DISSERTATION

HABITAT VARIATION EFFECTS ON CAVITY-NESTING BEE FITNESS, COMMUNITY ASSEMBLAGES, AND PARASITE INTERACTIONS IN THE COLORADO FRONT RANGE

Submitted by

Jessie M. Dodge

Department of Forest and Rangeland Stewardship

In partial fulfillment of the requirements

For the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Fall 2024

Doctoral Committee:

Advisor: Thomas S. Davis

Sara M. Galbraith
Mark Paschke
Jane E. Stewart

ABSTRACT

HABITAT VARIATION EFFECTS ON CAVITY-NESTING BEE FITNESS, COMMUNITY ASSEMBLAGES, AND PARASITE INTERACTIONS IN THE COLORADO FRONT RANGE

Although many dry forested ecosystems in the western US are shaped by disturbances like wildfire and forest management treatments, little is known about their effects on native solitary bee fitness. This is an important knowledge gap, as most bees in the western US are solitary and are crucial for pollination in forested ecosystems. Therefore, I test how wildfire and forest management treatments affect cavity-nesting solitary bee fitness traits including diet breadth and quality, provisioning ability, reproduction and brood development, parasite abundance, and community network metrics. This was done by deploying artificial nesting boxes in the ponderosa pine forest of Boulder County, CO that either burned at higher severity, thinned by hand, or were unburned and untreated control. For my first two chapters, I used the solitary bee, *Osmia lignaria* as a model species to evaluate bee fitness responses to variations in forest structure, floral density, and climatic conditions. I found that *O. lignaria* foraged for pollen from specific flora, regardless of on-site presence, which was affected by climate and forest structure, but effects varied from year to year. Otherwise, habitat variation did not affect *O. lignaria* nest provisioning, reproduction, or development. However, the abundance of their kleptoparasite, *Tricrania stansburyi*, decreased with increased wildland urban development. Finally, in my last chapter, I utilized artificial nest boxes to collect local cavity-nesting bees and wasps to compare differences in community composition, host-parasite interactions, and emergence rates among

Burned, Control, or Treated sites. The solitary bee, *Osmia calla* was found to be the most abundant species, indicative of burned sites whereas the kleptoparasite, *Nemognatha sparsa*, and parasitoid, *Monodontomerus spp.*, were the most abundant parasites found within all habitat types. Control sites were found to have the most host-parasite interactions, with parasites exhibiting more generalist relationships with hosts, followed by treated sites, with burned sites having the most specialized host-parasite interactions. Collectively, my results demonstrate that disturbance-caused habitat variations had little effect on the fitness of the solitary bee, *O. lignaria*, despite affecting their access to nutritional opportunities, suggesting they can reproduce within various dry, mixed conifer forested habitats. However, urbanization in forested ecosystems likely decreases exposure to nest parasites. Alternatively, local, cavity-nesting bee-parasite interactions differed among habitat types, with hosts inhabiting control sites portraying more parasitic pressure. Thus, some cavity-nesting bee species may be more influenced by habitat variations than *O. lignaria*, and this is likely mediated by interactions with parasitic species. The interacting effects of disturbances and parasite pressure on bee fitness found here can be used to inform native bee conservation strategies. For one, floral surveys may not reflect floral species bees are using for foraging so alternative methods investigating pollen sources bees are using for forage are suggested. Secondly, the loss of natural habitat with increasing urbanization within forested habitats can decrease kleptoparasite abundance but provide early season solitary bees with additional foraging sources. Finally, cavity-nesting bees and wasps in unburned and untreated habitats demonstrate higher parasitic pressure than burned and treated habitats, suggesting habitat variations caused by these disturbances may relieve parasitic pressure. Overall, monitoring bee parasite abundance may indicate healthy pollinator habitats within the forests of the Colorado Front Range.

ACKNOWLEDGEMENTS

I have received tremendous support and assistance from many people in the work presented here. First and foremost, I would like to express my gratitude to my advisor, TS Davis, for his guidance, advice, encouragement, and support. I am grateful to my committee member SM. Galbraith for her invaluable study design assistance, and for inspiring my research on wildfire effects on bees. Additionally, I am grateful to JE. Stewart for taking the time to mentor me on parasite and pathogen research and to M. Paschke for helping broaden my knowledge of ecology. I also appreciate J. Mola for including me in his lab meetings and pollinator "nerd" groups, as well as C. Stevens-Rumman, P. Fornwalt, and R. Gelles special thanks for their aid in the initial site selections.

I want to extend special thanks to the numerous field and lab technicians who assisted in data gathering and processing, including N. Comai, J. Ditzel, A. Fairchild, A. Hastings, GC Ohlson, and M. Perez. Lastly, I also want to express my gratitude to V. Scott and G. Jolma from CU Boulder for their invaluable assistance in guiding us with bee identification. I appreciate the support and guidance provided by Chris Wanner from the City of Boulder Open Space and Mountain Parks (OSMP), and Stefan Reinold, Therese Glowacki, and Nick Stremel from Boulder County Parks and Open Space (BCPOS), for granting us access and field assistance. Funding for my dissertation projects was provided by various sources, including the McIntire-Stennis Cooperative Forestry Research Program awarded to TS Davis and S Galbraith, and the USDA-NIFA Award 2020-67013-31864 awarded to TS. Davis, and the Boulder County Nature Association (BCNA) research grant awarded to JM. Dodge.

DEDICATION

To Devyn who has been my biggest supporter and kept me going when I wanted to quit.

To my friends and officemates (including my cats) who reminded me of the importance of taking breaks.

To myself for having a dream that seemed so unobtainable to one with my socioeconomic background yet fought to achieve it anyway.

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CHAPTER 1

INTRODUCTION

Animal pollinators are crucial in maintaining plant abundance and diversity (Ollerton, Winfree, and Tarrant 2011), directly impacting the genetic structure of plants (Burkle, Marlin, and Knight 2013) and shaping ecological networks (Loveless and Hamrick 1984). Bees are the predominant animal pollinators in most ecosystems and are responsible for most crop pollination (Winfree 2010). Nevertheless, in the past few decades, there has been a recorded decline in pollinators globally, with habitat loss being the primary cause of bee declines (Potts et al. 2010; Murray, Kuhlmann, and Potts 2009). As human populations continue to grow, land-use changes such as agriculture, grazing, logging, and developments, have also led to an increase in fire suppression efforts that change fire regimes (Johnstone et al. 2016; Hessburg, Agee, and Franklin 2005; Westerling et al. 2006) and, consequently, habitat structure (Carbone et al. 2019). The higher suppression efforts in conjunction with climate change have also led to more frequent and higher severity wildfires within western US forests (Johnstone et al. 2016; Hessburg, Agee, and Franklin 2005; Westerling 2016; Brown, Hall, and Westerling 2004). Land managers often use forest management treatments to mimic wildfire effects in fire-prone ecosystems, while also reducing wildfire risk (Fulé, Covington, and Moore 1997; Agee and Skinner 2005; Covington and Moore 1994; Covington et al. 1997). However, the effects of wildfire and forest management treatments on bee health and network interactions remain limited (Rivers et al. 2018). Given the significance of bees to floral communities, it's crucial to assess the impact of restoration treatments and wildfires, not only on plant-pollinator community networks, but also on bee fitness (Lopez-Uribe, Ricigliano, and Simone-Finstrom, 2020).

In North America, pollinator habitat conservation has been found to be very important and well established, but the effects of habitat variations on pollinators remains incomplete (Dicks et al. 2021). Few studies in temperate coniferous forests focus on habitat variations caused by wildfire or forest treatment effect on pollinators (Rivers et al. 2018; Carbone et al. 2019). Additionally, those studies tend to focus on effects on bee communities (Rivers et al. 2018), with fewer studies focusing on crucial bee fitness traits (Lopez-Uribe, Ricigliano, and Simone-Finstrom 2020), including brood development, reproduction (Galbraith, Cane, and Rivers 2021), diet (Simanonok and Burkle 2020), and parasitism (Forrest and Chisholm 2017).

Bees are fundamental in maintaining and promoting floral diversity and persistence in forested ecosystems (Ollerton, Winfree, and Tarrant 2011), particularly in open canopy conifer forests (Ulyshen et al. 2024). In return, these ecosystems provide foraging resources and nesting substrates for bee pollinator habitats (Hanula, Ulyshen, and Horn 2016; Rivers et al. 2018). However, open canopy conifer forests historically experienced frequent, low-severity wildfires (Moore, Covington, and Fulé 1999; Fulé, Covington, and Moore 1997) and without disturbances like wildfire or management treatments, forests become overcrowded and provide bees with fewer resources (Ulyshen et al. 2024). Thus, examining the impact of disturbances, such as wildfire and management interventions, is important for bee fitness within forested ecosystems. Such knowledge can help us understand key environmental drivers of bee fitness, inform land managers, and improve pollinator conservation efforts.

Here, I address the impact of habitat variations caused by wildfire and management treatments on bee fitness traits in dry, mixed conifer forests. In my first chapter, I explored how habitat variations caused by wildfire and forest thinning treatments affect the diets of the solitary bee, *Osmia lignaria*. Variations within *O. lignaria* foraged-pollen community assemblages and pollen protein content were investigated and compared to floral assemblages near their nests. The effects of diet content on *O. lignaria* reproduction and development were also tested. My second chapter addresses how disturbance-caused habitat variation affects *O. lignaria* nest provisioning and the abundance of their kleptoparasites, *Tricrania stansburyi*. Subsequently, I looked at kleptoparasitism rates in *O. lignaria* nests and how kleptoparasitism affects *O. lignaria* brood abundance and development. Lastly, my third chapter investigates the effects of habitat variation on cavity-nesting bees and parasite communities. I compared bee and wasp community assemblages among habitat types and host-parasite interactions within each habitat type are explored. I then determined emergence differences among species. My research demonstrates the variety of solitary cavity-nesting bee and wasp responses to habitat variations and, subsequently, the complex effects of diet and parasitism on bee fitness.

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CHAPTER 2

HABITAT VARIATION EFFECTS ON A CAVITY-NESTING BEE DIET BREADTH AND QUALITY

Introduction

Both anthropogenic and natural disturbances can shape bee community assemblages (Gelles, Davis, and Barrett 2023; Gelles, Davis, and Stevens-Rumann 2022; Davies, Davis, and Griswold 2023; Thapa-Magar, Davis, and Kondratieff 2020; Thapa-Magar, Davis, and Fernández-Giménez 2022; Ponisio et al. 2016). Disturbances that cause habitat loss or fragmentation, such as urbanization, can limit resources available to wild bees (Bommarco et al. 2010), including nesting substrates and forage availability (Donaldson et al. 2002; Howell, Alarc, and Minckley 2017; Driscoll et al. 2021; Rahimi, Barghjelveh, and Dong 2022). Although, other disturbances such as wildfire and restoration treatments in forested ecosystems, can improve bee habitats by providing more nesting substrates (Ulyshen et al. 2021; Gelles, Davis, and Stevens-Rumann 2022) and forage diversity and abundance (Dodson, Peterson, and Harrod 2008; Rossman et al. 2018; Metlen and Fiedler 2006), leading to increased bee diversity and abundance (Davies and Davis 2023; Thapa-Magar et al. 2023; Gelles, Davis, and Barrett 2023; Ponisio et al. 2016). However, the impact of disturbances on bee's diet and access to nutrition, and consequentially, their fitness, is not fully understood.

Pollen diversity and quality are crucial aspects of bee nutrition, with consequences for bee reproduction (Tasei and Aupinel 2008) and development (Di Pasquale et al. 2013; Bommarco et al. 2010). Bee larvae require both protein and carbohydrates in the form of pollen and nectar, respectively (Vaudo et al. 2015). Protein-rich pollen has been shown to increase bee larvae development (Tasei and Aupinel 2008) Pollen may have additional impacts on bee health, with microbes within pollen influencing rates of pathogen infection (Di Pasquale et al. 2013; Bryś, Skowronek, and Strachecka 2021; Adler et al. 2021; Fowler, Irwin, and Adler 2020; Fowler et al. 2020). Some studies suggest that because nutrition quality varies between pollen sources, bees may distinguish between high and low pollen quality when foraging (Hanley et al. 2008; Rasheed and Harder 1997). As pollen quality varies among floral resources, diet diversity can thus impact bee health as well, with larvae fed on higher-diversity diets having access to more nutrients, resulting in larger body mass (Tasei and Aupinel 2008; Bryś, Skowronek, and Strachecka 2021). Given that bees are central place foragers, transporting resources to their nests multiple times a day (Zurbuchen et al. 2010), the abundance and diversity of nutrients available within the plant community near their nest can significantly influence bee fitness.

Forage within forested bee habitat can thus vary depending on physiography, disturbance, tree stand structure, and climate. Topographic factors such as elevation, slope, and aspect can lead to differences in forest structure (Lentile, Smith, and Shepperd 2006; Lydersen and North 2012), fire severity (Beaty and Taylor 2001), and microclimates (Abella and Denton 2009; Zellweger et al. 2020). For example, in mixed-conifer forests of the western US, tend to be more mesic in northeastern facing aspects and xeric in southwestern facing aspects, making stands in southwestern slopes more likely to experience frequent wildfires (Beaty and Taylor 2001) and tree regeneration less likely (Stevens-Rumann and Morgan 2019; Ziegler et al. 2017). Increased slopes can also lead to increased wildfire severity (Stevens-Rumann and Morgan 2019). The combination of topography, disturbances, forest structure, and understory microclimates can thus lead to variations in bee habitat (Stangler, Hanson, and Steffan-Dewenter 2015; Bentrup et al. 2019). Therefore, it is important to understand how habitat variations caused by disturbances affect access to forage quality, with potential indirect effects on bee fitness.

Here I test how forest disturbances from wildfire and restoration treatments affect the composition and protein content of collected *Osmia lignaria* (Hymenoptera: Megachilidae; blue orchard bee) pollen provisions, with subsequent impacts on reproduction. *Osmia lignaria* is a North American native solitary cavity-nesting species (Rust 1974) with a wide foraging range (Palladini and Maron 2014; Greenleaf et al. 2007; Williams and Tepedino 2003). *Osmia lignaria* are commercially cultivated as pollinators, mostly in fruit-tree agricultural systems, and readily uses artificial nesting structures (Bosch and Kemp 2001). The study sought to answer the following questions: 1a) What plants are *O. lignaria* collecting pollen from and b) how does the species composition of provisions relate to local floral assemblages; 2) How is the species composition of collected pollen affected by habitat variations, including habitat type, topography (i.e. aspect, elevation, slope), tree stand composition (i.e. basal area, canopy cover), and climate (i.e. temperature and precipitation); and 3) Do pollen provisions metrics (i.e. richness, diversity, or protein content) predict bee reproduction? Answering these questions can improve our understanding of how habitat variation affects bee fitness, leading to better pollinator habitat management.

Methods and materials

Study area

Study sites were distributed in stands of dry mixed conifer montane forests in Boulder County, Colorado, (Figure 2.1) within Boulder County Parks and Open Space (BCPOS) and City of Boulder Open Space & Mountain Parks (OSMP) public land. Selected sites were dominated by ponderosa pine (*Pinus ponderosa* P. & C. Lawson), intermixed with Douglas fir (*Pseudotsuga menziesii* Mirb.) across an elevational range of 1800 – 2600 m above sea level. As Boulder County is one of the highest wildland-urban interface (WUI) counties in the country (Gude, Rasker, and Van Den Noort 2008), sites were distributed within the WUI at least 100 m away from roads, trails, or urban structure. Across the study region, the 30-year mean annual high and low temperatures were 15.0 ± 0.3 °C and 1.5 ± 0.2 °C, respectively, with 555.8 ± 3.3 mm of precipitation (PRISM Climate Group 2023). Most precipitation occurs in May (84.0 ± 0.8 mm) and the warmest and coldest months are July (mean temperature= 20.0 ± 0.2 °C) and December (mean temperature= -0.8 ± 0.2 °C, PRISM Climate Group 2023).

In 2020, fifteen study sites (Figure 2.1) were distributed at least 100 m apart within stands that experienced: (1) ≥80% tree canopy mortality from wildfires ('Burned', n= 5 sites; Key and Benson 2006); (2) tree density reduction treatments ('Thinned', n=5 sites; Stevens-Rumann and Fornwalt 2018); and (3) unburned and untreated sites ('Control', n=5 sites). Post-fire sites included areas within the Fourmile Canyon Fire (2010), Dome Fire (2010), Maxwell Fire (2011), and Flagstaff Fire (2012) burn perimeters. Thinned sites were hand-thinned between 2008-2012 for ecological restoration and fire-risk / fuel reduction purposes (Figure A1.1). In 2021, six of the original sites were excluded: three were burned in the 2020 Cal-Wood Fire, and three were excluded to increase the minimum distance between sites from 100 meters to 500 meters. Although *O. lignaria* typically forages within 100 meters of their nests (Bosch and Kemp 2001), they can forage up to 1 kilometer from their nests (Greenleaf et al. 2007; Guédot, Bosch, and Kemp 2009; Williams and Tepedino 2003). As a result, nine of the original sites were revisited in 2021, and 15 new sites were added, bringing the total to 24 sites with eight sites per habitat type (Figure 2.1).

Field methods

Nesting block deployment

Two 32-hole Binderboards^{TM} (Pollinator Paradise, Parma, ID) fitted with pre-slit glassine paper nest tubes (0.79 cm internal diameter) that were 15.40 cm in length (Jonesville Paper Tube Corp., Jonesville, MI) were used as nesting blocks and mounted at each site on metal T-post at ~1 m above ground. *Osmia lignaria* subsp. *propinqua* cocoons were obtained from a regional commercial vendor (Mountain West Mason Bees Riverton, UT). Cocoons containing pre-emergence *O. lignaria* were distributed into capped PVC emergence tubes (15.2 cm length × 1.9 cm diameter) fixed just below nesting blocks, at a ratio of 60: 40% male: female. In each emergence tube, a 6-mm diameter hole was drilled at one end through which bees could emerge, and bees emerged naturally from tubes following deployment in the field. In 2020, emergence tubes containing 15 male, and 10 female mason bees were affixed to nesting blocks between May 12 and 13; in 2021 emergence tubes contained 20 male and 16 female cocoons and were affixed to nesting blocks between May 24 and May 27 (Figure A1.2).

The nesting blocks were surveyed seven weeks after deployment in 2020 and three weeks after deployment in 2021. During each survey, two occupied nesting chambers with pollen provisions (if present) were randomly selected for pollen extraction. These samples were then placed on ice and stored at -20°C until further processing. Nesting blocks in 2020 were collected from study stands between July 26 and July 27 and nesting blocks in 2021 were collected between June 28 and July 1. Once in the lab, nesting blocks with inhabitants were placed in an enclosed box and kept at a constant ambient temperature (20 °C) to allow for development. In early November of each study year, nest tubes were removed using soft forceps, placed in plastic bags, and stored at -20 °C until further processing.

Habitat structural measurements and floral surveys

Circular fixed area plots (0.02 ha radius) were used to quantify stand structural characteristics including tree densities, stand basal area, species composition, and mortality status (live or dead). Only trees with a DBH > 10 cm were included in calculations of stand basal area, stand density, and stand species composition (Dodge et al. 2019). To estimate canopy cover, pictures were taken from the ground surface facing the canopy using a Samsung Galaxy S10+ phone on a flat surface 1 m from each nest box in each cardinal direction (n=16 per site in 2020, n=8 per site in 2021). Before taking photographs, the camera angle was adjusted to 0° using the level function. Recent methodological studies indicate that this approach of photographing the canopy using smartphone platforms yields reliable estimates of tree canopy cover (Smith and Ramsay 2018). Images were imported into ImageJ to calculate tree canopy cover, as described in Davis and Comai (2022). Canopy cover measurements were averaged together to yield a single site-level mean (Figure A1.1).

Floral resources were also surveyed, as floral abundance and richness are strongly linked with diversity and performance of bee assemblages (Kraemer, Oise, and Favi 2005; Palladini and Maron 2014; Hanula, Horn, and O'Brien 2015; Williams and Kremen 2007; Roulston and Goodell 2011). In 2020, understory floral density and species richness were measured using eight 1-m^2 quadrats: two were placed around each nesting block and 15 m upslope and downslope from the stand center with one quadrat 5 m to the west and one 10 m to the east of the transect (8 m^2 sampled per site; Figure 2.2). In 2021, a 25-× 2-m belt quadrat was placed between the two nest boxes (50 m^2 sampled per site). The number of stems of each forb plant species within each quadrat was recorded between July 16 – and Aug 1, 2020. In 2021, all stems of actively flowering understory plants were counted between May 27 and June 11.

Topographic and climatic metrics

Topographic variables including slope, aspect, and heat load index (HLI, a proxy for temperature and incident radiation) were also recorded for each site as these factors relate to thermal conditions and may have strong effects on bee forage availability and reproductive output (Bosch and Kemp 2004; Kemp and Bosch 2005; Radmacher and Strohm 2010; 2011; CaraDonna, Cunningham, and Iler 2018; Forrest and Chisholm 2017). Slope and aspect were extracted for each site using U.S. Geological Survey Earth Resources Observation and Science (USGS/EROS) slope and aspect files (USGS/EROS 2003) in ArcMap pro. Aspects were transformed following McCune and Keon (2002) such that 0 represented northeast-facing slopes and 180 represented southwest-facing slopes, classifying stands across a gradient of cool/wet to warm/dry. The heat load index (HLI) was then calculated for each stand using the equations of McCune and Keon (2002).

Landscape-level vegetation metrics for the study area were acquired using Existing Vegetation Type (EVT) data from LANDFIRE (LANDFIRE 2022). ArcMap Pro was used to convert the EVT raster to points and join point classification cells to a 500 m buffer around each site using slope and aspect files to account for surface cost distances. Cell counts of EVTs were categorized into broader landscape categories (Table 2.1). Afterward, cell counts for landscape categories were summarized within each site buffer and relativized using the function decostand in the R "vegan" package (Oksanen J. et al. 2022) to determine the proportion of each EVT within each site buffer. Landscape categories absent in 4 or more sites were omitted (i.e. Crops and Barran).

Climate variables include average precipitation (mm) and temperatures (°C) between January and June for 2020 and 2021 were also extracted within an 800 m radius around each site using PRISM Climate Group (PRISM Climate Group 2023). Accumulated growing degree days using a base temperature of 5°C (Pitts-Singer et al. 2008), were also calculated across study sites for the duration of each nest in the field; 63 ± 3 (mean ± standard error) in 2020, and 36 days in 2021 (Table 3.1).

Laboratory procedures

Pollen provisions collected from nest chambers as pollen samples (see above) were isolated, cleaned, homogenized, and pooled to the site level following methods described by Arstingstall et al. (2021). Once dried, homogenized pollen samples were divided into two equal subsamples.

One pollen subsample was used to determine pollen protein concentrations using the Bradford assay following procedures outlined in Vaudo et al. (2016). The other pollen subsample was sent for DNA metabarcoding (Jonah Ventures, Boulder, CO). Genomic DNA was obtained using the DNeasy 96 PowerSoil Pro Kit. Subsequently, a portion of the chloroplast trnL intron was PCR amplified using specific primers (Taberlet et al. 2007). The resulting amplicons were visually inspected using 2% agarose gel and cleaned before a second round of PCR was performed to integrate Illumina sequencing adapters and index sequences. The indexed amplicons were purified, normalized, and pooled to create library pools for sequencing on an Illumina MiSeq. Quality control was conducted before sequencing. Following sequencing, the reads were demultiplexed and merged before removing primer sequences and discarding low-quality reads. Reads affected by sequencing and PCR errors were removed using the unoise3 algorithm. Taxonomy was then assigned to each exact sequence variant (ESV) by mapping against reference data, and consensus taxonomy was generated. Only DNA sequencing reads that were identified to genus and had a 97 % match or higher were used. Sequencing depth of pollen DNA reads were compared between years (Figure A1.3).

Frozen bees were thawed, sorted by sex, and developmental stage (larvae or pupae) recorded. Cocoons from pupae were removed using forceps and tweezers, and pupae were then oven-dried and weighed to the nearest mg. All *O. lignaria* inhabitants (larvae and pupae) per straw were summed across the two blocks in each study stand to estimate total reproduction (total offspring). *Osmia lignaria* pupal weights were averaged across both nesting blocks in each stand as a corollary for ‘fitness’ (Calow 1977; Kim 1997; McCabe et al. 2021; Bosch and Kemp 2004).

Statistical analyses

The abundances of pollen, site floral, and landscape categories were relativized using the ‘decostand’ function in the “vegan” R package (Oksanen J. et al. 2022). Species area curves were made for both pollen and site floral within each year (Figure A1.4). Relativized abundances for pollen genera communities were used as a proxy for pollen genera proportions (%) within a site. Likewise, relativized abundances for landscape categories were used as a measure of landscape category proportions within a site. Richness and Pielou’s measure of species evenness were then calculated for pollen and floral communities and landscape type. Shannon’s diversity index was calculated using the ‘diversity’ function in the “vegan” R package (Oksanen J et al. 2022).

Distance-based tests were used to determine relationships between pollen communities collected by *O. lignaria* and site floral plant communities (Q1a). A Permutational Multivariate Analysis of Variance (PERMANOVA) was used to compare plant communities by source (either pollen or site floral), year (2020 or 2021), and the interaction between sources and year using the ‘adonis2’ function in the “vegan” R package (Oksanen J et al. 2022). A non-metric multidimensional scaling (NMDS) ordination was used to display the source/year relationships, using the Bray Curtis dissimilarity index and 999 Monte Carlo permutations. To determine what floral plant genera were more abundant (i.e. “indicative”) within each year and source and further determine what flora *O. lignaria* were foraging from (Q1b), an Indicator Species Analysis (Dufrêne et al. 1997) was performed using the “indicspecies” packages (De Cáceres and Legendre 2009).

A PERMANOVA was also used to test whether habitat variation affects pollen community assemblages within each year (Q2). However, to test which habitat variables explained the most variation within the pollen community without overfitting models, a distance-based Redundancy Analysis (db-RDA; Legendre and Andersson 1999) was run on principal coordinates derived from a Principal Coordinates Analysis (PCoA) using the Bray Curtis dissimilarity index and 999 Monte Carlo permutations, was first conducted (see Table A1.1 for a complete list of variables). Likewise, variables found to be multicollinear were omitted before implemented into the PERMANOVA model using the "vif.cca" goodness of fit function within the "vegan" R package (Oksanen J et al. 2022).

Lastly, pollen diversity, richness, and protein concentration were used as predictor variables to assess if pollen traits predicted bee fitness traits (Q3). Bee fitness traits included *O. lignaria* ratio (number of *O. lignaria* offspring that reached 2nd larval stage or higher / total number of provisioned cells), *O. lignaria* sex ratio (number of female *O. lignaria* offspring / total number of provisioned cells), and *O. lignaria* larvae mass (in 2020), male pupae mass (both years), and female pupae mass (2021). A Generalized Linear Model (GLM) with a Gaussian distribution was used to predict how pollen metrics affected all *O. lignaria* fitness traits, except for female pupae weight where, based on the histogram, a Gamma distribution was used. Sites with no pollen provisions, successful *O. lignaria* offspring growth, or positive protein concentration readings (i.e. non-true zeros) were omitted when analyzing Q3.

Results

What plants are O. lignaria collecting pollen from and how does the species composition of provisions relate to local floral assemblages?

In 2020 and 2021, there were 36 and 37 genera, respectively, identified in the pollen provisions collected by *O. lignaria* (Table A1.2). In contrast, 52 and 28 genera were found in the site flora communities in 2020 and 2021 (Table A1.3). The assemblage of plant genera represented in pollen provisions varied by year, source, and the interaction between year and source (Table 2.2, Figure 2.3). Pollen communities in 2020 had 11 significant indicator genera, dominated by *Berberis* spp., *Cerastium* spp., *Quercus* spp., and *Physocarpus* spp., and pollen communities from both years had 7 indicator genera, mostly dominated by tree pollen, but there were no significant indicator genera for 2021 pollen communities (Table 2.3, Figure 2.4). Similarly, there were more indicator genera for 2020 site flora communities than for 2021 flora communities (18 and 5, respectively), where *Achillea* spp*., Galium* spp*., Geranium* spp*., Lepidium* spp*.,* and *Symphoricarpos* spp. were the most abundant in 2020 and *Lomatium* spp*., Physaria* spp*.,* and *Erysimum* spp. were the more abundant in 2021. There were only 2 genera that were indicators for both study years; *Campanula* spp. and *Taraxacum* spp. Interestingly, the majority of genera *O. lignaria* foraged pollen from were from the Salicaceae and Rosaceae families, whereas local site flora were mostly within the Apiaceae, Asteraceae, Brassicaceae, Campanulaceae, Ericaceae, and Liliaceae families.

How is foraged pollen species composition affected by habitat variation?

In 2020, mean precipitation (mm) and mean temperature (°C) from Jan-July, transformed aspect, slope, and mean tree canopy cover (%), and landscape richness were all found to explain foraged pollen community variation (db-RDA adjusted r^2 = 66.8 %). However, only mean temperature (°C) from Jan-July and landscape richness were found to explain foraged pollen community variation in 2021 (db-RDA adjusted r^2 = 10.4 %). The 2020 db-RDA ordination found that three axes explained the most variation (82.1 %) within 2020 foraged pollen communities, where axis 1 was 53.9 %, axis 2 was 27.0 %, and axis 3 was 0.130 %.Transformed aspect (Table 2.5, Figure 2.5) and the 2020 pollen indicator genus *Berberis* spp. were found to be passively associated with both axes (Table A1.4) whereas mean tree canopy cover, average Jan-July precipitation, and the pollen indicator genera *Cercocarpus* spp. and *Salix* spp. were positively correlated with axes 1. This suggests that *Berberis* spp., *Cercocarpus* spp., and *Salix* spp. pollen was more abundant in areas with warmer aspects, higher mean tree canopy cover, and higher precipitation.

The 2021 db-RDA ordination found that two constrained axes explained 20.9 % of the variation, but most variation was explained by unconstrained axes (79.1%). Constrained axis 1 explained 18.4 % and axis 2 explained 2.5 %. of the 20.9% variation within 2021 foraged pollen communities. Average Jan-July temperature was positively correlated with axes 1 but negatively correlated with axis 2, whereas landscape richness was positively correlated with both axes. Likewise, the significant pollen indicator genus, *Cercocarpus* spp. was also positively correlated with axes 1 and negatively correlated with axis 2, suggesting foraged *Cercocarpus* spp. was more abundant in areas with higher temperatures in 2021 (Table A1.4). Interestingly, the significant pollen indicator genus, *Salix* spp., was negatively associated with both axes, suggesting that foraged *Salix* spp. in 2021 was more abundant in areas with lower temperatures and less landscape richness within 500 m of sites.

All habitat variables included in the 2020 model were found to predict pollen community composition except landscape diversity (Table 2.4, Figure 2.5). Inversely, the only habitat variable found to predict pollen community composition in 2021 was landscape diversity.

Does the pollen provision species richness, diversity, or protein content predict bee reproduction?

No pollen metrics were found to predict *O. lignaria* fitness traits (Table A1.5).

Discussion

The floral community composition represented within *Osmia lignaria* pollen provisions differed substantially from on-site floral assemblages across different stand treatments. Additionally, there were no indicator genera found within both foraged pollen and local site flora from either year, suggesting that *O. lignaria* were foraging for resources that were not found on site. *Osmia lignaria* have been found to forage long distances to collect tree pollen (Kraemer, Oise, and Favi 2005), specifically from *Salix* spp. (Williams and Tepedino 2003; Rust 1990). Very few of the floral species represented in pollen provisions were found near the bees' nests during the study (Table A1.2), further supporting our understanding that *O. lignaria* forages far afield for specific pollen sources. *Osmia lignaria* can travel up to 1 km from their nests (Williams and Tepedino 2003; Greenleaf et al. 2007; Guédot, Bosch, and Kemp 2009), and based on my study, may do so even when floral surveys show plentiful other resources near their nests. It is important to note that conifer species were significant indicator species identified in pollen communities in both study years. However, it is difficult to determine if conifer pollen was foraged for or if pollen was widely wind-dispersed and mixed with preferred forage pollen in large quantities.

The difference between flower species available surrounding nest sites and pollen provision contents was persistent despite different techniques being used to measure flowering species at the study site in 2020 and 2021. Although 2020 floral communities were more diverse with more indicator species than those in 2021 (Table 2.3, Table A1.6), indicating that 1-m^2 quadrats are better at capturing the flower diversity than belt transects. However, few preferred pollen sources were detected within either floral survey used (Figure 2.4, Table A1.2) suggesting that neither method was optimal in capturing *O. lignaria* forage preferences.

The later release of bees in 2021 compared to 2020 may have led to differences in forage availability, and thus differences in foraged pollen resources, richness, diversity, and protein seen between the two years. For example, many *Ribes* spp. in the area (e.g. *R. americanum* & *R. aureum*) bloom in mid-spring (USDA and NRCS 2024), were present in 2020 field surveys but not in 2021 (Table A1.3), indicating that the 2021 bees may have missed them. Similarly, the higher temperatures and lower precipitation in 2020 compared to 2021 (Figure A1.2) may have led to better foraging conditions (Forrest and Chisholm 2017).

Habitat variations were found to influence the species composition of foraged pollen provisions in both years, most notably landscape richness and mean temperatures from January to July. High severity wildfire (Strand et al. 2019; Burkle et al. 2015; Lentile et al. 2007; Ponisio et al. 2016) and restoration treatments (Morgan et al. 2015; Gelles, Davis, and Stevens-Rumann 2022; Heil and Burkle 2018; Kuenzi, Fulé, and Sieg 2008) have been shown to affect plant community assemblages. Thus, it is surprising that these habitat types (burned, treated, control) did not cause differences in pollen communities that *O. lignaria* foraged upon. Habitat type did cause variations in tree canopy cover (Figure A1.1), which was a predictor of foraged pollen communities in 2020, with higher tree canopy cover and warmer temperatures being correlated with more abundant *Berberis* spp., *Cercocarpus* spp., and *Salix* spp. pollen. This suggests foraging *O. lignaria* in 2020 were able to access preferred pollen sources associated with higher tree canopy cover, regardless of habitat type, including within burned patches. However, tree canopy cover did not predict foraged pollen community assemblages in 2021, even though *Cercocarpus* spp., and *Salix* spp. were abundant in 2021 foraged pollen as well (Figure 2.4, Table 2.3), suggesting interannual, or seasonal, habitat variations on bee diet composition.

As described earlier, many of the 2020 pollen indicator genera may have been post-peak flowering time when 2021 bees were released and thus were not a part of the 2021 pollen community. Farzan and Yang (2018) found that pollen diversity decreased steadily as the season progressed. Likewise, 2021 pollen provisions had lower diversity than 2020 provisions (Figure A1.5). This demonstrates the importance of early-season flowering plants for early-season bees (Kudo and Ida 2013; Malfi, Crone, and Williams 2019) and may foreshadow the effects of climate change on mismatched phenology (Kudo and Ida 2013; Farzan and Yang 2018; Forrest 2015).

Although increased pollen protein marginally increased the total provisioned cells in 2020, it was surprising to see that no other pollen traits affected *O. lignaria* fitness traits. Pollen protein content is essential for larval development (Roulston and Cane 2002; Westreich and Tobin 2024; Lawson, Kennedy, and Rehan 2021), but different bee species have different dietary requirements (Vaudo, Dyer, and Leonard 2024; Vaudo et al. 2020). Vaudo et al (2024) found that bees within the *Osmia* subgenus commonly interacted with around 3:5 protein-to-lipid ratios. Thus, differences in nectar might be more influential to *O. lignaria* fitness traits than protein alone (Williams and Tepedino 2003; Westreich and Tobin 2024). *Osmia lignaria* are generalists and will forage on available flowers (Kraemer, Oise, and Favi 2005), but suitable forage may decline as the season progresses (Farzan & Yang 2018). Many of the early-season flowering plants could contain more protein than later spring-season flowers, which were available to 2020-foraging *O. lignaria* but not 2021 foragers. However, there were no differences in total provisioned cells or brood count between 2020 and 2021 (Figure A1.6), despite less protein in 2021 pollen than in 2020 (Figure 2.6).

Osmia lignaria have been found to consistently mix pollen from several sources (Williams and Tepedino 2003). It is possible that each pollen species is nutritionally deficient but becomes nutritional when mixed. Low pollen mixing had been found to have little effect on *O. lignaria* provisioning rates or offspring fecundity (Williams and Tepedino 2003), as have low protein concentrations (Westreich and Tobin 2024). However, Farzan & Yang (2018) found a decrease in offspring count and mass of *O. lignaria* parents released mid-summer compared to spring. Therefore, if basic dietary needs are met, it appears that *O. lignaria* can reproduce viable offspring, regardless of habitat variation effects on pollen diversity, richness, and protein. content. However, the effects of habitat variations on pollen lipid concentrations (i.e. nectar) and the consequential effects on *O. lignaria* reproduction and development need to be further studied.

My results provide insights on generalist, cavity-nesting bee dietary preferences and variations caused by disturbances within dry, mixed conifer forests withing the Colorado Front

Range. Even though *O. lignaria* are generalists, my study demonstrates that they are willing to forage longer distances for preferred resources, despite having available pollen sources near their nests. Therefore, common floral survey methods (i.e. quadrates or belt transects), near cavity nesting bee nests, may not reflect floral sources within bee diets. Land managers may therefore need to use pollen identification methods (e.g. DNA metabarcoding or microscopy) to determine preferred foraging species and the habitat type associated with the preferred species (e.g. riparian areas for *Salix* spp.) within a landscape to better bee pollinator conservation efforts. Furthermore, we found habitat variations, but not type (burned, treated, control), influenced foraged pollen community assemblages in 2020 but not in 2021, suggesting temporal, either interannual or season, drivers. These findings highlight the importance of early season flowers for early season bee foragers and may have important implications for understanding the potential impacts of climate change on pollinator reproduction. Although we found no effects of *O. lignaria* diet variations on reproduction, this may not be true for other solitary bees. Future research in this area could further clarify the interconnectedness of habitat variations, diet, and pollinator fitness for other bee species, aiding in the development of targeted conservation and management strategies for sustaining healthy, local pollinator populations.

Tables

Table 2.1. Landscape category characterization of LANDFIRE Existing Vegetation Type (EVT).

Landscape Category	EVT
Barren	Rocky Mountain Cliff Canyon and Massive Bedrock
Coniferous Forest	Rocky Mountain Lodgepole Pine Forest, Rocky Mountain Subalpine Dry-Mesic Spruce-Fir Forest and Woodland, Southern Rocky Mountain Dry-Mesic Montane Mixed Conifer Forest and Woodland, Southern Rocky Mountain Mesic Montane Mixed Conifer Forest and Woodland, Southern Rocky Mountain Pinyon-Juniper Woodland, Southern Rocky Mountain Ponderosa Pine Savanna, and Southern Rocky Mountain Ponderosa Pine Woodland
Crops	Western Cool Temperate Pasture and Hayland
Deciduous Forest	Rocky Mountain Aspen Forest and Woodland and Rocky Mountain Lower Montane-Foothill Riparian Woodland
Rangeland	Great Basin & Intermountain Introduced Perennial Grassland and Forbland, Interior Western North American Temperate Ruderal Grassland, Southern Rocky Mountain Montane-Subalpine Grassland, Western Great Plains Foothill and Piedmont Grassland, Rocky Mountain Alpine-Montane Wet Meadow, Rocky Mountain Subalpine-Montane Mesic Meadow, Inter-Mountain Basins Montane Sagebrush Steppe, Rocky Mountain Gambel Oak-Mixed Montane Shrubland, and Rocky Mountain Lower Montane-Foothill Shrubland
Urban development	Developed -Low Intensity, Developed-Roads, Western Cool Temperate Developed Evergreen Forest, Western Cool Temperate Urban Evergreen Forest, Western Cool Temperate Urban Mixed Forest, Western Cool Temperate Urban Deciduous Forest, Western Cool Temperate Developed Herbaceous, Western Cool Temperate Urban Herbaceous, and Western Cool Temperate Urban Shrubland

Table 2.2. Summary of permutation adonis2 results testing the effects of study years – 2020 and 2021 (Year), source of community - pollen DNA and site floral stem (Source), and habitat type – sites burned at high severity, mechanically treated, and control (Habitat), and their interactions with each other on community composition. DF denotes degrees of freedom, bold face denotes significance at α = 0.05, whereas italic denotes marginal significance at α = 0.1.

Coefficients	**DF**	**Sum of Squares**	**R^2**	**F-value**	**P-value**
Year	1	1.187	0.040	3.400	**0.001**
Source	1	4.554	0.153	13.042	**0.001**
Year: Source	1	1.065	0.036	3.052	**0.001**
Residual	66	23.043	0.772		
Total	69	29.849	1		

Table 2.3. Significant genera found within year (2020 vs. 2021) – source (local site flora vs. foraged pollen) groups after an Indicator Species Analysis.

	Site flora			*Pollen*		
Group	**Genus**	***Statistic***	***P-value***	**Genus**	***Statistic***	***P-value***
2020	Achillea	0.683	0.001	Berberis	0.865	0.001
	Galium	0.683	0.001	Cerastium	0.655	0.001
	Geranium	0.682	0.001	Ribes	0.587	0.013
	Lepidium	0.575	0.001	Pseudotsuga	0.567	0.008
	Potentilla	0.574	0.004	Maianthemum	0.535	0.001
	Lupinus	0.572	0.003	Pelargonium	0.535	0.002
	Allium	0.528	0.021	Prosartes	0.535	0.003
	Symphoricarpos	0.503	0.01	Quercus	0.535	0.001
	Ceanothus	0.488	0.011	Populus	0.461	0.008
	Eriogonum	0.483	0.028	Physocarpus	0.455	0.01
	Phlox	0.47	0.015	Anemone	0.378	0.044
	Ambrosia	0.447	0.013			
	Arabis	0.447	0.014			
	Cirsium	0.447	0.02			
	Epilobium	0.447	0.021			
	Liliaceae	0.447	0.013			
	Opuntia	0.447	0.009			
	Verbascum	0.447	0.016			
2021	Lomatium	0.763	0.001	NA		
	Physaria	0.626	0.001			
	Erysimum	0.584	0.001			
	Alyssum	0.511	0.006			
	Stellaria	0.466	0.014			
Both	Campanula	0.513	0.016	Pinus	1	0.001
	Taraxacum	0.513	0.039	Cercocarpus	0.829	0.001
				Prunus	0.829	0.001
				Picea	0.771	0.001
				Acer	0.75	0.001
				Salix	0.63	0.003
				Rubus	0.504	0.045

Table 2.4. Summary of permutation adonis2 results testing the effects of habitat variables on pollen community composition sampled in each study year. DF denotes degrees of freedom and bold face denotes significance at $\alpha = 0.05$.

	Coefficients	**DF**	**Sum of Squares**	**R^2**	**F-value**	**P-value**
2020	Mean Jan-July precipitation (mm)	1	0.633	0.168	4.929	**0.008**
	Mean Jan-July temperature (°C)	1	0.550	0.146	4.284	**0.014**
	Transformed aspect	1	0.493	0.131	3.840	**0.019**
	Slope	1	0.466	0.124	3.627	**0.018**
	Mean tree canopy cover (%)	1	0.396	0.105	3.080	**0.036**
	Landscape richness	1	0.322	0.086	2.505	*0.065*
	Residual	7	0.899	0.239		
	Total	13	3.759	1		
2021	Mean Jan-July temperature (°C)	1	0.425	0.062	1.125	0.288
	Landscape diversity	1	0.737	0.108	1.952	**0.022**
	Residual	15	5.661	0.830		
	Total	17	6.823	1.000		

Table 2.5. Correlation coefficients associated with explanatory variables on the first 3 axes of db-RDA ordinations.

	Explanatory variables	**CAP1**	**CAP2**	**CAP3**
2020	Mean Jan-July precipitation (mm)	0.556	-0.642	0.070
	Mean Jan-July temperature (°C)	-0.042	0.507	-0.735
	Transformed aspect	0.587	0.120	-0.291
	Slope	-0.343	-0.467	-0.088
	Mean tree canopy cover (%)	0.326	-0.183	-0.054
	Landscape richness	0.059	0.346	0.736
2021	Mean Jan-July temperature (°C)	0.579	-0.815	NA
	Landscape diversity	0.553	0.833	NA

Figures

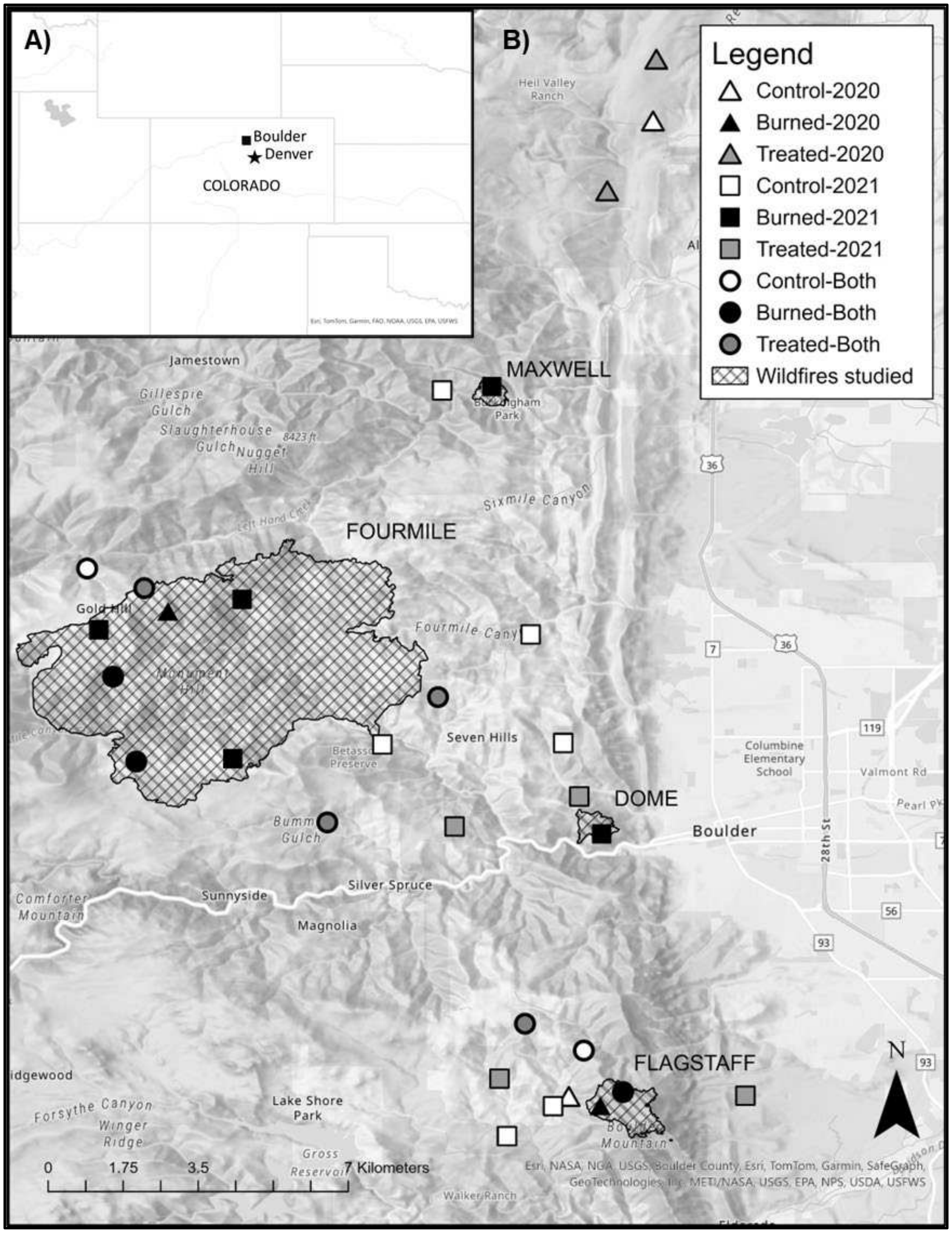

Figure 2.1. (A) Star shows the location of the study region within Colorado (near Boulder, CO); and (B) a map of study sites in Boulder County, Colorado. Site designations are as follows: burned: high severity wildfire (>80% tree canopy mortality) within the Dome (2010), Fourmile (2010), Maxwell (2011), and Flagstaff (2012) incidents; Thinned: managed for fuel reduction; and Control: non-burned and non-treated forested areas.

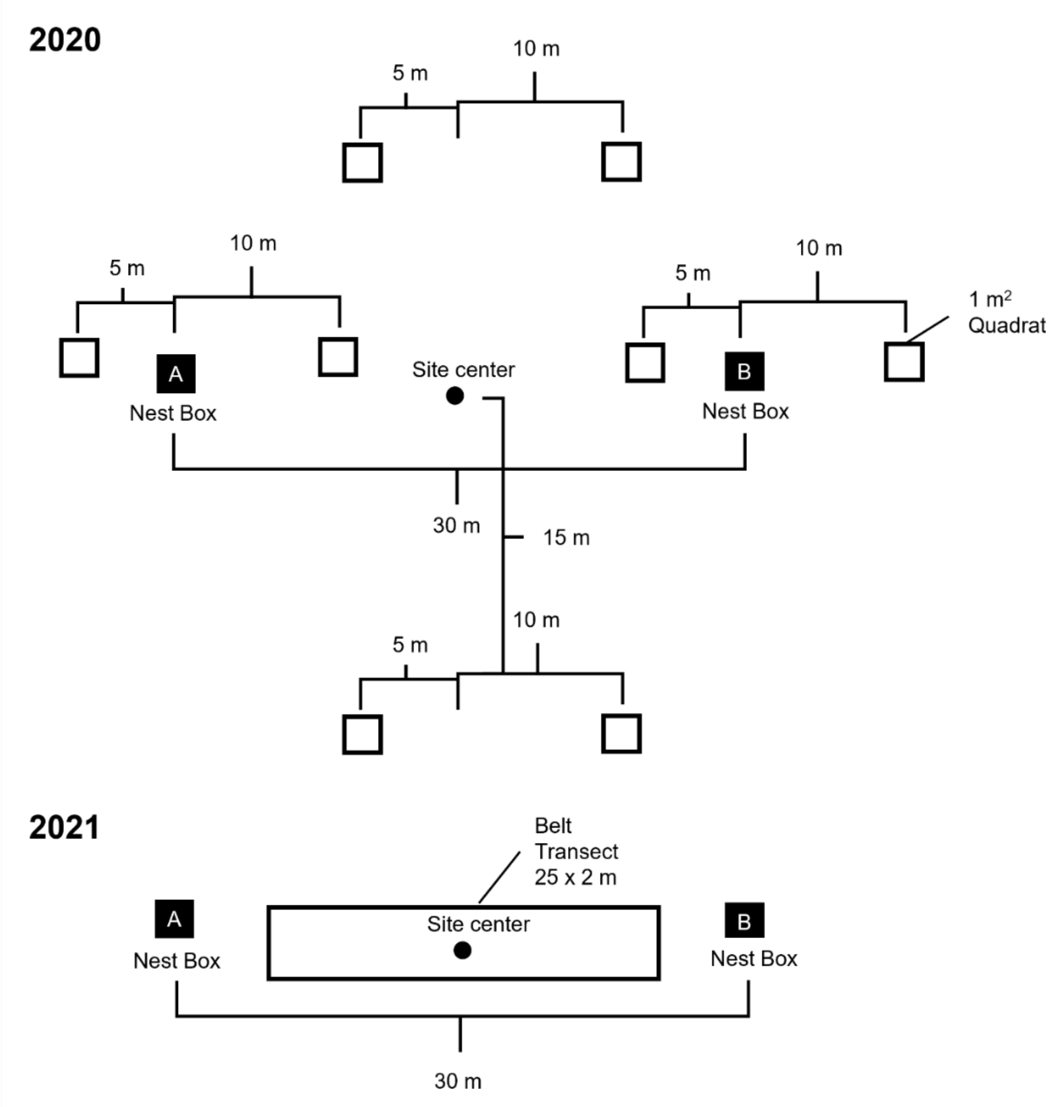

Figure 2.2. Sampling approaches used in A) 2020 to measure all forb stems and B) 2021 to measure all actively flowering forb stems.

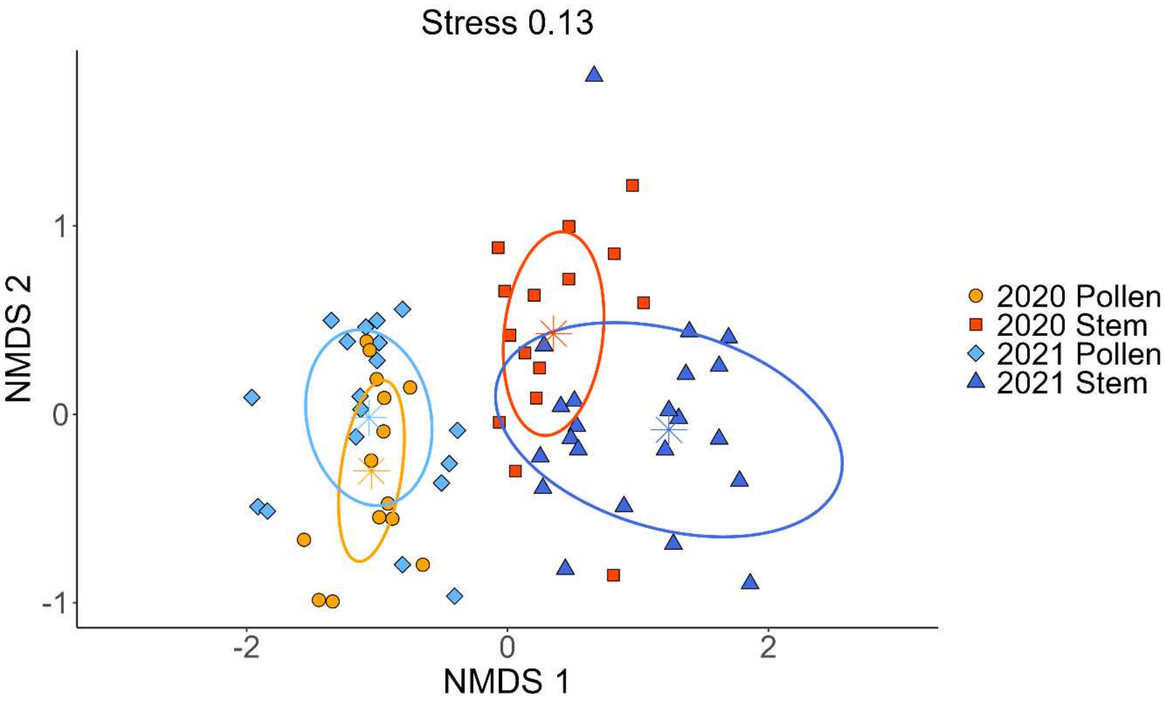

Figure 2.3. Non-metric Multi-dimensional Scaling (NMDS) of plant genera site ordinations between study years and plant source (i.e., from on-site stem counts vs. identified from metabarcoding of pollen). Stars in the middle of 95% confidence ellipses depict ordination centroid or mean ordination score.

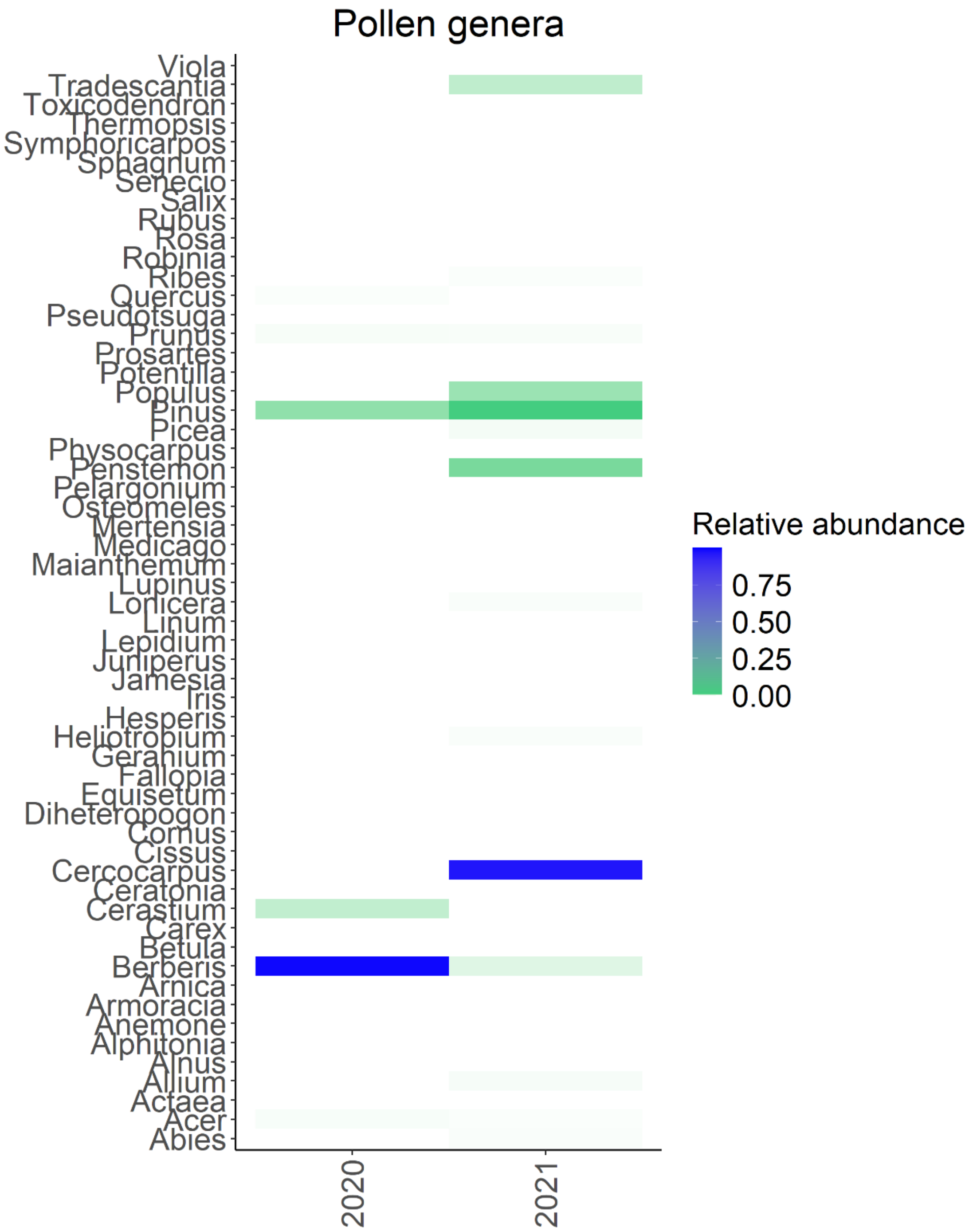

Figure 2.4. Heat map demonstrating most abundant pollen genera found within *O. lignaria* foraged pollen within site either burned at high severity (Burned), treated via hand-thinning (Treated), or unburned and untreated (Control) for each study year.

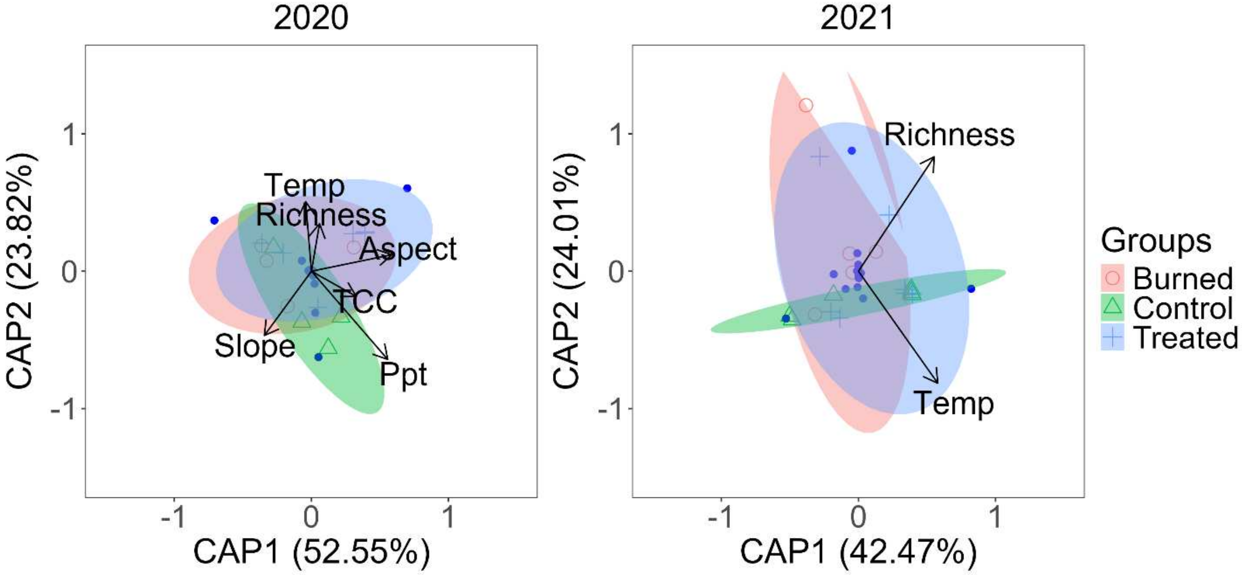

Figure 2.5. Principle Coordinates Analysis (PCoA) of *O. lignaria* pollen genera site ordinations and their correlations with habitat variables; slope, transformed aspect (Aspect), average precipitation from Jan-July (Ppt), average temperature from Jan-July (Temp), and mean tree canopy cover (TCC), and landscape richness (Richness), influences on pollen community assemblages in 2020 and 2021. Numbers in parentheses along each axis denote the amount of variance explained within the axis.

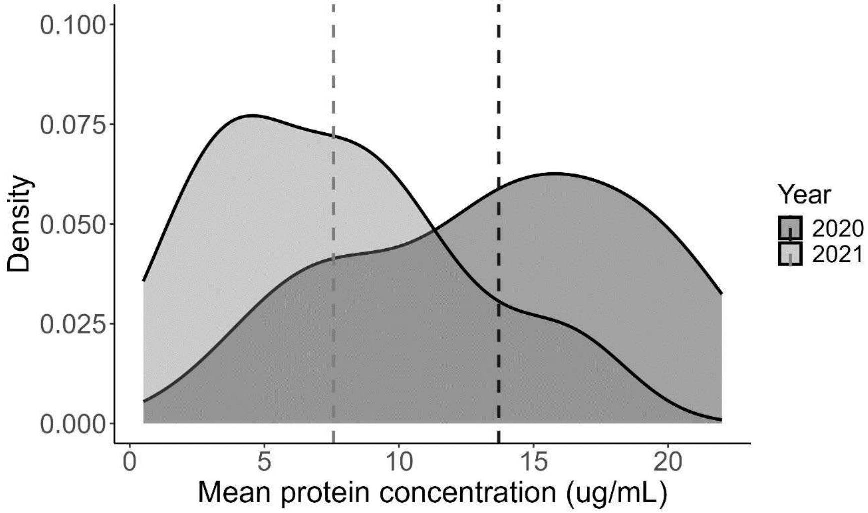

Figure 2.6. The distribution of pollen protein concentration across sites sampled in 2020 and 2021

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CHAPTER 3

HABITAT VARIATION EFFECTS ON A CAVITY-NESTING BEE PARASITE ABUNDANCE

Introduction

Forest management practices and disturbances that alter stand structure and composition can have cascading effects on plants and animals inhabiting forest ecosystems. For example, changes in forest canopy structure following wildfire or mechanical thinning are generally associated with more abundant and diverse floral resources, resulting in enhanced biodiversity of forest bee assemblages (Burkle et al. 2019; Metlen and Fiedler 2006; Dodson, Peterson, and Harrod 2008; Ponisio et al. 2016; Rossman et al. 2018; Ulyshen et al. 2021; Gelles, Davis, and Stevens-Rumann 2022; Davies, Davis, and Griswold 2023; Gelles, Davis, and Barrett 2023; Thapa-Magar et al. 2023). However, most research investigating these relationships focuses on forest disturbance effects on bee community composition, with comparatively few studies investigating bee fitness responses, such as foraging behavior, body size, phenology, and parasite abundance (López-Uribe, Ricigliano, and Simone-Finstrom 2020; Rittschof and Denny 2023). This precludes an understanding of how or why individual species respond to disturbances differently (Rivers et al. 2018). This is an important knowledge gap for forest managers as many bee populations are declining or are threatened (Cameron et al. 2011; Goulson et al. 2015) from factors such as habitat loss, resource degradation, and exposure to parasites (Murray, Kuhlmann, and Potts 2009; Potts et al. 2010; Dicks et al. 2021).

In addition to habitat changes caused by disturbances, many wild bees must contend with biotic challenges from various parasitic taxa with diverse lifecycles. For example, Meloid beetles within the genus *Tricrania (*Torchio and Bosch 1992; Farzan 2018) are common cavity-nesting bee kleptoparasites, or pollen predators (Linsley and MacSwain 1951; Erickson and Werner 1974). *Tricrania* spp. rely on parasitizing cavity-nesting bee nest cells to complete their larval development (Torchio and Bosch 1992). Both *Tricrania sanguinipennis* and *T. stansburyi* are particularly common in North America and are reported in association with multiple cavity-nesting bees (Batra 1980; Linsley and MacSwain 1951; Torchio and Bosch 1992). Early-instar larvae (triungulins) are relatively mobile and must attach to mature bees, where they are subsequently transported back to nests, along with provisions where each larva consumes pollen provisions and host larvae within a single nest cell (Torchio and Bosch 1992). Thus, adult *Tricrania* beetles are likely to select habitats that closely match the preferences of foraging bees for oviposition if their offspring are to be successful.

Like their hosts, bee parasite abundance varies greatly across landscapes (Gillespie 2010) and populations may respond to disturbance-caused habitat changes (Tobajas et al. 2021; Cohen et al. 2022; Grass et al. 2018). Presently, little is known about how habitats variations in dry, mixed-conifer forests (e.g. topography, forest structure, climate) changes affect *Tricrania* spp. abundance, or the combined effect of habitat and kleptoparasitism on bee fitness. A clearer understanding of where exposure to nest parasitism from *Tricrania* spp. is likely to occur and how kleptoparasitism affects bee fitness can have implications for solitary bee conservation and management. Here, my goal is to evaluate how habitat variation, including habitat type, topography (i.e. aspect, elevation, slope), tree stand composition (i.e. basal area, canopy cover), and climate (i.e. temperature and precipitation) affect *Osmia lignaria* Say (Hymenoptera:

Megachilidae) fitness traits such as nest provisioning, reproduction, and exposure to *T. stansburyi* parasitism. *Osmia lignaria* is a generalist pollinator native to North America (Rust 1974; Torchio 1991), and populations are commonly managed to supplement orchard pollination (Bosch, Kemp, and Peterson 2000). *Osmia lignaria* bees are cultivated commercially in large quantities and visit various flora including fruit trees, shrubs, woody plants, wildflowers, and crops. In addition, *O. lignaria* readily colonizes artificial nesting structures (Bosch and Kemp 2001) which can be collected and dissected to estimate provisioning success, reproduction, and parasitism rates (Williams and Tepedino 2003; Palladini and Maron 2014; Galbraith, Cane, and Rivers 2021). In this study, my objectives were to (1) determine how forested habitat variations affect *O. lignaria* nest provisioning and *T. stansburyi* abundances; (2) describe the basic rate of parasitism by *T. stansburyi*; and (3) evaluate the effects of parasite abundance on *O. lignaria* reproduction. These results have consequences for understanding nest parasitism of an agriculturally important cavity-nesting bee species, informing regional conservation efforts to improve solitary or cavity-nesting bee habitat within managed forests.

Materials and Methods

Field methods

The same study sites and field methods described in Chapter 2 were used here, with sites being distributed among dry-mixed conifer montane forests in Boulder County, Colorado (Figure 2.1). Likewise, the same habitat predictor variables were used in this chapter, except the topographic variables: elevation, aspect, and slope (Table 3.1). However, some landscape variables were added as predictor variables, including landscape diversity and the proportions of each landscape category within 500 m of each site. Site floral variables measured, described in Chapter 2, were also included as a predictor variable.

Laboratory procedures

During the process of dissecting nests from 2020 and 2021, nest parasites were identified and counted. The most abundant kleptoparasite was a meloid beetle *Tricrania stansburyi* Haldeman (Coleoptera: Meloidae) were observed - the beetle is a well-known parasite of *O. lignaria* brood (Torchio and Bosch 1992). The common *O. lignaria* parasitic chalcid wasp, *Monodontomerus* spp. (Hymenoptera: Torymidae) (Bosch and Kemp 2001) were also found. Accordingly, all parasitic broods (larvae, pupae, and adults) were likewise counted and summed for each site (i.e. count) and then divided by the sum of all *O. lignaria* provisioned cells to estimate the proportion (%) of nest parasitism.

Statistical analyses

Generalized linear models (GLM) with a Quasi-Poisson distribution were used to test how *O. lignaria* provisioned cells and *T. stansburyi* abundance (i.e. counts of either 2nd or higher instar larvae or pupae) were each affected by habitat variations (O1). To determine which predictor variables to include in the GLMs, an analysis workflow based on methods described by Ranganathan et al (2017) were used. Step 1) univariate GLMs with Quasi-Poisson distributions for each response variable (i.e. provisioned nests and *T. stansburyi* abundance) with each habitat predictor variable, including climate, floral, tree, landscape, and temporal factors (Table 3.1). Step 2) Pearson’s correlation tests were implemented within each predictor variable category (i.e. climate, floral, tree, and landscape) to test for significantly correlated variables at $\alpha = 0.1$. Step 3) Multivariate GLMs included significant univariate predictor variables at $\alpha = 0.1$ that were not significantly correlated at $\alpha = 0.1$ (Ranganathan, Pramesh, and Aggarwal 2017). Variables that were not found in 4 or more sites were also omitted (i.e. Barren and Crop Landscape proportions). During this process, an outlier site with a magnitude larger *T. stansburyi* count than counts from all other sites was found and was thus omitted from analyses.

To determine the rate of rate of *T. stansburyi* parasitism (O2), total *T. stansburyi* abundance (i.e. counts of either 2nd or higher instar larvae or pupae) was divided by total *O. lignaria* provisioned cells. To compare parasitism rates between years, a Chi-squared test was used to test the differences in *T. stansburyi* and *Monodontomerus* spp. parasitism ratios between study years. As *Monodontomerus* spp. can lay up to 10 eggs in one developing host (Bosch and Kemp 2001), only cells containing *Monodontomerus* spp. were used for *Monodontomerus* spp. ratio comparisons (i.e. counts of *Monodontomerus* spp. presence, not abundance). A GLM with a Quassi-Poisson distribution was also used to test how *O. lignaria* provisioning and brood abundance (i.e. counts of either 2nd or higher instar larvae or pupae) predicted *T. stansburyi* abundance (O3). Generalized linear regression models with a Gamma distribution were used to test how *T. stansburyi* abundance affected *O. lignaria* male and female pupae mass and GLMs with a binomial distribution were used to test *T. stansburyi* abundance effects on *O. lignaria* sex ratio. All analyses were implemented in the R programming language (R Core Team 2022). Modeled effects were interpreted as 'significant' using a Type I error rate of $\alpha = 0.05$.

Results

Objective 1: Determine how forested habitat variations affect O. lignaria *nest provisioning and T. stansburyi abundance*

Throughout the study, *O. lignaria* provisioned 1,420 cells (n=634 in 2020 and n=786 in 2021). Of these, 62.9% initiated development (i.e., contained *O. lignaria* larvae or pupae) in 2020, and 60.8% of initiated development in 2021. Neither landscape, floral, nor tree variables were strongly associated with *O. lignaria* nest provisioning (Table A2.1). The only variable that was a significant predictor of *T. stansburyi* abundance was the proportion (%) of the landscape represented by urban-developed land cover, which decreased with increased urban development cover (Table 3.2, Figure A2.1).

Objective 2: Describe the basic rate of parasitism by T. stansburyi

Parasitism rates were found to be significantly different between the study years (X2 = 20.813, df = 2, p-value < 0.001), with parasitism rates being around twice as high in 2020 (15.2 % in 2020, 9.5 % in 2021). In 2020, T. stansburyi were found in 9 out of 15 sites, with an O. lignaria brood cells parasitism rate of 12.9 % whereas in 2021, T. stansburyi were found in 15 out of 24 sites, but only had a parasitism rate of 6.2 %. The chalcid wasp, Monodontomerus spp. (Hymenoptera: Torymidae), an O. lignaria ectoparasitoid (Bosch and Kemp 2001), was found in 3.0 % of O. lignaria brood in 2020 and 5.4 % in 2021.

Objective 3: Evaluate the effects of parasite abundance on O. lignaria reproduction

Tricrania stansburyi abundances were positively associated with *O. lignaria* provisioning (β = 0.125, SE = 0.038, *z-value* = 3.300, *P-value* = 0.003, Figure 3.2A). Likewise, *T. stansburyi* abundance increased with *O. lignaria* brood abundance (β = 0.23, SE = 0.007, *t-value* = 3.169, *P-value* = 0.004, Figure 3.2B). However, no effects of *T. stansburyi* abundance on any other aspect of *O. lignaria* reproduction (i.e., pupal mass or male: female sex ratios) were found (Table 3.3).

Discussion

Osmia lignaria nest provisioning did not vary with habitat, landscape, or climate factors. However, nest colonization by the pollen predator *T. stansburyi* decreased along with the proportion of the landscape categorized as 'urban development'. This suggests that kleptoparasites in forest ecosystems may be more affected by habitat variation than their associated hosts (Tscharntke et al., 1998; Kruess and Tscharntke, 2000; Tscharntke and Brandl, 2004; Grass et al., 2018; Tobajas et al., 2021). This also suggests that Colorado Front Range bees may be less likely to experience nest parasitism in habitats with a higher development: forest ratio. (Figure 3.1). The mechanisms underlying this pattern are unknown but could indicate a mismatch between the environmental cues used by bees and their parasites during habitat selection. In other studies, increased urbanization generally corresponds to increased bee parasitism rates (Theodorou et al. 2016; Cohen et al. 2022; Gajger et al. 2022). This could be partially attributable to the life history of the parasite and their patterns of dispersal. *Tricrania stansburyi* adults lay eggs on nearby flowers where the first instar larvae (triungulins) emerge and, using their mandibles, attach to their host to be transported to their host's nest (Torchio and Bosch 1992). Thus, *T. stansburyi* females scout for host foraging habitats, but may be adapted to only search for floral species to which they have an evolutionary history. Since no deleterious effects of increased urban development on *O. lignaria* nest provisioning were found, urban development within forested habitats may provide foraging opportunities for *O. lignaria* (e.g. ornamental flowers, shrubs, and fruit trees) that female *T. stansburyi* may not utilize or access, possibly decreasing kleptoparasite exposure. To better inform bee conservation efforts, it would be useful to evaluate the floral species visited by dispersing *T. stansburyi*, as some floral species could serve as forage for bees without serving as a reservoir for parasite attachment.

Osmia lignaria nests had relatively low parasitism rates by *T. stansburyi* compared to rates of nest provisioning, indicating that parasites were more abundant in habitats that also represented good foraging conditions for bees (e.g., Sheffield et al. 2013). In the present study, *T. stansburyi* was found in 70.6 % of sites sampled, however, only 9.2% of all nest cells were parasitized on average. Although, parasitism rates were twice as high in 2020 compared to 2021, rates did not exceed 16%. Other recent studies report a similar pattern of more kleptoparasitism (~10% of brood cells) in areas with ample nest provisioning, and no clear negative effect on bee population growth (Tobajas et al. 2021). The present study and this earlier report collectively indicate that *O. lignaria* populations are generally tolerant of some parasitism under good environmental conditions. However, when environmental conditions are stressful (e.g. when low floral densities or ambient temperatures are elevated), bees may not be able to provision enough nests to support both reproduction and parasitism, resulting in population declines as parasitism rates exceed 20% of brood cells (Goodell 2003; Forrest and Chisholm 2017). In addition, *T. stansburyi* parasitism of *O. lignaria* can be inversely density-dependent (i.e. Farzan, 2018) and kleptoparasitism rates vary interannually, potentially decreasing solitary bee population growth rates over longer periods (Steffan-Dewenter and Schiele 2008; Tepedino and Torchio 1982) Accordingly, it will be important for future work to evaluate whether environmental stressors interact with parasitism to result in critical thresholds limiting population growth, and what those thresholds may be for different target bee species.

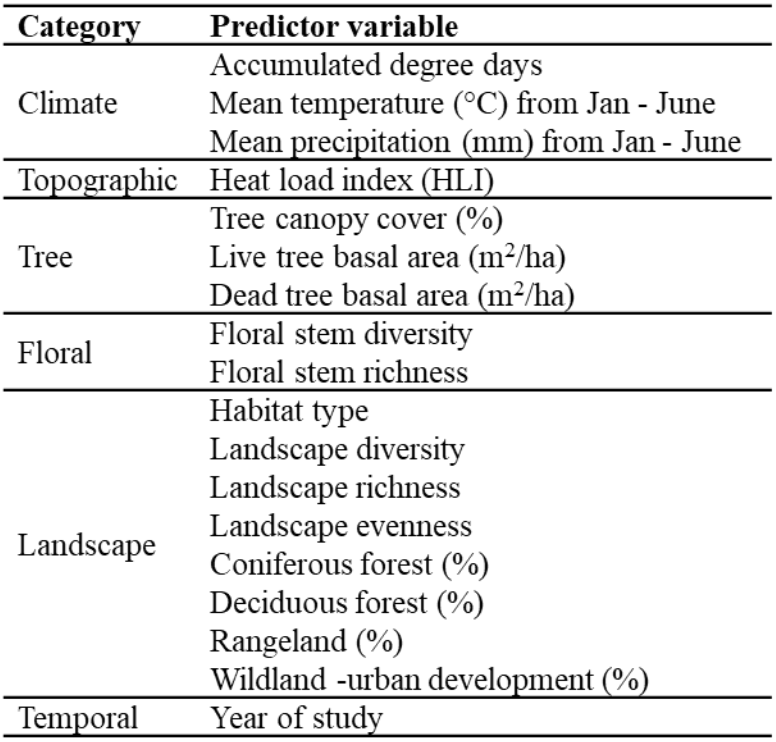
Since only one *T. stansburyi* larvae can develop within a host cell (Bosch and Kemp 2001; Torchio and Bosch 1992), it is not surprising that their presence did not affect the weight of surviving nest inhabitants, nor were any relationships between sex ratios of *O. lignaria* offspring and *T. stansburyi* abundance detected. Other authors report that sex ratios may be indirectly related to the quality of foraging habitats. For example, Seidelmann (2006) found that sex ratios and parasitism rates of *Osmia rufa* became more male-biased as provisioning efficiency decreased. In addition, parasitism rates of *Osmia* spp. increase as the foraging season progresses (Seidelmann 2006; Farzan and Yang 2018). This coincides with studies reporting more male-biased sex ratios under fewer available provisions as female brood typically weigh more than males, and thus require more provisions (Torchio and Tepedino 1980; Kim 1999).

This study design had several limitations that are important to consider when interpreting my findings. First, only offspring collected in 2021 were allowed to develop fully before freeze-killed and weighed and thus I was only able to test kleptoparasite effects on sex ratio in 2021. Secondly, bees were released and collected at different temporal periods in each study year, which could reflect differential access to some early flowering plants (Torchio and Tepedino 1980), as well as different thermal conditions, both of which may affect fat stores and ultimately longevity (Bosch and Kemp 2003). It is often suggested for *O. lignaria* deployment for crop pollination that nest boxes be collected quickly after larval development to avoid parasitism and predation (Bosch and Kemp 2001). Therefore, it is possible that removing nest boxes in July resulted in lower abundances of other parasitoids (i.e. *Monodontomerus* spp.) than might have been observed if boxes were left out longer. For example. female *Monodontomerus spp.* will chew holes into completed bee nests to lay their eggs inside developing bee larvae or pupae (Bosch and Kemp 2001). Thus, the removal of nests boxes in July may have missed peak *Monodontomerus* spp. activity were missed, resulting in the low *Monodontomerus* spp. abundance recorded.

In summary, my analyses indicate that forested habitat variation had little effect on *O. lignaria* nest provisioning, but the pollen predator *T. stansburyi* was sensitive to development in the wildland-urban interface, resulting in higher rates of parasitism in habitats with less urban development. Collectively, these findings indicate that the factors driving habitat use and site occupancy by foraging bees differ from that of an associated pollen predator, and exposure to parasitism may be more likely in natural habitats. Although parasitism rates were twice as high in 2020 compared to 2021, rates did not exceed 16% of brood cells. Increased *O. lignaria* nest provisioning and offspring abundance was a good predictor of *T. stansburyi* abundance, confirming density-dependent relationships between bees and their kleptoparasites. However, *T. stansburyi* abundance was not negatively correlated with *O. lignaria* abundance and had no relationship with the size or sex ratios of *O. lignaria* offspring. Future work will benefit from determining whether increased urban development in forested ecosystems affects other bee-parasite interactions similarly, and from a critical evaluation of the cues used by bees and parasites during habitat selection.

Tables

Table 3.1. Habitat predictor variables of *O. lignaria* nest provisioning and *T. stansburyi* abundance. Habitat variable extractions are described in Chapter 2.



Category	Predictor variable
Climate	Accumulated degree days Mean temperature (°C) from Jan - June Mean precipitation (mm) from Jan - June
Topographic	Heat load index (HLI)
Tree	Tree canopy cover (%) Live tree basal area (m^2/ha) Dead tree basal area (m^2/ha)
Floral	Floral stem diversity Floral stem richness
Landscape	Habitat type Landscape diversity Landscape richness Landscape evenness Coniferous forest (%) Deciduous forest (%) Rangeland (%) Wildland -urban development (%)
Temporal	Year of study

Table 3.2. Summary of a generalized linear regression model predicting effects of landscape evenness and the proportion of urban development landscapes on *T. stansburyi* abundance. Bold font indicates significance at α = 0.05.

Species	**Coefficients**	**Estimate (β)**	**Standard error**	***t*-value**	***P*-value**
T. stansburyi	Intercept	1.600	0.287	5.565	**< 0.001**
	Landscape evenness	-0.792	0.788	-1.005	0.324
	Urban development (%)	-15.185	6.773	-2.242	**0.033**

Table 3.3. Summary of generalized linear regression models analyzing effects of *T. stansburyi* abundance on *O. lignaria* fitness reproduction, including, pupae mass, and sex ratio. Note, only 2021 had enough female pupae to analyze female pupae mass and sex ratio. Bold font indicates significance at α = 0.05.

***O. lignaria* fitness trait**	**Coefficients**	**Estimate (β)**	**Standard error**	**Statistic**	***P*-value**
Male pupae mass (mg)	Intercept	23.656	1.091	21.686	**<0.001**
	T. stansburyi	-0.016	0.251	-0.063	0.950
Female pupae mass (mg)	Intercept	36.991	2.109	17.544	**<0.001**
	T. stansburyi	0.519	0.544	0.953	0.357
Female sex ratio (%)	Intercept	0.507	0.765	0.663	0.508
	T. stansburyi	-0.138	0.200	-0.689	0.491

Figures

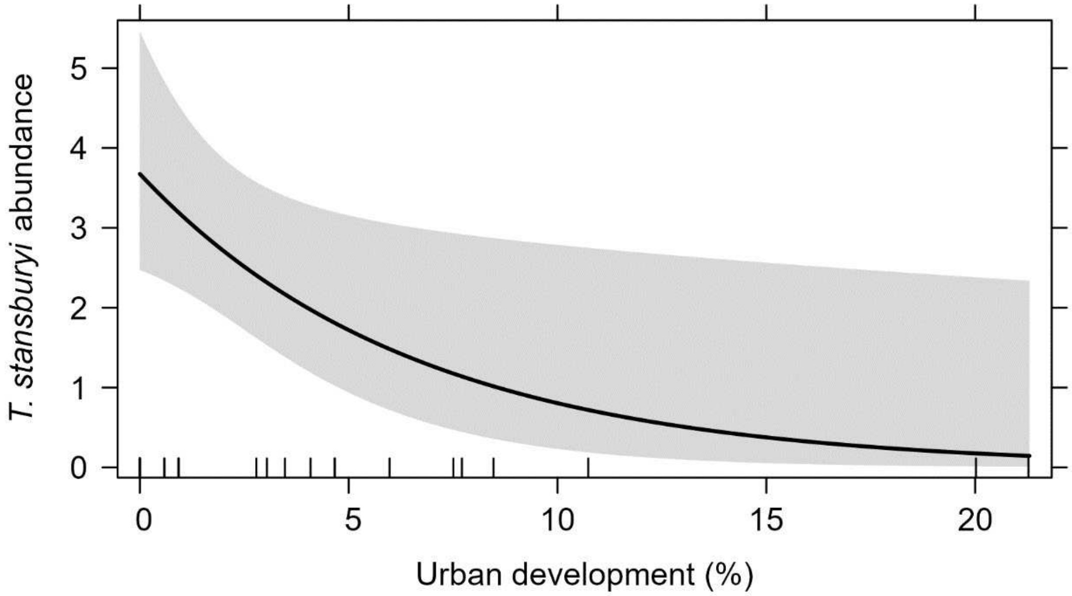


Figure 3.1. Predicted effects models depicting predicted effects of low-intensity urban development proportion within 500 m around site on *T. stansburyi* abundance. Shading denotes 95% confidence intervals; black line denotes significance at $\alpha = 0.05$.

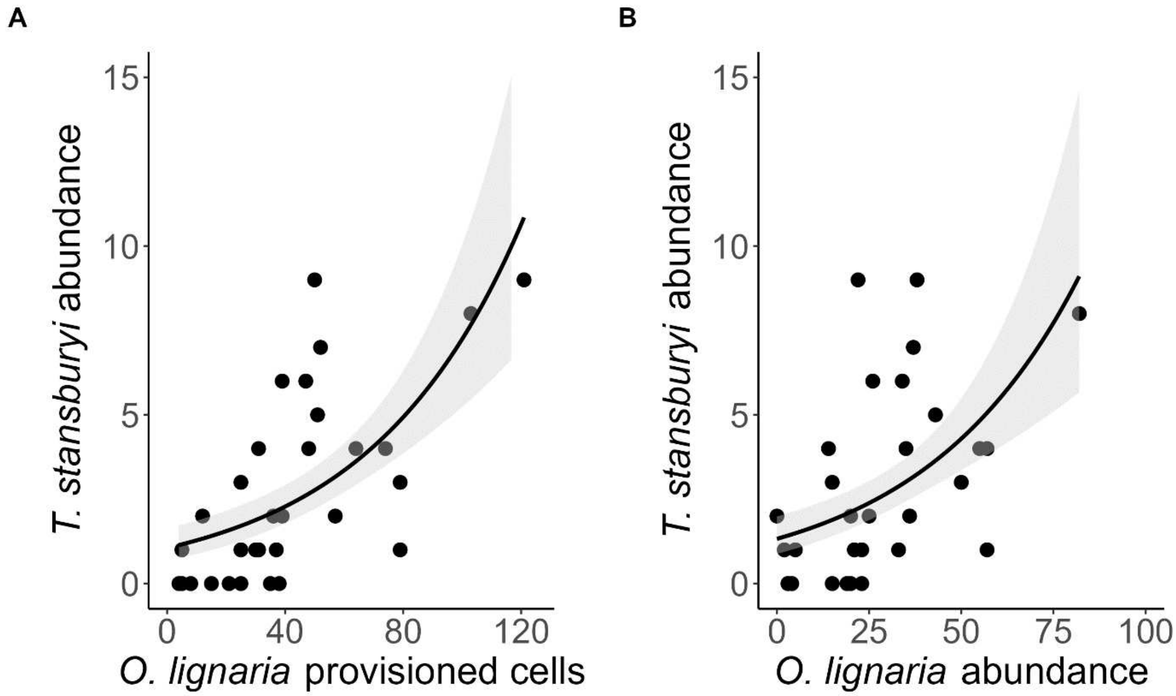


Figure 3.2. Parasites affect bee reproduction. Generalized linear model with Poisson distribution demonstrating predicted effects of (A) *O. lignaria* provisioned brood cells on *T. stansburyi* abundance (B) *T. stansburyi* abundance on *O. lignaria* abundance. Shading denotes 95% confidence intervals.

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CHAPTER 4

DISTURBANCE EFFECTS ON CAVITY-NESTING BEE AND WASP COMMUNITIES IN NORTHERN COLORADO

Introduction

Many dry forested ecosystems in the western US are shaped by wildfire and forest management practices to reduce wildfire risk (Cooper 1960; Covington and Moore 1994; Moore, Covington, and Fulé 1999). Although wildfires can increase foraging and nesting substrates availability for wild bees (Galbraith et al. 2019; Gelles, Davis, and Stevens-Rumann 2022), little is known about the effects of disturbances on cavity-nesting bee community interactions and brood development. As cavity-nesting bees and wasps readily use artificial nesting boxes (da Rocha-Filho et al. 2019; Tscharntke, Gathmann, and Steffan-Dewenter 1998; Gathmann, Greiler, and Tscharntke 1994), they can be used to quantify habitat variation effects on community assemblages, parasite abundance, and brood development (da Rocha-Filho et al. 2019; Tscharntke, Gathmann, and Steffan-Dewenter 1998).

In addition, habitat variation caused by wildfire and anthropogenic land use can also influence bee interactions with parasites (Cohen, McFrederick, and Philpott 2020; Cohen, Quistberg, and Philpott 2017; Kruess and Tscharntke 2000; Tobajas et al. 2021; Tscharntke, Gathmann, and Steffan-Dewenter 1998). There is a wide range of parasites that affect cavity-nesting bees, including kleptoparasites, or brood parasites, that consume host larval provisions (i.e., pollen and nectar), and parasitoids that consume bee host gradually either internally (endoparasitoids) or externally (exoparasitoids; Danforth, Minckley, and Neff 2019). However, parasites are intimately linked to the fate of their hosts and thus face similar threats as their hosts (Tscharntke and Brandl 2004; Grass et al. 2018) and can even be more sensitive to habitat variations if they're unable to find suitable hosts (Bordes et al. 2015; Sheffield et al. 2013). Yet, the interacting effects of parasitism and disturbance can have detrimental effects on bee fitness (Theodorou et al. 2016; Cohen et al. 2022; Gajger et al. 2022; Ponisio et al. 2024). For example, bumblebee parasitism rates in fragmented landscapes have been found to increase with resource availability but decrease with increased bee diversity (Cohen et al. 2022). Thus, understanding the dynamic relationships between cavity-nesting bees and their parasites across a heterogeneous landscape is vital for conservation efforts (Murray et al., 2009b; Goulson & Hughes, 2015; Goulson et al., 2015).

Therefore, the aim of this study is to 1) describe regional cavity-nesting bee fauna and evaluate how cavity-nesting bee and wasp communities vary by habitat type (burned, treated, and controlled); 2) describe the linkages between bees and their parasites across habitats; and 3) describe variation in emergence phenology among bee species. Understanding the relationships between cavity-nesting species and their parasites and how those relationships differ among habitats, can help us understand species coexistence, host and parasite co-evolution, and potential interacting threats that could be relevant for informing conservation efforts.

Materials and Methods

Field methods

In 2022, the same 24 study sites surveyed in 2021 for Chapters 2 and 3 were re-visited (Figure 4.1). The same 32-hole Binderboards^{TM} (Pollinator Paradise, Parma, ID) artificial nesting blocks described in Chapters 2 and 3 were also utilized, setting up 2 boxes at each site ~1 m above ground between May 30 and June 1, 2022. Nesting blocks were left in the field, collected between October 24 and October 26, and brought back to the lab where they were left in an enclosed storage box at ambient temperature (19 °C).

Laboratory procedures

Once in the lab, inhabitants from each nest were surveyed (November 1st through November 4th, 2022), and sealed nests were placed in an unsealed envelope and moved to a refrigerator at a constant temperature (3 °C). Nests were kept in the refrigerator through the winter for prepupal development (Bosch and Kemp 2001; Frohlich and Parker 1985). On April 12th, 2023, nests were removed from the refrigerator, and each nest was moved to a glass 50 mL test tube (24 x 150 mm) capped with a cotton ball and sealed with a steel screen (Hodge et al. 2022). Test tubes were then placed in an open cardboard box with nest caps (i.e. front) facing outward to emulate natural nest positioning. All nests were kept in the lab with an average temperature of 19°C and a 14:10 hour light: dark cycle and monitored daily for emergence. Once emerged, specimens were transferred to a labeled 5 mL capped glass vial, freeze-killed, and stored at -20 °C until further processing. Afterward, specimens were pinned and identified to the lowest taxonomic level possible using several sources (Evenhuis 1985; Evenhuis and Greathead 1999;

Sandhouse 1941; Grissell 2007; Silva 2013; Baker 1975; Timberlake 1943; Schwarz 1926; Scott et al. 2011; Sheffield et al. 2011; Sandhouse 1939; Garay 1979; Cockerell 1907; Parker and Bohart 1979; Enns 1955; Pinto and Bologna 1999; Goulet and Huber 1993). All specimen were identified to species except two parasites – one being a parasitoid identified to genus (*Monodontomerus* spp.) and the other a kleptoparasite identified to Subfamily (Sapyginae). Two HOBO temperature loggers were placed on either side of the workbench where nests were placed to monitor temperatures between the first day of removal from refrigeration (April 7th, 2023) and the final day that emergence was recorded (August 31st, 2023). Accumulated degree days using a base temperature of 5°C (Pitts-Singer et al. 2008) were calculated starting April 7th, 2023 (day 1) until inhabitants emerged, and each emerging individual was thus related to a specific degree-day accumulation.

Statistical analyses

Rarefied cavity-nest species richness and diversity were compared among habitat types using sample-based accumulation curves in the iNEXT R software package (Chao et al. 2014), where Hill numbers ($q = 0$ or 1 for species richness or Shannon's diversity, respectively) were used to calculate estimates. To compare cavity-nesting bee communities by habitat type (burned, controlled, or treated; Q1), a Permutational Multivariate Analysis of Variance (PERMANOVA) using the adonis2 function in the "vegan" R package (Oksanen J. et al. 2022) was used. A non-metric multidimensional scaling (NMDS) ordination was used to display habitat community ordinations (Bray Curtis dissimilarity, 999 Monte Carlo permutations). To determine if some species were indicative of a habitat type, an Indicator Species Analysis (ISA; Dufrêne et al.

1997) was done using the “indicspecies” packages (De Cáceres and Legendre 2009). Finally, an Analysis of Variance (ANOVA) was used to test differences in diversity metrics among habitat types. Diversity metrics included Shannon’s diversity index (H’), species richness, and species abundance for all species that successfully emerged. Shannon’s diversity index was calculated using the ‘diversity’ function in the “vegan” R package (Oksanen J et al. 2022). Abundance refers to counts of emerged species, except for *Monodontomerus* spp. where only counts of host pupae parasitized by *Monodontomerus* spp were used. Both abundance and richness values were square-root transformed to be normally distributed. Tukey’s Honest Significant Differences (HSD) was used to test for significant pairwise tests, using the “stats” R package (R Core Team 2013).

To measure parasite-host interactions and to test if those interactions varied by habitat type (Q2), network-level indices were measured including connectance, specialization ($H_2^{'}$), and weighted modularity of parasite-host networks within each habitat type as well as the species-level indices degree and species specificity using the “bipartite” R package (Dormann et al 2021). Connectance (C) is the proportion of observed interactions divided by all possible interactions between hosts and parasites. Specialization ($H_2^{'}$) values range from 0 to 1, with values close to 0 implying no specialization and values equal to 1 denoting perfect specialization within a network. Modularity (Q) measures the number of subgroups within a network with modularity indicating more interactions among parasite-host subgroups (i.e. module) than with other subgroups (Bordes et al 2015). Weighted modularity was measured using the “ComputeModules” function using the Beckett method (Beckett 2016).

To reduce network-level indices' sensitivity to network size differences (Song et al, 2017), network-level indices C and H_2' were transformed by subtracting the mean values from 2500 null-networks from the empirical mean, following methods described by Dormann (2021). Significant differences among habitat types were measured using z-scores calculated for each network using the formula:

$$z_I = \frac{I_{\text{observed}} - \bar{I}_{\text{nulls}}}{\sigma_{I_{\text{nulls}}}}.$$

Where “I” denotes the index for each network (Dormann 2021). Null-network distributions were created using the nullmodel function from the “vegan” R package (Olesen et al., 2007).

In addition, group-level metric indices; mean number of links, niche overlap, robustness, and generality (for parasites) or vulnerability (for hosts) were measured within each habitat type using the “bipartite” R package (Dormann et al 2021). Both kleptoparasites and parasitoids were included as “parasites” for all network and group-level analyses. Finally, Host, kleptoparasite, and parasitoid total abundance (i.e. sum of emerged individuals) were compared among habitat types using a generalized linear models (GLM) with a quasi-Poisson distribution.

A Kruskal-Wallis test was used to compare differences in accumulated degree days among species (Q3). Subsequently, a Dunn’s test with a Bonferroni p-value adjustment was used to test pairwise comparisons. Only species with 5 or more emergences were analyzed. R software was used for all analyses (R Core Team 2022), using the Type I error rate of $\alpha = 0.05$ to measure “significant” modeled effects.

Results

Q1) How do cavity-nesting bee community assemblages vary by habitat type?

In total, 433 cavity-nesting bees were successfully reared in the lab, consisting of 7 families, 11 genera, and 15 species. Nesting materials used varied by genus (Table 4.1). *Osmia calla* was the most abundant host species, *N. sparsa* was the most abundant kleptoparasite, and *Monodontomerus* spp. was the most abundant parasitoid (Table 4.1). Cavity nesting bee species differed significantly by habitat (Q1, Table 4.2, Figures 4.2 & 4.3). However, only abundance differed significantly among the habitat types (Table 4.3), with burned sites having higher abundance (27.375 ± 5.961) than treated sites (11.250 ± 3.294, Tukey HSD *p-value* = 0.016). *Osmia calla* was the only indicator species, indicative of burned sites (ISA, stat = 0.868, p-value = 0.001).

Q2) What are the parasite-host interactions within habitat types?

Network metric indices Δ C and Δ H_2' were significantly different than predicted in each habitat type, with Δ C between hosts and parasites being lower than predicted models and Δ H_2' being higher than predicted (Table 4.4). Burned sites had the lowest Δ C scores, with control and treated sites having lower and similar Δ C scores. However, burned sites had the highest $\Delta H_2'$ and Q values, followed closely by treated sites with control sites having the lowest values. Group-level indices showed that parasites and hosts in control sites had a higher mean number of links (interactions), niche overlap, general parasites, and vulnerable hosts than other habitat types (Table 4.5, Figure 4.4). Hosts in control sites were more robust than hosts in other habitats, but parasites in burned sites were more robust than in other habitats.

Monodontomerus spp. were the most generalist parasite, followed by the kleptoparasites *S. rudbeckiarum,* and *N. sparsa* in control sites, whereas *X. tigrinus, Monodontomerus* spp., and *C. deani,* were the most generalist parasites in treated sites (Table 4.6, Figure 4.4). All parasites in burned sites had 1 host except for *N. sparsa,* which were found in *D. ulkei* and *M. relativa* nests. The kleptoparasite *T. stansburyi* was only found in *O. calla* nests in burned sites, and the cavity wasp *T. clavatum* was only parasitized by the parasitoid *Monodontomerus* spp. in control and treated sites. Host abundance was higher in burned sites compared to treated sites (β = -0.862, SE = 0.354, t-value = -2.436, P-value = 0.019) and was marginally higher than control sites (β = -0.631, SE = 0.343, t-value = -1.841, P-value = 0.072). However, neither kleptoparasite nor parasitoid abundance was significantly different by habitat type (Figure 4.5).

Q3) Does emergence time differ among species?

Average emergence times varied significantly by species ($\chi^2 = 323.81$, df = 10, *p-value* < 0.001). *Osmia calla* significantly emerged before all other species except for their parasite *Monodontomerus* spp. (Figure 4.6). *D. ulkei* emerged significantly later than the cavity-nesting bee *M. relativa*, and their parasites *Monodontomerus* spp. and *S. montana*. Similarly, *T. clavatum* also emerged later than their parasite, *Monodontomerus* spp. All other species had similar emergence times.

Discussion

All host species found within artificial nests were native to the western USA (Ascher and Pickering 2020), and are common in Boulder County, CO (Scott et al. 2011). Of the 7 cavity-nesting bee and wasp families, all host species were within the family Megachilidae (Table 4.1), except for *T. clavatum,* which is a common cavity-nesting parasitic wasp that preys upon spiders (Medler 1967). Megachilids are known to use a wide variety of nesting substrates (Danforth, Neff, and Minckley 2019), and I observed several of these substrates in our nest blocks (Table 4.1). Bees in the genus *Osmia* use a wide variety of nesting substrates, including mud, bark, sand, and leaf pulp that are thought to vary by subgenus (Cane, Griswold, and Parker 2007). Bees in the *Megachile* genus typically use leaves for nest construction (Strickler, Scott, and Fischer 1996), *Dianthidium* spp. mostly construct nests out of resin (Danforth, Neff, and Minckley 2019; Frohlich and Parker 1985), and *Trypoxylon* spp. typically uses mud (Medler 1967).

Similarly, parasites reared in this study have recorded interactions with the host species reared. Three of the 6 kleptoparasites were cuckoo bees, also within the Megachilidae family, 2 were Meloid beetles, and the last kleptoparasite, Sapyginae, was a club-horned wasp (Table 4.1). *Stelis* spp. are known to covertly lay their eggs in unfinished *Osmia* spp nest cells while female hosts are foraging (Rozen and Hall 2011; Torchio 1989), as are many Sapyginae wasps (Rozen and Kamel 2009). Alternatively, female Meloid beetles will oviposit on floral resources used by hosts, where eggs hatch and latch on to foraging host females as mobile triungulin larvae (Batra 1980; Linsley and MacSwain 1951; Torchio and Bosch 1992). The parasitoids, *Monodontomerus* spp. and *L. affinis* have numerous hosts but mostly parasitize solitary bees and wasps (Grissell 2007), as do *X. tigrinus* (Bohart et al. 1960; Minckley 1989).

I found differences in cavity-nesting bee communities by habitat types, with burned sites having higher abundance but similar diversity and richness compared to treated and control sites. Wildfires have been shown to increase bee abundance, providing increased forage and nesting resources (Burkle et al. 2019; Galbraith et al. 2019; Gelles, Davis, and Stevens-Rumann 2022;). Alternatively, overly dense forests with reduced light and understory vegetation can reduce forage and nesting resources, and thus bee diversity (Hanula, Horn, and O'Brien 2015). Forest management treatments have been found to have lower bee diversity metrics compared to burned sites (Galbraith et al. 2019; Gelles, Davis, and Stevens-Rumann 2022), when prescribed fires are excluded from treatment plans (Gelles, Davis, and Barrett 2023; Heil and Burkle 2018).

Similarly, I found lower cavity-nesting bee and wasp abundances in treated sites compared to burned sites. However, kleptoparasite and parasitoid abundance did not differ among habitat types (Figure 4.5). Interestingly, although *O. calla* were the most abundant host species (Table 4.1), they were only parasitized by *T. stansburyi,* the least abundant kleptoparasite, in burned sites (Table 4.6, Figure 4.4). *Dianthidium ulkei*, the second most abundant host species, on the other hand, were parasitized by the most abundant parasites, regardless of habitat type, suggesting some host density dependence, at least in thinned and control sites (Figure 4.4).

Connectance was generally low among all habitat types, with undisturbed sites having the lowest connectance (Table 4.4). Other cavity-nesting Hymenoptera host-parasite studies have also found low connectance, (da Rocha-Filho et al. 2019; Nether, Dudek, and Buschini 2019). However, control sites also had lower specialization and modularity than burned and treated sites (Table 4.4). This suggests that parasites in control sites exhibited less specialized relationships with hosts than parasites in burned and treated sites, even if they were the same species. For example, the parasitoid, *X. tigrinus*, was found to be highly specialized with the host *D. ulkei* in burned and control sites but also interacted with *M. relativa* in treated sites (Table 4.6, Figure 4.5). It has been hypothesized that ecosystem stability, or resilience to change, increases with increased connectance, which is more likely in diverse ecological networks (Landi et al. 2018). Host-parasite connectance and modularity have been found to be negatively correlated with parasite abundance (D'Bastiani et al. 2020). However, I found connectance to be positively correlated with parasite abundance and negatively correlated with modularity. Here, control sites had higher connectance (Table 4.4), niche overlap, and highest host vulnerability (Table 4.5). As most of the host-parasite interactions in burned sites were specialized, whereas there were more generalist parasite-host interactions, it is possible that parasites within treated and controlled sites had slightly stronger selective pressure to utilize a wider range of hosts, because of lower host abundance (D'Bastiani et al. 2020).

Osmia calla and *D. ulkei* had the starkest emergence differences seen. Differences in emergence phenology can be a mechanism for species coexistence (Palmer, Stanton, and Young 2003). *Osmia* spp. are known to emerge early in the season, depending on spring blooming flora for forage (Bosch and Kemp 2000; 2003; 2005). The kleptoparasite, *T. stansburyi*, also emerges early, in synchrony with their hosts, *Osmia* spp. (Torchio and Bosch 1992). Interestingly, *S. montana* is recorded to have similar emergence times with *Osmia* spp., a common host as well (Torchio 1989). However, I found *S. montana* emergence to be statistically different than *O. calla*, which were unparasitized by *S. montana* - only *D. ulkei* and *Megachilie* spp. were found to be parasitized by *S. montana* and *S. montana* emerged significantly earlier than *D. ulkei* (Figure 4.6). Similarly, *Monodontomerus* spp. also emerged at significantly different times than some of their hosts. Parasites have been found to have higher adult emergence variation than their hosts (Osorio-Canadas et al. 2018; Macivor 2019). It is possible that the low abundance of parasites in this study did not fully capture the range of adult emergence. Alternatively, most parasites did not differ in emergence times from their hosts suggesting a co-evolutionary relationship between parasites and their hosts (Beani et al. 2018; Meeker et al. 2014; Osorio et al. 2015; Sedivy, Dorn, and Müller 2013).

These findings show how artificial nests can be used to monitor the reproduction and development of local cavity-nesting bees and wasps and shed light on the different groups of host-parasite communities and interactions in forested environments. I found that hosts within unburned and untreated dry forested ecosystems in northern Colorado had higher parasitic pressures compared to burned and thinned stands, suggesting that disturbances can help promote bee fitness. I also demonstrate temporal differences in emerging adult hosts, but more emerged synchrony between hosts and their parasites. These results can help inform land managers on better conservation strategies and the potential of using cavity-nesting communities and their parasites as bioindicators to determine habitat health (Tscharntke et al 1998, and Sheffield et al 2013).

Tables

Table 4.1. Cavity-nesting species successfully reared, abundance, proportions of sites found in, and the substrates hosts used to build nests.

Family	Species	Parasite type	Abundance	Site %	Nest materials
Megachilidae	*Dianthidium ulkei (Cresson 1878)*	Host	97	0.833	Sticks, sap/resin, small rocks
Megachilidae	*Megachile angelarum (Cockerell 1902)*	Host	11	0.125	Green leaves
Megachilidae	*Megachile fidelis (Cockerell 1899)*	Host	3	0.042	Green leaves
Megachilidae	*Megachile relativa (Cresson 1879)*	Host	27	0.292	Green leaves
Megachilidae	*Osmia calla (Cockerell 1897)*	Host	158	0.417	Veg walls
Crabronidae	*Trypoxylon clavatum (Say 1837)*	Host	35	0.25	Mud walls
Megachilidae	*Coelioxys deani (Cockerell 1909)*	Kleptoparasite	6	0.167	
Meloidae	*Nemognatha sparsa (LeConte 1868)*	Kleptoparasite	37	0.583	
Sapygidae	Sapyginae	Kleptoparasite	4	0.125	
Megachilidae	*Stelis montana (Cresson 1864)*	Kleptoparasite	17	0.167	
Megachilidae	*Stelis rudbeckiarum (Cockerell 1904)*	Kleptoparasite	5	0.083	
Meloidae	*Tricrania stansburyi*	Kleptoparasite	2	0.042	
Leucospidae	*Leucospis affinis (Say, 1824)*	Parasitoid	4	0.042	
Torymidae	*Monodontomerus* spp. (Westword)	Parasitoid	18	0.167	
Bombyliidae	*Xenox tigrinus (De Geer 1776)*	Parasitoid	9	0.292	

Table 4.2. Permutation adonis2 results testing the effects of habitat type – sites burned at high severity, mechanically treated, and control (Habitat) on cavity nesting bee community composition. DF denotes degrees of freedom, bold face denotes significance at $\alpha = 0.05$, whereas italic denotes marginal significance at $\alpha = 0.1$.

Coefficients	DF	Sum of Squares	R^2	F-value	P-value
Habitat	2	1.495	0.210	2.789	**0.004**
Residual	21	5.627	0.790		
Total	23	7.121	1.000		

Table 4.3. ANOVA results testing the effects of habitat type – sites burned at high severity, mechanically treated, and controlled (Habitat) on cavity-nesting bee community diversity, transformed richness, and transformed abundance. DF denotes degrees of freedom, bold face denotes significance at $\alpha = 0.05$, whereas italic denotes marginal significance at $\alpha = 0.1$.

Metric	Coefficients	DF	Sum of Squares	Mean Squares	F-value	P-value
Diversity	Habitat	2	0.516	0.258	1.122	0.344
	Residuals	21	4.827	0.230		
Richness	Habitat	2	0.132	0.066	0.279	0.759
	Residuals	21	4.974	0.237		
Abundance	Habitat	2	16.460	8.230	4.664	**0.021**
	Residuals	21	37.060	1.765		

Table 4.4. Comparison of network metric indices; transformed connectance (Δ C), transformed specialization (Δ H2'), and modularity (Q) among habitat types - burned at high-severity wildfire (Burned), thinned (Treated), and unburned and untreated (Control). Null model error values are shown in parentheses and stars denote significantly different values from null model distributions for ** $p < 0.001$ and *** $p < 0.0001$

Metrics	Burned	Control	Treated
ΔC	-0.21 (0.046) ***	-0.107 (0.031) ***	-0.103 (0.039) **
$\Delta H_2'$	0.622 (0.108) ***	0.312 (0.075) ***	0.615 (0.109) ***
Q	0.427	0.222	0.4

Table 4.5. Comparison of group metric indices between parasites and hosts among habitat types - burned at high-severity wildfire (Burned), thinned (Treated), and unburned and untreated (Control). Note, that "Generality" only applies to parasites, and "Vulnerability" only applies to hosts.

	Parasites			*Hosts*		
	Burned	**Control**	**Treated**	**Burned**	**Control**	**Treated**
Mean number of links	1.208	1.925	1.440	3.500	5.151	3.240
Niche overlap	0.349	0.863	0.382	0.035	0.219	0.145
Robustness	0.560	0.441	0.519	0.238	0.446	0.378
Generality/Vulnerability	1.135	1.583	1.400	3.081	4.042	2.109

Table 4.6. Species-level metrics for parasite-host species interactions within each habitat type; burned at high-severity (Burned), thinned (Treated), and unburned and untreated sites (Control).

	Habitat	**Species**	**Species specificity index**	**Degree**
Parasite	Burned	*Coelioxys deani*	1.000	1
		Leucospis affinis	1.000	1
		Nemognatha sparsa	0.721	2
		Sapyginae	1.000	1
		Stelis montana	1.000	1
		Tricrania stansburyi	1.000	1
		Xenox tigrinus	1.000	1
	Control	*Coelioxys deani*	1.000	1
		Monodontomerus spp.	0.429	3
		Nemognatha sparsa	0.939	2
		Stelis montana	1.000	1
		Stelis rudbeckiarum	0.775	2
		Xenox tigrinus	1.000	1
	Treated	*Coelioxys deani*	0.638	2
		Monodontomerus spp.	0.638	2
		Nemognatha sparsa	1.000	1
		Sapyginae	1.000	1
		Stelis montana	1.000	1
		Xenox tigrinus	0.577	2
Host	Burned	*Dianthidium ulkei*	0.435	4
		Megachile relativa	0.645	3
		Osmia calla	1.000	1
	Control	*Dianthidium ulkei*	0.343	6
		Megachile angelarum	1.000	1
		Megachile fidelis	1.000	1
		Osmia calla	1.000	1
		Trypoxylon clavatum	1.000	1
	Treated	*Dianthidium ulkei*	0.709	4
		Megachile relativa	1.000	1
		Megachile spp.	0.500	3
		Trypoxylon clavatum	1.000	1

Figures

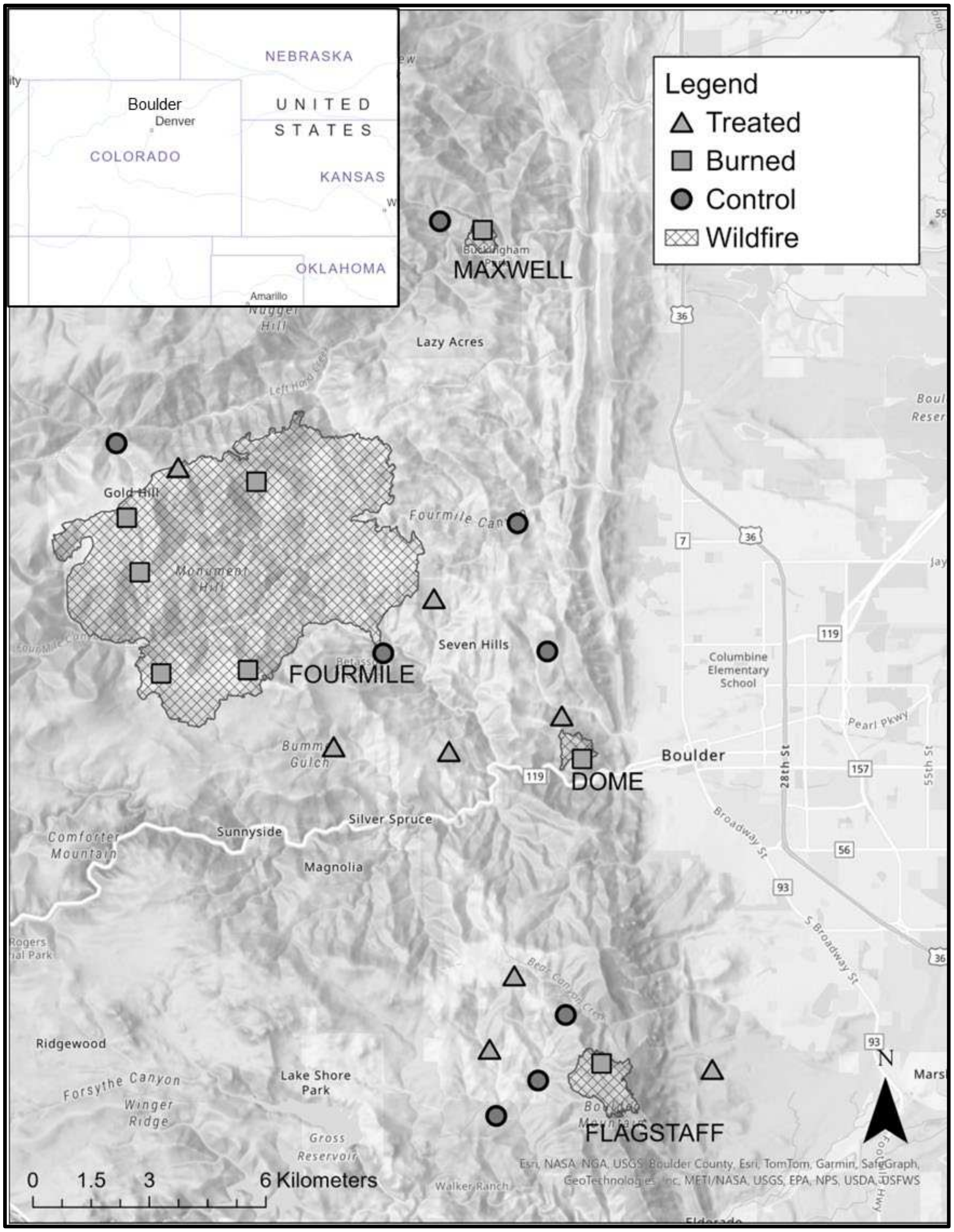

Figure 4.1. (A) Cutout of Boulder, Colorado, and (B) a map of study sites in Boulder County, Colorado. Site designations are as follows: burned: high severity wildfire (>80% tree canopy mortality) within the Dome (2010), Fourmile (2010), Maxwell (2011), and Flagstaff (2012) incidents; Thinned: managed for fuel reduction; and Control: non-burned and non-treated forested areas.

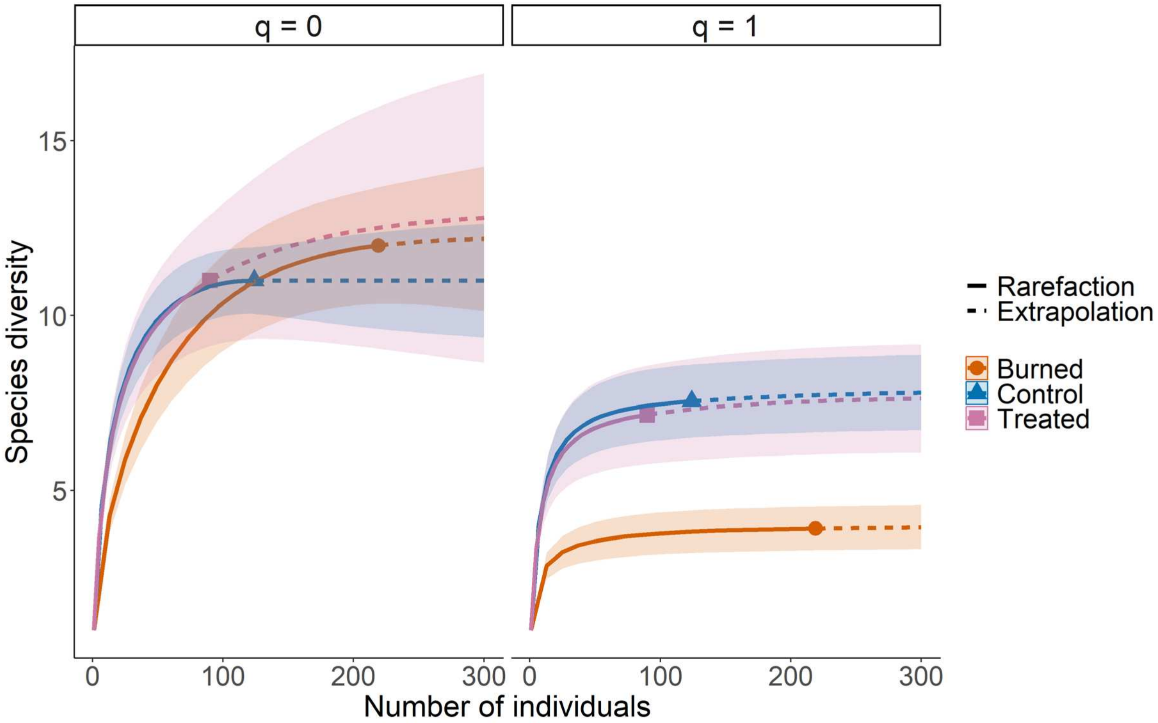

Figure 4.2. Sample-sized based accumulation curves among habitat types displaying rarefaction and extrapolation estimates calculated from Hill numbers of order (q) for species richness (q = 0) and Shannon diversity (q = 1). Shaded areas denote 95% confidence intervals for each curve.

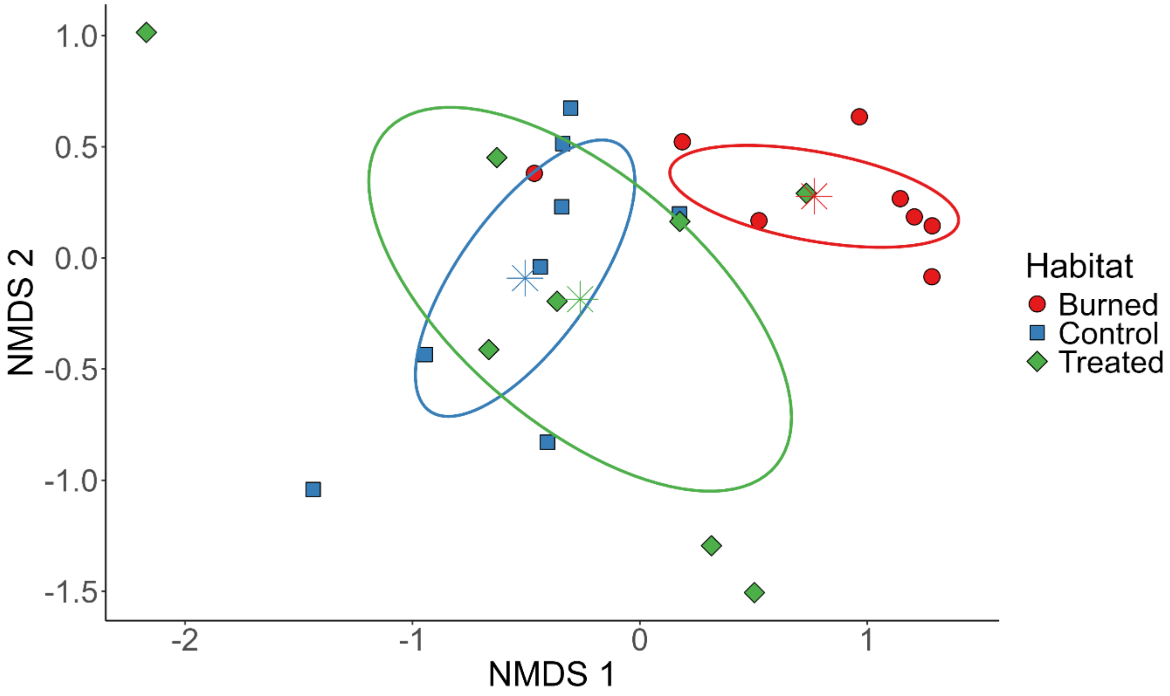

Figure 4.3. Non-metric Multi-dimensional Scaling (NMDS) of cavity bee species site ordinations among habitat groups. Ordination stress was 0.119 and Stars in the middle of 95% confidence ellipses depict ordination centroid or mean ordination score.

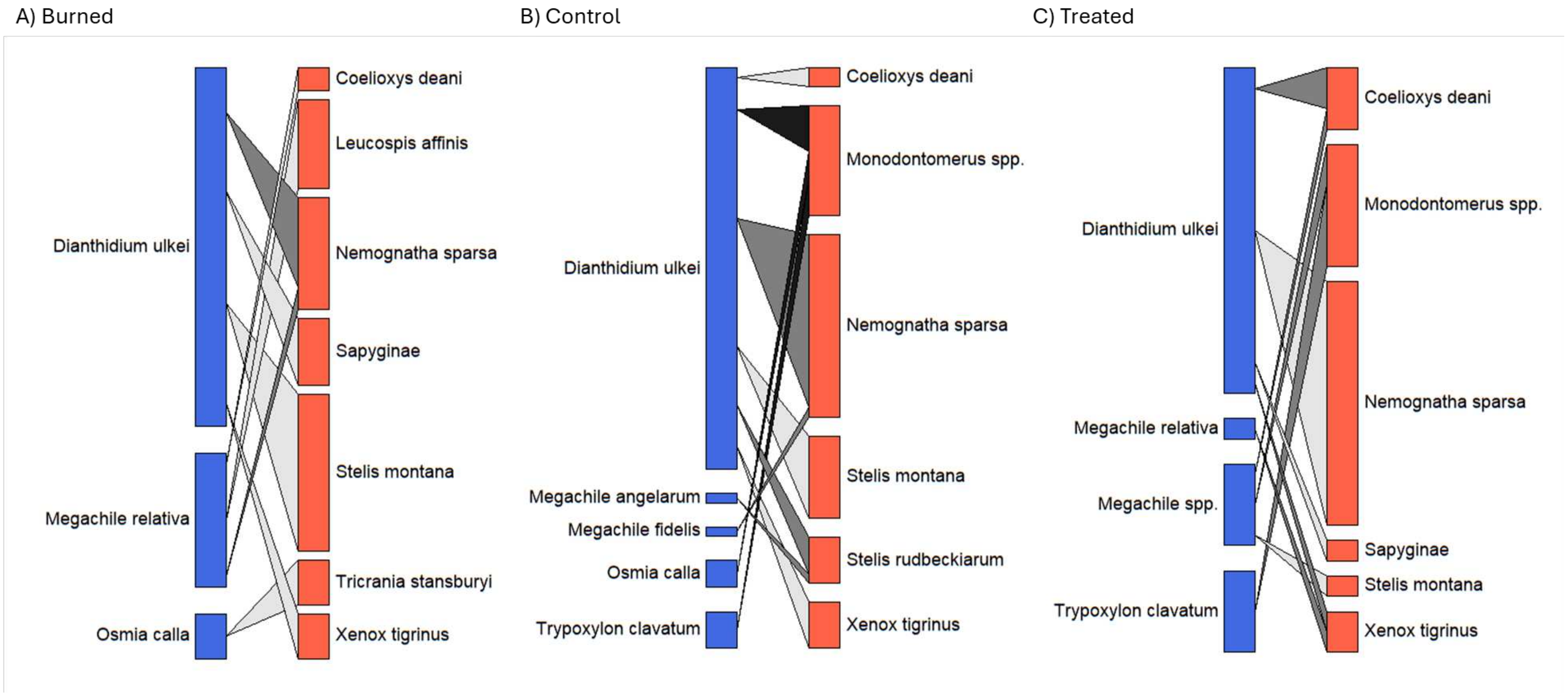

Figure 4.4. Parasite-host interactions pooled within (A) burned, (B) controlled, and (C) treated habitat types. The color of interaction arrows becomes darker with more interactions.

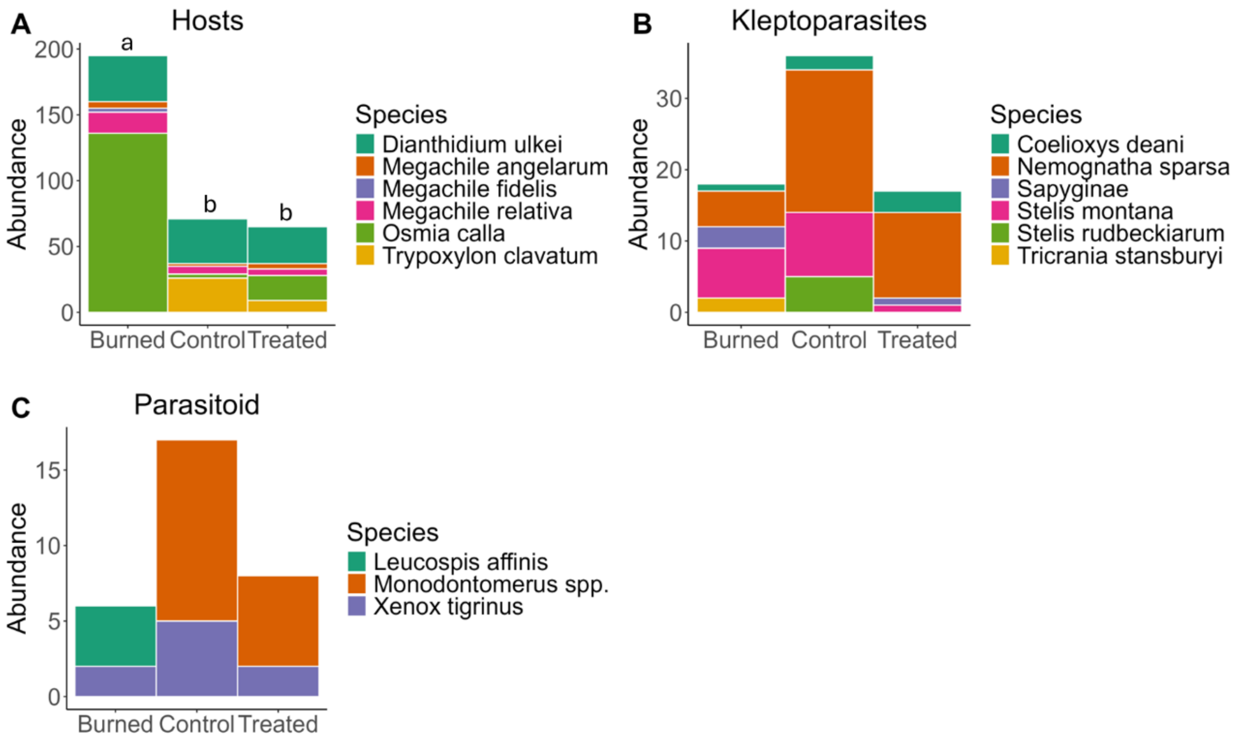

Figure 4.5. Abundance of emerged cavity-nesting (A) hosts, (B) kleptoparasites; and (C) parasitoids by habitat type; burned at high-severity wildfire (Burned), thinned (Treated), and unburned and untreated (Control). Letters denote significant GLM differences at α = 0.05. Note: *Monodontomerus spp.* abundance counts are not "true" abundance, but rather counts of host pupae infected by *Monodontomerus* spp.

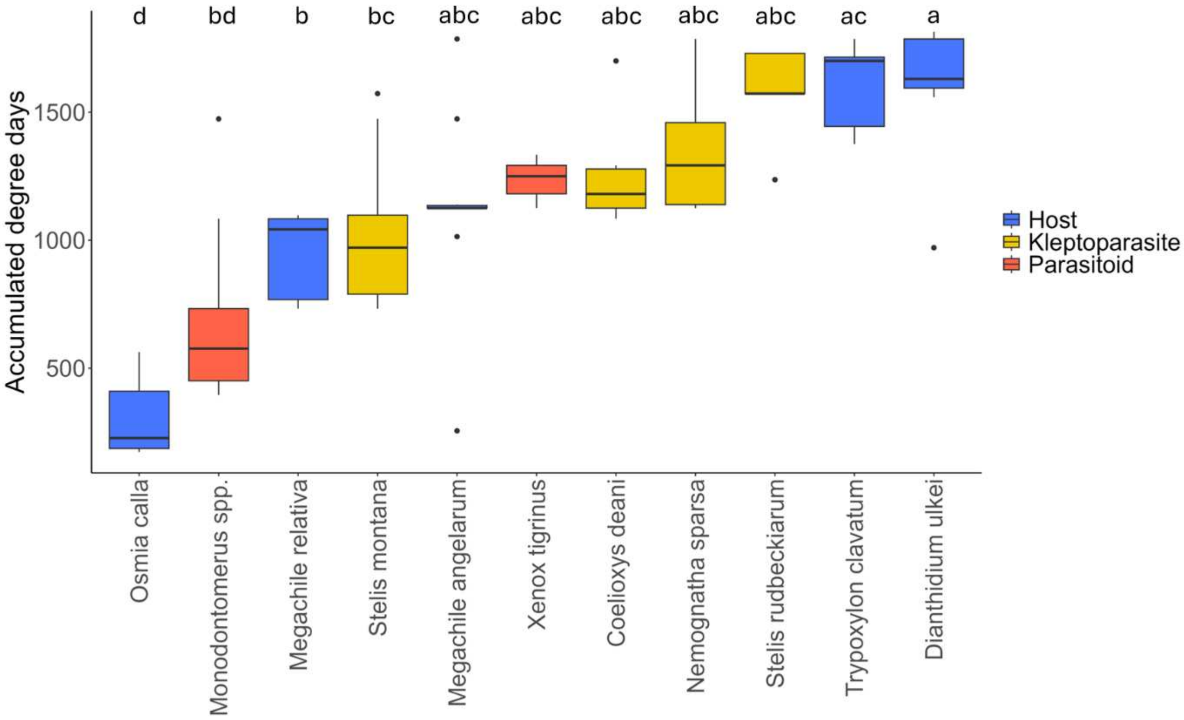

Figure 4.6. Degree days accumulated until emergence for each species in increasing order. Letters denote significant Dunn's Test pairwise comparisons among species emergence at $\alpha = 0.05$.

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CHAPTER 5

CONCLUSION

Most research on disturbance impacts on pollinators focuses on social bees or community assemblage differences. However, there is a notable lack of research on solitary, cavity-nesting bees and their fitness characteristics. My research addressed this literature gap by examining the influence of habitat variation on solitary bee diet, parasitism, and host-parasite community interactions.

In my initial chapter, I investigated how habitat variations influence bee diet, and consequently their reproduction. Despite differences in the types of flowers found in various habitats, *Osmia lignaria* primarily collected pollen from the Rosaceae and Salicaceae plant families, regardless of the specific floral makeup at each site. In 2020, the composition of pollen provisions was influenced by climate and landscape variations. However, in 2021, none of the habitat variables used predicted the composition of pollen. Interestingly, the study revealed that pollen provisions' diversity, richness, or protein content did not affect the reproduction or development of *O. lignaria*.

In my second chapter, I examined the impact of habitat variations on bee provisioning and kleptoparasite predation. The study revealed three key findings. First, I found that *O. lignaria* nest provisioning did not respond to habitat variation variables such as climate variation, forest structure, floral abundance, or land cover type. Second, I observed that the kleptoparasite, *T. stansburyi* abundance decreased with increased proportions of wildland-urban land cover.

Lastly, I found that *T. stansburyi* abundance was positively associated with *O. lignaria* nest provisioning and *O. lignaria* brood abundance. These results indicate that *O. lignaria*'s provisioning ability is less affected by habitat variations compared to its associated kleptoparasite. Habitats with abundant nest provisioning also supported larger populations of kleptoparasites, suggesting a higher likelihood of parasitism in such environments.

In my final chapter, I investigated cavity-nesting bee and parasite community assemblages and interactions within habitats that burned at high-severity (Burned), were thinned (Treated), or were unburned and untreated (Control). After collecting cavity-nest inhabitants, there were three key observations. Firstly, cavity-nesting bee and wasp communities varied by habitat, with burned sites having the highest abundance. Secondly, control sites had the most host-parasite interactions, with more parasite generality and host vulnerability than disturbed sites, which had fewer, more specialized parasite interactions. Lastly, emergence differed between a few cavity-nesting bee species, but generally, host-parasite pairs typically had synchronous adult emergence.

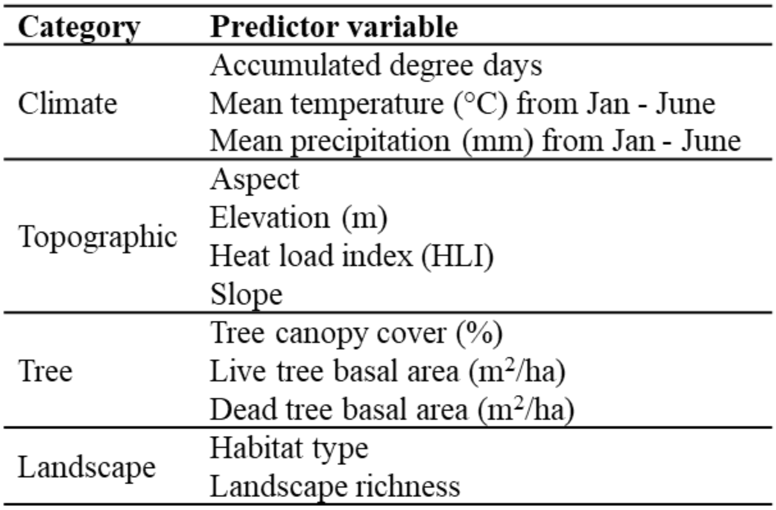
Collectively, my research indicates varying diet and parasite pressures across a landscape, but an overall perseverance of solitary bees. For example, even if forest disturbances cause variations in nutritional content, there was minimal impact on *O. lignaria* reproduction. However, landscape variations, such as increased urbanization in forested ecosystems, may pose threats to solitary bee pollen predators. Additionally, controlled sites displayed more general host-parasite interactions, suggesting 10-year-old wildfire may relieve parasitic pressure in dry forested ecosystems in Northern Colorado. Overall, these findings are crucial for understanding the responses of local, solitary bee communities to disturbances, which can be valuable for informing strategies for the management and conservation of native bees. Specifically, my results inform land managers that 1) floral surveys may not reflect preferred species for bee forage and surveying foraged pollen (e.g. microscopy or DNA metabarcoding) could lead to more targeted bee forage species and habitat types (e.g. riparian areas) conservation initiatives; 2) bee kleptoparasites could be used as indicator species for bee habitat health; and 3) disturbances like wildfire and thinning may relieve bees from parasitic pressure. Additionally, the presences of *D. ulkei* in all habitat types and the diversity of parasites that hosted upon *D. ulkei* suggests it might be a keystone species in dry, mixed-conifer forests of the Colorado Front Range and thus, could be a species to target for conservation management strategies.

APPENDICES

APPENDIX 1

Tables

Table A1.1. Habitat predictor variables used to test habitat variation on pollen community assemblages within each study year.



Category	Predictor variable
Climate	Accumulated degree days
	Mean temperature (°C) from Jan - June
	Mean precipitation (mm) from Jan - June
Topographic	Aspect
	Elevation (m)
	Heat load index (HLI)
	Slope
Tree	Tree canopy cover (%)
	Live tree basal area (m^2/ha)
	Dead tree basal area (m^2/ha)
Landscape	Habitat type
	Landscape richness

Table A1.2. Plant genera identified in site floral surveys (Site), within *O. lignaria* foraged pollen samples (Pollen), and genera identified in both floral surveys and pollen samples (Both) for each study year.

Study Year	Site	Pollen	Both
2020	Achillea	Actaea	Arnica
	Allium	Alnus	Senecio
	Ambrosia	Alphitonia	Tradescantia
	Arabis	Anemone	
	Carduus	Berberis	
	Ceanothus	Betula	
	Cirsium	Carex	
	Collinsia	Cerastium	
	Echinocereus	Ceratonia	
	Epilobium	Diheteropogon	
	Eriogonum	Equisetum	
	Gaillardia	Juniperus	
	Galium	Lonicera	
	Geranium	Maianthemum	
	Geum	Medicago	
	Grindelia	Pelargonium	
	Hieracium	Physocarpus	
	Jamesia	Populus	
	Lactuca	Prosartes	
	Lepidium	Pseudotsuga	
	Liliaceae	Quercus	
	Lupinus	Ribes	
	Mahonia	Sphagnum	
	Monarda		
	Opuntia		
	Phacelia		
	Phlox		
	Potentilla		
	Rosa		
	Sedum		
	Symphoricarpos		
	Tragopogon		
	Unk24		
	Verbascum		
	Yucca		

Study Year	Site	Pollen	Both
2021	Alyssum	Armoracia	NA
	Androsace	Cissus	
	Delphinium	Cornus	
	Erysimum	Fallopia	
	Leucocrinum	Heliotropium	
	Linaria	Hesperis	
	Lomatium	Robinia	
	Physaria		
	Stellaria		
Both	Campanula	Abies	NA
	Antennaria	Acer	
	Arctostaphylos	Cercocarpus	
	Astragalus	Iris	
	Erigeron	Linum	
	Mertensia	Osteomeles	
	Packera	Picea	
	Taraxacum	Pinus	
		Prunus	
		Rubus	
		Salix	
		Thermopsis	
		Toxicodendron	

Table A1.3. List of floral species identified in the field found in 2020, 2021, and both year surveys. Bold font denotes Indicator "Genera" found within foraged pollen community assemblages in Indicator Species Analysis.

2020 Species list	2021 Species list	Both
Achillea millefolium	Alyssum alyssoides	Allium spp.
Ambrosia tomentosa	Alyssum desertorum	Arctostaphylos uva-ursi
Antennaria spp.	Androsace occidentalis	Ceanothus fendleri
Arabis spp.	Antennaria rosea	Erigeron spp.
Arnica fulgens	Arnica cordifolia	Eriogonum spp.
Astragalus spp.	Astragalus spp.1	Erysimum capitatum
Campanula parryi	Astragalus spp.2	Lomatium spp.
Carduus nutans	Astragalus spp.3	Packera tridenticulata
Cirsium spp.	Astragalus spp.4	Senecio integerrimus
Collinsia parviflora	Campanula rotundifolia	Taraxacum officinale
Echinocereus viridiflorus	Delphinium occidentale	
Epilobium spp.	Leucocrinum montanum	
Gaillardia aristata	Linaria dalmatica	
Galium spp.	Mertensia lanceolata	
Geranium spp.	Packera spp.	
Geranium viscosissimum	Penstemon spp.1	
Geum triflorum	Penstemon spp.2	
Grindelia squarrosa	Phacelia hastata	
Hieracium spp.	Phlox longifolia	
Jamesia americana	Physaria bellii	
Lactuca serriola	Physaria spp.	
Lepidium spp.	Potentilla spp.	
Lupinus argenteus	**Rubus deliciosus**	
Lupinus spp.	Stellaria longifolia	
Mahonia repens		
Mertensia Lanceolata		
Monarda fistulosa		
Opuntia spp.		
Packera fendleri		
Penstemon spp.		
Phacelia spp.		
Phlox multiflora		
Phlox spp.		
Potentilla spp.		
Ribes spp.		

2020 Species list	**2021 Species list**	**Both**
Rosa acicularis		
Rubus idaeus		
Salix spp.		
Sedum lanceolatum		
Symphoricarpos albus		
Symphoricarpos spp.		
Tradescantia occidentalis		
Tragopogon spp.		
Unk Unk		
Unk Unk24		
Verbascum spp.		
Yucca glauca		

Table A1.4. Correlation coefficients associated with each genus on the first 3- and 2-axes of db-RDAs ran on 2020 and 2021 pollen communities, respectively. Bold font denotes significant indicator species within that year's pollen communities, and Bold and italic font denotes significant indicator species found within both year pollen communities.

	2020				*2021*	
Genus	**CAP1**	**CAP2**	**CAP3**	**Genus**	**CAP1**	**CAP2**
Abies	0.000	0.000	0.000	Abies	0.000	0.000
Acer	0.022	-0.040	0.139	***Acer***	-0.066	0.444
Actaea	0.000	0.000	0.000	Allium	0.000	0.000
Allium	-0.003	0.003	-0.003	Alphitonia	0.000	-0.004
Alnus	0.000	0.000	0.000	Armoracia	0.000	0.004
Alphitonia	0.016	0.008	-0.065	Berberis	-0.009	-0.059
Anemone	0.000	-0.001	0.003	***Cercocarpus***	1.127	-0.065
Arnica	0.000	0.001	-0.002	Cissus	0.002	-0.001
Berberis	1.243	0.760	-0.214	Cornus	0.000	0.001
Betula	0.000	-0.001	-0.001	Fallopia	-0.127	-0.065
Carex	0.003	0.002	0.004	Heliotropium	0.000	0.000
Cerastium	0.004	-0.004	-0.006	Hesperis	0.002	0.000
Ceratonia	-0.001	0.001	-0.001	Iris	0.000	0.000
Cercocarpus	-1.260	0.465	-0.030	Jamesia	-0.002	0.007
Diheteropogon	0.000	0.000	-0.001	Lepidium	0.000	0.004
Equisetum	0.000	0.000	0.000	Linum	0.000	0.002
Geranium	0.000	0.000	-0.001	Lonicera	0.000	0.000
Iris	0.000	0.000	0.000	Lupinus	-0.001	0.004
Jamesia	0.000	0.000	-0.001	Osteomeles	0.002	-0.005
Juniperus	0.000	0.000	0.000	Penstemon	-0.014	0.001
Linum	0.000	0.000	0.000	Physocarpus	0.000	0.002
Lonicera	0.000	0.000	0.003	***Picea***	-0.002	0.024
Lupinus	0.000	0.000	0.000	***Pinus***	-0.248	-0.011
Maianthemum	0.000	-0.001	-0.005	Populus	0.001	-0.002
Medicago	-0.002	0.002	-0.002	Potentilla	0.000	-0.002
Mertensia	-0.018	0.013	-0.014	***Prunus***	-0.011	0.066
Osteomeles	0.000	0.000	0.000	Pseudotsuga	-0.001	0.003
Pelargonium	-0.011	-0.015	-0.001	Ribes	-0.001	0.001
Penstemon	0.005	-0.027	-0.044	Robinia	-0.002	-0.006
Physocarpus	-0.001	0.001	-0.001	Rosa	0.024	-0.007
Picea	-0.006	0.007	-0.006	***Rubus***	0.003	-0.025
Pinus	-0.124	0.097	-0.152	***Salix***	-0.724	-0.174
Populus	0.049	-0.380	0.406	Symphoricarpos	0.000	-0.001

2020				*2021*		
Genus	**CAP1**	**CAP2**	**CAP3**	**Genus**	**CAP1**	**CAP2**
Prosartes	0.041	-0.115	0.500	Thermopsis	0.047	-0.100
Prunus	-0.040	0.006	0.044	Toxicodendron	0.002	-0.018
Pseudotsuga	0.003	-0.005	-0.002	Tradescantia	0.000	-0.020
Quercus	0.000	0.000	0.000	Viola	0.000	0.001
Ribes	0.000	-0.012	0.050		0.000	0.000
Rubus	0.007	0.004	-0.085			
Salix	0.091	-0.787	-0.493			
Senecio	0.000	0.000	0.000			
Sphagnum	-0.002	0.002	-0.002			
Symphoricarpos	0.000	0.000	0.000			
Thermopsis	-0.001	0.001	-0.002			
Toxicodendron	-0.002	0.002	-0.001			
Tradescantia	-0.012	0.012	-0.012			
Viola	0.001	0.001	-0.001			

Table A1.5. Summary of general linear regression models summarizing effects average pollen protein concentration (μg/mL, Protein), pollen diversity, and pollen richness, on total *O. lignaria* brood ratio, female sex ratio, male pupae weight, and female pupae weight within each study year. Bold face denotes significance at α = 0.05.

		2020				*2021*			
	Coefficients	**Estimate (β)**	**Std. Error**	***t-value***	***P-value***	**Estimate (β)**	**Std. Error**	***t-value***	***P-value***
Ratio (%)	Intercept	0.766	0.207	3.696	**0.004**	0.576	0.165	3.485	**0.005**
	Protein	0.002	0.010	0.172	0.867	0.008	0.015	0.492	0.632
	Diversity	0.113	0.200	0.564	0.585	-0.164	0.156	-1.056	0.312
	Richness	-0.020	0.030	-0.674	0.516	0.013	0.020	0.627	0.542
Sex ratio (%)	Intercept	NA	NA	NA	NA	0.671	0.165	4.075	**0.002**
	Protein	NA	NA	NA	NA	-0.003	0.015	-0.177	0.863
	Diversity	NA	NA	NA	NA	-0.146	0.148	-0.986	0.345
	Richness	NA	NA	NA	NA	-0.002	0.019	-0.105	0.918
Male pupae weight (mg)	Intercept	23.363	6.006	3.890	**0.012**	26.077	2.290	11.389	**0.000**
	Protein	-0.257	0.263	-0.978	0.373	-0.221	0.202	-1.098	0.298
	Diversity	-0.844	6.045	-0.140	0.894	-0.106	2.061	-0.051	0.960
	Richness	0.212	0.759	0.280	0.791	0.057	0.260	0.220	0.830
Female pupae weight (mg)	Intercept	NA	NA	NA	NA	0.025	0.003	8.633	**0.000**
	Protein	NA	NA	NA	NA	0.000	0.000	0.889	0.393
	Diversity	NA	NA	NA	NA	0.001	0.003	0.339	0.741
	Richness	NA	NA	NA	NA	0.000	0.000	-0.626	0.544
Larvae weight (mg)	Intercept	41.268	11.463	3.600	**0.006**	NA	NA	NA	NA
	Protein	-0.643	0.584	-1.100	0.300	NA	NA	NA	NA
	Diversity	-13.549	11.621	-1.166	0.274	NA	NA	NA	NA
	Richness	1.430	1.718	0.833	0.427	NA	NA	NA	NA

Table A1.6. Summary of stem counts identified to genus surveyed on site each year.

Genus	2020 Mean +/- SE	2021 Mean +/- SE
Achillea	5.204 +/- 1.31	0
Allium	1.167 +/- 0.167	1 +/- 0
Alyssum	0	3.168 +/- 1.352
Ambrosia	2.667 +/- 0.333	0
Androsace	0	1.035 +/- 0.035
Antennaria	3 +/- 0	6.75 +/- 0
Arabis	1 +/- 0	0
Arctostaphylos	9.75 +/- 7.25	6.758 +/- 2.439
Arnica	6.5 +/- 0	1 +/- 0
Astragalus	14.833 +/- 10.167	4.583 +/- 1.315
Campanula	5.45 +/- 2.376	1.188 +/- 0.188
Carduus	2 +/- 1	0
Ceanothus	32.5 +/- 11.303	8.333 +/- 0
Cirsium	1.833 +/- 0.833	0
Collinsia	2.25 +/- 1.25	0
Delphinium	0	1 +/- 0
Echinocereus	1 +/- 0	0
Epilobium	11.833 +/- 9.833	0
Erigeron	6 +/- 2.776	2.603 +/- 1.295
Eriogonum	3.976 +/- 1.023	9.367 +/- 8.367
Erysimum	1 +/- 0	1.029 +/- 0.029
Gaillardia	3 +/- 0	0
Galium	8.419 +/- 3.216	0
Geranium	4.857 +/- 1.993	0
Geum	4 +/- 1	0
Grindelia	2 +/- 0	0
Hieracium	1 +/- 0	0
Jamesia	10.25 +/- 0.25	0
Lactuca	1.5 +/- 0.5	0
Lepidium	26 +/- 13.604	0
Leucocrinum	0	1 +/- 0
Liliaceae	1 +/- 0	0
Linaria	0	1 +/- 0
Lomatium	1.833 +/- 0.441	2.308 +/- 0.388
Lupinus	5.98 +/- 1.343	0
Mahonia	11.75 +/- 0	0
Mertensia	3.167 +/- 0.833	1.157 +/- 0.085
Monarda	18 +/- 0	0

Genus	**2020 Mean +/- SE**	**2021 Mean +/- SE**
Opuntia	3.333 +/- 1.202	0
Packera	7.5 +/- 0.5	1.333 +/- 0.333
Penstemon	8.372 +/- 2.3	4.23 +/- 1.412
Phacelia	3.933 +/- 1.462	2.375 +/- 0
Phlox	16.333 +/- 9.866	1.3 +/- 0
Physaria	0	2.751 +/- 0.452
Potentilla	10 +/- 4.204	1.1 +/- 0.1
Ribes	3.5 +/- 0	0
Rosa	3.333 +/- 1.453	0
Rubus	3 +/- 0	2 +/- 0
Salix	6.333 +/- 0	0
Sedum	32 +/- 0	0
Senecio	1.5 +/- 0	1 +/- 0
Stellaria	0	1.943 +/- 0.275
Symphoricarpos	3.125 +/- 1.36	0
Taraxacum	3.583 +/- 1.714	2.272 +/- 0.719
Tradescantia	1 +/- 0	0
Tragopogon	1.75 +/- 0.25	0
Unk spp.1	2.25 +/- 0.75	0
Verbascum	2.333 +/- 1.333	0
Viola	0	1.56 +/- 0
Yucca	1 +/- 0	0

Figures

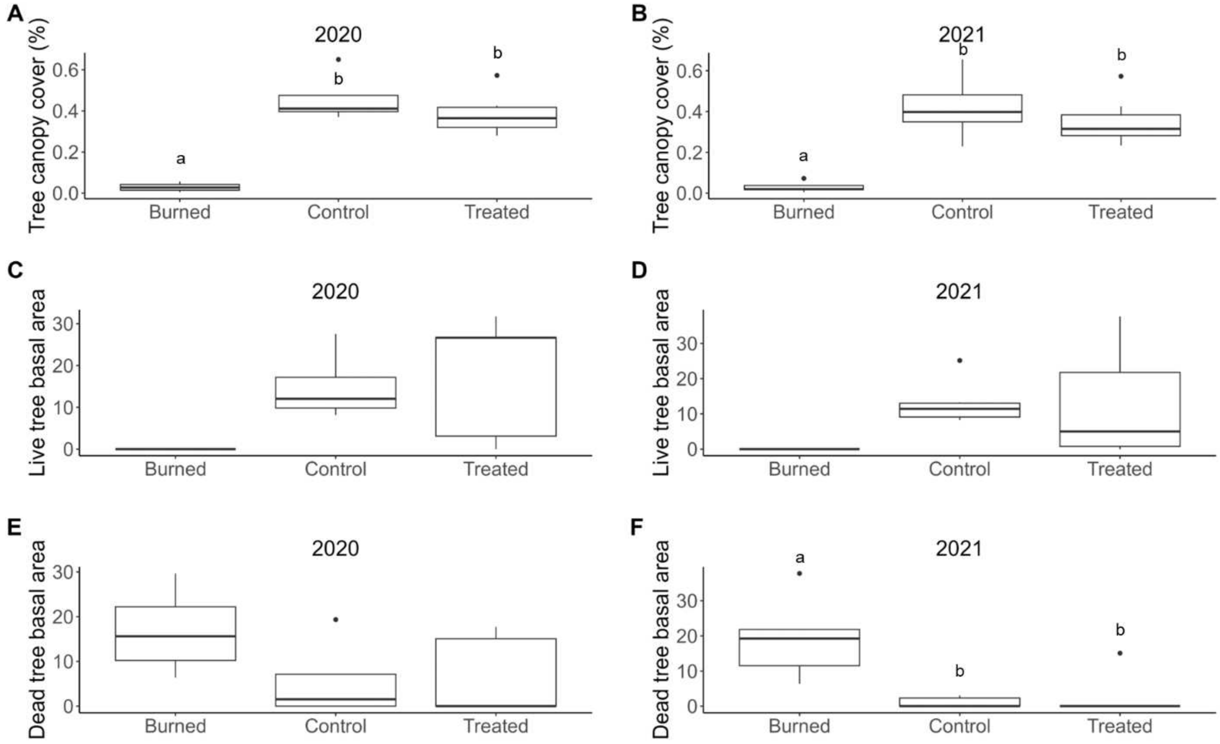


Figure A1.1. Differences of tree variables measured including mean tree canopy cover (%) in (A) 2020 and (B) 2021; live tree basal area m^2/ha^{-1} in (C) 2020 and (D) 2021; and dead tree basal area m^2/ha^{-1} in (E) 2020 and (F) 2021. Letters denote Tukey HSD significance at $\alpha = 0.05$.

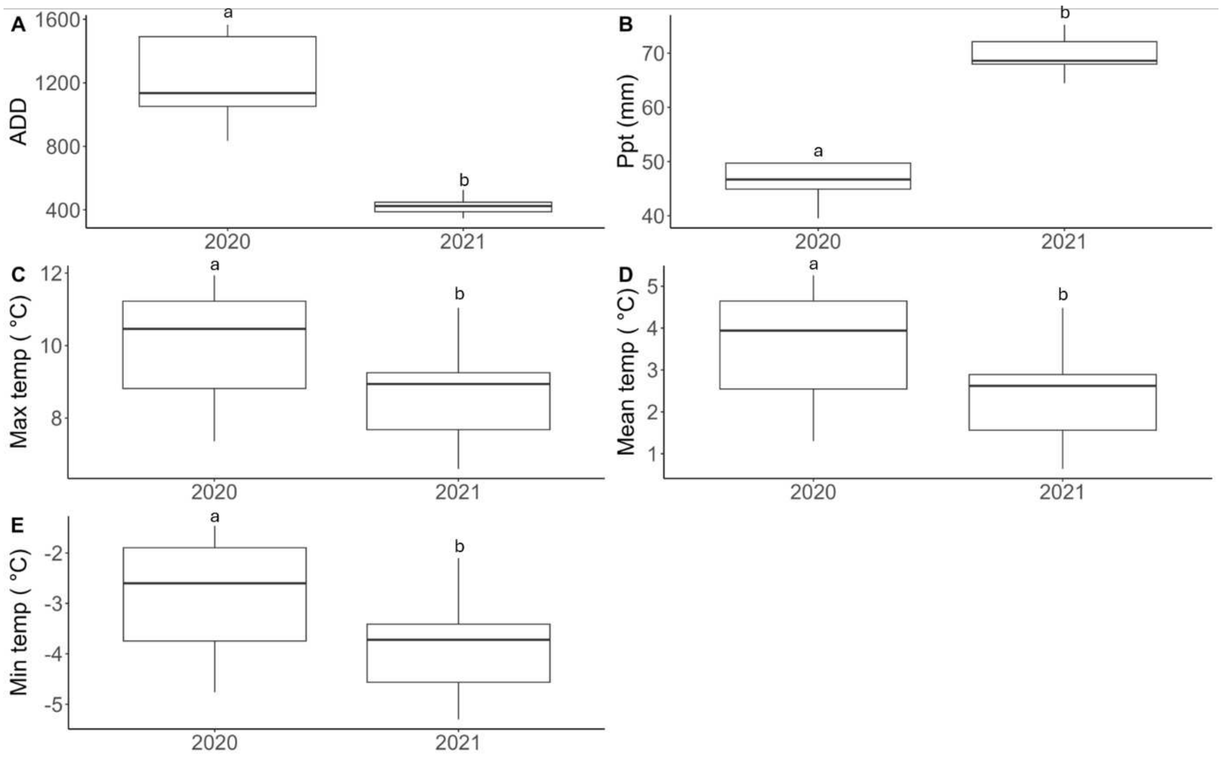


Figure A1.2. Average climate differences between January-July of each study year including: (A) accumulated degree days (ADD); (B) precipitation (ppt); (C) maximum temperature (max temp); (D) mean temperature (temp); and (E) minimum temperature (min temp). Letters denote ANOVA significance at α = 0.05.

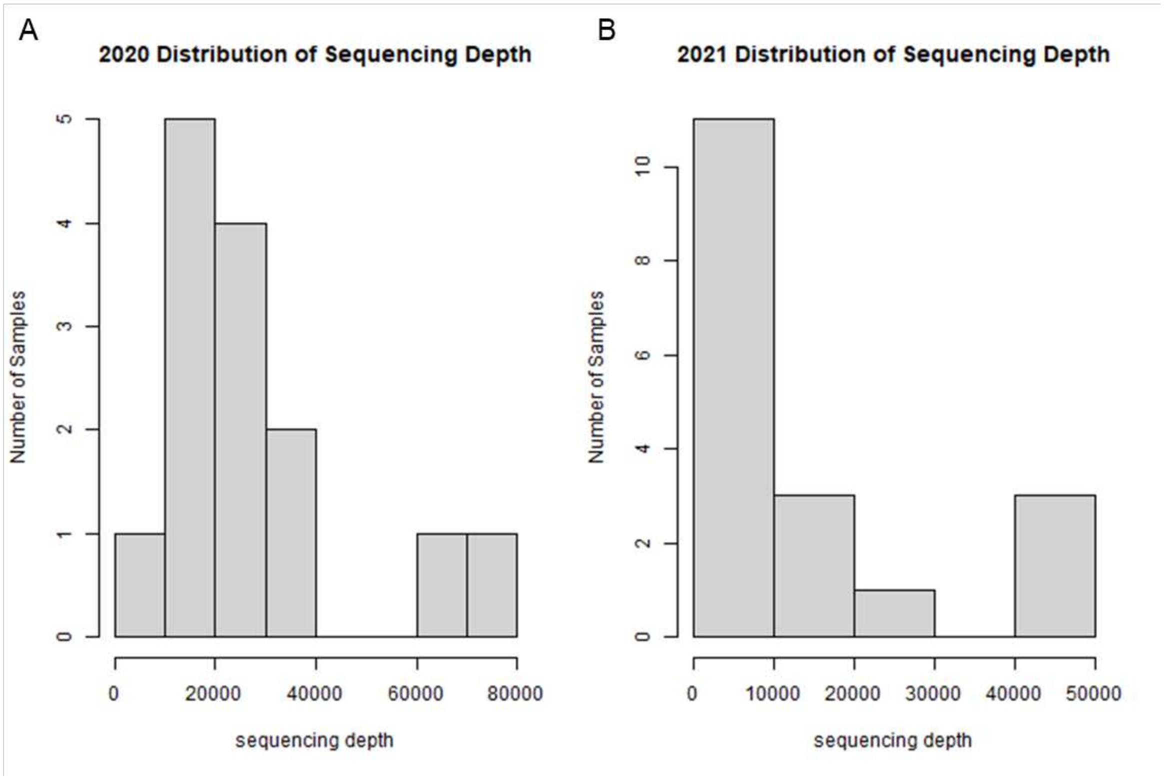


Figure A1.3. Sequencing depth found within pollen provision samples in (A) 2020 and (B) 2021.

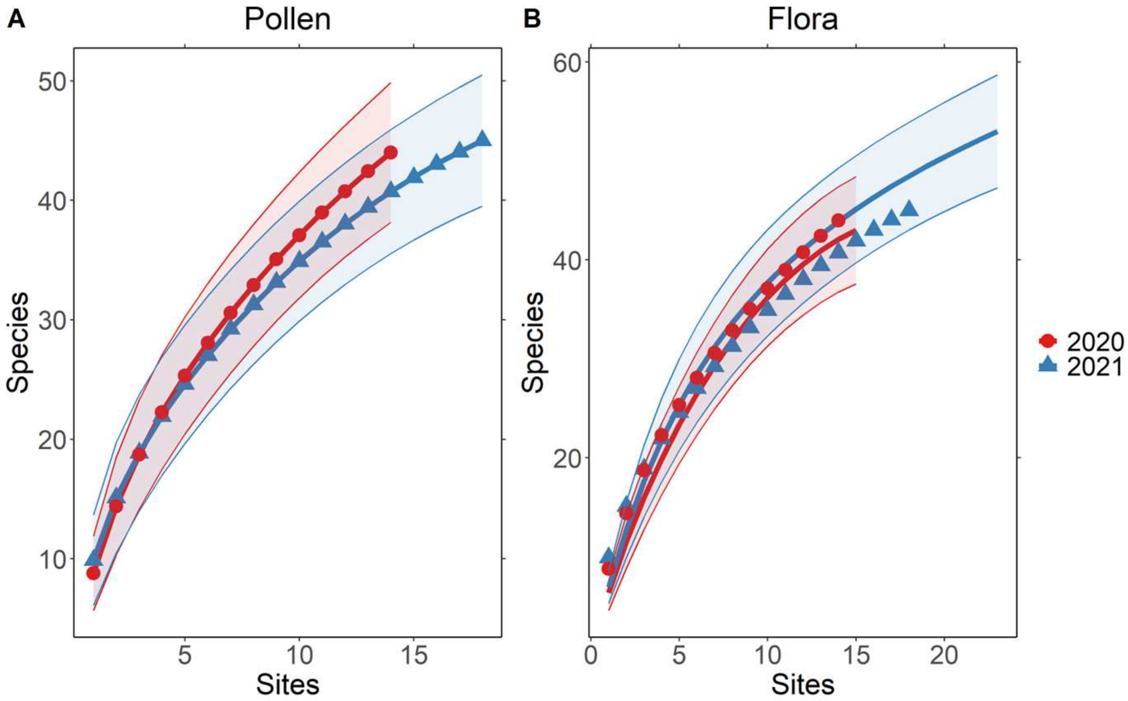


Figure A1.4. Species area curves for A) pollen provisions and B) site floral surveys within each study years.

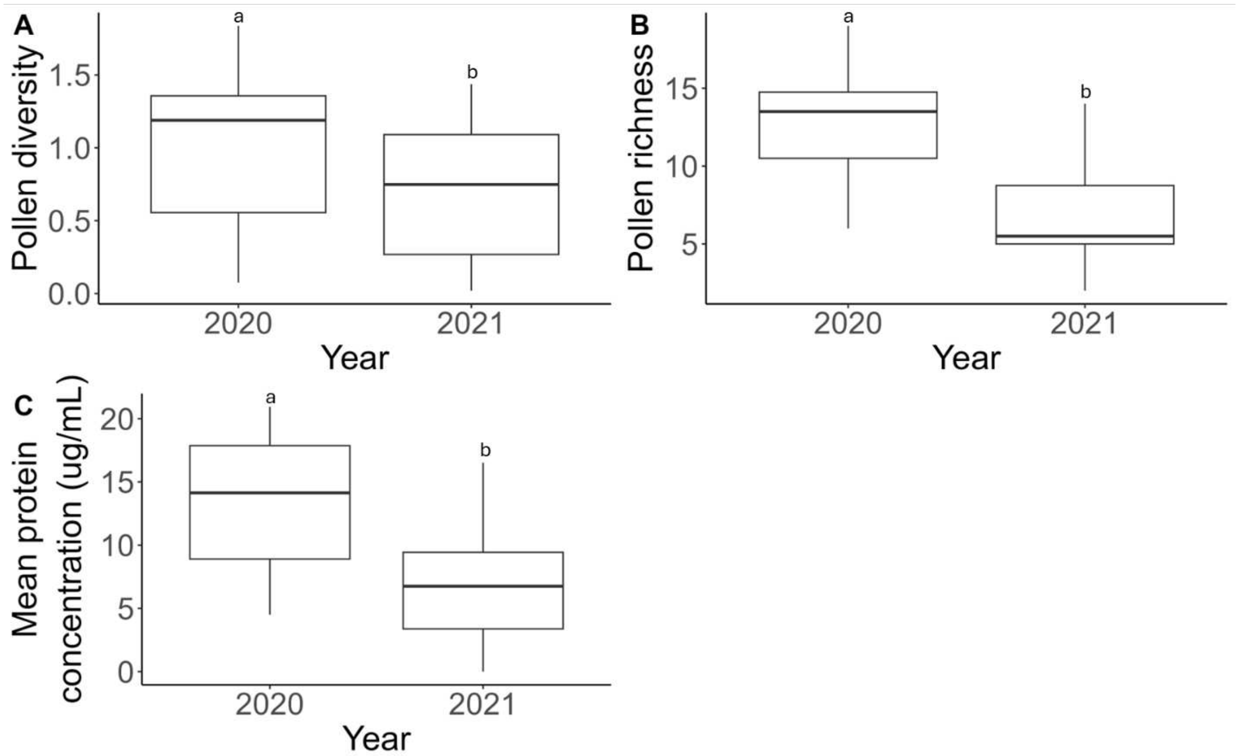


Figure A1.5. Differences in pollen DNA (A) Shannon's diversity, (B) richness, and (C) mean protein concentration between the two study years. Letters denote significance at α = 0.05 from ANOVA tests.

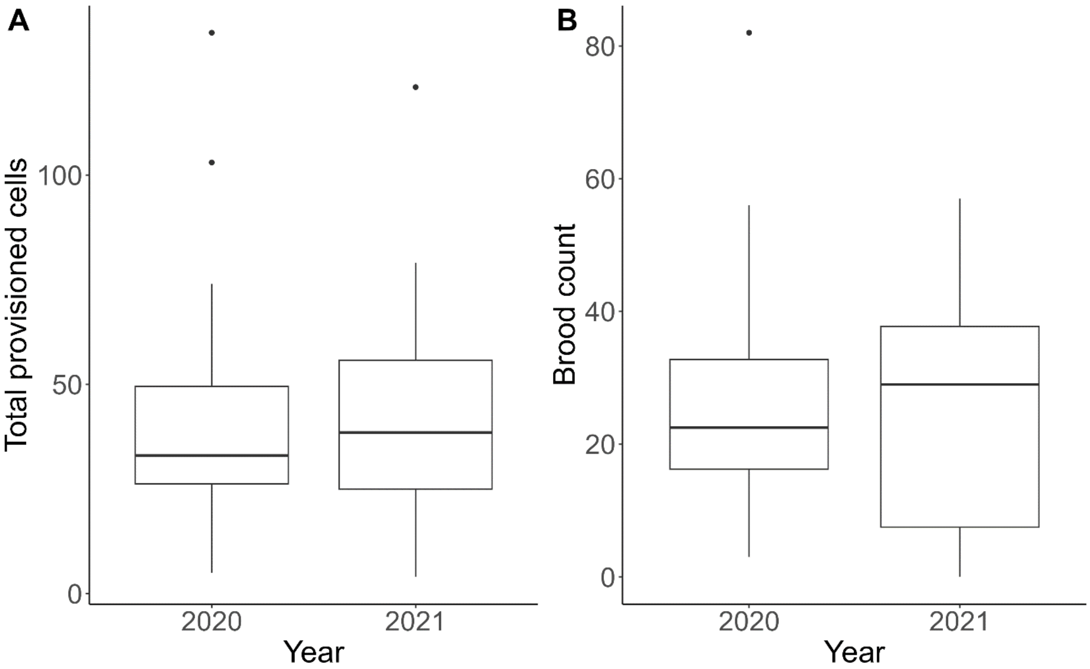


Figure A1.7. Boxplots displaying differences in *O. lignaria* (A) total provisioned nest cells; and (B) total brood (2nd larval instar or higher) count from all sites between each study year.

APPENDIX 2

Tables

Table A2.1. Summary of habitat variables predicting pollen *O. lignaria* provisioned nest cells and *T. stansburyi* abundance.

	Provisioned cells				*T. stansburyi abundance*			
Coefficients	**Estimate (β)**	**Standard Error**	***t-value***	***P-value***	**Estimate (β)**	**Standard Error**	***t-value***	***P-value***
Intercept	3.241	0.309	10.477	< **0.001**	0.684	0.389	1.756	*0.090*
Accumulated degree days	0.000	0.000	1.364	0.181	0.000	0.000	1.022	0.315
Intercept	4.322	0.734	5.887	< **0.001**	1.015	0.928	1.094	0.283
Jan-June avg. precip.	-0.012	0.012	-0.996	0.326	0.000	0.015	0.006	0.995
Intercept	3.214	0.408	7.887	< **0.001**	0.602	0.473	1.272	0.213
Jan-June avg. temp.	0.123	0.120	1.031	0.309	0.136	0.137	0.993	0.329
Intercept	3.691	0.254	14.520	< **0.001**	1.159	0.318	3.647	**0.001**
Heat Load Index (HLI)	0.083	0.183	0.455	0.652	0.118	0.228	0.517	0.609
Intercept	3.549	0.259	13.700	< **0.001**	0.967	0.349	2.768	**0.010**
Tree canopy cover (%)	0.165	0.757	0.218	0.828	0.175	0.963	0.182	0.857
Intercept	3.705	0.188	19.731	< **0.001**	1.097	0.249	4.408	< **0.001**
Live tree basal area	-0.014	0.014	-0.948	0.350	-0.005	0.017	-0.272	0.788
Intercept	3.725	0.189	19.668	< **0.001**	1.157	0.220	5.255	< **0.001**
Dead tree basal area	-0.018	0.016	-1.106	0.276	-0.015	0.020	-0.766	0.450
Intercept	3.696	0.376	9.833	< **0.001**	1.212	0.487	2.489	**0.019**
Floral stem diversity	-0.073	0.252	-0.291	0.772	-0.133	0.318	-0.420	0.678
Intercept	3.508	0.267	13.139	< **0.001**	0.804	0.325	2.472	**0.020**
Floral stem richness	0.013	0.032	0.403	0.690	0.030	0.036	0.843	0.406
Intercept	3.446	0.277	12.455	< **0.001**	0.560	0.440	1.273	0.214
Habitat-Control	0.019	0.397	0.049	0.961	0.539	0.532	1.012	0.320
Habitat-Treated	0.357	0.355	1.005	0.322	0.613	0.508	1.208	0.237
Intercept	3.859	0.269	14.355	< **0.001**	1.527	0.299	5.108	< **0.001**
Landscape diversity	-0.634	0.572	-1.109	0.275	-1.297	0.702	-1.849	*0.075*
Intercept	3.472	0.523	6.633	< **0.001**	1.790	0.561	3.191	**0.003**
Landscape richness	0.042	0.168	0.247	0.806	-0.260	0.187	-1.391	0.175
Intercept	3.913	0.275	14.204	< **0.001**	1.564	0.310	5.045	< **0.001**
Landscape evenness	-0.849	0.660	-1.286	0.206	-1.597	0.844	-1.894	*0.068*
Intercept	2.857	0.713	4.008	< **0.001**	-0.098	0.908	-0.108	0.915
Coniferous forest (%)	0.895	0.832	1.076	0.289	1.343	1.042	1.289	0.208
Intercept	3.572	0.193	18.489	< **0.001**	1.094	0.240	4.563	< **0.001**
Deciduous forest (%)	3.318	17.309	0.192	0.849	-9.832	21.498	-0.457	0.651
Intercept	3.697	0.181	20.390	< **0.001**	1.111	0.218	5.094	< **0.001**
Rangeland (%)	-0.741	0.852	-0.869	0.390	-0.675	0.999	-0.676	0.504
Intercept	3.689	0.170	21.637	< **0.001**	1.359	0.180	7.557	< **0.001**
WUI (%)	-3.290	3.432	-0.959	0.344	-16.319	6.612	-2.468	**0.020**
Intercept	3.744	0.223	16.818	< **0.001**	1.046	0.282	3.713	**0.001**
Year	-0.255	0.299	-0.853	0.399	-0.045	0.373	-0.119	0.906