THE INFLUENCE OF POST-WILDFIRE LOGGING ON FORB AND POLLINATOR COMMUNITIES AND FORB REPRODUCTIVE SUCCESS, GALLATIN NATIONAL FOREST, MONTANA

by

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DEDICATION

I dedicate this thesis to all of the science teachers I have had throughout my education. Thank you for your contagious excitement for science, for graciously sharing your knowledge, and for inspiring me to pursue a career in sharing my love of the natural world with future generations.

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ABSTRACT

Pollinators are in decline worldwide, and these declines have implications for flowering plants and their reproduction, given that 80% of flowering plants depend on insects for pollination. One potential contributor to pollinator species' declines is shifts in disturbance regimes, such as increased severity and frequency. Wildfires are essential natural disturbances that are important drivers of forest biodiversity in the western U.S., and there is often pressure to respond to wildfire with management including post-wildfire logging. This management strategy involves the removal of dead trees for economic value immediately following wildfire. Thus, is expected that post-wildfire logging has additional impacts on forest communities compared to non-salvage logging, and that it impacts forb and pollinator communities. Several studies have examined the short-term responses of forb and pollinator communities to wildfire and non-salvage logging individually, and one study examined their combined effects. However, no studies have examined the long-term effects of post-wildfire logging, on forb and pollinator communities and on forb reproduction. My research addresses these gaps in knowledge and asks: 1) how do floral and bee communities respond to post-wildfire logging and how do their responses differ between two different-aged fires, and 2) how does post-wildfire logging influence forb reproduction and pollen limitation of reproduction in an older wildfire? In the more recent fire, floral and bee density and species richness were higher in logged than unlogged areas. By contrast, in the older fire, forb and bee communities were similar between logged and unlogged areas. Unexpectedly, we found large inter- and intra-annual variation in the effects of post-wildfire logging. Lastly, in the older fire, there were no effects of post-wildfire logging on forb reproduction, but plants were pollen limited in unlogged areas. This suggests that plants in unlogged areas are able to augment their reproductive output with supplemental pollen resources, but plants in logged areas cannot. Together, these results suggest that post-wildfire logging is beneficial for forbs and pollinators in the short-term, and these positive effects depend on time of growing season and sampling year. However, post-wildfire logging may be detrimental for forb reproduction in the long-term.

INTRODUCTION

Disturbances play a key role in structuring terrestrial plant and animal communities worldwide and in driving spatial and temporal heterogeneity across multiple scales (Turner 2010). A disturbance is defined by White and Pickett (1985) as "any relatively discrete event that disrupts the structure of an ecosystem, community, or population, and changes resource availability or the physical environment". One of the greatest current threats to biodiversity and ecosystem services is unprecedented shifts in disturbance regimes (Turner 2010). According to the Intergovernmental Panel on Climate Change, it is expected that in response to climate change, natural disturbance events, such as wildfires, will become more severe and more frequent (IPCC 2013), which is likely to alter the land cover we see today.

Wildfires are essential natural disturbances that are important drivers of biodiversity in the forests of the western U.S. (Hansen *et al.* 1998) and are predicted to increase in intensity and frequency in the Greater Yellowstone Ecosystem (GYE) by the mid-21st century (Westerling *et al.* 2006; Morgan, Heyerdahl & Gibson 2008; Littell *et al.* 2009; Spracklen *et al.* 2009; Higuera, Whitlock & Gage 2010). The opening of the forest canopy by wildfire creates early successional habitat and can lead to increased plant productivity and plant diversity (Swanson *et al.* 2011). The long-term (11 + years post-wildfire) response of flowering plants to wildfire will be mediated by responses of pollinators and plant-pollinator interactions. Insect pollinators are essential for maintaining plant diversity in forest ecosystems (Kearns & Inouye 1997) as the majority (80%) of flowering plants depend on insects for pollination (Potts *et al.* 2010). Early successional habitats are essential for pollinator communities as they provide pollinators with important foraging and nesting resources (Potts *et al.* 2003a, 2005; Taki *et al.* 2013). Both flower and pollinator diversity increase in the short-term (0-10 years) after fire (Potts *et al.* 2003a; b; Grundel *et al.* 2010; Taki *et al.* 2013; Van Nuland *et al.* 2013).

In the Western U.S., there is often pressure to respond to increased wildfire frequency with management that includes post-wildfire logging (Lindenmayer, Burton & Franklin 2008; Congress 2013). Post-wildfire logging is a type of salvage logging that involves the removal of dead or dying trees for economic value specifically following wildfire disturbance (Lindenmayer *et al.* 2008). Post-wildfire logging may reduce fuels for future wildfires and advance regeneration in post-wildfire forests (Sessions *et al.* 2004). It also alters forest structural complexity, community composition, and ecosystem function by removing coarse woody debris, harvesting remaining biological legacies, and, harvesting trees at younger ages (Lindenmayer & Noss 2006).

These changes in land cover and land use in the GYE are expected to have major consequences for ecosystem functioning (Parmenter *et al.* 2003). Post-wildfire logging takes place immediately after wildfire during earlier successional stages unlike non-salvage logging (ex: clearcutting or forest thinning). Thus it is expected that post-wildfire logging will have effects on forest ecosystems additional to those of non-salvage logging including greater soil compaction and erosion, greater reductions in canopy cover, harvesting of larger sized stands of trees, and construction of more logging roads (McIver & Starr 2000; Morissette *et al.* 2002; Lindenmayer *et al.* 2008).

In light of these changes, it is important for ecologists to understand the long-term effects in addition to the short-term effects of increased human land use on biodiversity and ecosystem services (Turner 2010). Plants are key to stabilizing soils and reducing erosion in earlier successional stages. These short-term effects allow for the maintenance of soil resources that influence the future productivity of late-successional stages (Chapin III, Matson & Mooney 2002). It is important to evaluate the long-term effects of post-wildfire logging specifically because the combination of wildfire and post-wildfire logging may influence succession, and the long-term state of the forest ecosystem may impact the future fire regime of the logged region. For example, post-wildfire logging depletes, or at times eliminates, biological legacies. Biological legacies are organisms and organic structures that survive a disturbance event and can strongly influence the rate and pattern of succession through stabilization of ecosystem processes, providing habitat for some species, and modifying the environmental conditions (Franklin *et al.* 2000). It is thought that the abundance and spatial arrangement of biological legacies may be one of the key factors contributing to how succession differs across different disturbance severities (Turner, Donato & Romme 2013). Post-wildfire logging reduces the number of biological legacies more than wildfire naturally does, and this may lead to an altered process of succession (Lindenmayer *et al.* 2008). The results of this ecological alteration may not be observed until later on in successional time as different species are adapted to certain successional stages, and some species may be affected by the combination of wildfire and post-wildfire logging disturbances differently than others.

Furthermore, any changes in the process of succession may lead to differences in community structure at different successional times, which may have implications for natural fire regimes, relative to those the system has historically experienced. Surviving structures increase the structural complexity in post-disturbance ecosystems for decades to centuries beyond the short-term post-disturbance period. This structural complexity is important specifically for the recovery of forb and pollinator species (Ponisio *et al.* 2016). For example, biological legacies in the form of dead trees may provide increased diversity of micro-climates supporting a higher diversity of forbs (Franklin *et al.* 2000), as well as greater nesting habitat supporting a greater abundance and diversity of cavity-nesting pollinators (Harmon & Sexton 1996; Moretti *et al.* 2009; Williams *et al.* 2010; Mateos, Santos & Pujade-Villar 2011; Vázquez *et al.* 2011). Otherwise decades or centuries are required for these structures to develop.

The negative impact of post-wildfire logging on early successional forest habitat is also expected to impact forb and pollinator communities. Studies investigating the effects of non-salvage logging on forb and pollinator communities suggest that plants and pollinators respond similarly to logging as they do to wildfire; both plant and pollinator diversity increase immediately after logging (Romey *et al.* 2007; Pengelly & Cartar 2010; Jackson, Turner & Pearson 2014). In one study, pollinator richness was highest immediately following the combination of burning (prescribed fire) and logging (mechanical shrub removal) compared to burned only, logged only, and undisturbed (Campbell, Hanula & Waldrop 2007). However, short-term effects of fire or logging may be significantly different than the long-term effects (Siemann, Haarstad & Tilman 1997;

York 1999). For example, a small number of studies investigating the effects of time-since-fire or time-since-logging on plants and pollinators show flower richness and pollinator abundance and richness steadily decline with time (Potts *et al.* 2003a; b; Grundel *et al.* 2010; Dafni, Izhaki & Ne'eman 2012; Jackson *et al.* 2014). Though the responses of forb and pollinator communities to the combination of wildfire and post-wildfire logging may depend on time-since-fire, the long-term effects of post-wildfire logging on forb and pollinator communities are unknown.

An essential aspect of both short- and long-term post-wildfire forest recovery involves pollination and plant reproduction. Given that higher pollinator abundance has been associated with greater plant reproduction (Winfree *et al.* 2015), it is expected that the observed effects of post-wildfire logging on pollinator communities (Chapter 2) will subsequently influence plant reproduction. Plant reproduction is often limited by the receipt of pollen, and plants in disturbed areas may have lower reproduction than plants in undisturbed areas (Bierzychudek 1981; Galen 1985; Johnston 1991; Burd 1994; Parker 1997; Kearns, Inouye & Waser 1998; Ashman *et al.* 2004; Knight *et al.* 2005; Aizen & Harder 2007; Chen *et al.* 2016). In addition to being strongly influenced by the biotic conditions present (i.e., pollinator abundance and richness and pollen availability), plant reproduction is also driven by available abiotic resources (Burd 1994). As previously discussed, natural and anthropogenic disturbances can impact the biotic and abiotic resources necessary for plant growth and reproduction (Potts *et al.* 2003a).

As mentioned above, there has been a great deal of effort in studying the short-term response of forb and pollinator communities to wildfire and logging individually, and one study examining their combined effects. However, none of these studies have examined the long-term effects of post-wildfire logging in particular, on forb and pollinator communities and on forb reproduction. My research addressed these gaps in knowledge by focusing on the following questions: 1) how do floral and bee communities respond to post-wildfire logging, 2) how do the responses of floral and bee communities to post-wildfire logging differ between two different-aged fires, 3) How does post-wildfire logging influence forb reproduction in the long-term, and 4) How does post-wildfire logging influence pollen limitation of forb reproduction in the long-term?

The study area was located within the Greater Yellowstone Ecosystem (GYE) in the Gallatin National Forest near Pray, Montana (45°14'N, 110°33'W). While I was partially interested in testing the effect of time-since-fire on forb and bee communities and forb reproduction, I could not test this directly since that requires conducting a long-term study within one single wildfire, and this was not logistically feasible. Instead I selected two wildfires, the Wicked Creek fire and the Thompson Creek fire, that were similar to each other in every way logistically possible. These sites were located in adjacent watersheds, and likely experienced similar climatic conditions. They represented similar environmental conditions containing similar elevational, slope and aspect ranges. One way in which they differed was when they burned and when they were post-wildfire logged. The more recent fire, Wicked Creek, burned in 2007 and was logged in 2008. The older fire, Thompson Creek, burned in 1991 and was logged in 1993.

Within the two fire perimeters, in Chapter 2, I focused on addressing the first two questions by examining the influence of post-wildfire logging on floral and bee communities, how these effects varied across the growing season, between sampling years, and between two different aged fires. In Chapter 3, I addressed the third and fourth questions by examining the long-term effects of post-wildfire logging (using the older fire, Thompson Creek) on the reproductive success, and pollen limitation, of *Symphoricarpos albus* using a pollen supplementation experiment. *Symphoricarpos albus* is a widespread, fire adapted, and ecologically valuable shrub species common in post-wildfire vegetation communities of south-central Montana. *Symphoricarpos albus* also exhibits many characteristics that are advantageous for pollen supplementation experiments. I chose to address these questions in the older fire to assess the extent of any long-term effects of post-wildfire logging on forb reproduction, regardless of differences in forb or bee communities (addressed in Chapter 2).

My study area was located within a montane mixed conifer forests (elevation: 1,912.63 m-2,244.24 m). This area of south-central Montana is characterized by medium productivity and medium environmental moisture levels with mixed severity fires occurring every 35-200 years (Montana Field Guide 2010; U.S. Department of Agriculture, Forest Service & Missoula Fire Sciences Laboratory 2012). The biophysical conditions present within my study area are unique to montane mixed conifer forests and these conditions are important drivers of fire activity (severity and frequency) (Mcwethy *et al.* 2013). Areas at the productivity and environmental moisture extremes experience fire activity that is limited by sparse fuel loads or by high fuel moisture (Mcwethy *et al.* 2013). For example, temperate rain forest ecosystems such as those of the Pacific Northwest of the United States, are characterized by high productivity and moisture levels. These ecosystems experience low fire frequency as fuel moisture restricts the spread of fire. On the other hand, desert ecosystems such as those in the southwestern United States, are characterized by low productivity and moisture levels. They are limited by sparse fuels and experience infrequent, low severity fires (Mcwethy *et al.* 2013). While my study took place in an ecosystem in between these two productivity and moisture extremes, I can use the results from my study and what is known about the biophysical conditions and fire regimes of other ecosystems to predict how post-wildfire logging will impact forbs, pollinators and pollination services in other ecosystems.

To my knowledge, this is the first study to elucidate the long-term impacts of post-wildfire logging on native forb and pollinator communities and plant reproduction. Overall, addressing these gaps in knowledge will provide ecologically relevant information on how post-wildfire logging affects forb and pollinator communities, the extent of pollen limitation as a potential mechanism contributing to these observed effects on forbs, and insight into how post-wildfire forests can be managed to protect biodiversity of western U.S. forests.

THE EFFECTS OF POST-WILDFIRE LOGGING ON FORB AND POLLINATOR COMMUNITIES

Introduction

Wildfires are key drivers of biodiversity in forest ecosystems of the Western U.S. (Hansen *et al.* 1998). By opening up the forest canopy and creating early successional habitat, wildfires can lead to increased plant productivity and play a key role in structuring forest vegetative and animal communities (Swanson *et al.* 2011). In particular, because early successional habitats are beneficial for pollinator communities (Taki *et al.* 2013), wildfires may strongly influence pollinator nesting and foraging habitat, but these effects are not well understood.

Pollinator community structure is driven by foraging and nesting resources. Pollinators' main foraging resources include pollen and nectar. Floral communities are thought to be the primary driver of pollinator community structure (Potts *et al.* 2003a). Floral community characteristics such as floral diversity (Tepedino & Stanton 1981), floral patch size (Jha & Kremen 2013), and reward structure (pollen and nectar quantity and quality) (Potts *et al.* 2003a) are all important in structuring pollinator communities.

The required nesting resources vary between ground-nesting and cavity-nesting pollinators. For ground-nesting pollinators, important nesting resources include bare ground and pre-existing burrows (Potts *et al.* 2005). For cavity-nesting pollinators, resources include woody debris (Harmon & Sexton 1996; Moretti *et al.* 2009; Williams *et al.* 2010; Mateos *et al.* 2011; Vázquez *et al.* 2011), abandoned beetle galleries, and hollow stems (Potts *et al.* 2005). Numerous studies have investigated the importance of various nesting habitat characteristics and found the following to be important: soil texture (Cane 2016), soil compaction (Potts & Willmer 1997), soil moisture (Wuellner 1999), cavity shape and size (Schmidt & Thoenes 1992), and aspect and slope (Potts & Willmer 1997).

Pollinators are essential for maintaining plant diversity in forest ecosystems (Kearns & Inouye 1997), and it is expected that the long-term responses of flowering plants to wildfire will be partially mediated by the responses of pollinators and plant-pollinator interactions. Several studies have examined the short-term effects of fire on forb and pollinator communities, showing that both flower and pollinator diversity increase immediately after fire (Potts *et al.* 2003a; b; Grundel *et al.* 2010; Taki *et al.* 2013).

A common post-wildfire management practice is a type of salvage logging called post-wildfire logging, i.e. "the removal of dead trees or trees damaged or dying because of injurious agents (Lindenmayer *et al.* 2008)" specifically following wildfire disturbance. Post-wildfire logging is thought to aid in reducing fuels for subsequent fires and in stimulating regeneration in post-wildfire systems (Sessions *et al.* 2004). Post-wildfire logging also results in altered forest structural complexity, community composition, and ecosystem processes and functions (Lindenmayer & Noss 2006). Because it takes place during earlier successional stages compared to non-salvage logging, salvage logging in general has additional effects on forest ecosystems including greater soil compaction, increased erosion, greater reductions in canopy cover, harvesting of larger sized blocks of trees, harvesting trees at younger ages, and construction of more logging roads (McIver & Starr 2000, Morissette *et al.* 2002; Lindenmayer *et al.* 2008).

Since post-wildfire logging alters the conditions created by fire and significantly impacts early successional forest habitat (Swanson *et al.* 2011), post-wildfire logging could consequently influence forb and pollinator communities, and thus forest ecosystem functioning. The few studies that have investigated the effects of logging on forb and pollinator communities have focused on clearcutting and forest thinning, and have found patterns similar to those created by wildfire; both flower and pollinator diversity increase in the short-term after logging (between 2 and 9 years after logging) (Romey *et al.* 2007; Pengelly & Cartar 2010; Jackson, Turner & Pearson 2014). In addition, Campbell *et al.* (2007) considered the combined effects of fire (prescribed fire) and logging (mechanical shrub removal) on pollinator communities. They found that one to two years after disturbance, pollinator abundance and richness were highest in areas with both the shrub removal and experimental burn treatments relative to areas that were only burned, where only shrubs were removed, or were undisturbed (Campbell *et al.* 2007).

Importantly, ecological changes that occur in the short-term after fire or logging may be notably different than long-term changes that persist a number of years after the disturbance (Siemann *et al.* 1997; York 1999). All of the previously mentioned studies examined the short-term responses of forb or pollinator communities to fire and logging. The few studies examining the long-term responses of forb and pollinator communities to wildfire or logging have shown that flower richness and pollinator abundance and richness steadily decline with time-since-disturbance (Potts *et al.* 2003a; b; Grundel *et al.*

2010; Dafni *et al.* 2012; Jackson *et al.* 2014). Despite the potential additional impacts of wildfire and post-wildfire logging combined, and that these impacts may depend on time-since-wildfire, the long-term effects of post-wildfire logging on forb and pollinator communities are unknown.

In this study, I investigated the long-term influences of post-wildfire logging on floral and bee communities in the Gallatin National Forest, Montana, USA by comparing two adjacent, different-aged wildfires, Thompson Creek and Wicked Creek. The Thompson Creek wildfire occurred in 1991 and was post-wildfire logged in 1993 and 1995 (i.e., 23-24 years post-fire); the Wicked Creek wildfire burned in 2007 and was logged in 2008 (i.e., 7-8 years post-fire).

Within these two wildfires, I compared post-wildfire logged areas to unlogged areas and addressed the following questions: 1) how do floral and bee communities respond to post-wildfire logging, and 2) how do these community responses to post-wildfire logging differ between a more recent fire and an older fire? I also investigated inter-annual variability, intra-annual variability and their interactions on floral and bee communities. For my first question, I hypothesized that floral and bee density and species richness would be higher in post-wildfire logged areas as previous studies have shown that non-salvage logging opens up the canopy and increases sunlight availability, which have been shown to be beneficial for plant and bee habitat (Swanson *et al.* 2011; Taki *et al.* 2013). For my second question, I expected floral and bee density and species richness to be higher in the short-term (represented by Wicked Creek) compared to the long-term (represented by Thompson Creek) due to less canopy cover in the more recent wildfire (Taki *et al.* 2013).

To my knowledge, this research is the first to elucidate the long-term impacts of post-wildfire logging on native forb and pollinator communities. Overall, addressing this gap in knowledge will provide ecologically relevant information on how post-wildfire forests can be managed if plant and pollinator biodiversity is considered as a management goal.

Methods

Study Sites and Experimental Design

To quantify the effect of post-wildfire logging on forb and pollinator communities, I selected two wildfires that were similar to each other in every way logistically possible in that they were located in adjacent watersheds, and they were characterized by similar elevational, slope and aspect ranges. This allowed me to compare forb and pollinator communities between these two fires as a space-for time substitution for the effect of time-since-fire. This study was conducted in the Gallatin National Forest near Pray, Montana, USA (45°14’N, 110°33’W). Within the perimeters of the Thompson Creek (burned in 1991) and Wicked Creek (burned in 2007) wildfires, I selected two 15-hectare stands that were post-wildfire logged and two 15-hectare stands that were unlogged. Within each stand, I established nine sites that were randomly selected using a stratified design from the GRTS package in R (R Core Development Team 2013), for a total of 72 sites.

Quantification of Site Characteristics

I quantified coarse woody debris (CWD; downed trees > 5 cm in diameter) volume at each site because of its known ecological importance. For example, CWD is decreased by logging (Hopkins, Larson & Belote 2014), suppresses forb habitat (Tinker & Knight 2000; Vázquez *et al.* 2011), is an important nesting resource for cavity-nesting bees (Harmon & Sexton 1996; Moretti *et al.* 2009; Williams *et al.* 2010; Mateos *et al.* 2011; Vázquez *et al.* 2011), and it is important for long-term ecosystem nutrient cycling by affecting soil structure and providing organic matter inputs to forest ecosystems (Tinker & Knight 2000).To quantify CWD volume, along a 25 m transect at each site, I identified the species of, measured the diameter of, and recorded the decay classification of CWD (Lutes & Keane 2006). CWD was calculated using the formula from Harmon and Sexton (1996): $V = 9.869 * (\sum d^2)/8L$, where d is the piece diameter in cm, L is the length of the transect in meters, and V is CWD volume in m3/ha. I also used ArcGIS 10 to extract elevation, slope and aspect for each site. I included these site characteristics to account for any variability in environmental conditions between sites. However, none of these characteristics were included in our model set as none of them were statistically significant ($P > 0.05$ in all cases) predictors of floral density, floral species richness, bee density, or bee species richness.

Plant Sampling

Throughout the 2014 and 2015 growing seasons (1 June through 21 August), I visited each site once per week. During each site visit, I quantified the floral community by recording the density of open flowers of each species along a 25m X 2m band transect that was aligned to the center of the plot, perpendicular to the slope of the site.

Pollinator Sampling

During each site visit, I quantified the density of pollinators (# bees/20min./625 m^2) by hand-netting pollinators within a 25 m diameter circular plot centered on each site, for a total of 20 minutes. I considered pollinators to be any insect floral visitor that was observed flying from flower to flower and contacting the reproductive parts of the flowers. The pollinator communities of each plot were sampled for approximately 3 hours and 40 minutes over each growing season, with a total sampling time of 264 hours across all plots. The pollinators were collected individually in vials, immediately put on ice, and identified to species later in the lab.

Statistical Analyses

In order to assess the effects of post-wildfire logging on forb and pollinator communities, I used generalized linear mixed effects models (GLMMs) to analyze floral density and species richness and bee density and species richness all separately as response variables since these metrics were all correlated with one another ($R^2 > 0.3$). I assessed the effect of post-wildfire logging on these metrics and how these metrics varied between two different-aged fires, Wicked Creek (the more recent fire) and Thompson Creek (the older fire). I also assessed how these community metrics varied with CWD volume, over the course of the growing season, and between sampling years. Fixed factors included post-wildfire logging (presence or absence), fire ID (Thompson Creek or

Wicked Creek), CWD volume (CWD), Julian day (representing first day of each sampling week throughout summer growing season- 1 June through 21 August), sampling year (2014 and 2015). I also included two-way interactions between fire ID and post-wildfire logging, fire ID and CWD volume, and post-wildfire logging and CWD volume in order to address my original questions. I accounted for repeated measures within and across two sampling years by including Julian day and sampling year as fixed effects. Random factors included site nested with stand. A Poisson distribution was used for all response variables as they were all counts bounded at 0. I included CWD as an explanatory variable in the GLMMs due to its potential importance in structuring plant and insect communities. All analyses were performed in R 3.1.3 (R Core Development Team 2015). Mixed effects models were analyzed using the R package lme4 (Bates *et al.* 2015). Due to the contentious nature of using p-values and hypothesis testing with GLMMs, I decided to use F-values to make inference on overall main and interaction parameters.

To determine the best-supported models for my data predicting forb and pollinator communities, I used Akaike's Information Criteria (AIC) model selection. The top models for floral and bee density and species richness did not explain expected variation in the effects of logging and differences between the more recent fire and the older fire. Thus, I investigated these relationships further and included three-way interactions (fire ID x post-wildfire logging x Julian day, and fire ID x post-wildfire logging x CWD volume) in AIC model selection to determine the new best-supported model for my data. Using the top models for flower density and species richness and for pollinator density and species richness, I used the lsmeans R package for a post-hoc assessment of multiple comparison of means, and I based all significant differences in means on non-overlapping confidence intervals (Lenth 2016).

I used the adonis function (Oksanen 2015) to examine whether differences in floral and bee communities between logged and unlogged areas were driven by differences in community composition. I did this in the more recent fire only, where significant differences between logged and unlogged floral and bee communities were observed.

Results

Floral Density and Species Richness

Over 264 hours of observation, I sampled 3054 pollinator specimens of 201 species visiting 125 forb species. I also counted a total of 739,250 flowers representing 236 species.

Post-Wildfire Logging and Fire ID. Contrary to my hypotheses, there were no significant effects of post-wildfire logging or differences between the older fire and the more recent fire in mean floral density or mean floral species richness (Tables 1 & 2). However, as expected, the effects of logging on floral density and species richness depended on fire ID (i.e., logging by fire ID interaction) (Fig. 1 & 2). Floral density was 28% lower in logged than unlogged areas in the older fire (Thompson Creek), whereas it was 39% greater in logged than unlogged areas in the newer fire (Wicked Creek). There was no difference in floral species richness between logged and unlogged areas in the older fire, however, floral species richness was 23% higher in logged areas than in unlogged areas in the newer fire.

Table 1. Summary table for final model of floral density

	Df	SumSq	MeanSq	Fvalue
YEAR	1	3	3.20	3.16
logging	1	6	5.90	5.86
FIRE	1	3	3.10	3.10
Julian Day	11	89475	8134.10	8134.09
log.cwdv	1	6	6.30	6.27
YEAR × logging	1	118	117.60	117.57
YEAR × FIRE	1	1773	1773.20	1773.16
YEAR × Julian Day	10	22005	2200.50	2200.46
FIRE × Julian Day	10	6079	607.90	607.90
logging × Julian Day	11	17272	1570.20	1570.17
logging × FIRE	1	3	2.60	2.59
FIRE × log.cwdv	1	0	0.00	0.01
logging × log.cwdv	1	1	1.00	0.97
logging × FIRE × Julian Day	10	2702	270.20	270.20
logging × FIRE × log.cwdv	1	1	0.80	0.83

Table 2. Summary table for final model of floral species richness

	Df	SumSq	MeanSq	Fvalue
YEAR	1	0.51	0.51	0.51
logging	1	12.44	12.44	12.44
FIRE	1	0.40	0.40	0.40
Julian Day	11	293.03	26.64	26.64
log.cwdv	1	0.40	0.40	0.40
YEAR × logging	1	57.85	57.85	57.85
YEAR × FIRE	1	124.05	124.05	124.05
YEAR × Julian Day	10	45.79	4.58	4.58
FIRE × Julian Day	10	45.70	4.57	4.57
logging × Julian Day	11	8.32	0.76	0.76
logging × FIRE	1	2.08	2.08	2.08
FIRE × log.cwdv	1	0.54	0.54	0.54
logging × log.cwdv	1	0.59	0.59	0.59
logging × FIRE × Julian Day	10	29.47	2.95	2.95
logging × FIRE × log.cwdv	1	1.47	1.45	1.47

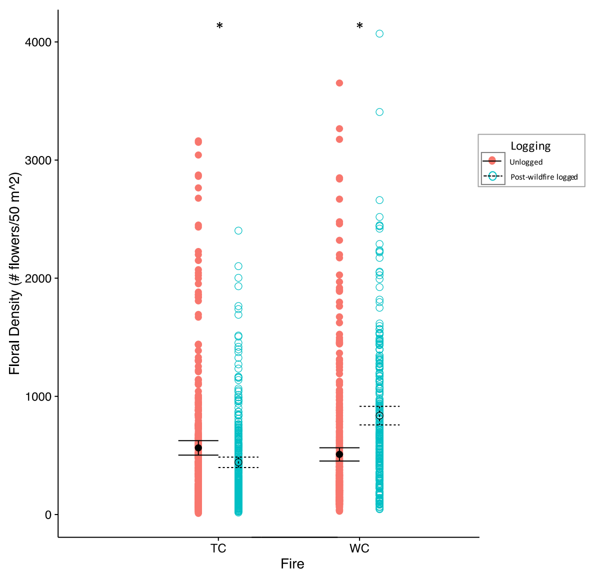

Figure 1. Significant differences in mean floral density between post-wildfire logged (blue) and unlogged (red) areas in Thompson Creek (older fire; TC) and Wicked Creek (newer fire; WC) are indicated by asterisks. The colored circles are site-specific floral density predictions from the final mixed model. The black circles represent the mean site-specific predicted floral density, and the error bars represent a 95% confidence interval around the mean for each logging, fire ID combination.

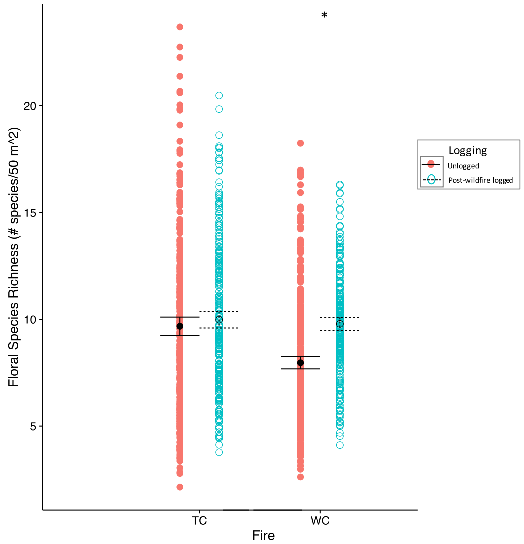

Figure 2. Significant differences in mean floral species richness between post-wildfire logged (blue) and unlogged (red) areas in Thompson Creek (older fire; TC) and Wicked Creek (newer fire; WC) are indicated by asterisks. The colored circles are site-specific floral species richness predictions from the final mixed model. The black circles represent the mean site-specific predicted floral species richness, and the error bars represent a 95% confidence interval around the mean for each logging, fire ID combination.

<u>Inter- and Intra-Annual Variability</u>. As expected, neither floral density nor floral species richness differed between sampling years (Tables 1 & 2). However, unexpectedly, the effects of logging on floral density and species richness varied by sampling year (Figures 3 & 4). In 2014, there were no differences in mean floral density or richness between logged and unlogged areas, while logged areas had 31% higher mean floral density and 20% higher mean species richness compared to unlogged areas in 2015.

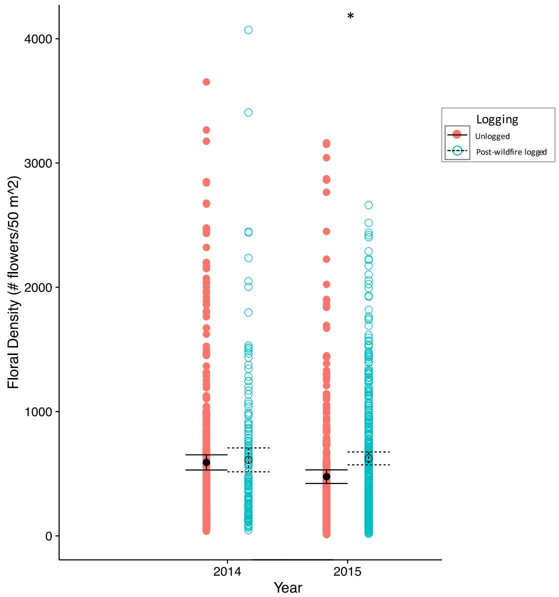

Figure 3. Significant differences in mean floral density between post-wildfire logged (blue) and unlogged (red) areas in 2014 and 2015 are indicated by asterisks. The colored circles are site-specific floral density predictions from the final mixed model. The black circles represent the mean site-specific predicted floral density, and the error bars represent a 95% confidence interval around the mean for each logging, year combination.

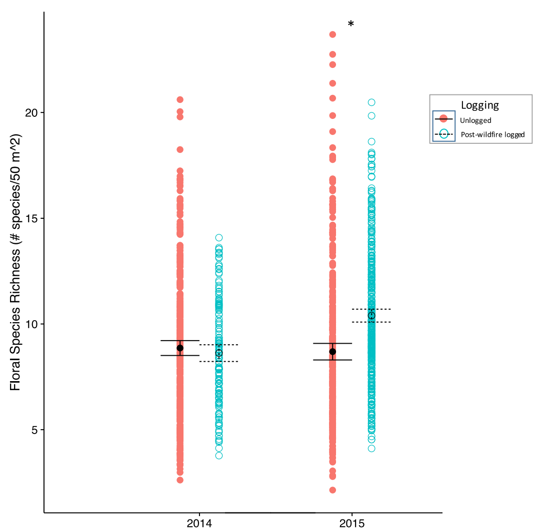

Figure 4. Significant differences in mean floral species richness between post-wildfire logged (blue) and unlogged (red) areas in 2014 and 2015 are indicated by asterisks. The colored circles are site-specific floral species richness predictions from the final mixed model. The black circles represent the mean site-specific predicted floral species richness, and the error bars represent a 95% confidence interval around the mean for each logging, year combination.

The difference in floral density and floral species richness between an older and more recent fire depended on sampling year (Tables 1 & 2). In 2014, floral density was 37% lower in the older fire (Thompson Creek) than in the more recent fire (Wicked Creek) (Fig. 5), whereas in 2015, there was no difference in mean floral density between the older fire and the newer fire. In 2014, there was no difference in mean floral species richness between the older fire and the more recent fire, whereas in 2015, the older fire had 37% lower mean floral richness than the newer fire (Fig. 6).

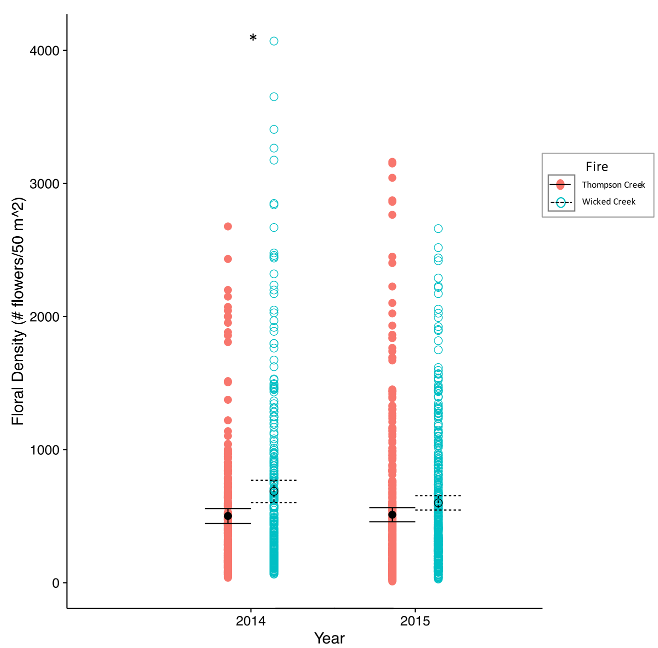

Figure 5. Significant differences in mean floral density between an older fire (Thompson Creek; red) and a more recent fire (Wicked Creek; blue) in 2014 and 2015 are indicated by asterisks. The colored circles are site-specific floral density predictions from the final mixed model. The black circles represent the mean site-specific predicted floral density, and the error bars represent a 95% confidence interval around the mean for each year, fire ID combination.

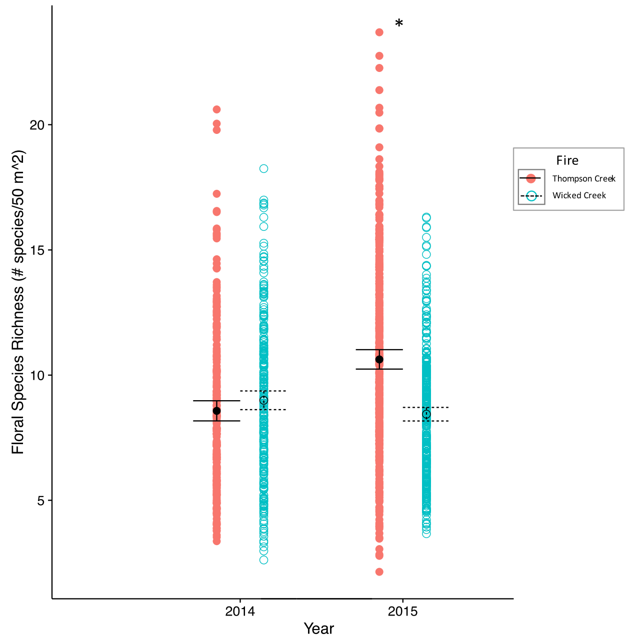

Figure 6. Significant differences in mean floral species richness between an older fire (Thompson Creek; red) and a more recent fire (Wicked Creek; blue) in 2014 and 2015 are indicated by asterisks. The colored circles are site-specific floral species richness predictions from the final mixed model. The black circles represent the mean site-specific predicted floral species richness, and the error bars represent a 95% confidence interval around the mean for each year, fire ID combination.

The effects of sampling year on floral density and floral species richness varied over the course of the summer (Tables 1 & 2, Fig. 7). Early and late in the 2014 growing season, mean floral density was higher and mean floral species richness was lower compared to 2015. These differences peaked at 100% higher floral density (Julian day 160, Fig. 7a) and 92% lower floral species richness (Julian day 167, Fig. 7b) in 2014 than 2015. However, during the peak growing season, there were no differences in mean flower density (Fig. 7a) or richness (Fig. 7b) between 2014 and 2015.

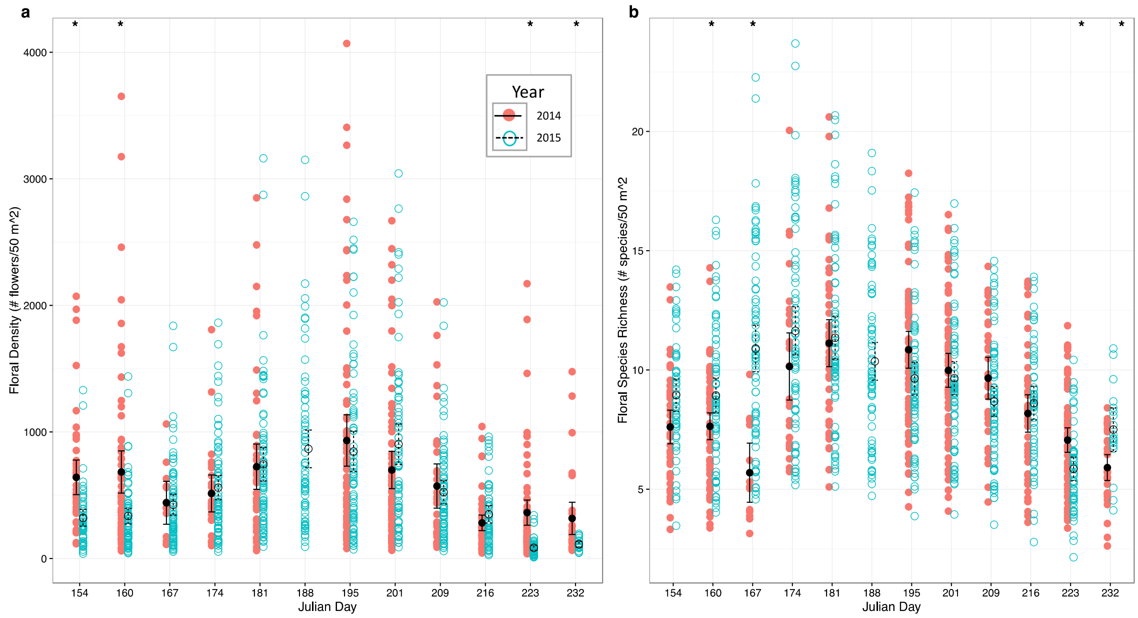

Figure 7. Significant differences (indicated by asterisks) in floral density (a) and floral species richness (b) between 2014 (red) and 2015 (blue) across the growing season (Julian Day; each Julian day represents first day of sampling week). The colored circles are site-specific floral density and floral species richness predictions from the final mixed model. The black circles show the mean site-specific predicted floral density and floral species richness, and the error bars represent a 95% confidence interval around the mean for each sampling week, year combination.

The effects of post-wildfire logging also varied across the summer growing season, and these effects differed between an older and a more recent fire (Fig. 8; Tables 1 & 2; logging by Julian Day by fire ID interaction). In the older fire, (Thompson Creek), there were minimal differences in floral density (Fig. 8a) or species richness (Fig. 8c) between logged and unlogged sites throughout most of the summer. By contrast, in the more recent fire (Wicked Creek) floral density (Fig. 8b) and species richness (Fig. 8d) in logged areas were higher than in unlogged areas throughout much of the summer. The difference between logged and unlogged floral density and species richness peaked at 86-89% higher during the early growing season (Julian days 167-195).

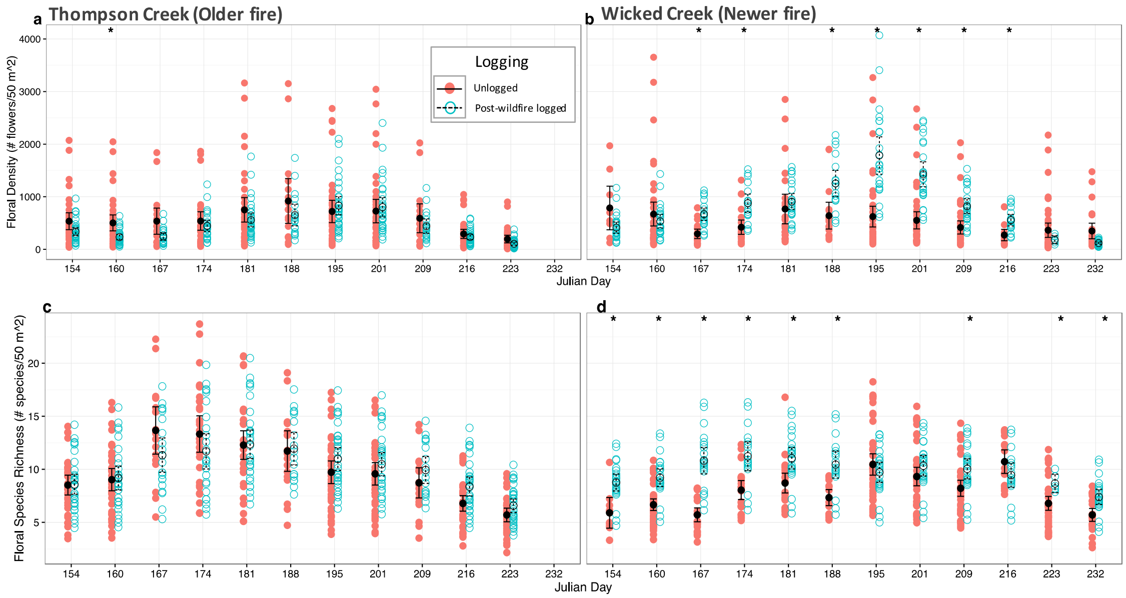

Figure 8. Significant differences (indicated by asterisks) in floral density (top panels) and floral species richness (bottom panels) for Thompson Creek (left panels) and Wicked Creek (right panels) between logged (blue) and unlogged (red) sites across the growing season (Julian Day) throughout both sampling years. Each Julian day represents the first day of sampling week from June through August. The colored circles are site-specific floral density and floral species richness predictions from the final mixed model. The black circles represent the mean site-specific predicted floral density and floral species richness, and the error bars represent a 95% confidence interval around the mean for each sampling week, logging treatment combination.

These differences in floral density and richness between logged and unlogged areas throughout the growing season in Wicked Creek were not driven by a specific suite of floral species (adonis: P = 0.3). In fact, there was high similarity in floral community composition between logged and unlogged areas in the early growing season when the difference between logged and unlogged floral density and richness was highest in Wicked Creek. Instead, the higher floral density in logged areas may have been driven by an increase in density of all species, which suggests post-wildfire logging affects all species similarly. The higher floral species richness in logged areas may be due to the presence of a few rare species in some of the logged areas.

Coarse Woody Debris. Floral density varied with CWD (Table 1). Mean floral density decreased by 15% with every doubling of CWD (Fig. 9).

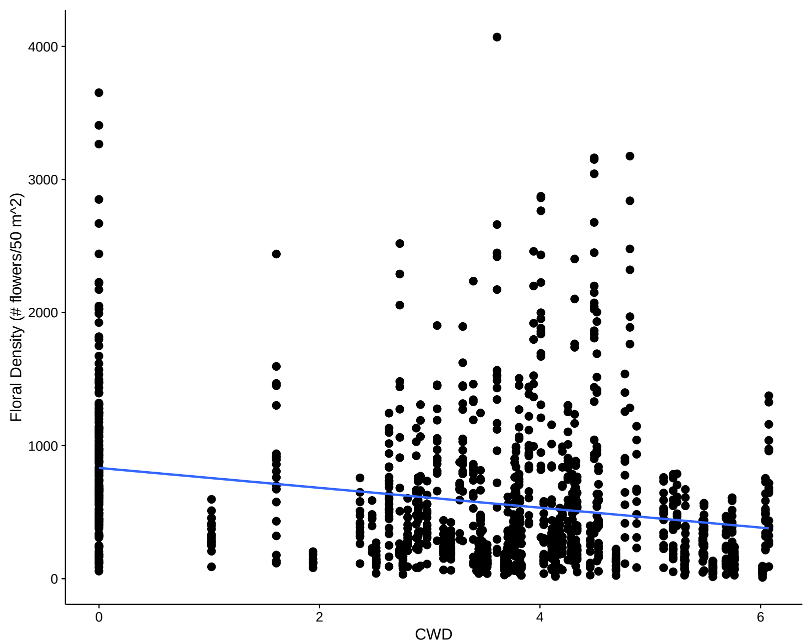

Figure 9. Floral density by coarse woody debris. The black points represent mean site-specific floral density predictions from the final mixed model and the gray error bounds represent a 95% confidence interval around the regression line.

Bee Density and Species Richness

Post-Wildfire Logging and Fire ID. Unexpectedly, there was no significant effect of post-wildfire logging on bee species richness (Table 3). However, mean bee density was 1.7 times higher in logged areas than unlogged areas, which was consistent with my hypothesis (Table 4). Contrary to my hypotheses, there were no significant effects of fire ID on bee density or bee species richness (Tables 3 & 4). However, as expected, the effects of logging on mean bee density and mean bee species richness depended on fire ID (Tables 3 & 4).

Table 3. Summary table for final model of bee species richness

	Df	SumSq	MeanSq	Fvalue
YEAR	1	188.90	188.90	188.90
logging	1	18.62	18.62	18.62
FIRE	1	23.39	23.39	23.39
Julian Day	11	114.47	10.41	10.41
YEAR × logging	1	29.03	29.03	29.03
YEAR × FIRE	1	5.29	5.29	5.29
YEAR × Julian Day	10	136.11	13.61	13.61
FIRE × Julian Day	10	16.21	1.62	1.62
logging × Julian Day	11	31.41	2.86	2.86
logging × FIRE	1	6.53	6.53	6.53
logging × FIRE × Julian Day	9	18.64	2.07	2.07

Table 4. Summary table for final model of bee density

	Df	SumSq	MeanSq	Fvalue
YEAR	1	539.33	539.33	539.33
logging	1	6.65	6.65	6.65
FIRE	1	6.37	6.37	6.37
Julian Day	11	455.24	41.39	41.39
YEAR × logging	1	16.17	16.17	16.17
YEAR × FIRE	1	12.77	12.77	12.77
YEAR × Julian Day	10	249.45	24.94	24.94
FIRE × Julian Day	10	22.03	2.20	2.20
logging × Julian Day	11	61.51	5.59	5.59
logging × FIRE	1	1.16	1.16	1.16
logging × FIRE × Julian Day	9	34.13	3.79	3.79

Intra- and Inter-Annual Variability. As expected, there were no significant effects of sampling year on bee density or bee species richness. Also as expected, the effects of logging on mean bee density and mean bee species richness between the older and more recent fire varied over the course of the growing seasons (Fig. 10; Tables 3 & 4). In the older fire, there were minimal differences in mean bee density (Fig. 10a) or richness (Fig.

10c) between logged and unlogged areas throughout the growing season. By contrast, in Wicked Creek, mean bee density (Fig. 10b) and richness (Fig. 10d) were up to 1.7 and 1.9 times higher, respectively, in logged areas than in unlogged areas early in the growing season. Bee richness was up to 100% higher in logged areas than in unlogged in the late growing season.

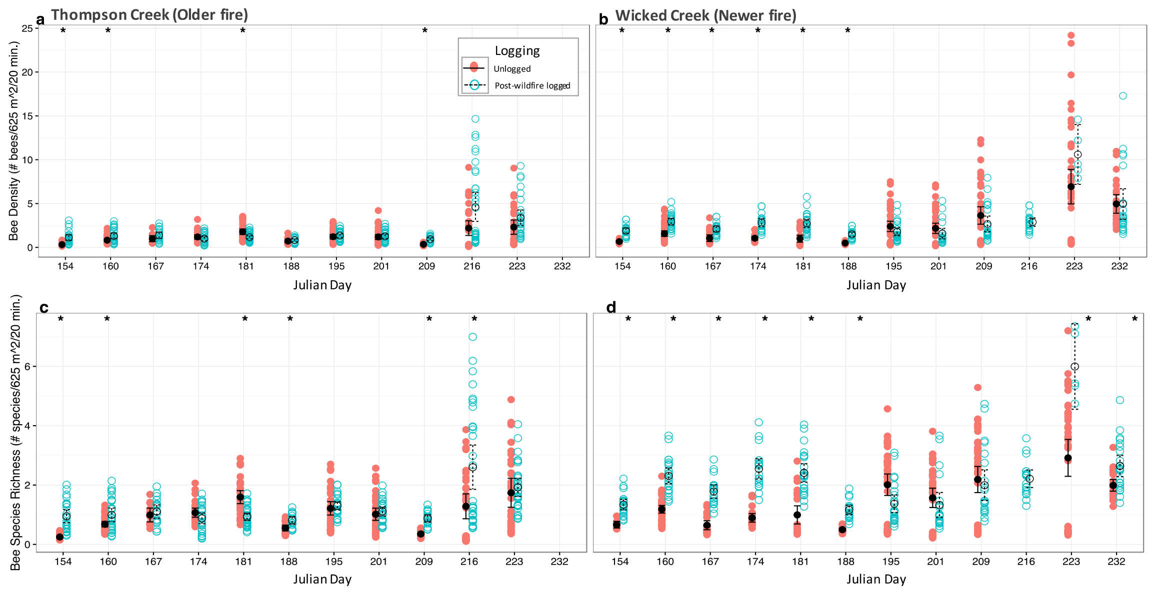

Figure 10. Significant differences (indicated by asterisks) in bee density (top panels) and bee species richness (bottom panels) in Thompson Creek (left panels) and Wicked Creek (right panels) between logged (blue) and unlogged (red) sites within sampling week across the growing season (Julian Day). Each Julian day represents the first day of each sampling week. The colored circles are site-specific bee density and bee species richness predictions from the final mixed model; red solid circles represent unlogged sites and blue open circles represent logged sites. The black circles represent the mean site-specific predicted bee density and bee species richness, and the error bars represent a 95% confidence interval around the mean for each sampling week, logging treatment combination.

These differences in bee density and richness between logged and unlogged sites were not driven by a specific suite of bee species (adonis: $P = 0.19$); there was high similarity in bee community composition between logged and unlogged areas. Instead, higher bee density in logged areas may be due to an increase in all bee species. The higher bee species richness in logged areas may be due to one or a few rare species that are present in logged areas.

These patterns of variation in bee density and bee species richness across the growing season differed by sampling year (Tables 3 & 4, Fig. 11). In the late growing season of 2014, mean bee density (Fig. 11a) and mean bee species richness (Fig. 11b) were up to 6.3 and 3.3 times higher, respectively, compared to 2015. The effects of logging on bee density and bee species richness also varied by sampling year. In 2014, there were no differences in mean bee density or richness between logged and unlogged sites. However, in 2015 mean bee density was 1.7 times higher and richness was 1.5 times higher in logged areas than in unlogged areas.

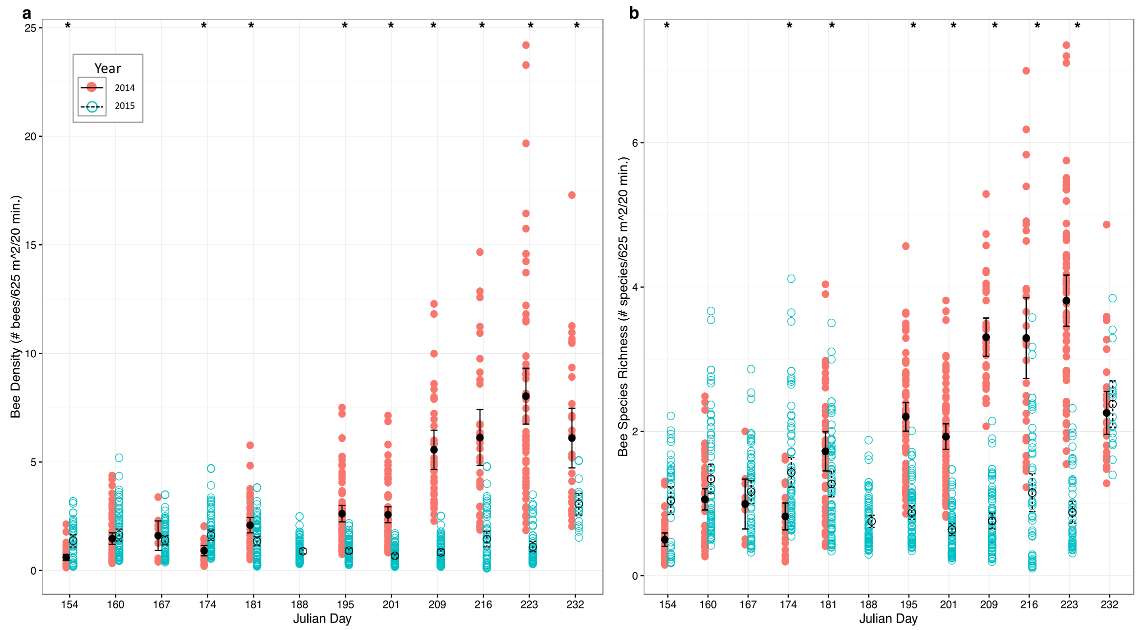

Figure 11. Significant differences (indicated by asterisks) in bee density (a) and bee species richness (b) between 2014 (red) and 2015 (blue) across the growing season. Each Julian day represents the first day of each sampling week. The colored circles are site-specific bee density and bee species richness predictions from the final mixed model. The black circles show the mean site-specific predicted bee density and bee species richness, and the error bars represent a 95% confidence interval around the mean for each sampling week, year combination.

The effects of fire ID on bee density and species richness varied by sampling year (Tables 3 & 4). Mean bee density was 100% higher in the newer fire than in the older fire in 2014 and 41% higher in the newer fire than in the older fire in 2015. Mean bee species richness was 66% higher in the newer fire than in the older fire in 2014, and 38% higher in the newer fire than in the older fire in 2015.

Discussion

Floral and bee density and richness were higher in post-wildfire logged areas than in unlogged areas in the short-term (Wicked Creek), but not long-term (Thompson

Creek), indicating that the benefits of post-wildfire logging on floral and bee communities diminishes over successional time, as expected. While a combination of wildfire and post-wildfire logging was beneficial for forb and bee communities, this effect depended on time of the growing season, sampling year and the specific fire. The effects of post-wildfire logging on floral and bee communities were dependent on a number of interacting variables.

Effects of Post-Wildfire Logging on Floral Communities

Post-wildfire logging was beneficial for floral communities in the short-term (Wicked Creek) but not in the long-term (Thompson Creek). Floral density and species richness were higher in logged areas compared to unlogged areas in the more recent fire, but there were few differences in the floral communities between logged and unlogged areas in the older fire. The difference in the effect of logging between the two different-aged fires is consistent with previous studies, and can emerge through a variety of mechanisms including increase in canopy cover over time, and less light availability for forb growth (Winfree, Griswold & Kremen 2007; Taki *et al.* 2013). My results are consistent with studies that show, over the long-term (from 8 to 178 years post-disturbance), floral communities of burned or logged areas become more similar to undisturbed sites (Potts *et al.* 2003a; Pengelly & Cartar 2010; Taki *et al.* 2013).

Floral density decreased with an increase in CWD volume, indicating that higher CWD volumes create less space for forb growth, which is consistent with a previous study (Tinker & Knight 2000). CWD provides suitable substrate for tree regeneration, and thus greater tree regeneration in areas of higher CWD volumes may increase competition between woody plants and for forbs (Heinemann & Kitzberger 2006; Lindenmayer *et al.* 2008; Stine *et al.* 2014). The higher floral density and species richness in logged areas in the newer fire may be due to lower CWD volumes as I found that logged areas had lower CWD volumes than unlogged areas ($P < 0.01$). The removal of woody biomass (standing trees in addition to CWD) by post-wildfire logging creates lower tree cover and greater sunlight availability, promoting forb growth (Lindenmayer *et al.* 2008).

Effects of Post-Wildfire
Logging on Pollinator Communities

Positive effects of post-wildfire logging on bee communities were observed in the newer fire (Wicked Creek) but not in the older fire (Thompson Creek), indicating that the influence of post-wildfire logging diminished over successional time, as expected. The attenuation of logging influence may be due to a variety of mechanisms, including increased canopy cover over time and reduced light availability for forb growth, which bees respond to directly through decreased foraging (Potts *et al.* 2003a; Campbell *et al.* 2007; Romey *et al.* 2007; Winfree *et al.* 2007; Grundel *et al.* 2010; Pengelly & Cartar 2010; Taki *et al.* 2013; Jackson *et al.* 2014; Rubene, Schroeder & Ranius 2015). Over the long-term, bee communities of burned and logged areas have been shown to become more similar to those of undisturbed sites (Potts *et al.* 2003a; Pengelly & Cartar 2010; Taki *et al.* 2013). My results show that, in the long-term (Thompson Creek), the bee communities of post-wildfire logged areas are the same as unlogged sites. However, in the short-term (Wicked Creek), my study shows that bee communities in post-wildfire logged areas are still different than those of unlogged areas.

Post-wildfire logging's effect on the pollinator community was also dependent on time of the growing season. Bee species with different life histories may be affected by post-wildfire logging differently and are active at different times throughout the summer growing season. For example, I sampled the greatest number of Halictid bees in the early growing season, Andrenids in the early and peak growing seasons, Megachilids in the peak growing season, Colletids in the peak and late growing season, and Apids in the late growing season. This variable effect may also be due to bees responding to changes in floral community and forage availability across the growing season (Potts *et al.* 2003a; Mateos *et al.* 2011; Jackson *et al.* 2014; Rubene *et al.* 2015). Overall forb density and species richness nearly doubles from the early to the peak growing season. Then, from the peak to the late growing season, both forb density and species richness decrease by nearly 65% and 35%, respectively.

In addition, logged areas may support some specific guilds of bees better than unlogged areas. I found that logged areas had lower CWD volumes than unlogged areas. Although I expected that greater CWD volume would benefit bee density communities by providing nesting habitat for cavity-nesting bees (Harmon & Sexton 1996; Moretti *et al.* 2009; Grundel *et al.* 2010; Williams *et al.* 2010; Mateos *et al.* 2011; Vázquez *et al.* 2011) or alternatively decrease bee density by limiting bare ground availability for ground-nesting bees, CWD volume was not a significant predictor of bee density or species richness ($P > 0.05$). This result suggests that bee communities are not limited by woody or ground-nesting resources in our system, that the amount of CWD volume present at my sites was not high enough to detect an effect, or that the amount of CWD volume was high enough across all sites, logged and unlogged, that I was unable to detect a difference.

Alternatively, ground-nesting bees may have been responding to increased availability of bare ground rather than CWD, and thus contributed to the increase in pollinator density in logged areas. Post-wildfire logging creates an increase in bare ground (Lindenmayer *et al.* 2008), and ground-nesting bees depend on bare ground for nesting resources (Potts *et al.* 2005; Campbell *et al.* 2007). Specifically, bee density for bees of ground-nesting families, Halictidae, Andrenidae and Apidae, were 43%, 45% and 23% greater in post-wildfire logged versus unlogged areas, respectively.

Inter-Annual Variability in Post-Wildfire
Logging's Effects on Forb and Bee Communities

Lastly, I found significant interannual variation in floral and bee community dynamics, and in the effects of post-wildfire logging on both floral and bee communities. Previous studies have also found interannual variation in forb and bee communities (Inouye, Saavedra & Lee-Yang 2003; Kudo & Hirao 2006; Alarcon, Waser & Ollerton 2008; Petanidou *et al.* 2008; Burkle & Irwin 2009; Devoto *et al.* 2009; Gallai *et al.* 2009; Hegland *et al.* 2009; Lambert, Miller-Rushing & Inouye 2010). The most notable differences between sampling years were seen in the pollinator communities, as the density bumble bee species (*Bombus spp.*) declined by 69% from 2014 to 2015. The bee density of all other families expect Andrenidae (Colletidae, Megachilidae, and

Halictidae) stayed relatively steady between 2014 and 2015. However, the bee density of Andrenidae increased by 23% from 2014 to 2015, suggesting that these bees responded positively to the reduction in *Bombus spp.* density.

This interannual variation may be due to forb and pollinator population dynamics, or may be due to fluctuations in climate patterns, including snowpack, precipitation, and temperature, between the sampling years. Recent warming in the GYE has been associated with earlier spring snowmelt and warmer summer temperatures (Romme & Turner 2015). Precipitation throughout the winter, as well as throughout the summer growing season, is important for forb growth, phenology, and reproduction, and pollinators respond to the presence and density of floral resources directly. These conclusions highlight the importance of conducting additional future research to better understand the interaction of temporal variability in climate and the effects of post-wildfire logging on forest biodiversity.

Implications of Post-Wildfire Logging on Forb-Bee Interactions

Post-wildfire logging similarly enhanced two interacting trophic levels -- forb and bee communities -- in the short-term (Wicked Creek). In the long-term (Thompson Creek), the benefits of post-wildfire logging on both forb and bee communities diminished. However, the timing of when the positive effects of post-wildfire logging were the strongest was different between forbs and bees. Forb density and species richness was highest in logged areas during the early and peak growing season, whereas bee density and species richness was highest in logged areas in the early and late growing season. These differences in timing may lead to mis-matches in important forb-bee interactions, which could have negative implications for forb reproduction.

Future Directions

I would expect that the effects of post-wildfire logging on forb and pollinator communities differs based on where the study takes place. This study took place in a montane mixed conifer forest, with medium productivity, medium moisture levels, and mixed severity fires occurring every 35-200 years. On one end of the productivity and moisture spectrum, the deserts of the southwestern U.S. are characterized by low productivity, low moisture levels and fire activity is limited by sparse fuels. In these desert ecosystems, I predict that post-wildfire logging would have a similar effect on forb and pollinator communities; forb and pollinator density and species richness would be higher in post-wildfire logged than unlogged areas. However, I would expect that these differences in forb and pollinator communities between logged and unlogged areas to remain for much longer. Given the low productivity, I would expect the process of succession to be much slower and therefore the forb and pollinator communities of post-wildfire logged areas of an older fire would still be different than those of unlogged areas, even past 25 years post-fire. On the other end of the spectrum, the temperate rain forests of the Pacific Northwest of the U.S. are characterized by high productivity and high moisture levels, and fire activity is limited by fuel moisture levels. In these types of ecosystems, I would expect that the effects of post-wildfire logging on forb and pollinator communities would diminish more quickly than they do in a mixed conifer forest. Specifically, I would predict that it would take less time for forb and pollinator communities in post-wildfire logged areas to become indistinguishable from unlogged areas, due to the high productivity and high moisture levels. Future studies may consider conducting a similar study in different ecosystems to test the hypothesis that the effects of post-wildfire logging on forb and pollinator communities depends on the ecosystems' biophysical conditions.

Additionally, the questions of this study were addressed with an observational-approach focused on floral and bee community dynamics patterns, and not a mechanistic-approach. Mechanisms underlying the patterns seen in the floral and bee communities due to post-wildfire logging may be addressed with field experiments. Manipulating the abiotic environment, for example soil moisture levels or sunlight availability, would allow future studies to gain a clearer understanding of the ecological processes underlying the effects of post-wildfire logging.

While this study focused on the effects of post-wildfire logging on bee foraging habitat (floral density and species richness), it did not directly assess pollinator nesting habitat. I would expect that the effects of post-wildfire logging on foraging habitat do not accurately represent the effects on nesting habitat since bee foraging and nesting habitat can be spatially separated (Westrich 1996). The availability of nesting sites and nesting resources has been found to be important for bee community structure (Potts *et al.* 2005), and timber harvesting likely disrupts potential nest sites for ground-nesting bees and removes biomass (Lindenmayer *et al.* 2008), which is potentially used by cavity-nesting bees. To gain a more complete understanding of how post-wildfire logging influences bee communities, future studies may also consider assessing bee nesting habitat.

Furthermore, I expect that the effects of post-wildfire logging would be different immediately after wildfire (1 year post-fire) or long after wildfire (60 years post-fire) than what I found 7-8 years (Wicked Creek) and 23-24 years (Thompson Creek) years after wildfire due to changes in forest community structure through successional time. Future studies must examine additional temporal differences in the effects of post-wildfire logging, especially the immediate and long-term effects, along with the mechanisms underlying those changes to gain an even deeper understanding of the temporal variation in how this type of forest management influences biodiversity.

Conclusions and Management Implications

To my knowledge, these results provide the first assessment of the responses of forb and pollinator communities to post-wildfire logging and are key to expanding our understanding of the effects of post-wildfire logging on forest biodiversity. Post-wildfire logging positively affected forb and pollinator communities in a more recent wildfire, but these effects diminished with time, suggesting short-term benefits. There may be longer-term negative effects of logging on the forb communities as suggested by Wyatt and Silman (2010) and Duffy and Meier (1992) and thus on the pollinator communities as well. These potential long-term negative effects could potentially lead to mismatched phenology between forbs and pollinators. The long-term effects of post-wildfire logging have received minimal attention, especially with regards to forb and pollinator communities. This study shows that over the long-term forb and pollinator communities in post-wildfire logged areas are more similar to unlogged areas than they are in the short-term. This implies that there are no negative long-term implications of post-wildfire logging on forb and pollinator density and species richness.

As changes in climate lead to more frequent and severe fires in the Greater Yellowstone Ecosystem (Westerling *et al.* 2006; Morgan *et al.* 2008; Littell *et al.* 2009; Spracklen *et al.* 2009; Higuera *et al.* 2010), the pressure for post-wildfire logging is likely to increase (Lindenmayer *et al.* 2008). The management of wildfire-affected landscapes must consider the effects of human land use on forest biodiversity, particularly floral and pollinator communities (Gaston 2006). Many ecological studies consider tree species richness and structural diversity in their assessment of the effects of timber harvesting (Belote & Aplet 2014). However, given the importance of early successional habitat to floral and bee communities (Taki *et al.* 2013) and that the most diverse ecoregions of Montana experience the greatest amount of timber harvesting, it is imperative that ecological assessments of logging consider additional indices of biodiversity (Belote & Aplet 2014), including floral and pollinator community dynamics. This study shows that post-wildfire logging has a beneficial effect on forb and bee communities, and these effects change through time.

THE EFFECTS OF POST-WILDFIRE LOGGING ON PLANT REPRODUCTIVE SUCCESS: A CASE STUDY USING *SYMPHORICARPOS ALBUS*

Introduction

The majority of flowering plant species (80%) require insect pollinators for reproduction (Potts *et al.* 2010). Furthermore, the reproduction of up to 73% of plant species is limited by pollen receipt (e.g., Bierzychudek 1981; Galen 1985; Johnston 1991; Burd 1994; Parker 1997; Ashman *et al.* 2004; Knight *et al.* 2005). This widespread pollen limitation of plant reproduction may have especially negative consequences for plant reproduction for plant species influenced by disturbances (Kearns *et al.* 1998; Aizen & Harder 2007; Chen *et al.* 2016). Investigating the extent of pollen limitation of plant reproductive success can provide insight into the mechanisms by which disturbances influence plant populations.

Because plant reproductive success is a product of both abiotic (e.g., soil nutrients, sunlight) and biotic resources (e.g., pollination services) (Burd 1994), both natural and anthropogenic disturbances that affect the availability of these resources (Potts *et al.* 2003a; Lindenmayer *et al.* 2008) may indirectly influence plant reproduction. In particular, by opening up the forest canopy, burned (i.e. wildfire and prescribed fires) and logged (i.e. forest thinning and clearcutting) areas create early successional habitat (Lindenmayer & Noss 2006; Swanson *et al.* 2011). Forb and pollinator abundance and diversity increase in early successional habitat (Potts *et al.* 2003a; Romey *et al.* 2007; Grundel *et al.* 2010; Pengelly & Cartar 2010; Jackson *et al.* 2014), and high pollinator abundance has been associated with increased plant reproductive success (Winfree *et al.*

2015). Wildfire can impact another fundamental abiotic resource for plant growth by augmenting levels of soil micronutrients that are important for seed development (i.e. P, K, and N) (Rundel 1981; Kutiel & Naveh 1987; le Maitre & Midgley 1992; Potts, Dafni & Neeman 2001), while logging can compact and erode soil, which restricts plant growth (Lindenmayer & Noss 2006).

The combination of fire and logging can have interactive effects on both abiotic and biotic conditions (Lindenmayer & Noss 2006; Campbell *et al.* 2007). Pollinator richness has been shown in an experimentally manipulated system to be higher in burned (i.e. prescribed fire) plus logged (i.e. mechanical shrub thinning) areas compared to areas that were only burned, only logged, or undisturbed (Campbell *et al.* 2007). Higher pollinator abundance in burned plus logged treatments may lead to increased plant reproductive success (Winfree *et al.* 2015). To my knowledge, only one previous study has examined the effect of the combination of fire (i.e., prescribed fire) and logging (i.e., tree retention logging- "retaining single trees or forest patches at the time of harvest") on plant reproductive success: Rodriguez et al. (2015) found that *Vaccinium myrtillus* (bilberry) reproduction was higher in areas that were unlogged (regardless of fire) when compared to areas that were logged. However, the same study found no difference in (lingonberry) reproduction (i.e. berry yield) between burned, logged or burned plus logged (Rodriguez & Kouki 2015). This study also assessed the effects of bee abundance and diversity on bilberry and lingonberry reproductive success to draw inference on the pollen limitation of plant reproduction in logged and burned areas. Rodriguez et al. (2015) found that the reproductive success of both plant species was independent of bee abundance and diversity. From this result, the authors inferred that the plants were not pollen limited since both plants were obligatory insect pollinated and had been found to have reduced fruit set in the absence of pollinators (Rodriguez & Kouki 2015).

Post-wildfire logging often takes place within one year following wildfire and thus is thought to have additional effects on forest abiotic properties including increased soil compaction, increased soil erosion, and greater reductions in forest canopy when compared to non-salvage logging (i.e. forest thinning or clearcutting) because seral vegetation has not yet developed to stabilize soils (McIver & Starr 2000; Morissette *et al.* 2002; Lindenmayer *et al.* 2008). Despite these additional ecological impacts, the effects of post-wildfire logging on plant reproductive success and pollen limitation is unknown.

Previous research suggests that non-salvage logging minimizes the degree of pollen limitation of plant reproduction via enhanced pollinator abundance and diversity compared to unlogged areas (Campbell *et al.* 2007; Rodriguez & Kouki 2015). In this study, I addressed the following questions: (1) how does post-wildfire logging influence forb reproductive success in an old fire and (2) how does post-wildfire logging influence pollen limitation of forb reproduction in an old fire? My first question does not separate the abiotic and biotic factors important for forb reproduction. Assessing the extent of pollen limitation of forb reproduction with my second question allows me to focus solely on the biotic component of forb reproduction, or the pollinators' roles in forb reproduction. I hypothesized that forb reproduction would be higher and less pollen limited in post-wildfire logged areas in the long-term, as previous studies suggest that logging enhances reproduction and minimizes the degree of pollen limitation of forb reproduction due to increased pollinator abundance and diversity in logged areas (Campbell *et al.* 2007; Rodriguez & Kouki 2015). However, I did not find higher pollinator density and species richness in post-wildfire logged areas compared to unlogged areas in the long-term (Chapter 2). Therefore, I adjusted my hypotheses and I expected that, if forb reproduction and pollen limitation of forb reproduction is driven by bee density and bee species richness, there would be no difference in forb reproduction, or forb pollen limitation between logged and unlogged areas.

In this study, I investigated the effects of post-wildfire logging on forb reproductive success in the same older wildfire from Chapter 2 (Thompson Creek, 2,824 hectares) in the Gallatin National Forest, Montana, USA. Within this fire perimeter, I performed a pollen supplementation experiment (PSE) on *Symphoricarpos albus* (snowberry) in post-wildfire logged and unlogged areas to investigate pollen limitation of reproductive success. I chose Thompson Creek for this PSE because I was interested in knowing whether or not there were any long-term repercussions on forb reproduction, regardless of what the community dynamics look like in response to post-wildfire logging. I selected *S. albus* because it is a widespread, self-incompatible, bee-pollinated, fire tolerant, and ecologically valuable shrub species.

To my knowledge, this field experiment is one of few studies that extends the investigation of responses of forb and pollinator communities to forest management practices by examining effects of post-wildfire logging on forb reproductive success and a potential mechanism, pollen limitation, in driving those effects.

Methods

Study System

This study was conducted in the Gallatin National Forest near Pray, Montana, USA (45°14’N, 110°33’W) within the Thompson Creek wildfire perimeter (burned in 1991, 2,824 hectares). I selected the Thompson Creek fire to conduct this experiment to be able to assess the long-term effects of post-wildfire logging on the pollen limitation of forb reproduction. To determine the degree to which forb reproduction is pollen limited in post-fire logged versus unlogged areas, I conducted a whole-plant pollen supplementation field experiment on *Symphoricarpos albus* individuals in July - August 2015.

Pollen supplementation experiments involve supplementally-pollinated and open-pollinated (i.e., naturally) plants. The supplementally-pollinated plants are assumed to receive maximum possible pollen resources for maximum plant reproduction. This is done by hand-pollinating the plants with a small paintbrush using pollen from nearby con-specific plants. These flowers are then left open to receive natural pollination as well. Open-pollinated plants serve as the control plants, and they represent natural pollination levels. The reproduction of supplementally-pollinated plants is compared to open-pollinated plants. If the reproduction of supplementally-pollinated plants is greater than that of open-pollinated plants, this indicates that plant reproduction is limited by the receipt of pollen. If there is no difference between supplementally-pollinated plants and open-pollinated plants, this indicates that the plants are not pollen limited.

I selected *S. albus* for this experiment because it has several characteristics that are advantageous for a pollen limitation experiment: it requires an insect pollinator for seed set; it is a small plant with few, big flowers, which is important for efficiency in the PSE; it was a common and widespread species throughout my study system as it was present at the majority of sites (10/18 sites per logging treatment); and it has 2 ovules with the capacity to produce a maximum of two seeds, which is also important for efficiency in measuring seeds. I conducted this experiment at four post-wildfire logged and four unlogged sites (total of 8 sites). In order to reduce variability in reproductive success metrics (fruit and seed size) that may be associated with plant size, I selected plants that were 1-2 feet tall and had at least 15 flowers, but no more than 60 flowers. To limit potential variability in abiotic conditions (e.g., sunlight, soil nutrients) that the plants experienced, all of the plants at a site were within 25 meters of each other.

Pollination Methods

Four *S. albus* plants at each of the 8 sites were randomly assigned to the supplemental pollination treatment and four were selected as control plants (i.e., N= 64 plants total). The control plants were exposed to open, natural pollination only. For the supplemental pollination treatment, I collected ten anthers from pollen donor plants within 25 meters of the focal plant and mixed them in a microcentrifuge tube. Using a small paintbrush, I transferred pollen from the pollen mixture to all open flowers on each designated plant (average of 27 flowers per plant). Pollen supplementation was done once during peak *S. albus* bloom (July 13th-July 24th) and the flowers were then left to receive natural pollination. Since *S. albus* has a short bloom time from early through late July and flowering lasts approximately 14 days (L. Heil, pers. obs.), supplementally-pollinating each plant once during peak bloom likely treated the majority of flowers on each plant.

Fruit Collection and Processing Methods

I collected all fruits from each plant as they matured throughout the last week of July and the first three weeks of August. To remove all moisture and measure the exact dry mass of the fruits and seeds, I dried the fruits in a drying oven for 48 hours at 50° C then dehumidified them in a desiccator for 30 minutes before weighing each fruit and seed individually. I also tested seed viability using the Tetrazolium test with a 0.1% Tetrazolium (Tz) solution (2, 3, 5 triphyenyltetrazolium chloride and water) after soaking the seeds in water for three hours (Kearns & Inouye 1993). I calculated mean mass per fruit, total fruit mass per plant, mean mass per seed, total seed mass per plant, number of seeds per plant, fruit set (# flowers/# fruits) per plant, and seed viability.

I selected one metric as my response variable in my analysis since all of these reproductive success metrics were correlated ($0.48 < R < 0.99$, $P < 0.01$ in all cases). Given all of these metrics, I chose mean mass per seed as the response variable in order to measure plant fitness in the most direct manner possible as the function of the seed is to pass on a plant's genetic material. Also, in general, there is a positive relationship between seed size and seed fitness (Smith & Fretwell 1974); seeds with greater seed mass have a greater chance of germinating as they are more tolerant of their conspecific neighbors (Lebrija-Trejos *et al.* 2016). There is also a positive relationship between number of seeds and seed fitness (Smith & Fretwell 1974). However, since *S. albus* only produces a maximum of two seeds per fruit, that leaves little room for any variability between plants to measure any effect on this metric, and thus I did not use the number of seeds metric. Alternatively, while the fruit size metrics are also related to fitness, fruit size is a less direct measure of plant fitness as fruits serve other functions in addition to housing the seed. These include both protecting the seed from frugivores and attracting frugivores for seed dispersal (Gurevitch, Scheiner & Fox 2006). Lastly, selecting seed size to represent plant reproductive success provides a more complete measure of fitness since both male and female parents' genetic material contribute to seed development, while fruit development is derived solely from the female plant (Lyons *et al.* 1989).

While I completed the Tetrazolium test to test for seed viability, I did not consider those results due to the subjective nature in interpreting the results. I felt that the results from objective fruit and seed measurements were a more precise representation of reproductive success.

Statistical Methods

To assess the effects of post-wildfire logging, pollination treatment and their interaction on the reproductive success (i.e. mean mass per seed) of *S. albus*, I used a 2-way ANOVA (R Core Development Team 2015). Using the results from the ANOVA, I used the lsmeans package to conduct a post-hoc assessment of multiple comparisons of means and investigate the interaction between logging and pollination treatments (Lenth 2016).

Results

Overall, pollination treatment (*P* = 0.047, t = -2.03, df=60; Fig. 12), post-wildfire logging (*P* = 0.048, t = -2.02, df = 60) significantly influenced *Symphoricarpos albus* reproductive success (i.e., mass per seed) and the effect of pollination treatment depended on the presence of post-wildfire logging (*P* = 0.052, t = 1.98, df=60). As expected, natural *S. albus* reproduction represented by open-pollinated (OP) plants was the same between post-wildfire logged and unlogged areas (*P* > 0.44, df = 60) in the long-term. This indicated that post-wildfire logging does not influence *S. albus* reproduction in an older fire. However, unexpectedly, the mean mass per seed for supplementally-pollinated plants in unlogged areas was, on average, 73% greater than that of plants in all other treatments (P < 0.05 in all cases, df = 60) and *S. albus* reproduction was similar in these other treatments (P > 0.44 in all cases, df = 60). This suggests that *S. albus* is pollen limited in unlogged areas but not in logged areas in the long-term.

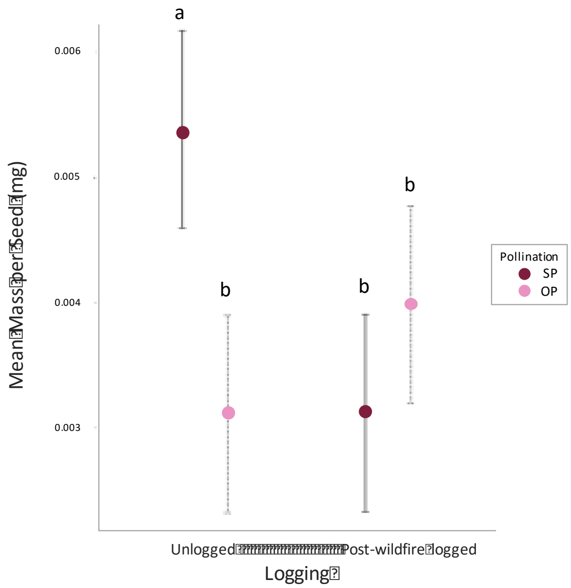

Figure 12. Mean mass per seed of supplementally-pollinated plants (SP; dark red) compared to that of open-pollinated plants (OP; pink) in unlogged areas versus post-wildfire logged areas. The error bars represent one standard error around the mean.

Discussion

Plant populations are often pollen limited (Bierzychudek 1981; Galen 1985; Johnston 1991; Burd 1994; Parker 1997; Ashman *et al.* 2004; Knight *et al.* 2005), and this may have reproductive consequences for plant populations affected by human activities (Kearns *et al.* 1998; Aizen & Harder 2007). I found that, in an old fire (Thompson Creek), post-wildfire logging had no impact on natural *S. albus* reproductive success (open-pollinated plants), and this was consistent with my hypothesis. However, contrary to my hypothesis, *S. albus* reproductive success (i.e., mass per seed) was limited by the receipt of pollen in unlogged areas (i.e., significant interaction between pollination and logging) in the old fire.

While plant reproductive success has been found to be pollen limited in areas that have experienced anthropogenic disturbances including prescribed fire, retention forestry, and urbanization (Johnson & Bond 1997; Aizen & Feinsinger 2003; Kolb 2005; Cheptou & Avendano V 2006), the few studies that have examined the effects of disturbances, particularly logging (retention logging), fire (prescribed burning), or the combination of both on plant reproductive success have yielded species-specific effects (i.e., both positive and negative responses). However, other studies show plant reproductive success in disturbed sites was not pollen limited compared to undisturbed areas (Potts *et al.* 2001; Rodriguez & Kouki 2015; Chen *et al.* 2016).

This result that *S. albus* reproduction was pollen limited in unlogged areas was inconsistent with the few similar studies previously mentioned (Potts *et al.* 2001; Rodriguez & Kouki 2015; Chen *et al.* 2016), but consistent with my original hypothesis. However, that hypothesis was based on my expectation that forbs in unlogged areas, but not logged areas, would be pollen limited due to lower bee density and species richness in unlogged areas. Since I previously found that there were no differences in bee density and species richness between logged and unlogged areas in the older fire in Chapter 2, the pollen limitation of *S. albus* must be due to abiotic factors, other biotic effects, or a combination of abiotic and other biotic factors (Ashman *et al.* 2004; Knight *et al.* 2005). Plants in unlogged areas may be able to take advantage of the extra pollen resources, which supplemental pollination provides them with, and produce larger seeds with those extra resources. However, forbs in logged areas may not be able to take advantage of these extra pollen resources as there was no difference between the mean mass per seed for open-pollinated plants and supplementally-pollinated plants in logged areas.

A possible explanation for this may be that post-wildfire logging influences soil structure, composition, or the microclimates that are present. This may happen through soil compaction or changes in soil nutrients that negatively affected seed development (Rundel 1981; Lindenmayer *et al.* 2008). Additionally, as decreased canopy cover may disrupt plant growth and reproduction (Franklin *et al.* 2000; Lindenmayer & Noss 2006), decreased canopy cover in logged areas may lead to drier soils, which could directly limit plant growth and reproductive success, given that *S. albus* grows best in moist soils (Gilbert 1995; Lindenmayer & Noss 2006). Therefore, even with the extra pollen resources, plants in post-wildfire logged areas are still unable to produce larger seeds.

In terms of biotic factors, differences in pollinator behavior, such as changes in visitation rates, between logged and unlogged areas may lead to greater mean mass per seed in unlogged areas than in logged areas. Overall, my results suggest that, in the long-term, post-wildfire logging does not lead to pollen limitation of *S. albus* reproduction, but may negatively influence the abiotic resources that are important for *S. albus* reproduction. However, this study did not examine these abiotic conditions.

Future Research Priorities

Similar to what I expected in Chapter 2, I expect that the results from this study depend on the biophysical conditions of where the study takes place. For example, I would expect that forbs in desert ecosystems would be more limited by abiotic factors, such as soil micronutrients or soil moisture, due to the low productivity and moisture levels characteristic of these ecosystems. Alternatively, I would predict that forbs in temperate rain forest ecosystems would be less limited by abiotic factors. While this study provides valuable information about *S. albus* reproduction in post-wildfire logged areas, it would be beneficial if future studies explicitly investigated the processes that are driving these patterns to further our understanding of plant reproduction. Specifically, to better inform how we conserve biodiversity and conduct post-wildfire management, it will be important to separate abiotic and biotic mechanisms underlying the effects of post-wildfire logging on forb reproduction and pollen limitation of forb reproduction. Manipulating the abiotic conditions, such as soil nutrient levels, and soil moisture levels, will allow us to make inferences on differences in the abiotic conditions between post-wildfire logged and unlogged areas. Future studies may incorporate a more community-wide approach and investigate inter-specific variation in plant reproductive responses to post-wildfire logging. It is expected that different species vary in how they respond to both natural and anthropogenic disturbances. Lastly, this study investigated the response of *S. albus* to post-wildfire logging in a 24-year old fire to investigate the presence of long-term implications of post-wildfire logging on plant reproduction. Future studies may gain insight into temporal variation in the effects of post-wildfire logging by examining whether the response of plant reproduction to post-wildfire logging depends on time-since-fire. Based on previous studies, forb and pollinator communities of disturbed areas become more similar to undisturbed areas with time-since-fire (Jackson *et al.* 2014). I observed differences in forb and bee density and species richness between post-wildfire logged and unlogged areas in an eight-year old fire (Chapter 2), and thus might expect plant reproductive success to be augmented in more recent fires in response to these community differences.

Conclusions

To my knowledge, this study is the first to show that post-wildfire logging has no effects on forb reproductive success but may have negative consequences for pollen limitation of forb reproduction in an old fire. Teasing apart the abiotic and biotic mechanisms of how post-wildfire management affects forb reproductive success is essential to advancing our understanding of the effects of wildfire and anthropogenic disturbances on forest ecosystems.

CONCLUSIONS

In a more recent fire (Wicked Creek), the effects of post-wildfire logging on forb and bee communities were beneficial: both floral and bee density and species richness were higher in logged areas compared to unlogged areas. In an older fire (Thompson Creek), by contrast, there were minimal effects of post-wildfire logging: the forb and bee communities were very similar between logged and unlogged areas. *Symphoricarpos albus* was pollen limited in unlogged areas in the long-term. The reproductive success of *S. albus* in logged areas was not limited by pollen, but it may have been limited by abiotic resources affected by post-wildfire logging.

As mentioned, this assessment of the effects of post-wildfire logging on forb and bee communities applies to a montane mixed-conifer forest of medium productivity, medium moisture levels, and mixed severity fires. In more productive ecosystems, I would expect that the ecosystem would return to its pre-disturbed state more quickly and would have relatively higher forb and pollinator density and species richness in a more recent fire after post-wildfire logging. In a less productive ecosystem, I would expect that the ecosystem would take longer to return to its pre-disturbed state and would have relatively lower forb and pollinator density and species richness in a more recent fire after post-wildfire logging (Huston 2014).

Current forest management, particularly post-wildfire management, focuses largely on tree growth and regeneration (Belote & Aplet 2014). Despite the fact that insect and understory plant species make up a large majority of forest biodiversity, and the most diverse areas of Montana experience the most logging, little attention is given to managing for biodiversity (Hagar 2007). As disturbance regimes change, it is essential for forest managers to understand community-wide effects of forest management on biodiversity. More importantly, it is imperative that forest managers anticipate expected increases in wildfire frequency and intensity and in post-wildfire logging activity and incorporate these predicted changes into their forest management planning. Lindenmayer and Noss (2006) urge that ecologically informed forest management policies regarding post-wildfire logging must be set in place before major natural disturbances occur so that haphazard decision making can be avoided.

The research herein depicts both the short-term and long-term effects that post-wildfire logging has on forb and pollinator community structure and forb reproduction, and the results of these two studies combined provide useful information for future post-wildfire management of south-central Montana forests. I recommend that forest managers consider the negative long-term implications demonstrated herein that post-wildfire logging has on the sustainability of forest ecosystems and pollination services when determining the extent of post-wildfire logging activity in wildfire-affected areas. However, it is clear that more research is needed to understand the spatial and temporal variability in the effects of post-wildfire logging on forb and pollinator communities and pollination services.

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APPENDIX A

TABLES

Table 5. AIC Model Selection summary table for floral density

Model selection based on AICc:						
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Model 10	65	342687.1	0.0	1	1	-171275.0
Model 9	64	342841.2	154.1	0	1	-171353.2
Model 8	64	344089.6	1402.6	0	1	-171977.4
Model 7	55	356576.3	13889.2	0	1	-178230.6
Model 6	63	344403.9	1716.8	0	1	-172135.6
Model 5	54	356592.6	13905.5	0	1	-178239.9
Model 4	54	357791.3	15104.3	0	1	-178839.3
Model 3	54	345574.9	2887.8	0	1	-172731.0
Model 2	53	357882.5	15195.4	0	1	-178885.9
Model 1	18	395786.8	53099.7	0	1	-197875.1

Table 6. AIC Model Selection summary table for floral species richness

Model selection based on AICc:						
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Model 10	65	6294.6	0.0	0.8	0.81	-3078.8
Model 7	55	6297.8	3.2	0.2	0.97	-3091.4
Model 3	54	6301.5	6.9	0.0	1	-3094.3
Model 9	64	6326.2	31.6	0.0	1	-3095.7
Model 5	54	6337.2	42.6	0.0	1	-3112.2
Model 8	64	6354.0	59.4	0.0	1	-3109.6
Model 4	54	6371.5	76.9	0.0	1	-3129.4
Model 6	63	6395.0	100.4	0.0	1	-3131.2
Model 2	53	6421.5	126.9	0.0	1	-3155.4
Model 1	18	6512.7	218.1	0.0	1	-3238.1

Table 7. AIC model selection summary table for bee density

Model selection based on AICc:						
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Model 19	60	4156.1	0.0	0.7	0.7	-2014.7
Model 30	62	4159.6	3.5	0.1	0.9	-2014.2
Model 29	62	4159.9	3.8	0.1	1.0	-2014.4
Model 35	63	4161.7	5.6	0.0	1.0	-2014.1
Model 3	54	4177.5	21.4	0.0	1.0	-2032.0
Model 10	59	4178.7	22.6	0.0	1.0	-2027.1
Model 23	61	4181.9	25.9	0.0	1.0	-2026.5
Model 22	61	4182.4	26.3	0.0	1.0	-2026.7
Model 34	62	4184.0	27.9	0.0	1.0	-2026.4
Model 32	62	4184.0	27.9	0.0	1.0	-2026.4
Model 13	59	4193.0	37.0	0.0	1.0	-2034.3
Model 26	61	4196.7	40.6	0.0	1.0	-2033.9
Model 25	61	4196.9	40.9	0.0	1.0	-2034.0
Model 31	62	4198.8	42.8	0.0	1.0	-2033.8
Model 6	58	4218.2	62.1	0.0	1.0	-2048.0
Model 17	60	4221.7	65.6	0.0	1.0	-2047.5
Model 16	60	4222.0	66.0	0.0	1.0	-2047.7
Model 28	61	4223.8	67.7	0.0	1.0	-2047.4
Model 9	50	4384.8	228.7	0.0	1.0	-2140.1
Model 21	52	4388.3	232.2	0.0	1.0	-2139.6
Model 20	52	4388.7	232.7	0.0	1.0	-2139.9
Model 4	49	4390.1	234.1	0.0	1.0	-2143.8
Model 33	53	4390.4	234.3	0.0	1.0	-2139.6
Model 12	51	4393.5	237.4	0.0	1.0	-2143.3
Model 11	51	4394.0	237.9	0.0	1.0	-2143.6
Model 24	52	4395.6	239.5	0.0	1.0	-2143.3
Model 5	49	4416.1	260.1	0.0	1.0	-2156.8
Model 15	51	4419.8	263.8	0.0	1.0	-2156.5
Model 14	51	4420.1	264.1	0.0	1.0	-2156.7
Model 27	52	4422.0	265.9	0.0	1.0	-2156.5
Model 2	52	4431.0	274.9	0.0	1.0	-2161.0
Model 1	19	4522.5	366.4	0.0	1.0	-2241.9
Model 8	49	4712.8	556.7	0.0	1.0	-2305.2
Model 7	49	4713.0	557.0	0.0	1.0	-2305.3
Model 18	50	4715.0	558.9	0.0	1.0	-2305.2

Table 8. AIC model selection summary table for bee species richness

Model selection based on AICc:						
	K	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Model 19	60	3393.6	0.0	0.7	0.7	-1633.4
Model 30	62	3396.8	3.2	0.1	0.8	-1632.8
Model 29	62	3397.2	3.6	0.1	0.9	-1633.0
Model 3	54	3398.3	4.7	0.1	1.0	-1642.4
Model 35	63	3398.9	5.3	0.1	1.0	-1632.8
Model 10	59	3412.6	19.0	0.0	1.0	-1644.1
Model 23	61	3415.3	21.7	0.0	1.0	-1643.2
Model 22	61	3416.0	22.4	0.0	1.0	-1643.5
Model 34	62	3417.4	23.8	0.0	1.0	-1643.1
Model 32	62	3417.4	23.8	0.0	1.0	-1643.1
Model 13	59	3431.1	37.5	0.0	1.0	-1653.3
Model 26	61	3434.4	40.8	0.0	1.0	-1652.7
Model 25	61	3434.7	41.1	0.0	1.0	-1652.9
Model 31	62	3436.6	43.0	0.0	1.0	-1652.7
Model 6	58	3451.8	58.3	0.0	1.0	-1664.8
Model 17	60	3454.6	61.0	0.0	1.0	-1664.0
Model 16	60	3455.3	61.7	0.0	1.0	-1664.3
Model 28	61	3456.8	63.2	0.0	1.0	-1663.9
Model 9	50	3509.3	115.8	0.0	1.0	-1702.4
Model 21	52	3512.5	118.9	0.0	1.0	-1701.7
Model 20	52	3512.9	119.3	0.0	1.0	-1701.9
Model 33	53	3514.5	120.9	0.0	1.0	-1701.6
Model 4	49	3515.0	121.4	0.0	1.0	-1706.3
Model 12	51	3517.6	124.0	0.0	1.0	-1705.4
Model 11	51	3518.4	124.8	0.0	1.0	-1705.8
Model 24	52	3519.7	126.1	0.0	1.0	-1705.3
Model 5	49	3550.4	156.8	0.0	1.0	-1724.0
Model 15	51	3553.5	159.9	0.0	1.0	-1723.3
Model 14	51	3554.0	160.4	0.0	1.0	-1723.6
Model 27	52	3555.7	162.1	0.0	1.0	-1723.3
Model 2	52	3564.5	170.9	0.0	1.0	-1727.7
Model 1	18	3585.5	191.9	0.0	1.0	-1774.4
Model 8	49	3681.1	287.5	0.0	1.0	-1789.3
Model 7	49	3681.7	288.1	0.0	1.0	-1789.6
Model 18	50	3683.2	289.7	0.0	1.0	-1789.3