



Salvage logging reduces wild bee diversity, but not abundance, in severely burned mixed-conifer forest



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ABSTRACT

Natural disturbances are critical for supporting biodiversity in many ecosystems, but subsequent management actions can influence the quality of habitat that follow these events. Post-disturbance salvage logging has negative consequences on certain components of forest biodiversity, but populations of some early seral-adapted organisms may be maintained in salvage-logged areas. We investigated the influence of an essential group of pollinators – wild bees – to recent post-wildfire salvage logging within managed mixed-conifer forest in the Pacific Northwest. We compared bee diversity (i.e., bee abundance, species richness, alpha diversity, and beta diversity) and habitat features (i.e., floral resources and available nesting substrates) in salvage-logged areas to unlogged sites, both of which experienced high-severity wildfire. Although we found no evidence for differences in bee abundance between salvage-logged and unlogged sites, interpolated estimates of species richness and both interpolated and extrapolated estimates of alpha diversity were greater in unlogged sites. Additionally, beta diversity was greater in unlogged sites when equal weight was given to rare species. Salvage logging did not select for specific functional groups of bees, as both logged and unlogged sites were dominated by generalist, social species that nest in the ground. However, habitat conditions for bees were influenced by salvage logging: flowering plant density was greater in salvage-logged sites during the latter half of the season, with fewer conifer snags and more woody debris than were available in unlogged sites. Our study indicates that salvage logging can support wild bee abundance, but that unlogged patches of severely burned forest supports slightly greater bee diversity within fire-prone mixed-conifer landscapes.

1. Introduction

Natural disturbances such as wildfires, droughts, insect outbreak, and windfall are hallmarks of forest ecosystems worldwide (Huston, 1979; Pickett and White, 1985; Hobbs and Huenneke, 1992). In temperate forests, high biodiversity and habitat heterogeneity are typically found in the early successional stage that follows severe disturbances with high tree mortality (Swanson et al., 2011; Thom and Seidl, 2016; Hilmers et al., 2018). Salvage logging, defined here as the removal of dead or dying trees after a forest disturbance, is often undertaken to recoup economic losses, reduce safety risks, and prepare sites for replanting within managed forests (Lindenmayer et al., 2008). Salvage logging is sometimes thought to have a greater impact on the biodiversity of plants and animals relative to harvesting undisturbed forest because of the additive and/or interacting effects that result from

harvests following disturbance (Franklin et al., 2002; Lindenmayer et al., 2008; Johnstone et al., 2016; Leverkus et al., 2018).

Pollinators are critical for biodiversity maintenance and their populations are influenced by environmental disturbances, including those that occur in managed forests (Hanula et al., 2016; Rivers et al., 2018a,b). Global concern for ongoing threats to pollinator populations has emphasized the need to understand how this group responds to anthropogenic activities (Pollinator Health Task Force, 2015; IPBES, 2016). Wild bees are often considered to be the most important pollinator groups, as they are abundant in a wide variety of ecosystems worldwide (Michener, 2007) and are frequent visitors to flowers in natural and anthropogenic systems (Neff and Simpson, 1993; Garibaldi et al., 2013). In temperate forests, wild bees are most abundant in forest openings (Hanula et al., 2016; Roberts et al., 2017) so management activities that reduce canopy cover, such as clear-cut harvest and

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thinning operations, are thought to promote bee populations in forest landscapes (Romey et al., 2007; Pengelly and Cartar, 2010; Hanula and Horn, 2011; Taki et al., 2013; Korpela et al., 2015; Rubene et al., 2015; Rodríguez and Kouki, 2017). Nevertheless, a recent review found a dearth of research on how bees and other pollinators respond to forest management activities, including post-disturbance salvage logging (Rivers et al., 2018a). As disturbances become more severe and widespread in forests worldwide (Diffenbaugh and Field, 2013; Millar and Stephenson, 2015), information is needed to understand how post-disturbance salvage logging could influence biodiversity, especially as it relates to organisms like wild bees that are often abundant in early seral forest habitats (Potts et al., 2003; Ponisio et al., 2016; Brown et al., 2017; Lazarina et al., 2017; Galbraith et al., 2019a; Lazarina et al., 2019).

To date only a single study has quantified how wild bee communities respond to post-fire salvage logging (Heil and Burkle, 2018). That work found greater bee density and species richness in logged sites 6 years after salvage logging occurred, with no differences in bee density and species richness 24 years after logging (Heil and Burkle, 2018). Of note, the study did not account for variation in local burn severity despite its importance in structuring post-fire bee communities (Galbraith et al., 2019a; Lazarina et al., 2019) which is likely to be relevant to areas subjected to post-fire salvage logging. Furthermore, bee communities can exhibit rapid temporal changes following forest disturbances (Potts et al., 2003; Moretti et al., 2006; Taki et al., 2013), responding to habitat conditions < 1 year after the initiation of stand-scale disturbance (Lazarina et al., 2019) and undergoing marked changes in abundance over successive seasons post-disturbance (Rivers et al., 2018b). Given that the influence of post-wildfire salvage logging on bees and their habitat appears to attenuate with time (Heil and Burkle, 2018), assessing how bee communities change shortly after salvage logging – while simultaneously considering burn severity – remains a critical step for understanding how components of biodiversity respond to post-fire harvest in forest ecosystems.

In this study, we quantified the effects of salvage logging on wild bees and their habitat soon after a large wildfire and subsequent salvage logging operations occurred in mixed-conifer forest in southern Oregon, USA. We hypothesized that bee abundance would be uninfluenced by salvage logging within severely burned forest because severe wildfire acts to remove the canopy and create favorable bee habitat in both logged and unlogged sites (Galbraith et al., 2019a). In contrast, we hypothesized that species richness and diversity would be reduced in salvage-logged sites relative to unlogged controls because of homogenizing effects of post-fire logging on habitats (Leverkus et al., 2014; Thorn et al., 2018). Specifically, we predicted that salvage logging would decrease habitat heterogeneity for wild bee taxa via the removal of nesting substrates like snags and stumps (McIver and Starr, 2001) and reduction of post-wildfire plant diversity (McIver and Starr, 2001; Beschta et al., 2004; Donato et al., 2006; Lindenmayer and Noss, 2006; Leverkus et al., 2014). In turn, this would result in lower alpha diversity (i.e., the effective number of species at the plot scale, weighed by their frequency; Jost, 2006) and beta diversity (i.e., between-plot diversity, or the proportion of species turnover between samples; Jost, 2006) in the salvage-logged sites relative to unlogged areas that experienced the same degree of fire severity.

In addition to measures of bee diversity, we also hypothesized that salvage logging would lead to distinct bee communities with respect to their functional traits. Bees are diverse in many aspects of their life history, including nesting substrates, degree of social behavior, and body size, and such traits are often linked to bee response to disturbance (Winfrey et al., 2007; Williams et al., 2010; Bartomeus et al., 2013; Harrison et al., 2018; Hall et al., 2019). Therefore, we predicted that bees that nest above-ground would be less abundant in logged sites due to the removal of potential woody nesting substrates (Cane et al., 2007; Moretti et al., 2009). We also expected that smaller bees would be disproportionately affected by salvage logging because bee body size

is positively linked to foraging distance (Gathmann and Tschardt, 2002; Zurbuchen et al., 2010), and that the shorter foraging range of small bees would lead to a slower population recovery from the combination of wildfire and logging disturbances. We also predicted that there would be more social species detected in salvage-logged sites, as the social colonies grow throughout the season, allowing workers to take advantage of dense patches of disturbance-adapted flowers often present in recently disturbed sites (Heil and Burkle, 2018; Mola and Williams, 2018). Finally, bees with a broad diet may be more competitive in heavily disturbed habitats because they have a greater likelihood of fulfilling their foraging requirements after a shift in resource availability (Bommarco et al., 2010). As such, we expected that floral generalists (i.e., bees that collect pollen from many plant taxa) would be relatively more abundant at salvage-logged sites than in unlogged areas.

2. Methods and materials

2.1. Study area and site selection

We undertook this research in the Klamath-Siskiyou ecoregion of southwestern Oregon USA (Fig. 1) during May–August of 2016 and 2017. This mountainous region is characterized by frequent, mixed-severity fires (Taylor and Skinner, 2003). Forests are composed of a mix of native conifers including Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Jeffrey pine (*Pinus jeffreyi*), and incense cedar (*Calocedrus decurrens*) intermixed with hardwoods, including tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), and madrone (*Arbutus menziesii*). There are > 3500 plant species recorded from this region, with many pollen- and nectar-rich forest understory species (particularly shrubs) flowering in the spring (April–May), such as *Gaultheria shallon*, *Vaccinium ovatum*, and *Ceanothus integerrimus*. In the summer, a diversity of flowering herbaceous perennials (e.g., *Campanula prenanthoides*, *Whipplea modesta*, *Apocynum pumilum*) can be common within regional forests (Whittaker, 1960).

Our study focused on the mixed-conifer forest region of the Klamath Mountains that burned in the Dad's Creek Fire and Rabbit Mountain Fire. Together, these burn areas comprised most of the Douglas Fire Complex. The Douglas Complex fires were ignited by lightning in July 2013, burned > 1 month, and resulted in a mosaic of fire severity across the landscape. The fires burned ~9400 ha in private forests and ~10,200 ha in public forests managed by the USDI Bureau of Land Management (BLM; Zald and Dunn, 2018). The BLM holdings within this region, from which we selected our study sites, were typically managed as even-aged Douglas-fir stands before the fire, with snags and live trees left after harvest for wildlife habitat. Salvage-logged sites were harvested in 2014 (Fig. 1), which included the removal of dead trees via cable logging, or less frequently, aerial fielding (BLM, 2014).

We determined burn severity of each site using the relative difference normalized burn ratio (RdNBR; Miller and Thode, 2007) using data from the Monitoring Trends in Burn Severity database (MTBS, 2014). RdNBR is a satellite imagery-based metric of pre- to post-fire change that correlates with basal area mortality (Reilly et al., 2017). We used this metric because it is widely available to scientists and land managers (Miller and Thode, 2007) and because it incorporates pre-fire spectral differences associated with variation in vegetation cover (Miller et al., 2009); thus, it accounts for pre-existing site characteristics (e.g., basal area) in measuring the degree of change caused by the wildfire.

To identify sampling locations, we overlaid a map of BLM salvage-logged harvest units with a burn severity map of the Douglas Complex and then randomly selected sampling locations within high-severity burn regions representing two treatments: salvage-logged sites ($n = 8$ sites, 7 of which were cable-logged and 1 that was helicopter-fielded) and unlogged control sites ($n = 9$ sites). Because the BLM only salvage-

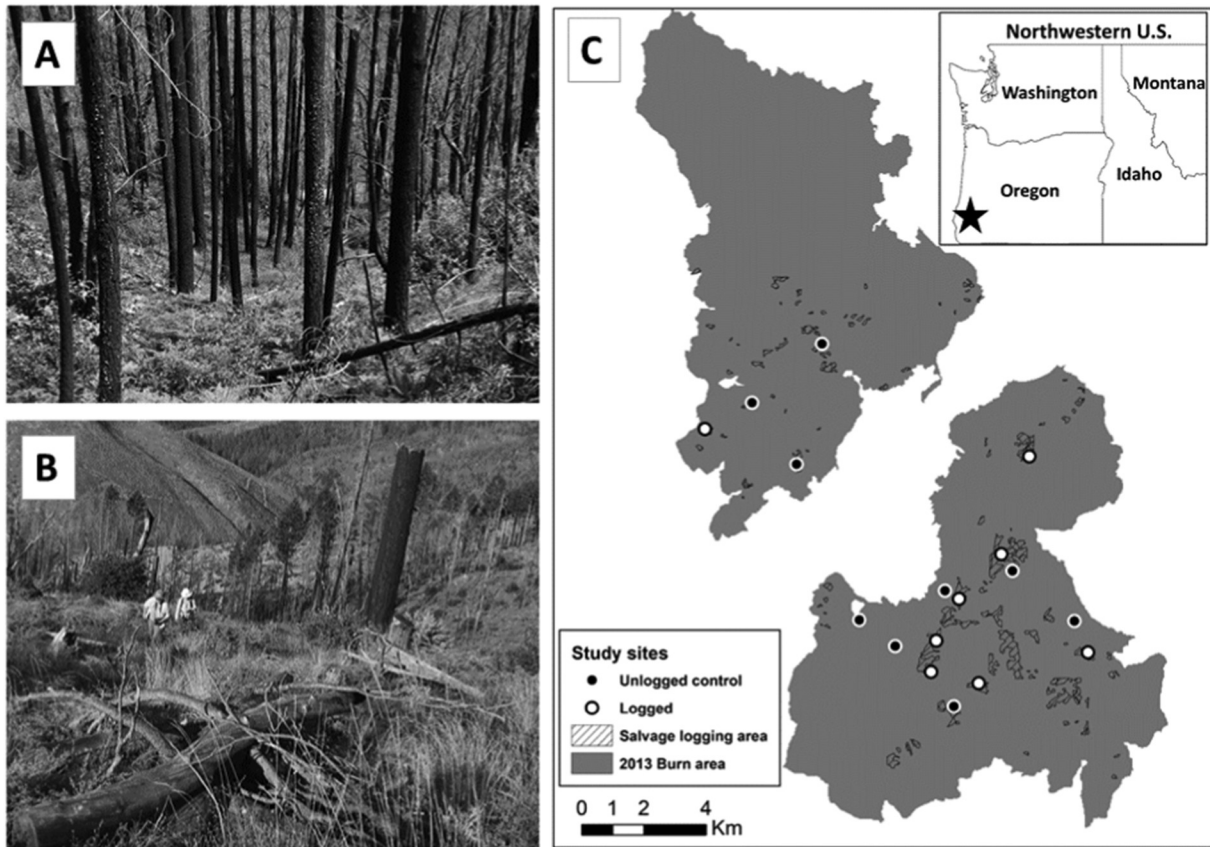


Fig. 1. Representative images for (A) an unlogged control site and (B) a salvage-logged site. Area map (C) shows the dispersion of study sites, which were located on Bureau of Land Management ownership in the Douglas Fire Complex. The burned area is shaded grey, with salvage-logged sections represented by cross-hatched polygons; study sites are marked with black circles (unlogged control sites) or white circles (salvage-logged sites).

logged units that burned severely, the randomly selected sites had similar fire severity, with RdNBR medians and quartiles for logged and unlogged sites within 100 units (from a total range of 395 units). We ensured that the two site types were spatially interspersed and that sites within the same treatment were a minimum of 1 km apart (mean = 5.8 km). This allowed us to consider sampling locations spatially independent, as most bee species found in temperate conifer forests are small- to moderate-sized bees (Rivers et al., 2018b) with foraging ranges expected to be < 1 km based on published size-foraging range relationships (Zurbuchen et al., 2010). In addition, we located all study sites > 50 m from the nearest active secondary road to minimize potential edge effects. Finally, we assessed several stand-level characteristics that are likely to influence bee communities as well as land managers' decision of where to salvage-log after a wildfire. We measured the elevation, aspect, and slope at the center of each sampling location and sought to limit the difference between these variables when choosing the study sites (see Supplementary Materials, T1).

2.2. Bee and habitat sampling

We collected bees and sampled bee habitat characteristics in the Douglas Complex as part of a related study investigating the influence of wildfire severity on wild bees (Galbraith et al., 2019a). Sampling took place during four sampling rounds each in 2016 and 2017: spring (collection period 1: late May), early summer (collection period 2: late June/early July), mid-summer (collection period 3: early August), and late summer (collection period 4: early September). These collection periods were selected to encompass variation in bee activity across the summer flight season, from the blooming of early-season flowering plants in May (e.g., *Vaccinium ovatum*, *Gaultheria shallon*) to the end of

bloom for late-season forbs by September. Active nearby wildfires prevented us from completing data collection period in 2017, so only eight of the 17 study sites were sampled during the final collection period in 2017.

During each collection period, we sampled bee communities using blue vane traps (BVTs; Springstar Inc., Woodinville, WA), which have UV-reflective vanes that attract a diversity of bee taxa (Stephen and Rao, 2005) and are effective in conifer forests (Rhoades et al., 2018; Rivers et al., 2018b). At each sampling site, we hung two traps with no killing agent or preservative, each on their own 1.8 m tall metal post, so that traps were at or above the height of most forbs. We placed the first trap 10 m from the geographic center of each severely burned patch along a randomly selected azimuth and the second trap was placed 10 m from the center 180° in the opposite direction. We avoided placing traps in dense vegetation patches to increase visibility for bees as much as possible. We left traps for 48 h, after which we removed them and placed them into a cooler with dry ice to kill captured insects; samples remained frozen until processing in the lab.

Floral resources are variable throughout the growing season in our study region (Whittaker, 1960), so we quantified flowering plant density at each study site within 1 week of each time that we sampled bees. We measured flowering plant density using ordered distance sampling, an efficient method in areas with patchy or sparse bloom (Nielson et al., 2004) which characterized our study sites. For this method, we established two transects that extended 50 m from each trap and identified and measured the distance to the 4th nearest flowering plant at every 10 m interval (Nielson et al., 2004). We initially used the 4th nearest plant to estimate species richness but found that it was likely to underestimate local flowering plant richness by biasing them towards abundant plants that were close to the transect (Galbraith, *personal*

observation). To improve our understanding of the flowering plant communities, in 2017 we recorded all flowering plant species observed within the sampling site while conducting searches for the ordered distance protocol (in addition to the 4th nearest flowering plant) to supplement our measure of species richness and floral composition.

In addition to floral resources, we also measured canopy cover, which is usually negatively correlated with bee diversity in temperate forest ecosystems (Hanula and Horn, 2011; Rubene et al., 2015). Using a convex spherical densiometer, we recorded percent canopy cover at each of the 10 m sampling points along transects that were used to quantify flowering plants. Similarly, we estimated exposed bare ground, which serves as an index of nesting availability for ground-nesting bees, by recording the percent bare ground visible within a 1 m radius of each of these points. We considered bare ground to be where soil or small pebbles (< 1 cm) were exposed from above.

Finally, we quantified the amount of dead wood within two 12.25-m radius plots per site by measuring snags, stumps, and other downed wood > 5 cm diameter because these substrates can provide nesting habitat for cavity-nesting bees (e.g., Michener, 1990; Cane et al., 2007). Within each plot, we counted and measured the width and length of coarse woody debris in three size categories (5–10 cm, 10–30 cm, and > 30 cm diameter) along a line transect through the plot center. We measured the height and diameter at breast height of all snags and the height and diameter at the top of stumps within the plots. When possible, we also identified whether standing dead wood was from a hardwood or conifer tree species. Using these data, we calculated the amount of snags and coarse woody debris that was available to cavity nesting bees. We also estimated the number of dead wood pieces that had potential nest sites by recording the number of beetle holes observed in a 1-m section of coarse woody debris crossing the transect and in the 1-meter section of snags and stumps at breast height. We only counted holes that were > 1 mm, as cavity-nesting bees often use exit holes from boring beetles as nesting locations (Cane et al., 2007).

2.3. Species identification and trait assignment

We assigned each captured bee to the lowest possible taxonomic level using keys from Michener (2007) and Stephen et al. (1969), as well as regional synoptic collections and local keys for *Agapostemon* (Stephen et al., 1969), *Anthophora* and *Ceratina* (www.discoverlife.org), *Bombus* (Williams et al., 2014), *Halictus* (Roberts, 1973), and *Xylcopa* (Hurd and Moure, 1963). Species-level identification was then carried out by A.R. Moldenke and L.R. Best. Species keys were unavailable for several groups in our region (e.g., *Lasioglossum* (*Dialictus*), *Osmia*), so in some taxa we could only identify specimens to morphospecies. If we were unable to associate male and female bees at the morphospecies level, we note these groups in Supplementary Materials (T2).

For all species, we used a Leica dissecting microscope and the measuring tool in Leica Microsystems LAS EZ software (Leica Microsystems, Buffalo Grove, IL) to measure intertegular distance (ITD) of up to 10 female specimens as a measure of body size (Cane, 1987). Body size is a strong predictor for foraging distance (Zurbuchen et al., 2010) and can predict bee response to environmental change (e.g., Renaud et al., 2016; Sydenham et al., 2016). We took the average of three replicate ITD measurements per individual and averaged individual-level measures for each species. We compiled information on bee sociality, nesting location, and pollen specialization using available literature and unpublished data from regional studies (Supplementary Materials, T2). Voucher specimens from this study are housed in the Oregon State University Arthropod Collection in Corvallis, OR (Galbraith et al., 2019b).

2.4. Statistical analysis

We modelled the effect of salvage logging on bee abundance and habitat features with generalized linear mixed models (GLMMs) using

the GLIMMIX function in SAS 9.4. (SAS Institute, Cary, NC). Least squares means of fixed effects were generated using the 'lsmeans' command in GLIMMIX. Unless otherwise noted, we report effect sizes as marginal model-derived parameter estimates (β) and their associated 95% CIs; both estimates were taken as the mean value for each covariate within each model. When a log-transformation was used in the model, we exponentiate reported estimates and CIs for ease of interpretation. Results for models using an identity link are additive differences, so we use a minus symbol ("−") when referring to parameter estimates. Results for models using a log link are multiplicative differences, so we use a division symbol ("÷") when referring to parameter estimates.

To assess the influence of salvage logging on observed bee abundance, we constructed a model that included year (2 levels: 2016, 2017), collection period (4 levels), treatment (2 levels: logged, unlogged), and a treatment × collection period interaction as fixed effects, with study site as a random effect. Including the treatment × collection interaction accounted for phenological environmental changes that may influence the magnitude of the effect of logging on bee populations. The model also included an offset for effort based on the number of traps per site, as traps were occasionally unavailable for sampling bees due to wind or animal disturbance. We used a negative binomial distribution with a log link to model bee abundance per site to eliminate overdispersion ($\chi^2/DF < 1$). Because two species in our dataset were especially abundant (*Halictus tripartitus* and *Bombus vosnesenskii*), we also assessed results of the bee abundance model after removing those species from the dataset to test whether bee abundance trends were driven by these common species (e.g., Miljanic et al., 2018). Finally, we tested for spatial autocorrelation of abundance measures over the course of the study by calculating the Moran's *I* Autocorrelation Index (Gittleman and Kot, 1990) from a matrix of inverse site distance weights using package "ape" in R.

We also used GLMMs to compare bee habitat between treatments and over time. For models predicting flowering plant density, we included year (2 levels: 2016, 2017), collection period (4 levels), treatment (2 levels: logged, unlogged), and a treatment × collection period interaction as fixed effects, with study site as a random effect. For flowering plant species richness, which was quantified in 2017, we included collection period (4 levels), treatment (2 levels: logged, unlogged) and a treatment × collection period interaction as fixed effects, with study site as a random effect. For the extent of canopy cover and bare ground, we calculated average values per site and modelled the response with year (2 levels: 2016, 2017) and treatment (2 levels: logged, unlogged) as fixed effects and study site as a random effect. Data were normally distributed in all cases, so we included a normal distribution and an identity link in our habitat models. As woody debris measurements were only taken once during the study, we report treatment medians and associated variation using boxplots, created using 'ggplot2' in R Studio version 3.4.2 (R Core Team, 2013).

Our final group of GLMMs estimated whether the abundance of different functional groups changed with treatment. For three models (nesting substrate, sociality, and diet specialization), we calculated the abundance of bees within each trait category at each sampling location. We then simplified the abundance model to only include three fixed effects: treatment ('logged' or 'unlogged'), a functional group variable (e.g., 'bee nesting habitat') and a treatment × functional group interaction. We again included the individual site as a random effect and an offset for trap effort. We chose a negative binomial distribution and 'log' link for each model to eliminate overdispersion ($\chi^2/DF < 1$). For bee size as measured by ITD, we modelled the mean ITD of bees collected per site per sampling event because body size may be influenced by seasonal changes in bee communities. Our resulting model had mean ITD as the response variable with year, collection, and treatment as fixed effects, site as a random effect, and an offset for effort. We used a normal distribution with an identity link for the ITD model, assessing residuals to ensure they were not overdispersed.

To compare species richness and Shannon alpha diversity between salvage-logged and unlogged sites, we generated sampling curves (Colwell et al., 2012) using package iNEXT v. 2.0.19 (Chao et al., 2014; Hsieh et al., 2016). Estimates were interpolated from individual-based abundance data to account for unequal sample sizes (Colwell et al., 2012) and then extrapolated to $2 \times$ the size of the smallest sample (Chao et al., 2014). We compared results between treatments using 95% CIs from bootstrapping. We calculated beta diversity, or the amount of spatial turnover between sites within each treatment, using R package vegetarian v1.2 (Charney and Record, 2009). We used two measures of beta diversity, the Jaccard index ($Q = 0$) and Shannon entropy ($[Q = 1]$; Jost, 2007) to represent the extent to which species are shared in two samples. These measures use different orders of 'Q', where a greater Q values puts less emphasis on rare observations in the sample (Jost, 2007). We compared results between treatments using standard errors from bootstrapping, as generated in the package.

3. Results

3.1. Bee community composition in logged and unlogged sites

We collected a total 3561 specimens representing 21 genera and 111 species/morphospecies of bees. The family Halictidae comprised 57% of specimens followed by Apidae (39%), Megachilidae (3%), Colletidae (< 1%), and Andrenidae (< 1%; Table 1). The most abundant species collected were *Halictus tripartitus*, *Bombus vosnesenskii*, *Xylocopa tabaniformis*, and *Apis mellifera*, which together composed 62% of the total sample. Species-level data are available in supplementary materials (T2).

Of the collected bees with known life history data, most individuals were classified as eusocial or primitively social (74%, $n = 2616$), including species within the genera *Apis*, *Bombus*, *Halictus*, and *Lasioglossum* (*Dialictus*), and most individuals were considered floral generalists (88%, $n = 3086$). We collected $> 6 \times$ more ground-nesting individuals ($n = 2866$) than above-ground nesters ($n = 451$), excluding an additional 6% ($n = 236$) that were cavity-nesting *Apis mellifera* that originated from managed and/or feral colonies.

Table 1

Number of specimens and species collected in each site type by genus for $n = 9$ unlogged sites and $n = 8$ salvage-logged sites. See Supplementary Materials (T2) for species-level functional traits with a list of references.

Genus	Num. collected in unlogged sites	Num. collected in logged sites	Species in unlogged sites	Species in logged sites
<i>Andrena</i>	6	5	5	4
<i>Anthidium</i>	4	3	2	1
<i>Anthophora</i>	19	15	3	2
<i>Apis</i>	92	144	1	1
<i>Ashmeadiella</i>	1	1	1	1
<i>Bombus</i>	304	374	8	8
<i>Ceratina</i>	4	0	1	0
<i>Colletes</i>	4	4	2	2
<i>Dianthidium</i>	5	3	3	2
<i>Dufourea</i>	1	0	1	0
<i>Eucera</i>	9	2	3	1
<i>Halictus</i>	546	744	5	4
<i>Hoplitis</i>	16	6	1	1
<i>Hylaeus</i>	13	7	9	4
<i>Lasioglossum</i>	357	362	26	21
<i>Megachile</i>	6	16	3	5
<i>Melecta</i>	2	0	1	0
<i>Melissodes</i>	47	127	5	6
<i>Osmia</i>	14	23	8	12
<i>Perdita</i>	2	2	1	1
<i>Xylocopa</i>	156	109	1	1

Table 2

Differences of treatment \times collection period across the season least squares means for bee abundance, bee abundance after removing the two most common bee species, flowering plant density, and flowering plant richness. All estimates have been exponentiated from their log-transformed values, though flowering plant density is on a scale of $\log^*(\text{flowers/ha})$.

Mean bee abundance (Unlogged/Logged)				
Collection period	Estimate	95% CI	T_{102}	P-value
Late spring	0.76	0.35, 1.61	-0.73	0.46
Early summer	0.86	0.41, 1.79	-0.41	0.68
Mid-summer	0.50	0.24, 1.03	-1.90	0.06
Late summer	1.16	0.51, 2.64	0.35	0.73
Mean bee abundance (Unlogged/Logged; Two species removed)				
Collection period	Estimate	95% CI	T_{102}	P-value
Late spring	0.87	0.44, 1.73	-0.39	0.70
Early summer	0.94	0.49, 1.82	-0.19	0.85
Mid-summer	0.58	0.30, 1.12	-1.65	0.10
Late summer	1.29	0.59, 2.83	0.65	0.52
Mean flowering plant density (Unlogged - Logged)				
Collection period	Estimate	95% CI	T_{98}	P-value
Late spring	0.44	-0.42, 1.30	1.02	0.31
Early summer	-0.88	-1.69, -0.06	-2.13	0.04
Mid-summer	-1.11	-1.92, -0.29	-2.69	< 0.01
Late summer	-1.46	-2.44, -0.50	-2.97	< 0.01
Mean flowering plant richness (Unlogged - Logged)				
Collection period	Estimate	95% CI	T_{33}	P-value
Late spring	0.41	-2.29, 3.11	0.31	0.76
Early summer	-1.59	-4.04, 0.84	-1.33	0.19
Mid-summer	1.06	-1.39, 3.50	0.88	0.39
Late summer	-1.52	-6.19, 3.15	-0.66	0.51

3.2. Bee abundance

We found no evidence that salvage logging influenced the mean abundance of bees collected per site (unlogged/logged treatment: $\beta = 0.79$, 95% CI [0.44, 1.40], $F_{1,102} = 0.66$, $P = .42$), nor did we detect a difference in bee abundance across years ($F_{1,102} = 2.25$, $P = .42$). Mean bee abundance differed relative to collection period ($F_{3,102} = 13.30$, $P < .01$), but this was consistent across treatments, as we found no treatment \times collection period interaction ($F_{3,102} = 1.46$, $P = .23$). Mean bee abundance per site was highly variable, particularly in the mid-summer, with large CIs around estimates that overlap with 1 (Table 2; Fig. 2A). Insufficient evidence for an influence of salvage logging on mean bee abundance remained after removing the two most common species (i.e., *Halictus tripartitus* and *Bombus vosnesenskii*) from the dataset (unlogged/logged treatment: $\beta = 0.88$, 95% CI [0.55, 1.44], $t = -0.50$, $F_{1,102} = 0.25$, $P = .62$; Table 2). We did not detect evidence of spatial autocorrelation between sites (Moran's $I = -0.09$, $P = .68$).

3.3. Floral resource measures

The mean density of flowering plants was 25% greater in sites subjected to salvage logging (unlogged - logged treatment: $\beta = -0.75$, [95% CI: -1.29, -0.22], $F_{1,98} = 7.73$, $P < .01$; Fig. 2B). Mean flowering plant density varied between collection periods ($F_{3,98} = 40.98$, $P < .01$) and we found an interaction between collection period \times treatment ($F_{1,98} = 4.18$, $P = .01$). For example, the 4th nearest flowering plant averaged 1.5 m from transects in both treatments during

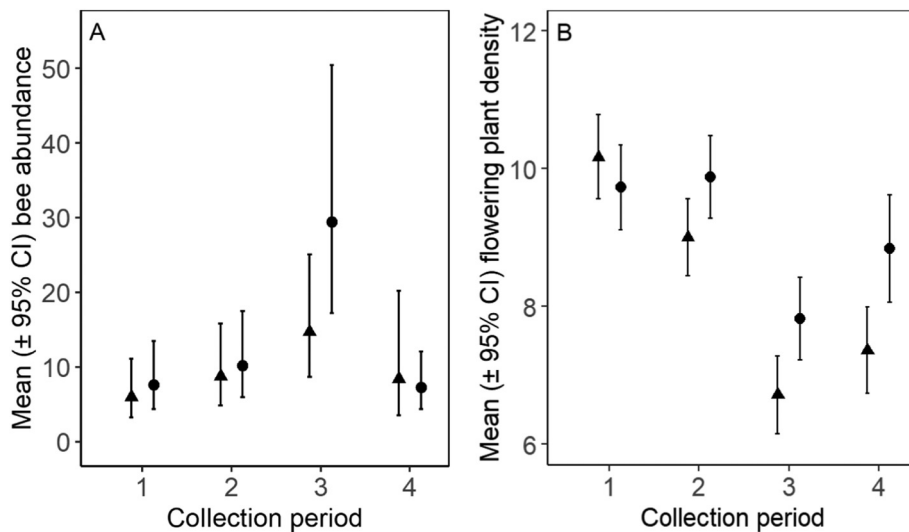


Fig. 2. Least squared means with 95% CIs plotted across collection periods while controlling for differences between years. Point estimates represent means for unlogged control (triangles) and salvage-logged sites (circles) sites across sampling periods for (A) bee abundance and (B) flowering plant density (number of flowering plants per hectare, natural log-transformed).

early spring when flowering plant density was similar (Table 1); in contrast, the 4th nearest flowering plant averaged 4.3 m from transects in logged sites and 19.1 m from transects in unlogged sites during mid-summer. We found no difference in mean flowering plant species richness between logged and unlogged sites (unlogged - logged treatment: $\beta = -0.41$, [95% CI: $-2.06, 1.24$], $F_{1,33} = 0.26$, $P = .62$) and no treatment \times collection period interaction ($F_{3,33} = 1.02$, $P = .39$; Table 2). Mean species richness declined throughout the season ($F_{1,33} = 9.38$, $P < .01$), and an average of only 10 plant species were observed flowering per site on a given visit over the course of the study. Canopy cover averaged $< 40\%$ in both control and treatment areas, and we did not find evidence for differences in mean canopy cover due to salvage logging (unlogged - logged treatment: $\beta = 10.99$, 95% CI: $-0.30, 23.28$], $F_{1,31} = 3.33$, $P = .08$) or year ($F_{1,31} = 0.03$, $P = .87$).

3.4. Bee species richness and diversity

Species accumulation curves showed converging bee species richness estimates in unlogged sites compared to logged sites when the number of individuals was standardized (Fig. 3A). Based on interpolated species richness curves, we would have detected an estimated 20 more species in unlogged sites compared to logged sites if we had

collected the same number of individuals in unlogged and logged sites. However, the extrapolated estimates eventually converged, meaning we had insufficient evidence that this trend would continue at greater sample sizes.

Estimates for alpha diversity were substantially lower than species richness estimates, indicating that bee populations in both treatments were dominated by a few species. Alpha diversity was greater in unlogged sites for both interpolated observations and extrapolated estimates, representing an estimated 3 fewer common species (Fig. 3B). Beta diversity was also greater within unlogged sites based on the Jaccard index, which gives equal weight to rare species ($Q = 0$). When less weight was given to rare species (Shannon entropy index, $Q = 1$), beta diversity was similar in logged and unlogged sites (Fig. 4).

3.5. Functional trait composition

We found no evidence that salvage logging influenced mean abundance of bees based on the bees' functional traits. There was no interaction between bee nesting habitat and salvage logging ($F_{1,15} = 0.63$, $P = .44$), as mean abundance of ground-nesting bees was greater than mean abundance of above-ground-nesting bees in both site types (above-ground/ground-nesting bee abundance: $\beta = 0.14$, 95% CI [0.08,

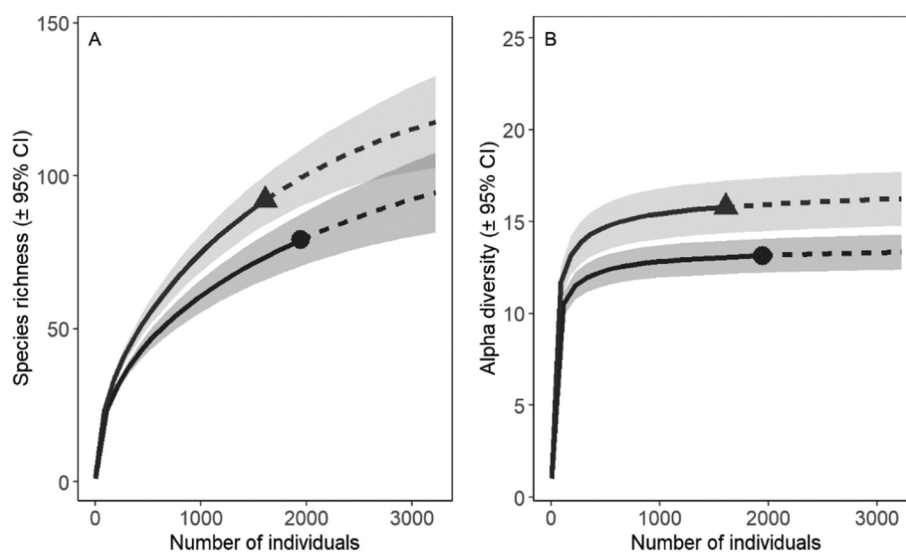


Fig. 3. A–B. Relationships between the number of individuals collected and (A) bee species richness and (B) Shannon alpha diversity of unlogged control (triangles) and salvage-logged sites (circles) using interpolated (solid line) and extrapolated (dotted line) species accumulation curves.

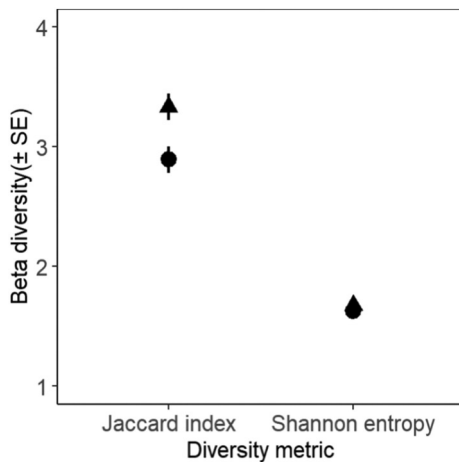


Fig. 4. The beta diversity of unlogged control (triangles) and salvage-logged sites (circles) sites estimated as numbers equivalents of the Jaccard index ($Q = 0$) and the Shannon entropy index ($Q = 1$) with standard error.

0.25], $F_{1,15} = 55.61$, $P < .01$). Likewise, we did not find evidence for an interaction between sociality \times treatment effect on bee abundance ($F_{1,15} = 0.55$, $P = .47$), as social bees were more abundant than solitary bees in both treatments (social/solitary bee species: $\beta = 2.35$, 95% CI [1.54, 3.60], $F_{1,15} = 18.54$, $P < .01$). Diet breadth and salvage logging also did not interact to predict bee abundance ($F_{1,15} = 0.20$, $P = .66$), with generalists consistently much more common than specialists (generalist/specialist bees: $\beta = 2.05$, 95% CI [1.69, 2.41], $F_{1,15} = 148.60$, $P < .01$). Likewise, we found no evidence that salvage logging was linked to bee body size (unlogged-logged treatment: $\beta = -0.11$, 95% CI [-0.52, 0.30], $t = -0.55$, $F_{1,100} = 0.24$, $P = .87$). Bee body size differed between collection periods ($F_{3,100} = 3.47$, $P = .02$), but there was no collection \times logging interaction ($F_{3,100} = 0.24$, $P = .87$) and no evidence for change in mean body size between years ($F_{1,100} = 0.04$, $P = .84$).

3.6. Nesting habitat availability

We detected no differences in the proportion of bare ground between logged and unlogged sites (unlogged - logged treatment: $\beta = 3.55$, 95% CI: -0.30, 23.28], $t = 0.80$, $F_{1,31} = 0.64$, $P = .43$), but there was 21% more bare ground during the first year of the study (between 2016 and 2017: $\beta = 21.09$, 95% CI: 12.04, 30.14], $F_{1,31} = 22.58$, $P < .01$). As expected, there were more conifer snags in unlogged sites compared to salvage-logged sites (Fig. 5A); in contrast, there was more coarse woody debris in salvage-logged sites (Fig. 5B). The number of snags, stumps, and coarse woody debris pieces containing beetle holes was also slightly greater in logged sites (Fig. 5C).

4. Discussion

Our study is the first to show the impacts of recent salvage logging on bee communities < 5 years after high-severity wildfire in a fire-prone mixed-conifer forest. We did not find differences in bee abundance between logged and unlogged control sites, but bee diversity was slightly greater in unlogged control sites. Although the areas we sampled were dominated by social, ground-nesting, and generalist bees, bee communities in salvage-logged sites were more homogeneous with fewer common species within sites (alpha-diversity) and fewer rare species between sites (beta-diversity) than burned areas not subjected to logging. There was also greater flowering plant density, but not observed flowering plant species richness, in logged sites, particularly during the period of mid- to late-summer. Thus, post-fire salvage logging appears to induce subtle changes to bee habitat and the

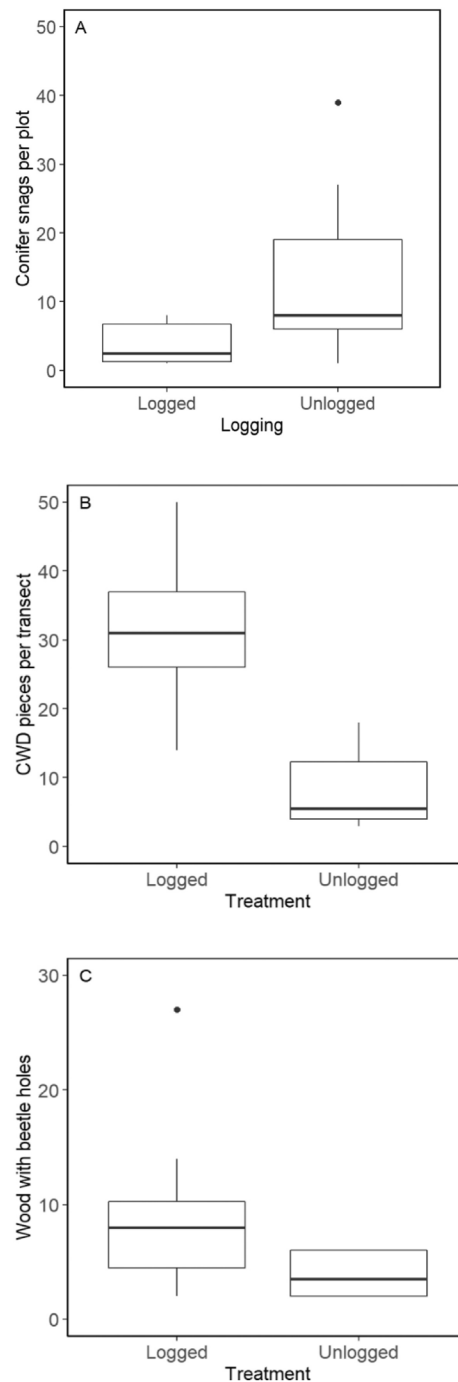


Fig. 5. Boxplots of (A) conifer snag density per plot, (B) the number of coarse woody debris pieces per plot, (C) the number of dead wood pieces containing beetle holes per plot.

composition of bee communities while maintaining the abundance of a few common species that may benefit disproportionately from the dense late-season resources in these areas.

Our results build upon the only previous study on the impacts of post-wildfire salvage logging on wild bee communities. Contrary to Heil and Burkle (2018), we did not find evidence for differences in bee abundance between salvage-logged and unlogged sites shortly after wildfire. We posit that this is likely because we limited our sampling to those sites that all experienced high local burn severity, which are the conditions typically chosen for post-wildfire salvage logging due to high tree mortality (Lindenmayer et al., 2008). Controlling for fire severity is essential for understanding the influence of post-fire salvage logging on

bee communities, as wildfire severity itself has a marked influence on bee diversity at local and landscape scales (Poniso et al., 2016; Galbraith et al., 2019a; Lazarina et al., 2019). In our previous work in this area (Galbraith et al., 2019a), we found that bee abundance and species richness increased markedly along the fire severity gradient, with $> 20\times$ more bees in the most severely compared to least severely burned forest sites. As such, the comparison between logged and unlogged sites within only severely burned forest in this study is critical for understanding how post-fire salvage logging may influence bee communities.

Although bee abundance was similar in unlogged and salvage logged sites, we did observe greater alpha- and beta- diversity of bees in unlogged sites. Alpha diversity, which takes both the species richness and evenness of a community into account, was greater in unlogged sites for both interpolated and extrapolated estimates. Differences in bee beta diversity, or the turnover in bee community composition between sites, depended on the amount weight given to rare species. When equal weight was given to rare species (i.e., $Q = 0$, the Jaccard index), we observed more spatial turnover of species in unlogged sites. When less weight was given to rare species in the sample ($Q = 1$, the Shannon entropy index), beta-diversity was equal between both treatments. Together, these findings indicate that bee communities were less homogenous in unlogged sites due to a reduced dominance of a few, common species and a greater presence of rare species.

We found no evidence that salvage logging resulted in the ecological filtering of specific functional groups of bees, but instead found that post-wildfire bee communities were characterized by a narrow range of functional characteristics in both treatments. This is evident from the substantial reduction in Shannon diversity estimates (12–15 species) compared to species richness estimates (> 100 species). Though our quantification of the bee community is likely biased towards bee species that are attracted to and captured by blue vane traps (see Geroff et al., 2014; Joshi et al., 2015; Gibbs et al., 2017), our findings are consistent with previous research showing that disturbed habitats often support wild bee communities that are comprised of abundant floral generalists (Devictor et al., 2008). Nearly 1/3 of all of the bees that we collected comprised just two species, *Bombus vosnesenskii* and *Halictus tripartitus*, both of which are eusocial floral generalists that prosper in highly disturbed areas, such as farmland (Kim et al., 2006; Rao and Strange, 2012) and urban areas (McFrederick and LeBuhn, 2006). These bees may have benefitted disproportionately from the floral resource availability after disturbance due to their social habit, which allows individual colonies to grow throughout the growing season. Additionally, both species nest in the ground, like most of the bee species collected in this study. The large proportion of species that are classified as ground-nesting in our study may be due to temperature effects of severe wildfire, as nests of ground-nesting bees are often protected from direct heating that causes mortality (Cane and Neff, 2011), whereas above-ground nesting bees may lose nesting substrates and/or experience direct mortality due to combustion (Moretti et al., 2009).

The availability of bare ground for ground-nesting bees decreased over the two years of the study, perhaps due to vegetative regrowth, but was similar between treatment types. Salvage logging can have marked direct and indirect effects on soil properties (McIver and Starr, 2001; Cambi et al., 2015), but the bare ground exposed by cable logging on our study sites may have been offset by the higher density of coarse woody debris in salvage-logged sites. This debris could have provided some nesting material for bees that nest in beetle holes or under the bark of trees (Cane et al., 2007), but it could also have decreased the suitability of habitat for ground-nesting species that need exposed mineral soil in which to build nest chambers. The soil types and properties preferred for nesting are known only from a few species (Cane, 1991), and it may be that our coarse measures of bare ground are insufficient for predicting bee communities. Therefore, future studies should focus on assessing the characteristics of forest soils that are available to ground-nesting bees to better understand fine-scale habitat use and

nest-site selection.

In contrast to the large number of ground-nesting bees captured, we collected few species that nest above-ground in dead conifers, pithy stems, or exit holes left by wood-boring beetles. As expected, salvage logging influenced the type of woody substrates available at the local scale (McIver and Starr, 2001; Lindenmayer and Noss, 2006; Russell et al., 2006). Woody materials were available in both treatments, but there were more conifer snags in unlogged sites, and more downed woody debris in salvage-logged sites. The most abundant above-ground nesting species we captured was *Xylocopa tabaniformis*, which nests in dead conifers (Michener, 1990) and was abundant in both salvage-logged and unlogged sites. In contrast, several stem-nesting species were only detected in unlogged sites, including one species of *Ceratina* and several species of *Hylaeus*. Although few specimens representing these genera were collected, we note that these taxa may have been particularly vulnerable to the combination of severe fire followed by salvage logging due to their preferred nesting substrates. As noted above, stem-nesting bees are likely less robust to high-severity fire because offspring will be killed by combustion of fine woody materials, so salvage logging may slow the accumulation of dead woody stems after the disturbance.

Land managers need to have information regarding the costs and benefits of salvage logging on wild bee communities for informed management decisions in post-fire forest landscapes (Lindenmayer et al., 2004). Because logging in unburned conifer forests generally supports pollinator diversity (Pengelly and Cartar, 2010; Taki et al., 2013; Korpela et al., 2015; Rubene et al., 2015), our findings highlight the need for more research regarding the different outcomes of logging in burned and unburned areas for wildlife habitat (Franklin et al., 2002; Lindenmayer et al., 2008; Johnstone et al., 2016; Leverkus et al., 2018), particularly for under-studied invertebrates (Wermelinger et al., 2017; Thorn et al., 2018). New studies should consider the degree of fire severity that typically precedes post-fire logging, as well as other conditions considered by land managers when they select areas for salvage logging (Lindenmayer et al., 2008). For example, stand age influences the abundance and diversity of pollinators in managed forests (Taki et al., 2013; Campbell et al., 2016; Rivers and Galbraith, unpublished data), and whether land managers generally choose to undertake salvage-logging in older stands (due to the greater economic value of larger trees) could drive additional habitat differences between logged and unlogged stands.

Although salvage-logged regions of severely burned forest in this study harbored greater bee habitat in the form of flowering plants, we did not find evidence that salvage logging influences the abundance of bees relative to unlogged forest that burned with similar severity. However, maximum bee diversity was found in the burned forest sites that were not salvage-logged. This adds new evidence that responses to salvage logging are often subtle and taxon-specific, even within a single group of pollinators (i.e., wild bees). Forest managers, particularly those working on public lands, are increasingly required to consider the diversity of wildlife like pollinators when making management decisions (White House, 2014; USDA, 2015), and this trend will likely continue as pollinators are added to lists of threatened and endangered species (e.g., IUCN Red List, 2019). Based on our results, land managers whose goals are to support wild bee diversity in managed landscapes where high severity fire and salvage logging may occur could consider increasing the abundance and diversity of pollen- and nectar-rich native plants throughout the summer flight season. Supplementing plant diversity has the potential to support populations of relatively rare solitary bees that are unable to take advantage of late-season flowering plants in the same manner as social species. Plants that flower earlier in the season might benefit solitary genera such as *Osmia* and *Andrena*, which include many species that are active in the spring. Furthermore, nesting substrates for bees that nest above-ground may be limiting in post-wildfire landscapes (Moretti et al., 2009), and populations of stem-nesting species are potentially further affected by activities like salvage

logging that slow the regeneration of plants with woody stems. Management activities that retain or supplement woody nesting substrates like pithy plants (e.g., *Rubus* species) and coarse woody debris (e.g., some standing snags) after wildfire and salvage logging could help support the recovery of cavity-nesting bees after these disturbances.

Declaration of Competing Interest

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

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The authors have no conflicts of interest related to this work.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117622>.

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