Temporal and Geographic Variation in the Effects of Wildfire and Forest Restoration on Bee and Social Wasp (Hymenoptera: Aculeata) Communities in Sierra Nevadan and Southwestern Conifer Forests of the United States

By

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DISSERTATION

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Dedication

I dedicate this dissertation to my mother, Marcia Zukosky. She ensured me a childhood full of numerous adventures to many of America’s natural wonders. If not for these experiences, I would not have chosen a career in ecology. I am forever grateful for her love, wisdom and support. I am lucky to be her son.

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Dissertation abstract

The introduction of livestock and wildfire suppression beginning in the mid-nineteenth century in the western United States have homogenized the structure of its mixed-conifer forests, where stands are unnaturally dense and exhibit higher rates of canopy and shrub cover compared to pre-suppression conditions. The increased continuity between surface fuels and tree crowns combined with climate change-driven droughts have exacerbated the severity—both in intensity and extent—of recent wildfires in the western US. Changes in vegetation and surface fuels resulting from altered disturbance regimes and human activities (e.g., silvicultural practices) are likely to influence the abundance and diversity of arthropod taxa and functional feeding guilds, many of which provide ecological services to forest ecosystems and surrounding landscapes. However, basic information on the community-level responses of most insect guilds to large-scale fire events is unavailable, despite increases in their occurrence in recent years. Similarly, thorough documentation of changes in insect community assemblages and diversity following various forest restoration efforts to prevent unnaturally large or severe wildfire is lacking for several ecoregions of the southwestern US. For this dissertation, I documented the community-level responses of bees (Hymenoptera: Apiformes) and yellowjacket wasps (Hymenoptera: Vespidae, Vespinae) to changes to forest structure following wildfire and restoration treatments in montane, coniferous forests of California and New Mexico, USA. Objectives and major findings from individual dissertation chapters are summarized below.

Chapter one: I documented the early successional responses of bee communities and individual bee functional groups to the 2020 Creek Fire, a large-scale disturbance that burned several thousand hectares of submontane, montane, and upper montane mixed-conifer forest within the Sierra National Forest, California. The objectives of this research were to document post-fire relationships between stand-level burn severity and local bee diversity within these different biotic zones. I further determined whether these relationships' general patterns varied with time (one vs. two years post-fire) or along an elevational gradient. Across all biotic zones, bee communities were generally more abundant and speciose in burned versus unburned stands one year post-fire, regardless of local burn severity. During the following summer, however, bee abundance and species richness were generally highest in stands that burned at severities more representative of the local ecosystem's natural fire regime. We observed similar patterns between the abundance of individual bee functional groups and local burn severity within individual biotic zones and between sample years. Variation in local community assemblages also increased with fire severity and time since fire across all biotic zones. Increases in grass or shrub layers between years were likely correlated with changes in local bee abundance and diversity, particularly at lower elevations. Overall, our findings suggest that stand-level relationships between post-fire bee abundance or diversity and fire severity may vary along elevational gradients or among different forest types found within a large-scale wildfire boundary. The pattern of these relationships may also change between the early, successive years following these disturbances. Importantly, our observations suggest low to moderate intensity fire characteristic of prescribed burns used to restore or maintain the function of lower elevation, mixed-conifer forests in the Californian Sierra Nevada mountains will likely benefit bee communities at both local and regional scales.

Chapter two: Regional-scale reductions in fire activity associated with centuries of logging and livestock grazing in the southwestern United States have contributed to the encroachment of pinyon pine and juniper (PJ) into high-elevation forests historically dominated by ponderosa pine. It is unclear whether alterations in overstory structure and ground cover conditions

following PJ encroachment into ponderosa pine forests influence the diversity or community compositions of ecologically important insect groups like wild and native bees. I documented bee community and functional group responses to 1) variation in ponderosa pine cover within a montane PJ-ponderosa pine forested landscape in Northern New Mexico, and 2) stand-thinning operations used to restore a ponderosa pine-dominant overstory across the broader landscape. Overall, bees were significantly more abundant in stands with moderate to high amounts of ponderosa pine cover in comparison to stands that were dominated by pinyon pine and juniper. However, neither bee diversity nor local community structures were significantly affected by variation in overstory tree composition, possibly due to the relative uniformity in canopy structure and ground cover conditions across the study site. While local bee abundance may be reduced in stands with high amounts of PJ cover, these findings suggest that PJ encroachment likely does not negatively impact bee communities residing in forested landscapes historically dominated by ponderosa pine in this ecoregion. Regardless, management practices that reduce canopy closure, maintain or increase ponderosa pine dominance, and preserve or create key habitat features (snags, bare soil patches, and floral resources) are likely to benefit wild bees in these ecosystems.

Chapter three: Documentation of the community-level responses of social yellowjacket wasps to wildfire in coniferous forests of the western United States is lacking, despite their ubiquitous distribution, ecological function and occasional pest status within these ecosystems. I sampled the local yellowjacket community along a burn severity gradient in montane, mixed-conifer stands located within various fire boundaries that occurred between 2015-2020 in the Californian Sierra Nevada mountains. I determined: 1) how post-burn patterns in yellowjacket abundance and diversity changed over time; and 2) how post-burn yellowjacket abundance and

diversity varied along a burn severity gradient within individual fire boundaries. Regardless of burn severity, wildfire significantly reduced yellowjacket abundance and species richness during the immediate (≤ two) years following stand disturbance, possibly due to flame-induced wasp mortality combined with the destruction of above-ground foraging, nesting and overwintering substrates. Stands that burned at high severity within older fire boundaries had high rates of shrub and grass cover, and were predominantly inhabited by large numbers of pestiferous *Vespula pennsylvanica* wasps. Forest-obligate yellowjacket species were generally only collected in unburned stands or in locations that burned at relatively low severity. Combined, these results suggest unnaturally high severity fire within these forests might facilitate increases in pestiferous yellowjacket populations due to favorable stand conditions. In contrast, lower severity burns characteristic of prescribed fire used to restore or maintain the function of mixed-conifer forests in the Central Sierra Nevada may provide the added benefit of short-term reductions in unwanted yellowjacket population levels in areas of concern.

Contents

Chapter one: Early successional patterns of wild bees (Hymenoptera: Apoidea) to an extreme wildfire event in the central Sierra Nevada Mountains of California

Abstract

We documented the early successional responses of bee communities and individual bee functional groups to the 2020 Creek Fire, a large-scale disturbance that burned several thousand hectares of submontane, montane, and upper montane mixed-conifer forest within the Sierra National Forest, California. Our primary objective was to document post-fire relationships between stand-level burn severity and local bee diversity within these different biotic zones. We further determined whether these relationships' general patterns varied with time (one vs. two years post-fire) and along an elevational gradient. Across all biotic zones, bee communities were generally more abundant and speciose in burned versus unburned stands one year post-fire, regardless of local burn severity. Increased availability of various foraging resources or nesting substrates following flame-induced reductions in canopy closure or surface fuels likely contributed to these local differences in bee abundance or diversity between burned versus unburned areas. During the following summer, however, bee abundance and species richness were generally highest in stands that burned at severities more representative of the local ecosystem's natural fire regime. We observed similar patterns between the abundance of individual bee functional groups and local burn severity within individual biotic zones and between sample years. Variation in local community assemblages also increased with fire severity and time since fire across all biotic zones. Increases in grass or shrub layers between years were likely correlated with changes in local bee abundance and diversity, particularly at lower elevations. Overall, our findings suggest that stand-level relationships between post-fire bee abundance or diversity and fire severity may vary along elevational gradients or among

different forest types found within a large-scale wildfire boundary. The pattern of these relationships may also change between the early, successive years following these disturbances. Importantly, low to moderate intensity fire characteristic of prescribed burns used to restore or maintain the function of lower elevation, mixed-conifer forests in the Californian Sierra Nevada mountains will likely benefit bee communities at both local and regional scales. Future studies that determine the optimal fire frequencies of these forest types for increasing or maintaining favorable habitat conditions for bees will help to refine larger regional strategies for conserving their communities in areas of concern.

Introduction

The introductions of livestock and wildfire suppression beginning in the mid-nineteenth century in the western United States have homogenized the structure of its mixed-conifer forests, where contemporary stands are generally denser and have higher rates of canopy and shrub cover compared to pre-suppression conditions (Allen et al. 2002, Miller and Safford 2017, Addington et al. 2018). The increased continuity between surface fuels and tree crowns combined with climate change-driven droughts have exacerbated the severity—both in intensity and extent—of recent wildfires in the western US (Miller et al. 2009, Parks and Abatzoglou 2020, Safford et al. 2022). Changes in an ecosystem's historical fire regime (the distribution, frequency and intensity of fires that occur within an area) may alter the structure of post-burn overstory and understory plant communities in coniferous forests (Denslow 1980, Stevens et al. 2016, Miller and Safford 2019). For example, plants that have historically evolved with periodical, low intensity wildfire may experience reduced rates of survival or reestablishment following high intensity fire (Collins et al. 2018, Etchells et al. 2020). Similarly, plants adapted to relatively infrequent, high intensity fire may experience population extirpations if fire occurs too frequently (resulting in insufficient time for seed production or storage) or if fire intensities are insufficient to stimulate germination (Keeley and Syphard 2018). Such alterations to plant understories within these ecosystems may further alter local plant-pollinator interactions that are important for maintaining landscape-scale biodiversity (Hurteau and Brooks 2011, Boscolo et al. 2017, Eckerter et al. 2022, Tarbill et al. 2023). However, documentation of the community-level responses of insect pollinators to extreme, large-scale wildfire events ('megafires') is unavailable for several ecoregions in western North America (Galbraith et al. 2018, Dole et al. 2023, Tarbill et al. 2023). Greater knowledge here can improve projections on how altered climate and disturbance regimes will affect broader ecological communities in forested landscapes throughout the region.

Wild, native bees (Hymenoptera: Apoidea) are the predominant pollinators in North American forests and grasslands (Hanula et al. 2016, Glenny et al. 2022). Aside from their broader function in maintaining or promoting landscape-level biodiversity in forest ecosystems (Loveless and Hamlick 1984, Potts et al. 2016), many bee-pollinated plants in these landscapes provide additional ecological services, including the protection of water quality and prevention of soil erosion (Wratten et al. 2012). However, bee populations are in decline globally, where land use change (Brown and Paxton 2009), loss of landscape-level heterogeneity (Kremen et al. 2007), and the degradation of habitat (Thapa-Magar et al. 2020) are primary factors that threaten their population sustainability (Koh et al. 2016, Drossart and Gerard 2020, Glenny et al. 2022). Declines in forest-associated bee populations may negatively impact native herbaceous plant diversity and overall forest ecosystem function. Consequently, investigation into what landscape and stand-level factors influence bee assemblages in North American forests has increased since the early 2000s, to identify potential strategies for bee conservation (reviewed in Hanula et al. 2016 and Glenny et al. 2022).

Well-established theories on habitat heterogeneity-biodiversity relationships (Pulliam 2000) suggest that forest patches with an increased variety of physical structures (e.g., multiple tree species, heterogeneous litter layers) or abiotic conditions (shaded and unshaded micro-habitats) can support a greater number of insect species with distinct life histories within a broader landscape (Uhey et al. 2020, Glenny et al. 2023) due to a greater abundance or diversity of available resources (Jha and Kremen 2013, Mallinger et al. 2016, Ponisio et al. 2016). In general, the removal of live canopy following fire events (Ponisio et al. 2016, Galbraith et al.

2018, Burkle et al. 2019, Mason Jr. 2021, Gelles et al. 2023), insect outbreaks (Davis et al. 2020, Foote et al.2020) and forest management operations (Taki et al. 2013, Rivers et al. 2019, Gelles et al. 2022, 2023) can indirectly benefit bees by opening the forest canopy, resulting in increasing light availability towards the understory which may promote the growth of their foraging resources (Anderson et al. 1969, Walters and Stiles 1996, McCabe et al. 2019). Reductions in canopy cover following tree death or removal may also alter microclimatic conditions associated with increased foraging activity by bees (Aleixo et al. 2017).

Reductions in fuel loads following fire have been demonstrated to benefit ground-nesting bees by increasing the amount of exposed, bare soil (Cane and Neff 2011, Hanula et al. 2016, Glenny et al. 2022). Increases in downed tree branches and boles following fire benefit cavity-nesting bees that utilize the abandoned galleries of bark beetles or wood borers (Simanonok and Burkle 2019, Fortuin and Ghandi 2021, Gelles et al. 2022). However, there are biological legacies (downed logs, snags) and various substrates (duff, leaf litter, coarse woody debris) in older (undisturbed) or denser stands that may be utilized as nesting material or overwintering sites by bees (Michener 2000, Williams et al. 2019, Simanonok and Burkle 2019, Fortuin and Ghandi 2021). Given that bees are central place foragers with limited foraging distances from their nests (Gathmann and Tscharntke 2002), large-scale wildfires may affect the quality and proximity of nesting and foraging resources in more extreme manners compared to less expansive or severe fire events (Burkle et al. 2019). As ‘megafires’ often burn over 10,000 ha of forest at relatively high and uniform intensities, these disturbances may homogenize overall landscape structures or significantly reduce the area of late-successional forests or fire refugia for bees (Le Breton et al. 2022) in comparison to smaller-scale, mixed-severity fire (McLaughlin et al. 2022, Dole et al. 2023, Tarbill et al. 2023).

Research on the thermal tolerances of grassland and forest-associated bees suggests above-ground nesting taxa are unlikely to survive temperatures produced by even low intensity wildfire (Busse et al. 2005, Cane and Neff 2011). By contrast, below-ground nesting bees that reside at depths of 10 cm or greater are likely to survive soil temperatures produced during even high intensity fire (Cane and Neff 2011). As understory plant responses to wildfire can vary along gradients of burn severity, elevation, and ecosystem productivity (Richter et al. 2019, Miller and Safford 2020, Brodie et al. 2021), insect pollinator responses to these disturbances may also vary with burn severity or among different forest types within a large-scale wildfire boundary. However, studies that have documented the effects of wildfire on forest-associated bee communities within the western US have largely sampled only one forest type within a broader region (Galbraith et al. 2018, Tarbill et al. 2023), or several years after the wildfire occurred (Ponisio et al. 2016, Burkle et al. 2019, Mason Jr. 2021). Therefore, it is unclear if relationships between stand-level burn severity and local bee diversity varies along an elevational gradient or with local forest productivity within a large-scale fire boundary. Overall, documentation of relatively immediate (e.g., < 3 years post-fire) responses of bee communities to wildfire is largely unavailable for the western US (Galbraith et al. 2019).

The primary objective of this study was to document the early-successional responses of bees to the 2020 Creek Fire, a large-scale disturbance that burned several thousand hectares of submontane, montane, and upper montane mixed-conifer forest within the Sierra National Forest, California. We determined relationships between stand-level burn severity and local bee diversity, and further evaluated whether the patterns of these relationships varied with time (one vs. two years post-fire) or among the various forest biotic zones we sampled. An additional objective was to describe the stand-level, structural attributes that influence local bee abundance and diversity within the ecoregion. Broadly, we hypothesized that post-fire bee abundance and diversity would increase with floral abundance and diversity, which would be highest in stands that burned at severities representative of the ecosystem's historic or natural fire regime. More specifically, we predicted: 1) fire severity would exhibit a negative relationship with post-fire bee diversity and abundance in ecosystems that historically burned at low severity (submontane woodlands and forest-woodland ecotones) because regional species pools in these ecosystems contain few plants (bee foraging resources) with adaptations to high-severity fire, 2) fire severity would exhibit a positive relationship with post-fire bee diversity and abundance in ecosystems that have been characterized historically by a substantial component of high severity fire (upper montane coniferous forests) due to competitive release within the understory plant community, and 3) the relationship between fire severity and bee diversity would plateau at intermediate levels of disturbance in ecosystems adapted to fire regimes with relatively moderate severities (montane, mixed-conifer forests).

Methodology

Research sites and plot selection criteria

We established 48 experimental plots (circular 1/20th hectares) within the 2020 Creek Fire burn boundary, along USDA Forest Service Roads 81 and 7 within Sierra National Forest (Bass Lake Ranger District). Plot locations across the entire study site ranged from 1150-2150 m in elevation, which encompassed the upper limits of the submontane biotic zone (from 550-900 m), the montane zone (900-1800 m), and up to the lower limits of the upper montane zone (1800 -2,700 m) (Allan 1992). Plots located within the submontane zone were co-dominated by gray pine (*Pinus sabiniana* Douglas ex D.Don), canyon live oak (*Quercus chrysolepis* Liebm.) and ponderosa pine (*P. ponderosa Douglas ex C.* Lawson). Plots located in the montane zone were co-dominated by ponderosa pine, incense cedar (*Calocedrus decurrens* [Torr.] Florin), and white fir (*Abies concolor* [Gordon] Lindley ex Hildebrand). Plots located in the upper montane zone were co-dominated by lodgepole pine (*P. contorta* Douglas), ponderosa pine, sugar pine (*P. lambertiana* Douglas), white fir, and red fir (*A. magnifica* A.Murray bis). Sixteen plots were established within each biotic zone, with four replicates per soil burn severity class (undisturbed, low, moderate, and high), using a soil burn severity map provided by the Burned Area Emergency Response (BAER) program (USGS 2020). Plots were spaced by a minimum of 0.75 km from one another and located in forest patches that had burned at uniform severity within a 300 m radius of plot centers.

Bee sampling and identification

Insect pan traps are an effective, passive method for sampling forest-associated bees (Campbell and Hanula 2007). Therefore, bees were sampled from each plot using a set of nine ultraviolet-painted polypropylene pan traps (256 mL cups). Traps were deployed along three transects separated by 120° (azimuths of 120°, 240°, and 360°). Pan traps were painted either white, fluorescent yellow, or fluorescent blue (three traps per color), with every color present along each transect. Traps were spaced six m apart along each transect. Traps were deployed for 48-hour periods, on an approximately biweekly basis during the summer of 2021 and 2022, June-September of each year. All bee specimens captured were stored in 70% ethanol until processed, pinned, and identified. Bees were identified to species or morphospecies using appropriate keys (Hurd and Michener 1955, Mitchell 1962, 1980, LaBerge 1989, Michener 2000, Gibbs 2010; Williams et al. 2014, Best et al. 2024), pictorial guides (Wilson and Carril 2012, discoverlife.org) and relevant reference material.

Quantifying forest structural attributes

During each year and for all experimental plots, both live and dead tree basal areas were quantified with variable radius sampling using a basal area factor of 10 m^2/ha at plot centers. Canopy cover was quantified using a hemispherical densiometer (Strickler 1959) from the average of four measurements, taken at plot center and the midpoint of each pan trap sampling transect (azimuths of 120°, 240°, and 360°). Forest floor cover composition was determined using a one square meter sampling quadrat, with measurements taken at plot center as well as 3, 9, and 15 m distances from plot centers along each pan trap transect for a total of 10 sampling points per plot. At each sampling point, the percentages of quadrat interior occupied or covered by rock, bare soil, leaf litter, grass, herbaceous plant, and shrubs were estimated visually. These values were averaged to yield plot-level mean for each cover class. The total number of flowering plant species within a 2 m buffer along pan trap transects was determined for each plot during every sampling period, the relative abundance of each species was estimated to the nearest multiple of 25 (i.e., 25, 50, 75, etc.) and these numbers summed to yield plot-level totals. The percentages of each 2 m buffer covered by coarse woody debris (diameter > 10 cm) or occupied by standing dead trees or logs were also estimated between quadrat sampling points and averaged to yield a plot-level estimate of coarse woody debris cover.

Statistical analyses

All statistical analyses were conducted using the R programming language (v 3.5.2 ‘Eggshell Igloo’, R Core Team), JMP 17 statistical software (SAS Institute Inc., Cary, NC) or PAST 4 statistical software (University of Oslo, Oslo, Norway). Prior to all analyses, the Shapiro-Wilk test and homogeneity of variance (HOV) tests were used to determine whether response variables were normally distributed and exhibited equal variance, respectively. Data not normally distributed were either log or square root-transformed, or otherwise analyzed with generalized regression techniques that could account for non-normal distributions.

Differences in bee diversity among soil burn severity classes and forest biotic zones

Differences in bee abundance, species richness, and diversity (Shannon-Weiner Index) across burn severity classes, time since fire and among biotic zones were determined using Three-way Analysis of Variance (ANOVA). Separate analyses were used for each response variable of interest. Additional ANOVA tests were used to determine differences in the abundance of individual bee functional groups between sample years (2021 and 2022) and among burn severity categories within each biotic zone. Following methods described by Forrest et al. (2015), species or morphospecies functional group assignments were based on information on life-history traits likely to affect bee habitat associations, including dietary specialization (polylectic vs. oligolectic), nesting location (above-ground vs. below-ground), sociality (social vs. solitary) and body size (small, medium and large-bodied).

Bee community composition was compared between burn severity classes and among forest biotic zones using the non-metric multidimensional scaling (NMDS) platform provided under PAST statistical software (Hammer et al. 2001) combined with permutational multivariate analyses of variance (PERMANOVA). Results were visualized using NMDS, depicting similarities in bee community compositions among the disturbance severity x biotic zone classes by their relative distances on a two-axis plane. Individual NMDS plots were also produced for each biotic zone, to assess for finer-scale degrees of similarity in community composition among burn severity classes and between years.

Relationships between forest structure and local bee diversity

We developed generalized linear models (Family: Poisson; Link: Log) to determine relative effect sizes of forest structural attributes as well as nesting and foraging habitat variables on bee abundance, species richness and Shannon's diversity, treating plot x year as the unit of analysis. Effects included canopy structure (both live and dead tree basal area, canopy cover), nesting resources (coarse woody debris and bare soil cover), and floral resources (i.e., total floral abundance and species richness). Separate models were generated for each dependent variable (bee abundance, species richness, and Shannon's diversity).

Results

Pan trap collections

We collected a total of 5251 bee specimens (1970 in 2021; 3281 in 2022) from 23 genera representing 53 species/morphospecies. Throughout the study site, the most prevalent genera collected were *Lasioglossum* (*Dialictus*) Curtis., *Halictus* Latrielle, *Lasioglossum* (*Lasioglossum*) Curtis, *Anthophora* Latrielle, *Osmia* Panzer, and *Anthidium* Fabricus, representing 48 %, 9 %, 6 %, 4 %, 4 % and 4 % of all captures, respectively. A total of 2,308 bees (854 in 2021, 1454 in 2022) were collected within the submontane zone, representing 45 % of total captures of across the study site. The most prevalent genera were *Lasioglossum* (*Dialictus*) (70 % of all captures), *Halictus* (9 %), *Lasioglossum* (*Lasioglossum*) (7 %), and *Anthophora* (5 %). A total of 1862 bees (510 in 2021, 1352 in 2022) were collected in the montane zone, representing 36 % of all captures across the study site. The most prevalent genera were *Halictus* (40 %), *Lassioglossum* (*Dialictus*) (20 %), *Chelostoma* Latrielle (7 %), *Andrena* Fabricus (5 %) and *Perdita* Smith (5 %). A total of 1018 bees (343 in 2021, 675 in 2022) were collected in the upper montane zone, representing 20

% of overall captures across the study site. The most prevalent genera *were Lasioglossum* (*Dialictus*) (32%), *Halictus* (10 %) *Anthophora* (10 %) *Osmia* (4 %) and *Bombus* Latrielle (3 %).

Differences in bee abundance and diversity among soil burn severity classes and biotic zones

Results from three-way ANOVA testing for significant (α = 0.05) effects of wildfire burn severity, time since fire, forest life zone, and their interactions on bee abundance, species richness, and Shannon's diversity are summarized in Table 1. Bee abundance was significantly affected by burn severity ($F_{3,92} = 6.47$; $p = 0.013$), year ($F_{1,94} = 2.17$; $p = 0.030$). The main effects of biotic zone and burn severity depended significantly on the level of the other ($F_{6,89} = 4.12$; $p = 0.005$), as did the interacting effects between life zone and year ($F_{2,93} = 7.15$; $p = 0.009$) (whole model: $F_{23,72} = 3.49$; $p < 0.001$). Bee species richness was significantly affected by burn severity ($F_{3,92} = 8.81$; $p = 0.004$), the interacting effects between life zone and severity ($F_{6,89} = 2.59$; $p = 0.044$), and the interacting effects between life zone and year ($F_{2,93} = 4.58$; $p = 0.036$) (whole model: $F_{23,72} = 3$; $p < 0.001$). Bee diversity was not significantly affected by burn severity ($F_{3,92} = 0.53$; $p = 0.467$), year ($F_{1, 94} = 1.47$; $p = 0.140$), nor their interactive terms (whole model: $F_{23,72} = 0.98$; $p = 0.490$).

Plot-level means and Tukey's HSD test of bee abundance, species richness, and Shannon's diversity among burn severity classes and forest biotic zones are illustrated in Figure 1. Across all biotic zones, bee abundance, species richness and diversity were generally lower in undisturbed plots compared to burned plots, regardless of time since fire. Plot-level means were greatest in plots within the montane zone during 2022, particularly in stands that had burned at medium or high severity. Bee abundance was generally reduced within the upper montane zone compared to plots located at lower elevations, particularly during 2021. Plot-level bee abundance and diversity were lowest in undisturbed areas within the submontane zone. Bee abundance, species richness and diversity increased from 2021 to 2022 in submontane plots that had burned at low or moderate severity, but significantly decreased in plots that burned at high severity. Within the montane zone, bee abundance and species richness were highest in plots that burned at high severity during 2021. Increases in bee abundance, species richness and diversity were observed across all burn severity categories in 2022, with the largest increases in medium and high burn severity areas. Within the upper montane zone during 2021, plot-level bee abundance and species richness were greatest in low severity plots and significantly reduced in medium severity plots by comparison. During 2022, increases in bee abundance, species richness and diversity were observed in undisturbed, medium and high severity plots, while local bee abundance within plots that burned at low severity decreased between years. Overall, plot-level bee abundance and diversity were lowest in medium severity and undisturbed plots during 2021 and 2022, respectively.

Variability in bee community assemblages across burn severity categories, biotic zones and over time

Results from NMDS analyses and associated PERMANOVA tests used to determine degrees of similarity in plot-level bee community composition between years and among burn severity classes for all biotic zones within the fire boundary are illustrated in Figure 2. Overall, similarity in plot-level bee community composition increased with time since fire, as points representing plot collections from 2022 were more variable with one another (spaced further apart) than points from 2021. Bee communities located within the upper montane zone were more similar (more concentrated) to one another in comparison to communities residing in the submontane and montane zones of (Fig. 2). Across all biotic zones, bee community composition was relatively uniform within undisturbed plots, whose 95% confidence ellipsoid encompasses less area than those representing other burn severity classes.

In the submontane zone (Fig. 3), variability in plot-level community composition increased from 2021 to 2022 within low and medium burn severity classes (stress = 0.03, Axis 1 R^2 = 0.97; Axis 2 R^2 = 0.02). During both years, the 95% confidence ellipsoids of medium and high severity burn classes encompassed more area than those of the undisturbed (particularly for 2021) and low severity classes, suggesting variation in bee community composition also increased with fire severity within the submontane zone. Several bee genera, including *Apis*, *Andrena*, B*ombus*, C*helostoma*, *Halictus*, *Lasioglossum*, *Megachile*, *Melissodes*, and *Anthophora* were located near the center of the ordination plot, indicating their general ubiquity across all burn severity classes. In contrast, *Anthidium*, *Ashmeadiella* and *Perdita* were closer to the centroids of the low severity and undisturbed ellipses (Fig. 3).

In the montane zone (Fig. 4), variation in plot-level bee community composition decreased from 2021 to 2022 (stress = 0.02, Axis 1 R^2 = 0.98; Axis 2 R^2 = 0.37). Increased variation between years was most pronounced in medium and high severity plots. Overall, variation in bee community composition increased with burn severity, as the 95% confidence ellipsoids of the medium and high severity burn classes encompassed extensively more area than both the low severity and undisturbed classes. The majority of genera observed within the montane zone were absent within the ellipsoids of the low severity and undisturbed classes, and in close proximity to the centroids of the high and medium severity burn classes (Fig. 4).

In the upper montane zone (Fig. 5), variation in plot-level bee community composition increased from 2021 to 2022, particularly in high severity plots (stress = 0.05, Axis 1 R^2 = 0.84; Axis 2 R^2 = 0.34) Overall, variability was greatest in high severity plots, whose 95 % confidence ellipsoid encompassed extensively more area than the other burn severity classes. Plots within medium severity plots exhibited the greatest similarity with one another within this biotic zone. Genera such as *Osmia*, *Halictus,* and *Chelostoma* were not encompassed by the confidence ellipsoids of medium and high severity burn classes, suggesting their relative absence in these burned areas.

Effects of forest structure on bee abundance and diversity

Results from generalized linear models describing variation in bee abundance, species richness, and Shannon's diversity due to environmental variables are summarized in Table 2. Variation in bee abundance was significantly affected by elevation (- correlation), basal area (+), floral species richness (FR) (+), shrub cover (+), grass cover (-), coarse woody debris (CWD) (+), % tree mortality (+), and time since fire (TSF) (+) (whole model: DF = 13; $\chi2 = 671.20$; $p < 0.0001$). Variation in bee species richness was significantly affected by basal area (+), FR (+), shrub cover (-), bare soil exposure (-), and grass cover (-) (whole model: DF = 13; $\chi2 = 97.69$; $p < 0.0001$). Floral species richness positively correlated with bee diversity and was the only significant environmental variable at the $\alpha = 0.05$ level (whole model: DF = 13; $\chi2 = 17.71$; $p < 0.1688$). Plot-level mean values of significant environmental variables associated with the forest floor among individual burn severity and biotic zone classes, separated by year, are depicted in Figure 6.

Effects of wildfire severity on bee functional groups

Polylectic bee abundance was significantly affected by biotic zone ($F_{2,93} = 5.45$; p = 0.0061), burn severity ($F_{3,92} = 2.74$; p = 0.049), and year ($F_{1,94} = 12.61$; p = 0.007). The interaction between biotic zone and burn severity ($F_{6,89} = 6.76$; p < 0.001) was also significant, where the main effects of either variable depended significantly on the level of the other (Table 3). One year post fire (2021), plot-level abundance was highest in burned plots within the submontane zone, particularly in stands that burned at high severity. The abundance of polylectic bees generally increased from 2021 to 2022 in burned areas throughout the study site. During 2022, these bees were the most abundant in plots that burned at low or high severity within the submontane and montane zones, respectively. Their plot-level abundance was generally reduced within the upper montane zone and in undisturbed stands (Fig. 7). Oligolectic bee abundance was significantly affected by biotic zone ($F_{2,93} = 15.56$; $p < 0.001$), burn severity ($F_{3,92} = 5.08$; $p = 0.0029$), and year ($F_{1,94} = 10.47$; $p = 0.0018$). The effects of biotic zone and burn severity ($F_{6,89} = 8.91$; $p < 0.001$) depended significantly on the level of the other, as did the interactions between burn severity and year ($F_{3,92} = 3.44$; $p = 0.0209$) (Table 3). Oligolectic bee abundance generally increased from 2021 to 2022 in burned areas throughout the study site. During 2022, they were the most abundant in plots that burned at low or high severity within the submontane and montane zones, respectively. Overall, their abundance was relatively low in undisturbed plots throughout the study site, regardless of year (Fig. 7).

Solitary bee abundance was significantly affected by biotic zone ($F_{2,93} = 9.11$; $p = 0.0003$), burn severity ($F_{3,92} = 3.25$; $p = 0.0263$) and year ($F_{1,94} = 9.68$; $p = 0.0026$). The interaction between biotic zone and burn severity ($F_{6,89} = 6.61$; $p < 0.001$) was also significant (Table 3). Their abundance generally increased from 2021 to 2022 in burned areas throughout the study site. During 2022, they were the most abundant in plots that burned at low or high severity within the submontane and montane zones, respectively. In general, plot-level solitary bee abundance was reduced in undisturbed plots compared to other local burn severity classes within the submontane and montane zones (Fig. 7). Social (both semi-social and eusocial) bee abundance was significantly affected by biotic zone ($F_{2,93} = 5.12$; $p = 0.0082$), burn severity ($F_{3,92} = 5.08$; $p = 0.0029$), and year ($F_{1,94} = 10.47$; $p = 0.0018$). The interactions between biotic zone and burn severity ($F_{6,89} = 8.91$; $p < 0.001$) as well as burn severity and year ($F_{3,92} = 3.44$; $p = 0.0209$) were also significant (Table 3). During 2021, social bees were the most abundant in burned plots within the submontane zone, particularly in stands that burned at medium or high severity. Aside from submontane plots that burned at high severity, social bee abundance generally increased from 2021 to 2022 in burned areas throughout the study site. During 2022, they were the most abundant in plots that burned at low or high severity within the submontane and montane zones, respectively. In general, social bees were less prevalent in undisturbed plots and throughout the upper montane zone (Fig. 7).

Small-bodied bee abundance was significantly affected by biotic zone ($F_{2, 93} = 5.2$; $p = 0.0076$), burn severity ($F_{3,92} = 3.72$; $p = 0.0148$) and year ($F_{1,94} = 10.83$; $p = 0.0015$). The interaction between biotic zone and burn severity ($F_{6,89} = 6.32$; $p < 0.001$) was also significant (Table 3). During 2021, small-bodied bees were most abundant in burned plots within the submontane zone, particularly in stands that burned at low or high severity. Their abundance generally increased from 2021 to 2022 in burned areas throughout the study site. During 2022, they were the most abundant in plots that burned at low or high severity within the submontane and montane zones, respectively. Plot-level abundance was relatively reduced in undisturbed plots and throughout the upper montane zone (Fig. 7). Medium-bodied bee abundance was significantly affected by biotic zone ($F_{2,93} = 4.35$; $p = 0.0163$) and year ($F_{1,94} = 8.25$; $p = 0.0053$). The interaction between biotic zone and burn severity ($F_{6,89} = 3.31$; $p = 0.0059$) was significant (Table 3). Medium-bodied bee abundance was relatively uniform across burn severity classes throughout all biotic zones in 2021. Increases in plot-level abundances were observed in burned plots during 2022. These increases were significant in low severity plots within the submontane and montane zones. Large-bodied bee abundance was significantly affected by year ($F_{1,94} = 5.65$; $p = 0.0199$). The interaction between biotic zone and burn severity ($F_{6,89} = 2.29$; $p = 0.0434$) was significant (Table 3). During 2021, these bees were generally more abundant in plots located in undisturbed rather than burned stands within the submontane and montane zones. Aside from submontane plots that burned at high severity, their abundance generally increased in burned plots from 2021 to 2022 throughout the study site. Overall, the greatest abundance of large-bodied bees was collected in upper montane plots that burned at high severity in 2022.

Above-ground nesting bee abundance was significantly affected by biotic zone ($F_{2,93} = 4.64$; $p = 0.035$), year ($F_{1,95} = 9.993$; $p = 0.0023$) and the interaction between biotic zone and burn severity ($F_{6,89} = 3.31$; $p = 0.0126$) (Table 3). Overall, they were the most abundant in plots that burned at low severity within the upper montane zone. Within the submontane and montane zone by comparison, these bees were generally more abundant in plots located in undisturbed rather than burned stands. Increases in plot-level abundances were generally observed in burned plots during 2022 throughout all biotic zones. However, submontane plots that burned at high severity were typically depleted of this group in 2022. Below-ground nesting bee abundance was significantly affected by biotic zone ($F_{2,93} = 4.53$; $p = 0.0138$), burn severity ($F_{3,92}= 4.21$; $p = 0.0082$), and year ($F_{1,95} = 11.9$; $p = 0.0009$). The interaction between biotic zone and burn severity ($F_{6,89} = 6.64$; $p < 0.001$) was also significant (Table 3). Aside from submontane plots that burned at high severity, below-ground nesting bee abundance generally increased from 2021 to 2022 in burned areas throughout the study site. During 2022, they were the most abundant in plots that burned at medium or high severity within the submontane and montane zones, respectively. Overall, their plot-level abundance was relatively reduced in the upper montane zone compared to other biotic zones (Fig. 7).

Discussion

Differences in bee abundance and diversity among soil burn severity classes and forest biotic zones

Regardless of local burn severity or time since fire, bee communities were generally more abundant and speciose in burned stands compared to nearby, undisturbed areas within submontane, montane, and upper montane forest ecosystems located within the 2020 Creek Fire boundary (Fig. 1). In general, bee communities were also more diverse in burned stands relative to in unburned stands, although no significant differences among burn severity categories were detected throughout the study site or within individual biotic zones (Table 1). We further determined that forest floor attributes, including exposed bare soil, floral species richness, and coarse woody debris (CWD) abundance, exhibited significant, positive correlations with bee abundance and diversity, while increased rock cover, as well as dense litter and grass layers were negatively correlated with these indices (Table 2). Such relationships between forest floor conditions and local bee biodiversity are well documented in studies that have investigated the landscape and stand-level factors regulating bee community assemblages in fire-adapted forests (Potts et al. 2003, 2005, Lazarina et al. 2016, 2017, Gelles et al. 2022, 2023). Overall, these results suggest that bee communities residing within coniferous forest landscapes of the western Sierra Nevada mountains may generally benefit from wildfire across a gradient of burn severities during early successional periods (<3 years post-fire), likely due to increased availability of various foraging resources or nesting substrates following flame-induced reductions in canopy closure or surface fuels (Table 2, Fig. 6). Importantly, increases in local bee abundance and species richness were observed one year post-fire within stands that burned at severities non-representative of the ecosystem's historical fire regime, for example, in lower elevation forests or woodlands that burned at high severity (Miller and Urban 1999, Stevens et al. 2015, Miller and Safford 2019). In contrast, bee abundance and species richness were generally highest in stands that burned at severities more representative of the local ecosystem's natural fire regime two years post-fire. Combined, our results suggest that, like their herbaceous foraging resources, bee community responses to wildfire may vary along gradients of ecosystem productivity driven by elevational or climatic factors (Richter et al. 2019, Miller and Safford 2020, Brodie et al. 2021). These general trends may also change during the immediate, successive years following stand disturbance as a greater abundance of bees or a broader range of bee species recolonize disturbed stands.

In submontane plots, bee abundance and species richness were significantly higher in stands that burned at low and high severity when compared to undisturbed stands in 2021 (Fig. 1). This pattern persisted for species richness during 2022, while bee abundance exhibited a relatively linear and negative relationship with increasing burn severity in submontane plots. Within lower montane, mixed-conifer forests of the Californian Sierra Nevada, fire-adapted shrubs and invasive grasses often rapidly dominate the forest floor after high severity fire, which may ultimately reduce understory plant species richness due to competitive exclusion over longer time periods than observed during this study (D'antonio and Vitousek 1992, Richter et al. 2019, Miller and Safford 2020, Brodie et al. 2021). Reductions in foraging resource (flowering forbs and shrubs) or nesting substrate visibility (e.g., exposed bare soil, abandoned burrows) following relatively large increases in local grasses layers could also help to explain the observed reductions in bee abundance and diversity within submontane stands that burned at high severity during 2022 when compared to plots that burned at lower severity (Fig.6). Relatively large increases in grass, shrub or even herbaceous plant cover in plots that burned at high severity may have also decreased the attractiveness, visibility or efficacy of pan traps used to sample bees within this biotic zone (Cane et al. 2000, Roulston et al. 2007). This potential issue may occur in all studies where passive trapping methods are used to assess changes in bee communities following forest disturbance. Incorporating other sampling techniques (e.g., aerial netting), while also identifying bee nesting locations within study sites can reduce the limitations of passive sampling methodologies used to document bee community responses to various forest disturbances.

Stands located within the montane zone were relatively depauperate of bees across all burn severity classes in 2021. However, significant increases in bee abundance and species richness were observed across all burn severity classes during 2022, particularly in stands that burned at medium or high severity (Fig. 1). Within the upper montane zone, bee abundance, species richness and diversity remained relatively uniform across burn severity categories, regardless of time since fire (Fig. 1). However, their communities were slightly more abundant and speciose in stands that burned at low and high severity in comparison to those that burned at medium severity or went undisturbed, particularly during 2021. It is unclear why plots within the montane and upper montane zones were relatively depleted of bees during 2021 in comparison to 2022 (Fig. 1), as various ground cover attributes positively correlated with either bee abundance or diversity (e.g., floral abundance and species richness, CWD abundance) remained relatively consistent between one- and two-years post-fire (Fig. 6). Overall, variable levels of ecosystem productivity (net rates of biomass production) among the biotic zones we sampled may help to explain the observed differences in local relationships between postfire biodiversity and burn severity (Connell 1978; Huston 1979, 1994, 2014; Kondoh, 2001, Hall et al. 2012, Richter et al. 2019). High productivity environments (e.g., montane, mixed-conifer forests) in the fire boundary with relatively dense stands and closed canopies may have required high fire intensities to significantly alter overstory conditions that could ultimately promote bee foraging activity or nest establishment two years post-fire (Galbraith et al. 2018, Burkle et al. 2019, Brodie et al. 2021). High intensity surface flames within the understory might have reduced the populations of highly competitive plant species, which may have allowed for less competitive species to proliferate in these ecosystems temporarily (Grimes 1973, Richter et al. 2019, Brodie et al. 2021). Any increases in herbaceous plant diversity following such instances of competitive release within the understory would likely benefit bees by providing them with a greater diversity (or abundance) of floral resources. However, these relatively high severity burns may have contributed to reduced bee abundance and diversity (both locally and regionally) during the immediate year post-fire, if they homogenized stand structures across the broader landscape, destroyed bee foraging, nesting or overwintering resources, or otherwise contributed directly to reduced population sizes or densities via flame-induced mortality (Breton et al. 2022, McLaughlin et al. 2022, Dole et al. 2023, Tarbill et al. 2023). Regardless of local burn severity, continued recolonization of bees and herbaceous plants into disturbed stands would naturally contribute to the observed plot-level increases in bee abundance and diversity from 2021 to 2022 within burned stands (Fig. 1).

Wildfire effects on bee community composition and individual functional groups

Within the submontane zone, variation in bee community composition was relatively uniform across all burn severity classes (Fig. 3). Several genera including *Apis, Andrena, Bombus,* *Chelostoma, Halictus, Lasioglossum*, *Megachile*, *Melissodes*, and *Anthophora*: were located near the center of the submontane ordination plot, indicating their general ubiquity across all burn severity classes. By contrast, *Anthidium*, *Ashmeadiella* and *Perdita* were in closer proximity to the centroids of the low burn severity and undisturbed ellipsoids, suggesting these taxa may be relatively maladapted to survive higher severity fires within submontane forests and woodlands (Fig. 3), possibly due to their nesting (e.g., above-ground) or overwintering behaviors (Forrest et al. 2015). Within the montane zone by comparison, we observed a more pronounced, linear relationship between burn severity and variation in bee community composition, where communities located within high severity burns were structurally less similar with one another in comparison to those residing in undisturbed stands or those that burned at low severity (Fig. 4). The majority of genera observed within these landscapes were absent within the ellipsoids of the low severity and undisturbed classes, and in close proximity to the centroids of the high and medium severity burn classes (Fig. 4). Variability in local community compositions was also greatest among high severity burned plots within the upper montane zone (Fig. 5), while those located in medium severity burns exhibited high degrees of similarity with one another. Genera including *Osmia*, *Halictus*, and *Chelostoma* were not encompassed by the confidence ellipsoids of medium and high severity burn classes, suggesting their relative absence in these burned areas (Fig. 5).

When grouping plots from all three biotic zones, we observed variation in local bee community composition to generally increase with fire severity as well as with time since fire (Fig. 3). In recently disturbed landscapes, variation in local bee community compositions may naturally increase over relatively short time periods as a greater number of individuals or an increased variety of species immigrate into disturbed areas (Potts et al. 2005, Williams et al.

2010, Haddad et al. 2008; Taki et al. 2013, Harrison et al. 2018). However, the high degree of variation in bee communities among plots that burned at high severity across our entire study site (Fig. 3) and within individual biotic zones (Figs. 3-5) conflicts with related studies that have suggested mixed-conifer forests that burn at lower or mixed severities should generally support a broader range of bee or herbaceous plant species compared to those that burn at predominantly at high severity (Ponisio et al. 2016, Galbraith et al. 2024). However, these studies have focused on bee community responses to fire severity gradients at scales larger than those assessed here (Lazarina et al. 2016, 2017, Ponisio et al. 2016, Burkle et al. 2022). During the immediate years following fire, open stands or non-forested patches created by high severity fire may have high amount of light availability which may attract bees or promote their foraging behavior within these locations (Aleixo et al. 2017), regardless of local resource availability. These contrasting results highlight the importance of considering spatial scale when assessing the effects of forest structure and disturbance on resident bee communities or populations (Galbraith et al. 2024).

We observed high amounts of similarity between bee functional groups and community-level responses to increased fire severity within individual biotic zones (Fig. 1, 7). Aside from submontane plots that burned at high severity, the abundance of individual functional groups generally increased from 2021 to 2022 in burned areas throughout the study site. Overall, functional traits including polylecty and high mobility may allow certain bee species to more readily colonize or better utilize forested areas that burn at high severity (Greenleaf et al. 2007, Dole et al. 2023). During 2022, several functional groups were highly abundant in plots that burned at low or high severity within the submontane and montane zones, respectively. Moderate to large-bodied bees and above-ground nesting species were highly prevalent in undisturbed stands, particularly within the upper montane zone during 2021 (Fig. 7). Other functional groups (e.g., below-ground nesters) were less abundant in undisturbed plots throughout the study site, regardless of year. Above-ground nesting bees are largely assumed to be relatively vulnerable to population reductions following wildfire (Cane and Neff 2011, Mason Jr. et al. 2021). Within the Creek Fire boundary, however, we collected various above-ground nesting species in montane and upper montane stands during the immediate year following fire, including within plots that burned at high severity (Fig. 7). This suggests that above-ground nesters residing within these ecosystems may be capable of emigrating away from burning areas or rapidly utilizing burned stands during the immediate year post-fire (Batista 2022, Dole et al. 2023). Given their flight capabilities, the majority of bee taxa present within the region may be capable of surviving even high severity wildfire at local scales. However, across larger areas and over longer time periods than observed during this study, expansive, high severity burn scars may homogenize overall landscape structures or significantly reduce the area of late-successional forests or fire refugia for bees (Le Breton et al. 2022, McLaughlin et al. 2022, Dole et al. 2023, Tarbill et al. 2023). Specifically, expansive, high severity burn scars may negatively affect certain bee taxa that are dependent on relatively specific resources, for example oligolectic bees or habitat specialists (Ponisio et al. 2016, Mason Jr. 2021). Overall, accounting for heterogeneity in stand- or patch-level burn severity within a broader landscape can improve projections of how these large-scale wildfire events alter bee species distributions and community compositions at both local and regional scales.

Conclusions

Our findings suggest that bee communities residing within coniferous forest landscapes of the western Sierra Nevada mountains may generally benefit from altered habitat conditions following wildfire across a gradient of burn severities during early successional periods (<3 years post-fire), likely due to increased availability of foraging resources or nesting substrates following flame-induced reductions in canopy closure or surface fuels (Table 2, Fig. 6). During the immediate year following fire, we collected high amounts of bees and bee species within stands that burned at severities non-representative of the ecosystem's historical fire regime, for example, in high severity burned areas within submontane ecosystems (Miller and Urban 1999, Stevens et al. 2016, Miller and Safford 2020). During the following summer, however, bee abundance and species richness was generally highest in stands that burned at severities more representative of the local ecosystem's natural fire regime (the distribution, frequency and intensity of fires that occur within an area). Overall, these observations suggest that stand-level relationships between post-fire bee abundance or diversity and fire severity may vary along elevational gradients or among different forest types within a large-scale wildfire boundary. These patterns may also change between the early, successive years following these disturbances. Increases in local grass and shrub layers, combined with varying levels of floral resources, may be among several factors that contribute to differences in stand-level bee abundance or diversity between years. Importantly, our observations corroborate with those from other studies that have determined low to moderate intensity fire characteristic of prescribed burns used to restore or maintain the function of lower elevation, mixed-conifer forests in the Californian Sierra Nevada mountains will likely benefit bee communities at both local and regional scales (Ponisio et al. 2016, Gelles et al. 2022, 2023, Glenny et al. 2022). Overall, long-term monitoring programs are necessary for determining how long favorable habitat conditions for bees persist following fire. Determining the frequency and optimal severity that a specific forest type should burn at (either naturally or via prescribed fire) in order to create or maintain favorable habitat conditions for bees can help refine regional strategies for conserving their communities in areas of concern.

Literature cited

Anderson, R. C., O. L. Loucks, and **A. M. Swain. 1969.** Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology* 50: 255-263.

Addington, R. N., G. H. Aplet, M. A. Battaglia, J. S. Briggs, P. M. Brown, A. S. Cheng, ... and **B. Wolk. 2018.** Principles and practices for the restoration of ponderosa pine and dry mixed-conifer forests of the Colorado Front Range.

Aleixo, K. P., C. Menezes, V. L. Imperatriz Fonseca, and **C. I. da Silva. 2017.** Seasonal availability of floral resources and ambient temperature shape stingless bee foraging behavior (*Scaptotrigona aff. depilis*). *Apidologie* 48: 117-127.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, and **J. T. Klingel. 2002.** Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12: 1418-1433.

Batista, E. K., J. E. Figueira, R. R. Solar, C. S. de Azevedo, M. V. Beirão, C. N. Berlinck, ... and **G. W. Fernandes. 2023.** In case of fire, escape or die: a trait-based approach for identifying animal species threatened by fire. *Fire* 6: 242.

Boscolo, D., P. M. Tokumoto, P. A. Ferreira, J. W. Ribeiro, and **J. S. dos Santos. 2017.** Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. *Perspectives in Ecology and Conservation* 15: 18-24.

Brodie, E. G., J. E. Miller, and **H. D. Safford. 2021.** Productivity modifies the effects of fire severity on understory diversity.

Brown, M. J., and **R. J. Paxton. 2009.** The conservation of bees: a global perspective. *Apidologie* 40: 410-416.

Burkle, L. A., M. P. Simanonok, J. S. Durney, J. A. Myers, and **R. T. Belote. 2019.** Wildfires influence abundance, diversity, and intraspecific and interspecific trait variation of native bees and flowering plants across burned and unburned landscapes. *Frontiers in Ecology and Evolution* 7: 252.

Burkle, L. A., R. T. Belote, and **J. A. Myers. 2022.** Wildfire severity alters drivers of interaction beta-diversity in plant-bee networks. *Ecography* 2022: e05986.

Campbell, J. W., and **J. L. Hanula. 2007.** Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation* 11: 399-408.

Cane, J. H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society* 64: 406-413.

Cane, J. H., and **J. L. Neff. 2011.** Predicted fates of ground-nesting bees in soil heated by wildfire: thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation* 144: 2631-2636.

Carril, O. M., T. Griswold, J. Haefner, and **J. S. Wilson. 2018.** Wild bees of Grand Staircase-Escalante National Monument: richness, abundance, and spatio-temporal beta-diversity. *PeerJ* 6: e5867.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, ... and **J. F. Franklin. 1999.** Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience* 49: 288-297.

Collins, B. M., J. M. Lydersen, R. G. Everett, and **S. L. Stephens. 2018.** How does forest recovery following moderate-severity fire influence effects of subsequent wildfire in mixed-conifer forests?. *Fire Ecology* 14: 1-9.

Davis, T. S., P. R. Rhoades, A. J. Mann, and **T. Griswold. 2020.** Bark beetle outbreak enhances biodiversity and foraging habitat of native bees in alpine landscapes of the southern Rocky Mountains. *Scientific Reports* 10: 16400.

Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia* 46: 18-21.

Dole, H. E., S. Villamarin-Cortez, and **L. A. Richards. 2023.** Facing the flames; insect responses to megafires and changing fire regimes. *Current Opinion in Insect Science* 101: 129.

Drossart, M., and **M. Gérard. 2020.** Beyond the decline of wild bees: Optimizing conservation measures and bringing together the actors. *Insects* 11: 649.

Eckerter, T., V. Braunisch, J. Buse, and **A. M. Klein. 2022.** Open forest successional stages and landscape heterogeneity promote wild bee diversity in temperate forests. *Conservation Science and Practice* 4: e12843.

Etchells, H., A. J. O'Donnell, W. L. McCaw, and **P. F. Grierson. 2020.** Fire severity impacts on tree mortality and post-fire recruitment in tall eucalypt forests of southwest Australia. *Forest Ecology and Management* 459: 117850.

Ferrenberg, S. M., D. W. Schwilk, E. E. Knapp, E. Groth, and **J. E. Keeley. 2006.** Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. *Fire Ecology* 2: 79-102.

Foote, G. G., N. E. Foote, J. B. Runyon, and **C. J. Fettig. 2020.** Changes in the summer wild bee community following a bark beetle outbreak in a Douglas-fir forest. *Environmental Entomology* 49: 1437-1448.

Forrest, J. R., R. W. Thorp, C. Kremen, and **N. M. Williams. 2015.** Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. *Journal of Applied Ecology* 52: 706-715.

Fortuin, C. C., and **K. J. Gandhi. 2021.** Functional traits and nesting habitats distinguish the structure of bee communities in clearcut and managed hardwood & pine forests in Southeastern USA. *Forest Ecology and Management* 496: 119351.

Galbraith, S. M., J. H. Cane, A. R. Moldenke, and **J. W. Rivers. 2019.** Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere* 10: e02668.

Galbraith, S. M., J. J. Valente, C. J. Dunn, and **J. W. Rivers. 2024.** Both Landsat- and LiDAR-derived measures predict forest bee response to large-scale wildfire. *Remote Sensing in Ecology and Conservation* 10: 24-38.

Gathmann, A., and **T. Tscharntke. 2002.** Foraging ranges of solitary bees. *Journal of Animal Ecology* 71: 757-764.

Gelles, R. V., T. S. Davis, and **C. S. Stevens-Rumann. 2022.** Wildfire and forest thinning shift floral resources and nesting substrates to impact native bee biodiversity in ponderosa pine forests of the Colorado Front Range. *Forest Ecology and Management* 510: 120087.

Gelles, R. V., T. S. Davis, and **K. J. Barrett. 2023.** 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. *Agricultural and Forest Entomology* 25: 435-448.

Glenny, W., J. B. Runyon, and **L. A. Burkle. 2022.** A review of management actions on insect pollinators on public lands in the United States. *Biodiversity and Conservation* 1-22.

Glenny, W., J. B. Runyon, and **L. A. Burkle. 2023.** Habitat characteristics structuring bee communities in a forest-shrubland ecotone. *Forest Ecology and Management* 534: 120883.

Greenleaf, S. S., N. M. Williams, R. Winfree, and **C. Kremen. 2007.** Bee foraging ranges and their relationship to body size. *Oecologia* 153: 589-596.

Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and **N. B. Pavlovic. 2010.** Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications* 20: 1678-1692.

Hanula, J. L., M. D. Ulyshen, and **S. Horn. 2016.** Conserving pollinators in North American forests: a review. *Natural Areas Journal* 36: 427-439.

Hammer, Ø., and **D. A. Harper. 2001.** Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: 1.

Harrison, T., J. Gibbs, and **R. Winfree. 2018.** Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology* 24: 287-296.

Holzschuh, A., I. Steffan-Dewenter, and **T. Tscharntke. 2010.** How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids?. *Journal of Animal Ecology* 79: 491-500.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, ... and **M. G. Turner. 2016.** Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment* 14: 369-378.

Hurteau, M. D., and **M. L. Brooks. 2011.** Short-and long-term effects of fire on carbon in US dry temperate forest systems. *BioScience* 61: 139-146.

Keeley, J. E., and **A. D. Syphard. 2018.** Historical patterns of wildfire ignition sources in California ecosystems. *International Journal of Wildland Fire* 27: 781-799.

Koh, I., E. V. Lonsdorf, N. M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and **T. H. Ricketts. 2016.** Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences* 113: 140-145.

Jha, S., and **C. Kremen. 2013.** Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences* 110: 555-558.

Kremen, C., N. M. Williams, and **R. W. Thorp. 2002.** Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences* 99: 16812-16816.

Lazarina, M., S. P. Sgardelis, T. Tscheulin, A. S. Kallimanis, J. Devalez, and **T. Petanidou. 2016.** Bee response to fire regimes in Mediterranean pine forests: the role of nesting preference, trophic specialization, and body size. *Basic and Applied Ecology* 17: 308-320.

Lazarina, M., S. P. Sgardelis, T. Tscheulin, J. Devalez, V. Mizerakis, A. S. Kallimanis, ... and **T. Petanidou. 2017.** The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. *Biodiversity and Conservation* 26: 115-131.

Le Breton, T. D., M. B. Lyons, R. H. Nolan, T. Penman, G. J. Williamson, and **M. K. Ooi. 2022.** Megafire-induced interval squeeze threatens vegetation at landscape scales. *Frontiers in Ecology and the Environment* 20: 327-334.

Loveless, M. D., and **J. L. Hamrick. 1984.** Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics* 15: 65-95.

Mallinger, R. E., J. Gibbs, and **C. Gratton. 2016.** Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees’ foraging periods. *Landscape Ecology* 31: 1523-1535.

Mason Jr, S. C., V. Shirey, L. C. Ponisio, and **J. K. Gelhaus. 2021.** Responses from bees, butterflies, and ground beetles to different fire and site characteristics: a global meta-analysis. *Biological Conservation* 261: 109265.

McCabe, T. D., and **M. C. Dietze. 2019.** Scaling contagious disturbance: A spatially-implicit dynamic model. *Frontiers in Ecology and Evolution* 7: 64.

McLaughlin, J. P., J. W. Schroeder, A. M. White, K. Culhane, H. E. Mirts, G. L. Tarbill, ... and **R. Sollmann. 2022.** Food webs for three burn severities after wildfire in the Eldorado National Forest, California. *Scientific Data* 9: 384.

Michener, C. D. 2000. *The bees of the world*. Vol. 1. JHU Press.

Miller, J. D., and **H. D. Safford. 2017.** Corroborating evidence of a pre-Euro-American low-to moderate-severity fire regime in yellow pine-mixed conifer forests of the Sierra Nevada, California, USA. *Fire Ecology* 13: 58-90.

Miller, C., and **D. L. Urban. 1999.** Forest pattern, fire, and climatic change in the Sierra Nevada. *Ecosystems* 2: 76-87.

Miller, J. E., and **H. D. Safford. 2020.** Are plant community responses to wildfire contingent upon historical disturbance regimes?. *Global Ecology and Biogeography* 29: 1621-1633.

Minott, J. A., and **T. E. Kolb. 2020.** Regeneration patterns reveal contraction of ponderosa forests and little upward migration of pinyon-juniper woodlands. *Forest Ecology and Management* 458: 117640.

North, M., B. Oakley, R. Fiegener, A. Gray, and **M. Barbour. 2005.** Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecology* 177: 13-24.

Nyoka, S. E. 2010. Can restoration management improve habitat for insect pollinators in ponderosa pine forests of the American southwest?. *Ecological Restoration* 28: 280-290.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'hara, ... and **M. J. Oksanen. 2013.** Package 'vegan'. Community ecology package, version 2: 1-295.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, ... and **H. Wagner. 2019.** *vegan*: Community ecology package. R package version 2.5-4.

Parks, S. A., and **J. T. Abatzoglou. 2020.** Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. *Geophysical Research Letters* 47: e2020GL089858.

Ponisio, L. C., K. Wilkin, L. K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, and **C. Kremen. 2016.** Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology* 22: 1794-1808.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and **P. Willmer. 2003.** Linking bees and flowers: how do floral communities structure pollinator communities?. *Ecology* 84: 2628-2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and **P. Willmer. 2005.** Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology* 30: 78-85.

Potts, S. G., V. Imperatriz-Fonseca, H. T. Ngo, M. A. Aizen, J. C. Biesmeijer, T. D. Breeze, ... and **A. J. Vanbergen. 2016.** Safeguarding pollinators and their values to human well-being. *Nature* 540: 220-229.

Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters* 3: 349-361.

Richter, C., M. Rejmánek, J. E. Miller, K. R. Welch, J. Weeks, and **H. D. Safford. 2019.** The species diversity × fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere* 10: e02882.

Rivers, J. W., C. L. Mathis, A. R. Moldenke, and **M. G. Betts. 2018.** Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest. *GCB Bioenergy* 10: 766-781.

Safford, H. D., and **J. T. Stevens. 2017.** Natural range of variation (NRV) for yellow pine and mixed conifer forests in the Sierra Nevada, southern Cascades, and Modoc and Inyo National Forests, California, USA. General Technical Report PSW-GTR-256, USDA Forest Service, Pacific Southwest Research Station, Albany, CA.

Safford, H. D., A. K. Paulson, Z. L. Steel, D. J. Young, and **R. B. Wayman. 2022.** The 2020 California fire season: A year like no other, a return to the past or a harbinger of the future?. *Global Ecology and Biogeography.*

Simanonok, M. P., and **L. A. Burkle. 2019.** Nesting success of wood-cavity-nesting bees declines with increasing time since wildfire. *Ecology and Evolution* 9: 12436-12445.

Steel, Z. L., M. J. Koontz, and **H. D. Safford. 2018.** The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. *Landscape Ecology* 33: 1159-1176.

Stevens, J. T., H. D. Safford, M. P. North, J. S. Fried, A. N. Gray, P. M. Brown, ... and **A. H. Taylor. 2016.** Average stand age from forest inventory plots does not describe historical fire regimes in ponderosa pine and mixed-conifer forests of western North America. *PLoS One* 11: e0147688.

Taki, H., R. Murao, K. Mitai, and **Y. Yamaura. 2018.** The species richness/abundance-area relationship of bees in an early successional tree plantation. *Basic and Applied Ecology* 26: 64-70.

Tarbill, G. L., A. M. White, and **R. Sollmann. 2023.** Response of pollinator taxa to fire is consistent with historic fire regimes in the Sierra Nevada and mediated through floral richness. *Ecology and Evolution* 13: e10761.

Thapa-Magar, K. B., T. S. Davis, and **B. Kondratieff. 2020.** Livestock grazing is associated with seasonal reduction in pollinator biodiversity and functional dispersion but cheatgrass invasion is not: Variation in bee assemblages in a multi-use shortgrass prairie. *PloS One* 15: e0237484.

Walters, B. B., and **E. W. Stiles. 1996.** Effect of canopy gaps and flower patch size on pollinator visitation of *Impatiens capensis*. *Bulletin of the Torrey Botanical Club* 123: 184-188.

Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and **N. Desneux. 2012.** Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems & Environment* 159: 112-122.

Williams, N. M., E. E. Crone, H. R. T'ai, R. L. Minckley, L. Packer, and **S. G. Potts. 2010.** Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143: 2280-2291.

Williams, N. M., and **C. Kremen. 2007.** Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications* 17: 910-921.

Williams, P. H., R. W. Thorp, L. L. Richardson, and **S. R. Colla. 2014.** *Bumble bees of North America: an identification guide.* Vol. 89. Princeton University Press.

Williams, N. M., J. M. Mola, C. Stuligross, T. Harrison, M. L. Page, R. M. Brennan, ... and **M. Rundlöf. 2019.** Fantastic bees and where to find them: locating the cryptic overwintering queens of a western bumble bee. *Ecosphere* 10: e02949.

Wilson, J. S., and **O. J. Messinger Carril. 2016.** *The bees in your backyard: a guide to North America's bees.* Princeton University Press.

Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and **N. Desneux. 2012.** Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems & Environment* 159: 112-122.

Uhey, D. A., H. L. Riskas, A. D. Smith, and **R. W. Hofstetter. 2020.** Ground-dwelling arthropods of pinyon-juniper woodlands: Arthropod community patterns are driven by climate and overall plant productivity, not host tree species. *PloS One* 15: e0238219.

Table 1. Results from two-way ANOVA testing for significant (α = 0.05) effects of wildfire burn severity, time since fire, forest life zone, and their interactions on bee abundance, species richness and Shannon's diversity.

Response	Parameter	DF	F	Prob > F
Abundance	Life zone	2	1.66	0.202
	Severity	3	6.47	0.013
	Year	1	2.17	0.030
	Life zone*Severity	6	4.12	0.005
	Life zone*Year	2	7.15	0.009
	Severity*Year	3	0.22	0.643
	Life zone*Severity*Year	6	1.17	0.334
	Whole model	23,72	3.49	<0.001
Richness	Life zone	2	0.02	0.893
	Severity	3	8.81	0.004
	Year	1	1.84	0.060
	Life zone*Severity	6	2.59	0.044
	Life zone*Year	2	4.58	0.036
	Severity*Year	3	0.16	0.689
	Life zone*Severity*Year	6	1.19	0.325
	Whole model	23,72	3	<0.001
Diversity	Life zone	2	0.28	0.600
	Severity	3	0.53	0.467
	Year	1	1.47	0.140
	Life zone*Severity	6	0.76	0.555
	Life zone*Year	2	0.22	0.639
	Severity*Year	3	0.6	0.441
	Life zone*Severity*Year	6	0.45	0.775
	Whole model	23,72	0.98	0.490

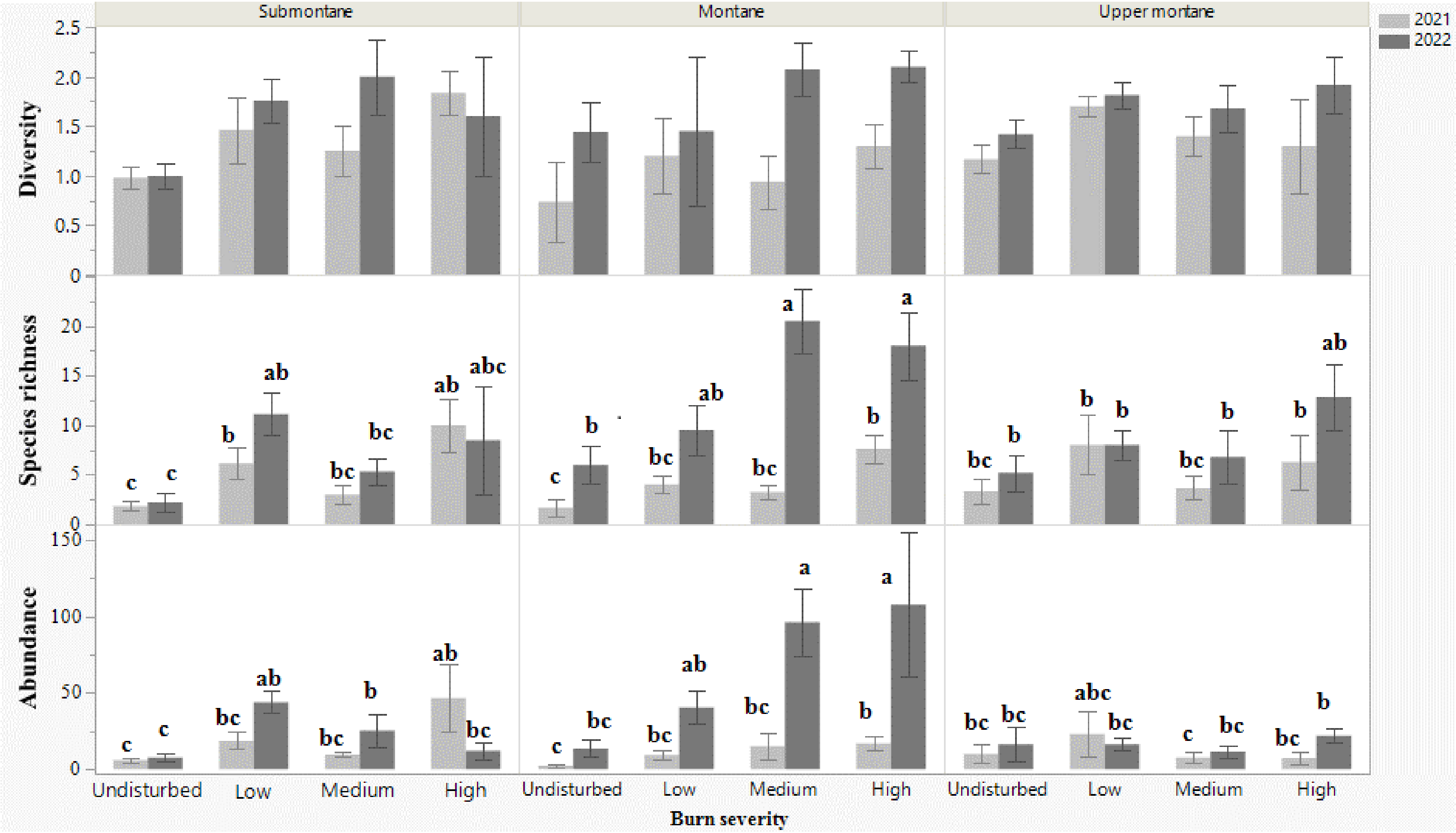

Figure 1. Plot-level means and Tukey's HSD test of bee abundance, species richness, and Shannon's diversity among burn severity classes, forest biotic zones and time since fire; means not sharing the same letter(s) within individual rows differ significantly (α = 0.05).

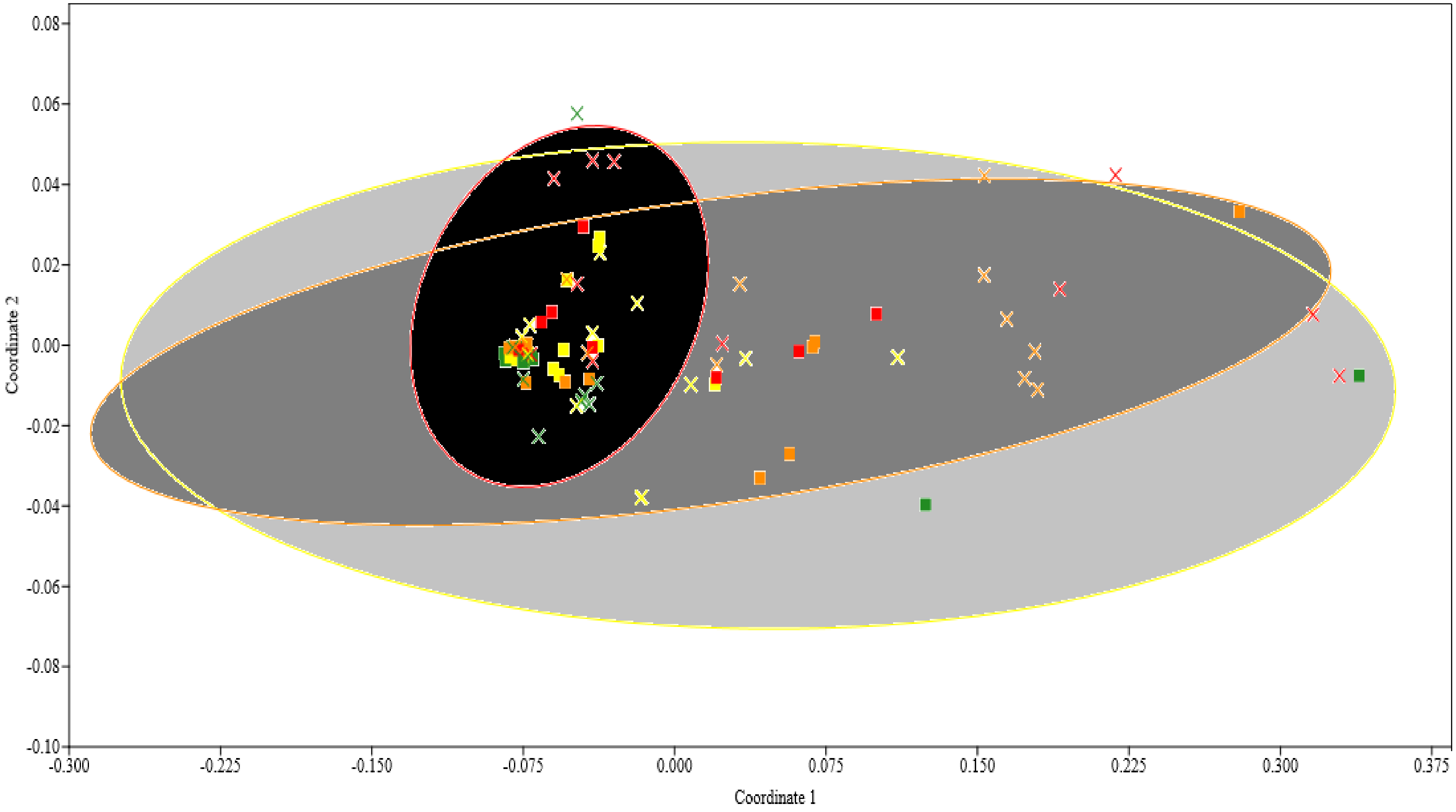

Figure 2. Results from NMDS analyses used to determine degrees of similarity in bee community assemblages among plots within individual forest biotic zones (black ellipsoid = upper montane zone; dark gray = montane zone; light gray = submontane zone) and burn severity classes (green = undisturbed; yellow = low severity; orange = medium severity; red = high severity), as well as between one (squares) and two (X's) years post-fire within the 2020 Creek Fire boundary located in Sierra National Forest, CA.

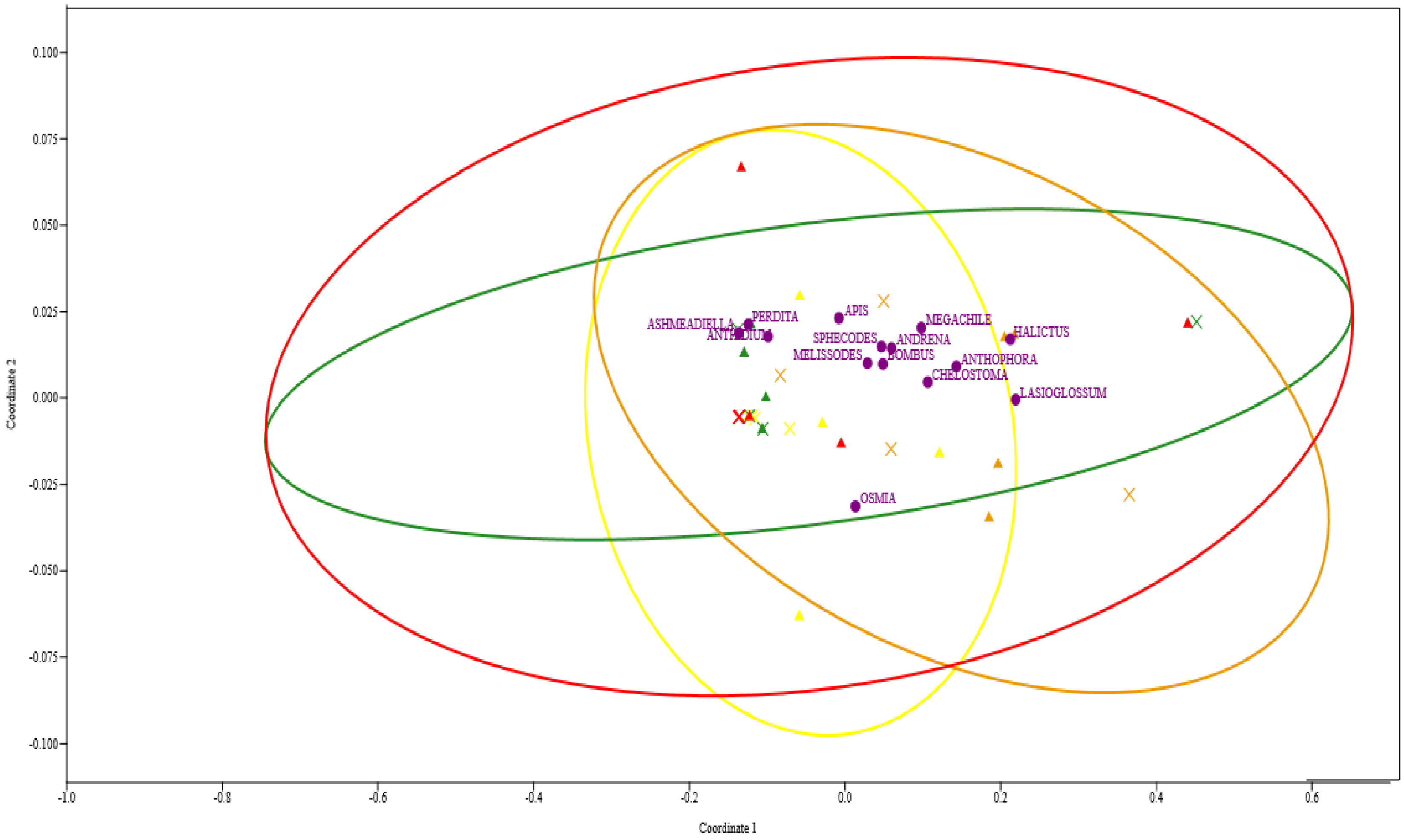

Figure 3. Bi-plot from Non-Metric Multidimensional Scaling (NMDS) analyses depicting degrees of similarity in bee community assemblages across burn severity classes (green = undisturbed; yellow = low severity; orange = medium severity; red = high severity) and between one (triangles) and two (X's) year's post-fire within submontane stands located in the 2020 Creek Fire boundary of Sierra National Forest, CA.

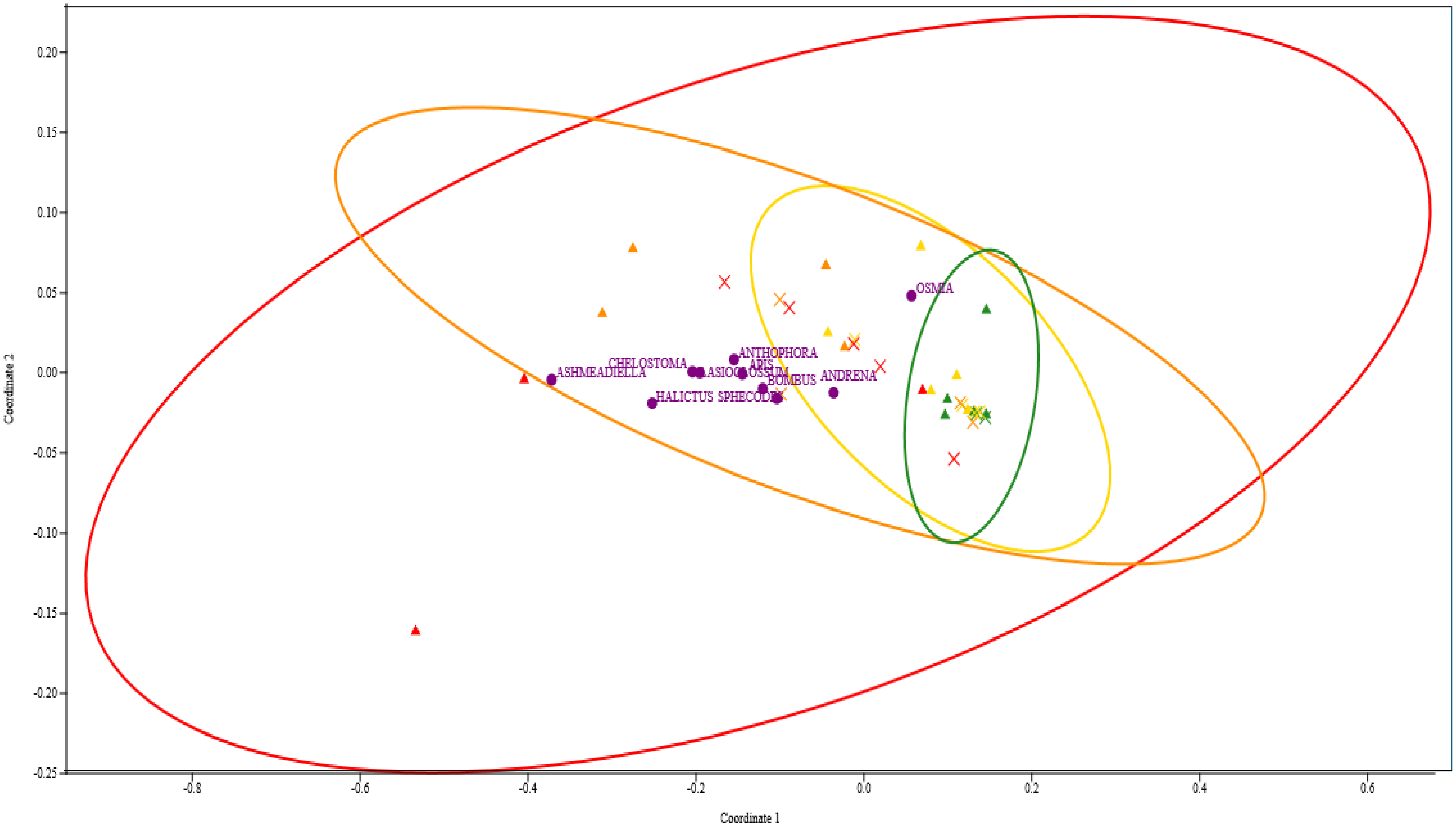

Figure 4. Bi-plot from Non-Metric Multidimensional Scaling (NMDS) analyses depicting degrees of similarity in bee community assemblages across burn severity classes (green = undisturbed; yellow = low severity; orange = medium severity; red = high severity) and between one (triangles) and two (X's) year's post-fire within montane stands located in the 2020 Creek Fire boundary of Sierra National Forest, CA.

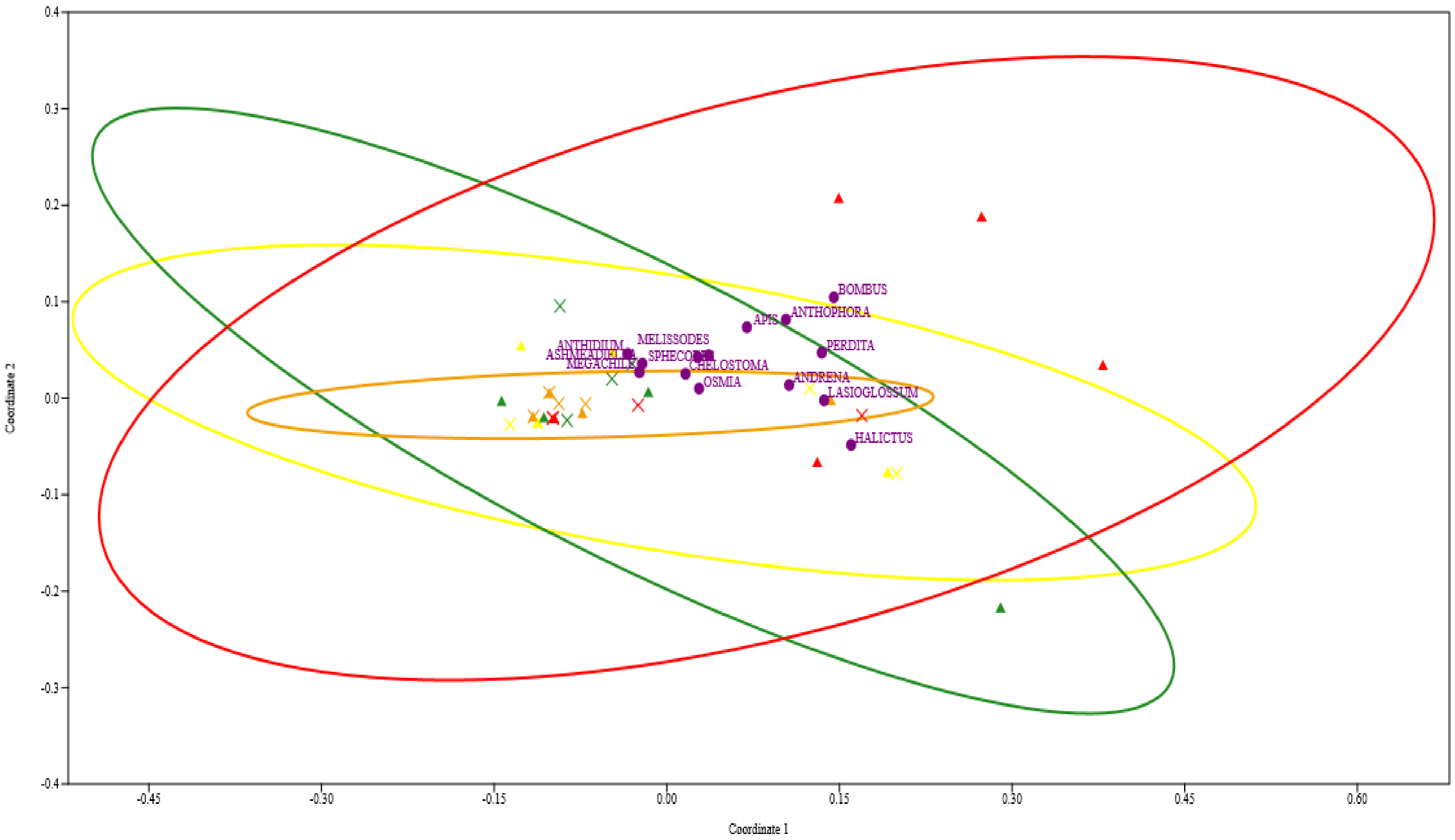

Figure 5. Bi-plot from Non-Metric Multidimensional Scaling (NMDS) analyses depicting degrees of similarity in bee community assemblages across burn severity classes (green = undisturbed; yellow = low severity; orange = medium severity; red = high severity) and between one (triangles) and two (X's) year's post-fire within upper montane stands located in the 2020 Creek Fire boundary of Sierra National Forest, CA.

Table 2. Summary of a generalized linear model analysis describing variation in bee assemblages due to effects of variation in elevation, basal area (BA), canopy closure (CC), floral abundance (FA), floral species richness (FR), litter cover (LC), shrub cover (SC), bare soil (BS), rock cover (RC), grass cover (GC), and coarse woody debris (CWD), percent tree mortality (% TM) and time since fire (TSF); emboldened Prob>|χ2| values indicate significant (α = 0.10) parameter effects.

Variable	**Parameter**	**β**	**SE**	**χ2**	**Prob>|χ2|**
Abundance	Intercept	2.4992	0.1898	173.05	<**.0001**
	ELEV.	-0.0001	<.0001	33.67	<**.0001**
	BA	0.0016	0.0002	59.18	<**.0001**
	CC	0.0007	0.0019	0.16	0.6931
	FA	-0.0001	0.0001	1.29	0.2567
	FR	0.2483	0.0153	263.42	<**.0001**
	LC	0.0005	0.0015	0.09	0.7645
	SC	0.0179	0.0017	108.54	<**.0001**
	BS	-0.0005	0.0016	0.09	0.7665
	RC	-0.0236	0.0053	21.02	<**.0001**
	GC	-0.0122	0.0013	90.11	<**.0001**
	CWD	0.0045	0.0014	10.13	0.0015
	% TM	0.0083	0.0009	90.00	<**.0001**
	TSF	0.2391	0.0395	36.29	<**.0001**
Species richness	Intercept	1.1232	0.3705	9.13	**0.0025**
	ELEV.	0.0001	<.0001	1.50	0.2199
	BA	0.0012	0.0005	6.95	**0.0084**
	CC	-0.0053	0.0037	2.04	0.1533
	FA	-0.0001	0.0001	1.10	0.2942
	FR	0.1864	0.0309	36.25	<**.0001**
	LC	-0.0028	0.0032	0.75	0.385
	SC	-0.0150	0.0033	20.23	<**.0001**
	BS	-0.0110	0.0035	10.16	**0.0014**
	RC	-0.0099	0.0101	0.96	0.3273
	GC	-0.0076	0.0026	8.92	**0.0028**
	CWD	0.0060	0.0030	3.80	**0.0512**
	% tree M	0.0031	0.0019	2.74	0.0977
	TSF	0.3340	0.0805	16.99	<**.0001**

Diversity	Intercept	0.5653	0.6524	0.75	0.3874
	ELEV.	0.0001	0.0001	3.01	0.0829
	BA	0.0010	0.0008	1.69	0.193
	CC	-0.0069	0.0064	1.14	0.2863
	FA	-0.0001	0.0003	0.14	0.7069
	FR	0.1258	0.0552	5.02	**0.0251**
	LC	-0.0035	0.0055	0.42	0.5178
	SC	0.0066	0.0060	1.17	0.2788
	BS	-0.0053	0.0060	0.75	0.3852
	RC	-0.0145	0.0174	0.69	0.4048
	GC	-0.0035	0.0046	0.56	0.4538
	CWD	0.0018	0.0055	0.11	0.7412
	% tree M	0.0004	0.0032	0.02	0.8884
	TSF	0.1472	0.1461	1.01	0.3154

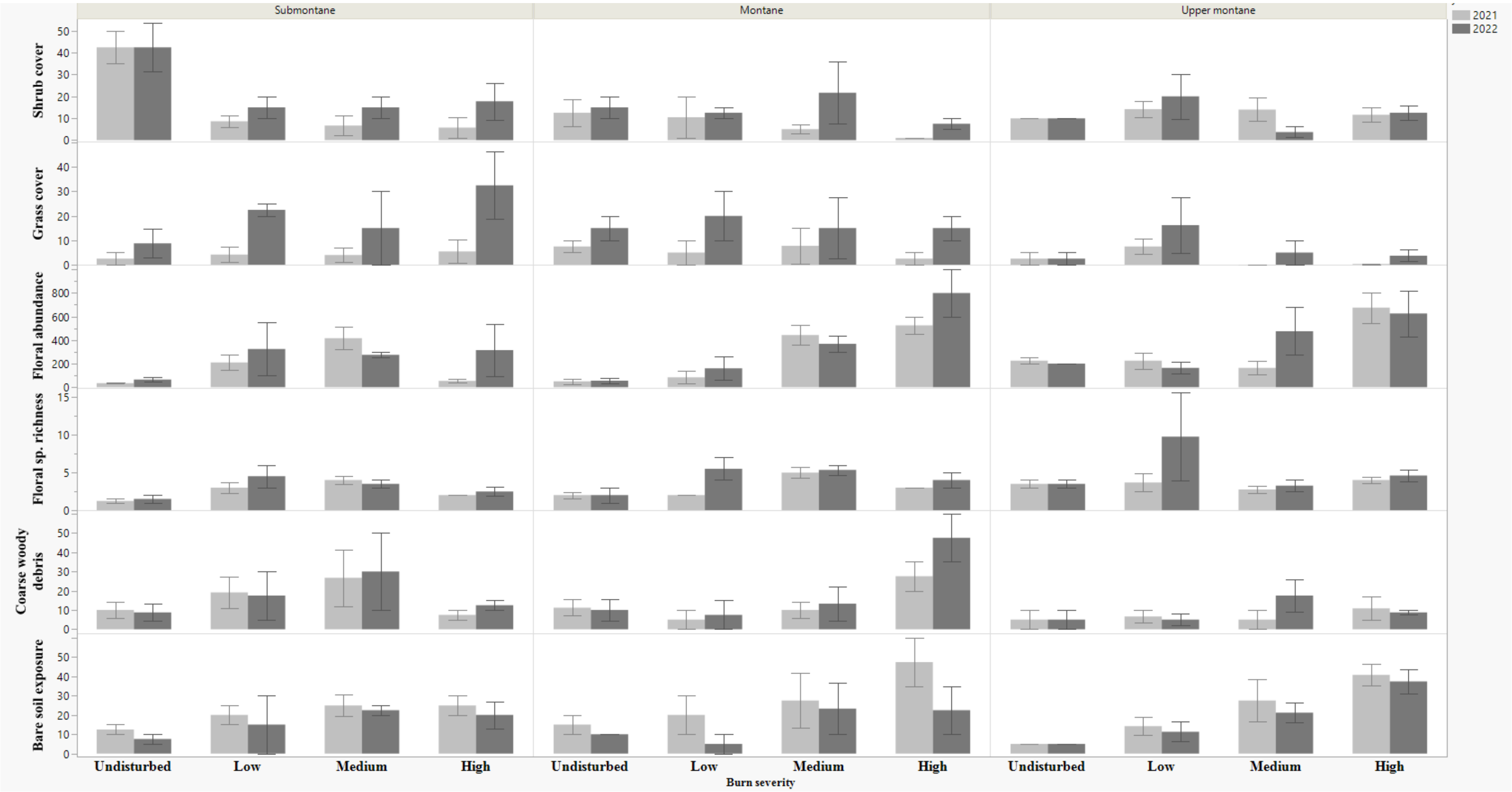

Figure 6. Plot-level means and associated standard errors of environmental attributes significantly (α = 0.05) correlated with bee abundance or diversity within the 2020 Creek Fire boundary of Sierra National Forest, CA. Individual means are separated by burn severity classes, forest biotic zones and time since fire.

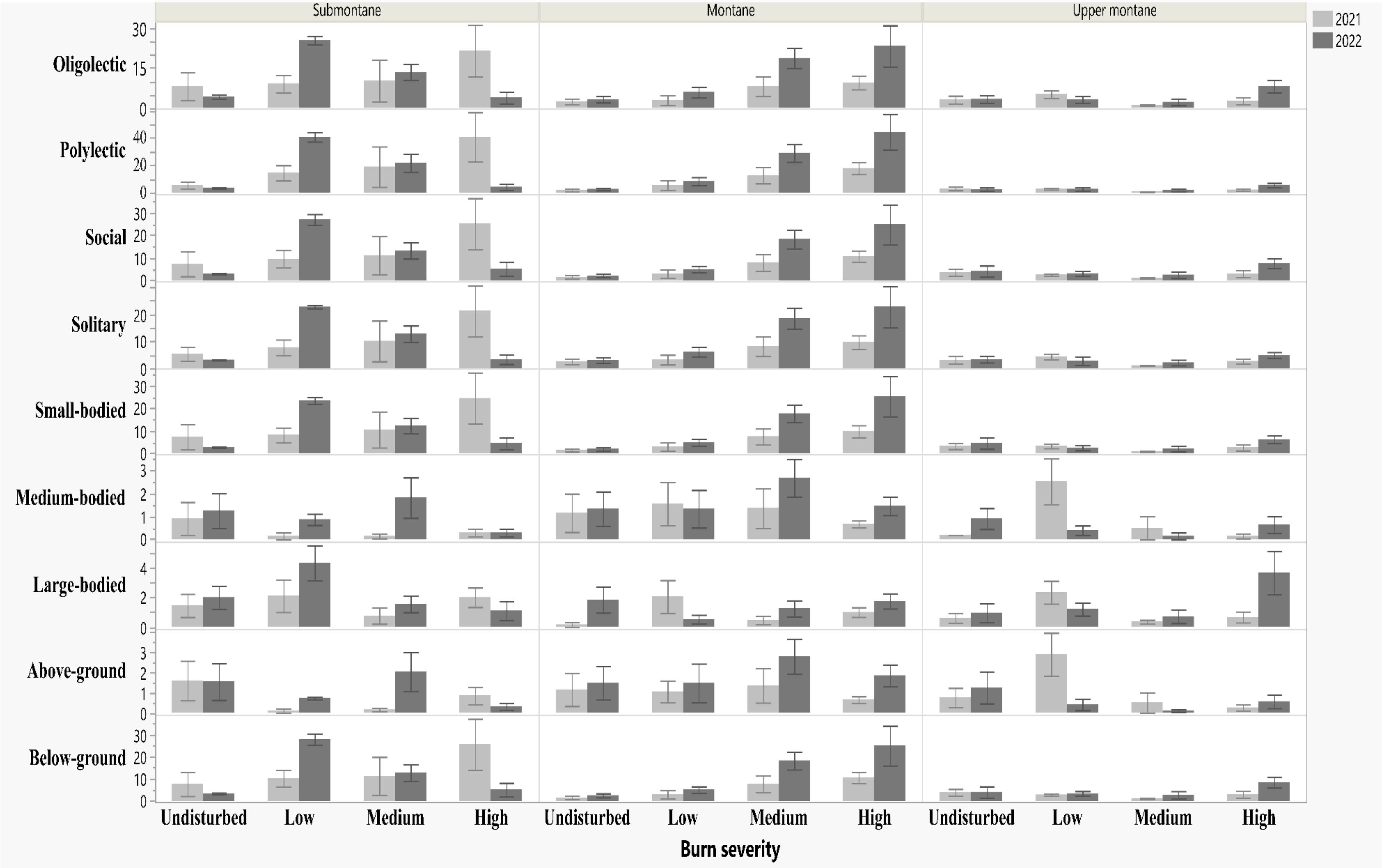

Figure 7. Differences among soil burn severity classes, forest biotic zones and time since fire (2021 vs. 2022) in plot-level abundances of bees associated with various functional traits (lecty, sociality, body size and nesting location). Means not connected by the same letter(s) within individual rows differ significantly ($\alpha = 0.05$).

Table 3. Results from Three-way ANOVA testing for significant (α = 0.05) effects of wildfire burn severity, time since fire, forest biotic zone and their interactions on the abundance of individual bee functional groups within the 2020 Creek Fire boundary of Sierra National Forest, CA.

Functional trait	**Parameter**	**DF**	**F**	**Prob > F**
Oligolectic	Life zone	2	15.56	<0.0001
	Severity	3	5.08	0.0029
	Year	1	10.47	0.0018
	Life zone*Severity	6	8.91	<0.0001
	Life zone*Year	2	1.38	0.2572
	Severity*Year	3	3.44	0.0209
	Life zone*Severity*Year	6	0.86	0.5221
	Whole model	23,72	5.54	<0.0001
Polylectic	Life zone	2	5.45	0.0061
	Severity	3	2.74	0.049
	Year	1	12.61	0.007
	Life zone*Severity	6	6.76	<0.0001
	Life zone*Year	2	1.42	0.2479
	Severity*Year	3	2.69	0.0517
	Life zone*Severity*Year	6	0.6	0.7276
	Whole model	23,72	3.71	<0.0001
Solitary	Life zone	2	9.11	0.0003
	Severity	3	3.25	0.0263
	Year	1	9.68	0.0026
	Life zone*Severity	6	6.61	<0.0001
	Life zone*Year	2	1.31	0.2737
	Severity*Year	3	2.45	0.0694
	Life zone*Severity*Year	6	0.51	0.7968
	Whole model	23,72	3.86	<0.0001

Social	Life zone	2	5.12	0.0082
	Severity	3	5.08	0.0029
	Year	1	10.47	0.0018
	Life zone*Severity	6	8.91	<0.0001
	Life zone*Year	2	1.38	0.2572
	Severity*Year	3	3.44	0.0209
	Life zone*Severity*Year	6	0.86	0.5221
	Whole model	23,72	5.54	<0.0001
Small-bodied	Life zone	2	5.2	0.0076
	Severity	3	3.72	0.0148
	Year	1	10.83	0.0015
	Life zone*Severity	6	6.32	<0.0001
	Life zone*Year	2	1.42	0.2475
	Severity*Year	3	2.74	0.0494
	Life zone*Severity*Year	6	0.6	0.7276
	Whole model	23,72	0.81	0.5637
Medium bodied	Life zone	2	4.35	0.0163
	Severity	3	1.7388	0.1662
	Year	1	8.25	0.0053
	Life zone*Severity	6	3.31	0.0059
	Life zone*Year	2	1.11	0.336
	Severity*Year	3	2.48	0.0667
	Life zone*Severity*Year	6	0.48	0.8155
	Whole model	23,72	2.3	0.0036
Large-bodied	Life zone	2	2.32	0.1048
	Severity	3	1.71	0.1716
	Year	1	5.65	0.0199
	Life zone*Severity	6	2.29	0.0434
	Life zone*Year	2	0.76	0.4675
	Severity*Year	3	2.65	0.0545
	Life zone*Severity*Year	6	0.45	0.8423
	Whole model	23,72	1.81	0.0281

Above-ground nester	Life zone	2	4.64	0.0453
	Severity	3	2.64	0.0555
	Year	1	9.993	0.0023
	Life zone*Severity	6	3.31	0.0126
	Life zone*Year	2	1.31	0.2762
	Severity*Year	3	3.02	0.0351
	Life zone*Severity*Year	6	0.17	0.9834
	Whole model	21,74	2.42	0.0021
Below-ground nester	Life zone	2	4.53	0.0138
	Severity	3	4.21	0.0082
	Year	1	11.9	0.0009
	Life zone*Severity	6	6.64	<0.0001
	Life zone*Year	2	1.23	0.2972
	Severity*Year	3	2.75	0.0486
	Life zone*Severity*Year	6	0.17	0.9834
	Whole model	21,74	0.98	0.4386

Chapter two: Effects of forest stand structure, overstory composition, and thinning treatments on wild bee communities in pinyon-ponderosa pine landscapes of northern New Mexico

Abstract

Regional-scale losses in fire activity associated with centuries of logging and livestock grazing in the southwestern United States have contributed to the encroachment of pinyon pine and juniper (PJ) into high-elevation forests historically dominated by ponderosa pine. It is unclear whether alterations in overstory structure and ground cover conditions following PJ encroachment into ponderosa pine forests influence the diversity or community compositions of ecologically important insect groups like wild and native bees. Similarly, documentation of bee community responses to common ecological restoration practices in PJ-ponderosa pine ecosystems is minimal. Here, we documented bee community and functional group responses to 1) variation in ponderosa pine cover within a montane PJ-ponderosa pine forested landscape in Northern New Mexico, and 2) stand-thinning operations used to restore a ponderosa pine-dominant overstory across the broader landscape. Ponderosa pine cover, snag abundance, and floral abundance exhibited significant, positive correlations with bee abundance, while snag abundance and bare soil exposure were significantly and positively correlated with bee diversity. Overall, bees were significantly more abundant in stands with moderate to high amounts of ponderosa pine cover in comparison to stands that were dominated by pinyon pine and juniper. However, neither bee diversity nor local community structures exhibited significant associations with overstory tree composition, possibly due to the relative uniformity in canopy structure and ground cover conditions across the study site. Minor but significant increases in bee abundance were observed in thinned areas between pre- and post-treatment years, particularly for polylectic, social, and above-ground nesting species. Aside from potentially reducing local abundance

levels, our analyses largely suggest that PJ encroachment likely does not negatively impact bee communities residing in forested landscapes historically dominated by ponderosa pine. Regardless, management practices that reduce canopy closure, maintain or increase ponderosa pine dominance, and preserve or create key habitat features (snags, bare soil patches, and floral resources) are likely to benefit wild bees in these ecosystems.

Introduction

The introduction of livestock and wildfire suppression beginning in the mid-nineteenth century in the southwestern United States have homogenized the structure of the region's mixed-conifer forests, where stands are far denser and exhibit higher rates of canopy and shrub cover compared to pre-suppression conditions (Allen et al. 2002, Miller and Safford 2017, Addington et al. 2018). Regional-scale reductions in fire activity have caused increases in shrub density and cover in contemporary stands, which has contributed to unnaturally high densities of shade-tolerant trees including pinyon pine, *Pinus edulis* Englemn., and juniper, *Juniperus* L., spp. developing within high elevation forests historically dominated by ponderosa pine, *P. ponderosa* Douglas ex. Lawson (Miller and Tausch 2002, Johnstone et al. 2016, Minott and Kolb 2020). Recent droughts have further exacerbated the conversion of ponderosa pine forests to pinyon-juniper (PJ) woodland (Huffman et al. 2008, Romme et al. 2009, Minott and Kolb 2020). Changes in fuel loads or overstory composition resulting from altered disturbance regimes and a changing climate may in turn alter the diversity and composition of insect communities in forest ecosystems (Ferrenberg et al. 2006, Williams et al. 2010, Dole et al. 2023). However, recent investigations into the relationships between habitat structure and insect diversity in pinyon pine ecosystems in the southwest pertain only to low-elevation, pinyon-juniper woodlands in Arizona and Colorado (Uhey et al. 2020, Davis and Comai 2022). It is unclear whether encroachment of pinyon-juniper into higher montane, ponderosa pine forests alters the diversity or structure of local insect communities. Similarly, documentation of the community-level responses of ecologically or economically important insect guilds (e.g., pollinators) to widely implemented forest management actions used to restore ponderosa pine dominance within these ecosystems is unavailable.

Wild and native bees (Hymenoptera: Apoidea) provide the majority of pollination services for herbaceous plant communities in North American forests (Hanula et al. 2016, Glenny et al. 2022). Aside from their function in maintaining broader ecological networks and promoting landscape-level biodiversity in forest ecosystems (Loveless and Hamlick 1984, Potts et al. 2016), many of these bee-pollinated plants provide additional ecological services, including the protection of water quality and prevention of soil erosion (Wratten et al. 2012). However, bee populations are in decline globally. Land use change (Brown and Paxton 2009), loss of landscape-level heterogeneity (Kremen et al. 2002), and the degradation of habitat (Thapa-Magar et al. 2020) are primary factors that threaten their sustainability (Koh et al. 2016, Drossart and Gerard 2020, Glenny et al. 2022). Declines in forest-associated bee populations may negatively impact native herbaceous plant diversity and overall forest ecosystem function. Consequently, investigation into what landscape and stand-level factors influence bee assemblages in North American forests has increased since the early 2000s, to identify potential strategies for their conservation (reviewed in Hanula et al. 2016 and Glenny et al. 2022). However, information on the biodiversity and habitat requirements of bees occupying pinyon-ponderosa pine ecotones and high-elevation, ponderosa pine forests is minimal for the southwest region, and for New Mexico, in particular (Carril et al. 2018, Glenny et al. 2022).

In general, open-stand conditions can promote the abundance and diversity of bees in temperate forests. Reductions in canopy cover following tree death or removal may also alter microclimatic conditions associated with increased foraging activity by bees (Aleixo et al. 2017). The removal of live canopy following fire events (Ponisio et al. 2016, Galbraith et al. 2019, Burkle et al. 2019), insect outbreaks (Davis et al. 2020, Foote et al.2020) as well as forest harvesting and management operations (Taki et al. 2013, Rivers et al. 2016, Gelles et al. 2022,

2023) can benefit bees by increasing light availability towards the understory which may promote herbaceous plant growth (Anderson et al. 1969), thereby increasing bee foraging resources (McCabe et al. 2019, Walters and Stiles 1996). Reductions in fuel loads following certain disturbances (primarily fire) may benefit ground-nesting bees by increasing the amount of exposed, bare soil (Cane and Neff 2011, Hanula et al. 2016, Glenny et al. 2022). However, it is unclear whether pinyon and juniper encroachment into higher elevation, ponderosa pine forests significantly alter overstory structure and local ground cover conditions that might ultimately affect local bee abundance or diversity. Such changes in overstory tree composition may have negative impacts on the local bee community if increases in PJ stem densities leads to higher rates of canopy closure, reduce light and surface temperatures on the forest floor, or increase fuel loads (litter, coarse woody debris, shrub cover). Alternatively, forests co-dominated by pinyon-juniper and ponderosa pine may have more heterogenous habitat patches with complementary floral and nesting resources or abiotic conditions that could support a broader species pool of bees with variable life histories (Pulliam 2000., Glenny et al. 2023).

We determined whether wild bee abundance or diversity varied along a gradient of pinyon-juniper cover within a montane forest of northern New Mexico historically dominated by ponderosa pine. We further described the stand-level factors associated with site-level variation in bee diversity and community assemblages. Finally, we documented bee community and functional group responses to stand-thinning operations conducted throughout the study site. These operations were focused on reducing pinyon and juniper stem densities to restore stand conditions to a ponderosa pine-dominant overstory and improve forest floor conditions for ungulates. We predicted that: 1) bee abundance and diversity would be maximized in areas with low amounts of canopy closure and high amounts of floral resources and nesting substrates (e.g., bare soil); 2) bee community assemblages would vary along a gradient of ponderosa pine cover across the study site if variability in canopy structure or ground cover composition between pinyon and ponderosa pine-dominant stands was also present; and 3) bee diversity or abundance would increase following thinning treatments across the study site if altered stand structures increased the amounts of their floral resources or nesting substrates on the forest floor.

Methods

Study site and plot descriptions

This research was conducted at Ignacio Chavez Wilderness Study Area (35.50493, -107.32737) at elevations of 2450-2500 m, located within Mesa Chivato, Cibola National Forest, NM during July-September of 2021 and 2022. Common tree species within the study area include ponderosa pine, pinyon pine, one-seed juniper, *J. monosperma* (Engelm.) Sarg., and Gambel oak, *Quercus gambelii* Nutt. Within the area, both pinyon pine and juniper have increased considerably in the understory of what historically was a frequent-fire ponderosa pine forest (Huffman et al. 2008). Common herbaceous plants include rabbit brush, *Crysothamnus* Nutt., spp., Bush mallow, *Malacothamnus* Green spp. Locust, *Robinia neomexicana* A. Gray, Beardtongue, *Penstemon* Schmidel spp., Fleabane, *Erigeron* L. prickly pear cacti, *Optunia* Mill spp. and Horsebrush, *Tetradymia* DC spp. A total of thirty experimental plots (n = 30) comprised of hexagonal units encompassing five hectares each were established in 2020. Plot boundaries were delineated by the New Department of Fish and Wildlife (NMDFW) prior to the beginning of an ecological restoration project designed to restore stand conditions back to historical (pre-1800s) densities of pinyon pine and juniper trees while retaining healthy ponderosa pine and oak. The overarching goal of these thinning treatments was to enhance wildlife habitat by reducing the density of tree cover, thereby facilitating the reestablishment of shrubs, grasses, and forbs

(Seybold and Graves personal communication 2019). Plots with canopy compositions of > 70 % pinyon pine and juniper (PJ) were assigned to a ‘pinyon-juniper (PJ) dominant’ group (n = 11). Plots with canopy compositions of 30-69 % PJ were assigned to a PJ-ponderosa-codominant’ group (n = 9). Plots with < 30% PJ were assigned to a ‘ponderosa pine dominant’ group (n = 10).

In October 2021, stands located in 20 of the 30 plots were thinned and received one of two residual slash removal treatments including: 1) full tree removal; or 2) lopping felled branch material to 1-1.2 m length pieces and scattering them around individual stumps (i.e, ‘lop and scatter). The remaining 10 were left as untreated controls. Variable slash removal strategies were used to determine differences in residual population levels of pinyon ips, *Ips confusus* Wood and Bright, among treatment groups in a separate study (Seybold and Graves personal communication 2019). Ponderosa pine growing above the pinyon-juniper canopy were retained (unless affected by dwarf mistletoe, *Arceuthobium vaginatum* (M.Bieb)., while all other conifers within a 10-meter radius (and below < 25 cm diameters at root collar) surrounding individual ponderosa pine were removed to reduce competition. Leave trees were retained in groups and spaced 6-15 m between one another. Individual groups consisted of trees of the same size or age class.

Sampling forest stand structure and forest floor composition

Diameters at breast height (DBH) and species of each overstory tree located within plot boundaries was determined in 2021 by the New Mexico Highlands Institute and NMDFW. Plot-level quadradic mean diameter (QMD) and basal area was determined from DBH measurements. Mean percent canopy closure per plot was determined from the average of five spherical densiometer readings taken at plot center as well as at 15, 30 and 45 m from plot center at azimuths of zero and 180 degrees (seven readings per plot) in 2021 and 2022. Plot-level herbaceous plant species richness and abundance (total number of inflorescences estimated in units of 20) was determined within a 10 x 50 m belt transect extending at azimuths of zero and 180 degrees from plot center (10 x 25 m belts per azimuth) during July and August of 2021 and 2022 by the Ecological Restoration Institute of Northern Arizona University and Foote. Forest floor composition was determined by using a square 1 x 1 m sampling quadrat, with measurements taken at five points spaced by 5 m each along belt transects with azimuths of zero and 180 degrees during July of 2021 and 2022. At each sampling point, proportions of the quadrat's interior occupied or covered by rock, bare soil, leaf litter, coarse woody debris (diameter ≥ 10 cm), grass and shrubs was estimated. Quadrat values from all 10 points were averaged to produce a plot-level mean for each ground cover category.

Bee community sampling

Insect pan traps are an effective, passive method for sampling forest-associated bees (Campbell and Hanula 2007). Therefore, bees were sampled using twelve pan traps per plot, deployed along the same N-S transect used for plot-level floral abundance and diversity measurements. Pan traps were constructed from 256 mL capacity polypropylene cups (8.75 cm mouth, 7.5 cm depth) containing approximately 250 mL distilled H_2O mixed with liquid soap detergent (for reducing surface tension) and were spray-painted either white, fluorescent yellow, or fluorescent blue (four traps per color) and spaced 4 m apart. Traps were deployed for 48-hour intervals, July 5-14, August 4-13, and September 8-17, during both 2021 and 2022; each plot was sampled during each interval. All bee specimens captured were stored in 70% ethanol until processed and identified. Bees were identified to species or morpho-species using appropriate keys (Hurd and Michener 1955, Mitchell, 1962, 1980, LaBerge 1989, Michener 2000, Gibbs

2010, Williams et al. 2014, Best et al. 2023) other pictorial guides (discoverlife.org) and relevant reference material.

Statistical analyses

All statistical analyses were conducted using the R programming language (v 3.5.2 ‘Eggshell Igloo’, R Core Team), JMP 17 statistical software (SAS Institute Inc., Cary, NC) or PAST 4 statistical software (University of Oslo, Oslo, Norway). Prior to all analyses, the Shapiro-Wilk test and homogeneity of variance (HOV) tests were used to determine whether response variables were normally distributed and exhibited equal variance, respectively. Data not normally distributed were either log or square root-transformed, or otherwise analyzed with generalized regression techniques that could account for non-normal distributions.

Differences in bee diversity among overstory classes and treatment groups

Differences in bee abundance, species richness, and diversity among overstory classes were determined using Analysis of Variance (ANOVA). Separate analyses were used for each response variable. Linear regression was used to illustrate the direction and magnitude of correlations between % ponderosa pine cover versus bee abundance, species richness and diversity. Separate models were developed for each response variable. Two-way ANOVA’ were conducted to determine differences in bee abundance, species richness and diversity between 2021 and 2022 and among treatment groups. Bee community composition was compared among overstory classes as well as between thinned and undisturbed treatment groups using a distance-based (Euclidean) framework under the non-metric multidimensional scaling (NMDS) platform provided under PAST (version 4.14) statistical software (Hammer et al. 2001) combined with permutational multivariate analysis of variance (PERMANOVA).

Differences in the abundance of bees associated with various functional groups among overstory classes were determined using ANOVA. Two-way ANOVA analyses were conducted to determine differences in functional group abundances between years and among thinning treatments. Following methods described by Forrest et al. (2015) and Williams et al. (2015), species or morphospecies functional group assignments were based off information on life-history traits likely to affect bee habitat associations, including dietary specialization (polylectic vs. oligolectic), nesting location (above-ground vs. below-ground) and sociality (social vs. solitary). Separate tests were conducted for each functional group.

Effects of forest structural attributes on bee diversity and bee functional groups

We used generalized linear models (Family: Poisson; link: Log) to determine relative effect sizes of forest structural attributes on bee abundance, species richness, and diversity, treating plot-level measurements (separated by year) as the unit of analysis. Model parameters included both live and dead tree basal area, plot-level quadratic mean diameter, canopy closure, % ponderosa pine cover, nesting resources (snags/ha, coarse woody debris and bare soil cover), and floral resources (floral abundance and floral species richness). Separate models were generated for each response variable of interest. We used stepwise model selection procedures (backwards selection) to evaluate which forest habitat variables were valid for entry into explanatory models accounting for variation in the abundance of individual bee functional groups. Variables considered for entry in the model were the same as described above, with a significance threshold of $p < 0.10$ determined by ordinary least squares (OLS) regression.

Results

Pan trap collections and summary of plot structural attribute data

We collected a total of 1154 bee specimens (591 in 2021; 563 in 2022) from 26 genera representing 48 species/morphospecies. The most prevalent genera collected in 2021 were *Lasioglossum* (*Dialictus*) Curtis spp., *Perdita* Smith spp., *Diadasia* Patton spp., *Dianthidium* Cockerell spp., and *Melissodes* Latrielle spp., accounting for 34 %, 18 %, 12 %, 4 % and 4 % of all captures, respectively. The most prevalent genera collected in 2022 were also *Lasioglossum* (*Dialictus*) spp., *Perdita* spp., *Diadasia* spp., *Dianthidium* spp., and *Melissodes* spp., accounting for 43 %, 24 %, 14 %, 4 % and 3 % respectively.

Plot-level means, associated standard errors (SE), and Tukey's honestly significant difference (HSD) are summarized in Table 1. The latter were used to test to determine differences in various structural attributes pertaining to the stand overstory structure and ground cover composition among tree overstory cover classes. Overall, overstory attributes including plot-level basal area (range: 0.8 - 44.5 m^2/ha; mean: 12.62 ± 1.64 m^2/ha), QMD (range: 6.9 – 83.8 cm; mean: 23.0 ± 0.3 cm) and canopy closure (range: 0-80 %; mean: 30.5 ± 4.4 %) did not significantly vary among overstory cover classes. Forest ground cover attributes including bare soil exposure (range: 10-40 %; mean: 21. 3 ± 2.1 %), coarse woody debris (CWD) cover (range: 0 – 30 %; mean: 13.5 ± 9.6), grass cover (range: 10 – 90 %; mean: 49.7 ± 4.3 %) and litter cover (range: 5 – 65 %; mean: 30.7 ± 3.3 %) also did not significantly differ among overstory cover classes. Mean floral abundance (range: 10 – 150 inflorescences; mean: 39.2 ± 4.8 inflorescences) did not significantly differ among overstory cover classes. However, mean floral species richness (range: 11 – 35 species; mean: 22.9 ± 8.5 species) was significantly lower in PJ-dominant plots compared to PJ-ponderosa-codominant and ponderosa-dominant plots (Table 1).

Differences in bee abundance and diversity among tree overstory classes

Overall, mean bee abundance was highest in ponderosa-dominant plots, and significantly reduced in PJ-dominant plots ($F_{2,27} = 3.5$; $p = 0.04$, Figure 1). There were no significant differences in bee species richness ($F_{2,27} = 0.58$; $p = 0.58$) nor diversity ($F_{2,27} = 1.09$; $p = 0.34$) among overstory classes (Fig. 1). Overall, % ponderosa cover exhibited a significant and positive relationship with bee abundance ($R^2 = 0.18$; $F_{1,28} = 5.31$; $p = 0.0288$) but not with bee species richness ($R^2 = 0.07$; $F_{1,28} = 1.20$; $p = 0.28$) nor bee diversity ($R^2 = 0.05$; $F_{1,28} = 0.01$; $p = 0.43$) across the study site (Figure 2).

Results from NMDS analyses demonstrated that the 95 % confidence ellipsoids of both PJ and PJ-ponderosa pine cover classes encompassed less area than that of the ponderosa pine cover class, whose associated plots were more variable with respective to local bee community composition (Figure 3). The greatest overlap or similarity with respect to plot-level community assemblages was observed between the ellipsoids of PJ-ponderosa and ponderosa cover classes. Axes one and two explained 70.0 and 9.7 %, respectively, of the total variance (stress = 0.06) present within plot-level community composition due to the relative abundance of individual bee species.

Differences in bee abundance and diversity among stand-thinning and slash management treatments

Results from two-way ANOVA determined no significant differences in bee abundance, species richness, and Shannon's diversity between 2021 and 2022 and among different thinning treatments (untreated, full tree removal and lop and scatter), including their interactive effects, (Table 3, Figure 4). Neither sampling year ($F_{1,58} = 0.11$; $p = 0.7314$), thinning treatment ($F_{2,57} = 2.7$; $p = 0.0703$) nor the interactive term between these factors ($F_{2,56} = 0.42$; $p = 0.6565$)

exhibited significant effects on bee abundance (whole model: $F_{5,54} = 1.31$; $p = 0.2739$). Neither sampling year ($F_{1,58} = 0.21$; $p = 0.6477$), thinning treatment ($F_{2,57} = 0.45$; $p = 0.6689$) nor their interactive term ($F_{2,56} = 0.08$; $p = 0. 9242$) exhibited significant effects of bee species richness (whole model: $F_{5,54} = 0.29$; $p = 0.945$.). Similarly, bee diversity (whole model: $F_{5,54} = 0.25$; $p = 0.938$) was not significantly affected by sampling year ($F_{1,58} = 0.22$; $p = 0.6385$), thinning treatment ($F_{2,57} = 0.31$; $p = 0.7344$) nor the interactive term ($F_{2,56} = 0.22$; $p = 0.8006$).

Results from NMDS analyses used to determine degrees of similarity in bee community assemblages among plots within individual treatment categories separated by year demonstrated that similarity in plot-level community composition increased from 2021 to 2022 (Figure 4). The 95 % confidence ellipsoids of both thinning treatment groups encompassed less area than the untreated control, reflecting greater plot-level similarity in local bee community composition within untreated areas. Axes one and two explained 55.6 and 37.8 %, respectively, of the total variance (stress = 0.097) present within plot-level community composition due to the relative abundance of individual species. Overall, Community assemblages within untreated plots also appeared to be less variable between 2021 and 2022 when compared to thinned plots (Figure 5).

Effects of forest structure on bee abundance and diversity

Results from generalized linear models determined bee abundance to be significantly affected by basal area (+ correlation), snag abundance (+), % ponderosa pine cover (+), shrub cover (-), floral abundance (+), litter cover (+) and CWD (-) (whole model: DF = 11; $\chi^2 = 146.71$; $p < 0.0001$, Table 4). Bee species richness was significantly affected by shrub cover (-) and bare soil exposure (+) (whole model: DF = 11; $\chi^2 = 47.30$; $p < 0.0001$). Snag abundance and bare soil exposure both exhibited positive relationships with bee diversity, and were the only environmental variables that were significant at the $\alpha = 0.05$ level (whole model: DF = 11; $\chi^2 = 46.27$; $p < 0.0001$). Plot-level mean values of significant environmental variables among thinning treatment classes are depicted in Figure 6.

Bee-functional group relationships with overstory composition and responses to thinning treatments

Results from ANOVA tests and Tukey's HSD testing for significant differences among overstory cover classes in their plot-level abundances of bees associated with various functional traits (lecty, sociality, and nesting location) are illustrated in Figure 7. Overall, the mean abundance of polylectic bees was greatest in ponderosa-dominant plots; however, means did not significantly differ among overstory cover classes ($F_{2,27} = 0.23$; $p = 0.7929$). The mean abundance of oligolectic bees was also greatest in PJ-ponderosa-codominant plots and significantly reduced within ponderosa-dominant plots ($F_{2,27} = 3.81$; $p = 0.0355$). The mean abundance of above-ground nesting bees was greatest in PJ-ponderosa-codominant plots and reduced in both ponderosa-dominant and PJ-dominant plots ($F_{2,27} = 3.24$; $p = 0.0552$). While it was also highest in PJ-ponderosa-codominant plots, the mean abundance of below-ground nesting bees did not significantly vary among overstory cover classes ($F_{2,27} = 1.16$; $p = 0.3288$), nor did the abundance of social ($F_{2,27} = 0.40$; $p = 0.6766$) or solitary bees ($F_{2,27} = 2.17$; $p = 0.1346$).

Results from two-way ANOVA, testing for significant differences in the abundance various bee functional groups between 2021 and 2022 and among different thinning treatments, including their interactive effects, are summarized in Table 5 and illustrated in Figure 8. Neither sampling year ($F_{1,58} = 0.22$; $p = 0.4851$), thinning treatment ($F_{2,57} = 0.08$; p = 0.9164) nor the interactive term between these factors ($F_{2,57} = 0.27$; $p = 0.76$) exhibited significant effects on the abundance of polylectic bees (whole model: $F_{5,54} = 0.24$; $p = 0.9392$). The abundance of oligolectic bees was significantly reduced in undisturbed plots compared to plots that were assigned to the 'lop and scatter' treatment ($F_{2,57} = 4.24$; $p = 0.0196$). However, neither sample year ($F_{1,58} = 0.58$; $p = 0.4473$) nor the interactive term between sample year and treatment ($F_{2,56} = 0.48$; $p = 0.61$), exhibited significant effects on their abundance (whole model: $F_{5,54} = 0.20$; $p = 0.0884$). The abundance of above-ground nesting bees was greatest in plots assigned plots assigned to the 'lop and scatter' treatment ($F_{2,56} = 5.7$; $p = 0.0056$), which increased in 2022 (Fig. 9). However, neither sample year ($F_{1,57} = 0.03$; $p = 0.9509$) nor the interactive term between sample year and treatment ($F_{2,57} = 0.25$; $p = 0.7855$), exhibited significant effects on their abundance (whole model: $F_{5,54} = 0.23$; $p = 0.0498$). The abundance of below-ground nesting bees was generally reduced in untreated plots compared to thinned plots, however, plot-level means did not significantly differ among treatment groups ($F_{2,57} = 0.57$; $p = 0.5696$) nor between years ($F_{1,58} = 0.21$; $p = 0.6453$), and was not significantly affected by their interactive term ($F_{2,57} = 0.57$; $p = 0.5696$) (whole model: $F_{5,54} = 0.42$; $p = 0.8267$). The abundance of social bees was highest in 2022 and within plots that were assigned to the 'lop and scatter' treatment', however, plot-level means did not significantly differ among treatment groups ($F_{2,57} = 1.25$; $p = 0.2942$) nor between years ($F_{1,58} = 0.96$; $p = 0.3296$), and was not significantly affected by their interactive term ($F_{2,57} = 0.41$; $p = 0.6651$) (whole model: $F_{5,54} = 0.86$; $p = 0.5103$). Plot-level means in solitary bee abundance increased from 2021 to 2022 across all treatment groups, and were highest in plots that were assigned to the 'full tree removal' treatment (Fig. 8). However, neither thinning treatment ($F_{2,57} = 0.21$; $p = 0.8090$), sampling year ($F_{1,58} = 0.51$; $p = 0.4762$), nor the interactive term ($F_{2,57} = 0.21$; $p = 0.8090$) between these factors exhibited significant effects on solitary bee abundance across the study site (Whole model: $F_{5,54} = 0.87$; $p = 0.5167$) (Table 5).

Results from stepwise regression procedures used to develop explanatory models on plot-level variation in bee functional group abundance due to local habitat structure are summarized in Table 6. The best model for explaining variation in plot-level, polylectic bee abundance included snag abundance (+ correlation), CWD abundance (-), shrub cover (-) and bare soil exposure (+) explanatory variables ($F_{4,55} = 3.62$; $p = 0.011$; $R^2 = 0.22$). A one unit change in snag abundance (± one snag or downed log), CWD cover (± 10%), shrub cover (± 10%) and bare soil exposure (± 10%) was estimated to change polylectic bee abundance by 0.4, 4.1, 1.6, and 1.7 %, respectively. The best model for explaining variation in plot-level, oligolectic bee abundance included QMD (+), CWD (-), SC (-), grass cover (-) and floral species richness (± one species) (+) as explanatory variables ($F_{5,54} = 3.05$; $p = 0.0171$; $R^2 = 0.22$). A one unit change in QMD (± 1 cm DBH), CWD, SC, GC (± 10%) and FR was estimated to change oligolectic bee abundance by 3.9, 0.9, 4.6, 1.2 and 4.3 %, respectively. The best model for explaining variation in plot-level abundance of above-ground nesting bees included basal area (BA) (-), SC (-) and GC (-) as negative, explanatory variables ($F_{3,56} = 7.04$; $p = 0.0004$; $R^2 = 0.28$). A one unit increase in BA (± 10 m^2/ha), SA, and GC was estimated to decrease above-ground nesting bee abundance by 3.6, 3.1 and 4.1 % respectively. Plot-level variation in below-ground nesting bee abundance was best explained by a model that included CWD and SC as negative, explanatory variables ($F_{2,57} = 6.54$; $p = 0.002$; $R^2 = 0.19$). A one unit increase in CWD and SC was estimated to reduce below-ground nesting bee abundance by 2.9 and 1.1 %, respectively. Plot-level variation in the abundance of social bees was best explained by a model that included CWD (-), SC (-) and BS (+) as explanatory variables ($F_{3,56} = 4.5$; $p = 0.0066$; $R^2 = 0.20$). A one unit change in CWD, SC and BS were estimated to change social bee abundance by 3.8, 1.9 and 2.1 %, respectively. Plot-level variation in solitary bee abundance was best explained by a model that included QMD (+), CWD (-), SC (-), GC (-) and FR (+) as explanatory variables ($F_{3,56} = 4.47$; $p = 0.003$; $R^2 = 0.19$). A one unit change in QMD, CWD, SC, GC and FR was estimated to change solitary bee abundance by 3.6, 4.3, 1.2, 0.7 and 4.4 %, respectively (Table 5).

Discussion

Differences in bee abundance and diversity among tree overstory classes

Regardless of year, bees were more abundant in stands with moderate to high amounts of ponderosa pine cover in comparison to stands that were dominated by pinyon pine and juniper across our study site (Figs. 1, 2). We further determined that % ponderosa pine cover, snag abundance, and floral abundance were positively correlated with bee abundance (Table 4). Bare soil exposure and snag about were positively correlated with bee diversity (Table 4) These relationships are well documented in related studies that collectively suggest structural elements like snags, exposed bare soil and an abundance of floral resources are important for both forest-associated bee communities (Potts et al. 2003, 2005, Lazarina et al. 2016, 2017, Galbraith et al. 2018, Burkle et al. 2019, Glenny et al. 2022). In comparison to PJ-dominant stands, our analyses suggest that areas with high amounts of ponderosa pine cover may have had more favorable conditions that promote local bee abundance, including reduced litter and shrub layers, increased floral diversity, or higher amounts of exposed, bare soils (Tables 1, 4, Fig. 6).

While bees were generally for abundant in ponderosa pine dominant stands, neither bee species richness nor diversity exhibited any significant associations with overstory tree composition (Fig. 1). Similarly, results from NMDS analyses suggest that bee community structure does not appear to be significantly affected by overstory tree composition, given the high degree of overlap between the NMDS 95% confidence ellipsoids of PJ-dominant, PJ-ponderosa-codominant, and ponderosa-dominant cover classes (Fig. 3). However, bee communities in plots located in PJ-dominant stands exhibited relatively high degrees of similarity with one another in regard to their respective community assemblages, potentially due to a smaller species pool residing in or utilizing these stands (Fig. 3). Overall, our analyses largely suggest that PJ encroachment likely does not negatively impact the diversity of bee communities residing in forested landscapes historically dominated by ponderosa pine. The general lack of variability in local bee diversity or community structure might be largely attributed to the overall, landscape-level homogeneity in stand structure (low basal area and canopy closure) observed across the study site (Table 1). These factors, along with various ground cover conditions (e.g., floral abundance, shrub cover) are known to influence bee diversity in PJ woodlands and ponderosa pine forests (Davis and Comai 2022, Gelles et al. 2022, Glenny et al. 2023).

Differences in bee abundance and diversity among stand-thinning and slash management treatments

We observed minor (< 10%) increases in bee abundance between pre- and post-treatment years of sampling within plots prescribed to either thinning treatment (Fig. 4). Similar patterns have been observed in other coniferous forests in the western US systems, where stand-thinning or tree harvests created open habitats and favorable abiotic conditions that likely enhanced bee floral resources or created additional nesting substrates for their populations (Rivers et al. 2016, Galbraith et al. 2019, Gelles et al. 2022, 2023). However, the observed increases in bee abundance were not significant (Table 3, Fig. 4). Bee species richness decreased from 2021 to 2022 in untreated areas as well as in ‘lop and scatter’ treated plots (Fig. 4), although these reductions in species richness were statistically insignificant as well (Table 3). Overall, plot-level bee diversity was unaffected by either thinning treatment (Fig. 4). The observed, marginal decline in species richness within 'lop and scatter' treated areas may partially be explained by increased amounts of tree debris on the ground following tree removal (Fig. 7), which may have obscured available nesting substrates utilized by certain taxa, or hindered herbaceous plant growth over relatively short time-periods (North et al. 2005). High amounts of tree material on the forest floor may have also reduced the attractiveness, visibility and therefore efficacy, of pan traps used to sample bees within our study site (Cane et al. 2000, Roulston et al. 2007). This potential issue may occur in all studies where passive trapping methods are used to assess changes in bee communities following forest disturbance. Incorporating other sampling techniques (e.g., aerial netting), while also identifying bee nesting locations within study sites can reduce the limitations of passive sampling methodologies used to document bee community responses to various forest disturbances.

We collected fewer bees and fewer bee species in untreated areas in 2022 compared to 2021 (Fig. 4). Increased uniformity in forest structure or connectivity of favorable habitat patches following thinning operations across the study site may have recruited bees towards disturbed areas, thereby reducing the concentrations of bees residing or foraging within untreated, ponderosa-dominant areas (Williams and Kremen 2007, Holzschuh et al. 2010, Gelles et al. 2022). Results from ordination analyses provide some evidence of this potential immigration. Specifically, similarity in plot-level community assemblages among all treatment categories increased from 2021 to 2022 across the study site, as the individual points of 2022 plots were in closer proximity to one another (Fig. 5). Overall, this increased similarity suggests that thinning operations designed to restore PJ-ponderosa forests to historical conditions may lead to more homogeneous bee communities across the broader landscape.

Bee-functional group relationships with overstory composition and responses to thinning treatments

Regardless of lecty, nest location or sociality, we generally observed higher abundances of bees in plots co-dominated by PJ and ponderosa pine in comparison to other overstory classes (Fig. 7). However, these differences were largely insignificant (Table 5, Fig. 8). Similarly, local abundances of individual bee functional groups were generally unaffected by the thinning operations conducted within this study site (Table 6, Fig. 8). Overall, forest patches with increased variety of physical structures (e.g., multiple tree species, heterogeneous litter layers) or abiotic conditions (shaded and unshaded micro-habitats) might support a greater number of bee species with distinct life histories within a broader landscape (Uhey et al. 2020, Glenny et al. 2023). The general landscape-level homogeneity of various overstory structural attributes (basal area, canopy closure) and ground cover conditions (Fig. 6, Table 1) present during both years of this study may have contributed to the relative lack of variation in local bee functional group abundances among overstory classes (Fig. 7) and between pre- and post-treatment years (Fig. 8).

We observed the highest abundance of polylectic (e.g., *Anthophora, Lasioglossum, Melissodes, Osmia* spp.) and oligolectic bees (e.g., various *Andrena, Diadasia* and *Mellitoma* spp.) in plots co-dominated by PJ and ponderosa pine (Fig. 7). Polylectic bee abundance was positively correlated with snag abundance and bare soil while oligolectic bee abundance was positively correlated with quadratic mean diameter (QMD) and floral species richness. The abundance of both functional groups was negatively correlated with CWD and shrub cover (Table 6). Overall, these observations suggest that both functional groups are likely relatively insensitive to short-term changes in habitat structure following thinning operations, provided that large amounts of CWD or dense shrub layers do not develop following stand thinning. Reducing these surface fuels via prescribed burning after thinning operations have been conducted may provide further benefits to bee communities inhabiting these ecosystems (Nyoka 2010). Such benefits have been demonstrated in ponderosa pine forests in Colorado (Gelles et al. 2023).

In general, the abundance of above-ground nesting bees (e.g., *Anthidium*, *Dianthidium* and *Osmia* spp.) was highest in PJ-ponderosa-codominant plots, lower in ponderosa-dominant plots and significantly reduced in PJ-dominant plots (Fig. 7). In contrast, below-ground nesting bee abundance (*Anthophora*, *Diadasia, Mellitoma* spp.; Halictid and Andrenid bees) did not significantly differ among overstory cover classes or thinning treatment categories (Fig. 7). Above-ground nesting bee abundance was highest in plots assigned to the ‘lop and scatter’ treatment in 2022 (Table 5, Fig. 8), positively correlated with both snag and CWD abundance, while and negatively correlated with basal area and grass cover (Table 6). Local above-ground nesting bees may prefer relatively open-stand conditions within this landscape. This fidelity might have compelled individuals to emigrate from untreated stands and towards thinned areas in 2022, thereby reducing their abundance in untreated locations. Below-ground nesting bee abundance was negatively correlated with CWD and shrub cover (Table 6). Related studies have suggested biological legacies like standing dead trees, downed logs can be utilized by various Anthophorine and Megachilid bees as nesting substrates (Simanonok and Burkle 2019, Fortuin and Ghandi 2021). Increases in downed tree branches and boles (CWD) following thinning operations (Fig. 6), may also benefit above-ground, cavity-nesting bees that utilize the abandoned galleries of bark beetles and wood borers over time. This has been demonstrated in thinned ponderosa pine forests in other ecoregions (Gelles et al. 2022). Similarly, natural disturbances that convert trees within PJ-ponderosa ecosystems into CWD could increase nesting sites for above-ground nesting species (Simanonok and Burkle 2019, Foote et al., 2020). Overall, these findings corroborate with results from related research that suggest maintaining a mosaic of ground cover conditions and preserving biological legacies within PJ-ponderosa pine ecosystems will likely benefit multiple bee functional groups (Ponisio et al. 2016, Glenny et al. 2022, 2023).

The abundance of social (e.g., subsocial *Anthophora*, *Halictus* and *Lasioglossum* spp.) and solitary bees (e.g., most Megachilid spp.) did not significantly vary among overstory cover classes (Fig. 7). Social bee abundance was negatively correlated with CWD and shrub cover, and positively correlated with bare soil exposure, while solitary bee abundance was positively correlated with QMD and floral species richness, and negatively correlated with CWD as well as shrub and grass cover (Table 6). These findings suggest that sparsely vegetated areas may be important for both solitary and aggregated bee nest establishment in PJ-ponderosa pine forests, further emphasizing the importance of bare ground for the populations of subterranean nesters (Cane 1991, Glenny et al. 2022). Solitary bee abundance increased from 2021 to 2022 across all thinning treatments, with the highest abundance in plots prescribed to the 'full tree removal' treatment (Fig 8). However, these increases were not significant (Table 5), indicating that solitary bees may be relatively unresponsive to habitat changes induced by thinning operations over short periods. However, a similar study that assessed the effects of forest structure on bee communities in PJ woodlands in the southwestern US reported a positive relationship between solitary bee abundance and canopy cover (Davis and Comai 2020). Therefore, negative effects of post-thinning reductions in canopy cover towards solitary taxa that preferentially utilize stands in later successional stages may develop over longer periods. Overall, long-term monitoring programs can improve our understanding of the temporal dynamics of bee community and individual functional group responses to these restoration practices, which can better guide bee conservation strategies in these ecosystems.

Conclusions

Aside from potentially lowering local abundance levels or foraging activity in denser stands, our analyses largely suggest that PJ encroachment does not negatively impact bee communities residing in forested landscapes historically dominated by ponderosa pine. Importantly, we found bee species richness and diversity to be relatively uniform among PJ-dominant, PJ-ponderosa-codominant and ponderosa pine-dominant stands within our study site. Furthermore, stand thinning and residual slash management operations designed to improve understory conditions for ungulates may not significantly affect local bee abundance or diversity within these ecosystems during the immediate years following disturbance, provided that relatively homogenous habitat conditions persist on the forest floor post-treatment. Overall, our findings corroborate with those from related studies that indicate creating or maintaining a mosaic of ground cover conditions and preserving biological legacies should benefit multiple bee functional groups within these ecosystems. Specifically, management practices or stand disturbances that reduce canopy closure, increase (or maintain) ponderosa pine dominance, and preserve or create key habitat features such as snags as well as high amounts of bare soil patches and floral resources are likely to promote the abundance or diversity of bees within the ecoregion. Reducing surface fuels via prescribed burning after thinning operations have been conducted may provide further benefits to bee communities inhabiting these ecosystems (Nyoka 2010).

The relative uniformity in bee abundance and diversity we observed across the study site may have resulted from landscape-level homogeneity in understory conditions or low variability in overstory structure. Quantifying habitat conditions along observational transects, combined with categorizing local overstory composition during this study may have not adequately captured significant variation in environmental attributes known to affect bee abundance or diversity across or within individual stands sampled during this study (Table 1). Sampling bees within additional forested landscapes co-occupied by PJ and ponderosa pine can help verify whether local bee abundance, diversity and composition of local bee communities are consistently uniform along a gradient of PJ or ponderosa pine cover throughout the southwest region. Future research should focus on long-term monitoring of bee communities in response to additional forest management practices (e.g., prescribed burning) to better guide conservation strategies in PJ-ponderosa pine ecosystems. Such studies should also incorporate landscape-level factors known to influence the distributions of bee populations, including habitat connectivity, land cover diversity, and proximity to intensively managed areas (e.g., agricultural lands or urban centers) when assessing the effects of these disturbances on their communities (Williams and Kremen 2007, Holzschuh et al. 2010). Knowledge gained from these efforts can provide a more comprehensive understanding of the drivers of bee diversity and abundance in PJ-ponderosa pine landscapes in the southwestern US, which can further guide future land management and bee conservation efforts across the region.

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Literature cited

Anderson, R. C., O. L. Loucks, and A. M. Swain. (1969). Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. *Ecology*, 50(2): 255-263.

Addington, R. N., G. H. Aplet, M. A. Battaglia, J. S. Briggs, P. M. Brown, A. S. Cheng, et al. (2018). Principles and practices for the restoration of ponderosa pine and dry mixed-conifer forests of the Colorado Front Range.

Aleixo, K. P., C. Menezes, V. L. Imperatriz Fonseca, and C. I. da Silva. (2017). Seasonal availability of floral resources and ambient temperature shape stingless bee foraging behavior (*Scaptotrigona aff. depilis*). *Apidologie*, 48: 117-127.

Allen, C. D., M. Savage, D. A. Falk, K. F. Suckling, T. W. Swetnam, T. Schulke, and J. T. Klingel. (2002). Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications*, 12(5): 1418-1433.

Brown, M. J., and R. J. Paxton. (2009). The conservation of bees: a global perspective. *Apidologie*, 40(3): 410-416.

Burkle, L. A., M. P. Simanonok, J. S. Durney, J. A. Myers, and R. T. Belote. (2019). Wildfires influence abundance, diversity, and intraspecific and interspecific trait variation of native bees and flowering plants across burned and unburned landscapes. *Frontiers in Ecology and Evolution*, 7: 252.

Burkle, L. A., R. T. Belote, and J. A. Myers. (2022). Wildfire severity alters drivers of interaction beta-diversity in plant–bee networks. *Ecography*, 2022(3): e05986.

Campbell, J. W., and J. L. Hanula. (2007). Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation*, 11(4): 399-408.

Cane, J. H. (1991). Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society*, 64(4): 406-413.

Cane, J. H., and J. L. Neff. (2011). Predicted fates of ground-nesting bees in soil heated by wildfire: thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation*, 144(11): 2631-2636.

Carril, O. M., T. Griswold, J. Haefner, and J. S. Wilson. (2018). Wild bees of Grand Staircase-Escalante National Monument: richness, abundance, and spatio-temporal beta-diversity. *PeerJ*, 6: e5867.

Chao, A., N. J. Gotelli, T. C. Hsieh, E. L. Sander, K. H. Ma, R. K. Colwell, and A. M. Ellison. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1): 45-67.

Chen, J., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, et al. (1999). Microclimate in forest ecosystem and landscape ecology: variations in local climate can be used to monitor and compare the effects of different management regimes. *BioScience*, 49(4): 288-297.

Davis, T. S., P. R. Rhoades, A. J. Mann, and T. Griswold. (2020). Bark beetle outbreak enhances biodiversity and foraging habitat of native bees in alpine landscapes of the southern Rocky Mountains. *Scientific Reports*, 10(1): 16400.

Davis, T. S., and N. Comai. **(2022).** Canopy cover and seasonality are associated with variation in native bee assemblages across a mixed pine-juniper woodland. *Agricultural and Forest Entomology*, 24(4): 497-505.

Dole, H. E., S. Villamarin-Cortez, and L. A. Richards. **(2023).** Facing the flames; insect responses to megafires and changing fire regimes. *Current Opinion in Insect Science*, 101-129.

Drossart, M., and M. Gérard. (2020). Beyond the decline of wild bees: Optimizing conservation measures and bringing together the actors. *Insects*, 11(9): 649.

Ferrenberg, S. M., D. W. Schwilk, E. E. Knapp, E. Groth, and J. E. Keeley. (2006). Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. *Fire Ecology*, 2(2): 79-102.

Foote, G. G., N. E. Foote, J. B. Runyon, D. W. Ross, and C. J. Fettig. **(2020).** Changes in the summer wild bee community following a bark beetle outbreak in a Douglas-fir forest. *Environmental Entomology*, 49(6): 1437-1448.

Fortuin, C. C., and K. J. Gandhi. **(2021).** Functional traits and nesting habitats distinguish the structure of bee communities in clearcut and managed hardwood & pine forests in Southeastern USA. *Forest Ecology and Management*, 496: 119351.

Galbraith, S. M., J. H. Cane, A. R. Moldenke, and J. W. Rivers. (2019). Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere*, 10(4): e02668.

Gelles, R. V., T. S. Davis, and C. S. Stevens-Rumann. **(2022).** Wildfire and forest thinning shift floral resources and nesting substrates to impact native bee biodiversity in ponderosa pine forests of the Colorado Front Range. *Forest Ecology and Management*, 510: 120087.

Gelles, R. V., T. S. Davis, and K. J. Barrett. **(2023).** 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. *Agricultural and Forest Entomology*, 25(3): 435-448.

Glenny, W., J. B. Runyon, and L. A. Burkle. **(2022).** A review of management actions on insect pollinators on public lands in the United States. *Biodiversity and Conservation*, 1-22.

Glenny, W., J. B. Runyon, and L. A. Burkle. **(2023).** Habitat characteristics structuring bee communities in a forest-shrubland ecotone. *Forest Ecology and Management,* 534: 120883.

Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. (2010). Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications*, 20: 1678–1692.

Hanula, J. L., M. D. Ulyshen, and S. Horn. **(2016).** Conserving pollinators in North American forests: a review. *Natural Areas Journal*, 36(4): 427-439.

Hammer, Ø., and D. A. Harper. **(2001).** Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4(1): 1.

Harrison, T., J. Gibbs, and R. Winfree. **(2018).** Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biology,* 24(1): 287-296.

Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. **(2010).** How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *Journal of Animal Ecology*, 79(2): 491-500.

Huffman, D. W., Crouse, J. E., Chancellor, W. W., & Fulé, P. Z. (2012). Influence of time since fire on pinyon–juniper woodland structure. *Forest Ecology and Management, 274*, 29-37.

Jha, S., & Kremen, C. (2013). Resource diversity and landscape-level homogeneity drive native bee foraging. *Proceedings of the National Academy of Sciences, 110*(2), 555-558.

Johnstone, J. F., C. D. Allen, J. F. Franklin, L. E. Frelich, B. J. Harvey, P. E. Higuera, et al. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment*, 14(7): 369-378.

Koh, I., E. V. Lonsdorf, N. M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T. H. Ricketts. (2016). Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl Acad. Sci, 113: 140–145.

Kremen, C., N. M. Williams, and R. W. Thorp. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*, 99(26): 16812-16816.

Lazarina, M., S. P. Sgardelis, T. Tscheulin, A. S. Kallimanis, J. Devalez, and T. Petanidou. (2016). Bee response to fire regimes in Mediterranean pine forests: the role of nesting preference, trophic specialization, and body size. *Basic and Applied Ecology*, 17(4): 308-320.

Lazarina, M., S. P. Sgardelis, T. Tscheulin, J. Devalez, V. Mizerakis, A. S. Kallimanis, et al. (2017). The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. *Biodiversity and Conservation*, 26: 115-131.

Loveless, M. D., and J. L. Hamrick. (1984). Ecological determinants of genetic structure in plant populations. *Annual Review of Ecology and Systematics*, 15(1): 65-95.

Mallinger, R. E., J. Gibbs, and C. Gratton. (2016). Diverse landscapes have a higher abundance and species richness of spring wild bees by providing complementary floral resources over bees' foraging periods. *Landscape Ecology*, 31: 1523-1535.

McCabe, T. D., and M. C. Dietze. **(2019).** Scaling contagious disturbance: A spatially-implicit dynamic model. *Frontiers in Ecology and Evolution*, 7: 64.

Miller, R. F., and R. J. Tausch. (2000). The role of fire in pinyon and juniper woodlands: a descriptive analysis. In *Proceedings of the Invasive Species Workshop: The Role of Fire in the Control and Spread of Invasive Species. Fire Conference* (pp. 15-30).

Minott, J. A., and T. E. Kolb. **(2020).** Regeneration patterns reveal contraction of ponderosa forests and little upward migration of pinyon-juniper woodlands. *Forest Ecology and Management*, 458: 117640.

North, M., B. Oakley, R. Fiegener, A. Gray, and M. Barbour. **(2005).** Influence of light and soil moisture on Sierran mixed-conifer understory communities. *Plant Ecology*, 177: 13-24.

Nyoka, S. E. (2010). Can restoration management improve habitat for insect pollinators in ponderosa pine forests of the American southwest? *Ecological Restoration*, 28(3): 280-290.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'hara, and M. J. Oksanen. **(2013).** Package 'vegan'. *Community Ecology Package, Version*, 2(9): 1-295.

Oksanen, J., F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, E. Szoecs, and H. Wagner. (2019). *vegan: Community Ecology Package*. R package version 2.5-4.

Ponisio, L. C., K. Wilkin, L. K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, and C. Kremen. (2016). Pyrodiversity begets plant–pollinator community diversity. *Global Change Biology*, 22(5): 1794-1808.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. (2003). Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology*, 84(10): 2628-2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, 30(1): 78-85.

Potts, S. G., V. Imperatriz-Fonseca, H. T. Ngo, M. A. Aizen, J. C. Biesmeijer, T. D. Breeze, et al. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, 540(7632): 220-229.

Pulliam, H. R. (2000). On the relationship between niche and distribution. *Ecology Letters*, 3(4): 349-361.

Walters, B. B., and E. W. Stiles. (1996). Effect of canopy gaps and flower patch size on pollinator visitation of *Impatiens capensis*. *Bulletin of the Torrey Botanical Club*, 123(3): 184-188.

Wratten, S. D., M. Gillespie, A. Decourtye, E. Mader, and N. Desneux. (2012). Pollinator habitat enhancement: benefits to other ecosystem services. *Agriculture, Ecosystems & Environment*, 159: 112-122.

Williams, N. M., E. E. Crone, T'ai, H. R., R. L. Minckley, L. Packer, and S. G. Potts. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, 143(10): 2280-2291.

Williams, N. M., and C. Kremen. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17(3): 910-921.

Simanonok, M. P., and L. A. Burkle. (2019). Nesting success of wood-cavity-nesting bees declines with increasing time since wildfire. *Ecology and Evolution*, 9(22): 12436-12445.

Taki, H., R. Murao, K. Mitai, and Y. Yamaura. (2018). The species richness/abundance–area relationship of bees in an early successional tree plantation. *Basic and Applied Ecology*, 26: 64-70.

Thapa-Magar, K. B., T. S. Davis, and B. Kondratieff. (2020). Livestock grazing is associated with seasonal reduction in pollinator biodiversity and functional dispersion but cheatgrass invasion is not: Variation in bee assemblages in a multi-use shortgrass prairie. *PLoS One*, 15(12): e0237484.

Uhey, D. A., H. L. Riskas, A. D. Smith, and R. W. Hofstetter. (2020). Ground-dwelling arthropods of pinyon-juniper woodlands: Arthropod community patterns are driven by climate and overall plant productivity, not host tree species. *PLoS One*, 15(8): e0238219.

Table 1. Plot-level means, associated standard errors (SE), and Tukey's honestly significant difference (HSD) test among tree overstory classes regarding various structural attributes of stand overstory structure and ground cover composition within a pinyon-ponderosa pine forest in Cibola National Forest, NM. Means not connected by the same letter(s) within individual columns differ significantly (α = 0.05).

	Overstory cover class								
	Pinyon-juniper			PJ-ponderosa			Ponderosa		
Attribute	Mean	SE	HSD	Mean	SE	HSD	Mean	SE	HSD
Basal area (m^2/ha)	68.7	11.2	a	58.1	5.6	a	42.5	7.1	a
QMD (cm)	9.2	0.6	a	10.6	1.9	a	7.6	0.6	a
Snag abundance	23.6	8.6	a	5.4	2.0	a	21.0	11.4	a
Canopy closure (%)	17.8	3.0	a	25.8	5.4	a	29.0	5.6	a
CWD cover (%)	13.6	1.4	a	15.7	0.9	a	13.5	1.4	a
Shrub cover (%)	41.3	3.5	a	40.1	3.8	a	37.0	4.5	a
Bare soil exposure (%)	18.6	2.5	a	15.8	2.7	a	23.0	2.7	a
Grass cover (%)	46.9	5.4	a	42.0	4.6	a	65.0	4.5	a
Litter cover (%)	32.7	4.0	a	42.2	3.6	a	21.8	3.7	a
Floral abundance	37.5	3.9	a	35.3	3.4	a	49.3	9.5	a
Floral spp. richness	19.2	1.3	b	25.2	0.8	a	24.3	1.1	a

Table 2. Plot-level means, associated standard errors (SE), and Tukey's honestly significant difference (HSD) test of bee abundance, species richness, and Shannon's diversity among tree overstory classes within a pinyon-ponderosa pine forest in Cibola National Forest, NM. Means not connected by the same letter(s) within individual columns differ significantly ($\alpha = 0.05$).

	Abundance			**Richness**			**Diversity**		
Overstory class	**Mean**	**SE**	**HSD**	**Mean**	**SE**	**HSD**	**Mean**	**SE**	**HSD**
PJ-dominant	14.27	1.95	b	6.73	1.09	a	2.00	0.23	a
PJ-ponderosa-codominant	19.56	2.36	ab	8.22	0.95	a	2.37	0.16	a
Ponderosa-dominant	25.80	4.55	a	8.00	1.22	a	1.97	0.21	a

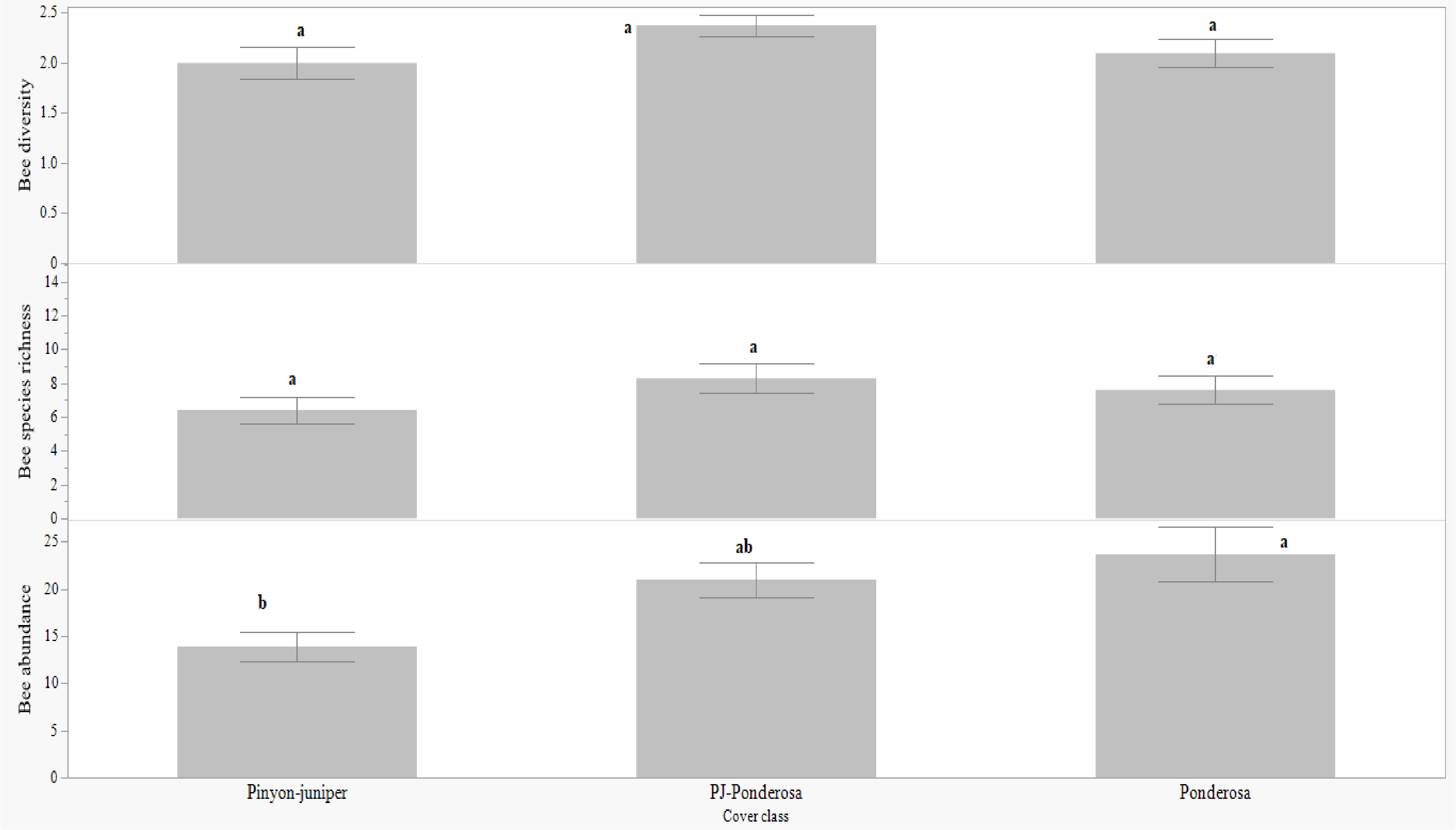

Figure 1. Plot-level means, associated standard errors (SE), and Tukey's honestly significant difference (HSD) test of bee abundance, species richness, and Shannon's diversity among tree overstory classes within a pinyon-ponderosa pine forest in Cibola National Forest, NM. Means not connected by the same letter(s) within individual rows differ significantly ($\alpha = 0.05$).

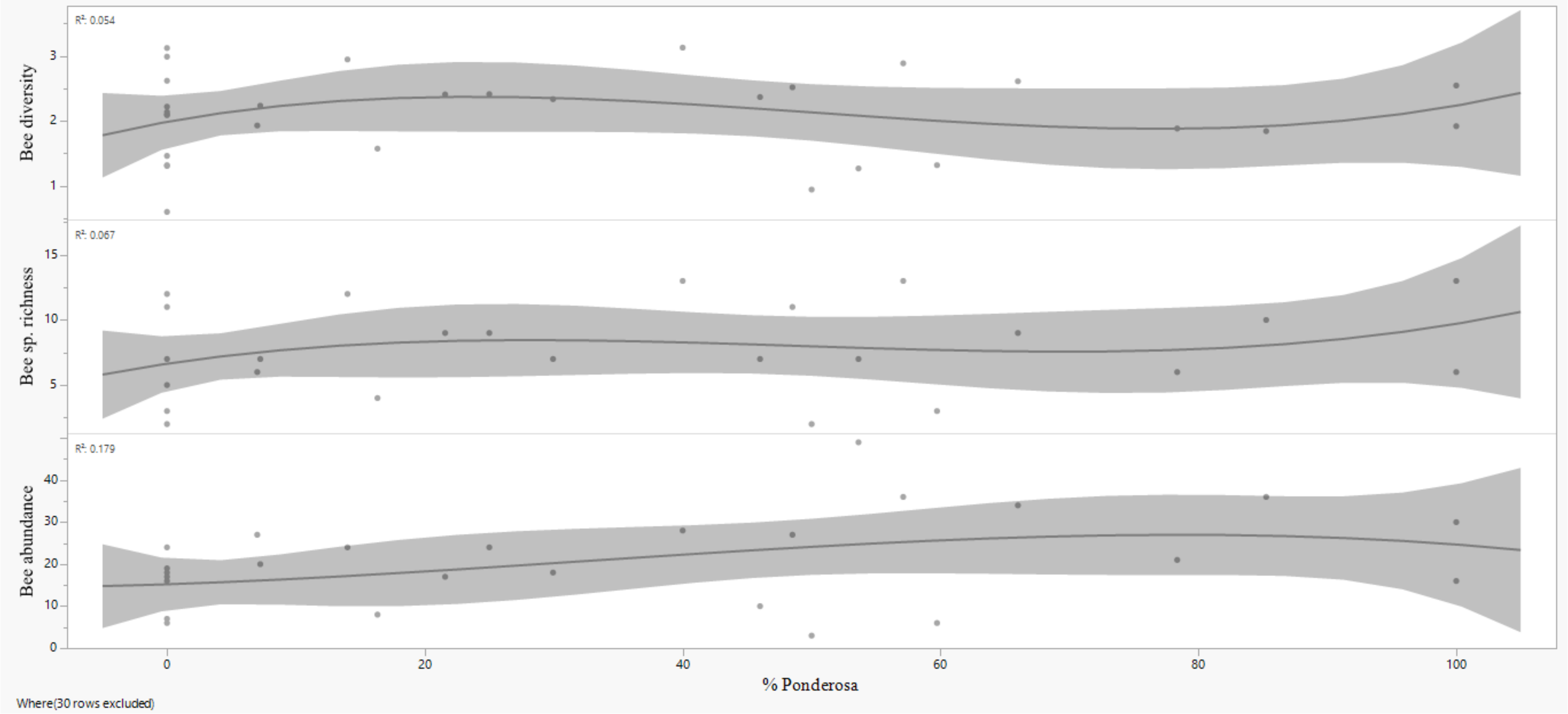

Figure 2. Results from linear regression used to illustrate the direction and magnitude of correlations between % ponderosa pine cover versus bee abundance ($R^2 = 0.18$; $F_{1,28} = 5.31$; $p = 0.0288$), species richness ($R^2 = 0.07$; $F_{1,28} = 1.20$; $p = 0.28$) and diversity ($R^2 = 0.05$; $F_{1,28} = 0.06$; $p = 0.54$) within a pinyon-ponderosa pine forest in Cibola National Forest, NM.

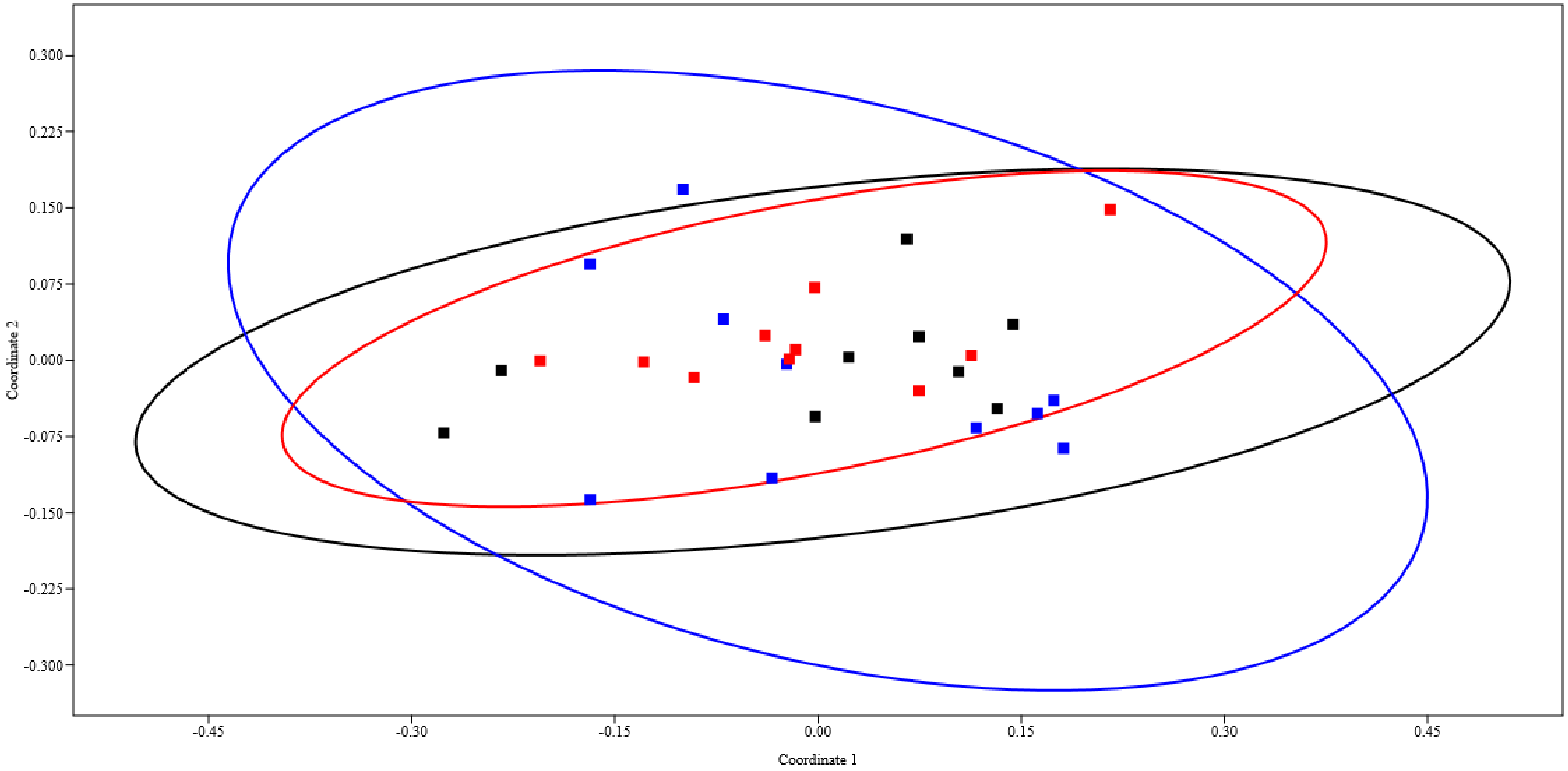

Figure 3. Results from NMDS analyses used to determine degrees of similarity in bee community assemblages among plots within individual tree overstory classes (blue = ponderosa-dominant; red = pinyon-juniper (PJ)-dominant; black = PJ-ponderosa-codominant) within a pinyon-ponderosa pine forest in Cibola National Forest, NM. Axes one and two explain 70.0 and 9.7 percent, respectively, of the total variance (stress = 0.06) present within plot-level community composition due to the relative abundance of individual bee species.

Table 3. Results from two-way ANOVA, testing for significant (α = 0.05) differences in bee abundance, species richness, and Shannon's diversity between 2021 and 2022 and among different thinning treatments (untreated, full tree removal and lop and scatter), including their interactive terms.

Response	**Parameter**	**DF**	**F**	**Prob > F**
Abundance	Treatment	2	2.7	0.0703
	Year	1	0.11	0.7314
	Treatment * year	2	0.42	0.6565
	Whole model	5,54	1.31	0.2739
Species richness	Treatment	2	0.45	0.6689
	Year	1	0.21	0.647
	Treatment * year	5	0.08	0.9242
	Whole model	5,54	0.29	0.945
Diversity	Treatment	2	0.31	0.2020
	Year	1	0.22	0.6385
	Treatment * year	2	0.22	0.8006
	Whole model	5,54	0.25	0.9380

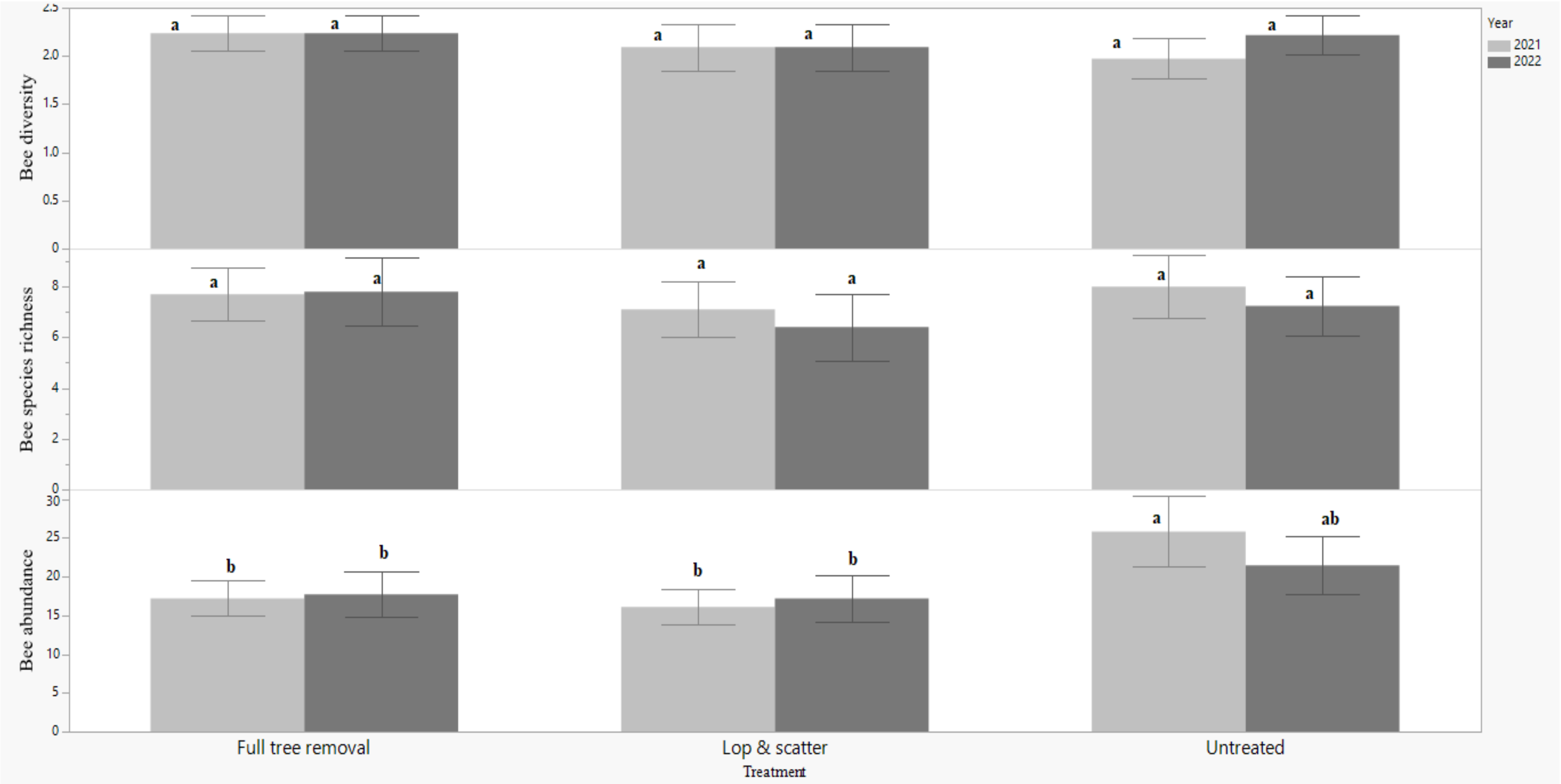

Figure 4. Plot-level means, associated standard errors (SE), and Tukey's honestly significant difference (HSD) testing for significant ($\alpha = 0.05$) differences in bee abundance, species richness, and Shannon's diversity between 2021 and 2022 and among different thinning treatments (untreated, full tree removal and lop and scatter), including their interactive terms in Cibola National Forest, NM. Means not connected by the same letter(s) within individual rows differ significantly ($\alpha = 0.05$).

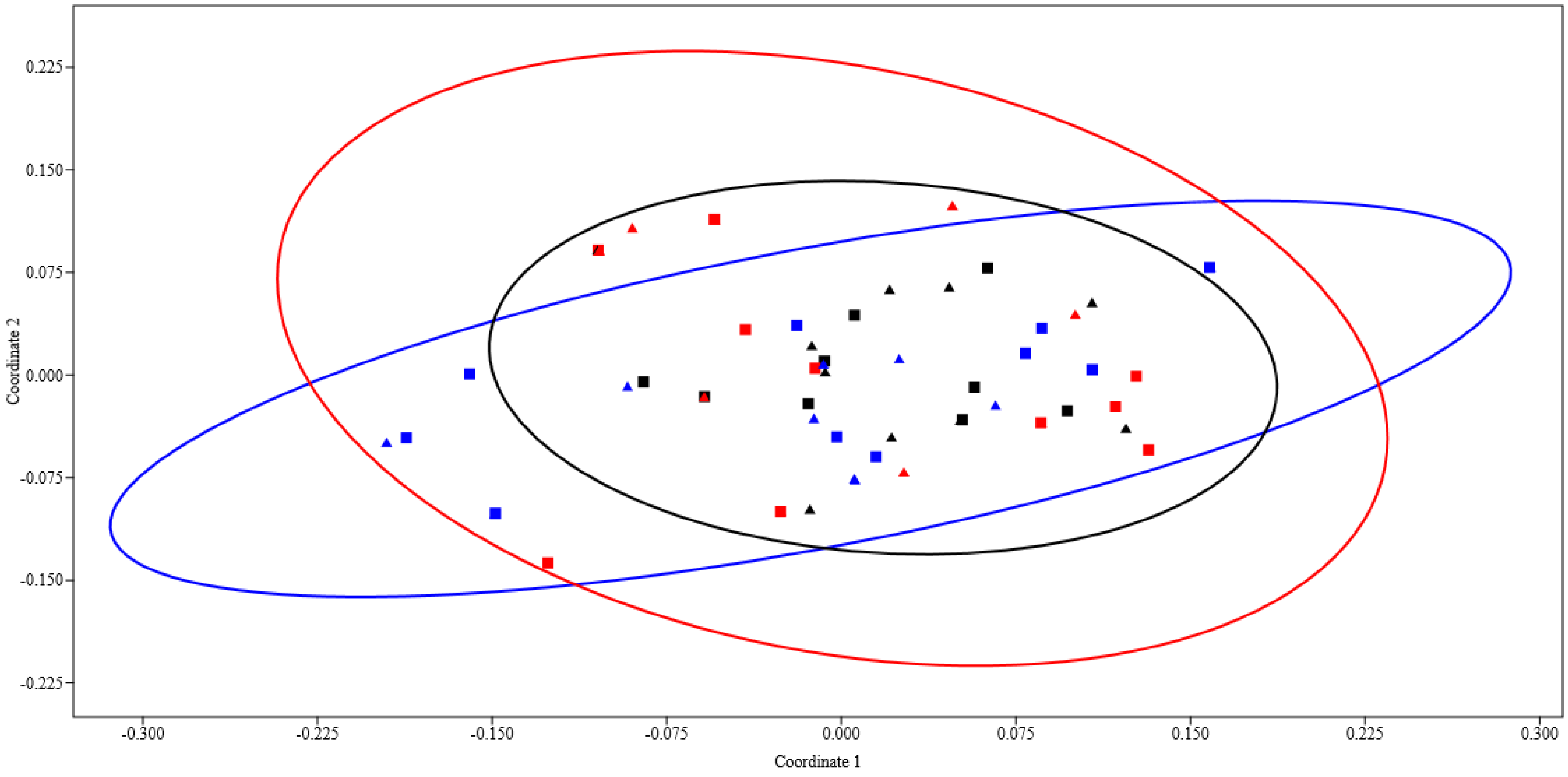

Figure 5. Results from NMDS analyses used to determine degrees of similarity in bee community assemblages among plots within individual treatment categories (black = full tree removal; blue = lop and scatter; red = untreated control) separated by year (2021 = squares; 2022 = triangles) within a pinyon-ponderosa pine forest in Cibola National Forest, NM. Axes one and two explained 55.6 and 37.8 percent, respectively, of the total variance (stress = 0.097) present within plot-level community composition due to the relative abundance of individual species.

Table 4. Summary of a generalized linear model analysis describing variation in bee abundance, species richness and Shannon's diversity due to effects of variation in basal area (BA), plot-level mean quadratic diameter (QMD), snag abundance (Snags), % ponderosa pine cover (% PIPO), shrub cover (SC), bare soil (BS), canopy closure (CC), grass cover (GC), floral abundance (FA), floral species richness (FR), litter cover (LC), and coarse woody debris (CWD). Emboldened Prob>|χ^2| values indicate significant ($\alpha = 0.05$) parameter effects.

Variable	Parameter	Estimate	SE	χ2	Prob>|χ2|
Abundance	Intercept	2.6429	0.2485	108.68	**<0.0001**
	BA	0.0022	0.0008	6.66	**0.0099**
	QMD	0.0121	0.0069	2.93	0.0868
	Snags	0.0020	0.0008	6.13	**0.0133**
	% PIPO	0.0053	0.0011	25.80	**<0.0001**
	SC	-0.0101	0.0021	23.19	**<0.0001**
	BS	0.0057	0.0030	3.56	0.0591
	CC	-0.0034	0.0017	4.17	**0.041**
	GC	0.0033	0.0018	3.53	0.0603
	FA	0.0030	0.0011	6.64	**0.0101**
	FR	-0.0083	0.0064	1.72	0.1901
	LC	-0.0057	0.0022	6.77	**0.0093**
	CWD	-0.0339	0.0007	21.25	**<0.0001**
Species richness	Intercept	1.4899	0.3897	14.29	**0.0002**
	BA	-0.0007	0.0014	0.28	0.5956
	QMD	0.0066	0.0123	0.28	0.5944
	Snags	0.0023	0.0013	3.30	0.0692
	% PIPO	-0.0002	0.0017	0.01	0.9161
	SC	-0.0098	0.0033	8.75	**0.0031**
	BS	0.0168	0.0049	11.69	**0.0006**
	CC	-0.0039	0.0027	2.11	0.1467
	GC	0.0047	0.0028	2.90	0.0887
	FA	0.0016	0.0019	0.71	0.3995
	FR	0.0052	0.0101	0.26	0.6078
	LC	0.0064	0.0035	3.42	0.0642
	CWD	-0.0117	0.0106	1.29	0.2553
Diversity	Intercept	1.4341	0.6012	5.44	**0.0197**
	BA	-0.0016	0.0021	0.55	0.4593
	QMD	0.0232	0.0160	2.06	0.1512
	Snags	0.0044	0.0019	5.14	**0.0234**
	% PIPO	-0.0016	0.0025	0.41	0.5237

Variable	Parameter	Estimate	SE	$\chi2$	Prob>|$\chi2$|
Diversity	SC	-0.0080	0.0048	2.65	0.1037
	BS	0.0180	0.0073	5.82	**0.0159**
	CC	-0.0026	0.0038	0.49	0.486
	GC	0.0067	0.0041	2.57	0.1088
	FA	0.0030	0.0032	0.87	0.3523
	FR	0.0048	0.0146	0.11	0.7433
	LC	0.0047	0.0052	0.83	0.3629
	CWD	-0.005	0.0180	0.08	0.7702

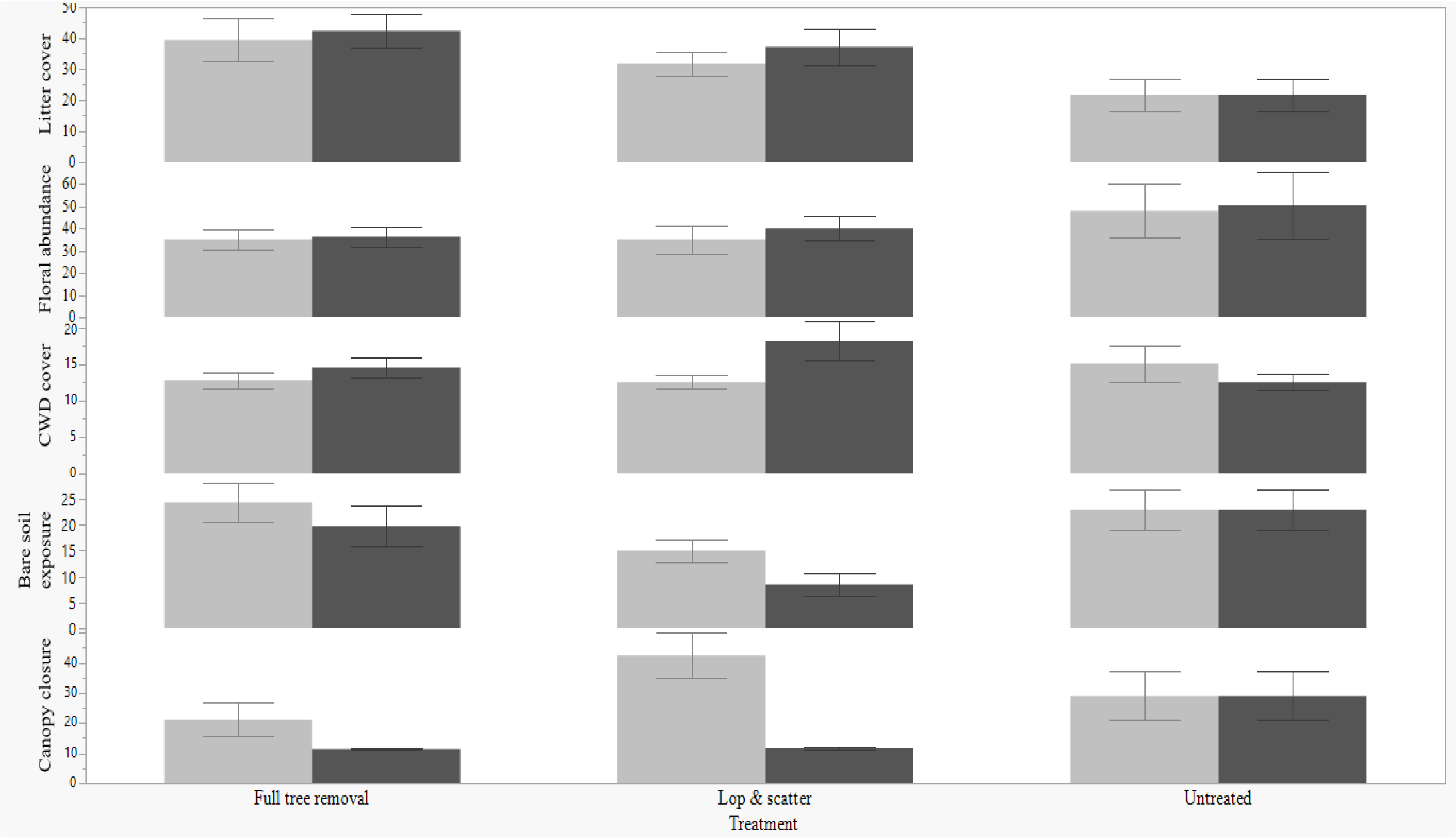

Figure 6. Plot-level means and associated standard errors of environmental attributes significantly (α = 0.05) correlated with bee abundance or diversity among different thinning treatments (untreated, full tree removal and lop and scatter), and between 2021 and 2022, within a pinyon-ponderosa pine forest in Cibola National Forest, NM.

Figure 7. Results from ANOVA tests and Tukey's HSD testing for significant differences among overstory classes in plot-level abundances of bees associated with various functional traits (lecty, sociality, and nesting location). Means not connected by the same letter(s) within individual rows differ significantly (α = 0.05).

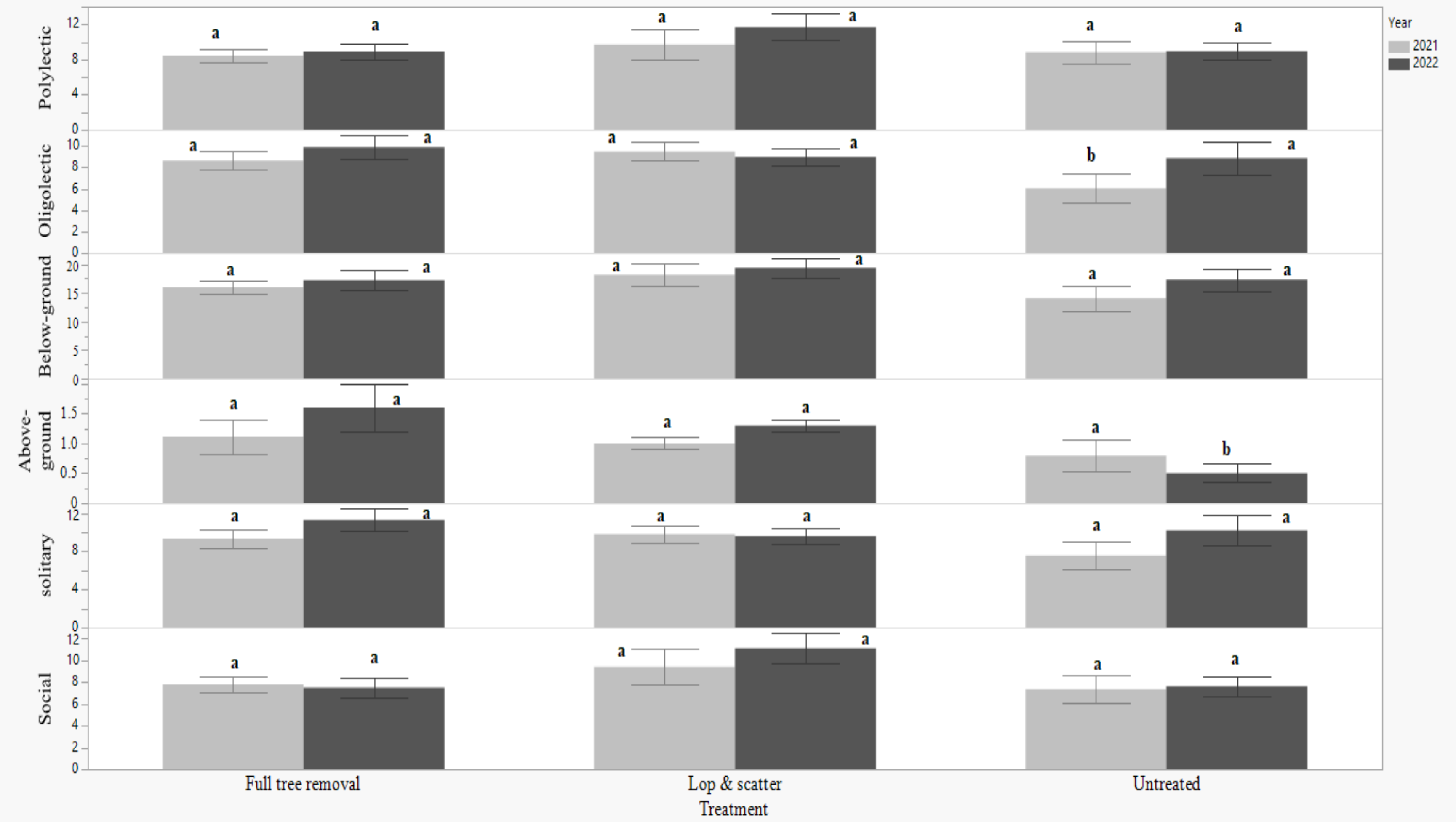

Figure 8. Results from ANOVA tests and Tukey's HSD testing for significant differences among various stand-thinning and residual slash management treatments in plot-level abundances of bees associated with various functional traits (lecty, sociality, and nesting location). Means not connected by the same letter(s) within individual rows differ significantly ($\alpha = 0.05$).

Table 5. Results from two-way ANOVA, testing for significant differences in the abundance of bees associated with various functional groups between 2021 and 2022 and among different thinning treatments (untreated, full tree removal and lop and scatter), including their interactive effects in Cibola National Forest, NM.

Functional group	Variable	DF	F	Prob > F
Polylectic bees	Treatment	2.00	0.09	0.9164
	Year	1.00	0.49	0.4851
	Treatment*Year	2.00	0.27	0.761
	Whole model	5, 54	0.24	0.93
Oligolectic bees	Treatment	2.00	4.24	0.0196
	Year	1.00	0.58	0.4473
	Treatment*Year	2.00	0.48	0.61
	Whole model	5, 54	0.20	0.0884
Above-ground nesting bees	Treatment	2.00	5.70	0.0056
	Year	1.00	0.03	0.9509
	Treatment*Year	2.00	0.25	0.7855
	Whole model	5, 54	0.23	0.0498
Above-ground nesting bees	Treatment	2.00	0.57	0.5696
	Year	1.00	0.21	0.6453
	Treatment*Year	2.00	0.67	0.4536
	Whole model	5, 54	0.42	0.8267
Social bees	Treatment	2.00	1.25	0.2942
	Year	1.00	0.96	0.3296
	Treatment*Year	2.00	0.41	0.6651
	Whole model	5, 54	0.86	0.5103
Solitary bees	Treatment	2.00	0.21	0.8090
	Year	1.00	0.41	0.6651
	Treatment*Year	2.00	0.21	0.8090
	Whole model	5, 54	0.87	0.5167

Table 6. Summary of stepwise regression procedures used to develop explanatory models regarding functional trait-specific relationships between wild bee abundance and habitat structure in a pinyon-ponderosa pine landscape within Cibola National Forest, NM.

Response variable (Y)	Prediction expression
Oligolectic bee abundance	log (Y) = 1.38 + 0.040 (QMD) - 0.045 (CWD) - 0.013 (SC) - 0.008 (GC) + 0.053 (FR)
Polylectic bee abundance	log (Y) = 3.19 + 0.003 (SA) - 0.045 (CWD) - 0.016 (SC) + 0.017 (BS)
Above-ground nesting abundance	log (Y) = 1.74- 0.030 (BA) + 0.032 (SA) - 0.042 (GC)
Below-ground nesting bee abundance	log (Y) = 3.23 - 0.029 (CWD) - 0.11 (SC)
Social bee abundance	log (Y) = 3.16 - 0.039 (CWD) - 0.195 (SC) + 0.021 (BS)
Solitary bee abundance	log (Y) = 1.65 + 0.035 (QMD) - 0.044 (CWD) - 0.012 (SC) - 0.007 (GC) + 0.043 (FR)

(QMD) = Quadratic mean diameter; (CWD) = Coarse woody debris; (SC) = Shrub cover; (GC) = Grass cover; (FR) = Floral species richness; (SA)= Snag abundance; (BS) = Bare soil exposure.

Chapter three: Temporal variation in the effects of wildfire on yellowjacket wasps (Hymenoptera: Vespidae, Vespinae) in mixed-conifer forests of the Sierra Nevada Mountains of California

Abstract

Documentation of the community-level responses of social yellowjacket wasps to wildfire in coniferous forests of the western United States is lacking, despite their ubiquitous distribution, ecological function and occasional pest status within these ecosystems. Here, we sampled the local yellowjacket community along a burn severity gradient in montane, mixed-conifer stands located within various fire boundaries that occurred between 2015-2020 in the Californian Sierra Nevada mountains. We documented: 1) how post-burn patterns in yellowjacket abundance and diversity changed over time; and 2) how post-burn yellowjacket abundance and diversity varied along a burn severity gradient within individual fire boundaries. We also developed descriptive models of forest habitat structure relationships with yellowjacket abundance, diversity and community composition across our study site. Our analyses suggest significant variation in yellowjacket abundance, diversity and community composition among burn severity and fire age classes, as well as differing species-level relationships between yellowjackets and the structural attributes of their forest habitat. Regardless of burn severity, wildfire significantly reduced yellowjacket abundance and species richness during the immediate (≤ two) years following stand disturbance, possibly due to flame-induced wasp mortality combined with the destruction of above-ground foraging, nesting and overwintering substrates. Post-fire yellowjacket communities were significantly more abundant within older fire boundaries (five- and seven-years-old), compared to those residing in one- and two-year-old boundaries. Stands that burned at high severity within older fire boundaries had high rates of shrub and grass cover, and were predominantly inhabited by large numbers of pestiferous

Vespula pennsylvanica wasps. Forest-obligate yellowjacket species were generally only collected in unburned stands or in locations that burned at relatively low severity. Combined, these results suggest unnaturally high severity fire within these forests might facilitate increases in pestiferous yellowjacket populations due to favorable stand conditions. In contrast, lower severity burns characteristic of prescribed fire used to restore or maintain the function of mixed-conifer forests in the Central Sierra Nevada may provide the added benefit of short-term reductions in unwanted yellowjacket population levels in areas of concern.

Introduction

Wildfire suppression policies enacted since the mid-nineteenth century in the western United States have homogenized the structural conditions of montane, mixed-conifer forests throughout the region, where stands are unnaturally dense and exhibit higher rates of canopy and shrub cover compared to pre-suppression conditions (Allen et al. 2002, Addington et al. 2018). The increased continuity between surface fuels and live canopies combined with climate-change-driven droughts have exacerbated the severity—both in intensity and extent—of recent wildfires in the western US (Miller et al. 2009, Steel et al. 2018, Parks and Abatzoglou 2020, Safford et al. 2022). Changes in understory vegetation and surface fuels resulting from altered fire regimes are likely to influence the abundance and diversity of arthropod taxa and functional feeding guilds (Moretti et al. 2004, Ferrenberg et al. 2006, Koltz et al. 2018), which may further impact nutrient cycling, soil decomposition rates, microclimates, and primary productivity within forest ecosystems (Peng and Apps 1999, Bowman et al. 2016, McLauchlan et al. 2020). Recent research pertaining to the effects of wildfire on forest-associated insect communities in temperate forest ecosystems has focused primarily on pollinators (Hanula et al. 2016, Mason Jr. et al. 2021, Glenny et al. 2022). Documentation of the community-level responses of ubiquitous insect predators (e.g., social wasps) to wildfire in the western US is largely unavailable (Ferrenberg et al. 2006). A better understanding of insect predator responses to wildfire can improve predictions on how altered climates and disturbance regimes will affect the overall structure and function of arthropod food webs in forested landscapes.

Social yellowjacket wasps (Hymenoptera: Vespidae, Vespinae) in the genera *Vespula* Thompson and *Dolichovespula* Rohwere are considered ubiquitous insect predators in temperate forests and help provide top-down regulation of lower-trophic arthropod populations (Akre et al.

1980, Kimsey and Carpenter 2012), some of which can be pests (Donovan 2003, Lichtenberg and Lichtenberg 2003). Yellowjacket venom is also painful and sometimes lethal towards humans (Golden 2007). Therefore, their presence in forests (especially in high-visitation areas such as national and state parks) often impedes management and recreational activities (Akre et al. 1980, Kimsey and Carpenter 2012). Numerous firefighters and forestry technicians are stung annually (Yosemite NP staff personal communication 2021, Safford personal communication 2022). Despite this, there is little information on what landscape- and stand-level factors regulate population levels and community assemblages of yellowjackets for the majority of forest cover types in the western US, and for the southwest region, in particular (Akre et al. 1976, 1980).

Yellowjackets nests are highly variable in size (from several dozen to thousands of cells) and constructed from a mixture of plant fibers and salivary secretions (Akre et al. 1980, Kimsey and Carpenter 2012). The nests of *Vepsula* yellowjackets are typically subterranean and frequently constructed beneath leaf litter and downed logs or large branches (although some species will build nests within hollow logs, trees, in patches of bare, exposed soil or in abandoned rodent burrows), while *Dolichovespula* nests are usually aerial and constructed in either tall shrubs or crowns of trees (Akre et al. 1976, 1980; Kimsey and Carpenter 2012). The queens of both genera often utilize downed logs or branch piles as overwintering substrates (MacDonald et al. 1975, Akre et al. 1976, 1980, MacDonald and Matthews 1981). As such, several yellowjacket species in the western US may be more prevalent in late-successional forest stands due to a relatively high abundance of nesting and overwintering resources (MacLean et al. 2021). Similarly, their communities may benefit from accumulated downed woody debris due to wildfire suppression. In contrast, forest fires (both natural and prescribed) may destroy above-ground yellowjacket nests or otherwise destroy nesting and overwintering resources present on the forest floor, thereby having deleterious effects on individual populations over short time periods. Alternatively, observed increases in understory plant diversity following fire events (e.g., Walters and Stiles 1996, Fahey et al. 2006, Hanula et al. 2016, McCabe et al. 2019) may indirectly benefit yellowjackets over longer time periods by promoting the abundance of their prey (herbivorous arthropods) or availability of nesting substrates (e.g., bare soil). However, few studies have tested these hypotheses or quantified basic relationships between yellowjacket diversity and forest structure in the western US, and only one study has assessed the effects of fire on Hymenopteran predators (aculeate wasps) in the Californian Sierra Nevada (Ferrenberg et al. 2006). Unlike the present study which encompasses a range of fire severity levels and times since fire, Ferrenberg et al. (2006) focused on prescribed burning treatments (which only include low intensity burning), only sampled one-year post-burn, and did not quantify forest structural attributes.

Recent wildfires in the Sierra National Forest, CA include the Sky Fire (2015), Railroad-Mission Fire (2017), and Creek Fire (2020). Using a network of observational plots, we sampled the local yellowjacket community using semiochemical attractants (Landholt and Zhang, 2016) along a burn severity gradient (undisturbed controls, low-, moderate-, and high-severity burn patches) in ponderosa pine, *Pinus ponderosa* Doug ex Laws, dominant stands within each fire boundary. We documented: 1) how post-burn patterns in yellowjacket abundance and diversity changed over time; 2) how post-burn yellowjacket abundance and diversity varied among burn severity classes within individual fire boundaries; and 3) how burn severity affects patterns of yellowjacket population and community growth rates following wildfire. Furthermore, we quantified various stand attributes (i.e., canopy structure and ground cover composition) at experimental plots to develop descriptive models of the relationships between yellowjacket diversity and forest habitat structure in the ecoregion. Overall, knowledge gained from this work can be utilized in future management plans focused on reducing local yellowjacket populations in areas of concern, for example recreational areas or households located within woodlands or montane forested landscapes.

Methods

Research site and plot descriptions

A total of 48 circular plots (0.05 hectares each) were established in burned and unburned stands located in the lower montane biotic zone (900-1800 m) of Sierra National Forest, CA (Bass Lake Ranger District: 37.35464, -119.54981). In addition to ponderosa pine, *P. ponderosa*, landscapes in this biotic zone are co-dominated by incense-cedar, *Calocedrus decurrens* (Torr.) Florin, and California white-fir, *Abies concolor var. lowiana* (Gordon & Glend.) A. Murray bis, at higher elevations. Sixteen plots were established in each fire boundary (the 2020 Creek, 2017 Mission-Railroad and 2015 Sky fires) representing unique age classes (one-two, five- and seven-years post-ignition), with four plots per burn severity class (undisturbed, low, moderate, and high). Plots located within the Creek fire boundary were established in June 2021. All other plots were established in June 2022. Plot locations were determined from vegetation burn severity maps provided by the USDA Forest Service Rapid Assessment of Vegetation Condition after Wildfire (RAVG) program (https://burnseverity.cr.usgs.gov/ravg/). Burn severity was uniform within a 300 m radius surrounding plot centers. This distance exceeds the foraging ranges of individual workers for the majority of *Vespula* spp. common in California (Akre and Davis 1978). All plots were spaced by ≥ 1 km.

Yellowjacket sampling

A combination of heptyl butyrate (HB), acetic acid (AA), and isobutanol (IB) has been shown to effectively sample yellowjacket diversity (reviewed in Landolt and Zhang 2016), and were therefore used as lures at each site. Following methods by Landolt et al. (2005), lures were composed of 10mL HB, 5 mL AA combined, and 5 mL IB, dispensed from 20 mL glass vials with (3 mm diameter) holes (3 mm diameter) punched through vial lids to ensure controlled release of the attractants. Vials were suspended inside traps fabricated from 1 L polypropylene bottles painted fluorescent yellow; the conical portion of each bottle was removed, then reattached inverted to allow for yellowjacket entry while preventing escape. Traps were deployed at plot center and operated monthly July through October over 48-hour periods. Collected specimens were stored in 70% ethanol until they were identified at the University of California, Davis using taxonomic keys (Akre et al. 1976, Kimsey and Carter 2012) and online pictorial guides (discoverlife.org).

Quantifying forest structural attributes

For all research plots, both live and dead tree basal areas were quantified via variable radius sampling using a basal area factor of 10 m^2/ha at plot centers. The mortality status of each tree censused was also determined during each year of sampling in July. Canopy closure was quantified using a hemispherical densiometer (Strickler 1959) from the average of four measurements, taken at plot center and 12 m distances from plot center at azimuths of 120°, 240°, and 360°.

Forest floor cover composition was determined using a one square meter sampling quadrat, with measurements taken at plot center as well as at four, eight and 12 m distances from plot centers along canopy closure sampling transects (azimuths of 120°, 240°, and 360°) for a total of 10 sampling points per plot. At each sampling point, the percentages of quadrat interior occupied or covered by rock, bare soil, leaf litter, grass, shrubs and coarse woody debris (material > 3cm in diameter) were estimated to the nearest multiple of 10 (e.g., 10 %, 20 %, etc.). These values were averaged to yield plot-level mean for each ground cover class. The total number of flowering plant species within each quadrat, and the relative abundance (# of inflorescences) of each species was estimated to the nearest multiple of 25 (i.e., 25, 50, 100, etc.). Quadrat-level abundances were summed to provide plot-level floral abundance values. Plot-level floral species richness was determined by summing the number of unique species found within all 10 quadrats.

Statisical analyses

All statistical analyses were conducted using the R programming language (v 3.5.2 'Eggshell Igloo', R Core Team), JMP 17 statistical software (SAS Institute Inc., Cary, NC) or PAST 4 statistical software (University of Oslo, Oslo, Norway). Prior to all analyses, the Shapiro-Wilk test and homogeneity of variance (HOV) tests were used to determine whether response variables were normally distributed and exhibited equal variance, respectively. Data not normally distributed were either log or square root-transformed ($\sqrt{[x + 0.01]}$), or otherwise analyzed with generalized regression techniques that could account for non-normal distributions.

Differences in yellowjacket abundance, diversity and community assemblages among burn severity and fire age classes

Differences in abundance, species richness, and Shannon Weiner index (diversity) across burn severity classes and time-since-burn (years post-ignition) were determined using two-way Analysis of Variance (ANOVA). Separate analyses were used for each response variable of interest. Linear regression was used to illustrate the direction and magnitude of correlations between % tree morality versus yellowjacket abundance, species richness and diversity. Separate models were developed for each response variable.

Degrees of similarity in yellowjacket community compositions among burn severity and fire age classes were visualized using a distance-based (Euclidean) framework (canonical correspondence analysis) under the non-metric multidimensional scaling (NMDS) platform provided under PAST (version 4.14) statistical software (Hammer et al. 2001). Canonical correspondence analyses were chosen over Non-Metric Multidimensional scaling (NDMS) to also visualize individual species relationships with canopy and forest floor structural attributes. Linear regression was also used to illustrate the direction and magnitude of correlations between % fire-induced tree morality versus yellowjacket abundance for each individual species collected during this study.

Relationships between forest structural attributes and yellowjacket diversity

We used generalized linear models (family: gaussian, link function: identity) to determine relative effect sizes of forest structural attributes on yellowjacket abundance, species richness, and diversity, treating plot-level measurements as the unit of analysis. Model effects included fire age, % tree mortality, canopy structure (both live and dead tree basal area, canopy closure), floral resources (floral abundance, floral species richness) and forest floor cover categories (bare soil, CWD, grass, shrubs). We used stepwise model selection procedures (backwards selection) to evaluate which forest habitat variables were valid for entry into explanatory models accounting for variation in the abundance of individual yellowjacket species collected within the study site. Variables considered for entry in the model were the same as described above, with a significance threshold of $p < 0.10$ for inclusion into a model determined by ordinary least squares (OLS) regression procedures.

Results

Differences in yellowjacket abundance, diversity and community assemblages among burn severity and fire age classes

A total of 1192 yellowjackets specimens were collected during the study, from five species including *V. pennsylvanica* (75 % of captures), *V. acadica* Sladen (11 %), *V. infernalis* Saussure (9 %), *V. sulphurea* de Saussure (8 %) and *V. atropilosa* Sladen (< 1 %). Overall, fire-induced tree mortality (%) exhibited significant correlations with the abundance of each individual yellowjacket species collected within the study site (Fig. 1). However, the direction and magnitude of these relationships varied among species. Percent tree mortality exhibited positive relationships with abundance of *V. pennsylvanica* ($R^2 = 0.11$; $F_{1,62} = 7.46$; $p = 0.0082$) and *V. atropilosa* ($R^2 = 0.19$; $F_{1,62} = 14.96$; $p = 0.0003$), and negative relationships with abundance of *V. acadica* ($R^2 = 0.19$; $F_{1,62} = 15.39$; $p = 0.0002$), *V. infernalis* ($R^2 = 0.21$; $F_{1,62} = 16.42$; $p = 0.0001$) and *V. sulphurea* ($R^2 = 0.17$; $F_{1,62} = 12.26$; $p = 0.0009$) (Fig. 1).

Plot-level means, associated standard errors (SE), and Tukey’s honestly significant difference (HSD) test of yellowjacket abundance, species richness, and Shannon’s diversity among burn severity classes and fire ages are summarized in Table 1 and illustrated in Figure 2 and 3. Overall, mean yellowjacket abundance was significantly reduced in low, medium and high severity burned plots within one- and two-year-old fire boundaries compared to plots located in unburned areas or in five-and seven-year-old fire boundaries (Table 1). Post-fire yellowjacket abundance was lowest within high severity burned areas one year following fire, and highest in high severity burned plots within five- and seven-year-old fire boundaries. Significant reductions in mean species richness and diversity among burn severity and fire age classes were limited to high burn severity plots within one- and seven-year old fire boundaries (Table 1; Figs. 2, 3).

Results from two-way ANOVA testing for significant ($\alpha = 0.05$) effects of wildfire burn severity, time since fire and their interactions on yellowjacket abundance, species richness and Shannon's diversity are summarized in Table 2. When categorically delineated, burn severity did not exhibit a significant effect on yellowjacket abundance ($F_{3,59} = 1.66$; $p = 0.187$). However, fire age ($F_{3,59} = 9.40$; $p < 0.0001$) and the interactive term between time since fire and burn severity classes ($F_{9,53} = 2.58$; $p = 0.017$) both exhibited significant effects of yellowjacket abundance (whole model: $F_{15,47} = 4.87$; $p < 0.0001$). Specifically, the main effect of time since fire depended significantly on the level of burn severity. Neither burn severity class ($F_{3,59} = 2,39$; $p = 0.08$), fire age ($F_{3,59} = 0.12$; $p = 0.948$), nor their interactive term ($F_{9,53} = 1.48$; $p = 0.182$) significantly affected yellowjacket species richness (whole model: $F_{15,47} = 2.39$; $p < 0.012$). Similarly, yellowjacket diversity (whole model: $F_{15,47} = 4.33$; $p = 0.001$) was not significantly affected by burn severity ($F_{3,59} = 2.24$; $p = 0.096$), fire age ($F_{3,59} = 1.26$; $p = 0.300$), nor their interactive term ($F_{9,53} = 1.12$; $p = 0.365$). Linear relationships regarding yellowjacket community-level abundance, species richness, and Shannon's diversity versus fire-induced tree mortality (%) are illustrated in Figure 4. Community-level abundance exhibited a significant, positive relationship with % tree mortality ($R^2 = 0.06$; $F_{1,62} = 4.16$; $p = 0.0456$), while species richness ($R^2 = 0.15$; $F_{1,62} = 11.19$; $p = 0.0014$) and diversity ($R^2 = 0.26$; $F_{1,62} = 22.55$; $p < 0.0001$) both exhibited significant, negative relationships with % tree mortality (Fig. 4).

Results from canonical correspondence analyses used to determine degrees of similarity of yellowjacket community assemblages among plots within individual fire age classes are illustrated in Figure 5. Axes one (eigenvalue = 0.333, p = 0.001) and two (eigenvalue = 0.024, *p* = 0.012) explained 90.4 and 6.5 %, respectively, of the total variance (stress = 0.09) present within plot-level community composition caused by environmental factors (forest canopy structure and ground cover composition). Overall, similarity in plot-level yellowjacket community composition increased with time since fire. The 95 % confidence ellipsoids of the seven-year-old fire encompassed less area than one- and two-year-old fires, whose associated plots were more variable (spaced further apart) with respective to local yellowjacket community composition (Fig. 5). In general, forest-obligate species such as the forest yellowjacket, *V. acadica,* and its nest-parasite, the cuckoo yellowjacket, *V. sulphurea,* (Carpenter and Kimsey 2012) were positively correlated with basal area, canopy closure and coarse woody debris, and negatively correlated with % tree mortality caused by wildfire (Figs. 1, 5). Conversely, species associated with non-forested habitats such as the western yellowjacket, *V. pennsylvanica,* and the prairie yellowjacket, *V. atropilosa*, exhibited positive relationships with % tree mortality and bare soil exposure as well as shrub and grass cover (Figs. 1, 5).

Relationships between forest structural attributes and yellowjacket diversity

Results from generalized linear models describing variation in yellowjacket abundance, species richness and Shannon's diversity due to environmental variables are summarized in Table 3. Given the disproportionate number of *V. pennsylvanica* collected in comparison to other yellowjacket species, analyses were conducted with and without the inclusion of *V. pennsylvanica* abundance data. With the inclusion of plot-level *V. pennsylvanica* abundance data, variation in community-level abundance was significantly affected by canopy closure (-correlation), bare soil (+), litter cover (+), coarse woody debris (-), floral abundance (+), shrub (+) and grass cover (-), as well as time since fire (+) (whole model: DF = 10; $\chi^2 = 746.27$; $p <$

0.0001). When excluding plot-level *V. pennsylvanica* abundance data in the analysis, variation in community-level abundance was significantly affected by % tree mortality (-), canopy closure (+), and bare soil (-) (whole model: DF = 10; $\chi^2 = 85.41$; $p < 0.0001$). Bare soil exhibited a negative relationship with yellowjacket species richness, which was the only variable that significantly affected species richness with the inclusion of plot-level *V. pennsylvanica* abundance data (whole model: DF = 10; $\chi^2 = 24.55$; $p = 0.0063$). When excluding plot-level *V. pennsylvanica* abundance data, no habitat variables exhibited significant effects on yellowjacket species richness at the $\alpha = 0.05$ level (whole model: DF = 10; $\chi^2 = 11.81$; $p = 0.298$). Yellowjacket diversity exhibited significant, negative relationships with % tree mortality, bare soil and time since fire with the inclusion of plot-level *V. pennsylvanica* abundance data in the analysis (whole model: DF = 10; $\chi^2 = 34.37$; $p = 0.0002$). When excluding plot-level *V. pennsylvanica* abundance data, variation in yellowjacket diversity was significantly affected by canopy closure (-), bare soil (-), floral abundance (+), and grass cover (-) (whole model: DF = 10; $\chi^2 = 27.44$; $p = 0.0022$) (Table 3).

Results from stepwise regression procedures used to develop explanatory models regarding species-specific relationships between yellowjacket abundance and habitat structure are summarized in Table 4. The best model for explaining variation in plot-level, forest yellowjacket (*V. acadica*) abundance included basal area, canopy closure, and shrub cover as explanatory variables ($F_{3, 60} = 7.67$; $p = 0.0002$; $R^2 = 0.29$), where abundance was negatively correlated with all three variables (Table 4). A one unit increase in basal area (+ 10 m^2/ha), canopy closure (+ 1%) or shrub cover (+ 10) % was estimated to decrease *V. acadica* abundance by 6.2, 2.1 and 3.9%, respectively. The best model for describing variation in plot-level prairie yellowjacket (*V. atropilosa*) abundance included % tree mortality, canopy closure, coarse woody debris and shrub cover as explanatory variables ($F_{4, 59} = 11.95$; $p < 0.0001$; $R^2 = 0.41$), where their abundance was positively correlated with % tree mortality and shrub cover, and negatively correlated with canopy closure and coarse woody debris (Table 4). A one unit change in % tree mortality, canopy closure, coarse woody debris (± 10%) or shrub cover was estimated to change *V. atropilosa* abundance by 2.0, 2.9, 3.9 and 3.1%, respectively. The best model for describing the variation in plot-level cuckoo yellowjacket (*V. infernalis*) abundance included % tree mortality, bare soil exposure, shrub and grass cover as well as time since fire (+1 year) as explanatory variables ($F_{5, 58} = 8.48$; $p < 0.0001$; $R^2 = 0.37$), where their abundance was positively correlated with shrub cover, and negatively correlated with % tree mortality, bare soil, grass cover and time since fire (Table 4). A one unit change in % tree mortality, bare soil exposure (± 10%), shrub and grass cover (± 10%) or time since fire (± 1 year) was estimated to change *V. infernalis* abundance by 3.0, 5.8, 7.3, 8.5 and 22.1 %, respectively. The best model for explaining variation in plot-level western yellowjacket (*V. pennsylvanica*) abundance included canopy closure, floral abundance and coarse woody debris as explanatory variables ($F_{3, 60} = 15.56$; $p < 0.0001$; $R^2 = 0.41$), where their abundance was positively correlated with floral abundance and negatively correlated with canopy closure as well as coarse woody debris (Table 4). A one unit change in canopy closure, floral abundance (+ 25 inflorescences) and coarse woody debris was estimated to change *V. pennsylvanica* abundance by 3.9, 4.8, and 13.1% respectively. The best model for explaining variation in plot-level California yellowjacket (*V. Sulphurea*) abundance included % tree mortality, floral abundance and basal area as explanatory variables ($F_{3, 60} = 4.60$; $p = 0.0005$; $R^2 = 0.18$), where their abundance was positively correlated with floral abundance and basal area, and negatively with % tree mortality (Table 4). A one unit change in % tree mortality, floral abundance or basal area was estimated to change *V. sulphurea* abundance by 4.9, 2.9 and 1.0%, respectively.

Discussion

Differences in yellowjacket abundance and diversity among burn severity and fire age classes

Results from ANOVA and Tukey's post-hoc tests indicate that yellowjacket abundance is significantly reduced during early successional periods (≤ two years) following fire in montane, mixed-conifer forests of the central Sierra Nevada, regardless of local burn severity or overstory tree morality (Tables 1, 2; Figs. 1, 2, 4). Our analyses demonstrated post-fire yellowjacket communities to be significantly more abundant within older fire boundaries (five- and seven-years-old), compared to those residing in one- and two-year-old boundaries, particularly in moderate and high severity burned areas (Tables 1, 2; Figs. 1, 2). Research on the thermal tolerances of subterranean-nesting bees suggest that high intensity fires that heat soils > 50 ° C may kill social Hymenopterans nesting at depths < 10 cm (Busse et al. 2005, Cane and Neff 2011). Portions or entire nests of several yellowjacket species collected during this study (*V. acadica, V. atropilosa, V. pennsylvanica*) have been documented at relatively shallow depths (3-15 cm), or even above-ground (within plant litter, shrubs, or underneath large piles of woody debris) in North America (MacDonald et al. 1975, Akre et al. 1980, MacDonald and Matthews 1981). Given such nesting behaviors, these early reductions in yellowjacket abundance across our study site may have resulted from even low intensity fire destroying above-ground nests, while higher intensity fire may have destroyed or irreparably damaged relatively shallow, subterranean nests throughout individual fire boundaries (Cane and Neff 2011).

Within older (≥ five years) fire boundaries, yellowjacket abundance and diversity was generally highest in areas that burned at moderate severity (Tables 1, 3; Figs. 1-4). These results coincide with both theoretical literature and empirical studies that propose a unimodal hump-shaped relationship between post-disturbance biodiversity and fire severity within forests that exhibit moderate levels of ecosystem productivity (net rate of biomass production), such as *P. ponderosa* landscapes in the western US (Connell 1978, Huston 1994, Hall et al. 2012, Richter et al. 2019). Increased light and nutrient availability on the forest floor resulting from altered stand structures following low to moderate severity fire might have promoted the abundance or diversity of the understory plant community in disturbed areas (Ponisio et al. 2016, Richter et al. 2019, Brodie et al. 2021) which may have promoted the abundance of flower-visiting arthropods (Potts et al. 2003, 2005, Lazarina et al. 2016, 2017) that are predated upon by yellowjackets (Akre et al. 1976, 1980). Relevant studies that have documented insect pollinator responses to wildifre suggest that the removal of fine surface fuels from low and moderate burn severities within fire-adapted forests can benefit their communities by exposing optimal nesting substrate or otherwise promoting the growth of community foraging resources (Potts et al. 2003, 2005, Lazarina et al. 2016, 2017, Ponisio et al. 2016, Mason Jr. et al. 2021, Glenny et al. 2022, Gelles et al. 2023). Well-established ecological theories on trophic cascades (Polis et al. 2000, Yang and Gratton 2014) and predator-prey dynamics (Holling 1961, 1966, Arditi and Ginzburg 1989, Berryman 1992) provide mechanisms as to why the abundance or diversity of insectivorous predators like yellowjackets might increase over time following the re-establishment and proliferation of herbaceous plant and flower-visiting insect communities in areas that burned at low or moderate severity.

Yellowjacket communities occupying stands that burned at high severity within older (≥ five years) fire boundaries were less speciose and diverse than those residing in unburned areas or locations that burned at relatively low severity (Table 1, Fig. 2, 3). In lower montane, mixed-conifer forests of the Californian Sierra Nevada, fire-adapted shrubs often rapidly dominate the forest floor after high severity fire, which may ultimately reduce understory plant species richness over early-successional periods due to competitive exclusion (Richter et al. 2019, Miller and Safford 2020, Brodie et al. 2021). Increased invasive grass cover following high severity wildfire in lower elevation, forested ecosystems may have similar, negative effects on local understory plant diversity (D’antonio and Vitousek 1992), while also obscuring nesting substrates (e.g., bare soil and rodent burrows) utilized by certain yellowjackets (Akre et al. 1980). The resulting reductions in herbaceous plant diversity and nesting substrate visibility could have caused cascading, negative effects on local yellowjacket populations and community diversity in high severity burn patches within our study site (Polis et al. 2000, Yang and Gratton 2014). Additionally, the destruction of downed and decaying logs, which are utilized by several yellowjacket species during nest construction (Akre et al. 1980, MacDonald and Matthews 1981) may have reduced nest densities within high severity burn patches, which could have potentially caused further reductions in species richness or diversity. Developing effective methods for efficiently locating yellowjacket nests within forested landscapes can improve our understanding of how wildfire affects yellowjacket colony density within a landscape or individual stand, and provide needed information on rates of colony re-establishment following fire.

Species-specific differences in yellowjacket responses to wildfire and relationships with forest structure

Results from ordination techniques and model selection procedures demonstrated noticeable variation in yellowjacket community composition among burn severity and fire age classes as well as species-specific relationships with various structural attributes of their forest habitat (Table 4; Fig. 5). Overall, similarity in plot-level yellowjacket community composition increased with time since fire, where the 95 % confidence ellipsoids of the seven-year old fire encompassed far less area and fewer species than one- and two-year-old fires (Fig. 5). In general, forest-obligate species such as the forest yellowjacket, *V. acadica,* and its nest-parasite, the cuckoo yellowjacket, *V. sulphurea*, (Carpenter and Kimsey 2012) were absent in older fire boundaries, positively correlated with basal area, canopy closure and coarse woody debris, and negatively correlated with % tree mortality (Table 4; Figs. 1, 5). Reductions in downed decaying logs or other coarse woody debris, particularly within those that burned at high severity, likely contributed to the general absence of these species which frequently construct their nests in these materials (MacDonald 1975). Conversely, species associated with non-forested habitats such as the western yellowjacket, *V. pennsylvanica,* and the prairie yellowjacket, *V. atropilosa*, exhibited positive relationships with % tree mortality as well as shrub and grass cover (Table 4; Figs. 1, 5). Traits including broad dietary breadth, high mobility or variable nesting behaviors might have allowed certain species (e.g., *V. pennsylvanica*) to colonize disturbed areas more readily or better utilize severely burned areas (Figs. 1, 3, 5) in comparison to species with restricted diets, foraging ranges or nesting habitats (Akre et al. 1980). Our results suggest an inverse relationship between plot-level yellowjacket diversity and *V. pennsylvanica* abundance (Fig. 3). Disproportionate immigration or proliferation of habitat generalists like *V. pennsylvanica* within these disturbed areas may have affected overall species evenness over time. While anecdotal, this observation also suggests potential interspecific competition within yellowjacket communities following fire, especially in areas that burned at high severities or in older fire boundaries, possibly due to homogenized habitat structures or low resource availability (Martin and Sapsis 1992, Ponisio et al. 2016, Harrison et al. 2018).

The direction and magnitude of relationships between various stand structural attributes and yellowjacket abundance or diversity was dependent on the inclusion of plot-level *V. pennsylvanica* abundance into our regression analyses (Table 3). For example, community-level abundance relationships with basal area and canopy closure were negative when including *V. pennsylvanica* data, and positive without (Table 3). This suggests that high severity wildfires in lower montane forests that significantly reduce the overstory might have detrimental effects on yellowjacket diversity over time, while also potentially creating conditions that promote pestiferous *V. pennsylvanica* populations. Altered yellowjacket community compositions with disproportionate amounts of generalist predators like *V. pennsylvanica* may have consequences for other arthropod functional guilds. For example, their workers have been found to aggressively defend carbohydrate-dense resources (e.g., floral nectar and honeydew) from other flower-visiting insects (Hanna et al. 2012, 2014). The disruption of local plant-pollinator networks due to such antagonistic interactions could potentially reduce the reproductive success of certain herbaceous species over time (Burkle and Alarcon 2011, Hanna et al. 2014). Future research that samples the local yellowjacket community in addition to insect pollinators and understory plant communities over an extensive chronosequence and burn severity gradient following wildfire can help determine how variation in burn severity and insect predator abundance affects the interactions between organisms within the lower trophic levels of arthropod food webs in western US forests over time.

Conclusions

Regardless of severity, wildfire significantly reduced yellowjacket abundance during the immediate years following disturbance across our study site (Fig. 2), likely due to flame-induced yellowjacket mortality combined with the destruction of their nesting and overwintering substrates (needle litter, shrub cover, coarse woody debris). This suggests that low to moderate intensity fire characteristic of prescribed burns used to restore or maintain the function of mixed-conifer forests in the Central Sierra Nevada may further benefit public safety via short-term reductions in local wasp population levels. Our data further suggests that these relatively low severity burns will likely not exhibit longer-term, negative effects on overall yellowjacket community diversity (Fig. 3). Conversely, high severity fire might create promote the population levels of certain pestiferous yellowjacket species (Tables 3, 4; Figs. 1, 3, 5), potentially through increases in resource availability, the development of favorable stand conditions, or lack of competitors. Future related research should investigate how other common forest disturbances (e.g., bark beetle outbreaks, windthrow events, stand-thinning operations) affect local yellowjacket populations via altering forest habitat structure or fine-scale abiotic conditions. Overall, generating predictive models on yellowjacket community responses to landscape disturbance and variation in forest structure can help inform land management agencies and private landowners of potential yellowjacket abundances, and therefore general pest status, in areas of concern.

Literature cited

Addington RN, Aplet GH, Battaglia MA, Briggs JS, Brown PM, Cheng AS, Wolk B. 2018. Principles and practices for the restoration of ponderosa pine and dry mixed-conifer forests of the Colorado Front Range. RMRS-GTR-373. Fort Collins (CO): *US Department of Agriculture, Forest Service, Rocky Mountain Research Station*. 121 p. 373

Akre RD, Davis HG. 1978. Biology and pest status of venomous wasps. *Annu Rev Entomol.* 23(1):215-238.

Akre RD, Reed HC. 1981. Population cycles of yellowjackets (Hymenoptera: Vespinae) in the Pacific Northwest. *Environ Entomol.* 10(3):267-274.

Akre RD, Garnett WB, MacDonald JM, Greene A, Landolt P. 1976. Behavior and colony development of Vespula pensylvanica and V. atropilosa (Hymenoptera: Vespidae). *J Kans Entomol Soc*. 63-84.

Allen CD, Savage M, Falk DA, Suckling KF, Swetnam TW, Schulke T, Klingel JT. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol Appl.* 12(5):1418-1433.

Arditi R, Ginzburg LR. 1989. Coupling in predator-prey dynamics: ratio-dependence. *J Theor Biol.* 139(3):311-326.

Berryman AA. 1992. The origins and evolution of predator-prey theory. *Ecology*. 73(5):1530-1535.

Bond WJ, Keeley JE. 2005. Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems. *Trends Ecol Evol.* 20(7):387-394.

Bond WJ, Woodward FI, Midgley GF. 2005. The global distribution of ecosystems in a world without fire. *New Phytol.* 165(2):525-538.

Bowman DM, Perry GL, Higgins SI, Johnson CN, Fuhlendorf SD, Murphy BP. 2016. Pyrodiversity is the coupling of biodiversity and fire regimes in food webs. Philos *Trans R Soc B Biol Sci*. 371(1696):20150169.

Brodie EG, Miller JE, Safford HD. 2021. Productivity modifies the effects of fire severity on understory diversity. *J Ecol.*

Burkle LA, Alarcón R. 2011. The future of plant–pollinator diversity: understanding interaction networks across time, space, and global change. *Am J Bot.* 98(3):528-538.

Burkle LA, Myers JA, Belote RT. 2015. Wildfire disturbance and productivity as drivers of plant species diversity across spatial scales. *Ecosphere*. 6(10):1-14.

Busse MD, Hubbert KR, Fiddler GO, Shestak CJ, Powers RF. 2005. Lethal soil temperatures during burning of masticated forest residues. *Int J Wildland Fire*. 14(3):267-276.

Cane JH. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *J Kans Entomol Soc*. 406-413.

Cane JH, Neff JL. 2011. Predicted fates of ground-nesting bees in soil heated by wildfire: thermal tolerances of life stages and a survey of nesting depths. *Biol Conserv*. 144(11):2631-2636.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr.* 84(1):45-67.

Connell JH. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. *Science*. 199(4335):1302-1310.

D'Antonio CM, Vitousek PM. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Ann. Rev Ecol Syst.* 23(1):63-87.

Donovan BJ. 2003. Potential manageable exploitation of social wasps, Vespula spp. (Hymenoptera: Vespidae), as generalist predators of insect pests. *Int J Pest Manag*. 49(4):281-285.

Fahey RT, Puettmann KJ. 2007. Ground-layer disturbance and initial conditions influence gap partitioning of understory vegetation. *J Ecol.*

Ferrenberg SM, Schwilk DW, Knapp EE, Groth E, Keeley JE. 2006. Fire decreases arthropod abundance but increases diversity: early and late season prescribed fire effects in a Sierra Nevada mixed-conifer forest. *Fire Ecol*. 2(2):79-102.

Galbraith SM, Cane JH, Moldenke AR, Rivers JW. 2019. Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere.* 10(4):e02668.

Gelles RV, Davis TS, Stevens-Rumann CS. 2023. Wildfire and forest thinning shift floral resources and nesting substrates to impact native bee biodiversity in ponderosa pine forests of the Colorado Front Range. *Forest Ecol Manag*. 510:120087.

Glenny W, Runyon JB, Burkle LA. 2022. A review of management actions on insect pollinators on public lands in the United States. *Biodiversity Conserv*. 1-22.

Golden DB, Breisch NL, Hamilton RG, Guralnick MW, Greene A, Craig TJ, Kagey-Sobotka A. 2006. Clinical and entomological factors influence the outcome of sting challenge studies. *J Allergy Clin Immunol*. 117(3):670-675.

Haddad NM, Holyoak M, Mata TM, Davies KF, Melbourne BA, Preston K. 2008. Species' traits predict the effects of disturbance and productivity on diversity. *Ecol Lett.* 11(4):348-356.

Hall AR, Miller AD, Leggett HC, Roxburgh SH, Buckling A, Shea K. 2012. Diversity–disturbance relationships: frequency and intensity interact. *Biol Lett.* 8(5):768-771.

Hanna C, Foote D, Kremen C. 2012. Short-and long-term control of Vespula pensylvanica in Hawaii by fipronil baiting. *Pest Manag Sci*. 68(7):1026-1033.

Hanna C, Foote D, Kremen C. 2014. Competitive impacts of an invasive nectar thief on plant–pollinator mutualisms. *Ecology*. 95(6):1622-1632.

Hammer Ø, Harper DA. 2001. Past: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*. 4(1):1.

Hanula JL, Ulyshen MD, Horn S. 2016. Conserving pollinators in North American forests: a review. *Nat Areas J*. 36(4):427-439.

Harrison T, Gibbs J, Winfree R. 2018. Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Global Change Biol.* 24(1):287-296.

Holling CS. 1961. Principles of insect predation. *Ann. Rev Entomol*. 6(1):163-182.

Holling CS. 1966. The functional response of invertebrate predators to prey density. *Mem Entomol Soc Can*. 98(S48):5-86.

Huston MA. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge (UK): *Cambridge University Press.*

Kimsey LS, Carpenter JM. 2012. The Vespinae of North America (Vespidae, Hymenoptera). *J Hymenoptera Res.* (28).

Koltz AM, Burkle LA, Pressler Y, Dell JE, Vidal MC, Richards LA, Murphy SM. 2018. Global change and the importance of fire for the ecology and evolution of insects. *Curr Opin Insect Sci.* 29:110-116.

Landolt PJ, Pantoja A, Green D. 2005. Yellowjacket wasps (Hymenoptera: Vespidae) trapped in Alaska with heptyl butyrate, acetic acid and isobutanol. *J Entomol Soc British Columbia*. 102:35-42.

Landolt P, Zhang QH. 2016. Discovery and development of chemical attractants used to trap pestiferous social wasps (Hymenoptera: Vespidae). *J Chem Ecol*. 42(7):655-665.

Lazarina M, Sgardelis SP, Tscheulin T, Kallimanis AS, Devalez J, Petanidou T. 2016. Bee response to fire regimes in Mediterranean pine forests: the role of nesting preference, trophic specialization, and body size. *Basic Appl Ecol*. 17(4):308-320.

Lazarina M, Sgardelis SP, Tscheulin T, Devalez J, Mizerakis V, Kallimanis AS, Petanidou T. 2017. The effect of fire history in shaping diversity patterns of flower-visiting insects in post-fire Mediterranean pine forests. *Biodivers Conserv*. 26:115-131.

Lichtenberg JS, Lichtenberg DA. 2003. Predation of caterpillars on understory saplings in an Ozark forest. *Southeastern Nat.* 2(3):423-432.

MacDonald JF, Akre RD, Hill WB. 1975. Nest associates of Vespula atropilosa and V. pensylvanica in southeastern Washington state (Hymenoptera: Vespidae). J *Kans Entomol Soc*. 53-63.

MacDonald JF, Matthews RW. 1981. Nesting biology of the eastern yellowjacket, Vespula maculifrons (Hymenoptera: Vespidae). *J Kans Entomol Soc*. 433-457.

MacLean JL, van Akker L, Van Hezewijk BH. 2021. The structure of temperate yellowjacket communities is affected by land development and loss of forest cover. *Agric Forest Entomol*. 23(3):269-275.

Martin RE, Sapsis DB. 1992. Fires as agents of biodiversity: pyrodiversity promotes biodiversity. In Proceedings of the conference on biodiversity of northwest California ecosystems. *Cooperative Extension, University of California, Berkeley* (pp. 150-157).

Mason Jr SC, Shirey V, Ponisio LC, Gelhaus JK. 2021. Responses from bees, butterflies, and ground beetles to different fire and site characteristics: a global meta-analysis. *Biol Conserv*. 261:109265.

McCabe TD, Dietze MC. 2019. Scaling contagious disturbance: a spatially-implicit dynamic model. Front Ecol Evol. 7:64.

McLauchlan KK, Higuera PE, Miesel JR, Rogers BM, Schweitzer J, Shuman JK, Watts AC. 2020. Fire as a fundamental ecological process: research advances and frontiers. *J Ecol*. 108(5):2047-2069.

Miller JD, Safford HD, Crimmins M, Thode AE. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and southern Cascade Mountains, California and Nevada, USA. *Ecosystems.* 12(1):16-32.

Miller JD, Safford HD. 2017. Corroborating evidence of a pre-Euro-American low-to moderate-severity fire regime in yellow pine-mixed conifer forests of the Sierra Nevada, California, USA. *Fire Ecol*. 13(1):58-90.

Moretti M, Obrist MK, Duelli P. 2004. Arthropod biodiversity after forest fires: winners and losers in the winter fire regime of the southern Alps. *Ecography*. 27(2):173-186.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'hara RB, Oksanen MJ. 2013. Package 'vegan'. Community ecology package, version, 2(9):1-295.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H. 2019. vegan: Community ecology package. R package version 2.5-4

Parks SA, Abatzoglou JT. 2020. Warmer and drier fire seasons contribute to increases in area burned at high severity in western US forests from 1985 to 2017. *Geophys Res Lett.* 47(22):e2020GL089858.

Peng C, Apps MJ. 1999. Modelling the response of net primary productivity (NPP) of boreal forest ecosystems to changes in climate and fire disturbance regimes. *Ecol Modell.* 122(3):175-193.

Polis GA, Sears AL, Huxel GR, Strong DR, Maron J. 2000. When is a trophic cascade a trophic cascade?. *Trends Ecol Evol.* 15(11):473-475.

Ponisio LC, Wilkin K, M'Gonigle LK, Kulhanek K, Cook L, Thorp R, Kremen C. 2016. Pyrodiversity begets plant–pollinator community diversity. *Global Change Biol.* 22(5):1794-1808.

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P. 2003. Linking bees and flowers: how do floral communities structure pollinator communities?. *Ecology*. 84(10):2628-2642.

Potts SG, Vulliamy B, Roberts S, O'Toole C, Dafni A, Ne'eman G, Willmer P. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecol Entomol.* 30(1):78-85.

Richter C, Rejmánek M, Miller JE, Welch KR, Weeks J, Safford H. 2019. The species diversity× fire severity relationship is hump-shaped in semiarid yellow pine and mixed conifer forests. *Ecosphere*. 10(10):e02882.

Safford HD, Paulson AK, Steel ZL, Young DJ, Wayman RB. 2022. The 2020 California fire season: a year like no other, a return to the past or a harbinger of the future?. *Global Ecol Biogeogr.*

Steel ZL, Koontz MJ, Safford HD. 2018. The changing landscape of wildfire: burn pattern trends and implications for California's yellow pine and mixed conifer forests. *Landscape Ecol.* 33(7):1159-1176.

Strickler GS. 1959. Use of the densiometer to estimate density of forest canopy on permanent sample plots. *PNW Old Series Research Notes No. 180*, p. 1-5, 180.

Syphard AD, Radeloff VC, Hawbaker TJ, Stewart SI. 2009. Conservation threats due to human-caused increases in fire frequency in Mediterranean-climate ecosystems. *Conserv Biol.* 23(3):758-769.

Walters BB, Stiles EW. 1996. Effect of canopy gaps and flower patch size on pollinator visitation of Impatiens capensis. *Bull Torrey Bot Club*. 184-188.

Williams NM, Crone EE, T'ai HR, Minckley RL, Packer L, Potts SG. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biol Conserv*. 143(10):2280-2291.

U.S. Geological Survey. 2020. Rapid Assessment of Vegetation Condition after Wildfire (RAVG). [accessed 2020 Oct]. https://burnseverity.cr.usgs.gov/ravg/.

Yang LH, Gratton C. 2014. Insects as drivers of ecosystem processes. *Curr Opin Insect Sci*. 2:26-32.

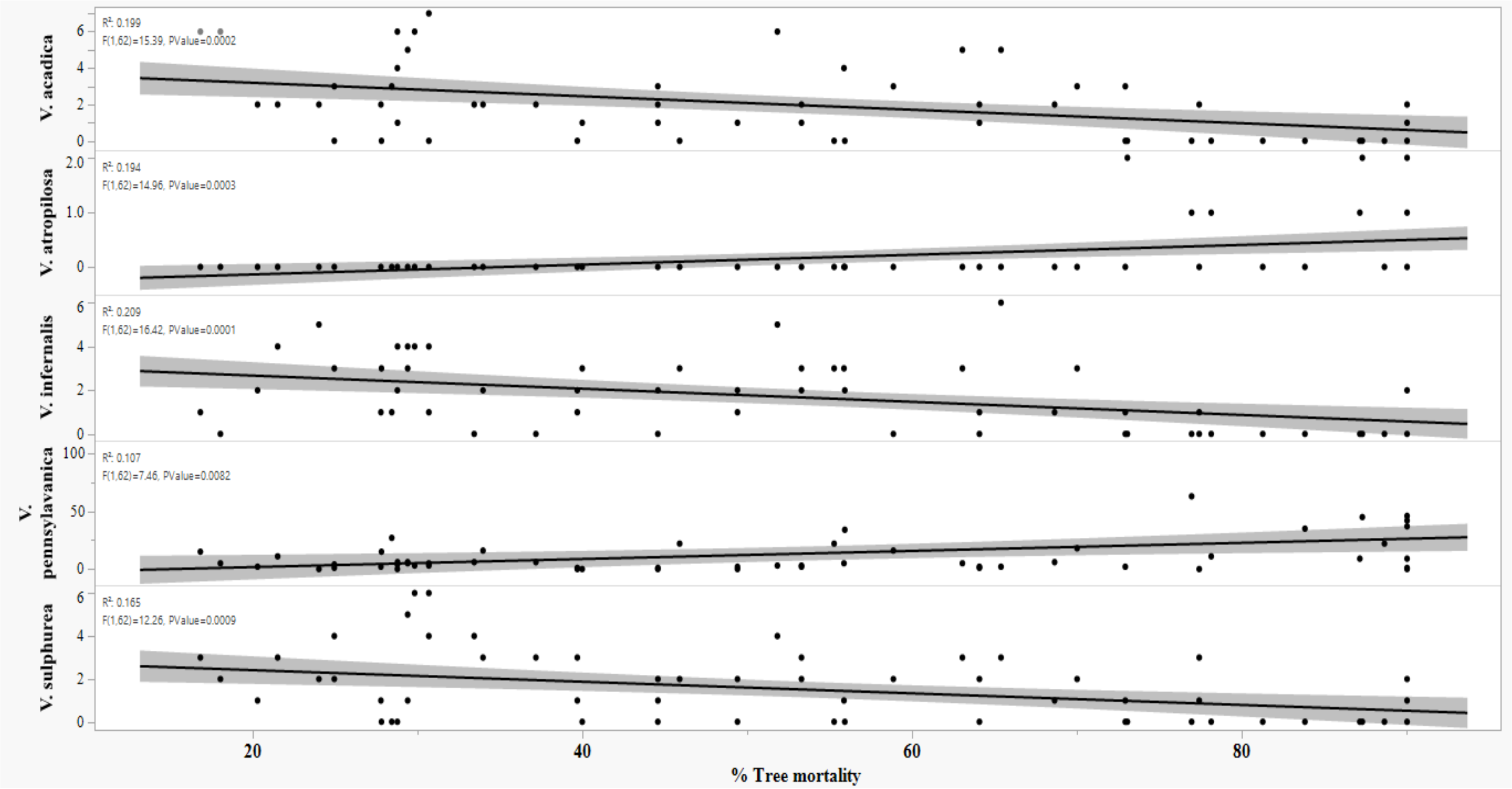

Figure 1. Results from simple linear regression used to determine the direction and magnitude of correlations between fire-induced tree mortality (%) versus species-level yellowjacket abundance within montane forested landscapes of Sierra National Forest, California.

Table 1. Plot-level means, associated standard errors (SE), and Tukey’s honestly significant difference (HSD) test of yellowjacket abundance, species richness, and Shannon’s diversity among burn severity classes and fire ages; means not connected by the same letter(s) within individual columns differ significantly ($\alpha = 0.05$).

Burn Severity	**Fire Age (years)**	**Abundance**			**Richness**			**Diversity**		
		Mean	**SE**	**HSD**	**Mean**	**SE**	**HSD**	**Mean**	**SE**	**HSD**
Undisturbed	1	14.5	1.7	abc	3.8	0.3	ab	1.2	0.1	abc
	2	11	2.9	abc	3	0.4	ab	1	0.2	abc
	5	13	2.2	abc	3.3	0.3	ab	1.1	0.1	abc
	7	14.5	4.7	abc	4	0	a	1.2	0.1	abc
Low	1	4.3	1.1	bc	2.8	0.8	ab	0.8	0.3	bc
	2	4	0.9	bc	2.5	0.6	ab	0.7	0.3	bc
	5	11.3	2.9	abc	3	0.4	ab	1	0.2	abc
	7	24.8	2.8	abc	3	0.4	ab	0.6	0.1	abc
Medium	1	4.8	1.4	bc	2.8	0.8	ab	0.8	0.3	bc
	2	6.5	1.4	bc	3.3	0.5	ab	1.1	0.2	bc
	5	13.8	1.4	abc	4	0	a	1.3	0.1	abc
	7	24	1.5	abc	3	0.6	ab	0.7	0.2	abc
High	1	2.8	0.6	c	2	0.4	ab	0.6	0.2	c
	2	35.8	9.2	ab	3	0.7	ab	0.4	0.1	ab
	5	59.8	31	a	1.8	0.3	ab	0.1	0.1	a
	7	52.3	23.1	a	1.5	0.3	b	0.1	0.1	a

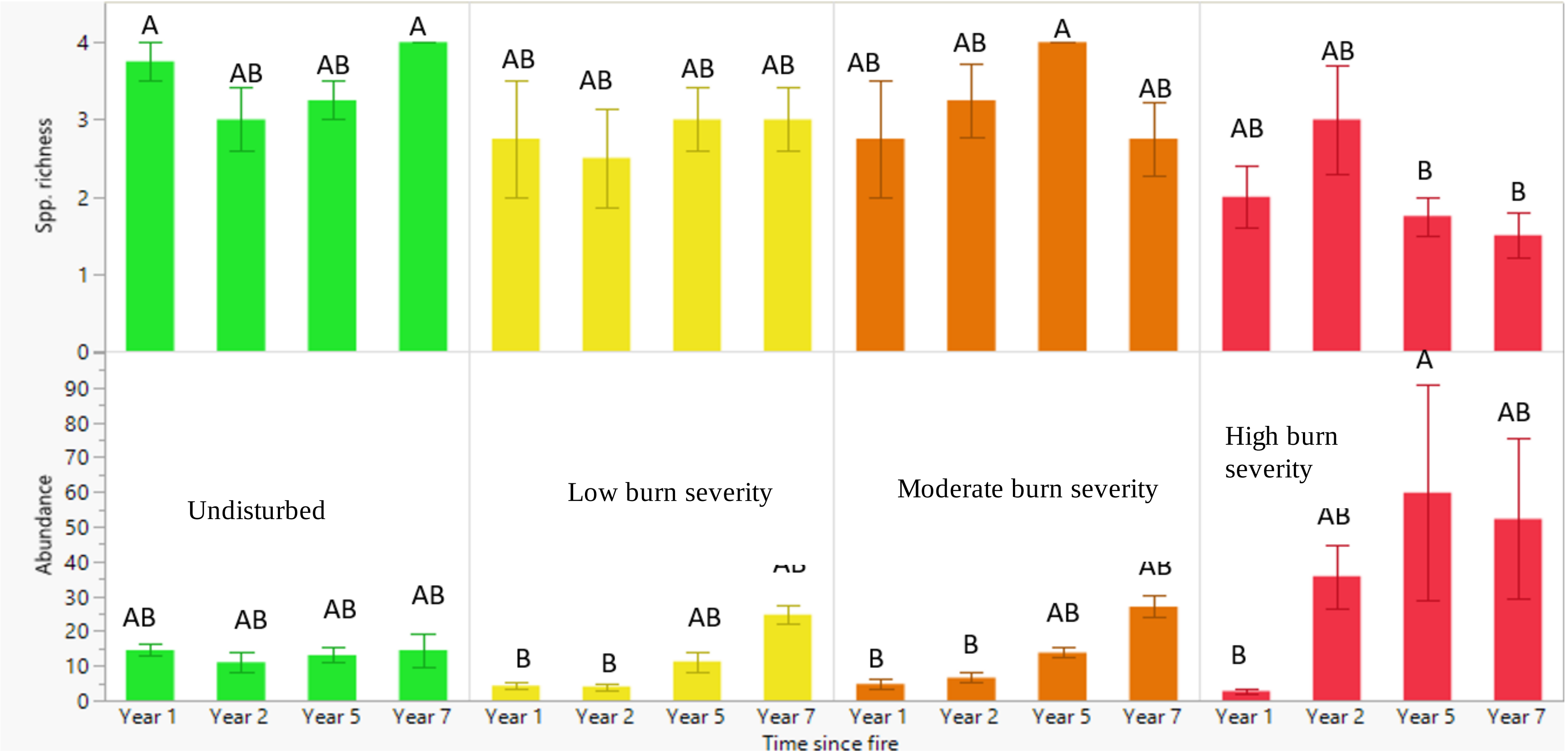

Figure 2. Plot-level means, associated standard errors (SE), and Tukey's honestly significant difference (HSD) test of yellowjacket abundance, and species richness among burn severity classes and fire ages; means not connected by the same letter(s) within individual columns differ significantly (α = 0.05).

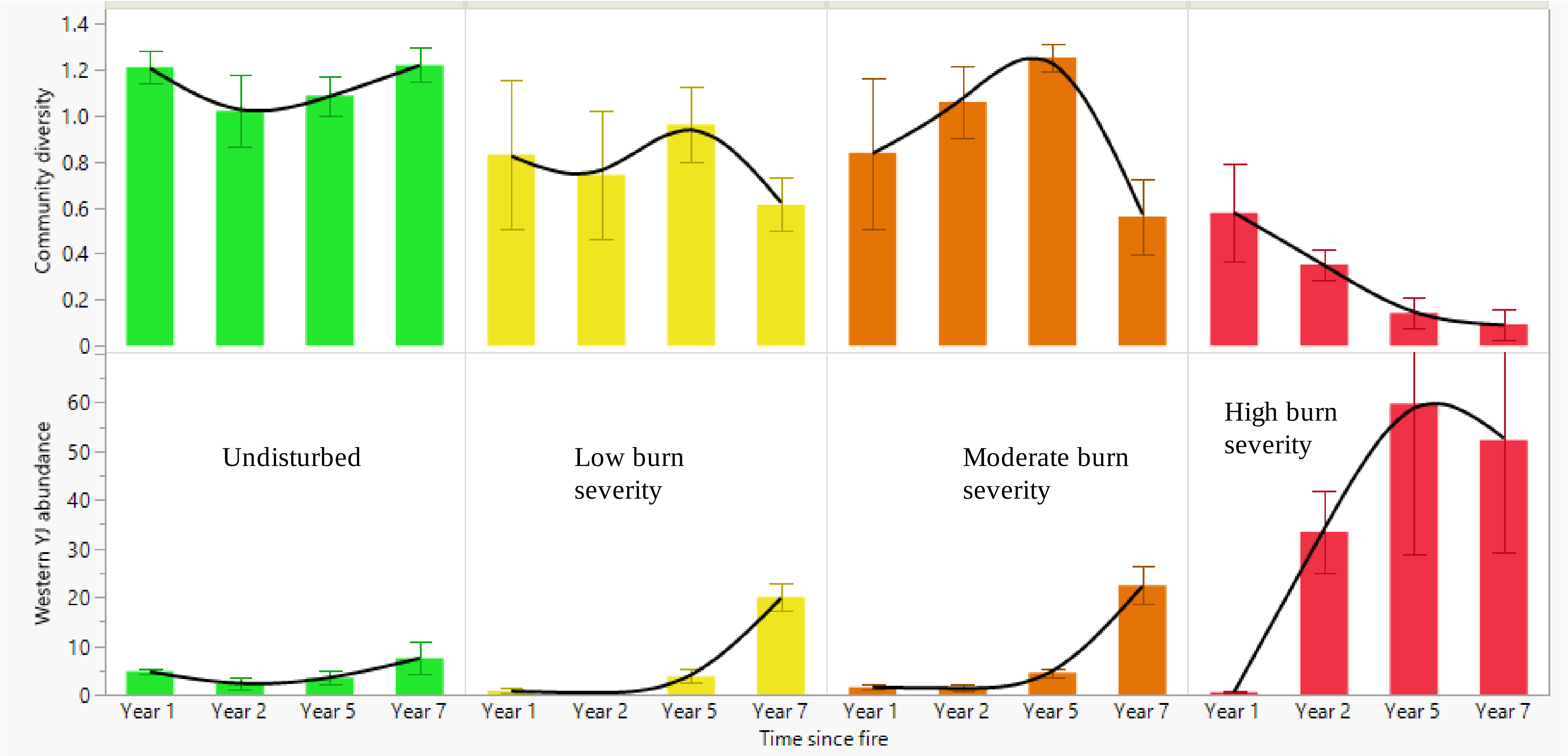

Figure 3. Bar graph illustrating differences in mean yellowjacket Shannon's diversity (top) and western yellowjacket, *Vespula pennsylvanica*, abundance (bottom) among burn severity classes and fire ages within montane forested landscapes of Sierra National Forest, California. Spline lines (lamdba = 0.05) are provided to illustrate general patterns between *V. pennsylvanica* abundance vs. overall yellowjacket diversity among burn severity and fire age classes.

Table 2. Results from two-way ANOVA testing for significant ($\alpha = 0.05$) effects of wildfire burn severity, time since fire and their interaction on yellowjacket abundance, species richness and Shannon's diversity.

Response	**Parameter**	**DF**	**F**	**Prob > F**
Abundance	Severity	3	1.66	0.187
	Fire age (years)	3	9.40	<0.001
	Severity*Fire age (years)	9	2.58	0.017
	Whole model	15,47	4.87	<0.001
Richness	Severity	3	2.39	0.080
	Fire age (years)	3	0.12	0.948
	Severity*Fire age (years)	9	1.48	0.182
	Whole model	15,47	2.39	0.012
Diversity	Severity	3	2.24	0.096
	Fire age (years)	3	1.26	0.300
	Severity*Fire age (years)	9	1.12	0.365
	Whole model	15,47	4.43	<0.001

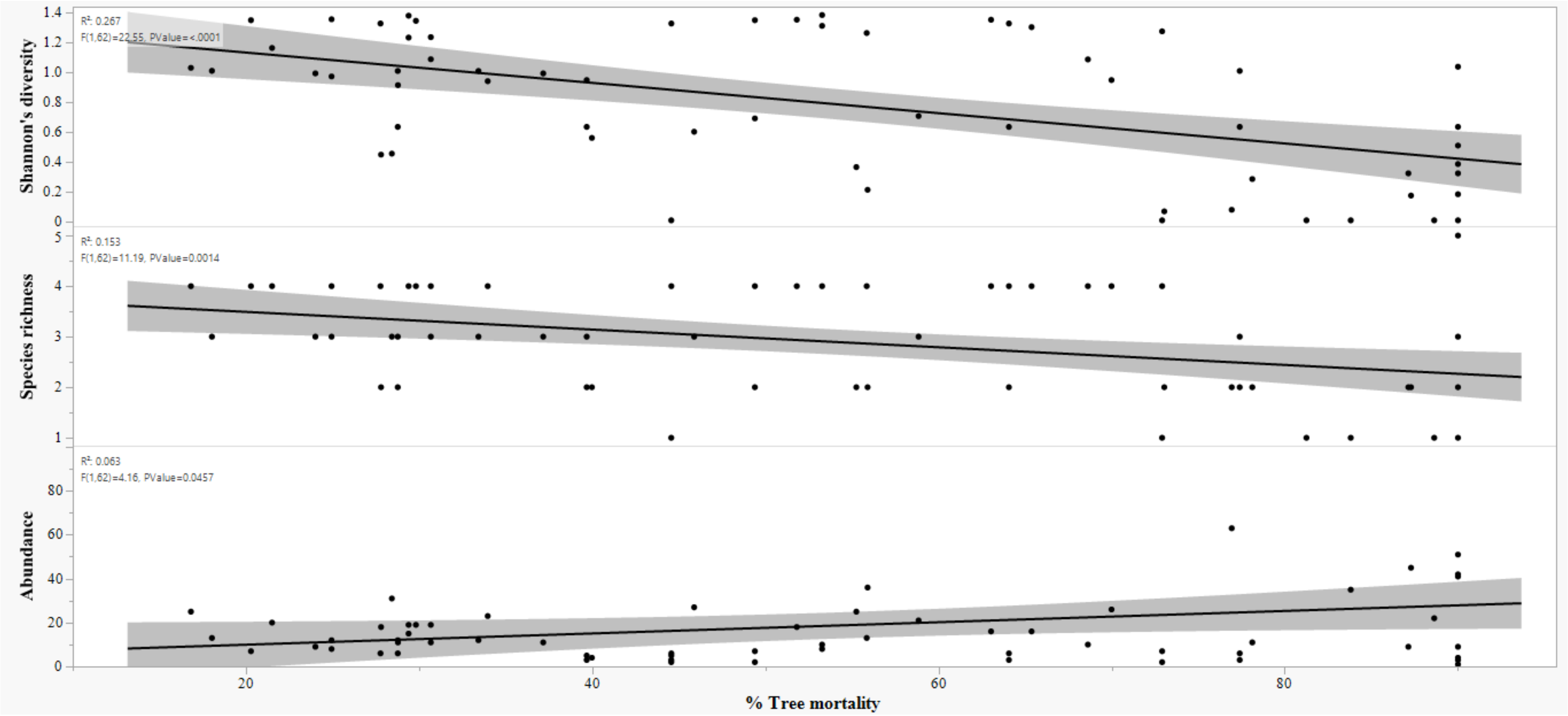

Figure 4. Results from simple linear regression used to determine the direction and magnitude of correlations between fire-induced tree mortality (%) versus yellowjacket abundance (bottom), species richness (middle) and Shannon's diversity (top) within montane forested landscapes of Sierra National Forest, California.

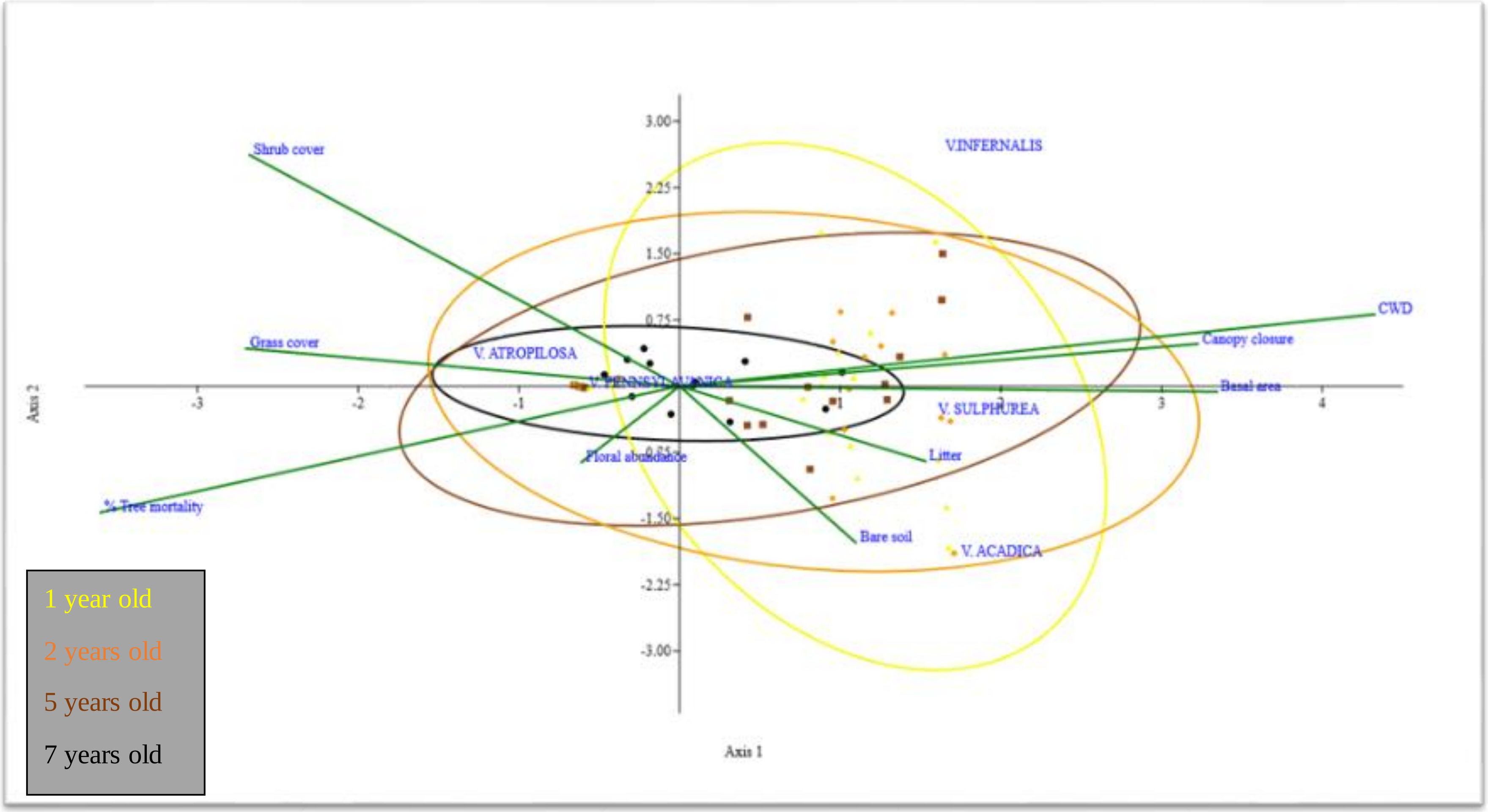

Figure 5. Tri-plot from canonical correspondence depicting degrees of similarity in yellowjacket community assemblages across fire age classes (ellipsoids), and individual species relationships (direction, magnitude) with stand structural attributes and fire-induced tree mortality (green vectors).

Table 3. Summary of a generalized linear model analysis describing variation in yellowjacket assemblages due to effects of variation in fire-induced tree mortality (% M), basal area (BA), canopy closure (CC), bare soil (BS), litter cover (LC), coarse woody debris (CWD), floral abundance (FA), shrub cover (SC), grass cover (GC) and time since fire (TSF). Analyses were conducted with and without the inclusion of *Vespula pennsylavanica* abundance data in the model; emboldened Prob>$\lvert\chi^2\rvert$ values indicate significant (α = 0.05) and almost significant (α = 0.10) parameter effects.

Variable	**Parameter**	**Estimate**		**SE**		χ^2		**Prob>$\lvert\chi^2\rvert$**	
		with	***without***	***with***	***without***	***with***	***without***	***with***	***without***
Abundance	% M	0.003	-0.010	0.002	0.004	2.827	6.842	**0.0927**	**0.0089**
	BA	-0.001	0.001	0.001	0.001	1.587	0.500	0.2078	0.4793
	CC	-0.023	0.012	0.003	0.004	69.753	8.730	**<.0001**	**0.0031**
	BS	0.019	-0.018	0.003	0.007	37.591	7.202	**<.0001**	**0.0073**
	LC	0.004	0.000	0.001	0.002	9.701	0.018	**0.0018**	0.8939
	CWD	-0.083	0.005	0.008	0.008	159.738	0.366	**<.0001**	0.5452
	FA	0.003	0.001	0.001	0.001	25.998	0.303	**<.0001**	0.5817
	SC	0.018	0.002	0.004	0.008	18.260	0.054	**<.0001**	0.817
	GC	-0.016	-0.003	0.003	0.006	30.356	0.304	**<.0001**	0.5816
	TSF	0.177	-0.039	0.018	0.038	100.689	1.065	**<.0001**	0.302
Species richness	% M	-0.009	-0.006	0.007	0.006	1.457	0.986	0.2274	0.3207
	BA	-0.002	-0.002	0.003	0.002	0.583	0.495	0.445	0.4815
	CC	0.000	0.002	0.009	0.007	0.000	0.146	0.9911	0.702
	BS	-0.039	-0.016	0.011	0.010	11.168	2.928	**0.0008**	**0.0871**
	LC	0.003	0.000	0.004	0.003	0.637	0.014	0.4248	0.9049
	CWD	0.016	0.014	0.017	0.012	0.879	1.206	0.3484	0.2722
	FA	0.000	-0.001	0.002	0.002	0.015	0.132	0.9031	0.7166
	SC	0.008	0.004	0.016	0.013	0.227	0.094	0.6338	0.7586
	GC	-0.010	-0.004	0.011	0.009	0.941	0.163	0.3319	0.6864
	TSF	-0.084	-0.074	0.070	0.057	1.407	1.702	0.2356	0.192

Table 3 (continued). Summary of a generalized linear model analysis describing variation in yellowjacket assemblages due to effects of variation in fire-induced tree mortality (% M), basal area (BA), canopy closure (CC), bare soil (BS), litter cover (LC), coarse woody debris (CWD), floral abundance (FA), shrub cover (SC), grass cover (GC) and time since fire (TSF). Analyses were conducted with and without the inclusion of *Vespula pennsylavanica* abundance data in the model; emboldened Prob>$|\chi^2|$ values indicate significant ($\alpha = 0.05$) and almost significant ($\alpha = 0.10$) parameter effects.

Variable	**Parameter**	**Estimate**		**SE**		χ^2		**Prob>$\|\chi^2\|$**	
		with	***without***	***with***	***without***	***with***	***without***	***with***	***without***
Shannon's diversity	% M	-0.004	0.004	0.002	0.003	3.880	2.437	**0.0489**	0.1185
	BA	0.000	-0.002	0.001	0.001	0.165	1.970	0.6849	0.1605
	CC	0.002	0.006	0.003	0.003	0.922	3.826	0.337	**0.0504**
	BS	-0.009	-0.016	0.003	0.004	7.348	12.514	**0.0067**	**0.0004**
	LC	0.001	0.001	0.001	0.001	0.435	0.919	0.5096	0.3378
	CWD	0.009	0.011	0.005	0.006	3.402	3.107	**0.0651**	**0.078**
	FA	0.000	0.002	0.001	0.001	0.079	4.184	0.779	**0.0408**
	SC	0.002	0.002	0.005	0.006	0.183	0.178	0.6692	0.6735
	GC	-0.001	-0.008	0.003	0.004	0.170	4.288	0.6797	**0.0384**
	TSF	-0.043	-0.003	0.021	0.026	4.032	0.012	**0.0447**	0.911

Table 4. Summary of stepwise regression procedures used to develop explanatory models regarding species-specific relationships between yellowjacket abundance and habitat structure within montane, forested landscapes of Sierra National Forest, California.

Response variable (Y)	Prediction expression
V. acadica abundance	log (Y) = -4.58 + 0.02 (BA) + 0.06 (CC) - 0.04 (SC)
V. atropilosa abundance	log (Y) = -3.9 + 0.02 (% M) - 0.03 (CC) - 0.04 (CWD) + 0.03 (SC)
V. infernalis abundance	log (Y) = 3.06 - 0.03 (% M) - 0.06 (BA) + 0.07 (SC) - 0.06 (GC) - 0.25 (TSF)
V. pennsylvanica abundance	log (Y) = 2.41 - 0.04 (CC) - 0.14 (CWD) + 0.05 (FA)
V. sulphurea abundance	log (Y) = 4.54 - 0.05 (% M) + 0.01 (BA) + 0.26 (FA)

BA = Basal area; CC = Canopy closure; SC = Shrub cover; % M = % tree mortality; CWD = Coarse woody debris; TSF = Time since fire; FA = Floral abundance.