FINAL REPORT

Title: Prescribed fire use promotes native bee biodiversity in a semi-arid forest ecosystem

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ABSTRACT

Insect pollinators, especially bees, are an essential component ecosystem function. Native bees provide key ecosystem services and shape the structure and composition of plant communities. However, recent research suggests a large-scale decline in bee populations, compelling the need for further research of the drivers and mechanisms influencing this decline. Within ponderosa pine ecosystems, fire suppression policies in the late 19th and early 20th century have led to the growth of dense stands with closed canopies and low understory production-this forest structure is widely considered undesirable for a variety of reasons. One approach to restoring the historic structure of these forests is to re-introduce fire disturbances to the landscape. Although the effects of managed or 'prescribed' fire on vegetation structure and composition are well-studied, relatively few studies have investigated whether prescribed fires have cascading effects on ecological communities important to ecosystem function, including native bees.

To address this knowledge gap, blue vane traps were used to sample native bee community assemblages across the growing season in ponderosa pine-forest sites in northern Colorado to evaluate the effects of prescribed fire restoration treatments, and time since treatment (1-yr post-fire, 3-yrs post-fire. non-treated controls), on bee populations. We quantified bee abundance, richness, and diversity as well as foraging resources (floral abundance and richness) and nesting habitat (coarse woody debris). From this, 5 key findings emerged: (1) Overall γ-diversity consisted of 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 25 genera, and at least 58 species. Predominant genera include bumblebees (*Bombus* sp.), mason bees (O*smia* spp.), and digger bees (*Anthophora* spp.) which accounted for 61.4%, 13.9%, and 8% of collected specimens, respectively. (2) Pooled bee abundances varied across the season, with highest captures occurring early in the growing season; bee species richness and α-diversity varied across treatment type and were highest within 1-year post-fire stands. (3) Unique bee community compositions were associated with different treatment types but also varied across the season. (4) Treatment type and seasonality were associated with differences in bee nesting habit. (5) Floral resource abundances and richness were associated with increased bee abundances, richness, and diversity, though stand basal area was negatively correlated with bee abundance and species richness.

Results here provide evidence that fire-disturbed forest stands generally promote bee site occupancy, but this effect is likely to peak shortly after fires and then decline. In addition, distinct bee assemblages were found in stands that were in varying states of time-since-fire, indicating that a mosaic of treatments likely support the greatest bee biodiversity at a landscape-scale. Further, findings here elucidate habitat structural components, specifically stand basal area and floral resource richness, that can be targeted by land managers to facilitate bee site occupancy. With this, we conclude the use of prescribed fire as a forest restoration method likely promote pollinator abundance and diversity in semi-arid ponderosa pine forests of the southwestern United States.

OBJECTIVES

The objectives of this proposed project are to 1) to assess differences in bee community assemblages across non-treated control and prescribed fire treatment sites, 2) to analyze differences in bee community assemblages relative to time-since-treatment and 3) identify how prescribed fire impacts components of bee habitat, such as floral resources and coarse wood debris (large surface fuels) and describe the effects of these components on bee abundance and species richness.

BACKGROUND

Pollinators are critical components of healthy ecosystems where they provide pollination services to trees, shrubs, and herbaceous plants (Hanula et al. 2015). Within forested ecosystems, native pollinators are responsible for most pollination interactions (Hanula et al. 2016); for example, pollination of ~87% of wild plant species are directly dependent on insects (Ollerton et al. 2011), mainly native bees (Potts et al. 2010). Yet, despite their crucial role in ecosystem productivity - and evidence of their widespread decline (Gilgert and Vaughan 2011) - there is currently little known about factors regulating abundance or diversity of bee pollinators in Colorado or in forested systems in general (Koh et al. 2016). Forest management is widespread and utilized for a variety of goals, thus, it is likely that forest management methods impact pollination on large spatial scales.

Throughout much of the U.S. southwest region, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) is a predominant forest cover type (Reynolds et al. 2013) that historically experienced frequent low- or mixed-severity fire events (Addington et al. 2018). These fires assisted in the maintenance of a heterogenous, open forest structure with large interspaces between trees within stands. However, habitat conditions within southwestern pine forests have shifted as a result of past forest management (Covington and Moore 1994). In the late 19th and early 20th century widespread policies of fire exclusion, and extirpation of fire disturbances, resulted in high stem densities with closed canopies and low understory production in southwestern ponderosa pine systems (Allen et al. 2002). These uncharacteristically dense conditions pose as a threat to native bee populations by moving landscapes away from a mosaic forest structure and towards a homogenous forest structure (Nyoka 2010). High-density forest stands with closed canopies also reduces connectivity between habitat patches, hindering bee foraging or migration and potentially contributing to pollinator decline. For instance, closed canopy stands typically express reduced understory growth, leading to a lack of available food and nesting resources. Additionally, closed canopies prevent light from reaching the forest floor, reducing opportunity for thermoregulation; temperature and light are also important abiotic factors affecting bee foraging behaviors (Polatto et al. 2014). Consequently, the current 'non-historic' structure of regional southwestern ponderosa pine forests are likely to have various cascading effects on native bee populations, many of which could be deleterious. Despite these impacts, surprisingly few studies have examined how disturbances such as fire or restoration practices, including thinning and prescribed fire, impact bee communities.

In particular, prescribed fire is an important tool for natural resource stewards; restoring fire as a key ecosystem process can assist in reducing stand densities and maintaining desirable elements of ecosystem structure, function, and composition (Baker et al. 2007). Recent studies demonstrate that forest management and fire alter the structure of forest vegetation, but also site occupancy of forbaceous species (Laughlin and Fule 2008; Strahan et al. 2015; Kerns and Day 2018) – both factors are important to pollinator communities in forest ecosystems. Accordingly, it is probable that both fire and fire prevention strategies indirectly impact pollinator communities through effects on forest structure and forb abundance. The effects of prescribed fire on native bee communities remains relatively unexplored, indicating a need for research on interactions between fire disturbances, bee foraging and nesting habitats, and bee communities across a wide variety of forest cover types. Knowledge of these relationships is essential to better plan and implement forest management for the conservation of bee biodiversity, and to describe the effects of forest restoration efforts on pollination services.

Here, we ask the question "How does prescribed fire impact a native bee assemblage in a forest system?"; We test the hypothesis that prescribed fire restoration treatments facilitate increases in abundance and species richness of native bees compared to non-treated forest stands. We sampled bee communities in areas that spanned multiple time-since-fire treatments to test: (a) how bee abundances, species richness, and diversity of bees vary with time-since-fire, and (b) how nesting and floral resources (i.e., tree density, stand basal area, canopy cover, coarse woody debris, floral species richness) may affect those relationships and differ among treatments. Our findings have implications for understanding how a widespread forest restoration tactic (i.e., implementation of prescribed fire) affects communities of native bees over time, with consequences for biodiversity and function of forest ecosystems.

MATERIALS AND METHODS

Study system

Bees were collected from a total of 14 lower-montane sites in Red Feather Lakes, Colorado (40˚51′17″ N, 105˚35′16″ W; 2513m elevation) during the growing seasons of 2018 using passive trapping methods. In the growing season of 2020, additional sites and treatments were included, for a total of 26 sites sampled at the conclusion of data collection (Fig. 1). Overstory vegetation in stands selected from this study were predominantly ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson), though lodgepole pine (*Pinus contorta* Douglas) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) reached the overstory in some areas. Sites were selected to represent three treatment types including sites that were (1) 1-year post-prescribed fire (n = 8), (2) 3-year post-prescribed fire (n = 9), and (3) non-treated control sites (n = 9).

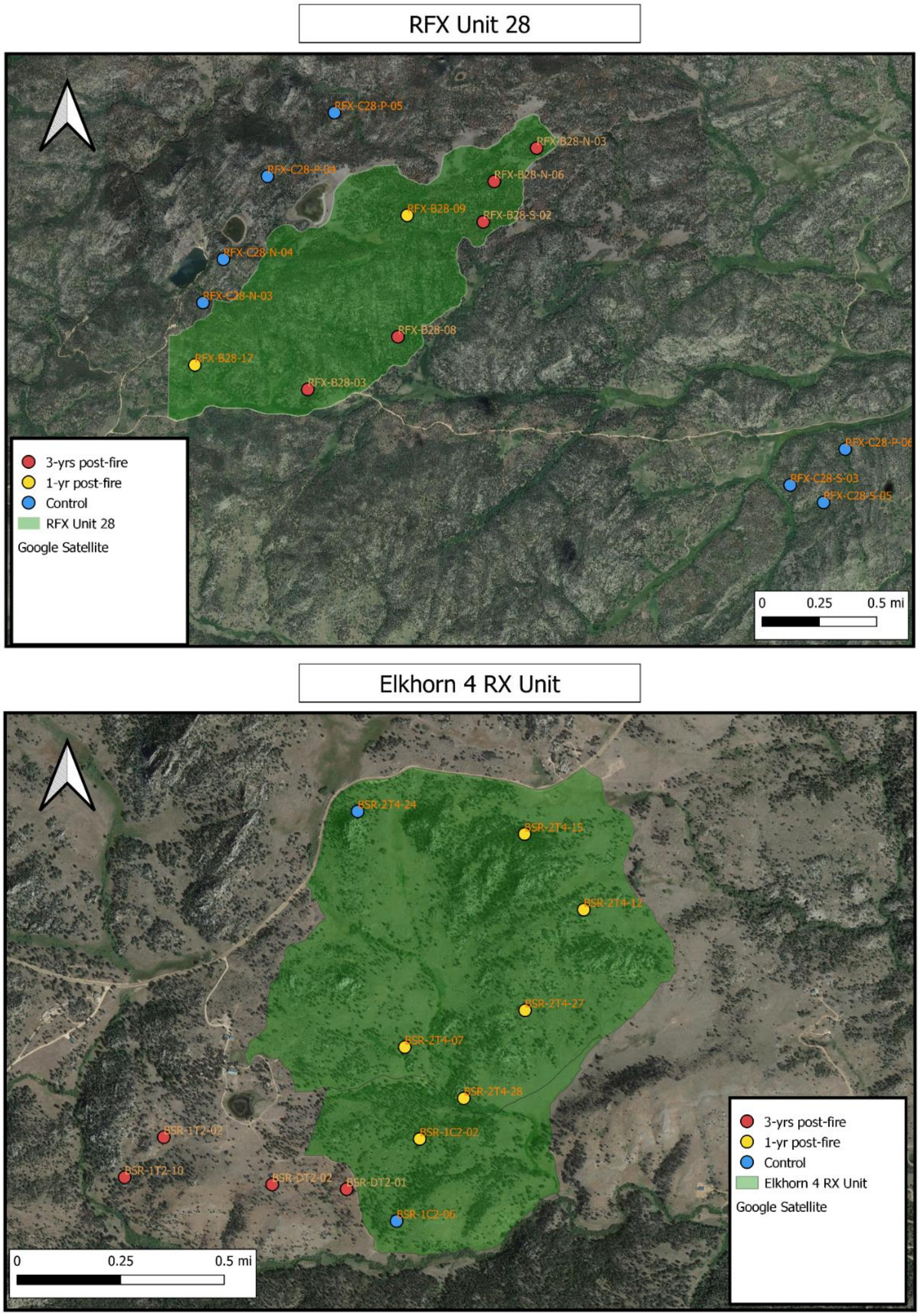

Figure 1. Map of sites at (a) Red Feather Lakes, CO and (b) Ben-Delatour Scout Ranch with plots labeled and prescribed burn treatment area denoted (in green).

Bee sampling procedure

Sites were sampled four times in each year of the study to capture seasonal variation in bee assemblages (Rhoades et al. 2018), including May, June, July, and August (N = 160 total bee sampling events). To sample bees, blue vane traps (Springstar, Inc. Woodinville, WA, USA) were hung during each collection event from existing vegetation at a height of 1.3m for 48-h during periods of favorable weather at a density of one trap per site. Each trap included a wire mesh insert to provide refugia to trapped specimens in the case of unfavorable weather and three 1 mm drilled holes to reduce the probability of inundation with water. Upon the end of each sample period, traps were collected, and trapped specimens were euthanized by placing on dry ice. Specimens were then brought to the lab where all bees were pinned and identified to the lowest taxonomic level possible. In most cases this was genus to species, but some specimens could only be sorted to morphospecies. Voucher specimens are curated at the C.P. Gillette Museum of Arthropod Diversity at Colorado State University.

Forestry and understory measurements

At each collection location, site forest structural information was collected within a 0.01-ha fixed-area plot (10 m^2). In each plot, trees were censused and their species identity as well as diameter at breast height (dbh) were recorded. Overstory canopy cover was recorded along two 8 m transects running north and south from plot center using a densitometer. The presence of both live and dead overstory cover above breast height was tallied. From these data basic forestry measurements were computed and used as variables for analysis, including stand basal area (m^2/ha^{-1}), tree density (trees/ha^{-1}), and overstory canopy cover (%).

Site structural elements important to bee foraging and nesting were also measured. Coarse woody debris availability is an important predictor of potential nesting habitat, particularly for solitary bees (Rodriguez and Kouki 2015). To measure the availability of coarse woody debris (both sound and rotting material on the ground surface with proximal diameter >7.6cm), a 0.015-ha (6.9m radius) fixed-area plot around the trap location was utilized. Diameters of both ends of debris, as well as length, were recorded and included as a site-level estimate surface loading calculation in megagrams per hectare (MG/ha) (Brown et al. 1974).

In addition to nesting habitat created by woody debris, floral resource availability also directly influences bee site occupancy as a key foraging resource (Hanula et al. 2016). At each collection period, floral species richness was recorded using quadrats. At each site and collection period, five replicate 1m^2 quadrats were deployed and the total number of unique species represented by active floral displays were recorded. One quadrat was placed directly beneath the trap location, with additional quadrats placed 2m in each cardinal direction. Quadrat measurements were treated as a subsample, and values from all five quadrats at each site were averaged together to yield a site-level mean floral abundance and richness for each collection period.

Data analyses

All statistical analyses were conducted using the R programming language

(V3.5.2, "Eggshell Igloo"). A Type I error rate of α = 0.05 was assigned for statistical significance to modeled effects.

A one-way ANOVA model was used to compare mean basal area, tree density, canopy cover (%), coarse woody debris surface loading, and floral richness due to the effects of prescribed fire (treatments = 1-yr post-fire, 3-yr post-fire, and non-treated control stands). Two-way ANOVA was used to analyze the fixed effects of site treatment type (1-yr post-fire, 3-yr post-fire, and non-treated control), seasonality (May, June, July, August), and the treatment × seasonality interaction on the responses of mean bee abundance, bee species richness, and bee α-diversity (as described by the Shannon-Weiner H′ statistic); sample year was incorporated as a random effect (2018 or 2020). This analysis used site × month × year observations as the unit of replication (N = 160). Bee abundance data was log-transformed to conform to assumptions of normality prior to analysis. Shannon's H′ cannot be calculated when no species are present (H′ = 0 when a single species is present), therefore collections where no catches occurred were omitted from consideration when analyzing model effects on Shannon's H′ (18.4% of observations); however, zeros were incorporated in analyses on bee abundance and species richness.

Bee β-diversity across treatments was analyzed using rarefaction curves (Colwell et al. 2012) produced by the 'iNEXT' package (Hseih et al. 2020). Estimates were interpolated from sample-based abundances to account for different numbers of bee captures and extrapolated to approximately 2x the size of the largest sample (Chao et al. 2014), and multiple metrics were considered (q = 0, 1, and 2). In addition to species accumulation rates, bee community compositions were compared between treatment types using a distance-based framework. Species-abundance matrices of bee captures from all sites (rows = sites, columns = bee species counts) were transformed into matrices of Bray-Curtis dissimilarities and effects of treatment type were analyzed using the 'adonis2' function (permutational multivariate analysis of variance, n permutations = 9,999) in the R add-on package 'vegan' (Oksanen et al. 2019). Results were visualized using non-metric multidimensional scaling (NMDS). Additionally, chi-squared tests were used to assess whether the proportion of bee functional groups (as assigned by nesting behavior) varied by month of collection and treatment type. Nesting behaviors were divided into four categories based on exhibited life history strategies of each species: above ground nesters, below ground nesters, nesting generalists (above and below ground nesters), and parasitic species.

In addition to the effects of prescribed fire treatments, a generalized linear model framework (family: gaussian, link function: identity) was used to compare relative effect sizes of forest structure and foraging habitat variables on bee assemblages, treating unique site and treatment combinations (n = 31) as the unit of analysis. Bee community metrics were averaged across the two years of collection to produce site-level averages (i.e., mean bee abundance, richness, and diversity). Selected independent variables used in the model were stand basal area, tree density, canopy cover, woody debris surface loadings, and floral species richness. Tree density was omitted from analysis due to high correlation with basal area (Pearson's correlation coefficient $r = 0.821$). Response variables include mean bee abundance, bee species richness, and Shannon-Weiner diversity. Both independent and dependent variables were standardized to ($\mu = 0$, $\sigma = 1$) prior to analysis to simplify interpretation.

RESULTS AND DISCUSSION

How do bee abundance, species richness, and diversity of bees vary with time-since fire?

Characteristics of overstory vegetation between treatment types were similar. Tree density did not differ significantly between treatment types (1-yr post-burn = 129.3 trees per ha, 3-yr post-burn = 131.8 trees per ha, non-treated control = 158.3 trees per ha; $F_{2, 30} = 0.476$, $P = 0.626$), nor did stand basal area (1-yr post-burn = 13.4 m^2/ha, 3-yr post-burn = 12.6 m^2/ha, non-treated control = 11.3 m^2/ha; ; $F_{2, 30} = 0.120$, $P = 0.887$) or canopy cover (1-yr post-burn = 30%, 3-yr post-burn = 26%, non-treated control = 37%; ; $F_{2, 30} = 0.632$, $P = 0.539$).

Typical flora taxa identified during surveying include *Achillea millefolium*, *Cedum lanceolatum*, *Collinsia parviflora*, *Corydalis aurea*, *Geranium caespitosum*, *Penstemon virens*, *Phacelia* sp., *Potentilla fissa, Potentilla hippiana*, and *Solidago* spp. Mean floral richness was unaffected by a collection period × treatment interaction ($F_{3, 147} = 1.551$, $P = 0.166$), though across all treatment types floral richness was higher mid-growing season (June, July) than in other months of survey ($F_{3, 147} = 18.959$, $P < 0.001$; Fig. 2a). Mean floral richness was also highest in 1-yr post-burn plots across all months of data collection with a 75.7% and 61.6% increase from non-treated control and 3-year post-burn plots, respectively ($F_{2, 147} = 6.360$, $P = 0.002$; Fig. 2b). Year-to-year- variation accounted for ~32% of modeled variance in floral richness but was not statistically significant ($P = 0.494$). Bee nesting habitat (coarse woody debris) did not differ significantly between treatment types ($F_{2, 30} = 2.349$; $P = 0.114$), though was 66.2% and 48.5% higher in non-treated control stands than in 1-yr and 3-yr post-burn plots, respectively.

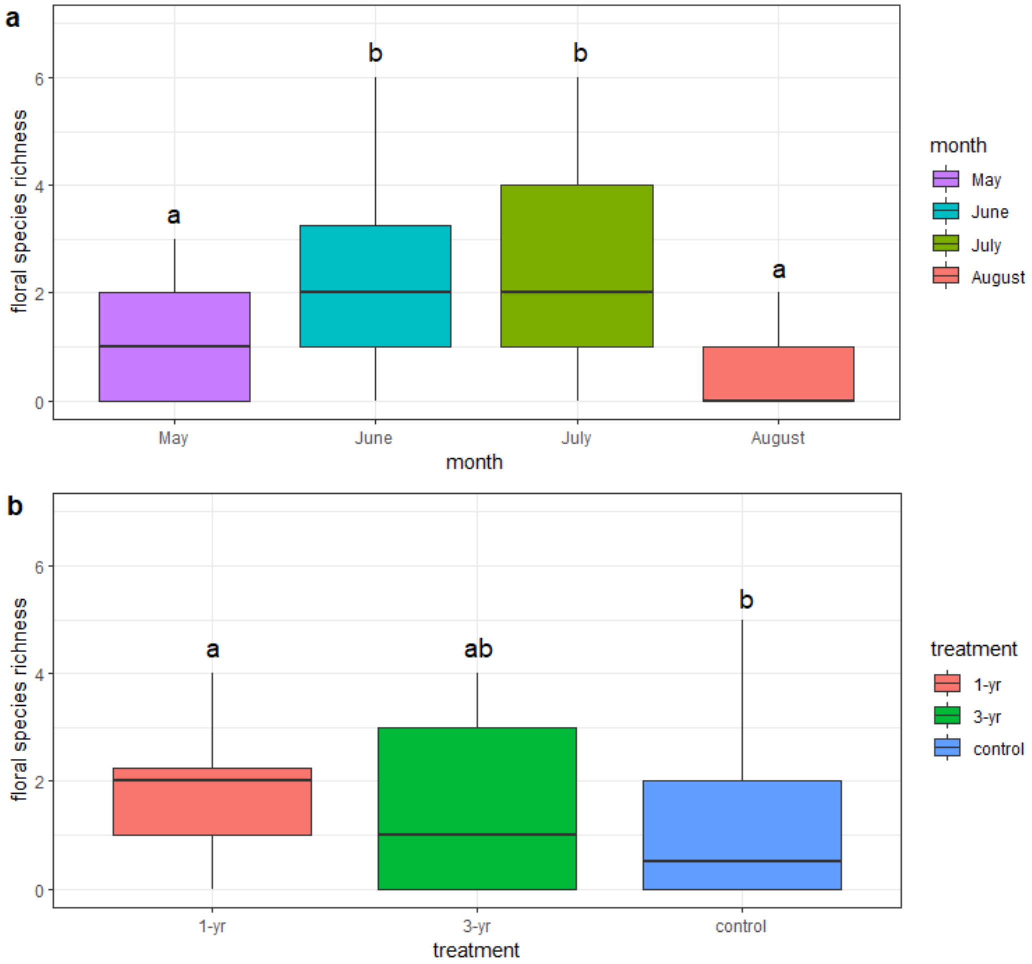

Figure 2. Distribution of bee foraging habitat across (a) collection period and (b) treatment type. Lettering denotes Tukey's HSD test; boxplots not connected by the same letter differ significantly in mean value.

A total of 1,096 bee specimens were collected across the two-year sampling period. Bee γ-diversity was represented by 5 families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 25 genera, and at least 58 species. Predominant genera include bumblebees (*Bombus* sp.), mason bees (O*smia* spp.), and digger bees (*Anthophora* spp.), accounting for 61.4%, 13.9%, and 8% of collected specimens, respectively (Table 1). Dominant species within our sample include *Bombus centralis* Cresson (18.7%), *Bombus bifarius* Cresson (9.7%), and *Bombus melanopygus* Nylander (7.9%).

Family	**Genus**	**Treatment**		
		1-yr post-fire	3-yr post-fire	control
Andrenidae	*Andrena*	4	1	4
Apidae	*Anthophora*	51	15	22
	Apis	1	1	0
	Bombus	317	106	249
	Diadasia	1	0	0
	Epeolus	0	0	1
	Eucera	0	0	1
	Melecta	0	3	1
	Melissodes	10	4	14
	Nomada	1	0	0
	Triepeolus	0	1	0
Colletidae	*Colletes*	0	1	3
	Hylaeus	3	1	2
Halictidae	*Agapostemon*	3	0	1
	Dialictus	2	0	2
	Evylaeus	6	0	0
	Halictus	3	3	5
	Lasioglossum	30	10	7
	Sphecodes	3	0	0
	Unknown	1	0	0
Megachilidae	*Ashmeadiella*	1	0	2
	Dianthidium	4	0	4
	Hoplitis	10	4	5
	Megachile	9	2	5
	Osmia	91	7	54
	Stelis	1	2	0

Table 1. A summary of bee genera captured in this study and their abundances by treatment type (i.e., time-since-fire and non-treated control stands).

Bee abundance significantly varied as result of seasonality ($F_{3, 147} = 12.686$, $P < 0.001$) and marginally varied due to the main effect of treatment type ($F_{2, 147} = 2.551$, $P = 0.082$). No significant variation in bee abundance was detected due to a treatment × seasonality interaction ($F_{6, 147} = 0.733$, $P = 0.624$). The average number of bee captures was 42.2% and 68.4% higher in 1-yr post-fire stands than in non-treated control and 3-yr post-fire stands, respectively (Fig. 3a). Further, bee abundances were highest early in the growing season (May), with 50.7%, 73.5% and 32.1% higher captures compared to that of June, July, and August, respectively (Fig. 4a). Year effects accounted for 29.7% of modeled variance in bee abundance but were not statistically significant ($P = 0.489$).

Bee richness varied significantly as a result of treatment ($F_{3, 147} = 5.497$, $P = 0.005$); however, bee species richness did not vary as a result of seasonality ($F_{3, 147}=$

1.926, $P = 0.128$; Fig. 4b) or a treatment × seasonality interaction ($F_{6, 147} = 1.573$, $P = 0.159$). Bee richness was 37.6% and 61.1% higher in 1-year post-fire stands than in non-treated control and 3-year post-fire stands, respectively (Fig. 3b). Year effects account for 9.1% of modeled variance in bee richness but were not statistically significant ($P = 0.513$).

Bee α-diversity varied significantly as a result of treatment ($F_{3, 147} = 5.460$, $P = 0.005$), though diversity did not vary as a result of seasonality ($F_{3, 147} = 1.601$, $P = 0.192$; Fig. 4c) or a treatment × seasonality interaction ($F_{6, 147} = 0.992$, $P = 0.434$). Shannon-Weiner diversity was 30.5% and 68.1% higher in 1-year post-fire stands than in non-treated control and 3-year post-fire stands, respectively (Fig. 3c). Year effects account for 26.2% of modeled variance in bee diversity, though this was not statistically significant ($P = 0.491$).

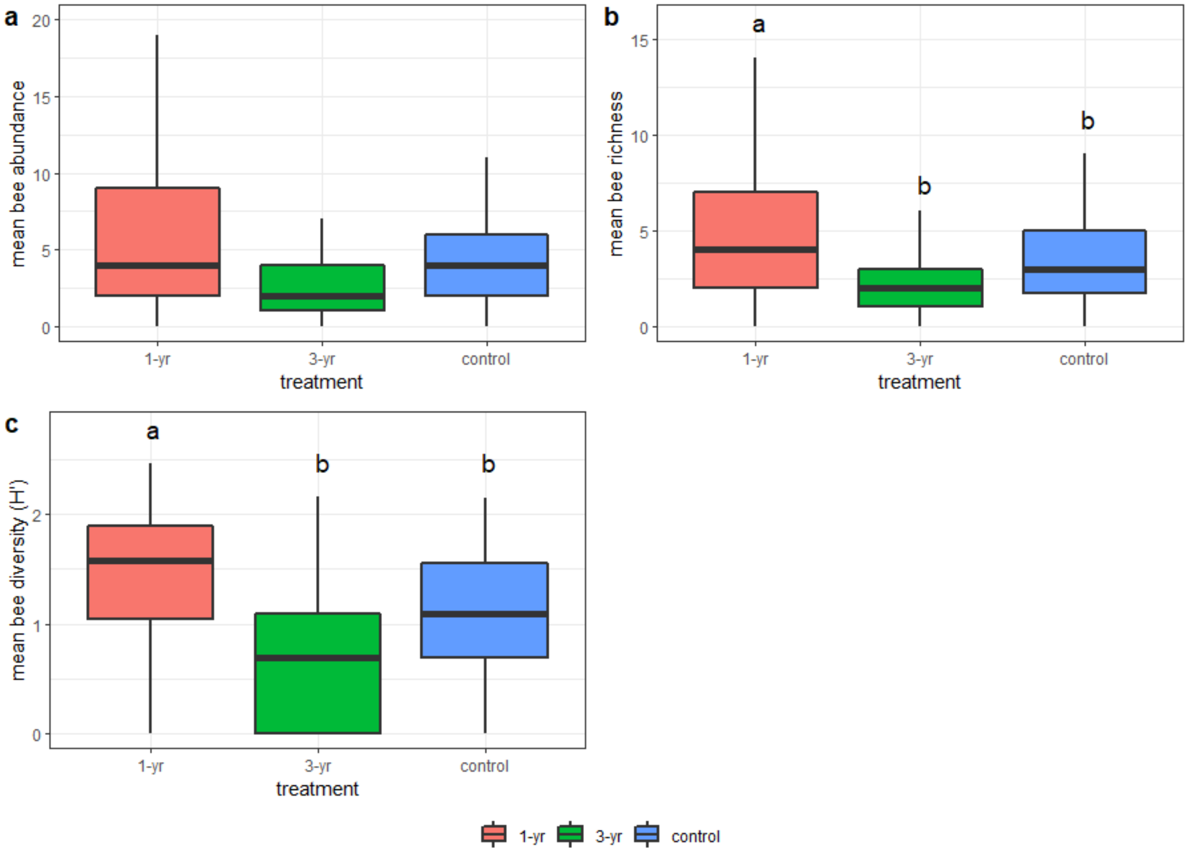

Figure 3. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (Shannon's H' statistic) due to the effects of prescribed fire treatment. Lettering indicates Tukey's HSD test, and boxplots not connected by the same letter in each panel are significantly different.

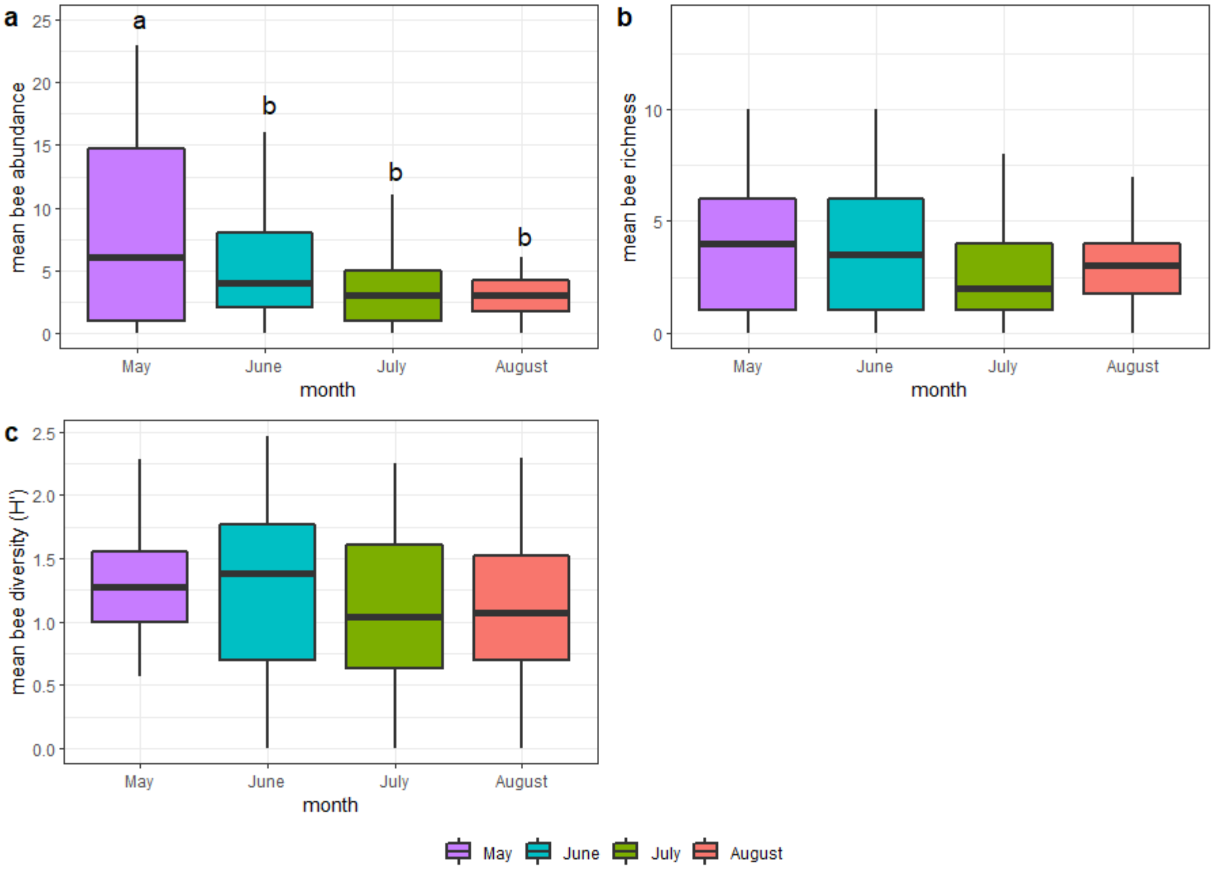

Figure 4. The distribution of (a) mean bee abundance, (b) mean bee richness, and (c) mean bee diversity (H') across collection period. Lettering indicates Tukey's HSD test, and boxplots not connected by the same letter in each panel are significantly different.

Analysis of β-diversity using rarefaction curves coupled with bootstrapped confidence intervals indicated that accumulation of bee biodiversity in 1-year post-fire stands exceeded that of recorded from other treatment types (Fig. 5), with bee biodiversity declining to below that of non-treated control stands by 3-years post prescribed fire. Additionally, species composition of bee community assemblages differed significantly across collection period ($F_{3, 92} = 3.069$, $P = 0.001$; Fig. 6a). Turnover ratios of *Bombus*, *Osmia*, *Anthophora*, and *Melissodes* primarily drove this difference, with *Bombus* captures highest in May, *Osmia* captures highest in June, and *Anthophora* and *Melissodes* most frequently encountered in August. Community assemblages also differed between treatment types ($F_{2, 28} = 1.327$, $P = 0.033$; Fig. 6b), with distinct turnover expressed by multiple genera of bees, including: *Diadasia*, *Nomada*, *Evylaeus*, *Sphecodes*, *Epeolus*, *Eucera*, and *Triepeolus* (Table 1).

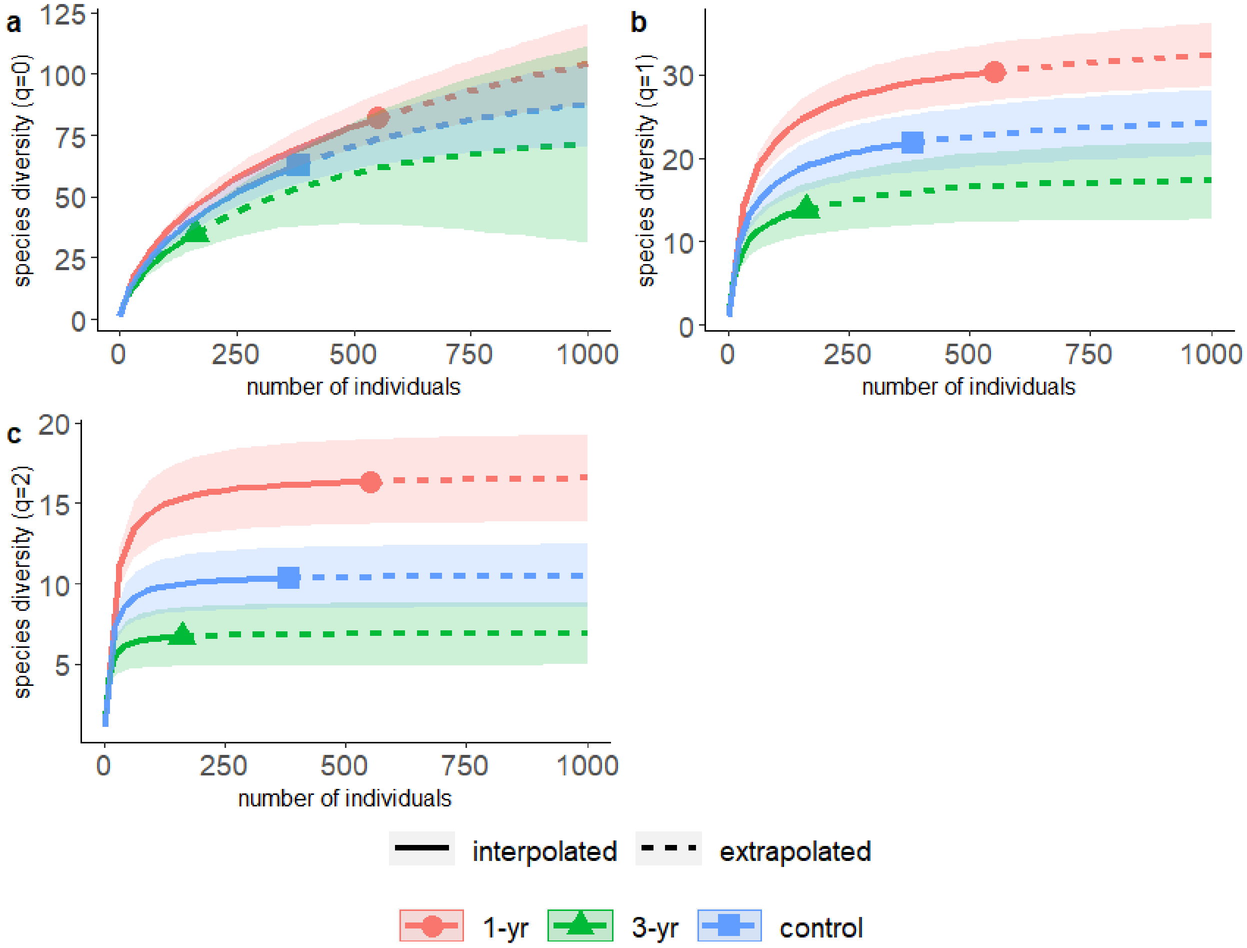

Figure 5. Sample-based accumulation of bee species diversity within treatment types with Hill's numbers representing (a) species richness (*q* = 0), (b) Shannon's diversity (*q* = 1), and (c), Simpson diversity (*q* = 2). Shading represents the bootstrap-estimated 95% confidence interval for each sampling curve.

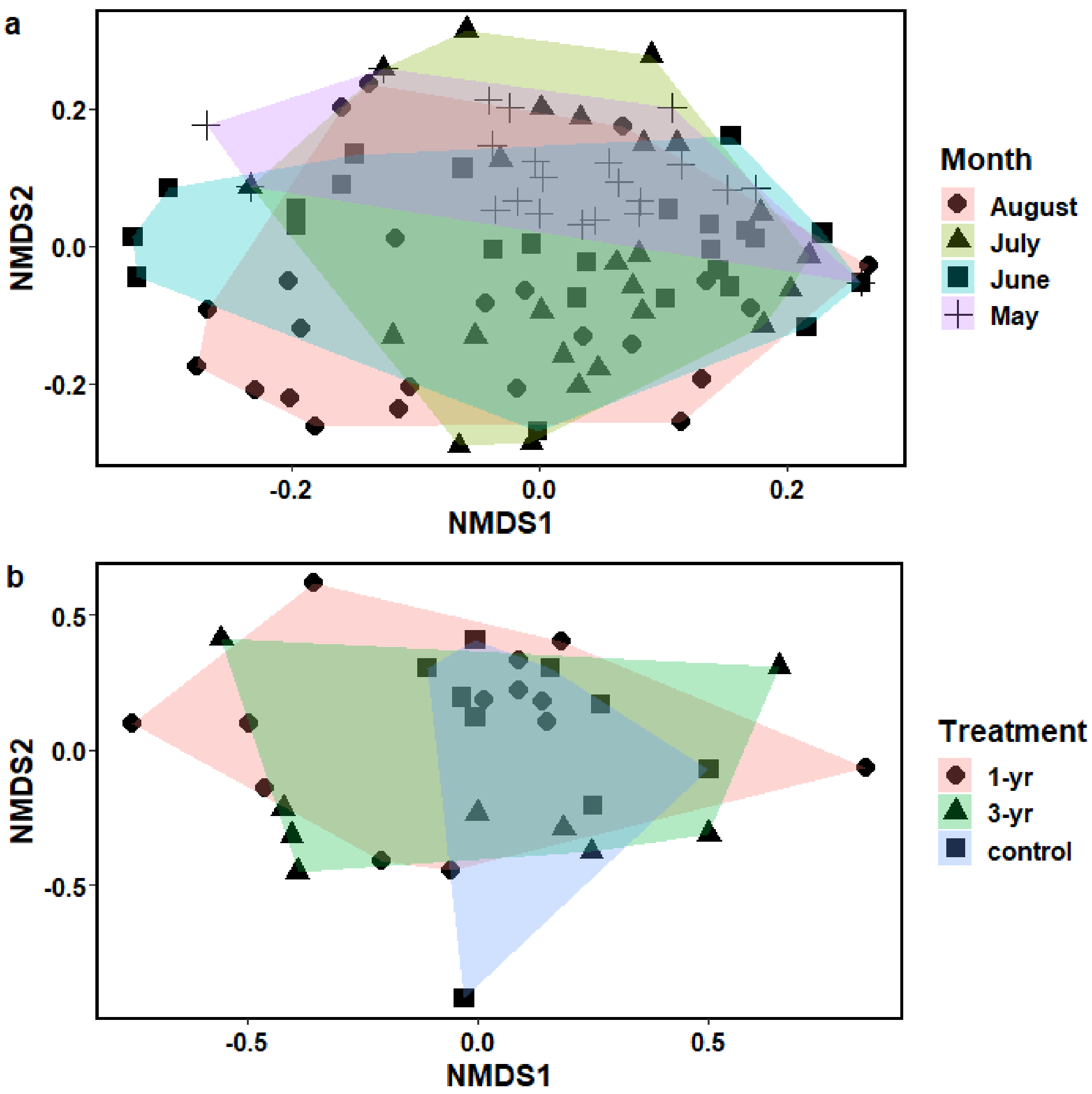

Figure 6. Ordination of bee community assemblages (non-metric multi-dimensional scaling) across (a) collection period and (b) treatment type.

Proportions of bee functional groups (as described by nesting habit) differed due to the effect of collection period ($X^2 = 76.317$, $P < 0.001$; Fig. 7a). Early-season (May) captures contained higher proportions of above ground nesting specialists, whereas late-season captures included higher proportions of nesting generalists. Proportions of bee functional groups represented in the sample also significantly differed between treatment types ($X^2 = 42.714$, $P < 0.001$) with higher ratios of nesting generalists in 1-year post-fire stands, whereas 3-year post-fire stands experienced higher ratios of below ground nesting and parasitic species (Fig. 7b).

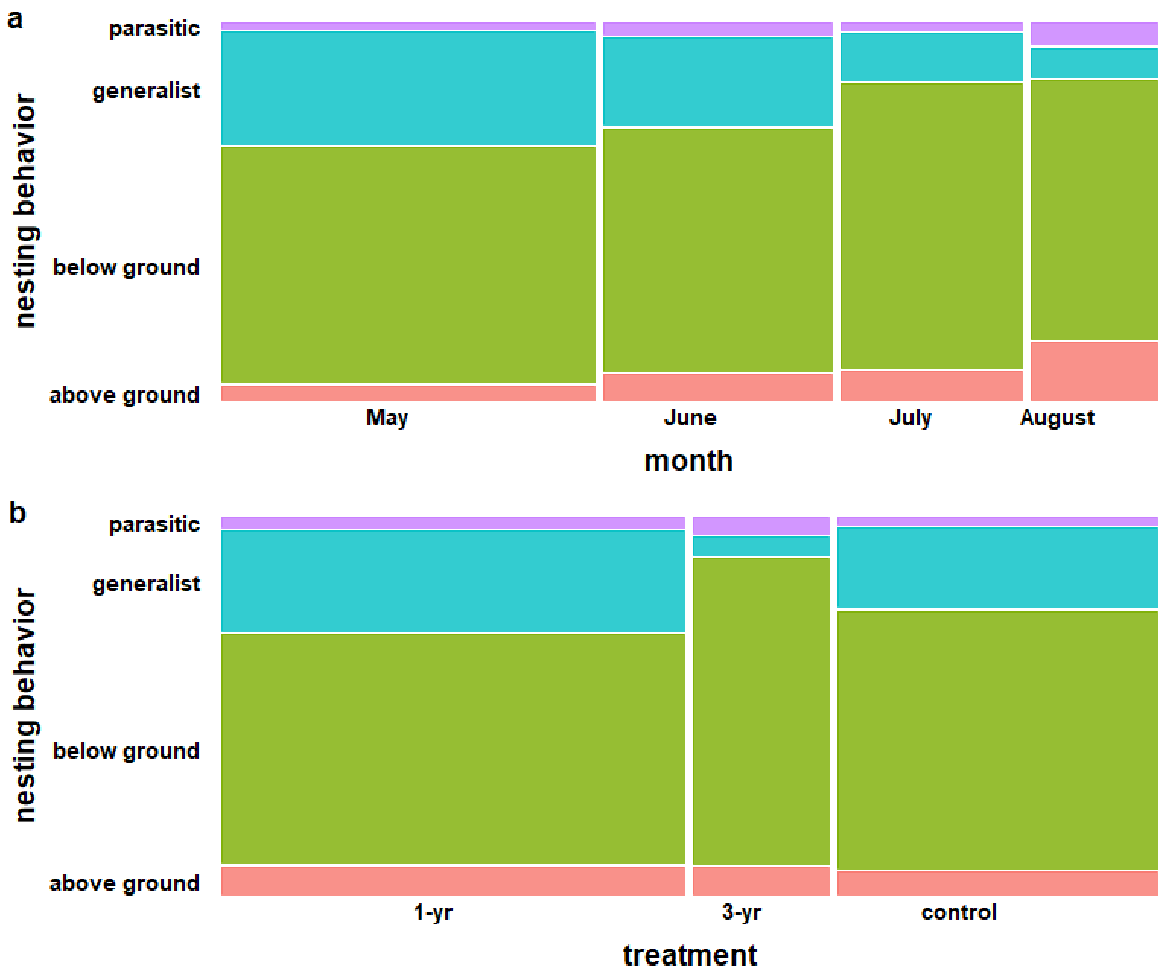

Figure 7. Mosaic plot illustrating ratios of observed nesting behavior among captured bees within each (a) collection period and (b) treatment type.

What are the relative effects of forest structure and foraging habitat on bee assemblages across the landscape?

Across all sampled stands, bee abundance was positively associated with increasing floral richness (β = 0.564, $P < 0.001$) and negatively associated with increasing stand basal area (β = -0.472, $P = 0.012$; Fig. 8a, b). Mean bee species richness was also positively associated with increasing floral species richness (β = 0.670, $P < 0.001$) and negatively associated with increasing stand basal area (β = -0.406, $P = 0.028$; Fig. 8c, d). Likewise, Shannon-Weiner diversity was associated with increasing floral species richness (β = 0.670, $P < 0.001$; Fig. 8e; Table 2).

Response variable	Parameter	Estimate (β)	SE	F	*P*
Bee abundance	Intercept	-0.032	0.133	-	0.809
	Floral richness	**0.564**	**0.140**	**13.307**	**< 0.001**
	Canopy cover	0.313	0.159	3.168	0.057
	Basal area	**-0.472**	**0.177**	**5.854**	**0.012**
	Coarse woody debris	0.126	0.168	0.462	0.456
Bee richness	Intercept	0.001	0.134	-	0.994
	Floral richness	**0.581**	**0.140**	**14.072**	**< 0.001**
	Canopy cover	0.256	0.160	2.107	0.117
	Basal area	**-0.407**	**0.177**	**4.329**	**0.028**
	Coarse woody debris	0.209	0.168	1.262	0.221
Shannon-Weiner diversity	Intercept	-0.032	133	-	0.812
	Floral richness	**0.670**	**0.14**	**18.831**	**< 0.001**
	Canopy cover	0.165	0.159	0.882	0.305
	Basal area	-0.270	0.177	1.912	0.135
	Coarse woody debris	0.225	0.168	1.475	0.187

Table 2. Summary of a generalized linear model analysis to describe variation in bee assemblages due to effects of forest structure and foraging habitat. Significant ($P < 0.05$) effects are bolded.

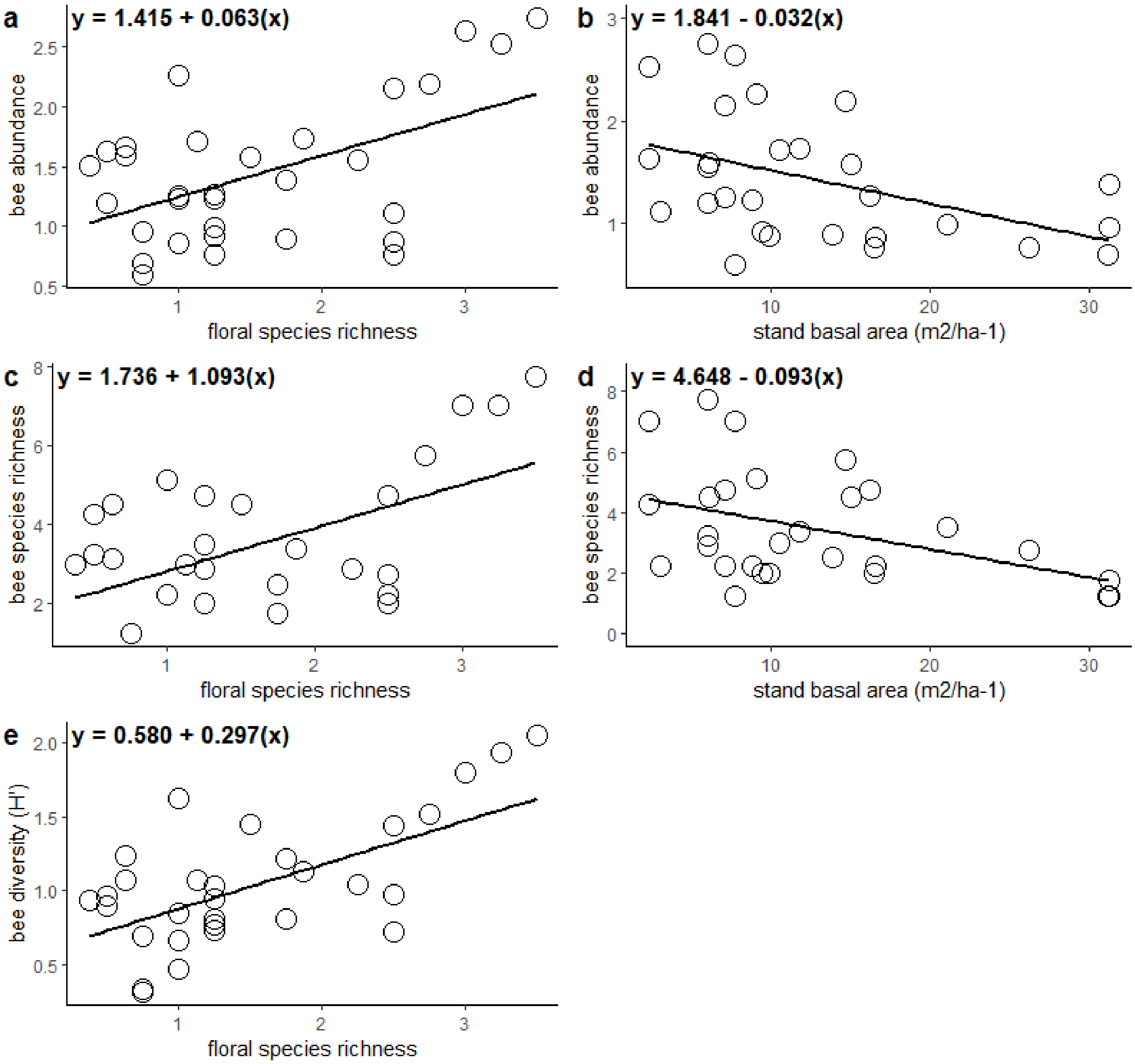

Figure 8. Linear models describing the relationship between bee abundance and (a) stand basal area and (b) floral species richness; bee species richness and (c) stand basal area and (d) floral species richness; and (e) bee diversity and floral richness. All regression models are significant at a Type I error rate of α= 0.05.

Discussion

Our analyses demonstrate that low-intensity prescribed surface fires in southwestern ponderosa pine forests impact foraging resources (floral richness) important for native bees, and these effects cascade to impact bee assemblage α- and β-diversity. At 1-year post-fire, floral richness was enhanced in burned stands (Fig. 2b) and floral richness was positively correlated with bee abundance, richness, and diversity (Fig. 8). However, by 3-years post-fire this effect was diminished, and bee α-diversity was not different from non-treated control stands. This increase and then decline in diversity following prescribed fire was also associated with a shift in β-diversity, and bee assemblages were predominated by below-ground nesting specialists in 3-year post-fire habitats (Fig. 7). Collectively, these results suggest that prescribed fire use in southwestern ponderosa pine forests can have immediate positive effects on bee abundance and richness in forest stands and may also drive functional changes in bee communities over time.

In addition to prescribed fire effects, stands with lower basal area were associated with increased bee abundance and species richness. Reduction of stand basal area can increase penetration of sunlight to the forest floor, promoting growth of forb species necessary for successful bee foraging (Eltz et al. 2002; Jha and Vandermeer 2010; Rubene et al. 2015), increasing opportunity for thermoregulation and further supporting foraging behavior as insects are most active in sunlit areas (Nyoka 2010). Although canopy cover itself did not emerge as a good predictor of bee abundance or richness in our models, basal area and canopy cover did exhibit relative correlation (r = 0.475, *P* = 0.011) to whereas stand basal area increased canopy cover did as well.

Stands sampled 1-year post-fire exhibited increases in bee richness and diversity compared to stands that were 3-year post-fire and non-treated control stands. Stands that were 1-year post-fire also exhibited the highest mean floral richness, suggesting that prescribed fire use caused an increase in the availability of foraging resources for bees. Other studies have shown that prescribed fire can stimulate germination of existing seedbanks with heat or smoke (Read et al. 2000), which may explain the observed increase in floral richness. Moreover, bees often forage in early-seral habitats as these areas are typically have higher forb densities (Roberts et al. 2017), and as floral resource availability becomes consistent across the growing season a greater variety of foraging niche requirements are met (Bennett and Gratton 2013; Dorado and Vasquez 2014). Similar positive relationships between fire, floral richness, and bee diversity have been previously reported from other dry mixed-conifer forests of the western U.S. but have focused primarily on wildfire (Galbraith et al. 2018; Burkle et al. 2019). In more mesic ecosystems, researchers have found evidence of prescribed fire promoting bee diversity at lesser years post-fire (Moylett et al. 2020), whereas in more arid systems floral and bee diversity may not peak until 2 years following wildfire events (Potts et al. 2003). There are also several key differences in the effects of prescribed fire and wildfire on forest structure that could have important consequences for the habitat resources that bees rely on. For example, prescribed fires are often managed to burn at low intensity and severity, whereas wildfires burn at variable intensities and may result in extensive tree mortality at large spatial scales, leading to contrasting landscape characteristics indicating the potential for varying habitat conditions available for bees. Additionally, prescribed fire is often administered in spring or fall, whereas wildfires often burn during summer months (Brown and Sieg 1996) with the potential for differential impacts on insect and plant communities.

There was evidence of distinct bee species turnover due to differences in time-since-fire treatments. *Bombus* (bumblebees, Apidae) were the most abundant taxa found across all treatment types, comprising 61% of total captures. The single most abundant species was *Bombus centralis* Cresson, a foraging generalist that comprised ~18% of the total collection and was found most frequently within 1-year post-fire and non-treated control stands. Other species were only found in specific habitats, including *B. fernaldae* Franklin (Fernald's cuckoo bumblebee, a parasitic species) and *B. fervidus* F. (golden northern bumblebee), which were captured in 3-year post-fire and non-treated control stands, respectively. *Osmia* spp. (mason bees, Megachilidae) are generalist foragers and were relatively abundant in all habitats, though were most commonly collected in 1-year post-fire and non-treated control stands. In contrast, *Anthophora* spp. (digger bees, Megachilidae) were most abundant in 1-year and 3-year post-fire stands, indicating a potential preference for recently disturbed habitats. This is consistent with the life history of *Anthophora* as all species within the genus nest below ground and rely on bare soil substrate for suitable nesting sites (Wilson and Carril 2015; Youngsteadt 2020), which is likely increased in recently burned stands.

Bee community compositions also shifted significantly due to seasonal effects. The most abundant genera (*Bombus*, *Osmia*, and *Anthophora*) were captured in all months of collection. Though bee α-diversity was unaffected by seasonality, abundances of most genera varied across the collection period. Some taxa exhibited specific phenologies and were captured only at certain times in the growing season; for example, *Melecta* and *Sphecodes* were found early-season (May) whereas *Ashmeadiella*, *Colletes*, *Dianthidium*, *Epeolus*, *Eucera*, *Stelis*, and *Triepeolus* appeared late-season (July and August). Many of the genera exhibiting seasonal specificity are either specialist foragers or parasitic (Wilson and Carril 2015), and these groups may exhibit greater sensitivity to seasonal pulses in floral resources or host bee reproductive cycles.

Analyzing bee abundances by their nesting behaviors indicated evidence for functional variation in bee communities across the growing season and across treatment type. We observed higher numbers of nesting generalists in 1-year post-fire stands relative to other treatment types, whereas 3-year post-fire stands bees that specialize in below-ground nesting were more frequent. This pattern may be attributed to physical effects of prescribed fire treatments: burning consumes woody debris and surface vegetation and increases bare soil cover (Allen et al. 2002; Nyoka 2010), altering habitat availability for cavity-nesting and ground-nesting bees, respectively. This aligns with a recent study from southeastern forests, which showed that prescribed fire led to higher densities of ground-nesting bees (Ulyshen et al. 2021). However, we did not detect a positive response of ground-nesting bee species to prescribed fire until 3 years post-fire, potentially indicating a delayed response of bee functional variation to fire disturbance in more arid forest systems.

CONCLUSIONS AND IMPLICATIONS

Conclusions

This study is among the first to assess effects of prescribed fire treatment and associated time-since-fire effects on native bee communities in a southwestern ponderosa pine forest system. The analyses reported here contribute to a growing body of evidence that fire disturbance, including low intensity prescribed fire use, is associated with near-term benefits for forest bees (Campbell et al. 2018, Burkle et al. 2019, Galbraith et al. 2019, Ulyshen et al. 2021). Here, different post-fire timesteps were associated with distinct bee community composition and functional variation. Further, land managers can manipulate stand basal area and floral resources to control site-level bee assemblages but are recommended to facilitate a heterogenous forest structure to promote landscape-level bee biodiversity. Future studies can explore connections between underlying mechanisms of bee response (e.g., floral resource characteristics, landscape-level factors, bee life history traits) to prescribed fire treatments to contribute further understanding on how to manage, or account, for native bee conservation in a time of widespread insect pollinator decline and a shifting climate.

Implications

Several limitations should be considered when interpreting our results. Foremost, abiotic factors that may have contributed to site variability were not accounted for in our study design. Physical conditions including mean site temperature, humidity, and windspeed likely impact both plant phenology and insect behavior (Fucini et al. 2014) at the microsite level and provide additional insight on drivers of bee species distributions. Future studies may benefit from including such measurements to parse out which fire-driven physical changes influence environmental shifts that may impact bee site occupancy. Second, our study design does not include landscape factors known to drive distributions of insect populations at large scales, including land cover richness, habitat connectivity, and proximity to heavily managed ecosystems such as agricultural lands, urban systems, or other extensive land management operations. Due to bees have varying foraging ranges, with some taxa foraging at distances greater than 1000 m (Zurbuchen et al. 2010), inclusion of regional to landscape-level factors in future analyses could help develop improved models of bee species distributions that incorporate comparison of effects between small- and large-scale factors. Lastly, our collection method uses only single approach (vane traps), but inclusion of multiple collection methods (e.g., vane traps, colored pan traps, and aerial netting) reflects a broader representation of bee biodiversity overall (Rhoades et al. 2017).

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APPENDIX A

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APPENDIX B

- This study will be submitted to *Journal of Forest Ecology and Management* by September 1, 2021 as:

  Gelles, R.V., Davis, T.S., Stevens-Rumann, C.S., Barrett, K.J. (2021). Prescribed fire use promotes native bee biodiversity in a semi-arid forest ecosystem. *Journal of Forest Ecology and Management.*

- Upon completion of this publication, all data will be made available on the Dryad digital repository.
- The findings of the preceding publication were presented at the 8th International Fire Ecology and Management Congress hosted by the Association of Fire Ecology in Tucson, AZ on November 18, 2019.
- The M.S. thesis was successfully defended on May 12, 2021.
- The findings of this study are to be presented at a webinar for JFSP Southern Rockies Fire Science Network in Fall 2021.
- Findings of this study will be presented at a Science Lab hosted by the Colorado Forest Restoration Institute in Fall 2021.
- A pamphlet by Colorado State University Extension detailing Colorado native bees and relevant management is in production and is to be published come Spring 2022.

APPENDIX C

The data collected from this project include identification and abundances of bee specimen caught throughout the duration of the study. Habitat data including tree stand density, stand basal area, canopy cover, floral abundances, and floral species identifications. Coarse woody debris measurements were also calculated and used to calculate site-level surface fuel loadings. The data collected and used here did not deviate from the proposed data management plan. Metadata will be available for access on the Dryad digital repository.