

PLANT-POLLINATOR NETWORK ASSEMBLY AFTER WILDFIRE

by

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DEDICATION

To Stacy for your endless love and patience through this entire ordeal.

And to Geoff, I'll see what I can do about carrying that fire.

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ABSTRACT

Plant-pollinator networks are threatened by anthropogenic influence due to habitat loss, changing fire regimes, climate change and other factors. Furthermore, we have little current knowledge for how species interactions and processes like pollination assemble and recover post-disturbance. Studying the mechanisms by which plant-pollinator interactions assemble in a post-disturbance landscape, particularly across gradients of disturbance intensity and successional time, would greatly help in building foundational ecological knowledge regarding the assembly of species interactions as well as provide specific information to aid conservation and management. Therefore, we investigated plant-pollinator network assembly after wildfire, between mixed- and high-severity burns and across time-since-burn, and we asked i) how do network structure and the network roles of persistent species vary ii) how does wildfire change the nutritional landscape of available floral pollen quality and how does that influence bumble bee foraging and nutrition, and iii) how do nesting and floral resources affected by wildfire influence wood-cavity-bee nesting success and richness?

Our study design involved four wildfires from the Absaroka Mountains of southwest Montana, USA, which included a range of burn severities as well as a 1-25 year chronosequence of time-since-burn sampled primarily from 2014 to 2016. Bees were sampled via hand netting and nesting boxes alongside floral census transects and pollen sampling to assess metrics important to plant-pollinator network assembly, available floral pollen quality, bumble bee nutrition, and wood-cavity-nesting bee nesting success.

The primary findings are that i) plant-pollinator network structure does not dramatically shift with burn severity or time-since-burn, nor do the network roles of persistent species, ii) available floral pollen quality and bumblebee nutrition are limited by high-severity burns, and iii) burn severity has little effect on the nesting success of wood-cavity-nesting bees. The conclusions that follow these results are mainly that i) evidence of constant structure and low variance of species' roles provides evidence for preferential attachment over opportunistic attachment in assembling plant-pollinator networks post-disturbance, ii) varied species composition between mixed- and high-severity burns may mean that bumble bees are nutritionally limited in high-severity burns, and iii) nesting resources do not appear to strongly limit nesting success or richness of wood-cavity-nesting bees.

INTRODUCTION

Community ecology has always been oriented towards understanding patterns in the diversity and distribution of species, and modern research has maintained that initial heading by investigating the processes which organize or control the assembly of community composition (Vellend 2010). In recent years, focus has turned towards the importance of species interactions in structuring communities for purposes of assessing e.g., their function, resilience, or stability and persistence when facing both natural perturbations as well as anthropogenic effects (Bascompte and Stouffer 2009, Tylianakis et al. 2010). For a community assembling after disturbance there are factors which will determine the species that can initially be present in the post-disturbance landscape. For example, seed banks can affect the regeneration of the vegetative community (Brown et al. 2015), and environmental filters, such as soil changes due to disturbance (e.g., Carbone and Aguilar 2017) can affect which species are successful in establishing from that legacy seed bank. Furthermore, as succession progresses, other factors which control assembly may begin to dominate. Changing environmental conditions may allow the dispersal of new species into the area, or cause local extinction of previously established species, while ecological drift of species' abundances may cause species' presence to change dramatically across the landscape (Vellend 2010).

The processes which dictate assembly are relatively well integrated into community ecology theory, however evidence for when or how these individual processes of assembly are dominant and how different communities assemble after disturbance is poorly understood for most animal communities, particularly for species

that are tied to essential ecological functions like pollination (Driscoll et al. 2010, Brown et al. 2017). Plant-pollinator networks are an example of two communities and their resulting species interactions that are at the forefront of developing theory for the assembly of species interactions, as they represent an essential ecosystem function, pollination, that is under threat from anthropogenic changes (Potts et al. 2010, Tylianakis et al. 2010). Furthermore, we still have a poor understanding of the factors which determine species interactions, particularly during assembly. In the face of habitat loss, climate change, and other anthropogenic factors, building an understanding of how communities and species interactions assemble, particularly post-disturbance, will be essential for proper conservation and management in the twenty-first century (Tylianakis et al. 2008, 2010).

Fire is an essential ecosystem process for many systems globally, and an important example of a natural disturbance that has undergone significant alteration in the Anthropocene such as increasing spatial extent of burns, increased burn severity, and greater burn frequency (Bowman et al. 2009). In the context of community and network assembly, changing fire regimes presents an ecological opportunity, in that we can study different ages of burns that assembled along different trajectories to look for commonalities as well as differences which can be used to gain insight on how species interactions assemble. Furthermore, on a practical level, it can provide information essential for future fire management.

The overarching theme of this dissertation is the assembly of plant-pollinator networks after wildfire, with particular focus on how different components of a post-burn

ecosystem may determine or limit the assembly of plant and pollinator communities as well as the interactions which form those networks. In the first chapter we directly focus on network assembly, individually assessing how plant and pollinator communities change with burn severity and time-since-burn before addressing changes in network structure and species' network roles across those same gradients. The second chapter takes a look at how nutrition may drive species interactions, as we investigate how wildfire can shape the landscape-scale available floral pollen quality, as well as how post-burn variance in the available floral pollen quality correlates with bumblebee foraging and bumblebee nutrition. In the third chapter, we take an environmental filtering approach to community assembly, in that we attempt to test whether environmental factors altered by wildfire (i.e., nesting and floral resources) play a role in determining the nesting success of wood-cavity-nesting bees, and whether those patterns may differ between burn-severity and time-since-burn.

PLANT-POLLINATOR NETWORK MOTIFS AND SPECIES' ROLES DO NOT
CHANGE WITH BURN SEVERITY OR TIME-SINCE-BURN

Introduction

Disturbance is an important driver of community assembly, as it creates opportunities for species to disperse and colonize previously inaccessible areas, allowing for the assembly of founding communities which then encounter environmental filters that dictate the outcomes of species establishment and community assembly (Chase and Leibold 2003). Ecological disturbances, such as wildfire, provide exceptional opportunities to track the assembly of communities by comparing community composition and structure across gradients of disturbance severity or through successional time. Fire is a globally occurring process essential for biodiversity, yet it has experienced marked increases in severity due to fire suppression and climate change (Bowman et al. 2009). Wildfire can have profound effects on community assembly by influencing dispersal and species sorting, i.e., which species persist through fire, colonize afterwards, and successfully establish (Brown et al. 2015). Furthermore, the resulting patterns of community composition are likely to change through successional time post-burn (Abella and Fornwalt 2015). Post-fire plant community assembly has recently been shown to be highly controlled by legacy effects (e.g., seed banks) with environmental filters playing a secondary role after initial establishment by species and increasing in importance with successional time post-burn (Brown et al. 2015). While vegetation community assembly post-burn has been widely studied, and the theory driving plant

community assembly is well developed, the responses of animal communities and their interactions with the plant community are poorly understood (Brown et al. 2017). One of the biggest factors currently limiting our understanding of the effects of fire, and disturbance generally, on community assembly is the lack of data regarding species interactions, particularly for species involved in processes like pollination that directly affect plant reproduction and thus have the potential to influence community assembly (Driscoll et al. 2010). Concurrently, pollinator biodiversity is declining globally, with habitat loss or degradation via changing fire regimes implicated as one of the many contributors (Potts et al. 2010).

We have a general understanding of how communities respond to wildfire: greater burn severity or lower variability among patches in burn severity tends to decrease species richness of both bees and flora (Ponisio et al. 2016), while mixed-severity burns, those with higher variability in local burn severity, demonstrate greater bee and floral diversity (Ponisio et al. 2016). Both bee and floral richness also tend to peak in the years immediately post-burn, and gradually decline with increasing time-since-burn (Potts et al. 2003, Potts et al. 2005, Grundel et al. 2010, Abella and Fornwalt 2015, Burkle et al. 2015). This temporal pattern has not been studied in tandem with burn severity for bee communities to our knowledge; however, the trajectories of floral community species richness post-burn can vary with burn severity, with high-severity burns requiring greater time-since-burn to approach pre-burn diversity levels (Abella and Fornwalt 2015). Additionally, time-since-burn influences bee communities in other ways as well: ground nesting bees are more abundant in fresh burns, generalists are more abundant in areas of

recent and frequent burns, and bee body size increases with greater time-since-burn (Lazarina et al. 2016), suggesting environmental filtering on certain taxa or traits that vary with time-since-burn. Therefore, it generally seems that plant communities are likely to be structured by legacy effects post-burn (Brown et al. 2015), while the associated pollinator communities assemble following combinations of foraging, nesting, or other trait-focused environmental filters (e.g., Lazarina et al. 2016, Peralta et al. 2017).

However, plant and pollinator communities are not isolated from one another in their post-disturbance assembly, given that the structure and function of species interactions and the resulting network (i.e., web of species interactions between trophic levels) can change dependently and independently of the basic biodiversity and species turnover of the individual communities (Dyer et al. 2010, Tylianakis et al. 2010). Plant-pollinator networks are an important example of two trophic levels (i.e., flowering forbs and pollinating bees) impacted by wildfire, with calls having been made for the conservation of ecological networks generally (Tylianakis et al. 2010), and plant-pollinator networks specifically, due to their sensitivity to anthropogenic effects (Burkle et al. 2013) such as increasing burn severity, extent, and frequency (Bowman et al. 2009, Potts et al. 2010). High-severity burns have been found to have greater interaction richness than moderate- or low-severity burned sites, however high pyrodiversity of an area (i.e., “mixed-severity” burns with a diversity of low-, moderate-, and high-severity burned patches) can have higher interaction richness compared to areas of low pyrodiversity (i.e., homogenous, high-severity burns, Ponisio et al. 2016). A better understanding of the assembly of pollinator communities and plant-pollinator networks in

the context of different burn severities, and how those patterns change through time, is essential for building an empirical understanding of how species interactions assemble as well as providing information relevant for the management and conservation of pollinators and pollination services, which is still lacking despite recent practical and conceptual progress (Brown et al. 2017).

Assembly of plant-pollinator networks is believed to be non-random with species organizing themselves around a tightly nested core of persistent species and interactions (i.e., specialist interactions are a subset of generalist pairings, Bascompte et al. 2003). Generally, plant-pollinator networks can be typified by high species and interaction turnover through space, time, and across environmental gradients, with variable ranges of that turnover being caused by rewiring of interactions (~20-80%, Oleson et al. 2008, Petanidou et al. 2008, Simanonok and Burkle 2014, Cirtwill et al. 2018). Pollinators are generally thought to follow a pattern of preferential attachment during assembly, in which species entering the network are more likely to interact with species which are already highly connected (e.g., Olesen et al. 2008, Bascompte and Stouffer 2009). However, competing evidence suggests that pollinators are more likely to form links opportunistically within the network, where the most persistent species in the network are frequently rewiring their links to interact with other species (e.g., Ponisio et al. 2017). Additionally, in primary succession, plant-pollinator networks have been found to contrast with niche-selection theories of pollination specialization (i.e., networks do not become more specialized through time), but rather plant-pollinator networks become more diverse in both species and interaction richness with greater niche breadth through

time (Albrecht et al. 2010). However, recently burned areas have been observed to have greater abundances of generalist species compared to older burns and feeding behavior does not vary with increasing time-since-burn (Peralta et al. 2017), suggesting that mechanisms of community assembly like niche selection may not act similarly in secondary succession (e.g., post-burn). Network-level metrics tend to stabilize within a few years post-burn, i.e., they closely mirror pre-burn networks structurally, suggesting that plant-pollinator networks are resilient to fire and that species interactions assemble quickly (Peralta et al. 2017). Since the measures of species interactions and resulting network structure are tied to measures of biodiversity as well as species and interaction turnover, examining community and network assembly across different burn severities, where species abundance, richness, and composition typically vary, allows for examination of how species interactions are formed in assembling networks. Furthermore, doing so across a successional gradient can provide insights into whether the mechanisms that organize species interactions (e.g., preferential vs. opportunistic attachment) change with successional time, such as they do with assembling plant communities (e.g., legacy effects vs. environmental filtering, Brown et al. 2015).

One method for examining changes in network links concurrent with species-level measurements of their interactions is quantifying species' roles via testing for changes in species interaction patterns (e.g., network motifs, Milo et al. 2002), as they can elucidate differences which may be obscured by previously preferred methods such as network-level metrics of connectance or nestedness (Stouffer et al. 2012). Network motifs, the “building blocks of networks” (Milo et al. 2002), are unique patterns of species

interactions comprising two to six species, in which species roles in a network are made apparent by their direct and indirect interactions across motifs (Figure 1). While only recently implemented for bipartite networks, such as with plant-pollinator networks (Cirtwill et al. 2018), the occurrence and frequency of different motifs in networks may provide new insights into understanding species function in their communities (Baker et al. 2015), how varying species composition may shape network structure (Cirtwill et al. 2018), or how species roles in motifs may confer stability (Stouffer and Bascompte 2010). Likewise, these tools may help provide insight into how species interactions assemble after disturbance. For example, it is still poorly understood how species interactions, and plant-pollinator networks specifically, assemble (Brown et al. 2017). It has also been suggested that rare species roles may change more rapidly than abundant species (Cirtwill et al. 2018). Similarly, pollinators tend to have highly variable species roles through time, both within- and between-years (Ponisio et al. 2017, Cirtwill et al. 2018). In other types of networks (e.g., unipartite-parasitoid, food webs), consistent presence of network motifs around core species has been identified as conferring persistence to the species in those networks (Stouffer and Bascompte 2010, Baker et al. 2015). By using network motifs (Milo et al. 2002, Bascompte & Stouffer 2009), we can investigate whether the identities and frequencies of species interactions change at the network, community, or species-specific level. Additionally, examination of common species shared between networks following a gradient of time-since-burn allows for testing if core species are persistent (Bascompte et al. 2003, Bascompte and Stouffer 2009) or dynamic (Ponisio et al. 2017, Cirtwill et al. 2018) in their network roles during

assembly. To expand this idea, looking between burn severities and across time-since-burn can tell us when and why persistent species are stable or dynamic in their roles, as disturbance and time-since-disturbance have not been examined as drivers of species role changes in plant-pollinator networks. For example, if motif patterns are similar between burn severities, or become less variable through successional time, it could suggest a strong role of preferential attachment in determining species interactions. By contrast, if network motif patterns for persistent species are highly variable between burn severities or highly variable across time-since-burn, then we could infer that species are more opportunistic in forming their network links.

Therefore, to determine the factors which contribute towards network assembly in a post-burn environment, we sought to 1.) assess measures of bee and floral abundance, richness, species composition, species turnover, and interaction turnover to understand baseline patterns in the communities between mixed- and high-severity fires as well as with time-since-burn, 2.) test for changes in network motif identities and frequencies as well as the network roles of shared species across fire severities and time-since-burn by comparing the presence and frequencies of network motifs between mixed- and high-severity fires and across time-since-burn. To our knowledge, changes in species roles in plant-pollinator networks, particularly those addressed by examining network motifs, have not been studied regarding assembly post-disturbance.

Methods

Field Sampling

Four wildfires from the Absaroka Mountains of southwest Montana, USA were selected which contained a variety of burn severities and covered a range of time-since-burn (Table 1). Additionally, we selected unburned sites (i.e., controls) which have not burned in at least 75 years, located 4km from any burned sites. We selected two 15ha blocks of high-severity burn (>95% high severity) and two 15 ha blocks of mixed-severity burn (containing low-, moderate-, and high-severity) within each fire perimeter. Within the unburned areas, two 15 ha blocks were selected. Fire severities were determined by the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al. 2007). Within each block, nine sampling plots were placed randomly using Generalized Random Tessellation Stratified Spatial Sampling (GRTS), which accounts for the spatial distribution of plots to prevent clustering (Kincaid & Olsen 2011). Placement of plots within each mixed-severity block were further constrained such that there were 3 low-severity, 3 moderate-severity, and 3 high-severity plots. This design resulted in a total of 162 sampling plots. Each sampling plot consisted of a 25m diameter circular plot centered on a 25m x 2m band transect. We performed floral censuses of all plant species in bloom within each band transect and 20 minutes of pollinator hand netting within each circular plot at least every other week over the course of the flowering season (Early June – Late August) in 2014, 2015, and 2016; the Wicked Creek fire and unburned area were also sampled in 2013, and the mixed-severity plots in the Thompson Creek fire were not sampled in 2016. This resulted in a total of 450 hours of hand netting observation. With

the range of burn ignition dates represented (Table 1), this sampling design covered a chronosequence of 1-25 years post-burn.

Analyses

To assess pollinator and floral species abundance and richness changes with burn severity and time-since-burn, we used linear mixed-effects models in the packages lme4 and lmerTest for R (Bates et al. 2015, Kuznetsova et al. 2017), with year, transect ID, and block ID as random effects to account for repeated measurements of the same plots through time. Species turnover was calculated using Whittaker's beta-diversity as its wide use (Koleff et al. 2003) allows for direct comparison with recent studies performing similar work. Interaction turnover was calculated using the betalink package for R as betalink provides the additive contributions of species turnover and interaction rewiring to interaction turnover (Poisot et al. 2012) which can help in understanding changes in network motif patterns. To assess the effects of burn-severity and time-since-burn on metrics of species and interaction turnover, we compared pairwise dissimilarities of species and interaction turnover across time-since-burn and then separately investigated trends for mixed- and high-severity plots using linear and polynomial regression as trends dictated (see Results). Furthermore, we used the community matrices from the turnover analyses to test for compositional differences between burn-severities and across time-since-burn using a PERMANOVA via the adonis function in vegan for R (Oksanen et al. 2018). In the PERMANOVA we tested for compositional differences in the plant and pollinator communities across burn severity, time-since-burn, their interaction, year, transect ID, and block ID.

To investigate network motif patterns and species roles, network motifs positions and frequencies were calculated for yearly summaries of each sampling plot using the `bmotif` package in R (Simmons et al. 2018). For example, for each sampling plot in each year, we created an interaction matrix of species from the hand-netting data. For each interaction matrix, `bmotif` quantifies the frequency of all unique combinations of pre-defined motifs (e.g., Figure 1) which contain two to six species. Yearly networks were chosen for these analyses for several practical reasons. In a given week, few, if any, plant-pollinator interactions were observed at each plot. Thus, using weekly or monthly interaction networks would have limited our analyses to only extremely simple motifs and thereby restricted testing for differences between burn severities and across time-since-burn. While yearly network summaries introduce the potential for forbidden links (i.e., places species together which did not necessarily overlap in space and/or time, Bascompte et al. 2003), they do so evenly across all years without introducing within-season variability. Ideally, sampling methods for this chapter would have had fewer sampling plots with greater time spent at each plot so as to capture a larger network at each plot; furthermore, we did not spatially combine plots to achieve a similar effect as it would provide the same problem of forbidden links, would not work evenly within mixed-severity plots compared to high-severity plots due to the plot-level severity varying, and would add the additional issue of spatial auto-correlation. The literature and goals of this chapter have changed significantly over the four years since the inception of this study design, and I believe that using yearly networks for these analyses provides the best, most widely-comparable insight into their function with the available data and study

design. Therefore, we make no statements regarding within-year network motif patterns or species role changes, focusing only on interannual variation.

We tested for yearly plot-level differences in network motifs compared across burn severity, time-since-burn, their interaction, and year of sampling with a PERMANOVA. Following significant PERMANOVA results, we tested for differences among factor levels with post-hoc Tukey HSD tests. To test for changes in “core” common species roles across burn-severities and time-since-burn, we used three different groups of shared species: 1.) species present across all years of sampling, in both mixed- and high-severity burns, and across all years of time-since-burn, 2.) species present across all years of sampling and all years of time-since-burn yet only from mixed-severity plots, and 3.) species present across all years of sampling and all years of time-since-burn yet only from high-severity plots. Sampling data from 2013 was excluded from these species role analyses (but from no other analyses) due to differences in sampling effort which could have caused us to miss shared species (2 weeks in 2013 vs. average of 10 weeks in all other years) as well as from unburned plots due to extremely low pollinator visitation. Changes in species roles were then tested for each species between burn-severities and across time-since-burn using a PERMANOVA via the `adonis` function in `vegan` for R (Oksanen et al. 2018). All analyses were performed in R (R Core Team 2018).

Results

We hand netted 6,230 bees which were identified to 263 species and morphospecies, and we counted 845,994 flowers from 278 species in floral censuses, 134 of which were visited by bees in our hand-netting observations.

Bee abundance was significantly higher in mixed- (estimate = 58.88, $t = 4.22$, $P < 0.01$) and high-severity plots (est. = 60.26, $t = 4.24$, $P < 0.01$) compared to unburned, but did not differ between mixed- and high-severity ($t = -0.04$, $P = 0.96$, Figure 2). Floral abundance followed the same trend with greater abundance in mixed- (est. = 125.89, $t = 4.46$, $P < 0.01$) and high-severity plots (est. = 74.13, $t = 3.96$, $P < 0.01$, Figure 2) compared to unburned plots. Floral abundance did not differ between mixed- and high-severity plots ($t = 0.94$, $P = 0.37$, Figure 2). Neither bee abundance ($t = 0.34$, $P = 0.74$) nor floral abundance ($t = 0.82$, $P = 0.42$) varied with time-since-burn (Figure 2). Bee species richness was also greater in mixed- (est. = 42.97, $t = 6.94$, $P < 0.01$) and high-severity plots (est. = 40.4, $t = 6.85$, $P < 0.01$) relative to unburned plots, but did not differ between mixed- and high-severity ($t = 0.24$, $P = 0.82$, Figure 2). Floral species richness in mixed- (est. = 18.02, $t = 5.04$, $P < 0.01$) and high-severity (est. = 11.24, $t = 4.21$, $P < 0.01$) plots was greater relative to unburned, while no difference was observed between mixed- and high-severity ($t = 1.56$, $P = 0.14$, Figure 2). Bee species richness increased by 1.28 species per year with increasing time-since-burn ($t = 2.11$, $P = 0.05$), while floral species richness increased by 9.18 species per year with increasing time-since-burn as well ($t = 4.43$, $P < 0.01$, Figure 2)

Bee species composition (Table 2) significantly varied with burn severity (though no significant differences between mixed-, high-severity, or unburned were found via Tukey's HSD post-hoc), time-since-burn, year of sampling (2014 was significantly different from 2015 and 2016, Tukey HSD $P < 0.01$, and 2015 was different from 2013, Tukey HSD $P < 0.01$), transect, as well as the interaction of burn severity and time-since-burn. Floral species composition (Table 3) varied significantly with burn severity (mixed severity was significantly different from both unburned and high-severity, Tukey HSD $P < 0.01$), time-since-burn, year of sampling (2016 was different from 2014 and 2015, Tukey HSD $P < 0.01$), transect ID, as well as the interaction of burn severity and time-since-burn. Note that the degrees of freedom representing number of site:year combinations are lower for the pollinator data as we did not observe any pollinator visitation at some sites.

Bee species turnover was greater in mixed-severity plots compared to high-severity plots (0.84 vs. 0.79 for high-severity) and significantly increased difference in time-since-burn (Overall: $F_{2,109275} = 4690$, $P < 0.01$, Mixed: $F_{1,22364} = 270.2$, $P < 0.01$, High: $F_{1,25423} = 1184$, $P < 0.01$, Figure 3). Similarly, floral species turnover was greater in mixed- compared to high-severity plots (0.71 vs. 0.64) and increased with time-since-burn (Overall: $F_{1,135979}$, $P < 0.01$, Mixed: $F_{1,23218} = 1418$, $P < 0.01$, High: $F_{1,27259}$, $P < 0.01$, Figure 3). Interaction turnover was marginally greater in mixed-severity plots (0.93 vs. 0.90) and increased nonlinearly with time-since-burn (Overall: $F_{2,109275} = 3149$, $P < 0.01$, Mixed: $F_{2,22363} = 307.3$, $P < 0.01$, High: $F_{2,25422} = 394.5$, $P < 0.01$, Figure 4). The mean contribution of shared species to turnover, or interaction rewiring, was minimal

(0.18) and significantly decreased nonlinearly with increasing time-since-burn ($F_{2,109275} = 1346$, $P < 0.01$, Figure 4), although the estimate of decrease was marginal (-0.00003).

Network motif identity and frequency was significantly different between burn severities ($F_{2,467} = 14.43$, $P < 0.01$, Table 4), and this result was due to significant differences between the unburned and mixed-severity plots (Tukey HSD $P = 0.01$). There were significant differences between sampling years ($F_{1,467} = 5.27$, $P < 0.01$); 2015 was different from other sampling years (Tukey HSD 2015:2014 $P < 0.01$, 2016:2015 $P = 0.05$). Common shared species between mixed- and high-severity and across all years of time-since-burn were *Bombus bifarius* and *Megachile relativa* for bee species, *Chamerion angustifolium* and *Spiraea betulifolia* for floral species. For these species, the only significant motif differences were observed for *Spiraea betuloides* with time-since-burn (Table 5). Investigating high- and mixed-severity plots separately, additional shared species were the floral species *Arnica cordifolia* and *Euribia conspicua* for high-severity, and pollinators *Bombus insularis*, *Bombus rufocinctus*, *Megachile frigida*, and *Megachile lapponica*, along with floral species *Achillea millefolium* and *Campanula rotundifolia* for mixed-severity plots. Examining species roles within-severity for these species, only *Megachile lapponica* had dissimilar motif patterns with time-since-burn (Tables 6, 7).

Discussion

We found bee and floral abundance and richness to be greater in plots that burned with mixed- and high-severity relative to unburned plots, but surprisingly did not identify differences in floral abundance and richness between mixed- and high-severity,

indicating no effect of burn severity on baseline metrics of biodiversity. Bee and floral abundance did not vary with time-since-burn, while bee and floral species richness both increased with time-since-burn, suggesting that burn severity has little effect on baseline diversity metrics. These results for both communities contrast with evidence of peaks in richness and abundance occurring soon after fire with subsequent declines over time (e.g., Potts et al. 2003), suggesting that plant-pollinator communities in our system may respond differently from other published evidence. Despite minimal observed changes in baseline measurements of biodiversity (i.e., richness and abundance), species composition was dramatically different for both the bee and floral communities. Bee community composition differed between unburned areas and those that burned with mixed-severity, while floral communities that burned with mixed-severity were different in composition from unburned areas or those that burned with high-severity. Likewise, the composition of both floral and bee communities varied significantly with time-since-burn. Similarly, species turnover was extremely high for bee and floral communities, being higher on average in mixed-severity plots compared to high-severity plots, with turnover tending to increase with greater difference in time-since-burn. Compositional and turnover results are consistent with findings that greater pyrodiversity, such as that experienced in a mixed-severity burn, can increase pollinator turnover (Ponisio et al. 2016) and that turnover within plant-pollinator networks increases through successional time during assembly (Albrecht et al. 2010). We found patterns of network motifs to be relatively unchanged with burn severity or time-since-burn, with significant differences only between our mixed-severity burn and our unburned sites as well as due to variability

in one of our sampling years. This suggests that while unburned areas have structurally different networks compared to mixed-severity burns, the species roles occupied in plant-pollinator networks are relatively unchanged by burn severity in spite of significant variance in species composition between burn severities. Therefore, it may be that while common species are mostly stable in their roles, less persistent species are more opportunistic in forming network links. Furthermore, we found that the most persistent species, those that were present among our burn severity and time-since-burn gradients across sampling years, tended to have consistent, unchanging network roles, with only a few species presenting as exceptions. These results contrast with recent research which has suggested that plant-pollinator networks, and the core, persistent species, demonstrate highly dynamic network motif patterns and changing species roles through time (Ponisio et al. 2017, Cirtwill et al. 2018), and suggests that in our study system plant-pollinator interactions assemble more preferentially.

Bee and floral abundance and richness patterns contrasted with published patterns of post-burn responses. Surprisingly, we did not observe differences between burn severities for floral or bee abundance, instead only finding that abundances were dramatically lower in our unburned plots. A study in a similar ecosystem (montane mixed-conifer forests) found that increasing pyrodiversity predictably increased the number of bee species observed (Ponisio et al. 2016), yet we did not observe any change between mixed- and high-severity burns on species richness. The distinction may lay in our definition of mixed-severity, in that our mixed-severity blocks are designed to contain pockets of low, moderate, and high severity so as to replicate a historical fire

regime, whereas pyrodiversity as a true gradient would assess finer-scale spatial burn patterns (Ponisio et al. 2016), to which bees are highly sensitive for habitat selection (Grundel et al. 2010). However, we did observe significant compositional differences and high levels of species turnover between burn severities, consistent with previous findings (Ponisio et al. 2016). In other systems, specifically Mediterranean shrubland (Potts et al. 2003, 2005) and mixed savanna-forest landscapes (Grundel et al. 2010), bee abundance and richness tended to peak in the years soon after fire and decline through successional time. Our patterns contrast in that we find no signature of time-since-burn on bee or floral abundances, and positive relationships of bee and floral richness with increasing time-since-burn. Examination of the patterns, however, (Figure 2) indicates that floral, but not bee, abundance and richness, peaks at a much later point in succession, from 23-25 years post-burn. Species and interaction turnover should generally be greater where the landscape and its communities are patchy (e.g., Ponisio et al. 2016), which we did observe with higher plant and pollinator turnover in mixed-severity compared to high-severity sites. However, with greater turnover, we also expect network structure and function to change in tandem (e.g., Cirtwill et al. 2018) resulting in different network patterns based on the heterogeneity of the landscape and communities.

Network motif identity and frequency was not observed to be different between mixed- and high-severity sites and did not vary with time-since-burn. A lack of difference between mixed- and high-severity sites suggests that the basic structure and interaction patterns of networks present in these burns are relatively similar, and that despite having significantly different species compositions, the interactions in those networks assembled

along predictable, orderly paths (e.g., Bascompte et al. 2003). Furthermore, the low level of interaction rewiring coupled with our observation that network motif patterns do not change between severities suggests that most species are well established and stable in their network roles, consistent with predictions of preferential attachment in network assembly (Bascompte and Stouffer 2009). This is further supported by our individual assessment of the network motif patterns of common, shared species across burn severities and time-since-burn, as all but one of those species did not change their motif identities or frequencies across burn-severity and time-since-burn. Additionally, we detected a difference in general network motif patterns when comparing mixed-severity to unburned sites. As plant community development is can be driven by legacy effects in post-burn systems (Brown et al. 2015), it may be that the unburned community assembled from a different seed bank, under different fire regimes, and therefore along a different trajectory. Similarly, as our mixed-severity treatment design (i.e., 3 low, moderate, and high severity plots) includes some high-severity plots, it may be the case that our severity treatments are more similar than we intended. Furthermore, while burn severity of individual plots was objectively determined (Eidenshink et al. 2007), ground-truthing of local burn severity was not always intuitively aligned with the reported severity (pers. obs.).

Network motif identities and frequencies also demonstrated variability among sampling years. This agrees with recent results showing high inter-annual variation of species roles within plant-pollinator networks sampled at the same locality, which suggested that species turnover was a driving cause, i.e., that changes in species

composition resulted in different observed network motifs (Cirtwill et al. 2018). Plant-pollinator networks are known to have high spatial and interannual variation in species composition and interactions (Olesen et al. 2008, Simanonok & Burkle 2014), and likewise we observed significant levels of both across increasing dissimilarity in time-since-burn. However, whereas another study observed common species rewiring their interactions between years during network assembly (Ponisio et al. 2017), we instead observed common species to maintain similar roles over our gradients of interest. This discrepancy is potentially due to the analysis used: our study used meso-scale measures which can be species-specific, whereas Ponisio et al. (2017) utilized change point analyses which are only able to detect large-scale changes in network structure, i.e., we were assessing our study networks at different scales. More likely, however, is that there were large ecological differences between the studies, in that Ponisio et al. (2017) were investigating an assembling network at native restoration sites in what was previously agricultural land, whereas our study sites are montane conifer forests and burn scars. Therefore, the factors controlling community and network assembly are likely to be very different: in the restoration sites the majority of flowering plants are planted, whereas our resulting floral communities are likely primarily a result of the seed bank present, while the pollinator communities would also be different between agricultural and relatively natural landscapes.

Despite no overarching changes in network motifs between burn severities or with time-since-burn, we detected changes in the network roles of a few persistent species across our study design. *Spiraea betulifolia*, which was an extremely abundant species

across all study areas, accounted for 6.5% of observed pollinator visitation (403 of 6230 interactions) and bloomed across all months and years of our study. *Spiraea betulifolia* has been previously identified to be an early successional species after fire which resprouts from rhizomes and then declines with increasing time-since-burn (Doyle et al. 1998), therefore our observation of this species changing network roles with time-since-burn may be due to declines in abundance or species composition with time-since-burn. This is somewhat consistent with our results, as while *S. betulifolia* was extremely abundant across all our burned sites, it was nearly absent from our unburned plots. When looking at species role changes within burn severity, we also observed dissimilar network roles for *Megachile lapponica* with time-since-burn in mixed-severity burns. As an oligolectic species (i.e., specializing its diet on only a few plant species), *M. lapponica* primarily visited *Chamerion angustifolium* in our study (78.2%, 122 of 156 interactions), and while *C. angustifolium* was present across all mixed-severity burns, it was much less abundant at our oldest mixed-severity burn (i.e., in mixed-severity sites of the Thompson Creek Fire, *Chamerion angustifolium* flowers represented 2.3%, 644 of 27,599 of the total). It is possible that the observed changes in network roles for *M. lapponica* are thus driven by declines in the preferred forage of *C. angustifolium*, and the observed role changes are due to *M. lapponica* rewiring late during post-burn assembly. Although, network role changes may occur without rewiring, and it could be a result of compositional shifts around *M. lapponica* which change the context and therefore the network motifs of its interactions. In both of these species-specific responses, network role changes were likely driven by changes in species composition with increasing time-

since-burn, presenting evidence of environmental filtering or ecological drift (random changes in species relative abundances) as important factors in the assembly of these communities and networks (Vellend 2010) with increasing time-since-burn.

Generally, our results support the idea that plant-pollinator networks assemble via preferential attachment, in that network motifs were not variable between mixed- and high-severity burns with no change observed across time-since-burn either. We base this on the idea that motifs would be less consistent for individual species were opportunistic attachment to be the dominating network assembly factor. Furthermore, the most persistent species were highly stable in their network roles, suggesting that these species fill specific niches within their networks and these roles do not shift via environmental differences (e.g, mixed- vs. high-severity) or with successional time. This work helps contribute to the ongoing exploration of the governing factors of the organization and assembly of species interactions, particularly for plant-pollinator networks. A future study which compares multiple scales of network structure analyses on the same dataset to further elucidate discussed differences would be helpful for advancing our understanding of how species interactions assemble.

Table 1: Name, location, size, and ignition date of burns. Note that Location is an approximate centroid of sampling plots located within the burn perimeter.

Fire Name	Location	Burned Area (Acres)	Ignition Date
Emigrant	45.23°, -110.73°	11,834	August 16, 2013
Pine Creek	45.52°, -110.50°	8,572	August 29, 2012
Wicked Creek	45.26°, -110.47°	28,674	August 8, 2007
Thompson Creek	45.24°, -110.55°	6,979	July 16, 1991
Unburned	45.25°, -110.41°	-	-

Table 2: PERMANOVA results of bee species composition.

	d.f.	Sum of Squares	Mean Sum of Squares	F	R²	P
Burn Severity	2	6.16	3.08	9.05	0.03	< 0.01
Time-Since-Burn	1	5.54	5.54	16.30	0.03	< 0.01
Sampling Year	1	2.17	2.17	6.37	0.01	< 0.01
Transect ID	154	66.79	0.43	1.28	0.36	< 0.01
Burn Severity/ Time-Since-Burn Interaction	2	1.00	0.50	1.47	0.01	0.03
Residuals	307	104.39	0.34		0.56	

Table 3: PERMANOVA results of floral species composition.

	d.f.	Sum of Squares	Mean sum of Squares	F	R²	P
Burn Severity	2	15.51	7.75	30.58	0.07	< 0.01
Time-Since-Burn	1	6.62	6.62	26.11	0.03	< 0.01
Sampling Year	1	2.33	2.33	9.18	0.01	< 0.01
Transect ID	158	102.63	0.65	2.56	0.47	< 0.01
Burn Severity/ Time-Since-Burn Interaction	2	2.05	1.02	4.03	0.01	< 0.01
Residuals	357	90.52	0.25		0.41	

Table 4: Network motif identity and frequency PERMANOVA summary.

	d.f.	Sum of Squares	Mean Sum of Squares	F	R²	P
Burn Severity	2	7.38	3.69	14.43	0.06	< 0.01
Time-Since-Burn	1	0.16	0.16	0.62	< 0.01	0.67
Sampling Year	1	1.35	1.35	5.27	0.01	< 0.01
Transect ID	154	39.92	0.26	1.01	0.31	0.42
Burn Severity Time-Since-Burn Interaction	2	1.44	0.22	0.86	< 0.01	0.56
Residuals	307	78.51	0.26		0.61	

Table 5: Network motif identity and frequency PERMANOVA output for shared species across mixed- and high-severity plots and all years of time-since-burn.

	d.f.	Sum of Squares	Mean Sum of Squares	F	R²	P
<i>Bombus Bifarius</i>						
Time-Since-Burn	1	0.29	0.27	0.92	0.05	0.47
Burn Severity	1	0.11	0.11	0.38	0.02	0.92
Burn Severity Time-Since-Burn	1	0.19	0.19	0.66	0.04	0.66
Interaction						
Residuals	15	4.39	0.29		0.88	
<i>Megachile relativa</i>						
Time-Since-Burn	1	0.18	0.18	0.52	0.03	0.74
Burn Severity	1	0.06	0.06	0.17	0.01	0.99
Burn Severity Time-Since-Burn	1	0.28	0.28	0.81	0.05	0.53
Interaction						
Residuals	15	5.23	0.35		0.9	
<i>Chamerion angustifolium</i>						
Time-Since-Burn	1	0.4	0.4	1.36	0.08	0.23
Burn Severity	1	0.1	0.1	0.35	0.02	0.9
Burn Severity Time-Since-Burn	1	0.15	0.15	0.51	0.03	0.77
Interaction						
Residuals	15	4.38	0.29		0.87	
<i>Spiraea betulifolium</i>						
Time-Since-Burn	1	0.97	0.97	3.47	0.17	< 0.01
Burn Severity	1	0.26	0.26	0.94	0.05	0.43
Burn Severity Time-Since-Burn	1	0.16	0.16	0.59	0.03	0.76
Interaction						
Residuals	15	4.21	0.28		0.75	

Table 6. Network motif identity and frequency PERMANOVA output for species present in high-severity plots and all years of time-since-burn.

	d.f.	Sum of Squares	Mean Sum of Squares	F	R²	P
<i>Arnica cordifolia</i>						
Burn Severity	1	0.46	0.46	1.33	0.14	0.22
Residuals	8	2.74	0.34		0.86	
<i>Eurybia conspicua</i>						
Burn Severity	1	0.3	0.3	0.88	0.1	0.44
Residuals	8	2.67	0.33		0.9	

Table 7: Network motif identity and frequency PERMANOVA output for species present in mixed-severity plots and all years of time-since-burn.

	d.f.	Sum of Squares	Mean Sum of Squares	F	R²	P
<i>Bombus insularis</i>						
Burn Severity	1	0.22	0.22	0.68	0.09	0.62
Residuals	7	2.25	0.32		0.91	
<i>Bombus rufocinctus</i>						
Burn Severity	1	0.38	0.38	1.26	0.15	0.26
Residuals	7	2.11	0.3		0.85	
<i>Megachile frigida</i>						
Burn Severity	1	0.31	0.31	0.99	0.12	0.41
Residuals	7	2.23	0.32		0.88	
<i>Megachile lapponica</i>						
Burn Severity	1	0.84	0.84	3.05	0.3	0.03
Residuals	7	1.92	0.27		0.7	
<i>Achillea millefolium</i>						
Burn Severity	1	0.49	0.49	2.05	0.23	0.14
Residuals	7	1.69	0.24		0.77	
<i>Campanula rotundifolium</i>						
Burn Severity	1	0.19	0.19	0.68	0.09	0.68
Residuals	7	1.99	0.28		0.91	

Figure 1: Conceptual network motif figure. Motifs can be thought of as subunits of networks, comprised of two to six species. For example, we can see if species are involved in multiple direct and indirect species interactions which can be separately considered as subunit motifs. If we look at the yellow bee species in our network (top left), we can identify individual 2-species subunits (top right), as well as 3-species subunits (bottom row). For each species we can quantify their position in these motifs (i.e., “motif identity”) as well as the frequency with which those motifs occur.

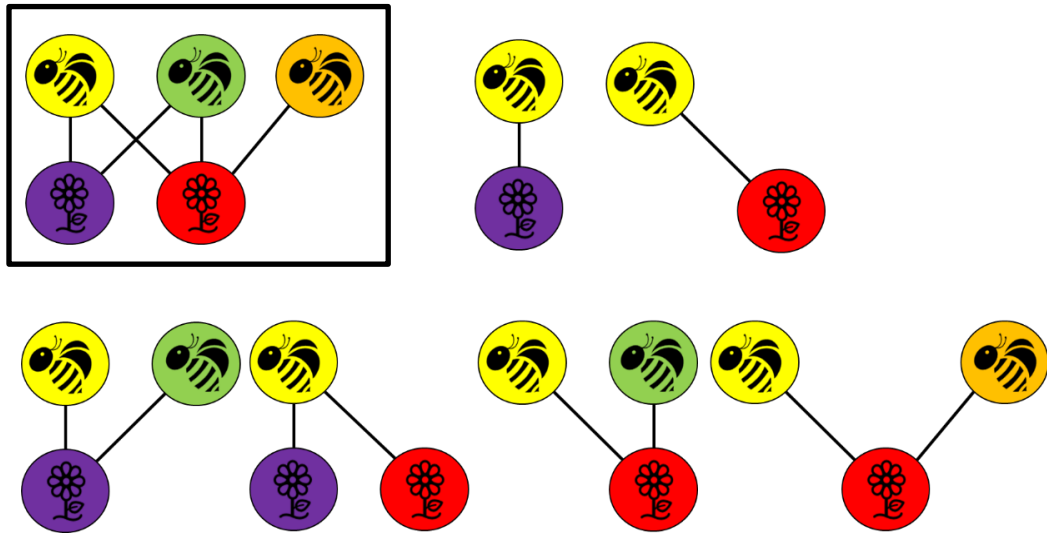


Figure 2: Floral abundance, floral species richness, bee abundance, and bee species richness. Blue is for mixed-severity plots, red for high-severity plots, and green for unburned plots.

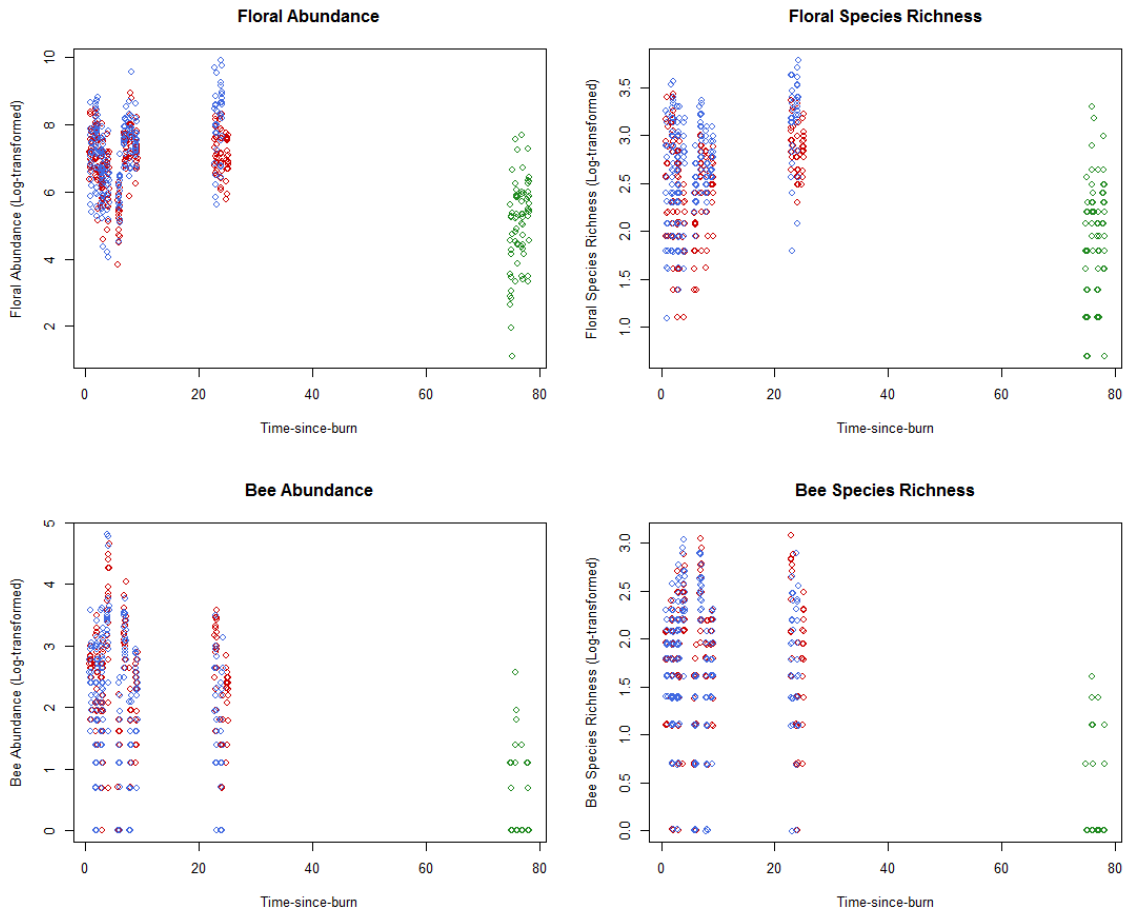


Figure 3: Floral species turnover (left column) and bee species turnover (right column) across pairwise differences in time-since-burn. Top row plots are across all sites, the middle row is for high-severity plots, and the bottom row is mixed-severity plots.

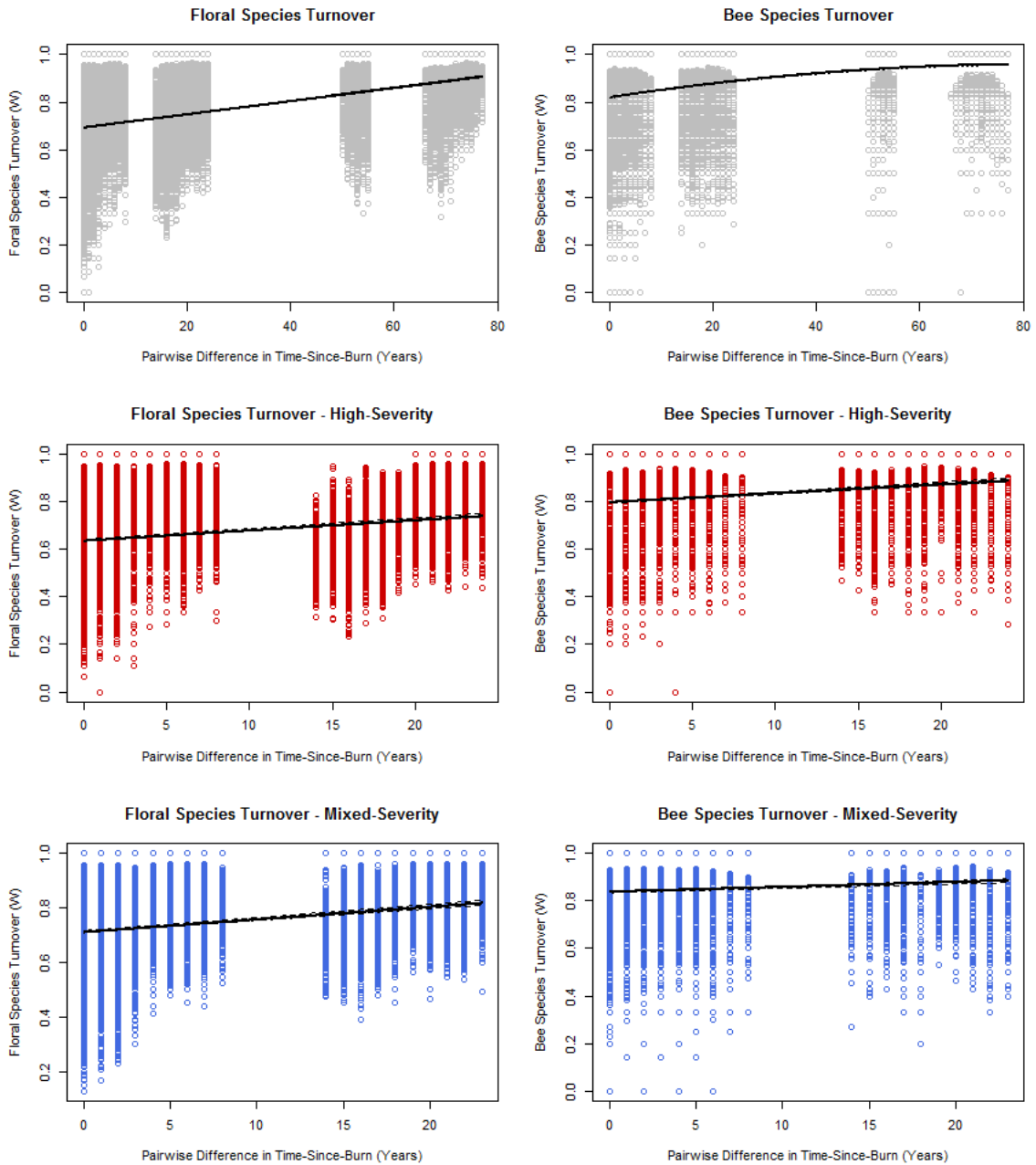
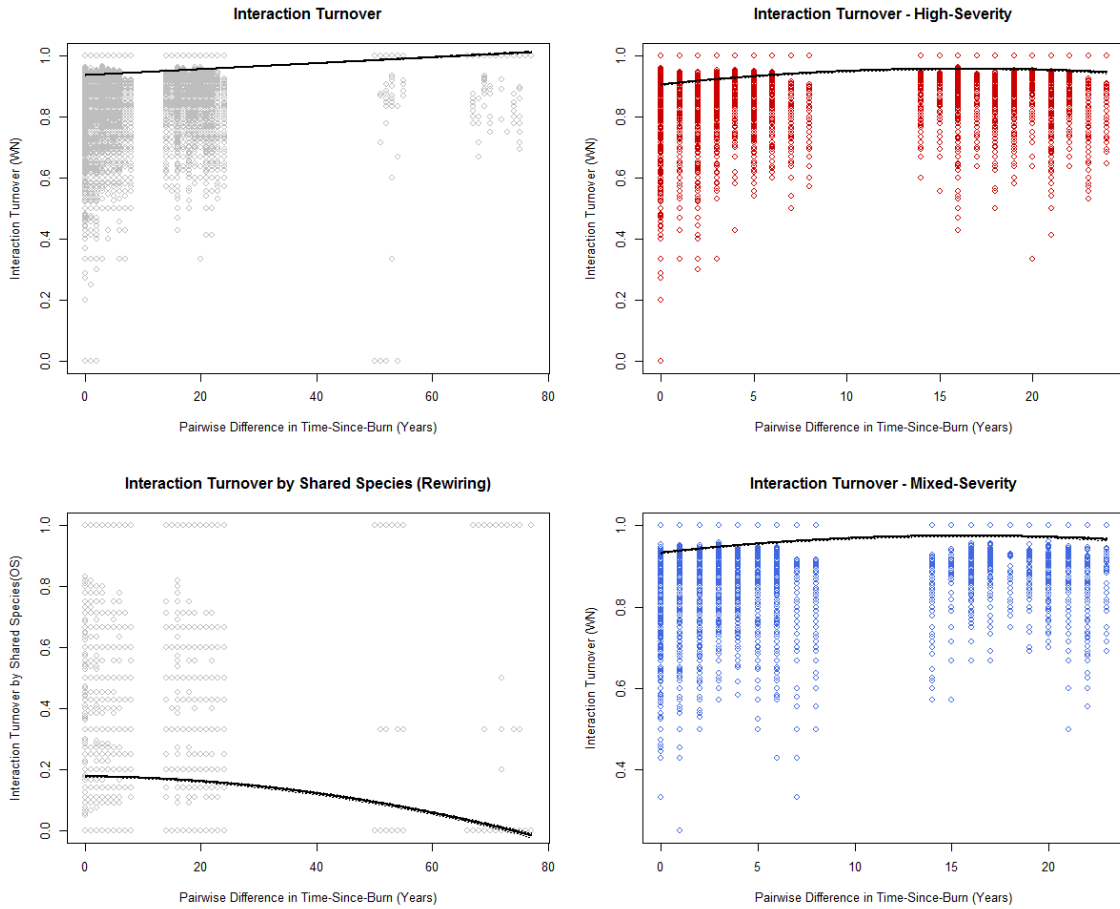


Figure 4: Interaction turnover across pairwise differences in time-since-burn. Top left is interaction turnover across all sites, top right is only high-severity plots, bottom left is the interaction turnover due to shared species changing their interacting partner (i.e., rewiring) for all sites, and bottom right is only mixed-severity plots.



HIGH-SEVERITY WILDFIRE LIMITS BUMBLEBEE NUTRITION AND
AVAILABLE FLORAL POLLEN QUALITY COMPARED TO MIXED-SEVERITY
BURNS

Introduction

Pollen provides bumblebees (*Bombus spp.*) with nearly all proteins, lipids, and other non-carbohydrate nutrients received during their lifetime, with pollen primarily provisioned to individuals when they are larvae (Roulston & Cane 2000). There is ample evidence that foraging bumblebees can differentiate among pollen from different plant species based on the quality of pollen (Ruedenauer et al. 2015, 2016), and, subsequently, that the quality of nutrition received during larval development can dramatically influence adult bumble bees. For example, higher pollen nitrogen, a common proxy for protein content and for pollen quality (Roulston et al. 2000), can increase the number of larvae developing within a colony (Looper & Berdel 1980), larval weight and body size (Tasei & Aupinel 2008, Vanderplanck et al. 2014), and adult survival (Di Pasquale et al. 2013). Importantly, experiments that simply increase the quantity of pollen provided to a colony or to individual larvae do not yield similar benefits as those that provide pollen of adequate quality; low quality pollen diets are often insufficient in certain nutrients, amino acids, or their stoichiometric balance (Filipiak et al. 2018).

Bumblebees discriminate among pollens that differ in quality and do so using a combination of visual, tactile, and olfactory cues (Dobson et al. 1999, Mapaland et al. 2008, Kitaoka & Nieh 2009, Ruedenauer et al. 2015, 2016, Vaudo et al. 2016). As a

result, floral species with higher quality pollen receive more floral visitors (Hanley et al. 2008, Somme et al. 2015). Of the two bumblebee species (*Bombus impatiens* and *Bombus terrestris*) whose workers have been tested thus far, both preferentially forage for high quality pollen (Kitaoka & Nieh 2009, Ruedenauer et al. 2016), thereby providing their colonies with high quality pollen and balanced nutrition. Currently however, most of what we know regarding pollen quality preferences is known from experimental studies in laboratory settings (e.g., Muth et al. 2016, Filipiak et al. 2018). Generally, bumblebees tend to prefer to forage in areas where flowering plant species richness is high and variation in species composition between patches is low (Jha and Kremen 2013), but also where pollen availability (Harder 1990) and quality are high (Rasheed et al. 1997, Robertson et al. 1999). Corbicular pollen loads often include a mixture of plant species (Ruedenauer et al. 2016, Filipiak et al. 2018), and the composition of pollen collected is often similar across colonies within the same landscape (Saifuddin and Jha 2014), which, when coupled with evidence of pollen quality preferences in the laboratory, suggests that bumblebees in natural settings forage based on available quality of pollen rather than abundance. However, while we have a general understanding of how pollen quality influences bumblebee foraging as well as how pollen quality can affect bumblebee nutrition, we have little knowledge as to how these relationships function outside of the laboratory. In a field setting, the availability of species whose pollen differs in quality and thus the available nutritional landscape may influence those patterns of foraging and resulting bumblebee nutrition in ways that cannot be explored experimentally (Woodard and Jha 2017). Furthermore, as the composition of floral communities – and thus the

suites of available pollen quality –vary across space and time, often due to anthropogenic factors, then too might patterns of bumblebee foraging and nutrition (Woodard and Jha 2017).

Disturbances, like wildfire, that influence the diversity and composition of floral resources (Hessburg et al. 1999, Abella and Fornwalt 2015, Burkle et al. 2015) could strongly affect bumblebee foraging and nutrition. With increasing fire severities and changing fire regimes, areas historically dominated by patchy, mixed-severity fires are becoming more typified by large-scale, homogenizing high-severity burns (Arno & Fiedler 2005, Hessburg et al. 2005, Bowman et al. 2009). In particular, burn severity and time-since-burn can influence floral community composition patterns (See Chapter 2, Abella and Fornwalt 2015). Burn severity may thereby affect the available nutrient landscape for pollen-foraging workers. Mixed-severity burns are comprised of a patchwork of low- to high-severity burns, can generate a greater diversity of habitats and species across the landscape, and thus could provide foraging bumblebees with a greater diversity of pollen when compared to high-severity burns (Arno & Fiedler 2005). High-severity burns are characterized by high tree mortality (i.e., minimal canopy cover), creating large open meadows where early successional forbs and shrubs tend to thrive (Pierce et al. 2004, Arno & Fiedler 2005). These large open meadows, while having a greater abundance of floral resources than lower-severity burns or unburned areas, may provide a lower diversity of pollen resources and therefore potentially lower quality pollen resources as well. While we did not observe baseline species richness differences in the floral community between burn severities, mixed- and high-severity burns did have

compositionally different communities where the available floral pollen quality could differ. The effects of wildfire severity on the suite of floral species available for bee foraging may also change with successional time, e.g., the floral communities in mixed-severity burns may more rapidly approach compositions similar to unburned communities than would communities in high-severity burns (e.g., Abella and Fornwalt 2015), and we did observe compositional changes in the floral community with time-since-burn for both mixed- and high-severity plots. Only in the years immediately following wildfire may the effects of wildfire for mixed-severity burns be evident on floral communities (Abella and Fornwalt 2015) and bumblebee nutrition, as floral richness can increase with increasing time-since-burn (See Chapter 2). Additionally, the effects of high-severity burns may persist (Abella and Fornwalt 2015), highlighting the importance of understanding how available floral resources and nutrition may differ between burn severities. Given that bumblebees are diet generalists in that they receive different components of their nutrition (e.g., certain amino acids) from different floral species (Filipiak et al. 2018), being forced to “specialize” on a single, dominant species in high-severity burns may be detrimental to bumblebee nutrition. Previous research shows species richness of both bees and forbs typically peaking in the years soon after fire and declining through successional time (Potts 2003, Potts 2005, Swanson et al. 2011, Taki et al. 2013, Abella and Fornwalt 2015); however, we saw a general pattern of increasing species richness through time post-burn. In either case, successional changes in the floral community with time-since-fire could then influence bee foraging, the quality of pollen collected, and subsequent offspring nutrition. Therefore, for post-burn landscapes, understanding how

floral resources – like the suites of pollen available after wildfire – influence bumblebee foraging and nutrition could help with conserving and managing pollinators (Woodard and Jha 2017).

We sought to investigate how shifts in floral resources due to wildfire influence bumblebee foraging as well as bumblebee nutrition. Comparing mixed- and high-severity burns across three wildfires ranging from one to seven years post-burn in southwest Montana USA, we investigated differences in 1) the quality (i.e., percent nitrogen) of available floral pollen in the environment, 2) the quality of pollen in corbicular loads of bumblebees, and 3) bumblebee nutrition, specifically using body percent nitrogen. To our knowledge, this study is the first to investigate the links between pollen quality, bee nutrition, and foraging in a field setting.

Methods

Study System

To study the ecological effects of wildfire on bumblebee nutrition and foraging, we used a chronosequence (Hutto & Belote 2012) of three wildfires from the Absaroka Mountains, Montana USA (Table 1). Wildfires occurred within 30km of each other and are therefore similar except for time-since-burn. Our sampling of this time-since-burn chronosequence covered one, two, and seven years post-burn. To compare bee foraging and nutrition between mixed- and high-severity burns, I selected two 15ha sampling blocks of homogenous high-severity burn and two of heterogeneous mixed-severity burn within each fire perimeter. Fire severity data was acquired from the Monitoring Trends in

Burn Severity (MTBS) project (Eidenshink et al. 2007). Within each block, I established nine sampling plots, for a total of 108 plots. A mixed-severity block was comprised of three low-severity plots, three moderate-severity plots, and three-high severity plots. Plots were randomly placed using Generalized Random Tessellation Stratified Spatial Sampling (GRTS), which accounts for the spatial distribution of those plots to minimize clustering (Kincaid & Olsen 2011).

Field Sampling

Each plot was a 25m diameter circle ($\sim 490 \text{ m}^2$) and contained a 25m x 2m band transect centered on the plot. We censused floral densities of each plant species within the band transect. In the circular plot, we hand-netted bumblebees that were observed visiting open flowers for 20 minutes in each plot at least every other week over the course of the flowering season, resulting in ~ 133 total observation hours (Early June – Late August) in 2014. All bees collected were workers; queens were not destructively sampled. A subset ($N = 73$ individuals, Appendix A3) of collected bumblebees were selected for chemical analyses based on the presence of corbicular pollen on the individual. These bumblebees were used to test their nutritional state, and their corbicular pollen samples were used to test the quality of their corbicular pollen loads (Appendix A4). To assess pollen percent nitrogen and the available pollen quality at sampling plots, undehisced anthers were collected from floral species known to be visited by bumblebees in this system (Appendix A5). Pollen samples from each floral species were pooled across all plots in 2014 and 2015 because pollen protein content is phylogenetically

conserved, generally not influenced by environmental conditions, and does not exhibit variability between years (Roulston et al. 2000).

Lab Methods

We quantified percent nitrogen for all bee and pollen samples (both corbicular and anther). To do this, we removed corbicular pollen from each bee, then lyophilized whole bee specimens and pollen samples for eight hours and weighed them afterward. Bumblebees were then homogenized using a mortar and pestle, from which a ≤ 5 mg subsample was taken. Anthers were suspended in ethanol, sonicated for one minute at 40kHz, and then centrifuged for one minute at 2400rpm. All samples (bee, corbicular pollen, and plant pollen) were combusted in a Costech ECS 4010 Nitrogen/Protein Analyzer to determine total nitrogen content.

Statistical Analyses

To compare the quality of available floral pollen between burn severities and across time-since-burn, we calculated the mean pollen percent nitrogen available to each individual bee in each plot by using the anther-collected percent nitrogen of all floral species during the week in which that bee species was collected from that plot. To test for differences in available pollen quality (i.e., percent nitrogen) we used a linear mixed effects model comparing mean available pollen quality between mixed- and high-severity, time-since-burn, their interaction, and including sampling plot as a random effect. To test for differences in corbicular pollen quality (i.e., percent nitrogen) across burn-severities and time-since-burn as well as to investigate whether corbicular pollen

quality was affected by the quality of available pollen at the site from which the bee was captured during the same week of sampling, we used a linear mixed effects model of corbicular pollen quality compared against burn severity, time-since-burn, their interaction, available pollen quality at the site, pollen quality of the species of flower from which the bee was netted, and we included sampling plot as a random effect. Finally, to test for changes in bee nutrition across burn severities and time-since-burn, we used a linear mixed effects model comparing bee percent nitrogen against burn severities, time-since-burn, their interaction, and again included sampling plot as a random effect. Sampling plot identity was included as a random effect in all models so as to account for repeated measures, given that multiple bees included in this study were often sampled from a single plot. All analyses were performed in R with the lme4, and lmerTest packages (Bates et al. 2015, Kuznetsova et al. 2017, R core team 2018).

Results

Quality of Available Floral Pollen

Anther-collected pollen varied from 1.07 to 5.24 %N for the 32 floral species collected. Available floral pollen percent nitrogen was 0.82 %N greater in mixed- vs. high-severity plots ($t = 2.29$, $P = 0.03$), yet there was no significant change with time-since-burn ($t = 1.25$, $P = 0.22$) and no interactive effect between burn-severity and time-since-burn ($t = 0.45$, $P = 0.65$) (Figure 5).

Quality of Corbicular Pollen

Corbicular pollen samples ranged from 2.58 to 7.44 %N. Corbicular pollen percent nitrogen was marginally greater by 0.60 %N in mixed-severity plots than in high-severity plots ($t = 1.722$, $P = 0.09$), with no significant change across time-since-burn ($t = 0.85$, $P = 0.40$), and no evidence of an interaction between burn-severity and time-since-burn ($t = -1.08$, $P = 0.29$, Figure 6). Corbicular pollen percent nitrogen increased by 0.52 %N with increasing available floral pollen percent nitrogen ($t = 3.05$, $P < 0.01$, Figure 7). However, corbicular pollen percent nitrogen was unrelated to the pollen percent nitrogen of the plant from which the bee was collected ($t = 1.21$, $P = 0.23$).

Bumblebee Nutrition

Bumblebee percent nitrogen ranged from 6.97 to 12.52 %N. Bumblebee percent nitrogen was 1.16 %N higher in mixed- than in high-severity plots ($t = 2.36$, $P = 0.02$), and also increased by 0.33 %N per year with increasing time-since-burn ($t = 3.58$, $P < 0.01$, Figure 8). There was no evidence for an interactive effect between burn severity and time-since-burn ($t = -1.62$, $P = 0.11$).

Discussion

Taken together, our findings suggest that the quality of pollen available to bumblebees and bumblebee nutrition may be negatively affected by high-severity burns, likely via changes in the quality of available pollen relative to mixed-severity burns. For the floral community, available pollen percent nitrogen was significantly greater in mixed- compared to high-severity burns for all years of time-since-burn, indicating that

burn severity effects on the available nutrition do not attenuate in the early years post-burn (Abella and Fornwalt 2015). Similarly, corbicular pollen collected from bumblebees foraging in mixed-severity plots had marginally greater percent nitrogen than that of bumblebees collected in high-severity plots. Further, corbicular pollen quality closely followed the quality of available floral pollen, indicating that bumblebees foraging in high-severity burns are foraging on poorer nutritional sources. Furthermore, bumblebee nutrition was different between burn severities, with workers from high-severity plots having lower percent nitrogen than those from mixed-severity plots, suggesting that bumblebees in high-severity burns both receive lower quality forage and are of poorer nutrition themselves. Additionally, bumblebee percent nitrogen increased with greater time-since-burn, indicating that despite the stability in quality of available floral pollen across time-since-burn, bumblebees are able to mitigate the effects of burn severity independent of available pollen quality. These findings of reduced quality of available pollen in high-severity areas, associated with reduced corbicular pollen quality and poor bumblebee nutrition in high-severity burns, could have implications for reduced colony- or landscape-level bee health following homogenizing disturbances like high-severity wildfires.

Quality of Available Pollen

It is well established that plant communities can change dramatically following disturbances like wildfire, and that these changes vary both with the severity of burn as well as successional time post-disturbance (Abella and Fornwalt 2015). Canopy clearing “stand-replacement” fire events generally help to promote vegetation community

diversity and abundance (Swanson et al. 2011). However, our results demonstrate that wildfire severity can affect the quality of available pollen in these resulting communities, and that these severity effects do not attenuate with increasing time-since-burn. Our finding of high-severity plots having lower pollen quality (i.e., percent nitrogen) suggests that although canopy-clearing burns (i.e., high-severity) typically result in quantitatively greater floral resources for pollinators (e.g., Potts et al. 2003), this abundance of resources may provide nutritionally inadequate or lower quality pollen resources. Furthermore, the lower quality pollen in high-severity burns is still apparent 7 years post-burn, implying that the effects of severe wildfires on the quality of available pollen, as well as potentially on species which rely on those floral resources, persist at least that long as a biological legacy of high-severity burns. Additionally, we observed the quality of available pollen to be strongly correlated with the quality of corbicular pollen, providing evidence that the lower pollen quality availability in high-severity burns is thereby lowering the quality of nutrition bumblebees are able to forage on there.

Bumblebee Nutrition

The quality and quantity of pollen resources are important for bee nutrition (Di Pasquale et al. 2013), bee abundance, and bee species diversity (Potts et al. 2003), yet their relative importance is not well understood. There is strong general support for how organisms can be limited by, or show different nutritional states with, available nutrition (e.g., Elser et al. 2000). For pollinating insects like bumblebees, the quality of floral resources, particularly pollen, is undeniably important for bumblebee nutrition (Ruedenauer et al. 2016). In our study, we observed that the quality of corbicular pollen

was lower in high-severity compared to mixed-severity burns, indicating that bumblebees in high-severity burns are foraging for and receiving poorer nutrition. However, despite the available pollen quality and corbicular pollen remaining quite dissimilar between mixed- and high-severity areas seven years post-burn, bumblebee nutrition appeared to only show strong differences between burn severities in the years immediately post-burn (1-2 years). This growing discrepancy between pollen percent nitrogen and bee percent nitrogen in high-severity burns over time suggests that the effects of high-severity burns on bumblebee nutrition are greatest in the years immediately post-burn yet the effects are mitigated to approximately the same levels as mixed-severity burns after 7 years post-burn. Alternatively, if bumblebees are nutritionally constrained, there could be tradeoffs at the colony-level: e.g., if a colony is nutritionally limited by protein from pollen, they may produce fewer or smaller workers. While evidence does not suggest that bumblebees compensate for low-quality pollen resources by increasing consumption or larval provisioning (Roulson and Cane 2002), bumblebees have been observed to increase foraging rates based on the quantity of current pollen stores in the colony as well as the quality of available floral pollen (Kitaoka & Nieh 2009). However, we are unaware of any study which considers colony-wide bumblebee nutrition and could address this question of whether production and quality of workers in wild colonies can be phenotypically plastic with available pollen resources.

Disturbance & The Nutritional Landscape

Anthropogenic influences on floral resources important for bumblebees, both via the diversity of flora as well as the quality of available nutrition (i.e., both pollen and

nectar abundance and quality), has been cited as one of the most important issues facing wild bumblebee species (Woodard and Jha 2017). Our research has begun to investigate how the nutritional landscape may be altered by disturbance and how wildfire severity may leave legacies on the quality of available floral pollen and bumblebee nutrition which are apparent many years post-disturbance. In the Anthropocene, ecosystems are not limited to single disturbances like changing fire regimes, as other factors such as habitat loss and climate change act in concert (Potts et al. 2010). In this system, we observed that high-severity burns have lower quality pollen nutrition available for bees. We also observed that bees have poorer nutritional states and collect poorer quality pollen in high-severity burns. As high-severity burns continue to increase in frequency and spatial scale (Bowman et al. 2009), there are likely to be more severe impacts on bumblebee communities, due at least in part from nutritional limitations. While much is known about pollen nutrition and bumblebee foraging in experimental settings (e.g., Muth et al. 2016, Ruedenauer et al. 2016), field studies testing the effects of pollen quality on bumblebee foraging following disturbances like wildfire could provide more realistic assessments of the potential for disturbances to influence the nutrition of bumblebees and other pollinators. More detailed nutritional measurements of pollen (e.g., stoichiometric or geometric framework methods, Filipiak et al. 2018) would provide additional insights into the effects of available nutrition on bumblebees. Future studies may consider studying bee colony density alongside measures of bee nutrition and colony health (e.g., larval mass, number) in the years following wildfire in order to determine the degree to which bumblebees exhibit trade-offs to adjust to variation in nutrition

availability, such as worker longevity, number, or size. Additionally, field-based colony-level measurements of nutrition could help to address the relative importance of quality and quantity of floral resources, particularly post-disturbance.

Figure 5: Available floral pollen quality in percent nitrogen across time-since-burn in years. Red represents high-severity and blue represents mixed-severity. Solid lines represent the linear models while dashed lines are 95% confidence intervals.

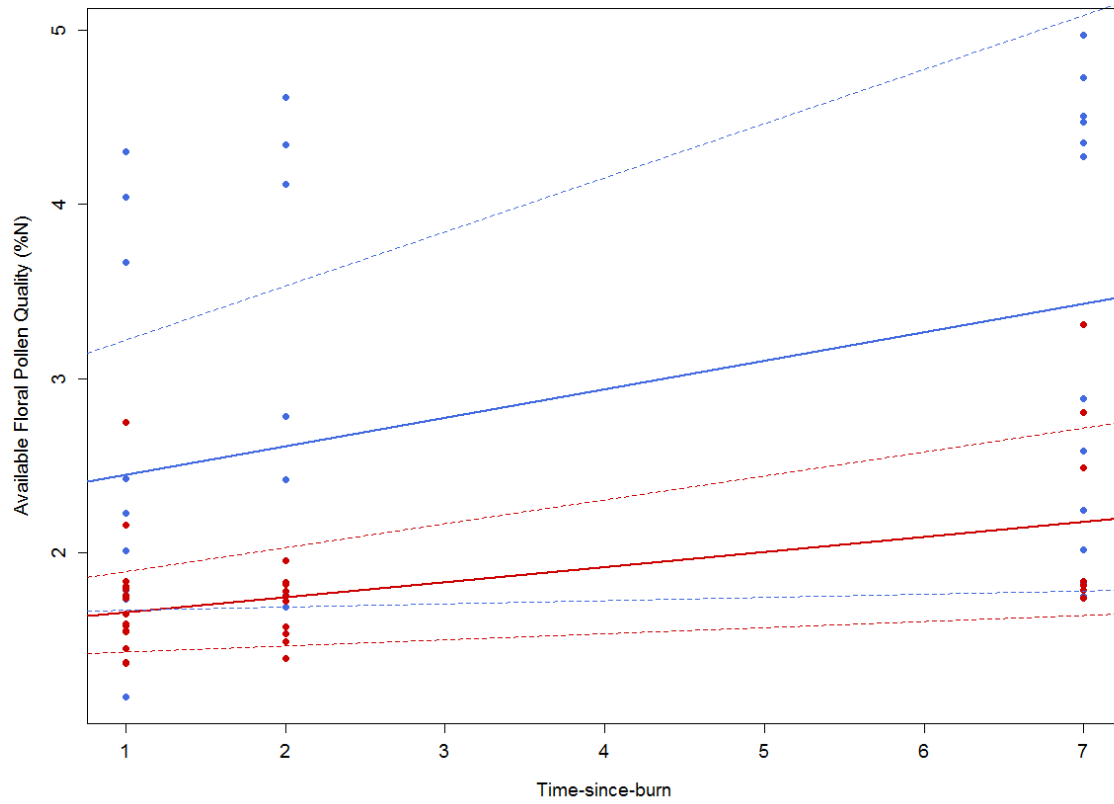


Figure 6: Corbicular pollen quality in percent nitrogen across time-since-burn in years. Red represents high-severity and blue represents mixed-severity. Solid lines represent the linear models while dashed lines are 95% confidence intervals.

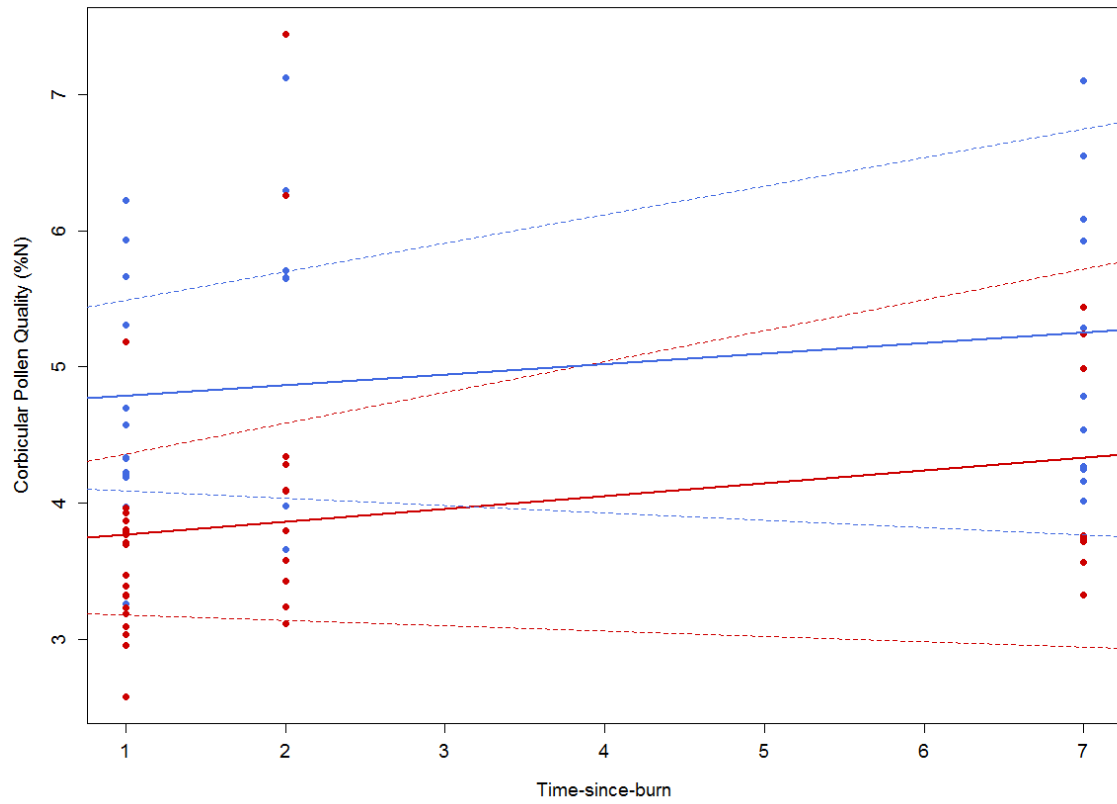


Figure 7: Corbicular pollen quality in percent nitrogen across the quality of available floral pollen in percent nitrogen. Red represents high-severity and blue represents mixed-severity. Solid lines represent the linear models while dashed lines are 95% confidence intervals.

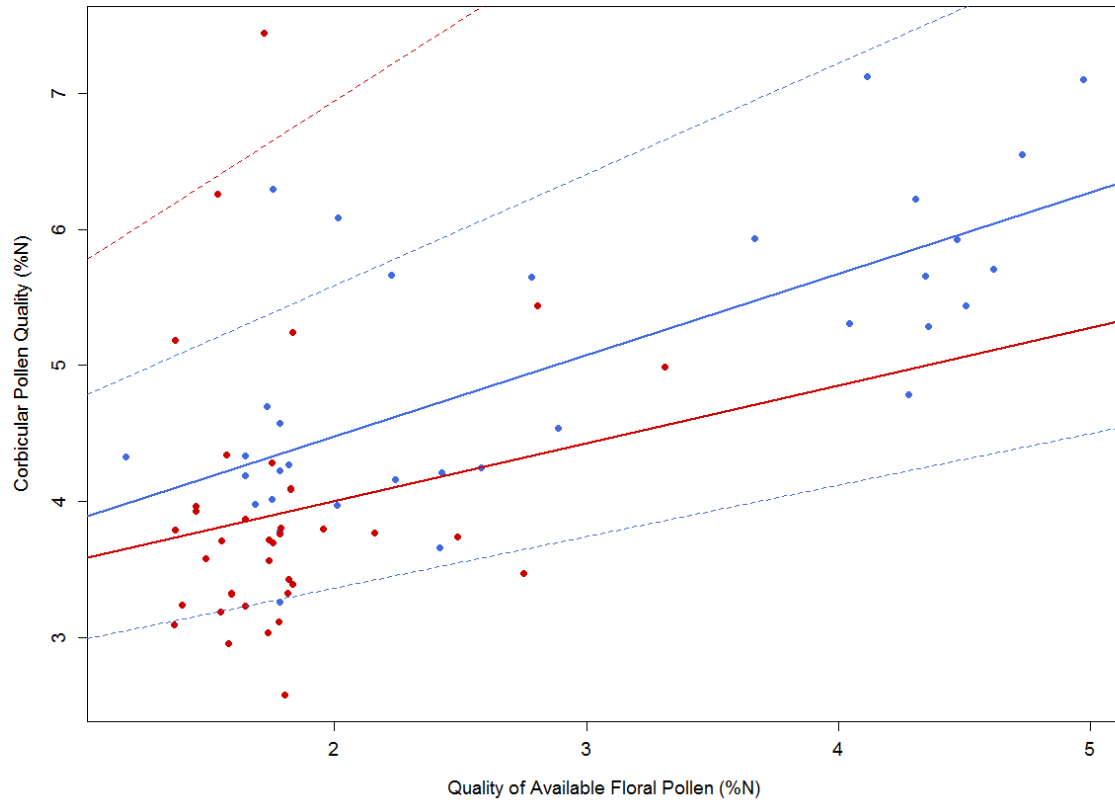
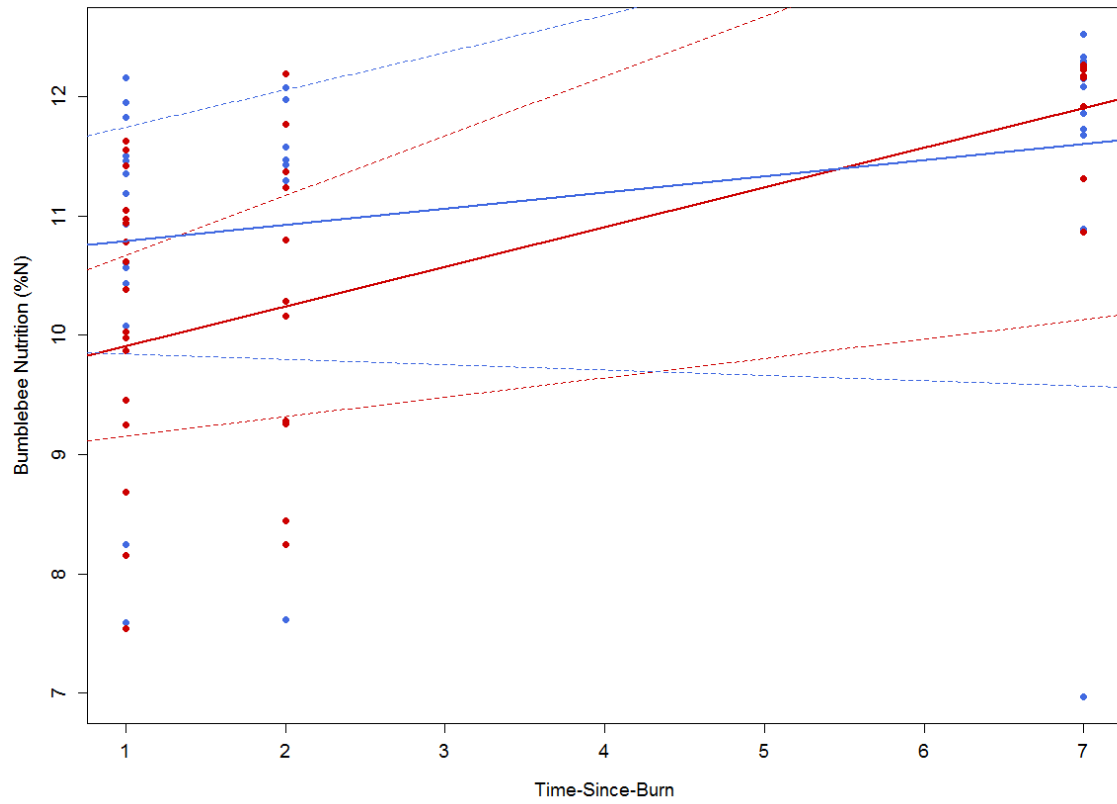


Figure 8: Bumblebee nutrition measured as percent nitrogen across time-since-burn in years. Red represents high-severity and blue represents mixed-severity. Solid lines represent the linear models while dashed lines are 95% confidence intervals.



NESTING SUCCESS OF WOOD-CAVITY-NESTING BEES AFTER WILDFIRE
DECLINES WITH INCREASING TIME-SINCE-BURN BUT IS UNAFFECTED BY
BURN SEVERITY

Introduction

Bees require both nesting and foraging habitats for survival and successful reproduction, yet these two resources do not always overlap spatiotemporally (i.e., floral and nesting habitats are individually “partial habitats;” Westrich 1996). This is particularly true for wood-cavity nesting bees, as many of the characteristics associated with wood-cavity nesting habitat, such as large standing tree snags, abundant coarse woody debris, or high canopy cover, represent physical characteristics which may restrict floral abundance or diversity (Potts et al. 2005, Peterson et al. 2007). Additionally, bees are central-place foragers, typically foraging within a few hundred meters of their nests (Gathmann & Tscharnke 2002). This combination of short foraging distances from a central location and necessity for ample nesting and floral resources makes the relative spatial proximity and arrangement of bees’ nesting and foraging habitats essential for nesting success (Westrich 1996).

Disturbances, such as wildfire, can affect the quality, quantity, and spatial distribution of nesting and floral resources for bees (Potts et al. 2005, Peralta et al. 2017). Wildfire is a globally occurring phenomenon and a natural, necessary part of many ecosystems, yet fire suppression and climate change have amplified the extent and severity of fires (Bowman et al. 2009). Large scale, high-severity fires have

homogenizing effects across the landscape, causing high tree mortality and removing coarse woody debris along with other vegetation (Pierce et al. 2004). The homogenization of landscapes by high-severity burns (Bowman et al. 2009) could strongly affect the presence and relative proximities of both nesting and foraging habitats for wood-cavity-nesting bees, creating landscapes where suitable nesting resources are either unavailable or too distant from sufficient floral resources. High-severity burns generally have lower species richness and site-to-site variation across the landscape for both bee and floral communities (Ponisio et al. 2016). By contrast, mixed-severity burns create a mixture of low- to high-severity patches, providing a variety of biological legacies (e.g., snags or coarse woody debris) and floral communities across the landscape (Arno and Fiedler 2005). Greater landscape diversity post-burn, such as that which occurs with mixed-severity burns, has also been associated with increased bee and floral species richness (Ponisio et al. 2016). Additionally, the vegetation and biological legacies, including old solitary bee nesting cavities, that survive low-severity burns are noted as important nesting resources (Robinson et al. 2013, Brown et al. 2017), highlighting how wood-cavity nesting bees may be particularly vulnerable to the effects of high-severity wildfires.

The effects of wildfire severity are often dependent on successional processes, and may develop, attenuate, or persist with time-since-burn (Abella and Fornwalt 2015). Bee abundance and richness have been observed to be greatest in recent burns (i.e., <10 years post-burn, Potts et al. 2003, Potts et al. 2005, Grundel et al. 2010), with both abundance and richness tending to decline through successional time (Potts et al. 2003).

These changes in the bee community have been associated with declines in the availability of nesting resources post-burn (Potts et al. 2005, Grundel et al. 2010), suggesting that nesting resource availability may limit both bee abundance and species richness with increasing time-since-burn. Many nesting resources associated with wood-cavity-nesting bees appear to vary with time-since-burn: the number of available cavities can be highest in the years immediately post-burn, yet the amount of coarse woody debris may peak in older burns (ca. 16 years post-burn, Potts et al. 2005). In another system, wood-cavity nesting bees were more abundant in older burns (20-28 years post-burn, Lazarina et al. 2016). Together, these patterns suggest that wood-cavity-nesting bees may be limited by nesting resources, and the availability of these resources changes with time-since burn (Potts et al. 2005). However, while the potential for specific nesting resource limitation remains relatively unknown, there is evidence that wood-cavity nesting bees recover quickly post-burn, and diet-generalist species can dominate community composition in recently burned sites (Peralta et al. 2017). Similarly, for the floral community, floral abundance and diversity tend to peak in the years soon after fire and decline with increasing time-since-burn (Potts et al. 2003, Peralta et al. 2017), however low-, moderate-, and high-severity burns exhibit different rates of change in their floral communities with time-since-burn (Abella and Fornwalt 2015). While broad community measurements such as richness and abundance of bees and flora tend to be positively correlated post-burn, the composition of the floral community has been found to be a poor predictor of bee community composition (Grundel et al. 2010, Lazarina et al. 2017). Bee nesting is notoriously difficult to measure, particularly for wood-cavity-nesting bees

(Roulston & Goodell 2011), and studies investigating their nesting resources have often used passive trapping via bee-bowls (e.g., Grundel et al. 2010) or hand-netting of foraging bees (e.g., Potts et al. 2005) to infer use of local bee nesting resources. One study used artificial nests post-burn to investigate changes in foraging patterns and network structure (Peralta et al. 2017) but did not relate these patterns to any direct measurements of nesting resources. Therefore, while general hypotheses exist regarding bees' use of nesting and foraging habitats following fire, the use of nesting habitats and resources has not been adequately demonstrated independently of foraging and floral resources for wood-cavity-nesting bees (Roulston and Goodell 2011).

We investigated how different species of wood-cavity nesting bees utilize artificially-provided nesting habitat after wildfire, and how nesting and floral resource differences across mixed- and high-severity burns as well as time-since-burn may affect the community of nesting bees and their nesting success. We placed bee nesting boxes in mixed- and high-severity burns across a time-since-burn gradient using the chronosequence approach (Hutto & Belote 2012) to ask: i) how does species richness and nesting success of wood-cavity nesting bees vary with burn severity and time-since-burn and ii) how do habitat characteristics which are altered by burn severity and time-since-burn (specifically, coarse woody debris, wood cavity density, canopy cover, and floral resources) contribute to bee richness and nesting success? Specifically, we expected burn-severity and time-since-burn to affect nesting resources and floral resources, which would in turn affect bee nesting success and species richness, i.e., the effects of burn-severity and time-since-burn would indirectly act on nesting success and

species richness via nesting and floral resources. We hypothesized that i) species richness and measures of nesting success (e.g., emergence from nesting boxes) would both be greater in mixed-severity burns due to greater availability of nesting resources; however, we expected species richness to increase and nesting success to increase with increasing time-since-burn. We expected that ii) measures of nesting success would increase with available coarse woody debris, density of available wood cavities, canopy cover, floral richness, and floral abundance. Furthermore, we expected nesting resources and floral resources to vary with burn severity and time-since-burn. Specifically, we expected that nesting resources would generally be more available in mixed-severity burns and become more available with time-since-burn. Further, we expected that floral resources would be more abundant in high-severity burns but more species rich in mixed-severity burns, and that floral abundance would decline while floral richness would increase with time-since-burn. Finally, we anticipated that nesting resources would be more strongly associated with measures of nesting success than would floral resources in high-severity burns and in recent wildfires (i.e., minimal time-since-burn), as nesting resources are more likely to be limited in such situations. In summary, we expected burn severity and time-since-burn to influence nesting and floral resources which would in turn affect nesting bee richness and nesting success (i.e., burn severity and time-since-burn have indirect effects on bee richness and nesting success via nesting and floral resources).

Methods

Study Site

Four wildfires from the Absaroka Mountains of southwest Montana, USA were selected to include a range of burn-severities and time-since-burn (Table 1). Additionally, we selected unburned sites which have not burned in at least 75 years, located approximately 4 km from all burned sites so as to be ecologically similar yet distant enough to minimize chances of bees moving between burned and unburned sites (Table 1). We selected two 15ha sampling blocks of high-severity burn and two of mixed-severity burn within each wildfire perimeter. Fire severities were determined by the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al. 2007). A high-severity block was an area of 15ha which is >95% high-severity, containing three 25m diameter circular sampling plots. A mixed-severity block was a 15ha area containing one low-severity sampling plot, one moderate-severity plot, and one high-severity plot. There were a total of 54 study plots sampled for this chapter.

Field Sampling

Within each plot, a bee nesting box was affixed to the snag nearest to the center of the plot in early June 2016. When no standing snags were present, the highest coarse woody debris (for 9 of 54 plots) or stump (for 5 of 54 plots) nearest to the center of the plot was used. Nest boxes were always placed with their cavity openings facing southeast, and approximately 1m in height whenever possible. Nesting boxes were constructed out of pine or poplar, and each box had 16 drilled cavities for cardboard bee

nesting tubes. Four sizes of tubes were used in each box (3mm, 4mm, 5mm, and 6mm) to maximize the number of species which could potentially nest in the boxes (Figure 9). Nest boxes were checked at least every other week from June through August; full nesting tubes were removed and replaced with unused, empty tubes. Full tubes were then individually stored in plastic bottles with 1.5mm air holes and overwintered in the ambient conditions of an uninsulated shed in Bozeman, MT from September 2016 until emergence was first noted in April 2017. Once bees began to emerge, tubes were moved into room temperature lab conditions and checked twice per week from April-August for new emergence. After emergence, bees were frozen and identified to species. We recorded proportion of bee nesting tubes which emerged along with bee species richness.

Habitat characteristics of each plot were sampled once. Along a 25m transect through the center of each plot we calculated coarse woody debris (CWD) as volume in m^3/ha following Harmon and Sexton (1996). The number of wood cavities, defined as $\geq 3\text{mm}$ holes, were recorded for all CWD, snags, and trees along a 2m x 25m transect. Canopy photographs were taken from the center of the plot using a fish-eye lens and canopy cover was calculated using Gap Light Analyzer (Frazer et al. 1999). The floral community was measured every other week along a 2m x 25m transect, where all open flowers of each species were identified and counted to provide floral richness and abundance at the plot level. Floral data were matched to know foraging habits of collected bee species (Chapter 2), and only floral species on which collected bee species were known to visit were included analyses. It is also important to note that since we used a subset of sampling plots from Chapter 2 in this study, and this chapter only

includes data from 2016, that floral abundance and richness summaries had the potential to show different results. Furthermore, as we could not be certain of the exact floral community from which the bee nests were provisioned, floral data compared against nesting success and bee richness is taken from all weeks prior to when the tube was retrieved from the field.

Statistical Analysis

To assess the effects of burn severity and time-since-burn on nesting and floral resources and their subsequent effects on overall bee nesting success we used structural equation modelling (Figure 10). We used this approach to test our general hypothesis that burn severity and time-since-burn would alter nesting resources (canopy cover, coarse woody debris, and availability of wood cavities) as well as floral resources (floral species richness and abundance) and both would then affect measures of wood-cavity-nesting bee nesting success (bee emergence, bee species richness for all species). All analyses were performed in R using the lavaan package (Rosseel 2012, R Core Development Team 2018).

Results

We collected 641 total filled nesting tubes: 307 (47.9%) had no emergence, 241 (37.6%) had successful bee emergence, and 93 (14.5%) had emergence of non-bee insects. A total of 676 adult bees emerged, representing 18 species, primarily *Megachile lapponica* (402) and *Hoplitis albifrons argentifrons* (129) (Appendix A6). No emergence

(bee or otherwise) was observed from any of the 47 filled nesting tubes collected in our unburned sampling plots.

Overall SEM fit was exceptionally poor, with a significant chi-square ($\chi^2(11) = 1312.02$, $P < 0.01$, Figure 11) and weak indices of fit (CFI = 0.67, TLI = -0.34, RMSEA = 0.43, SRMR = 1.79). Despite the poor fit, there were interesting correlations revealed through the regressions within the SEM which can still be utilized for discussion, as they can be explored to help explain alternative hypotheses for why our structural model does not represent reality. For nesting resources, canopy openness, volume of coarse woody debris, and number of wood cavities were greater in both mixed- and high-severity plots relative to unburned (Table 8). Number of wood cavities was much greater in high severity relative to mixed-severity. Canopy openness, volume of coarse woody debris, and number of wood cavities increased with time-since-burn (Table 8). Floral richness and abundance were both lower in unburned plots yet relatively similar in mixed- vs. high-severity, and both floral richness and abundance increased with greater time-since-burn (Table 8). Bee emergence showed no significant differences with burn severity and declined with increasing time-since-burn. Bee richness was not significantly different between burn severities and also declined with increasing time-since-burn (Table 8). The effects of nesting resources were variable on measures of bee nesting success. Bee emergence was greater with increasing canopy openness but did not significantly vary with any other measure of nesting or floral resources (Table 8). Bee richness was greater with increased canopy openness and declined with increasing number of wood cavities

(Table 8). Neither bee emergence nor bee richness showed any direct correlations to floral richness or abundance (Table 8).

Discussion

By using nesting boxes in both mixed- and high-severity burns across a chronosequence of time-since-burn, we sought to study the use and relative importance of nesting resources and foraging resources for wood-cavity-bee nesting success and species richness post-burn. We found no evidence that burn-severity affected the nesting success or species richness of nesting bees via nesting and floral resources. However, increasing time-since-burn was associated with declines in both bee nesting success and bee species richness, highlighting the importance of early successional habitats for wood-cavity-nesting bees in post-burn ecosystems. Additionally, we observed that *all* nesting and floral habitat measurements (canopy cover, coarse woody debris, wood cavity density, floral richness, and floral abundance) were significantly positively associated with mixed- and high-severity fire (compared to unburned) as well as positively correlated with increasing time-since-burn. However, these severity and succession induced habitat patterns had little effect on nesting success or bee richness; the one exception was that canopy cover was negatively correlated with nesting success and bee richness, with a greater magnitude of effect than any other habitat or treatment predictor, providing evidence for the importance of early-successional post-burn habitats for wood-cavity-nesting bees.

Early successional habitats, noted as having relatively low canopy cover, which can contribute towards high productivity and diversity of plants (i.e., abundant floral resources, Swanson et al. 2011), are hypothesized to be exceptionally important for bee species (Taki et al. 2013). Empirical support for the importance of early successional habitats for bees, particularly wood-cavity-nesting bees, is mixed. In one system, wood-cavity-nesting bees recovered in the years immediately following fire (Peralta et al. 2017), while, in another system, cavity-nesting bee abundance peaked as many as 20-28 years after fire (Lazarina et al. 2017). Our results for nesting bee richness are consistent with trends suggesting that bee richness peaks in the years immediately post-burn and then gradually declines through successional time (Potts et al. 2003, Potts et al. 2005, Grundel et al. 2010, Peralta et al. 2017). We observed that some nesting resources, such as wood cavity density, which has been previously found to positively correlate with bee abundance and richness (Potts et al. 2005), increased with increasing time-since-burn. Surprisingly, this wood cavity density, which should provide for increased nesting opportunities, was negatively associated with nesting bee richness, however the estimate of decline was marginal. Our other measure of nesting resources, coarse woody debris, which also increased with greater time-since-burn, was unrelated to nesting success or species richness. Taken together, these results suggest that wood-cavity-nesting bee richness may not be limited by nesting resources in post-burn systems. While our study does not show evidence for floral resources affecting nesting bee richness, bee richness and floral richness often follow similar trends, as evidenced in Chapter 2 and elsewhere (e.g., Potts et al. 2003).

To our knowledge, nesting success had not previously been quantified at a community level for bees, particularly in a post-burn ecosystem. The closest comparison is the direct study of wood-cavity-nesting bees which were sampled using trap-nests (Peralta et al. 2017), yet that study was focused on use of floral resources and did not measure or address nesting resources. We anticipated that nesting resources would become more abundant with increasing time-since-burn, and that this would result in greater nesting success, if nesting resources are more limiting than floral resources. Our results suggest that there are changes in nesting resources with burn severity as well as with time-since-burn, which agrees with other studies (e.g., Potts et al. 2005); however, we were unable to detect a link between nesting resources and bee nesting success or richness. Canopy openness was strongly positively correlated with nesting success and bee richness. It's possible that canopy cover could act a proxy for nesting resources, e.g., more trees and snags could imply more available nesting sites. If so, then our results that nesting success and bee richness were higher in early burns (1-2 years post-burn) in sampling plots with lower canopy cover could imply that wood-cavity-nesting bees are not limited by nesting resources in early post-burn systems.

Surprisingly, despite dramatic differences having been previously detected between mixed- and high-severity burns (Chapter 2, Chapter 3) along with burn severity being significantly correlated with all measures of nesting and floral habitat, we observed no significant differences between burn severities for either nesting success or nesting bee richness. One possibility for this discrepancy with other chapters' results may relate to the species which were captured by our artificial nesting boxes. Our nesting boxes

were dominated by diet generalist species which were also abundant in our foraging data (Chapter 2), with two species comprising 78.6% of bees which emerged from our nesting boxes. Given the abundant and diet-generalist nature of these species, we could infer that we did not find floral resources to significantly affect bee nesting success simply because the species which comprised most of our samples have very flexible demands for foraging habitat. The low abundance and patchy distribution of rarer species prevented explicit testing of whether their nesting success was influenced by burn severity or time-since-burn. Another likelihood is that our artificial nesting boxes do not accurately reflect nesting success or the species richness of bees which are nesting in the area. For example, whether or not nesting resources are limiting, we provided an unnatural nesting option for bees in that area. If their nesting success is dependent on the material in which they are nesting, then having nearly identical artificial nesting habitat across burn severities would be unable to discern a difference. Furthermore, we observed other strange discrepancies regarding burn severities. For example, and contrary to expectations, coarse woody debris was more abundant in high- vs. mixed-severity burns, although coarse woody debris levels were not associated with bee emergence or richness. Given that coarse woody debris increased more with time-since-burn than did the difference between mixed- and high-severity, this pattern may result from increased coarse woody debris at older burns, via increased fuel loads accumulating through time post-burn. High-severity burns typically result in high tree mortality (Pierce et al. 2004), and our coarse woody debris measurements may have been greater with increasing time-since-burn as more coarse woody debris could have entered the plot via snags that

previously were outside the plot fell into the plot. To illustrate this possibility, we had two snags with nesting boxes affixed fall during the study period; both were in our older fire, at two high-severity plots in the Wicked Creek Fire.

While sampling foraging bees remains standard practice, it remains difficult and inefficient to locate their natural nesting places, particularly for wood-cavity nesting bees (Roulston and Goodell 2011). Prior to our decision to use artificial nesting boxes in this study, we attempted using several other approaches to locate natural nests which were not successful. For example, we captured foraging bees, coated them with UV-fluorescent powder, released them, and returned at night to search for nests with a UV flashlight. This method was unsuccessful as we discovered that bees would land soon after being powdered to groom, well before returning to their nest. Furthermore, when we tested UV-fluorescent powder on *Megachile lapponica* bees with known, artificial nests, we discovered that the inside of the nesting cavity would be thoroughly powdered yet almost none was deposited on the outside or entrance, thus making it highly unlikely that wild nests would be able to be located. We also placed small, double-sided insect sticky-traps inside wood cavities in snags and coarse woody debris and revisited these sticky-traps 24h later to search for bees caught in the traps. This method was unsuccessful in trapping any bees. In one particular instance we discovered a wood cavity with a Megachilidae bee deep inside. We placed a sticky trap inside the entrance, but upon returning later discovered both the bee and sticky trap to be gone. Likely possibilities for this method failing include 1. Failure of the double-sided trap, 2. Too light-weight of traps so that the bees were able to escape with the trap attached, or 3. Predation of the trapped bee. In any

case, effectively locating above-ground nesting bees remains difficult, and we therefore continue to have a poor understanding of how wood-cavity-nesting bees select nesting habitat.

In this study we did not find any strong evidence for wood-cavity-nesting bees to be limited by natural nesting resources, and we were generally unable to link nesting and floral resources affected by fire to bee nesting success or species richness. Our one significant highlight is the finding that increasing canopy cover is very strongly correlated with a decline in wood-cavity-nesting bee nesting success and species richness. Future studies need to consider a wider range of habitat characteristics which could be influenced by wildfire, as it remains difficult to assess or predict whether nesting resources will be limiting as well as how these species respond to disturbances such as wildfire.

Table 8: Structural equation modelling output.

Regressions		Estimate	Std. Error	Z	P
High Severity	Time-since-burn	-0.08	0.02	-4.17	<0.01
Mixed Severity	Time-since-burn	-0.09	0.02	-4.35	<0.01
Canopy	Time-since-burn	0.01	0.004	2.75	<0.01
	High Severity	0.43	0.01	56.35	<0.01
Coarse wood debris	Mixed Severity	0.41	0.01	53.35	<0.01
	Time-since-burn	0.71	0.03	24.99	<0.01
	High Severity	0.97	0.05	18.07	<0.01
Wood cavities	Mixed Severity	0.57	0.05	10.7	<0.01
	Time-since-burn	1.17	0.07	17.62	<0.01
	High Severity	2.26	0.13	18.04	<0.01
Floral richness	Mixed Severity	2.46	0.12	19.84	<0.01
	Time-since-burn	0.17	0.01	12.7	<0.01
	High Severity	1.34	0.03	52.57	<0.01
Floral abundance	Mixed Severity	1.46	0.03	58.05	<0.01
	Time-since-burn	0.65	0.04	17.55	<0.01
	High Severity	5.59	0.07	79.95	<0.01
Nesting success	Mixed Severity	5.88	0.07	84.97	<0.01
	Canopy	0.47	0.19	2.55	0.01
	Coarse woody debris	0.03	0.03	1.04	0.3
	Floral richness	0.04	0.06	0.79	0.43
	Floral abundance	-0.02	0.02	-0.72	0.47
	Wood cavities	-0.003	0.01	-0.29	0.77
	Time-since-burn	-0.2	0.03	-5.93	<0.01
Bee richness	High Severity	-0.25	0.17	-1.52	0.13
	Mixed Severity	-0.15	0.17	-0.88	0.38
	Canopy	1.49	0.19	8.02	<0.01
	Coarse woody debris	0.02	0.03	0.81	0.42
	Floral richness	0.06	0.06	1.09	0.28
	Floral abundance	0.01	0.02	0.31	0.76
	Wood cavities	-0.09	0.01	-7.46	<0.01
Time-since-burn	High Severity	-0.12	0.03	-3.54	<0.01
	High Severity	-0.07	0.17	-0.4	0.69
	Mixed Severity	-0.24	0.17	-1.41	0.16

Figure 9: Example of a nesting box, at a high-severity plot in the Pine Creek fire. Note the different sizes of tubes.



Figure 10: Hypothetical pathway of how burn severity and time-since-burn may affect bee nesting success and species richness, and how associations in our structural equation model were scripted. All lines are directional from top to bottom with solid lines representing positive and dashed representing negative.

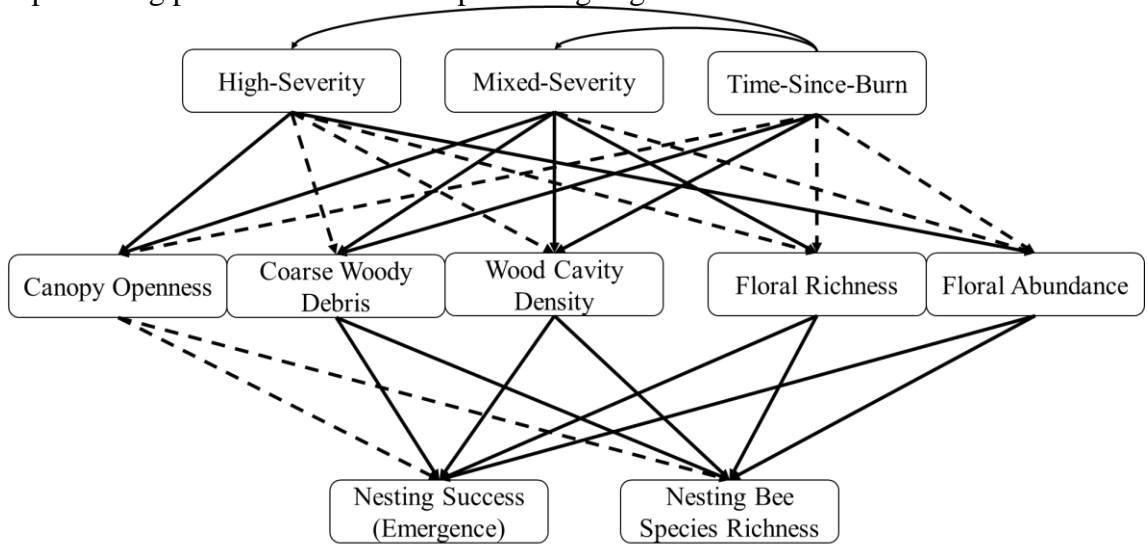
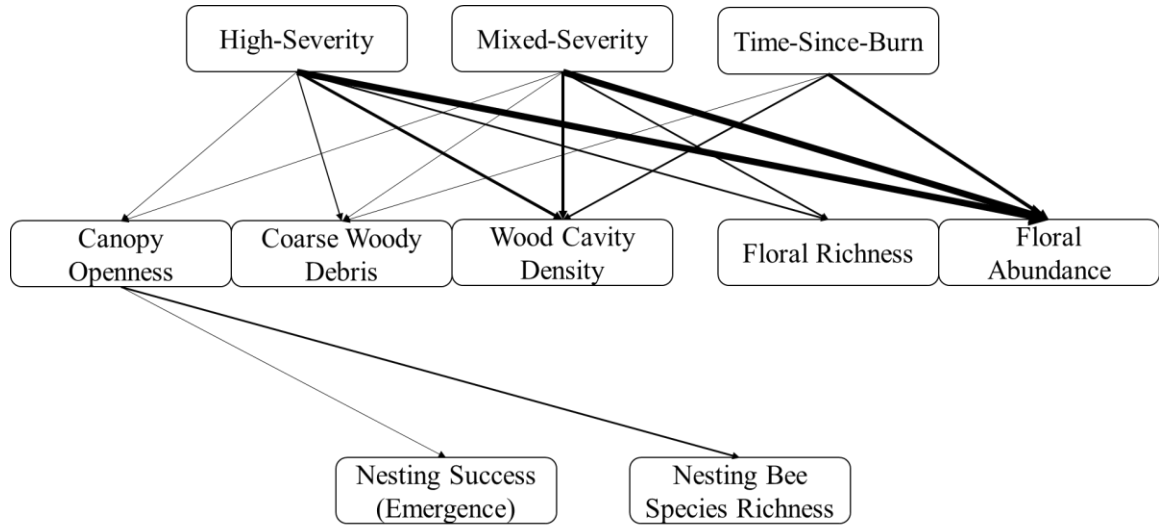


Figure 11: Structural equation modeling results. Only statistically significant correlations with estimates greater than 0.2 are included. Solid lines represent positive effects, and lines widths are weighted by their estimate from Table 8.



CONCLUSIONS

Taken together, these studies help to inform patterns in the assembly of plant and pollinator communities and their network interactions. The network motif analyses help to suggest that species' roles in networks are not dramatically altered by burn severity, and that despite changing species composition, highly persistent species are generally also persistent in their network roles. This could suggest that pollinators follow some form of preferential attachment in making their network interactions in our study system, because if pollinators were opportunistic in forming links we may expect low consistency of their network roles. However, our results leave open the possibility that less common or less persistent species are highly flexible in their network positions and that they may still form links opportunistically. This is evidenced by our finding that general network motifs changed with one of our study years, as we find, and expect (Oleson et al. 2008), pollinator turnover to be high interannually.

Our nutrition results begin to explore a mechanism for determining plant-pollinator interactions that until now had not been studied in a field setting: pollen quality. We found that the quality of available floral pollen was much greater in mixed- vs. high-severity burns, that this pattern correlated with bumblebee corbicular pollen quality, and that bumblebees had a stronger nutritional state in mixed-severity burns. While our network results did not find any broad-scale differences across burn severities, these results show that different floral community composition between mixed- and high-severity can result in different available forage quality, with significant effects for bumblebees. Therefore, while summary patterns of abundance, richness, and network

roles did not significantly vary with burn severity, our nutrition results highlight that there may be secondary effects of changes in species composition which are dependent on the quality of forage within that composition and the resulting nutritional landscape. In the context of the assembly of species interactions, the nutrition results do not clearly point towards preferential vs. opportunistic attachment; the higher quality pollen being collected in mixed-severity plots could either simply reflect opportunity of more higher quality plants being present or could suggest that bumble bees preferentially forage for that higher quality pollen. The only further inference we can glean is that the relationship of available pollen quality vs. corbicular pollen quality is lower than 1:1, whereas if foraging were perfectly opportunistic we may expect a 1:1 relationship.

In testing for changes in wood-cavity-bee nesting, we found that burn severity does not appear to directly or indirectly affect wood-cavity-bee nesting success or species richness via nesting or floral resources. However, nesting success and bee richness did appear to decline with increasing time-since-burn, and surprisingly this occurs concurrently with increases in nesting resources with time-since-burn. With our artificial sampling it is difficult to draw conclusions from this finding; e.g., if we were able to sample natural nesting density and success then finding declining nesting success concurrent with increasing nesting resources would suggest that wood-cavity-nesting bees are unlikely to be limited by nesting resources after wildfire. As it stands, an important conclusion is that innovation in sampling for nesting bees is gravely needed, as it remains exceedingly difficult to efficiently locate wild nesting bees, and many methods have proven unsuccessful. Considering community assembly, the vast majority of bees

which emerged from our traps consisted of just two species, and thus it limits our inference towards the importance of nesting resources at a community level. However, an early peak in bee nesting success and species richness that subsequently declined with increasing time-since-burn suggests that early successional burns are important periods for wood-cavity-nesting bees.

All together, our results paint a complicated picture of the complicated processes of community and network assembly, where burn severity and time-since-burn often have inconsistent or inconclusive findings. Subsequent analyses of these data may allow insights which can account for shortcomings of the studies as presented. Future work investigating these themes across multiple layers, e.g., integrating a nutritional context into the assembly of species interactions and network structure, or accounting for nesting resources in bipartite species interaction networks, would help break new conceptual ground as well as provide clarity on understanding the motivations behind assembling species interactions.

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APPENDIX A

SPECIES LISTS

Appendix A1: Bee species sampled via hand netting by locality and burn severity combinations. EM is Emigrant, PC is Pine Creek, WC is Wicked Creek, TC is Thompson Creek, and UN is unburned for localities while HI is high-severity and MX is mixed-severity.

Species	EM HI	EM MX	PC HI	PC MX	WC HI	WC MX	TC HI	TC MX	UN	Total
<i>Agopostemon texanus</i>			1							1
<i>Agopostemon virescens</i>			1							1
<i>Andrena amphibola</i>	1	1	6	4	1	4				17
<i>Andrena Andrena1</i>	2	1		2						5
<i>Andrena Andrena2</i>	1		1	5						7
<i>Andrena candida</i>					1					1
<i>Andrena cartaegi</i>		1	1	3						5
<i>Andrena cleodora</i>	1		3							4
<i>Andrena crataegi</i>					2				1	3
<i>Andrena cupreotincta</i>				3						3
<i>Andrena knuthiana</i>	1	1		2		1				5
<i>Andrena medionitens</i>	1		1			1				3
<i>Andrena melanothroa</i>									1	1
<i>Andrena microandrena2</i>	1									1
<i>Andrena milwaukeeensis</i>	1			1	1	1				4
<i>Andrena miranda</i>	15	12	69	59	16	11	3	5		190
<i>Andrena nasonii</i>				1						1
<i>Andrena nigrocaerulea</i>		1	2	1		1				5
<i>Andrena</i>				5						5

<i>nivalis</i>										
<i>Andrena pronorum</i>	1	2		1						4
<i>Andrena prunorum</i>						1				1
<i>Andrena Q1</i>	1									1
<i>Andrena Q2</i>			1							1
<i>Andrena Q3</i>		1								1
<i>Andrena s.str. sp.1</i>								2		2
<i>Andrena saccata</i>	1	1	2	4	3	5	2	3		21
<i>Andrena salicifloris</i>						1				1
<i>Andrena scurra</i>			1	1						2
<i>Andrena sp.F10</i>								1		1
<i>Andrena sp.F11</i>	1									1
<i>Andrena sp.F12</i>		1								1
<i>Andrena sp.F13</i>		1	3	2						6
<i>Andrena sp.F14</i>				3						3
<i>Andrena sp.F15</i>						2		1		3
<i>Andrena sp.F4</i>								1		1
<i>Andrena sp.F7</i>				1					1	2
<i>Andrena sp.F8</i>	1									1
<i>Andrena sp.F9</i>		3	1	3						7
<i>Andrena sp.M2</i>								1		1
<i>Andrena surda</i>	1		1							2
<i>Andrena</i>					1	4				5

<i>thaspis</i>										
<i>Andrena topazana</i>	2	1		2	11	6	4	10		36
<i>Andrena transnigra</i>				1						1
<i>Andrena vierecki</i>					1	1				2
<i>Anthidium atrifrons</i>							1			1
<i>Anthidium mormonum</i>	1		3			1				5
<i>Anthidium tenuiflorae</i>					2					2
<i>Anthophora terminalis</i>	4		1	21		1	1	1		29
<i>Anthophora urbana</i>		1								1
<i>Anthophora ursina</i>	1			2						3
<i>Apis Apis1</i>	1									1
<i>Apis mellifera</i>	33	42	483	519	4	3				1084
<i>Ashmeadiella Ashmeadiella1</i>		1								1
<i>Ashmeadiella cactorum</i>					1	2	3			6
<i>Ashmeadiella cadorum</i>	1	1	1							3
<i>Ashmeadiella californica</i>					1		1			2
<i>Ashmeadiella pronitens</i>					2	3	1	2		8
<i>Bombus appositus</i>	12	11	2	27	22	10	8	6		98
<i>Bombus bifarius</i>	147	114	373	176	236	221	84	52	3	1406
<i>Bombus borealis</i>				1						1
<i>Bombus centralis</i>	10	46	17	29	9	8	8	16	8	151
<i>Bombus fervidus</i>		1			1	1	1			4
<i>Bombus</i>			1		1		14	1		17

<i>sodalis</i>										
<i>Colletes fulgidus</i>	1	1	2	5	2	3	3			17
<i>Colletes hyalinus</i>	1	1		3						5
<i>Colletes hyalinus</i>					5	4				9
<i>Colletes kincaidii</i>		1	2	1						4
<i>Colletes lutzi</i>						2				2
<i>Colletes phaceliae</i>		1		1						2
<i>Dianthidium singulare</i>		1								1
<i>Dianthidium subparvum</i>	2									2
<i>Dufourea maura</i>		3			2	5	2			12
<i>Epeolus sp.</i>				1						1
<i>Eucera edwardsii</i>						1				1
<i>Eucera frater</i>						1				1
<i>Halictus confusus</i>	2	3		2	4	2		2		15
<i>Halictus farinosus</i>	3	3		4			1			11
<i>Halictus ligatus</i>	1		1							2
<i>Halictus rubicundus</i>	9	5	20	29	4	6	3	1	2	79
<i>Halictus virgatellus</i>				1						1
<i>Heriades carinata</i>	1			4						5
<i>Heriades cressoni</i>	2	7	2	10		1				22
<i>Heriades variolosa</i>		1	1	1						3
<i>Hoplitis albifrons argentifrons</i>		3	13	8	23	19	24	3		93

<i>Hoplitis chlorosmia2</i>	1									1
<i>Hoplitis fulgida</i>		5		3	7	9	20	5		49
<i>Hoplitis producta</i>					1		2			3
<i>Hoplitis robusta</i>	1	3			1			2	2	9
<i>Hoplitis sp.</i>								1		1
<i>Hoplitis sp.F1</i>							1			1
<i>Hoplitis truncata</i>			1							1
<i>Hylaeus affinis</i>	1		1							2
<i>Hylaeus annulatus</i>				1	2	1	1			5
<i>Hylaeus basalis</i>	2	1	3	6	2	7	17	5	1	44
<i>Hylaeus coloradensis</i>	1	3		8		1	1			14
<i>Hylaeus episcopalis</i>		1				2			1	4
<i>Hylaeus Hylaeus1</i>				2						2
<i>Hylaeus mesillae /rudbeckiae</i>							1			1
<i>Hylaeus modestus</i>	1	3		1	5	15	29			54
<i>Hylaeus sp.</i>						1	1	2		4
<i>Hylaeus sp.M/F1</i>						1				1
<i>Hylaeus sp.M2</i>						1				1
<i>Hylaeus verticalis</i>		3				2	3			8
<i>Hylaeus wootoni</i>				4	1	5	3	1		14
<i>Lasioglossum albipenne</i>					1	1	1			3
<i>Lasioglossum</i>					2		2			4

<i>anhypops</i>										
<i>Lasioglossum egregium</i>					1					1
<i>Lasioglossum ephialtum</i>						1	1			2
<i>Lasioglossum marinense</i>					11	7	27		1	46
<i>Lasioglossum nigroviride</i>					18	29	29			76
<i>Lasioglossum nr.pavoninum</i>						2				2
<i>Lasioglossum obnubilum</i>					4		1			5
<i>Lasioglossum planatum</i>						1	1			2
<i>Lasioglossum ruidosense</i>						2				2
<i>Lasioglossum sedi</i>							1			1
<i>Lasioglossum sisymbrii</i>					1					1
<i>Lasioglossum sp.</i>						1	2	37		40
<i>Lasioglossum sp.F1</i>					5		1		2	8
<i>Lasioglossum sp.F17</i>						2				2
<i>Lasioglossum sp.F2</i>							1			1
<i>Lasioglossum sp.F27</i>						1	1			2
<i>Lasioglossum sp.F3</i>					2	3				5
<i>Lasioglossum sp.F5</i>					7	1	9			17
<i>Lasioglossum sp.F6</i>					2	1				3
<i>Lasioglossum sp.M4</i>					18	2	4			24
<i>Lasioglossum sp.M5</i>							2			2
<i>Lasioglossum sp.M6</i>						1				1
<i>Lasioglossum</i>					7	8	1			16

<i>tenax</i>										
<i>Lassioglossum albipenne</i>				4						4
<i>Lassioglossum anhypops</i>	1	1	3	1						6
<i>Lassioglossum egregium</i>			1							1
<i>Lassioglossum Erylaeus1</i>		1								1
<i>Lassioglossum heterorhinum</i>	1	1		1						3
<i>Lassioglossum laevissimum</i>				1						1
<i>Lassioglossum lampronotum</i>	1									1
<i>Lassioglossum marinense</i>		3	2	2						7
<i>Lassioglossum nigroviride</i>	1	2		1						4
<i>Lassioglossum pacatimum</i>				1						1
<i>Lassioglossum paraforbesii</i>	1	1								2
<i>Lassioglossum ruidosense</i>	1	1								2
<i>Lassioglossum sedi</i>	1	1	2	1						5
<i>Lassioglossum sp.F1</i>	1									1
<i>Lassioglossum sp.F2</i>		2								2
<i>Lassioglossum sp.F5</i>	4	8	13	7						32
<i>Lassioglossum sp.F6</i>	1	1	5	6						13
<i>Lassioglossum sp.M3</i>	1									1
<i>Lassioglossum sp.M4</i>	3									3
<i>Lassioglossum tenax</i>	1	1								2
<i>Lassioglossum timothyii</i>	1			1						2
<i>Lassioglossum</i>	1		9	6						16

<i>titusi</i>										
<i>Lassioglossum trizonatum</i>				1						1
<i>Lassioglossum zonulum</i>	2		1							3
<i>Megachile angularum</i>	2	2		2		1				7
<i>Megachile apicalis</i>							1			1
<i>Megachile centucularis</i>		1	1	1						3
<i>Megachile fortis</i>	1	1		3						5
<i>Megachile frigida</i>	1	9	21	6	34	27	14	4		116
<i>Megachile gemula</i>	2	3	3	3	1	1	6	6		25
<i>Megachile inermis</i>	3	3	1	5						12
<i>Megachile lapponica</i>	8	33	12	13	33	41	12	4		156
<i>Megachile latimanus</i>	2	3	5	3						13
<i>Megachile Megachile1</i>		1								1
<i>Megachile melanophaea</i>	3	5	2		3	12	4	1		30
<i>Megachile montivaga</i>		2					1			3
<i>Megachile perihirta</i>	14	6	8	4		2	4	2	1	41
<i>Megachile pugnata</i>	11	9	9	7	7	7	3	1		54
<i>Megachile relativa</i>	2	24	16	12	12	9	21	5		101
<i>Melissodes coreopsis</i>	6		6							12
<i>Melissodes microsticta</i>	1		1		3	1				6
<i>Melissodes sp.M1</i>				1						1
<i>Nomada sp.F3</i>							1			1
<i>Nomada</i>							1			1

<i>sp.F6</i>										
<i>Nomada</i> <i>sp.F8</i>			2							2
<i>Nomada</i> <i>sp.M1</i>				1						1
<i>Nomada</i> <i>sp.M2</i>				1						1
<i>Osmia</i> <i>aff.paradisica</i>		1				5		1		7
<i>Osmia</i> <i>aff.pusilla</i>							1			1
<i>Osmia</i> <i>albolateralis</i>	1	1		1	16	14	4	2		39
<i>Osmia</i> <i>atrocyanea</i>		1		1		2	1	1		6
<i>Osmia</i> <i>brevis</i>			1		3		1	1		6
<i>Osmia</i> <i>bruneri</i>				1						1
<i>Osmia</i> <i>bucephala</i>			1		11	4	6	2		24
<i>Osmia</i> <i>californica</i>	2	1	1	2						6
<i>Osmia</i> <i>coloradensis</i>	12	40	13	13	3	2	6	1		90
<i>Osmia</i> <i>densa</i>	1			2	1	1	1	1		7
<i>Osmia</i> <i>dolorosa</i>								2		2
<i>Osmia</i> <i>ednae</i>		1			1		2	11		15
<i>Osmia</i> <i>grindeliae</i>		1		2	1			3		7
<i>Osmia</i> <i>inermis</i>	2	1	1	5	2	2				13
<i>Osmia</i> <i>juxta</i>	1		2	2	2	2	9	8	3	29
<i>Osmia</i> <i>lignaria</i> <i>propinqua</i>				2	1		1			4
<i>Osmia</i> <i>longula</i>					2					2
<i>Osmia</i> <i>montana</i>	5	2	5	4	5	4	2			27

<i>Osmia nanula</i>					1					1
<i>Osmia nigrifrons</i>					3	4		1		8
<i>Osmia nigriventris</i>					1	1				2
<i>Osmia nr. simillima</i>								2		2
<i>Osmia odontogaster</i>								1		1
<i>Osmia odontogaster gr.sp.1</i>					2					2
<i>Osmia odontogaster gr.sp.2</i>	1	1				1		1		4
<i>Osmia Osmia1</i>	1									1
<i>Osmia Osmia2</i>				2						2
<i>Osmia Osmia5</i>			1	1						2
<i>Osmia paradisica</i>					4	2		1	1	8
<i>Osmia pentstemonis</i>		1			2	6	2	3		14
<i>Osmia phacelia</i>								2		2
<i>Osmia phaceliae</i>	1	6	1	2	4	5	3		1	23
<i>Osmia physariae</i>						1				1
<i>Osmia pikei</i>							2			2
<i>Osmia proxima</i>					3	3	5			11
<i>Osmia pusilla</i>	1				2	1	1			5
<i>Osmia sculleni</i>							1	1		2
<i>Osmia simillima</i>	1	2								3
<i>Osmia sp.</i>		1	6	2	2	2	5		2	20

<i>Stelis</i> <i>sp.F2</i>							1			1
<i>Stelis</i> <i>sp.F6</i>					2					2
<i>Stelis</i> <i>sp.notch</i>	1									1
<i>Stelis</i> <i>sp.proto</i>			1	1						2
<i>Triepeolus</i> <i>paenepectoralis</i>	1		1							2
<i>Total</i>	472	598	1314	1235	818	777	607	334	75	6230

Appendix A2: Floral species sampled along floral census transects by locality and burn severity combinations. EM is Emigrant, PC is Pine Creek, WC is Wicked Creek, TC is Thompson Creek, and UN is unburned for localities while HI is high-severity and MX is mixed-severity.

Species	EM HI	EM MX	PC HI	PC MX	WC HI	WC MX	TC HI	TC MX	UN	Total
<i>Achillea millefolium</i>	2861	255 6	42	135 2	6662	2479 0	880 1	3528 7	95	8244 6
<i>Actaea rubra</i>							27	533	103	663
<i>Agastache urticifolia</i>							0	2794		2794
<i>Agoseris aurantiaca</i>					3	40	3	60		106
<i>Agoseris glauca</i>	143	13		13	0	2	5	5		181
<i>Allium acuminatum</i>								0		0
<i>Allium cernuum</i>									0	0
<i>Allium textile</i>	16	2		0						18
<i>Amelanchier alnifolia</i>			2	256	0	19	75	3		355
<i>Anaphalis margaritacea</i>	17	48	188	42	7339	2385	180 74	563	0	2865 6
<i>Anemone multifida</i>								0	0	0
<i>Angelica arguta</i>							5	0		5
<i>Antennaria alpina</i>					0		6			6
<i>Antennaria anaphaloides</i>						18				18
<i>Antennaria corymbosa</i>					13		6	527		546
<i>Antennaria media</i>						0				0
<i>Antennaria microphylla</i>					52	301	906			1259
<i>Antennaria neglecta</i>		43	0	0	807	859	271 5	670	38	5132

<i>Antennaria racemosa</i>		705		0	976	7721	107 8	4808	948	1623 6
<i>Antennaria rosea</i>		36			549	1536	421 3	256	6	6596
<i>Antennaria umbrinella</i>	0	39						527		566
<i>Apocynum androsaemifolium</i>				340						340
<i>Aquilegia flavescens</i>								46	246	292
<i>Arabis drummondii</i>		0				20				20
<i>Arabis glabra</i>								91		91
<i>Arabis hirsuta</i>						6		8		14
<i>Arabis holboellii</i>	25	214		31	26	678	114			1088
<i>Arabis lemmonii</i>								263		263
<i>Arabis lyallii</i>		7		0						7
<i>Arabis microphylla</i>							6			6
<i>Arabis sp.</i>						0				0
<i>Arctostaphylos uva-ursi</i>					0	0				0
<i>Arenaria capillaris</i>		196		9		9	2			216
<i>Arenaria congesta</i>					1	50	0	748		799
<i>Arenaria sp.</i>		145		0						145
<i>Arnica chamissonis</i>							0	0		0
<i>Arnica cordifolia</i>	4979	862	123 93	763 4	703	341	131 4	524	144	2889 4
<i>Arnica latifolia</i>		24		23	97	14	68		61	287
<i>Arnica longifolia</i>	305	17	18	147	0		9	20		516
<i>Arnica</i>	571	452	370	120				40		1553

<i>lanceolata</i>										
<i>Clematis hirsutissima</i>	0									0
<i>Clematis occidentalis</i>					187	28	216	224	34	689
<i>Clintonia uniflora</i>									0	0
<i>Collinsia parviflora</i>	1017 2	158 78	0	230 9				4549		3290 8
<i>Collomia linearis</i>	1007 4	585 9	0	651	98	26	65			1677 3
<i>Collomia tinctoria</i>								4989		4989
<i>Corallorhiza maculata</i>									10	10
<i>Corallorhiza trifida</i>					3				0	3
<i>Cornus sericea</i>							231			231
<i>Corydalis aurea</i>	563	115 0	50	57						1820
<i>Crepis acuminata</i>								29		29
<i>Crepis atribarba</i>					30	420	58		1	509
<i>Crepis intermedia</i>	1293	130		7	0					1430
<i>Crepis modocensis</i>	50	0		35						85
<i>Crepis tectorum</i>	279	6	0	31	1	0		18		335
<i>Cynoglossum officinale</i>	0	0		35			0			35
<i>Delphinium barbeyi</i>							277	782		1059
<i>Delphinium bicolor</i>	97	55		293			793	350		1588
<i>Descurainia sophia</i>	2591	221		274						3086
<i>Dracocephalu m parviflorum</i>	970	315	196 2	263 7	0	0				5884
<i>Epilobium brachycarpum</i>	994	212 9	576	142	15	5	133			3994

<i>Epilobium ciliatum</i>	20	93	40	4			0			157
<i>Epilobium lactiflorum</i>								25		25
<i>Epilobium minutum</i>						0				0
<i>Erigeron acris</i>		0	4		211	15	55		2	287
<i>Erigeron caespitosus</i>		0		0						0
<i>Erigeron concinnus</i>									0	0
<i>Erigeron divergens</i>					2	0				2
<i>Erigeron glabellus</i>	4	96	4	72	20	1	26	879		1102
<i>Erigeron lonchophyllus</i>									4	4
<i>Erigeron ochroleucus</i>						0				0
<i>Erigeron peregrinus</i>		0			0	29	36			65
<i>Erigeron speciosus</i>	223	140	37	699	4	0	0			1103
<i>Erigeron ursinus</i>					3					3
<i>Eriogonum umbellatum</i>	0	0		19						19
<i>Erysimum asperum</i>	0	1	0	0			0	28		29
<i>Erysimum cheiranthoides</i>	9	407 4	2	230 5						6390
<i>Erysimum inconspicuum</i>							8			8
<i>Euphorbia esula</i>	30			12						42
<i>Eurybia conspicua</i>	2716	106	221 9	393	1282	944	675	104	0	8439
<i>Fragaria virginiana</i>	14	117	0	8	869	1120	141 5	1658	108 4	6285
<i>Fritillaria atropurpurea</i>						3		96		99
<i>Gaillardia aristata</i>	94	367		13						474

<i>Galium boreale</i>	3176	548		542	5422	1177 5	196 0	3793	125	2734 1
<i>Galium triflorum</i>		37		48	16		245	1950	5	2301
<i>Gaura coccinea</i>				0						0
<i>Gayophytum spp.</i>						0				0
<i>Gentianella tenella</i>							12		0	12
<i>Geranium carolinianum</i>	1116	122 9	422 5	112 7						7697
<i>Geranium richardsonii</i>	23	69			1	46	590	130	308	1167
<i>Geranium viscosissimum</i>	959	984	0	695		136	1	244	10	3029
<i>Geum aleppicum</i>						3	9			12
<i>Geum macrophyllum</i>							184	1		185
<i>Geum triflorum</i>		13		23						36
<i>Goodyera oblongifolia</i>						1				1
<i>Hackelia floribunda</i>	294	167 8		468			3	6249		8692
<i>Hedysarum sulphurescens</i>	2	3			1421 4	1546 9	326		0	3001 4
<i>Helianthella uniflora</i>	7		17	30						54
<i>Heracleum maximum</i>							131	460		591
<i>Heracleum sp.</i>							0			0
<i>Heterotheca villosa</i>		0	0	28	0	0				28
<i>Heuchera cylindrica</i>					455	0	0	105		560
<i>Heuchera parviflora</i>								271		271
<i>Hieracium albiflorum</i>	30	15	3	38	718	3026	969	626	144	5569
<i>Hieracium aurantiacum</i>					0	207	39			246

<i>Hieracium cynoglossoides</i>	31									31
<i>Hieracium gracile</i>	2			4	1	5	0	77		89
<i>Hieracium scouleri</i>					0	1		365		366
<i>Hieracium umbellatum</i>	130				0	0	0		0	130
<i>Hydrophyllum capitatum</i>								1468		1468
<i>Lactuca serriola</i>								0		0
<i>Leptarrhena pyrolifolia</i>									0	0
<i>Lesquerella montana</i>						7				7
<i>Linaria dalmatica</i>							61			61
<i>Linaria vulgaris</i>			0	0						0
<i>Linnaea borealis</i>					386	750	445 9	3050	818 5	1683 0
<i>Linum lewisii</i>					10	0				10
<i>Listera cordata</i>					0			1271	497	1768
<i>Lithophragma parviflorum</i>	1704	120 7		46						2957
<i>Lithospermum ruderale</i>	3	33		344		5		0		385
<i>Lithospermum arvense</i>								139		139
<i>Lomatium dissectum</i>				1				50		51
<i>Lomatium ambiguum</i>		0		7						7
<i>Lonicera involucreta</i>					0				27	27
<i>Lonicera utahensis</i>					767	207	261	408	624	2267
<i>Lupinus argenteus</i>					7315	7717	614		0	1564 6
<i>Lupinus sericeus</i>	2006	256 4	0	201 1	3951	1105 2	578	2258 5	6	4475 3

<i>Mahonia repens</i>			61	4	237	966	167 7	3354	978	7277
<i>Maianthemum racemosum</i>	0	1	0	25	0	1	91	2075	1	2194
<i>Maianthemum stellatum</i>	0			51	0	1	87		32	171
<i>Medicago lupulina</i>						1	9		11	21
<i>Melilotus officinalis</i>				3	13	0				16
<i>Mertensia ciliata</i>	34	425		126						585
<i>Mertensia longiflora</i>						0	279	3708		3987
<i>Mertensia oblongifolia</i>							120			120
<i>Mimulus guttatus</i>							135			135
<i>Minuartia austromontana</i>		150		313						463
<i>Mitella pentandra</i>							0			0
<i>Mitella stauropetala</i>									1	1
<i>Mitella trifida</i>								195	14	209
<i>Moehringia lateriflora</i>		30				0		381		411
<i>Monarda fistulosa</i>			0	182 4						1824
<i>Moneses uniflora</i>									0	0
<i>Myosotis asiatica</i>							4	3909	0	3913
<i>Oreostemma alpigenum</i>						3				3
<i>Orthilia secunda</i>			2		0		5		33	40
<i>Osmorhiza berteroi</i>						0	2		98	100
<i>Osmorhiza depauperata</i>							0	296	47	343
<i>Oxytropis besseyi</i>							0			0

<i>sp.</i>										
<i>Ranunculus acriformis</i>							29	4		33
<i>Ranunculus uncinatus</i>					0		825	447		1272
<i>Ribes cereum</i>					15	0	477	420	225	1137
<i>Ribes hudsonianum</i>			0	450	17	0	20	53	200	740
<i>Ribes lacustre</i>							352	65	306	723
<i>Ribes laxiflorum</i>									5	5
<i>Rosa woodsii</i>	209	6	6	209	119	231	89	75	8	952
<i>Rubus idaeus</i>	9	0	12	14		0	236	42		313
<i>Rubus parviflorus</i>	24		96	46	6	0	53	179	26	430
<i>Sambucus nigra cerulea</i>							5			5
<i>Sambucus racemosa</i>			2	0	0		268	391	1	662
<i>Saxifraga spp.</i>			143	0					34	177
<i>Sedum lanceolatum</i>	25					0	162	2961	0	3148
<i>Sedum spp</i>							30			30
<i>Senecio integerrimus</i>								214		214
<i>Senecio serra</i>					356	27	15	1383	0	1781
<i>Senecio sp.</i>					76	360	67		0	503
<i>Senecio triangularis</i>						2	19		0	21
<i>Senecio lugens</i>								50		50
<i>Shepherdia canadensis</i>					0	0			109	109
<i>Silene latifolia</i>	1285	889		974	4	3	0	258		3413

<i>Silene menziesii</i>								1553		1553
<i>Sisymbrium altissimum</i>	201	334 4	0	574						4119
<i>Solidago canadensis</i>	2	0	3	170	27	17	705		120	1044
<i>Solidago gigantea</i>					5	238				243
<i>Solidago missouriensis</i>	128	0	19	5	0	0	80	787	4	1023
<i>Solidago multiradiata</i>	0	6	5	164	27	2	214		216	634
<i>Solidago simplex</i>						6		30		36
<i>Sonchus arvensis</i>	120	160 7	0	34						1761
<i>Sonchus asper</i>	526	168 9	55	27						2297
<i>Sonchus oleraceus</i>	70	1	25	303						399
<i>Sorbus scopulina</i>						0				0
<i>Sphaeralcea coccinea</i>							0			0
<i>Spiraea betulifolia</i>	2121	953	559 7	371 3	4147	3546	300 3	1381 6	317	3721 3
<i>Stellaria longipes</i>	0	69	0	10		416	1			496
<i>Stellaria media</i>	102	524	0	30						656
<i>Streptopus amplexifolius</i>									2	2
<i>Symphoricarpos albus</i>	1816 4	213 5	851	133 30	144	518	142 0	1347 1	0	5003 3
<i>Symphoricarpos ascendens</i>						3				3
<i>Symphoricarpos ericoides</i>						0				0
<i>Symphoricarpos foliaceum</i>	51	0	12	86		23	0	0		172

<i>Zigadenus elegans</i>									4	4
<i>Zigadenus venenosus</i>	17	65		13						95
<i>Total</i>	1027 13	790 35	417 23	707 92	1114 70	1429 70	863 32	1893 57	216 02	8459 94

Appendix A3: Bumblebees used for nutritional analyses with their location of collection (EM = Emigrant, PC = Pine Creek, WC = Wicked Creek, “HIGH” and “MIX” refer to local burn severity), species, percent nitrogen, percent carbon, total bee mass, and the mass of the subsample used for combustion.

Site	Species	%N	%C	Bee Mass (mg)	Combusted Sample Mass (mg)
EMHIGH	<i>B. bifarius</i>	9.87	47.29	38.10	4.58
EMHIGH	<i>B. bifarius</i>	7.54	45.13	63.30	6.86
EMHIGH	<i>B. bifarius</i>	11.04	47.98	31.70	4.45
EMHIGH	<i>B. bifarius</i>	8.15	45.18	45.20	5.27
EMHIGH	<i>B. bifarius</i>	10.97	48.36	37.30	5.02
EMHIGH	<i>B. bifarius</i>	9.25	47.01	38.10	4.21
EMHIGH	<i>B. bifarius</i>	8.68	46.72	42.30	5.89
EMHIGH	<i>B. bifarius</i>	10.38	47.76	35.40	5.57
EMHIGH	<i>B. huntii</i>	9.98	48.14	38.70	5.71
EMHIGH	<i>B. bifarius</i>	10.94	47.49	36.60	4.73
EMHIGH	<i>B. bifarius</i>	8.16	45.91	52.80	5.05
EMHIGH	<i>B. bifarius</i>	7.54	45.74	65.20	6.31
EMHIGH	<i>B. bifarius</i>	10.78	48.30	28.20	4.27
EMHIGH	<i>B. mixtus</i>	11.55	48.10	30.20	4.83
EMHIGH	<i>B. mixtus</i>	9.46	46.82	38.20	4.96
EMHIGH	<i>B. bifarius</i>	11.63	48.22	23.10	4.72
EMHIGH	<i>B. bifarius</i>	11.42	48.90	28.70	4.46
EMHIGH	<i>B. rufocinctus</i>	10.03	46.93	37.10	5.72
EMHIGH	<i>B. bifarius</i>	10.62	47.67	39.40	4.34
EMMIX	<i>B. mixtus</i>	11.51	50.79	23.60	5.66
EMMIX	<i>B. mixtus</i>	11.19	47.97	37.90	4.66
EMMIX	<i>B. bifarius</i>	11.35	49.80	30.50	3.79
EMMIX	<i>B. bifarius</i>	7.59	44.96	53.70	5.68
EMMIX	<i>B. bifarius</i>	10.08	47.40	24.30	5.07
EMMIX	<i>B. bifarius</i>	8.25	46.36	35.80	6.23
EMMIX	<i>B. bifarius</i>	10.93	48.04	27.30	5.05
EMMIX	<i>B. mixtus</i>	11.19	47.86	31.80	4.39
EMMIX	<i>B. rufocinctus</i>	11.95	47.80	33.30	4.64
EMMIX	<i>B. mixtus</i>	11.46	47.72	40.80	4.58
EMMIX	<i>B. mixtus</i>	10.57	47.68	40.70	5.87
EMMIX	<i>B. bifarius</i>	10.61	48.00	39.40	4.32
EMMIX	<i>B. bifarius</i>	10.44	47.80	36.30	4.34
EMMIX	<i>B. bifarius</i>	11.83	47.91	31.60	4.33
EMMIX	<i>B. centralis</i>	12.16	50.57	32.40	5.15
PCHIGH	<i>B. bifarius</i>	9.28	46.91	40.30	3.84

PCHIGH	<i>B. bifarius</i>	8.25	46.43	64.80	7.00
PCHIGH	<i>B. bifarius</i>	10.80	48.17	29.20	4.85
PCHIGH	<i>B. occidentalis</i>	11.37	48.35	24.20	4.40
PCHIGH	<i>B. bifarius</i>	10.16	48.23	52.50	8.43
PCHIGH	<i>B. centralis</i>	9.26	48.38	41.10	4.81
PCHIGH	<i>B. occidentalis</i>	8.45	46.21	88.80	7.31
PCHIGH	<i>B. bifarius</i>	10.28	47.57	53.00	5.09
PCHIGH	<i>B. bifarius</i>	11.24	47.80	31.30	4.02
PCHIGH	<i>B. centralis</i>	11.77	50.99	32.60	5.43
PCHIGH	<i>B. bifarius</i>	12.19	49.83	22.30	4.90
PCMIX	<i>B. rufocinctus</i>	11.30	47.70	41.90	4.41
PCMIX	<i>B. bifarius</i>	11.58	47.85	30.30	4.37
PCMIX	<i>B. mixtus</i>	12.08	48.69	29.80	4.24
PCMIX	<i>B. centralis</i>	11.97	53.10	34.00	5.53
PCMIX	<i>B. bifarius</i>	7.61	49.35	34.20	6.25
PCMIX	<i>B. bifarius</i>	11.48	48.45	27.80	4.40
PCMIX	<i>B. rufocinctus</i>	11.43	48.38	35.90	5.08
WCHIGH	<i>B. bifarius</i>	12.25	49.31	27.60	4.71
WCHIGH	<i>B. bifarius</i>	12.27	49.82	26.70	5.40
WCHIGH	<i>B. bifarius</i>	10.86	48.60	42.00	5.19
WCHIGH	<i>B. bifarius</i>	11.92	48.92	30.80	5.49
WCHIGH	<i>B. bifarius</i>	11.32	49.53	43.80	5.09
WCHIGH	<i>B. bifarius</i>	12.17	49.94	27.10	4.37
WCHIGH	<i>B. mixtus</i>	12.13	48.70	58.10	4.58
WCHIGH	<i>B. bifarius</i>	12.16	49.12	31.20	5.29
WCHIGH	<i>B. bifarius</i>	12.22	49.69	31.20	4.86
WCMIX	<i>B. bifarius</i>	11.86	49.40	29.20	4.68
WCMIX	<i>B. bifarius</i>	10.89	49.60	31.00	5.65
WCMIX	<i>B. bifarius</i>	6.97	45.07	28.90	5.35
WCMIX	<i>B. bifarius</i>	11.73	50.63	24.80	4.93
WCMIX	<i>B. bifarius</i>	12.08	49.26	26.40	5.03
WCMIX	<i>B. bifarius</i>	12.30	49.08	26.50	4.65
WCMIX	<i>B. bifarius</i>	12.52	49.21	18.00	4.81
WCMIX	<i>B. bifarius</i>	12.28	49.39	38.80	4.77
WCMIX	<i>B. bifarius</i>	12.34	49.40	29.40	4.69
WCMIX	<i>B. bifarius</i>	12.15	48.82	30.20	5.56
WCMIX	<i>B. bifarius</i>	12.25	49.22	27.50	3.59
WCMIX	<i>B. bifarius</i>	11.68	49.87	27.60	4.69

Appendix A4: Bees used for nutritional analysis with the flower species from which they were hand netted, the floral pollen percent nitrogen of that species, the percent nitrogen of that bee's corbicular pollen, the percent carbon of that bee's corbicular pollen, and the total corbicular pollen mass used for analysis.

Site	Species	Visited Flower	Floral Pollen %N	Corbicular Pollen		
				% N	%C	Mass (mg)
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.39	45.49	3.73
EM HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.19	45.69	1.57
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.71	45.46	5.45
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.77	46.67	1.88
EM HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.32	44.34	2.55
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.33	43.64	2.25
EM HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.23	41.43	1.65
EM HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.87	43.71	0.83
EM HIGH	<i>B. huntii</i>	<i>Symphoricarpos albus</i>	1.57	2.58	46.19	7.88
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.47	46.99	0.97
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	2.95	44.62	4.97
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.03	45.66	4.32
EM HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	5.18	47.98	3.84
EM HIGH	<i>B. mixtus</i>	<i>Symphoricarpos albus</i>	1.57	3.10	45.85	1.54
EM HIGH	<i>B. mixtus</i>	<i>Symphoricarpos albus</i>	1.57	3.79	46.84	4.86
EM HIGH	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	3.70	47.12	3.39
EM HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.80	47.99	2.64

EM HIGH	<i>B. rufocinctus</i>	<i>Chamerion angustifolium</i>	1.84	3.9 7	46.3 8	1.81
EM HIGH	<i>B. bifarius</i>	<i>Phacelia hastata</i>	NA	3.9 3	47.1 8	4.61
EM MIX	<i>B. mixtus</i>	<i>Eurybia conspicua</i>	NA	4.2 1	48.4 6	2.26
EM MIX	<i>B. mixtus</i>	<i>Spiraea betulifolia</i>	1.07	3.9 7	47.1 2	4.64
EM MIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	5.6 7	49.0 1	1.14
EM MIX	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	3.2 6	46.3 0	6.26
EM MIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.7 7	47.8 5	4.10
EM MIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.7 8	47.6 2	5.09
EM MIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	4.2 3	47.8 8	5.04
EM MIX	<i>B. mixtus</i>	<i>Spiraea betulifolia</i>	1.07	4.5 7	47.8 9	1.33
EM MIX	<i>B. rufocinctus</i>	<i>Campanula rotundifolia</i>	2.97	5.9 4	45.8 0	0.37
EM MIX	<i>B. mixtus</i>	<i>Lupinus sericeus</i>	4.98	5.3 1	48.5 9	1.02
EM MIX	<i>B. mixtus</i>	<i>Spiraea betulifolia</i>	1.07	4.1 9	47.3 3	2.82
EM MIX	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	4.3 4	47.6 8	5.08
EM MIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	4.3 3	46.6 7	6.31
EM MIX	<i>B. bifarius</i>	<i>Phacelia linearis</i>	4.24	4.7 0	48.0 9	0.81
EM MIX	<i>B. centralis</i>	<i>Lupinus sericeus</i>	4.98	6.2 3	47.7 8	1.39
PC HIGH	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	3.5 8	46.8 4	0.53
PC HIGH	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	3.7 9	47.1 2	2.66
PC HIGH	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	3.4 3	48.0 3	2.35
PC HIGH	<i>B. occidentalis</i>	<i>Chamerion angustifolium</i>	1.84	3.2 4	50.4 2	1.25
PC HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	4.3 4	46.6 9	1.16

PC HIGH	<i>B. centralis</i>	<i>Eurybia conspicua</i>	NA	3.1 1	45.9 0	1.80
PC HIGH	<i>B. occidentalis</i>	<i>Spiraea betulifolia</i>	1.07	4.0 9	47.0 0	4.40
PC HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	4.0 9	46.6 5	5.72
PC HIGH	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	6.2 6	45.7 8	0.33
PC HIGH	<i>B. centralis</i>	<i>Chamerion angustifolium</i>	1.84	4.2 8	47.6 6	2.10
PC HIGH	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	7.4 4	49.3 6	3.26
PC MIX	<i>B. rufocinctus</i>	<i>Campanula rotundifolia</i>	2.97	7.1 3	48.5 5	0.70
PC MIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	5.7 1	47.2 3	3.14
PC MIX	<i>B. mixtus</i>	<i>Rosa woodsii</i>	3.36	5.6 5	47.4 9	2.02
PC MIX	<i>B. centralis</i>	<i>Lupinus sericeus</i>	4.98	6.3 0	47.4 8	4.01
PC MIX	<i>B. bifarius</i>	<i>Symphoricarpos albus</i>	1.57	3.9 8	46.4 1	0.83
PC MIX	<i>B. bifarius</i>	<i>Geranium viscosissimum</i>	2.54	5.6 6	49.6 7	0.61
PC MIX	<i>B. rufocinctus</i>	<i>Campanula rotundifolia</i>	2.97	3.6 6	45.1 7	5.62
WC HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.7 4	46.7 7	2.05
WC HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	5.4 4	49.9 4	1.87
WC HIGH	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	5.2 4	47.9 5	6.05
WC HIGH	<i>B. bifarius</i>	<i>Hedysarum sulphurescens</i>	NA	4.9 9	37.2 5	4.40
WC HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.3 3	46.0 9	3.68
WC HIGH	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.7 6	46.7 2	3.50
WC HIGH	<i>B. mixtus</i>	<i>Lonicera utahensis</i>	NA	5.5 5	48.3 9	2.88
WCHIG H	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	3.7 2	45.1 3	3.34
WCHIG H	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	3.5 7	47.1 1	3.98

WCMIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	4.2 7	47.8 2	4.14
WCMIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	6.5 5	47.6 3	1.84
WCMIX	<i>B. bifarius</i>	<i>Chamerion angustifolium</i>	1.84	4.2 5	46.5 7	3.77
WCMIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	5.2 9	47.3 8	8.18
WCMIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	5.4 4	47.6 5	3.78
WCMIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	4.0 1	47.0 7	4.73
WCMIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	5.9 3	46.7 1	2.28
WCMIX	<i>B. bifarius</i>	<i>Trifolium repens</i>	NA	4.5 4	46.6 6	3.86
WCMIX	<i>B. bifarius</i>	<i>Hedysarum sulphurescens</i>	NA	6.0 8	47.6 0	3.41
WCMIX	<i>B. bifarius</i>	<i>Lupinus sericeus</i>	4.98	7.1 1	48.8 3	4.63
WCMIX	<i>B. bifarius</i>	<i>Trifolium repens</i>	NA	4.7 9	46.0 7	3.58
WCMIX	<i>B. bifarius</i>	<i>Spiraea betulifolia</i>	1.07	4.1 6	47.8 1	6.11

Appendix A5: Floral pollen samples used to determine available floral pollen quality. Species, percent nitrogen, percent carbon, nitrogen mass of sample, carbon mass of sample, and total pollen sample mass.

Species	% N	%C	N Mass (mg)	C Mass (mg)	Sample Mass (mg)
<i>Anaphalis margaritacea</i>	1.7 6	46.0 2	0.06	1.64	3.56
<i>Arnica cordifolia</i>	3.6 3	50.0 8	0.02	0.27	0.54
<i>Arnica mollis</i>	1.5 2	54.0 1	0.01	0.31	0.57
<i>Campanula rotundifolia</i>	2.9 7	50.0 4	0.18	2.44	2.59
<i>Carduus nutans</i>	3.7 8	51.4 2	0.08	1.30	4.75
<i>Cerastium arvense</i>	4.8 2	46.2 9	0.04	0.35	0.76
<i>Chamerion angustifolium</i>	1.8 4	49.1 4	0.09	2.37	4.83
<i>Cirsium arvense</i>	2.2 2	50.7 2	0.11	2.44	4.81
<i>Cirsium vulgare</i>	2.1 1	48.7 8	0.05	1.08	2.22
<i>Delphinium bicolor</i>	4.0 8	45.4 9	0.09	0.95	2.08
<i>Epilobium brachycarpum</i>	1.5 1	45.0 3	0.07	2.06	4.58
<i>Erigeron glabellus</i>	2.0 9	44.8 8	0.07	1.46	3.24
<i>Erigeron glabellus</i>	2.2 4	46.6 7	0.10	2.01	4.31
<i>Erigeron speciosus</i>	3.0 9	48.5 8	0.05	0.72	1.48
<i>Gaillardia aristata</i>	3.5 1	50.1 4	0.12	1.75	3.49
<i>Galium boreale</i>	3.2 0	50.9 1	0.13	2.09	4.10
<i>Geranium carolinianum</i>	3.2 4	43.4 4	0.04	0.55	1.27
<i>Geranium viscosissimum</i>	2.5 4	46.0 8	0.06	1.15	2.49
<i>Lupinus sericeus</i>	4.9 8	47.9 1	0.11	1.02	2.13

<i>Monarda fistulosa</i>	1.9 1	50.6 6	0.02	0.57	1.13
<i>Phacelia linearis</i>	4.2 4	49.1 6	0.04	0.44	0.88
<i>Physocarpus malvaceus</i>	1.4 8	46.9 3	0.08	2.36	5.03
<i>Potentilla diversifolia</i>	2.6 8	46.9 0	0.15	2.54	5.41
<i>Ribes hudsonianum</i>	4.1 0	46.8 6	0.05	0.52	1.11
<i>Rosa woodsii</i>	3.3 6	51.1 3	0.03	0.42	0.83
<i>Rubus parviflorus</i>	4.3 8	42.2 4	0.06	0.53	1.25
<i>Silene latifolia</i>	5.2 4	49.1 3	0.21	1.93	3.93
<i>Solidago multiradiata</i>	2.0 6	48.9 0	0.10	2.26	4.62
<i>Spiraea betulifolia</i>	1.0 7	47.8 9	0.01	0.46	0.95
<i>Symphoricarpos albus</i>	1.5 7	47.8 5	0.08	2.32	4.85
<i>Tragopogon dubius</i>	4.5 1	49.0 0	0.06	0.68	1.39

Appendix A6: Emerged nesting tubes by species, with tube size, fire locality (EM = Emigrant, PC = Pine Creek, WC = Wicked Creek, and TC = Thompson Creek), treatment (HI = high-severity, MX = mixed-severity), date of tube collect (Month-Day for 2016), and the number of bees which emerged from that tube.

Species	Tube Size (mm)	Fire	Treatment	Date	Number Emerged
<i>Ashmeadiella californica</i>	3	WC	MX	8-16	5
<i>Coelioxys moesta</i>	6	EM	MX	7-14	1
<i>Coelioxys moesta</i>	6	EM	MX	8-08	1
<i>Coelioxys moesta</i>	6	EM	MX	8-07	1
<i>Coelioxys moesta</i>	6	TC	HI	8-01	1
<i>Coelioxys moesta</i>	6	WC	HI	8-01	1
<i>Heriades carinatus</i>	3	PC	MX	8-11	1
<i>Hoplitis albifrons argentifrons</i>	5	EM	HI	7-20	1
<i>Hoplitis albifrons argentifrons</i>	6	EM	HI	8-12	1
<i>Hoplitis albifrons argentifrons</i>	5	EM	HI	7-12	3
<i>Hoplitis albifrons argentifrons</i>	4	EM	HI	7-28	5
<i>Hoplitis albifrons argentifrons</i>	5	EM	MX	7-21	1
<i>Hoplitis albifrons argentifrons</i>	6	EM	MX	7-14	1
<i>Hoplitis albifrons argentifrons</i>	5	EM	MX	7-14	2
<i>Hoplitis albifrons argentifrons</i>	5	PC	HI	8-13	2
<i>Hoplitis albifrons argentifrons</i>	5	PC	HI	7-26	3
<i>Hoplitis albifrons argentifrons</i>	5	PC	HI	7-26	3
<i>Hoplitis albifrons argentifrons</i>	4	PC	HI	8-03	2
<i>Hoplitis albifrons argentifrons</i>	5	PC	MX	6-27	4
<i>Hoplitis albifrons argentifrons</i>	5	PC	MX	8-11	1
<i>Hoplitis albifrons argentifrons</i>	6	PC	MX	8-11	3

<i>Hoplitis albifrons argentifrons</i>	5	PC	MX	8-11	4
<i>Hoplitis albifrons argentifrons</i>	5	TC	HI	8-15	2
<i>Hoplitis albifrons argentifrons</i>	5	TC	HI	8-01	1
<i>Hoplitis albifrons argentifrons</i>	6	TC	HI	8-01	2
<i>Hoplitis albifrons argentifrons</i>	4	TC	HI	8-15	1
<i>Hoplitis albifrons argentifrons</i>	5	TC	HI	8-01	3
<i>Hoplitis albifrons argentifrons</i>	4	TC	MX	7-08	2
<i>Hoplitis albifrons argentifrons</i>	4	WC	HI	8-01	1
<i>Hoplitis albifrons argentifrons</i>	4	WC	HI	8-01	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	8-16	1
<i>Hoplitis albifrons argentifrons</i>	4	WC	HI	8-01	3
<i>Hoplitis albifrons argentifrons</i>	4	WC	HI	8-01	2
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	8-01	2
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	8-01	3
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	8-01	4
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	7-07	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	7-07	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	HI	8-01	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	HI	7-07	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	HI	7-07	2
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	8-15	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	1

<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	7-07	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	7-07	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-15	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	7-07	2
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	7-07	2
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	7-07	3
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-15	3
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	7-07	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-01	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	7-07	2
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	2
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	8-01	3
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-01	3
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	4
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	6-30	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	1
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	6-30	2
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	6-30	2
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	6-30	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	6-30	1

<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-01	1
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	7-07	2
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	2
<i>Hoplitis albifrons argentifrons</i>	5	WC	MX	8-01	2
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	6-30	2
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-01	2
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	7-07	3
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	8-01	3
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	8-01	4
<i>Hoplitis albifrons argentifrons</i>	4	WC	MX	8-16	1
<i>Hoplitis albifrons argentifrons</i>	6	WC	MX	6-30	1
<i>Hoplitis fulgida fulgida</i>	4	TC	HI	8-01	6
<i>Hylaeus basalis</i>	3	EM	HI	8-12	9
<i>Hylaeus colorodensis</i>	3	EM	HI	8-12	1
<i>Hylaeus modestus</i>	3	EM	HI	8-12	2
<i>Hylaeus modestus</i>	4	EM	MX	8-12	11
<i>Hylaeus modestus</i>	4	PC	HI	7-26	1
<i>Hylaeus modestus</i>	3	PC	HI	7-26	2
<i>Hylaeus modestus</i>	3	PC	HI	7-26	2
<i>Hylaeus modestus</i>	3	TC	HI	8-15	7
<i>Hylaeus modestus</i>	3	TC	HI	7-08	2
<i>Hylaeus modestus</i>	3	WC	MX	8-15	5
<i>Hylaeus verticalis</i>	4	EM	HI	8-12	5
<i>Hylaeus verticalis</i>	3	EM	HI	7-13	12
<i>Hylaeus verticalis</i>	3	EM	MX	8-12	1
<i>Hylaeus verticalis</i>	3	TC	MX	8-15	7
<i>Hylaeus verticalis</i>	3	WC	MX	8-15	2
<i>Megachile centuncularis</i>	6	WC	HI	8-01	1
<i>Megachile lapponica</i>	6	EM	HI	8-12	1
<i>Megachile lapponica</i>	6	EM	HI	8-12	2
<i>Megachile lapponica</i>	6	EM	HI	8-12	1

<i>Megachile lapponica</i>	6	EM	HI	8-12	1
<i>Megachile lapponica</i>	6	EM	MX	7-14	3
<i>Megachile lapponica</i>	6	EM	MX	7-21	4
<i>Megachile lapponica</i>	6	EM	MX	8-12	5
<i>Megachile lapponica</i>	6	EM	MX	7-21	6
<i>Megachile lapponica</i>	6	EM	MX	7-21	6
<i>Megachile lapponica</i>	6	EM	MX	7-27	1
<i>Megachile lapponica</i>	5	EM	MX	8-12	3
<i>Megachile lapponica</i>	6	EM	MX	7-27	3
<i>Megachile lapponica</i>	6	EM	MX	8-08	3
<i>Megachile lapponica</i>	6	EM	MX	8-08	4
<i>Megachile lapponica</i>	6	EM	MX	7-20	8
<i>Megachile lapponica</i>	6	EM	MX	8-08	2
<i>Megachile lapponica</i>	6	EM	MX	8-08	2
<i>Megachile lapponica</i>	6	EM	MX	8-08	2
<i>Megachile lapponica</i>	6	EM	MX	8-07	1
<i>Megachile lapponica</i>	6	EM	MX	8-07	2
<i>Megachile lapponica</i>	6	EM	MX	7-21	3
<i>Megachile lapponica</i>	6	EM	MX	7-21	3
<i>Megachile lapponica</i>	6	EM	MX	7-21	3
<i>Megachile lapponica</i>	6	EM	MX	8-07	4
<i>Megachile lapponica</i>	6	EM	MX	7-27	9
<i>Megachile lapponica</i>	6	EM	MX	8-09	1
<i>Megachile lapponica</i>	6	EM	MX	7-14	2
<i>Megachile lapponica</i>	6	EM	MX	7-21	2
<i>Megachile lapponica</i>	6	EM	MX	8-09	3
<i>Megachile lapponica</i>	6	EM	MX	8-09	3
<i>Megachile lapponica</i>	6	EM	MX	7-14	4
<i>Megachile lapponica</i>	6	EM	MX	7-21	4
<i>Megachile lapponica</i>	6	EM	MX	7-21	4
<i>Megachile lapponica</i>	6	EM	MX	7-14	6
<i>Megachile lapponica</i>	6	EM	MX	7-21	6
<i>Megachile lapponica</i>	6	EM	MX	8-09	6
<i>Megachile lapponica</i>	5	EM	MX	7-27	7
<i>Megachile lapponica</i>	6	EM	MX	7-27	7
<i>Megachile lapponica</i>	6	EM	MX	7-27	8
<i>Megachile lapponica</i>	5	EM	MX	8-12	20
<i>Megachile lapponica</i>	6	EM	MX	8-12	2
<i>Megachile lapponica</i>	6	EM	MX	7-27	4
<i>Megachile lapponica</i>	6	EM	MX	7-27	4
<i>Megachile lapponica</i>	6	EM	MX	7-21	5

<i>Megachile lapponica</i>	6	PC	HI	7-18	1
<i>Megachile lapponica</i>	6	PC	HI	7-18	6
<i>Megachile lapponica</i>	6	PC	HI	7-18	6
<i>Megachile lapponica</i>	6	PC	HI	8-11	6
<i>Megachile lapponica</i>	6	PC	HI	7-26	1
<i>Megachile lapponica</i>	6	PC	HI	7-26	2
<i>Megachile lapponica</i>	6	PC	HI	7-26	3
<i>Megachile lapponica</i>	6	PC	HI	7-26	5
<i>Megachile lapponica</i>	6	PC	HI	8-03	1
<i>Megachile lapponica</i>	6	PC	HI	7-26	2
<i>Megachile lapponica</i>	6	PC	HI	7-26	3
<i>Megachile lapponica</i>	6	PC	HI	7-26	6
<i>Megachile lapponica</i>	6	PC	HI	8-11	1
<i>Megachile lapponica</i>	6	PC	HI	7-26	2
<i>Megachile lapponica</i>	6	PC	HI	7-26	5
<i>Megachile lapponica</i>	6	PC	HI	7-26	1
<i>Megachile lapponica</i>	6	PC	HI	8-03	2
<i>Megachile lapponica</i>	6	PC	MX	8-02	1
<i>Megachile lapponica</i>	5	PC	MX	7-19	1
<i>Megachile lapponica</i>	6	PC	MX	8-11	1
<i>Megachile lapponica</i>	6	PC	MX	8-02	2
<i>Megachile lapponica</i>	6	PC	MX	7-19	3
<i>Megachile lapponica</i>	6	PC	MX	8-02	4
<i>Megachile lapponica</i>	6	PC	MX	7-14	5
<i>Megachile lapponica</i>	6	PC	MX	7-19	6
<i>Megachile lapponica</i>	6	PC	MX	7-19	2
<i>Megachile lapponica</i>	6	PC	MX	7-19	3
<i>Megachile lapponica</i>	6	PC	MX	7-19	5
<i>Megachile lapponica</i>	6	PC	MX	8-11	3
<i>Megachile lapponica</i>	5	TC	HI	8-15	3
<i>Megachile lapponica</i>	6	TC	HI	8-01	3
<i>Megachile lapponica</i>	6	TC	HI	8-15	1
<i>Megachile lapponica</i>	6	TC	HI	8-01	4
<i>Megachile lapponica</i>	6	TC	HI	8-15	1
<i>Megachile lapponica</i>	6	TC	HI	8-01	3
<i>Megachile lapponica</i>	6	TC	HI	8-01	4
<i>Megachile lapponica</i>	6	TC	HI	8-11	7
<i>Megachile lapponica</i>	6	WC	HI	8-01	1
<i>Megachile lapponica</i>	5	WC	HI	8-01	2
<i>Megachile lapponica</i>	5	WC	HI	8-01	5
<i>Megachile lapponica</i>	6	WC	HI	8-01	8

<i>Megachile lapponica</i>	6	WC	HI	8-01	1
<i>Megachile lapponica</i>	6	WC	HI	8-01	1
<i>Megachile lapponica</i>	6	WC	HI	8-01	2
<i>Megachile lapponica</i>	4	WC	HI	8-15	1
<i>Megachile lapponica</i>	6	WC	HI	8-15	1
<i>Megachile lapponica</i>	6	WC	HI	8-01	2
<i>Megachile lapponica</i>	6	WC	HI	8-01	1
<i>Megachile lapponica</i>	6	WC	HI	8-01	1
<i>Megachile lapponica</i>	6	WC	HI	8-15	2
<i>Megachile lapponica</i>	6	WC	MX	8-15	1
<i>Megachile lapponica</i>	6	WC	MX	8-15	1
<i>Megachile lapponica</i>	6	WC	MX	8-15	3
<i>Megachile lapponica</i>	6	WC	MX	7-07	4
<i>Megachile lapponica</i>	6	WC	MX	8-01	4
<i>Megachile lapponica</i>	6	WC	MX	8-15	2
<i>Megachile lapponica</i>	5	WC	MX	8-01	3
<i>Megachile lapponica</i>	5	WC	MX	8-01	7
<i>Megachile lapponica</i>	6	WC	MX	8-15	1
<i>Megachile lapponica</i>	6	WC	MX	7-07	2
<i>Megachile lapponica</i>	6	WC	MX	7-07	3
<i>Megachile lapponica</i>	4	WC	MX	8-15	1
<i>Megachile lapponica</i>	6	WC	MX	8-15	1
<i>Megachile lapponica</i>	6	WC	MX	8-01	2
<i>Megachile lapponica</i>	6	WC	MX	8-01	2
<i>Megachile lapponica</i>	6	WC	MX	8-15	2
<i>Megachile lapponica</i>	6	WC	MX	8-01	4
<i>Megachile lapponica</i>	6	WC	MX	8-01	6
<i>Megachile lapponica</i>	5	WC	MX	8-15	7
<i>Megachile lapponica</i>	6	WC	MX	8-16	1
<i>Megachile lapponica</i>	6	WC	MX	8-16	2
<i>Megachile lapponica</i>	6	WC	MX	8-16	3
<i>Megachile lapponica</i>	6	WC	MX	8-01	2
<i>Megachile lapponica</i>	6	WC	MX	8-01	3
<i>Megachile lapponica</i>	4	WC	MX	8-16	4
<i>Megachile lapponica</i>	6	WC	MX	8-01	4
<i>Megachile lapponica</i>	6	WC	MX	8-01	4
<i>Megachile pugnata</i>	5	PC	HI	7-26	1
<i>Megachile relativa</i>	6	PC	HI	8-01	3
<i>Megachile relativa</i>	6	PC	HI	8-11	9
<i>Megachile relativa</i>	6	PC	MX	7-18	3
<i>Megachile relativa</i>	6	WC	HI	8-16	2

<i>Megachile relativa</i>	6	WC	HI	8-16	3
<i>Megachile relativa</i>	6	WC	HI	8-15	2
<i>Megachile relativa</i>	6	WC	MX	8-15	4
<i>Osmia juxta</i>	6	WC	HI	8-01	2
<i>Osmia juxta</i>	5	WC	HI	7-07	3
<i>Osmia juxta</i>	6	WC	HI	8-15	2
<i>Osmia lignaria propinqua</i>	6	EM	HI	8-12	1
<i>Osmia pusilla</i>	3	EM	MX	8-12	8
<i>Osmia spl</i>	4	PC	HI	7-26	1
<i>Stelis montana</i>	5	EM	HI	7-20	1
<i>Stelis montana</i>	6	PC	HI	8-11	1
<i>Stelis montana</i>	5	PC	HI	7-26	2
<i>Stelis montana</i>	5	TC	MX	8-01	1
<i>Stelis montana</i>	5	WC	HI	8-01	1
<i>Stelis montana</i>	4	WC	MX	8-01	1
<i>Stelis montana</i>	4	WC	MX	8-01	1
<i>Stelis montana</i>	5	WC	MX	8-01	1