

THESIS

DRIVERS AND PHENOLOGY OF NATIVE BEE-FLOWER INTERACTIONS IN
RESTORED PONDEROSA PINE FORESTS

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ABSTRACT

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Many ecosystems, globally, are degraded or transformed as a result of anthropomorphic activities. Ecological restoration can manage ecosystem processes by reintroducing disturbance and returning systems to historical conditions. There is a particular need for restoration treatments in forested ecosystems, such as the conifer forests along the Colorado Front Range, as changes due to a century of fire-suppression policies and logging practices have led to overly-dense, even age forest stands that are prone to stand-replacing wildfires that are hazards to human property and ecosystem health.

Most flowering plants are pollinated by animals; native bees are especially important pollinators in many terrestrial systems. However, native bees are facing challenges due to rapid land use change, which have led to population declines. While there is evidence that ecological restoration can improve native bee habitat, the effects of restoration treatments on native bee populations and bee-flower interactions are poorly understood. Additionally, the mechanisms driving interactions, especially within forested ecosystems, are understudied.

To address these knowledge gaps, this thesis aims to 1) summarize current understanding of the effects of ecological restoration on native bee communities, 2) use structural equation modelling to determine the mechanisms driving differences between bee-flower interactions in thinned and non-thinned forest sites, 3) further explore potential site and floral characteristics

driving these interactions in canopy gap habitats, and 4) examine phenological matching between bees and floral abundance/nutrition.

Bee-flower interactions were surveyed in two separate studies located in ponderosa pine (*Pinus ponderosa* Dougl. Ex. Laws.) dominated forests along the Colorado Front Range treated under the Collaborative Forest Landscape Restoration Program (CFLRP), which aims to restore ecological health. In the first study, native bee assemblages and interactions were compared between thinned and non-thinned stands in relation to site characteristics such as forest structure, temperature, floral resources, and nesting habitat. In the second study, over 6,500 bee-flower interactions were observed in canopy gap habitats and analyzed to understand phenological matching and interaction drivers such as floral availability, nutritional value, and visual traits. Overall, these studies suggest that native bee communities respond positively to ecological restoration in ponderosa pine forests along the Colorado Front Range. Specifically, structural equation modeling suggests that changes to forest structure result in cascading effects altering temperature, foraging availability, and nesting resources which increase native bee abundance, species richness, diversity, and interactions. The degree of phenological mismatch was site-specific and more severe for certain functional groups, such as small-sized bees. While at a site level higher pollen protein content may increase total interactions, bees tended to select flowers based on visual signals, such as color, display area, and height.

These findings have important implications for ecosystem management. Specifically, the data suggest thinning and gap creation are important management practices for restoring ecological services, such as pollination, and increasing bee and floral diversity. Our results suggest that managers should consider bee functional diversity and floral phenological diversity in planning restoration projects. Both studies also identify floral species that play key roles in maintaining

ecological networks, including invasive species that are often targeted for eradication in management plans. While ecosystem restoration likely benefits native bees, additional consideration should be given to maximize these benefits to ensure continued ecosystem function under uncertain future conditions.

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PREFACE

The chapters in this thesis are formatted for journal submission, hence formatting may differ throughout. Chapter 1 (Forest restoration treatments enhance plant-pollinator networks via floral- and temperature-mediated resource cascades) is formatted for the *Journal of Applied Ecology*. Chapter 2 (Phenological mismatch of native bees and floral nutrition and drivers of bee-flower interactions in canopy gap habitats) is formatted for *Ecological Applications*.

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INTRODUCTION: DIRECT AND INDIRECT EFFECTS OF ECOLOGICAL RESTORATION ON NATIVE BEE POPULATIONS

INTRODUCTION

Habitat loss is a global threat to native bee populations (Winfree et al., 2009). While the importance of native bees for ecosystem function is well established, few studies consider how land management affects native bee communities and populations (Harmon-Threatt & Chin, 2016). Pollination is a vital ecosystem function that may be impacted by ecological restoration practices. Restoration activities could benefit or impede pollination services depending on variation in pollinator life histories, elements of ecosystem structure and composition, or specific restoration implementations. These effects on native bee communities can be either direct or indirect. Direct effects include activities that immediately increase or decrease pollinator populations sizes, such as unintentional mortality of bees from pesticide or herbicide applications, destruction of nests by equipment, burning, or other implementations. Indirect effects more typically include longer-term effects of restoration activities that impact bee populations over time mediated via floral communities and nesting habitat.

This review synthesizes literature examining important consequences ecological restoration activities have on native bee communities. For this review, the term “ecological restoration” is used as defined by the Society for Ecological Restoration: ‘the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed’ (Society for Ecological Restoration International Science & Policy Working Group, 2004). Ecological restoration practices discussed in this review are seed and tree planting, invasive plant removal,

prescribed burning, and forest thinning. While this review broadly considers the interactions between native bees and restoration practices, it specifically examines how restoration in forest ecosystems affects native bees.

To identify previous research in this field, I conducted a systematic literature search in Web of Science using a combination of keywords including restoration/restor*, “native bees”, and “wild bees” (Clarivate Analytics, 2021; Figure 1.1). I limited the search for research papers to include recent studies (since 2005), although it should be noted that this field of inquiry is relatively nascent, so early literature is limited. For example, using the search restor* “native bees”, Web of Science returns 75 results with only three results occurring prior to 2008. Since 2008, the number of publications per year generally increased in this field. Based on papers available in Web of Science the term “ecological restoration” does not appear until 1988 and it is not until 1998 that pollinators are mentioned within the ecological restoration field. Studies included in this review must directly compare bee abundance, richness, diversity, or species composition between restored and non-restored habitats. To review the field appropriately, my analysis interprets several other literature reviews and meta-analyses.

General effects of ecological restoration on native forest bee communities

In a meta-analysis examining how habitat restoration benefits native bees, Tonietto & Larking (2018) found that across 28 studies all restoration efforts increased bee abundance. The studies include a range of habitat types, geographic regions, and restoration treatments. Bee species richness increased in all restored categories (restoration, burning, grazing, invasive plant removal, mowing, and seeding) across studies, except for those restored by mowing (Tonietto & Larkin, 2018). However, bee and plant species responses differed between various restoration methods and habitats, so it is important to look at each system and location separately (Harmon-

Threatt & Chin, 2016; Tonietto & Larkin, 2018). Most of the research examining the effect of restoration on native bees focuses on agricultural systems (Winfree, 2010). Agricultural habitat restoration includes methods such as restoring the surrounding habitat in buffer areas, setting aside or converting some fields to pollinator-friendly habitat, farming in-production fields less intensively, and organic farming which decreased detrimental impacts on pollinators from pesticides (Winfree, 2010). These practices are more common in the European Union where farmers are compensated for ecological restoration (Winfree, 2010). While restoration in agricultural systems is important, this area only represents a subset of issues facing pollinators.

Studies in many forest ecosystems demonstrate that native bees benefit from more open forest conditions (Hanula et al., 2016; Roberts et al., 2017). These studies find that abundance and species richness of bees are greater in forests with lower basal area (*i.e.* fewer large trees resulting in more open conditions) (Hanula et al., 2015; Romey et al., 2007). Basal area predicted bee diversity better than any other forest conditions measured (Hanula et al., 2015). Even in non-restored areas where heavy logging has taken place bee diversity is positively correlated with open forest conditions (Romey et al., 2007). An exception to this trend is in tropical forests where the problem is usually destruction of habitat by land-use changes instead of fire suppression. In these tropical systems forest restoration usually involves planting trees that can restore bee populations (Montoya-Pfeiffer et al., 2020).

Native bees and floral communities can have complex interactions, so effects of restoration efforts on bees may differ even in apparently similar forest ecosystems. For example, two studies evaluating restoration of riparian forests in different parts of the United States reported contrasting results. One study in Georgia found that restoration of riparian forests increases bee abundance, species richness, and plant-bee interactions (Hanula & Horn, 2011). In

the riparian forests of central California, studies comparing restored to non-restored habitats found no difference in bee abundance or diversity, but some difference in species composition (Williams, 2011). The differences in findings of these two studies may be explained by how the restoration efforts altered the environment. For example, in Georgia, there was an increase in floral diversity whereas in California, floral resources did not change. These differences highlight the importance of studying multiple types of ecosystems, especially if available resources differ, when trying to define general principles and suggest using caution when in extrapolating or generalizing results across various systems.

The literature suggests that restorative treatments can have both direct and indirect effects. However, even in comparatively well-studied systems (*i.e.*, agricultural habitats), the mechanism of reported effects may be poorly understood (Tonietto & Larkin, 2018). It is possible that some of these restorative treatments directly affect bee communities, but it is also possible that they influence other factors such as the floral community which in turn affects native bees. Understanding what factors are most important for ensuring bee population success and how those factors are altered in restoration is vital to ensuring success of native bee conservation efforts (Winfree, 2010).

Direct effects of ecological restoration on native bee communities

Certain restoration methods cause direct harm to native bee communities. For example, prescribed burning can heat the soil to temperatures beyond bees' thermal tolerances (Cane & Neff, 2011). However, for lower intensity burns used in restoration projects, the majority of bees likely survive. Controlled burning is most damaging to shallow-nesting bees, such as ground-nesting *Osmia* and *Megachile* (Cane & Neff, 2011). Burning of above-ground material could also result in physical destruction of nests. Similarly, other restoration methods that remove

vegetation, particularly from the understory, could destroy or disrupt nests (Fortuin & Gandhi, 2021).

Pesticides, including herbicides and insecticides, are often used in restoration projects to eliminate invasive species. However, pesticides can be extremely detrimental to native bees (Hatfield et al., 2021; Prendergast et al., 2022). For example, Hatfield et al. (2021) documented the use of a neonicotinoid insecticide (dinotefuran) in an isolated area killed up to 100,000 bumblebees. The accumulation of toxins and rate of mortality is dependent on functional traits such as body size/fat storage and how heavily bees utilize the species being treated (Longing et al., 2020). Life-history characteristics, such as nesting substrate can also play a critical role in determining the magnitude of effect from pesticides. For example, ground-nesting bees are more sensitive due to exposure to pesticides, especially herbicides, that leach into the soil (Main et al., 2020). While chemical herbicides can be detrimental, there may be alternative methods for invasive control such as bio-herbicides or biological control agents that do not affect pollinators (Mbundi et al., 2021), and should therefore be considered in restoration practices.

Indirect effects of ecological restoration on bee communities

While there are some direct effects of ecological restoration, the majority of effects result from indirect mechanisms initiated by environmental changes. The two main categories of factors that can limit bee population growth are the availability of nesting substrates and floral resources. The extent to which these factors can limit bee population growth depends on the species of bees and their life-history traits. For example, solitary species that are floral specialists and ground-nesters, such as *Andrena hattoriana* (Andrenidae) and *Dieunomia triangulifera* (Halictidae) are controlled primarily by availability of pollen resources since they visit a specific host plant and bare ground is commonly available (Larsson & Franzén, 2007; Minckley et al., 1994). There is

evidence for floral resources as potential limiting factors in other genera with life-history traits such as eusociality (*Bombus*) and cavity-nesting, often in woody substrates (*Osmia* and *Megachile*) (Bowers, 1986; Gathmann et al., 1994; Williams & Kremen, 2007). These studies provide evidence that bee populations increase along with floral resource availability, likely due to the rate in which these species are able to provision their colonies/cells. However, in systems with abundant floral resources and augmented nesting, bee populations of *Osmia rufa* increase as nesting resources increase, rather than pollen availability, suggesting limitation by nest site availability and a potential threshold to the benefits of increased floral abundance (Steffan-Dewenter & Schiele, 2008).

Effects mediated via floral resources

Restoration treatments that involve sowing or broadcasting of seed mixes can benefit native bee populations as increased flower availability is often correlated with increased abundance and species richness of bees (Lane et al., 2020; Woodcock et al., 2014). However, knowledge gaps exist in the understanding of which flowers native bees are using and therefore restoration activities do not always align with the desired outcome (Cariveau et al., 2020). For example, in some seeding restorations only one (*Ranunculus acris*) out of 15 plant species within foraging range are used by common solitary bees (Gresty et al., 2018). Warming global temperatures are also a concern in restoration efforts aimed at directly benefiting native bees as changing climate may alter floral phenology (Cariveau et al., 2020). Specifically, many floral species may bloom earlier, whereas bee emergence will remain relatively constant, causing phenological mismatch resulting in reduced floral reproduction and altered available nutrition for bee survival (CaraDonna et al., 2014; Rafferty & Ives, 2011). Relations between floral and bee increases could be influenced by an indirect effect through restorative techniques such as prescribed

burning. Burning can cause an increase in floral availability by creating open spaces for plants to grow, which increases native bee abundance (Buckles & Harmon-Threatt, 2019; Decker & Harmon-Threatt, 2019; Harmon-Threatt & Chin, 2016).

Many restoration projects aim to remove non-native, invasive plant species (*i.e.*, weeds) to return habitats to historical conditions, reduce competition with native plants, and improve ecosystem function. Studies that remove invasive plant species for restoration purposes found that decreasing invasive plants leads to increased plant pollination networks (Fiedler, Landis, & Arduser, 2012; Hanula & Horn, 2011). Invasive plants decrease floral diversity, so by removing them there is an increase in the complexity of plant-pollinator networks, which may be more resilient to disturbance (Kaiser-Bunbury et al., 2017). This trend exists in several ecosystems, namely wetlands (Fiedler et al., 2012), riparian forests (Hanula & Horn, 2011), and inselbergs (Kaiser-Bunbury et al., 2017). However, some invasive species may express traits that are particularly attractive to pollinators, and therefore be key species in bee-flower interaction networks (Theis, 2006). To preserve resiliency and connectivity in pollinator networks, managers should consider replacing invasives with species expressing similar inflorescences and functional traits (Goldstein & Zych, 2016).

Both thinning evenly throughout a stand, and gap creation (clumped thinning), are beneficial to native bees by creating open forest conditions (Hanula et al., 2016). Due to wildfire concerns, most forest thinning projects focus more on fuel reduction treatments than the ecological restoration of specific forest ecosystem functions. However, these fuel treatments can still lead to increases in abundance and diversity of native bees (Campbell et al., 2007; Nyoka, 2010; P. R. Rhoades et al., 2018). Thinning projects that both selectively remove trees and clear understory shrub cover most greatly increase native bee abundances and species richness

(Hanula et al., 2015). Decreasing the basal area, a measurement of forest stand density, and canopy cover increase the abundance and diversity of flowering plants by increasing light availability and growing space (Campbell et al., 2007; Cho et al., 2017; P. R. Rhoades et al., 2018). In turn, this greater abundance of flowering plants in open forest conditions can support a greater abundance of native bee communities (Campbell et al., 2007; Rhoades et al., 2018). In addition to supporting more floral resources, physical factors such as light intensity and temperature are also correlated with increased foraging frequency of native bee species (Polatto et al., 2014), and both factors may increase in stands that have experienced canopy removal or reduction.

Effects mediated via nesting habitat

Burning or similar restoration methods can affect soil properties (e.g., soil texture, compaction, permeability, etc.) important for habitat utilization by ground-nesting bee species (Buckles & Harmon-Threatt, 2019).. While there is evidence that prescribed fires can improve soil conditions which create greater nesting habitat for native bees, this area has not been well explored in forested ecosystems (Buckles & Harmon-Threatt, 2019). Burning, thinning, and other practices that decrease vegetation cover can increase nesting habitat for ground-nesting bees, who benefit from patchy sun-exposed ground (Vaughan et al., 2015).

Restoration treatments aiming to decrease both overstory and understory vegetation likely change nesting availability depending on how removed vegetation is treated. For example, in clearcuts with removed woody debris, ground-nesting bees increase more than other groups (Fortuin & Gandhi, 2021). Salvage-logging, removal of dead/dying trees after disturbance, while often not implemented as a restoration treatment demonstrates potential effects of removing woody debris from native bee habitat. While bee abundance increases following

salvage-logging, species richness and diversity decrease, suggesting negative impacts towards cavity-nesting bees that rely on woody debris (Galbraith et al., 2019). Alternatively, woody materials left on-site can increase the population of cavity-nesting bees and negatively affect soil nesting bees due to a lack of bare ground availability (Fortuin & Gandhi, 2021). Further consideration should be given to how treatment of removed material affects functional bee diversity and the importance of various patches of treatments across a landscape.

Knowledge gaps and methodological challenges

One challenge of studying native bees is the lack of long-term monitoring projects of populations and evaluation of habitat conditions (Winfree, 2010). Habitat conditions, especially floral resources can vary significantly within a year. A chronosequence approach can be useful for understanding the changes in bee, plants, and bee-flower interactions throughout a season. In particular, frequent evaluation of habitat conditions is needed to discern significant community differences and species turnover at restored sites. Many studies that compare native bee populations in restored and non-restored habitats have limited number of sampling bouts throughout a season and are therefore only a snapshot of the community composition. Additionally, many restoration treatments are poorly evaluated and do not consider native bees in the evaluation process (Winfree, 2010). Some of these knowledge gaps stem from lack of communication between pollinator biologists and land managers, suggesting that outreach programs designed to educate land managers on the importance of implementing restoration plans — specifically those which consider effects on conditions important for native pollinators — could be beneficial as a conservation effort (Menz et al. 2011).

Another gap in pollination biology is that the ecology and population dynamics of most bee species are unstudied (Winfree, 2010). Enhanced understanding of population biology and

life-history strategies would improve interpretation of results in similar studies, especially to assess why restoration efforts might increase abundance in certain bee functional groups but not others. To evaluate the success of a restoration project and its effect on native bee species, it is important to know how many individuals are required for maintaining minimum viable population sizes.

The few studies examining potential limiting factors illustrate that limitation of bee population growth is dependent on species and life-history traits. Even if more information on native bee life-history traits and factors limiting population growth were available, it would still be challenging to predict the mechanisms of restoration effects in forested ecosystems because there is often little information on what species are present. Restoration projects can alter floral resources, nesting availability, and physical properties. Therefore, to improve the understanding of effect mechanisms, studies evaluating restoration projects should examine native bee and interaction diversity and as well as a variety of important habitat factors. Without knowing what limits bee populations, it is difficult to evaluate the success of restoration projects.

Methodological issues such as the techniques used for capturing bees must also be considered. Different sampling techniques result in varying bee abundances and species representation (Rhoades et al., 2017). For example, blue vane traps are biased towards larger bees, whereas pan traps are biased towards smaller bees. Passive trapping (blue vane, pan, and malaise traps) often results in incorrect conclusions about the bee community composition (Prendergast & Hogendoorn, 2021). Passive trapping also may lead to increased capture in poor habitat and decreased capture in quality habitat where bees are more attracted to floral resources (Kuhlman et al., 2021; Prendergast & Hogendoorn, 2021). Of the 13 studies directly comparing restored and non-restored habitats within a single system, only three used multiple approaches to

analyze differences in native bee populations. The five capture methods used throughout the literature were netting, observation, pan traps, malaise traps, and blue vane traps. The most popular method was pan traps which were used in six of the 13 studies. Net and observation were used in 4 studies each; malaise and blue vane traps were each used in a single study. Despite the issues listed above, passive trapping (*i.e.*, blue vane and pan traps) are useful because they allow for simultaneous observations over large areas with little possible overlap in observer bias. In contrast, netting gives specific information about which plants and plant traits are particularly important in supporting networks, but it is difficult to standardize accuracy across multiple observations.

By only including one method, or in some cases two, these studies are only sampling a subset of the overall community and therefore underestimating species diversity or missing some interactions. In the future, projects comparing restored and non-restored habitats should incorporate multiple sampling methods to gain clarity on the differences in native bee populations.

CONCLUSIONS

Current research indicates that forest restoration treatments do affect native bee populations, regardless of the primary intent of the project. Most research shows a positive relationship between bee populations and restored habitat. Although there are a couple studies that show no impact of restoration on native bees, none of the reviewed studies reported negative effects on native bees. However, certain restoration practices, such as prescribed burning and pesticide/herbicide application, can negatively affect native bees under some conditions. To maximize the benefits to native bee populations and habitat from future restoration treatments, research must develop better understanding of the mechanisms behind community change.

Additionally, many studies demonstrate that certain functional and taxonomic groups are disproportionately affected by certain restoration practices, such as the removal of woody debris used for nesting material. Therefore, future studies must evaluate the effectiveness of restoration on various groupings and consider how sampling method may influence the results. Agricultural systems have been a primary focus until recently, so there is a need to evaluate restoration projects in different ecosystems. This need is especially apparent in forested habitats that span very large areas and where the interactions of bee population and restoration projects are very poorly understood. While there is strong evidence that native bees benefit from restored forest conditions, and many have argued that pollination should be considered in restoration, few studies have evaluated the impacts of forest restoration treatments on pollinators, particularly in the western United States (Handel, 2019; Hanula et al., 2016; Winfree, 2010).

The need for studying pollinators in forests is especially apparent in managed mixed conifer forests common throughout the Colorado Front Range (Rivers et al., 2018). Based on the findings in previous literature, the objective of my research is to evaluate how the ecological restoration treatment of thinning in ponderosa pine-dominant forests in the Front Range affects native bee populations and bee-flower interactions. My research first directly compares restored and non-restored forested areas to determine the mechanisms driving changes to bee-flower interactions and the second further evaluates drivers of these interactions in canopy gap habitats.

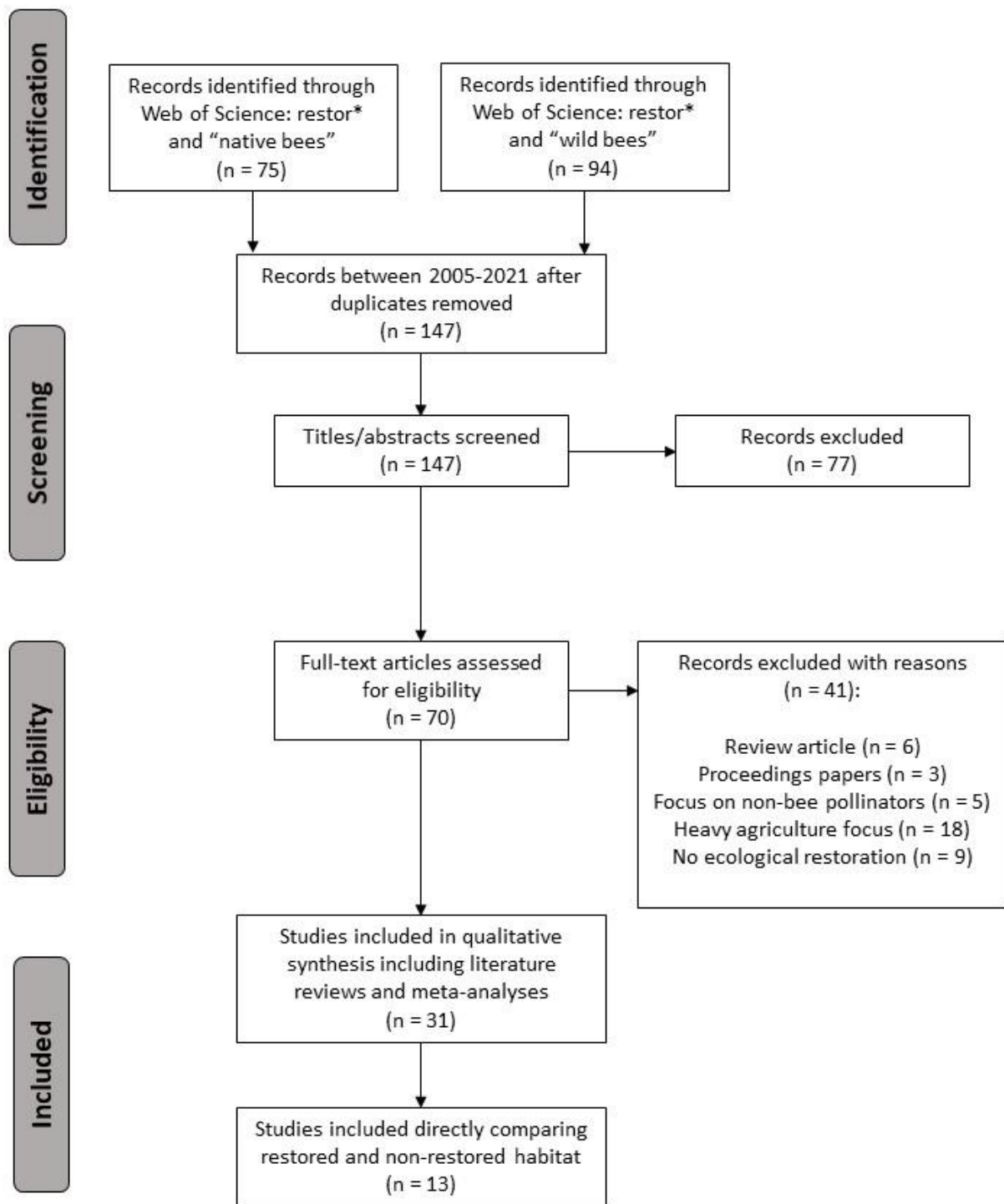


Figure 1.1. PRISMA diagram to illustrate the process for selecting studies to be included in the qualitative synthesis. Records exclude based on titles/abstracts did not directly compare bee abundance, richness, diversity, or species composition between restored and non-restored habitats.

CHAPTER 1: FOREST RESTORATION TREATMENTS ENHANCE PLANT-POLLINATOR NETWORKS VIA FLORAL- AND TEMPERATURE-MEDIATED RESOURCE CASCADES

SUMMARY

1. Anthropomorphic activities transform and degrade habitats which often need specific tactics and reintroduction of disturbance regimes to restore essential ecosystem processes.

In North American conifer forests, stem density reduction via thinning operations is broadly implemented as a means of ecological restoration and fire hazard reduction. Effects of thinning on forest bee communities are poorly understood but could be important for conservation of biodiversity and ecosystem services. Here, we test the hypothesis that forest thinning initiates a resource cascade that affects pollinator community assemblages and bee-flower interactions.

2. Native bee assemblages and interactions were compared between mechanically thinned and non-treated stands in ponderosa pine forests. Associations between bee communities, nesting and foraging resources, and forest structure were analyzed using parametric statistics and network analyses. Structural equation models were constructed to determine how thinning affects ecosystem structural components important for pollination.
3. Thinned sites had greater canopy openness, temperature, floral abundance and diversity, and bare ground cover. Native bee abundance, richness, and diversity were 120%, 53%, 37% greater at thinned sites, respectively. Thinned sites had more interactions and their network metrics suggested improved resiliency. Increased growing space, increased light and higher temperatures initiated a resource cascade which resulted in greater foraging resources

causing increases in bee richness and abundance, and ultimately resulting in more interactions.

4. Floral abundance was the strongest predictor of bee abundance and diversity; bee abundance and richness were the most important factors predicting interaction abundance and richness, respectively. We conclude that forest thinning for ecological restoration in ponderosa pine habitats within 2-8 years post-treatment is likely to improve resources utilized by native bees and is associated with increased bee abundances in the wildland-urban interface.
5. *Synthesis and applications.* Native bee assemblages and plant-bee interactions positively respond to the cascading effects of thinning treatments that alter temperature and foraging resources. Analyzing multiple site-level factors provides insight on how to conduct forest thinning operations to maximize native bee conservation while improving forest conditions. We show that decreasing canopy cover initiates an increase in floral resources which ultimately benefit native bees that provide essential ecosystem services.

INTRODUCTION

Ecological restoration is an important practice, globally, for managing ecosystem processes. Restoration generally aims to recover ecosystems previously degraded, damaged, transformed, or destroyed as a result of anthropomorphic activities by reintroducing natural disturbance patterns and returning the system to historical conditions (SER, 2004). Although specific tactics vary across ecoregions and cover types, restoration is often approached through manipulation of dominant vegetation or specific disturbance processes (Leite et al., 2013). In many parts of western North America, stem densities in forest ecosystems have increased far beyond historical conditions as a result of fire suppression policies, extensive logging practices, encroachment of the wildland-urban interface, and changing climate conditions (P. M. Brown et al., 2015;

Rodman et al., 2019). To address these structural shifts, restoration treatments consisting of intensive thinning operations are often implemented to reduce forest stand densities, facilitate or re-introduce fire as a disturbance process, and reduce wildfire hazard in the wildland-urban interface (Dennis & Sturtevant, 2007). These ecological restoration and fuel reduction treatments generally aim to remove small-diameter trees, increase canopy base height, and reduce canopy connectivity (Fulé et al., 2001).

Despite the widespread use of stand density reduction as a restoration practice in the western North American landscape, the effects of these changes in dominant vegetation on ecological networks and biotic communities that provide key ecosystem support services are poorly understood. For example, native bee pollinators are in decline worldwide due to habitat loss from land-use changes; native bee species in forested landscapes may be particularly sensitive to vegetation changes (Potts et al., 2010; Winfree et al., 2009). The majority of angiosperms rely on animal pollinators, of which bees are especially important for ensuring functional and genetic diversity (Fontaine et al., 2006). While the importance of native bees for ecosystem function is well established, few studies consider how land management actions affect native bee communities and populations (Harmon-Threatt & Chin, 2016). There is evidence that native bees could benefit from restored forest conditions and some authors suggest that pollination services should be considered in restoration efforts, but few studies have evaluated the impacts of forest restoration treatments on pollinators (Handel, 2019; Rivers et al., 2018). Understanding factors that drive bee-plant interactions and how those factors are altered by restoration is therefore critical for maximizing native bee conservation and sustaining ecosystem services (Winfree, 2010).

The Collaborative Forest Landscape Restoration Program (CFLRP) is one example of a program in the western United States that aims to restore ecological health and reduce wildfire risk, with the additional goal of monitoring ecosystem services, such as pollination. The CFLRP was created by congress in 2009 to enhance long-lasting ecological, social, and economic benefits on National Forest System (NFS) lands. One project area is located on the Front Range of Colorado, where people throughout the wildland-urban interface widely extirpated fire from ponderosa pine (*Pinus ponderosa* Dougl. Ex. Laws.) dominated forests, necessitating a widespread need for forest restoration efforts (Addington et al., 2018). Interior ponderosa pine forests have historically supported mixed-fire regimes with frequent fire return intervals (Dickinson, 2014); mature trees are fire-tolerant (Oliver & Ryker, 1990). The FR-CFLRP aims to treat ~13,000 hectares of predominately ponderosa pine forests with diverse understory forb and native bee communities (Addington et al., 2014; P. R. Rhoades et al., 2018). While there are many benefits to thinning in ponderosa forests, it is often difficult to complete thinning treatments due to low economic returns (Ager et al., 2017). Despite the prevalence of both fuel reduction and ecological restoration treatments in Colorado's ponderosa pine forests, there are still significant gaps in the understanding of the influence of forest thinning practices along the Front Range.

To address the plant-pollinator networks knowledge gap, we analyze these interactions in the Colorado Front Range and model how various elements of ecosystem structure hierarchically impact native bee communities and associations with flowering plants. We use a conceptual model (Figure 2.1; path justifications are described in Table S1.1) to assess the causal relationships between site factors altered by restoration and plant-pollinator interactions. We hypothesize that restored areas (a) differ in vegetation structure that ultimately changes physical

properties and increases foraging and nesting resources, (b) have greater abundance and diversity of native bee communities and plant-pollinator interactions, and that (c) these increases are driven by a cascade of resources initiated by thinning treatments. Our results have important implications for understanding how ecosystem management influences biotic communities of global concern that provide invaluable ecosystem services.

METHODS

Site selection

The treatment areas (mechanical thinning) on the Front Range are primarily in ponderosa pine (*Pinus ponderosa*) dominated forests, with components of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), lodgepole pine (*Pinus contorta* Dougl. Ex. Loud.), common juniper (*Juniperus communis* L.), and quaking aspen (*Populus tremuloides* Michx.) at 7,000 to 9,000 feet elevation (Figure 2.2). Treatment areas ranged from 224 to 311-hectare patches. Sites (n=30) are in the Roosevelt National Forest where thinning treatments were completed in 2012 and the Pike National Forest where thinning treatments were completed in 2017 and 2018. Elevation, aspect, and slope were recorded for all sites.

Characterization of forest structure

Overstory vegetation at sites was sampled using 0.1-hectare fixed-area plots (~32 m²); a total of 15 thinned and 15 non-thinned sites across the entire study region were sampled. Thinned sites were located near the interior of treatment areas to avoid edge effects and at least 500 meters apart to ensure sampling independence (Figure S1.1). Non-thinned sites were located nearby, but outside of, treatment areas with similar elevation, slope, and aspect. In each plot, basal area (m²/ha)—a measurement of forest stand density—was recorded using an angle gauge at ten points where floral quadrats were deployed (described below), such that at each sample site there

were ten measurements of basal area that were subsampled to yield a site-level average basal area. Photos of the canopy were also taken at each point to analyze canopy openness. Canopy openness was computed using the Gap Light Analyzer (GLA ver. 2) software (Frazer et al., 2000). All trees within each plot were censused and species were recorded. Basal area and tree density differed between site types, confirming that forest structure differed significantly between post-thinning and non-thinned stands. On average, non-thinned sites had 3.6 times greater basal area and 3.8 times greater tree density (Figure 2.3A, B). Quadratic mean diameter (QMD) did not differ between site types (Figure 2.3C), and canopies were 21.1% more open at thinned sites compared to non-thinned sites (Figure 2.3D).

Characterization of foraging resources, nesting habitat, and stand physical properties

To estimate floral resource availability, the number of flowers for each floral species was counted within meter-squared quadrats. A flower was defined as a complete inflorescence, such that compound flowers counted as a single flower, where a single plant could have multiple inflorescences. At each site, 10 quadrats were deployed. One quadrat was placed in the center of the plot, four quadrats were then placed in each cardinal direction extending three meters away from center, another four quadrats were placed an additional three meters from the previous four, and one quadrat was randomly deployed at any point within the plot (without overlap). The quadrats were treated as subsamples, such that for each site there was a single mean value for floral density and richness. To account for seasonal variation, floral quadrats were re-sampled three times throughout the growing season synchronously with bee sampling, approximately once every 4 weeks (June to August 2020).

Ground cover, an important indicator of ground-nesting bee habitat, was also measured. To measure ground cover, five 20-meter point-intercept transects were placed equidistantly

radiating from the center of the fixed-area plot (100 total intercepts). The primary ground cover was recorded every half meter. Ground cover (%) was categorized as 1) bare ground, 2) forbs, 3) grass, 4) litter, 5) moss, 6) rock, 7) shrub, 8) tree, or 9) wood.

Surface woody debris loadings, potential nesting habitat for cavity-nesting bee species, were estimated using transects. Coarse woody debris (CWD) was measured along five 25-meter transect lines from the center of the plot (Lutes et al., 2006). CWD was characterized as logs of at least one meter in length with a diameter of $\geq 8.0\text{cm}$ and the center point above the duff layer. Diameter was measured where any CWD intersected the transect line, perpendicular to the log length. The volume of CWD at each site was subsequently computed using the equation of $V = \pi^2 \sum_{i=1}^n d^2 / 8l$ (Van Wagner, 1968).

During the second sampling period (July), a data logger (HOBO Pendant Temp/Alarm One Channel Data Logger 8K Model, Onset Computer Corp., Pocasset, MA) was deployed to record ambient temperature every 30 minutes at each site until the last sampling time in August. The data loggers were placed in small cardboard boxes enclosed in a plastic bag attached to the north side of a tree located near the middle of each plot to minimize direct solar radiation.

Bee sampling and identification

Bees were captured once a month throughout the growing season in June, July, and August for a total of three sampling times (n=90 bee collections). At each site, blue vane traps (SpringStar, Woodinville, WA, USA) and pan traps (~350ml) were set and left for 48 hours. The blue vane trap was placed at the center of the plot and three colored pan traps (blue, white, and yellow) were placed equidistant from one another in a triangular arrangement approximately two meters from center. In addition to passive trapping, bees were also captured via active netting for an hour at each site between the hours of 08:00 and 14:00. All samplings took place during

generally sunny conditions. Flower species visited by bees were recorded to inform network analyses.

After collection, bees were dried, pinned, and identified using various guides and available literature (Ascher & Pickering, 2020; Michener et al., 1994; Scott et al., 2011). Most bees were identified to the species level. If species-level identification was not possible, bees were separated into subgenera or morphospecies. The genus *Lasioglossum* was separated into the subgenera *Dialictus* or *Lasioglossum* s.s.. There were five bee specimens out of 1,432 (two from non-thinned sites and three from thinned sites) that were damaged and were not identifiable. These specimens were therefore omitted in diversity analyses but were still included with regards to abundance.

Data analyses

All statistical analyses were completed using R Studio Version 4.0.2, “Taking Off Again” (R Core Team, 2021). A Type I error rate of $\alpha = 0.05$ was used for assigning statistical significance in all analyses.

a) Effects of thinning on temperature, nesting, and foraging resources

A two-sample Students t-test was used to compare elements of forest structure and temperature between thinned and non-thinned stands. Mean floral density and floral species richness were compared across all months between thinned and non-thinned stands using an Analysis of Variance (ANOVA) model that included treatment, observation period (month), and a month \times treatment interaction as fixed effects.

b) Effects of thinning on bee abundance, diversity, and plant-pollinator interactions

A two-factor ANOVA was used to analyze the effects of seasonality (June, July, and August), treatment (thinned and non-thinned stands), and the seasonality \times treatment interaction on

metrics of bee community α -diversity. Shannon-Weiner diversity index H' was calculated using the 'vegan' package (Oksanen et al., 2020). The H' statistic could not be computed for three site-months (all at non-thinned sites) due to no bee captures but were included as zero in the bee abundance and species richness analyses.

Bee species β -diversity was analyzed with sample-based accumulation curves using the 'iNEXT' package (Hsieh et al., 2020). Estimates were interpolated from sample-based incidence frequency and were extrapolated to twice the number of replication units. Estimates were calculated using three different Hill numbers including species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$). Number of sampling units was extrapolated to two times the number of sampling units ($n=90$) (Chao et al., 2014).

Community composition was analyzed between thinned and non-thinned sites using a distanced-based framework (Bray-Curtis dissimilarities). The effects of site status on community composition were analyzed using permutational multivariate analysis of variance via the 'adonis2' function in package 'vegan'. To visualize these results a non-metric multidimensional scaling (NMDS) plot was produced with the 'metaMDS' function.

A one-way ANOVA was used to analyze the effects of capture method (net, blue vane, and pan trap) on bee abundance. The analysis used site and method as the unit of replication ($n=90$ site \times method combinations). Community composition was analyzed between the three capture methods using the same method as above.

The linkages and interactions of bees and floral species were analyzed using the 'bipartite' package (Dormann et al., 2008). The bee specimens included were only those netted while visiting flowers. To quantify these interactions, three metrics were calculated (Dormann, 2021; Kelly & Elle, 2020): (1) Network-level specialization ($H2'$), (2) Modularity (Q), and (3)

Weighted nestedness (WNODF). To determine significance between thinned and controlled sites, we calculated z-scores by comparing observed differences in indices to null distributions such that $z_I = \frac{I_{observed} - \bar{I}_{nulls}}{\sigma I_{nulls}}$ (Dormann, 2021). We constructed the null distributions of network metrics from random networks using the ‘nullmodel’ function. To identify species with potentially important ecological roles in the pollinator networks, we determined standardized connection c and participation z values for all species (Olesen et al., 2007). We defined objective thresholds by using the 95% quantiles from null models for critical values (Dormann, 2021).

c) Modeling resource cascades of forest structure on plant-bee interactions

Piecewise structural equation modeling was used to explore causal relationships between the various site characteristics and bee assemblages by combining multiple linear models (Shipley, 2009). Specifically, a structural equation model (SEM) was used to assess the effects of forest structure, foraging habitat, nesting habitat, and physical properties on bee assemblages and bee-flower interactions. Since we were modeling bee-flower interactions, we only used data from bees that were captured via netting. The SEM was constructed with linear mixed-effects models (LMMs), fitted using the ‘lme’ function in the package ‘nmle’ (Pinheiro et al., 2021). The LMMs were generated based on a hypothesized SEM model (Figure 2.1; Table S1.1). All models included a random intercept for sample site. The SEM was fit using the R package ‘piecewiseSEM’ (Lefcheck, 2016). All variables used in the SEM were normalized to make effect sizes comparable. Model fit was evaluated following methods outlined in Shipley (2009) by using direct separation (d-sep) tests. The d-sep test is based on Fisher’s C statistic that follows a χ^2 distribution, where the resulting P -value represents the probability of observing the model by chance assuming a causal relationship.

RESULTS

a) Effects of thinning on temperature, nesting, and foraging resources

Mean temperature was on average 0.7°C higher in thinned stands ($18.84 \pm 0.16^{\circ}\text{C}$) compared to non-thinned stands ($18.11 \pm 0.18^{\circ}\text{C}$; $t_{28} = -2.957$, $P = 0.006$; Figure S1.2A). Maximum temperature was on average 3.5°C higher in thinned stands (thinned: $37.04 \pm 1.13^{\circ}\text{C}$; non-thinned: $33.45 \pm 0.74^{\circ}\text{C}$; $t_{28} = -2.666$, $P = 0.013$; Figure S1.2B). Minimum temperature was on average 0.9°C higher in thinned stands, but this difference was not significant (thinned: $8.22 \pm 0.27^{\circ}\text{C}$; non-thinned: $7.34 \pm 0.49^{\circ}\text{C}$; $t_{28} = -1.560$, $P = 0.130$; Figure S1.2C).

Nesting resources varied between site types. Bare ground cover was 5.33% greater in thinned stands, and this difference was significant (thinned: 8.47 ± 1.67 % cover; non-thinned: 3.13 ± 1.38 % cover; $t_{28} = -2.462$, $P = 0.020$; Figure 2.3G). However, woody nesting substrates (CWD volume), did not differ between site types (thinned: $23.58 \pm 6.45 \text{ m}^3\text{ha}^{-1}$; non-thinned: $27.55 \pm 7.03 \text{ m}^3\text{ha}^{-1}$; $t_{28} = 0.416$, $P = 0.681$, Figure 2.3H). The 10 most common floral taxa across sites (*i.e.*, occurred in the greatest number of sites) included *Penstemon virens*, *Achillea millefolium*, *Geranium caespitosum*, *Jamesia americana*, *Mertensia lanceolata*, *Sedum lanceolatum*, *Arctostaphylos uva-ursi*, *Solidago missouriensis*, *Antennaria parvifolia*, and *Heterotheca villosa* with the most abundant being *P. virens*, *A. parvifolia*, and *S. lanceolatum*.

Mean floral abundance and floral species richness were greater at thinned sites across all months (Table 2.1; Figure S1.3). Both treatment and month had a significant effect on floral abundance and species richness, and there was no interaction effect between treatment and month. Floral density was on average 145%, 245%, and 638% greater in June, July, and August, respectively, in thinned sites. Similarly, the difference between floral species richness increased between site types throughout the summer, with floral species richness being 104%, 179%, and

217% greater in June, July, and August, respectively, in thinned sites. Linear regression analysis indicated a negative association between floral abundance and basal area (Figure 2.4A).

However, the trend was only significant in non-thinned stands (Floral abundance = $200 - 4.8BA$; $R^2 = 0.37$, $P = 0.017$). Similarly, floral species richness increased as basal area decreased (Figure 2.4B), and the trend was only significant at non-thinned sites (Floral richness = $10 - 0.19BA$; $R^2 = 0.41$, $P = 0.010$).

b) Effects of thinning on bee abundance, diversity, and plant-pollinator interactions

In total 1,432 (1,427 identified) bees were captured during sampling efforts, comprising five families, 31 genera, and 124 species (Table S1.2). The most abundant genera were *Lasioglossum* (Halictidae), *Bombus* (Apidae), and *Osmia* (Megachilidae) which accounted for 26%, 24%, and 9% of the total bees captured, respectively. Aside from *Lasioglossum*, which was not identified to the species level, the most abundant bee species were *Bombus centralis* (9%), *Bombus bifarius* (8%), *Hylaeus* spp. (Colletidae) (4%).

Overall, mean bee abundance was 118% greater in thinned stands than non-thinned stands ($F_{1,84} = 24.470$, $P < 0.001$). Bee abundances varied seasonally ($F_{2,84} = 7.009$, $P = 0.002$) and increased throughout the growing season (Figure 2.5A). There was no evidence of an interaction between site type and seasonality ($F_{2,84} = 0.740$, $P = 0.480$).

Bee species richness varied due to effects of thinning treatments and was on average 127.4% higher in thinned stands ($F_{1,84} = 42.278$, $P < 0.001$). Species richness also varied significantly due to seasonal effects with 18.5% and 25.8% more species present in June than in July and August, respectively (Figure 2.5B; $F_{2,84} = 4.399$, $P = 0.015$). There was no evidence of an interaction between treatment and seasonality ($F_{2,84} = 1.199$, $P = 0.307$).

Shannon-Weiner diversity (H') varied significantly between site types and was on average 66.9% higher in thinned stands ($F_{1,81} = 30.596$, $P < 0.001$). Shannon-Weiner diversity only varied marginally due to seasonal effect (Figure 2.5C; $F_{2,81} = 2.505$, $P = 0.088$), and there was no evidence of an interaction effect between treatment and month ($F_{2,84} = 1.618$, $P = 0.205$).

Sample-based accumulation of bee species diversity using rarefaction curves indicated that accumulation of bee biodiversity in thinned forest stands was substantially greater than non-thinned stands (Figure 2.5D). Bee species compositions differed significantly between site type (Figure S1.4; $F_{1,29} = 2.793$, $P = 0.002$). The difference in composition was driven by the ratios of *Bombus:Hylaeus* and *Lasioglossum:Hylaeus*, which increased 6.5 and 6.3 times, respectively, in the non-thinned stands due to lower proportions of *Hylaeus*.

Bee abundances were also analyzed relative to capture methods. Capture method did not have a significant effect on abundance (Figure S1.5; $F_{2,87} = 0.448$, $P = 0.641$). Bee species compositions differed significantly between capture methods ($F_{2,83} = 5.595$, $P < 0.001$). The most common genus captured via both blue vane traps and netting was *Bombus*; however, using the blue vane traps *Bombus* represented 44% of the total capture whereas using netting *Bombus* only represented 20%. The majority (53%) of bees captured via pan traps were members of the genus *Lasioglossum*. Of the 124 species identified, only 27 were captured using all three methods (Figure S1.6). Netting yielded the highest number of unique species (34).

Specialization of plant-pollinator networks, the deviation of a species' total unique interactions from that expected (Dormann et al., 2009), were similar between site types (thinned: $H_2' = 0.388$; non-thinned: $H_2' = 0.312$; $P = 0.206$; Figure S1.7A). However, both thinned ($P < 0.001$) and non-thinned sites ($P < 0.001$) were more specialized than expected by null models (Figure S1.8A). The thinned sites had 622% greater weighted nestedness (WNODF) suggesting

that when accounting for interaction intensity more specialized species interact with subsets of the species generalists (Bascompte & Jordano, 2007) (thinned: $WNODF = 6.747$; non-thinned: $WNODF = 0.935$; $P = 0.024$; Figure S1.7B). Weighted nestedness was not different than expected by null models in non-thinned sites ($P = 0.232$) but was significantly more nested in thinned sites ($P = 0.002$; Figure S1.8B). Modularity was 36% greater in the non-thinned sites than thinned sites (non-thinned: $Q = 0.726$; thinned: $Q = 0.533$; $P < 0.001$; Figure S1.7C; Figure S1.9). At the non-thinned sites, no bee or flower species played a significant role in the network (Figure S1.10A, B). At the thinned sites, 4 out of 40 floral species and 8 out of 84 bee species had high among module connectivity (*i.e.*, “connectors”), and 3 bee species (*Lasioglossum* (*sensu stricto*) spp., *Bombus centralis*, *Ashmeadiella californica*) had high within module degrees making them “module hubs” (Olesen et al., 2007; Figure S1.10C, D). There were ~8 times more total interactions (thinned: 391 interactions; non-thinned: 49 interactions) and five times the number of unique linkages in the thinned sites (thinned: 208 links; non-thinned: 41 links; Figure 2.6).

c) Modeling resource cascades of forest structure on plant-bee interactions

The resulting structural equation model was a strong fit, suggesting causal relationships between forest structure, foraging resources, bee species richness/abundance, and plant-bee interactions (Fisher's $C = 14.20$; $P = 0.894$; $df = 22$; Figure 2.7; Table S1.3). Bee abundance was the only factor that had a significant direct effect on interaction abundance (total number of interactions; $\beta = 0.994$, $P < 0.001$), while bee richness and bee abundance had significant direct effects on interaction richness ($\beta = 0.735$, $P < 0.001$; $\beta = 0.221$, $P = 0.045$). Maximum temperature and floral abundance had significant direct effects on bee abundance ($\beta = 0.440$, $P = 0.001$; $\beta = 0.663$, $P = 0.004$) and bee richness ($\beta = 0.363$, $P < 0.001$; $\beta = 0.606$, $P < 0.001$). Canopy

openness directly affected floral abundance ($\beta = 0.412$, $P = 0.028$) and species richness ($\beta = 0.362$, $P = 0.044$) and indirectly affected bee richness and abundance through increasing the maximum temperature ($\beta = 0.481$, $P = 0.007$). Bare ground, representing nesting habitat, did not significantly affect bee assemblages but did increase floral richness ($\beta = 0.403$, $P = 0.026$).

DISCUSSION

Here we show that restoration-motivated forest thinning practices drive a series of direct and indirect effects that cascade to increase plant-pollinator interactions in a forest type widespread across landscapes of the western United States. Cutting of overstory trees resulted in substantial reduction of the canopy, which increased floral density and richness, as well as site-level thermal conditions. These shifts drove differences in the α - and β -diversity of bee assemblages with consequences for interactions between bees and flowers, and improved network resiliency. Accordingly, thinning has repercussions for conservation of native bee assemblages via multiple pathways, with potential impacts on pollination services.

While there are concerns for bee species decline with global warming (Zhao et al., 2021), the activity of flying insects is temperature-dependent (Heinrich, 1974) and bees often prefer warmer nectar (Norgate et al., 2010). Structural equation modeling revealed that increases in maximum temperature directly affected α - and β -diversity of bee assemblages, and indirectly their interactions. With greater maximum temperatures in thinned sites, and under the changing climate, it is important that we understand the potential beneficial threshold to increasing temperatures and increasing resiliency to environmental changes (Song et al., 2017).

Higher nestedness could be advantageous for persistence and stability of plant-bee interactions in a changing environment, particularly with increases in temperature (Bascompte & Jordano, 2007; Song et al., 2017). We found that weighted nestedness was much greater in

thinned sites, suggesting greater structural stability of networks in restored forests. While mutualist interactions are often more nested than by chance (Bascompte & Jordano, 2007), non-thinned sites were not different from null models which further illustrates the importance of forest restoration for pollinator network resiliency.

We also observed higher modularity in non-thinned sites, which is assumed to decrease resiliency because there are less redundancies in the network, hence isolating clusters from one another (Soares et al., 2017). Modularity generally increases with the size of the network (Olesen et al., 2007), therefore our finding of lower modularity in thinned sites is particularly significant. Even in large networks, the number of species that play key roles are often limited (Olesen et al., 2007). We found only two network hubs (those with high values of connectivity and network participation) in the thinned sites, *Bombus bifarius* and *Lasioglossum* (sensu stricto) spp., which are both generalists. While these taxa were among the most abundant in our study, they still require extra attention in conservation efforts due to their important roles in these systems.

High specialization can decrease ecological resilience due to increased importance of individual species (Soares et al., 2017). Modularity is usually correlated with specialization, and the level of specialization is often greater in smaller networks or with less sampling effort (Dormann, 2021). We therefore expected the non-thinned sites to have greater specialization but found no evidence that non-thinned sites were more specialized than thinned sites suggesting selectivity, perhaps due to increased availability of floral resources, in thinned sites. Both site types were more specialized than null models which is expected in mutualistic networks where pollinators often visit flowers selectively. Specialized interactions are more easily lost, especially under environmental change—therefore, it is important that we identify highly specialized species to direct conservation efforts (Soares et al., 2017).

Approximately a quarter of unique interactions were from bees visiting just three floral species: *Solidago missouriensis* (8.8%), *Heterotheca villosa* (8.0%), and *Geranium caespitosum* (6.4%). These species were among the 10 most common (occurring across many sites) floral taxa across sites, but not the most abundant (high abundance within sites). This finding highlights the potential attractive qualities of these floral species, and the differences in bee species composition across sites. While these floral species increased the number of unique interactions, they were not considered network connectors. Of the 10% of floral species considered connectors, *Achillea millefolium*, *Penstemon virens* and *H. villosa* were among the most common, with *P. virens* being the most abundant. This suggests that the other connector species (*Erysimum capitatum*) may have traits that make it attractive to a wide range of pollinators. Considering floral species roles in network function is important to improve management strategies to better conserve pollinators. Seed mixes should include species with important ecological roles, or species that possess similar traits.

While many studies call for use of multiple capture methods (Portman et al., 2020), few studies examining bee biodiversity across landscapes employ more than one method. Without the inclusion of multiple capture methods, we would decrease the number of unique species identified. For example, only using blue vane traps would have resulted in a >50% reduction in observed species richness. Blue vane traps were biased towards larger bees (*Bombus*) with greater foraging distances, especially in sites with less floral resources. Flight range increases with body size (Greenleaf et al., 2007), therefore the large bees that were over represented likely come from further distances without utilizing any resources in the site. Small to mid-sized bees (e.g., *Lasioglossum*) were more common in the pan traps. Studies using capture methods reliant on visual attraction (i.e., blue vane and pan traps) should interpret results with caution when

examining site-level bee assemblages. Because visual traps could be poor representations of smaller scale resource utilization, multiple capture methods should be deployed for accurate site-level community composition.

Our model suggests that the forest thinning via creation of canopy openings and bare ground is a potential strategy for conservation of declining bee communities across large landscapes. We expect to see diminishing benefits as the canopy regrows post-treatment. Therefore, regular introduction of disturbances is not only important for forest health but will also improve pollinator networks. We show that in thinned forests 2-8 years post-treatment, foraging habitat is improved which increases plant-bee interactions. High interactions support high pollinator services which ensure ecosystem function and resiliency (Kaiser-Bunbury et al., 2017). This research contributes to the few studies examining the importance of vegetation restoration efforts for improving plant-pollinator networks (Kaiser-Bunbury et al., 2017), and can be used as a framework for analyzing the effect mechanism of site-level factors on native bee populations and bee-flower interactions across different ecological restoration projects. Yet, more research is needed to understand the complexities of these resource cascades to better understand ecological restoration effects on pollinator networks and to improve recommendations for future restoration projects.

Table 2.1. ANOVA table summarizing differences in mean floral abundances and floral species richness between thinned and non-thinned stands ('Treatment'), in the context of seasonal monthly variation. Significant effects are highlighted in bold text.

Variable	Source	SS	df	F	P
Mean floral density/m ²	Treatment (thinned vs. control)	132.38	1	20.64	<0.001
	Month	220.52	2	17.19	<0.001
	Treatment × Month	25.06	2	1.95	0.1482
	Residuals	538.75	84	-	-
Number of floral species/10m ²	Treatment (thinned vs. control)	127.21	1	29.31	<0.001
	Month	136.42	2	15.72	<0.001
	Treatment × Month	7.49	2	0.86	0.4257
	Residuals	364.53	84	-	-

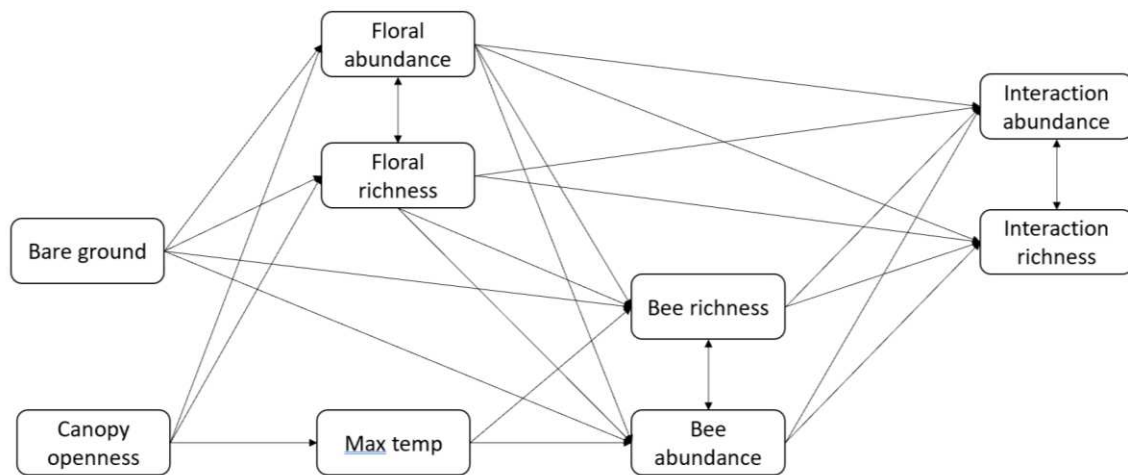


Figure 2.1. Directed acyclic graph describing hypothesized causal relationships between forest structure, foraging habitat, nesting habitat, physical properties, bee assemblages, and bee-flower interactions. Arrows indicate the direction of the relationship. Bidirectional arrows signify correlated errors. See Table S1.1 for pathway justifications.

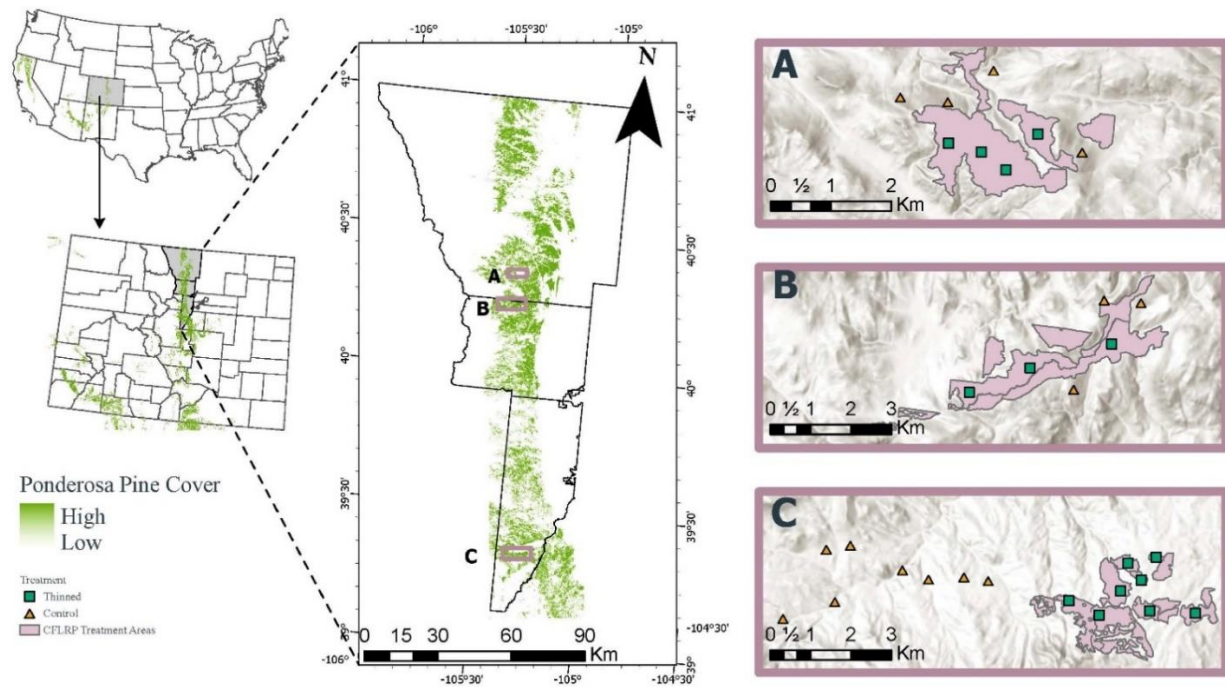


Figure 2.2. Map highlighting study region in the Colorado Front Range (Larimer, Jefferson, and Boulder counties). Pink rectangles show the forest areas used in the study: (A) Roosevelt National Forest- Thompson River; (B) Roosevelt National Forest- Estes Valley; (C) Pike National Forest. Green shows areas of high *Pinus ponderosa* cover. Squares represent sites in thinned forested areas and orange triangles represent untreated forested sites.

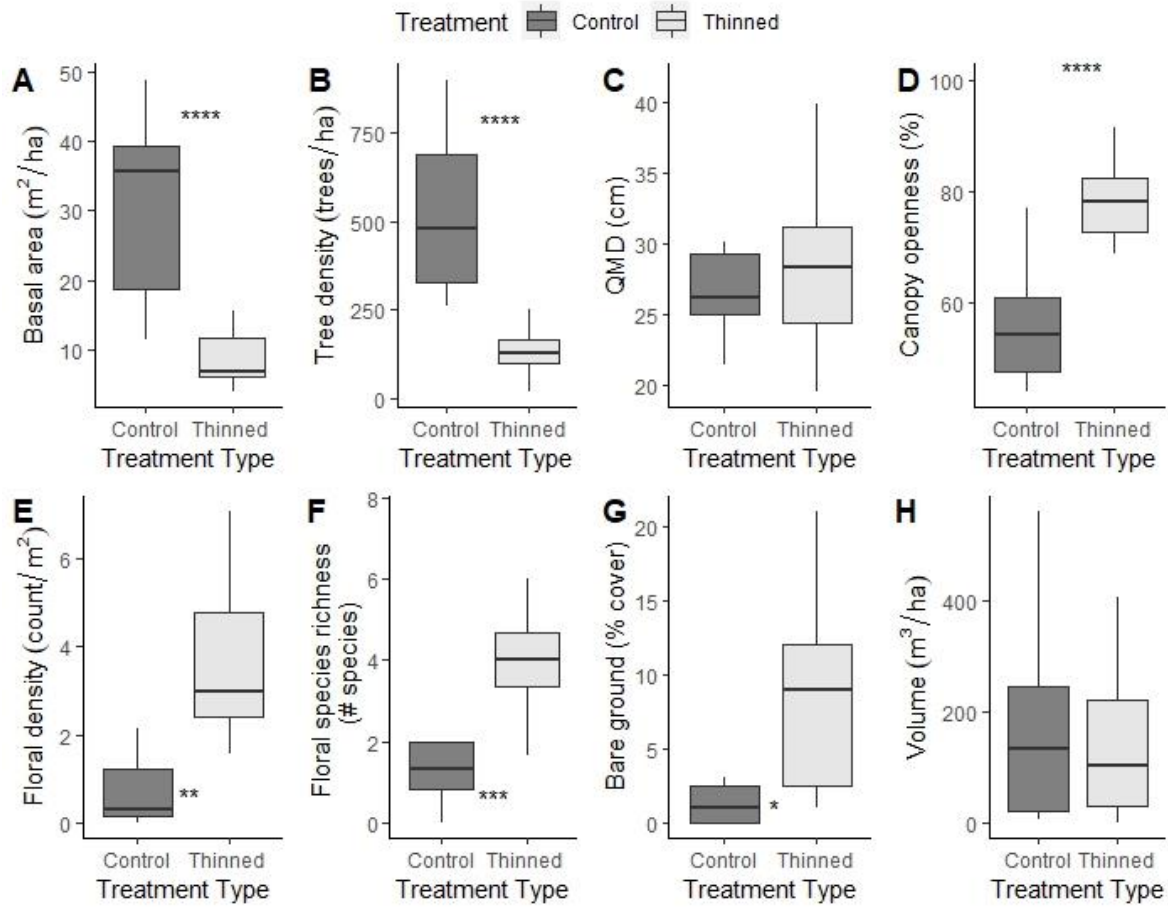


Figure 2.3. A comparison of forest structure variables between thinned and non-thinned stands. A) forest basal area ($\text{m}^2 \text{ ha}^{-1}$), B) tree density, C) quadratic mean diameter (cm), D) canopy openness (%), E) mean floral density pooled across months (count/ m^2), F) floral species richness pooled across month (total number of species), G) bare ground cover (%), and H) CWD Volume (m^3/ha). Statistical significance from t-tests p-values denoted by asterisks (Significance codes: '****' $P < 0.001$ '***' $P < 0.01$ '*' $P < 0.05$).

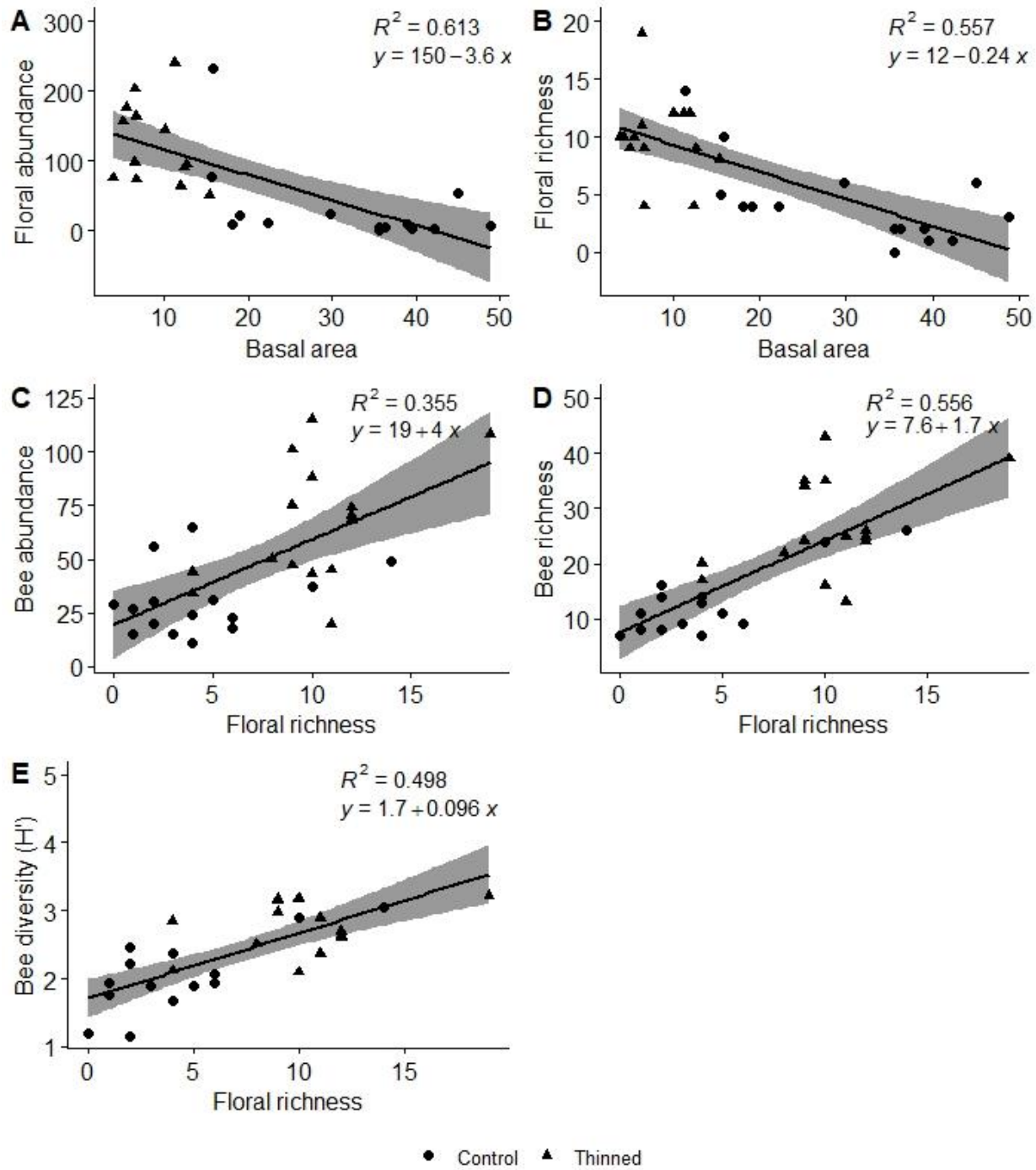


Figure 2.4. Relationship between foraging habitat and forest structure (A, B) and foraging habitat and bee communities (C, D, E) in ponderosa pine stands. Linear regressions between (A) Basal area (m²ha⁻¹) and floral abundance (count/m²), (B) basal area and species richness, (C) floral richness and bee abundance, (D) floral richness and bee species richness, and (E) floral richness and bee species diversity (Shannon-Wiener H'). Circles represent non-thinned stands and triangles represent thinned forest stands. Shaded areas denote 95% confidence intervals of regression models. All relationships shown are significant ($P < 0.05$).

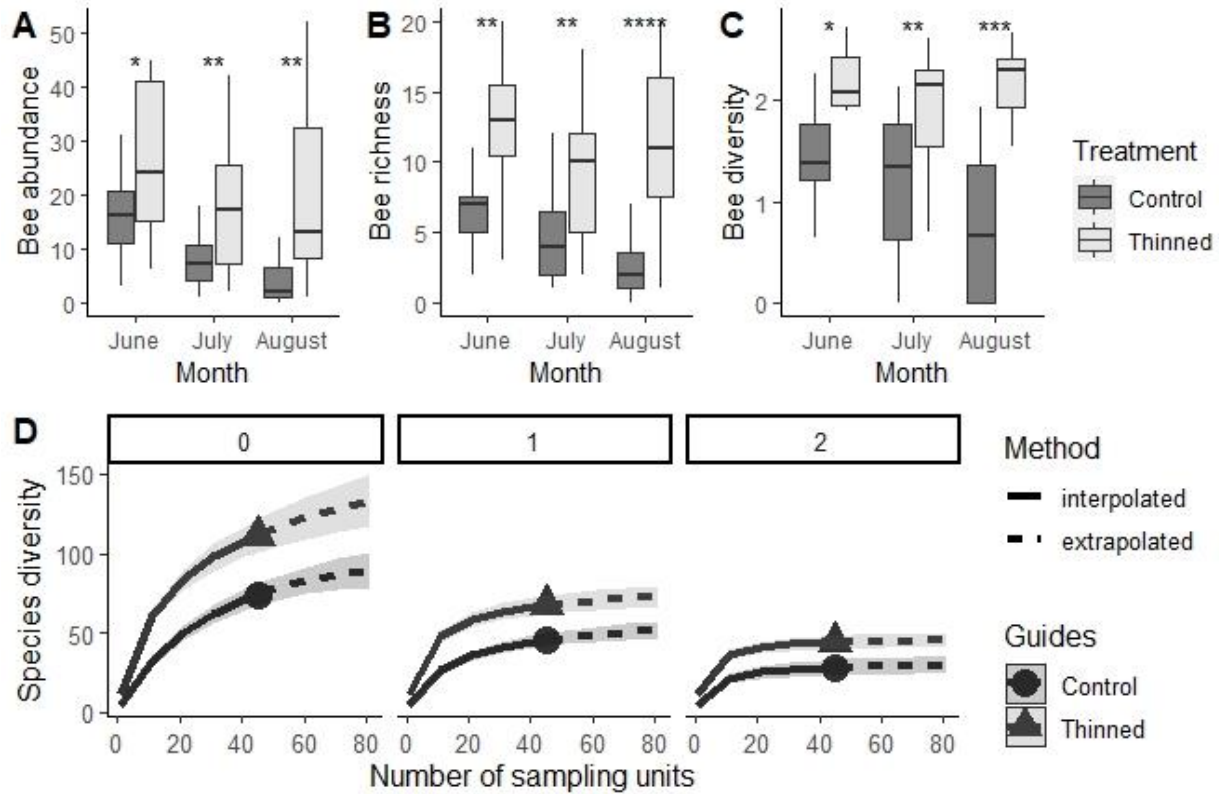


Figure 2.5. The distribution of native bee (A) abundance, (B) species richness, and (C) Shannon-Weiner diversity averaged across all capture methods relative to collection month (seasonality) between thinned and non-thinned forest stands. Statistical significance by p-values denoted with asterisks (Significance codes: $P < 0.0001$ '****'; $P < 0.001$ '***'; $P < 0.01$ '**'; $P < 0.05$ '*'). (D) Sample-based accumulation of bee species diversity from thinned and non-thinned stands showing the three measures of Hill numbers of order q : species richness ($q = 0$), Shannon diversity ($q = 1$, the exponential of Shannon entropy) and Simpson diversity ($q = 2$, the inverse of Simpson concentration). Shaded areas represent 95% confidence intervals of each curve.

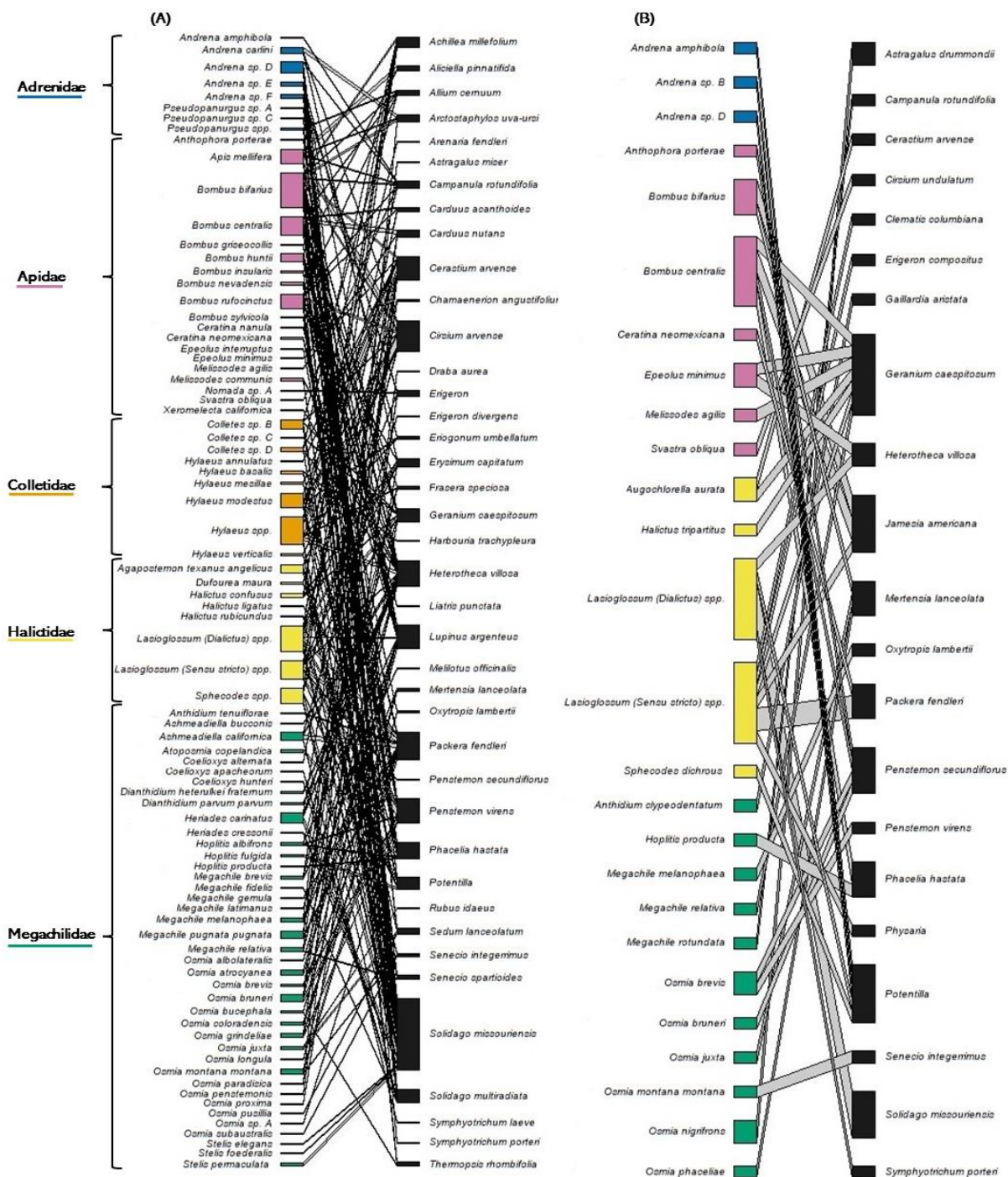
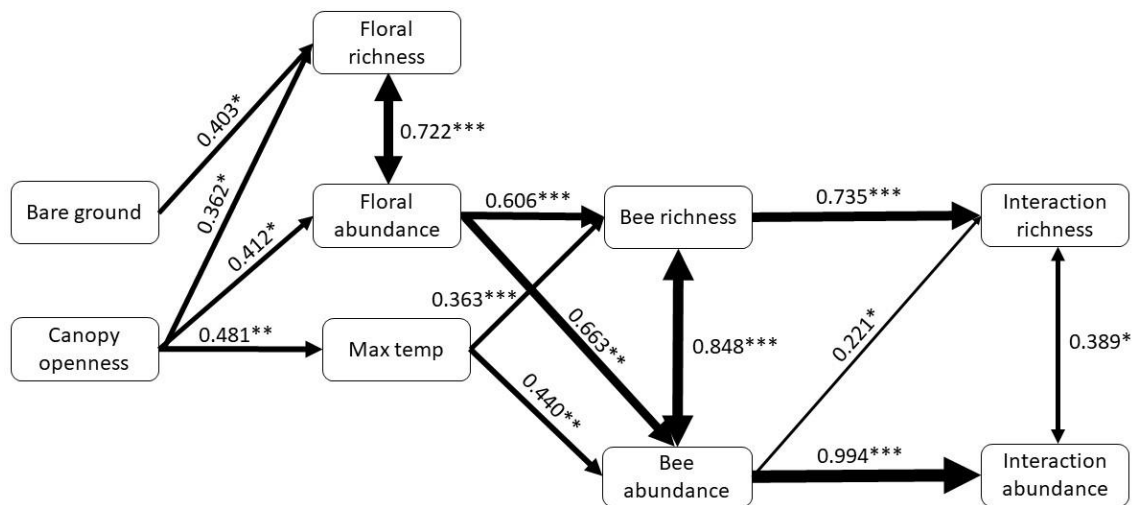


Figure 2.6. Networks of flower and bee interactions in Ponderosa pine forested sites in the Colorado Front Range: (A) thinned forest sites and (B) non-thinned forest sites. The size of the line represents the number of interactions between bees and flowers and the size of the box shows the number of interactions. Box colors represent different bee families: blue = Andrenidae, pink = Apidae, orange = Colletidae, yellow = Halictidae, green = Megachilidae.



signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05

Figure 2.7. Structural equation model evaluating the effects of forest structure, nesting habitat, physical conditions, and foraging habitat on bee assemblages and bee-flower interactions. Line size is representative of the effect size. Significance (P -value) is represented by * following the coefficient (Significance codes: $P < 0.0001$ '***' $P < 0.001$ '**' $P < 0.01$ '*' $P < 0.05$).

CHAPTER 2: PHENOLOGICAL MISMATCH OF NATIVE BEES AND FLORAL NUTRITION AND DRIVERS OF BEE-FLOWER INTERACTIONS IN CANOPY GAP HABITATS

SUMMARY

Many forest restoration projects create canopy gaps of varying sizes to mimic historical forest structures and improve ecosystem function. Canopy gaps can promote high floral diversity and may be a valuable resource for native bees with consequences for bee-flower interactions and community structure in forest habitats. Here, we recorded bee-flower interactions in canopy gaps of varying sizes to test how variation in floral availability, pollen nutritional value, and bee and floral traits impact bee-flower networks. We observed ~6,500 bee-flower interactions throughout the growing season to model bee and pollen protein phenology and relate floral visitation to visual traits (flower display area, color, ultraviolet reflectance, height). Three important findings emerged: (1) although gap size was not strongly associated with phenological matching of foraging bee abundances and protein density, bee body size predicted activity periods and foraging activity of small-to-medium sized bees was mismatched with periods of peak protein density; (2) across all sites, protein density ($\mu\text{g}/\text{m}^2$) and floral species richness were the only predictors of interaction abundance and richness, respectively; and (3) floral visual traits predicted visitation, with more interactions recorded for tall species with large floral display areas. We present a ‘pollinator importance index’ that combines interaction richness and abundance with pollen protein content to estimate relative value of floral species for native bees; this approach revealed that an invasive species (*Carduus nutans*, musk thistle) has very high value for bees in forest canopy gaps. Our results suggest that canopy gap creation is likely to

have similar impacts on bee-flower interaction networks regardless of gap size, but phenological mismatch between bees and pollen protein is much more likely for small-bodied bees with short foraging ranges. Interpretation of a pollinator importance index indicates that removal of a common noxious weed species may have detrimental effects on floral resources used by bees, but networks could be supplemented by favoring or planting floral species with specific traits that were associated with high visitation rates.

INTRODUCTION

Native bees are essential animal pollinators for ensuring genetic and functional diversity of angiosperms (Fontaine et al., 2006). However, native bee species are in global decline due to land-use changes, particularly those that alter vegetation in forested landscapes (Potts et al., 2010; Winfree et al., 2009). Ecosystem management focusing on habitat restoration can increase native bee abundance and richness, fostering increased bee-flower interactions with consequences for improved ecosystem services such as pollination (Tonietto & Larkin, 2018). Despite the essential ecosystem functions bees provide and the benefits they receive from ecosystem restoration, many projects do not consider native bees in the design or evaluation of project success (Winfree, 2010). Projects that manage for pollination services often focus on increasing floral availability (Isaacs et al., 2009), but do not consider how that may alter pollination networks if increases in floral species are disproportionally utilized by certain functional or genomic grouping of bees.

In forested ecosystems, restoration methods such as thinning evenly throughout a stand, and clumped thinning (gap creation) can benefit native bee communities by creating open forest conditions (Hanula et al., 2016). These changes in forest structure can alter bee-flower interactions by promoting recruitment of floral resources, often resulting in increased

specialization (Hall et al., 2022). Interpreting bee life history and functional traits can inform our understanding of how canopy gaps may affect bee-flower interactions (Williams et al., 2010). For example, body size predicts bee foraging distances, so bees of different sizes will likely respond differently to canopy gaps depending on gap size and distribution across the landscape (Walther-Hellwig & Frankl, 2000; Zurbuchen et al., 2010). Some of these changes may stem from shifts in the floral community and available pollen protein, which differs between species (Pamminger et al., 2019; Simanonok & Burkle, 2020). Changes in floral availability and nutritional quality are critical to consider due to implications for bee health (Schenk et al., 2018), and some floral species may be more valuable to bees than others. In addition to nutrition, floral visual traits play a role in driving bee-flower interactions and may signal resource value. Common garden experiments suggest that floral area is an important morphological trait related to visitation patterns, and that bee functional groups may have unique responses to different floral morphologies (Rowe et al., 2020). By evaluating floral traits, flowers with a high use value to bees can easily be selected for based on visual characteristics and nutritional value.

The timing in which plant species flower and bees foraging occurs can have important implications for successful pollination, bee health, and overall biodiversity (Nürnberger et al., 2019; Petanidou et al., 2014; Rafferty & Ives, 2011); however, creation of canopy gaps may drive phenological shifts in flowering plant communities with consequences for pollinators. Specifically, accelerated snowmelt and increased light may result in earlier bloom times within canopy gaps (Galloway & Burgess, 2012). Phenological mismatch, the difference between floral bloom periods or nutritional value and native bee emergence/foraging (Figure 3.1), can decouple ecological networks and result in species loss (Kudo & Ida, 2013; Ogilvie & Forrest, 2017). However, phenological shifts in both floral bloom periods and bees are highly species-specific

and poorly understood (Solga et al., 2014). Since phenological shifts can be unique to individual species, there are often redistributions of community composition and floral abundance throughout the season (CaraDonna et al., 2014). Accordingly, in addition to examining the relative value of floral resources in post-restoration landscapes, it is also critical to determine whether changes in forest canopy conditions affect timing of bee foraging activity.

In the western United States, many forest restoration projects decrease basal area and create larger gaps in the canopy (R. T. Brown et al., 2004), conditions that resemble historical, pre-settlement forest structures (P. M. Brown et al., 2015; Stoddard et al., 2021). In the Front Range region of Colorado, USA, extensive logging, and a general policy of fire suppression during the 20th century coincided with the rapid growth of the wildland-interface, with consequences for ecosystem function. For example, extensive logging followed by suppression policies gradually resulted in undesirable forest structures including stands with high stem densities and an increased risk of severe wildfire (Rodman et al., 2019). To address these changes in forest structure and mitigate risk of wildfire, various land management collaboratives have been established that share a common goal of ecosystem restoration.

One such group is the federally-directed Collaborative Forest Landscape Restoration Program (CFLRP) (Addington et al., 2014), which aims to reduce wildfire risk and restore ecological health by reintroducing natural disturbances to reduce basal area and create canopy openings (gaps). The Front Range CFLRP project has largely succeeded in reducing basal area to close to historical levels, but there remain fewer canopy gaps than historically indicated (Cannon et al., 2018). Gap creation can increase floral diversity and play many other important roles in ecosystem function (Muscolo et al., 2014). However, there is often hesitancy by managers to

create gaps and much deliberation on the appropriate size and spatial distribution of canopy gaps (Kern et al., 2017).

To inform ecological restoration efforts, we analyze whether canopy gap size impacts bee-flower interactions, emphasizing bee and floral traits to model interaction networks on CFLRP lands in the Colorado Front Range. We develop models to compare the phenology of floral availability, nutrition, and native bee populations throughout the growing season, and to analyze the drivers of bee-flower interactions. Specifically, we test the following hypotheses: (1) phenological trends in the accumulation of floral resources and nutrition align with bee abundances at a site-level, but may differ due to bee functional traits, and (2) bee-flower interactions can be predicted by floral nutritional value and visual traits. We also develop and interpret a pollinator importance index, which can help managers to determine which species are of high value to bees in canopy gaps. An enhanced understanding of bee-flower interactions in canopy gap habitats could inform forest management decisions by promoting conservation of ecosystem services and maintenance of ecological networks.

METHODS

Site selection

This project took place in the Front Range of Colorado (U.S.A.) in the Roosevelt National Forest at 2,100 to 2,700 meters elevation (Figure 3.2). Sites were selected from aerial imaging to identify canopy gaps across a size gradient. Gaps were defined by having no mature trees and >5 saplings. The border of the gap was delineated by the canopy drip line. Canopy gaps ranged from 0.16 to 2.96 hectares; there was a total of $n = 8$ canopy gaps, located at least a kilometer apart to ensure sampling independence. While larger bees (*i.e.*, some *Bombus* species) can forage up to 1,750m from their nesting locations, most species forage within 1,000m, often >300m for

smaller, solitary species (Walther-Hellwig & Frankl, 2000; Zurbuchen et al., 2010). All gaps were located within or adjacent to the boundaries of area treated under the Front Range Collaborative Forest Landscape Restoration Program (FR-CFLRP). Across the FR-CFLRP treatment areas, mean basal area was reduced 35%, and mean tree density was reduced 53% following restoration treatments (Cannon et al., 2018).

Floral density, richness, and diversity

In each canopy gap, floral density and diversity were measured within three replicate 1 m wide × 25 m long belt transects. Transects were laid parallel to one another and arranged equidistantly across gaps, such that distance between transects was dependent on gap size and shape (ranging between 25m and 80m apart). Within each transect, the total number of flowers was counted, and species were recorded. Flowers were defined as complete inflorescence, such that a single plant with multiple flower heads was counted as multiple flowers for floral abundance. Transects were sampled the same day as bees were sampled, approximately once every 14 days beginning May 21 and ending September 12, 2021, for a total of $n = 9$ sampling periods and $n = 72$ sampling events.

Floral trait measurements

For every blooming floral species recorded, five inflorescences were photographed and measured to characterize floral structure and height of inflorescence from the ground. The ImageJ software (Schneider et al., 2012) was used to measure the floral display area for all images and determine the color of floral displays based on Red, Green, Blue (RGB) values. Flowers were assigned a color group (blue, yellow, white) based on dominant RGB values, such that “blue” flowers were blue dominant, “yellow” approximately equivalent red and green values, and “white” equivalent red, green, and blue values. Height was measured to the nearest 5 mm in the field. A blacklight

was used to observe ultra-violet reflectance which was recorded as a binary variable. The five replicates per species were treated as a subsample, such that for each species there was a single mean value for each measured trait.

Pollen protein quantification

For each floral species with more than ten flowers recorded within transects, several flowers were harvested from which pollen was extracted. Flowers were harvested from different plants located proximal to, but outside of sampled canopy gaps to prevent elimination of resources within study sites. 17.5% of the floral species observed within the sites were not collected due to limited availability outside the site boundary. The number of flowers harvested depended on the size of flower and amount of pollen, such that enough flowers were harvested to ensure a quantifiable pollen mass (ranging between 5 and 150 flowers/species). Flowers were harvested as buds close to opening or recently opened to maximize the amount of pollen collected.

Harvested flowers were returned to the lab for processing. Pollen extraction methods were adapted from Hicks et al. (2016), as follows. Flowers from each species were pooled to achieve a quantifiable amount of pollen. Anthers were removed from flowers and placed in a 1.5 ml Eppendorf tube containing 1.0 ml of 70% ethanol. Samples were vortexed for 30 seconds to separate the pollen from the anthers. Anthers were then removed from the tubes and examined under a microscope to confirm that all pollen had been removed. If all pollen was not removed, the sample Eppendorf was vortexed again. Tubes containing pollen and 70% ethanol were centrifuged for 10 minutes at 13,000 rpm. Ethanol was decanted and the resulting pollen pellets were air-dried at room temperature under fumigation hoods until all ethanol evaporated. Samples were then weighed using a high-sensitivity balance to the nearest 0.01 mg. The mass was then corrected to mean per inflorescence.

Bradford assays (Bradford, 1976; Roulston et al., 2000) were used to measure pollen protein content. The pollen pellets were diluted with equal volume distilled water. Pollen and water were vortexed until homogenous. A 10 μ l aliquot of the pollen-water solution was added to a sterile polystyrene flat-bottomed, 96-well plate (CELLTREAT, Pepperell, MA, Lot #229196). For each flower species, 10 μ l was added to three wells. There were a few flower species that had such small amounts of pollen that only 5 μ l could be added. Distilled water was then added to the wells to bring total volume to 160 μ l. The pollen and water were further mixed by repeatedly pipetting 20 μ l of the mixture, eight times per well. After mixing, 40 μ l of Bradford reagent (Sigma, St. Louis, MO, Lot # SLCG1879) was added to each well and mixed as previously. After 20 minutes, the absorbance of the wells was read at 595 nm wavelength using a BioTek Heatwave plate reader and Gen5 Software.

Protein quantity was then determined based on a bovine γ -globulin protein standard (Bio-Rad, Hercules, CA, Lot #5000005) (0.05 mg/mg) that was used at eight dilutions— volumes of 4, 8, 16, 30, 70, 130, 160 μ l with distilled water added until total volume reached 160 μ l— in the first column of every plate. The standard was mixed as previously detailed for the pollen samples, and 40 μ l of Bradford reagent was added to wells. Based on the standard, a second-order polynomial linear model was constructed using the known protein concentrations. The unknown protein quantities of the pollen samples were then calculated by solving the equation using the non-negative root from the quadratic formula.

Bee sampling

Bee diversity and abundance were measured via aerial netting. Bees were only captured if they were actively alighting on or visiting a flower (*i.e.*, landed on a mature inflorescence); species of flower was recorded for all observed interactions. Netting was done in 30-minute intervals

throughout each canopy gap, three times throughout the day. To account for differences in bee activity throughout the day, the sampling intervals occurred in the morning (08:00-11:00), midday (11:00-14:00), and afternoon (14:00-17:00), and results were pooled. During the 30-minute netting, each canopy gap was strategically walked to cover the entire site and avoid resampling flowers. Bees captured were identified in the field to the lowest taxonomic grouping that could be determined with confidence, usually to genus, and on occasion to species. Bees were then released upon identification to avoid biasing collections over the course of the growing season by reducing local population sizes. As bees were released upon capture, some individuals were possibly captured multiple times.

Data analysis

All statistical analyses were completed using R Studio Version 4.0.2, “Taking Off Again” (R Core Team, 2021). A Type I error rate of $\alpha = 0.05$ was used for assigning statistical significance in all analyses.

a) Phenological trends of floral availability, pollen protein, and bee-flower interactions

The phenology of floral resources and bee-flower interactions were first analyzed by examining change-over-time. A two-way mixed analysis of variance (ANOVA) model was used to fit mean floral density, pollen protein density, floral richness, and floral diversity to a model that included ordinal day, gap size (ha), and size \times day interaction as fixed effects, and site as a random effect. Models were fitted by residual maximum likelihood using the ‘lmer’ function as part of the lme4 package (Bates et al., 2014). Significance was determined from F -values using Satterthwaite’s method (Luke, 2017). Pollen protein density was log transformed for all models to normalize the distribution. An identical model was used to fit bee-flower interactions, bee richness, and bee diversity.

The relationship between the proportion of large, medium, and small bees across the growing season and patch size gradient was analyzed using chi-square tests calculated using the ‘chisq.test’ function from the stats package (R Core Team, 2021). Body size was assigned to bee genera qualitatively based on average size relative to *Apis mellifera* where large was larger than, mid-sized was approximately equivalent to, and small was smaller than *A. mellifera* (Scott et al., 2011).

Phenological similarity between nutritional resource availability and bee abundances during sampling periods was compared across all sites by analyzing the rate of accumulation of protein density and bee-flower interactions over time. Two-parameter logistic models were fit to protein density and bee captures as a function of ordinal day, using the R add-on package ‘nplr’ (Commo & Bot, 2016). Logistic models were solved to calculate 33, 50, and 90% accumulation protein density and bee captures, consistent with initiation, peak, and cessation of blooming and bee activity periods (e.g., Dell and Davis 2019). 33% was selected based on the maximum within site accumulation at the first sampling period to avoid extrapolation. We estimated phenological mismatch by comparing the dates of each threshold (i.e., modeled date of 33, 50, and 90% accumulation) for protein density and bee abundance (Figure 3.1). We used a one-sample Student’s t-test to test the null hypothesis that the difference between threshold dates of protein density and bee abundance was zero.

Phenological mismatch was also analyzed as a function of bee body size. Large-bodied bees have larger foraging ranges and lipid reserves than small-bodied bees and may be able to travel long distances to access floral resources (Greenleaf et al., 2007). In contrast, foraging of small-bodied bees is often confined to the immediate area. The same methods as above were used to construct logistic regression models for each body size group (i.e., large-, medium-, and

small-bodied bees). Differences between the groups were analyzed using one-way ANOVA, treating bee body size as a fixed effect on the response of mismatch (i.e., the mean difference between 33, 50, and 90% accumulation of protein density and bee-flower interactions in days). Tukey's HSD test was used to make all pairwise comparisons among sample means.

b) Effects of floral nutrition and visual traits on bee-flower interactions

A pollinator importance index for each flower species was created based on total number of interactions, interaction richness (number of unique interactions), and protein concentration. All values were normalized to occur between 0 and 1. Due to the inclusion of protein concentration, only species for which protein concentration was measured were included in these indices (n= 57).

Mixed effect models were used to analyze which habitat factors were associated with bee-flower interaction abundance and richness. Floral density, floral species richness, pollen protein density, and canopy gap size were treated as fixed effects and collection period was treated as a random effect. Models were fitted by residual maximum likelihood using the 'lmer' function as part of the lme4 package (Bates et al., 2014). Significance was determined from *P*-values calculated from t-tests using Satterthwaite's method (Luke, 2017). Collection period × site was treated as an experimental unit such that n = 72.

Mixed effect models were used to analyze whether variation in floral traits is associated with variation in bee-flower interactions. Flower color based on RGB values (blue, yellow, white; see above), native vs. introduced status, flower height, flower display size, ultraviolet reflectance, pollen protein concentration, floral density, and relative abundance (abundance of flower species / total abundance within site-day) were treated as fixed effects and collection period as a random effect. Models were fit and analyzed using the same methods as above. Floral

density and relative abundance were included to determine if selection was due to nutritional value and visual traits or availability. Since flower species were of interest in this analysis, collection period \times site \times flower species were treated as an experimental unit ($n=992$). However, since pollen protein was not measured for some species, 290 observations had to be excluded from this analysis resulting in $n=702$. Initial models for habitat factors and floral traits also included site as a random effect, but the random intercept did not account for any variance and therefore was omitted from the final models.

RESULTS

a) Phenology of floral availability, pollen protein, and bee-flower interactions

Floral density was greatest towards the end of the growing season (~day 210 (July 29)), although at some sites floral density peaked earlier in the season (between ~day 150 (May 30) and ~day 175 (June 24)). Floral richness had a similar trend to floral density, where the greatest number of species present was between days 200 (July 19) and 220 (August 8), with some differences between sites. However, neither floral density ($F_{1,76} = 2.0581$, $P = 0.156$; Figure S2.1a) nor floral richness ($F_{1,62} = 0.001$, $P = 0.972$; Figure S2.1b) varied by day of year. Mean floral diversity (H') was highest earlier in the season (~day 175 (June 24)) and remained consistent throughout the growing season until ~day 225 (August 13) ($F_{1,68} = 0.610$, $P = 0.438$; Figure S2.1c). This trend was similar across all sites. Protein density remained relatively low across all sites until day 200 (July 19) when it rose to peak around day 230 (August 18). This trend was largely driven by two sites that had a large spike in protein density later in the season, although protein density did not vary significantly by day of year ($F_{1,68} = 1.774$, $P = 0.188$; Figure S2.1d). When accounting for site variation, floral diversity ($F_{1,66,292} = 7.530$, $P = 0.007$) and protein density ($F_{1,66,812} = 17.464$, $P < 0.001$) varied by canopy gap size, whereas floral density ($F_{1,76} = 0.239$, $P = 0.626$)

and richness ($F_{1,66.856} = 2.229$, $P = 0.140$) did not (Figure S2.2). Floral density ($F_{1,76} = 0.119$, $P = 0.731$) and floral richness ($F_{1,62} = 2.276$, $P = 0.137$) had no interaction effects between ordinal day and gap size; however, there was an interaction effect when examining floral diversity ($F_{1,62} = 7.674$, $P = 0.007$) and protein density ($F_{1,62} = 20.561$, $P < 0.001$).

Overall, 6,474 bee-flower interactions were observed over the course of the growing season. Bee-flower interactions peaked around the same time as floral availability, but also did not vary by day of year ($F_{1,68} = 2.192$, $P = 0.143$; Figure S2.3a). Bee richness was highest between day 200 (July 19) and 210 (July 29) (Figure S2.3b). Like floral diversity, bee diversity was highest earlier in the season but began to decline by day 210 (July 29) (Figure S2.3c). Neither bee richness nor diversity differed by day of year (richness: $F_{1,65} = 0.007$, $P = 0.0.934$; diversity: $F_{1,65} = 2.379$, $P = 0.128$). Bee-flower interactions ($F_{1,68} = 2.068$, $P = 0.155$), bee species richness ($F_{1,65} = 2.524$, $P = 0.117$), and diversity ($F_{1,65} = 0.941$, $P = 0.336$) did not vary by gap size (Figure S2.4). There was no interaction effect across any of the bee population variables (abundance: $F_{1,68} = 2.014$, $P = 0.160$; richness: $F_{1,65} = 1.760$, $P = 0.189$; diversity: $F_{1,65} = 0.638$, $P = 0.427$).

However, bee body sizes did vary across sampling periods and gap size. The proportion of the three body size categories changed over the summer, primarily driven by the increasing proportion of large-bodied bee species ($\chi^2 = 2116.5$, $P < 0.001$; Figure 3.3a). Body size ratio also varied by gap size, with 212% greater proportions of mid-sized bees in the smallest canopy gap compared to the largest ($\chi^2 = 253.9$, $P < 0.001$; Figure 3.3b).

The rate of accumulation of bee-flower interactions pooled across body sizes was similar across all sites, but the accumulation of pollen protein density differed resulting in some site-to-site variation in terms of phenological mismatch (Figure S2.5). Across sites, there was no

evidence of mismatch at the 50% or 90% accumulation thresholds (50%: $t = 1.54$; $P = 0.17$; 90%: $t = -0.45$; $P = 0.67$). However, at the initial accumulation (33%), protein density and bee abundance accumulation significantly differed ($t = 2.868$; $P = 0.024$). Canopy gap size showed no significant correlation to phenological mismatch ($R^2 = 0.227$; $P = 0.243$).

There was evidence of phenological mismatch due to variation in bee body size, but these differences were early- and mid-season and eroded by the end of the growing season (Figure 3.4). At both 33% and 50% accumulation of protein density and bee abundances, mismatch significantly varied by body size (33%: $F_{2,21} = 13.400$, $P < 0.001$; 50%: $F_{2,21} = 7.562$, $P = 0.003$), particularly with differences between the large bees and medium/small bees (Figure 3.5a, b). However, at 90% accumulation, mismatch did not vary significantly between body sizes ($F_{2,21} = 0.608$, $P = 0.554$; Figure 3.5c).

b) Effects of habitat factors and floral traits on bee-flower interactions

Floral species varied considerably in nutritional value (protein concentration), and the most nutritious species were *Oenothera coronopifolia* (55.34 $\mu\text{g/ml}$), *Lupinus argenteus* (26.91 $\mu\text{g/ml}$), *Artemisia frigida* (19.83 $\mu\text{g/ml}$), *Penstemon virens* (17.20 $\mu\text{g/ml}$), and *Linaria vulgaris* (16.85 $\mu\text{g/ml}$) (Table 3.1). However, nutritional value was not necessarily associated with interaction abundance, and most interacted-with species were *Carduus nutans*, *Heterotheca villosa*, *Geranium caespitosum*, *Monarda fistulosa*, and *Ericameria nauseosa*. Of those species, *C. nutans*, *H. villosa*, and *G. caespitosum* were also notable for supporting many unique interactions (*i.e.*, they had high interaction richness). The five species with the greatest pollinator importance index values were *C. nutans* (0.162), *H. villosa* (0.109), *L. argenteus* (0.104), *G. caespitosum* (0.056), and *Calochortus gunnisonii* (0.034; Table 3.1; Figure 3.6).

Across canopy gaps, the total number of bee-flower interactions varied due to changes in protein density ($t = 3.058$, $P = 0.003$; Table 3.2; Figure 3.7a). However, floral density, species richness, and gap size did not affect total bee-flower interactions. The number of unique interactions between bees and flowers varied due to changes in floral richness ($t = 2.315$, $P = 0.024$; Table 3.2; Figure 3.7b), but not by any other variables.

Floral traits were also associated with bee-flower interactions (Table 3.3). Total interactions and interaction richness varied based on flower color, with blue/pink/purple (blue) flowers having on average 43% and 68% more total interactions than yellow and white flowers, respectively (Figure S2.6A). Blue flowers also had 28% and 45% greater interaction richness than yellow and white flowers (Figure S2.6B). Introduced flowers on average had 24% more total interactions ($t_{1,692.5} = -0.109$, $P = 0.913$), but 12% fewer unique interactions ($t_{1,689.3} = 2.313$, $P = 0.021$). Of the introduced flowers, *C. nutans* made up 70% of the total interactions and 46% of interaction richness. Taller flowers had more total interactions ($t_{1,667.7} = 5.147$, $P < 0.001$) and greater interaction richness ($t_{1,688.7} = 2.167$, $P = 0.031$). Flowers with greater floral display area had more total interactions ($t_{1,667.8} = 4.428$, $P < 0.001$) and greater interaction richness ($t_{1,692.8} = 5.531$, $P < 0.001$). Flowers with ultraviolet reflection had 42% more total interactions, but this effect was not significant ($t_{1,690} = -0.324$, $P = 0.746$); ultraviolet reflectance was associated with 35% greater interaction richness ($t_{1,693} = 1.782$, $P = 0.075$). There were more total interactions and unique interactions as floral density (total: $t_{1,360} = 5.761$, $P < 0.001$; unique: $t_{1,476.7} = 4.987$, $P < 0.001$) and relative abundance (total: $t_{1,351} = 4.309$, $P < 0.001$; unique: $t_{1,461.7} = 3.293$, $P = 0.001$) increased within a canopy gap. Nutritional value (protein concentration) had no significant effect on total interaction and unique interactions.

DISCUSSION

We found no evidence for phenological mismatch between bees-flower interactions and pollen protein density due to variation in canopy gap size. In addition, there were similar numbers of interactions and similar interaction richness for bees and flowers across gap sizes, indicating that even small canopy gaps are likely to benefit bee-flower networks. However, when bees were separated into functional groups based on body size, there was clear evidence of mismatch between protein availability for small- and medium-sized bees. This pattern was pronounced at the beginning of the season, which has important implications for bee survival and bee and floral biodiversity (Petanidou et al. 2014) and indicates that bees are likely to respond differently to climate- or management-driven changes in phenology of floral resources depending on their sizes and foraging range. In addition, we show that the highest-value floral resource in our system is a noxious weed, which has consequences for pollination networks under a policy of weed eradication. However, supplemental seeding with native floral taxa that have tall height and large floral display areas help may offset the impacts of noxious weed removal for native bees.

While large-bodied bees are able to travel longer distances to access floral resources (Greenleaf et al., 2007), foraging by small-bodied bees may be restricted to the immediate area. Therefore, the mismatch between their emergence and availability of nutrition on a site level is concerning for conservation of biodiversity. Bees were categorized into size classes (large, medium, and small) based on genera; some genera have considerable variation in size so our results should be considered as relating to broad functional groupings rather than specific taxa. This study only considered bee body size, but other bee functional traits such as overwintering strategy and nest location may also be important for interpreting phenological matching with

floral resources (Stemkovski et al., 2020). For example, in forested systems, gap creation may disproportionately benefit ground-nesting bees as thinning increases bare ground cover but may decrease other nesting materials (Fortuin & Gandhi, 2021). Future studies and forest restoration projects should therefore consider consequences on functional pollinator diversity by critically examining floral availability, phenology, and nesting habitat.

Continued warming and frequent drought are both projected for the southwestern ecoregion of the United States in coming decades (Cayan et al., 2010), which may shift timing of floral blooms and bee emergence, and further exacerbate phenological mismatch between flowers and native bee pollinators (Stemkovski et al., 2020). Our results indicate that certain bee taxa may experience phenological mismatch to a greater degree than others; extra emphasis should be placed on those functional groups to maintain biodiversity and ecosystem function. Climate change may also reduce pollen protein concentrations in floral species (Ziska et al., 2016), and therefore it will be important to identify high protein floral species for use in ecosystem restoration projects. Currently, many restoration treatments involving seed planting mixes include floral species that are not used by native bees and therefore do not foster bee-flower interactions (Cariveau et al., 2020). In our study system, native floral species had the highest protein concentrations and included *Oenothera*, *Lupinus*, *Artemisia*, and *Penstemon* (Table 3.1). Accordingly, we recommend these as potential inclusions for regional seed mixes as a nutritional supplement for native bees. In addition, practitioners should consider floral phenological diversity in floral availability so that phenological mismatch across all functional groups is limited (Havens & Vitt, 2016).

We present a pollinator importance index that accounts for combined effects of nutritional quality of floral species, bee visitation rates, and the number of unique interactions (richness)

supported by floral species. Our interpretation of this index illustrates the importance of both native and introduced species in maintaining pollinator networks. Specifically, *Carduus nutans*, a particularly invasive and abundant thistle in the region, played a critical role in providing nutritional value and supporting bee diversity. This finding suggests that there may be consequences of invasive species removal in restoration projects. Land managers must consider the immediate effects of removal, such as pesticide use which can be extremely detrimental to native bees (Hatfield et al., 2021; Prendergast et al., 2022), and the longer-term effects from the loss of species providing essential sources of nutrition, particularly if invasive species provide early-season resources to small- and medium-sized bees. To mitigate potential consequences, restoration projects can replace invasives with similar native species (e.g., *Cirsium undulatum* in our system). In addition, replacement taxa can be selected based on floral traits that were associated with high interaction richness or abundance such as display area and display height.

Despite the importance of nutritional value to bee health, our results indicate that bees may not be selecting for floral species with high protein concentrations, and rather selecting visually attractive and highly abundant species. However, on a site level, protein density was an important factor in determining the total bee-flower interactions, suggesting that bees may select areas where quality resources are abundant. Another factor that should be considered in future studies is nectar sugar content and lipid: protein ratios in the pollen which may drive bee species' floral preferences and in the case of nectar sugar content can directly impact foraging ranges or foraging duration by providing immediate energy (Vaudo et al., 2020). Although nectar sugar content was not measured, larger floral display area is correlated to greater nectar sugar content in some floral taxa (Guezen & Forrest, 2021), suggesting that bees were attracted to visual traits that signal nectar quality rather than pollen protein concentration.

Floral density did not predict bee-flower interaction abundance or richness. While dense floral displays can be more attractive for certain bee taxa or functional groups, dense patches are avoided by others to reduce exploitation competition (Barley et al., 2021). Our results are consistent with findings that highly mobile insect herbivores tend to be unresponsive to vegetation density because they can readily move between patches (Denno, 1994). Additionally, canopy gap size was not associated with pooled biodiversity of bee-flower interactions though there were differences in bee functional traits (body size) with smaller gaps generally supporting a higher proportion of small- and medium-sized bees (Figure 3.3). This potentially indicates that bees prefer large canopy gaps when they can forage distal to nesting locations. Based on these findings, canopy gap size between ~0.1 and 3 ha is not important for fostering interactions. However, creation of many small (<0.75 ha) canopy gaps may support more smaller-bodied bees which are threatened based on flight distances and phenological mismatch.

Our results highlight some considerations for future forest restoration practices in the Colorado Front Range. This research presents a method for examining phenological mismatch of important mutualistic interactions based on pollen protein which allows for population stability as the main nutritional resource for bee larvae. We also identify floral species that play a key role in the maintenance of these ecological networks. Some of the most attractive floral species in this study are also exotic invasives/noxious weeds so may be subject to removal under restoration treatments. We suggest that these species be replaced by species that match the phenology, nutritional value, and visual traits associated with abundant and diverse bee-flower interactions. Restoration projects aiming to promote biodiversity should manage for bee functional diversity due to potentially increased sensitivity of certain groups to phenological shifts and habitat alteration. The findings presented here add to the growing field of knowledge that reduced

overstory or biotic disturbance have a generally positive effect on native bee communities (Davis et al., 2020; Gelles et al., 2021; P. R. Rhoades et al., 2018). This general trend, then, can be exploited to not only meet management goals (*e.g.*, fire risk reduction and restoration in the CFLRP) but also so increase diversity, enhance plant-pollinator networks, and potentially support ecosystem function.

Table 3.1. Summary table of all flower species observed during the study, their nutritional value (pollen protein concentration), and number of interactions with bee species (total interactions and total number of unique interactions). Introduced/non-native species are noted by an asterisk (*).

Family	Flower (*introduced)	Protein concentration ($\mu\text{g/ml}$) \pm SE	Total interactions	Interaction richness	Pollinator importance index
Amaryllidaceae	<i>Allium cernuum</i>	-	25	9	-
	<i>Allium geyeri</i>	9.714 ± 0.688	8	4	2.10×10^{-4}
Apiaceae	<i>Harbouria trachyleura</i>	4.716 ± 1.417	43	11	0.001
Asparagaceae	<i>Leucocrinum montanum</i>	7.302 ± 1.703	16	6	4.67×10^{-4}
Asteraceae	<i>Achillea millefolium</i>	14.056 ± 3.482	106	15	0.015
	<i>Agoseris aurantiaca</i>	-	1	1	-
	<i>Agoseris glauca</i>	-	134	12	-
	<i>Antennaria corymbosa</i>	5.192 ± 0.950	1	1	3.39×10^{-6}
	<i>Arnica fulgens</i>	0.362 ± 0.362	9	4	0.000
	<i>Artemisia frigida</i>	19.832 ± 14.532	5	2	1.36×10^{-4}
	<i>Artemisia ludoviciana</i>	3.921 ± 0.353	1	1	2.49×10^{-6}
	<i>Carduus nutans</i> *	12.897 ± 2.115	837	22	0.162
	<i>Cirsium arvense</i> *	-	9	4	-
	<i>Conyza canadensis</i>	-	3	2	-
	<i>Dieteria bigelovii</i>	-	1	1	-
	<i>Ericameria nauseosa</i>	4.797 ± 0.213	411	17	0.022
	<i>Erigeron divergens</i>	2.794 ± 0.304	14	6	1.43×10^{-4}
	<i>Erigeron flagellaris</i>	7.394 ± 0.319	10	4	1.97×10^{-4}
	<i>Erigeron speciosus</i>	-	170	17	-
	<i>Gaillardia aristata</i>	6.607 ± 0.360	123	18	0.010
	<i>Grindelia squarrosa</i>	9.562 ± 1.048	52	9	0.003
	<i>Heliomeris multiflora</i>	-	5	2	-
	<i>Heterotheca villosa</i>	8.312 ± 0.635	631	31	0.109
	<i>Lactuca serriola</i>	-	0	0	-
	<i>Liatris punctata</i>	-	5	2	-
	<i>Packera fendleri</i>	8.592 ± 2.267	4	3	6.92×10^{-5}
	<i>Senecio integerrimus</i>	7.445 ± 2.637	29	7	0.001
	<i>Solidago multiradiata</i>	4.378 ± 1.385	90	12	0.003
	<i>Symphyotrichum ericoides</i>	-	4	2	-
	<i>Symphyotrichum laeve</i>	-	8	2	-
	<i>Symphyotrichum porteri</i>	10.726 ± 5.377	40	10	0.003
	<i>Taraxacum officinale</i> *	3.554 ± 0.987	165	22	0.008
	<i>Tragopogon dubius</i> *	4.545 ± 1.543	10	6	1.76×10^{-4}
Boraginaceae	<i>Cryptantha ambigua</i>	-	3	3	-
	<i>Lappula occidentalis</i>	-	7	7	-
	<i>Mertensia lanceolata</i>	7.276 ± 1.348	62	17	0.005
	<i>Phacelia hastata</i>	-	28	4	-
Brassicaceae	<i>Arabis glabra</i>	-	3	3	-

	<i>Camelina microcarpa</i> *	8.330 ± 1.561	7	3	1.17 × 10 ⁻⁴
	<i>Descurainia pinnata</i>	-	2	2	-
	<i>Descurainia sophia</i> *	-	0	0	-
	<i>Draba aurea</i>	5.886 ± 0.445	2	2	1.55 × 10 ⁻⁵
	<i>Erysimum capitatum</i>	7.683 ± 1.320	14	9	6.47 × 10 ⁻⁴
	<i>Lesquerella montana</i>	-	3	1	-
	<i>Noccaea fendleri</i>	0.909 ± 0.325	33	9	1.14 × 10 ⁻⁴
	<i>Thlaspi arvense</i> *	6.065 ± 1.776	11	6	2.64 × 10 ⁻⁴
Campanulaceae	<i>Campanula rotundifolia</i>	6.476 ± 0.364	213	23	0.021
Caprifoliaceae	<i>Symphoricarpos occidentalis</i>	-	1	1	
Caryophyllaceae	<i>Arenaria fendleri</i>	11.356 ± 3.098	7	3	1.62 × 10 ⁻⁴
	<i>Cerastium arvense</i>	10.42514	52	10	0.004
Crassulaceae	<i>Sedum lanceolatum</i>	7.787 ± 0.973	11	6	3.44 × 10 ⁻⁴
Fabaceae	<i>Astragalus agrestis</i>	-	2	2	-
	<i>Astragalus flexuosus</i>	3.875 ± 1.380	130	15	0.005
	<i>Astragalus miser</i>	-	21	10	-
	<i>Astragalus parryi</i>	2.965 ± 1.257	13	6	1.42 × 10 ⁻⁴
	<i>Lupinus argenteus</i>	26.909 ± 6.442	311	18	0.104
	<i>Oxytropis lambertii</i>	11.706 ± 2.672	150	10	0.012
	<i>Thermopsis montana</i>	10.512 ± 4.170	58	10	0.004
	<i>Trifolium pratense</i> *	-	2	1	-
Gentianaceae	<i>Frasera speciosa</i>	7.025 ± 0.319	35	8	0.001
Geraniaceae	<i>Geranium caespitosum</i>	6.608 ± 1.546	511	25	0.056
Grossulariaceae	<i>Ribes cereum</i>	-	32	11	-
Lamiaceae	<i>Monarda fistulosa</i>	-	444	16	-
	<i>Scutellaria brittonii</i>	4.836 ± 0.561	0	0	0.000
Liliaceae	<i>Calochortus gunnisonii</i>	9.223 ± 0.460	259	21	0.034
Melanthiaceae	<i>Toxicoscordion venenosum</i>	4.099 ± 0.580	0	0	0.000
Montiaceae	<i>Claytonia lanceolata</i>	3.836 ± 0.891	36	6	5.26 × 10 ⁻⁴
Onagraceae	<i>Epilobium brachycarpum</i>	-	2	1	-
	<i>Oenothera coronopifolia</i>	55.344 ± 18.638	7	4	0.001
Orobanchaceae	<i>Orthocarpus luteus</i>	-	11	2	-
Plantaginaceae	<i>Collinsia parviflora</i>	-	5	5	-
	<i>Linaria dalmatica</i> *	-	36	4	-
	<i>Linaria vulgaris</i> *	16.845 ± 4.233	66	8	0.006
	<i>Penstemon glaber</i>	-	5	3	-
	<i>Penstemon secundiflorus</i>	-	1	1	-
	<i>Penstemon virens</i>	17.203 ± 6.049	38	7	0.003
	<i>Veronica plantaginea</i>	6.331 ± 1.285	70	9	0.003
Polemoniaceae	<i>Collomia linearis</i>	7.831 ± 0.746	8	4	1.68 × 10 ⁻⁴
Polygonaceae	<i>Eriogonum umbellatum</i>	3.566 ± 0.623	283	21	0.013
	<i>Polygonum douglasii</i>	-	1	1	-
Ranunculaceae	<i>Clematis hirsutissima</i>	11.634 ± 1.712	6	2	9.48 × 10 ⁻⁵

	<i>Delphinium nuttallianum</i>	6.455 ± 1.242	115	14	0.007
	<i>Pulsatilla nuttalliana</i>	3.998 ± 1.097	70	5	8.92 × 10 ⁻⁴
	<i>Ranunculus glaberrimus</i>	6.533 ± 0.725	0	0	0.000
Rhamnaceae	<i>Ceanothus herbaceus</i>	6.482 ± 0.870	30	6	7.72 × 10 ⁻⁴
Rosaceae	<i>Potentilla fissa</i>	1.169 ± 0.592	81	13	5.96 × 10 ⁻⁴
	<i>Potentilla gracilis</i>	-	57	9	-
	<i>Potentilla hippiana</i>	8.986 ± 2.788	77	14	0.007
	<i>Potentilla pensylvanica</i>	-	4	2	-
	<i>Potentilla pulcherrima</i>	-	14	4	-
	<i>Rosa woodsii</i>	8.197 ± 4.402	3	3	4.94 × 10 ⁻⁵
	<i>Rubus deliciosus</i>	-	2	2	-
Saxifragaceae	<i>Saxifraga rhomboidea</i>	4.565 ± 0.459	2	2	1.18 × 10 ⁻⁵
Scrophulariaceae	<i>Verbascum thapsus</i> *	-	47	7	-

Table 3.2. Linear mixed model analysis summarizing variation in bee-flower interactions due to effects of floral availability, nutrition, and canopy-gap size. Significance is determined using t-test (Satterthwaite's method) with significant ($P < 0.05$) effects bolded. Only fixed effects are shown in table; sample period ($n = 9$) was treated as a random effect in both models.

Response variable	Parameter	Estimate (β)	SE	df	t-score	P
Total bee-flower interactions	Intercept	87.001	22.948	23.112	3.791	0.001
	Floral density (/m ²)	0.374	0.953	64.098	0.393	0.696
	Floral richness	-0.509	1.388	63.409	-0.367	0.715
	Protein density ($\mu\text{g}/\text{m}^2$)	8.489	2.776	63.703	3.058	0.003
	Canopy gap size (ha)	-4.697	5.080	58.139	-0.924	0.359
	Residual variance	-	-	1164	-	-
Unique bee-flower interactions	Intercept	19.301	5.313	20.938	3.633	0.002
	Floral density (/m ²)	-0.113	0.211	63.337	-0.534	0.595
	Floral richness	0.711	0.307	62.661	2.315	0.024
	Protein density ($\mu\text{g}/\text{m}^2$)	0.584	0.614	62.844	0.950	0.346
	Canopy gap size (ha)	-1.796	1.120	57.972	-1.603	0.114
	Residual variance	-	-	56.52	-	-

Table 3.3. Linear mixed model analysis summarizing variation in bee-flower interactions due to effects of floral visual traits, nutrition, and abundance. Significance is determined using t-test (Satterthwaite's method) with significant ($P < 0.05$) effects bolded. Only fixed effects are shown in table; sample period ($n = 9$) was treated as a random effect in both models.

Response variable	Parameter	Estimate (β)	SE	df	t-score	P
Total interactions	Intercept	1.093	2.267	268.5	0.482	0.630
	Color White	-5.957	1.425	689.3	-4.180	<0.001
	Color Yellow	-4.759	1.263	691.7	-3.768	<0.001
	Status (Native)	-0.179	1.645	692.5	-0.109	0.913
	Floral display area	0.004	0.001	667.8	4.428	<0.001
	Floral display height	0.015	0.003	667.7	5.147	<0.001
	UV reflectance (yes)	-0.375	1.157	690.0	-0.324	0.746
	Protein concentration (ug/mg)	0.047	0.075	691.2	0.634	0.526
	Floral density	2.432	0.422	360.0	5.761	<0.001
	Relative abundance	22.480	5.217	351.1	4.309	<0.001
	Residual variance	-	-	159.21	-	-
Interaction richness	Intercept	0.703	0.399	118.4	1.762	0.081
	Color White	-1.096	0.235	686.1	-4.662	<0.001
	Color Yellow	-0.866	0.209	692.2	-4.143	<0.001
	Status (Native)	0.628	0.272	689.3	2.313	0.021
	Floral display area	0.001	<0.001	692.8	5.531	<0.001
	Floral display height	0.001	<0.001	688.7	2.167	0.031
	UV reflectance (yes)	0.341	0.192	693.0	1.782	0.075
	Protein concentration (ug/mg)	0.004	0.012	692.3	0.338	0.736
	Floral density	0.359	0.072	476.7	4.987	<0.001
	Relative abundance	2.936	0.892	461.7	3.293	0.001
	Residual variance	-	-	4.319	-	-

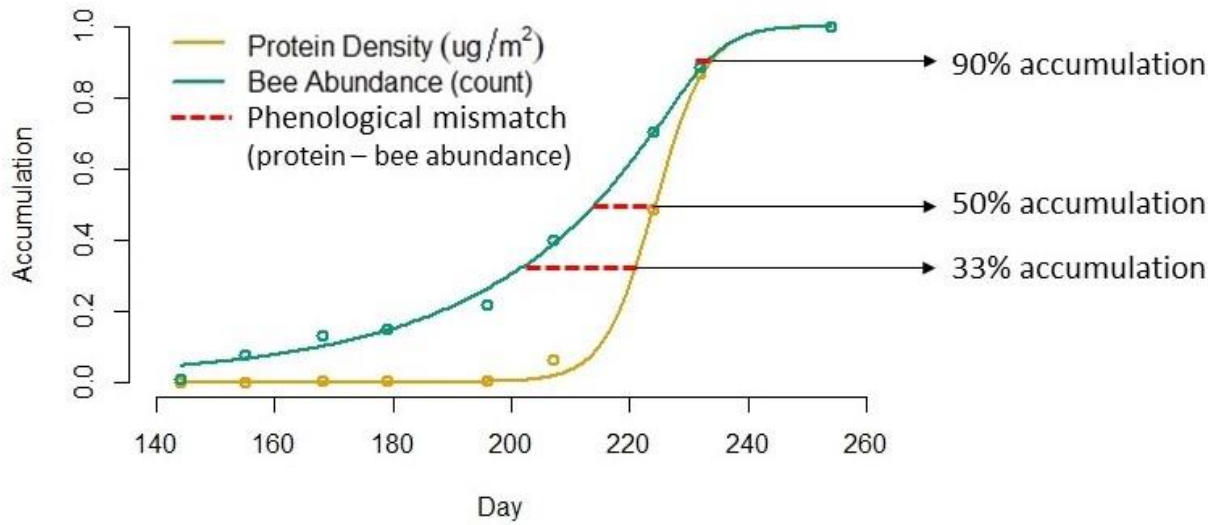


Figure 3.1. Conceptual figure showing the calculation of phenological mismatch. Orange solid line shows the logistic model of the accumulation of protein density (ug/m^2) and green solid line shows logistic model of bee abundance accumulation. The red dashed line shows the phenological mismatch (number of days between protein accumulation and bee abundance accumulation) at three different time points (33%, 50%, and 90% accumulation).

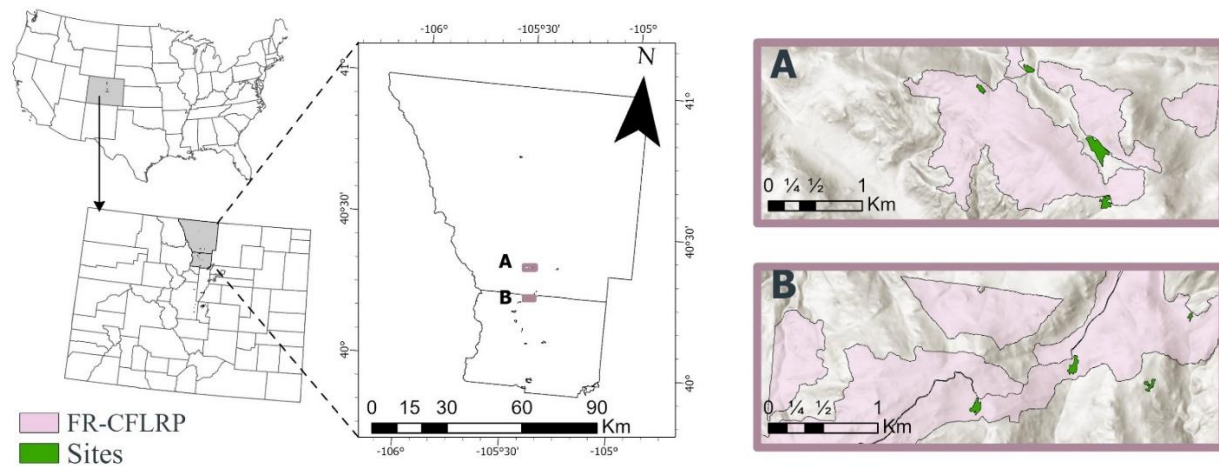


Figure 3.2. Map highlighting study region in the Colorado Front Range (Larimer and Jefferson counties). Pink rectangles show the forest areas used in the study: (A) Roosevelt National Forest-Thompson River; (B) Roosevelt National Forest- Estes Valley. Green polygons show the canopy gaps (n=8) included in the study; pink polygons show the areas treated under Front Range Collaborative Forest Landscape Restoration Program (FR-CFLRP).

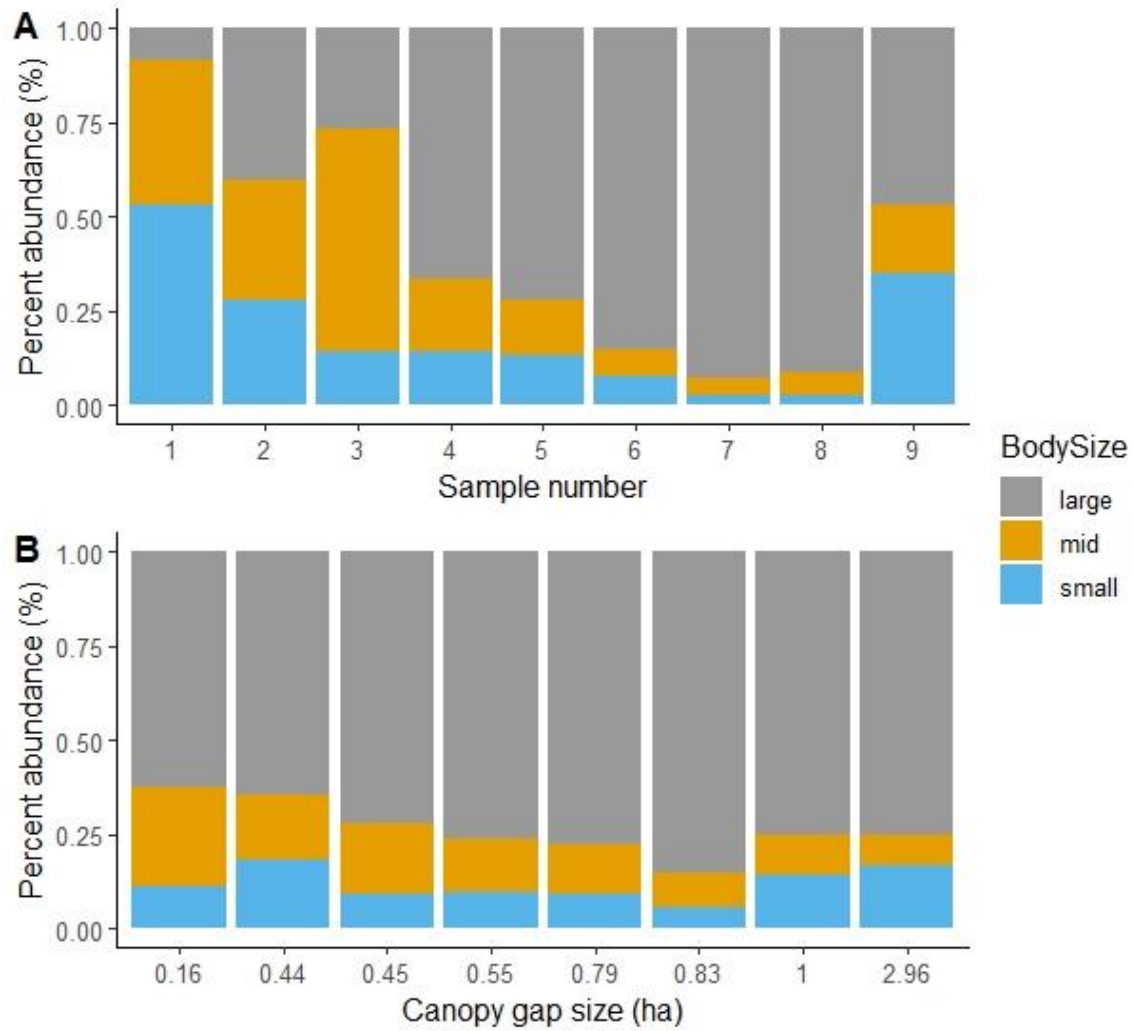


Figure 3.3. Proportion of large, medium, and small bees compared across (A) time (sampling period) and (B) canopy gap sizes (ha). Grey bars show percent large bees, orange bars show percent mid-sized bees, and blue bars show percent small-sized bees.

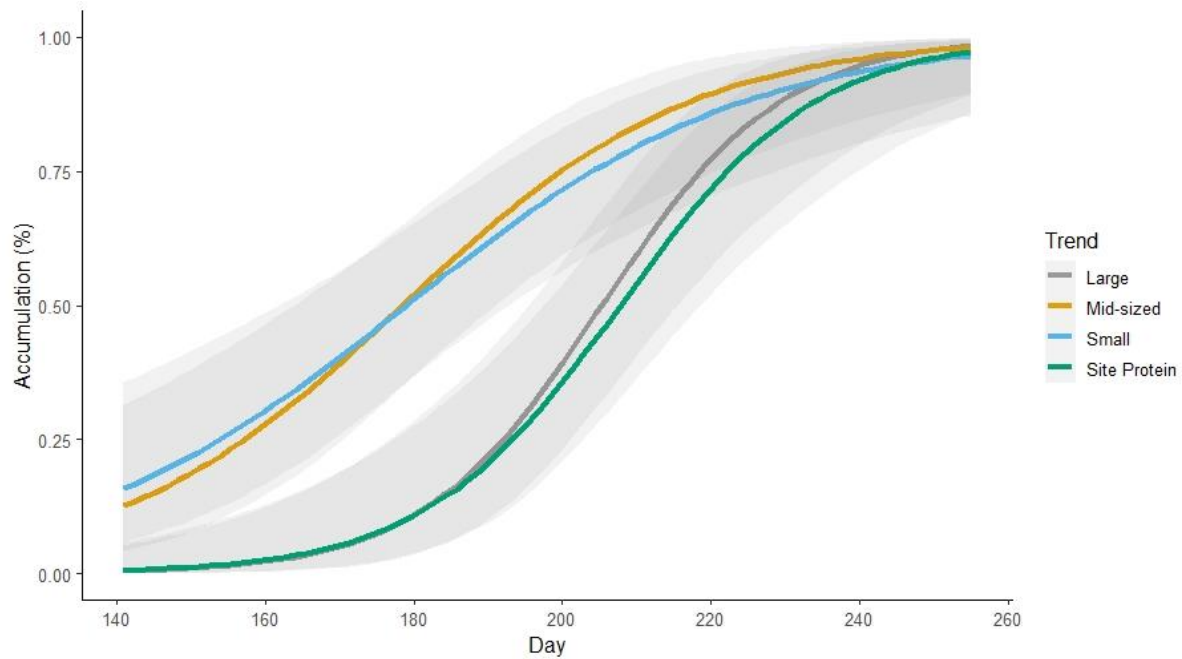


Figure 3.4. Seasonal accumulation of protein density and bee abundance relative to bee body size. Lines show logistic regressions fit for canopy gap protein density (green) and bee abundance separated by body size (large = grey, mid-sized = orange, small = blue). Gray shading represents the 95% confidence interval.

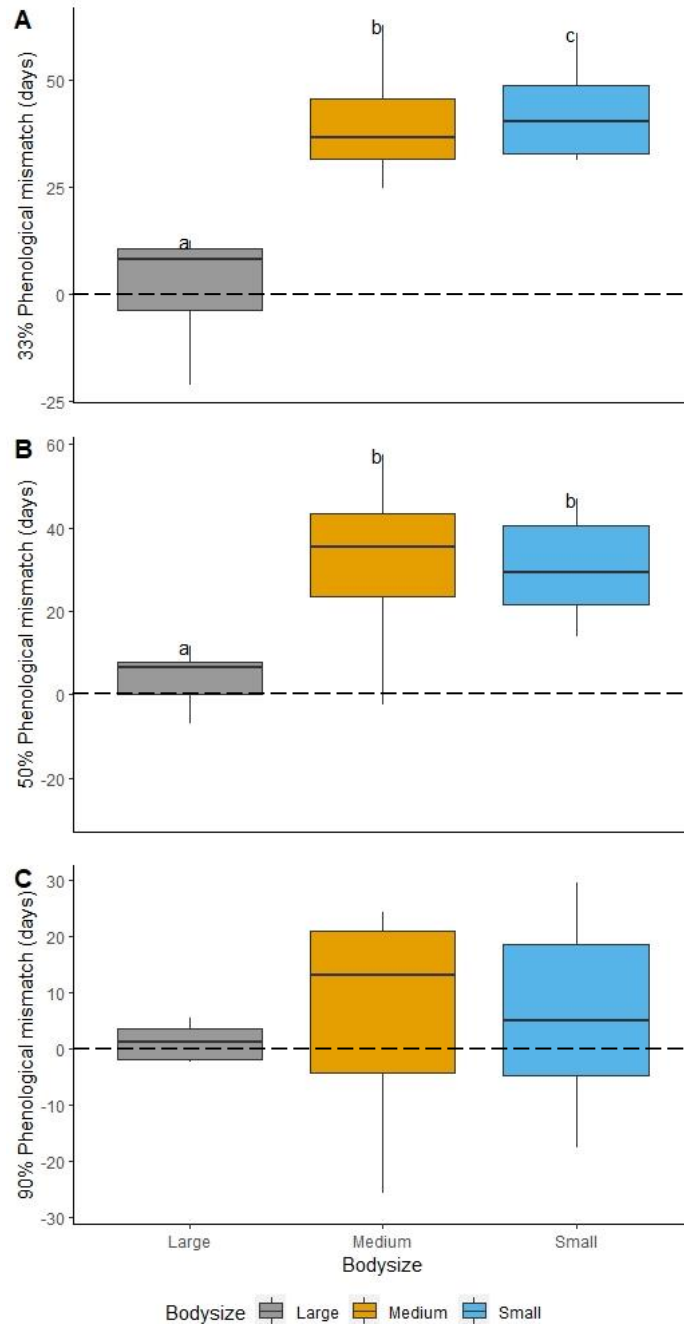


Figure 3.5. Comparison of phenological mismatch between protein density and bee abundance across bee body size at different time points throughout the season: (A) difference of number of days between 33%, (B) 50%, and (C) 90% accumulation of protein density and bee abundance. Letters represent significant differences ($P < 0.05$) between groups based on Tukey HSD values. Dashed line shows 0 days mismatch.

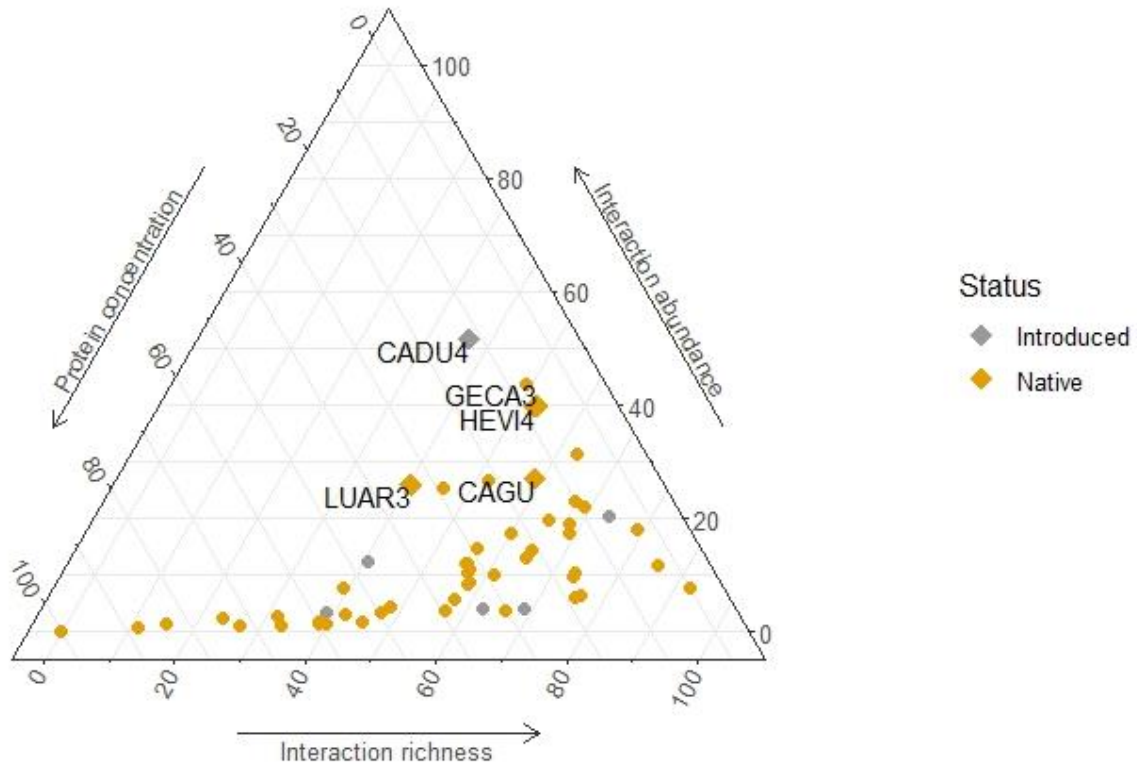


Figure 3.6. Pollinator importance index of floral species grouped by native (orange) and introduced (grey) species, ordinated along three axes: protein concentration (left), interaction abundance (right), and interaction richness (bottom). The five species with the greatest pollinator important index values are represented by diamonds and labeled with USDA species symbols (CADU4 = *Carduus nutans*, HEVI4 = *Heterotheca villosa*, LUAR3 = *Lupinus argenteus*, GECA3 = *Geranium caespitosum*, CAGU = *Calochortus gunnisonii*).

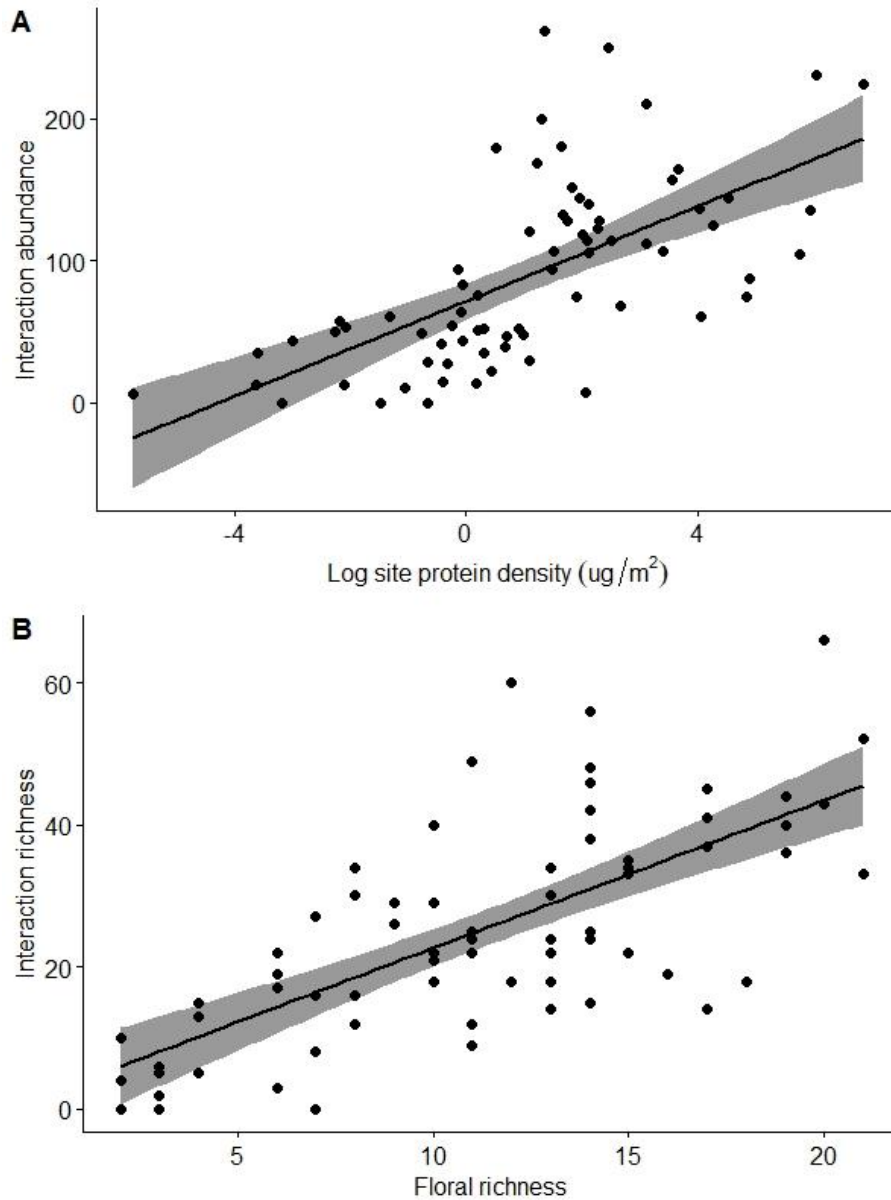


Figure 3.7. Relationship between interactions and significant floral population variables. Linear regressions between (A) interaction abundance and log transformed site protein density (ug/m²) and (B) interaction richness and floral richness. Circles represent each site-day sampling period. Shaded areas denote 95% confidence intervals of regression models.

CONCLUSION

Ecological restoration is valuable for managing ecosystem processes, such as interactions between native bees and flowering plants. In forested ecosystems, restoring forest structure closer to historical conditions via mechanical thinning and gap creation result in cascading effects that ultimately increase bee-flower interactions. Here, we develop a structural equation model that suggests a causal mechanism stemming from changes in forest structure. Our model shows that forest thinning and creation of bare ground increases temperature and foraging resources, increasing bee abundance and richness, and ultimately leading to more bee-flower interactions. These studies also show that canopy gap habitats provide diverse floral resources and support native bee populations. However, the phenology of bees and floral nutrition can be site-specific and differ by bee functional groups. For example, we found that smaller bees have greater phenological mismatch, and therefore may require additional consideration from managers to support continued diversity. Our models also suggest that higher protein levels may be able to support greater bee abundance, but that bees tend to select flowers based on visual signals.

Together these studies add to the current knowledge of bee communities in managed ponderosa pine forest along the Colorado Front Range (Davis et al., 2020; Gelles et al., 2021; P. R. Rhoades et al., 2018). Here, we expand on existing information by using active trapping (netting) to focus on bee-flower interactions instead of only community composition. By including these interactions in our models, we develop a better understanding of the underlying mechanisms that lead to changes in pollinator networks. These findings, therefore, have important implications for ecosystem management. Specifically, decreased basal area leads to

increases in floral and bee diversity, as well as bee-flower interactions. Canopy gaps support high diversity of bee-flower interactions, but canopy gap size variation between ~0.1 and 3 ha does not determine differences in these interactions. We identify floral species that play critical roles in maintaining ecological networks. Managers considering seed mixes should include species occupying these roles or expressing similar traits to promote native bee diversity and ecological services, such as pollination. Seed mixes should also be phenologically diverse to minimize mismatch between bees and flowers (Havens & Vitt, 2016). Some species identified as key network modulators are invasive species that may be targeted for eradication in management plans. Due to their potentially important roles in these networks, managers should consider replacements that display similar visual and functional traits. Our results suggest that special consideration should be given to bee functional diversity and floral phenology diversity, especially in bee functional groups that may be particularly susceptible to phenological mismatch, such as small-bodied bees.

Improving ecological restoration is especially important under the changing climate. Hotter, drier climates and rises in CO₂ may lead to decreased foraging and nutritional resources (Ziska et al., 2016). Phenological mismatch may also increase as bloom times are more susceptible than bee emergence to climatic variation (Bartomeus et al., 2011; Kudo & Ida, 2013). Although we show that ecosystem restoration likely benefits native bees and supports ecological services, additional research is needed to ensure continued ecosystem function. Particularly, these studies are limited to one year of data. Annual variation and community composition turnover are important considerations for future research and management projects. While this data illustrates that 2-8 years post-treatment foraging habitat is improved, resulting in increased bee-plant

interactions, we expect diminishing benefits over time. Long-term studies are needed to advise the frequency return interval for introduction of disturbance (*i.e.*, thinning).

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APPENDICES

APPENDIX I: CHAPTER 1 SUPPLEMENTAL MATERIAL

Table S1.1. Justifications for the linear regressions included in the linear mixed-effects models to construct the structural equation model.

Variable 1	Variable 2	Rationale	References
Bare Ground	Floral abundance & richness	More growing space available for floral species	Kane, J. M., Varner, J. M., Knapp, E. E., & Powers, R. F. (2010). Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest. <i>Applied Vegetation Science</i> , 13(2), 207–220. https://doi.org/10.1111/j.1654-109X.2009.01062.x
	Bee abundance & richness	Importance for ground nesting bees	Buckles, B. J., & Harmon-Threatt, A. N. (2019). Bee diversity in tallgrass prairies affected by management and its effects on above- and below-ground resources. <i>Journal of Applied Ecology</i> , 56(11), 2443–2453. https://doi.org/10.1111/1365-2664.13479 Harmon-Threatt, A., & Chin, K. (2016). Common Methods for Tallgrass Prairie Restoration and Their Potential Effects on Bee Diversity. <i>Natural Areas Journal</i> , 36(4), 400–411. https://doi.org/10.3375/043.036.0407
Canopy openness	Max temp	Increased insolation causes increased temperature	Ma, S., Concilio, A., Oakley, B., North, M., & Chen, J. (2010). Spatial variability in microclimate in a mixed-conifer forest before and after thinning and burning treatments. <i>Forest Ecology and Management</i> , 259(5), 904–915. https://doi.org/10.1016/j.foreco.2009.11.030
	Floral abundance & richness	Sunlight promotes floral species	Kane, J. M., Varner, J. M., Knapp, E. E., & Powers, R. F. (2010). Understory vegetation response to mechanical mastication and other fuels treatments in a ponderosa pine forest. <i>Applied Vegetation Science</i> , 13(2), 207–220. https://doi.org/10.1111/j.1654-109X.2009.01062.x Wolk, B., & Rocca, M. E. (2009). Thinning and chipping small-diameter ponderosa pine changes understory plant communities on the

			Colorado Front Range. <i>Forest Ecology and Management</i> , 257(1), 85–95. https://doi.org/10.1016/j.foreco.2008.08.014
Max temp	Bee abundance & richness	Insects are poikilotherms and activity may change across temperatures	Hanula, J. L., Ulyshen, M. D., & Horn, S. (2016). Conserving Pollinators in North American Forests: A Review. <i>Natural Areas Journal</i> , 36(4), 427–439. https://doi.org/10.3375/043.036.0409 Polatto, L., Chaud-Netto, J., & Vieira, V. (2014). Influence of Abiotic Factors and Floral Resource Availability on Daily Foraging Activity of Bees: Influence of Abiotic and Biotic Factors on Bees. <i>Journal of Insect Behavior</i> , 27. https://doi.org/10.1007/s10905-014-9452-6
Floral abundance & richness	Bee abundance & richness	More floral resources can support higher abundance and diversity of bees	Lane, I. G., Herron-Sweet, C. R., Portman, Z. M., & Cariveau, D. P. (2020). Floral resource diversity drives bee community diversity in prairie restorations along an agricultural landscape gradient. <i>Journal of Applied Ecology</i> , 57(10), 2010–2018. https://doi.org/10.1111/1365-2664.13694
	Bee-flower interactions	Increased interaction abundance and diversity requires having abundant and diverse flower species	Bendel, C. R., Kral-O'Brien, K. C., Hovick, T. J., Limb, R. F., & Harmon, J. P. (2019). Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition. <i>Ecosphere</i> , 10(1), e02569. https://doi.org/10.1002/ecs2.2569 Kaiser-Bunbury, C. N., Vázquez, D. P., Stang, M., & Ghazoul, J. (2014). Determinants of the microstructure of plant–pollinator networks. <i>Ecology</i> , 95(12), 3314–3324. https://doi.org/10.1890/14-0024.1
Bee abundance & richness	Bee-flower interactions	Increased interaction abundance and diversity requires having abundant and diverse bee species	Bendel, C. R., Kral-O'Brien, K. C., Hovick, T. J., Limb, R. F., & Harmon, J. P. (2019). Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition. <i>Ecosphere</i> , 10(1), e02569. https://doi.org/10.1002/ecs2.2569 Forup, M. L., Henson, K. S. E., Craze, P. G., & Memmott, J. (2008). The restoration of ecological interactions: Plant–pollinator networks on ancient and restored heathlands. <i>Journal of Applied Ecology</i> , 45(3), 742–752.

			https://doi.org/10.1111/j.1365-2664.2007.01390.x Kaiser-Bunbury, C. N., Vázquez, D. P., Stang, M., & Ghazoul, J. (2014). Determinants of the microstructure of plant–pollinator networks. <i>Ecology</i> , 95(12), 3314–3324. https://doi.org/10.1890/14-0024.1
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Table S1.2. Summary of bee γ -diversity from 30 sample sites distributed in the Pike National Forest and the Roosevelt National Forest in the Front Range of northern Colorado. Specimens grouped to distinct morphospecies but were identified as ‘sp.’ if species level could not be determined.

Family	Genus	(Subgenera) species	Treatment	
			Control	Thinned
Andrenidae	<i>Andrena</i>	<i>amphibola</i>	2	5
		<i>carlini</i>	3	7
		sp. A	0	2
		sp. B	1	0
		sp. C	0	2
		sp. D	2	11
		sp. E	0	4
		sp. F	1	4
		spp.	1	1
	<i>Pseudopanurgus</i>	sp. A	2	1
		sp. B	1	0
		sp. C	0	1
		spp.	4	15
Apidae	<i>Anthophora</i>	<i>bomboides</i>	3	1
		<i>montana</i>	8	7
		<i>occidentalis</i>	1	0
		<i>porterae</i>	9	12
		<i>terminalis</i>	7	7
		<i>urbana</i>	0	2
		<i>walshii</i>	3	0
	<i>Apis</i>	<i>mellifera</i>	0	15
	<i>Bombus</i>	<i>appositus</i>	4	27
		<i>bifarius</i>	24	86
		<i>californicus</i>	3	1
		<i>centralis</i>	88	43
		<i>griseocollis</i>	0	1
		<i>huntii</i>	3	13
		<i>insularis</i>	1	3
		<i>melanopygus</i>	1	4
		<i>nevadensis</i>	1	6
		<i>occidentalis</i>	1	0
		<i>rufocinctus</i>	7	17
		<i>sylvicola</i>	0	3
	<i>Ceratina</i>	<i>nanula</i>	0	3
		<i>neomexicana</i>	4	5
	<i>Epeolus</i>	<i>interruptus</i>	0	3
		<i>minimus</i>	2	1
	<i>Habropoda</i>	<i>morrisoni</i>	1	0
	<i>Melissodes</i>	<i>agilis</i>	1	3

		<i>communis</i>	4	10
		<i>tristis</i>	2	5
	<i>Nomada</i>	sp. A	0	1
		sp. B	1	0
		sp. C	0	1
	<i>Svastra</i>	<i>obliqua</i>	3	3
	<i>Xeromelecta</i>	<i>californica</i>	0	1
Colletidae	<i>Colletes</i>	sp. A	1	0
		sp. B	2	9
		sp. C	0	1
		sp. D	0	5
	<i>Hylaeus</i>	<i>annulatus</i>	0	4
		<i>basalis</i>	0	4
		<i>mesillae</i>	1	2
		<i>modestus</i>	4	31
		<i>rudbeckiae</i>	1	0
		spp.	2	54
		<i>verticalis</i>	2	5
Halictidae	<i>Agapostemon</i>	<i>texanus angelicus</i>	1	20
	<i>Augochlorella</i>	<i>aurata</i>	2	0
	<i>Dufourea</i>	<i>maura</i>	2	5
	<i>Halictus</i>	<i>confusus</i>	3	4
		<i>farinosus</i>	0	1
		<i>ligatus</i>	0	1
		<i>rubicundus</i>	2	3
		<i>tripartitus</i>	15	17
	<i>Lasioglossum</i>	(<i>Dialictus</i>) spp.	59	108
		(<i>Sensu stricto</i>) spp.	86	123
	<i>Sphecodes</i>	<i>dichrous</i>	1	0
		spp.	5	21
Megachilidae	<i>Anthidium</i>	<i>clypeodentatum</i>	1	0
		<i>placitum</i>	0	1
		<i>tenuiflorae</i>	0	2
	<i>Ashmeadiella</i>	<i>bucconis</i>	0	1
		<i>cactorum</i>	0	9
		<i>californica</i>	0	9
		<i>pronitens</i>	0	1
	<i>Atoposmia</i>	<i>abjecta abjecta</i>	0	2
		<i>copelandica</i>	0	3
	<i>Coelioxys</i>	<i>alternata</i>	0	1
		<i>apacheorum</i>	0	1
		<i>hunteri</i>	0	1
		<i>moesta</i>	0	1
	<i>Dianthidium</i>	<i>heterulkei fraternum</i>	1	7
		<i>parvum parvum</i>	0	3

	<i>Heriades</i>	<i>carinatus</i>	2	19
		<i>cressonii</i>	0	2
	<i>Hoplitis</i>	<i>albifrons</i>	4	22
		<i>fulgida</i>	0	4
		<i>producta</i>	3	1
		<i>robusta</i>	0	1
	<i>Lithurgus</i>	<i>apicalis</i>	0	1
	<i>Megachile</i>	<i>brevis</i>	1	6
		<i>centuncularis</i>	1	1
		<i>fidelis</i>	0	1
		<i>gemula</i>	0	2
		<i>latimanus</i>	1	3
		<i>melanophaea</i>	6	8
		<i>pugnata pugnata</i>	0	7
		<i>relativa</i>	1	4
		<i>rotundata</i>	1	0
	<i>Osmia</i>	<i>(Melanosmia) sp. B</i>	0	1
		<i>albolateralis</i>	1	2
		<i>atrocyanea</i>	1	8
		<i>brevis</i>	6	8
		<i>bruneri</i>	3	14
		<i>bucephala</i>	7	6
		<i>coloradensis</i>	0	4
		<i>densa</i>	3	1
		<i>grindeliae</i>	1	8
		<i>juxta</i>	11	17
		<i>kincaidii</i>	0	1
		<i>longula</i>	0	2
		<i>montana montana</i>	1	6
		<i>nigrifrons</i>	2	0
		<i>paradisica</i>	0	6
		<i>penstemonis</i>	1	1
		<i>phaceliae</i>	1	1
		<i>proxima</i>	0	1
		<i>pusillia</i>	0	1
		<i>sp. A</i>	0	1
		<i>subaustralis</i>	0	1
	<i>Stelis</i>	<i>elegans</i>	0	1
		<i>foederalis</i>	0	2
		<i>permaculata</i>	0	7

Table S1.3. Table with all coefficients from structural equation model. Abbreviations are as follows: beeab2 = bee abundance (net only), beerich2 = bee richness (net only), Bare = bare ground cover, floralab = floral abundance, floralrich = floral species richness, MaxTemp = maximum site temperature, Sky = canopy openness, interactionab = interaction abundance (total interactions), interactionrich = interaction richness (unique interactions). Statistical significance denoted by asterisks (Significance codes: ‘****’ $P < 0.001$ ‘***’ $P < 0.01$ ‘**’ $P < 0.05$).

Response	Predictor	β	SE	DF	Crit. Value	P-Value
beeab2	Bare	0.081	0.147	25	0.550	0.587
beeab2	MaxTemp	0.440	0.122	25	3.620	0.001**
beeab2	floralab	0.663	0.209	25	3.176	0.004**
beeab2	floralrich	-0.164	0.218	25	-0.751	0.460
beerich2	Bare	0.206	0.109	25	1.895	0.070
beerich2	MaxTemp	0.363	0.090	25	4.035	<0.001****
beerich2	floralab	0.606	0.155	25	3.924	<0.001****
beerich2	floralrich	-0.025	0.161	25	-0.156	0.877
floralab	Sky	0.412	0.178	27	2.316	0.028*
floralab	Bare	0.318	0.178	27	1.789	0.085
floralrich	Sky	0.362	0.172	27	2.111	0.044*
floralrich	Bare	0.403	0.172	27	2.350	0.026*
interactionab	floralrich	0.005	0.014	25	0.373	0.712
interactionab	floralab	-0.021	0.016	25	-1.266	0.217
interactionab	beerich2	0.018	0.028	25	0.650	0.522
interactionab	beeab2	0.994	0.023	25	43.41	<0.001****
interactionrich	floralrich	-0.003	0.065	25	-0.04	0.965
interactionrich	floralab	0.054	0.074	25	0.726	0.475
interactionrich	beerich2	0.735	0.126	25	5.827	<0.001****
interactionrich	beeab2	0.221	0.105	25	2.108	0.045*
MaxTemp	Sky	0.481	0.166	28	2.899	0.007**
floralab	floralrich	0.722	-	30	5.419	<0.001****
beeab2	beerich2	0.848	-	30	8.328	<0.001****
interactionab	interactionrich	0.389	-	30	2.195	0.019*

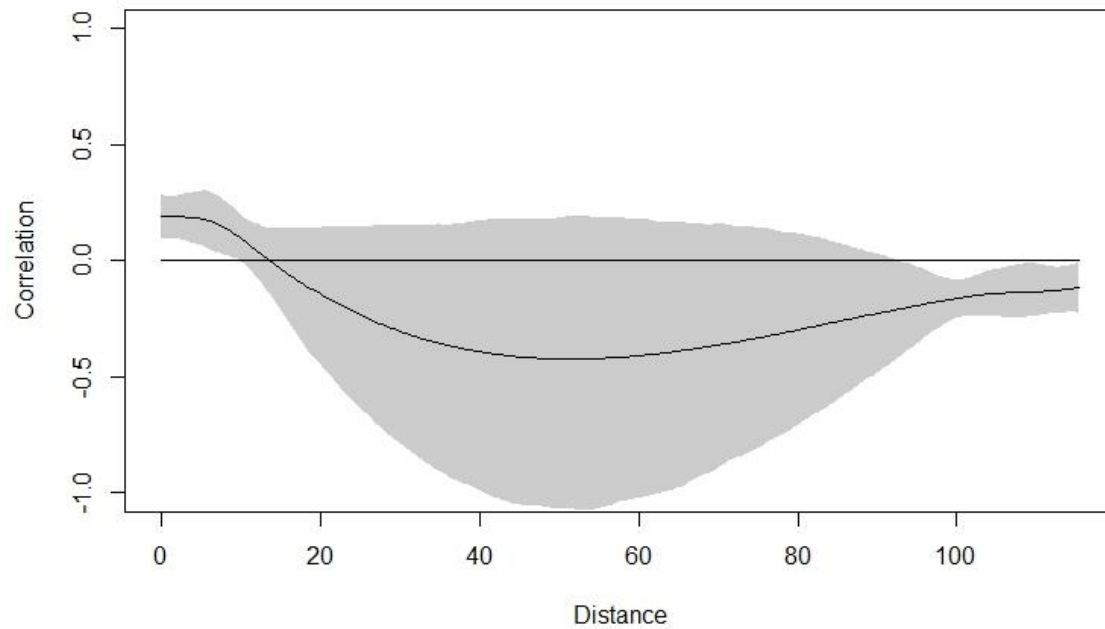


Figure S1.1. Spline correlogram from spatial data based on x = longitude and y = latitude of site locations ($n=30$), with z = bee species abundance matrix (rows = site, columns = bee species abundances). Gray shading represents the 95% confidence interval; distance is in kilometers. Nonparametric spatial correlogram was constructed using the ‘ncf’ R package with resampling = 1,000 (Bjornstad & Falck, 2001). Departure of 95% confidence intervals of spline correlogram was considered evidence of spatial autocorrelation at the given scale.

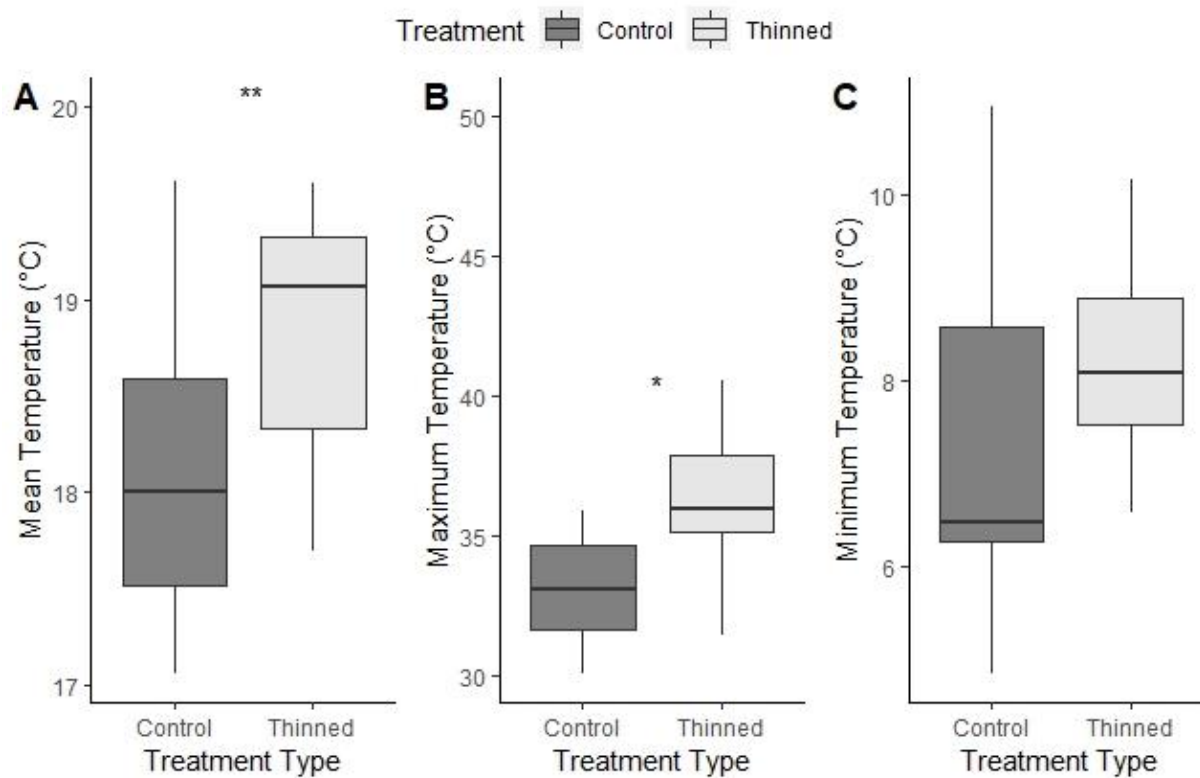


Figure S1.2. A comparison of site temperature between thinned and non-thinned stands during summer months: A) mean temperature, B) maximum temperature, C) minimum temperature. Statistical significance from t-tests p-values denoted by asterisks (Significance codes: ‘***’ $P < 0.001$ ‘**’ $P < 0.01$ ‘*’ $P < 0.05$).

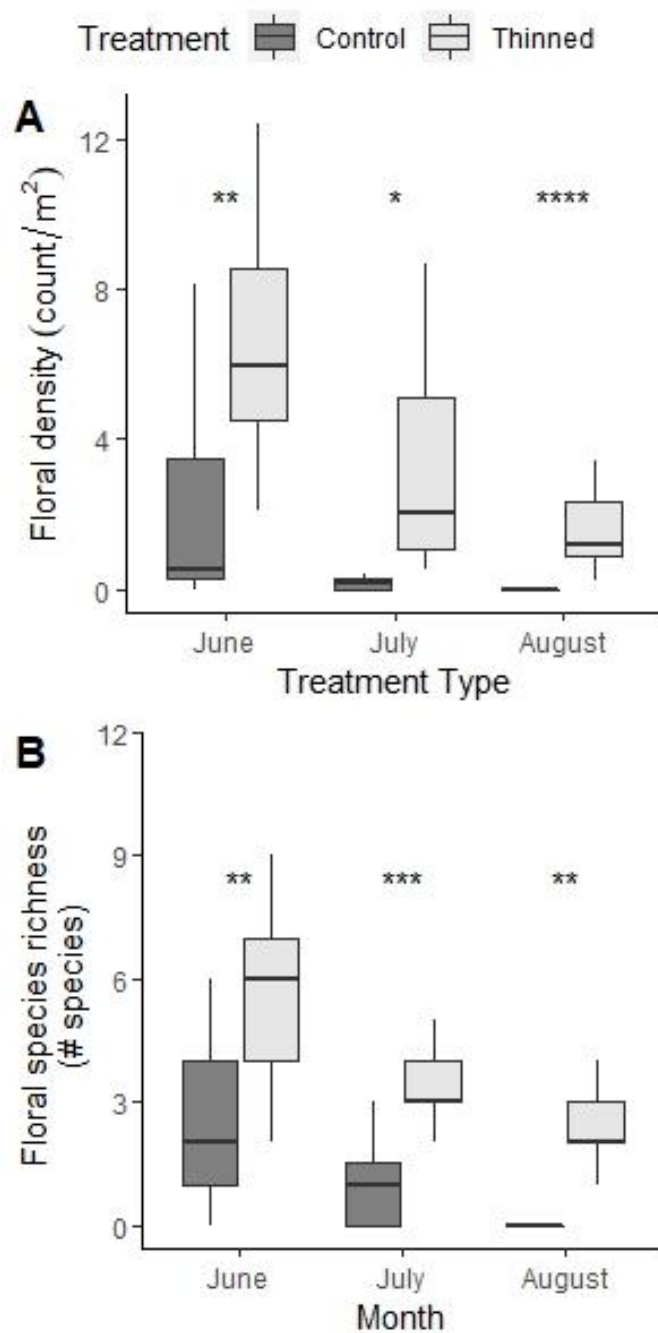


Figure S1.3. Foraging habitat variables (A) floral density (count/m²), and (B) floral species richness (total number of species counted within quadrats). Statistical significance by p-values denoted with asterisks Significance codes: ‘***’ $P < 0.001$ ‘**’ $P < 0.01$ ‘*’ $P < 0.05$.

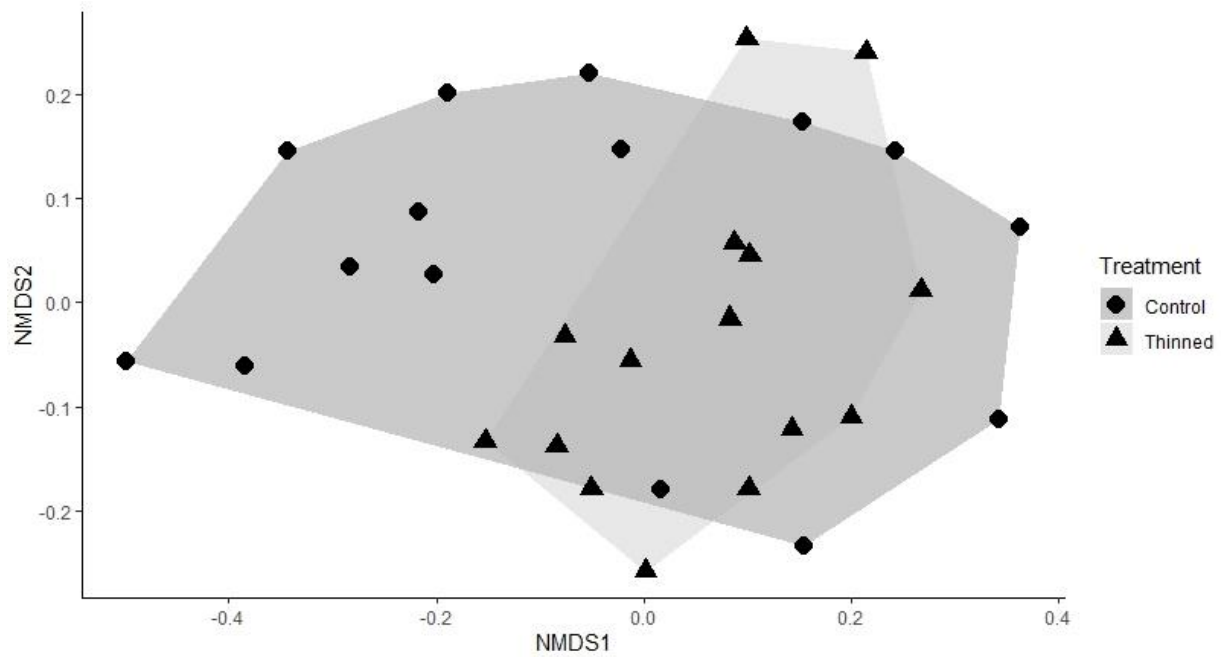


Figure S1.4. Ordination of bee community assemblages (NMDS), compared between thinned and non-thinned (control) sites (stress: 0.240).

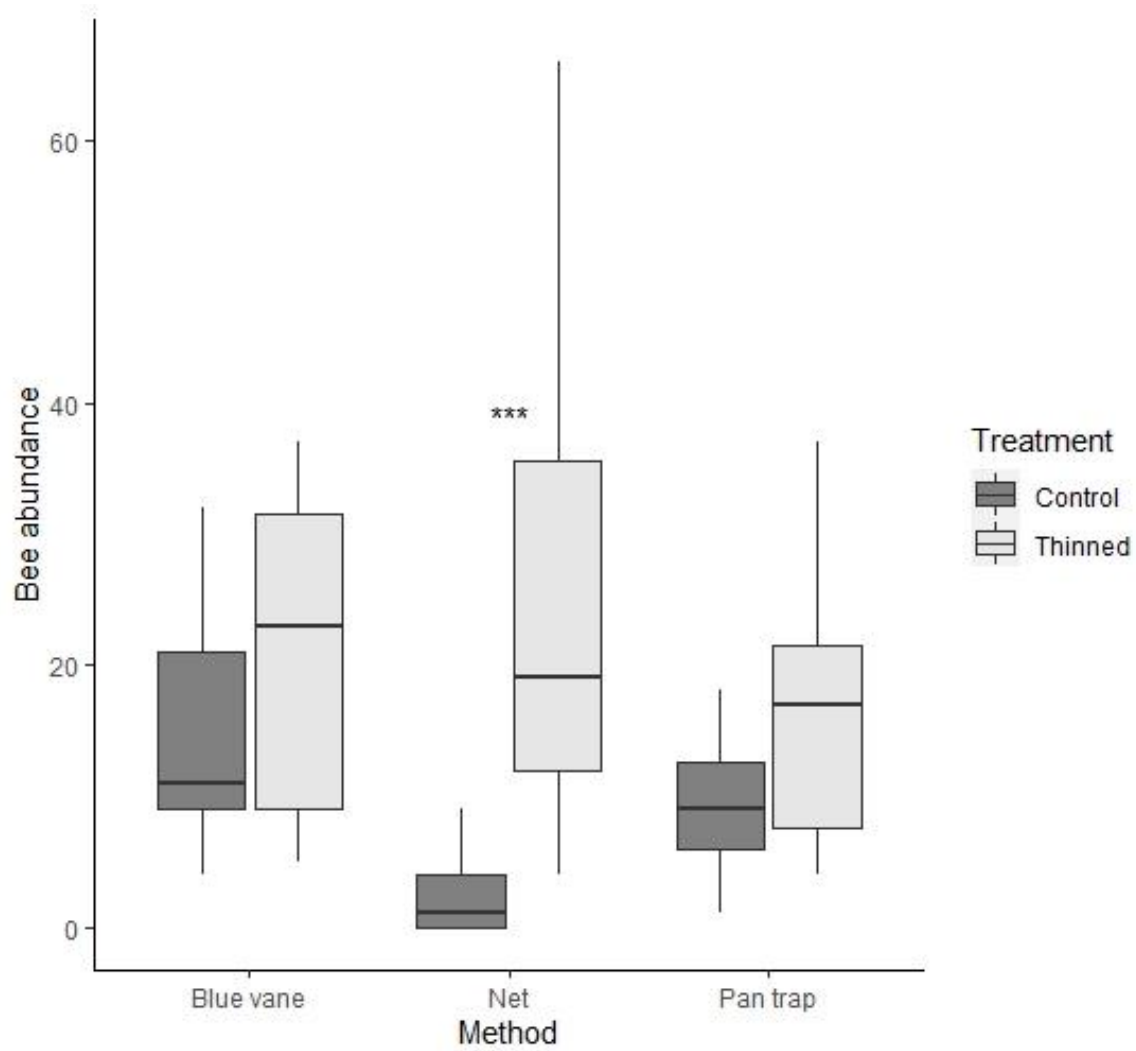


Figure S1.5. The distribution of bee abundance averaged across all months relative to collection method. Statistical significance by p-values denoted with asterisks Significance codes: ‘***’ $P < 0.001$ ‘**’ $P < 0.01$ ‘*’ $P < 0.05$).

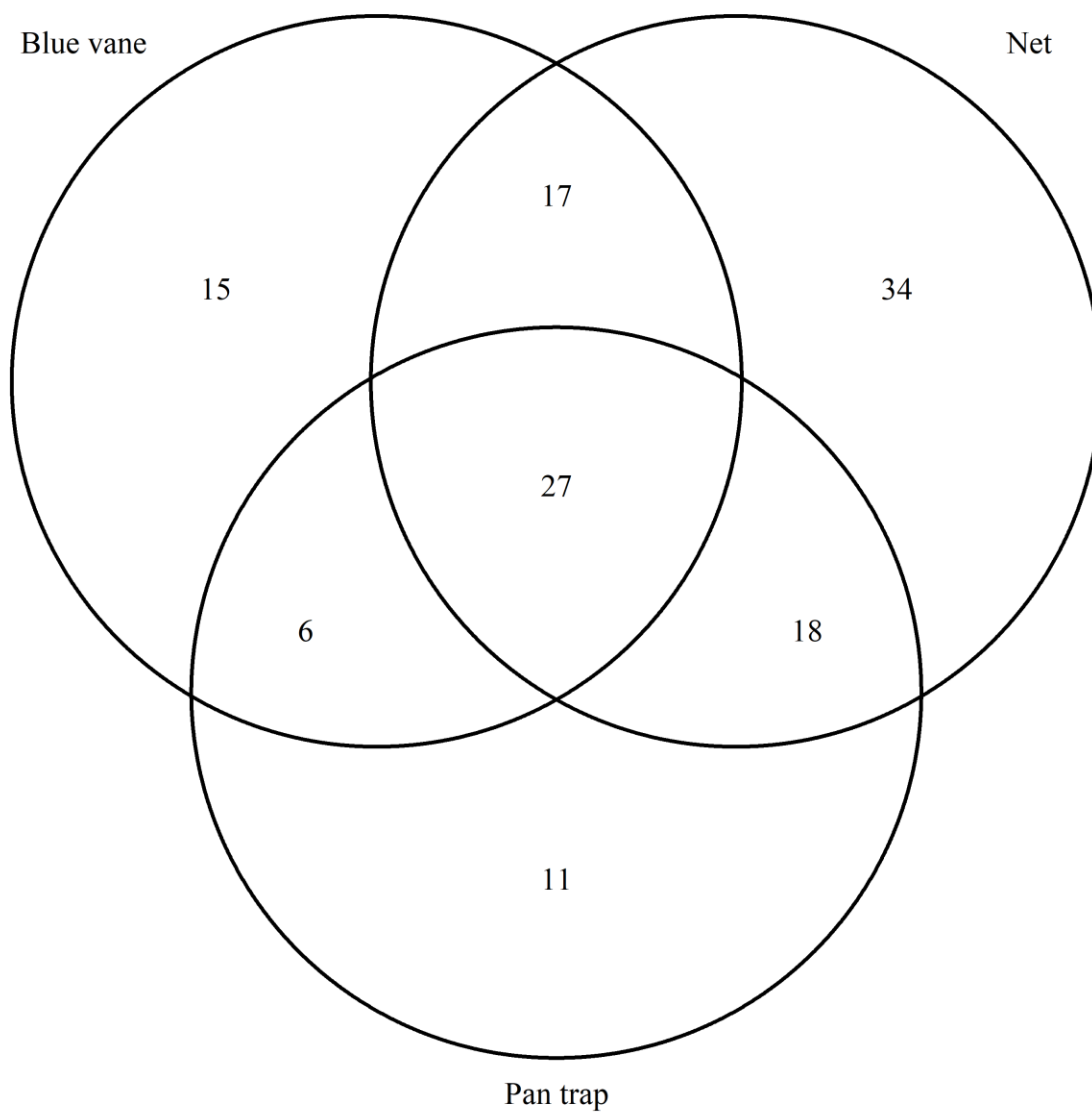
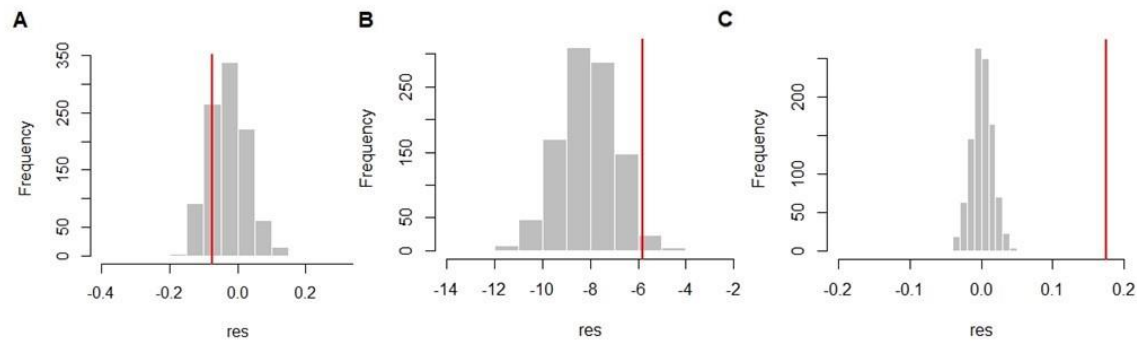


Figure S1.6. Comparison of bee communities by capture method. Venn diagram showing the number of species captured using each method (blue vane, net, and pan trap). Numbers indicate number of unique species.



Figure

S1.7. Comparison of difference between non-thinned and thinned sites for network metrics A) network-level specialization (H_2'), B) weighted nestedness (WNODF), and C) modularity (Q) compared to differences between null distributions. Null distributions were calculated from $n=1000$ random networks using the 'nullmodels' function in the 'bipartite' package. Red vertical lines represent the observed difference of network metrics between site types (non-thinned, thinned).

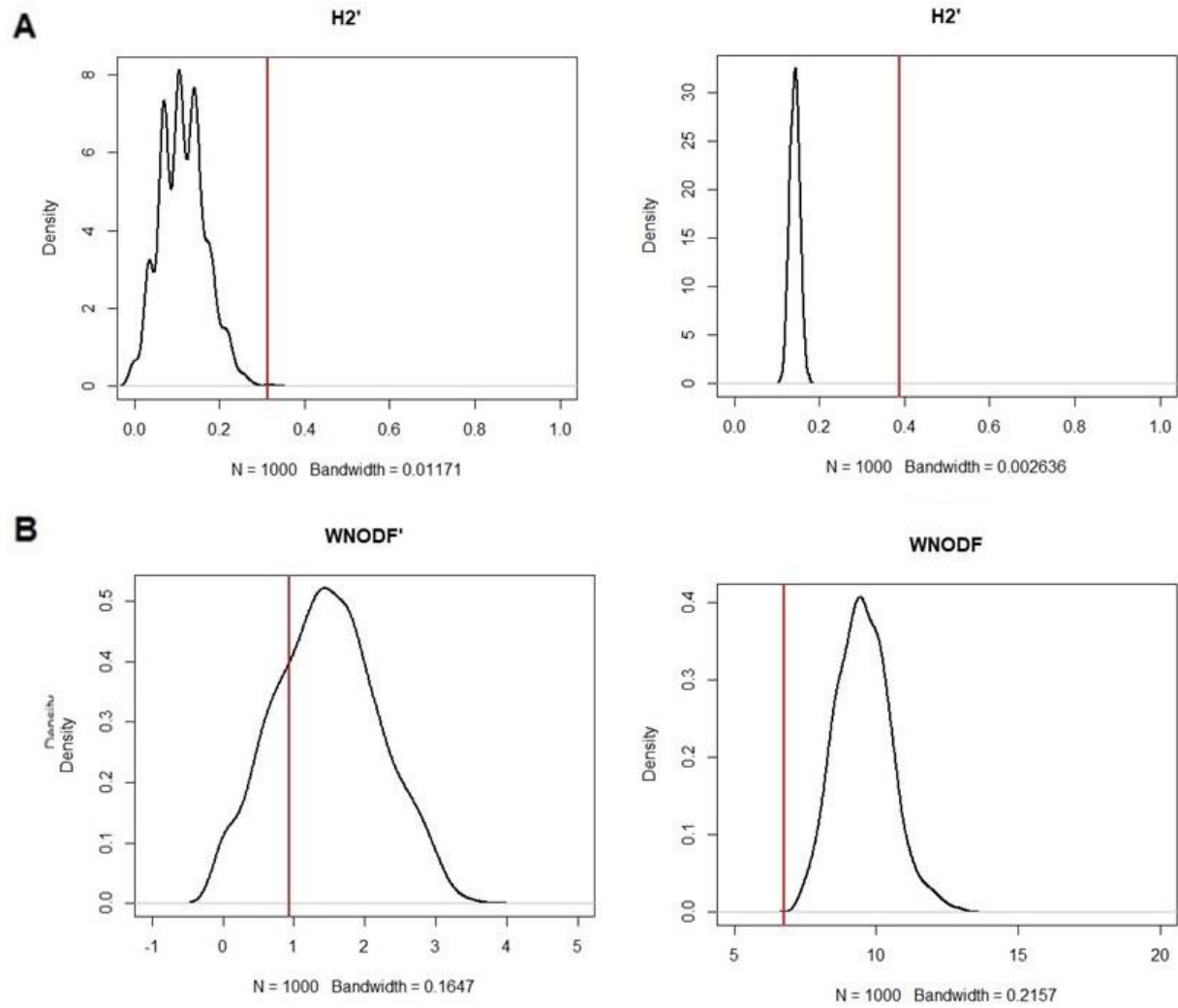


Figure S1.8. Comparison of difference between non-thinned (left) and thinned (right) sites for network metrics A) network-level specialization ($H2'$) and B) weighted nestedness (WNODF) compared to differences between null distributions. Null distributions were calculated from $n=1000$ random networks using the 'nullmodels' function in the 'bipartite' package. Red vertical lines represent the observed network metrics at each site types.

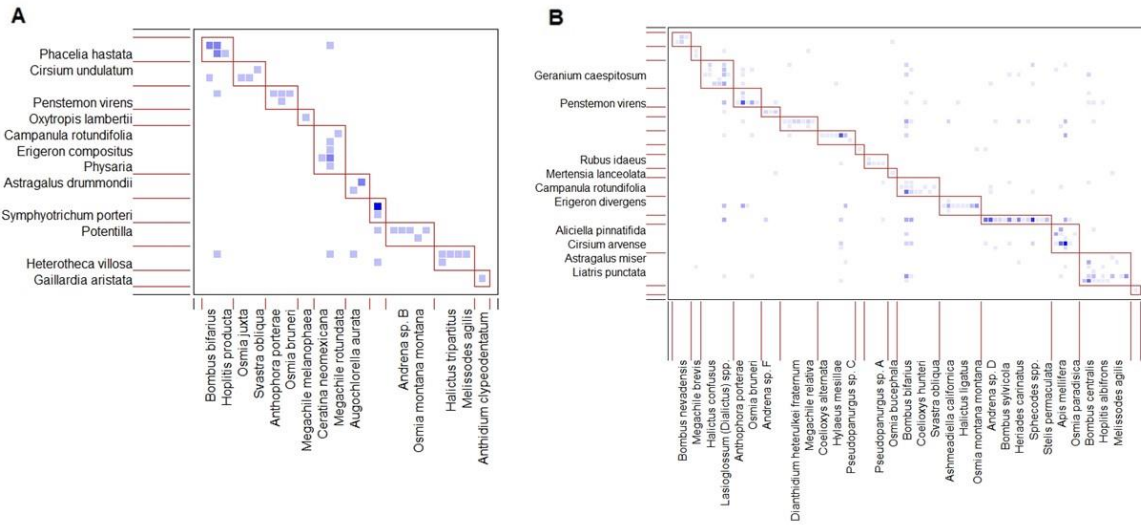


Figure S1.9. Interaction matrix showing networks from A) non-thinned sites ($Q = 0.712$) and B) thinned sites ($Q = 0.538$). Darker squares represent more frequent interactions and red lines delineate the modules. Modules computed using 'computeModule' function and plotted with 'plotModuleWeb'.

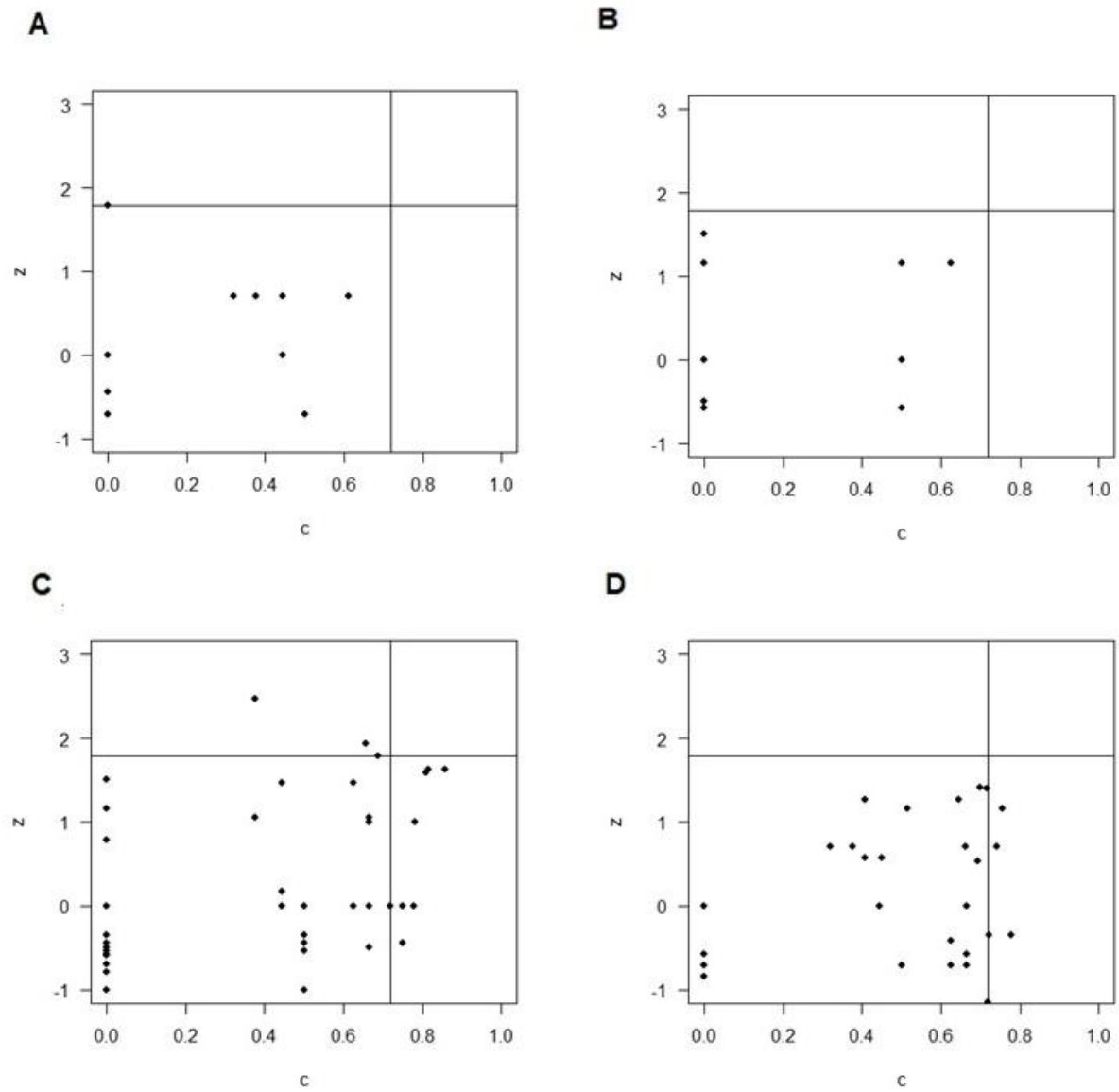


Figure S1.10. Connection (c) and participation (z) values for pollinators (left) and plants (right) in the non-thinned (A, B) and thinned (C, D) networks. Lines indicate 95% quantiles generated from 100 null models.

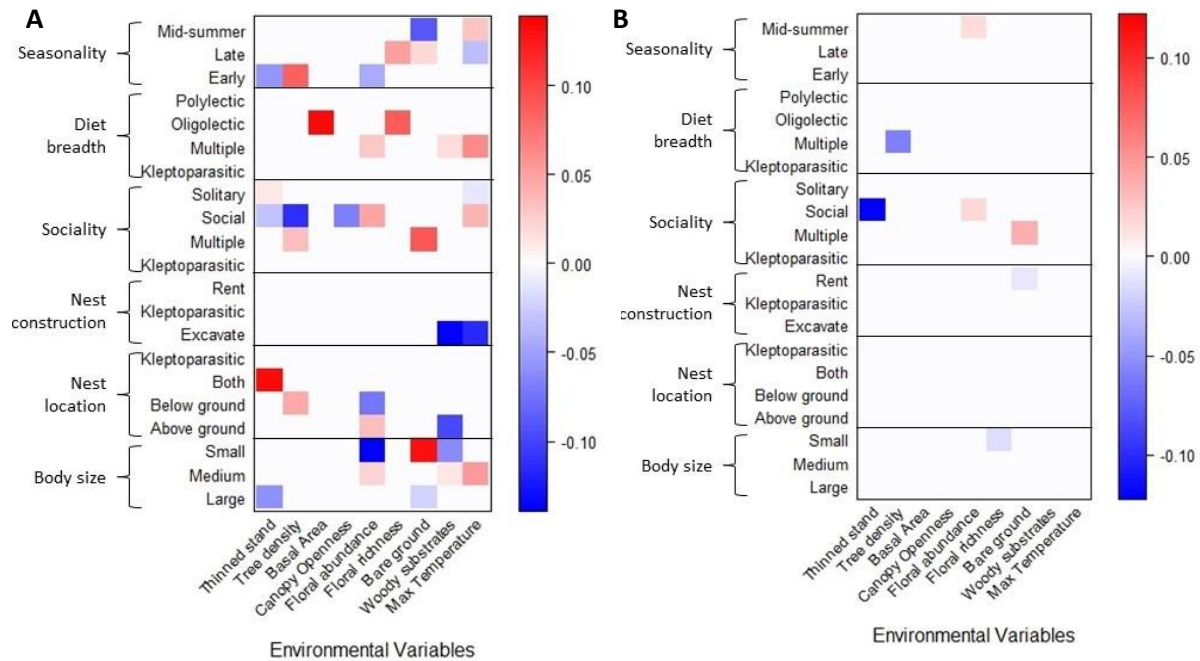


Figure S1.11. Fourth-corner analysis modeling bee genus abundances as a function of environmental factors × bee functional traits. Colored cells indicate significant correlations ($P < 0.05$), where the darker colors indicate a larger effect size (greater regression coefficient). Red cells indicate positive regression coefficients and blue cells indicate negative coefficients. A) Fourth-corner using abundances from all sampling methods (model deviance = 192.9, $P = 0.025$). B) Fourth-corner using abundances from bees captured by netting (model deviance = 169.5, $P = 0.190$).

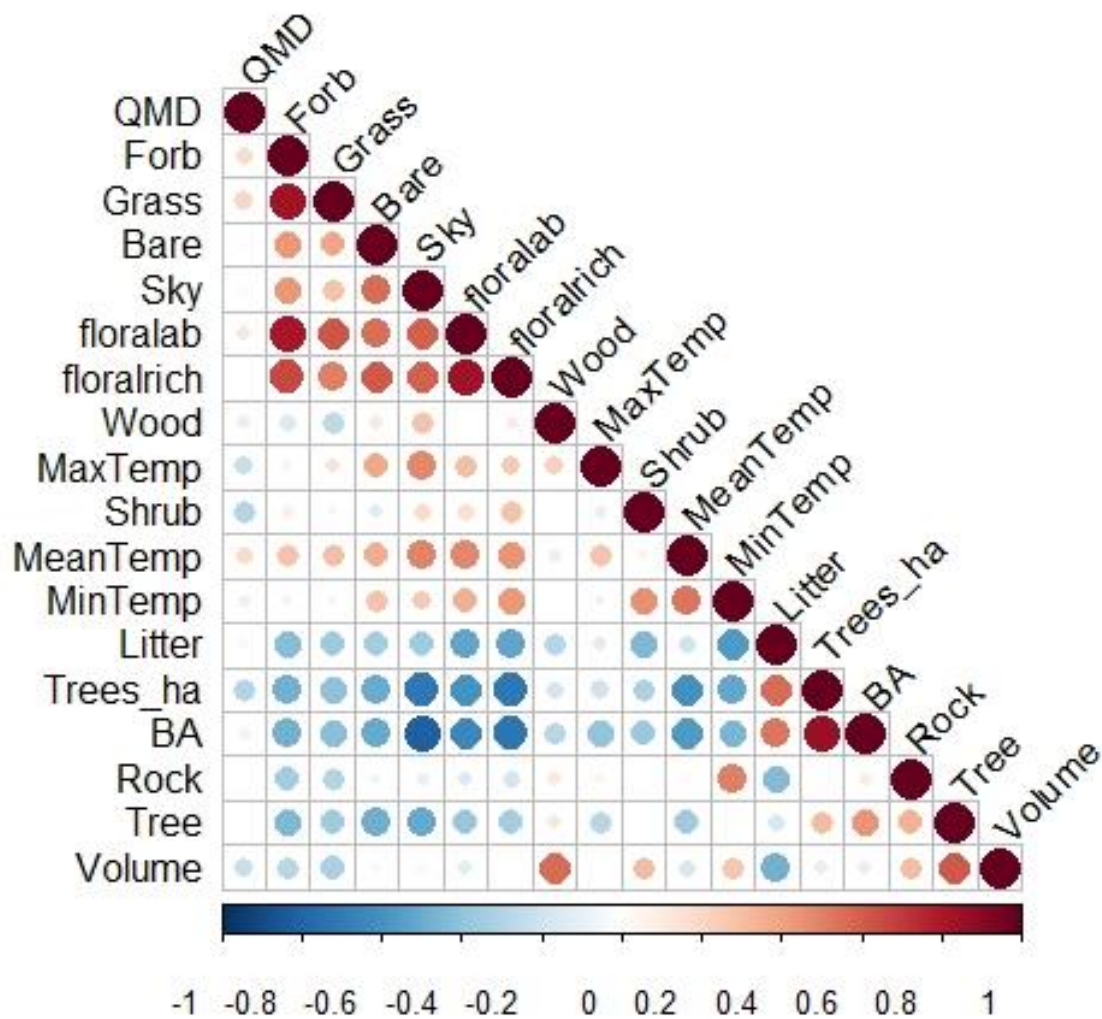


Figure S1.12. Heat map grid of correlation coefficients for forest structure and foraging habitat variables with larger circles representing high correlation. Blue represents negative and red represents positive correlations. Abbreviations are as follows: QMD = quadratic mean diameter, Bare = bare ground cover, floralab = floral abundance, floralrich = floral species richness, Forb = forb ground cover, Grass = grass ground cover, Wood = wood ground cover, MaxTemp = maximum site temperature, MeanTemp = mean site temperature, MinTemp = minimum site temperature, Sky = canopy openness, Litter = litter ground cover, Trees_ha = tree density per hectare, BA = basal area, Rock = rock ground cover, Tree = tree ground cover, Volume = volume of coarse wood debris (CWD).

APPENDIX II: CHAPTER 2 SUPPLEMENTAL MATERIAL

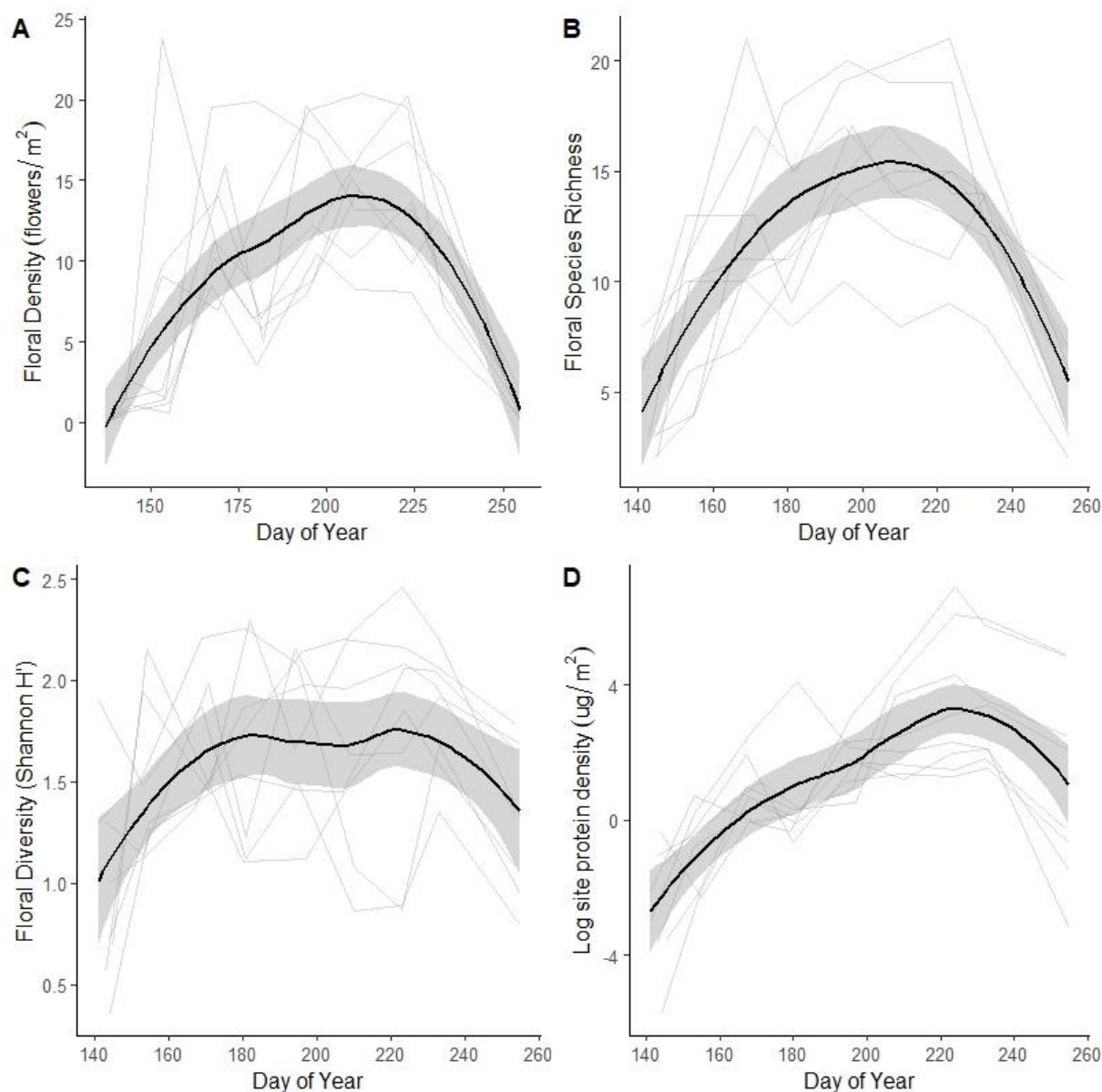


Figure S2.1. Floral phenology during the growing season: (A) floral density (flowers/m²); (B) floral species richness; (C) floral diversity (Shannon H'); (D) protein density (ug/m²) log transformed. Grey lines show trends at each site (n=8); black line shows overall trend with surround grey indicating 95% confidence interval.

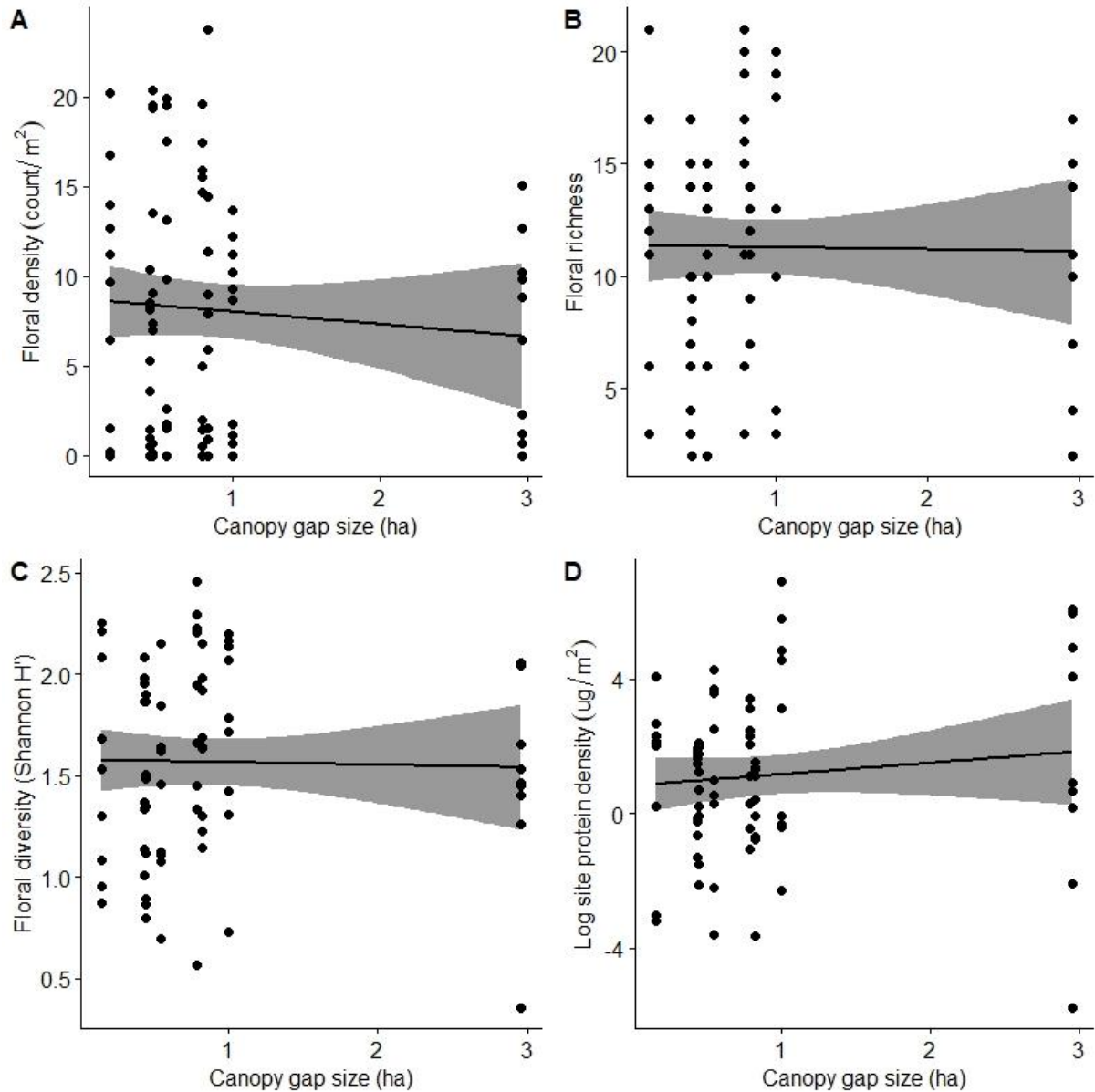


Figure S2.2. Relationship between floral population variables and canopy gap size (ha). Linear regressions between (A) floral diversity, (B) floral species richness, (C) floral Shannon H' diversity, and (D) site protein density (ug/m²) log transformed. Circles represent each site-day sampling period. Shaded areas denote 95% confidence intervals of regression models.

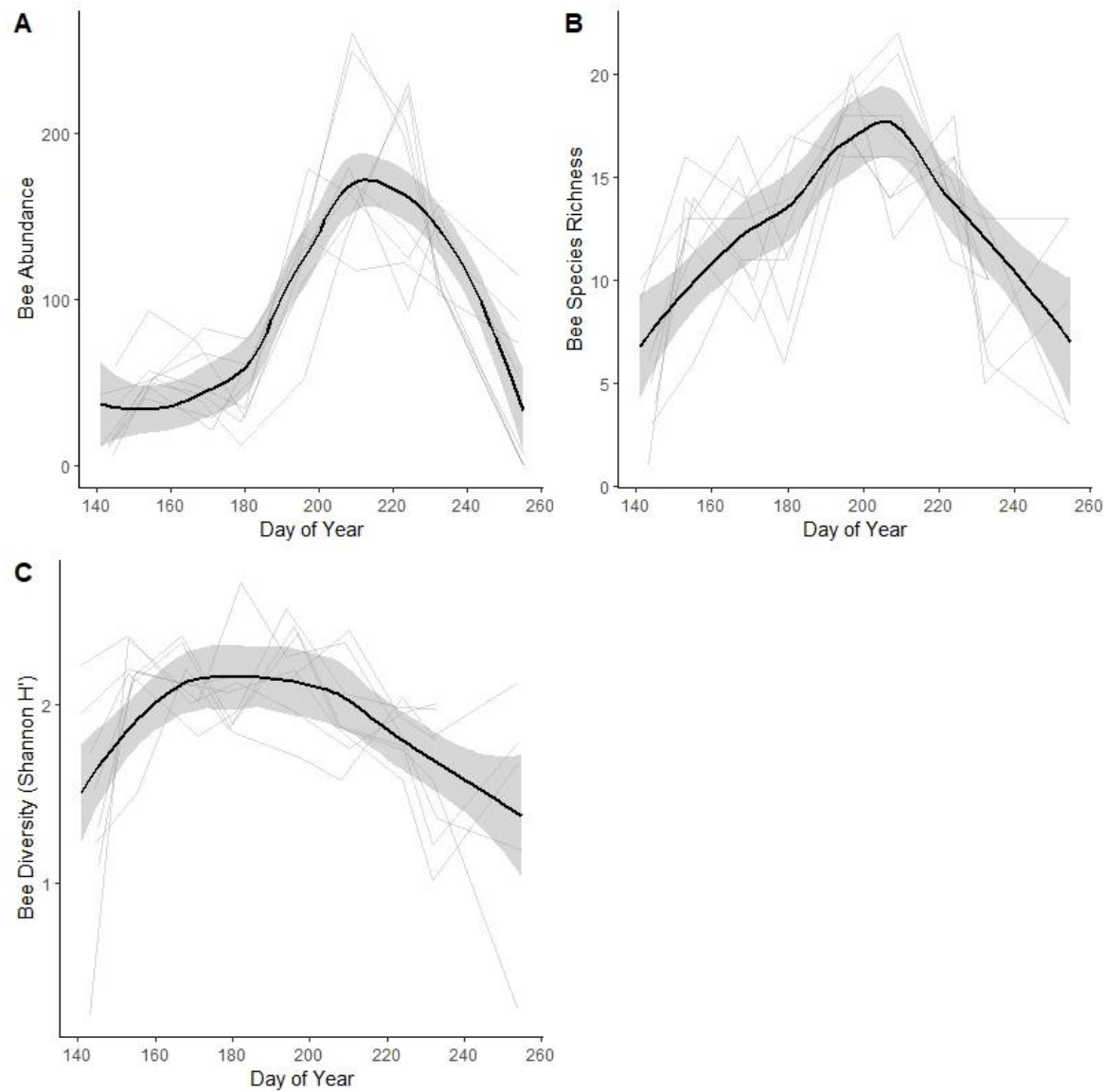


Figure S2.3. Bee phenology during the growing season: (A) bee density (bees/m²); (B) bee abundance (total number of bees); (C) bee species richness; (D) bee diversity (Shannon H'). Grey lines show trends at each site (n=8); black line shows overall trend with surround grey indicating 95% confidence interval.

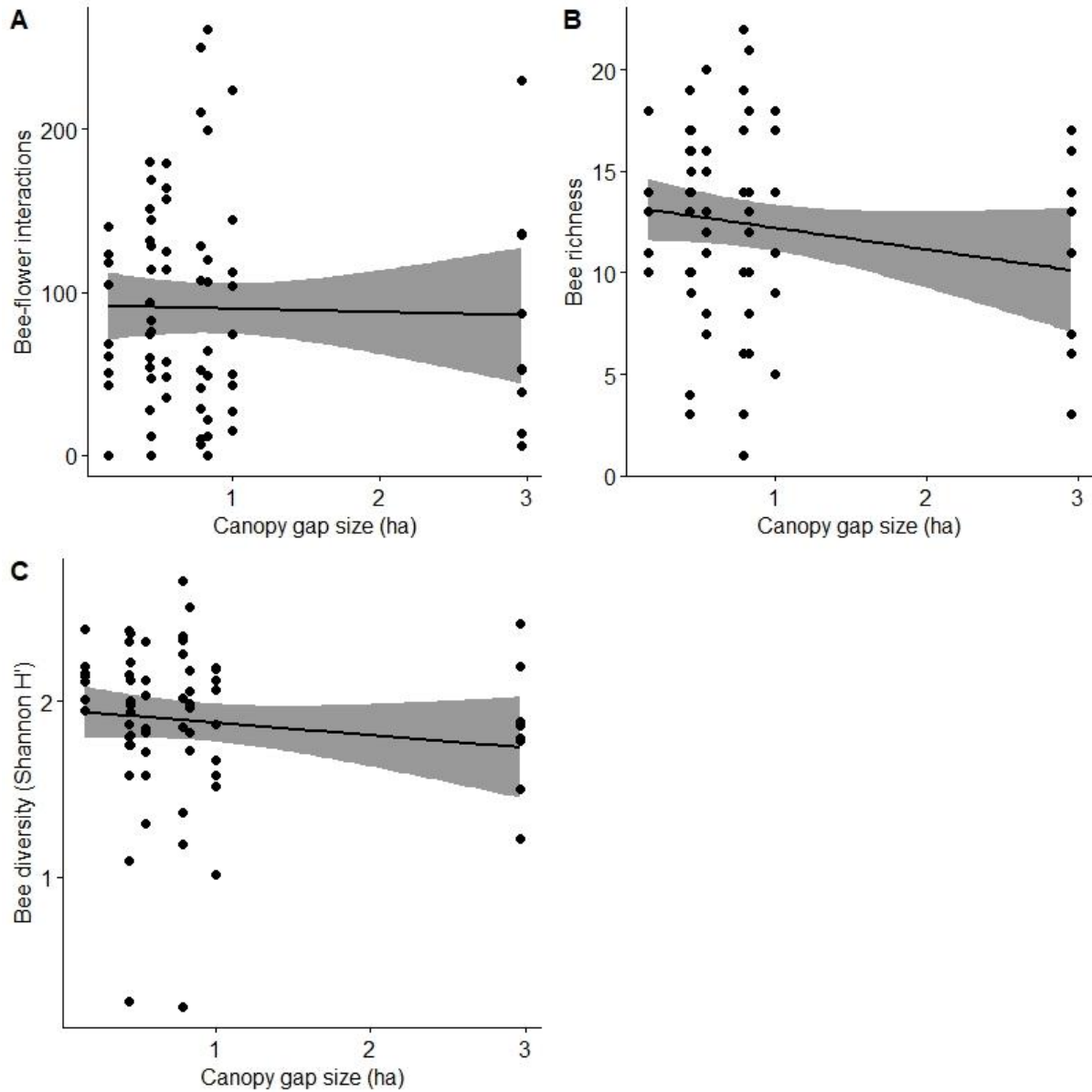


Figure S2.4. Relationship between bee population variables and canopy gap size (ha). Linear regressions between (A) bee-flower interactions/bee abundance, (B) bee species richness, and (C) bee Shannon H' diversity. Circles represent each site-day sampling period. Shaded areas denote 95% confidence intervals of regression models.

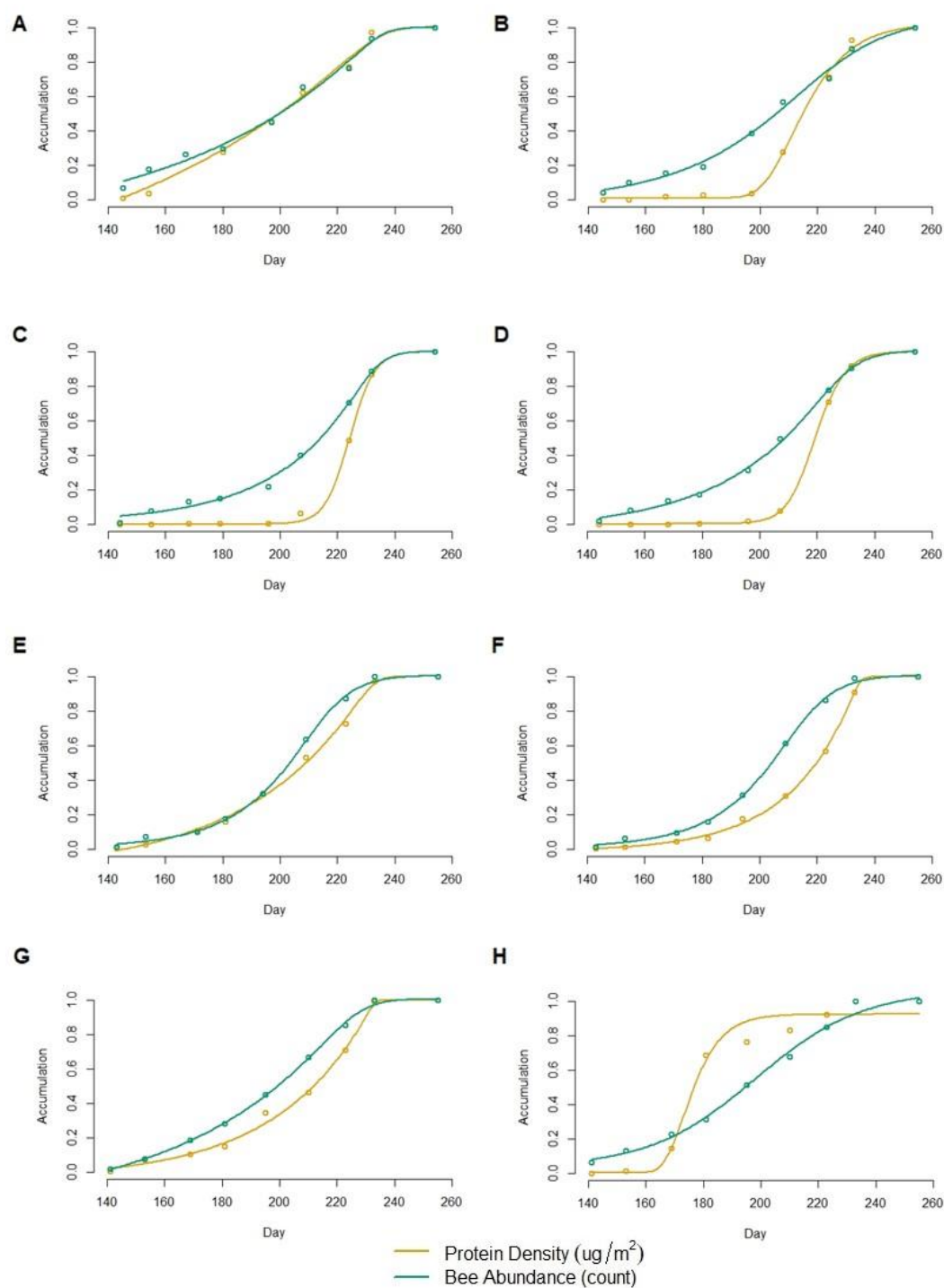


Figure S2.5. Comparison across sites of accumulation of protein density and bee abundance over the growing season. A-H show logistic curves for sites 1-8 respectively. Orange lines show accumulation of protein density ($\mu\text{g}/\text{m}^2$) across each site; green lines show accumulation of bee abundance (count).

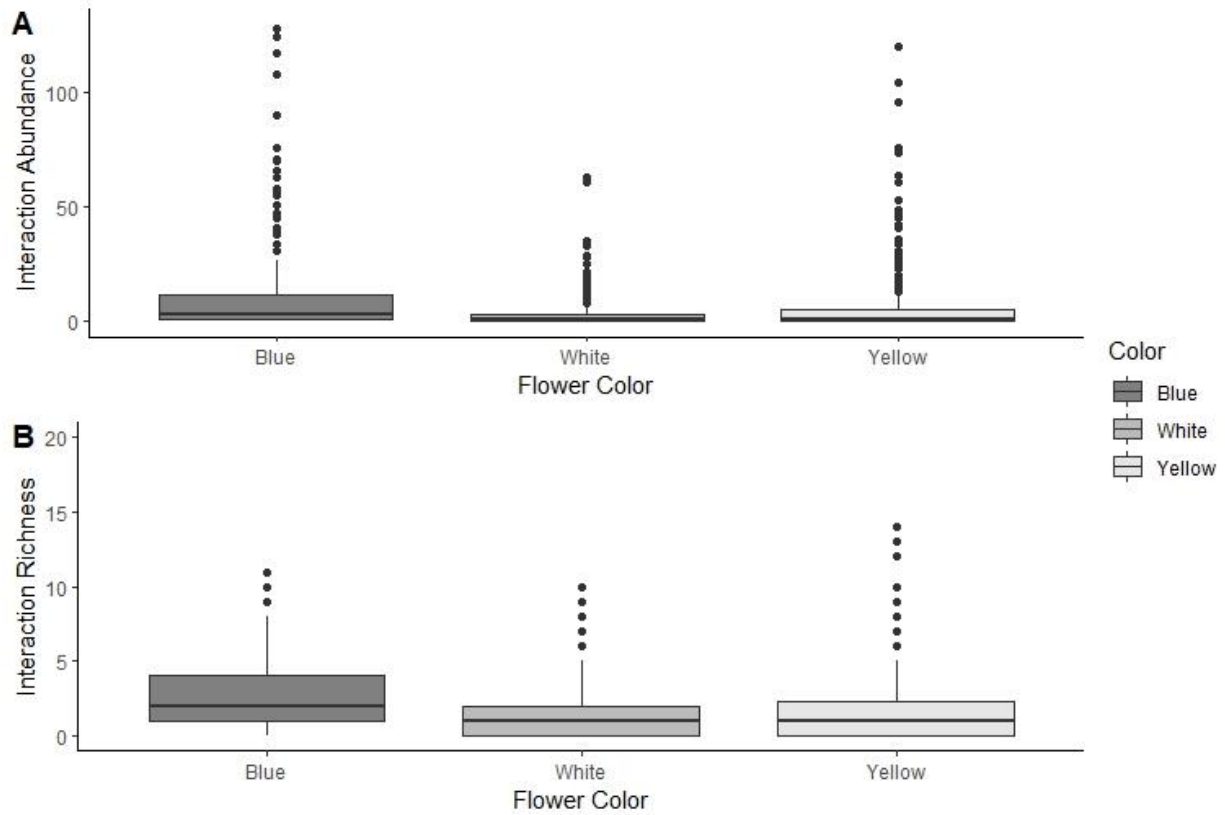


Figure S2.6. Comparison between flower colors and (A) interaction abundance and (B) interaction richness. Flower colors grouped by blue (includes pinks, purples, and blues), yellow (including orange and yellow), and white. Black circles represent outliers.