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# Prescribed fire is associated with increased floral richness and promotes short-term increases in bee biodiversity in the ponderosa pine forest of the Southern Rocky Mountains

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## Abstract

1. Managed low-severity surface fires are frequently implemented in efforts to restore disturbance processes to forests of North America; although the effects of managed fire on forest structure are well-studied, few studies investigate whether these disturbances cascade to impact pollinator communities.
2. We analysed bee-habitat relationships in fire-treated (1- and 3-years post-treatment) and non-treated ponderosa pine stands in Colorado to test wild bee population responses.
3. Observed bee richness and α-diversity were highest in stands 1-year post-fire and had more *Anthophora*, *Bombus*, *Osmia* and *Lasioglossum* spp. in comparison to 3-year post-fire and non-treated stands. Bee functional groups were responsive to treatments, with more below-ground nesting taxa present in stands 3 years post-fire.
4. Floral richness was the highest mid-growing season (June, July) and within 1-year post-fire stands.
5. A model analysing the effects of foraging and nesting habitat variation on bee assemblages indicated positive association between floral richness and bee α-diversity, but negative relationships with stand basal area. Nesting habitat was not associated with variation in bee assemblages.
6. We conclude that managed fire has positive short-term effects on bee biodiversity that are likely mediated by floral richness. However, these effects were not detectable by 3 years post-treatment in the southern Rocky Mountain region.

KEYWORDS
forest management, pollinator, ponderosa pine, prescribed fire

## INTRODUCTION

Pollinators are critical components of healthy ecosystems where they provide pollination services to trees, shrubs, and herbaceous plants (Hanula et al., 2015). Within forested systems, native insect pollinators are responsible for most pollination interactions (Hanula et al., 2016). For example, pollination of ∼87% of wild plant species is directly dependent on insects (Ollerton et al., 2011), mainly native bees (Potts et al., 2010). Yet, despite their crucial role in ecosystem productivity—and significant public concern about bee populations

(Cameron et al., 2011; Gilgert & Vaughan, 2011) and the decline of insects in general (Eisenhauer et al., 2019)—there is currently little known about factors regulating abundance or diversity of bee pollinators in forested systems (Koh et al., 2016; Rivers et al., 2018). However, anthropogenic activities including land management and land-use change may alter habitats used by bees and have emerged as among the strongest factors known to impact bee populations (Dicks et al., 2021).

Throughout much of western North America, 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). Fires promoted heterogeneous, open forest structures with large interspaces between trees (Allen et al., 2002). However, widespread policies of fire suppression over the last century have led to shifts in habitat conditions including increased tree densities, closed canopies and low understory productivity (Allen et al., 2002). High forest tree densities and climate change have set the stage for subsequent high-severity fire events that occur across very large spatial extents; these events are increasing in frequency and often cause extensive damage to property and forest resources within wildland-urban interfaces (Dennison et al., 2014; Schoennagel et al., 2017). Dense forest conditions may also affect native bee populations by moving landscapes towards a more homogenous forest structure (Nyoka, 2010). High-density forest stands with closed canopies reduce connectivity between habitat patches, hindering bee foraging or migration and potentially contributing to population decline. Additionally, closed canopies prevent light from reaching the forest floor and alter temperature conditions, potentially reducing opportunities for thermoregulation (Polatto et al., 2014) and suppressing understory productivity (Laughlin et al., 2011) and therefore bee foraging opportunities. Consequently, 'non-historic' structures in ponderosa pine forests are likely to have various cascading effects on native bee populations, many of which could be deleterious.

In the southern Rocky Mountain region of North America, regional ecological restoration efforts often focus on re-introducing fire disturbances to ponderosa pine forests in a controlled manner, using managed or 'prescribed' fire as a tool to attain desirable structures prior to extensive and uncontrolled disturbances (i.e., wildfire, Baker et al., 2007). Recent studies demonstrate that managed fire may alter dominant vegetation (canopy cover) and can drive recruitment of forbaceous species (Kerns & Day, 2018; Laughlin & Fulé, 2008; Strahan et al., 2015)—both factors (canopy cover and forb diversity) are important to pollinator communities in forest ecosystems (Gelles et al., 2022; Odanaka et al., 2020). The effects of prescribed fire on native bee communities are seldom explored (but see Campbell et al., 2018, Ulyshen et al., 2021), indicating a need for research on interactions between managed fire, bee foraging and nesting habitats, and bee communities (Carbone et al., 2019) across a wide variety of forest cover types. Knowledge of these relationships is essential to better plan and implement forest management strategies that promote the conservation of bee biodiversity and pollination services.

Here, we ask the question, 'How does managed fire impact native bee assemblages in a fire-adapted ponderosa pine forest?' We test how fire restoration treatments ('prescribed fire') impact abundance and observed richness of native bees compared to non-treated forest stands over time. We sampled bee communities in areas that spanned multiple time-since-fire treatments to test: (1) whether bee abundances, observed richness, and diversity of bees vary with time-since-fire, and (2) how variation in forest structure, nesting habitats, and floral resources affect bee assemblages across sites. Our findings have implications for understanding how a widespread forest restoration tactic (implementation of prescribed fire) affects communities of native bees over time, with consequences for biodiversity and the function of forest ecosystems.

# METHODS

## Study system

Bees were collected from a total of 14 lower-montane sites in the vicinity of Red Feather Lakes, Colorado, USA (40°51′17″N, 105°35′16″W; 2513 m elevation) during the growing season of 2018. In the growing season of 2020, additional sites and treatments were included, for a total of 26 sites sampled during the study (Figure 1). Overstory vegetation in stands selected for study was 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. Study sites had not experienced burns within the past century, though prescribed burns here took place in the spring of 2017, and summer or early-fall of 2019. Thus, 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 ($n = 9$) (Table S1). Burn units selected for study included the Elkhorn burn unit (~205 ha, burned in October 2019) and the Red Feather Lakes burn unit (~215 ha, burned in November 2017). Both fires were 'prescribed' (managed) for the purposes of future fire risk reduction and had similar outcomes of primarily low-intensity surface fire with a high degree of understory consumption and tree scorching, but very little overstory tree mortality.

## Bee sampling procedures

Sites were sampled four times each year to capture seasonal variation in bee assemblages (Rhoades et al., 2018), including May, June, July, and August ($N = 160$ total collection events). To sample bees, blue vane traps (Springstar, Inc. Woodinville, WA) were hung during each collection event from existing vegetation at a height of 1.3 m for 48 h during periods of favourable weather at a density of one trap per site. Traps were placed at a minimum spacing of 300 m and average spacing of ~500 m. Placement relative to the interior of burn units varied, with some traps placed relatively near unit edges and some placed in the interior (Figure 1). Blue vane traps may bias sampling towards

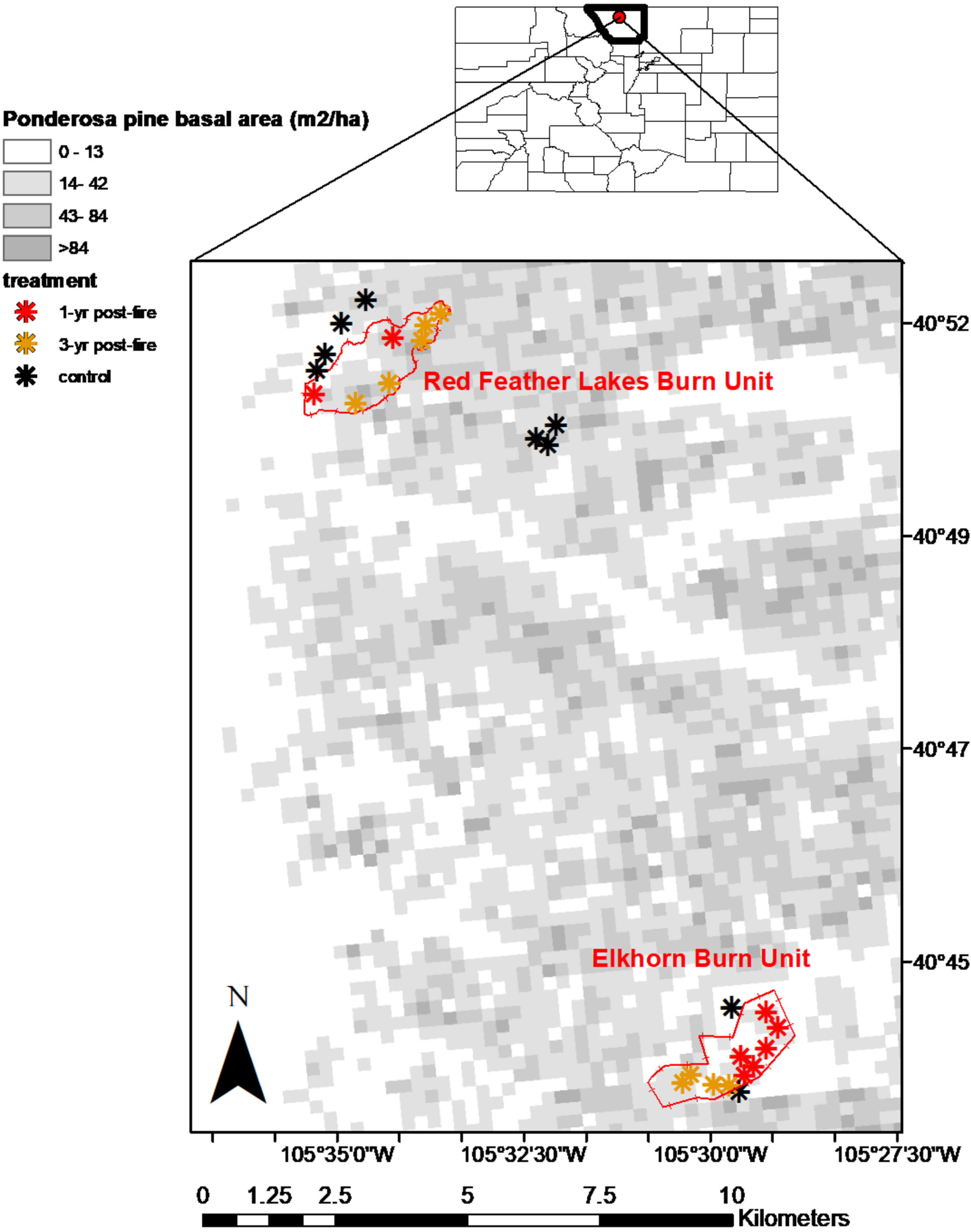

**FIGURE 1** Location of study sites in the Red Feather Lakes region of northern Colorado (USA). Prescribed fire footprints are denoted by red lines; shading shows ponderosa pine basal area ($m^2/ha^{-1}$).

various taxonomic groups, particularly larger bodies bees (Gibbs et al., 2017). Nonetheless, use of vane traps offers the benefit of efficiency when sampling large landscapes over short time frames, reducing potential effects of differences in species phenologies and limiting bias due to variation in observer skill when utilizing active methods (such as netting; Nielsen et al., 2011) Each trap included a wire mesh insert to provide refugia to trapped specimens in the case of unfavourable weather and three 1 mm drilled holes to reduce probability of inundation with water. Following each sampling bout 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 species, if possible, using DiscoverLife bee species keys (Ascher & Pickering, 2020) and the keys of Michener (2000) and Koch et al. (2012). Collections from the present study were also cross-referenced with Scott et al. (2011) and specimens at the C. P Gillette Museum of Arthropod Diversity (Colorado State University) or the personal collections of the authors (e.g., Davis et al., 2020; Davis & Comai, 2022; Gelles et al., 2022; Rhoades et al., 2018).

Morphospecies designations were used when specimens were identifiable as a distinct taxonomic group, but species-level identifications were not feasible. Appropriate voucher specimens were archived in the C.P. Gillette Museum of Arthropod Diversity.

## Forestry and understory measurements

At each collection location, structural information was collected within a 0.04-ha fixed-area plot. In each plot, trees were censused and their species identity as well as diameter at breast height (dbh) were recorded. Overstory canopy cover (closure) was recorded along two 8 m transects running north and south from plot centre using a densitometer. The presence of both live and dead overstory cover above breast height was tallied. We computed stand basal area ($m^2/ha^{-1}$), tree density ($trees/ha^{-1}$), and canopy cover (%) from these data.

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 (Rodríguez & Kouki, 2015). To measure the availability of coarse woody debris (both sound and rotting material on the ground surface with proximal diameter >7.6 cm), a 0.015-ha (6.9 m 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 of surface loading, calculated in megagrams per hectare (MG/ha) after the methods of Brown (1974). Though woody debris measurements are valuable in relating habitat-driven mechanisms to bee response, bee flight ranges likely exceed the area at which these estimates are made and should be taken into consideration when interpreting results.

In addition to coarse woody debris, floral resource availability also influences bee assemblages as a foraging resource (Hanula et al., 2016). At each collection period, floral species richness was recorded using quadrats; floral density was not considered as prior studies have shown richness to be a more important factor contributing to bee site occupancy and foraging (Jha & Kremen, 2013; Potts et al., 2003). At each site and collection period, five replicate 1 $m^2$ quadrats were deployed, and the total number of unique species represented by active floral displays was recorded. One quadrat was placed directly beneath the trap location, with additional quadrats placed 2 m 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 richness for each collection period.

## Data analysis

All statistical analyses were conducted using the R programming language (V3.5.2, 'Eggshell Igloo', R Core Team, 2022). A Type I error rate of $\alpha = 0.05$ was used for assigning statistical significance to modelled effects.

A one-way ANOVA model was used to analyse variation in elements of forest structure (mean basal area, tree density, canopy cover, coarse woody debris surface loading, and floral richness) due to the effects of prescribed fire (treatments = 1-year post-fire, 3-year post-fire, and non-treated control stand). All pairwise comparisons of means were made using Tukey's Honest Significant Difference (HSD) test.

Two-way ANOVA was used to analyse the fixed effects of site treatment type (1-year post-fire, 3-year post-fire, and non-treated control), seasonality (May, June, July, August), and the treatment × seasonality interaction on the responses of mean bee abundance, observed bee richness, and bee diversity (as measured by the Shannon-Weiner H′ statistic); sample year (2018 or 2020) was incorporated as a random effect. 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 analysing model effects on Shannon's H′ (18.4% of observations); zeros were incorporated in analyses on bee abundance and observed richness.

To estimate the relationship between sampling effort and observed bee biodiversity at study sites, bee α-diversity was analysed using Hill numbers (Colwell et al., 2012) extracted from the 'iNEXT' package (Hseih et al., 2020). Estimates and rarefaction curves were interpolated from sample-based abundances to account for different numbers of bee captures and extrapolated to approximately 2× the size of the smallest sample per treatment type (Chao et al. 2014), and multiple Hill numbers were considered (i.e., $q = 0$ {species richness}, 1 {Shannon diversity}, and 2 {Simpson diversity}). In addition to richness 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 genus counts) were transformed into matrices of Bray-Curtis dissimilarities and effects of treatment type were analysed using the 'adonis2' function (permutational multivariate analysis of variance; PERMANOVA, $n = 9999$ permutations) in the R add-on package 'vegan' (Oksanen et al., 2021), such that the analysis was performed at the morphospecies level. Results were visualized using non-metric multidimensional scaling (NMDS). Prior to interpreting PERMANOVA output, we first confirmed equivalent homogeneity of variance between treatment groups ($F_{2,\ 28} = 1.375$, $p = 0.269$) using a multivariate analog of Levene's test (function 'betadisper' from package 'vegan'). Seasonal variation was not analysed within this framework as seasonal variation did not exhibit a homogenous variance ($F_{3,\ 92} = 4.115$, $p = 0.008$). Additionally, chi-squared tests were used to assess whether the proportion of bee functional groups (as assigned by nesting behaviour, Table S2) varied by month of collection and treatment type. Nesting behaviours were divided into four categories based on life history strategies of each genus (Wilson & Carril, 2015; Wright et al., 2017, Danforth et al. 2020) and included above ground nesters, below ground nesters, taxa that exhibit flexible behaviours (i.e., bees that nest either below ground or within cavities), and cleptoparasitic species.

A generalized linear model framework (family: gaussian, link function: identity) was used to compare relative effect sizes of forest

**TABLE 1** Summary of variation in forest structure, foraging and nesting habitat variables, and bee diversity metrics

| | | Treatment group | | |
|---|---|---|---|---|
| **Category** | **Variable** | **1-year post-fire** | **3-year post-fire** | **Control** |
| Forest structure | Basal area (m$^2$ ha) | 13.39 ± 2.65 | 12.57 ± 3.24 | 11.25 ± 1.91 |
| | Stem density (stems/ha) | 129.26 ± 24.26 | 131.79 ± 23.30 | 158.35 ± 15.76 |
| | Canopy cover (%) | 0.30 ± 0.06 | 0.27 ± 0.07 | 0.38 ± 0.07 |
| Foraging habitat | Floral richness (per m$^2$) | 2.00 ± 0.25 **A** | 1.25 ± 0.24 **AB** | 1.16 ± 0.19 **B** |
| Nesting habitat | Coarse woody debris (Mg/ha) | 4.47 ± 1.84 | 6.82 ± 2.44 | 13.24 ± 4.62 |
| Bee $\alpha$-diversity | Abundance | 9.18 ± 1.33 | 4.50 ± 1.19 | 1.98 ± 0.85 |
| | Observed richness | 4.55 ± 0.42 **A** | 2.41 ± 0.39 **B** | 3.11 ± 0.27 **B** |
| | Diversity (Shannon's H′) | 1.40 ± 0.09 **A** | 0.69 ± 0.12 **B** | 1.03 ± 0.08 **B** |

*Note*: Values shown are means ± SE. Lettering denotes Tukey's HSD test for groups where significant ($p < 0.05$) pairwise differences were identified.

structure and foraging habitat variables on bee assemblages, treating unique sites and treatment combinations ($n = 31$ total experimental units) as the unit of analysis. Bee community metrics were averaged across the 2 years of collection to produce site-level estimates of mean bee abundance, observed richness, and diversity. Independent variables used in model development 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 (Table S3). Response variables include mean bee abundance, observed bee richness, and Shannon diversity. Both independent and dependent variables were standardized to ($\mu = 0, \sigma = 1$) prior to analysis to simplify interpretation of coefficients.

# RESULTS

## Effects of burn treatment on environmental variables

Characteristics of overstory vegetation between treatment types were similar (Table 1). Tree density did not differ significantly between treatment types (1-year post-prescribed burn = 129.3 trees per ha, 3-year post-prescribed 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-year post-prescribed burn = 13.4 m$^2$/ha, 3-year post-prescribed 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-year post-prescribed burn = 30% cover, 3-year post-prescribed burn = 26% cover, non-treated control = 37% cover; $F_{2, 30} = 0.632$, $p = 0.539$).

Typical flora taxa identified during surveying include *Achillea millefolium*, *Sedum 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 ($F_{3, 147} = 18.959$, $p < 0.001$; Figure 2). Mean floral richness in 1-year post-prescribed burn sites was 75.7% greater than non-treated control sites and 61.6% greater than 3-year post-prescribed burn sites ($F_{2, 147} = 6.360$, $p = 0.002$; Table 1). Year-to-year-variation accounted for $\sim$32% of the modelled variance in floral richness but was not statistically significant ($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 nesting habitat in non-treated control sites was 66.2% greater than in 1-year post-fire sites and 48.5% greater than in 3-year post-fire sites.

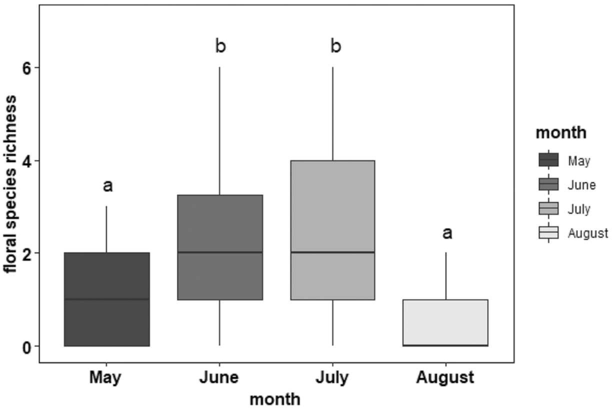

**FIGURE 2** Distribution of floral species richness across collection period. Lettering denotes Tukey's HSD test; boxplots not connected by the same letter differ significantly in mean value.

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

A total of 1096 bee specimens were captured in vane traps. Bee $\gamma$-diversity was represented by five families (Andrenidae, Apidae, Colletidae, Halictidae, and Megachilidae), 25 genera (including *Dialictus* and *Evylaeus*, subgenera of genus *Lasioglossum*), and at least 55 species. Predominant genera include bumblebees (*Bombus* spp.), mason bees (*Osmia* spp.), and digger bees (*Anthophora* spp.), accounting for 61.4%, 13.9%, and 8% of collected specimens, respectively (Table 2). Dominant species within our sample include *Bombus centralis* Cresson (18.7%), *Bombus bifarius* Cresson (9.7%), and *Bombus melanopygus*

**TABLE 2** Abundances of bees, summarized by species, captured in blue vane traps in each treatment type (i.e., time-since-fire and non-treated control stands).

| | | | Treatment type | | |
|---|---|---|---|---|---|
| **Family** | **Genus** | **Species** | **1-year post-fire** | **3-year post-fire** | **Control** |
| Andrenidae | *Andrena* | *carlini* | 0 | 0 | 1 |
| | | *geranii* | 0 | 1 | 0 |
| | | sp. 1 | 1 | 0 | 1 |
| | | sp. 2 | 3 | 0 | 0 |
| | | sp. 3 | 0 | 0 | 1 |
| | | sp. 4 | 0 | 0 | 1 |
| Apidae | *Anthophora* | *bomboides* | 2 | 0 | 0 |
| | | *californica* | 1 | 0 | 0 |
| | | *montana* | 8 | 4 | 6 |
| | | *porterae* | 22 | 11 | 7 |
| | | *terminalis* | 10 | 0 | 9 |
| | | *ursina* | 7 | 0 | 0 |
| | | sp. 1 | 1 | 0 | 0 |
| | *Apis* | *mellifera* | 1 | 1 | 0 |
| | *Bombus* | *appositus* | 33 | 8 | 21 |
| | | *bifarius* | 23 | 55 | 28 |
| | | *californicus* | 4 | 0 | 2 |
| | | *centralis* | 87 | 20 | 98 |
| | | *fernaldae* | 0 | 1 | 0 |
| | | *fervidus* | 0 | 0 | 2 |
| | | *flavifrons* | 38 | 0 | 32 |
| | | *griseocollis* | 2 | 2 | 1 |
| | | *huntii* | 11 | 0 | 3 |
| | | *insularis* | 10 | 0 | 5 |
| | | *melanopygus* | 59 | 0 | 27 |
| | | *nevadensis* | 10 | 10 | 8 |
| | | *occidentalis* | 1 | 1 | 0 |
| | | *rufocinctus* | 20 | 7 | 9 |
| | | *sylvicola* | 18 | 2 | 13 |
| | | sp. 1 | 1 | 0 | 0 |
| | *Diadasia* | sp. 1 | 1 | 0 | 0 |
| | *Epeolus* | *americanus* | 0 | 0 | 1 |
| | *Eucera* | *speciosa* | 0 | 0 | 1 |
| | *Melecta* | *pacifica* | 0 | 3 | 1 |
| | *Melissodes* | *agilis* | 3 | 0 | 0 |
| | | *bimaculata* | 0 | 0 | 1 |
| | | sp. 1 | 1 | 2 | 2 |
| | | sp. 2 | 1 | 1 | 2 |
| | | sp. 3 | 1 | 0 | 6 |
| | | sp. 4 | 3 | 1 | 2 |
| | | sp. 5 | 1 | 0 | 1 |
| | *Nomada* | sp. 1 | 1 | 0 | 0 |
| | *Triepeolus* | sp. 1 | 0 | 1 | 0 |

(Continues)

**TABLE 2** (Continued)

| Family | Genus | Species | Treatment type<br>1-year post-fire | 3-year post-fire | Control |
|---|---|---|---|---|---|
| Colletidae | *Colletes* | sp. 1 | 0 | 1 | 2 |
| | | sp. 2 | 0 | 0 | 1 |
| | *Hylaeus* | *basalis* | 1 | 0 | 1 |
| | | sp. 1 | 1 | 1 | 1 |
| | | sp. 2 | 1 | 0 | 0 |
| Halictidae | *Agapostemon* | *angelicus/texanus* | 2 | 0 | 1 |
| | | *viriscens* | 1 | 0 | 0 |
| | *Halictus* | *confusus* | 0 | 0 | 1 |
| | | *ligatus* | 1 | 0 | 0 |
| | | *parallelus* | 1 | 0 | 3 |
| | | *rubicundus* | 0 | 3 | 0 |
| | | sp. 1 | 1 | 0 | 1 |
| | *Lasioglossum* (*Dialictus*) | sp. 1 | 2 | 0 | 0 |
| | | sp. 2 | 0 | 0 | 2 |
| | *Lasioglossum* (*Evylaeus*) | sp. 1 | 3 | 0 | 0 |
| | | sp. 2 | 2 | 0 | 0 |
| | | sp. 3 | 1 | 0 | 0 |
| | *Lasioglossum* (*s. stricto*) | sp. 1 | 2 | 1 | 0 |
| | | sp. 2 | 3 | 0 | 0 |
| | | sp. 3 | 4 | 0 | 2 |
| | | sp. 4 | 1 | 2 | 0 |
| | | sp. 5 | 1 | 1 | 3 |
| | | sp. 6 | 6 | 0 | 1 |
| | | sp. 7 | 8 | 3 | 0 |
| | | sp. 8 | 4 | 3 | 1 |
| | | sp. 9 | 1 | 0 | 0 |
| | *Sphecodes* | *eustictus* | 2 | 0 | 0 |
| | | sp. 1 | 1 | 0 | 0 |
| | Unknown | sp. 1 | 1 | 0 | 0 |
| Megachilidae | *Ashmeadiella* | *bucconis* | 1 | 0 | 0 |
| | | *californica* | 0 | 0 | 2 |
| | *Dianthidium* | *concinnum* | 0 | 0 | 1 |
| | | sp. 1 | 1 | 0 | 1 |
| | | sp. 2 | 1 | 0 | 1 |
| | | sp. 3 | 2 | 0 | 1 |
| | *Hoplitis* | *albifrons* | 5 | 4 | 3 |
| | | *fulgida* | 4 | 0 | 2 |
| | | *truncata* | 1 | 0 | 0 |
| | *Megachile* | *augustini* | 1 | 1 | 0 |
| | | *dentitarsus* | 0 | 0 | 1 |
| | | *gemula* | 0 | 0 | 1 |
| | | *parallela* | 3 | 1 | 1 |
| | | *pugnata* | 1 | 0 | 0 |
| | | sp. 1 | 3 | 0 | 2 |
| | | sp. 2 | 1 | 0 | 0 |

(Continues)

**TABLE 2** (Continued)

| Family | Genus | Species | Treatment type<br>1-year post-fire | <br>3-year post-fire | <br>Control |
|---|---|---|---|---|---|
| | *Osmia* | *bruneri* | 1 | 0 | 0 |
| | | *bucephala* | 47 | 4 | 28 |
| | | *longula* | 4 | 0 | 3 |
| | | *penstemonis* | 3 | 0 | 0 |
| | | *simillima* | 3 | 1 | 1 |
| | | sp. 1 | 6 | 0 | 5 |
| | | sp. 2 | 11 | 1 | 7 |
| | | sp. 3 | 6 | 0 | 3 |
| | | sp. 4 | 4 | 0 | 2 |
| | | sp. 5 | 3 | 1 | 0 |
| | | sp. 6 | 1 | 0 | 1 |
| | | sp. 7 | 2 | 0 | 3 |
| | | sp. 8 | 0 | 0 | 1 |
| | *Stelis* | *foederalis* | 1 | 1 | 0 |
| | | *permaculata* | 0 | 1 | 0 |

*Note*: Bees that were sorted as morphospecies but could not be definitively identified based on available taxonomic resources are denoted as 'sp.1', 'sp.2', etc.

Nylander (7.9%). Across treatment type, *Bombus* were the most captured genera comprising 57.4% of 1-year post-fire collections, 65.4% of 3-year post-fire collections, and 65.2% of control stand collections (Table S4). Collections within 1-year post-fire and non-treated control stands had large portions of *Osmia* (16.5%, 14.1%) and *Anthophora* (14.1%, 5.8%), whereas 3-year post-fire stands experience frequent encounters with *Osmia* (9.3%) and *Lasioglossum* (6.2%).

Bee abundances varied significantly due to the effect of seasonality ($F_{3,\,147} = 12.686$, $p < 0.001$), though there was no evidence of variation in mean bee abundances due to a treatment effect ($F_{2,\,147} = 2.551$, $p = 0.082$) or a treatment × seasonality interaction ($F_{6,\,147} = 0.733$, $p = 0.624$). The average number of bee captures in 1-year post-fire stands was 68.4% greater than 3-year post-fire stands and 42.4% greater than non-treated control stands (Table 1). Bee abundances in May were 50.7% greater than June, 73.5% greater than July, and 32.1% greater than August captures (Figure S1). Year effects accounted for 29.7% of the modelled variance in bee abundance but were not statistically significant ($p = 0.489$).

Mean observed bee richness varied significantly due to the effect of treatment ($F_{3,\,147} = 5.497$, $p = 0.005$); however, observed bee richness did not vary due to the effect of seasonality ($F_{3,\,147} = 1.926$, $p = 0.128$) or a treatment × seasonality interaction ($F_{6,\,147} = 1.573$, $p = 0.159$). Observed bee richness in 1-year post-fire stands was 61.1% greater than in 3-year post-fire stands and 37.6% greater than in non-treated control stands (Table 1). Year effects account for 9.1% of the modelled variance in observed bee richness but were not statistically significant ($p = 0.513$).

Bee diversity (Shannon's H′) varied significantly due to the effect of treatment ($F_{3,\,147} = 5.460$, $p = 0.005$), but not due to seasonality ($F_{3,\,147} = 1.601$, $p = 0.192$) or a treatment × seasonality interaction ($F_{6,\,147} = 0.992$, $p = 0.434$). Shannon-Weiner diversity in 1-year post-fire stands was 68.1% greater than in 3-year post-fire stands and 30.5% greater than in non-treated control stands (Table 1). Year effects account for 26.2% of the modelled variance in bee diversity, though this was not statistically significant ($p = 0.491$).

Analysis of α-diversity using rarefaction curves and Hill numbers coupled with bootstrapped confidence intervals indicated that accumulation of bee biodiversity in 1-year post-fire stands exceeded that of other treatment types (Figure S2), with bee biodiversity declining to below that of non-treated control stands by 3-years post prescribed fire. Additionally, there was evidence that community assemblages differed between treatment types ($F_{2,\,28} = 1.327$, $p = 0.033$; Figure 3), with turnover observed in multiple bee genera including *Diadasia*, *Nomada*, *Evylaeus*, *Sphecodes*, *Epeolus*, *Eucera*, and *Triepeolus* (Table 2).

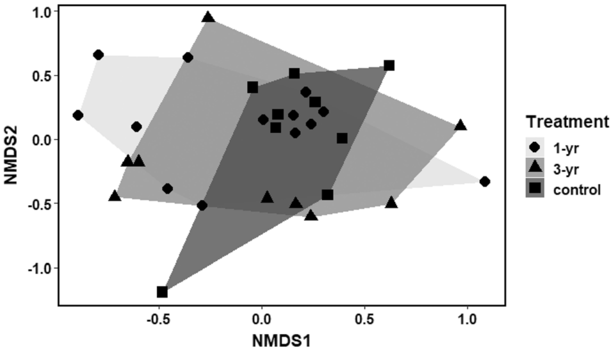

**FIGURE 3** Ordination of bee community composition (non-metric multidimensional scaling) across treatment categories.

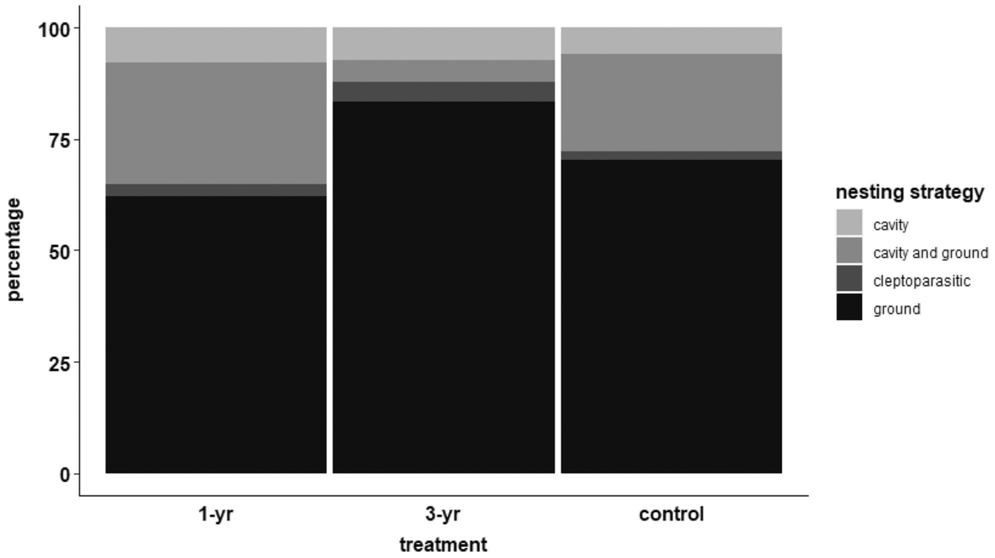

**FIGURE 4** Variation in the proportion of captured bees exhibiting different nesting behaviours across treatment type.

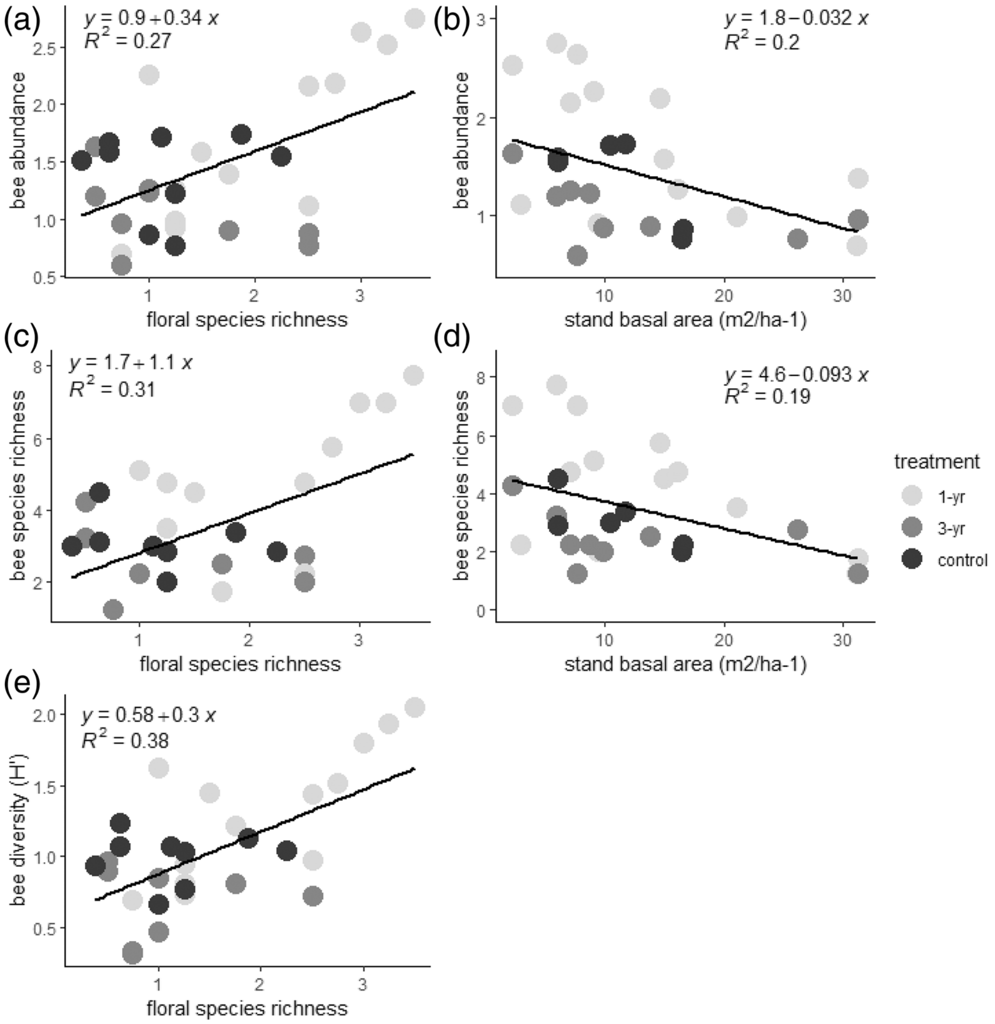

**FIGURE 5** Linear models describing the relationship between bee abundance and (a) stand basal area and (b) floral species richness; observed bee species richness and (c) stand basal area and (d) floral species richness; and (e) bee diversity and floral richness.

**TABLE 3** Summary of a generalized linear model analysis describing variation in bee assemblages due to effects of variation in forest structure and foraging habitat.

| Response variable | Parameter | Estimate ($\beta$) | SE | *t*-score | *p* |
|---|---|---|---|---|---|
| Bee abundance | Intercept | −0.032 | 0.133 | −0.220 | 0.809 |
| | **Floral richness** | **0.564** | **0.140** | **3.648** | **<0.001** |
| | Canopy cover | 0.313 | 0.159 | 1.780 | 0.057 |
| | **Basal area** | **−0.472** | **0.177** | **−2.419** | **0.012** |
| | Coarse woody debris | 0.126 | 0.168 | 0.680 | 0.456 |
| Observed bee richness | Intercept | 0.001 | 0.134 | 0.007 | 0.994 |
| | **Floral richness** | **0.581** | **0.140** | **3.751** | **< 0.001** |
| | Canopy cover | 0.256 | 0.160 | 1.452 | 0.117 |
| | **Basal area** | **−0.407** | **0.177** | **−2.081** | **0.028** |
| | Coarse woody debris | 0.209 | 0.168 | 1.123 | 0.221 |
| Shannon's H′ | Intercept | −0.032 | 0.133 | −0.216 | 0.812 |
| | **Floral species richness** | **0.670** | **0.140** | **4.339** | **<0.001** |
| | Canopy cover | 0.165 | 0.159 | 0.939 | 0.305 |
| | Basal area | −0.270 | 0.177 | −1.383 | 0.135 |
| | Coarse woody debris | 0.225 | 0.168 | 1.215 | 0.187 |

*Note*: Significant ($p < 0.05$) effects are denoted in bold text.

Proportions of bee functional groups (as assigned by nesting habit) differed with the collection period ($\chi^2 = 76.317$, df $= 9$, $p < 0.001$). Early-season (May) captures contained higher proportions of above ground nesting specialists, whereas late-season captures included higher proportions of bees that nest below ground or within cavities. Proportions of bee nesting groups represented in the sample also significantly differed between treatment types ($\chi^2 = 42.714$, df $= 6$, $p < 0.001$) with higher ratios of bees that nest below ground or cavity nesters in 1-year post-fire stands, whereas 3-year post-fire stands exhibited higher ratios of below ground nesting and cleptoparasitic species (Figure 4).

## How do variations in forest structure, nesting habitat, and floral resources affect bee assemblages across sites?

Across all sampled stands, bee abundance was positively associated with increasing floral richness ($\beta = 0.564$, $p < 0.001$) and negatively associated with increasing stand basal area ($\beta = -0.472$, $p = 0.012$; Figure 5a, b). Mean observed bee richness was also positively associated with increasing floral species richness ($\beta = 0.670$, $p < 0.001$) and negatively associated with increasing stand basal area ($\beta = -0.406$, $p = 0.028$; Figure 5c, d). Likewise, diversity (Shannon's H′) was associated with increasing floral species richness ($\beta = 0.670$, $p < 0.001$; Figure 5e). However, canopy cover and coarse woody debris had no detectable effect on variation in bee assemblages (Table 3).

## 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-diversity. At 1-year post-fire, floral richness was enhanced in burned stands (Table 1) and floral richness was positively correlated with bee abundance, observed richness, and diversity (Figure 6a, c, e). By 3 years post-fire this effect was diminished and bee diversity was not different from non-treated control stands. This increase and then decline in diversity following the prescribed fire was also associated with a shift in bee life history traits, and bee assemblages were predominated by below-ground nesting specialists in 3-year post-fire habitats (Figure 4). Collectively, these results suggest that prescribed fire use in southwestern ponderosa pine forests can have immediate positive effects on observed bee richness in forest stands and may also drive functional changes in bee communities over relatively short timeframes.

In addition to prescribed fire effects, stands with a lower basal area were associated with increased bee abundance and observed richness. Reduction of stand basal area can increase penetration of sunlight to the forest floor, promoting the growth of forb species necessary for successful bee foraging (Eltz et al., 2002; Jha & Vandermeer, 2010; Rubene et al., 2015), increasing opportunities for thermoregulation and further supporting foraging behaviour as insects are most active in sunlit areas (Nyoka, 2010).

Stands sampled 1-year post-fire exhibited increases in observed bee richness and diversity compared to stands that were 3-year post-fire and non-treated control stands. These findings are consistent with those from a recent study in a longleaf pine system (Moylett et al., 2020), where bee abundance and diversity declined rapidly with increasing time-since-fire. 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 the 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 typically have high forb densities (Roberts et al., 2017). 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 wildfires (Burkle et al., 2019; Galbraith et al., 2019). Collectively, these studies and the present study converge on general support for the 'pyrodiversity hypothesis' proposed by Ulyshen et al. (2022) and could indicate that a policy of frequent burn rotations across fire-adapted forest landscapes will garner rapid short-term general benefits for bees and other pollinators.

In more mesic ecosystems, there is also evidence of fire promoting bee diversity immediately following fire events (Moylett et al., 2020; Ulyshen et al., 2021), whereas in more arid systems floral and bee diversity may not peak until 2 years post-fire (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 areas of tree mortality, leading to contrasting landscape characteristics. Additionally, prescribed fire is often administered in spring or fall, whereas wildfires often burn during summer months (Brown & Sieg, 1996) with the potential for differential impacts on insect and plant communities. Prescribed fire events are recommended during the growing season, when insects are in mobile phases of their life history and have higher potential to recolonize or escape fire-induced mortality (Nyoka, 2010). However, mid-season burns may negatively impact diversity of plant communities leading to cascading effects on pollinator communities (Roberton & Rebar, 2022), such as decreased habitat complexity and nesting opportunity, as bees exhibit differential preferences for habitat conditions which may or may not provide optimal nesting opportunities depending on the specific taxa considered.

This assertion is supported by our analysis of bee nesting strategies relative to time-since-fire. We observed higher numbers of bees with flexible nesting strategies (i.e., those that nest below ground or within cavities) in 1-year post-fire stands relative to other treatment types, whereas within 3-year post-fire stands bees that specialize in below-ground nesting were more frequent. This pattern may be explainable due to the 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 matches 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.

There was also evidence of turnover in bee species due to the effects of time-since-fire treatments. *Bombus* (bumblebees, Apidae) were the most abundant taxa found across all treatment types, comprising the majority of captures. The single most abundant species was *Bombus centralis* Cresson, a foraging generalist that comprised ~18% of the total collection and was found most abundantly 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 socially parasitic species) and *B. fervidus* F. (golden northern bumblebee), which were captured in 3-year post-fire and non-treated control stands, respectively (Table S4). *Osmia* spp. (mason bees, Megachilidae) are generalist foragers and were relatively abundant in all habitats, though were most abundant in 1-year post-fire and non-treated control stands. In contrast, *Anthophora* spp. (digger bees, Apidae) 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 & Carril, 2015), which increases in recently burned stands. Moylett et al. (2020) found similar results, with strong evidence of turnover in bee community composition associated with fire-driven shifts in habitat variables, including nesting substrate and canopy cover. Thus, there is evidence that some species may be adapted to take advantage of conditions created by prescribed fire treatments, such as ground nesting bees who may find increased bare soil cover opportune, or larger bodied bees who may more readily recolonize disturbed areas due to greater foraging distances (Greenleaf et al., 2007). However, some bee taxa may be disadvantaged by prescribed fire treatments. Cavity nesters who nest in woody material or vegetation above the ground surface, such as various *Bombus* species, could be at risk of decreased populations due to fire-induced destruction of nests. Sites that have recently experienced fire may lack established populations of bees with these life history strategies. Further, our analyses suggest differences in floral richness and communities between treatments, potentially leading to variation in bee communities as bee taxa may rely on specific host plants, or flower morphological traits, for foraging (Potts et al., 2003).

This study has several limitations that should be considered for the design of subsequent projects. Foremost, abiotic factors that may have contributed to site variability were not measured but have the potential to impact bee sampling. Physical conditions including mean site temperature, humidity, and windspeed likely impact both plant phenology and insect behaviour (Fucini et al., 2014) at the microsite level and provide additional insight on drivers of bee species distributions. 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. 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 a single approach (vane traps). Inclusion of multiple collection methods (e.g., vane traps, coloured pan traps, and aerial netting) may reflect a broader representation of bee biodiversity overall (Rhoades et al., 2017).

This study is the first to assess the effects of prescribed fire treatment and associated time-since-fire effects on native bee communities in semi-arid ponderosa pine forests of the southern Rocky Mountain region (but see Campbell et al., 2018 for a description of these effects in southern hardwood forests, and Gelles et al., 2022 for a description of wildfire and thinning effects in ponderosa pine forests). 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 bee assemblages. 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 impact site-level bee assemblages. Prescribed fire treatments are often paired with basal area reduction (thinning) treatments, directly altering tree density and associated canopy cover. Though thinning treatments were not incorporated in the design of the present study design, the combination of a thin and burn prescription can positively influence bee site occupancy as a reduction in forest canopy associated with tree removal may benefit the growth of forbaceous species that provide foraging and nesting resource to insect pollinators. Future studies should focus on the underlying mechanisms of bee responses (e.g., floral resource characteristics, variation in nesting habitats, landscape-level factors, and bee life history traits) to prescribed fire treatments to contribute further understanding of how to manage forest structure to conserve native bee populations in a shifting climate.

## AUTHOR CONTRIBUTIONS

**Ryleigh V Gelles:** Conceptualization; data curation; formal analysis; investigation; methodology; writing – original draft; writing – review and editing. **Thomas Seth Davis:** Conceptualization; formal analysis; funding acquisition; methodology; project administration; supervision; writing – review and editing. **Kevin J Barrett:** Conceptualization; funding acquisition; investigation; resources; writing – review and editing.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Data S1.** Supporting Information

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