2020

Bird and Native Bee Responses to Habitat Treatments

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Recommended Citation

Oja, Emily Bea, "Bird and Native Bee Responses to Habitat Treatments" (2020). *Graduate Student Theses, Dissertations, & Professional Papers*. 11599.
https://scholarworks.umt.edu/etd/11599

BIRD AND NATIVE BEE RESPONSES TO HABITAT TREATMENTS

By

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B. S. Fisheries and Wildlife
Michigan State University, East Lansing, MI, 2016

Thesis

presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife Biology

The University of Montana
Missoula, MT

May 2020

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ABSTRACT

Oja, Emily B., M.S., Spring, 2020 Wildlife Biology

BIRD AND NATIVE BEE RESPONSES TO HABITAT TREATMENTS

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As forests across the United States have been altered due to fire suppression in the last century, their structure has been altered, resulting in increased fuel loads. Subsequently, managers have been increasingly implementing habitat treatments including prescribed burning, mechanical thinning, and a combination of both treatments to reduce fuel loads and enhance habitat for ungulates. The Rocky Mountain Elk Foundation has partnered with agencies to complete over 10,000 of these treatments across the United States to enhance elk habitat. As treatment impacts to other wildlife species are not well understood, we evaluated the effects of these treatments on the bird and bee communities over varying temporal and spatial factors.

We sampled these communities across eastern Oregon, northern Idaho, and Montana over the summers of 2018 and 2019 at sites treated with prescribed burns, mechanical thins, and thin plus burns, along with paired controls. We evaluated impacts to birds through estimation of the abundance of four focal species and groups of birds, species richness, and species diversity. We found that Mountain Chickadees responded negatively to treatments, and decreased in abundance as surrounding treated area increased, while Bluebirds responded positively to treatments due to removal of the forest canopy. Species richness, diversity, and abundance of Dark-eyed Juncos and Woodpeckers were not impacted by treatments.

Similarly to birds, we estimated abundance, species richness, and species diversity of bees at treated and control sites to assess treatment impacts. Abundance, species richness, and species diversity of bees increased following treatments, largely due to decreased canopy cover at treated sites. Surrounding landscape impacted bee responses, with species diversity increasing with increasing treated area, and abundance increasing with surrounding open area.

Both communities were most impacted by thin-burns than burn treatments, and response to treatment type likely differed because thin-burn treatments removed more canopy and understory vegetation than burn treatments. However, these impacts were time-dependent, with treated sites returning to pre-treatment conditions between 10 and 15 years post-treatment. Overall, we observed positive impacts to the bee community to habitat treatments, while the bird community was largely unaffected by treatments.

ACKNOWLEDGMENTS

There are so many people who need to be acknowledged in helping me to reach the finish line of my graduate career. First, I owe so much to my advisors Dr. Josh Millspaugh and Dr. Chad Bishop, who were amazing and supportive while guiding this whole process. Thank you Josh, for always offering support and advice and reasoning through my crazy analysis ideas, and always reassuring me that things will be OK. Thank you Chad, for your constant encouragement and helping me to relate my findings back to the elk/ungulate habitat treatment world. I'm sorry we didn't discover a new bee species, but I will remember you both if I ever do get the chance to name a new species. I also need to thank my other committee members, Jeff Good and Tom Toman, for being so supportive and offering great insight through this whole process. Additionally, thank you Tom for helping us to coordinate with RMEF, and to RMEF for funding this project.

I would also like to thank the faculty here for providing such a great education and opportunities for growth. I also need to thank Dr. Sandy DeBano, for offering so much knowledge and experience about bees that I was lacking when this project began.

Thank you to my field crews for hiking many miles across the northern Rocky Mountains (which isn't an easy feat). Thank you for working so hard every day and filling endless cups with soapy water. In a similar vein, I am so grateful for all of the Forest Service and BLM biologists who truly made this project possible with help in finding study sites and getting permission to sample.

To the Millspaugh and Bishop labs, thank you for being great friends and always offering guidance. I owe a lot to Stephanie Berry, who was a great mentor at the beginning of this project,

and taught me so much about being a graduate student a field crew leader. And also how to make amazing and gross food in the field. Thank you Chris Hansen, for being my unofficial personal TA and with all of the help and patience with coding, when I probably could have just Googled things half the time. To Dr. Hannah Specht, I do not know how this project would have come together without all of your continuous help in analysis and just thinking about these nongame habitat treatment problems with me. I also need to thank some amazing friends I met during this experience, Chloe Wright, Jess Krohner, and Lauren Snobl, for commiserating and maintaining my sanity, mostly through drinking wine and/or watching reality television with me on a weekly basis.

Finally, I need to thank my family. My mom, Valerie Oja, was truly so supportive through this whole process, and always believed in me and encouraged me to chase after what I want from life. My uncle, Curtis Oja, was also such a huge supporter and has been there for me through it all. Although he’s not here to see me finish this whole process, I would also like to thank my dad, Michael Oja, for making me a (kind of) tough wildlife woman and teaching me how to enjoy and respect the outdoors. To Andersen Beauchine, my partner in life, I cannot express how grateful I am to you. I can’t believe you moved to Montana and stayed through all of this craziness, but I truly could not have done it without your love and support. And also to Jynx, for being an amazing stress relieving kitty, and being there to sit on my lap and purr contentedly whenever I needed you.

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CHAPTER 1

NATIVE BEE RESPONSE TO PRESCRIBED BURNING AND MECHANICAL THINNING IN EASTERN OREGON, NORTHERN IDAHO, AND MONTANA

ABSTRACT

Insect pollinators, and especially bees, are critical for the pollination of wild plants globally, but have experienced huge declines recently in part due to habitat loss. Habitat treatments, including prescribed burning, mechanical thinning, and a combination of both are commonly conducted across the western United States to mitigate wildfire risk through reducing fuel loads, and also to enhance wildlife habitat, primarily for ungulates. As these treatments also affect the bee community, we examined the effects of these treatments on the bee community across eastern Oregon, northern Idaho, and Montana. We found that decreased canopy cover was an important predictor of bee abundance, species richness, and species diversity. As habitat treatments reduced canopy cover and also exposed bare ground cover, an important nesting resource, burn and thin plus burn treatments resulted in increased bee abundance, richness, and species diversity. We found that thin-burn treatments were more beneficial to the bee community than burn treatments, and that these benefits generally decreased over time, with re-treatment recommended at 10-15 years to maintain these benefits. Larger treatments were also more beneficial in increasing bee species diversity than smaller treatments, and higher bee densities were available in open landscapes.

INTRODUCTION

Pollination of crops and wild plants, often by insects, is an important ecosystem service (Buchmann and Nabhan 1996, Kearns et al. 1998, Biesmiejer 2006). Declines in pollinators have been linked to declines in distribution of insect-pollinated plants (Biesmiejer 2006), and in temperate regions, it is estimated that 78% of plant species are pollinated by animals (Ollerton et al. 2011). Of all animal pollinators, many consider bees to be the most important group (Klein et al. 2007, Hopwood 2008, Westphal et al. 2008, Winfree et al. 2009, Potts et al. 2010, Geroff et al. 2014). Although honey bees are considered more economically valuable (Klein et al. 2007), wild bees and insects have been found to increase fruit sets of crops compared to honey bees (Garibaldi et al. 2013). Wild bees also play a critical role in ecosystem functioning of wildlands, pollinating many native wild plants (Biesmiejer 2006, Potts et al. 2010). The important ecosystem services that bees provide are now being threatened, as bee populations decline across the globe (Kearns et al. 1998, Biesmiejer et al. 2006, Burkle et al. 2013). The reasons for these declines are numerous, and include climate change, modern agricultural practices and pesticide use, invasive species, and habitat fragmentation and changes in land use (Kearns et al. 1998, Brown and Paxton 2009, Potts et al. 2010). Of these, habitat fragmentation and land use changes may be the biggest threat that bees face (Brown and Paxton 2009, Potts et al. 2010). Because of this, managing land to conserve bee habitat may be an important tool in ensuring the persistence of bee communities.

Conservation of bees is an increasing conservation priority for many managers, and habitat loss is a critical threat to bees—thus understanding how common habitat management practices affect bee communities may be crucial for their persistence. Two common habitat treatments implemented in forested regions are prescribed burning and mechanical thinning. These treatments are implemented for a variety of reasons, including wildfire mitigation, providing more forage for ungulates and livestock, and altering forest tree species composition and structure (Covington et al. 1997, Graham et al. 1999, Pollet and Omi 2002, Pilliod et al. 2006, Harrod et al. 2007). The Rocky Mountain Elk Foundation (RMEF) has treated over 7 million acres of land across the U.S., primarily with the objective of elk (*Cervus canadensis*) habitat improvement. The treatments used are typically either mechanical thinning, prescribed burning, or a combination of both. Generally, impacts resulting from prescribed burning can include higher production of herbaceous plants, increases in canopy height, structural complexity, and reduction of snags and downed logs (Covington et al. 1997, Pilliod et al. 2006, George and Zack 2008). Mechanical thinning can provide more control in removing specific trees, and can result in greater reduction in the forest canopy (Harrod et al. 2007), which can be beneficial to species that utilize open habitats, such as deer, elk, and some bird species (Pilliod et al. 2006).

Although it is generally understood how these treatments impact ungulates and other wildlife (Converse et al. 2006, Pilliod et al. 2006, Long et al. 2008), impacts to the bee community are less well known (Rivers et al. 2018). Some studies have found that burning and thinning increase bee richness and abundance (Campbell et al. 2007, Hanula et al. 2015). Higher abundance in treated forests could be due to a lower basal area, decreased canopy cover, or an increase in herbaceous cover (Potts et al. 2003*a*, Campbell et al. 2007, Grundel et al. 2010, Hanula et al. 2015). Higher species richness may be attributed to a higher floral species richness, or an increase in nesting resources, primarily in the form of bare ground (Potts et al. 2003*a*, Campbell et al. 2007, Hopwood 2008, Hanula et al. 2015). However, the effectiveness of treatments is likely limited in time as the forest canopy closes, the tree density increases, and floral abundance and diversity decreases post-treatment (Potts et al. 2003*a*, Hanula et al. 2015). Landscape context may also influence the response of the bee community to habitat treatments. Past studies have found that landscape surrounding a study patch (e.g. proportion of surrounding meadow, semi-natural habitat, arable land) affects species richness and abundance of bees at a patch, however the impact of patch size on species richness and abundance is not clear (Steffan-Dewenter 2002, Steffan-Dewenter 2003, Hatfield and Lebuhn 2007, Heard et al. 2007).

We determined the effects of prescribed burning and mechanical thinning on the bee community in Montana, northern Idaho, and eastern Oregon. To determine the impacts of these habitat treatments on the bee community, we hypothesized the following:

1) Treatments will result in increased bee richness and abundance due to increased floral species richness and abundance.
2) Treated sites surrounded by open, grassland habitat will have a higher abundance, species richness and diversity of bees than those surrounded by forest.
3) Treated sites will have a lower bee abundance and species richness as time since treatment increases due to canopy closure over time, and declining floral abundance and species richness.
4) Larger treatments will have a higher bee abundance and species richness than smaller treatments, because there will be more floral and nesting resources resulting from the treatment.

STUDY AREA

Our study occurred in five general regions in the northern Rocky Mountains across eastern Oregon, northern Idaho, and Montana. These regions include the Starkey Experimental Forest, Clearwater Region, north Idaho and Kootenai Region, Lolo National Forest Region, and eastern Montana Region (Figure 1). Forests in these regions have been altered by fire suppression following European settlement (Covington and Moore 1994), but past conditions were likely a product of fires burning at varying intensities throughout these forest types (Habeck and Mutch 1973, Arno 1980). These regions are all located within the northern Rocky Mountains, and confined to coniferous forests primarily composed of ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*). The terrain across this region is complex and slopes can range up to 40 degrees.

The Starkey Experimental Forest is located in northeastern Oregon. Starkey is surrounded with game proof fencing to support ungulate research (Rowland et al. 1997). Forests at our sites sampled in Starkey are composed primarily of ponderosa pine and Douglas fir, but also contained lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and grand fir (*Abies grandis*). The elevation in this region ranges between 1220 and 1520 meters, and precipitation averages 51 cm per year (Skovlin 1991). The average temperatures in mid-summer are between 12°C and 31°C (Rapp 2004). The Starkey Experimental Forest is composed primarily of ponderosa pine and Douglas fir forests (Skovlin 1991, Long et al. 2008).

The Clearwater Region is primarily located in east-central Idaho, and ranged from about 740 meters to 1505 meters in elevation at our study sites. Warm, moist Pacific air masses affect the climate of much of the Clearwater River Sub-basin, and precipitation varies across the Sub-basin between 30 cm up to 228 cm per year (Clark and Harris 2011). Summer temperatures average between approximately 15˚ C to 21˚ C (Clark and Harris 2011). The forests at our study sites in this region were primarily composed of Douglas fir and ponderosa pine, but also contained western larch and grand fir, while the understory ranges from grass/forb to seral shrub to closed forest canopy with little understory vegetation (Unsworth et al. 1998).

The Kootenai/north Idaho region is composed of areas in the Kootenai National Forest and the Idaho Panhandle National Forest. The forests at our study sites in this region were primarily composed of ponderosa pine and Douglas fir, but also contained grand fir, lodgepole pine, and western larch. Elevation in our sites in this region ranged from approximately 820 meters to 1740 meters. Average annual precipitation ranges from 35 cm to 92.7 cm (Kuennen and Nielsen-Gerhardt 1995). Average summer temperatures in locations across this region range from 14°C to 21°C (Arguez et al. 2010).

The Lolo Region is primarily in west-central and southwestern Montana, and elevations in the Lolo Region at our study sites ranged from 994 meters to 1969 meters. The average temperatures in the Lolo National Forest are approximately 19°C in midsummer, and annual precipitation ranges from 38 cm to over 254 cm (Sasich and Lamotte-Hagen 1989). Forests in our study sites in the Lolo region were primarily composed of Douglas fir and ponderosa pine, but also contained grand fir and lodgepole pine. The fire frequency in this area is approximately 30-100 years (Sasich and Lamotte-Hagen 1989). There are a combination of grasslands and coniferous forests of primarily Ponderosa pine and Douglas fir in this region (Bourne 1959).

The eastern Montana region is composed of Bureau of Land Management (BLM) land bordering the Flathead National Forest, parts of the Beaverhead Deer Lodge National Forest, and Tin Can Hill, BLM land in central eastern Montana which borders the Musselshell River. The Beaverhead National Forest section of this area receives between 30 and 140 cm of precipitation and the average summer temperature is 17°C (Greene 2007). Forests in the Beaverhead-Deer Lodge and Ovando areas in this region were composed primarily of ponderosa pine and Douglas fir, but also contained lodgepole pine, grand fir, Rocky Mountain juniper (*Juniperus scopulorum*), and western larch. Elevation at study sites in this part of the region ranged from 1230 meters to 2150 meters. The Tin Can Hill area of this region is a mixed area of BLM lands and private agricultural area. The elevation in this area ranged from 710 to 906 meters and the forests were primarily composed of ponderosa pine, Douglas fir, and Rocky Mountain Juniper.

METHODS

Site Selection

Our study sites were managed by state and federal agencies who used matching funds from RMEF to conduct habitat treatments to primarily benefit elk. Sites were treated with either prescribed burning, mechanical thinning, or both. Sites were selected to represent our five study regions and forest stand age classes as equally as possible (Table 1). After identifying available sites within the regions, we selected sites within to ensure an equal distribution as possible of forest stand ages, with access to the sites and the retreatment of older sites limiting our ability to equally represent sites with stand ages greater than 15 years. Within the Starkey Experimental Forest, most of the treatment units were too small to accommodate multiple points, so we selected treatment units that could contain at least two points, and selected the nearest control unit(s) (which were already identified for other research projects within Starkey) that could also accommodate the same number of points. Once sample sites were identified, we chose a control unit near the treated unit that was as similar as possible with respect to potential vegetation type, aspect, and slope (Figure 2). One of our control units in the Idaho Clearwater region was used for two treated sites that were close in proximity and had limited appropriate controls available in the area. If there were multiple units treated, we paired control units with each unit where possible. Within the control unit(s), we randomly selected points in the same way as treatment sampling points were selected. Though we sampled three treatment types, we were only able to sample two mechanical thins, so we only assessed burns and thin-burns.

Sample Point Selection

This study was conducted in conjunction with a retrospective study of bird abundance, and to increase efficiency, sample points for this study coincided with points used for the bird study. In each treatment and control unit, four points were randomly selected that were at least 100 meters from a road, 100 meters from the edge of a treatment unit, and a minimum of 250 meters apart. Points were also selected to fit as many points into a treatment unit as possible within our sampling constraints. Therefore, units selected contained at least 100 meters by 300 meters of available sample area to be used for the study. Due to the need to maximize our sampling effort within limited time across complex terrain, sampling points were within 2.5

kilometers of a road, and no more than 4 kilometers apart, unless they were less than 750 meters from a road. At one site with especially challenging terrain, points were selected so that the closest two points were within 1500 meters of a road and 650 meters apart. If a treatment was composed of multiple distinct units, starting points were within 1 km of a road. Of the four points selected, the two points closest to a road were used in bee sampling. We used 100 meter long transects to sample bees, randomizing the direction of the transect from the sampling point.

Field Methods

We collected bees along two, 100 meter long transects in each treatment and control unit (Heard et al. 2007, Popic et al. 2013). To capture variation throughout the summer, we sampled the same transects three times between May 15th and August 24th, 2018 and May 7th and August 2nd, 2019. To collect bees, we used a combination of pan traps and hand netting to represent species that may not be efficiently captured by one method alone (Westphal et al. 2008, Popic et al. 2013). Pan trap sampling is a method of trapping bees which utilizes brightly colored bowls filled with water and soap; when a bee is attracted to the color of the trap, it flies into the trap and drowns, and is collected at the end of the sampling period (Cane et al. 2000, Westphal et al. 2008). The pan traps were UV blue, UV yellow, and white. These colors have been shown to be attractive to many bee species (Droege 2006, Popic et al. 2013). Along each transect, 6 groups of three pan traps (one of each color, placed in a triangle formation) were spaced 20 meters apart, resulting in 18 pan traps per transect. To reduce competition amongst the 3 traps within a cluster, they were spaced 5 meters apart (Droege 2006, Westphal et al. 2008). Additionally, as previous studies have shown that elevated pan traps may collect a higher bee species richness and abundance (Tuell and Isaacs 2009, Geroff et al. 2014), we elevated one pan trap of each group to the height of the tallest blooming flower within a meter. The elevated pan was the blue pan at 0 and 60 meters along the transect, the white pan at 20 and 80 meters along the transect, and the yellow pan at 40 and 100 meters along the transect. If there were not blooming flowers within a meter of the pan, the pan was not elevated. We filled the traps in the morning between 07:00 and 11:00, and collected the traps between 14:00 and 15:00. We recorded weather conditions (cloud cover, temperature, rain, wind speed) throughout the day that may affect catch rate, especially unfavorable weather conditions.

To collect bees that may not be represented by the pan traps (Popic et al. 2013), we also netted along transects twice a day for 30 minutes between 9 am and 12 pm, and 12 pm and 3 pm (Lebuhn et al. 2003, Popic et al. 2013). Observers began netting at the starting point of transects, recording approximate distance walked during the netting period and their end coordinate. Netting was conducted only in favorable weather conditions (temperature greater than 12 C, little to no wind (less than 5 m/s), low cloud cover (less than 60% cloud cover), and no rain). All bees collected were sent to Utah State University for identification.

To assess vegetation characteristics related to the bee community at each site, we used (50 cm x 50 cm) quadrats along the transect next to each pan trap, totaling 18 quadrats along the transect (Ockinger and Smith 2007). Within the quadrats, we measured floral diversity and abundance, and visually woody debris, and cover of bare ground (Campbell et al. 2007, Ockinger and Smith 2007, Hopwood 2008, Grundel et al. 2010, Hanula et al. 2015). We generally rounded woody debris and bare ground cover to the nearest 5%, however we estimated values between 0% and 2% to the nearest 1% during the 2019 sampling year. Within each quadrat, floral abundance was measured by counting the number of 10 cm x 10 cm squares (out of 25 total squares) that contained blooming flowers, and floral diversity as the number of species of blooming flowers present within 50 x 50 cm plot (Ockinger and Smith 2007). At each pan trap, we also measured canopy cover using a Moosehorn (Robinson 1947, Cook et al. 1995, Grundel et al. 2010), and we measured slope and aspect along 20 meter intervals of the transect where the traps were located. Finally, to assess effects of surrounding landscape on bee richness and abundance, we used ArcGIS and data from the National Land Cover Database (NLCD 2016; Yang et al. 2018) to determine the percent of surrounding landscape within 800 meters of the transect that was open/grassland area (Steffan-Dewenter 2003, Grundel et al. 2010).

Analytical Methods

Abundance

Due to scarcity of data with a very large number of pans collecting zero bees, a zero inflated Poisson model did not work at the pan level. Additionally, with the low number of replicates of our treatment types and few bees collected in the Lolo region control sites, our model would not converge with spatial random effects and weather covariates. Therefore, we took an alternative approach of modeling the effects of continuous habitat covariates on bee abundance. We also tested the effects of treatments on these habitat covariates, which allowed us to examine habitat-bee relationships, habitat-treatment relationships, and treatment-bee relationships.

We used Generalized Linear Models with a negative binomial distribution and number of bees caught at the transect-level within visits as our response. Due to inconsistent levels of netting effort, we only used bees captured in our pans in these analyses. We also included categorical weather variables to account for variation in weather during our sampling periods (Table 2). We standardized all covariates and tested for correlations between variables that may be highly related, including floral species richness and the number of elevated traps along a transect, which were highly correlated (r^2=0.48). Since floral species richness explained more variation in the data, and floral abundance was more highly correlated with the number of elevated traps than with floral richness, we retained floral richness in our models and removed the sum of elevated pan traps.

Our models were based on *a priori* habitat and landscape hypotheses, and all models, including our null model, contained covariates to account for variation due to amount of active trap time (in minutes), date of sampling, and our weather covariates (Table 2). Our *a priori* models included a floral community model (floral abundance and floral species richness measured as the sum of blooming flowers and the sum of blooming species along a transect), nesting resources model (percent cover of bare ground and dead woody debris), a canopy cover model, a landscape model (including percent of surrounding open habitat and treated area within 800 meters), and combinations of those models (Table 3). Since we collected data on percent of bare ground in a more specific manner in 2019 than 2018, we used mean values of percent bare ground in 2019 and applied those values to matching transects sampled in 2018. For transects sampled in 2018 and not 2019 (n=25), we applied the mean bare ground estimate from the region level to those transects. For all other missing transect-level habitat covariates, we imputed the mean value of that covariate across all of our samples. We also derived the mean and standard error for our vegetation covariates measured across our treatment types to compare values between treatments and their paired controls, and evaluate any differences across time since treatment (binned as 1-5 years, 6-10 years, 11-22 years).

We used Akaike's Information Criterion corrected for small sample sizes ("AICc"; Burnham and Anderson 2002) to select our top model, but did not interpret parameters that were likely uninformative based on confidence intervals (Arnold 2010). With our top model, we predicted bee abundance over the mean values of covariates in each of our paired treatment and control sites (estimating one value for mean abundance across the paired treatment transects and control transects on each sampling visit, since we would not expect a static abundance across the summer after removing bees). We then subtracted the predicted control mean abundance from the mean treated abundance within each site (with a "site" being unique to a treatment type, time since treatment, and overall location), propagated our error through this process, and plotted these values over time since treatment to evaluate the hypothesis that habitat characteristics of treatment sites (and resultant changes in bee abundance) converges with that of their paired controls with greater time since treatment.

Species Richness and Diversity

We used the same analytical process to evaluate bee species richness and diversity across our treatment types as we did for abundance. Species richness was measured as the number of distinct species caught at a transect on a specific date, since our collection involves removing bees and we therefore would not expect a static community across our sampling events. We used the package vegan in R (Oksanen et al. 2019) to obtain Shannon diversity estimates applied at the same level. We excluded diversity estimates of 0 from our model as they were not informing the model and were skewing our data towards 0. We also generated species accumulation curves using the package iNEXT in R (Chao et al. 2014, Hsieh et al. 2019), to compare species accumulated across our sampling effort between treatments and their paired controls. Effort was calculated as the number of transects that collected bees on a unique date (meaning that the same transect could be represented up to six times in our accumulation curves).

RESULTS

Habitat

Across all times since treatment (groups of 1-5 years, 6-10 years, and 11-22 years) and treatment types (burns and thin-burns), canopy cover was lower in treatments than in their respective controls (Figure 2). Floral abundance and richness were not different between treatments and their respective controls in any time since treatment (Figure 3). However mean floral abundance was lower and mean floral richness was higher in burn treatments, regardless of their stand age, relative to their controls. In thin-burn treatments, floral abundance was higher irrespective of time since treatment, and floral species richness was higher in the 1-5 year and 11-22 year groups, but lower in the 6-10 year group. In both thin-burn and burn only treatments, downed woody debris was lower in treated sites when compared with controls (Figure 4). Treatments also exposed bare ground cover, as bare ground cover was higher in thin-burn treatments between 6 and 22 years post-treatment, while mean bare ground cover was higher in burns compared to controls (Figure 4).

Bee Collection

Over our field sampling seasons, we captured 5,769 bees representing 225 distinct species. Of the captured bees, ten species were only captured by net, and we used 4,614 bees captured in pans in our analyses, representing 214 species. Overall, sweat bees were most captured, with the most numerous species being the sweat bees of the species *Halictus tripartitus* (n=1339), Pruinose Metallic-Sweat Bee (*Lasioglossum pruinosum* (n=295)), Confusing Metallic Furrow Bee (*Halictus confuses* (n=195)), sweat bee of the species *Lasioglossum marinense* (n=178), sweat bee of the species *Lasioglossum incompletum* (n=174), Cooley’s Sweat Bee (*Lasioglossum cooleyi* (n=128)), and the Orange-legged Furrow Bee (*Halictus rubicundus* (n=100)). Some rare species captured included mining bees *Andrena shoshoni and Andrena gardineri,* long-horned bees *Eucera actuosa, Eucera delphinii, Eucera hamata, Eucera lepida, Eucera pallidihirta, Melissodes composite,* and *Melissodes verbesinarum,* sweat bee *Nomia* *universitatis,* cuckoo bee *Neopasites n. sp.,* mason bees *Osmia indeprensa, Osmia iridis,* and *Osmia malina,* and cuckoo bees *Stelis callura* and *Stelis labiata.*

Abundance

The top model for bee abundance was the global model, including covariates for canopy cover, percent of surrounding area that is open and surrounding treated area within 800 meters, floral covariates, and nesting covariates (Tables 4, 5). The amount of time that traps were active was positively associated with abundance, and date was negatively associated with abundance, meaning more bees were available for capture later in the season. Weather also correlated with the abundance of bees caught, with less bees available for capture on days that were mostly cloudy for some portion of the day, and days colder than 12°C.

Important habitat and landscape predictors of bee abundance included canopy cover, percent of surrounding open area, dead woody debris cover, and percent of bare ground cover. Canopy cover was negatively associated with bee abundance (Figure 5); over an increase in canopy cover from 0 to 100%, we would expect a 73% decrease in the relative abundance of bees. Percent of surrounding open area was positively associated with bee abundance (Figure 5), with an increase of surrounding open area from 0.09% to 73% associated with an increase in relative abundance of 412%. Dead woody debris was negatively associated with bee abundance, with an expected decrease in relative abundance of 63% over an increase in dead woody debris cover from 0 to 52.2% (Figure 5). Percent of bare ground cover was positively associated with bee abundance, with an expected increase in bee abundance of 355% over an increase in percent bare ground over 0 to 40.3% (Figure 5). There were also signals that bee abundance was negatively related to floral abundance and percent of surrounding treated area, but confidence intervals slightly overlapped with 0 (Table 5).

Burn treatments had an overall positive effect on bee abundance, but benefits from treatment declined over time since treatment (Figure 6). The mean predicted abundance at thin-burn treatment sites were all higher than their respective controls except for two sampling occasions (two different sites measured on unique days), and as time since treatment increased, the difference in abundance between treatments and paired controls became smaller. Thin-burns had a larger positive effect than burns on bee abundance because thin-burns had a larger impact on reducing canopy cover and exposing bare ground, however that effect was ameliorated over time (Figure 6).

Species Richness and Diversity

The top model for species richness was the nesting resource plus canopy cover model (Tables 6, 7). For diversity, the top model was the canopy cover plus landscape model (Tables 8, 9). The amount of time that traps were active was positively associated with richness and diversity, and date was negatively associated with richness and diversity, meaning more bee species were available for capture later in the season. Weather covariates were important predictors of bee richness, but not diversity. Therefore, bee species were less available for capture on days that were mostly cloudy for some portion of the day, and days colder than 12°C, but this was not an important determinant in the Shannon diversity of the species available.

Habitat and landscape predictors important for bee species richness were canopy cover and percent of bare ground, while canopy cover and percent of surrounding treated area were important predictors for bee species diversity. Increasing canopy cover had a negative effect on both species richness and diversity (Figures 7,8). Over an increase of 0% to 100% canopy, we would expect a relative decrease of 79% in bee richness and 42% decrease in relative bee species diversity. Percent of bare ground had a positive effect on species richness (Figure 7). Over an increase in percent bare ground from 0% to 40.3% we would expect an increase in relative species richness of 124%. Percent of surrounding treated area had a positive effect on species diversity (Figure 8). Over an increase of surrounding treated area from 0% to 99.96%, we would expect a relative increase of 60.4% in species diversity. Our model signaled that surrounding open area may also have a negative effect on bee diversity, but confidence intervals slightly overlapped 0.

Predicted bee species diversity and richness was higher in most thin-burns and most burns relative to controls, and over time, the difference between treatments and controls in species diversity and richness became smaller (Figure 6). It is likely that richness and diversity were generally higher in treatments than controls partly because of reduced canopy cover. We suspect that larger treatments also have a more positive impact on species diversity relative to smaller treatments, given the positive effect of surrounding treated area on species diversity. Our species accumulation curves showed support for the positive effects of treatments on bee species richness that our models suggested (Figure 9). While we did not reach the number of samples necessary to sample the whole bee community, species were accumulated at a significantly higher rate in burns and thin-burns than in their respective controls, indicating a higher species richness at treated sites relative to their respective controls.

DISCUSSION

Overall, our results showed that decreased canopy cover and increased bare ground cover are important habitat predictors of higher abundance and species richness of bees in the northern Rocky Mountains. Habitat treatments reduced canopy cover and increased bare ground cover, which resulted in overall higher bee abundance and richness in treated sites than their paired controls. Thin-burn treatments were more effective in removing canopy and exposing bare ground, and therefore resulted in higher bee abundance and bee species richnessthan burn treatments. Bee abundance and species diversity were also predicted by the surrounding landscape, with bee abundance positively associated with surrounding open landscape, and bee species diversity positively associated with surrounding treated area.

Floral abundance and richness were unexpectedly not important predictors of the bee community. While some past studies have found that floral resources are important in structuring the bee community (Potts et al. 2003*b*, Hopwood 2008), others have found that floral abundance is not strongly linked to bee abundance (Tepedino and Stanton 1981), and that the bee community overall is weakly predicted by the plant community (Grundel et al. 2010). There are a few reasons that could explain the weak connection between the floral and bee communities in our study. Different species of flower provide varying level of foraging resources (Potts et al. 2003*b*) so some plant species may have been more important than others for the bee community sampled, or there may not have been strong links between specific bee and plant species (Grundel et al. 2010). It is also possible that a different sampling method or a higher effort in sampling the floral community surrounding transects may have resulted in a stronger link between bee responses and floral communities at our sampled sites. Overall, although our results indicated canopy cover and bare ground cover were more important predictors of the bee community than floral abundance and richness, this is not to say that floral resources are not critical for bees.

Canopy cover and bare ground cover were much more important predictors of the bee community than floral resources. This result could help managers to evaluate treatments over time for impacts on bees because it is much simpler to measure canopy cover and bare ground than to sample the floral community. Reduced canopy cover or reduced basal area, generally related with more open habitat, has been linked with increased bee abundance by past studies (Campbell et al. 2007, Grundel et al. 2010, Hanula et al. 2015). Increased bee abundance could be due to increased herbaceous cover, or simply increased microhabitat quality, as warmer sunnier conditions are more suitable for bees (Campbell et al. 2007, Chaplin-Kramer et al. 2011). The importance of bare ground relative to woody debris for bee abundance and richness indicated by our results suggests that the bee community sampled may have been composed of more ground-nesters than wood-nesters. Nesting resources are an important consideration when treating habitat for bees, because while treatments that involve prescribed burning can expose bare ground, they will likely also result in reduced woody debris (Figure 4).

While habitat impacts from treatments are clearly important predictors for the bee community, our results also indicated that surrounding landscape matrix may be an important consideration for managers deciding where to conduct treatments. We found that surrounding open area was an important predictor for bee abundance, and was slightly negatively associated with bee species diversity. Our landscape results indicate that open landscapes are highly productive for a few dominant bee species, whereas the composition of the bee community in forested areas may be more even. Additionally, our results indicated that bee communities at treated sites were more even than at control sites, and that surrounding treated area increased bee diversity, potentially indicating that larger treatments are more beneficial in increasing bee species diversity than smaller treatments. Habitat treatments in these areas may have increased habitat heterogeneity, increasing general habitat suitability for a suite of species which were found in a more even distribution. These results could also be partly influenced by some of our control sites in the very open landscape of the Tin Can Hill area of our Eastern Montana region, which were extremely productive for some species (especially *Halictus tripartitus*). Treated sites in this area were also much larger than other treated sites in our study, potentially influencing the result that surrounding treated area was weakly negatively associated with bee abundance (Table 5). These controls may have also driven the result that bee diversity increased with surrounding treated area, if a few species in the Tin Can controls were very dominant and drove down the species diversity in that area.

The final major consideration when conducting habitat treatments to benefit wildlife species concerns time, and what an appropriate time frame is to re-treat previously treated areas to maintain benefits to wildlife species. Although it is difficult to specify an exact time frame that would maximize benefits for bees with consideration to costs and effort of conducting treatments, our results suggest that at 10 to 15 years, benefits of treatments to bees seem to decrease as treated sites become more similar to their assumed pre-treatment condition. This result fits with the historical fire regime in this region, which indicates that low-intensity fires occurred every 15-30 years before the fire suppression era (Arno 1980).

However, it is difficult to fully evaluate the effect of time since treatment, as we did not have any thin-burn treatments available to sample that were between 1 and 3 years post-treatment. Additionally, landscape and treatment intensity may also play an important role in answering this question. The thin-burn treatments that were 8-10 years post-treatment were both conducted in a generally open woodland area in our eastern Montana region, so treatments may not have caused as dramatic of an impact as the thin-burn treatments that were 4-6 years post-treatment in the more densely forested Lolo and north Idaho regions. Our time since treatment figure (Figure 6) supports this idea, as we can see a decrease in bee abundance, richness, and diversity at the 8-10 year mark post-treatment in thin-burns, however these metrics generally increase again at the 15-17 year mark, which represents our Starkey sites. Treatments at Starkey were conducted in a denser forest type compared to the eastern Montana region, and may have burned at a higher intensity than treatments in the eastern Montana region. So although there is likely a pattern of time since treatment, especially for species richness and diversity, landscape and other treatment factors may also be influencing bee responses.

Although there is a strong indication that treatments positively impacted the bee community, this is in relation to controls, which can be difficult to choose when completing these retrospective habitat studies. First, it was difficult to find an appropriate control based on our criteria in some situations where a lot of the surrounding landscape was treated, burned by a wildfire, or a different habitat type. It is also difficult to assess if any management activities have taken place on the control plots, and natural events, such as windstorms or bark beetle outbreaks, may impact them differently than the treatments. For example, our sites at the Starkey Experimental Forest experienced a past bark beetle outbreak, but agencies may not know or record this information for all of the public lands they manage. A before-after control-impact design may be better to address some of these concerns, but this study design is often not possible for studies that are trying to assess impacts from treatments conducted 20-30 years ago. However, as there seems to be strong patterns and indications in our results using multiple lines of evidence, we are confident that the prescribed burns and burn-thins as implemented and described are having positive impacts on the bee communities.

Overall, based on this research, we would recommend that managers wishing to maximize treatment benefits to bees should consider a combination of thinning and burning which will likely be more positively impactful than prescribed burn treatments alone. Additionally, managers may see larger positive impacts to species diversity by conducting larger treatments in forested areas. Finally, if managers wish to sustain these benefits created by opening the forest with habitat treatments, re-treatment may be necessary between 10 and 15 years post-treatment.

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TABLES AND FIGURES

Table 1: Descriptions of our sites sampled including the year of treatment, region, and size in acres.

Treatment Type	Region	Year of Treatment	Size
Thin-burn	Starkey	2001	271 acres
Thin-burn	Starkey	2003	675 acres
Burn	Eastern Montana	1997	212 acres
Burn	Eastern Montana	1997	54 acres
Thin	Eastern Montana	2012	243 acres
Thin-burn	Eastern Montana	2009	244 acres
Thin-burn	Eastern Montana	2010	208 acres
Burn	Eastern Montana	2010	1361 acres
Burn	Eastern Montana	2012	3853 acres
Burn	Eastern Montana	2015	6657 acres
Burn	Eastern Montana	2017	2509 acres
Burn	Lolo	2004	90 acres
Thin	Lolo	2006	566 acres
Thin-burn	Lolo	2014	124 acres
Burn	Lolo	2016	3275 acres
Thin-burn	North-Idaho Kootenai	2013	167 acres
Burn	North-Idaho Kootenai	2018	40 acres
Burn	North-Idaho Kootenai	2013	553 acres
Burn	Clearwater	2008	1019 acres
Burn	Clearwater	2011	1207 acres
Burn	Clearwater	2014	967 acres
Burn	Clearwater	2018	223 acres

Table 2: Descriptions of how weather was categorized in our analysis.

Weather covariate	Category	Description
Cloud	0	Sunny to partly cloudy all or most of day
Cloud	1	Mostly cloudy (>60%) for some time less than half of the sampling time
Cloud	2	Mostly cloudy (>60%) for a majority of the sampling time
Temperature	0	Temperature less than 12°C for more than half of the day
Temperature	1	Temperature less than 12°C for less than half of the day, between 12°C and 16°C the rest of the day
Temperature	2	Temperature greater than 12°C for the majority to all day
Rain	0	No rain all day
Rain	1	Brief rain showers to intermittent brief showers throughout the day

Table 3: The *a priori* models used in the bee analysis, along with covariates and descriptions of the hypotheses tested.

Model name[1]	Hypothesis	Variables included
Floral	The availability of floral resources will determine the bee response tested	Floral species richness+ floral abundance
Nesting	The availability of nesting resources will determine the bee response tested	Dead woody debris + bare ground
Canopy Cover	Reduced canopy cover will determine the bee response tested	Canopy cover
Landscape	The surrounding landscape (within 800 meters) will determine the bee response tested	Open area + treated area
Canopy Cover Floral	Reduced canopy cover and the availability of floral resources will determine the bee response tested	Canopy cover + floral species richness+ floral abundance
Canopy Cover Nesting	Reduced canopy cover and the availability of nesting resources will determine the bee response tested	Canopy cover+ dead woody debris + bare ground
Canopy Cover Landscape	Reduced canopy cover and the surrounding landscape will determine the bee response tested	Canopy cover+ open area + treated area
Global	All floral, nesting, canopy, and landscape variables will determine the bee response tested	Canopy cover+ floral richness+ floral abundance + dead woody debris + bare ground + open area + treated area

[1] The base model is trap time+cloud+temperature+rain+date. All models contain these covariates in addition to explanatory habitat and landscape covariates.

Table 4: The global model containing habitat and landscape covariates was the top ranking model for bee abundance. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into abundance models for bees in the northern Rocky Mountains 2018-2019.

Model[1]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Global	17	2017.399	0	0.999904	0.999904
Canopy Cover Landscape	13	2035.956	18.55775	9.34E-05	0.999998
Canopy Cover Nesting	13	2043.494	26.09538	2.15E-06	1
Canopy Cover Floral	13	2062.739	45.34023	1.43E-10	1
Landscape	12	2063.314	45.91494	1.07E-10	1
Landscape Floral	14	2064.036	46.63727	7.46E-11	1
Canopy Cover	11	2064.839	47.44	4.99E-11	1
Nesting	13	2070.365	52.96644	3.15E-12	1
Base	10	2150.447	133.048	1.29E-29	1
Floral	12	2154.538	137.1394	1.66E-30	1

Table 5: Coefficients (Coeff), standard errors (SE), and p (Pr(>|z|) values for covariates in the global abundance model for bees in the northern Rocky Mountains in 2018-2019.

Coeff	Estimate	SE	Pr(>|z|)
(Intercept)	-0.3	0.44	0.49
time	0.29	0.072	3.51E-05
Cloud1	-0.54	0.18	0.002
Cloud2	-1.2	0.3	5.94e-05
Cloud3	-2.6	0.44	2.65e-09
Temp1	1.75	0.56	0.0019
Temp2	2.72	0.44	9.02e-10
Rain1	-0.22	0.27	0.42
Date	-0.55	0.086	1.48e-10
Canopy	-0.40	0.097	3.91e-05
Floral Richness	-0.12	0.083	0.16
Floral Abundance	-0.14	0.074	0.052
Downed Woody Debris	-0.20	0.094	0.037
Bare Ground	0.27	0.071	0.00018
Open Area	0.45	0.085	1.31e-07
Treated Area	-0.12	0.07	0.082

Table 6: The canopy cover nesting model was the top ranking model for bee richness. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into richness models for bees in the northern Rocky Mountains 2018-2019.

Model[1]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Canopy Cover Nesting	13	1624.036	0	0.5	0.5
Global	17	1625.5	1.47	0.24	0.74
Canopy Cover Landscape	13	1625.72	1.68	0.21	0.95
Canopy Cover	11	1629.40	5.37	0.034	0.99
Canopy Cover Floral	13	1631.21	7.17	0.014	1
Nesting	12	1664.79	40.76	7.03E-10	1
Landscape	12	1676.057	52.021	2.52E-12	1
Landscape Floral	14	1679.93	55.89	3.63E-13	1
Base	10	1713.8	89.76	1.61E-20	1
Floral	12	1717.18	93.14	2.97E-21	1

Table 7: Coefficients (Coeff), standard errors (SE), and p (Pr(>|z|) values for covariates in the canopy cover and nesting richness model for bees in the northern Rocky Mountains in 2018-2019.

	Estimate	Std. Error	Pr(>|z|)
(Intercept)	-0.072	0.33	0.83
time	0.27	0.051	2.41e-07
Cloud1	-0.27	0.12	0.031
Cloud2	-0.56	0.21	0.0071
Cloud3	-1.95	0.35	1.82e-08
Temp1	1.08	0.4	0.0073
Temp2	1.72	0.33	2.70e-07
Rain1	-0.3	0.18	0.11
Date	-0.39	0.055	1.21e-12
canopy	-0.48	0.068	1.73e-12
Downed woody debris	-0.059	0.064	0.36
Bare Ground	0.14	0.049	0.004

Table 8: The canopy cover landscape model was the top ranking model for bee diversity. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into diversity models for bees in the northern Rocky Mountains 2018-2019.

Model[1]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Canopy Cover Landscape	13	358.11	0	0.8	0.8
Landscape	12	361.96	3.85	0.12	0.92
Global	17	364.89	6.78	0.027	0.94
Canopy Cover	11	365.75	7.63	0.018	0.96
Landscape Floral	14	366.33	8.22	0.013	0.98
Base	10	366.99	8.87	0.0095	0.98
Nesting	12	367.39	9.27	0.0078	0.99
Nesting canopy cover	13	368.72	10.61	0.004	1
Canopy Cover Floral	13	369.85	11.74	0.0023	1
Floral	12	371.4	13.29	0.001	1

Table 9: Coefficients (Coeff), standard errors (SE), and p (Pr(>|t|)) values for covariates in the canopy cover landscape diversity model for bees in the northern Rocky Mountains in 2018-2019.

	Estimate	Std. Error	Pr(>|t|)
(Intercept)	1.08	0.32	0.00083
time	0.12	0.04	0.0022
Cloud1	0.011	0.098	0.91
Cloud2	-0.047	0.15	0.76
Cloud3	-0.28	0.4	0.48
Temp1	-0.08	0.36	0.83
Temp2	0.39	0.32	0.22
Rain1	-0.17	0.15	0.26
Date	-0.16	0.042	7.11e-05
canopy	-0.11	0.044	0.016
Open	-0.085	0.044	0.054
Treated Area	0.13	0.041	0.0018

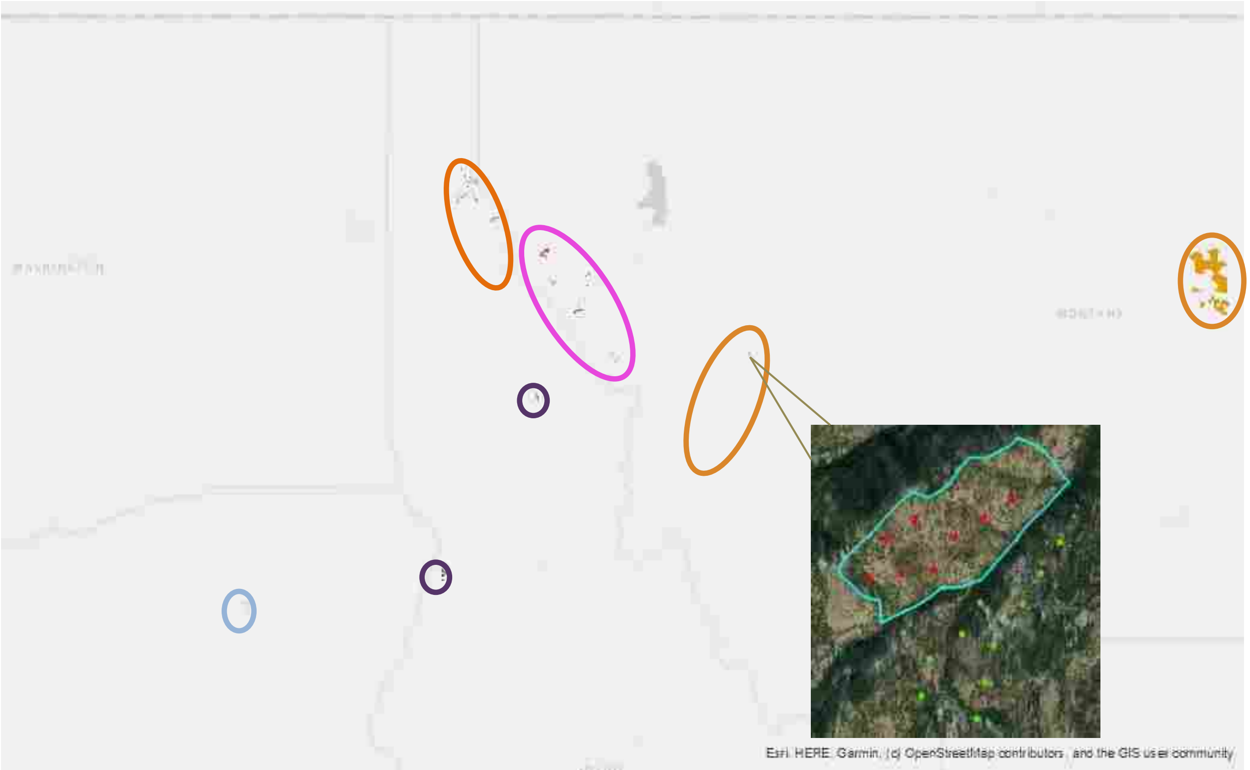

Figure 1: Map of our study region. The Starkey region is shown in blue on the lower left, the Clearwater region is shown in purple, the Lolo region in pink, the north Idaho-Kootenai region in dark orange, and the eastern Montana region in light orange. Also pictured is an image of an example of a treatment and paired control unit with the border of the treatment unit in light blue, the treatment points in red, and the control points in light green. All points (including points exclusively used for point counts) are shown, with the point closest to the road and the point closest to that being used for bee transects.

Figure 2: A representation of a typical treated stand and nearby control area that would be sampled for this study. Photo credit: Stephanie Berry.

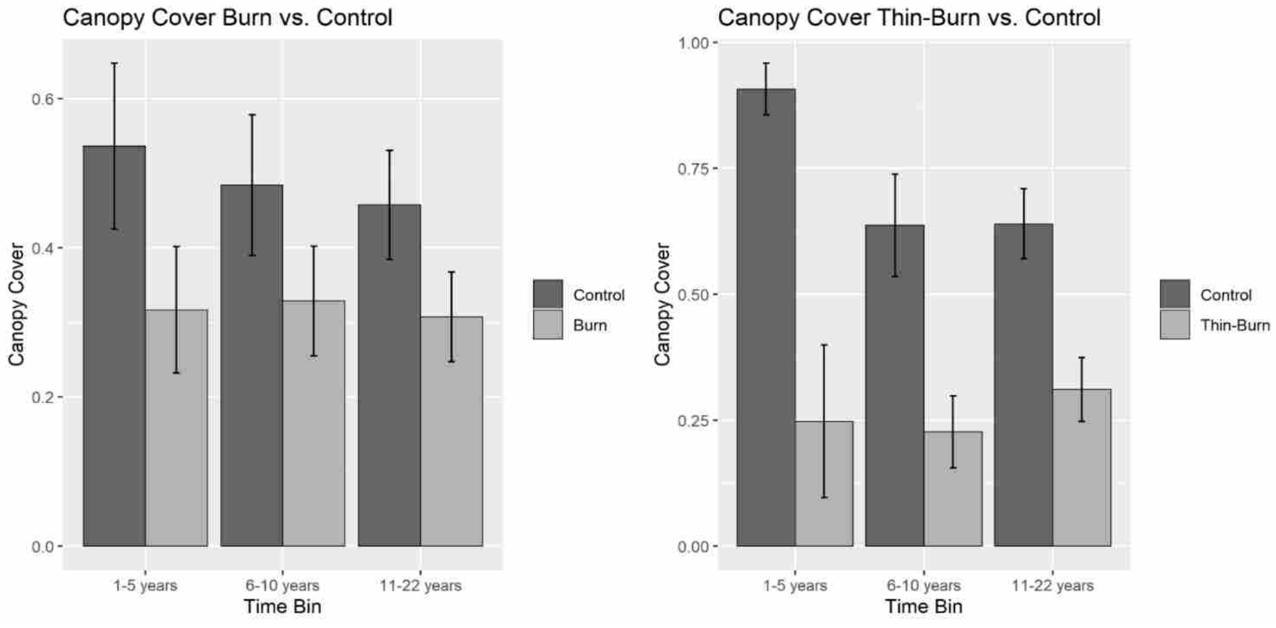

Figure 3: Canopy cover in burn (left) and thin-burn (right) vs. their paired controls.

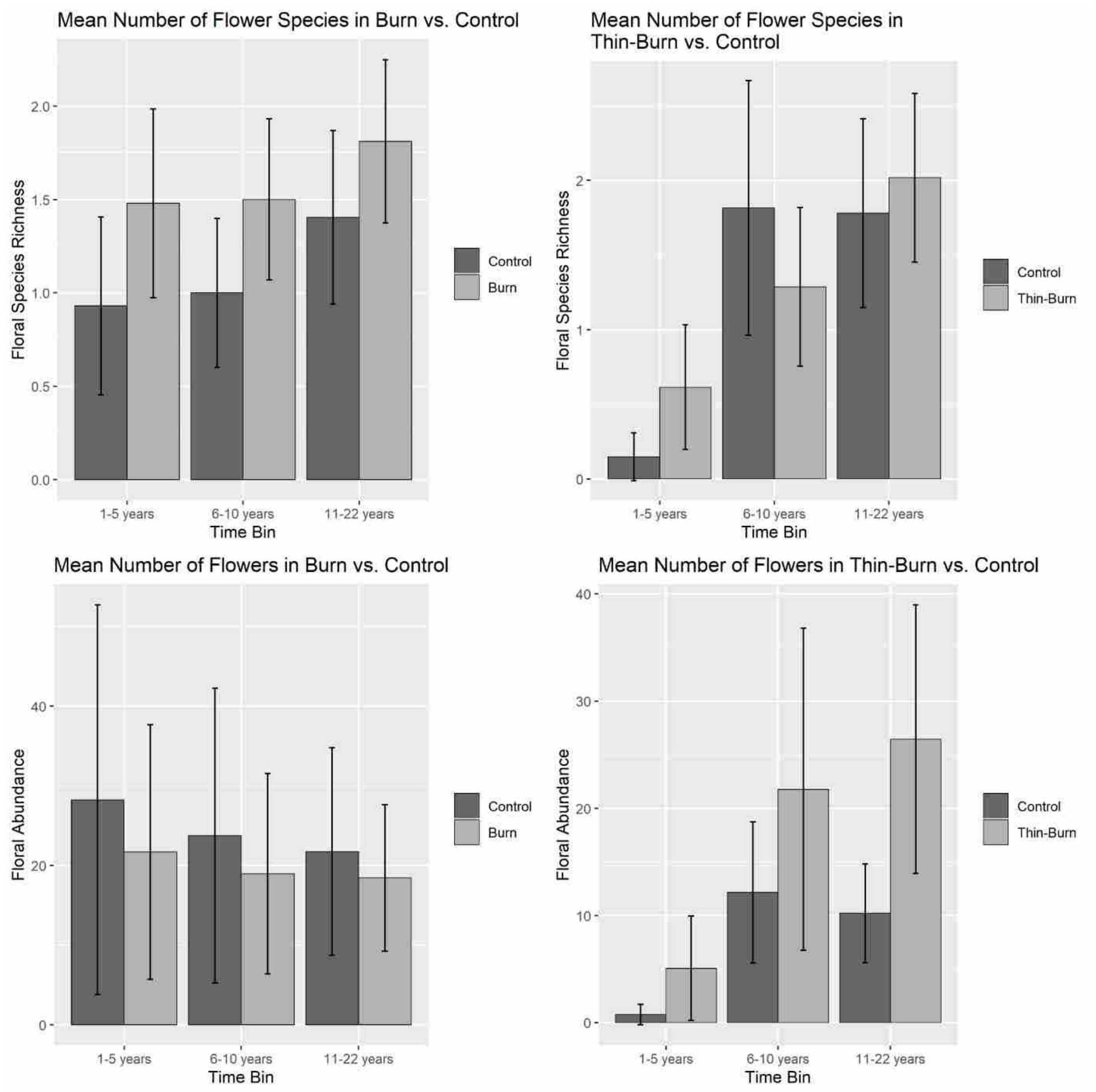

Figure 4: Mean floral species richness in burn (top left) and thin-burn (top right) vs. control, and mean floral abundance in burns (bottom left) and thin-burns (bottom right) vs. control.

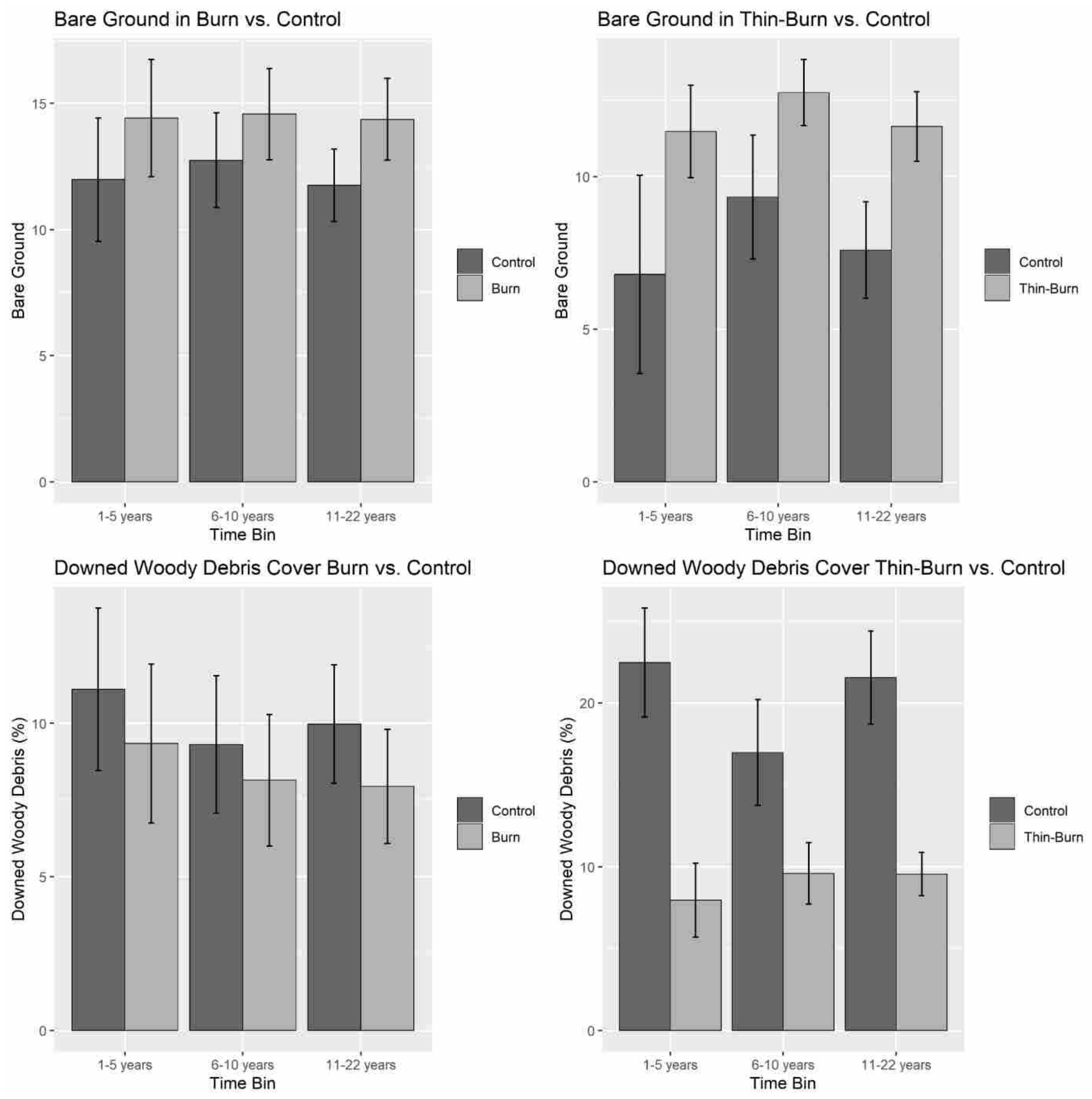

Figure 5: Bare ground in burn (top left) and thin-burn (top right) vs. control, and dead woody debris in burn (bottom left) vs. thin-burn (bottom right).

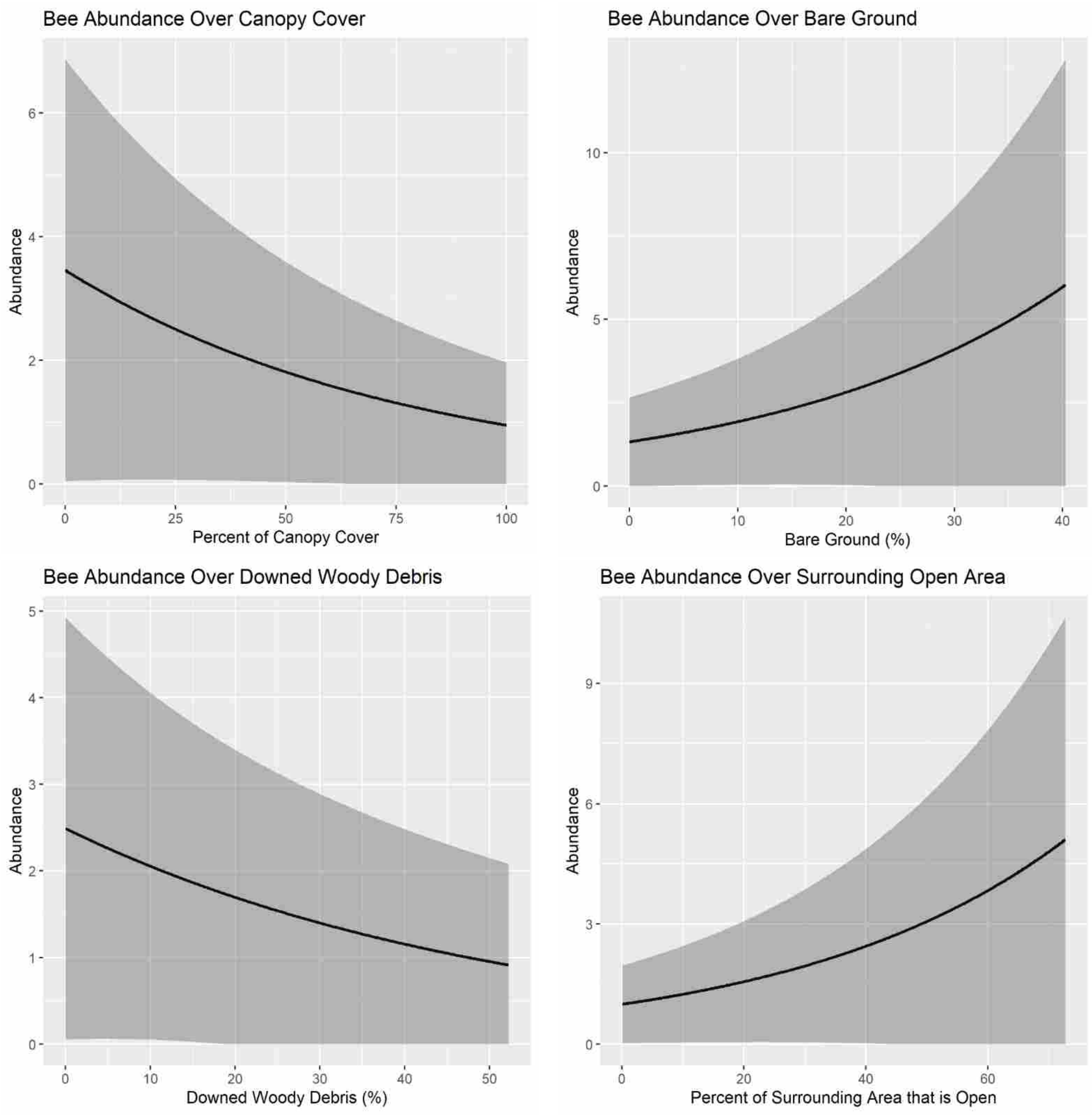

Figure 6: Bee abundance over canopy cover (top right), bare ground cover (middle right), top right (floral abundance), surrounding treated area (bottom left), downed woody debris cover (bottom middle), and surrounding open area (bottom right).

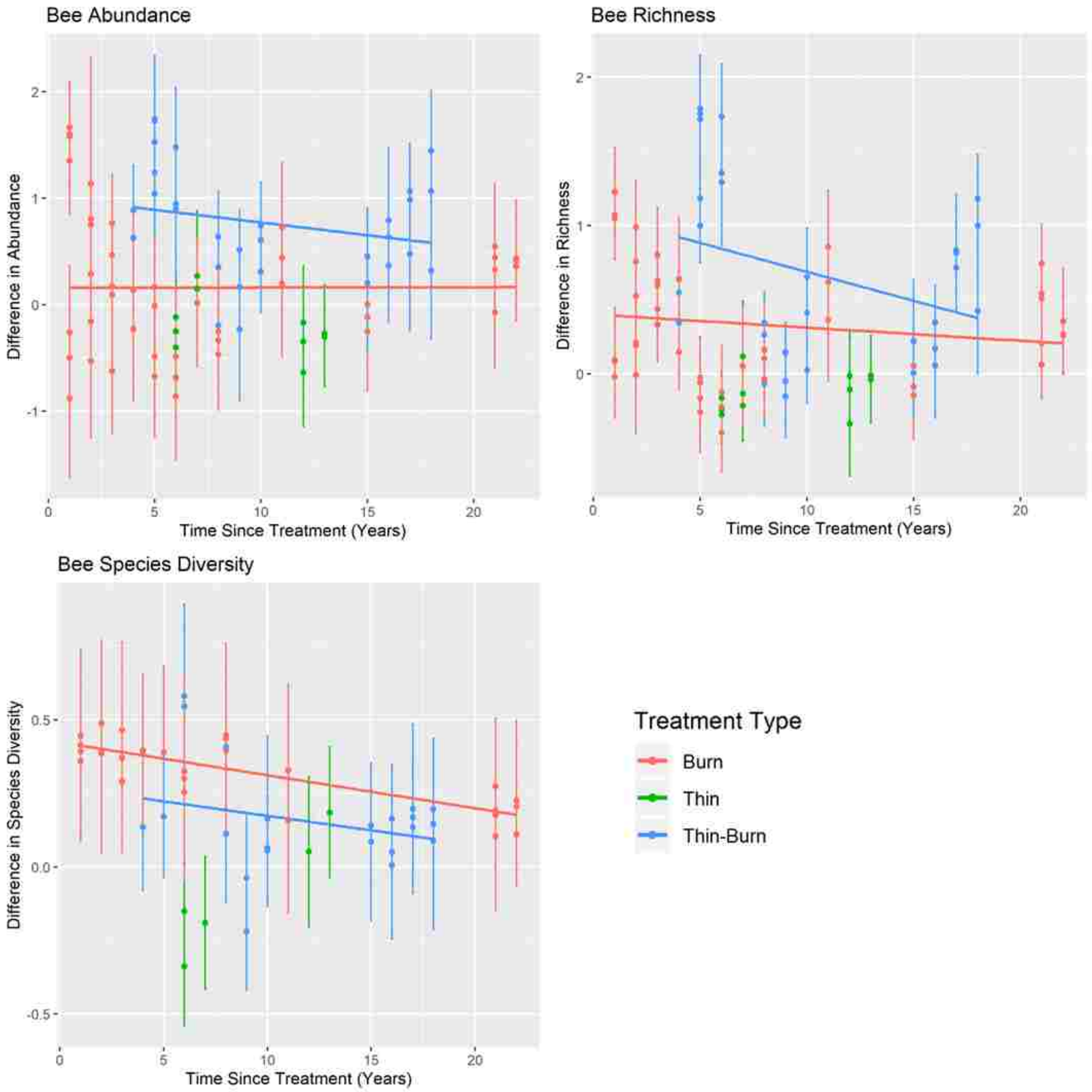

Figure 7: Difference in bee abundance (top left), species richness (top right), and Shannon species diversity (bottom left) in treatments vs. their paired control, with burns in red, thins in green, and thin-burns in blue.

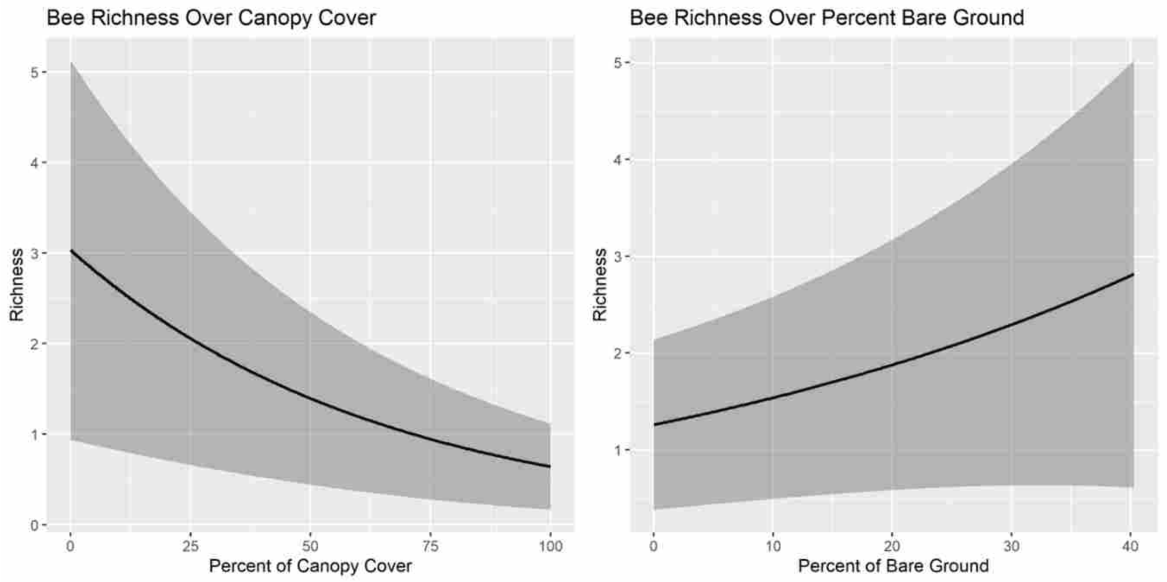

Figure 8: Bee species richness over percent canopy cover (left), and percent of bare ground cover (right).

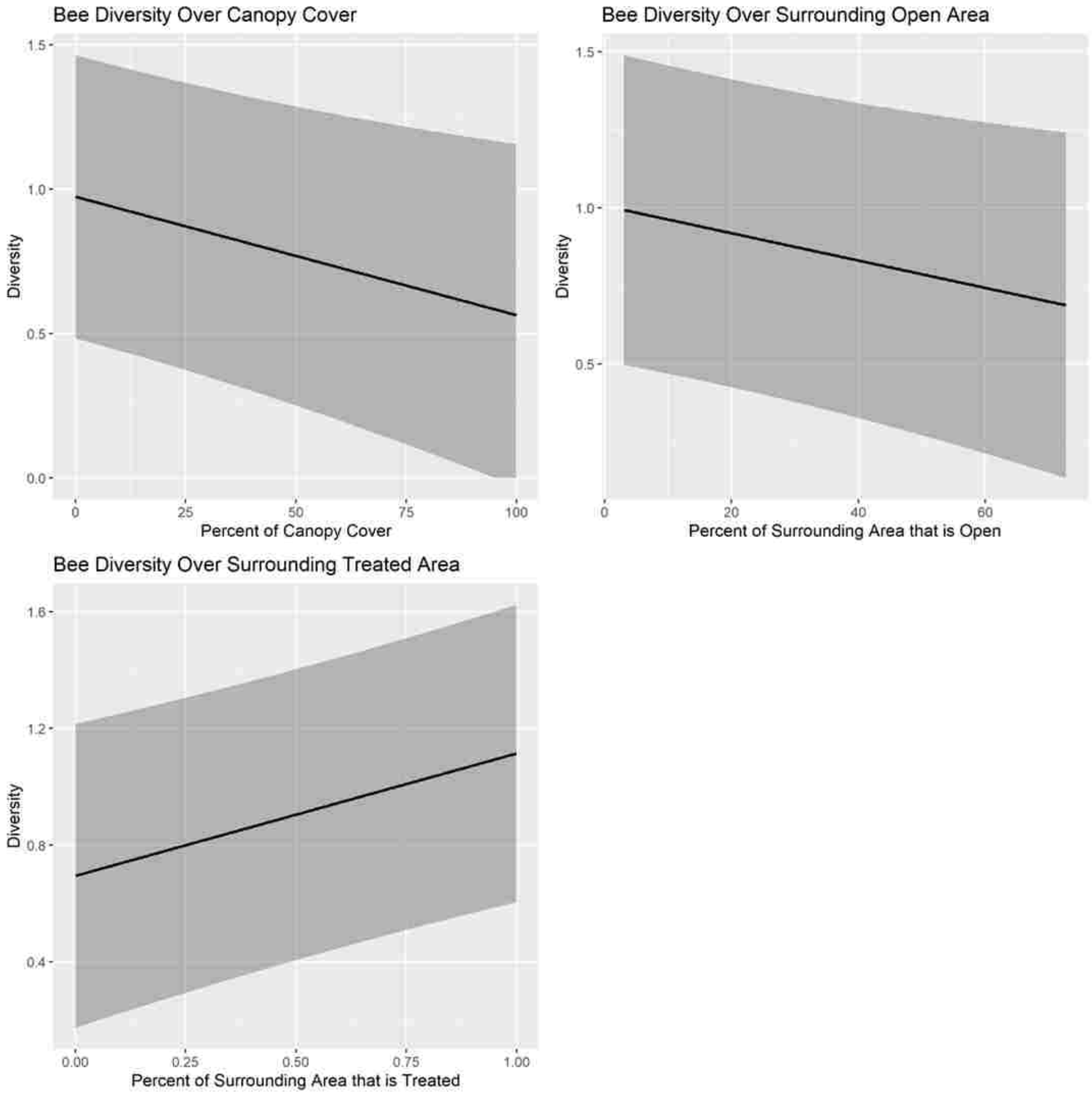

Figure 9: Bee species diversity over percent canopy cover (top left), percent of surrounding open area (top right), and percent of surrounding treated area (bottom left).

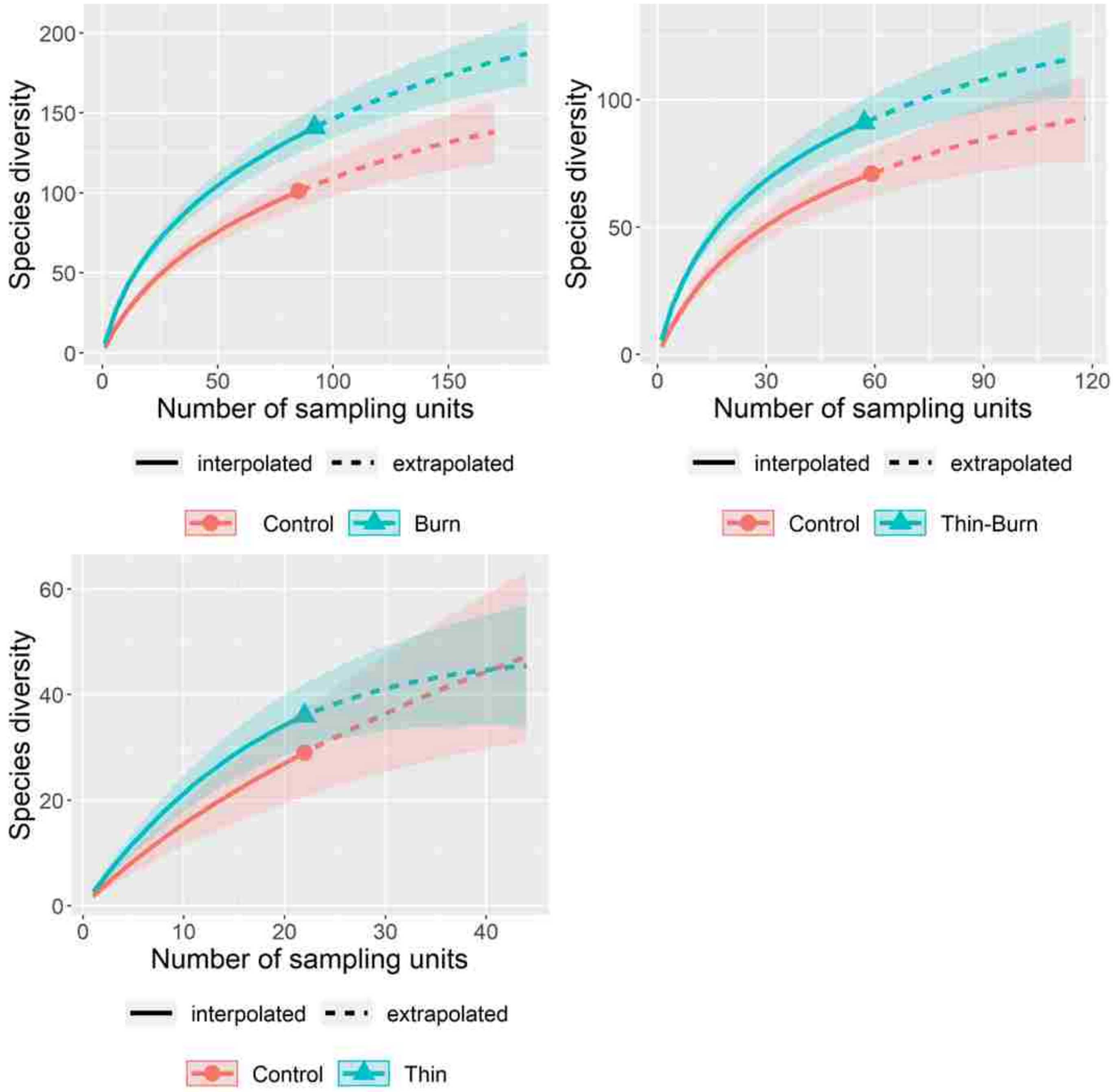

Figure 10: Species accumulation over number of sampling units (number of unique transect date combinations) in thin-burns (top left), burns (top right), and thins (bottom left).

CHAPTER 2

BIRD RESPONSE TO PRESCRIBED BURNING AND MECHANICAL THINNING IN EASTERN OREGON, NORTHERN IDAHO, AND MONTANA

ABSTRACT

Habitat treatments including mechanical thinning, prescribed burning, and a combination of both are being increasingly conducted across the western United States to mitigate wildfire risk through the reduction in fuel loads, enhance ungulate habitat quality, and increase overall habitat heterogeneity. Little is known about bird response, especially over long periods of time since treatment and over a variety of habitat types. We conducted point counts and measured habitat responses to such habitat treatments over the summers of 2018 and 2019 to evaluate bird response to treatment type, landscape, and temporal factors. We evaluated the density of four focal species/groups and species richness and diversity at paired treatment and control sites. We found a negative response exhibited by Mountain Chickadees (*Poecile gambeli*), and a positive response to treatments from bluebirds, and no effect of treatments on species richness or diversity. Thin-burns had larger impacts compared with burn only treatments, and there were stronger declines in abundance over time since treatment in thin-burn treatments than burn treatments. Overall, we did not see strong responses from the bird community to habitat treatments, suggesting these treatments would have to be conducted at a higher intensity or over a larger scale to detect impacts.

INTRODUCTION

Habitat treatments such as mechanical thinning, prescribed burning, and a combination of thinning and burning are frequently conducted by managers across the United States. After the fire exclusionary period post Euro-American settlement, forest conditions changed and fuel loadings have increased (Covington and Moore 1994). Therefore, treatments are increasingly being conducted by managers to mitigate wildfire risk and impacts (Graham et al. 1999, Agee and Skinner 2005). These treatments may serve a multitude of purposes, including reduction of fuels, improving habitat quality for ungulates and livestock, and modifying forest composition and structure (Covington et al. 1997, Graham et al. 1999, Pollet and Omi 2002, Pilliod et al. 2006, Harrod et al. 2007, Stephens et al. 2012). Impacts from prescribed burning can include increased herbaceous plant production, structural complexity, and decreased tree density (Covington et al. 1997, Pollet and Omi 2002, Pilliod et al. 2006, Harrod et al. 2007). Mechanical thinning can allow for greater control in selecting which trees to remove, allows for an altered species composition, and can reduce the forest canopy cover (Graham et al. 1999, Harrod et al. 2007). In combination, these treatments can result in higher scorch and removal of trees, lower basal area, reduced canopy cover, and lower recruitment of trees in the future (Harrod et al. 2007, Stephens et al. 2009) .

The Rocky Mountain Elk Foundation (RMEF) has treated over 7 million acres of land since the late 1980's with such treatments across the U.S. These treatments were primarily conducted to improve elk habitat quality, as past studies have shown that similar treatments improve ungulate habitat quality through nutritional quantity and quality (Pilliod et al. 2006, Long et al. 2008). However, these treatments, alone and in combination, can impact the habitat of many other species, including small mammals, carnivores, invertebrates, and birds (Pilliod et al. 2006).

Birds are a critical component of many forests and grasslands, providing invaluable ecosystem services and recreational opportunities. Ecosystem services provided include pest control, nutrient cycling, pollination, and seed dispersal (Wenny et al. 2011). Additionally, a large percentage of the United States population enjoys bird watching, and contributes over $40 billion annually on trip and equipment expenses (Carver 2013). However, many bird species are in decline due to habitat loss (Brawn et al. 2001, Schmiegelow and Mönkkönen 2002, Soykan et al. 2016). Therefore, appropriately managing existing bird habitat is a conservation priority for many managers.

Treatment impacts on birds vary by species, and are usually dependent on how a species utilizes its habitat for food and nesting. For this study, we estimated abundance of two focal species and two guilds of birds in treated and control sites. These species were selected because they represent a range of habitat types and a variety of foraging guilds. These species, in past studies, have all exhibited positive, neutral/mixed, or negative responses to prescribed burning and mechanical thinning. Our focal species included Dark-eyed Juncos (*Junco hyemalis*), Mountain Chickadees (*Poecile gambeli*), a bluebird guild (which included Western Bluebirds (*Sialia mexicana*) and Mountain Bluebirds (*Sialia currucoides*), and a woodpecker guild (which included Northern Flickers (*Colaptes auratus*), Hairy Woodpeckers (*Picoides villosus*), and Downy Woodpeckers (*Picoides pubescens*).

Foliage insectivore species like mountain chickadees may be negatively impacted by treatments like prescribed burning and mechanical thinning, which can remove some of the needles and twigs that they use in foraging (Bock and Lynch 1970, Tobalske et al. 1991, Kotliar et al. 2002, Bock and Block 2005, Bateman and O'Connell 2006, Hurteau et al. 2008*a,b*). Species that tend to nest and forage on the ground and in shrubs, such as Dark-eyed Juncos, may be negatively impacted by prescribed burning due to decreased shrub cover and litter, or positively impacted due to increased insect prey availability following increased herbaceous cover (Bock and Bock 1983, Artman 2003, Sperry et al. 2008, Bagne and Purcell 2011, Bayne and Nielsen 2011, Hutto and Patterson 2016). Cavity nesters, such as woodpeckers, may also benefit from snag creation resulting from burn treatments (Bateman and O'Connell 2006). Mechanical thin plus burn treatments have been found to have a larger positive effect on some bird species relative to thinning and burning alone, especially those associated with more open conditions (Fontaine and Kennedy 2012). For example, Woodpecker species and Western Bluebirds have been found to respond positively to thin-burn treatments, which remove more small trees than burning or thinning alone, increasing availability of insects in trees and on the forest floor (Harrod et al. 2007, Lyons et al. 2008, Hurteau et al. 2008*a,b*, Fontaine and Kennedy

2012). However, most studies have not looked at these impacts over a broad spatial scale that includes a multitude of habitat types or long-term responses to treatments.

While changes in abundance or occupancy of some bird species may occur in response to treatments, species richness may also be impacted by treatments. However, bird species richness response to treatments has not been consistent across studies. While some studies have found an increase in species richness after prescribed burning (Bock and Lynch 1970, Brawn et al. 2001, Bock and Block 2005), others have found no species richness response (Bateman and O'Connell 2006, George and Zack 2008, Russell et al. 2009). Similarly, some studies have shown that thinning increases species richness of birds (Hagar et al. 2004, Bayne and Nielsen 2011) while others found no change in species richness after thinning (Artman 2003, George and Zack 2008). Bayne and Nielsen (2011) analyzed studies that determined the impacts of forest thinning on the bird community, and found that most studies in coniferous forests showed an increase in richness post treatment, while most studies in deciduous forests found a decrease in bird species richness post treatment. It has been hypothesized that species richness of birds increases after habitat treatments because these treatments increase the structural complexity of forests, increasing the likelihood that more bird species will select these forests as their habitat (Bayne and Nielsen 2011).

Overall, impacts of treatments on groups of birds will likely be affected by the time since the treatment and the landscape context of the treatment. For example, Bagne and Purcell (2011) found that within one year, aerial foragers and riparian species responded positively to prescribed fire, while bark foragers increased between 3 and 6 years post treatment. Changes in abundance may be due to changes in tree or other vegetation characteristics, like shrub and herbaceous growth, or creation of snags (Bock and Bock 1983, Bateman and O'Connell 2006). Typically when prescribed burning and mechanical thinning are used to treat forests, forb and grass regrowth occurs within 1-2 years and shrub regrowth occurs within 1-10 years (Pilliod et al. 2006). Additionally, many species will be found in higher abundances when patches are surrounded by similar habitat, as more resources are available (forest patch surrounded by forest, etc.) (Blake and Karr 1984, Connor et al. 2000, Desrochers et al. 2010). Overall, larger patches surrounded by “natural” landscapes (i.e. not fragmented) may support more species and a higher abundance of birds than fragmented landscapes (McIntyre 1995). This may indicate that smaller treatments, or treatments surrounded by non-suitable habitat will not support as many bird species.

We aimed to understand the impacts of forest treatments on bird communities by examining the influence of prescribed burning and mechanical thinning forest treatments, alone and in combination, on bird abundance, richness, and diversity through the impact of these treatments on vegetation structure. We further sought to understand the impacts of time since treatment, the treatment size, and landscape context on bird-related metrics through comparison to controls.

Our hypotheses were as follows:

1) Treated sites will have lower Mountain Chickadee abundance due to lower canopy cover and tree density, providing fewer foraging opportunities.
2) Treated sites will have higher Bluebird and Dark-eyed Junco abundance due to increased insect prey availability caused by higher understory growth.
3) Treated sites will have higher Woodpecker abundance due to increased snag and large tree availability, which will increase foraging and nesting opportunities.

4) As treated patch size and percent of surrounding forested landscape increases, species richness and abundance of Woodpeckers and Dark-eyed Juncos will increase due to increased availability of resources.
5) As time since treatment increases, predicted effects of treatments on species richness and abundance of our focal species will diminish, as treated sites return to pre-treated conditions.
6) Habitat treatments will increase overall species richness of the bird community due to increased diversity of forest and vegetation characteristics

STUDY AREA

Our study occurred in five general regions in the northern Rocky Mountains across eastern Oregon, northern Idaho, and Montana (Figure 1). These regions included the Starkey Experimental Forest, Clearwater Region, north Idaho and Kootenai Region, Lolo National Forest Region, and eastern Montana Region. Forests in these regions have been altered by fire suppression following European settlement (Covington and Moore 1994), but past conditions were likely a product of fires burning at varying intensities throughout these forest types (Habeck and Mutch 1973, Arno 1980). These regions are all located within the northern Rocky Mountains, and confined to coniferous forests primarily composed of ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*). The terrain across this region is complex and slopes can range up to 40 degrees.

The Starkey Experimental Forest is located in northeastern Oregon. Starkey is surrounded with game-proof fencing to support ungulate research (Rowland et al. 1997). Forests at our sites sampled in Starkey were composed primarily of ponderosa pine and Douglas fir, but also contained lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and grand fir

(*Abies grandis*). The elevation in this region ranged between 1220 and 1520 meters, and precipitation averages 51 cm per year (Skovlin 1991). The average temperatures in mid-summer were between 12°C and 31°C (Rapp 2004).

The Clearwater Region is primarily located in east-central Idaho, and ranged from about 740 meters to 1505 meters in elevation at our study sites. Warm, moist Pacific air masses affect the climate of much of the Clearwater River Subbasin, and precipitation varies across the Subbasin between 30 cm up to 228 cm per year (Clark and Harris 2011). Summer temperatures averaged between approximately 15˚ C to 21˚ C (Clark and Harris 2011). The forests at our study sites in this region were primarily composed of Douglas fir and ponderosa pine, but also contained western larch and grand fir, while the understory ranged from grass/forb to seral shrub to closed forest canopy with little understory vegetation (Unsworth et al. 1998).

The Kootenai/north Idaho region is composed of areas in the Kootenai National Forest and the Idaho Panhandle National Forest. Our study sites were primarily composed of ponderosa pine and Douglas fir, but also contained grand fir, lodgepole pine, and western larch. Elevation at these sites ranged from approximately 820 meters to 1740 meters. Average annual precipitation ranged from 35 cm to 92.7 cm (Kuennen and Nielsen-Gerhardt 1995). Summer temperatures in locations across this region ranged from 14°C to 21°C (Arguez et al. 2010).

The Lolo Region is primarily in west-central and southwestern Montana, and elevations in the Lolo Region at our study sites ranged from 994 meters to 1969 meters. The average temperatures in the Lolo National Forest are approximately 19°C in midsummer, and annual precipitation ranges from 38 cm to over 254 cm (Sasich and Lamotte-Hagen 1989). Forests in our study sites in the Lolo region were primarily composed of Douglas fir and ponderosa pine, but also contained grand fir and lodgepole pine. The fire frequency in this area is approximately

30-100 years (Sasich and Lamotte-Hagen 1989). There are a combination of grasslands and coniferous forests of primarily Ponderosa pine and Douglas fir in this region (Bourne 1959).

The eastern Montana region is composed of Bureau of Land Management (BLM) land bordering the Flathead National Forest, parts of the Beaverhead Deerlodge National Forest, and Tin Can Hill, BLM land in central eastern Montana which borders the Musselshell River. The Beaverhead National Forest section of this area receives between 30 and 140 cm of precipitation and the average summer temperature is 17°C (Greene 2007). Forests in the Beaverhead-Deerlodge and Ovando areas in this region were composed primarily of ponderosa pine and Douglas fir, but also contained lodgepole pine, grand fir, Rocky Mountain juniper (*Juniperus scopulorum*), and western larch. Elevation at study sites in this part of the region ranged from 1230 meters to 2150 meters. The Tin Can Hill area of this region is a mixed area of BLM lands and private agricultural area. The elevation in this area ranges from 710 to 906 meters and the forests are primarily composed of ponderosa pine, Douglas fir, and Rocky Mountain Juniper.

METHODS

Site Selection

Our study sites were managed by state and federal agencies who used matching funds from RMEF to conduct habitat treatments to primarily benefit elk. Sites were treated with either prescribed burning, mechanical thinning, or both. Sites were selected to represent our five study regions and forest stand age classes as equally as possible (Table 1). After identifying available sites within the regions, we selected sites within to ensure an equal distribution as possible of forest stand ages, with access to the sites and the retreatment of older sites limiting our ability to equally represent sites with stand ages greater than 15 years. Within the Starkey Experimental Forest, most of the treatment units were too small to accommodate multiple points, so we selected treatment units that could contain at least two points, and selected the nearest control unit(s) (which were already identified for other research projects within Starkey) that could also accommodate the same number of points. Once sample sites were identified, we chose a control unit near the treated unit that was as similar as possible with respect to potential vegetation type, aspect, and slope (Figure 2). If there were multiple units treated, we paired control units with each unit where possible. One of our control units in the Idaho Clearwater region was used for two treated sites that were close in proximity and had limited appropriate controls available in the area. Within the control unit(s), we randomly selected points in the same way as treatment sampling points were selected. Though we sampled three treatment types, we were only able to sample two mechanical thins, and were not able to fit more than four points in those treatments due to their small size, so we were only able to fully assess burns and thin-burns.

Sampling Design

At each site, up to four, 250-500-meter long transects (or as many as would fit in the treated site, up to four) were used to conduct bird point counts and measure vegetation characteristics. The start point and direction of each transect was randomly selected within the site, and points were selected to fit the maximum number of points into a site possible. All points were located at least 100 meters from a road and edge, so as to avoid nuisance edge or road effects (Hutto et al. 1986, Hutto 1995, Hagar et al. 2004). Sites in the eastern Montana region were open woodlands or grasslands interspersed with patches of forest and naturally contained many edge-like features, so points were placed as best as possible to avoid edges, but it was not always possible. Two of our treated points in the Starkey region were located approximately 60 meters from a treated edge due to other edge and fencing constraints. Points were spaced 250 meters apart to avoid double counting of birds (Hutto 1986). Study design was constrained by the capacity to access survey points within the short daily window when avian point counts could be conducted to maximize detection probability. To maximize the number of points that could potentially be sampled within these constraints, points were within 2.5 kilometers of a road, and all starting points of a transect were no further than 4 kilometers apart, unless they were less than 750 meters from a road. Points at one site with particularly challenging terrain were selected so that the first two starting points were within 1500 meters of a road and within 650 meters of each other, to try to maximize the probability of sampling more than 3 points in the morning sampling period. If a treatment site was composed of multiple distinct units, starting points were within 1 kilometer of a road to facilitate driving from one unit to the next within time constraints.

Field Methods

Point counts were conducted in the study area between May 15th and August 24th, 2018 and May 7th and August 2nd, 2019. Point counts began at official sunrise and ended approximately 4 hours later. At each point count station, an observer recorded birds heard or seen within a 50 meter radius for 10 minutes, GPS coordinates, and weather conditions. We used rangefinders to determine the 50 meter radius, however two of the rangefinders measured distance in yards, so it is likely that some birds outside of a 50 yard radius may not have been recorded. Additionally, the first sampling season, observers recorded the actual distance to the bird, which may have excluded some birds high in trees that should have been counted. Upon detection of a bird, observers recorded the species and the minute interval (out of the 10 minute point count) that a bird was detected. Observers were trained in species identification before the season began, and made every attempt to only record birds that they were certain were unique individuals. Additionally, we constrained point counts used in abundance estimation to the first 6 minutes to reduce the probability that birds used in our abundance analysis were double-counted. We excluded fly-overs and fly-throughs from our analyses.

Vegetation Sampling

At each bird point count location, we measured aspect, slope, forestry data, and understory vegetation characteristics within an 11.3 meter radius. We recorded forestry data at each point including basal area with a 10 Basal Area Factor gauge, dominant tree species, dominant size class, and canopy cover. Dominant size class was classified as: none, sapling (<12.5 cm DBH), pole timber (12.5-27.5 cm DBH), and saw timber (>27.5 cm DBH). We only used one measurement of these characteristics in our analysis, as these do not change over the season. We assessed canopy cover using a Moosehorn (Robinson 1947, Cook et al. 1995) and understory vegetation along an 11.3 meter radius perpendicular to the point count transect at the beginning and end of the sampling season. Along this transect (11.3 meter radius, 22.6 meter diameter), we used 0.1 m^2 Daubenmire frames (Daubenmire 1959) spaced 2 meters apart. In each frame, we visually estimated percent coverage of grasses, dead plants standing and lying flat on the ground, forbs, bare ground, dead woody debris, and woody vegetation (shrubs) (Winter and Faaborg 1999, Sperry et al. 2008). We generally rounded understory vegetation cover to the nearest 5%, however we estimated values between 0% and 2% to the nearest 1% during the 2019 sampling year. Additionally, we used Arc GIS and data from the National Land Cover Database (NLCD 2016; Yang et al. 2018) to determine percent cover of forest and the percent cover of treated area in the 1250 meter radius surrounding each bird point count station (Taylor and Krawchuk 2005).

Analytical methods: Focal species relative abundance

To estimate abundance of focal bird species, we attempted to use three-level hierarchical models that would allow us to estimate detection probability (σ), availability (φ), and abundance (λ) in a Bayesian framework. This model would have estimated availability (the probability that a bird is available during a count) across sites and sampling visits, as we expected our focal species to emigrate out of our points over our sampling period (Chandler et al. 2011). However, scarcity of data and zero-inflation created by lack of occurrence limited our approach, as we did not have enough detections to support the complexity of this model structure.

Therefore, we took an alternative approach and used N-Mixture models with the function gpcount in the R package unmarked to estimate abundance of focal bird species (Fiske and Chandler 2011). This function estimates abundance, detection probability, and availability for count data collected over multiple periods using a robust design in a maximum likelihood framework. Our primary sampling occasions were our two years of data collection, with secondary periods of three sampling occasions within each year. This function assumes openness between primary periods (years) and closure between secondary periods (within season counts); we likely violated the closure assumption across sampling occasions within each year. This means that we are estimating relative use by focal species at our sampling points rather than true abundance. We also did not have sufficient detections in all sites to include a random effect of site to account for habitat characteristics that differ across our study area.

Overview of multi-stage model-building.

To account for imperfect detection, we tested *a priori* models with detection varying by minute after sunrise that the point count started (minute), day of the year (date), and the year that the point count occurred (year) and constant abundance. We tested all of these models in both a Poisson and Negative Binomial distribution, and selected the top model of these using Akaike's Information Criterion corrected for small sample sizes ("AICc"; Burnham and Anderson 2002) to determine which detection covariates and distribution we would include in our habitat abundance models. All continuous covariates were centered and scaled to facilitate comparison with each other, and we imputed missing detection covariates with the function imputeMissing in unmarked.

For each of our focal species, we built models to reflect *a priori* habitat hypotheses that abundance would vary by understory vegetation (herbaceous, shrub, and woody debris cover), forest characteristics (canopy cover and basal area), landscape (cover of forest and treated area), or over all of these (Table 2). We also constructed models to explore potential combinations of these covariates not included initially but that our models indicated may be important, such as combinations of specific vegetation covariates and landscape variables.

First, to test effects of vegetation covariates that change across the season and between sampling years, we considered approaches for summarizing data across both seasons into a single covariate for abundance models. We compared models of the vegetation covariate minimum, mean, and maximum using AICc, and adopted the summarization approach that ranked highest for the vegetation covariates, and did this process separately for canopy cover. We applied this approach for each focal species or group. We also incorporated landscape-level covariates into our models including percent of surrounding forest cover and treated area within 1250 meters. If habitat measurements were missing at any of our points, we imputed the mean of that covariate to include in the place of the missing data. We then used a model selection framework and AICc to select the top model to use in abundance estimates for each of our focal species and groups (Arnold 2010). However, we did not interpret parameters that are likely uninformative based on confidence intervals.

With our top model for each species, we estimated relative abundance for each focal species and group at each treatment and paired control site at the mean of the covariates associated with the points included in each site. We calculated the difference in predicted relative abundance between each treatment and its paired control, subtracting the mean abundance in the control site from the mean abundance in the paired treated site, and propagating the error through this step from the initial estimates. We then plotted these differences against time since treatment to examine the hypothesis that treatments and controls will become more similar in habitat quality over time.

Analytical methods: species richness and diversity

To assess differences in species richness and diversity between treatments and controls, we used the same overall model structure and selection process as we did for focal species abundance, but without accounting for imperfect detection. We used species richness (number of species) and Shannon's Diversity Index (Shannon 1948), calculated with the package vegan in R (Oksanen et al. 2019) aggregated over all sampling occasions as responses. Habitat variables and *a priori* models were the same as used for focal species abundance, but we also included the percent of non-vegetated cover in our vegetation model category. Since we did not account for sampling effort in our species richness and diversity models, we calculated sample-based rarefaction curves with the package iNEXT in R (Chao et al. 2014, Hsieh et al. 2019), and used them to compare species accumulation between points at each of our treatment types and their paired controls. Each unit of effort used in these curves was a point count sampling occasion, meaning that most points are represented multiple times in each curve, since we sampled most points over multiple occasions (up to six times).

RESULTS

Habitat Responses

Habitat treatments did not have significant impacts on habitat, overall (Figures 3-10). Basal area was not different in burns or thin-burns and their paired controls (Figures 3-4). Canopy cover was not different in burns or thin-burns and their paired controls, however the mean of the canopy cover measurements was lower in thin-burns in all age classes (Figures 3-4). Herbaceous cover was not different for burns or thin-burns and their paired controls, however the mean of the maximum measurement was higher after 6 years of treatment in burns vs controls, while the thin-burn maximum measurement was higher in 5 years (Figures 5-10). The minimum measurement of herbaceous cover was also higher 10 years post-treatment in burn vs. control, and lower in 11-22 years post-treatment for thin-burn treatments vs control (Figures 7, 10). Woody debris was lower 11-22 years post treatment for thin-burns vs. controls, and not different in burns vs. controls (Figures 5-10). The mean woody debris measurements, however, were lower in 1-5 years and 11-22 years post-burn vs. control (Figure 6). The mean and minimum measurements of shrub cover were lower in thin-burns 5 years post-treatment, and the maximum measurements of shrub cover were not different in thin-burns than controls in all age classes (Figures 8-10). Shrub cover was not different in burns vs controls, however the maximum and mean measurements of shrub cover in thin-burns were lower in 1-5 and 11-22 years post-treatment compared to their paired controls (Figures 5-10). Non-vegetated cover was higher in the thin-burns 11-22 years post-treatment and not different from controls 5 years post-treatment (though the mean was higher in thin-burns) (Figure 8). Non-vegetated cover was not different in burn vs. controls, however the mean was higher in burns less than 5 years post-treatment and 11-22 years post-treatment (Figure 5).

Abundance

Over both seasons, we conducted 765 point counts, with 98 detections of Mountain Chickadees, 84 detections of Dark-eyed Juncos, 28 detections of Bluebirds, and 48 detections of Woodpeckers.

Habitat treatments did not have a clear effect on the relative abundance of any of our focal species in comparison with paired controls. However, of our focal species, Mountain Chickadees showed the strongest negative response to treatment (Figure 11). The top model for Mountain Chickadees included minute and year effects on detection (Table 3) and mean woody debris and percent of surrounding treated area effects on abundance (Table 4). There was a negative effect of percent of surrounding treated area on chickadee abundance (Table 5; Figure 11). We would expect an 87% decrease in relative abundance of chickadees over an increase of 0 to 100% surrounding treated area within 1250 meters. A majority of sites had a higher predicted mean abundance of chickadees in the controls than the treatments (across treatment type), indicating a potential negative effect of treatment, even though confidence intervals overlap zero (Figure 11). We found that relative abundance of Mountain Chickadees decreased at treatment sites relative to controls with increasing time since treatment at thin-burn sites (n=6), but found no trend of time since treatment at burn sites (Fig2).

There was little evidence that treatments impacted Dark-eyed Junco abundance (Figure 12). The top model for Dark-eyed Juncos included detection covariates of minute, date, and year (Table 6), along with abundance covariates for the maximum values of vegetation cover measured over our sampling periods (Table 7). Dark-eyed Junco abundance increased with increasing herbaceous cover and woody debris cover (Table 8). We would expect an increase in the relative abundance of Dark-eyed Juncos of approximately 219% over an increase in herbaceous cover of 3.5% to 92.5%. Herbaceous cover was not different in either burns or thin-burns (Figures 5, 8). However, mean herbaceous cover increased over time since treatment in burns, while decreasing over time since treatment relative to controls in thin-burns. Woody debris was also significantly lower in the 11-22 thin-burn treatments relative to controls, potentially driving the greater estimated difference in Dark-eyed Junco abundance between thin-burn treatments and controls in older treatments (Figures 5, 8). We would predict an increase in the relative abundance of juncos of approximately 484% over an increase of 0% and 100% woody debris cover. There was no difference between treated and control sites overall for any treatment type, except both thin sites had more juncos predicted in the paired controls (Figure 12). However, there was a slight increasing trend in abundance over time since treatment in burned sites (n=14), and a strong negative trend in time since treatment for thin-burn sites (n=6).

There was also not a strong treatment effect on focal woodpecker species at our study sites. The top selected model included no detection covariates (Table 9) and abundance covariates included minimum vegetation values sampled across our seasons (Table 10). Woodpecker abundance was positively related with downed woody debris (Table 11). Woody debris cover at burned sites was not different from controls in any time bin, however was lower at thin-burn sites in the 11-22 year time bin (Figures 7, 10). We would expect a relative increase of 556% as many woodpeckers over an increase of 0 to 46% woody debris cover. There was little difference in abundance between treatments and controls at most burn sites, and no apparent trend over time since treatment (Figure 13). The thin-burn treatments may have had slightly more of an effect than the burns, with higher abundance of woodpeckers in sites treated less than 10 years ago compared with their paired controls, and lower abundance in sites at 10 or more years post-treatment.

Our last focal species, bluebirds, showed a somewhat positive treatment response to burns, and a completely positive response thin-burns (Figure 14). The top model selected for bluebirds included an effect of date^2 (Table 12) on detection and basal area and minimum canopy measurements on abundance (Table 13). Bluebird abundance decreased with higher canopy cover (Table 14). We would expect a decrease in relative abundance of bluebirds of approximately 92% as canopy cover increases from 0 to 100%. There was not a strong trend of time since treatment on bluebird abundance (Figure 14). Canopy cover was not different in burn sites and control sites, but mean canopy cover was consistently lower in thin-burn sites than in controls (Figures 3, 4).

Species Richness and Diversity

Over both sampling seasons, we detected 85 species of birds at our sample points. Our top selected model for species richness of birds was the global model, including understory vegetation, forest vegetation, and landscape covariates (Table 15). Forest cover, canopy cover, and percent of surrounding treated area were negatively associated with species richness, while herbaceous cover, woody debris, and non-vegetated cover were all significantly positively related with species richness (Table 15). We would expect a 25% decrease in relative species richness over an increase of 0 to 100% in canopy cover and surrounding treated area within 1250 meters, and a 31% decrease in species richness over forest cover ranging from 17% to 98%. Herbaceous cover was not significantly different in burn or thin-burn sites from control sites (Figures 5, 8). However, maximum herbaceous cover was slightly lower in the 1-5 year time post-treatment and increases compared to the control over time in burn sites, while herbaceous cover was higher in the 1-5 year time post-treatment and became more similar to controls over time at thin-burn sites. We would expect an increase in relative species richness of approximately 109% over our minimum herbaceous cover (3.5%) to our maximum herbaceous cover (92.5%). Maximum woody debris cover is lower in both treatment types at all times post treatment except burns between 6-10 years post treatment, and is significantly lower in thin-burn sites between 11-22 years post-treatment. We would expect an increase in relative species richness of approximately 313% over 0% to 100% woody debris cover. Non-vegetated cover is not significantly different between burn and control sites, but is significantly higher in the thin-burn sites between 11-22 years post-treatment. We would expect an increase in relative species richness of approximately 174% over our non-vegetated cover range of 2% to 91%.

The top selected model for bird species diversity was the landscape and vegetation model. Similarly to bird species richness, surrounding forest cover was negatively associated with bird species diversity, while maximum herbaceous cover, maximum woody debris, and maximum non vegetated cover were positively surrounded with bird species diversity. There was also a signal that surrounding treated area negatively impacted bird species diversity, however confidence intervals slightly overlapped with 0.

Overall, there was little indication that treatments had an effect on species richness or diversity. Species richness was higher in the thin-burn site five years post-treatment compared to the paired control, but decreased over time since treatment until it is significantly lower in thin-burns 16 years or greater post-treatment (Figures 15, 16). Mean species richness was generally lower in burned sites less than 5 years post-treatment compared to controls, but increased over time since treatment. Species accumulation curves also indicated that there was no effect of treatment on species richness (Figure 17), however we were not able to produce reliable accumulation curves or standard error estimates with our data.

DISCUSSION

Results of this study were largely consistent with past studies. Although confidence intervals did not support a strong treatment response for any of our focal species, there seemed to be some patterns and signals as evidenced by abundance means and trends over time since treatment. Overall, thin-burns had a stronger impact on habitat characteristics measured and most of our focal species abundance and species richness and diversity.

The strongest response in either direction was a negative response to all treatment types by Mountain Chickadees. This response has been confirmed by past similar studies (Bock and Lynch 1970, Bateman and O'Connell 2006, Hurteau et al. *2008a,b*, Bagne and Purcell 2011). None of the vegetation responses we measured explain this response, however others have hypothesized that this response is largely due to their foraging habits. Past research has found that chickadees select large diameter live conifer trees for foraging, of which there may be less in treated stands (Bock and Lynch 1970, Bateman and O'Connell 2006, Lyons et al. 2008). However, this does not fully explain the negative response to burn treatments, since we found no significant effect of burns on canopy cover or basal area. While we did not measure the number of snags in stands, if prescribed burns were killing a significant number of trees, we may expect to find a lower basal area and canopy cover in treated stands, which we did not. Bateman and O'Connell (2006) also found a persistent negative response of chickadees to treatments from 3-6 years after treatment, suggesting there may be another mechanism to explain the negative response that we did not measure.

Bluebirds also responded somewhat expectedly to treatments, though not as positively to burn-only treatments as we would expect. Past studies have found that both bluebird species respond positively to thin, burn, and thin-burn treatments (Bock and Bock 1983, Saab and Powell 2004, Wightman and Germaine 2006, Hurteau et al. 2008*a,b,* Russell et al. 2009). We found that Bluebirds were negatively associated with canopy cover, probably because reduced canopy cover increased open spaces and perch availability and opportunities for hunting ground invertebrates (Bock and Lynch 1970, Wightman and Germaine 2006). Therefore, a negative association of bluebirds with canopy cover is likely why mean abundance estimates for bluebirds indicate a positive treatment response to thin-burn treatments, since those treatments decreased canopy cover more than burn treatments. Bluebirds showed a positive response to burn treatments at most sites, except for our eastern Montana Tin Can Hill sites, where the controls were generally more open than the treated sites, as it was difficult to find appropriately forested control sites in that area. There was not a distinctive trend of bluebird abundance over time since treatment, though we did not find that canopy cover significantly increased over time since treatment for either treatment type, so that is likely why there wasn't a temporal trend.

The woodpecker response to treatment was less clear. There seemed to be no response to burn treatments, and a possible slight response to thin-burn treatments which decreased over time since treatment. None of the forest characteristics we measured were significant for woodpecker species, however the woody debris was significant, probably due to their foraging habits (Bock and Lynch 1970). Additionally, burn treatments likely did not increase availability of snags for woodpecker nesting, which is probably key in their past positive response to burn-only treatments (Zarnowitz and Manuwal 1985, Bateman and O'Connell 2006, Lyons et al. 2008). It is possible that the negative time since treatment trend was due to the decrease in foraging substrate quality in older snags and downed logs, which have less bark remaining over time since creation (Bateman and O'Connell 2006).

Like woodpeckers, Dark-eyed Juncos also did not exhibit a clear treatment response, but also like woodpeckers, seemed to have a negative time since treatment trend in thin-burn treatments. Unlike woodpeckers, there was a positive trend of time since treatment in burn treatments. Many studies have also found that the Dark-eyed Junco response to habitat treatments can vary from negative to positive to neutral (Tobalske et al. 1991, Sperry et al. 2008, Hurteau et al. 2008*a,b*). Their response, like many other bird species, is likely related to their foraging and nesting habits. Sperry et al. (2008) found that Junco nesting was not adversely affected by treatments in the first year post-fire, however low-flying arthropod biomass was lower due to reduced vegetation cover. There may be a positive time since treatment trend in burn treatments as herbaceous cover increased over time since treatment in burns, thereby increasing insect availability. Similarly, Juncos may be decreasing over time since treatment in thin-burn treatments due to the decrease in woody debris in 11-22 year age classes. This is likely not because of treatments, but two of our sites in that age class were impacted by bark beetle infestation, and woody debris was much higher in control sites there.

The overall species richness response to treatments was mixed, however there was no definite positive or negative response to either treatment type, which is consistent with past studies (Bateman and O’Connell 2006, George and Zack 2008, Hurteau et al. 2008*a*, Russell et al. 2009). If anything, our results indicated a slightly negative species richness response to treatment, as species richness slightly decreased over increasing treated area.

It is likely that the treatments did not have a large impact on the overall bird community, but also possible that the number of birds benefited by treatments was the same as the number of birds negatively impacted. It is also possible that variation in control sites made it difficult to tease out impacts to birds from treatments and how they differed across treatment types, over time, and over landscape. However, consistent with past studies, we did not see many significant impacts to vegetation or forest characteristics that we measured, so treatments at this small of a scale and of a lower intensity may not be significantly impacting the community (Hurteau et al. 2008*a*). The burn treatments, similar to other studies in the past, likely had a very low impact on the forest compared to thin-burn treatments (Bock and Bock 1983, Lyons et al. 2008, Hurteau et al. 2008*a*, Bagne and Purcell 2011). Surprisingly, we only saw an effect of landscape scale (forest cover and cover of treated area) for Mountain Chickadees. However, treated area was significantly larger for burn treatments than thin-burn or thin treatments, so more research would need to be conducted to look specifically at the effect of treated area for thin-burn treatments, which likely have a larger impact in general on the focal species we measured. If managers want to have an impact on specific bird species in a community that would benefit from more open habitat, they should consider that thin-burn treatments will be more impactful than burn treatments in opening the forest and changing vegetation cover characteristics, and that small scale treatments applied across a landscape mosaic will likely not have a measureable effect on the bird community. If managers apply treatments across a large portion of the landscape, they are more likely to alter bird communities consistent with our results. However, as we saw in Dark-eyed Juncos, woodpeckers, and overall species richness, these treatments may have negative impacts over time since treatment, so goals of the treatments and times at which sites are retreated should be considered carefully.

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TABLES AND FIGURES

Table 1: Sites sampled across our study area in 2018 and 2019 and the treatment type, region, year of treatment, and size that each site sampled represented.

Treatment Type	Region	Year of Treatment	Size
Thin-burn	Starkey	2001	271 acres
Thin-burn	Starkey	2003	675 acres
Burn	Eastern Montana	1997	212 acres
Burn	Eastern Montana	1997	54 acres
Thin	Eastern Montana	2012	243 acres
Thin-burn	Eastern Montana	2009	244 acres
Thin-burn	Eastern Montana	2010	208 acres
Burn	Eastern Montana	2010	1361 acres
Burn	Eastern Montana	2012	3853 acres
Burn	Eastern Montana	2015	6657 acres
Burn	Eastern Montana	2017	2509 acres
Burn	Lolo	2004	90 acres
Thin	Lolo	2006	566 acres
Thin-burn	Lolo	2014	124 acres
Burn	Lolo	2016	3275 acres
Thin-burn	North-Idaho Kootenai	2013	167 acres
Burn	North-Idaho Kootenai	2018	40 acres
Burn	North-Idaho Kootenai	2013	553 acres
Burn	Clearwater	2008	1019 acres
Burn	Clearwater	2011	1207 acres
Burn	Clearwater	2014	967 acres
Burn	Clearwater	2018	223 acres

Table 2: The *a priori* models used in the bird analysis, along with covariates and descriptions of the hypotheses they were testing. After running these models, we explored combinations of these models not initially tested that we thought may be significant.

Model name[1]	Hypothesis
Forestry	The canopy cover and basal area will determine the bird response tested
Landscape	The surrounding area composed of forest and treated area will determine the bird response tested
Vegetation	The understory vegetation will determine the bird response tested
Global	All variables will determine the bird response tested

Table 3: The Negative Binomial model for minute and year effects on detection probability is the top-ranking model for Mountain Chickadees. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into detection probability (σ) models for Mountain Chickadees in the northern Rocky Mountains 2018-2019.

Model[1,2]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
NB (σ) (min+year)	6	598.38	0	0.41	0.41
NB (σ) (year)	5	598.97	0.59	0.31	0.72
NB (σ) (min+date+year)	7	599.83	1.45	0.2	0.91
NB (σ) (min+date^2+year)	8	601.52	3.14	0.085	1
NB (σ) (min)	5	618.75	20.37	1.55E-05	1
NB (σ) (.)	4	618.86	20.48	1.46E-05	1
P (σ) (min+date+year)	6	619.31	20.94	1.17E-05	1
P (σ) (min+date^2+year)	7	619.61	21.23	1.01E-05	1
NB (σ) (date)	5	620.31	21.93	7.08E-06	1
NB (σ) (min+date)	6	620.34	21.96	6.98E-06	1
P (σ) (min+year)	5	620.35	21.97	6.94E-06	1
NB (σ) (date^2)	6	621.053	22.68	4.88E-06	1
P (σ) (year)	4	621.068	22.69	4.85E-06	1
NB (σ) (min+date^2)	7	621.32	22.94	4.28E-06	1
P (σ) (date^2)	5	635.88	37.5	2.95E-09	1
P (σ) (min+date^2)	6	636.11	37.73	2.63E-09	1
P (σ) (min+date)	5	636.58	38.2	2.08E-09	1
P (σ) (date)	4	636.59	38.21	2.07E-09	1
P (σ) (min)	4	638.34	39.96	8.62E-10	1
P (σ) (.)	3	638.85	40.47	6.67E-10	1

[1] Distributions: NB=Negative binomial and P=Poisson

[2] date=day of year, min=minutes since sunrise, year=year

Table 4: Surrounding treated area and mean woody debris cover was the top-ranking model on abundance for Mountain Chickadees. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into abundance (λ) models for Mountain Chickadees in the northern Rocky Mountains 2018-2019.

Model[3,4]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Trt area+ Woody Debris	8	589.55	0	0.37	0.37
Trt area+ Canopy cover	8	590.16	0.61	0.27	0.65
Trt area + Canopy Cover + Woody debris	9	591.21	1.66	0.16	0.81
Landscape	8	592.0037	2.45	0.11	0.92
Global	10	594.38	4.83	0.033	0.95
Vegetation mean	9	595.34	5.79	0.021	0.97
Vegetation maximum	9	595.38	5.84	0.02	0.99
Vegetation minimum	9	598.32	8.77	0.0046	1
Forestry minimum	8	599.5	9.95	0.0026	1
Forestry mean	8	600.8	11.25	0.0013	1
Forestry maximum	8	601.99	12.44	0.00074	1
Null	4	618.86	29.31	1.61E-07	1

[3] trt area=Percent of surrounding area that is treated within 1250 meters, Vegetation models=herbaceous cover+ shrub cover+ woody debris cover, Forestry models=Basal Area+Canopy cover, Landscape models= percent of surrounding area that is forested +Percent of surrounding area that is treated within 1250 meters

[4] Global=Basal area + canopy cover + surrounding forest area + surrounding treated area

Table 5: Coefficients (Coeff), standard errors (SE), and p (P(>|z|)) values for covariates in the most supported abundance model for Mountain Chickadees in the northern Rocky Mountains in 2018-2019.

	Coeff	SE	P(>|z|)
(Intercept)	1.16	0.39	0.0026
Trt area	-0.56	0.22	0.011
Mean woody debris cover	0.24	0.14	0.088

Table 6: The Poisson model for minute, date, and year effects on detection probability is the top-ranking model for Dark-eyed Juncos. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into detection probability (σ) models for Dark-eyed Juncos in the northern Rocky Mountains 2018-2019.

Model[1,2]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
P (σ) (min+date+year)	6	544.86	0	0.29	0.29
P (σ) (min+date^2+year)	7	545.21	0.34	0.25	0.54
NB (σ) (min+date+year)	7	545.96	1.1	0.17	0.71
NB (σ) (min+date^2+year)	8	546.57	1.71	0.13	0.84
P (σ) (min+date)	5	549.47	4.61	0.029	0.87
P (σ) (date)	4	549.54	4.68	0.028	0.9
NB (σ) (date)	5	550.15	5.29	0.021	0.92
NB (σ) (min+date)	6	550.18	5.32	0.021	0.94
P (σ) (date^2)	5	550.52	5.66	0.017	0.96
P (σ) (min+date^2)	6	550.52	5.66	0.017	0.97
NB (σ) (date^2)	6	551.38	6.51	0.011	0.98
NB (σ) (min+date^2)	7	551.45	6.59	0.011	0.995
NB (σ) (min+year)	6	555.69	10.82	0.0013	0.997
NB (σ) (year)	5	556.054	11.19	0.0011	0.998
P (σ) (min+year)	5	556.76	11.9	0.00077	0.999
P (σ) (year)	4	557.41	12.55	0.00056	0.999
NB (σ) (min)	5	558.72	13.86	0.00029	0.9995
NB (σ) (.)	4	559.37	14.51	0.00021	0.9997
P (σ) (min)	4	559.73	14.87	0.00017	0.9999
P (σ) (.)	3	560.65	15.79	0.00011	1

Table 7: Maximum herbaceous, woody debris, and shrub cover was the top-ranking model for abundance of Dark-eyed Juncos. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into abundance (λ) models for Dark-eyed Juncos in the northern Rocky Mountains 2018-2019.

Models[3,5,6]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Vegetation maximum	9	539.55	0	0.51	0.51
Vegetation mean	9	540.91	1.37	0.26	0.77
Landscape+vegetation	11	542.18	2.63	0.14	0.91
Global	13	544.67	5.12	0.04	0.95
Vegetation minimum	9	545.69	6.15	0.024	0.97
Landscape	8	546.69	7.14	0.014	0.99
Forestry minimum	8	548.9	9.35	0.0048	0.99
Forestry maximum	8	548.95	9.4	0.0047	1
Forestry mean	8	548.95	9.4	0.0047	1
Null	3	560.65	21.1	1.34E-05	1

[5] Global model=Basal area + canopy cover+ percent of surrounding forested area + percent of surrounding treated area +herbaceous cover + shrub cover + woody debris,

[6] Landscape+vegetation= percent of surrounding treated area + percent of surrounding forested area + herbaceous cover + shrub cover + woody debris

Table 8: Coefficients (Coeff), standard errors (SE), and p (P(>|z|)) values for covariates in the most supported abundance model for Dark-eyed Juncos in the northern Rocky Mountains in 2018-2019.

	Coeff	SE	P(>|z|)
(Intercept)	1.9	0.56	0.00072
Maximum herbaceous	0.24	0.11	0.034
Maximum shrub	-0.21	0.14	0.14
Maximum woody debris	0.25	0.084	0.0034

Table 9: The Poisson model for no effects on detection probability is the top-ranking model for Woodpeckers. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into detection probability (σ) models for Woodpecker species in the northern Rocky Mountains 2018-2019.

Model[1,2]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
P (σ) (.)	3	373.38	0	0.21	0.21
NB (σ) (.)	4	374.55	1.17	0.12	0.32
P (σ) (date)	4	374.57	1.19	0.11	0.44
P (σ) (year)	4	375.05	1.66	0.09	0.53
P (σ) (min)	4	375.37	1.99	0.077	0.61
NB ccccc	5	375.68	2.3	0.066	0.67
NB (σ) (year)	5	376.26	2.87	0.049	0.72
NB (σ) (min)	5	376.58	3.2	0.042	0.76
P (σ) (min+date)	5	376.61	3.23	0.041	0.8
P (σ) (date^2)	5	376.67	3.29	0.04	0.84
P(σ) (min+year)	5	377.05	3.67	0.033	0.88
NB (σ) (min+date)	6	377.75	4.37	0.023	0.9
NB (σ) (date^2)	6	377.79	4.41	0.023	0.92
NB(σ) (min+year)	6	378.3	4.92	0.018	0.94
P(σ) (min+date+year)	6	378.33	4.95	0.018	0.96
P (σ) (min+date^2)	6	378.73	5.35	0.014	0.97
NB (σ) (min+date+year)	7	379.52	6.14	0.0096	0.98
NB(σ) (min+date^2)	7	379.89	6.51	0.008	0.99
P(σ) (min+date^2+year)	7	380.46	7.08	0.006	0.997
NB(σ) (min+date^2+year)	8	381.68	8.3	0.0033	1

Table 10: Minimum herbaceous, woody debris, and shrub cover was the top-ranking model for woodpecker abundance. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into abundance (λ) models for Woodpeckers in the northern Rocky Mountains 2018-2019.

Models[3,5,7]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Vegetation minimum	6	365.19	0	0.55	0.55
Landscape+vegetation	8	365.92	0.73	0.38	0.93
Global	11	371.87	6.68	0.029	0.96
Landscape	5	372.56	7.37	0.014	0.97
Vegetation mean	6	372.97	7.78	0.011	0.98
Null	3	373.38	8.19	0.0091	0.99
Forestry maximum	5	376.75	11.36	0.0019	0.99
Forestry mean	5	376.83	11.38	0.0019	0.997
Forestry minimum	5	376.96	11.52	0.0017	0.998
Vegetation maximum	6	377.036	11.85	0.0015	1

[7] Landscape+vegetation= Percent of surrounding forested area+percent of surrounding treated area+ herbaceous cover+shrub cover+woody debris cover

Table 11: Coefficients (Coeff), standard errors (SE), and p (P) values for covariates in the most supported abundance model for Woodpeckers in the northern Rocky Mountains in 2018-2019.

	Coeff	SE	P(>|z|)
(Intercept)	1.45	0.83	0.079
Minimum herbaceous	0.19	0.13	0.15
Minimum shrub	-0.38	0.22	0.085
Minimum woody debris	0.42	0.12	0.00075

Table 12: The Poisson model for quadratic date effects on detection probability is the top-ranking model for Bluebirds. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into detection probability (σ) models for Bluebird species in the northern Rocky Mountains 2018-2019.

Model[1,2]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
P (σ) (date^2)	5	236.48	0	0.34	0.34
P (σ) (min+date^2)	6	238.25	1.77	0.14	0.48
NB (σ) (date^2)	6	238.6	2.12	0.12	0.6
P (σ) (date)	4	238.62	2.14	0.12	0.71
P (σ) (min+date^2+year)	7	239.8	3.32	0.064	0.78
P (σ) (min+date)	5	240.07	3.59	0.056	0.83
NB (σ) (min+date^2)	7	240.39	3.91	0.048	0.88
NB (σ) (date)	5	240.72	4.24	0.041	0.92
P (σ) (min+date+year)	6	241.63	5.15	0.026	0.95
NB (σ) (min+date^2+year)	8	241.96	5.48	0.022	0.97
NB (σ) (min+date)	6	242.18	5.7	0.02	0.99
NB (σ) (min+date+year)	7	243.75	7.27	0.0089	0.997
P (σ) (.)	3	247.96	11.48	0.0011	0.998
P (σ) (year)	4	249.26	12.78	0.00057	0.999
P (σ) (min)	4	249.34	12.86	0.00055	0.999
P (σ) (min+year)	5	250.67	14.19	0.00028	1
NB (σ) (year)	5	251.31	14.83	0.0002	1
NB (σ) (min)	5	251.41	14.93	0.00019	1
NB (σ) (min+year)	6	252.73	16.25	0.0001	1

Table 13: Minimum canopy cover and basal area is the top ranking model for bluebird abundance. Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into abundance (λ) models for Bluebirds in the northern Rocky Mountains 2018-2019.

Model[3,5,6]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Forestry minimum	7	233.5	0	0.71	0.71
Forestry mean	7	236.51	3.007	0.16	0.87
Forestry maximum	7	239.037	5.53	0.045	0.91
Landscape	7	240.27	6.76	0.024	0.93
Vegetation minimum	8	240.6	7.094	0.02	0.95
Vegetation maximum	8	240.64	7.14	0.02	0.97
Vegetation mean	8	240.8	7.29	0.018	0.99
Global	12	243.99	10.49	0.0037	1
Vegetation+landscape	10	244.75	11.25	0.0026	1
Null	3	247.96	14.45	0.00052	1

Table 14: Coefficients (Coeff), standard errors (SE), and p (P) values for covariates in the most supported abundance model for Bluebirds in the northern Rocky Mountains in 2018-2019.

	Coeff	SE	P(>|z|)
(Intercept)	1.8	1.28	0.16
Basal area	0.3	0.26	0.24
Minimum canopy cover	-0.8	0.33	0.015

Table 15: Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into models for bird species richness in the northern Rocky Mountains 2018-2019.

Models[8]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Global	9	1061.67	0	0.66	0.66
Landscape + vegetation	7	1063.15	1.48	0.32	0.98
Forestry + vegetation	7	1068.65	6.97	0.02	1
Vegetation maximum	5	1076.29	14.61	0.00045	1
Vegetation minimum	3	1106.5	44.82	1.22E-10	1
Landscape	3	1123.44	61.77	2.56E-14	1
Forestry minimum	3	1131.09	69.42	5.59E-16	1
Vegetation mean	5	1131.79	70.12	3.93E-16	1
Forestry maximum	3	1141.28	79.61	3.43E-18	1
Forestry mean	3	1143.31	81.64	1.24E-18	1

[8] Vegetation models= herbaceous cover + shrub cover + woody debris cover + non-vegetated cover, Forestry models= canopy cover + basal area, Forestry+ vegetation= basal area + canopy cover + herbaceous cover + shrub cover + woody debris cover + non-vegetated cover, Landscape=percent of surrounding forested area + percent of surrounding treated area, Landscape + vegetation= surrounding forest cover + surrounding treated area + herbaceous cover + shrub cover + woody debris + non-vegetated cover, Global=surrounding forest cover + surrounding treated area + canopy cover + basal area + herbaceous cover + shrub cover + woody debris + non-vegetated cover

Table 16: Coefficients (Coeff), standard errors (SE), and p (P) values for covariates in the top model for bird species richness in the northern Rocky Mountains in 2018-2019.

	Coeff	SE	P(>|z|)
Intercept	1.6	0.031	< 2e-16
Forest cover	-0.11	0.042	0.0095
Trt area	-0.079	0.033	0.018
Minimum canopy cover	-0.093	0.039	0.017
Basal Area	0.036	0.039	0.35
Maximum herbaceous cover	0.15	0.034	1.36e-05
Maximum shrub cover	0.018	0.031	0.57
Maximum woody debris	0.2	0.029	1.32e-11
Maximum non-vegetated cover	0.23	0.036	4.59e-10

Table 17: Number of parameters (K), AICc, ΔAICc, Akaike weight (AICcwt) based on Akaike's Information Criteria, and cumulative Akaike weight (Cum.Wt) for covariates incorporated into models for bird species diversity in the northern Rocky Mountains 2018-2019.

Models[8]	K	AICc	Delta_AICc	AICcWt	Cum.Wt
Landscape + vegetation	8	402.94	0	0.64	0.64
Global	10	404.68	1.74	0.27	0.91
Forestry + vegetation	8	407.33	4.39	0.071	0.98
Vegetation maximum	6	409.6	6.66	0.023	1
Vegetation minimum	4	428.21	25.27	2.08E-06	1
Landscape	4	443.79	40.85	8.61E-10	1
Forestry minimum	4	446.3	43.36	2.45E-10	1
Vegetation mean	6	447.98	45.037	1.06E-10	1
Forestry maximum	4	450.82	47.88	2.56E-11	1
Forestry mean	4	451.37	48.43	1.95E-11	1

Table 18: Coefficients (Coeff), standard errors (SE), and p (P) values for covariates in the most supported model for bird species diversity in the northern Rocky Mountains in 2018-2019.

	Coeff	SE	Pr(>|t|)
(Intercept)	1.2	0.041	< 2e-16
Forest cover	-0.15	0.052	0.0056
Trt area	-0.084	0.043	0.054
Maximum herbaceous cover	0.21	0.049	2.70e-05
Maximum shrub cover	0.051	0.044	0.24250
Maximum woody debris	0.25	0.048	5.54e-07
Maximum non-vegetated cover	0.31	0.049	1.78e-09

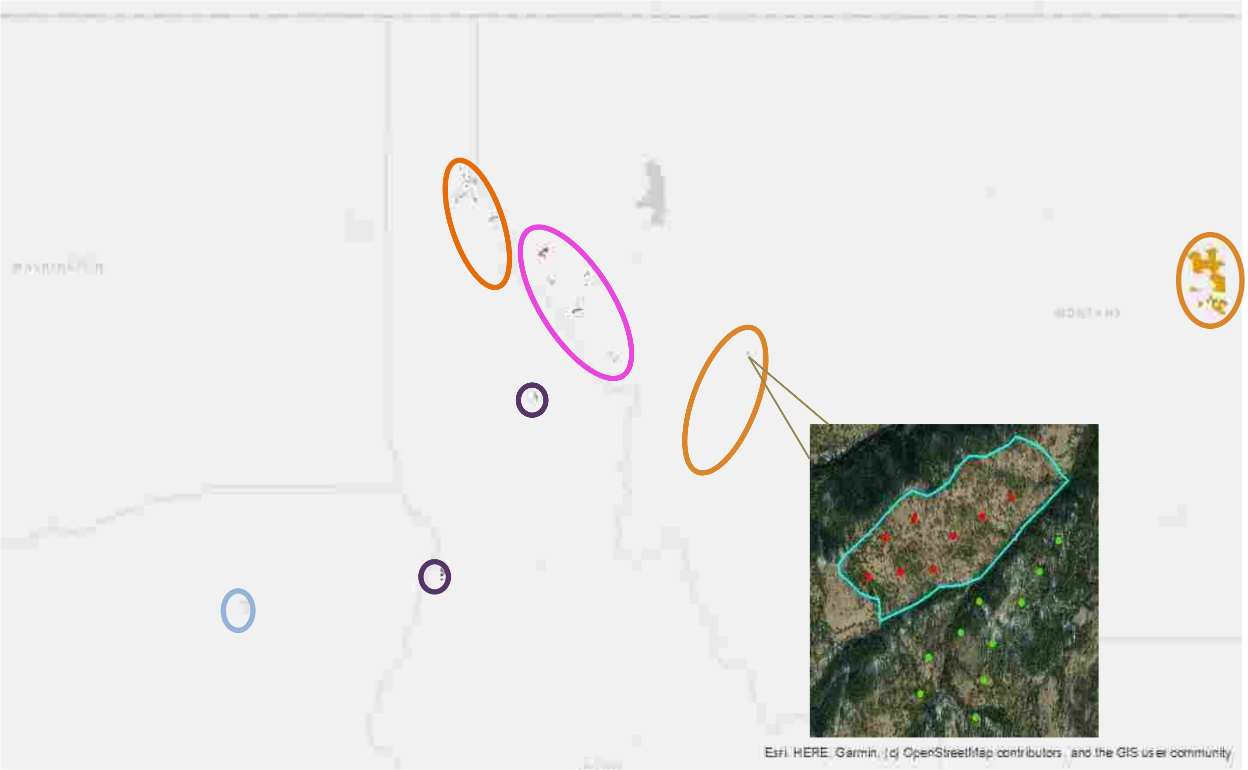

Figure 1: Map of our study region. The Starkey region is shown in blue on the lower left, the Clearwater region is shown in purple, the Lolo region in pink, the north Idaho-Kootenai region in dark orange, and the eastern Montana region in light orange. Also pictured is an image of an example of a treatment and paired control unit with the border of the treatment unit in light blue, the treatment points in red, and the control points in light green

Figure 2: A representation of a typical treated stand and nearby control area that would be sampled for this study. Photo credit: Stephanie Berry.

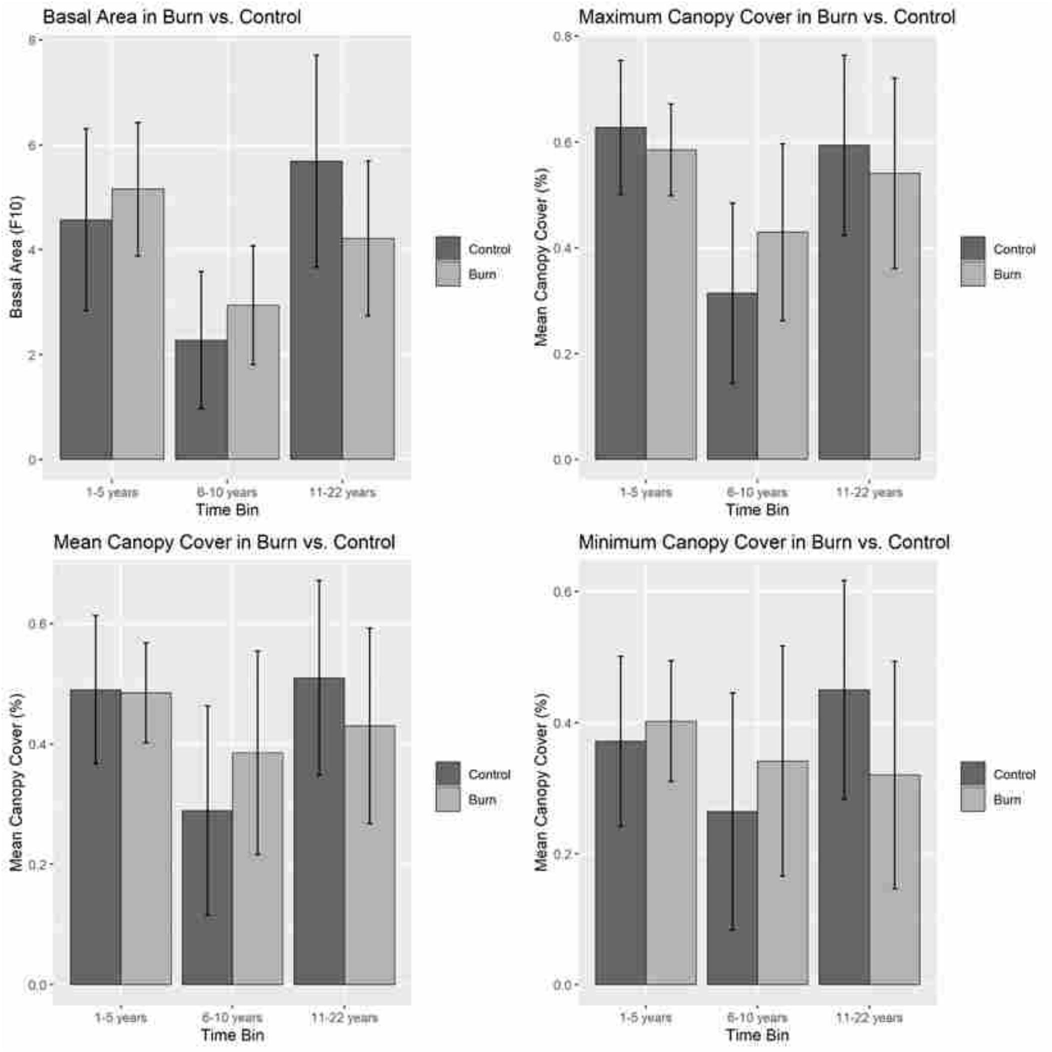

Figure 3: Basal area (top left) and maximum (top right), mean (bottom left), and minimum canopy cover (bottom right) measured throughout both seasons at burned and control sites.

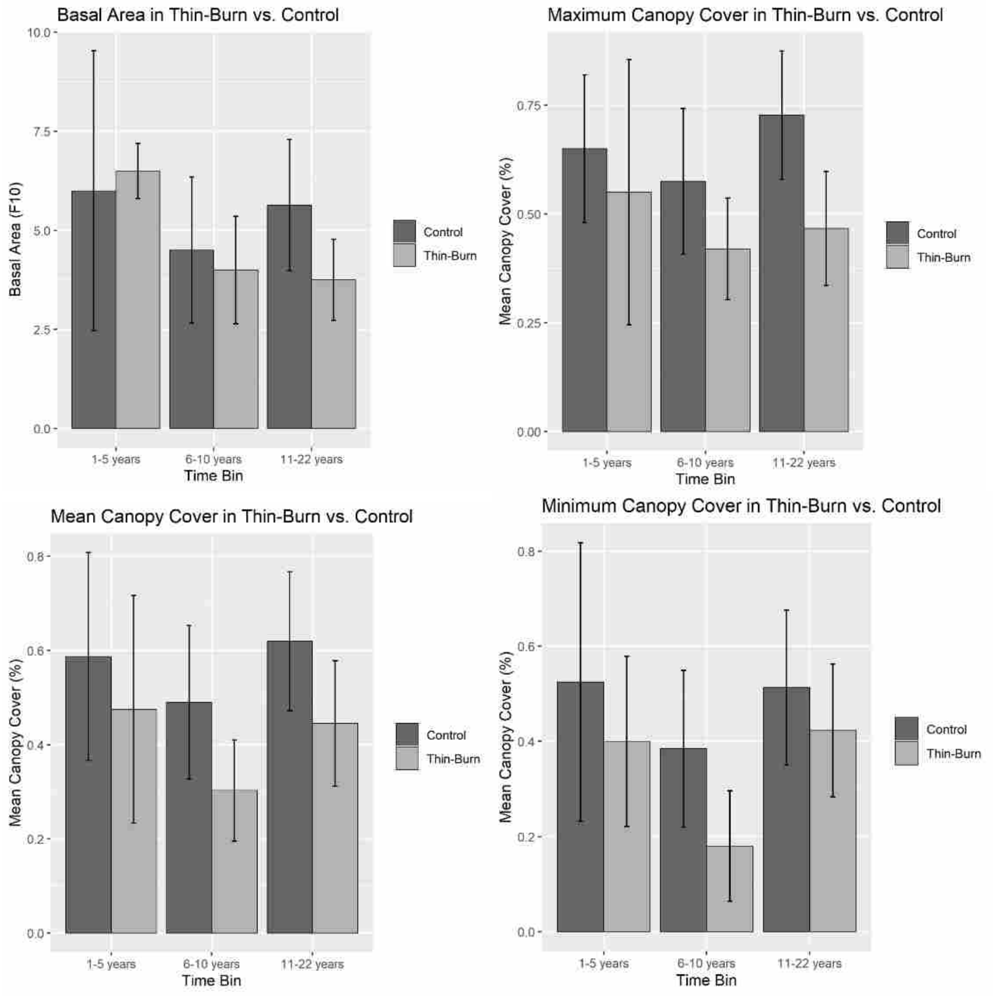

Figure 4: Basal area (top left) and maximum (top right), mean (bottom left), and minimum canopy cover (bottom right) measured throughout both seasons at thin-burned and control sites.

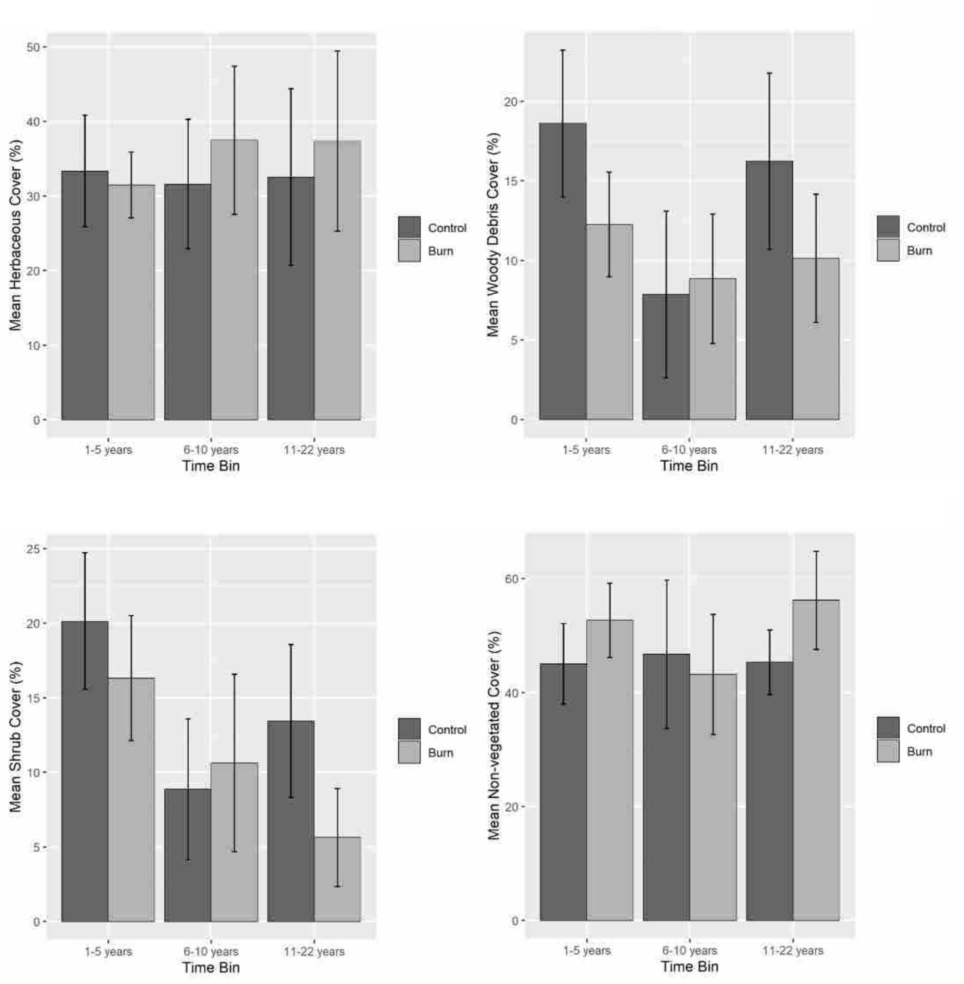

Figure 5: Maximum vegetation values measured throughout both seasons of sampling at paired burn and control sites, with herbaceous cover (top left), woody debris (top right), shrub cover (bottom left), and non-vegetated cover (bottom right).

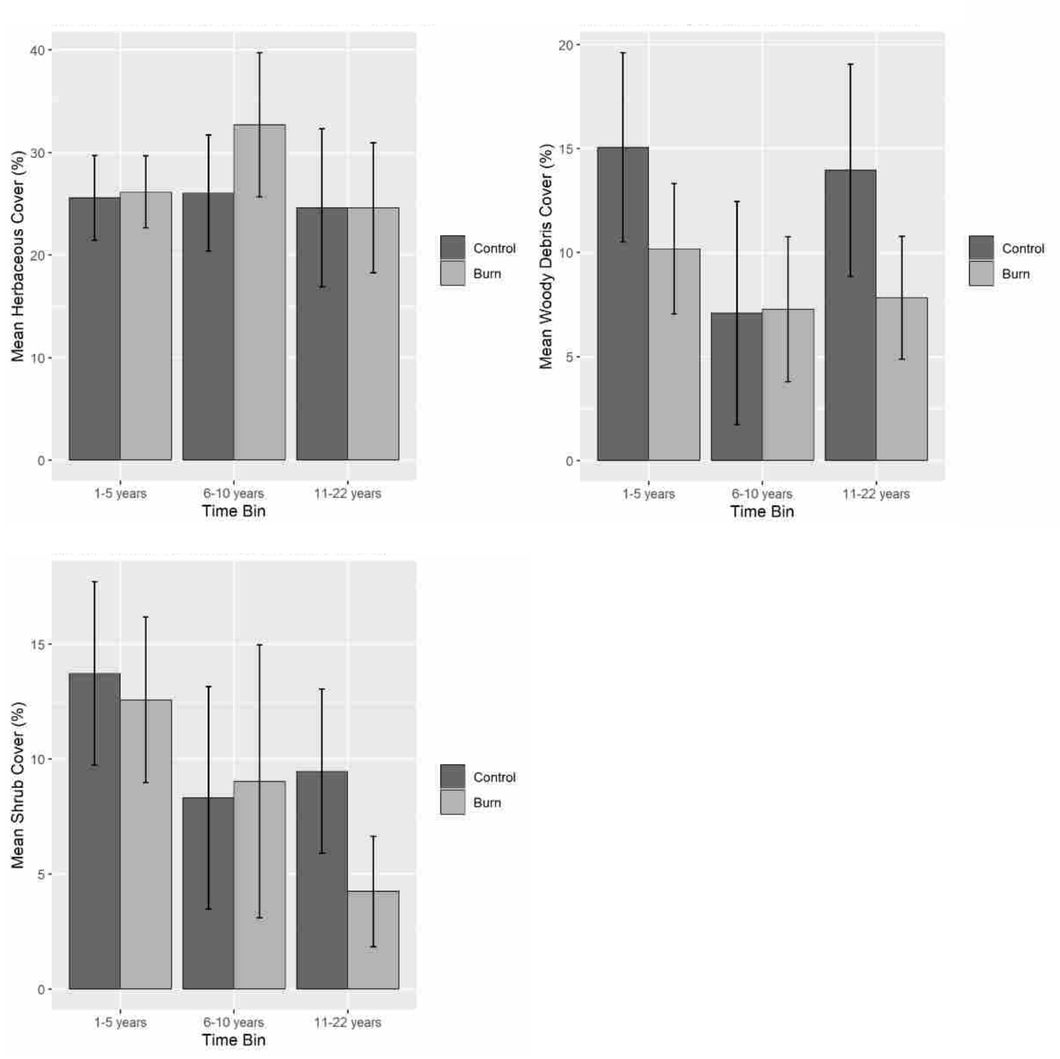

Figure 6: Mean vegetation values measured throughout both seasons of sampling at paired burn and control sites, with herbaceous cover (top left), woody debris (top right), and shrub cover (bottom left).

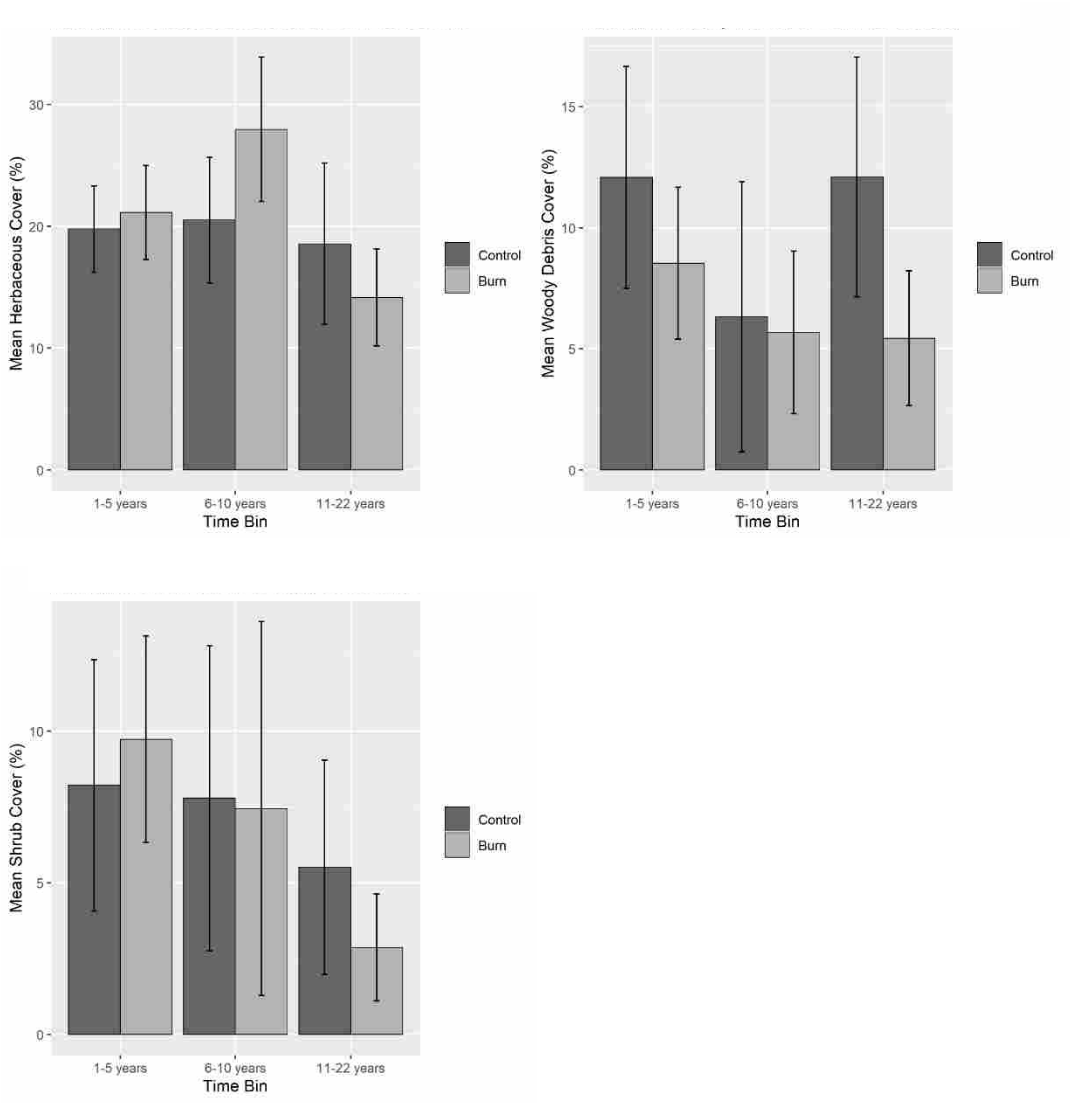

Figure 7: Minimum vegetation values measured throughout both seasons of sampling at paired burn and control sites, with herbaceous cover (top left), woody debris (top right), and shrub cover (bottom left).

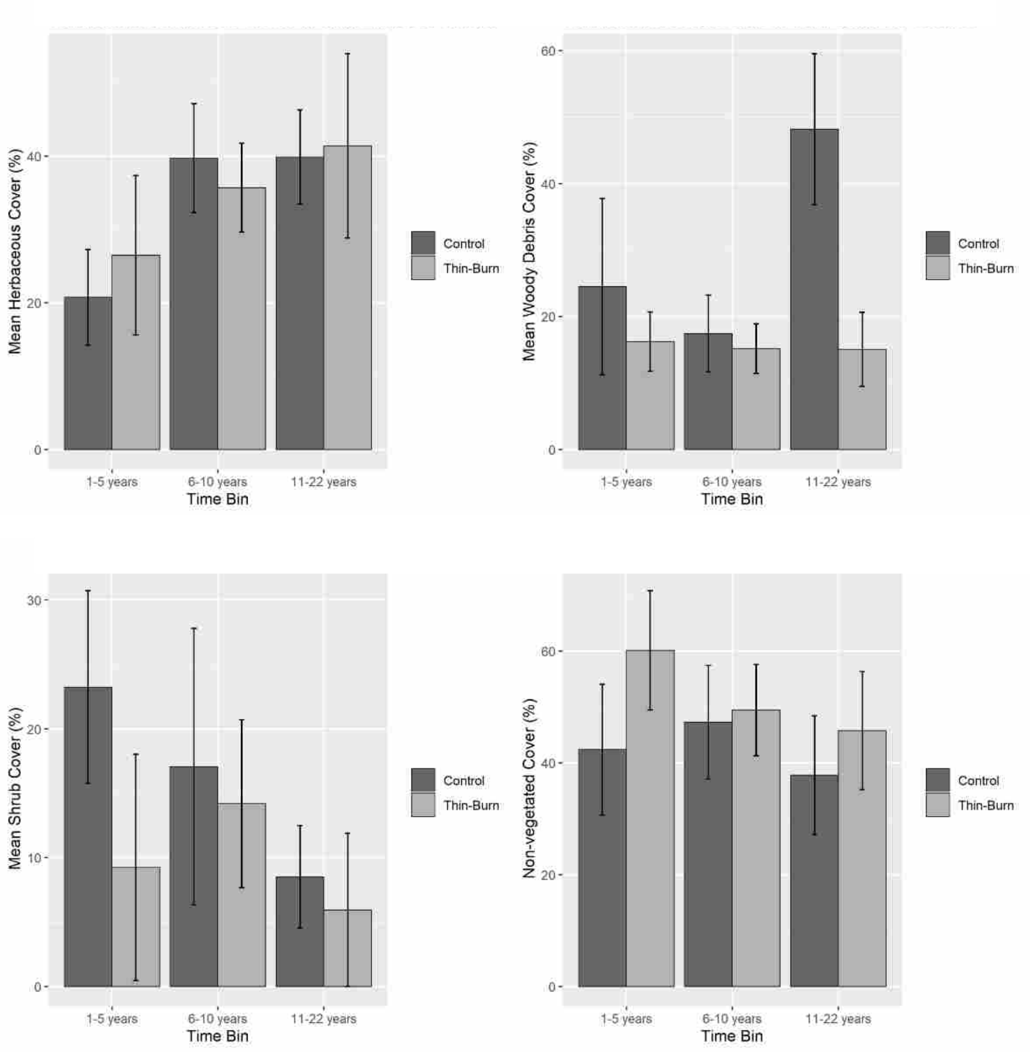

Figure 8: Maximum vegetation values measured throughout both seasons of sampling at paired thin-burn and control sites, with herbaceous cover (top left), woody debris (top right), shrub cover (bottom left), and non-vegetated cover (bottom right).

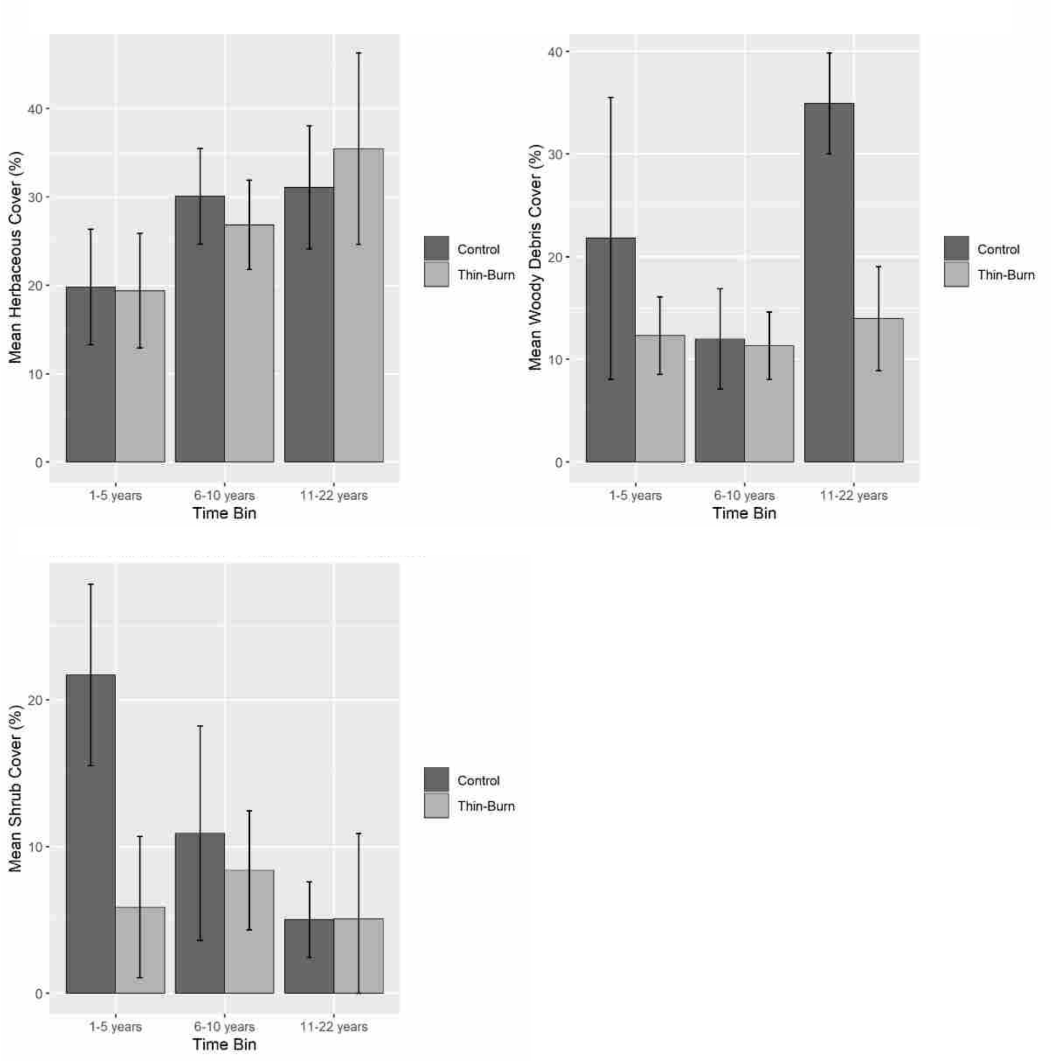

Figure 9: Mean vegetation values measured throughout both seasons of sampling at paired thin-burn and control sites, with herbaceous cover (top left), woody debris (top right), and shrub cover (bottom left).

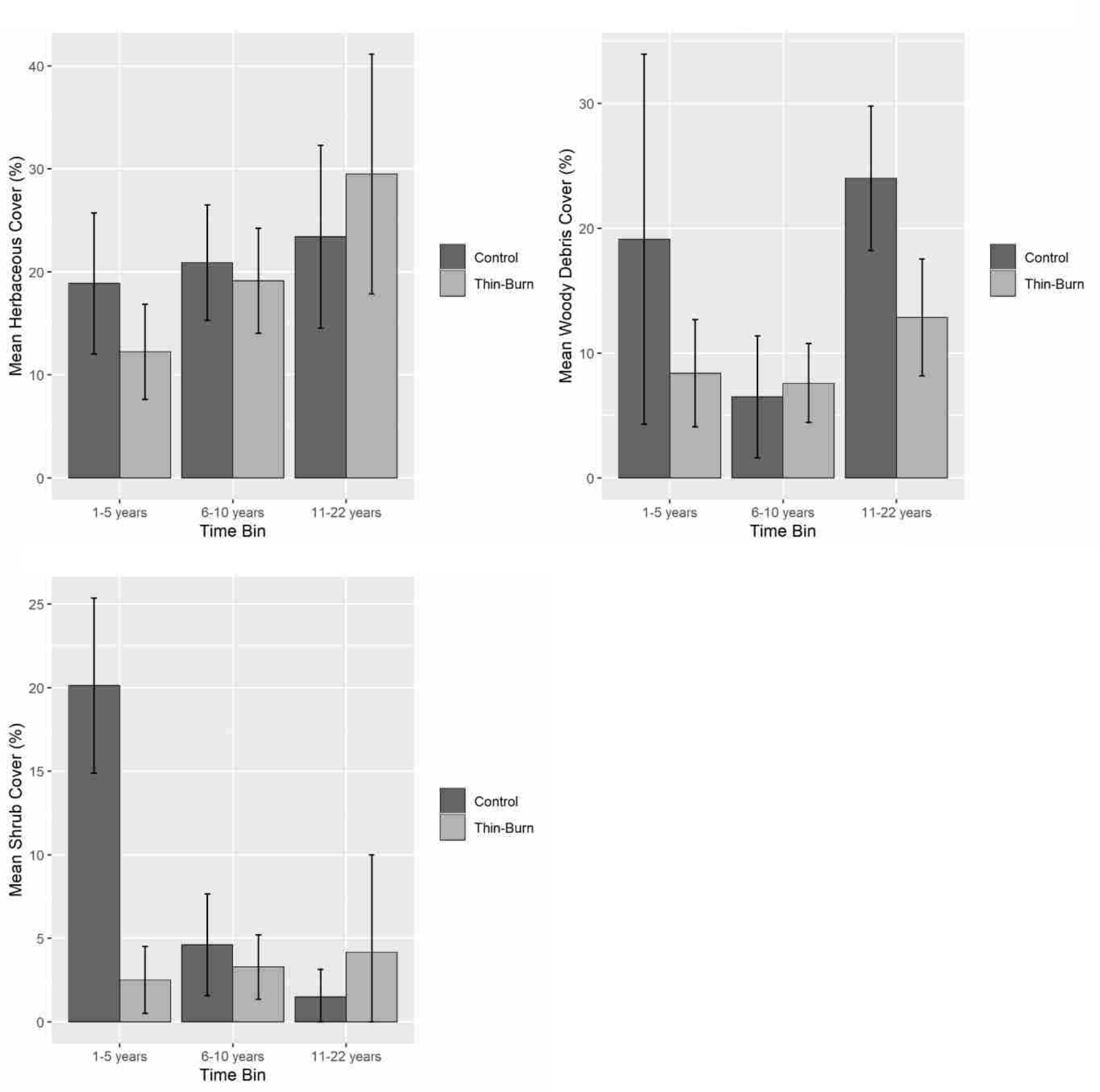

Figure 10: Minimum vegetation values measured throughout both seasons of sampling at paired burn and control sites, with herbaceous cover (top left), woody debris (top right), and shrub cover (bottom left).

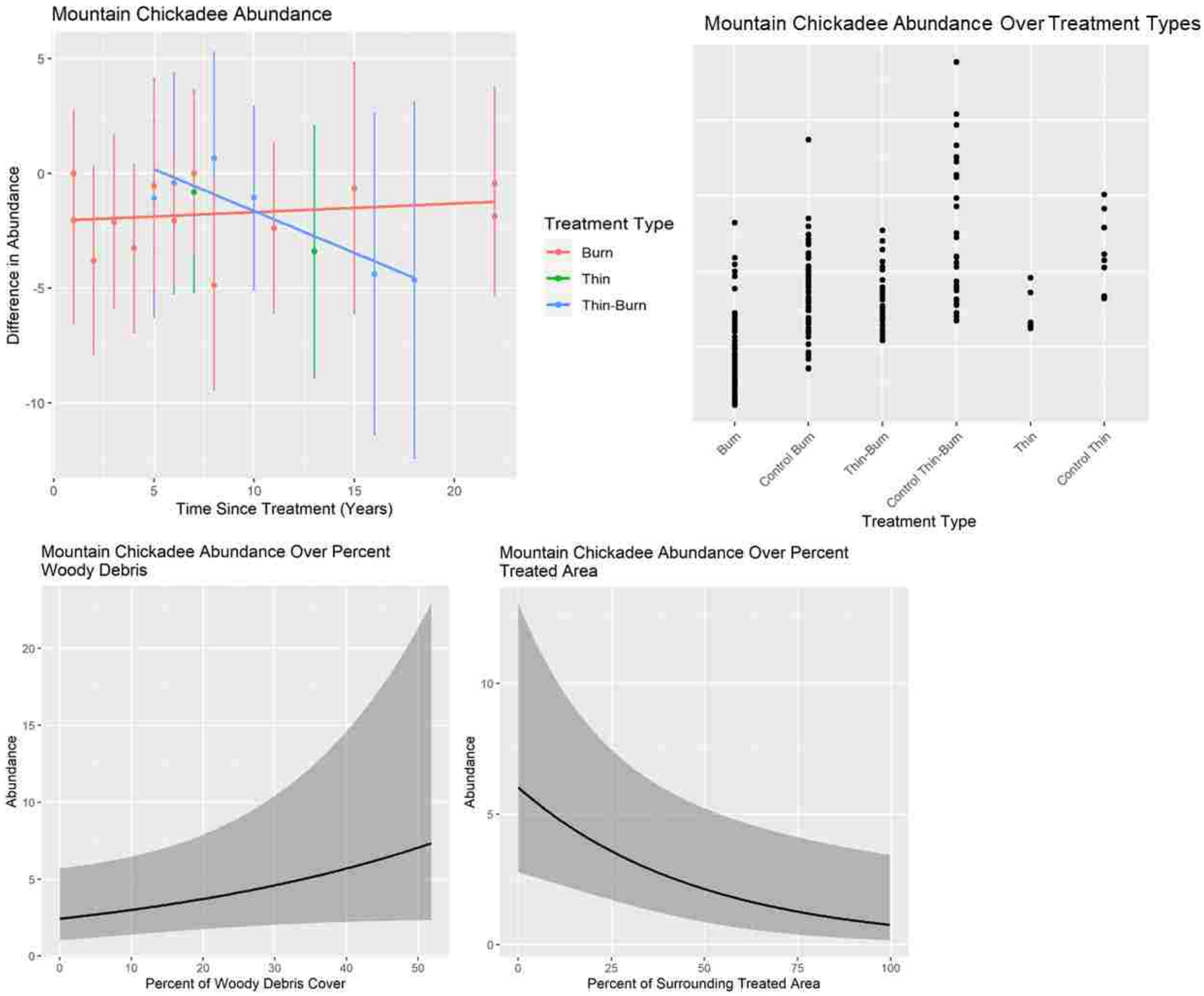

Figure 11: Mountain Chickadee predicted abundance over time since treatment (top left), predicted abundance across points in burns, thin-burns, and thins, and their paired controls (top right), and predicted abundance of chickadees over percent of woody debris cover and percent of surrounding area. Mountain Chickadee abundance difference over time since treatment was calculated as treatment minus control, so means below 0 represent a higher mean abundance in controls than their paired treatments.

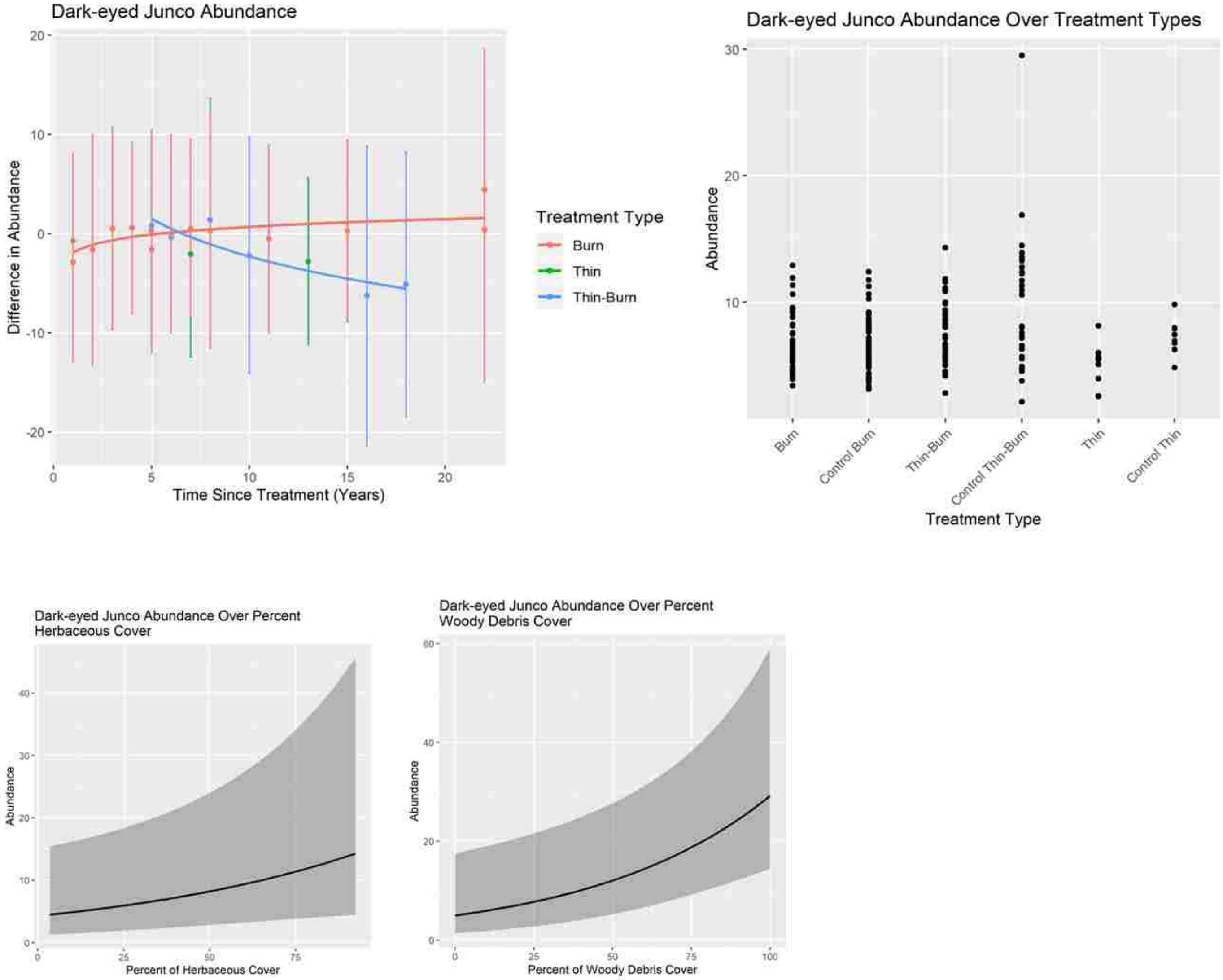

Figure 12: Dark-eyed Junco predicted abundance over time since treatment (top left), predicted abundance across points in burns, thin-burns, and thins, and their paired controls (top right), and predicted abundance of junco over percent of herbaceous cover (bottom left), and woody debris cover (bottom center). Dark-eyed Junco abundance difference over time since treatment was calculated as treatment minus control, so means below 0 represent a higher mean abundance in controls than their paired treatments.

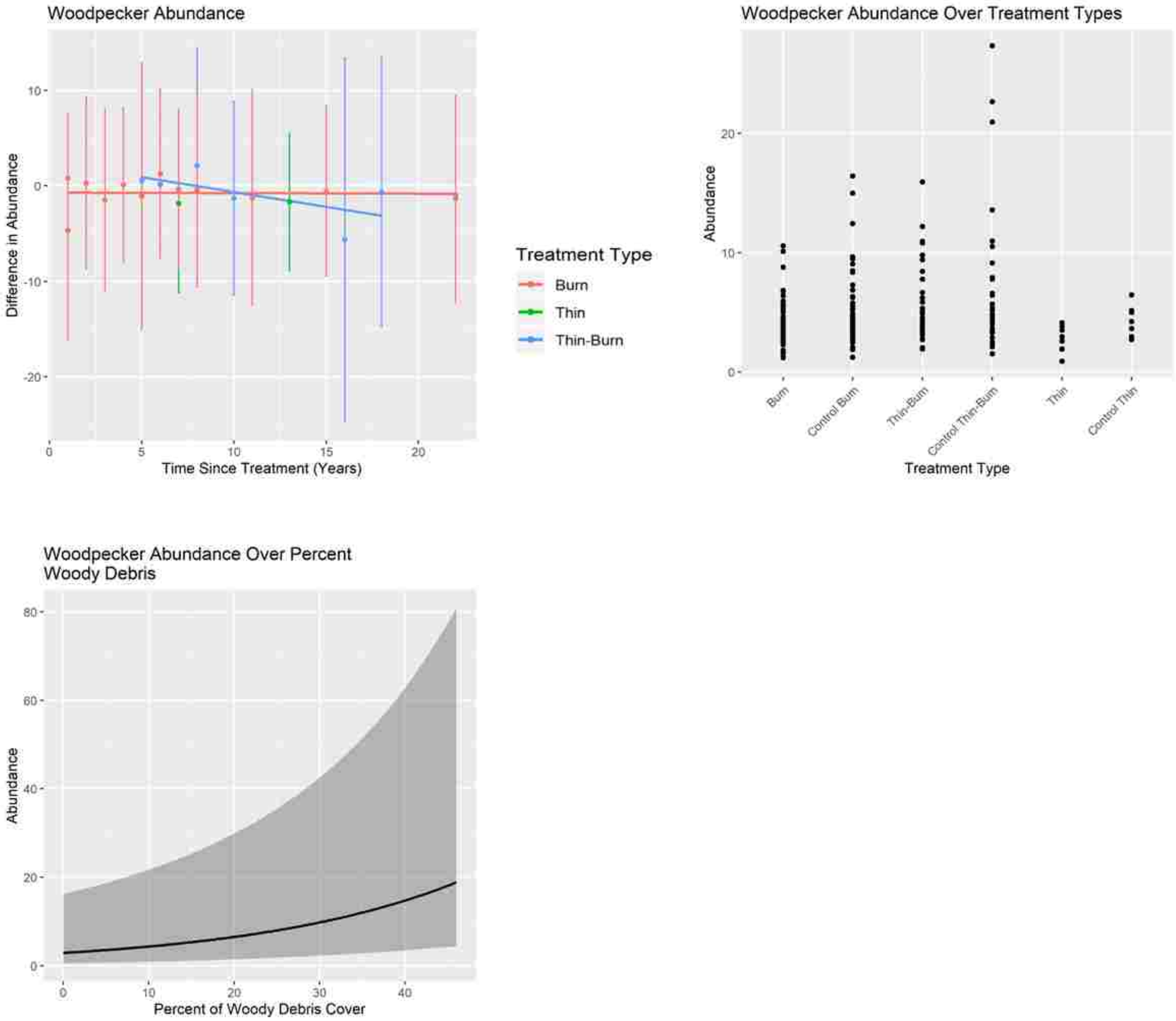

Figure 13: Woodpecker predicted abundance over time since treatment (top left), predicted abundance across points in burns, thin-burns, and thins, and their paired controls (top right), and predicted abundance of woodpeckers over percent of woody debris cover (bottom left), and shrub cover (bottom center). Dark-eyed Junco abundance difference over time since treatment was calculated as treatment minus control, so means below 0 represent a higher mean abundance in controls than their paired treatments.

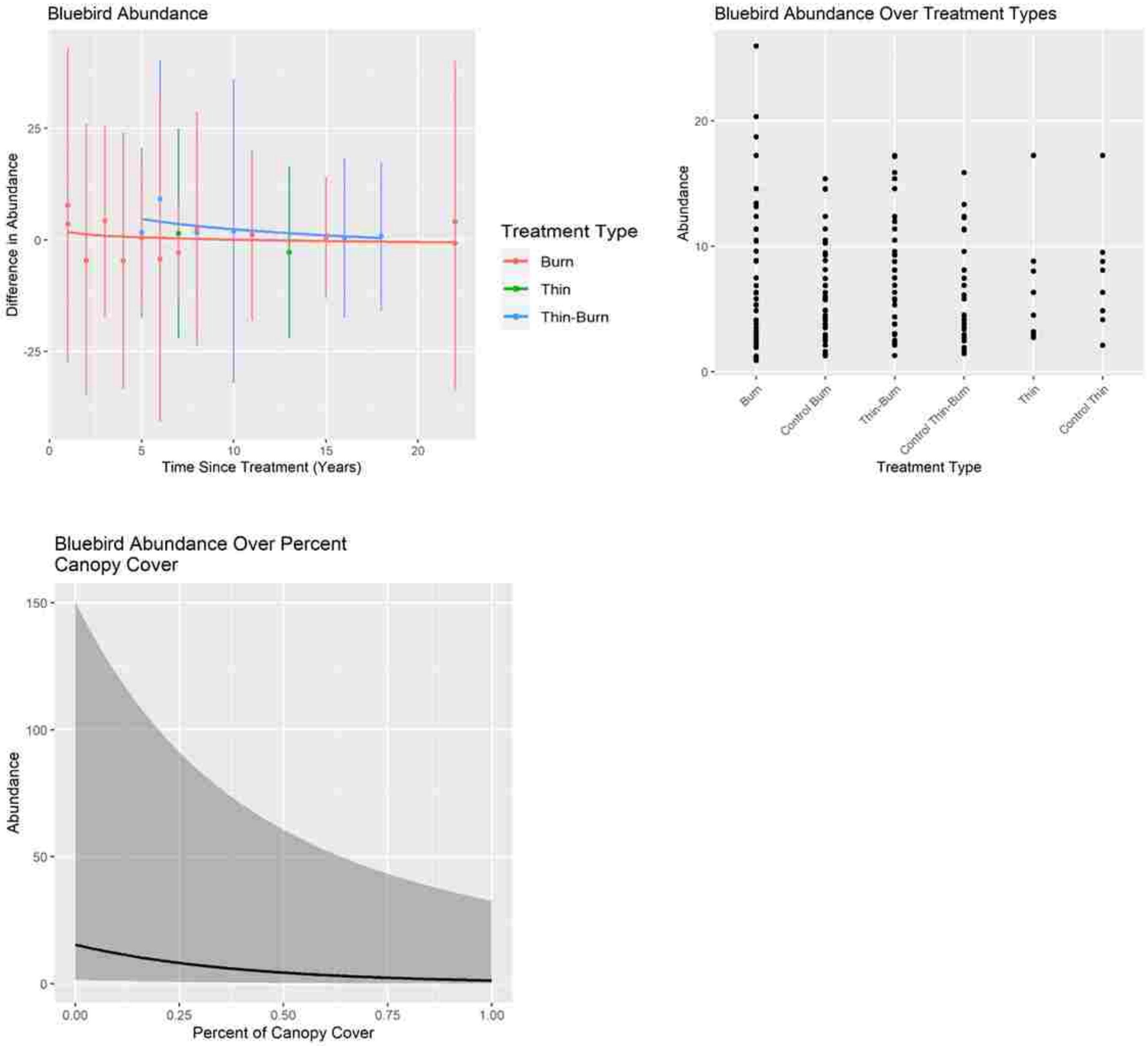

Figure 14: Bluebird predicted abundance over time since treatment (top left), predicted abundance across points in burns, thin-burns, and thins, and their paired controls (top right), and predicted abundance of bluebird over percent of canopy cover (bottom left). Bluebird abundance difference over time since treatment was calculated as treatment minus control, so means below 0 represent a higher mean abundance in controls than their paired treatments.

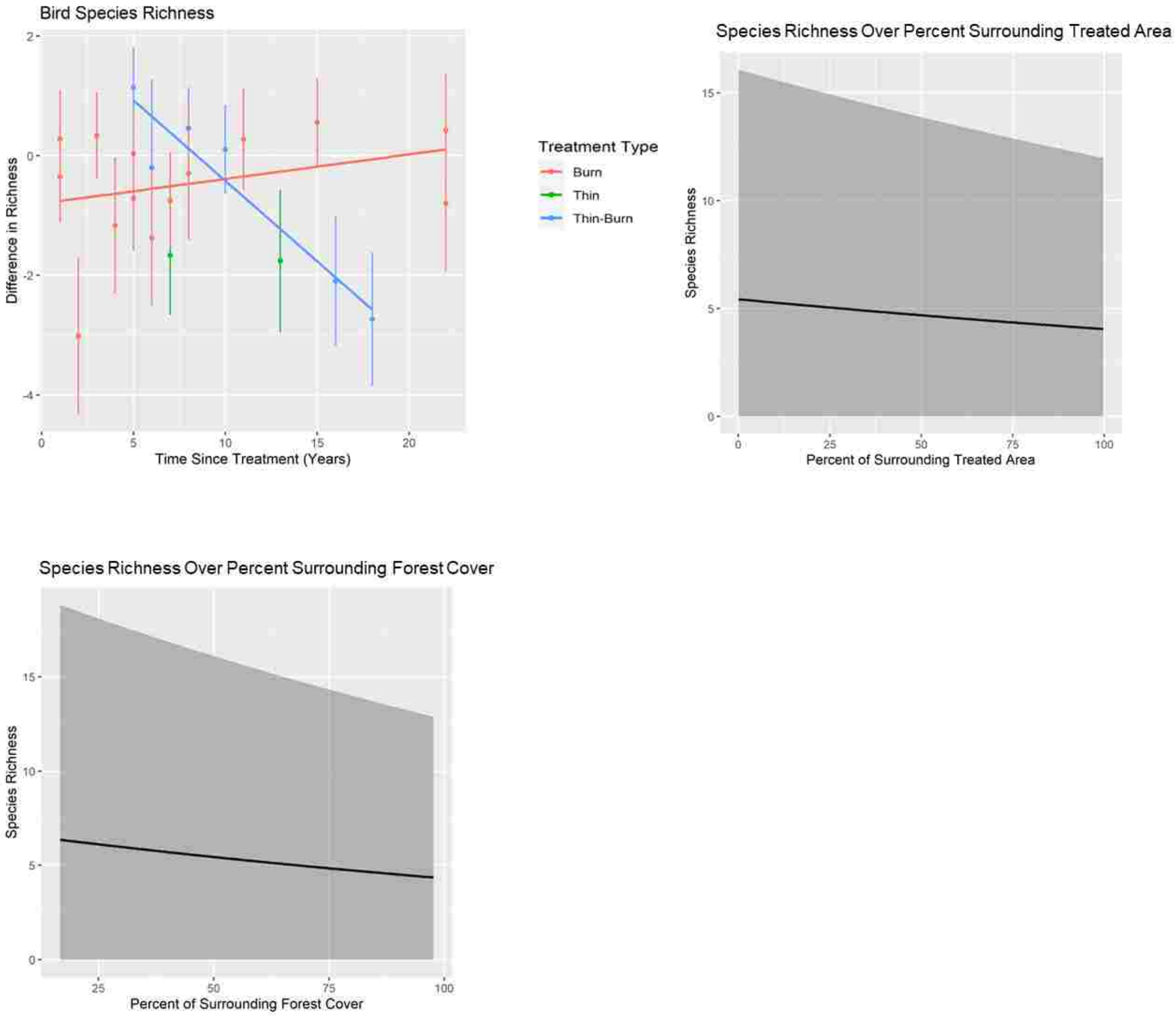

Figure 15: Predicted species richness over time since treatment (top left), predicted species richness over treated area (top right), and predicted species richness over surrounding forest cover. Species richness difference over time since treatment was calculated as treatment minus control, so means below 0 represent a higher mean abundance in controls than their paired treatments.

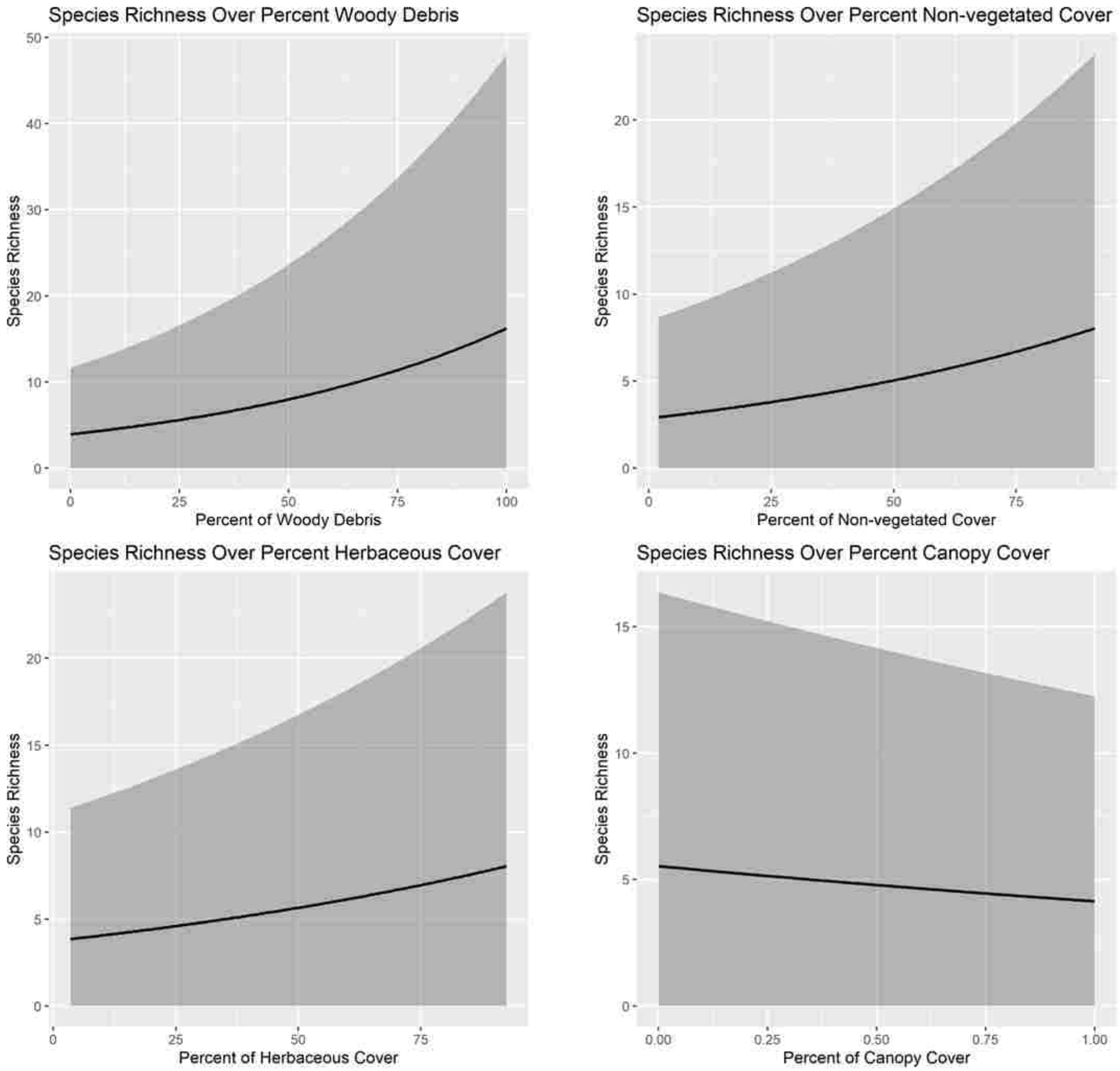

Figure 16: Predicted species richness over percent of woody debris (top left), percent of non-vegetated cover (top right), percent of herbaceous cover (bottom left), and percent of canopy cover (bottom right).

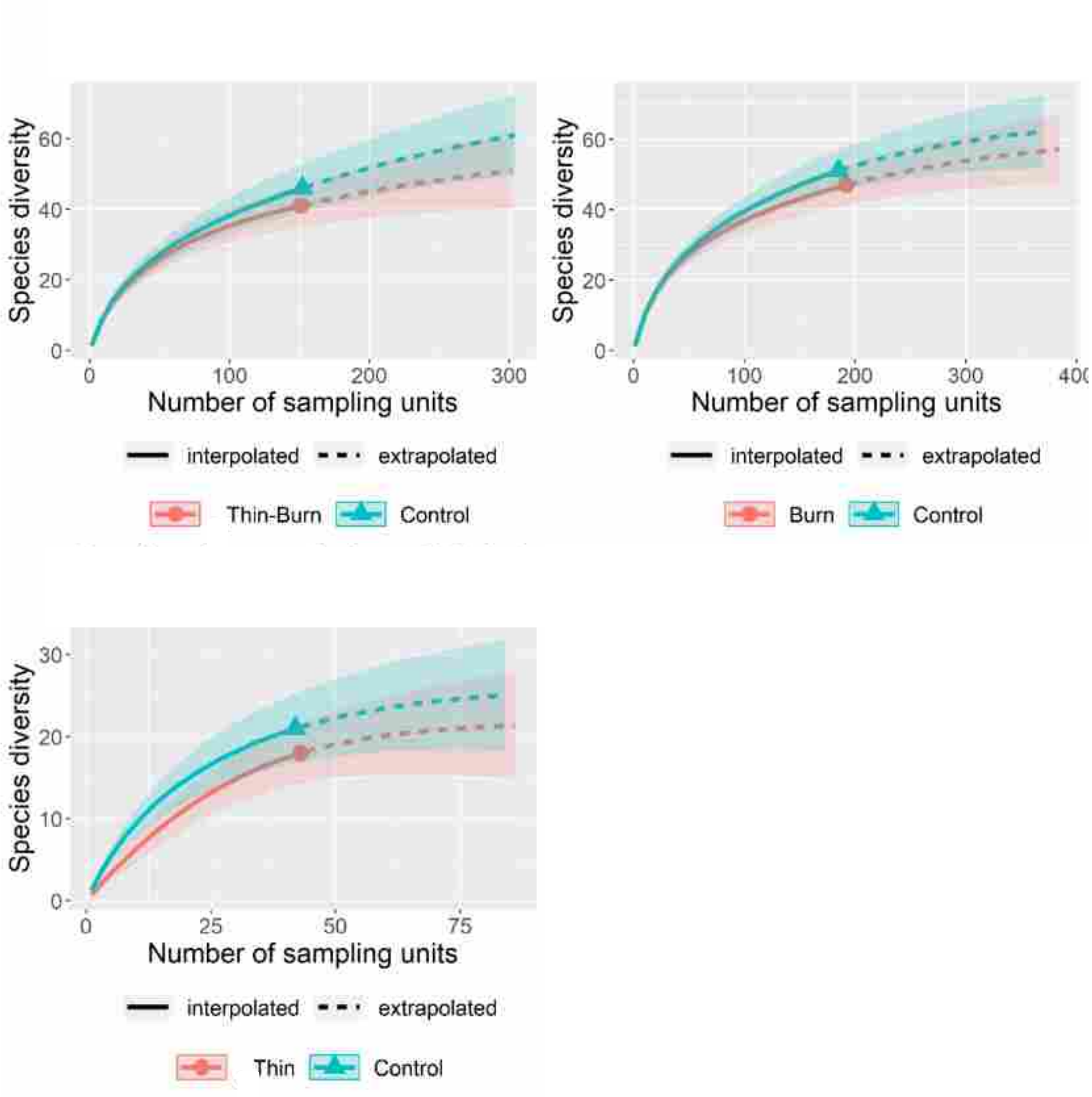

Figure 17: Species accumulation over number of point counts completed in each treatment type and their paired controls.

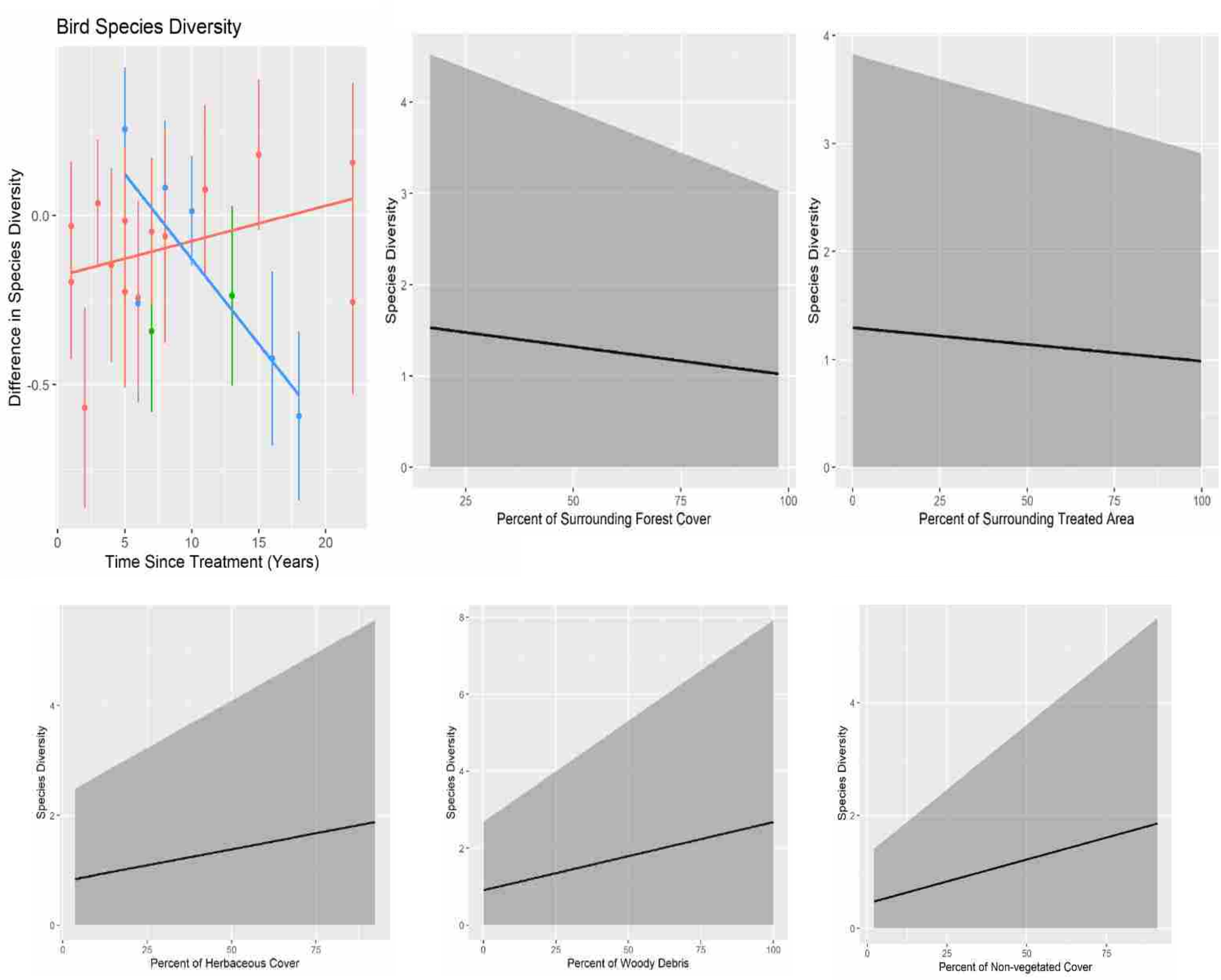

Figure 17: Predicted species diversity over time since treatment (top left), predicted species diversity over forest cover and treated area (top right), and predicted species diversity over herbaceous cover (bottom left), woody debris (bottom center), and non-vegetated cover (non-vegetated cover). Species richness difference over time since treatment was calculated as treatment minus control, so means below 0 represent a higher mean abundance in controls than their paired treatments.

SUMMARY

Summary of Retrospective Habitat Treatment Analysis of Bird and Native Bee Communities

Across the western United States, fire exclusion has changed forest structure, with patterns of increasing tree density, fuel loads, and closure of the forest canopy, leading to higher wildfire severity and risk (Covington and Moore 1994). Habitat treatments such as prescribed burning, mechanical thinning, and a combination of the two can mitigate these issues arising from fire exclusion (Graham et al. 1999, Agee and Skinner 2005). These treatments are also used to improve habitat quality for species that utilize early-successional, or open habitat, such as elk (*Cervus canadensis*) (Pilliod et al. 2006, Long et al. 2008). The Rocky Mountain Elk Foundation (RMEF) has helped to fund more than 7 million acres of habitat treatments across the U.S., primarily with the objective of increasing elk habitat quality. When these treatments are conducted, other species of wildlife might be impacted.

Two communities potentially impacted by these treatments are birds and native bees, however we understand much less about their responses to habitat treatments than elk responses. Both of these communities provide important ecosystem services, with bees being hugely important in pollination of wild plants and agricultural crops (Ollerton et al. 2011, Garibaldi et al. 2013), and birds playing an important role in pest control, nutrient cycling, and seed dispersal (Wenny et al. 2011), in addition to the recreational opportunities that birds provide in the form of bird watching (Carver 2013). Unfortunately, these communities are also experiencing declines in part due to habitat loss (Brawn et al. 2001, Schmiegelow and Monkkonen 2002, Biesmiejer 2006, Soykan et al. 2016). Since habitat availability is an important factor in the persistence of bird and bee communities, it is important to know the impacts of habitat treatments like prescribed burning and mechanical thinning, which are increasingly being conducted across the western United States.

To understand how habitat treatments impact bird and bee communities, we sampled them across eastern Oregon, northern Idaho, and Montana during the summers of 2018 and 2019. We completed our sampling in habitat treatments (prescribed burning, mechanical thinning, and a combination of both, henceforth described as “thin-burns”) that were conducted between 1997 and 2018 and ranged between 40 and 6,657 acres. We also sampled nearby paired control areas for comparison with communities present in the treatments. We sampled multiple treatment types, a wide range of locations, sizes of treatments, and times since treatment to assess how these factors impacted bird and bee responses to treatment. To sample birds, we completed point counts within a 50 meter radius of the sample point, recording all birds seen and heard within 10 minutes. To sample bees, we used pan traps (colored bowls filled with soapy water, to attract and trap bees) and hand netting (Cane et al. 2000, Westphal et al. 2008, Popic et al. 2013). In addition to the wildlife sampling, we also completed vegetation and forest sampling, measuring herbaceous, bare ground, and woody debris cover, flower abundance and species richness, canopy cover, and basal area. In this way, we were able to measure how treatments changed habitat characteristics, and therefore how habitat changes were related to wildlife impacts resulting from treatments.

To assess bird response to treatments, we estimated bird species richness and diversity along with abundance of a few focal species and groups of birds that represented different foraging and nesting strategies, so we could relate responses of these species to other birds with similar strategies. We estimated abundance of Dark-eyed Juncos (*Junco hyemalis*), Mountain Chickadees (*Poecile gambeli*), Woodpeckers (including Hairy Woodpeckers (*Picoides villosus*), Downy Woodpeckers (*Picoides pubescens*), and Northern Flickers (*Colaptes auratus*)), and Bluebirds (including Western and Mountain Bluebirds). Dark-eyed Juncos nest on the ground (Sperry et al. 2008), while Mountain Chickadees, Woodpeckers, and Bluebirds nest in tree cavities (Bock and Block 2005, Bateman and O'Connell 2006). Dark-eyed juncos also forage on the ground for seeds and insects (Artman 2003, Sperry et al. 2008, Bayne and Nielsen 2011), while Mountain Chickadees forage on the foliage for insects (Bateman and O'Connell 2006), Woodpeckers forage on trees, logs, and the ground for insects (Elchuk and Wiebe 2002, Bateman and O'Connell 2006), and Bluebirds are ground-foragers, primarily for insects (Wightman and Germaine 2006).

Overall, we found no dramatic impacts on our focal bird species from the treatments. Mountain chickadees were most negatively impacted by treatments of all types in all times post-treatment out of our focal species, and their abundance decreased 87% with increasing percent of surrounding treated area within a 1250 meter radius from 0% to 100%. Chickadees were most negatively impacted by burns within 0-5 years of treatment, and thin-burns 10 years post-treatment. Dark-eyed Juncos did not show a clear response to treatment, however they decreased in thin-burn treatments over time since treatment, and thin-burn treatments 10 years or older post treatment had a negative impact on junco abundance. The woodpecker response was very similar to the Dark-eyed Junco response. Woodpeckers did not show a clear response to treatments overall, but their abundance declined over time since treatment in thin-burn treatments. Thin-burn treatments less than 10 years post-treatment were optimal for woodpeckers, but after that point, their abundance declined below control levels in thin-burn sites. Bluebirds showed a more positive response to treatments, and especially thin-burn treatments. Bluebird treatment response was likely because bluebirds were negatively associated with canopy cover, which was lower in thin-burns (which burned more intensively than prescribed burns along) respective to their controls than burns. There was no trend over time since treatment for bluebird abundance, so treatments at all times were similarly beneficial for bluebirds. There was little indication that bird species richness and diversity was different in treated or control sites, with 85 bird species detected over all of our sampling effort.

To assess the bee response to treatments, we estimated relative abundance, species richness, and species diversity of bees at our study sites. There was a much more dramatic response to treatments by the bee community than the bird community to habitat treatments. Burns and thin-burns positively impacted bee abundance, species richness, and species diversity, partly due to reduction in canopy cover by these treatments. Thin-burns had a more positive impact on bee abundance and richness than burn treatments, again likely due to the fact that thin-burns burn more intensively and therefore remove more canopy than burns alone. However, these benefits declined over time, with bee abundance, richness, and diversity becoming more similar to control sites at around 10-15 years. Additionally, bare ground, a nesting resource for many bees, was positively associated with bee abundance and richness, which was made available by habitat treatments. The landscape matrix that treatments were conducted was also important for the bees sampled, as open landscapes (within 800 meters) were associated with higher bee abundance and lower bee diversity. The size of the habitat treatments were also important for bee diversity, with relative bee diversity increasing 57% over our range of surrounding treated area, up to 497 acres, suggesting that larger treatments (up to 497 acres that we measured) may be more effective at increasing bee diversity than smaller treatments.

Our results showed interesting patterns about type of treatment, time since treatment, and the overall differences between the bee and bird communities. Overall, thin-burns more dramatically impacted bee and bird communities in our study area than burns, likely because thin-burns are typically more intense and remove more trees than burns alone (Harrod et al. 2007, Stephens et al. 2009). However, desirable impacts to wildlife from thin-burns declined more over time since treatment than burns in comparison with their respective controls, with benefits typically declining between 10 and 15 years. It is possible that thin-burns are changing a site's natural trajectory, whereas burns alone are not changing sites that dramatically, so over time, burns return to the control state whereas thin-burns may move to another state. If this is the case, then re-treatment between 10 and 15 years may be optimal for these treatments in order to avoid negative impacts on wildlife. However, not all treatment impacts were linear. In some cases, such as bee species richness, there is an overall decrease in richness at thin-burns between 8 and 10 years, but then an increase in sites between 15 and 17 years post-treatment. These inconsistent temporal trends suggest that other factors are at play, and may be more a question of habitat type or intensity of the treatment initially conducted. Overall, there are likely trends in wildlife responses over time since treatment, but there are clearly other treatment and landscape factors affecting these responses.

Our results also show that bees respond much more dramatically in a positive direction than birds, which could be a question of scale. Many solitary bee species likely forage and live locally (within 10s of meters; Potts et al. 2003) compared with many bird species. For example, a Northern Flicker's home range size is around 25 hectares (Elchuk and Wiebe 2003). While this home range size is well within the average size of our treatments, this could make it difficult to measure a bird response statistically at such a small scale, with habitat treatments potentially only causing an increase in a few breeding pairs of a species over the whole treatment. So while an event like a wildfire will likely have more dramatic impacts on both communities, a relatively smaller-scale, less intense treatment such as the habitat treatments we sampled, may be more impactful to bees, which seem to respond very positively to any treatment that opens the canopy. However, with respect to bee responses, our results show that benefits from treatment seem to decline over time since treatment. If managers wish to use these treatments to benefit bees specifically, it may be wise to retreat sites after around 10 to 15 years, and use thin-burn rather than burn treatments to maximize benefits if possible. Benefits to certain bird species, such as bluebirds or woodpeckers, would also likely be maximized following these guidelines, though treatments much larger in scale would likely be required to see any dramatic responses from the bird community overall. With habitat treatments such as these, there will always be winners and losers (such as conifer obligates including chickadees), however overall impacts to birds were minimal, while benefits to bees were substantial.

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APPENDIX

Table A1: Bee species caught by region and by method of capture (either pan or net). The bees caught by pan in this table represent bees used in our analyses. The Tin Can Hill and Beaverhead-Deerlodge areas of the “Eastern Montana” region were separated for this appendix, since a large number of bees were caught in the Tin Can Hill, or “Eastern Montana” region here. Region names are abbreviated here to fit the table, where BD=”Beaverhead-Deerlodge”, CL=”Clearwater”, EM=”Eastern Montana”, LO=”Lolo”, NI=”North-Idaho/Kootenai”, and ST=”Starkey”.

Species	BD		CL		EM		LO		NI		ST	
	pan	net	pan	net	pan	net	pan	net	pan	net	pan	net
Agapostemon angelicus / texanus	26	1	3	0	68	0	0	0	0	0	0	0
Agapostemon femoratus	0	0	0	0	7	0	0	0	0	0	0	0
Agapostemon sp.	0	0	0	0	1	0	0	0	0	0	0	0
Agapostemon texanus	6	0	0	0	86	0	0	0	0	0	0	0
Agapostemon virescens	1	0	0	0	38	0	0	0	0	0	0	0
Andrena ablegata	2	0	0	0	0	0	0	0	0	0	8	0
Andrena amphibola	2	0	0	0	18	1	0	0	0	0	5	0
Andrena astragali	0	0	0	0	1	0	0	0	0	0	2	0
Andrena caerulea	0	0	0	0	0	0	1	0	0	0	7	0
Andrena cressonii	0	0	0	0	3	0	0	0	0	0	0	0
Andrena cyanophila	3	0	0	0	0	0	0	0	0	0	0	0
Andrena evoluta	3	0	0	0	0	0	0	0	0	0	3	0
Andrena gardineri	0	0	0	0	1	0	0	0	0	0	0	0
Andrena hamulata	0	0	0	0	0	0	0	0	0	0	1	0
Andrena laminibucca	1	0	0	0	0	0	0	0	0	0	0	0
Andrena medionitens	1	0	0	0	0	0	0	0	0	0	0	0
Andrena melanochroa	2	0	0	0	0	0	0	0	0	0	10	1
Andrena microchlora	7	0	2	0	0	1	0	0	0	0	9	0
Andrena miranda	0	1	0	0	2	0	0	0	0	0	0	0
Andrena nigrihirta	1	0	7	0	1	0	0	0	5	0	7	0
Andrena nigrocaerulea	9	0	4	1	0	0	1	0	2	0	9	0
Andrena nivalis	9	0	2	0	1	1	0	0	0	0	4	0
Andrena nothocalaidis	0	0	0	0	1	0	0	0	0	0	0	0
Andrena pallidifovea	4	0	0	0	0	0	0	0	0	0	0	0
Andrena prunorum	0	0	1	0	0	0	0	0	0	0	1	0

Andrena rufosignata	0	0	4	0	0	0	0	0	0	0	1	0
Andrena salicifloris	0	0	0	0	1	0	0	0	0	0	2	0
Andrena shoshoni	1	0	0	0	0	0	0	0	0	0	0	0
Andrena sp.	0	0	0	0	0	0	0	0	1	0	0	0
Andrena sp. 1	0	0	0	0	0	0	0	0	1	0	0	0
Andrena sp. 2	1	0	0	0	0	0	0	0	0	0	0	0
Andrena sp. 3	0	0	0	0	0	0	1	0	0	0	0	0
Andrena sp. A	1	0	0	0	0	0	0	0	0	0	0	0
Andrena sp. C	0	0	1	0	0	0	0	0	0	0	0	0
Andrena sp. D	0	0	1	0	0	0	0	0	0	0	0	0
Andrena transnigra	0	0	1	0	0	0	0	0	3	0	2	0
Andrena trizonata	0	0	1	0	0	0	0	0	0	0	0	0
Andrena vicinoides	0	3	0	0	0	0	0	0	0	0	1	0
Andrena vierecki	0	0	0	0	0	0	0	0	0	0	1	0
Andrena w-scripta	1	0	0	0	0	0	0	0	0	0	0	0
Anthidium atrifrons	0	0	0	0	0	0	1	0	0	0	0	0
Anthidium utahense	0	0	0	0	4	0	0	0	0	0	0	0
Anthophora affabilis	0	0	0	0	8	0	0	0	0	0	0	0
*Anthophora bomboides**	0	0	0	0	0	1	0	0	0	0	0	0
*Anthophora pacifica**	0	0	0	0	0	0	0	0	0	0	0	2
Anthophora ursina	0	5	0	0	0	0	0	0	0	0	1	5
Ashmeadiella cubiceps	0	0	0	0	0	0	0	0	0	0	1	0
Atoposmia anthodyta	0	0	1	0	0	0	0	0	0	0	0	0
Bombus appositus	1	1	0	0	0	0	0	0	0	0	1	2
Bombus bifarius	22	38	3	2	1	0	10	2	8	5	9	22
Bombus californicus	1	6	3	0	1	0	0	0	0	0	2	0
Bombus centralis	4	2	0	0	5	1	0	1	0	0	3	3
Bombus fernaldae	0	0	0	0	0	0	0	0	1	0	0	0
Bombus fervidus	0	0	0	0	6	4	0	0	0	0	0	0
Bombus flavifrons	3	5	3	2	0	0	2	1	3	1	6	11
*Bombus griseocollis**	0	0	0	0	0	1	0	0	0	0	0	0
Bombus huntii	0	0	0	0	24	14	0	0	0	0	0	0
Bombus insularis	4	3	0	0	1	0	0	1	0	0	2	2
Bombus mixtus	2	2	0	0	0	0	3	2	3	3	5	10
*Bombus nevadensis**	0	0	0	0	0	2	0	0	0	0	0	0
Bombus rufocinctus	0	2	0	0	4	0	1	1	0	0	1	0
Bombus vosnesenskii	0	0	0	0	0	0	0	0	0	0	1	1
Calliopsis andreniformis	0	0	0	0	10	0	0	0	0	0	0	0
Ceratina acantha	0	0	1	0	0	0	1	0	3	0	1	0
Ceratina nanula	2	0	0	0	1	0	0	0	1	0	0	0
Ceratina neomexicana	6	0	0	0	0	0	0	0	0	0	0	0
Colletes brevicornis	0	0	0	0	1	0	0	0	0	0	0	0
Colletes consors	1	0	0	0	0	0	0	0	0	0	0	0

*Colletes fulgidus**	0	0	0	0	0	0	0	0	0	0	0	1
*Colletes kincaidii**	0	1	0	0	0	0	0	0	0	0	0	0
Colletes nigrifrons	1	0	0	0	0	0	0	0	0	0	0	0
Diadasia australis	0	0	0	0	11	0	0	0	0	0	0	0
Diadasia diminuta	0	0	0	0	4	0	0	0	0	0	0	0
Dianthidium heterulkei	0	0	0	0	0	0	0	0	0	0	1	0
Dianthidium parvum	0	0	0	0	2	0	0	0	0	0	0	0
Dianthidium pudicum	6	0	0	0	0	0	0	0	0	0	0	0
Dianthidium ulkei	0	0	0	0	2	0	0	0	0	0	0	0
Dufourea dilatipes	0	0	0	0	0	0	4	0	0	0	59	0
Dufourea maura	1	2	0	0	0	0	7	0	1	0	0	0
Dufourea trochantera	6	0	0	0	2	0	0	0	0	0	0	0
Eucera actuosa	0	0	0	0	8	0	0	0	0	0	0	0
Eucera delphinii	0	0	0	0	1	0	0	0	0	0	0	0
Eucera frater	2	0	0	0	3	0	0	0	0	0	2	0
Eucera hamata	0	0	0	0	5	0	0	0	0	0	0	0
Eucera hurdi	1	4	0	0	0	0	0	0	0	0	4	2
Eucera lepida	0	0	0	0	3	0	0	0	0	0	0	0
Eucera pallidihirta	0	0	0	0	1	0	0	0	0	0	0	0
Halictus confusus	9	0	1	0	193	1	0	0	0	0	1	0
Halictus farinosus	0	0	3	0	11	1	0	0	0	0	7	0
Halictus ligatus	4	0	6	0	15	0	0	0	0	0	3	0
Halictus rubicundus	23	0	4	0	29	1	10	0	2	0	23	2
Halictus tripartitus	21	0	33	0	1305	0	10	0	3	0	30	0
*Heriades variolosus**	0	0	0	0	0	1	0	0	0	0	0	0
Holcopasites calliopsidis	0	0	0	0	1	0	0	0	0	0	0	0
Hoplitis albifrons	2	1	0	0	3	1	3	0	0	0	1	0
Hoplitis fulgida	9	1	0	0	4	0	1	0	0	0	3	0
Hoplitis grinnelli	0	0	0	0	2	0	0	0	0	0	0	0
Hoplitis hypocrita	1	0	0	0	0	0	0	0	0	0	0	0
Hoplitis pilosifrons	0	0	0	0	1	0	0	0	0	0	0	0
Hoplitis producta	0	0	1	0	3	0	0	0	0	0	0	0
Hylaeus basalis	0	0	2	0	0	0	1	0	1	0	4	0
Hylaeus coloradensis	1	0	0	0	0	0	0	0	0	0	0	0
Hylaeus mesillae	0	0	0	0	0	0	2	0	0	0	0	0
Hylaeus modestus	6	0	1	0	0	0	3	0	0	0	1	0
Hylaeus sp.	1	0	0	0	0	0	0	0	0	0	0	0
Hylaeus wootoni	2	0	0	0	0	0	1	0	0	0	0	0
Lasioglossum aberrans	0	0	0	0	3	0	0	0	0	0	0	0
Lasioglossum albipenne	18	0	0	0	34	0	0	0	1	0	0	0
Lasioglossum anhypops	9	0	7	0	0	0	0	0	1	0	4	1
Lasioglossum cooleyi	87	1	8	0	1	0	8	0	0	0	13	0
Lasioglossum egregium	11	1	1	0	19	0	3	0	0	0	2	0

Lasioglossum glabriventre	0	0	0	0	0	0	0	0	0	0	2	0
Lasioglossum hudsoniellum	0	0	0	0	12	0	0	0	0	0	0	0
Lasioglossum incompletum	0	0	19	0	63	0	1	0	0	0	30	0
Lasioglossum knereri	1	0	0	0	0	0	1	0	1	0	4	0
Lasioglossum laevissimum	1	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum leucozonium	0	0	0	0	1	0	0	0	0	0	0	0
Lasioglossum lilliputense	0	0	0	0	1	0	0	0	0	0	0	0
Lasioglossum marinense	14	0	33	0	6	0	25	0	85	4	18	0
Lasioglossum nevadense	54	0	18	0	12	0	30	0	6	0	45	0
Lasioglossum olympiae	0	0	0	0	0	0	0	0	0	0	2	1
Lasioglossum perdifficile	0	0	0	0	2	0	0	0	0	0	0	0
Lasioglossum perpunctatum	0	0	0	0	4	0	0	0	0	0	0	0
Lasioglossum prasinogaster	24	0	0	0	6	0	0	0	0	0	1	0
Lasioglossum pruinosum	4	0	0	0	301	0	0	0	0	0	0	0
Lasioglossum punctatoventre	5	1	4	0	3	1	1	0	0	0	12	0
Lasioglossum ruidosense	9	0	3	0	9	0	1	0	2	0	8	0
Lasioglossum sandhousiellum	31	0	1	0	3	0	1	0	2	0	44	0
Lasioglossum sedi	34	0	1	0	0	0	0	0	0	0	42	0
Lasioglossum semicaeruleum	0	0	0	0	4	0	0	0	0	0	0	0
Lasioglossum sisymbrii	0	0	0	0	3	0	0	0	0	0	0	0
Lasioglossum sp.	12	0	10	0	23	0	5	0	0	1	6	0
Lasioglossum sp. 1	6	0	0	0	36	0	0	0	0	0	1	0
Lasioglossum sp. 2	8	0	4	0	1	0	0	0	0	0	7	0
Lasioglossum sp. 3	11	0	12	0	3	0	2	0	5	0	26	0
Lasioglossum sp. 4	2	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum sp. 5	0	0	0	0	1	0	0	0	0	0	0	0
Lasioglossum sp. 6	1	0	0	0	0	0	0	0	1	0	0	0
Lasioglossum tegulare	0	0	0	0	8	0	0	0	0	0	0	0
Lasioglossum tenax	0	0	0	0	0	0	3	0	0	0	0	0
Lasioglossum titusi	0	0	1	0	0	0	0	0	0	0	0	0
Lasioglossum trizonatum	33	2	0	0	2	0	1	0	0	0	17	1
Lasioglossum zonulum	0	0	0	0	1	0	0	0	0	0	0	0
Megachile apicalis	0	0	0	0	0	0	0	0	1	0	0	0
Megachile brevis	0	0	0	0	3	1	0	0	0	0	0	0
Megachile campanulae	1	0	0	0	0	0	0	0	0	0	0	0
Megachile melanophaea	0	0	0	0	1	0	0	0	0	0	0	1
Megachile montivaga	0	0	1	0	1	0	0	0	2	0	0	0
Megachile onobrychidis	0	0	0	0	1	0	0	0	0	0	0	0
Megachile parallela	1	0	0	0	0	0	0	0	0	0	0	0
Megachile perihirta	6	5	0	0	0	0	1	0	0	0	0	0
Megachile pugnata	0	0	0	0	0	0	0	0	1	0	0	0
Megachile relativa	0	0	1	0	0	0	1	0	0	0	0	0
Melecta pacifica	1	2	0	0	2	0	0	0	0	0	0	0

Melissodes agilis	0	0	0	0	1	0	0	0	0	0	0	0
Melissodes bimatris	0	0	0	0	1	0	0	0	0	0	0	0
Melissodes communis	0	0	0	0	4	0	0	0	0	0	0	0
Melissodes composita	0	0	0	0	1	0	0	0	0	0	0	0
Melissodes lupina	4	0	0	0	21	1	0	0	0	0	0	0
Melissodes lupinus	0	0	0	0	10	0	0	0	0	0	0	0
Melissodes lutulenta	0	0	0	0	19	0	0	0	0	0	0	0
Melissodes microsticta	14	2	0	0	0	0	0	0	1	0	2	0
Melissodes montana	2	0	0	0	0	0	0	0	0	0	0	0
*Melissodes sp. 1**	0	0	0	0	0	1	0	0	0	0	0	0
Melissodes sp. A	0	0	0	0	1	0	0	0	0	0	0	0
Melissodes tristis	0	0	0	0	2	0	0	0	0	0	0	0
Melissodes verbesinarum	0	0	0	0	1	0	0	0	0	0	0	0
Neopasites n. sp.	1	0	0	0	0	0	0	0	0	0	0	0
Nomada sp. 1	0	0	0	0	0	0	0	0	1	0	0	0
Nomada sp. 2	0	0	0	0	0	0	0	0	0	0	1	0
Nomada sp. 3	0	0	0	0	0	0	0	0	0	0	1	0
Nomada sp. A	0	0	1	0	0	0	0	1	0	0	0	0
Nomada sp. C	0	0	1	0	0	0	0	0	0	0	0	0
*Nomia universitatis**	0	0	0	0	0	2	0	0	0	0	0	0
Osmia albolateralis	2	1	1	0	25	2	0	0	0	0	5	0
Osmia atrocyanea	1	0	1	0	0	0	0	0	0	0	6	0
Osmia bella	0	0	1	0	0	0	0	0	0	0	2	0
Osmia brevis	0	0	1	0	2	0	1	0	0	0	0	0
Osmia bruneri	0	0	0	0	9	0	1	0	0	0	0	0
Osmia bucephala	1	0	0	0	0	0	0	0	0	0	5	1
Osmia californica	1	0	0	0	0	0	0	0	0	0	3	0
Osmia calla	0	0	0	0	1	0	0	0	0	0	0	0
Osmia coloradensis	3	0	0	1	0	0	1	0	0	0	3	1
Osmia densa	3	0	4	0	9	0	9	0	1	0	12	1
Osmia ednae	0	0	0	0	2	0	1	0	0	0	0	0
Osmia grindeliae	0	0	0	0	2	0	0	1	0	0	2	0
Osmia indeprensa	1	0	1	0	0	0	0	0	0	0	3	0
Osmia inermis	0	0	0	0	0	0	1	0	0	0	0	0
Osmia integra	0	0	0	0	5	0	0	0	0	0	0	0
Osmia iridis	0	0	0	0	1	0	0	0	0	0	0	0
Osmia juxta	8	2	1	0	0	0	5	0	0	0	28	1
Osmia kincaidii	1	0	1	0	3	0	0	0	1	0	4	0
Osmia lignaria	1	0	0	0	0	0	0	0	0	0	2	2
Osmia longula	0	1	0	0	0	0	0	0	0	0	0	0
Osmia malina	0	0	1	0	0	0	1	0	1	0	0	0
Osmia montana	0	0	3	0	0	0	0	0	0	0	5	1
Osmia obliqua	0	0	0	0	0	0	0	0	0	0	1	0

Osmia paradisica	4	2	0	0	0	0	0	0	0	0	0	0
Osmia pusilla	0	0	1	0	10	0	0	0	0	0	7	0
Osmia simillima	0	0	0	0	1	0	0	0	0	0	0	0
Osmia sp.	6	0	1	1	12	0	0	0	0	0	4	0
Osmia sp. A	0	0	0	0	1	0	0	0	0	0	0	0
Osmia subaustralis	0	0	1	0	0	0	0	0	0	0	0	0
Osmia torchioi	0	0	0	0	2	0	0	0	0	0	0	0
Osmia trevoris	3	0	1	0	76	3	0	0	0	0	2	0
Osmia tristella	2	0	4	0	1	0	1	0	0	0	0	1
Panurginus atriceps	33	0	0	0	0	0	0	0	1	0	0	0
Panurginus sp.	1	0	0	0	0	0	0	0	0	0	0	0
Panurginus sp. 1	2	0	0	0	0	0	0	0	0	0	0	0
Panurginus torchio	0	0	8	0	4	0	0	0	0	0	1	0
*Perdita sp. 1**	0	0	0	0	0	1	0	0	0	0	0	0
Perdita torchioi	0	0	0	0	0	0	0	0	1	0	0	0
Pseudopanurgus didirupa	1	0	0	0	0	0	0	0	0	0	0	0
Sphecodes sp.	6	1	2	0	0	1	1	0	0	0	2	0
Stelis callura	1	0	0	0	0	0	0	0	0	0	0	0
Stelis holocyanea	1	0	0	0	0	0	0	0	0	0	0	0
Stelis labiata	0	0	0	0	1	0	0	0	0	0	0	0
Stelis montana	1	0	0	0	0	0	0	0	0	0	0	0
Stelis monticola	0	0	0	0	0	0	1	0	0	0	0	0

Table A2: Bee species caught by region and by method of capture (either pan or net). The bees in this table represent bees not used in our analyses, as they were used in a collaborative effort for another project and did not fit with our sampling design. Some bees here were from transects or sites removed due to inadequate controls. The Tin Can Hill and Beaverhead-Deerlodge areas of the "Eastern Montana" region were separated for this appendix, since a large number of bees were caught in the Tin Can Hill, or "Eastern Montana" region here. Region names are abbreviated here to fit the table, where BD="Beaverhead-Deerlodge", CL="Clearwater", EM="Eastern Montana", LO="Lolo", NI="North-Idaho/Kootenai", and ST="Starkey".

Species	BD		CL		EM	LO		ST	
	pan	net	pan	net	net	pan	net	pan	net
Agapostemon angelicus / texanus	2	0	1	0	0	0	0	0	0
Andrena ablegata	0	0	1	0	0	1	0	10	0
Andrena amphibola	0	0	0	0	0	0	0	2	0
Andrena angustitarsata	0	0	0	0	0	0	0	1	2
Andrena caerulea	0	0	0	0	0	0	0	2	0
Andrena cressonii	0	0	1	0	0	0	0	0	0
Andrena melanochroa	0	0	0	0	0	0	0	6	3
Andrena microchlora	0	0	0	0	0	0	0	42	1
Andrena nigrihirta	1	0	0	0	0	0	0	10	0
Andrena nigrocaerulea	0	0	0	0	0	0	0	6	2
Andrena nivalis	0	0	0	0	0	0	0	3	1
Andrena nothocalaidis	0	0	0	0	0	0	0	1	0
Andrena prunorum	0	0	0	0	0	0	0	1	0
Andrena rufosignata	0	0	0	0	0	0	0	0	1
Andrena salicifloris	0	0	0	0	0	0	0	1	0
Andrena sp. 4	0	0	0	0	0	0	0	1	0
Andrena sp. B	0	0	0	0	0	0	0	2	0
Andrena thaspii	0	0	0	0	0	0	0	1	0
Andrena transnigra	0	0	0	0	0	0	0	1	0
Andrena vierecki	0	0	0	0	0	0	0	1	0
Anthophora affabilis	0	0	1	0	0	0	0	0	0
Anthophora ursina	0	0	0	0	0	0	0	0	4
Apis mellifera	2	18	1	0	1	0	0	0	0
Bombus appositus	0	0	1	0	0	0	0	0	1
Bombus bifarius	0	0	0	0	0	4	1	3	1

Bombus californicus	0	0	0	0	0	0	0	1	0
Bombus fernaldae	0	0	0	0	0	0	0	1	0
Bombus flavifrons	0	0	0	0	0	0	0	7	6
Bombus insularis	0	0	0	0	0	0	0	0	1
Bombus mixtus	0	0	0	1	0	0	0	1	0
Bombus rufocinctus	0	0	1	0	0	0	0	0	0
Ceratina acantha	0	0	4	0	0	0	0	0	0
Ceratina sequoiae	0	0	1	0	0	0	0	0	0
Dianthidium heterulkei	0	0	0	0	0	0	0	1	0
Dufourea dilatipes	0	0	0	0	0	5	0	36	0
Eucera delphinii	0	0	1	0	0	0	0	0	0
Eucera frater	0	0	0	0	0	0	0	2	0
Eucera hurdi	0	0	0	0	0	0	0	1	0
Habropoda cineraria	0	0	0	0	0	0	0	1	1
Halictus confusus	0	0	0	0	0	0	0	1	0
Halictus farinosus	0	0	1	0	0	0	0	3	0
Halictus ligatus	0	0	5	0	0	0	0	1	0
Halictus rubicundus	1	0	8	0	0	1	0	17	1
Halictus tripartitus	0	0	34	0	0	13	0	34	0
Hoplitis fulgida	0	0	0	0	0	0	0	1	0
Hoplitis producta	0	0	1	0	0	0	0	0	0
Hylaeus episcopalis	0	0	1	0	0	0	0	0	0
Hylaeus modestus	0	0	0	0	0	0	0	3	0
Lasioglossum albipenne	1	0	0	0	0	0	0	0	0
Lasioglossum anhypops	0	0	0	0	0	0	0	8	0
Lasioglossum cooleyi	2	0	14	0	0	2	0	8	0
Lasioglossum egregium	0	0	1	0	0	0	0	0	0
Lasioglossum incompletum	1	0	61	0	0	0	0	26	0
Lasioglossum marinense	0	0	3	0	0	1	0	7	0
Lasioglossum nevadense	2	0	10	0	0	3	0	33	0
Lasioglossum olympiae	0	0	0	0	0	0	0	2	0
Lasioglossum prasinogaster	1	0	0	0	0	0	0	6	0
Lasioglossum pruinosum	0	0	0	0	0	0	0	1	0
Lasioglossum punctatoventre	0	0	6	0	0	0	0	15	0
Lasioglossum ruidosense	1	0	0	0	0	1	0	13	0
Lasioglossum sandhousiellum	0	0	0	0	0	0	0	40	0
Lasioglossum sedi	0	0	1	0	0	0	0	21	0
Lasioglossum sisymbrii	0	0	0	0	0	1	0	1	0
Lasioglossum sp.	0	0	6	0	0	0	0	6	0
Lasioglossum sp. 2	0	0	0	0	0	0	0	6	0
Lasioglossum sp. 3	0	0	0	0	0	0	0	18	1
Lasioglossum titusi	0	0	14	0	0	0	0	0	0
Lasioglossum trizonatum	1	0	1	0	0	0	0	14	0

Megachile apicalis	0	0	0	0	0	1	0	0	0
Melecta pacifica	0	0	0	0	0	0	0	2	0
Melecta separata	0	0	0	0	0	0	0	2	0
Melissodes lupinus	0	0	1	0	0	0	0	0	0
Nomada sp. 4	0	0	0	0	0	0	0	1	0
Nomada sp. 5	0	0	0	0	0	0	0	3	0
Nomada sp. B	0	0	0	0	0	0	0	2	0
Osmia albolateralis	0	0	0	0	0	0	0	6	0
Osmia atrocyanea	0	0	0	0	0	0	0	5	0
Osmia bella	0	0	0	0	0	0	0	3	0
Osmia brevis	0	0	0	0	0	0	0	1	0
Osmia bruneri	0	0	0	0	0	0	0	1	0
Osmia bucephala	0	0	0	0	0	0	0	15	1
Osmia coloradensis	0	0	1	0	0	0	0	3	0
Osmia densa	1	0	1	0	0	0	0	13	1
Osmia ednae	0	0	0	0	0	0	0	1	0
Osmia indeprensa	0	0	0	0	0	1	0	9	1
Osmia juxta	0	0	0	0	0	0	0	52	0
Osmia kincaidii	0	0	0	0	0	0	0	13	0
Osmia lignaria	0	0	0	0	0	0	0	1	0
Osmia longula	0	0	0	0	0	0	0	3	0
Osmia montana	0	0	0	0	0	0	0	15	0
Osmia pusilla	0	0	1	0	0	1	0	10	0
Osmia sp.	0	0	0	0	0	0	0	4	2
Osmia trevoris	1	0	0	0	0	0	0	0	0
Osmia tristella	0	0	0	0	0	0	0	5	3
Panurginus atriceps	0	0	0	0	0	1	0	0	0
Panurginus sp.	0	0	1	0	0	0	0	0	0
Panurginus torchio	0	0	4	0	0	0	0	1	0
Sphecodes sp.	0	0	0	0	0	0	0	3	0

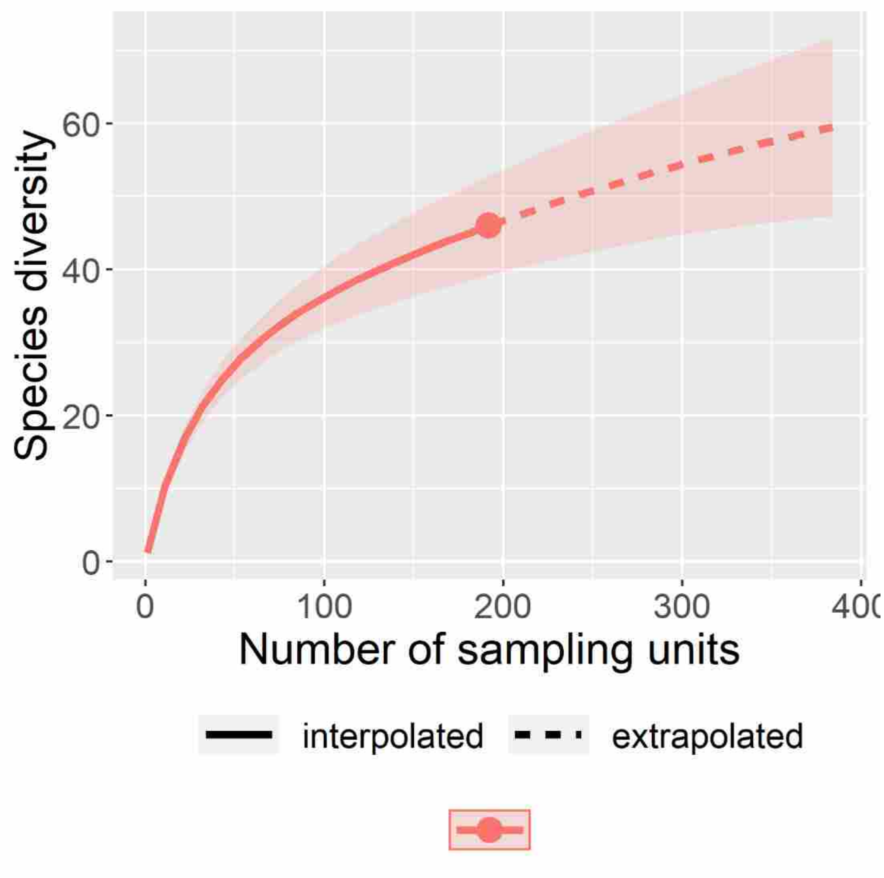

Figure A1: Bee netting data species accumulation curve.