FINAL REPORT

Title: Effects of wildfire burn severity on cavity-nesting bee and wasp habitat and community composition two decades post fire

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List of Abbreviations

CWD: coarse woody debris dNBR: Difference Normalized Burn Ratio MTBS: Monitoring Trends in Burn Severity

Keywords

Hymenoptera, trap-nests, disturbance, habitat, wood

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Effects of wildfire burn severity on cavity-nesting bee and wasp habitat and community composition two decades post-fire

Abstract

Wildfires can impact the availability of insect habitat, including nesting habitat. We studied the effects of wildfire burn severity on cavity-nesting bee and wasp abundance and diversity, and nesting habitat across burn severities (high, low, unburned) in two mixed-severity fires in ponderosa pine, *Pinus ponderosa*, forest that burned >20 years ago. We collected cavity-nesters with 36 trap-nests consisting of bundles of hollow reeds across 18 sites. We used a new key for nest caps to identify our specimens before rearing them out over the winter. We also measured habitat factors that could provide natural cavities for bees and wasps, such as coarse woody debris, standing dead wood, and shrub stems. We found no effects of fire severity on cavity-nesting bee and wasp abundance or diversity. We also found that high severity sites had more coarse woody debris for potential nesting habitat factors. Our results indicate that fire, even high severity fire, does not have lasting negative impacts on cavity-nesting bees and wasps.

Objectives

Our objective was to study the lasting effects of wildfire burn severity on cavity-nesting bees and wasps. Specifically, our research questions were: 1. Are cavity-nesting bee and wasp abundance and richness affected by fire severity more than twenty years post-fire? 2. How does fire severity impact nesting resources? 3. Are cavity-nesting bee and wasp community metrics associated with the amount of nesting resources available, or could other factors be at play? Our aim with this study is to provide land managers with information about the effect of fire on cavity-nesting bees and wasps and their habitat. This is important because cavity-nesting bees and wasps provide vital ecosystem services such as pollination, and in the case of wasps, both pollination and predation on herbivorous pests.

Background

Insect habitat loss is worrisome considering growing reports of global insect declines (Hallmann et al. 2017; Wagner 2020; Montgomery et al. 2020). Insects are highly diverse (Gaston 1991) and provide a multitude of ecosystem services such as decomposition, pestcontrol, nutrition for humans and other animals, and pollination (Scudder 2009). Fire is a disturbance that can both create and destroy insect habitat (New 2014). While fire naturally occurs in many ecosystems (Bowman et al. 2013), fire suppression and climate change (Jolly et al. 2015; Sullivan et al. 2022) impact the frequency and severity of wildfires. In some ecosystems, fire severity and frequency are predicted to increase dramatically from historical patterns (Westerling et al. 2006; Jolly et al. 2015); in others, suppression and human development have decreased the frequency of natural fire (Doerr and Santín 2016). While we know that global change is affecting insects, less is known about the effects of individual stressors like fire on insects (Koltz et al. 2018; Wagner 2020).

Some species of insect are fire-adapted, while others are more sensitive. For example, some species are pyrophilic, like fire beetles (*Melanophila acuminata*) that seek out burned trees to lay their eggs (Bell 2023). Other insects are not so well-adapted to fire; butterfly and moth species (order: Lepidoptera) seem to be more sensitive to fire (Carbone et al. 2019; Bieber et al. 2023) and benefit from unburned refugia containing undisturbed vegetation (Swengel and Swengel 2007). Post-fire environments tend to favor insects that either survive the flames, such as ground-nesting species (Brokaw et al. 2023), or that effectively colonize burned areas from unburned ones, such as mobile, generalist species (Koltz et al. 2018). Fire can be a driver of insect community dynamics, but the exact mechanisms and effects on specific taxa are less clear (Koltz et al. 2018).

How insect pollinators are affected by fire is still understudied. Many bees and wasps (order: Hymenoptera) are insect pollinators that provide essential pollination services both to human crops and to natural vegetation (Page et al. 2021). Global meta-analyses disagree on the effects of fire on bee and wasp habitat: Carbone et al. (2019) found positive effects of wildfire for Hymenoptera abundance and richness, while Bieber et al. (2023) found no positive effects overall for Hymenoptera, and Mason et al. (2021) found positive effects of wildfire on bee abundance. More studies are needed to improve our understanding of fire's effect on vital pollinators as concerns about habitat loss and fragmentation increase (Potts et al. 2010; Powney et al. 2019).

Cavity-nesting bees and wasps (hereafter cavity-nesters) in particular can be excellent indicators of environmental stress caused by disturbance-mediated habitat changes (Tscharntke et al. 1998; Staab et al. 2018). This sensitivity to environmental change, as well as their multiple roles in ecosystems, makes cavity-nesters interesting subjects for studying the effects of wildfire on bees and wasps. These species nest in cavities in dead wood, and hollow, pithy plant stems (Evans 1966; Krombein 1967). This functional guild also fills important roles in the ecosystem; cavity-nesting solitary wasps are pollinators as well as predators of other arthropod species (Brock et al. 2021), and cavity-nesting bees are both pollinators of plants and hosts to kleptoparasitic bees and wasps (Krombein 1967). Some cavity-nesting species even have commercial value for agriculture, like the blue orchard bee (*Osmia lignaria*) that pollinates fruit trees (Torchio 1976). There is some evidence for positive effects of fire on cavity-nesting bees (e.g. Potts et al. 2005; Lazarina et al. 2016; Burkle et al. 2019; Simanonok and Burkle 2019; Gelles et al. 2022) and for the resilience of wood-nesting bee communities to fire (Peralta et al. 2017). However, a few of these studies found that effects differ with time post-fire (Potts et al.

2005; Lazarina et al. 2016; Peralta et al. 2017; Simanonok and Burkle 2019). In Mediterranean ecosystems, Lazarina et al. (2016) found more cavity-nesting bees in older burn sites (20-28 years old) and Potts et al. (2005) found more in intermediate-aged sites (10 years post-fire). In Montana, Simanok and Burkle (2019) found that time-since-fire was a better predictor than severity for nesting success and bee richness, with both declining with increasing time-since-fire. There is even less literature available for cavity-nesting wasps (e.g. Cruz-Sánchez et al. 2011; Rubene et al. 2015), which is not surprising as wasps are often neglected in general in pollinator research (Sumner et al. 2018). Furthermore, only a few studies focus exclusively on either cavity-nesting bees or wasps (e.g. Peralta et al. 2017; Simanonok and Burkle 2019), emphasizing the need for more research into this functional group.

An advantage to studying cavity-nesting species is that they can be studied with artificial "trap" nests consisting of either drilled holes or hollow reeds (Krombein 1967; Staab et al. 2018). These trap nests have the benefit of capturing just individuals that are actively nesting in an area, excluding foragers that are only passing through, as opposed to netting or other trapping methods such as pan traps that sample the entire bee and wasp community (Staab et al. 2018). Trapnesting can therefore be a good measure of the suitability of the local habitat when examining ecological change on local scales (Tscharntke et al. 1998; Staab et al. 2018). Only a few studies have used trap nests to study the effects of fire on bees (e.g. Peralta et al. 2017; Burkle et al. 2019; Simanonok and Burkle 2019) and wasps (e.g. Rubene et al. 2015) and even fewer report any standardized method for measuring burn severity (but see Burkle et al. 2019; Simanonok and Burkle 2019). Given that fire changes cavity-nesting bee and wasp habitat such as downed woody debris (Burkle et al. 2019; Gelles et al. 2022), snags (Chambers and Mast 2005), and pithy stems (Potts et al. 2005), we suspected that this nesting guild might be sensitive to the effects of wildfire severity, even up to two decades post-fire.

In our study, we investigated the lasting effects of wildfire burn severity on cavity-nesting bee and wasp abundance and diversity. We established sites in areas of high and low severity fire, as well as unburned control areas, across a mixed-coniferous forest that burned in two separate fires more than twenty years ago. We hypothesized that: 1) cavity-nesting bee and wasp abundance and richness would increase with increasing fire severity, 2) nesting habitat, such as coarse woody debris, snags, and stems, would increase with increasing fire severity, and 3) cavity-nesting bee and wasp abundance and richness would be correlated with the availability of nesting habitat. Our study describes the effects of fire severity on an understudied but ecologically relevant nesting guild in a mature post-fire environment. We aim to provide insight into the lasting effects of fire on pollinator communities.

Materials and Methods

Site selection

We established our study sites in spring of 2023 in the lower montane zone of the Front Range of Colorado in an area that experienced two mixed-severity wildfires over twenty years ago. The 4,731 hectare Buffalo Creek fire occurred in 1996, and the 3,888 hectare High Meadows fire occurred in 2001 (Figure 1). We selected these fires because of their proximity to each other, similar age, and range of burn severities. We determined fire severity using data overlays provided by the United States Forest Service (Monitoring Trends in Burn Severity (MTBS)) and difference Normalized Burn Ratio (dNBR) (MTBS Data Access: Fire-Level Geospatial Data, 2022). We established eighteen total sites that spanned both fires and our target burn severities. We established three 50x50m sites per severity per fire using our MTBS severity overlays. We considered MTBS high to moderate severities as high severity areas, low to lowunburned to be low severity, and unburned areas outside of the fire boundaries to be unburned control sites. We lost one of our Buffalo Creek unburned sites (site B_U2) to a prescribed fire in mid-July. However, we kept this site in our analyses as we had already recorded all habitat measures and collected specimens from that trap over several sampling visits prior to the burn.

At each site, we verified the burn severity reported by our MTBS overlays by measuring canopy cover, as well as observing evidence of past fire such as charring on logs, stumps, live trees, and snags. We considered sites with no canopy cover besides small regrowth to be high severity stands, and sites within the fire boundaries with evidence of fire such as charring, but with little impacts on the overstory canopy, to be low burn sites. We classified unburned sites as sites outside the burn area with no evidence of fire. We also avoided areas that had been thinned by looking for cut stumps. We established our sites by selectively locating a representative area within the target burn severity, and then to randomize the location of the center of the site, we walked 50m along a random compass azimuth to the site center. From the site center, we established a 50x50m square site. We estimated canopy cover at our sites to confirm our assumptions that high severity fire should reduce canopy cover. We did this by haphazardly choosing a 'representative' tree in each quarter (North, South, East, West) of our sites and measuring canopy cover with a densiometer at each of the cardinal directions at the edge of that tree's canopy (following methods described in Paul E. Lemmon 1956). We calculated mean canopy cover at a site by averaging all measurements at that site (n=16 individual measurements). Many of these sites have been used for previous studies in the area (Bieber et al. 2024, Murphy et al. 2018).



Figure 1: Map of our eighteen site locations across both fires in Colorado, USA: Hi Meadows (upper left) and Buffalo Creek (lower right). Our study sites are displayed with shapes: unburnt sites are triangles, low sites are circles, and high burn sites are squares. Fire boundaries are shown with MTBS dNBR data and colors indicate burn severity: high severity locations are indicated in red, moderate in yellow, low in teal, and low-to-unburned in green. For our purposes, we considered high and moderate burn areas (red, yellow) as high severity, and low and low-to-unburned areas (teal, green) as low severity if there was visual evidence of fire.

Trap-nesting of bees and wasps

We installed two trap nests at the center of each site (Figure 2). We constructed traps by binding together bamboo and natural reeds. To create trap nests that would collect the greatest number of bee and wasp species, we used a variety of reed and bamboo sizes. Each trap contained 7 larger diameter (cavity diameter >4mm) bamboo, 4 medium diameter (<4mm) bamboo, and 20 small diameter (<3mm) natural reeds to provide a variety of nesting sizes. We cut the reeds so that one end was sealed by a node and one end was open for the bees and wasps to use. We attached one nest to a wooden stake at the height of 0.5m, and the other nest on a separate stake at 1m high; these stakes were 2m apart from each other, with all open ends facing east (per recommendations from Staab et al. 2018). We checked trap nests monthly (April-October) and removed and replaced all occupied reeds, which were recognized by a sealed nest cap.

Each time we checked the trap nests, we recorded the number of occupied reeds in each trap, as well as nest cap material, nest cap depth (defined as the distance from the top of the reed to the cap surface), reed diameter, and reed length. We used these factors, along with the date the nest was finished, to preliminarily identify the trap occupants. We identified bees to genus and wasps to family using a newly developed nest cap key for Colorado cavity-nesters (Jolma 2023). From this key, we calculated average trap-nested bee abundance and genus richness, and average trap-nested wasp abundance. We did not calculate wasp richness because we only collected two families of cavity-nesting wasps and did not feel that this level of identification was suitable for considerations of wasp diversity at our sites. We also recorded trap nest occupancy (the number of reeds that were occupied by a bee or wasp out of the total number of reeds in the trap) from both traps at each site. One occupant that we could not key out to a clear bee or wasp abundance and richness calculations.



Figure 2: An example of our trap-nest orientation and position at one of our high severity burn sites at the Hi Meadows fire. Trap-nests consisted of various sizes of hollow bamboo and natural reeds. We installed two trap-nests at each site at the site center, one at 0.5m tall and the other at 1m tall.

Coarse woody debris

We measured coarse woody debris (dead and down wood over 8 cm in diameter, hereafter CWD) using woody debris size classes and methods from Brown (1974). We modified the planar-intercept transects by splitting our 50x50m sites into four equal quarters. Within each quarter, we established a 25m transect along a random compass azimuth at a random starting point along the north-south boundary-line of the quarter. We limited the possible azimuth ranges to directions that pointed our transect into the targeted quarter; however, transects were allowed to intersect neighboring quarters. We measured each piece of CWD intersecting our transect from 5 to 25m and recorded its diameter and length. To estimate CWD volume at our sites from our measurements of CWD diameter and length, we used Huber's and DeVries' formulas (Husch et al. 1972; DeVries 1973). We analyzed both CWD count (the total pieces of CWD from all 4 transects at each site) and CWD volume.

Snag basal area

To calculate snag (standing dead tree) basal area, we measured the diameter at breast height (dbh) of all snags over 3m tall within our sites. We summed the basal area of all snags at a site to estimate the snag density. Basal area is often used as a measure of snag density as the standing dead wood is important wildlife habitat and this measure accounts for both the number and diameter of individual snags (Cade 1997). We also considered basal area because the number of cavities from wood-boring beetles, which are often utilized by cavity-nesting bees and wasps (Westerfelt et al. 2015), have been previously shown to increase with larger snag size (Thibault and Moreau 2016).

Woody shrub stem number

To measure the potential availability of woody shrub stems for nesting, we counted the number of main stems at the base of each shrub along four 50m transects running north-south across our sites. At every 0.5m along our 50m transects, if a shrub was intersected, we recorded the stem number for both live and dead shrubs. We measured shrub stem number because some cavity-nesting species use woody twigs and stems, including the pithy stems of shrubs like *Rubus* spp. (Stephen et al. 1969).

Statistical Analyses

We used R programming language for all statistical analyses (V 4.3.2, R Core Team 2022). We performed ANOVAs, Kruskal-Wallis tests, and linear models using the *lme4* package (Bates et al. 2015) and the *stats* package in the base R program (R Core Team 2022). To analyze abundance and richness of cavity-nesting bees and wasps, as well as overall trap occupancy, we used ANOVAs with a fixed effect of *severity* (unburned, low, and high) and a random effect of *fire identity* (Buffalo Creek vs. Hi Meadows fires). We included fire as a random effect to account for the non-independence of sites located at the same fire site. We pooled trap nest occupancy, bee/wasp abundance, and bee genus richness at each site (n = 18 sites) across both traps and across all sample periods (April-October). We checked all response variables for assumptions of normality and homogeneity of variance. We used a Box-Cox transformation to transform bee abundance to fit the assumptions of normality. Bee genus richness could not be transformed to completely fit the assumptions of normality. We determined

an ANOVA was still appropriate, however, because the variance was homogenous and ANOVAs are relatively robust to departures from normality if the assumption of homogeneity of variance is met (Sheng 2008). We performed pairwise, post-hoc comparisons using *emmeans* (Lenth et al. 2024) of all significant ANOVA results for cavity-nester analyses.

We analyzed canopy cover differences by *severity* with a Kruskal-Wallis non-parametric test and a post-hoc Dunn's test. To analyze the nesting habitat factors of CWD count, CWD volume, and snag basal area, we used ANOVAs with the fixed effect of burn *severity* and random effect of *fire identity*. Our unit of replication was the individual site (n = 18 sites). To meet the assumptions of normality and homogeneity of variance, we log(x+1) transformed CWD count and CWD volume and square root transformed snag basal area. We could not transform shrub stem number to meet the assumptions of normality or homogeneity of variance as it was highly skewed, so we performed a non-parametric Kruskal-Wallis test on shrub stem number with a fixed effect of *severity*. We performed pairwise, post-hoc comparisons using *emmeans* (Lenth et al. 2024) for all significant ANOVA results for habitat analyses.

To analyze the relationship between cavity-nester abundance and richness and the availability of nesting habitat, we used linear models with fixed-effects of *CWD volume*, *snag basal area*, and *shrub stem number* with each site as the unit of analysis (n = 18). We excluded *CWD count* because it was highly correlated with *CWD volume*. We also analyzed the relationship between the latter nesting habitat variables (*CWD volume, snag basal area*, and *shrub stem number*) and our response variables of overall trap-nest occupancy, bee abundance, bee genus richness, and wasp abundance. We checked all models for assumptions of normality of residuals and homoscedasticity.

Results

Trap-nested bees and wasps

We collected a total of 140 individual nests from all our sites with 90 occupied by wasps and 49 occupied by bees, with one unknown nest (Table 1). Of the wasp species we collected, 85% belonged to the family Eumeninae with the rest from the family Crabronidae. Of the bee species we collected, 94% of the bees belonged to Megachilidae and only 3 individuals belonged to the family Colletidae. For bees, Osmia spp. were the most common with 32 individuals. Total trap occupancy (bees + wasps), cavity-nesting bee richness, cavity-nesting bee abundance, and cavity-nesting wasp abundance did not differ by *severity* (Table 2). **Table 1:** List of cavity-nesting bee and wasp taxa (Hymenoptera) and number of individuals collected from trap-nests from each burn severity. Taxa are organized by family. We identified cavity-nesters using a newly developed nest cap key for Colorado, and IDs are to the lowest taxonomic level possible using only nest caps.

Family	Identification	Fire severity		
Hymenoptera		Unburned	Low severity	High severity
Colletidae	<i>Hylaeus</i> spp.	1	0	2
Crabronidae	<i>Trypoxylon</i> spp.	4	6	1
	Unknown spp.	1	0	1
Vespidae	Eumeninae spp.	16	29	32
Megachilidae	Ashmeadiella spp.	0	1	0
	Anthidium spp.	2	0	0
	Dianthidium ulkei	0	0	4
	Hoplitis spp.	0	4	3
	Osmia lignaria	2	0	1
	Osmia spp.	8	3	18

Table 2: ANOVA tests with a fixed effect of severity and random effect of fire identity on trapnest occupancy, bee abundance, bee genus richness, and wasp abundance for cavity-nesters we collected via trap-nesting.

Fixed effects	d.f.	F-stat	p-value
Trap-nest occupancy			
Severity	2,15	1.52	0.25
Box-Cox (Bee abundance)			
Severity	2,14	3.21	0.07
Bee genus richness			
Severity	2,14	0.44	0.65
Wasp abundance			
Severity	2,15	0.75	0.49

Canopy cover and nesting habitat factors

We confirmed that canopy cover at our sites differed by *severity* (KW₂ = 11.91, P = 0.003) and was significantly less at high severity sites than low (Z = 2.62, P = 0.013) or unburned sites (Z = 3.17, P = 0.005). Both CWD count and CWD volume varied by *severity* (Table 3). We found 161% greater CWD counts at high severity sites versus unburned sites (P = 0.013). CWD counts at high and low severity sites were not different (P = 0.30) nor were CWD counts at low and unburned sites (P = 0.21) (Figure 3a). CWD volume was also 232% higher at high severity sites when compared to unburned sites (P = 0.002). CWD volume was not different between high and low severity sites (P = 0.16) or between low and unburned sites (P = 0.063) (Figure 3b). Snag basal area did not vary by *severity* (Table 3). Shrub stem number also did not vary by *severity* (Table 3).

Table 3: ANOVA tests with a fixed effect of severity and random effect of fire on nesting habitat factors: log(CWD count +1), log(CWD volume +1), and \sqrt{snag} basal area, and a Kruskal-Wallis non-parametric test on shrub stem number by severity. Bold values indicate significant predictor variables and interactions.

Fixed effects	d.f.	F-stat	p-value
Log(CWD count + 1)			
Severity	2,14	5.55	0.02
Log(CWD volume + 1)			
Severity	2,15	9.86	0.002
$\sqrt{(Snag \ basal \ area)}$			
Severity	2,14	2.22	0.15
Response	d.f.	KW	p-value
Shrub stem number			
Severity	2	3.95	0.14



Figure 3: Measures of cavity-nester nesting habitat at our sites of (a) CWD count, (b) CWD volume (m3/ha) (CWD vol.) as affected by burn severity. We log(x+1) transformed CWD count and CWD volume to meet assumptions of normality. Data are shown as boxplots with the center line as the median, the top and bottom segments of the colored bars as the first and third quartiles, and the whiskers are the minimum and maximum (excluding outliers, which are represented as black circles). Each bar represents a different burn severity (high, low, unburned). Lowercase letters represent the results of Tukey's HSD post-hoc tests, and different letters between bars indicate significant differences between severities.

Relationship between cavity-nester assemblages and nesting habitat variables

We found a weak positive relationship between trap-nest bee abundance and *shrub stem number* (Table 4). Trap-nest occupancy, bee genus richness, and wasp abundance were not associated with any of the habitat variables.

Parameter	Coeff.	SE	t-score	p-value
Trap-nest occupancy				
Intercept	5.93	1.61	3.68	0.003
Shrub stem number	0.04	0.04	0.96	0.35
CWD volume	0.0007	0.005	0.14	0.89
Snag basal area	5.18	4.60	1.13	0.28
Trap-nest bee abundance				
Intercept	1.41	0.75	1.88	0.08
Shrub stem number	0.04	0.02	2.09	0.06
CWD volume	0.002	0.002	0.69	0.50
Snag basal area	2.16	2.15	1.01	0.33
Trap-nest bee genus richness				
Intercept	1.21	0.35	3.43	0.004
Shrub stem number	0.01	0.009	1.39	0.19
CWD volume	-0.0004	0.001	-0.40	0.70
Snag basal area	-0.04	1.01	-0.04	0.97
Trap-nest wasp abundance				
Intercept	4.43	1.33	3.33	0.005
Shrub stem number	0.00008	0.03	0.02	0.98
CWD volume	-0.0007	0.004	-0.17	0.87
Snag basal area	2.91	3.79	0.77	0.46

Table 4: Linear models of trap-nest occupancy, trap-nest bee abundance, trap-nest bee genus richness, trap-nest wasp abundance, netted bee abundance, and netted bee morphospecies richness in relation to nesting habitat factors.

Discussion

We demonstrated that the effects of high severity fire on the landscape, such as the reduction of tree canopy cover and increased CWD, are still evident 20 years post-fire. However, cavitynester richness and abundance in our trap nests was the same in high severity, low severity, and unburned areas, suggesting that both burned and unburned areas provide sufficient nesting habitat to support active nesting of bees and wasps. Our results add to growing evidence that fire does not negatively impact bee communities (Potts et al. 2003; Grundel et al. 2010; Mola and Williams 2018; Simanonok and Burkle 2019); however, we also failed to detect any positive effects of wildfire on cavity-nesting bees in contrast to the findings of Simanonok and Burkle (2019) and Burkle (2019). We also found no effects of burn severity on cavity-nesting wasps. Knowledge of the effects of fire on wasp communities is more limited, and previous studies have found no effects of fire on wasps (Johansson et al. 2020) to positive effects (Cruz-Sánchez et al. 2011; Bogusch et al. 2015; Rubene et al. 2015) to negative effects (Lockwood et al. 1996; Campbell et al. 2018). Our results show that fire does not seem to negatively affect the functional group of cavity-nesting wasps, and that both burned and unburned areas provide sufficient habitat.

We found that areas burned by high severity fire could potentially provide more nesting habitat in the form of CWD than unburned areas. Fires initially decrease the amount of CWD through consumption, but the amount of CWD can increase again, especially after high severity fire, as fire-affected trees die and become CWD (Monsanto and Agee 2008). Cavity-nesting bees and wasps use wood-boring beetle holes in CWD and a few will excavate cavities themselves (Evans 1966; Scott et al. 2011; Westerfelt et al. 2015). Bee diversity and abundance has been previously linked to CWD abundance (Gelles et al. 2022; Glenny et al. 2023). Interestingly, we did not find a direct relationship between CWD and the abundance or richness of cavity-nesters. We still know little about how cavity-nesters select suitable wood for nesting, partially due to the difficulty of identifying natural nests in the field (Roulston and Goodell 2011). It has been suggested that cavity-nesters may prefer dry, fresh wood to rotten wood (Westerfelt et al. 2015); although, a few species do specifically excavate cavities in softer, rotten wood (Anthophora terminalis, for example) (Scott et al. 2011). It is possible that we did not find a relationship between CWD and cavity-nesters because of the age of our sites, resulting in a lack of fresh CWD from fire-related tree mortality. In fact, we found that standing snag basal area was not different in high severity sites compared to low severity and unburned sites. This finding, combined with almost no canopy cover in our high severity sites, suggests that the existing CWD in our high severity sites is from trees that were killed by the Buffalo Creek and Hi Meadows fires at least twenty years ago. We also may not have found a relationship between cavity-nesters and woody resources because we did not count the number of cavities on each piece of CWD or snag, which could be more important than the volume of woody nesting habitat available (Potts et al. 2005; Westerfelt et al. 2015; Rubene et al. 2015). Simanonok and Burkle (2019) previously showed that cavity-nesting bee richness decreases with time post-fire, despite increasing CWD in older burns, possibly due to decreasing natural cavities in CWD with time post-fire. Interestingly, 3-4 years post-fire, Galbraith et al. (2019) found a decrease, rather than an increase, of CWD at high severity burn sites; however, they found an increase in the number of cavities with increasing fire severity. They found that bee diversity and abundance in general was correlated with increased burn severity but did not specify the effects on cavity-nesters alone, nor did they attempt to relate the increase in bees directly to the increased nesting habitat. Future studies should further investigate the mechanism behind the varying effects of fire on the number of available cavities, as well as the specific nesting preferences of cavity-nesting bees and wasps that use these cavities. Aspects of the CWD itself like soundness and species, or microclimate factors such as shading or slope, could affect nest selection.

Our study contributes to increasing evidence that wildfire does not negatively impact bees and wasps. Notably, we demonstrated that high severity fire does not have lasting negative ramifications for a functional guild that is sensitive to environmental change (Tscharntke, Gathmann, and Steffan-Dewenter 1998; Staab et al. 2018). However, despite increases in CWD at high severity sites, we did not observe more cavity-nesters in high severity areas than low severity or unburned areas. We were also not able to clearly identify any nesting habitat factors at our sites that were directly associated with cavity-nesting bee and wasp community metrics. This suggests that cavity-nesters may not be nest-limited in our study system, and that they are able to nest just as well in areas with less CWD as areas with more. It is possible that cavity-nesters are limited by other factors that we did not measure such as forage, and that both burned and unburned areas provide similar amounts. More knowledge of what habitat factors limit cavitynesters is necessary to better conserve this functional group.

Conclusions and Implications for Management

Fire and land managers should consider the habitat value of increased CWD in high severity burn areas for bee and wasp nesting habitat when conducting burned area rehabilitation. Removal of snags, CWD, and shrubs are often part of management actions to increase treeseedling recruitment and reduce the likelihood of reburn after high severity fire (McGinnis et al. 2010); however, these actions could be removing valuable nesting habitat for pollinators (bees and wasps) and predators (wasps) that provide ecosystems services towards plant reproduction and regrowth. While we did not find a direct relationship between CWD and cavity-nesters, other research has shown that the removal of CWD and snags by land managers after a disturbance event can have significant negative effects on cavity-nesting bees (Carper and Bowers 2017). Small patches and areas that will not impact public safety should be left to remain in an opencanopy state and to naturally regenerate. Furthermore, our findings challenge the notion that low severity fires are the only "good fires" that should be returned to the landscape and add to growing evidence that high severity fires are not always detrimental to ecosystems (Gordon, Price, and Tasker 2017; He, Lamont, and Pausas 2019; Burkle et al. 2019; Gelles, Davis, and Stevens-Rumann 2022). While large areas of repeated high severity fire are likely bad for biodiversity and should be prevented (Ponisio et al. 2016), some insect functional groups like cavity-nesters seem to be resilient to small patches of high severity fire and are able to exist equally as well in burned and unburned areas.

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Appendix B: List of Completed/Planned Scientific/Technical Publications/Science Delivery Products

Deliverable type	Description	Delivery Date
Presentations	Smith, Alaina, Carper, Adrian L., Murphy, Shannon	November 2023
	M. Effects of wildfire burn severity on wild bee	
	communities two-decades post-fire. Entomological	
	Society Annual Meeting, Nov. 5th-8th 2023, National	
	Harbor, MD.	
	Smith, Alaina, Walheim, Micheala, Schroder, Norah,	December 2023
	Hicks, Sarah, and Murphy, Shannon M. Effects of	
	wildfire burn severity on cavity-nesting bee and wasp	
	habitat and community composition. 10th	
	International Fire Ecology and Management	
	Conference, Dec. 4-8th 2023, Monterey, CA.	
Written Outreach	Manager-relevant pollinator habitat fact sheet	Planned for
	summarizing findings	Winter 2025
Peer-reviewed	Smith, Alaina, Walheim, Micheala, Schroder, Norah,	In preparation,
publications	Hicks, Sarah, Murphy, Shannon M. Effects of wildfire	planned for Fall
	burn severity on cavity-nesting bee and wasp habitat	2025
	and community composition.	
Master's thesis	Smith, Alaina (2024). The Effects of Wildfire Burn	June 2024
	Severity on Bee and Wasp Communities Two Decades	
	Post-Fire. Master's thesis, University of Denver	

Appendix C: Metadata

The data collected for this project reflect trap-nest captures of cavity-nesting bee and wasp communities and accompanying habitat data, collected on the Pike National Forest near Bailey, Colorado between April and October 2023. These data originate from trap-nests consisting of bundles of hollow bamboo reeds. Two trap nests (one 1m tall, another at 0.5m tall) were placed in the center of each site, for a total of 36 trap nests between 18 sites. We established 3 sites per burn severity (unburned, low, high) per fire (Buffalo Creek or Hi Meadows fires). Trap nests were visited and occupied reeds replaced approximately once monthly. Habitat data, including CWD, snags, and shrub stems, were collected once at each site. CWD was counted along 4 modified Brown's transects per site, snags were counted for the whole site, and shrub stems were counted along four 50m North-South transects.

Nature of Data to be archived:

We have two kinds of data: 1) data recorded from field data that is currently on both paper data sheets that were used in the field and entered on our lab computers and backed up, 2) bees and wasps that emerged from our deployed trap nests. Data sheets include preliminary identifications of cavity-nesting bees and wasps by nest cap material (PikeNF_cavitynestingbeeswasps.csv), counts of CWD and corresponding volume calculations (PikeNF_CWD.csv), snag counts and basal area (PikeNF_snags.csv), and shrub stem counts (PikeNF_shrubs.csv). The bees are currently at the University of Colorado Museum where experts are identifying them to species. Once they are done identifying them, we will retrieve them and then label them appropriately.

Where data will be archived:

All of our data will be archived at DRYAD (datadryad.org), which is a non-profit archive of ecological data. Our bees, once appropriate labeled, will be returned to the University of Colorado Museum where they will be vouchered, digitized, and stored.

Timeline for completing data archival:

The bees are currently being identified, but we should have them back soon. We plan to get them all labeled before the end of May 2025 and then return them to the University of Colorado Museum for vouchering in June or July 2025. Once that is done, then we can finalize our data and meta-data for our DRYAD submission. We plan to have all data archived by October 2025.