the ‘scale of effect’ and incorporating biological rationale for said scale should help to create objective and repeatable methods (Jackson & Fahrig 2015). Studies that investigated the relationship between pyrodiversity and pollinator diversity demonstrated general positive effects of pyrodiversity on pollinators (Ponisio et al. 2016, Ulyshen et al. in press) and detailed mechanisms of how changes in pyrodiversity impacted pollinator communities and plant-pollinator networks (Ponisio 2020). It is unclear if this relationship will hold true for other species/communities within an ecosystem (Jones & Tingley 2021), and it is likely that one ‘fire mosaic’ will not be able to accommodate the needs for all species (Bradstock et al. 2005). This will require multiple macroecological studies of the pyrodiversity-biodiversity relationship.

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APPENDICES

Appendix A - Chapter 2 Appendix

Table S2.1: References and effect sizes extracted from studies analyzing effect of fire on pollinator communities. Additional citations are included for sources used to calculate the effect sizes (ES) based on statistical information published in each study.

ID	Study	Year	Hedges' d	Estimated Variance	Citation for ES Calculation	Mean Burn Size (ha.)	Pollinator	Type of Data	Geographical Region
1	Kwilosz & Knutson 1999	1999	0.733944084	0.044855508	Rosenberg et al. 2013	42	Butterflies	Counts of *L. melissa*	Indiana
2	Fleishman 2000	2000	0.414	0.5837	Lüdecke 2019	10.7	Butterflies	Richness	Nevada
3	Potts et al. 2003	2003	1.733238771	0.7	Lajeunesse 2013	266	Bees	Abundance	Israel
3	Potts et al. 2003	2004	1.607836222	0.7	Lajeunesse 2013	266	Bees	Richness	Israel
4	Campbell et al. 2007	2007	-0.307	0.6745	Lüdecke 2019	10	Hymenoptera	Abundance	North Carolina
4	Campbell et al. 2007	2007	0.349	0.6768	Lüdecke 2019	10	Hymenoptera	Abundance	North Carolina
4	Campbell et al. 2007	2007	-1.644	0.8918	Lüdecke 2019	10	Hymenoptera	Richness	North Carolina
4	Campbell et al. 2007	2007	0.045	0.6668	Lüdecke 2019	10	Lepidoptera	Abundance	North Carolina
4	Campbell et al. 2007	2007	0.754	0.714	Lüdecke 2019	10	Lepidoptera	Abundance	North Carolina
4	Campbell et al. 2007	2007	1.174	0.7815	Lüdecke 2019	10	Lepidoptera	Richness	North Carolina
5	Powell et al. 2007	2007	-0.591	0.0648	Lüdecke 2019	6.7	Butterflies	Counts of *S. idalia*	Kansas
6	Vogel et al. 2007	2007	-1.185	0.310584397	Rosenberg et al. 2013	48.6	Butterflies	Abundance	Iowa
6	Vogel et al. 2007	2007	0.712	0.282505159	Rosenberg et al. 2013	48.6	Butterflies	Richness	Iowa
6	Vogel et al. 2007	2007	1.515	0.338426958	Rosenberg et al. 2013	48.6	Butterflies	Diversity	Iowa
7	McIver & Macke 2014	2014	-0.317	0.225	Lüdecke 2019	16	Butterflies	Abundance	CA, OR, NV, UT
7	McIver & Macke 2014	2014	0.113	0.2226	Lüdecke 2019	16	Butterflies	Richness	CA, OR, NV, UT
7	McIver & Macke 2014	2014	0.789	0.308	Lüdecke 2019	41.4	Butterflies	Abundance	OR, NV, UT, ID, WA
7	McIver & Macke 2014	2014	1.273	0.3436	Lüdecke 2019	41.4	Butterflies	Richness	OR, NV, UT, ID, WA
8	Nowicki P, Marczyk J 2015	2015	0.043	0.0769	Lüdecke 2019	160	Butterflies	*M. teleius*	Poland
8	Nowicki P, Marczyk J 2015	2015	0.115	0.0771	Lüdecke 2019	160	Butterflies	*M. nausithous*	Poland
9	Rodriguez & Kouki 2017	2017	11.57864489	2.959687866	Lajeunesse 2013	3.95	Bees	Richness	Finland

10	Campbell et al. 2018	2018	1.747	0.6907	Lüdecke 2019	14	Bees	Abundance	North Carolina
10	Campbell et al. 2018	2018	1.365	0.6164	Lüdecke 2019	14	Bees	Richness	North Carolina
10	Campbell et al. 2018	2018	2.480	0.8843	Lüdecke 2019	14	Bees	Diversity	North Carolina
11	Henderson et al. 2018	2018	-0.0074	0.2857	Lüdecke 2019	31	Butterflies	Counts of *S. idalia*	Wisconsin
12	Lettow et al. 2018	2018	0.876	0.438391382	Rosenberg et al. 2013	0.8	Bees	Abundance	Michigan
12	Lettow et al. 2018	2018	1.754	0.5537501	Rosenberg et al. 2013	0.8	Bees	Abundance	Michigan
12	Lettow et al. 2018	2018	-0.571	0.416316337	Rosenberg et al. 2013	0.8	Bees	Richness	Michigan
12	Lettow et al. 2018	2018	0.571	0.416316337	Rosenberg et al. 2013	0.8	Bees	Richness	Michigan
12	Lettow et al. 2018	2018	-0.571	0.416316337	Rosenberg et al. 2013	0.8	Bees	Diversity	Michigan
12	Lettow et al. 2018	2018	0.903	0.440790843	Rosenberg et al. 2013	0.8	Bees	Diversity	Michigan
13	Mola & Willians 2018	2018	1.4519	0.6787	Lüdecke 2019	2.95	Bees	Counts of *B. vosnesenskii*	California
14	Buckles & Harmon-Threatt 2019	2019	1.451	0.505289114	Rosenberg et al. 2013	1	Bees	Abundance	Missouri
14	Buckles & Harmon-Threatt 2019	2019	0.997	0.44974493	Rosenberg et al. 2013	1	Bees	Richness	Missouri
15	Decker & Harmon-Threatt 2019	2019	-3.326911798	0.895963602	Lajeunesse 2013	7.56	Bees	Abundance	Illinois
15	Decker & Harmon-Threatt 2019	2019	-9.984116563	4.923883667	Lajeunesse 2013	4.33	Bees	Abundance	Illinois
15	Decker & Harmon-Threatt 2019	2019	-3.894687574	1.082338565	Lajeunesse 2013	7.56	Bees	Richness	Illinois
15	Decker & Harmon-Threatt 2019	2019	-7.264631	2.791714578	Lajeunesse 2013	4.33	Bees	Richness	Illinois
15	Decker & Harmon-Threatt 2019	2019	-0.949605736	0.433845827	Lajeunesse 2013	7.56	Bees	Diversity	Illinois
15	Decker & Harmon-Threatt 2019	2019	-0.470462218	0.402917811	Lajeunesse 2013	4.33	Bees	Diversity	Illinois
16	Dicarlo et al. 2019	2019	0.898	0.2446	Lüdecke 2019	400	Bees	Abundance	Oregon
16	Dicarlo et al. 2019	2019	0.974	0.2486	Lüdecke 2019	400	Bees	Richness	Oregon
16	Dicarlo et al. 2019	2019	1.065	0.2537	Lüdecke 2019	400	Bees	Diversity	Oregon
17	Tucker & Rehan 2019	2019	0.434094849	0.682369861	Rosenberg et al. 2013	23	Bees	Abundance	New Hampshire
17	Tucker & Rehan 2019	2019	0.285923106	0.673479335	Rosenberg et al. 2013	23	Bees	Richness	New Hampshire
18	Moylett et al. 2020	2020	1.242606752	0.298252236	Rosenberg et al. 2013	19.5	Bees	Abundance	North Carolina
18	Moylett et al. 2020	2020	2.577339574	0.457583728	Rosenberg et al. 2013	19.5	Bees	Richness	North Carolina
19	Simmons & Bossart 2020	2020	0.091101225	0.333679143	Rosenberg et al. 2013	207	Bees	Abundance	Louisiana and Mississippi
19	Simmons & Bossart 2020	2020	-0.074710693	0.333565904	Rosenberg et al. 2013	207	Bees	Richness	Louisiana and Mississippi

Table S2.2: Synopsis of models used in the different hierarchical mixed effects meta-analysis, expressed in R language syntax, using the ‘metafor’ package (Viechtbauer, 2010). IVWd=Inverse-Variance-Weighted Hedges’ d. IVd=inverse-variance of Hedges’ d, Paper=paper identity.

Test for Overall Effect
rma.mv(IVWd, IVd, method=”REML”, random=list(~1|Paper))
Test for predictor variable (fire size, pollinator taxa)
rma.mv(IVWd, IVd, mods=~predictor_variable, method=”REML”, random=list(~1|id))

Table S2.3: Results for publication bias results using the Egger’s regression test.

Response Variable	Estimate	P value
Abundance	0.0998	0.545
Richness	0.2462	0.651
Diversity	0.6258	0.669

Table S2.4: Results of preliminary tests for abundance, richness, and diversity for overall and moderator models.

Response Variable	Moderators	Category	Hedges' d	P value	CI
Abundance	Overall	-	1.1129	0.0742	(-0.1087 - 2.3346)
	Burn Size	Large (intercept)	2.9693	0.1219	(-0.7931 - 6.7317)
		Medium	-1.5386	0.5004	(-6.0138 - 2.9365)
		Small	-2.2079	0.2962	(-6.3502 - 1.9345)
	Pollinator	Butterflies	-0.3901	0.6964	(-2.3494 - 1.5692)
Richness	Overall	-	1.4738	**0.0209**	(0.2230 - 2.7246)
	Burn Size	Large (intercept)	2.9734	0.1277	(-0.8527 - 6.7995)
		Medium	-1.8831	0.4331	(-6.5920 - 2.8257)
		Small	-2.3535	0.272	(6.5530 - 1.8461)
	Pollinator	Butterflies	1.9972	0.0907	(-0.3165 - 4.3109)
Diversity	Overall	-	1.7673	0.1343	(-0.546 - 4.0806)
	Burn Size	Large	4.1963	0.1344	(-1.2978 - 9.6904)
		Medium	0.2814	0.9416	(-7.2405 - 7.8033)
		Small	-3.6887	0.2327	(-9.7459 - 2.3686)

Table S2.5: Results of heterogeneity for abundance, richness, and diversity models.

Response Variable	Moderators	d.f.	Q*	P value
Abundance	Overall	20	80.4537	< 0.0001
	Burn Size	3	1.3493	0.7175
Richness	Overall	14	103.817	< 0.0001
	Burn Size	3	3.8037	0.2835
Diversity	Overall	4	11.4648	0.0218
	Burn Size	2	2.7552	0.2522

Table S4.6: Results following the sensitivity analysis for abundance, richness, and diversity for overall and moderator models.

Response Variable	Moderators	Category	Hedges' d	P value	CI
Abundance	Overall	-	1.3005	**0.0179**	(0.2240 - 2.3770)
	Burn Size	Large (intercept)	2.9251	0.0647	(-0.1780 - 6.0282)
		Medium	-1.7901	0.3595	(-5.6190 - 2.0387)
		Small	-1.8661	0.2830	(-5.2729 - 1.5408)
		Butterflies	-0.0041	0.9967	(-1.928 - 1.9146)
Richness	Overall	-	1.1653	0.059	(-0.0445 - 2.3751)
	Burn Size	Large (intercept)	2.9497	0.0993	(-0.5579 - 6.4573)
		Medium	-2.0843	0.3479	(-6.4363 - 2.676)
		Small	-2.8691	0.1475	(-6.7515 - 1.0132)
		Butterflies	2.1245	0.0623	(-0.1096 - 4.3586)
Diversity	Overall	-	2.1324	0.0693	(-0.1683 - 4.4332)
	Burn Size	Large (intercept)	4.1963	0.1558	(-1.5988 - 9.9914)
		Medium	0.2814	0.9448	(-7.6795 - 8.2423)
		Small	-3.1906	0.3325	(-9.6434 - 3.2623)

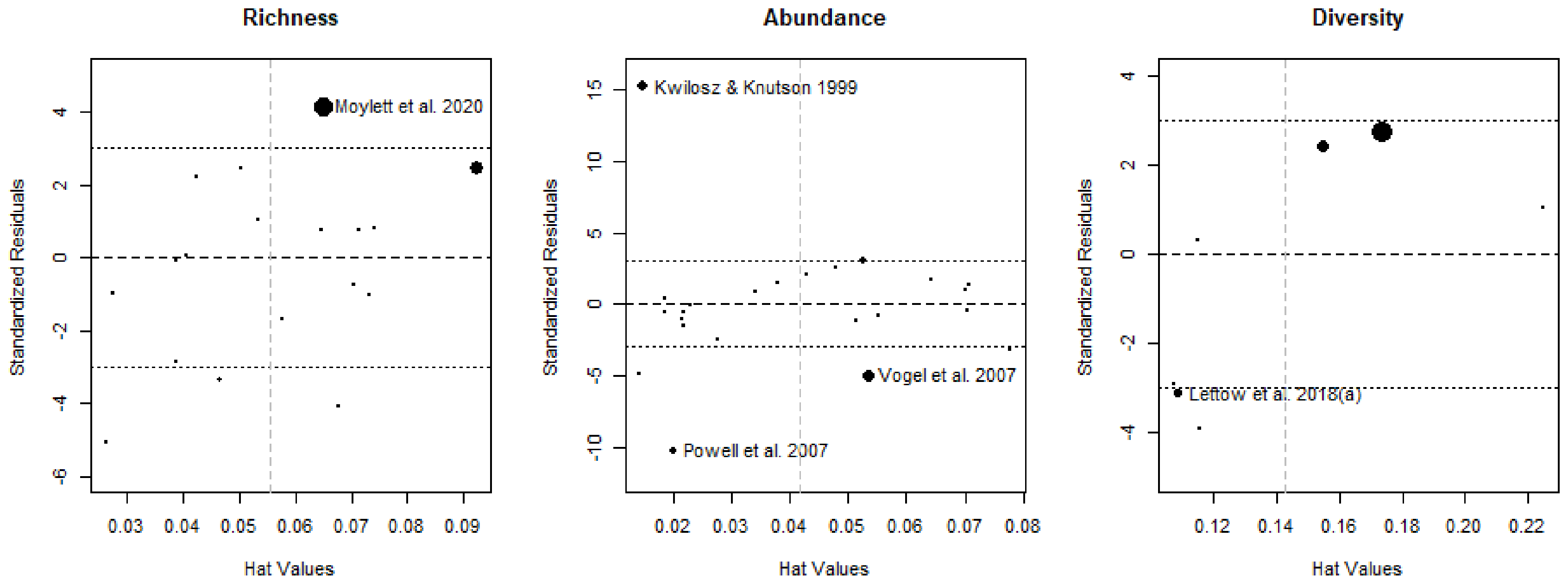

Figure S4.1: Plots of standardized residuals and hat values for richness abundance and diversity.

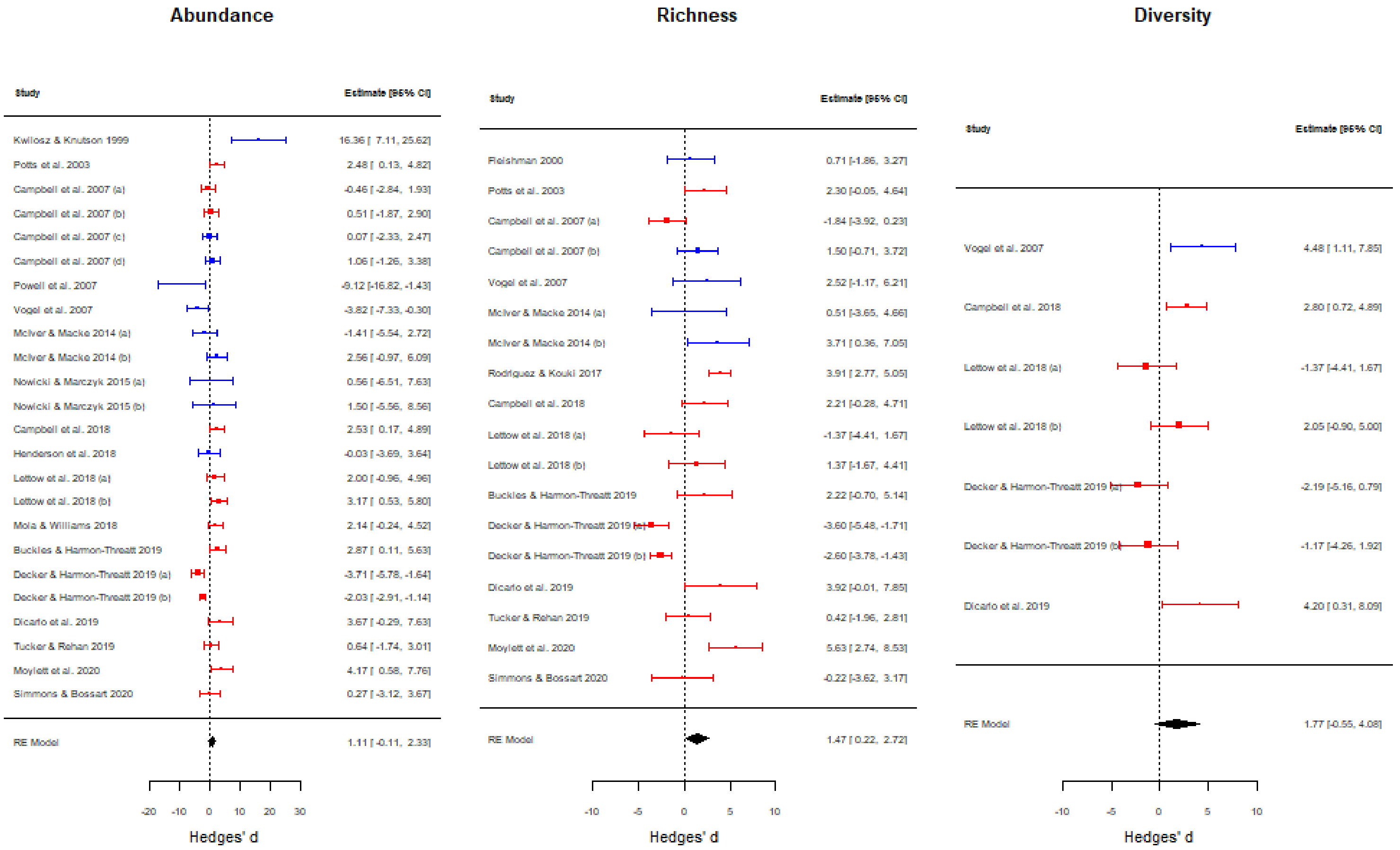

Figure S4.2: Funnel graphs showing the individual and overall effect sizes for each study included in the abundance richness and diversity models. Data shown are from bee taxa (red) or butterfly taxa (blue).

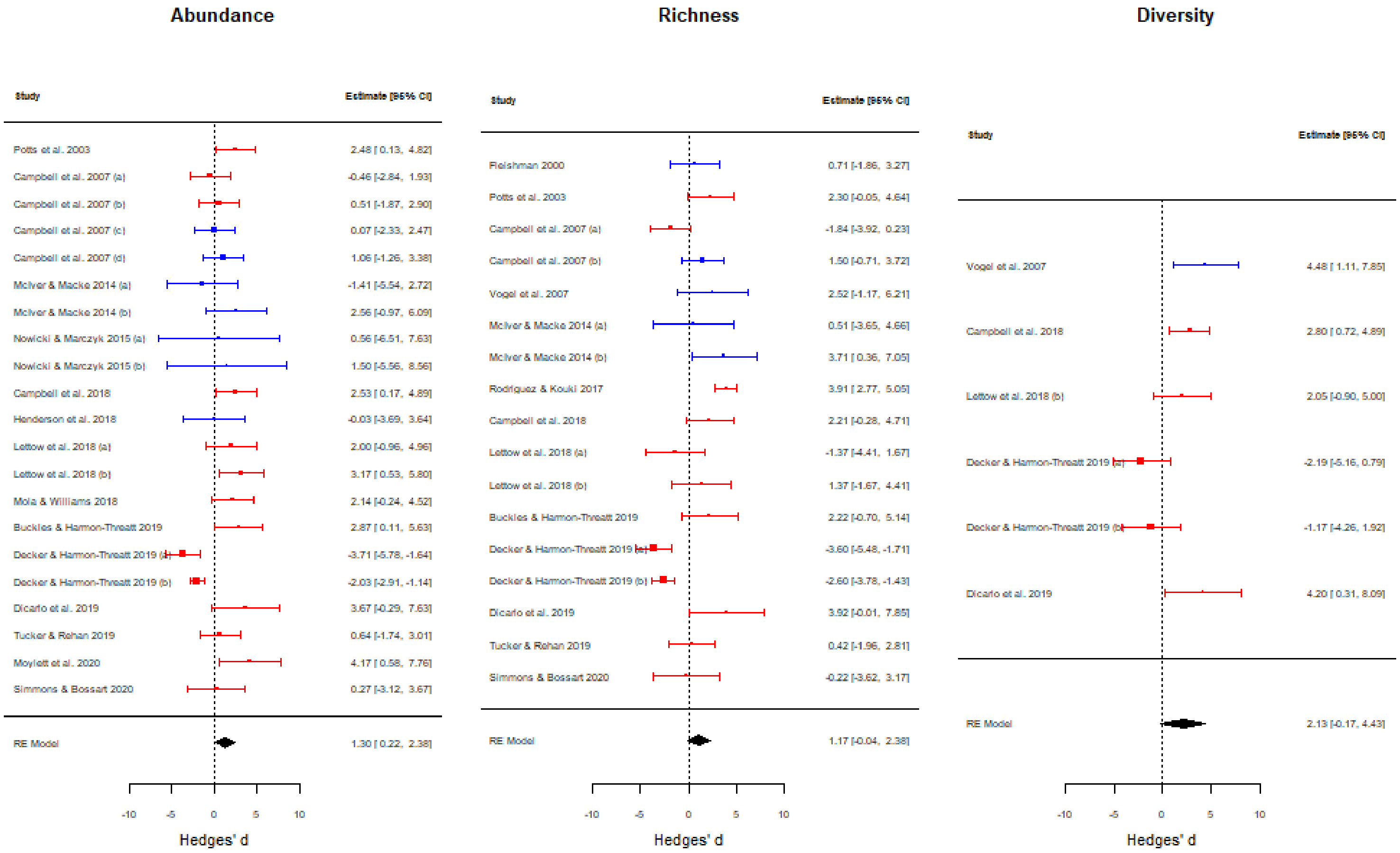

Figure S4.3: Funnel graphs showing the individual and overall effect sizes for each study included in the abundance richness and diversity models with the influential potential outliers removed. Data shown are from bee taxa (red) or butterfly taxa (blue).

Appendix B - Chapter 3 Appendix

Table S3.1. Table of sampling locations with GPS coordinates in WSGS and UTM (17N) format and elevation.

ID	Location	Distance	Lat (WSGS)	Lon (WSGS)	Lat (UTM)	Long (UTM)
1	Five Points	0	33.03730999	-83.655494	252003	3658557.7
2	Five Points	50	33.03689601	-83.655696	251983	3658512.2
3	Five Points	100	33.03649703	-83.65592298	251960.6	3658468.5
4	Five Points	150	33.03609302	-83.65617502	251936	3658424.3
5	Five Points	200	33.03569396	-83.65639396	251914.4	3658380.6
6	Five Points	250	33.03532197	-83.65667501	251887.1	3658340
7	Five Points	300	33.034896	-83.65696401	251858.9	3658293.4
8	Five Points	350	33.03449099	-83.65724003	251832	3658249.1
9	Five Points	400	33.03411003	-83.657493	251807.3	3658207.5
10	Five Points	450	33.03372304	-83.65772199	251784.8	3658165.1
11	Five Points	500	33.03334602	-83.65783799	251772.9	3658123.6
12	Five Points	0	33.03739096	-83.65548402	252004.1	3658566.6
13	Five Points	50	33.03782498	-83.65537103	252015.9	3658614.5
14	Five Points	100	33.03826997	-83.65522301	252031	3658663.5
15	Five Points	150	33.03871103	-83.65502704	252050.5	3658712
16	Five Points	200	33.03911998	-83.65481598	252071.4	3658756.8
17	Five Points	250	33.03948199	-83.65465597	252087.4	3658796.6
18	Five Points	300	33.03991903	-83.65445103	252107.7	3658844.6
19	Five Points	350	33.04035698	-83.65429597	252123.4	3658892.8
20	Five Points	400	33.04068203	-83.65419899	252133.4	3658928.6
21	Five Points	450	33.04106802	-83.653898	252162.6	3658970.7
22	Five Points	500	33.04137999	-83.65375701	252176.7	3659005
23	Natural Rock	0	33.07698204	-83.68740298	249134.8	3663033.6
24	Natural Rock	50	33.07737398	-83.68728203	249147.2	3663076.7
25	Natural Rock	100	33.07782199	-83.68717298	249158.6	3663126.2
26	Natural Rock	150	33.07832298	-83.687134	249163.7	3663181.6
27	Natural Rock	200	33.07876596	-83.68699201	249178.2	3663230.4
28	Natural Rock	250	33.07912898	-83.68695203	249183	3663270.6
29	Natural Rock	300	33.07959401	-83.68690903	249188.3	3663322.1
30	Natural Rock	350	33.08001696	-83.68689202	249191.1	3663368.9
31	Natural Rock	400	33.08042902	-83.68683804	249197.3	3663414.5
32	Natural Rock	450	33.08082598	-83.68675204	249206.5	3663458.3
33	Natural Rock	500	33.08122898	-83.68671499	249211.1	3663502.9
34	Natural Rock	0	33.07784303	-83.69300301	248614.3	3663142.5
35	Natural Rock	50	33.07769802	-83.69342898	248574.1	3663127.4
36	Natural Rock	100	33.07745	-83.69386601	248532.6	3663100.9

37	Natural Rock	150	33.07721003	-83.694439	248478.4	3663075.7
38	Natural Rock	200	33.07699897	-83.69478601	248445.4	3663053.1
39	Natural Rock	250	33.07679798	-83.69524199	248402.3	3663031.9
40	Natural Rock	300	33.07656898	-83.69565999	248362.6	3663007.5
41	Natural Rock	350	33.076399	-83.69608403	248322.5	3662989.7
42	Natural Rock	400	33.07622298	-83.69653397	248280	3662971.3
43	Natural Rock	450	33.07600002	-83.69704703	248231.4	3662947.8
44	Natural Rock	500	33.075781	-83.69745397	248192.8	3662924.4
45	Caney Creek	0	33.13160196	-83.72479498	245800.7	3669181.7
46	Caney Creek	50	33.13133097	-83.72443004	245834	3669150.7
47	Caney Creek	100	33.13105202	-83.72400801	245872.5	3669118.8
48	Caney Creek	150	33.13085203	-83.723604	245909.7	3669095.6
49	Caney Creek	200	33.13056998	-83.72315699	245950.6	3669063.2
50	Caney Creek	250	33.130343	-83.72264997	245997.2	3669036.8
51	Caney Creek	300	33.13011199	-83.72228201	246030.9	3669010.3
52	Caney Creek	350	33.12984997	-83.72187599	246068	3668980.3
53	Caney Creek	400	33.12962299	-83.72144599	246107.5	3668954.1
54	Caney Creek	450	33.12940699	-83.72096999	246151.3	3668929
55	Caney Creek	500	33.129093	-83.72054804	246189.8	3668893.1
56	Caney Creek	0	33.13705103	-83.71986399	246276.5	3669774.1
57	Caney Creek	50	33.13721398	-83.72044201	246223.1	3669793.6
58	Caney Creek	100	33.13728598	-83.72099899	246171.3	3669802.9
59	Caney Creek	150	33.13744297	-83.72158497	246117.1	3669821.7
60	Caney Creek	200	33.137505	-83.72213398	246066	3669830
61	Caney Creek	250	33.13761597	-83.72274502	246009.3	3669843.7
62	Caney Creek	300	33.13780298	-83.72333301	245955	3669865.9
63	Caney Creek	350	33.13791001	-83.72390198	245902.2	3669879.2
64	Caney Creek	400	33.13807103	-83.72446801	245849.9	3669898.4
65	Caney Creek	450	33.13825903	-83.72493999	245806.4	3669920.4
66	Caney Creek	500	33.13843799	-83.72553502	245751.4	3669941.7

Table S3.2. Table of plant species collected including their Abundance and the proportion of sampling locations each species was present in 2015 and 2016.

		2015		2016	
Common Name	Scientific Name	Abundance	Proportion	Abundance	Proportion
3 Seeded Mercury	*Acalypha rhomboidea*	10	0.136	3	0.045
Chalk Bark Maple	*Acer leucoderme*	14	0.076	13	0.106
Red Maple	*Acer rubrum*	122	0.379	99	0.364
Annual Ragweed	*Ambrosia artemisiifolia*	4	0.030	1	0.015
Indianhemp	*Apocynum cannabinum*	0	0.000	1	0.015
Pawpaw	*Asimina triloba*	1	0.015	2	0.030
Ebony Spleenwort	*Asplenium platyneuron*	1	0.015	0	0.000
Aster sp.	*Aster* sp.	0	0.000	13	0.121
Asteraceae	*Asteraceae* 1	10	0.061	0	0.000
Asteraceae	*Asteraceae* 2	0	0.000	36	0.303
American Beautyberry	*Callicarpa americana*	22	0.212	17	0.167
Trumpet Creeper	*Campsis radicans*	0	0.000	1	0.015
Hickory	*Carya* sp.	31	0.364	25	0.242
Sugarberry	*Celtis laevigata*	2	0.030	8	0.076
Spurred Butterfly Pea	*Centrosema virginianum*	71	0.348	82	0.379
Redbud	*Cercis canadensis*	6	0.091	7	0.061
Partridge Pea	*Chamaecrista fasciculata*	54	0.227	18	0.212
Blue Mistflower	*Conoclinium coelestinum*	3	0.045	13	0.106
Canadian Horseweed	*Conyza canadensis*	1	0.015	0	0.000
Greater Tickseed	*Coreopsis major*	0	0.000	8	0.015
Whorled Tickseed	*Coreopsis verticillata*	10	0.061	5	0.045
Flowering Dogwood	*Cornus florida*	40	0.288	34	0.303
Hawthorn	*Crataegus* sp.	12	0.121	10	0.136
Woodvamp	*Decumaria barbara*	2	0.015	1	0.015
Tick Trefoil	*Desmodium* sp.	21	0.227	29	0.242

Rosette Grass	*Dichanthelium* sp.	110	0.636	128	0.773
Poor Joe	*Diodia teres*	2	0.030	4	0.045
Common Persimmon	*Diospyros virginiana*	24	0.242	24	0.242
Wood Fern	*Dryopteris* sp.	0	0.000	1	0.015
Carolina Elephantsfoot	*Elephantopus carolinianus*	30	0.318	30	0.258
American Burnweed	*Erechtites hieraciifolius*	9	0.076	19	0.167
Eastern Daisy Fleabane	*Erigeron annuus*	0	0.000	5	0.061
Fleabane	*Erigeron* sp.	0	0.000	14	0.121
Strawberrybush	*Euonymus americanus*	3	0.045	30	0.288
Dog Fennel	*Eupatorium capillifolium*	1	0.015	0	0.000
Yankeeweed	*Eupatorium compositifolium*	6	0.076	1	0.015
Flowering Spurge	*Euphorbia corollata*	5	0.061	7	0.091
Sweetscented Joe Pye Weed	*Eutrochium purpureum*	10	0.106	9	0.091
American Beech	*Fagus grandifolia*	1	0.015	1	0.015
Green Ash	*Fraxinus pennsylvanica*	5	0.061	9	0.091
Milk Pea	*Galactia* sp.	41	0.227	82	0.424
Stickwilly	*Galium aparine*	0	0.000	8	0.091
Coastal Bedstraw	*Galium hispidulum*	5	0.061	0	0.000
Eastern Teaberry	*Gaultheria procumbens*	1	0.015	2	0.030
Yellow Jessamine	*Gelsemium sempervirens*	20	0.106	16	0.061
Carolina Silverbell	*Halesia carolina*	0	0.000	2	0.015
American Witchhazel	*Hamamelis virginiana*	1	0.015	3	0.015
Sunflower	*Helianthus* sp. 1	3	0.015	0	0.000
Sunflower	*Helianthus* sp. 2	11	0.061	0	0.000
Sunflower	*Helianthus* sp. 3	0	0.000	12	0.076
Little Brown Jug	*Hexastylis arifolia*	1	0.015	1	0.015
St. Johnswort	*Hypericum perforatum*	13	0.121	12	0.182
American Holly	*Ilex opaca*	1	0.015	0	0.000
Holly	*Ilex* sp.	2	0.030	0	0.000
Canada Lettuce	*Lactuca canadensis*	0	0.000	1	0.015
Sericea Lespedeza	*Lespedeza cuneata*	2	0.030	2	0.030

Lespedeza	*Lespedeza* sp.	48	0.379	53	0.348
Sweetgum	*Liquidambar styraciflua*	215	0.667	236	0.621
Tuliptree	*Liriodendron tulipifera*	13	0.106	2	0.030
Japanese Honeysuckle	*Lonicera japonica*	42	0.212	27	0.212
Angular Fruit Milk Vine	*Matelea gonocarpos*	1	0.015	0	0.000
Common Moonseed	*Menispermum canadense*	1	0.015	3	0.030
Nepalese Browntop	*Microstegium vimineum*	0	0.000	1	0.015
Littleleaf Sensitive-Briar	*Mimosa microphylla*	4	0.061	0	0.000
Partridge Berry	*Mitchella repens*	4	0.045	0	0.000
Blackgum	*Nyssa sylvatica*	6	0.045	4	0.045
Hophornbeam	*Ostrya virginiana*	12	0.061	23	0.136
Panic Grass	*Panicum* sp.	26	0.242	21	0.227
Virginia Creeper	*Parthenocissus quinquefolia*	18	0.136	18	0.106
Purple Passionflower	*Passiflora incarnata*	1	0.015	0	0.000
Loblolly Pine	*Pinus taeda*	35	0.409	29	0.318
Grass	*Poaceae*	501	0.970	499	0.955
Smartweed	*Polygonum* sp.	0	0.000	1	0.015
Juniper Leaf	*Polypremum procumbens*	0	0.000	1	0.015
Christmas Fern	*Polystichum acrostichoides*	37	0.106	35	0.136
Dwarf Cinquefoil	*Potentilla canadensis*	16	0.182	0	0.000
Common Selfheal	*Prunella vulgaris*	0	0.000	1	0.015
Black Cherry	*Prunus serotina*	27	0.182	23	0.182
Rabbit-Tobacco	*Pseudognaphalium obtusifolium*	0	0.000	2	0.030
Mountain Mint	*Pycnanthemum* sp.	2	0.030	3	0.045
White Oak	*Quercus alba*	53	0.348	48	0.424
Southern Red Oak	*Quercus falcata*	34	0.258	35	0.303
Water Oak	*Quercus nigra*	28	0.273	30	0.273
Northern Red Oak	*Quercus rubra*	19	0.182	4	0.061
Post Oak	*Quercus stellata*	3	0.045	4	0.045
Littleleaf Buttercup	*Ranunculus abortivus*	2	0.030	0	0.000
Fragrant Sumac	*Rhus aromatica*	12	0.076	13	0.091

Winged Sumac	*Rhus copallinum*	81	0.439	109	0.485
Rose	*Rosa* sp.	12	0.091	11	0.076
Blackberry	*Rubus* sp.	114	0.439	140	0.470
Rudbeckia sp.	*Rudbeckia* sp.	1	0.015	0	0.000
Carolina Wild Petunia	*Ruellia caroliniensis*	2	0.030	4	0.061
Rosepink	*Sabatia angularis*	0	0.000	1	0.015
Rosinweed	*Silphium* sp.	31	0.318	0	0.000
Small Hairy Leafcup	*Smallanthus uvedalius*	0	0.000	1	0.015
Greenbrier	*Smilax* sp.	54	0.530	42	0.455
Carolina Horsenettle	*Solanum carolinense*	0	0.000	1	0.015
Solidago sp.	*Solidago* sp. 1	16	0.136	0	0.000
Solidago sp.	*Solidago* sp. 2	0	0.000	2	0.030
Solidago sp.	*Solidago* sp. 3	0	0.000	3	0.030
Johnsons Grass	*Sorghum halepense*	31	0.273	59	0.288
Sidebeak Pencilflower	*Stylosanthes biflora*	2	0.030	1	0.015
Calico Aster	*Symphyotrichum lateriflorum*	0	0.000	6	0.061
Virginia tephrosia	*Tephrosia virginiana*	0	0.000	1	0.015
Eastern poision ivy	*Toxicodendron radicans*	3	0.045	1	0.015
Noseburn	*Tragia urticifolia*	6	0.061	3	0.030
Unknown	Unknown	1	0.015	0	0.000
Winged Elm	*Ulmus alata*	33	0.288	15	0.091
Stinging Nettle	*Urtica dioica*	0	0.000	1	0.015
Farkleberry	*Vaccinium arboreum*	17	0.076	0	0.000
High Bush Blueberry	*Vaccinium corymbosum*	0	0.000	11	0.076
Elliot's Blueberry	*Vaccinium elliottii*	0	0.000	27	0.288
Blueberry	*Vaccinium* sp.	67	0.485	0	0.000
Deer Berry	*Vaccinium stamineum*	0	0.000	20	0.227
Violet	*Viola* sp.	3	0.030	1	0.015
Muscadine	*Vitis rotundifolia*	424	0.894	356	0.879

Table S3.3. Table of butterfly species collected from 2015, 2016, and the total and size group to which each species belongs. Abbreviations are Caney Creek (C.C.), Five Points (F.P.), and Natural Rock (N.R.).

		2015			2016			
Species	Body Size Guild	C.C.	F.P.	N.R.	C.C.	F.P.	N.R.	Total
Abaeis nicippe (Cramer 1779)	Large	2	2	1	1	4	2	12
Achalarus lyciades (Geyer 1832)	Medium	1	3	2	4	0	0	10
Agraulis vanillae (L. 1758)	Large	0	2	0	0	1	0	3
Amblyscirtes aesculapius (F. 1793)	Medium	1	1	1	3	0	21	27
Amblyscirtes alternata (Grote & Robinson 1867)	Small	2	0	1	1	0	1	5
Amblyscirtes belli H. Freeman 1941	Medium	0	0	15	0	0	3	18
Amblyscirtes hegon (Scudder 1863)	Small	7	2	1	3	0	1	14
Ancyloxypha numitor (F. 1793)	Small	1	0	0	0	0	0	1
Battus philenor † (L. 1771)	Large	9	7	13	12	14	9	64
Calycopis cecrops † (F. 1793)	Small	13	20	8	2	10	2	55
Chlosyne nycteis (E. Doubleday [1847])	Large	2	0	0	0	0	0	2
Cupido comyntas (Godart [1824])	Small	0	1	0	1	3	1	6
Cyllopsis gemma (Hübner, 1808)	Medium	0	2	1	2	0	1	6
Epargyreus clarus (Cramer 1775)	Large	0	0	1	0	0	1	2
Erynnis horatius (Scudder & Burgess 1870)	Medium	0	0	0	1	0	0	1
Erynnis juvenalis (F. 1793)	Medium	0	0	3	1	0	1	5
Erynnis zarucco (Lucas 1857)	Medium	0	0	0	0	1	0	1
Euphyes vestris (Boisducal 1852)	Small	0	3	4	2	4	1	14
Hermeuptychia sosybius † (F. 1793)	Medium	7	12	4	4	16	24	67
Hylephila phyleus (Drury 1773)	Medium	1	3	0	2	0	0	6
Junonia coenia Hübner [1822]	Large	0	0	2	0	0	0	2
Lerema accius † (J. E. Smith 1797)	Medium	307	272	437	292	294	252	1854
Megisto cymela (Cramer 1777)	Medium	4	0	2	0	1	1	8
Nastra lherminier † (Latreille [1824])	Small	104	29	51	55	25	13	277
Neographium marcellus (Cramer 1777)	Large	0	0	0	0	0	3	3
Oligoria maculata † (W. H. Edwards 1865)	Medium	11	20	22	45	70	39	207

Phoebis sennae (L. 1758)	Large	1	13	4	3	3	2	26
Phyciodes tharos (Drury 1773)	Medium	5	5	5	0	4	5	24
Poanes hobomok (T. Harris 1862)	Small	0	0	0	0	0	2	2
Poanes zabulon (Boisduval & Le Conte [1837])	Medium	25	11	15	5	8	10	74
Polites origenes † (F. 1793)	Small	15	8	9	12	25	8	77
Polites vibex † (Geyer 1832)	Small	12	17	7	7	8	2	53
Pompeius verna (W. H. Edwards 1862)	Small	7	3	11	0	3	1	25
Problema byssus (W. H. Edwards 1880)	Medium	1	2	3	3	5	3	17
Pterourus glaucus † (L. 1758)	Large	9	10	8	7	19	12	65
Pterourus troilus (L. 1758)	Large	3	0	2	0	2	0	7
Pyrisitia lisa (Boisduval & Le Conte [1830])	Medium	1	1	3	0	2	1	8
Thorybes bathyllus (J. E. Smith 1797)	Medium	5	3	5	5	3	3	24
Thorybes confusis (E. Bell 1923)	Medium	4	0	0	1	2	1	8
Thorybes pylades (Scudder 1870)	Medium	10	4	5	9	4	3	35
Urbanus proteus (L. 1758)	Large	1	1	1	0	0	1	4
Wallengrenia egeremet (Scudder 1863)	Small	11	4	1	11	4	4	35
Wallengrenia otho (J. E. Smith, 1797)	Small	0	0	0	0	0	3	3
Total Abundance		580	461	648	494	535	437	3155
Total Richness		29	28	32	27	26	34	43

*: † indicates species with greater than 50 individuals collected.

Table S3.4. Table of bee species collected during the first and second year (species with greater than 50 individuals are in bold) and the size group to which each species belongs. Abbreviations are Caney Creek (C.C.), Five Points (F.P.), and Natural Rock (N.R.).

			2015			2016			
Species	Body Size Guild	Nesting Guild	C.C.	F.P.	N.R.	C.C.	F.P.	N.R.	Total
Agapostemon splendens (Lepeletier 1841)	Large	Soil	0	0	1	0	0	0	1
Andrena atlantica Mitchell 1960	Medium	Soil	0	0	0	4	0	4	8
Andrena barbara Bouseman & LaBerge 1979	Large	Soil	0	0	0	4	0	0	4
Andrena cressonii Robertson 1891	Medium	Soil	0	0	0	1	1	0	2
Andrena distans Provancher 1888	Medium	Soil	1	0	1	0	0	2	4
Andrena hirticincta Provancher 1888	Large	Soil	0	0	0	1	0	0	1
Andrena ilicis Mitchell 1960	Medium	Soil	0	0	0	1	2	1	4
Andrena imitatrix Cresson 1872	Medium	Soil	0	0	0	0	0	1	1
Andrena perplexa Smith 1853	Large	Soil	0	0	0	1	0	0	1
Andrena rubi Mitchell 1960	Medium	Soil	0	0	0	1	0	0	1
Andrena sp.	Medium	Soil	1	1	0	0	0	0	2
Andrena fenningeria Viereck 1922	Medium	Soil	0	0	0	4	0	1	5
Andrena violae Robertson 1891	Medium	Soil	0	0	0	0	1	0	1
Anthophora abrupta Say 1838	Large	Soil	1	0	0	1	1	0	3
Apis melifera L. 1758	Large	Wood/Ground	0	0	0	0	1	1	2
Ashmeadiella floridana (Robertson 1897)	Medium	Wood	0	0	0	0	1	0	1
Augochlora pura † (Say 1837)	Medium	Rotting Wood	48	40	74	2	18	9	191
Augochloropsis metallica (F. 1793)	Medium	Soil	3	2	1	0	0	1	7
Augochlorella aurata † (Smith 1853)	Small	Soil	323	524	829	129	131	271	2207
Bombus bimaculatus Cresson 1863	Large	Wood/Ground	9	4	6	5	6	5	35
Bombus fraternus (Smith 1854)	Large	Wood/Ground	0	0	0	0	1	0	1
Bombus griseocollis (De Geer 1773)	Large	Wood/Ground	12	6	9	5	0	2	34
Bombus impatiens † Cresson 1863	Large	Wood/Ground	68	28	69	32	32	34	263

Bombus pensylvanicus (De Geer 1773)	Large	Wood/Ground	0	0	1	2	1	1	5
Calliopsis andreniformis Smith 1853	Medium	Soil	1	0	1	0	0	0	2
Ceratina calcarata † Robertson 1900	Medium	Wood	35	25	32	27	19	31	169
Ceratina cockerelli H. S. Smith 1907	Small	Wood	1	0	1	0	0	0	2
Ceratina dupla Say 1837	Medium	Wood	4	0	2	0	0	3	9
Ceratina strenua † Smith 1879	Small	Wood	27	35	26	5	18	25	136
Colletes inaequalis Say 1837	Large	Soil	0	0	0	0	0	1	1
Eucera hamata (Bradley 1942)	Large	Soil	0	0	1	0	1	0	2
Eucera rosae (Robertson 1900)	Large	Soil	0	1	3	3	0	1	8
Halictus confuses Smith 1853	Medium	Soil	0	1	0	0	0	0	1
Halictus ligatus Say 1837	Medium	Soil	4	1	4	0	0	3	12
Halictus rubicundus (Christ 1791)	Large	Soil	1	0	0	0	0	0	1
Heriades carinatus Cresson 1864	Medium	Wood	1	0	0	0	0	0	1
Heriades variolosa (Cresson 1872)	Medium	Wood	0	0	1	0	0	0	1
Hoplitis producta (Cresson 1864)	Medium	Wood	0	1	2	0	0	1	4
Hoplitis truncate (Cresson 1878)	Medium	Wood	2	0	0	0	0	3	5
Hylaeus affinis (Smith 1853)	Small	Wood	1	1	2	0	0	1	5
Hylaeus floridanus (Robertson 1893)	Small	Wood	0	1	0	0	0	0	1
Hylaeus modestus Say 1837	Small	Wood	0	3	0	0	0	1	4
Lasioglossum admirandum † (Sandhouse 1924)	Small	Soil	15	23	56	4	2	4	104
Lasioglossum apopkense † (Robertson 1892)	Small	Soil	245	19	102	94	16	22	498
Lasioglossum bruneri † (Crawford 1902)	Medium	Soil	440	209	848	50	65	175	1787
Lasioglossum callidum (Sandhouse 1924)	Small	Soil	1	0	1	0	0	0	2
Lasioglossum cattellae (Ellis 1913)	Small	Soil	1	1	1	0	0	0	3
Lasioglossum ceanothi † (Mitchell 1960)	Small	Soil	10	37	31	3	3	13	97
Lasioglossum coeruleum (Robertson 1893)	Medium	Soil	2	4	11	0	1	2	20
Lasioglossum coreopsis (Robertson 1902)	Small	Soil	2	4	10	5	1	5	27
Lasioglossum creberrimum (Smith 1853)	Small	Soil	0	1	1	0	0	0	2
Lasioglossum cressonii (Robertson 1890)	Medium	Soil	0	0	0	1	0	0	1
Lasioglossum gotham Gibbs 2011	Medium	Soil	8	3	8	6	2	1	28
Lasioglossum hitchensi † Gibbs 2012	Small	Soil	90	45	141	9	7	16	308

Lasioglossum illinoense † (Robertson 1892)	Small	Soil	189	84	171	44	16	25	529
Lasioglossum imitatum † (Smith 1853)	Small	Soil	81	47	84	2	9	10	233
Lasioglossum lionotum (Sandhouse 1923)	Small	Soil	1	0	1	0	0	2	4
Lasioglossum longifrons (Baker 1906)	Small	Soil	0	0	0	2	1	2	5
Lasioglossum nymphale (Smith 1853)	Small	Soil	0	0	0	1	0	0	1
Lasioglossum obscurum (Robertson 1892)	Medium	Soil	0	1	0	0	0	0	1
Lasioglossum pilosum † (Smith 1853)	Medium	Soil	89	5	44	9	5	4	156
Lasioglossum raleighense † (Crawford 1932)	Small	Soil	91	65	84	56	39	46	381
Lasioglossum smilacinae (Robertson 1897)	Medium	Soil	0	0	1	0	0	0	1
Lasioglossum subviridatum (Cockerell 1938)	Small	Soil	3	0	1	0	0	0	4
Lasioglossum sp.	Small	Soil	0	0	0	0	0	1	1
Lasioglossum tegulare † (Robertson 1890)	Small	Soil	131	55	108	45	16	21	376
Lasioglossum timothyi Gibbs 2010	Small	Soil	0	0	0	0	0	1	1
Lasioglossum trigeminum † Gibbs 2011	Small	Soil	85	110	269	29	25	36	554
Lasioglossum weemsi † (Mitchell 1960)	Small	Soil	27	15	69	3	0	3	117
Lasioglossum zephyrum (Smith 1853)	Small	Soil	0	1	1	0	1	0	3
Lasioglossum birkmanni † (Crawford 1906)	Small	Soil	11	15	28	4	5	6	69
Lasioglossum foxii (Robertson 1895)	Small	Soil	0	0	0	0	0	1	1
Lasioglossum macoupinense (Robertson 1895)	Small	Soil	0	0	1	0	0	1	2
Lasioglossum pectorale † (Smith 1853)	Small	Soil	21	6	35	2	0	3	67
Lasioglossum sopinci (Crawford 1932)	Medium	Soil	0	2	3	0	0	2	7
Lasioglossum fuscipenne (Smith 1853)	Medium	Soil	0	0	0	0	0	3	3
Megachile campanulae (Robertson 1903)	Large	Wood	1	1	0	0	0	0	2
Megachile frigida Smith 1853	Large	Wood	1	2	1	0	0	0	4
Megachile gemula Cresson 1878	Large	Wood	1	0	0	0	1	0	2
Megachile georgica Cresson 1878	Large	Wood	1	1	1	1	1	0	5
Megachile latimanus Say 1823	Large	Wood	1	0	0	0	0	0	1
Megachile mendica Cresson 1878	Large	Wood	2	2	2	0	1	4	11
Megachile petulans Cresson 1878	Large	Wood	1	0	1	0	0	1	3
Megachile sculpturalis Smith 1853	Large	Wood	0	0	1	0	0	0	1
Melissodes agilis Cresson 1878	Large	Soil	3	1	4	2	0	0	10

Melissodes bimaculatus † (Lepeletier 1825)	Large	Soil	19	21	2	5	3	3	53
Melissodes comptiodes Robertson 1898	Large	Soil	15	12	14	3	1	1	46
Melissodes dentiventris Smith 1854	Large	Soil	0	1	0	0	0	0	1
Melissodes desponsus Smith 1854	Large	Soil	0	2	0	1	0	0	3
Melissodes manipularis Smith 1854	Large	Soil	0	0	1	0	0	0	1
Melitoma taurea (Say 1837)	Large	Soil	2	1	0	0	15	3	21
Melitta Americana (Smith 1853)	Large	Soil	0	0	1	2	0	2	5
Nomada annulata Smith 1854	Medium	Soil	0	0	0	0	1	0	1
Nomada depressa Cresson 1863	Medium	Soil	0	0	0	0	0	1	1
Nomada imbricata Smith 1854	Medium	Soil	0	0	0	4	1	0	5
Nomada ovata (Robertson 1903)	Medium	Soil	0	0	0	1	0	0	1
Nomada parva Robertson 1900	Small	Soil	0	0	3	0	0	1	4
Nomada perplexa Cresson 1863	Medium	Soil	0	0	0	1	0	0	1
Nomada sayi Robertson 1893	Small	Soil	0	0	10	0	0	2	12
Nomada sp.	Medium	Soil	0	0	0	1	0	0	1
Nomada sulphurata Smith 1854	Medium	Soil	0	0	0	0	1	1	2
Nomia nortoni Cresson 1868	Large	Soil	1	0	0	0	0	0	1
Osmia atriventris Cresson 1864	Medium	Wood	1	0	2	0	0	1	4
Osmia chalybea Smith 1853	Large	Wood	0	1	2	2	1	0	6
Osmia collinsiae Robertson 1905	Large	Wood	1	0	0	0	0	0	1
Osmia conjuncta Cresson 1864	Medium	Wood	0	1	0	0	2	1	4
Osmia distincta Cresson 1864	Medium	Wood	0	0	0	0	0	3	3
Osmia georgica Cresson 1878	Medium	Wood	0	1	0	1	1	1	4
Osmia inspergens Lovell & Cockerell 1907	Large	Wood	0	0	1	0	0	0	1
Osmia pumila Cresson 1864	Medium	Wood	0	0	1	0	1	2	4
Osmia sandhouseae Mitchell 1927	Medium	Wood	1	1	0	0	1	3	6
Osmia texana Cresson 1872	Large	Wood	0	0	0	0	0	3	3
Panurginus potentillae (Crawford 1916)	Small	Soil	0	0	0	1	0	0	1
Perdita bishoppi Cockerell 1906	Small	Soil	0	0	6	0	0	2	8
Pseudopanurgus sp.	Small	Soil	0	0	1	0	7	2	10
Sphecodes antennariae Robertson 1891	Small	Soil	0	0	0	0	1	0	1

Sphecodes banskii Lovell 1909	Small	Soil	0	0	0	1	1	0	2
Sphecodes pimpinellae Robertson 1900	Medium	Soil	0	0	1	0	0	1	2
Stelis lateralis Cresson 1864	Small	Wood	1	0	0	0	0	0	1
Svastra atripes (Cresson 1872)	Large	Soil	0	0	0	0	0	1	1
Svastra obliqua (Say 1837)	Large	Soil	0	1	0	1	0	0	2
Svastra petulca (Cresson 1878)	Large	Soil	0	0	1	0	0	0	1
Trachusa ridingsii (Cresson 1878)	Large	Soil	1	0	1	1	0	0	3
Xylocopa virginica (L. 1771)	Large	Wood	5	1	1	1	0	0	8
Total Abundance			2144	1476	3234	626	488	847	8815
Total Richness			58	54	68	54	49	69	124

*: † indicates species with greater than 50 individuals collected.

Table S3.5: ANOVA results for the effects of distance (Dist), burn cycle (BC), year (Yr), plant Richness (PR) (plant height is not included in these final models as it was not a significant covariate), the interaction of distance and burn cycle, the interaction of distance and year, the interaction of burn cycle and year, and the interaction of distance burn cycle and year on sqrt-transformed large (Lrg.) bee Abundance, sqrt-transformed large bee Richness, Shannon's large bee Diversity (H'), sqrt-transformed small (Sm.) bee Abundance, sqrt-transformed small bee Richness, and Shannon's small bee Diversity using Kenward-Roger denominator degrees of freedom approximation method.

	Sqrt(Lrg. Bee Abundance)	Sqrt(Lrg. Bee Richness)	Lrg. Bee H'	Sqrt(Sm. Bee Abundance)	Sqrt(Sm. Bee Richness)	Sm. Bee H'
Dist	$F_{1,57.3}=9.67^{**}$	$F_{1,58.1}=9.18^{**}$	$F_{1,58.1}=7.76^{**}$	$F_{1,58.0}=0.18$	$F_{1,57.4}=9.44^{**}$	$F_{1,58.1}=15.64^{***}$
BC	$F_{1,2.0}=1.07$	$F_{1,2.0}=0.13$	$F_{1,2.0}=0.59$	$F_{1,2.0}=2.62$	$F_{1,2.0}=1.14$	$F_{1,2.0}=0.03$
Yr	$F_{1,2.0}=8.60$	$F_{1,2.0}=8.50$	$F_{1,2.0}=15.38$	$F_{1,2.0}=49.83^{*}$	$F_{1,1.9}=210.55^{**}$	$F_{1,2.0}=27.38^{*}$
PD	$F_{1,98.5}=4.30^{*}$				$F_{1,94.2}=4.12^{*}$	
PH						
Open						
BG						
Dist*BC	$F_{1,57.8}=2.29$	$F_{1,58.1}=3.15$	$F_{1,58.1}=1.89$	$F_{1,58.0}=0.55$	$F_{1,57.9}=0.03$	$F_{1,58.1}=0.16$
Dist*Yr	$F_{1,57.6}=0.60$	$F_{1,58.1}=0.27$	$F_{1,58.2}=0.95$	$F_{1,58.1}=2.02$	$F_{1,57.8}=3.16$	$F_{1,58.1}=1.02$
BC*Yr	$F_{1,2.0}=2.83$	$F_{1,2.0}=0.37$	$F_{1,2.0}=0.43$	$F_{1,2.0}=50.34^{*}$	$F_{1,2.0}=46.84^{*}$	$F_{1,2.0}=24.76^{*}$
Dist*BC*Yr	$F_{1,57.8}=8.33^{**}$	$F_{1,58.1}=11.88^{**}$	$F_{1,58.2}=9.31^{**}$	$F_{1,58.1}=0.37$	$F_{1,58.0}=1.79$	$F_{1,58.1}=4.81^{*}$

*: symbols indicating level of significance (alpha=0.05), *p<0.05, **p<0.01, ***p<0.001

Table S3.6: ANOVA results for the effects of distance (Dist), burn cycle (BC), year (Yr), plant Richness (PR), plant height (PH), the interaction of distance and burn cycle, the interaction of distance and year, the interaction of burn cycle and year, and the interaction of distance burn cycle and year on ln-transformed soil bee Abundance, sqrt-transformed soil bee Richness, Shannon's soil bee Diversity (H'), sqrt-transformed wood bee Abundance, sqrt-transformed wood bee Richness, and Shannon's wood bee Diversity using Kenward-Roger denominator degrees of freedom approximation method.

	Ln(Soil Bee Abundance)	Sqrt(Soil Bee Richness)	Soil Bee H'	Sqrt(Wood Bee Abundance)	Sqrt(Wood Bee Richness)	Wood Bee H'
Dist	$F_{1,58.0}=0.17$	$F_{1,59.4}=6.39^{*}$	$F_{1,59.5}=12.87^{***}$	$F_{1,58.1}=2.86$	$F_{1,58.1}=5.91^{*}$	$F_{1,58.7}=7.53^{*}$
BC	$F_{1,2.0}=0.59$	$F_{1,2.0}=2.42$	$F_{1,2.0}=1.66$	$F_{1,2.0}=0.01$	$F_{1,2.0}=0.01$	$F_{1,2.0}=0.11$
Yr	$F_{1,2.0}=227.38^{**}$	$F_{1,1.6}=165.33^{*}$	$F_{1,1.7}=22.20$	$F_{1,2.0}=3.39$	$F_{1,2.0}=1.44$	$F_{1,2.0}=0.78$
PD		$F_{1,67.8}=6.32^{*}$	$F_{1,58.9}=4.41^{*}$			
PH						
Open		$F_{1,23.5}=3.68$	$F_{1,29.5}=4.02$			$F_{1,81.8}=3.79$
BG						
Dist*BC	$F_{1,58.0}=0.39$	$F_{1,57.2}=0.50$	$F_{1,57.1}=2.45$	$F_{1,58.1}=0.01$	$F_{1,58.1}=0.22$	$F_{1,57.3}=0.04$
Dist*Yr	$F_{1,58.1}=3.55$	$F_{1,58.4}=0.57$	$F_{1,58.4}=0.001$	$F_{1,58.1}=3.24$	$F_{1,58.1}=3.02$	$F_{1,58.8}=0.51$
BC*Yr	$F_{1,2.0}=64.71^{*}$	$F_{1,2.2}=26.52^{*}$	$F_{1,2.2}=30.95^{*}$	$F_{1,2.0}=1.18$	$F_{1,2.0}=1.15$	$F_{1,2.1}=4.55$
Dist*BC*Yr	$F_{1,58.1}=1.48$	$F_{1,60.4}=2.19$	$F_{1,60.4}=5.41^{*}$	$F_{1,58.1}=0.75$	$F_{1,58.1}=1.78$	$F_{1,60.3}=2.34$

*: symbols indicating level of significance (alpha=0.05), *p<0.05, **p<0.01, ***p<0.001

Table S3.7: ANOVA results for the effects of distance (Dist), burn cycle (BC), year (Yr), plant Richness (PR) (plant height is not included in these final models as it was not a significant covariate), the interaction of distance and burn cycle, the interaction of distance and year, the interaction of burn cycle and year, and the interaction of distance burn cycle and year on sqrt-transformed *Bombus impatiens* Abundance, sqrt-transformed *Lasioglossum tegulare* Abundance, sqrt-transformed *Lasioglossum imitatum* Abundance, sqrt-transformed *Lasioglossum illinoense* Abundance, and sqrt-transformed *Lasioglossum hitchensi* Abundance and community composition using Kenward-Roger denominator degrees of freedom approximation method.

	Sqrt(*Melissodes bimaculatus*)	Sqrt(*Lasioglossum raleighense*)	Sqrt(*L. apopkense*)	Ln(*Ceratina calcarata*)	Ln(*L. bruneri*)	Sqrt(*L. birkmanni*)
Dist	$F_{1,56.4}=8.34$	$F_{1,58.7}=8.36^{**}$	$F_{1,58.1}=11.11^{**}$	$F_{1,58.1}=0.37$	$F_{1,57.3}=0.14$	$F_{1,58.1}=0.04$
BC	$F_{1,2.0}=2.08$	$F_{1,2.0}=3.15$	$F_{1,2.0}=3.71$	$F_{1,2.0}=0.26$	$F_{1,2.0}=0.07$	$F_{1,2.0}=0.09$
Yr	$F_{1,2.0}=3.62$	$F_{1,1.9}=18.85$	$F_{1,2.0}=4.39$	$F_{1,2.0}=1.24$	$F_{1,2.0}=23.46^{*}$	$F_{1,2.0}=8.94$
PD	$F_{1,86.8}=4.70^{*}$				$F_{1,111.0}=4.60^{*}$	
PH	$F_{1,92.3}=4.07^{*}$					
Open		$F_{1,66.2}=4.12^{*}$				
BG						
Dist*BC	$F_{1,56.7}=3.51$	$F_{1,57.5}=0.21$	$F_{1,58.1}=1.93$	$F_{1,58.1}=0.55$	$F_{1,57.8}=0.32$	$F_{1,58.1}=3.37$
Dist*Yr	$F_{1,58.1}=24.69^{***}$	$F_{1,58.7}=2.34$	$F_{1,58.1}=0.92$	$F_{1,58.1}=0.55$	$F_{1,57.5}=2.99$	$F_{1,58.1}=1.47$
BC*Yr	$F_{1,2.2}=2.20$	$F_{1,2.1}=1.47$	$F_{1,2.0}=16.51$	$F_{1,2.0}=0.02$	$F_{1,2.0}=0.18$	$F_{1,2.0}=1.85$
Dist*BC*Yr	$F_{1,57.8}=4.40^{*}$	$F_{1,59.7}=0.31$	$F_{1,58.1}=0.78$	$F_{1,58.1}=0.05$	$F_{1,57.7}=1.19$	$F_{1,58.1}=0.17$

*: symbols indicating level of significance (alpha=0.05), *$p<0.05$, **$p<0.01$, ***$p<0.001$

Table S3.8: ANOVA results for the effects of distance (Dist), burn cycle (BC), year (Yr), plant Richness (PR) (plant height is not included in these final models as it was not a significant covariate), the interaction of distance and burn cycle, the interaction of distance and year, the interaction of burn cycle and year, and the interaction of distance burn cycle and year on sqrt-transformed *Bombus impatiens* Abundance, sqrt-transformed *Lasioglossum tegulare* Abundance, sqrt-transformed *Lasioglossum imitatum* Abundance, sqrt-transformed *Lasioglossum illinoense* Abundance, and sqrt-transformed *Lasioglossum hitchensi* Abundance and community composition using Kenward-Roger denominator degrees of freedom approximation method.

	Sqrt(*Bombus impatiens*)	Sqrt(*Lasioglossum tegulare*)	Sqrt(*L. imitatum*)	Sqrt(*L. illinoense*)	Sqrt(*L, hitchensi*)	Axis 1	Axis 2	Axis 3
Dist	$F_{1,58.1}=1.64$	$F_{1,58.1}=6.20^{*}$	$F_{1,58.1}=7.78^{**}$	$F_{1,57.3}=4.29^{*}$	$F_{1,59.1}=0.16$	$F_{1,58.1}=2.04$	$F_{1,58.1}=13.75^{***}$	$F_{1,57.1}=0.01$
BC	$F_{1,2.0}=0.98$	$F_{1,2.0}=3.58$	$F_{1,2.0}=0.38$	$F_{1,2.0}=5.75$	$F_{1,2.0}=5.21$	$F_{1,2.0}=0.05$	$F_{1,2.0}=0.23$	$F_{1,2.0}=0.93$
Yr	$F_{1,2.0}=3.28$	$F_{1,2.0}=26.39^{*}$	$F_{1,2.0}=31.0^{*}$	$F_{1,2.0}=22.80^{*}$	$F_{1,2.0}=14.51$	$F_{1,2.0}=10.46$	$F_{1,2.0}=0.02$	$F_{1,2.0}=64.53^{*}$
PD				$F_{1,100.3}=4.69^{*}$	$F_{1,98.4}=6.76^{*}$			
PH								$F_{1,81.9}=5.63^{*}$
Open					$F_{1,102.1}=4.27^{*}$			
BG								
Dist*BC	$F_{1,58.1}=0.19$	$F_{1,58.1}=0.02$	$F_{1,58.1}=0.04$	$F_{1,57.8}=0.25$	$F_{1,56.6}=0.32$	$F_{1,58.1}=0.21$	$F_{1,58.1}=4.32^{*}$	$F_{1,57.1}=0.13$
Dist*Yr	$F_{1,58.1}=0.01$	$F_{1,58.2}=10.01^{**}$	$F_{1,58.1}=6.45^{*}$	$F_{1,57.7}=4.33^{*}$	$F_{1,58.3}=1.85$	$F_{1,58.1}=1.46$	$F_{1,58.1}=14.94^{***}$	$F_{1,58.4}=3.18$
BC*Yr	$F_{1,2.0}=6.89$	$F_{1,2.0}=42.05^{*}$	$F_{1,2.0}=2.27$	$F_{1,2.0}=85.78^{*}$	$F_{1,2.1}=2.35$	$F_{1,2.0}=3.10$	$F_{1,2.0}=0.27$	$F_{1,2.2}=2.96$
Dist*BC*Yr	$F_{1,58.1}=3.98$	$F_{1,58.2}=1.76$	$F_{1,58.1}=0.85$	$F_{1,57.9}=4.24^{*}$	$F_{1,60.6}=5.80$	$F_{1,58.1}=0.15$	$F_{1,58.1}=0.30$	$F_{1,58.1}=0.59$

*: symbols indicating level of significance (alpha=0.05), *p<0.05, **p<0.01, ***p<0.001

Table S3.9: ANOVA results for the effects of distance (Dist), burn cycle (BC), year (Yr), plant Richness (PR), plant height (PH), the interaction of distance and burn cycle, the interaction of distance and year, the interaction of burn cycle and year, and the interaction of distance burn cycle and year on sqrt-transformed large (Lrg.) butterfly Abundance, sqrt-transformed large butterfly Richness, Shannon's large butterfly Diversity (H'), sqrt-transformed small (Sm.) butterfly Abundance, sqrt-transformed small butterfly Richness, and Shannon's small butterfly Diversity and community composition using Kenward-Roger denominator degrees of freedom approximation method.

	Sqrt(Lrg. Butterfly Abundance)	Sqrt(Lrg. Butterfly Richness)	Lrg. Butterfly H'	Sqrt(Sm. Butterfly Abundance)	Sqrt(Sm. Butterfly Richness)	Sm. Butterfly H'	Axis 1	Axis 2	Axis 3
Dist	$F_{1,56.4}=4.48^{*}$	$F_{1,57.2}=6.43^{*}$	$F_{1,57.3}=0.94$	$F_{1,57.2}=3.20$	$F_{1,57.3}=0.46$	$F_{1,58.2}=0.23$	$F_{1,57.5}=1.95$	$F_{1,57.4}=0.46$	$F_{1,58.1}=1.12$
BC	$F_{1,2.0}=1.34$	$F_{1,2.0}=0.35$	$F_{1,2.0}=1.66$	$F_{1,2.0}=0.02$	$F_{1,2.0}=0.001$	$F_{1,2.0}=0.03$	$F_{1,2.0}=1.57$	$F_{1,2.0}=1.03$	$F_{1,2.0}=0.01$
Yr	$F_{1,2.0}=0.15$	$F_{1,2.0}=0.02$	$F_{1,2.0}=0.10$	$F_{1,2.0}=3.44$	$F_{1,2.0}=2.63$	$F_{1,2.0}=4.54$	$F_{1,1.9}=1.58$	$F_{1,1.9}=4.30$	$F_{1,2.0}=4.41$
PD	$F_{1,69.9}=10.06^{**}$	$F_{1,76.6}=5.62^{*}$	$F_{1,61.8}=3.28$	$F_{1,96.7}=4.89^{*}$	$F_{1,88.8}=3.46$		$F_{1,98.2}=8.19^{**}$	$F_{1,59.6}=3.80$	
PH	$F_{1,84.1}=5.43^{*}$								
BG									
Dist*BC	$F_{1,56.7}=0.01$	$F_{1,57.5}=0.23$	$F_{1,57.6}=0.08$	$F_{1,57.7}=0.01$	$F_{1,57.7}=0.003$	$F_{1,58.2}=0.03$	$F_{1,57.9}=0.12$	$F_{1,57.7}=6.27^{*}$	$F_{1,58.1}=0.11$
Dist*Yr	$F_{1,58.3}=0.04$	$F_{1,58.0}=0.16$	$F_{1,58.0}=0.05$	$F_{1,57.7}=1.90$	$F_{1,57.8}=3.53$	$F_{1,58.2}=0.60$	$F_{1,57.6}=0.92$	$F_{1,58.0}=0.01$	$F_{1,58.1}=0.07$
BC*Yr	$F_{1,2.4}=10.72$	$F_{1,2.0}=8.02$	$F_{1,2.0}=4.71$	$F_{1,2.0}=0.12$	$F_{1,2.0}=0.02$	$F_{1,2.0}=1.07$	$F_{1,2.1}=1.80$	$F_{1,2.0}=5.58$	$F_{1,2.0}=0.21$
Dist*BC*Yr	$F_{1,58.1}=0.98$	$F_{1,58.1}=0.07$	$F_{1,58.1}=0.32$	$F_{1,57.9}=2.55$	$F_{1,58.0}=3.03$	$F_{1,58.1}=2.71$	$F_{1,57.9}=0.33$	$F_{1,58.1}=0.01$	$F_{1,58.1}=1.01$

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, $^{***}p<0.001$

Table S3.10: Pearson and Kendall correlations with ordination axes from bee community composition (n=132).

Axis:	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Distance	0.123	0.015	0.104	-0.352	0.124	-0.234	0.009	0	-0.001
Openness	-0.047	0.002	-0.027	0.174	0.03	0.117	-0.058	0.003	-0.015
Plant Richness	0.248	0.061	0.177	-0.202	0.041	-0.133	0.074	0.005	0.062
Plant Diversity	0.22	0.049	0.16	-0.207	0.043	-0.156	0.117	0.014	0.06
Plant Height	0.106	0.011	0.105	0.041	0.002	0.062	0.088	0.008	0.046
Percent Bare Ground	-0.109	0.012	-0.089	-0.074	0.005	-0.067	-0.048	0.002	-0.062
Bee Richness	-0.586	0.344	-0.445	0.46	0.212	0.357	0.508	0.258	0.369
Bee Abundance	-0.512	0.262	-0.428	0.183	0.033	0.136	0.62	0.384	0.5
Bee Diversity	-0.526	0.277	-0.379	0.637	0.405	0.475	0.158	0.025	0.126
Augochlora pura	-0.179	0.032	-0.124	-0.055	0.003	-0.058	0.551	0.303	0.496
Augochlorella aurata	-0.145	0.021	-0.069	-0.267	0.071	-0.272	0.49	0.24	0.375
Bombus impatiens	-0.434	0.188	-0.36	0.475	0.226	0.427	0.165	0.027	0.063
Ceratina calcarata	-0.472	0.222	-0.378	-0.112	0.013	-0.095	-0.181	0.033	-0.148
C. strenua	-0.26	0.068	-0.188	0.177	0.031	0.176	0.224	0.05	0.155
Lasioglossum admirandum	-0.307	0.095	-0.294	0.175	0.03	0.207	0.425	0.18	0.383
L. apopkense	-0.37	0.137	-0.341	0.314	0.098	0.406	0.19	0.036	0.049
L. bruneri	-0.366	0.134	-0.311	0.155	0.024	0.217	0.48	0.23	0.392
L. ceanothi	-0.147	0.022	-0.149	-0.126	0.016	-0.095	0.414	0.171	0.351
L. hitchensi	-0.37	0.137	-0.279	0.2	0.04	0.228	0.515	0.266	0.439
L. illinoense	-0.447	0.2	-0.406	0.303	0.092	0.295	0.382	0.146	0.263
L. imitatum	-0.446	0.199	-0.418	0.275	0.076	0.249	0.387	0.15	0.366
L. pilosum	-0.259	0.067	-0.284	0.154	0.024	0.175	0.194	0.038	0.151
L. raleighense	-0.404	0.163	-0.312	0.316	0.1	0.279	0.172	0.029	0.143
L. tegulare	-0.407	0.166	-0.311	0.326	0.106	0.337	0.31	0.096	0.217
L. trigeminum	-0.218	0.048	-0.137	-0.135	0.018	-0.082	0.539	0.291	0.425
L. weemsi	-0.297	0.088	-0.286	0.135	0.018	0.133	0.453	0.206	0.452
L. birkmanni	-0.32	0.102	-0.301	-0.428	0.183	-0.362	0.211	0.045	0.125
L. pectoral	-0.218	0.047	-0.157	0.051	0.003	0.032	0.355	0.126	0.315
Melissodes bimaculatus	-0.28	0.078	-0.237	0.302	0.091	0.278	0.161	0.026	0.092

Table S3.11: Pearson and Kendall correlations with ordination axes from butterfly community composition (n=132).

Axis	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Distance	0.166	0.028	0.11	0.075	0.006	0.042	0.079	0.006	0.058
Plant Richness	0.345	0.119	0.23	0.184	0.034	0.131	-0.026	0.001	-0.031
Plant Diversity	0.343	0.117	0.253	0.204	0.042	0.126	0.014	0	-0.008
Openness	0.004	0	-0.019	0.081	0.007	0.057	0.094	0.009	0.078
Butterfly Richness	-0.763	0.581	-0.598	-0.225	0.051	-0.186	-0.311	0.097	-0.234
Butterfly Abundance	-0.741	0.549	-0.572	-0.156	0.024	-0.143	-0.203	0.041	-0.139
Butterfly Diversity	-0.666	0.444	-0.462	-0.305	0.093	-0.229	-0.309	0.096	-0.197
Battus philenor	-0.41	0.168	-0.349	-0.263	0.069	-0.23	0.26	0.068	0.203
Calycopis cecrops	-0.235	0.055	-0.172	-0.094	0.009	-0.025	-0.118	0.014	-0.121
Hermeuptychia sosybius	-0.081	0.007	-0.079	-0.194	0.038	-0.143	-0.029	0.001	-0.078
Lerema accius	-0.542	0.294	-0.386	0.01	0	-0.04	-0.135	0.018	-0.083
Nastra lherminier	-0.491	0.241	-0.373	0.101	0.01	0.036	-0.181	0.033	-0.208
Oligora maculate	-0.399	0.159	-0.378	-0.339	0.115	-0.223	0.051	0.003	0.052
Poanes zabulon	-0.192	0.037	-0.139	0.251	0.063	0.227	-0.566	0.32	-0.523
Polities origenes	-0.293	0.086	-0.321	-0.159	0.025	-0.075	0.04	0.002	-0.026
P. vibex	-0.375	0.141	-0.294	-0.238	0.056	-0.225	-0.026	0.001	0.025
Pterourus glaucus	0.068	0.005	0.093	-0.72	0.519	-0.644	-0.122	0.015	-0.109

Table S3.12: Pearson and Kendall correlations with ordination axes from plant community composition (n=132).

Axis	1			2			3		
	r	r-sq	tau	r	r-sq	tau	r	r-sq	tau
Openness	-0.503	0.253	-0.389	-0.024	0.001	-0.024	-0.261	0.068	-0.203
Plant Height	-0.49	0.24	-0.41	-0.063	0.004	-0.049	-0.187	0.035	-0.203
Plant Richness	-0.355	0.126	-0.245	0.048	0.002	0.054	-0.585	0.342	-0.448
Plant Diversity	-0.269	0.072	-0.184	0.08	0.006	0.067	-0.531	0.281	-0.366
Bee Abundance	0.131	0.017	0.074	0.036	0.001	0.003	-0.043	0.002	0.016
Distance	0.042	0.002	0.046	0.066	0.004	0.053	0.051	0.003	0.032
Bee Diversity	-0.045	0.002	-0.08	-0.153	0.023	-0.099	0.061	0.004	0.033
Butterfly Diversity	0.048	0.002	0.004	-0.026	0.001	-0.031	0.075	0.006	0.057
Bee Richness	0.035	0.001	0.02	-0.043	0.002	-0.029	0.034	0.001	0.029
Butterfly Richness	0.015	0	-0.018	-0.045	0.002	-0.034	0.037	0.001	0.041
Butterfly Abundance	-0.018	0	-0.035	-0.04	0.002	-0.014	0.107	0.011	0.078

Table S3.13: Data of the daily average of weather data collected from the Brender weather station on the burn dates included in this study.

Burn Block	Burn Dates	Temp. (F)	Rel. Humidity (%)	Wind Dir. (DEG)	Wind Speed (MPH)	Max. Wind Speed (MPH)	Hourly Rainfall (IN)
Caney Creek	30-Jan-15	47.29167	51.625	232.4583	1.3333333	6.875	0
Natural Rock	7-Feb-15	43.125	53.95833	108.625	0.625	2.958333	0
Five Points	10-Mar-15	67.79167	65.91667	165.1667	1.4166667	6.375	0
Caney Creek	13-Feb-16	40.70833	37.25	289.7083	1.2083333	6.25	0
Natural Rock	1-Mar-16	60.04167	71.45833	251.5	1.375	6.083333	0.01916667
Five Points	14-Mar-16	66.25	72.41667	208.1667	0.9583333	4.916667	0

Table S3.14: Data on the daily average dead fuel variables collected from the Brender weather station on the burn dates included in this study.

Burn Block	Burn Dates	Fuel Stick Moisture (%)	Fuel Stick Temperature (%)	1 Hr. Dead Fuel Moisture (%)	10 Hr. Dead Fuel Moisture (%)
Caney Creek	30-Jan-15	10.9125	47.45833	10.9125	10.9125
Natural Rock	7-Feb-15	9.754167	43.16667	9.754167	9.754167
Five Points	10-Mar-15	11.458333	68.70833	11.458333	11.458333
Caney Creek	13-Feb-16	8.891667	42.41667	8.891667	8.891667
Natural Rock	1-Mar-16	13.5	62.08333	13.5	13.5
Five Points	14-Mar-16	14.983333	67.41667	14.983333	14.983333

Table S3.15: Data on the daily average National Fire Danger Rating System (NFDRS) Indices collected from the Brender weather station on the burn dates included in this study.

Burn Block	Burn Dates	Spread Component (FT/MIN)	Energy Release Component (BTU/FT^2)	Burning Index (*0.1FT)	Ignition Component (%)
Caney Creek	30-Jan-15	0.8083333	9.416667	7.608333	2.904167
Natural Rock	7-Feb-15	0.7791667	10.85	7.920833	3.479167
Five Points	10-Mar-15	0.8541667	8.683333	7.4875	3.020833
Caney Creek	13-Feb-16	0.8833333	11.841667	8.729167	3.933333
Natural Rock	1-Mar-16	0.6375	6.95	5.608333	2.454167
Five Points	14-Mar-16	0.5541667	6.15	5.05	2.233333

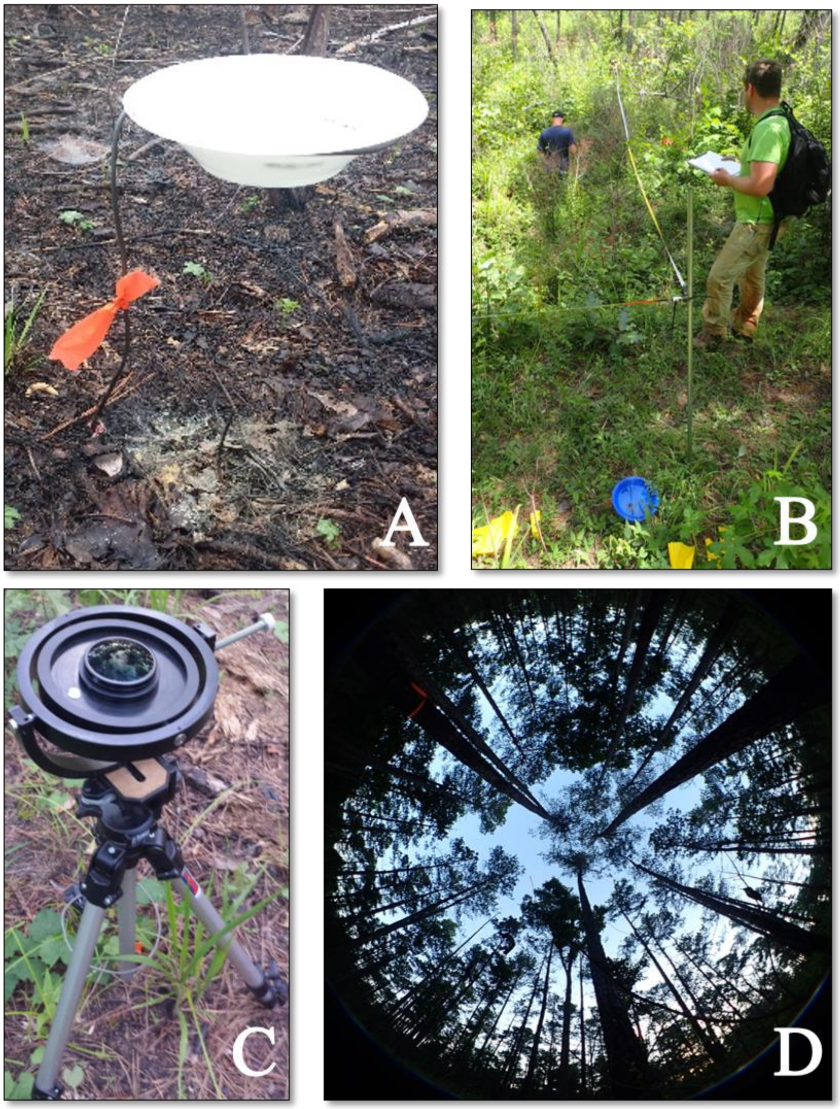

Figure S3.1: A: Image of the colored pan traps suspended approximately 30 cm above the ground. B: Image demonstrating the collection of the herbaceous vegetation surrounding each sampling location. C: Image of the camera used to collect images for canopy openness data. D: Image of the canopy coverage at one location at the Piedmont National Wildlife Refuge.

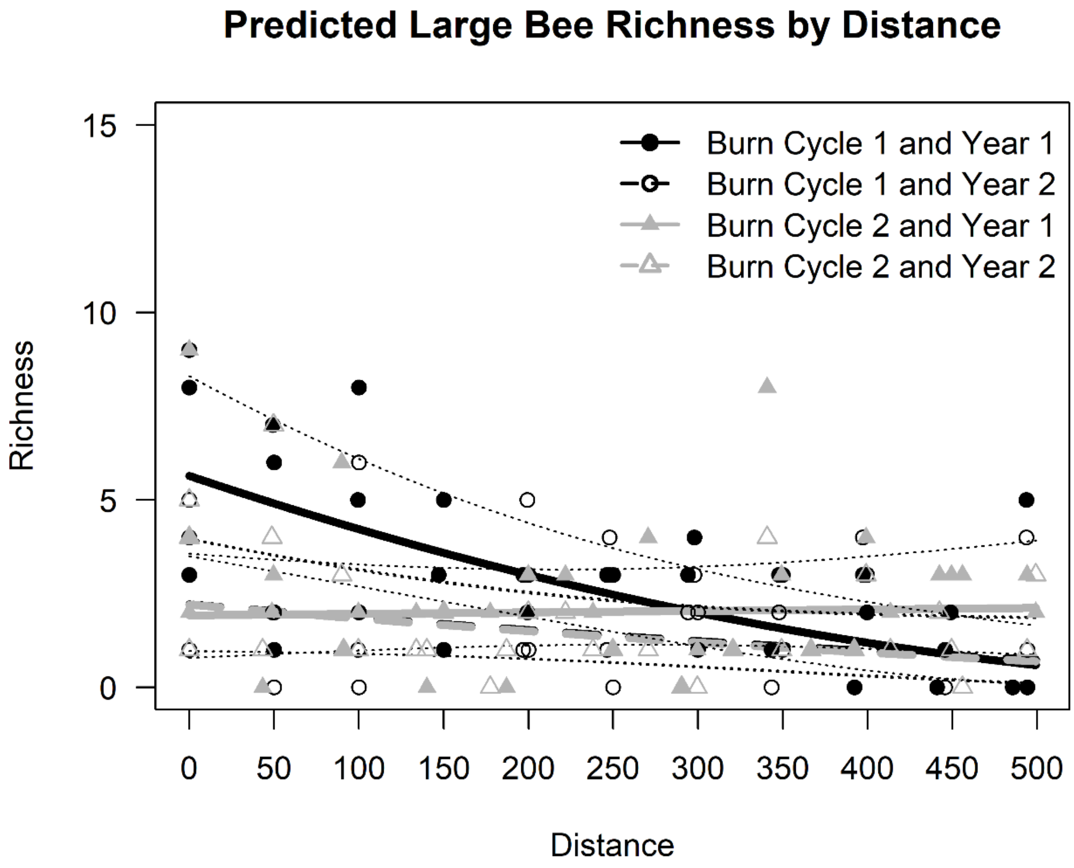

Figure S3.2: Predicted large bee Richness as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.5*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

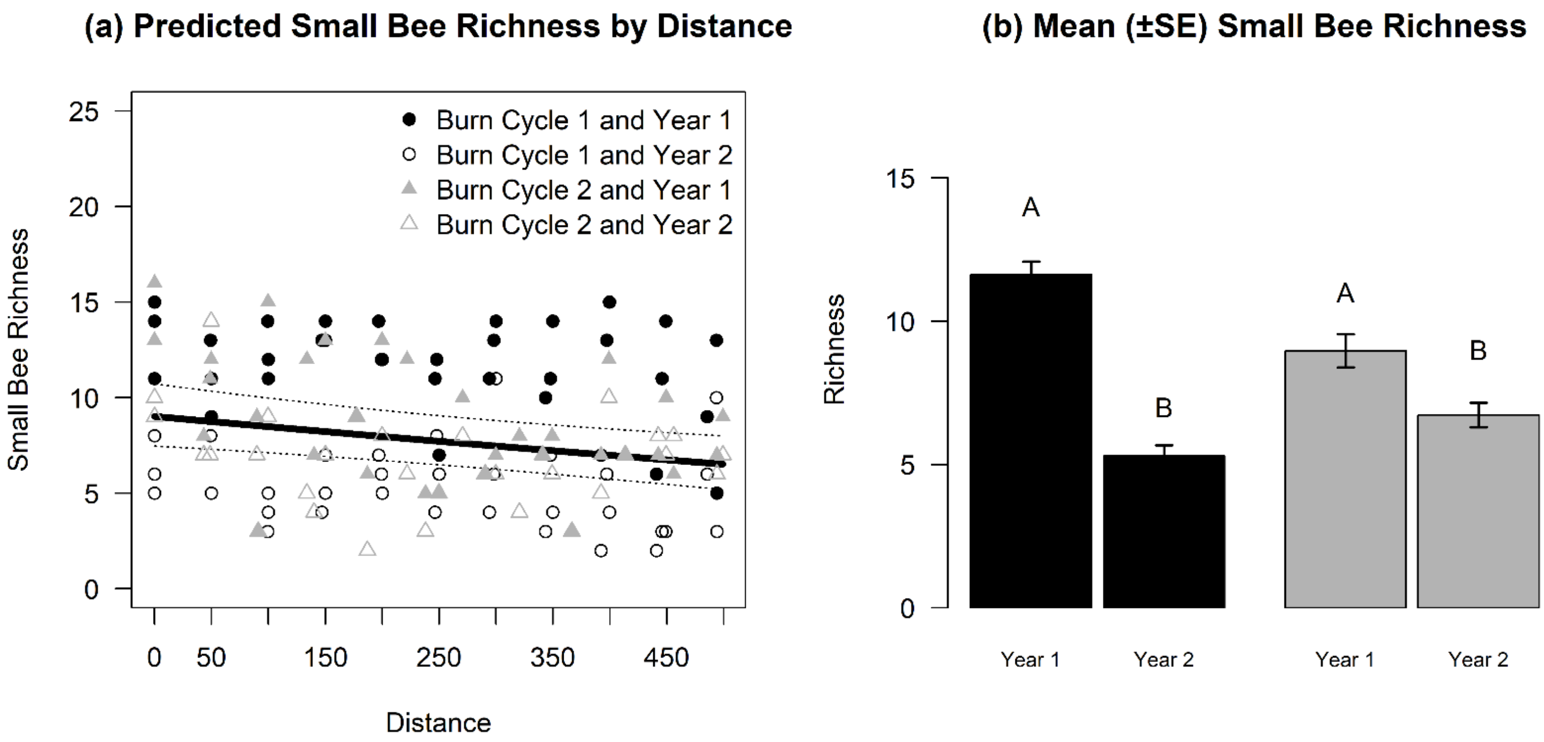

Figure S3.3: Predicted small bee Richness as a function of distance into burn blocks (a), mean (±SE) small bee Richness for each burn cycle and year (b) (see *Table S3.5*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

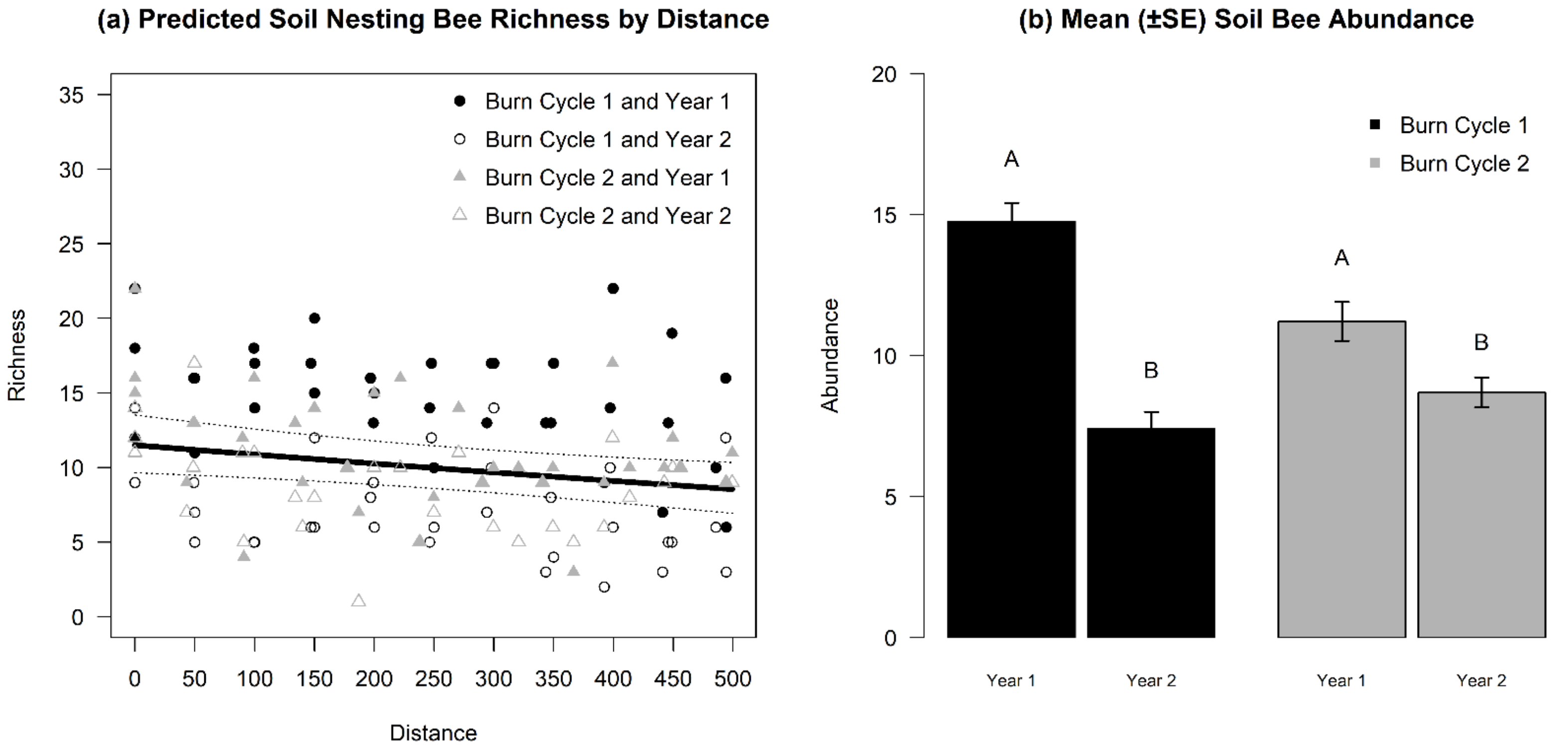

Figure S3.4: Predicted soil nesting bee Richness as a function of distance into burn blocks (a), mean (±SE) soil nesting bee Richness for each burn cycle and year (b) (see *Table S3.6*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

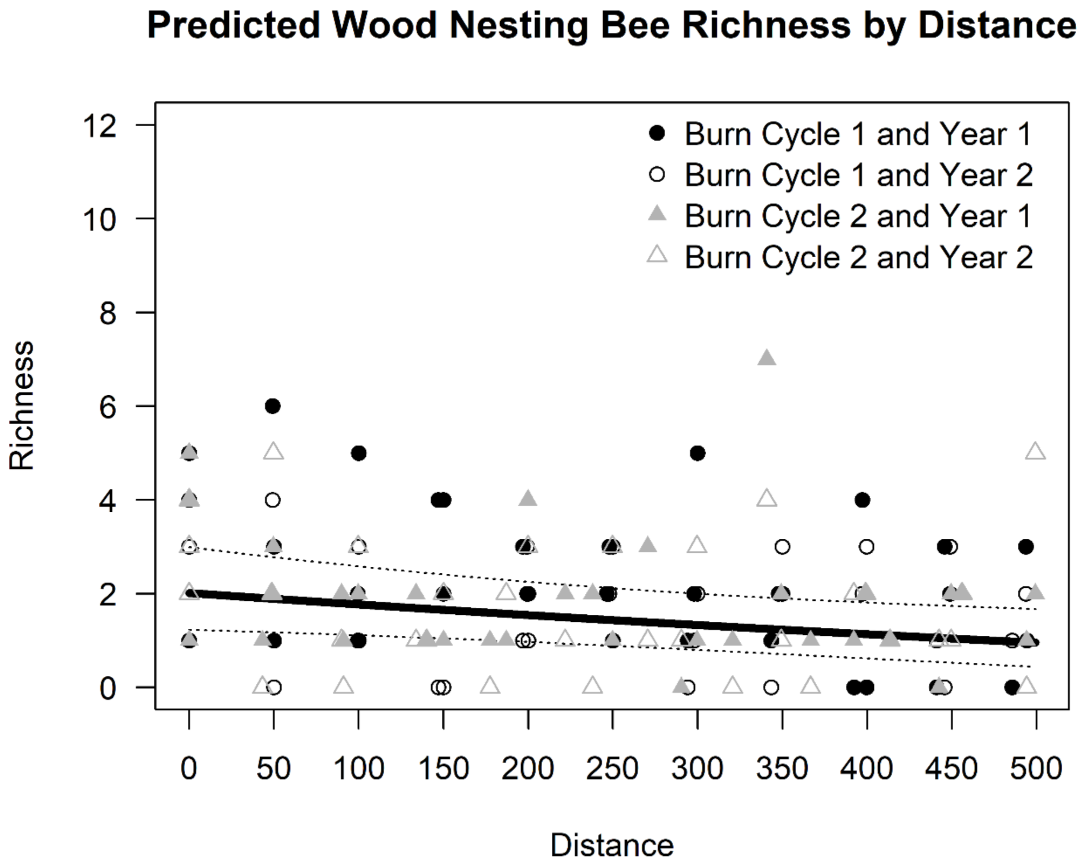

Figure S3.5: Predicted wood nesting bee Richness as a function of distance into burn blocks (see *Table S3.6*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

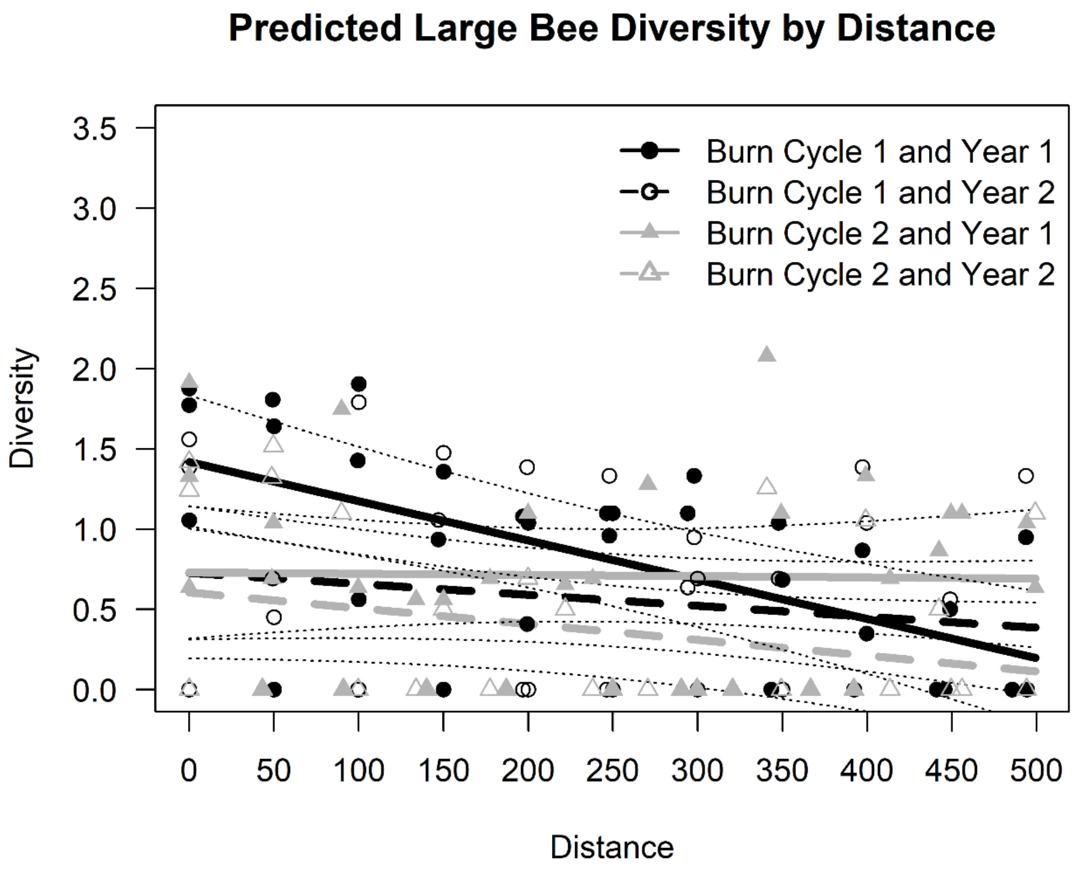

Figure S3.6: Predicted large bee Diversity as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.5*).

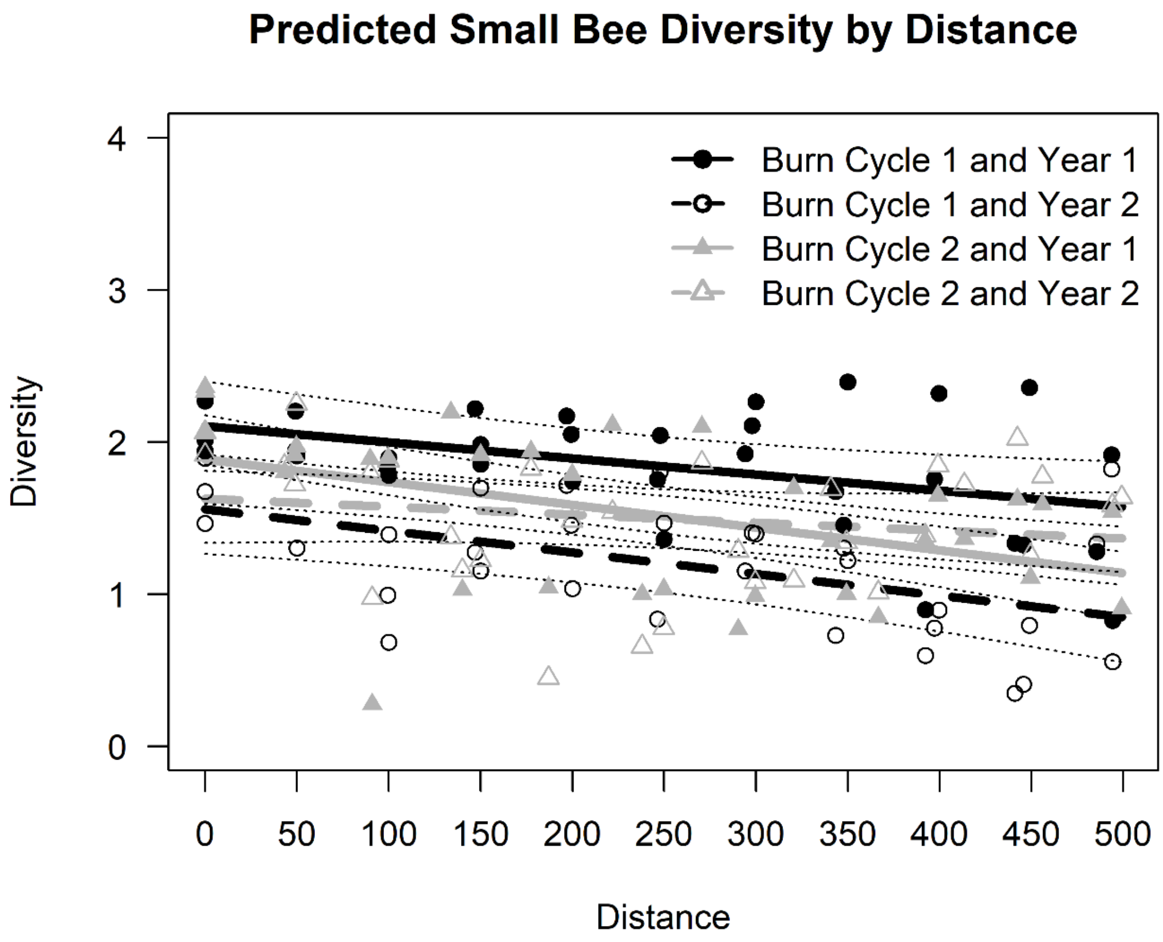

Figure S3.7: Predicted small bee Diversity as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.5*).

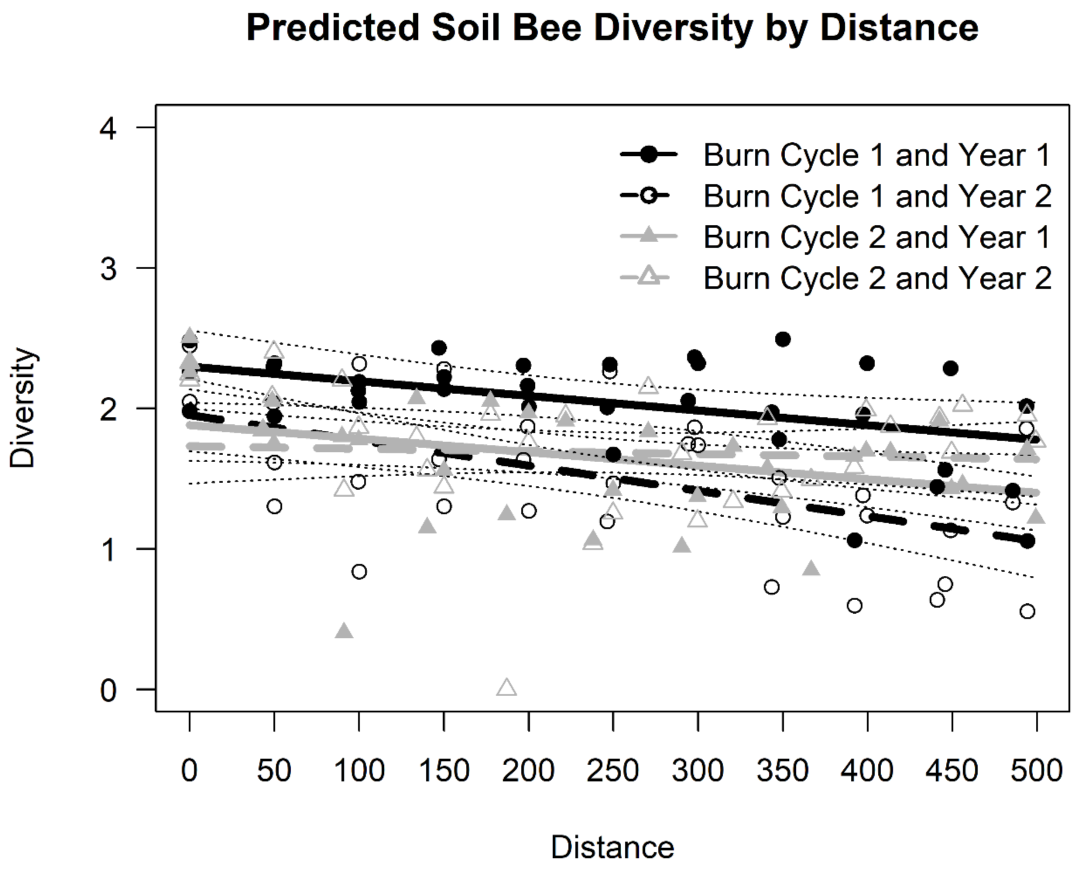

Figure S3.8: Predicted soil nesting bee Diversity as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.6*).

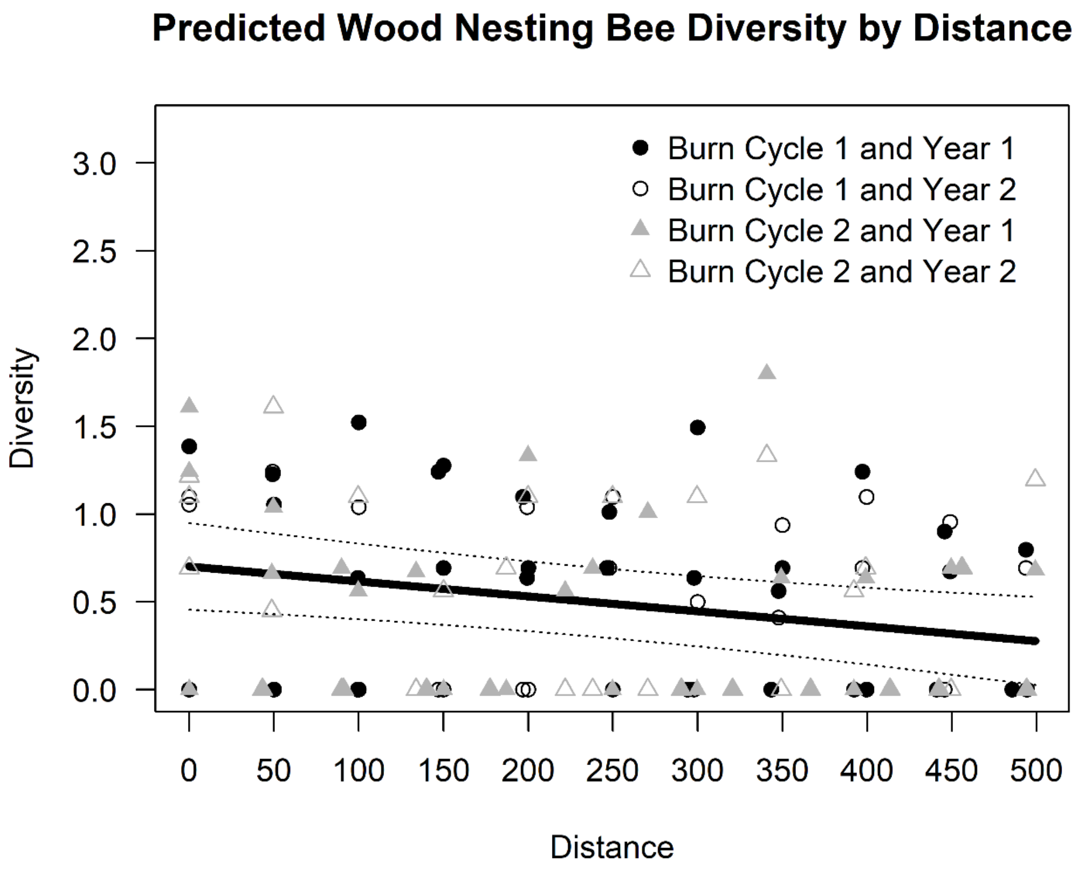

Figure S3.9: Predicted wood nesting bee Diversity as a function of distance into burn blocks (see *Table S3.6*).

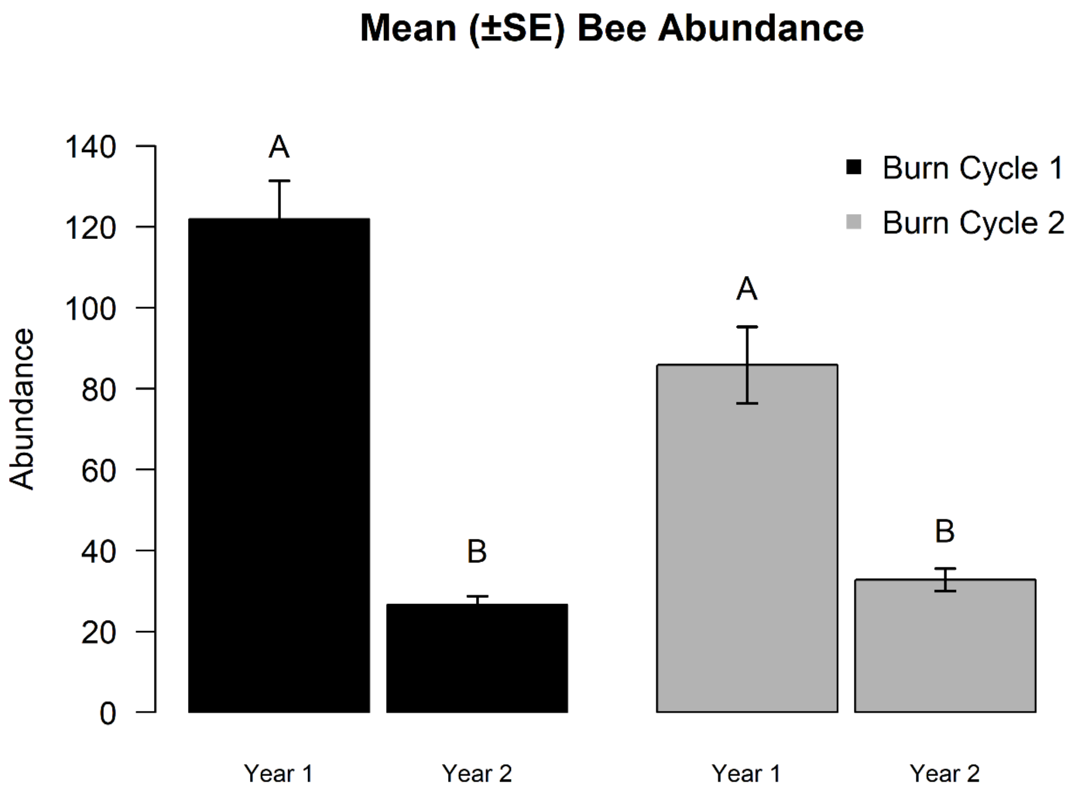

Figure S3.10: Mean (±SE) bee Abundance for each burn cycle and year (see *Table 3.2*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here.

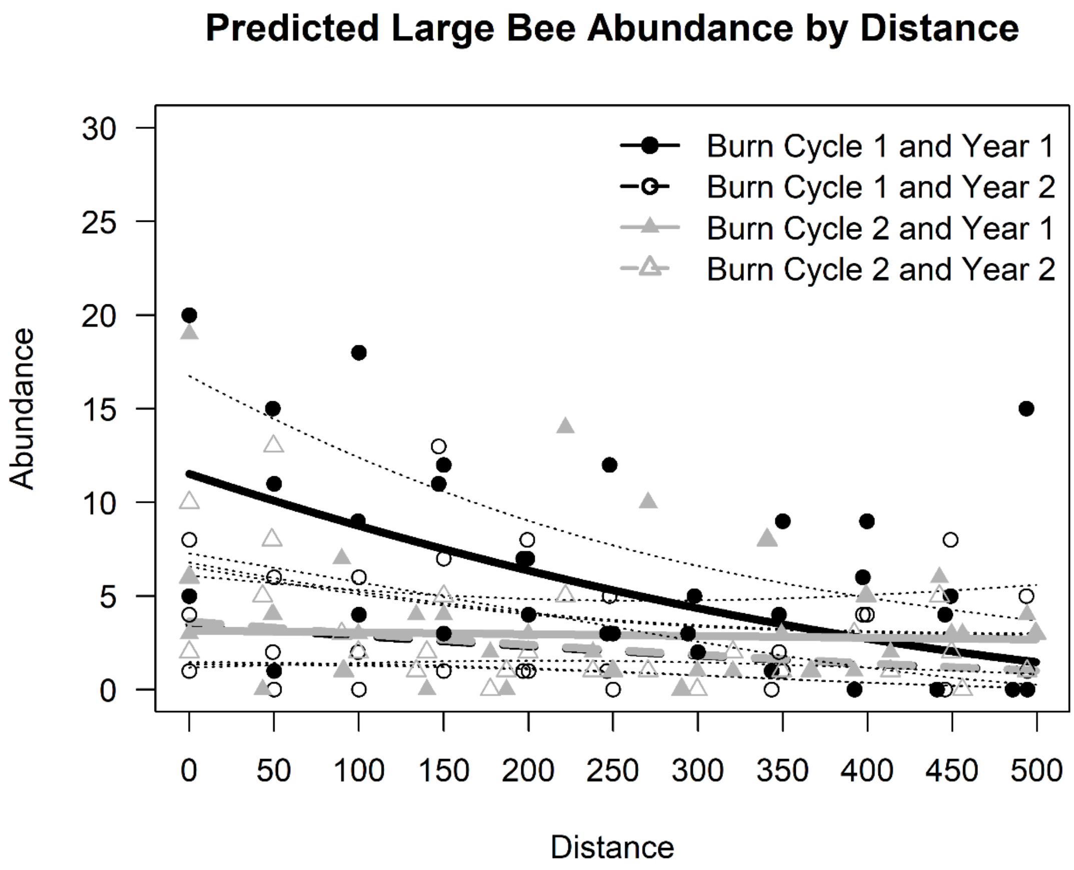

Figure S3.11: Predicted large bee Abundance as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.5*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

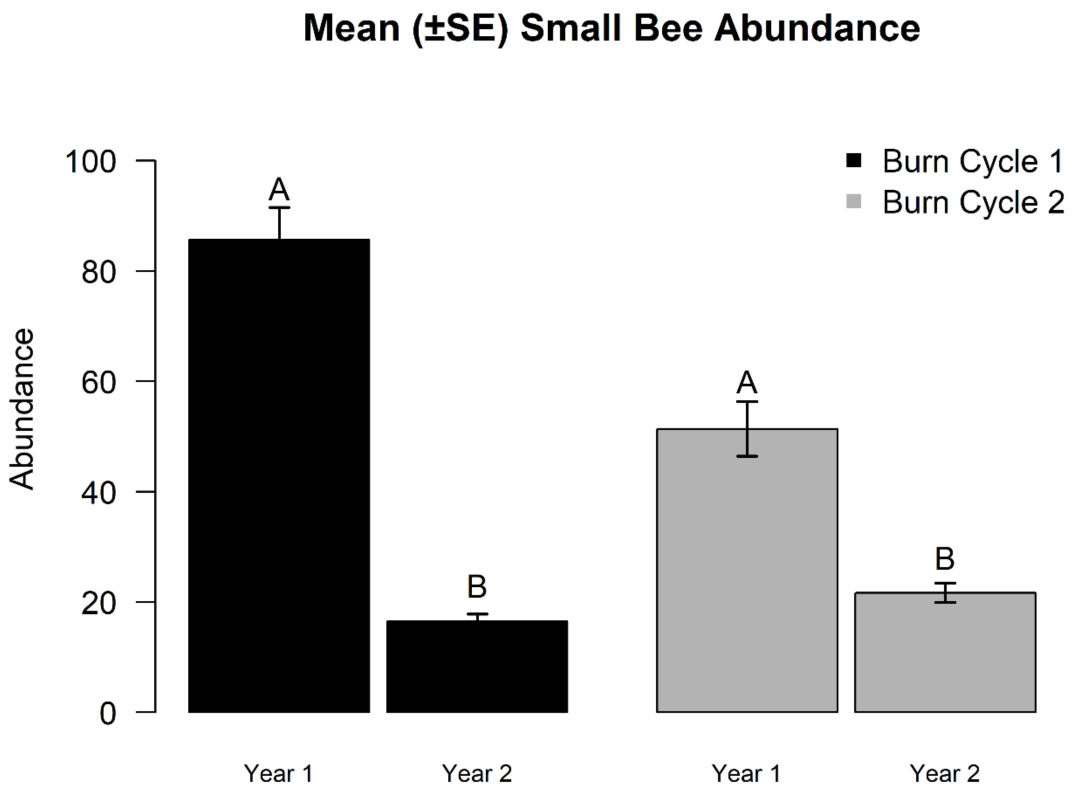

Figure S3.12: Mean (±SE) small bee Abundance for each burn cycle and year (see *Table S3.5*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here.

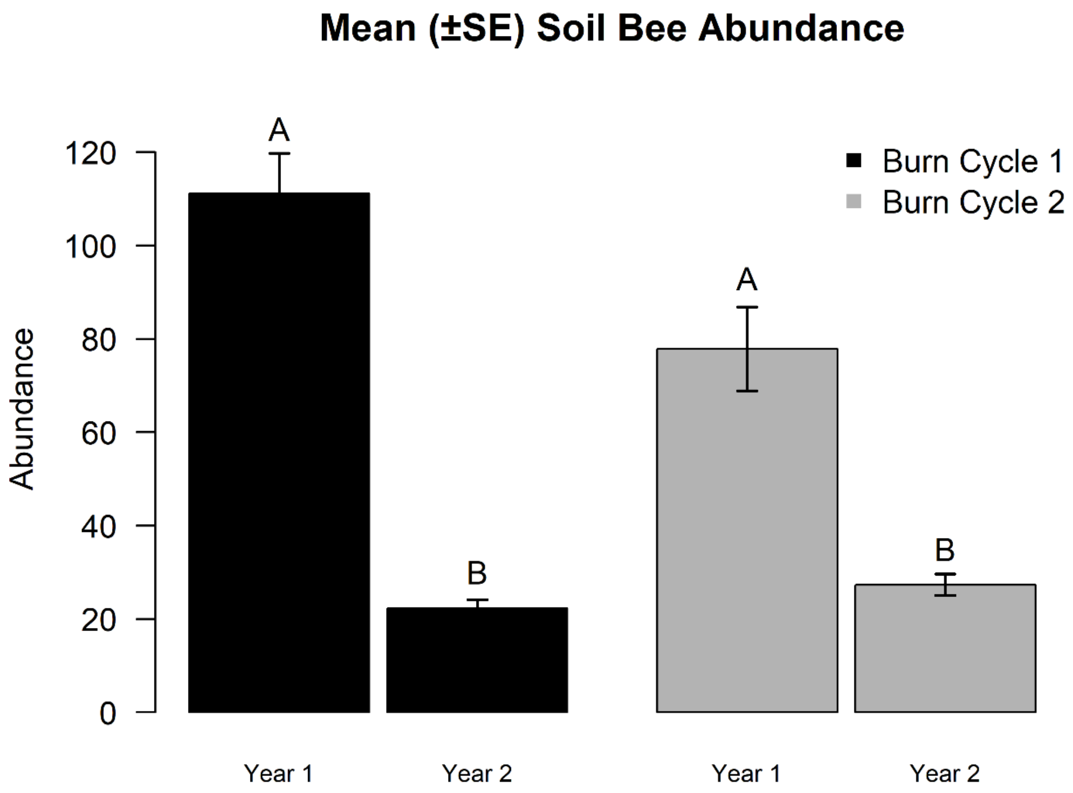

Figure S3.13: Mean (±SE) soil bee Abundance for each burn cycle and year (see *Table S3.6*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here.

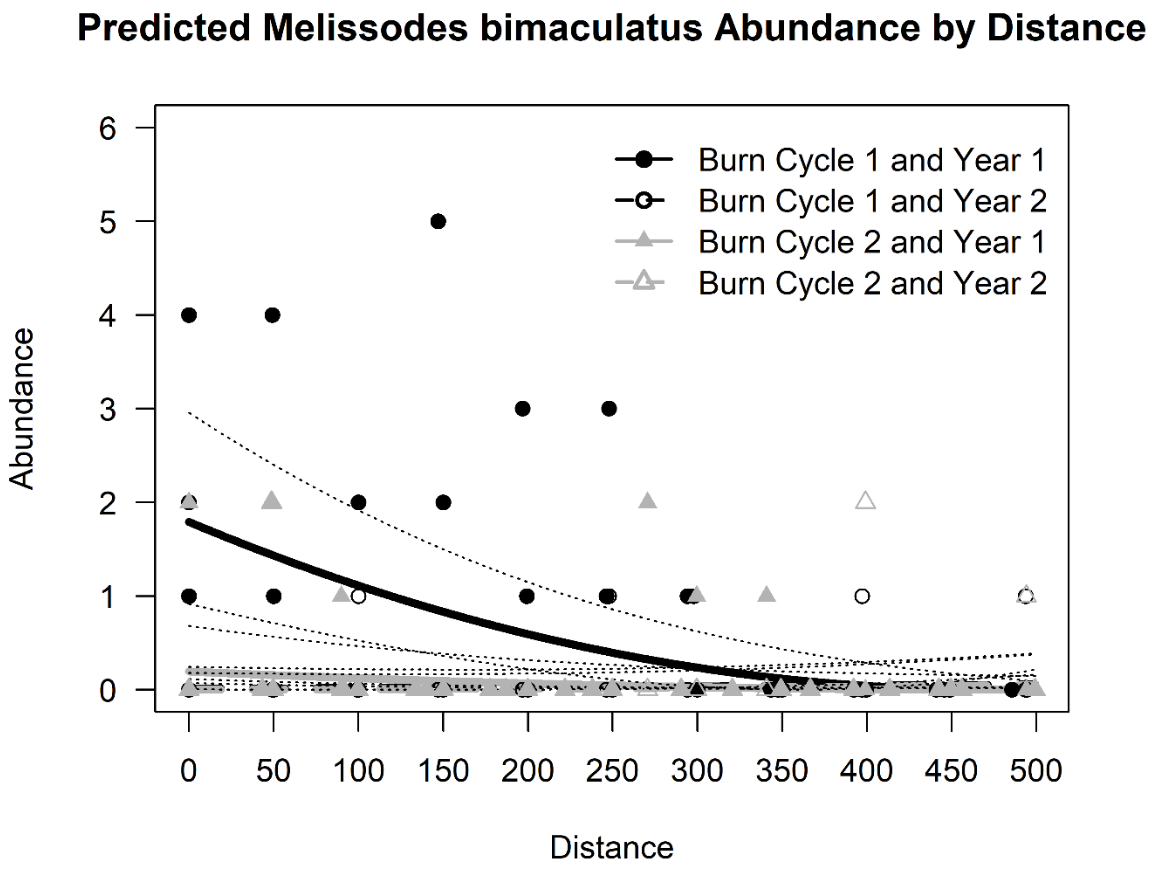

Figure S3.14: Predicted Abundance of *Melissodes bimaculatus* as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.7*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

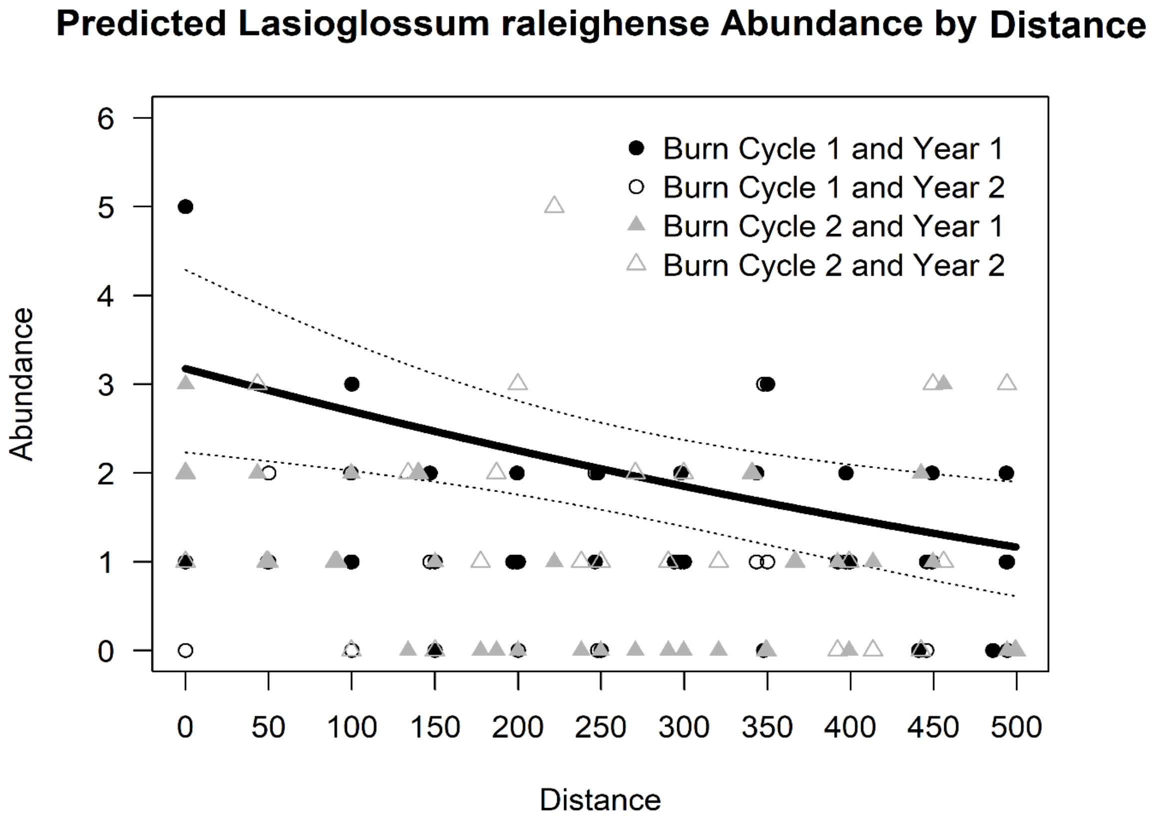

Figure S3.15: Predicted Abundance of *Lasioglossum raleighense* as a function of distance into burn blocks (see *Table S3.7*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

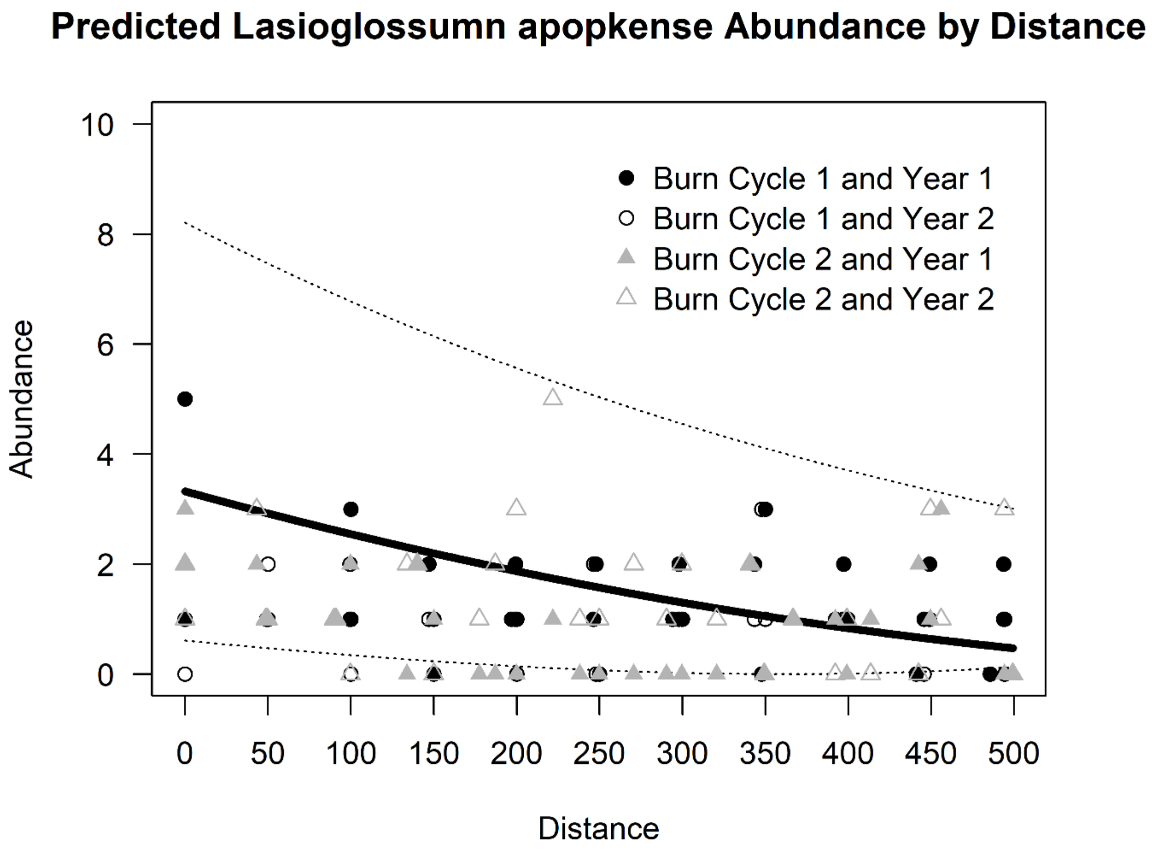

Figure S3.16: Predicted Abundance of *Lasioglossum apopkense* as a function of distance into burn blocks (see *Table S3.7*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

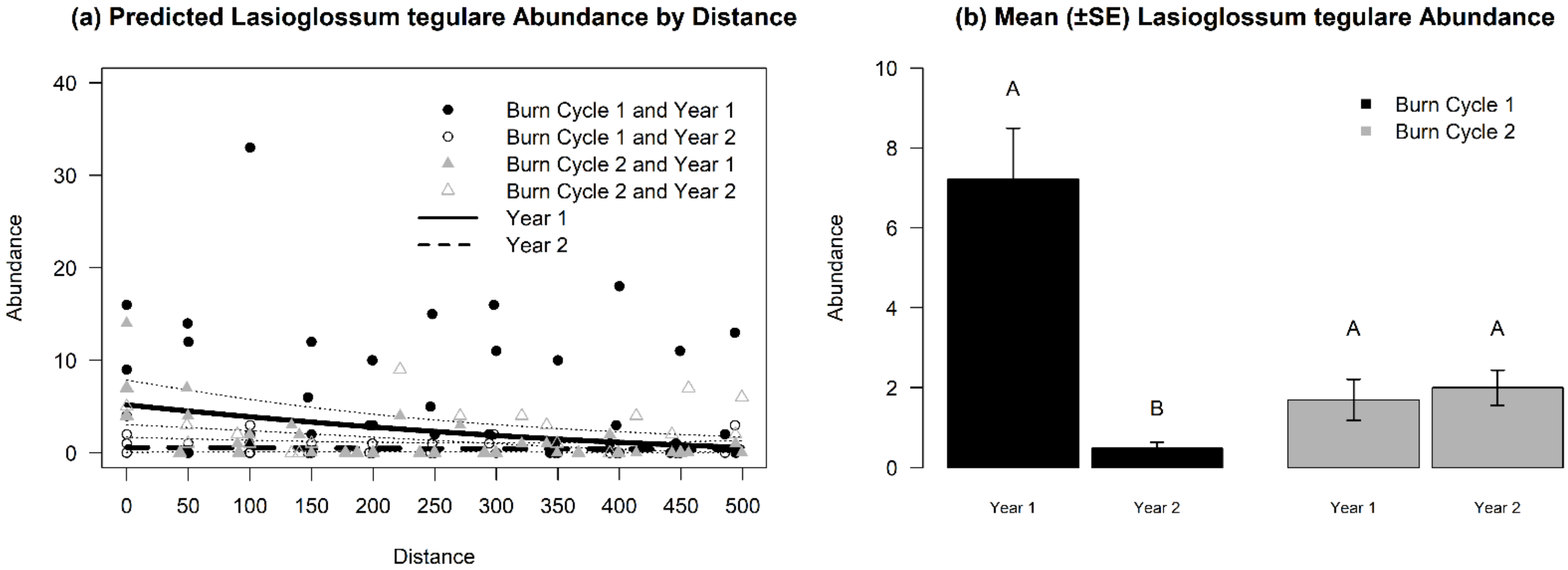

Figure S3.17: Predicted Abundance of *Lasioglossum tegulare* as a function of the interaction of distance into burn blocks, and year (a), mean (±SE) soil nesting bee Richness for each burn cycle and year (b) (see *Table S3.8*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

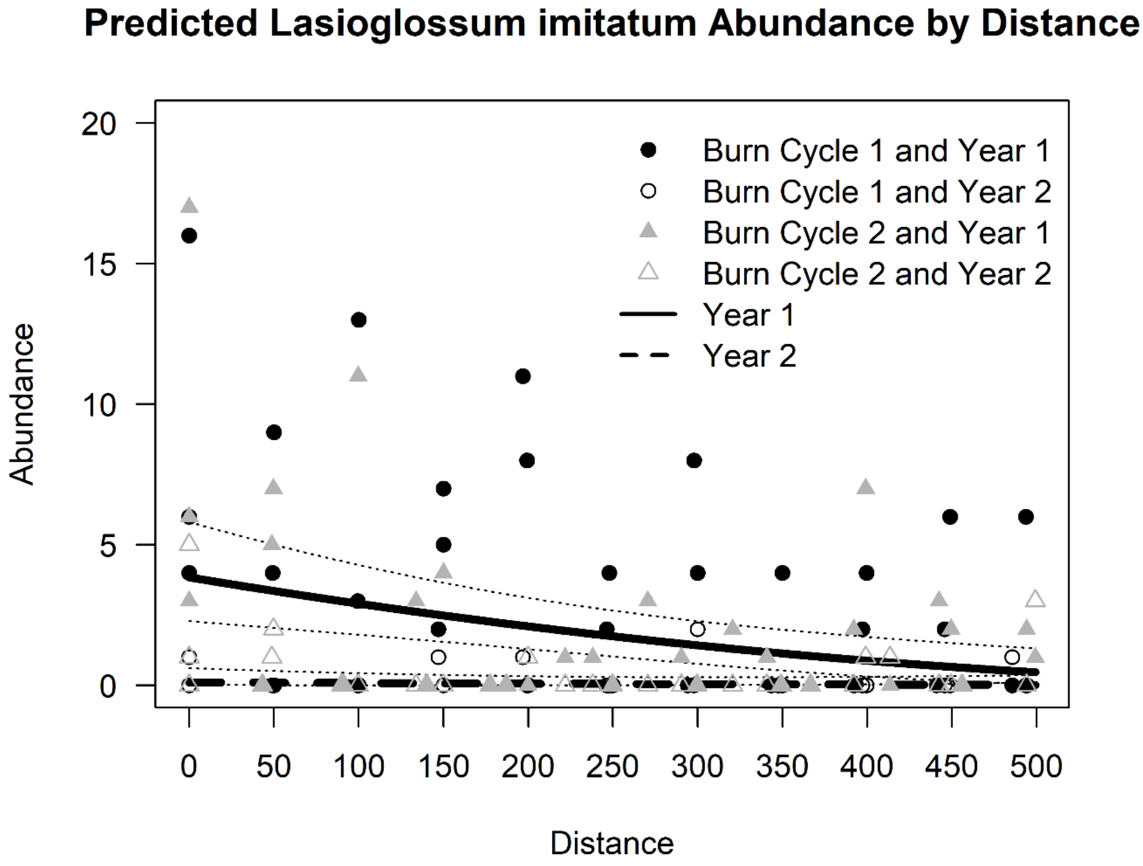

Figure S3.18: Predicted Abundance of *Lasioglossum imitatum* as a function of the interaction of distance into burn blocks, and year (see *Table S3.8*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

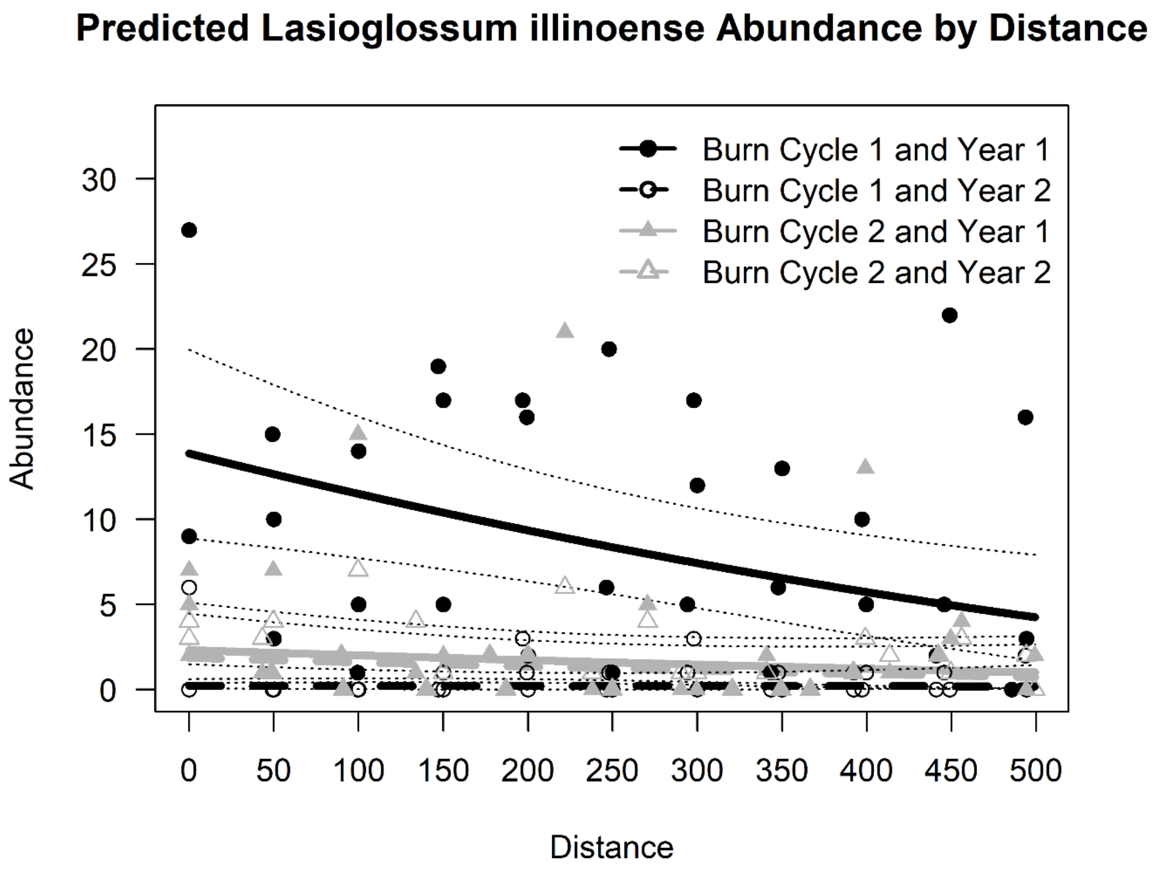

Figure S3.19: Predicted Abundance of *Lasioglossum illinoense* as a function of the three-way interaction of distance into burn blocks, burn cycle, and year (see *Table S3.8*). Different letters indicate statistical significance based on estimated marginal means. Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

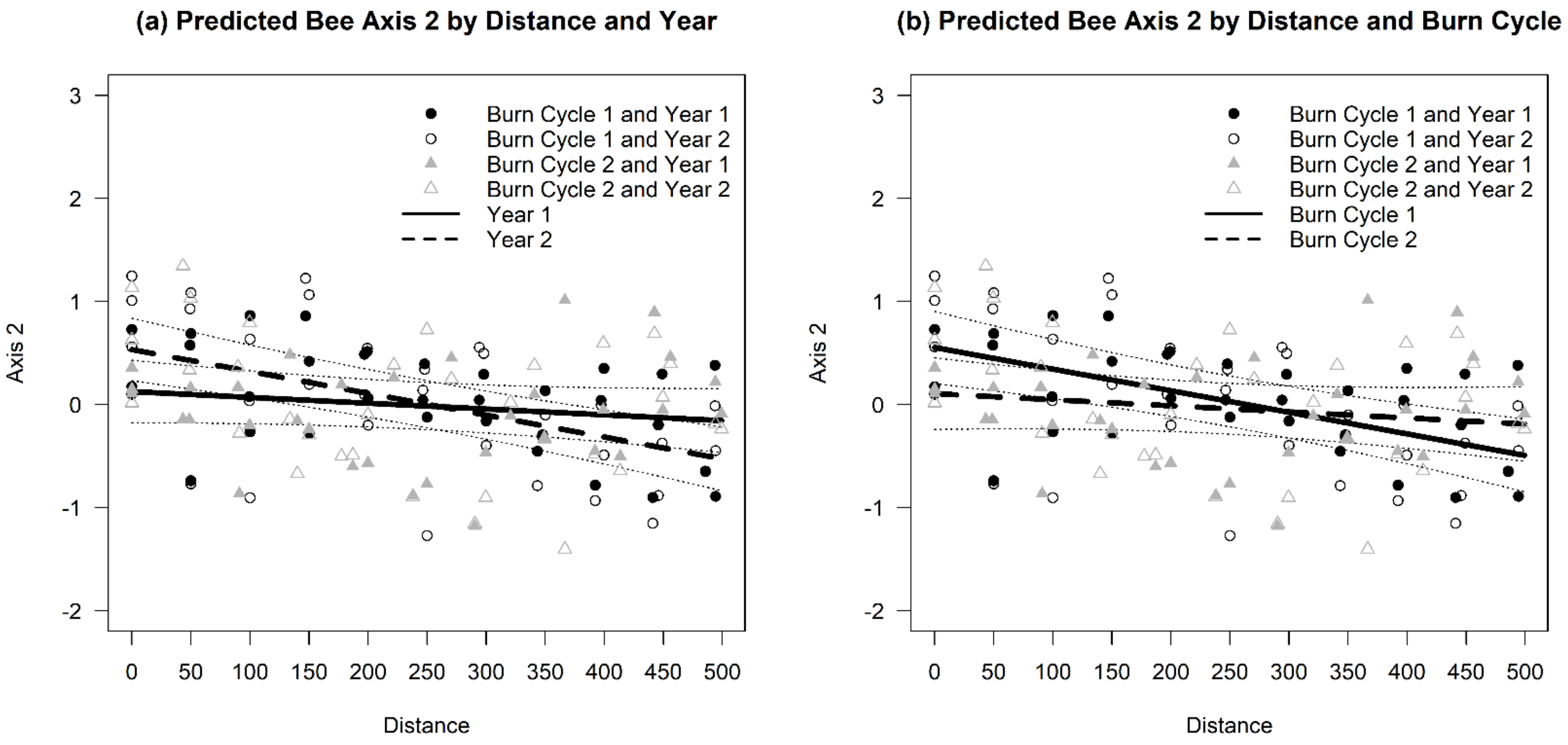

Figure S3.20: Predicted change in the bee community composition for axis 2 as a function of the interaction of distance into burn blocks, and burn cycle (a), and the interaction of distance into burn blocks, and year (b) (see *Table S3.8*).

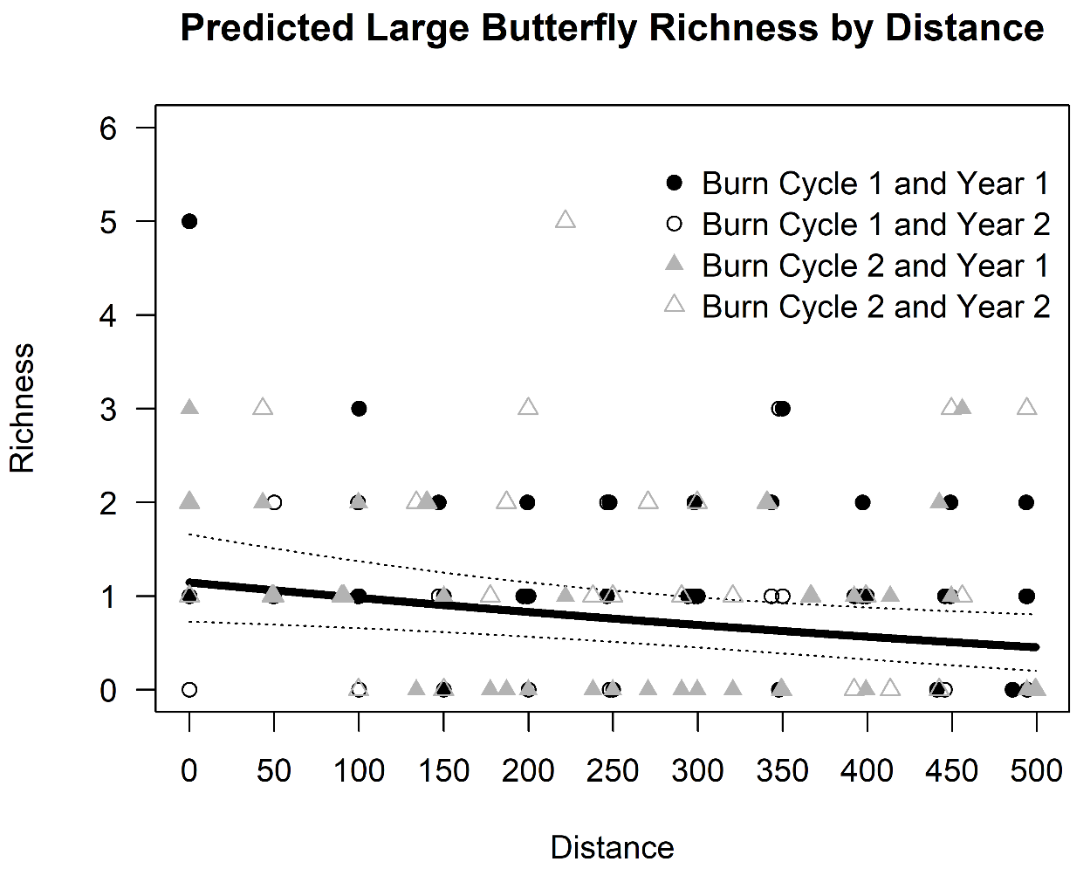

Figure S3.21: Predicted large butterfly Richness as a function of distance into burn blocks (see *Table S3.9*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

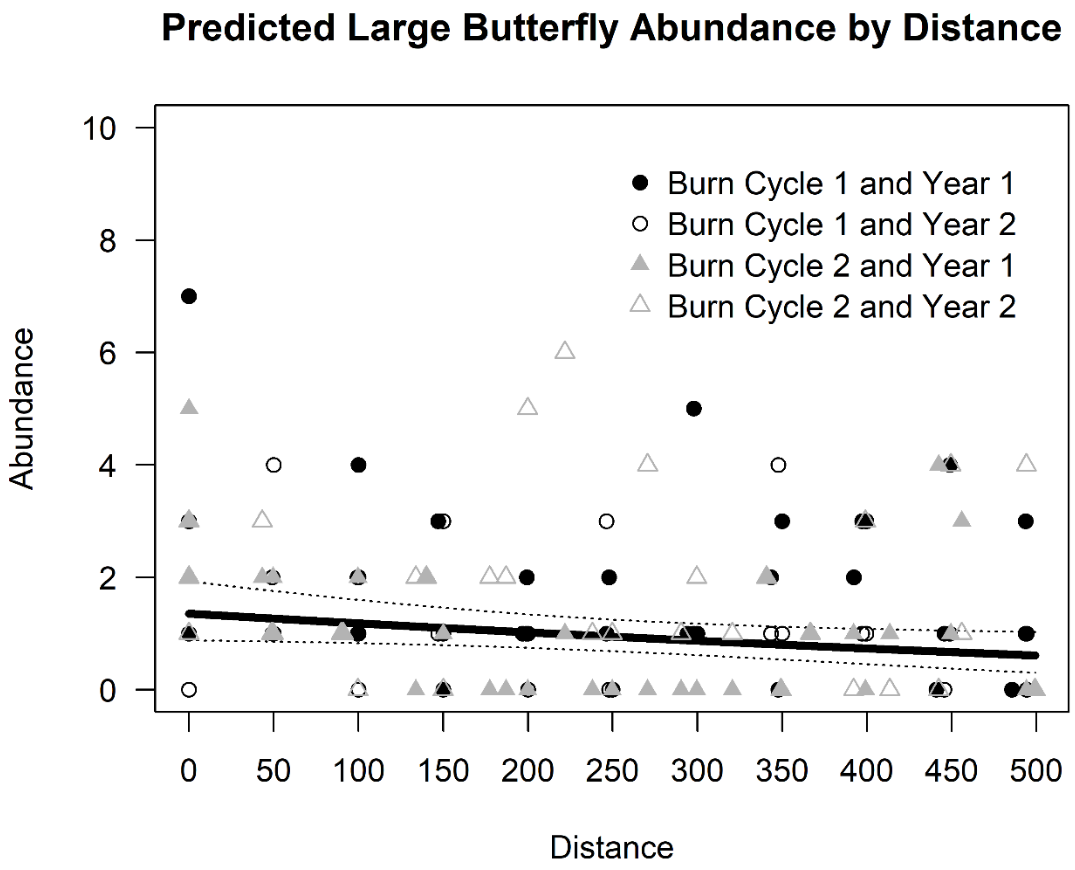

Figure S3.22: Predicted large butterfly Abundance as a function of distance into burn blocks (see *Table S3.9*). Although transformed data were used in the analyses (see *Data analysis*), raw data are presented here (open and closed circles and triangles).

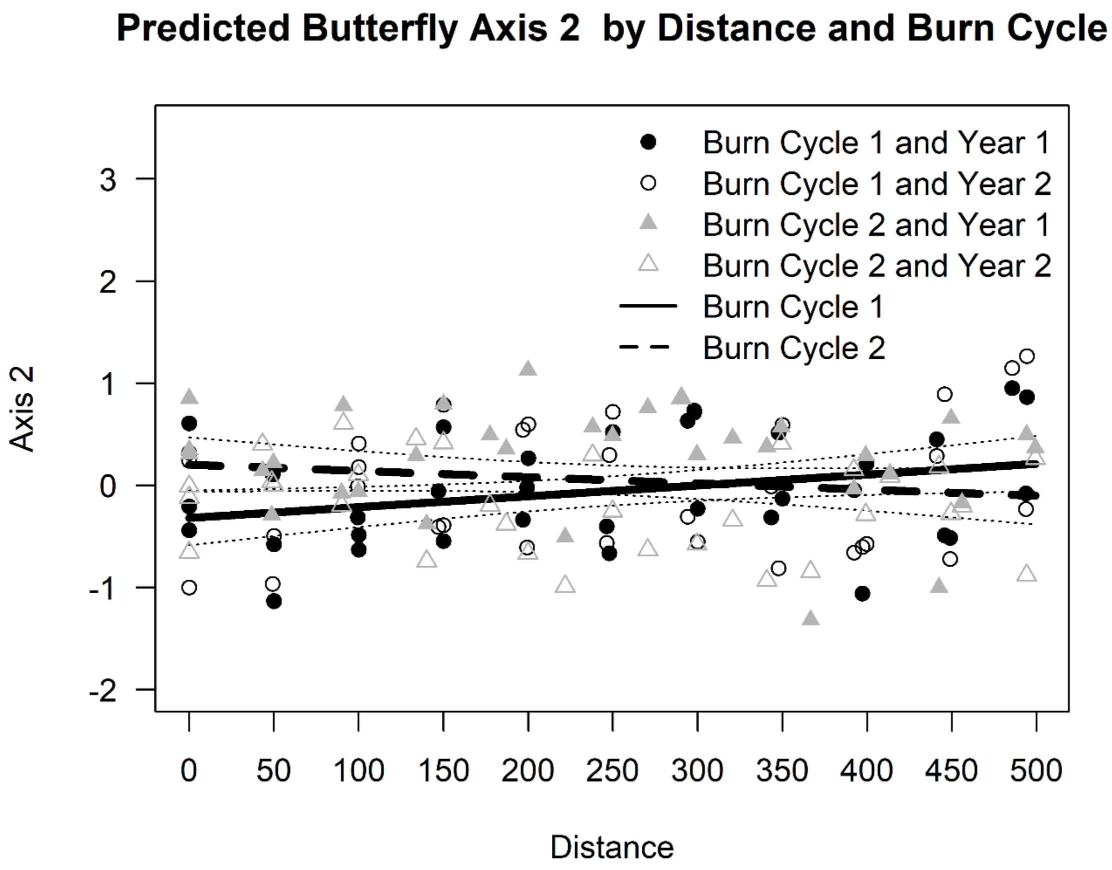

Figure S3.23: Predicted change in the butterfly community composition for axis 2 as a function of the interaction of distance into burn blocks and burn cycle (see *Table S3.9*).

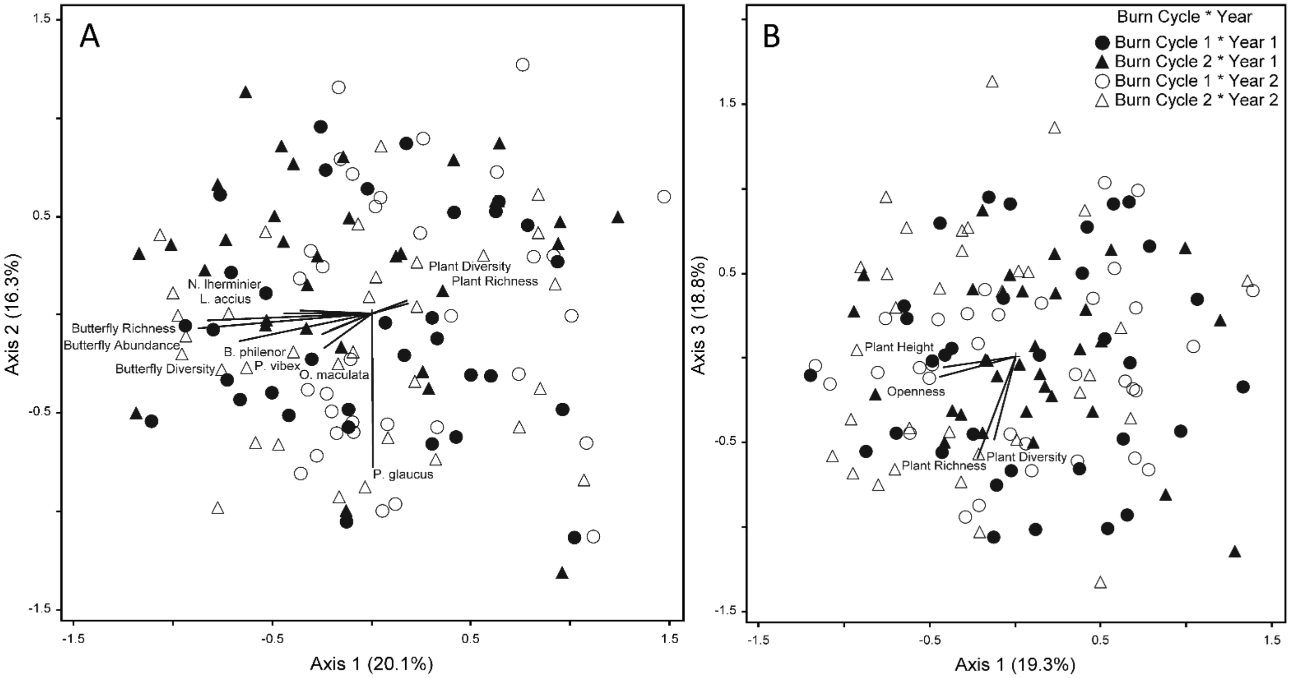

Figure S3.24: Non-metric multidimensional ordination of the butterfly (A) and plant (B) community observed along a gradient of distance into burn blocks in the Piedmont National Wildlife Refuge, with joint plots of Butterfly Abundance, Butterfly Richness, Butterfly Diversity, Plant Richness, Plant Diversity, and Abundance of *Battus philenor* (B. philenor), *Lerema accius* (L. accius), *Nastra lherminier* (N. lherminier), *Oligoria maculata* (O. maculata), *Polites vibex* (P. vibex), and *Pterourus glaucus* (P. glaucus) correlated with axis one or two for the butterfly community and with joint plots of Plant Richness, Plant Diversity, Plant Height, and Openness correlated with axis one or three for the plant community (*see Table S3.9 and S3.10*).

Appendix C - Chapter 4 Appendix

Table S4.1: Sampling Locations from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB).

Study	Block	Location	A/B	Lat (WSGS)	Lon (WSGS)
ANF	233	center	A	30.3302277	-84.547237
ANF	233	center	B	30.330336	-84.5472206
ANF	233	edge1	A	30.33572202	-84.54464704
ANF	233	edge1	B	30.33585797	-84.54474603
ANF	233	edge2	A	30.32151796	-84.52890599
ANF	233	edge2	B	30.321726	-84.52890096
ANF	240	center	A	30.265784	-84.67610504
ANF	240	center	B	30.26575601	-84.67608098
ANF	240	edge1	A	30.26367503	-84.68831998
ANF	240	edge1	B	30.263699	-84.68826399
ANF	240	edge2	A	30.27464502	-84.66080102
ANF	240	edge2	B	30.27466396	-84.66087
ANF	243	center	A	30.26811903	-84.60315297
ANF	243	center	B	30.26816597	-84.60307896
ANF	243	edge1	A	30.25828304	-84.59341496
ANF	243	edge1	B	30.25821799	-84.59350498
ANF	243	edge2	A	30.26575701	-84.61306399
ANF	243	edge2	B	30.265798	-84.61297899
ANF	248	center	A	30.31489701	-84.36163598
ANF	248	center	B	30.31513296	-84.36208298
ANF	248	edge1	A	30.32558796	-84.36789399
ANF	248	edge1	B	30.325623	-84.36808803
ANF	248	edge2	A	30.33342102	-84.39182499
ANF	248	edge2	B	30.33359301	-84.39177403
ANF	328	center	A	30.14822597	-84.63978399
ANF	328	center	B	30.14817098	-84.63984802
ANF	328	edge1	A	30.14878102	-84.65043504
ANF	328	edge1	B	30.14881002	-84.65038299
ANF	328	edge2	A	30.157724	-84.651594
ANF	328	edge2	B	30.15778896	-84.65155302
EAB	F7	center	A	30.58517701	-86.83474903
EAB	F7	center	B	30.58510602	-86.83470796
EAB	F7	edge1	A	30.59851999	-86.82723499
EAB	F7	edge1	B	30.59848798	-86.82734898
EAB	F7	edge2	A	30.58887896	-86.85329801
EAB	F7	edge2	B	30.58883001	-86.85321503
EAB	F25	center	A	30.59260304	-86.76083196

EAB	F25	center	B	30.59254697	-86.760695
EAB	F25	edge1	A	30.59871898	-86.77334698
EAB	F25	edge1	B	30.598765	-86.77326601
EAB	F25	edge2	A	30.58965102	-86.73875201
EAB	F25	edge2	B	30.58973299	-86.73875403
EAB	G8	center	A	30.52947097	-86.60535201
EAB	G8	center	B	30.52952302	-86.60523601
EAB	G8	edge1	A	30.53197699	-86.59688403
EAB	G8	edge1	B	30.53198302	-86.59697698
EAB	G8	edge2	A	30.53904603	-86.61874001
EAB	G8	edge2	B	30.538954	-86.618695
EAB	J13	center	A	30.67544399	-86.45951796
EAB	J13	center	B	30.67544801	-86.45938897
EAB	J13	edge1	A	30.68958904	-86.459625
EAB	J13	edge1	B	30.68950203	-86.45968803
EAB	J13	edge2	A	30.681284	-86.47053204
EAB	J13	edge2	B	30.68125097	-86.47043799
EAB	K8	center	A	30.61721398	-86.47393702
EAB	K8	center	B	30.61722203	-86.47384096
EAB	K8	edge1	A	30.60765803	-86.47518802
EAB	K8	edge1	B	30.60775702	-86.47517301
EAB	K8	edge2	A	30.61006699	-86.50123696
EAB	K8	edge2	B	30.61007998	-86.50114803

Table S4.2: Table of bee species collected, their body size and nesting guild, and the relative abundance from the Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB) sampling locations.

Row Labels	Body Size	Nesting Guild	ANF	EAB	Grand Total
Agapostemon splendens (Lepeletier 1841)	Large	Soil	3	0	3
Andrena cressonii Robertson 1891	Medium	Soil	13	0	13
Andrena ziziaeformis Cockerell 1908	Medium	Soil	0	1	1
Anthophora abrupta Say 1838	Large	Soil	0	2	2
Anthophora ursina Cresson 1869	Large	Soil	0	5	5
Apis melifera L. 1758	Large	Other	6	1	7
Ashmeadiella floridana (Robertson 1897)	Medium	Wood	1	4	5
Augochlora pura (Say 1837)	Medium	Rotting Wood	1	2	3
Augochloropsis metallica (F. 1793)	Medium	Soil	193	20	213
Augochloropsis sumptuosa (Smith 1853)	Large	Soil	16	8	24
Augochorella aurata (Smith 1854)	Small	Soil	170	47	217
Bombus bimaculatus Cresson 1863	Large	Other	1	0	1
Centris lanosa Cresson 1872	Large	Soil	1	0	1
Ceratina calcarata Robertson 1900	Medium	Wood	0	1	1
Ceratina dupla Say 1837	Medium	Wood	1	3	4
Coelioxys galactiae Mitchell 1962	Large	Wood	1	16	17
Lasioglossum alachuense (Mitchell 1960)	6 mm	Soil	58	3	61
Lasioglossum apokense (Robertson 1892)	Small	Soil	444	585	1029
Lasioglossum floridanum (Robertson 1892)	Medium	Soil	46	118	164
Lasioglossum foxii (Robertson 1895)	Small	Soil	1	0	1
Lasioglossum illinoense (Robertson 1892)	Small	Soil	46	204	250
Lasioglossum longifrons (Baker 1906)	Small	Soil	53	3	56
Lasioglossum nymphale (Smith 1853)	Small	Soil	447	306	753
Lasioglossum pectorale (Smith 1853)	Small	Soil	3	2	5
Lasioglossum puteulanum Gibbs 2009	Small	Soil	7	4	11

Lasioglossum raleighense (Crawford 1932)	Small	Soil	32	70	102
Lasioglossum reticulatum (Robertson 1892)	Medium	Soil	42	70	112
Lasioglossum sopinci (Crawford 1932)	Medium	Soil	0	59	59
Lasioglossum tamiamense (Mitchell 1960)	Small	Soil	7	3	10
Lasioglossum vierecki (Crawford 1904)	Small	Soil	7	0	7
Lasioglossum weemsi (Mitchell 1960)/hitchensi Gibbs 2012	Small	Soil	7	3	10
Megachile deflexa Cresson 1878	Large	Wood	0	4	4
Megachile frugalis Cresson 1872	Large	Wood	0	34	34
Megachile georgica Cresson 1878	Large	Wood	0	2	2
Megachile integra Cresson 1878	Large	Wood	8	32	40
Megachile mendica Cresson 1878	Large	Wood	2	9	11
Megachile mucida Cresson 1878	Large	Wood	0	1	1
Megachile parallela Smith 1853	Large	Wood	0	1	1
Megachile petulans Cresson 1878	Large	Wood	0	1	1
Megachile pseudobrevis Mitchell 1935	Large	Wood	18	0	18
Megachile texana Cresson 1878	Large	Wood	17	23	40
Melissodes bimaculata (Lepeletier 1825)	Large	Soil	0	1	1
Melissodes communis Cresson 1878	Large	Soil	5	0	5
Nomia maneei Cockerell 1910	Large	Soil	1	0	1
Osmia cordata Robertson 1902	Large	Wood	3	1	4
Osmia distincta Cresson 1864	Medium	Wood	1	0	1
Osmia inspergens Lovell & Cockerell 1907	Medium	Wood	1	1	2
Perdita octomaculata (Say 1824)	Small	Soil	0	1	1
Svastra atripes (Cresson 1872)	Large	Soil	0	2	2
Xylocopa micans Lepeletier 1841	Large	Wood	1	0	1
Xylocopa virginica (L. 1771)	Large	Wood	2	1	3
Total Richness			37	40	51
Total Abundance			1666	1654	3320

Table S4.3. ANOVA results for the effects of location, canopy openness (Openness), percent wetland (% wetland), bare ground (BG), plant abundance (PA), and plant richness (PR) on square root-transformed bee abundance (N), square root-transformed bee richness (S), and Shannon's bee diversity (H') for soil nesting bees using Kenward-Roger denominator degrees of freedom approximation method from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB).

	ANF			EAB		
	Sqrt(Bee N)	Sqrt(Bee S)	Bee H'	Sqrt(Bee N)	Sqrt(Bee S)	Bee H'
Location	$F_{1,6.8}=1.08$	$F_{1,9.0}=1.35$	$F_{1,9.1}=3.60$	$F_{1,0.6}=1.41$	$F_{1,1.5}=3.15$	$F_{1,4.7}=0.04$
Openness				$F_{1,0.7}=4.14$	$F_{1,0.7}=9.38$	
% Wetland	$F_{1,7.5}=2.34$			$F_{1,1.0}=0.20$	$F_{1,1.6}=0.75$	
BG	$F_{1,6.2}=3.50$			$F_{1,0.9}=0.01$	$F_{1,1.8}=0.38$	
PA	$F_{1,7.3}=5.21$		$F_{1,10.8}=4.13$	$F_{1,6.4}=0.61$	$F_{1,1.3}=2.63$	$F_{1,2.3}=2.53$
PR				$F_{1,1.1}=0.10$		
PH	$F_{1,7.0}=3.23$		$F_{1,9.5}=4.26$	$F_{1,1.8}=0.11$	$F_{1,1.0}=0.49$	

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, and $^{***}p<0.001$

Table S4.4. ANOVA results for the effects of location, canopy openness (Openness), percent wetland (% wetland), bare ground (BG), plant abundance (PA), and plant richness (PR) on square root-transformed bee abundance (N), square root-transformed bee richness (S), and Shannon's bee diversity (H') for wood nesting bees using Kenward-Roger denominator degrees of freedom approximation method from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB).

	ANF			EAB		
	Sqrt(Bee N)	Sqrt(Bee S)	Bee H'	Sqrt(Bee N)	Ln(Bee S)	Bee H'
Location	$F_{1,7.0}=11.78^{*}$	$F_{1,8.3}=1.45$	$F_{1,8.3}=0.19$	$F_{1,2.0}=74.76^{*}$	$F_{1,3.1}=0.86$	$F_{1,3.1}=0.50$
Openness				$F_{1,2.0}=4.74$	$F_{1,4.6}=2.19$	$F_{1,4.6}=2.13$
% Wetland	$F_{1,9.3}=3.05$			$F_{1,1.3}=89.71^{*}$		
BG	$F_{1,8.7}=4.95$	$F_{1,9.5}=5.83^{*}$	$F_{1,10.6}=7.00^{*}$		$F_{1,5.0}=1.98$	$F_{1,5.0}=1.66$
PA				$F_{1,1.1}=13.75$		
PR				$F_{1,1.5}=0.69$		
PH	$F_{1,7.6}=3.28$			$F_{1,1.3}=7.18$		

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, and $^{***}p<0.001$

Table S4.5. ANOVA results for the effects of location, canopy openness (Openness), percent wetland (% wetland), bare ground (BG), plant abundance (PA), and plant richness (PR) on natural log-transformed bee abundance (N), sqrt-transformed bee richness (S), and Shannon's bee diversity (H') for small bees using Kenward-Roger denominator degrees of freedom approximation method from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB).

	ANF			EAB		
	Ln(Bee N)	Sqrt(Bee S)	Bee H'	Ln(Bee N)	Ln(Bee S)	Bee H'
Location	$F_{1,9.0}=0.01$	$F_{1,9.0}=1.45$	$F_{1,9.1}=2.56$	$F_{1,1.1}=3.28$	$F_{1,1.0}=0.43$	$F_{1,2.3}=0.21$
Openness				$F_{1,1.4}=3.09$	$F_{1,1.1}=21.14$	$F_{1,2.5}=5.02$
% Wetland	$F_{1,3.9}=4.83$			$F_{1,1.5}=1.43$	$F_{1,1.3}=2.18$	$F_{1,3.3}=4.31$
BG				$F_{1,0.4}=0.81$	$F_{1,1.2}=0.97$	$F_{1,2.4}=6.42$
PA			$F_{1,10.8}=2.78$			
PR				$F_{1,2.0}=0.51$	$F_{1,1.9}=4.07$	
PH			$F_{1,9.5}=2.58$	$F_{1,0.2}=2.23$	$F_{1,0.8}=4.01$	

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, and $^{***}p<0.001$

Table S4.6. ANOVA results for the effects of location, canopy openness (Openness), percent wetland (% wetland), bare ground (BG), plant abundance (PA), and plant richness (PR) on natural log-transformed bee abundance (N), square root-transformed bee richness (S), and Shannon's bee diversity (H') for large bees using Kenward-Roger denominator degrees of freedom approximation method from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB).

	ANF			EAB		
	Sqrt(Bee N)	Ln(Bee S)	Bee H'	Sqrt(Bee N)	Sqrt(Bee S)	Bee H'
Location	$F_{1,6.6}=12.54^{*}$	$F_{1,9.0}=4.18$	$F_{1,9.0}=0.80$	$F_{1,0.0}=0.00$	$F_{1,1.0}=0.05$	$F_{1,0.7}=0.02$
Openness	$F_{1,4.0}=3.25$			$F_{1,0.0}=0.00$	$F_{1,1.9}=0.000$	$F_{1,0.8}=0.01$
% Wetland		$F_{1,3.7}=14.67^{*}$	$F_{1,3.7}=12.21^{*}$	$F_{1,0.0}=0.00$		$F_{1,1.2}=0.03$
BG	$F_{1,5.4}=16.68^{**}$			$F_{1,0.0}=0.00$	$F_{1,1.7}=0.02$	$F_{1,1.1}=0.09$
PA				$F_{1,0.0}=0.00$	$F_{1,1.4}=0.01$	$F_{1,5.8}=0.03$
PR	$F_{1,6.6}=4.76$			$F_{1,0.0}=0.00$	$F_{1,1.4}=0.01$	$F_{1,1.2}=0.04$
PH	$F_{1,8.2}=3.61$			$F_{1,0.0}=0.00$	$F_{1,0.8}=0.004$	$F_{1,2.2}=0.05$

*: symbols indicating level of significance (alpha=0.05), $^{*}p<0.05$, $^{**}p<0.01$, and $^{***}p<0.001$

Table S4.7. PerMANOVA results for the effect of location from Apalachicola National Forest (ANF) and Eglin Air Force Base (EAB) sampling locations.

ANF	D.F.	S.S.	M.S.	F Statistic	P Value
Location	2	0.4549	0.22745	0.80316	0.7056
Residual	12	3.3983	0.28320		
Total	14	3.8532			
EAB	D.F.	S.S.	M.S.	F Statistic	P Value
Location	2	0.2022	0.10111	0.4568	0.9158
Residual	6	1.328	0.22133		
Total	8	1.5302			

Figure S4.1: Image of the colored pan traps suspended approximately 30 cm above the ground.

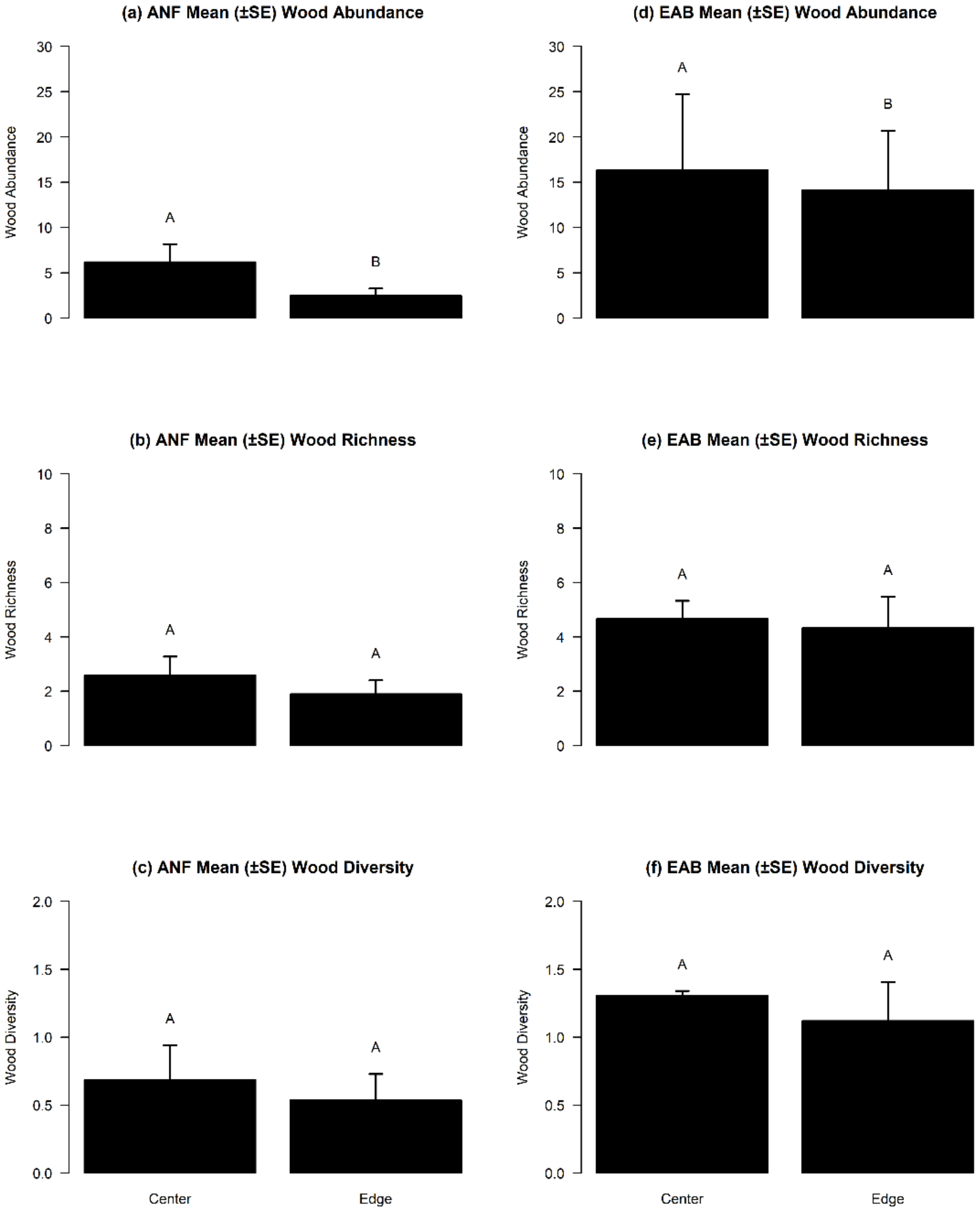

Figure S4.2: Bar graphs of mean (±SE) wood nesting bee abundance, richness, and diversity collected from the center, and edge locations at Apalachicola National Forest (ANF), and Eglin Air Force Base (EAB).

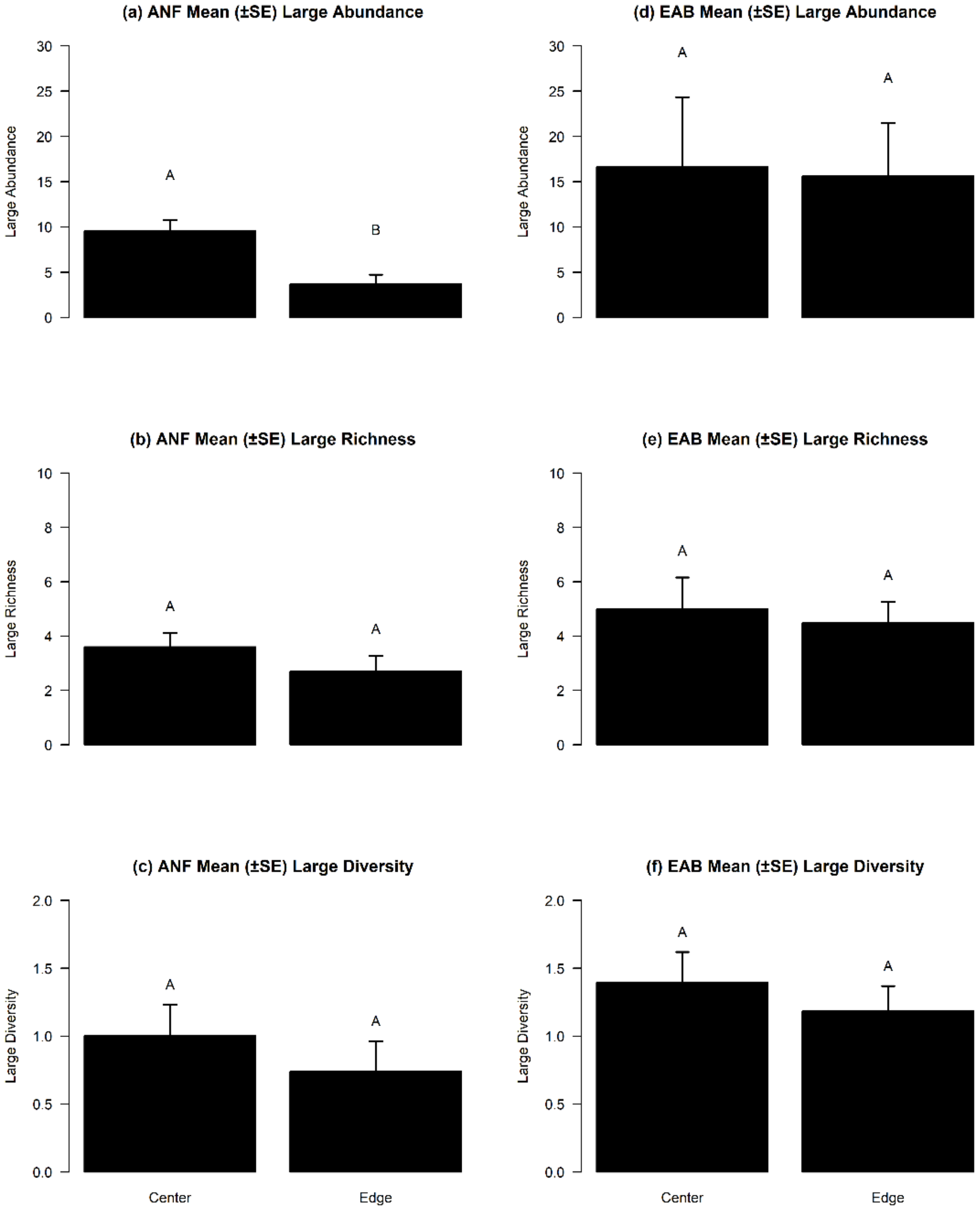

Figure S4.3: Bar graphs of mean (±SE) large bee abundance, richness, and diversity collected from the center, and edge locations at Apalachicola National Forest (ANF), and Eglin Air Force Base (EAB).

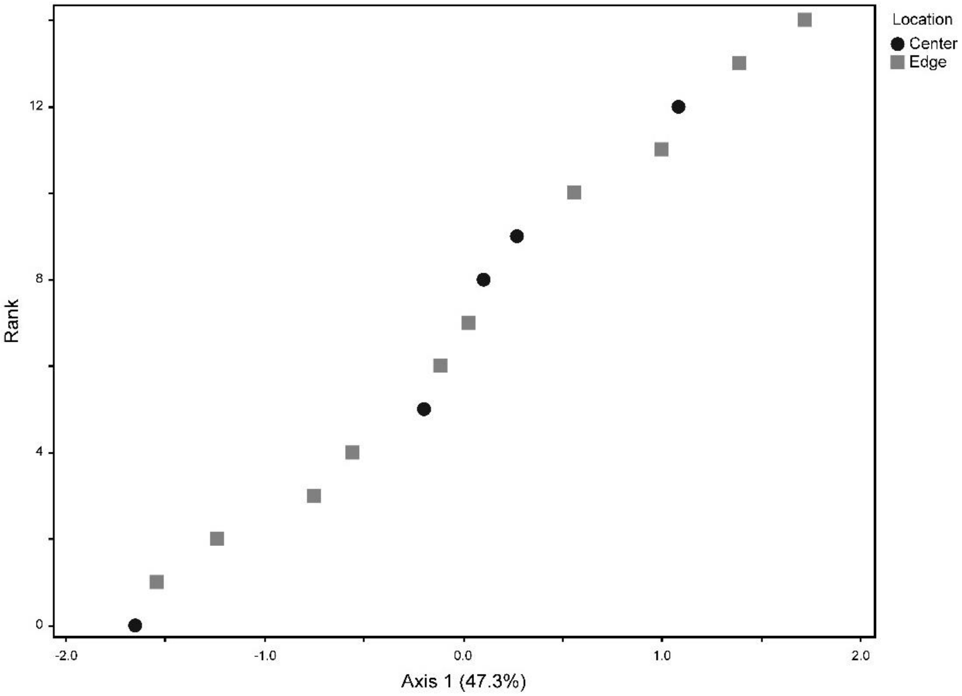

Figure S4.4: Non-metric multidimensional ordination of the bee community observed from the 15 sampling locations at the Apalachicola National Forest.

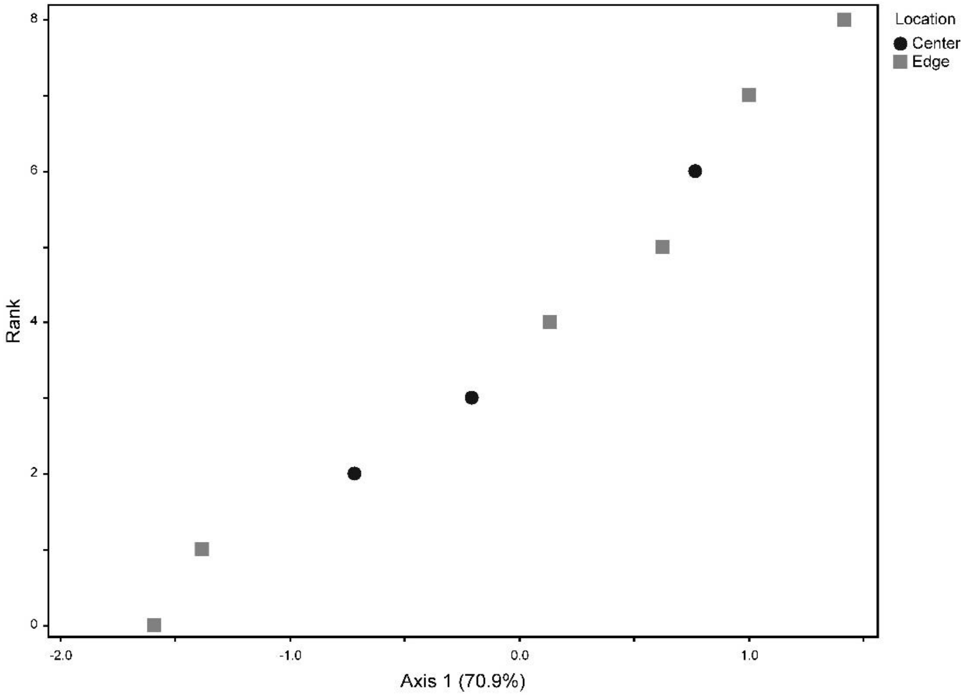

Figure S4.5: Non-metric multidimensional ordination of the bee community observed from the nine sampling locations at the Eglin Air Force Base.

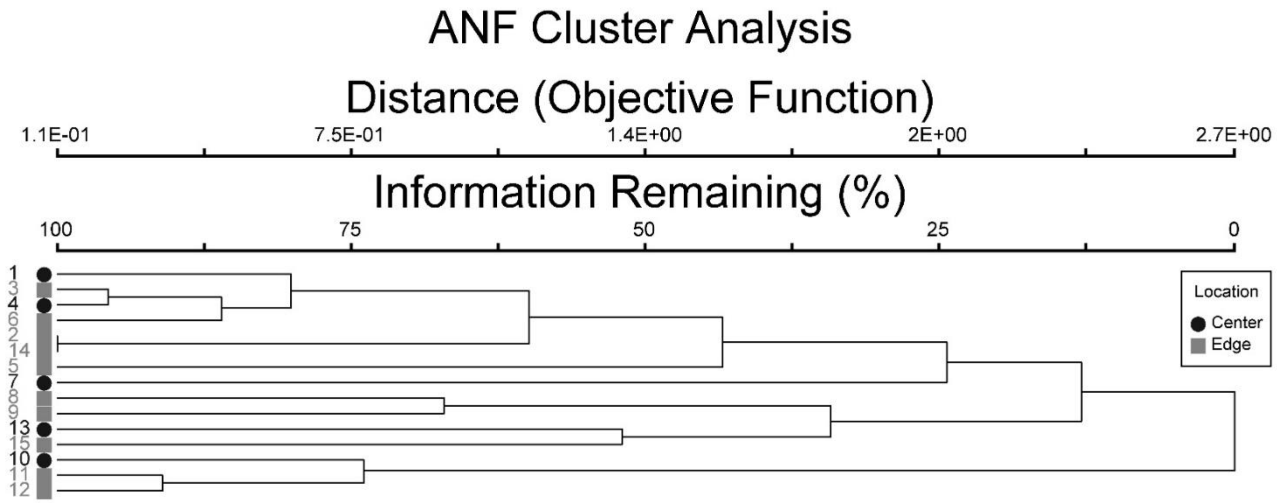

Figure S4.5: ANF Cluster Analysis for sampling locations from Apalachicola National Forest (ANF).

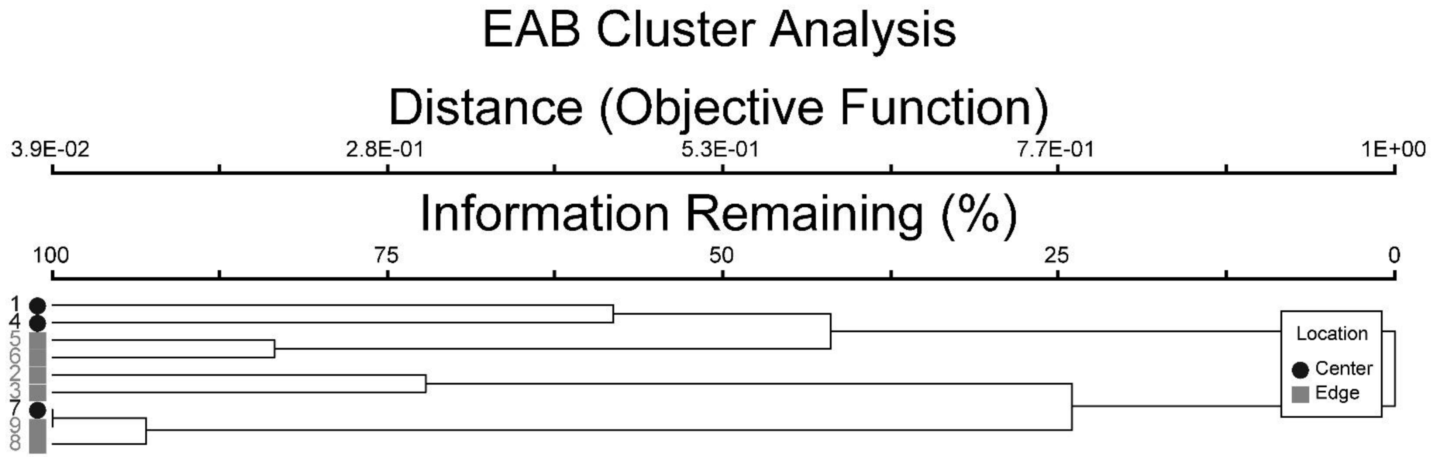

Figure S4.6: EAB Cluster Analysis for sampling locations from Eglin Air Force Base (EAB).