



Original Research Article

Shaded fuel breaks support diverse bee communities in fire-prone managed conifer forests

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ABSTRACT

Fuels management is critical for wildfire mitigation, yet our understanding of how this practice influences forest insect pollinators is limited. In this study, we evaluated bee communities in shaded fuel breaks ($n = 27$) and untreated reference sites ($n = 9$) on private conifer forests of northern California during 2023–2024. Across both years we captured 17,124 bees comprising 5 families, 33 genera, and 188 species. We found bee abundance was $3.2 \times$ greater in shaded fuel breaks relative to reference sites, whereas fuel breaks only averaged 2.4% more species than reference sites. Using Hill numbers to assess diversity, we found species richness ($q = 0$) and Simpson diversity ($q = 2$) were similar between treated and reference sites, whereas Shannon diversity ($q = 1$) was greater for reference sites due to the presence of locally rare species. Thus, shaded fuel breaks supported a less diverse bee community with a greater abundance of common taxa, whereas reference sites contained more locally rare species. These findings indicate that both shaded fuel breaks and untreated mature forest contribute distinct components to the broader bee community, and that fuel break creation boosts bee abundance in fire-prone conifer forests.

1. Introduction

The historical fire regime of dry coniferous forests in western North America consisted of frequent, low-severity fires supplemented by Indigenous cultural burning practices and led to multi-aged forests with varying degrees of canopy openness (Mallek et al., 2013; Marks-Block and Tripp, 2021; Miller and Safford, 2012; van de Water and Safford, 2011). Fire suppression efforts of the early 20th century altered fire activity within many western forests (Beaty and Taylor, 2001; Marks-Block and Tripp, 2021; Miller and Safford, 2012; Williams et al., 2023) and ultimately contributed to increases in the size and severity of wildfires (Abatzoglou et al., 2021; Dennison et al., 2014; Mallek et al., 2013; Riegel et al., 2006). Despite a decrease in fuels, the size and intensity of wildfires are projected to increase due to climate change (Abatzoglou et al., 2021) and a widespread fire deficit (Parks et al., 2025), requiring management interventions to reduce wildfire risk.

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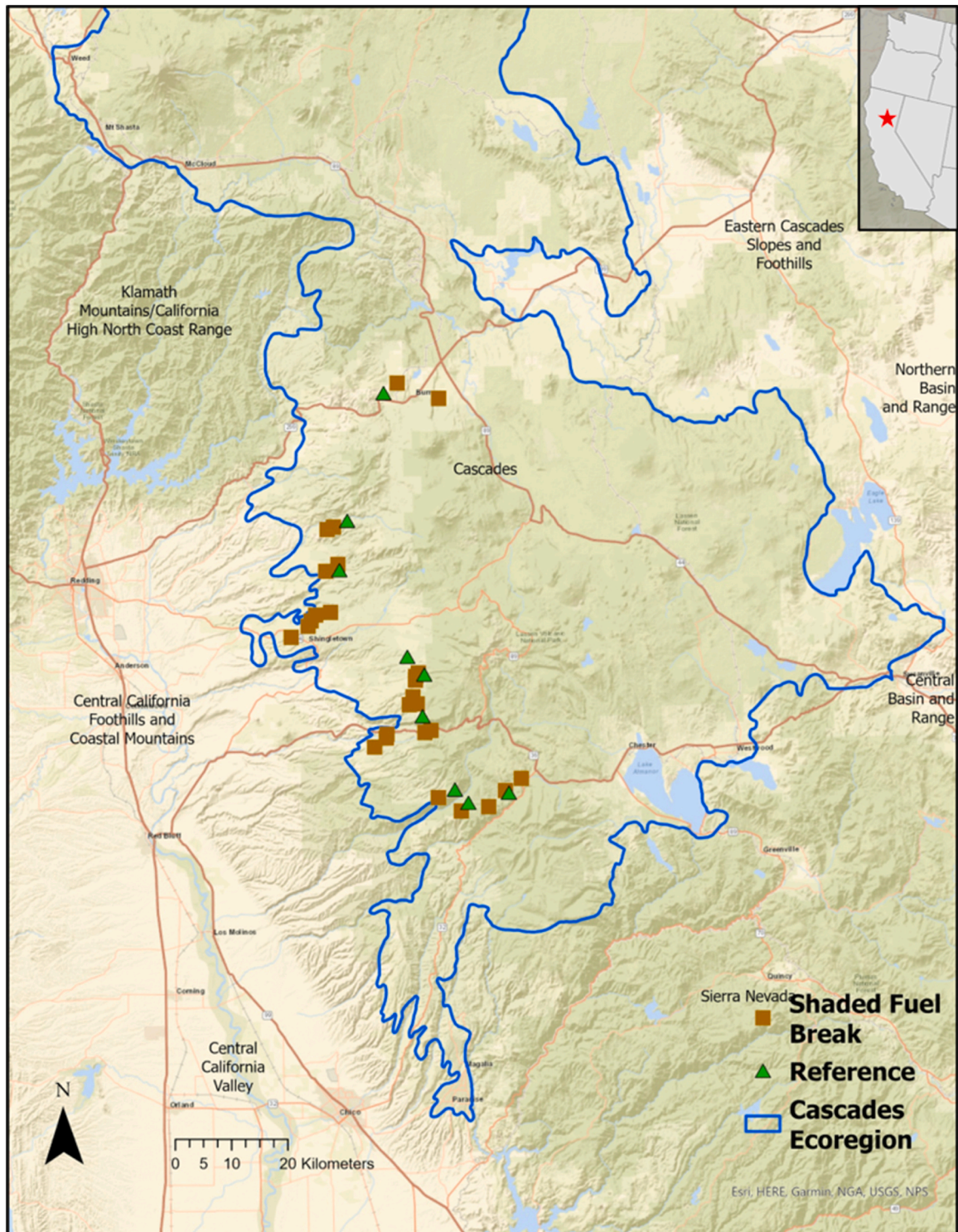


Fig. 1. This research was undertaken in the Cascades Ecoregion (bounded by blue lines) of northeastern California; 27 shaded fuel breaks (brown squares) and 9 mature forest reference sites (green triangles) were sampled for bees, floral resources, and environmental conditions during summer 2023–2024. The red star on the inset map indicates the general study area within the western United States.

Fuel breaks are used as a management tool to decrease wildfire effects by reducing fuel amounts to slow and/or stop the spread of wildfire (Agee et al., 2000; Bajinath-Rodino et al., 2023; Low et al., 2023). Shaded fuel breaks are specific to forests and are created along roads and access points via treatments that retain some large, well-spaced overstory trees while reducing canopy cover and decreasing woody fuels (Agee et al., 2000; Ascoli et al., 2018; Green, 1977). Local conditions (e.g., forest type, elevation) dictate the degree to which fuels are removed and whether machinery is used in the creation of shaded fuel breaks. Despite this variation, shaded fuel breaks can be effective at reducing burn severity relative to adjacent untreated areas while maintaining vegetation health over the long term (Agee et al., 2000; Bajinath-Rodino et al., 2023; Kennedy et al., 2019; Low et al., 2023). Although they have been implemented widely (Kennedy et al., 2019; McKinney et al., 2022; Roche et al., 2024), how shaded fuel breaks influence forest biodiversity remains largely unexplored, even for keystone groups such as pollinating insects.

Insect pollinators are crucial in natural ecosystems for maintaining biodiversity through their pollinating services (Ollerton et al., 2011, 2022). Despite being well-studied in agricultural settings, how forest insect pollinators respond to natural disturbances and management activities has received limited study (Rivers and Ulyshen, 2026; Rivers et al., 2018). Wildfire in forests often creates open conditions that supports insect pollinator communities (Carbone et al., 2019; Mason et al., 2021), including fire-prone forests of western North America (Frank et al., 2026; Galbraith et al., 2019; Ponisio et al., 2016). Similarly, forest management that reduces forest canopy and promotes floral resources and nesting areas can also support diverse insect pollinator communities (Briggs et al., 2024; Fan Brown et al., 2026; Gelles et al., 2022; McDonald et al., 2026; Mitchell et al., 2026; Rivers and Betts, 2021; Roberts et al., 2017; Zitomer et al., 2023). However, limited research has evaluated the degree to which shaded fuel breaks support insect pollinator communities within managed forests, a topic of growing importance given projected increases in fuels management activity (Abatzoglou et al., 2021; Roche et al., 2024).

In this study, we evaluated the extent to which shaded fuel breaks (hereafter, fuel breaks) supported wild bee communities in mixed conifer forests of northern California. We first quantified how stand-scale characteristics, such as canopy openness and the cover of live vegetation, differed between fuel breaks and untreated reference sites. Additionally, we hypothesized that floral resources would differ between fuel breaks and reference sites, and we predicted greater floral richness and abundance in fuel breaks. We also hypothesized that bee communities would differ between treatments, and predicted bee communities in fuel breaks would be characterized by greater abundance, species richness, and diversity, relative to reference sites. Finally, we hypothesized that fuel breaks would differ in the nesting substrates they provide to wild bees, and we predicted that fuel breaks would have greater coverage of bare ground and less coarse woody debris (Antoine and Forrest, 2021; Davis and LaBerge, 1975).

2. Methods

2.1. Study area

We conducted our study during May–August 2023–2024 in the Cascades Ecoregion of northern California (Fig. 1). This region is characterized by a Mediterranean climate with cool, wet winters and warm, dry summers. Annual precipitation averages ~71 cm and ~140 cm on the east and west sides, respectively; in contrast, mean July daily minimum (east: 6.2 °C; west: 5.9 °C) and maximum temperatures (east: 30.8 °C; west: 27.1 °C) are similar (Western Regional Climate Center, 2025). Dominant tree species in this region include Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), lodgepole pine (*Pinus contorta* ssp. *murrayana*), and Jeffrey pine (*Pinus jeffreyi*) with several hardwood tree species (e.g., big leaf maple [*Acer macrophyllum*], oaks [*Quercus* spp.]) and shrubs (e.g., *Ceanothus*, *Arctostaphylos*, *Symphoricarpos*; Skinner and Taylor, 2006).

2.2. Experimental design

We established 36 study sites on privately owned managed forests consisting largely of Douglas-fir and pine (*Pinus* spp.); 27 were treated as fuel breaks 2–9 years prior to sampling (mean: 5 years), with 9 serving as untreated reference sites. The number of sampling sites was constrained by recent logging, large-scale wildfires (e.g., 2021 Dixie Fire), and logistical considerations, leading us to sample fewer reference sites. Although we attempted to include fuel breaks that spanned a broader range of time since treatment, there was insufficient variation in our area to support such a design. All study sites were (1) located along a secondary road, (2) at least 80 m wide, (3) at least 1 km distant from large-scale disturbance (i.e., timber harvest or wildfire) that occurred in the previous 10 y, and (4) situated ≥ 2 km from other sites being sampled to maintain spatial independence. The fuel breaks we evaluated were located in areas with variable logging traffic and ridgelines, and they were treated such that ground fuels were limited and live tree density were reduced relative to untreated surrounding areas (Figure S1). In contrast, reference sites were characterized by $\geq 60\%$ canopy cover (California Forest Observatory, 2020) and experienced no major disturbance for a minimum of 10 y prior to sampling. Therefore, both fuel breaks and reference sites represented operational conditions in the region.

2.3. Measurement of site characteristics

In summer 2023, we established 4 subplots (3 m x 15 m) on each site for hand-netting bees and quantifying floral resources. We typically established 2 subplots on each side of a forest access road; however, we were forced to place all subplots on one side of a road in 10 instances (i.e., 8 fuel breaks, 2 reference sites). In summer 2024, we established 4 additional transects per site, each 35 m in length, to characterize environmental conditions that may have influenced bee communities. We alternated their placement with hand-netting subplots to avoid trampling floral resources. To quantify site-scale characteristics, we recorded all vegetation and ground

cover in contact with a metal stake that was placed vertically every 1 m along the length of each transect from which we calculated percent cover of live vegetation (i.e., shrubs, forbs, grasses, trees, and/or ferns) and ground cover (i.e., bare ground, rock, and/or coarse woody debris). At the same locations, we also recorded the degree of canopy openness (%) using a GRS densiometer, and relative litter depth (cm) given its potential relationship to bee nesting (Antoine and Forrest, 2021) and overwintering sites (Michener, 2007; Williams et al., 2019).

2.4. Floral resource sampling

To quantify floral resources, we counted all flowering species in bloom within each subplot when we hand-netted bees (see below). We used dichotomous keys to identify plants for northern California flora (CalFlora, 2025; Oswald, 2002; Sullivan, 2023); we identified > 95% of the 1437 plants we detected to species. To estimate the average number of flowers available per blooming stem during each hand-netting round, we counted the total number of stems in bloom for each species, and we counted all open flowers on up to 10 stems per species. We then took the average number of flowers per stem, multiplied it by the total number of blooming stems for each species on each subplot. Next, we summed the total number of blooms across the four subplots to obtain a site-level estimate of bloom density during each sampling round, and then multiplied that value by the number of times we recorded floral resources on each sampling site. Because we did not sample all sites equally due to access issues (see below), we standardized floral resources to bloom density per 1 m².

2.5. Bee community sampling

To sample bees, we conducted 3 rounds of hand-netting and 2 rounds of passive trapping each year. Hand-netting and trapping alternated every 2–3 weeks to provide temporally consistent sampling of bee communities. We conducted hand-netting during favorable weather conditions (i.e., 15.5–32.0° C, wind < 19 km/h) by walking at an even pace along one half of each subplot lengthwise for 15 min, and then returning along the other half of the same subplot for an additional 15 min. This resulted in 30 min surveys on each subplot and therefore 2 h of hand-netting per site during each round. We used insect nets (91.4 cm handle, 30.5 cm diameter hoop) to capture bees contacting flowers within subplot boundaries. After netting a bee, we placed it in a vial of 70% ethanol and recorded the plant species from which it was captured. In contrast, we placed each queen bumble bee (*Bombus* spp.) into an empty vial on ice, photographed it, and then released it after hand-netting was completed.

We also used passive trapping to sample bee communities by placing 1 blue vane trap (BVT; Banfield Bio Inc., Woodinville, WA) and a cluster of 3 pan traps (96 ml each; New Horizons, Upper Marlboro, MD) adjacent to each subplot. Each cluster had 1 pan trap painted blue, white, and yellow with fluorescent paint; this yielded 4 BVTs and 12 pan traps per site. We deployed traps after bumble bee queens nest establishment to reduce sampling impacts as much as possible. We filled BVTs with soapy water and pan traps with a 1:3 ratio of propylene glycol to water to reduce evaporation. We set out all traps simultaneously on each site and left them in place for 48 h, rinsing specimens and moving them to 70% ethanol immediately after removal from traps. After each trapping round, we checked traps for the presence of the western bumble bee (*B. occidentalis*), a species of conservation concern. Due to permitting constraints, we did not reset passive traps at 3 sites in 2023 where we trapped this species, although we did sample those sites the following year. In 2024, the Park Fire led to closures during the second round of passive trapping that restricted sampling to $n = 8$ sites (7 fuel breaks, 1 reference) with traps placed out for only half of the typical sampling period (i.e., 24 h). These differences in sampling effort led us to explicitly incorporate sampling effort into our statistical analyses (see below).

2.6. Bee specimen identification

We transferred all specimens to the USDA bee lab at Utah State University, where SB made species determinations using taxonomic keys (Table S1) and reference specimens from the U.S. National Pollinating Insect Collection. Our classifications for family, genus, and subgenus follow Michener (2007) except for some *Lasioglossum* subgenera, which instead follow Gibbs et al. (2012). Bees that could be distinguished from each other morphologically but not to species were separated into morphospecies and given alphanumeric titles; for these, we included the sex with the larger number of morphospecies in species counts to avoid inflating species richness estimates. For specimens that were damaged in a way that prevented confident species-level identification, we report them to the genus level.

2.7. Statistical analysis

We conducted all statistical analyses using the R statistical environment (v4.5.1; R Core Team, 2025). We first summarized site-scale environmental factors (i.e., canopy openness, bare ground, shrub cover, litter cover, coarse woody debris) to assess how they were influenced by treatments. Next, we fit a generalized linear mixed model (GLMM) using the package 'glmmTMB' (Brooks et al., 2017; McGillicuddy et al., 2025) to assess the effect of treatment on bloom density. We modeled bloom density as realizations of a Tweedie distribution because we had true zeros in otherwise positive, continuous data (Dunn and Smyth, 2005). We included treatment and year as covariates to account for variation across sites within the same treatments, and sampling site as a random effect. In this model, we did not include a sampling offset because we standardized bloom density by area sampled. To assess treatment effect on richness of plant species in bloom, we used the package 'glmmTMB' to fit a negative binomial GLMM with a log link. We included treatment and year as covariates to account for variation across sites within treatments, sampling site as a random effect, and an offset for sampling effort because sampling was uneven due to several factors (e.g., wildfire closures, wildlife disturbance). We assessed

model fit for all models using simulated quantile residuals from the package ‘DHARMA’ (Hartig, 2022). Because of the log-link function, we exponentiated estimates and confidence intervals to present multiplicative differences ($\exp(\hat{\beta})$) on the scale of the response variables.

We used the ‘iNEXT’ package (Chao et al., 2014; Hsieh et al., 2024) to estimate the diversity of flowering plant species in bloom. This method uses Hill numbers (q) to give different weights to groups of species according to their relative abundance (Chao et al., 2014; Hsieh et al., 2016): $q = 0$ is equivalent to species richness, $q = 1$ is equivalent to Shannon diversity, and $q = 2$ is equivalent to Simpson diversity (Chao et al., 2014; Roswell et al., 2021). Additionally, we calculated sample coverage to assess sampling completeness and estimate the proportion of species missing from a particular sample (Chao et al., 2014; Roswell et al., 2021).

To assess the effect of treatment on bee abundance, we used the package ‘glmmTMB’ to fit a negative binomial GLMM with a log link to account for high dispersion in the data. We included treatment (2 levels [fuel break, reference site]) as a fixed effect, and bloom density (continuous), year (2 levels), amount of shrubs (%), amount of coarse woody debris (%), and amount of shrubs along forest edge transects (%) as covariates to account for variation across sites. We included sampling site as a random effect, and we used a sampling effort offset. Because bee capture rates varied by sampling method (Sampognaro, 2025), we added sampled method to the abundance model as a fixed effect to adjust for effort after accounting for differing capture rates across sampling approaches. Because residuals plots showed variability in dispersion across capture methods, we also allowed the dispersion parameter to vary by capture method.

To assess treatment effects on bee richness, we used individual-based rarefaction by standardizing richness to the lowest number of individuals captured for each year $\times$ site $\times$ sampling method combination (minimum range: 1–14). We then used bootstrapping to resample individuals at each year, site, and sampling method, totaling richness over all sampling methods, and fitted the same GLMM for each bootstrap resample to estimate standard errors and confidence intervals for the treatment effect of interest. For the richness

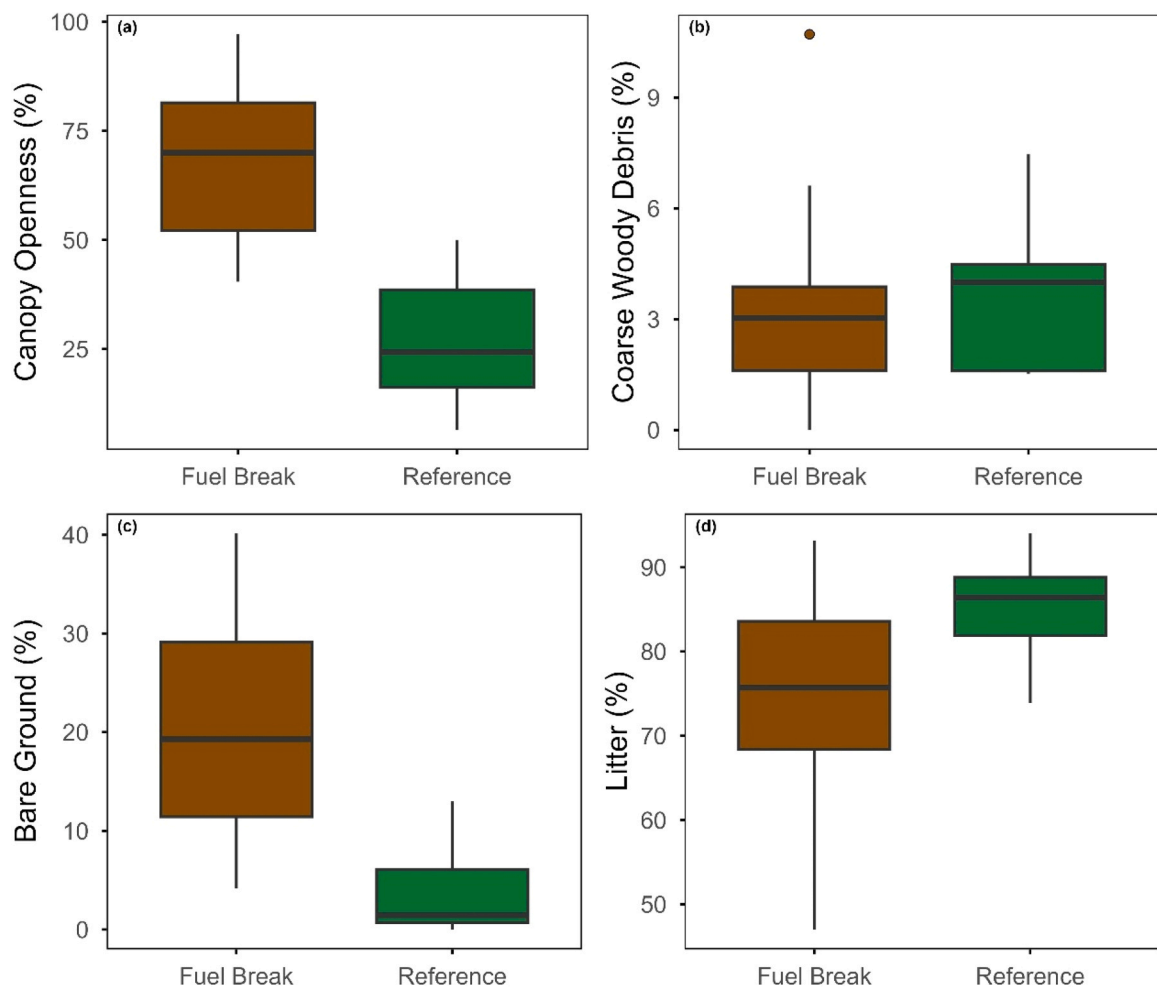


Fig. 2. Boxplots illustrating differences in local environmental factors by treatment including (a) canopy openness, (b) bare ground, (c) coarse woody debris, and (d) litter cover. Estimates of canopy openness and bare ground were greater in shaded fuel breaks whereas estimates of coarse woody debris and litter cover were greater in untreated reference sites.

model, we fitted a zero-truncated generalized Poisson model to account for the absence of zeros in our richness data, and we included treatment and year as fixed factors with site as a random effect. We included bloom density, plant species richness (continuous), and percent coarse woody debris as covariates to account for variation across sites. To account for large differences in scale among the variables and to improve model convergence, we standardized all covariates. In addition to modeling abundance and richness while controlling for vegetation characteristics, we also quantified bee diversity across treatments using Hill numbers and the iNEXT package (Chao et al., 2014; Hsieh et al., 2024) as described above for floral resources.

Finally, we used two complementary approaches to quantify how bee species composition varied between treatments. In the first, we used the R package ‘indicspecies’ (De Caceres and Legendre, 2009) to assess which species were associated with the treatments. This analysis provides an indicator value for species highly associated with a treatment, based on two components: specificity (i.e., the exclusivity of a species within a particular treatment) and fidelity (i.e., the frequency of a species belonging to a particular treatment; De Caceres and Legendre, 2009). In the second approach, we used nonmetric multidimensional scaling (NMDS) in the ‘vegan’ package (v2.6–10; Oksanen et al., 2025). This allowed us to investigate community compositional difference via the use of estimating Bray-Curtis distance measures for 4 ordinations. We plotted sampling sites at the level of both species and genera to visualize how bee communities clustered due to treatments. We used a similar approach to examine patterns of functional traits at the generic level. Prior to analysis, we removed 58 rare species from the species-level data and 8 genera from the genus-level data that occurred at < 3% of sites. We log-transformed species data (Jackson et al., 2012; Legendre and Gallagher, 2001; McCune and Grace, 2002; Sgarbi et al., 2020) due to large differences in the number of individuals captured among species, and stress plots confirmed that NMDS plots accurately represented the dissimilarity between treatments. We performed ordinations separately for nesting and sociality traits, using Zitomer (2023) to assign traits; for species lacking nesting information, we assigned it the most common nesting trait for its genus via the same database. We then plotted sites in “nesting trait space” and “sociality trait space” to quantify differences in these characteristics for bees captured in the two treatments. We included this analysis to determine if variation in community composition was associated with nesting functional traits and, therefore, implied differences in the nesting resources available or degree of sociality of bees using the different treatments.

3. Results

3.1. Treatment effects on site characteristics

We found strong differences between site-scale characteristics in fuel breaks and reference sites (Fig. 1). Canopy openness was $2.4 \times$ greater in fuel breaks (mean = 68.0%, SD = 17.4%) than in reference sites (mean = 28.4%, SD = 13.4%; Fig. 2a). Bare ground was approximately $6 \times$ greater in fuel breaks (mean = 24.3%, SD = 12.1%) than in reference sites (mean = 4.1%, SD = 4.3%; Fig. 2b), whereas coarse woody debris was only $1.2 \times$ greater in reference sites (mean = 3.9%, SD = 1.7%) compared to fuel breaks (mean = 3.2%, SD = 2.2%; Fig. 2c). We found that litter cover was similar between treatments, with reference sites having $1.2 \times$ greater litter cover (mean = 86.8%, SD = 6.0%) than fuel breaks (mean = 71.6%, SD = 12.5%; Fig. 2d).

3.2. Treatment effects on floral resources

We detected 114 plant species in bloom that were restricted to fuel breaks and 8 unique plant species in bloom at reference sites; 35 species were shared across both treatments (Table S2). Of these, 89% were classified as native species and 11% were non-native

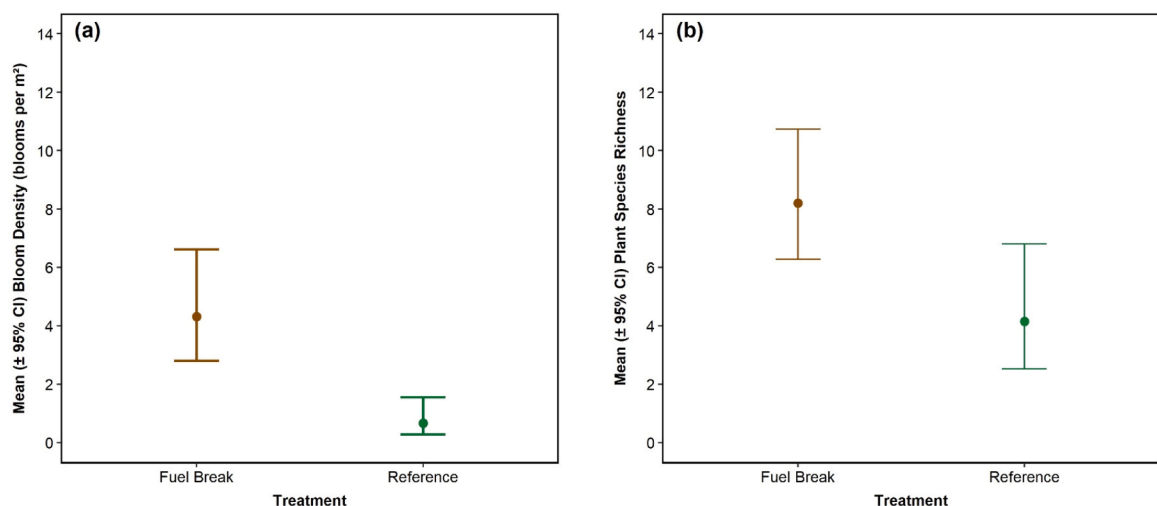


Fig. 3. Model estimated means ($\pm$ 95% CI) for (a) bloom density and (b) blooming plant species richness between shaded fuel breaks and untreated reference sites.

(Table S2). Fuel breaks had approximately $6.5 \times$ greater bloom density ($\exp(\hat{\beta}) = 6.45$; 95% CI: [2.59, 16.10]) compared to reference sites (Fig. 3a), and they supported approximately twice the richness of flowering plant species in bloom ($\exp(\hat{\beta}) = 1.97$; 95% CI: [1.13, 3.46]) compared to reference sites (Fig. 3b). Floral richness did not change between years; however, bloom density decreased by an estimated 71% in the second year of sampling (2024 effect: $\exp(\hat{\beta}) = 0.29$, 95% CI: [0.18, 0.47]), and this decrease was observed in both fuel breaks and reference sites (Figure S2).

When assessing diversity using Hill numbers, sample coverage for flowering plants in bloom was high in fuel breaks (97%), with a lower estimate for reference sites (85%). When comparing plant diversity between treatments and standardizing sample size to the smaller of both samples (i.e., $n = 43$ flowering plant species, reference sites), estimates of all three Hill measures were greater in fuel break than in reference sites (Table S3, Figure S3) with non-overlapping 95% CIs. The estimate of rarified species richness (Hill number: $q = 0$) was lower in fuel breaks (82 species; 95% CI: [78.5, 85.4]) than observed species richness (149 species). In reference sites, the opposite occurred; estimated species richness (57 species; 95% CI: [44.1, 70.0]) was greater than observed species richness (43 species; Table S3, Figure S3).

3.3. Overview of bee communities

During the 2023–2024 field seasons, we collected 17,124 bees representing 5 families, 33 genera, and 188 species (Table S4). More

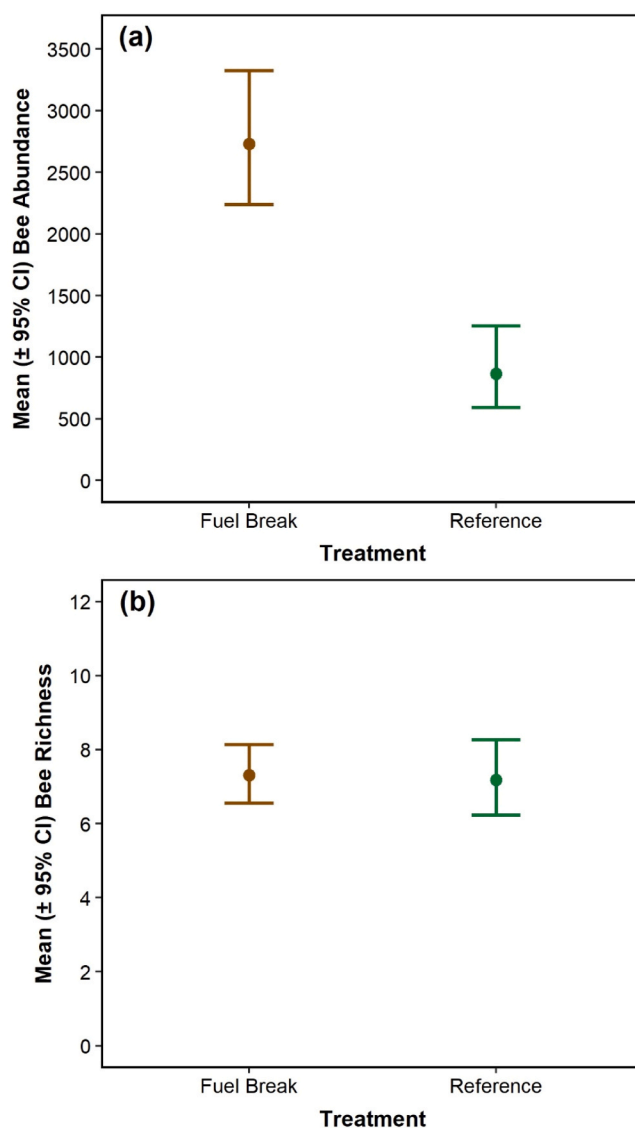


Fig. 4. Model estimated means ($\pm$ 95% CI) for (a) mean bee abundance and (b) mean bee species richness between shaded fuel breaks and untreated reference sites.

than twice as many bees were collected in 2023 as in 2024 (12,393 and 4731 individuals, respectively), likely due to a substantial reduction in flowering resources in 2024 (Figure S2). Overall, 16,122 bees were collected in 27 fuel breaks (mean individuals per site: 597 ± 395 SD), and 1002 bees were collected in 9 reference sites (mean individuals per site: 111 ± 63 SD). Species richness across both treatments was greater in 2023 relative to 2024 (157 vs. 134 species, respectively) with 54 species unique to 2023, 31 species unique to 2024, and 103 species shared between years. Fuel breaks had an observed bee species richness of 183 species (mean bee richness per site: 40 ± 10 SD), whereas reference sites had an observed richness of 74 species (mean bee richness per site: 21 ± 8 SD). Overall, 114 bee species were restricted to fuel breaks, 5 bee species were restricted to reference sites, and 69 bee species were shared between treatments. Across both treatments and years of sampling, hand-netting consistently yielded fewer bee specimens than passive trapping (Table S5).

The most abundant genera we collected were *Bombus* (6771 individuals, 13 species), *Lasioglossum* (4246 individuals, 21 species), and *Halictus* (3810 individuals, 5 species), which together comprised approximately 87% of the total captures. We caught 10 western bumble bees (3 queens, 7 workers) in passive traps across both treatments; none were detected during hand-netting. We rarely captured the western honey bee (*Apis mellifera*), with only with 51 individuals captured at 13 fuel breaks and 2 individuals captured at 2 reference sites.

3.4. Treatment effects on bee communities

After controlling for site characteristics, our data supported the hypothesis of greater bee abundance in fuel breaks (contrast: fuel breaks – reference sites; $z = 5.24$, $p < 0.001$). We estimated that mean bee abundance, averaged over year and trap type, was approximately $3.2 \times$ greater (95% CI [2.05, 4.85]) in fuel breaks (mean: 2728 individuals per site [95% CI: 2238, 3326]) relative to reference sites (mean: 864 individuals per site [95% CI: 595, 1255]; Fig. 4a), after accounting for site-scale factors. For coarse woody debris, we estimated a decrease in mean bee abundance of 13% with a 1% linear increase in woody debris cover ($\exp(\hat{\beta}) = 0.87$, 95% CI: [0.81, 0.95]).

After accounting for differences in bees caught across sites using individual rarefaction, we estimated a relatively small difference in mean species richness between treatment and reference sites. When holding plant species richness and coarse woody debris cover constant, we found that fuel break sites had, on average, only 2.4% more species than reference sites ($\exp(\hat{\beta}) = 1.024$, 95% bootstrapped CI: [0.91, 1.16]), given the data (Fig. 4b). Bee richness was not meaningfully linked to bloom density after accounting for the other variables in the model including the treatment effect, which was associated with bloom density. We estimated that, for each additional 100 blooms in the 45 m² survey area, bee richness was reduced by ~12%, on average, but could be as much as an 82% increase or a 60% decrease given uncertainty in the estimate (95% CI of multiplicative effect: [0.40, 1.82]). Bee richness had a negative association with coarse woody debris, but with very high uncertainty ($\hat{\beta} = -0.71$, 95% CI: [-3.45, 0.78]). Rarefied bee species richness was estimated to be about 29.5% lower in 2024 relative to 2023, consistent with a decrease in bloom density and bee abundance in 2024 (contrast: 2024 / 2023: $\exp(\hat{\beta}) = 0.71$; 95% CI: [0.63, 0.78]).

Sample coverage estimates for bees, calculated using the bootstrap resampling method, were high and estimated at $> 98\%$ for both fuel breaks and reference sites. When comparing extrapolated bee diversity between treatments after rarefaction to the smaller of both samples (i.e., $n = 1002$ bees captured at reference sites), bee diversity estimates for all three Hill measures were greater at reference sites, yet bootstrapped 95% confidence intervals overlapped between treatments for species richness and Simpson diversity (Table 1, Fig. 5).

Using indicator species analysis, we found that multiple species were characteristic of fuel breaks. We detected *Lasioglossum incompletum* (indicator value [IV] = 0.90, specificity = 1.00, fidelity = 0.82, $p = 0.001$) and *Xylocopa tabaniformis* (IV = 0.86, specificity = 1.00, fidelity = 0.74, $p = 0.005$) exclusively in fuel breaks. We also classified *Halictus farinosus* (IV = 0.94, specificity = 0.99, fidelity = 0.89, $p = 0.003$), *Melissodes lupina* (IV = 0.95, specificity = 0.94, fidelity = 0.96, $p = 0.001$), *Hoplitis albifrons* (IV = 0.82, specificity = 0.86, fidelity = 0.78, $p = 0.02$), and *Lasioglossum kneri* (IV = 0.74, specificity = 0.92, fidelity = 0.60, $p = 0.04$) as indicator species for fuel breaks. In contrast, *Osmia pentstemonis* was the lone indicator species we detected for reference sites (IV = 0.75, specificity = 1.00, fidelity = 0.56, $p = 0.002$); it was restricted to reference sites, and found it in approximately half of the reference sites we surveyed.

Table 1

Observed and estimated bee diversity using Hill numbers for shaded fuel breaks and untreated reference sites in northern California sampled May through August of 2023–2024. We found that reference sites had greater values for estimated species richness and estimated Shannon diversity, with no clear difference in estimated Simpson diversity between treatment groups. Hill numbers use the parameter q to give different weights to groups of species according to rarity; $q = 0$ gives leverage to rare species, $q = 1$ gives leverage to species by proportional abundance with balanced influence from rare and common species, and $q = 2$ gives greater leverage to dominant species.

Treatment	Diversity measure	Hill #	Observed richness	Estimated diversity	Lower 95% CI	Upper 95% CI
Shaded fuel break	Species richness	$q = 0$	183	92.6	89.4	95.7
	Shannon diversity	$q = 1$	–	13.2	12.8	13.6
	Simpson diversity	$q = 2$	–	6.0	5.8	6.1
Reference	Species richness	$q = 0$	74	97.1	81.9	112.3
	Shannon diversity	$q = 1$	–	15.4	13.7	17.1
	Simpson diversity	$q = 2$	–	6.6	5.8	7.4

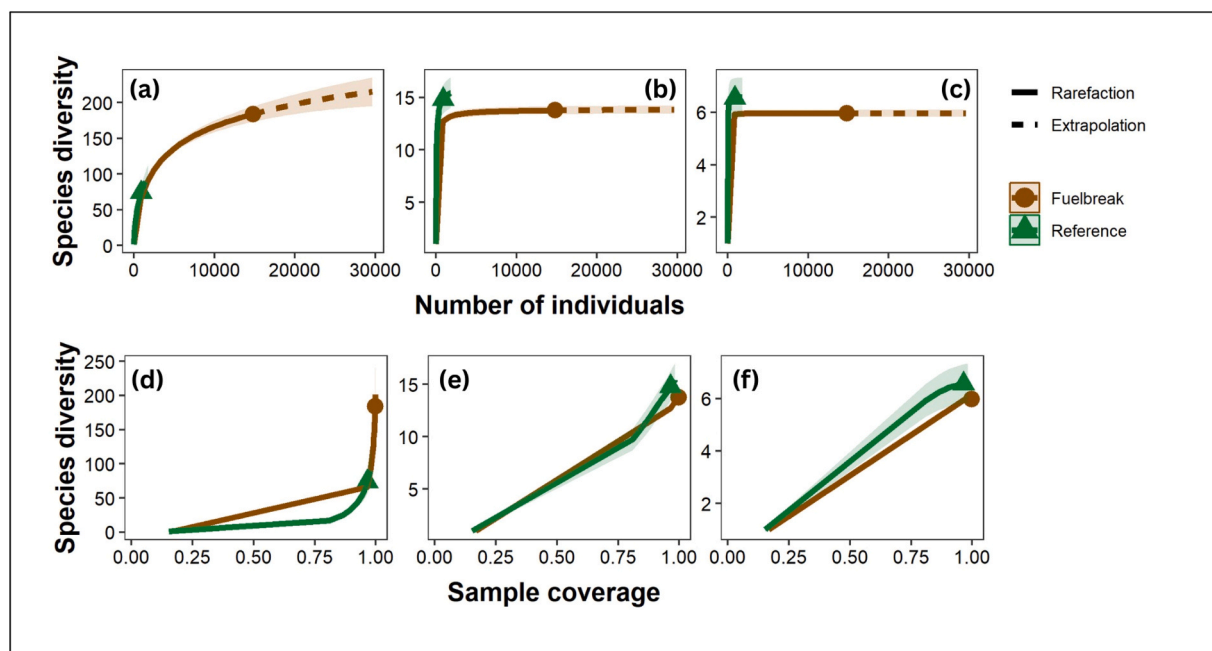


Fig. 5. Sample-size-based (a–c) and coverage-based (d–f) rarefaction/extrapolation plots of bee species diversity based on Hill numbers for shaded fuel breaks (brown circles) and untreated reference areas (green triangles). Plots a–c show bee species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$) and are based on the number of individuals; plots d–f show sample coverage. Coverages in curves (d–f) were extrapolated to 98.3% for shaded fuel breaks and to 98.2% for reference sites.

When using ordination to characterize bee communities at the generic level, we found that species in the genus *Osmia* were strongly associated with reference sites; in contrast, *Megachile*, *Hoplitis*, *Halictus*, and *Melissodes* were strongly associated with fuel breaks (Fig. 6). There was a reasonable fit for the ordination distance compared to the observed dissimilarity (non-metric fit: $R^2 = 0.961$, linear fit: $R^2 = 0.857$, stress: 0.196) at the generic level. When characterizing communities at the species level, we found more variation in bee communities across reference sites than fuel breaks (Figure S4), with the stress plot showing a reasonable fit for the ordination distance compared to the observed dissimilarity (non-metric fit: $R^2 = 0.988$, linear fit: $R^2 = 0.961$, stress: 0.111). This analysis found that species were shared between treatments; of these, two species (i.e., *Halictus farinosus*, *Melissodes lupina*) had a stronger association with fuel breaks whereas two other species (i.e., *Bombus melanopygus*, *Lasioglossum anhypops*) had a stronger association with reference sites. Finally, when we visualized sites in trait-space, we observed that fuel breaks represented a subset of reference sites (Figure S5a). Fuel breaks mainly contained species with ground-nesting traits, and reference sites contained species with ground, stem, and cavity-nesting traits. When considering sociality, we found that fuel break communities had increased primitively eusocial, social, and kleptoparasitic species, whereas reference sites had several social classes but tended to have a stronger association with solitary and social species (Figure S5b).

4. Discussion

Our study found that fuel breaks in northern California conifer forests supported a diversity of wild bees, and these areas contained more individuals, though not more species, than reference sites. Our compositional analysis found species with diverse natural histories in fuel breaks, some of which were not shared with reference sites. This finding, along with estimates of bee abundance, suggests that fuel breaks play an important role in providing habitat for wild bees in managed conifer forests. Indeed, the abundance of dominant bee species in a community can drive pollination services, and abundance may be better than species richness when considering ecosystem function (Winfree et al., 2018, 2025). Moreover, dominant species in a community can enhance pollination through greater floral visitation rates, increased pollen transfer, and more consistent interactions between bees and flowering plants (Winfree et al., 2015). In this context, fuel breaks are important for supporting wild bees and the pollination services they provide in conifer forests.

Although reference sites supported fewer bees overall, they were more diverse when assessed via measures of species richness and Shannon diversity, which contributed to the differences in community composition between treatments. This finding suggests that fuel breaks and reference sites together provide important habitat for the broader bee community, in addition to other areas known to be favorable to bees, such as roadside areas (Hanula et al., 2016) and regenerating stands (Briggs et al., 2024; Rivers and Betts, 2021; Roberts et al., 2017; Zitomer et al., 2023). The different bee assemblages found in fuel breaks and reference sites likely reflect variation in floral resources and nesting substrates required by wild bees, both of which were altered by the creation of fuel breaks. For example,

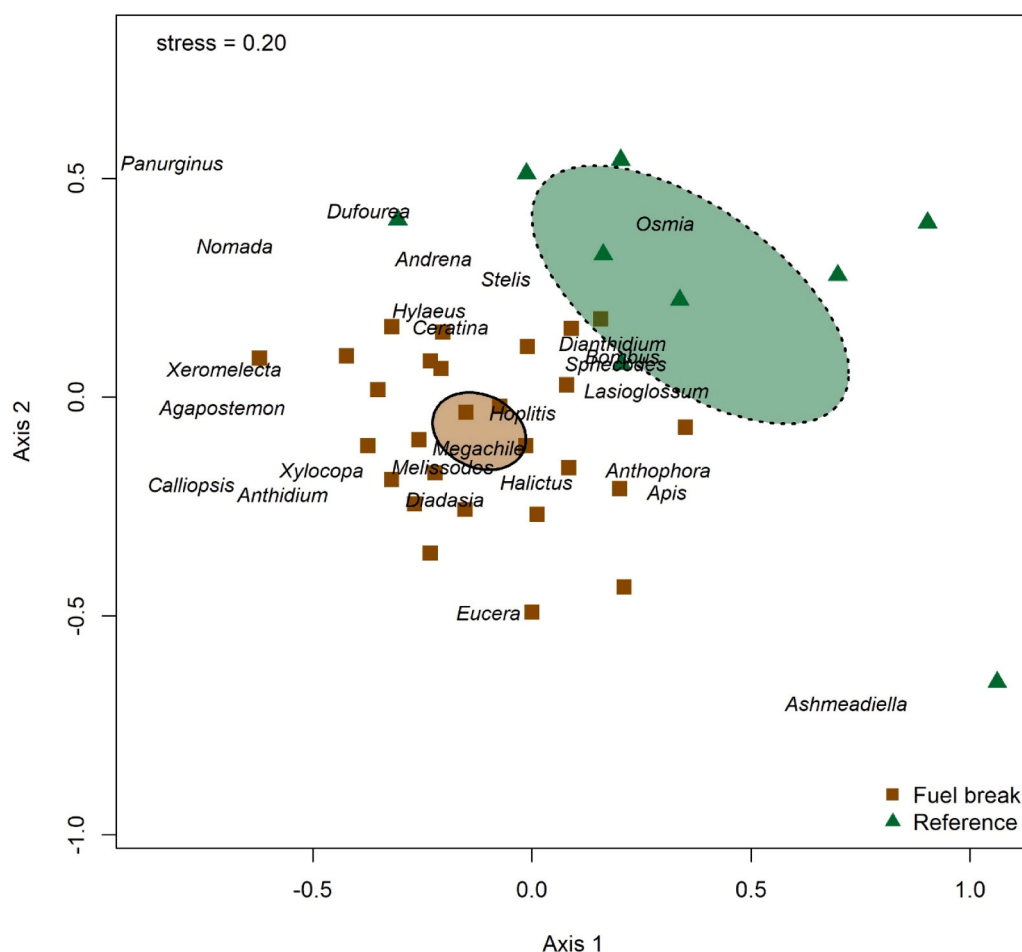


Fig. 6. Nonmetric multidimensional scaling (NMDS) plot with shaded fuel breaks (brown squares, brown ellipse) and untreated reference sites (green triangles, green ellipse). Genera stress values are shown in black text by genus name, with reference sites closest in space to the genus *Osmia*, which represent cavity nesting species, and shaded fuel breaks closest in space to the genera *Megachile*, *Melissodes*, *Halictus* and *Hoplitis*, most of which are ground nesting species. The lack of overlap of the two ellipses indicates strong differentiation in community composition for genera between shaded fuel breaks and untreated reference sites.

fuel breaks have decreased canopy cover through the removal of overstory trees which, in turn, increases light availability for flowering plants in the understory (Agee et al., 2000; Ascoli et al., 2018). This pattern was evident in our study, as fuel breaks had greater canopy openness and more floral resources when compared to reference sites. Species richness of blooming flowering plants and measures of floral diversity were also greater in fuel breaks; thus, the greater abundance of bees in fuel breaks is likely due to greater floral availability and/or floral diversity (Doublet et al., 2022; Gerner and Sargent, 2022; Hyjazie and Sargent, 2022; Potts et al., 2003).

In addition to having greater floral resources, we also found that fuel breaks had more bare ground and less coarse woody debris than reference sites, likely providing nesting opportunities for the ground-nesting species that typically dominate bee communities (Cane and Neff, 2011; Harmon-Threatt, 2020). For example, nesting traits of bees in reference sites included genera with ground-, stem-, and cavity-nesting species; in contrast, bees captured in fuel breaks were limited largely to ground-nesting taxa. Additionally, several of the indicator species identified for fuel breaks were classified as ground-nesting species (Antoine and Forrest, 2021; Danforth, 2002), suggesting bare ground within fuel breaks may be used for nesting. However, other indicator species for fuel breaks nest in excavated woody materials (*Xylocopa tabaniformis*; Stephen et al., 1969) or pre-existing cavities/stems (*Hoplitis albifrons*; Sedivy et al., 2013), so shaded fuel break sites may also support wood-nesting species. Alternatively, these species may have nested elsewhere and instead visited fuel breaks to consume floral resources. In contrast, the lone indicator species for reference sites, *Osmia pentstemonis*, uses pithy stems for nesting (Cane et al., 2007), potentially indicating a greater presence of this nesting resource in untreated areas. We note that although we detected the western bumble bee in both treatments, reference sites may better serve as underground overwintering sites for bumble bee queens because litter provides protection against extreme heat and cold (Martin et al., 2023; Williams et al., 2019). Therefore, it is worth assessing how forest management may support overwintering queens of this species. More broadly, our findings indicate that bee communities of fuel breaks differed relative to those in reference sites, and those

differences may have been driven by nesting requirements.

We found that fuel breaks supported diverse and abundant bee communities, which compliments other studies that found bee communities respond positively to canopy reduction in dry conifer forest. For example, research undertaken in pinyon-juniper woodlands of Arizona found greater bee abundance and species richness in thinned areas, with stronger effects when thinning was combined with prescribed fire (Nyoka, 2010). More recently, Davies et al. (2023) found that bee communities were more diverse in thinned ponderosa pine stands relative to untreated reference stands, a pattern also observed for bumble bees in thinned conifer forest in California, either alone or when combined with prescribed fire (Cole et al., 2025). Our findings are concordant with studies in other regions where bee communities respond positively to canopy reduction in both deciduous (Milam et al., 2018; Roberts et al., 2017) and coniferous forests (Briggs et al., 2024; Taki et al., 2013; Zitomer et al., 2023). Additional studies have found that untreated stands support wild bee communities in dry conifer forests (Davies et al., 2023; Gelles et al., 2022; Mitchell et al., 2026); therefore, closed canopy stands may play larger roles than previously realized in supporting wild bees, and these areas should be considered in pollinator conservation efforts.

5. Conclusions

Growth in the extent and severity of recent wildfires (Abatzoglou and Williams, 2016), along with projected increases in wildfire activity (Abatzoglou et al., 2021), have led to increased calls for managing fuels to reduce wildfire risk (Pausas and Keeley, 2021; Stephens et al., 2020). Fuel reduction treatments, including fuel breaks, are effective in moderating fire behavior and restoring dry conifer forests to historical disturbance regimes (Agee and Skinner, 2005; Kalies and Yocom Kent, 2016; Gannon et al., 2023; Low et al., 2023). Our study has demonstrated that fuel breaks in conifer forests are characterized by diverse wild bee communities and abundant floral resources, and they may also serve as areas for nesting. It also has shown that untreated reference stands support distinct and locally rare taxa. Together, this suggests that shaded fuel breaks can support wild bee communities while also reducing wildfire risk, indicating a “win-win” scenario whereby fuels management results in habitat creation for insect pollinators. However, we have an incomplete understanding of how fuel breaks are used by pollinating insects, so long-term studies that evaluate bee nesting within fuel breaks and quantify temporal variation in floral resource quality are needed, especially investigations focused on native and non-native plants (Merriam et al., 2006). Given that floral resource availability appears to drive bee use of fuel breaks, seeding native flowering plants into disturbed ground within fuel breaks may increase their value to pollinators (McDonald et al., 2026). Additionally, investigations that assess the long-term response of other pollinating insect groups – including flies, beetles, and moths and butterflies – to the creation and maintenance of fuel breaks will be particularly valuable, and they will broaden our understanding of how pollinator conservation may be compatible with forest management undertaken to reduce wildfire risk.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2026.e04431](https://doi.org/10.1016/j.gecco.2026.e04431).

Data availability

Data will be made available on request.

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