Journal of Forestry (2025) 124:41–85
https://doi.org/10.1007/s44392-025-00016-1

ORIGINAL PAPER

Comparison of Early Seral Forest Bee Communities Following Clearcutting or Wildfire Depends on Stand Age and Nesting Guild

Graham S. Frank[1] · James W. Rivers[2] · Jake Verschuyl[3] · Lincoln R. Best[4] · Matthew G. Betts[1] · Andrew J. Kroll[5,6] · Mark E. Swanson[2,7] · Meg A. Krawchuk[1]

Received: 1 October 2024 / Accepted: 21 February 2025 / Published online: 28 April 2025

Abstract

Forest harvesting can create habitat for wild bees, but with potentially different characteristics from habitats created by natural disturbance such as wildfire. We evaluated how bee communities varied between early seral stands regenerated by wildfire or intensively managed stands regenerated by clearcut harvest up to 20 years post-disturbance, using a chronosequence design in southwest Oregon. We also compared bee communities supported by post-fire salvage logging, 6–9 years post-disturbance. Clearcut stands supported higher bee abundance (90% CI: 36, 255%) and species richness (90% CI: 24.6, 44.8%) than fire-origin stands initially, but lower abundance (90% CI: –21, –71%) and species richness (90% CI: –51.4, –66.5%) in the oldest stands. Solitary nesting species associated with dead wood (mostly *Osmia* spp.) were more abundant in fire-origin stands. Our results indicate that clearcut harvest creates habitat for most wild bees adapted to stand-replacing fire but compromises habitat longevity and limits dead wood nesting habitat.

Keywords Biodiversity · Early successional forest · Intensive forest management · Pollinators · Salvage logging · Klamath Mountains

---

Study Implications Our results indicate that intensive forest management may be compatible with supporting the pool of wild bee species that occur in response to stand-replacing wildfire, except for species reliant on dead wood. Greater retention of downed dead wood may help alleviate these differences. Wild bee habitat within regenerating stands lasted longer following wildfire disturbance than clearcutting with intensive forest management. Therefore, retaining broadleaf vegetation likely prolongs bee habitat but may trade off with bee abundance during stand initiation. It is also possible that the large total extent of regenerating stands in some managed landscapes offsets shorter habitat longevity for bees.

Extended author information available on the last page of the article

Introduction

Wild bees (Hymenoptera: Anthophila) are the most important pollinator in many ecosystems (Neff and Simpson 1993) and their pollination services maintain plant diversity and energy-rich food webs (Morandin and Winston 2005, Fontaine et al. 2006; Kremen et al. 2007, Kudo et al. 2008). However, wild bees are experiencing widespread population declines in North America (Potts et al. 2010; Kopec and Burd 2017), many of which are due to habitat loss through land-use change (Goulson et al. 2005; Williams and Osborne 2009; Winfree et al. 2009; Potts et al. 2010). In forest ecosystems, disturbances that create or maintain an open canopy promote bee habitat, providing light energy to the forest floor (Hanula et al. 2016; Rodríguez and Kouki 2017; Galbraith et al. 2019a; Ulyshen et al. 2024). However, contemporary disturbance regimes in many productive forest landscapes are dominated by timber harvests (Brown et al. 2018), and the degree to which these emulate natural disturbance processes and support characteristic native bee communities is poorly understood.

Bee habitat may be especially dependent on disturbance in conifer-dominated forests, where foraging resources are limited after canopy closure (Taki et al. 2013; Zitomer et al. 2023; Ulyshen et al. 2024). With approximately three-fourths of the lumber produced in the United States harvested from conifer forests (Brandeis et al. 2021), it is important to understand bee responses to forest harvest in these contexts. In the Pacific Northwest, USA, intensive forest management on private forests accounts for most harvested timber volume (Zhou and Daniels 2018) and includes clearcut harvests on 30–50-year rotations, herbicide treatments for site preparation and crop tree release, and planting improved conifer seedlings (Talbert and Marshall 2005). Harvest disturbance in conifer forests has been shown to promote bee abundance and diversity compared to closed-canopy forests (Winfree et al. 2007; Rhoades et al. 2017, 2018; Chase et al. 2023), including harvests with intensive management practices (Taki et al. 2013; Rivers et al. 2018b; Rivers and Betts 2021; Zitomer et al. 2023). However, it is unclear how similar these bee communities are to those associated with natural disturbance, and managers of conifer forests often cite a lack of information on conservation targets and the effects of specific practices as barriers to incorporating pollinator habitat into their decision-making (Rivers et al. 2018a).

Natural disturbance processes can provide benchmarks for evaluating biodiversity outcomes of forest management (Hunter 1993; Attiwill 1994; North and Keeton 2008). Wildfire is a prominent natural disturbance process in Pacific Northwest forests (Spies et al. 2018) and often promotes bee abundance and diversity, especially when fire severity is moderate or high (Bogusch et al. 2015; Burkle et al. 2019; Galbraith et al. 2019a). Reduced canopy cover post-fire can increase floral resource availability, in turn enhancing wild bee populations (Potts et al. 2003a; Zurbuchen et al. 2010; Mola and Williams 2018). Bare soil exposed by surface fuel combustion can increase nesting substrate availability for ground-nesting species (Potts et al. 2005; Lazarina et al. 2016), and dead wood generated by fire-induced tree mortality provides substrates for many solitary bees that nest in aboveground cavities (Bogusch et al. 2015; Galbraith et al. 2019a). The characteristics of post-fire bee habitat can also be altered by salvage logging, which removes dead or injured trees following disturbance (Lindenmayer et al. 2008). As many natural forest disturbances increase in extent and severity with changes in climate and management

(Sommerfeld et al. 2018, Halofsky et al. 2020), it is also critical to understand how pollinators respond to salvage logging in regenerating forests.

Habitat for wild bees provided by regenerating early seral forest stands following harvest may differ from fire-origin stands in several ways. For one, longevity of bee habitat in intensively managed conifer forests can be short compared to that of naturally regenerating stands (Taki et al. 2013). In the absence of planting and silvicultural herbicides, conifers can be slower to attain dominance over broadleaf vegetation (Collins and Roller 2013; Tepley et al. 2014). Conversely, silvicultural herbicides could improve bee habitat during stand initiation by delaying development of shrub-layer vegetation, promoting flowering forbs (Kormann et al. 2021). Limited bare soil and dead wood in harvested stands compared to fire-origin stands may also reduce nesting habitat for bees (Rodríguez and Kouki 2015), though nest site preferences of ground-nesting species can be multifaceted (Cane 1991; Antoine and Forrest 2021) and many aboveground-nesting solitary bees use a variety of cavity substrates (Cane et al. 2007). Salvage logging reduces dead wood volume, but previous studies in conifer forests have not found evidence that bee species responses to salvage logging depend on whether those species nest in cavities (Heil and Burkle 2018; Galbraith et al. 2019b).

To evaluate the degree to which habitat for early seral forest bees following stand-replacing fire (fire-origin stands) is emulated by clearcutting with intensive forest management (clearcut stands) or altered by post-fire salvage logging, we studied bee communities within a fire-adapted, mixed-evergreen forest landscape in southwest Oregon, USA. We investigated (1) how the abundance and species richness of wild bees varied among disturbance types and stand ages (i.e., time since disturbance); (2) how habitat characteristics relevant to foraging and nesting explain variability in bee community responses; and (3) how bee responses vary among key life history traits: nest location and sociality. Many bees respond positively to forest canopy removal, so we expected high bee abundance and species richness with all disturbance types (Galbraith et al. 2019a, b; Zitomer et al. 2023). However, we expected bee responses between disturbance types to vary with stand age because herbicide treatments in clearcut stands can enhance floral resources by reducing shrub cover (Kormann et al. 2021) but suppress them later in stand development by accelerating conifer growth (Kroll et al. 2020). Finally, we expected bee responses to vary with sociality and nest location because belowground-nesting species tend to respond more positively to disturbance than aboveground-nesting species, and social species are often more resistant than solitary species to management intensification in agricultural settings (Williams et al. 2010). Furthermore, fire-origin stands contain abundant dead wood, an important nesting substrate for many solitary aboveground-nesting species (Danforth et al. 2019).

Materials and Methods

Study Area and Design

We studied bees as one component of a broader multi-taxa biodiversity study that included bees, birds, beetles, and plant communities in the Klamath Mountains of southwest Oregon, USA (Fig. 1; Frank 2023). High severity fire is part of the

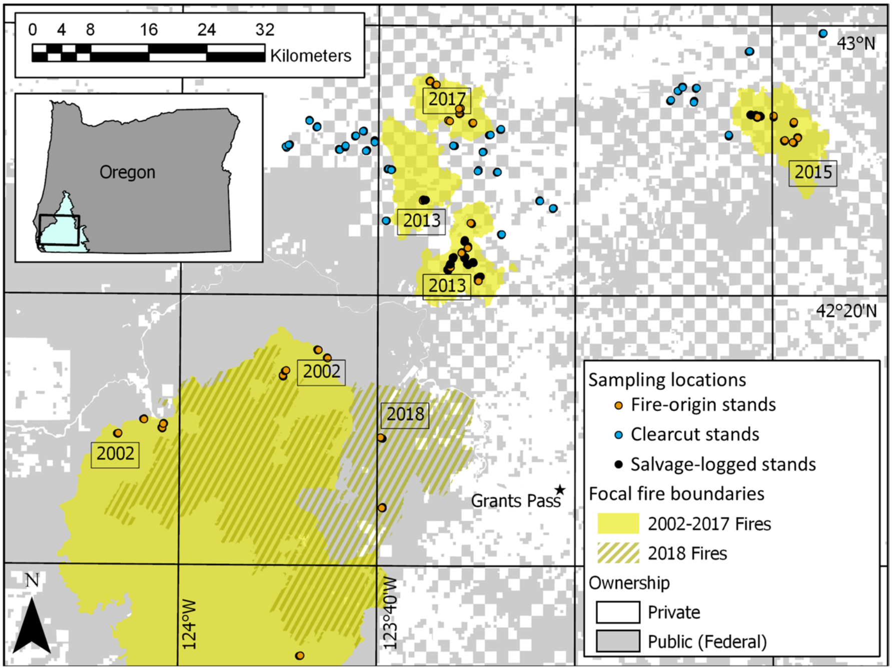


Fig. 1 Map of sampling locations for early seral forest bee assemblages in southwest Oregon, overlaid on land ownership pattern and fire footprints in which we sampled. Point colors correspond to the three disturbance types in our study design. Numeric labels correspond to the year of each fire

mixed-severity historic fire regime in the Klamath Mountains (Spies et al. 2018), and has increased in recent decades due to a warming climate and fuel accumulation (Taylor et al. 2021). Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) forest types dominate middle elevations in the Klamath Mountains, and we constrained our sampling to stands with climax vegetation modeled as Douglas-fir or Douglas-fir/Tanoak (*Notholithocarpus densiflorus*; Henderson 2013).

We stratified sampling locations across three disturbance types and three stand age classes. Disturbance types included: stand-replacing fire (fire-origin stands) and post-fire salvage logging (salvage-logged stands) on federal forestlands, and clearcut harvest with intensive management on private forestlands (clearcut stands). Stand age classes included: 2–5 yr (young), 6–9 yr (intermediate), and 16–20 yr (advanced), based on the timing of canopy removal. We defined fire-origin stands as patches that burned at high severity, based on an RdNBR (Relativized difference in the Normalized Burn Ratio) corresponding to > 75% basal area mortality (> 649; Reilly et al. 2017). Some younger fire-origin stands were planted, but with minimal influence on stand structure due to suppressed seedling growth and high mortality (first author, personal observation). We defined salvage-logged stands similarly, but with clearcut salvage harvest following the fire. Salvage-logged stands were planted but were not treated with herbicides. We only sampled salvage logged stands in the intermediate age class, as unforeseen fires and management during site selection limited availability of young and advanced candidate stands. We defined clearcut stands as those regenerating from clearcut harvest on unburned, privately managed forestlands, with intensive management practices outlined above. All stands were patches > 4 ha meeting our criteria that had not been harvested or burned within 45 years of the focal disturbance, based on harvest records and fire history maps. Our final study design included 69 sampled stands from seven disturbance × stand age combinations of early seral forest: young, intermediate, and advanced fire-origin and clearcut stands, and intermediate salvage-logged stands (Table 1).

Data Collection

We sampled each stand for bee community and habitat variables in one of three years: 2019, 2021, or 2022. We established three plots within each stand, with centers ≥ 100 m apart and ≥ 50 m from an identifiable stand edge such as a road, harvest edge, or lower burn severity. Plot centers were typically (96.6% of plots) within 150 m of an adjacent plot, though some were farther due to irregular stand shapes.

Bee Communities

We sampled bee communities using blue vane traps with yellow collection bottles (BanfieldBio, Woodinville, Washington, USA). Passive sampling methods including blue vane traps eliminate observer biases and are less labor intensive than hand netting, which was not logistically feasible in our study. Compared to passive pan trapping, blue vane traps often result in higher asymptotic species richness estimates (Joshi et al. 2015; Rhoades et al. 2017), though the two methods can yield distinct species composition, with blue vane traps collecting larger bees on average (Rhoades et al. 2017; McCravy et al 2019). When sampling stands, we set traps for two days in each of two rounds, late spring (May 16 to June 6) and mid-summer (July 11 to August 1). We randomly assigned sampling dates to stands within

Table 1 Sample sizes and means of non-floral habitat variables for disturbance × stand age combinations of early seral forest in the Klamath Mountains of Southwest Oregon (SD in parentheses). Boxplots of these variables and other metrics of forest vegetation structure are presented in Appendix 1

Age class	Disturbance type	*n*	Snag basal area (m^2 ha^{-1})	CWD volume (m^3 ha^{-1})	Pithy-stemmed plant cover (%)	Vegetation height (m)	Bare ground (%)
2 – 5 yr	Fire	10	55.0 (6.9)	101 (87)	0.40 (0.77)	1.8 (0.5)	16.9 (17.1)
	Clearcut	10	0.3 (0.5)	139 (79)	0.29 (0.49)	1.2 (0.5)	10.4 (4.0)
6 – 9 yr	Fire	10	47.8 (13.8)	195 (79)	0.42 (0.49)	3.0 (0.4)	11.1 (10.4)
	Clearcut	10	0.5 (0.5)	121 (80)	0.41 (0.47)	2.2 (1.0)	6.8 (6.2)
	Salvage	11	5.1 (3.8)	218 (51)	0.55 (0.65)	2.4 (0.6)	14.9 (7.6)
16 – 20 yr	Fire	9	21.8 (18.4)	180 (55)	0.10 (0.17)	4.7 (1.2)	14.0 (6.9)
	Clearcut	9	1.1 (1.7)	106 (48)	0.28 (0.61)	9.1 (1.3)	9.2 (8.0)

CWD Coarse woody debris >7.62 cm diameter each round. During each sampling round, crews attached traps to T-posts at each plot center and filled them with soapy water. Trap height measured to the top of the collection bottle averaged 0.91 m (SD: 0.12 m). Sampling effort varied due to trap destruction by wildlife and small deviations from our schedule, which we accounted for in analysis. Crews transferred samples to 95% ethanol upon collection. A single individual (LRB) identified all bee specimens using morphological keys, supported by DNA barcoding, and identified 99.4% of specimens to the species level (Frank et al. 2024).

Habitat Variables

We quantified floral resources in four 100 m^2 circular subplots at each plot during each two-day sampling period. We centered three subplots 18 m from the blue vane trap at 0-, 120-, and 240-degree azimuths, and a fourth subplot 9 m from the trap at a random azimuth of 60, 180, or 300 degrees. As a metric of floral resource availability, crews estimated percent floral cover as the maximum projected surface area of the corolla of each open flower in any one plane, aggregated within species at each subplot (Carrié et al. 2018; Spiesman et al. 2019). To minimize variability among observers, we estimated floral cover in intervals that were broader for higher values: 0.01% increments up to 0.3%, 0.1% increments from 0.3 to 2%, and 1% increments thereafter. Observers calibrated estimates using 10×10 cm squares, which represent 0.01% of 100 m^2. We treated values recorded as “trace” ($<0.005\%$) as 0.0025% for analyses. As a metric of stand development, we split each floral resource subplot into four quadrants and measured height (m) of the tallest woody vegetation in each quadrant. Crews also recorded visual estimates of percent bare ground within each subplot, to the nearest 10%. For analysis, we summarized measurements to stand-scale floral richness, mean floral cover, mean bare ground, and mean vegetation height.

We quantified coarse woody debris volume (CWD; $m^3\ ha^{-1}$), an important nesting substrate for some bee species, using line intercept transects. Transects extended 5–40 m from plot center along 0°, 120°, and 240° azimuths, and we measured diameter of all logs >7.62 cm at the point of intersection. We summarized diameters to a stand-scale estimate of dead wood volume using: $\pi^2 * \sum(d^2 \div 8L)$, where d is the piece diameter (m) and L is transect length (m; Harmon et al. 1986). For snags, we measured diameter of all stems 10–50 cm diameter at breast height (dbh, 1.37 m) in the same 100 m^2 subplots used to quantify floral cover. We measured larger snags >50 cm dbh in 25 m radius circular plots (1963 m^2) centered on each blue vane trap. If there were fewer than three snags >50 cm dbh within 25 m, we expanded the plot to 50 m (7854 m^2). For analysis, we summarized snag data into estimated basal area ($m^2\ ha^{-1}$) for each stand: $\sum(\pi * (dbh \div 2)^2 \div A)$, where dbh is that of each snag (m) and A is the plot area (hectares). We also collected ocular cover estimates of plant species with hollow, pithy stems known to provide nesting habitat for stem-nesting bees (*Sambucus* spp., *Stachys* spp., and *Rubus* spp. except for *R. ursinus* due to small stem diameter; Danforth et al. 2019), in smaller 25 m^2 circular subplots nested within each 100 m^2 subplot.

Data Analysis

Bee Abundance

We used two separate hierarchical models to (1) compare species- and community-level bee abundance among disturbance × stand age combinations of early seral forest ("comparative model") and (2) evaluate relationships between bee responses and habitat characteristics, including floral resources and nesting substrates ("explanatory model"). We also examined how these responses varied with bee sociality and nest location traits. We fit both models using the R package HMSC (Tikhonov et al. 2020), a flexible Bayesian framework for joint species distribution models (Ovaskainen et al. 2017). HMSC integrates species-specific models each relating counts to environmental covariates, allowing for information to be shared among species and for evaluating the degree to which responses are influenced by traits (Ovaskainen and Abrego 2020).

We modeled counts of a subset of (morpho)species with sufficient captures in our dataset, defined as those detected in at least 10% of stands and with ≥ 10 individuals captured (Appendix 2, Table 5). We aggregated species counts across all three traps within a stand × sampling round. For the comparative model, we modeled counts of each species as a function of sampling round, disturbance type, stand age class, and the interaction between disturbance and age class. For the explanatory model, we modeled species counts as a function of sampling round, flowering species richness, log-transformed floral cover, snag basal area, CWD volume, bare ground, and percent cover of pithy-stemmed plants. In both models, we included an offset for sampling effort and assumed a lognormal Poisson distribution and log link function. We calculated sampling effort as the time each trap was available to pollinators active during daylight hours (08:00–20:00), summed across the three traps in each stand.

We modeled species responses to disturbance × stand age combinations or habitat characteristics as a function of sociality (social or solitary) and nest location (below or aboveground). These traits may predict bee responses to disturbance (Williams et al. 2010), are available for most species (Appendix 2, Table SB1), and are relatively consistent within species. However, *Bombus fervidus*, *B. melanopygus*, and *B. mixtus* can nest above- or belowground, and we analyzed these species as aboveground nesters. To account for multiple sampling rounds within stands and for spatial dependencies in species responses, we included a spatially explicit random effect based on the geographic center of the three blue vane traps in each stand. We evaluated model convergence, model fit, and spatial autocorrelation in model residuals before interpreting results (Appendix 3).

For inference, we calculated posterior distributions of predicted species abundances within each disturbance × stand age category (comparative model) or across observed ranges of habitat characteristics (explanatory model). We summed individual species abundance predictions to generate posterior distributions of total abundance, incorporating the uncertainty in individual species estimates. We expected patterns in total abundance to be driven by a few especially abundant species, which may have distinct responses to disturbance types and stand age. Moreover, blue vane traps may be biased towards larger species (Rhoades et al. 2017; McCravy et al. 2019), which would give these species undue influence on total abundance in our sample. Therefore, we also calculated relative abundance for each species to evaluate patterns with each species weighted equally, dividing by the sum of predicted abundance for that species across all categories. We then calculated mean relative abundance across all species, and across species within specific guilds (i.e., combinations of sociality and nesting traits). Similarly, to summarize guild-level responses to habitat characteristics, we summed relevant linear combinations of HMSC gamma parameters, which reflect trait influences on species responses (Brown et al. 2014). We calculated 90% highest density credible intervals for parameter estimates and contrasts, and Bayesian p-values representing the proportion of posterior draws for which a contrast is < 0.

Rarefied Species Richness

We used sample-based rarefaction to compare species richness between disturbance types while accounting for differences in sampling effort. Sample-based rarefaction is a technique that resamples entire sample units without replacement, and we pooled bees across plots and seasons into stand-level sample units. Sample-based rarefaction was more appropriate for our data than individual-based rarefaction because social bees and those that nest in aggregations are unlikely to exhibit random spatial dispersion. During rarefaction, we weighted samples by sampling effort. Richness estimates from sample-based rarefaction reflect both species richness and any systematic differences in abundance between categories (Gotelli and Colwell 2001).

To determine values of sampling effort at which to compare species richness among disturbance types, we fit a nonlinear regression model to each of the 2000 permutations of each rarefaction curve and calculated the slope for the average curve in each disturbance × stand age combination. Comparing species richness at a common rate of species accumulation accounts for the possibility that equivalent sampling effort does not always result in equivalent sampling completeness (the degree to which species richness is fully characterized) under different environmental conditions (Roswell et al. 2021). We used the shallowest slope attained across disturbance × stand age combinations as a common slope value at which to estimate rarefied richness values for each category. We generated permutation-based confidence intervals for these point estimates and for contrasts between categories. We made rarefaction calculations using the vegan package in R (Oksanen et al. 2022).

Habitat Characteristics

Habitat characteristics included floral resource metrics (floral richness and total floral cover) and non-floral aspects of habitat (i.e., bare ground, snag basal area, CWD volume, pithy-stemmed plant cover, and vegetation height). We calculated means and SDs of bee habitat characteristics within disturbance × stand age combinations and made comparisons among these categories using linear models. We made separate comparisons of floral resources for spring and summer sampling rounds. For linear models, we log-transformed habitat characteristics as necessary to meet model assumptions. To evaluate whether characteristics varied across categories generally, we used likelihood ratio tests comparing a model with all seven categories against an intercept-only model. We also evaluated planned contrasts between disturbance types in the same age classes, and among age classes of the same disturbance types, using single-step adjustments to correct CIs for multiple comparisons. All analyses were conducting using R statistical software version 4.3.1 (R Core Team 2023).

Results

We collected 9861 bees representing 27 genera and 139 species/morphospecies, mostly from the families Apidae, Halictidae, and Megachilidae (Appendix 2). We collected most bees (73%) during the summer sampling round. There were 51 species available for inclusion in HMSC multispecies abundance models, representing 97.6% of bees collected (Table 2).

Composition and Abundance Comparisons

Comparisons of bee abundance between disturbance types varied across stand age classes (Fig. 2a). Predicted bee abundance was 124% higher (90% CI: 36, 255%) for young clearcut stands and 74% higher for intermediate clearcut stands (90% CI: 16, 154%) than fire-origin stands of the same age. Predicted bee abundance for salvage-logged stands, sampled only in the intermediate age class, was 3 × higher than for intermediate fire-origin stands (90% CI: 2.1, 4.7 ×). Bee abundance declined with age of clearcut stands, but we found little evidence for this pattern in fire-origin stands (Fig. 2a). Abundance was 83% lower (90% CI: 73, 90%) in advanced than young clearcut stands, whereas any evidence for a decline in fire-origin stands was weak (90% CI: 114% decline, 20% increase). Consequently, estimates of bee abundance were 52% lower (90% CI: 21, 71%) for advanced clearcut stands than advanced fire-origin stands.

Patterns in mean relative abundance across bee species were similar to those for overall bee abundance (Fig. 2b). Mean relative abundance was 93% higher

Table 2 Summary of bees collected in early seral forests of the Klamath Mountains according to guild membership, sampling round, and inclusion in hierarchical multispecies abundance models. Species excluded from models had fewer than 10 total individuals or were detected in < 10% of sampled stands

			Species			Individuals		
	Sociality	Nest location	Spring	Summer	Total	Spring	Summer	Total
Modelled	Social	Aboveground	4	4	4	93	143	236
		Belowground	12	12	12	1101	4454	5555
	Solitary	Aboveground	14	14	16	466	693	1159
		Belowground	18	19	21	872	1804	2676
Not modelled	–	–	47	60	87	115	120	235
Totals			95	109	138	2647	7214	9861

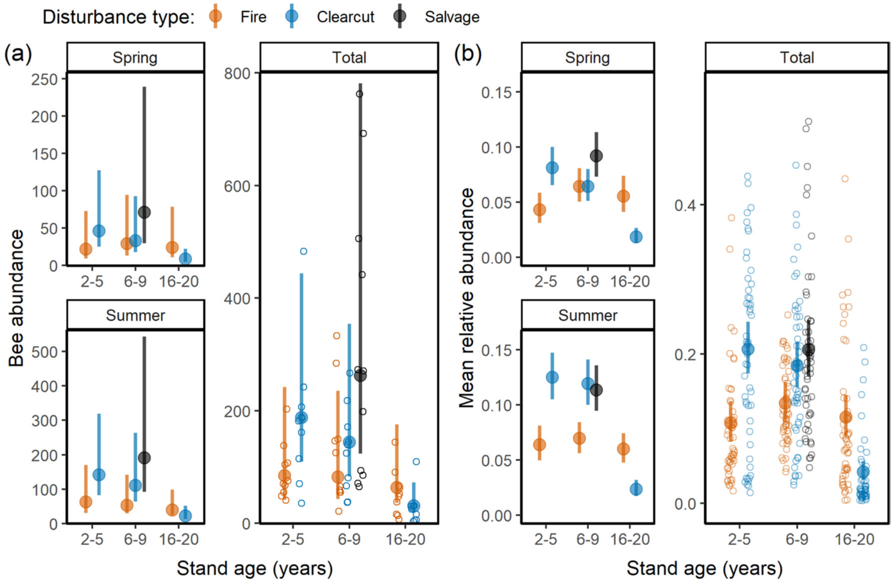
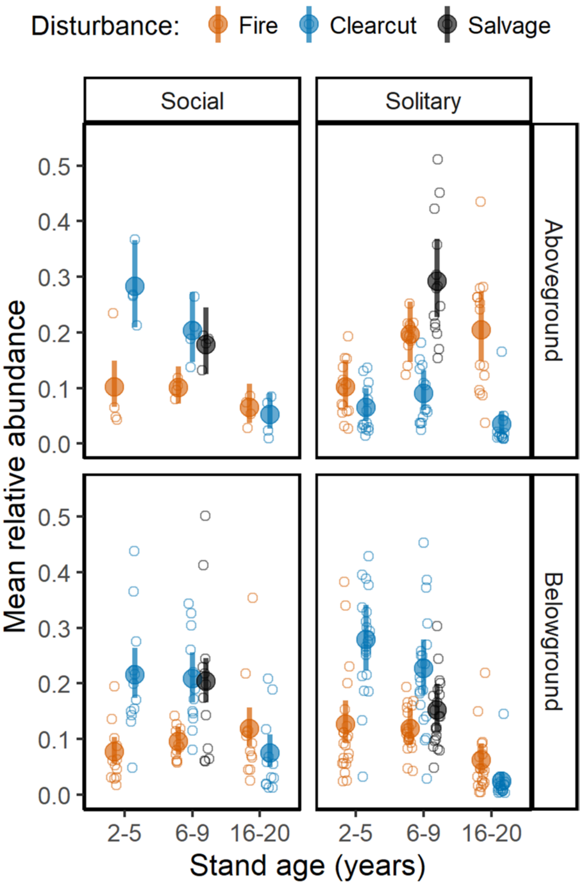


Fig. 2 Comparisons of (**a**) total bee abundance and (**b**) relativized abundance among disturbance × stand age combinationsof early seral forest. Total bee abundance represents predicted total captures for all species over six trap-days per sampling round. Relative abundance represents predicted abundance of a given species for each disturbance × age combination, relative to the sum of its predicted abundances across categories; therefore, mean relative abundance reflects abundance patterns across species. Dots and vertical lines represent posterior medians and 90% credible intervals. Small circles represent (**a**) data from individual stands, standardized for sampling effort, or (**b**) posterior median estimates for relative abundance of individual species

(90% CI: 39, 165%) for clearcut than for fire-origin stands in the young age class and 38% higher (90% CI: 4, 83%) in the intermediate age class, but 63% lower (90% CI: 47, 75%) in the advanced age class. For salvage-logged stands, mean relative abundance was 54% higher (90% CI: 16, 107%) than for fire-origin stands in the intermediate age class.

Comparisons of guild-level responses showed clear differences in bee community composition among disturbance × stand age combinations (Fig. 3). Responses of solitary aboveground-nesting species diverged from those of the broader bee community, with higher predicted mean relative abundance for fire-origin than clearcut stands, especially in older age classes. Estimates for mean relative abundance of solitary aboveground-nesting species were 36% lower (90% CI: 65% lower, 16% higher) for clearcut than fire-origin stands in the young age class, 54% lower (90% CI: 24, 72%) in the intermediate age class, and 83% lower (90% CI: 69, 91%) in the advanced age class. For the remaining guilds, comparisons between clearcut and fire-origin stands generally followed broader community-level patterns (Fig. 3). Bee composition in salvage-logged stands was less distinct from fire-origin stands. For example, we found no evidence for the negative response of the solitary aboveground-nesting guild (90% CI: 1% lower, 129%

Fig. 3 Comparisons of bee community composition among early seral forest categories, based on mean relative abundance of species within each guild, separated by sampling round. Mean relative abundance is the guild-level mean of species abundance predictions for a disturbance-age category, relativized for each species by the sum of predicted abundances across categories. Dots and vertical lines represent posterior medians and 90% credible intervals for guild-level means. Small circles represent posterior median estimates for relative abundance of individual species



higher mean relative abundance in salvage-logged stands) that we observed for clearcut stands in the intermediate age class, or for the positive response of the solitary belowground-nesting guild (90% CI: 13% lower, 90% higher). Our decision to analyze *Bombus fervidus*, *B. melanopygus*, and *B. mixtus* as aboveground nesting species did not influence comparisons (Appendix 4).

Species Richness

Species richness comparisons among disturbance types varied with stand age. Using the common rate of species accumulation per unit sampling effort (2.6 species 10 trap-days^{-1}), rarefied species richness for young clearcut stands was 34% higher (90% CI: 24.6%, 44.8%) than that of young fire-origin stands (Fig. 4). Estimated species richness increased by 46% for intermediate fire-origin stands and was 14% higher (90% CI: 5.6%, 21.7%) than the estimate for intermediate clearcut stands. Species richness declined for both disturbances between the intermediate and advanced age classes, but more sharply for clearcut stands such that species richness

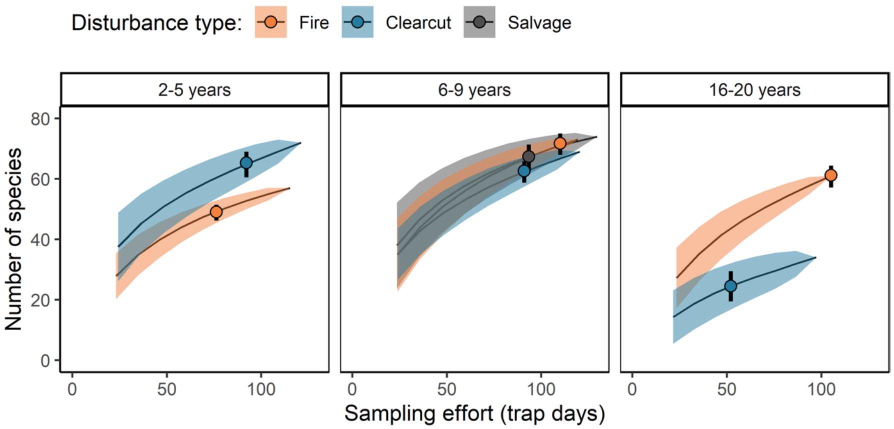


Fig. 4 Sample-based rarefaction curves for species richness across all stands sampled in each disturbance-age category, scaled by effort for each sample. Shading represents 90% confidence intervals for each rarefaction curve. Point estimates are at the shallowest slope in common among age classes, based on a quadratic logarithmic function ("Gitay model") fit to each rarefaction permutation, and include 90% confidence intervals (vertical lines)

in advanced clearcut stands was 60% lower (90% CI: 51.1%, 66.7%) than for fire-origin stands. We found no evidence that species richness for salvage-logged stands differed from unlogged fire-origin stands in the intermediate age class (90% CI: 1.6% lower, 13.7% higher in fire-origin).

Habitat Variables

Floral resource metrics varied among disturbance types, stand ages, and sampling rounds. In both spring and summer sampling rounds, flowering species richness in fire-origin stands decreased with stand age (Table 3). Spring floral richness was less variable with clearcut stand age, though summer floral richness was markedly lower for the advanced age class than young (57% lower; 90% CI: 2, 17 fewer species) or intermediate (61% lower; 90% CI: 4, 18 fewer species) age classes. Floral cover in the summer sampling round was very low for most disturbance × stand age combinations, except where stands had substantial Asteraceae components, including young fire-origin stands, and young and intermediate clearcut stands (Table 3). Overall, 97% of Asteraceae floral cover was from exotic species, especially *Hypochaeris radicata* (54%), *Senecio sylvaticus* (21%), and *Crepis capillaris* (11%). Variability in floral cover among disturbance × stand age combinations was weaker during the spring sampling round ($F_{6,61} = 2.25$, $p = 0.05$) compared to summer ($F_{6,62} = 17.41$, $p < 0.01$). Notably, variability within categories was much higher for floral cover than floral richness (Table 3).

Disturbance types also differed in some non-floral habitat characteristics. Snags were virtually absent from plots in clearcut stands and were most abundant in the youngest fire-origin stands (Table 1). Salvage-logged stands sampled in the intermediate age class also contained few snags. However, salvage-logged stands contained

Table 3 Means of floral resource variables for disturbance × stand age combinations of early seral forest in the Klamath Mountains of southwest Oregon, within spring and summer sampling rounds (SD in parentheses)

Round	Age class	Disturbance type	*n*	Floral richness	Total floral cover (%)	Asteraceae floral cover (%)
Spring	2 – 5 yr	Fire	9	20.3 (4.4)	0.438 (0.662)	0.009 (0.015)
		Clearcut	10	14.2 (6.2)	0.165 (0.334)	0.101 (0.309)
	6 – 9 yr	Fire	10	17.9 (5.0)	1.842 (2.984)*	0.001 (0.001)
		Clearcut	10	18.8 (6.5)	0.658 (0.900)	0.012 (0.015)
		Salvage	11	21.1 (6.2)	2.877 (7.152)**	0.006 (0.010)
	16 – 20 yr	Fire	9	9.2 (4.1)	0.208 (0.260)	0.001 (0.002)
		Clearcut	9	13.6 (5.6)	0.288 (0.307)	0.000 (0.000)
Summer	2 – 5 yr	Fire	10	17.7 (5.6)	0.172 (0.256)	0.150 (0.258)
		Clearcut	10	16.9 (6.3)	0.431 (0.470)	0.412 (0.472)
	6 – 9 yr	Fire	10	10.3 (6.2)	0.040 (0.046)	0.007 (0.009)
		Clearcut	10	18.3 (8.4)	0.353 (0.490)	0.301 (0.500)
		Salvage	11	9.6 (5.6)	0.019 (0.019)	0.008 (0.009)
	16 – 20 yr	Fire	9	3.1 (3.8)	0.002 (0.003)	0.000 (0.001)
		Clearcut	9	7.2 (6.7)	0.011 (0.011)	0.001 (0.001)

*excluding outliers: mean = 0.552, SD = 0.898; **excluding outliers: mean = 0.731, SD = 0.766

the highest volume of CWD (i.e., downed dead wood) of any category, on average, followed closely by intermediate and advanced fire-origin stands. Within age classes, there was little evidence for differences in CWD volume between clearcut and fire-origin stands due to high variability among stands. Woody vegetation height was similar between clearcut and fire-origin stands in young ($p = 0.25$) and intermediate ($p = 0.55$) age classes. However, vegetation was nearly twice as tall on average (90% CI: 3.4, 5.4 m taller) in clearcut than fire-origin stands for the advanced age class. Comparisons in the cover of pithy-stemmed plants and bare ground among disturbance × stand age combinations were weak (pithy plants: $F_{6,62} = 1.77, p = 0.11$; bare ground: $F_{6,62} = 2.05, p = 0.07$).

Bee Relationships with Habitat Variables

Bee community responses varied across gradients in floral and non-floral habitat variables. The proportion of variation in species counts captured by parameters in the explanatory model (pseudo-R^2) ranged from 0.01 to 0.59 (median = 0.21) and was strongly correlated with total captures (log-transformed) of each species ($r = 0.88$).

Relationships between bee abundance and floral resources were specific to the different metrics (floral cover or richness) and varied by sampling round and species traits. Across a floral richness gradient of 3–33 species, which was within ranges observed in both sampling rounds, predicted bee abundance increased 3.0× (90%

CI: 1.5×, 5.5×) for the spring sample but only 7% (90% CI: –49, 141%) for the summer sample. This contrast between sampling rounds was driven in part by the higher proportion of solitary bees in the spring sample (53%) than the summer sample (21%); predicted spring abundance of solitary bees increased 7.1×(90% CI: 3.3×, 16.0×) across the floral richness gradient, whereas we found no evidence for higher spring abundance of social bees across the same gradient ($p = 0.31$; Fig. 5a). The relationship between solitary bee abundance and floral richness was also weaker for the summer sampling round, with a 116% (i.e., 2.16×; 90% CI: –11, 425%) increase across the gradient (Fig. 5a). We found no evidence for a positive relationship between overall bee abundance and floral cover ($p = 0.77$), though several *Megachile* and *Melissodes* species captured almost exclusively during the summer sampling round were strongly associated with floral cover (Fig. 6a). Species associations with floral cover were related to seasonality more broadly, as coefficient estimates for sampling round and floral cover were correlated (r = 0.70, 90% CI: 0.57, 0.84; Fig. 6a).

In addition to floral resource variables, gradients in dead wood abundance helped explain variability in bee responses. Solitary aboveground-nesting species were more positively related to snag basal area and CWD volume than other functional groups (Figs. 5b and 6b). Across the observed gradient of 0–69 $m^2\ ha^{-1}$ snag basal area, abundance of solitary aboveground-nesting bees was expected to increase 95% (90% CI: –14, 381%), which was distinct from the negative abundance response of other guilds (–68%; 90% CI: –34, –83%). For these other guilds, the relationship between abundance and CWD volume was neutral (Figs. 5b and 6b) across the observed gradient of 2.3–364.3 $m^3\ ha^{-1}$ (90% CI: –56%, 167% change in abundance). In comparison, abundance of solitary aboveground nesting bees

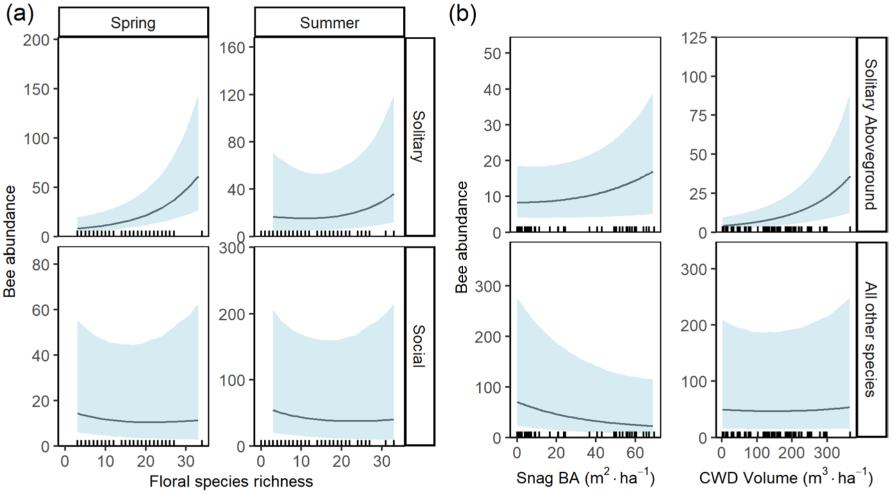


Fig. 5 Predicted bee abundance responses to (**a**) observed flowering species richness, (**b**) snag basal area (BA) and coarse woody debris (CWD) volume. Shaded areas represent 90% credible intervals and lines represent posterior medians. Abundance responses to CWD and snags are for both sampling rounds combined

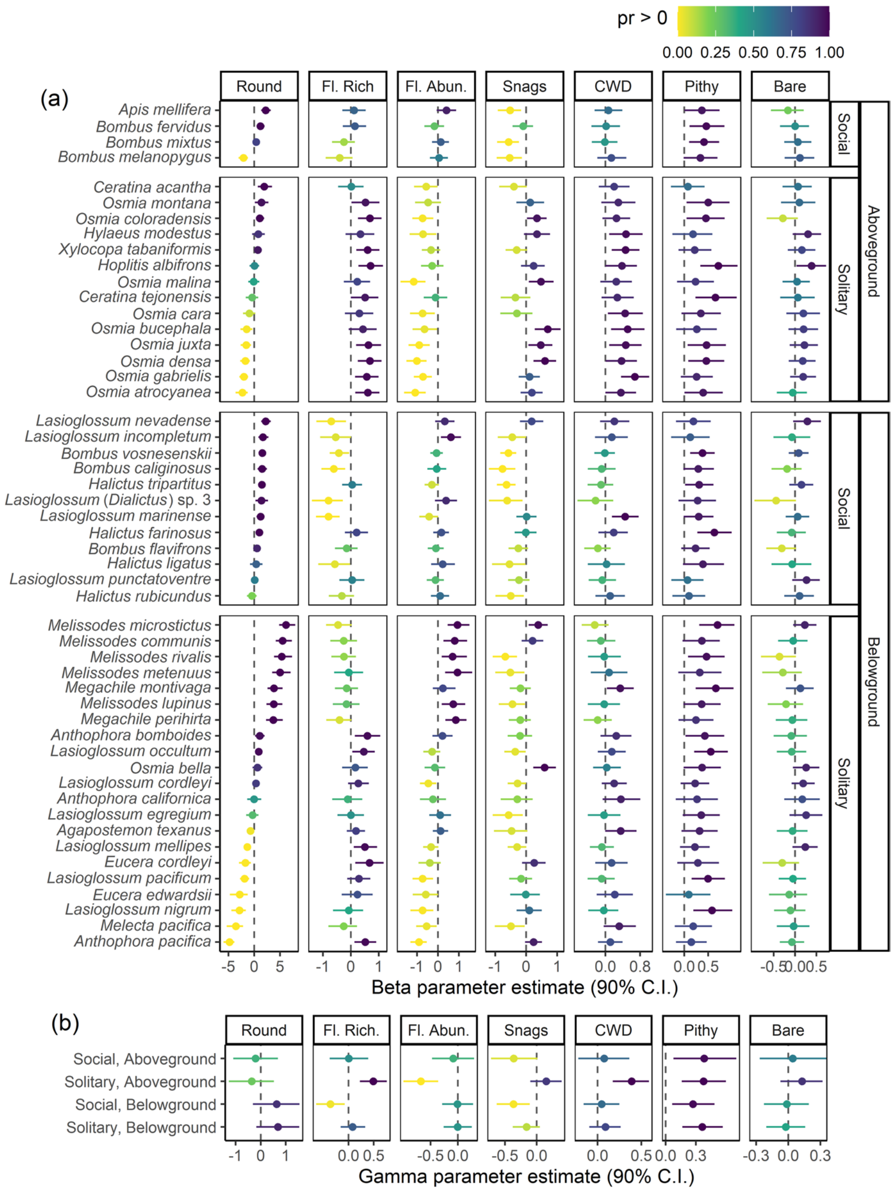


Fig. 6 Species-specific beta parameter estimates for explanatory HMSC model (**a**) and gamma parameters summarizing group-level responses (**b**). Beta parameter estimates correspond to the expected multiplicative increase in abundance of a given species for a one SD increase in the explanatory variable, labeled in the panel header. Round = spring vs. summer sampling round, with positive estimates corresponding to summer; Fl. Rich. = observed flowering species richness; Fl. Abund = log-transformed floral cover; CWD = coarse woody debris; Snags = standing dead snags; Pithy Stem = cover of pithy-stemmed plants. Note that *Bombus* categorized as aboveground nesters can also nest belowground

was predicted to increase 8.6×(90% CI: 3.6×, 20.2×) over the same gradient in CWD volume (Fig. 5c). Most (9 of 14) solitary aboveground-nesting species were *Osmia* spp., especially those associated with the spring sampling round (Fig. 6a). Bee abundance was positively related to both pithy-stemmed plant cover and bare ground, but these relationships were not specific to stem-nesting or ground-nesting species (Appendix 5).

Discussion

In a temperate forest ecosystem, forest harvest appears to emulate natural stand-replacing disturbance for much of the wild bee community, but this depended on stand age and nesting guild. We found that, for at least the first nine years after disturbance, clearcut stands supported comparable or greater bee abundance than stands regenerating after fire, with the important exception of solitary species that nest primarily in dead wood. Bee abundance declined with stand age as harvested forests regenerated, reinforcing the importance of ephemeral, disturbance-generated habitat for wild bees in temperate forest landscapes (Taki et al. 2013; Carbone et al. 2019; Rivers and Betts 2021; Mathis et al. 2021; Zitomer et al. 2023). However, we also found that habitat for wild bees lasted longer following wildfire than clearcutting, as fire-origin stands supported higher bee abundance and species richness in the oldest age class. Salvage-logging resulted in comparable species richness and high bee abundance relative to unlogged fire-origin stands, including the solitary, aboveground-nesting group, potentially due to abundant down dead wood in salvage-logged stands and their adjacency to snag forests. Taken together, our results suggest that clearcutting with intensive forest management is compatible with conserving most wild bees supported by stand-replacing wildfire, providing considerable habitat on many managed landscapes, but compromises the duration of the early seral period and limits nesting habitat (dead wood).

Our study revealed complex relationships between bee abundances and floral resource metrics and aligned with previous work connecting wild bees and flowering plants in early seral forest stands (Potts et al. 2003b; Roberts et al. 2017; Mathis et al. 2021). Among the belowground-nesting solitary bees, species captured almost exclusively in the summer were strongly associated with the higher summer floral cover in clearcut stands, contributing to high bee abundance in these stands relative to fire-origin stands for the younger age classes. This group included several species of *Melissodes*, a genus that appears to be common in clearcut stands in the Pacific Northwest (Rivers et al. 2018a, b; Rivers and Betts 2021; Zitomer et al. 2023). Many *Melissodes* prefer or even specialize on Asteraceae pollen (Wright 2018), which declined between young and intermediate fire-origin age classes but were higher initially and maintained longer in clearcut stands. Silvicultural herbicides can promote colonization by exotic Asteraceae (Stokely et al. 2020), and our results suggest that this interaction may prolong habitat for some species dependent on the stand initiation phase.

Other solitary species were associated with floral richness rather than amount of bloom, and we found little evidence that social species were related to either metric of floral resources. We modeled associations between bee abundance and floral resource metrics observed in discrete two-day samples, which may not reflect season-long factors like floral resource continuity necessary for social species to maintain and grow colonies (Kaluza et al. 2018; Hemberger et al. 2022). Even for the comparatively short life cycles of solitary bees, floral richness may be a better proxy than abundance (floral cover) for continuous availability of foraging resources (Ogilvie and Forrest 2017). Diverse flowering plants may also be more likely to provide key nutrients lacking when floral resources are abundant but homogeneous (Filipiak et al. 2022). Additionally, flowering pulses from early-flowering shrubs (e.g., *Arctostaphylos*, *Ceanothus*) drove floral cover estimates in the spring, and the floral resource provided by shrubs may be outweighed by their negative effect on herbaceous floral resources (Mathis et al. 2021). Although our decision to use blue vane traps facilitated a large and diverse sample of bees, studies using multiple sampling methods consistently report weaker relationships between bee and bloom metrics with passive trapping than with hand netting (Rhoades et al. 2017; Krahner et al. 2024). This discrepancy may indicate a bias in passive methods that is worth continued investigation (Mathis et al. 2024). However, netting relies on active observers who may detect bees more easily when bloom abundance is high. A positive relationship between bloom abundance and detection probabilities would artificially inflate estimates of bee-bloom relationships in netting studies and has not been examined.

Stand structure may also influence bee habitat use by modifying foraging patterns independent of floral resource availability (Ulyshen et al. 2024). Bee foraging activity can be limited by cool temperatures (Corbet et al. 1993), and both standing snags (Fontaine et al. 2010) and differences in vegetation structure (Thompson et al. 2017) can produce cooler microclimates. Obstacles in structurally complex environments, such as snags or dense vegetation, can force bees to take slower, more circuitous flight paths (Crall et al. 2015), reducing foraging efficiency. Structural complexity is considered an important attribute for ecological functioning in early seral forest stands (Donato et al. 2012; DellaSala et al. 2014), and future work is necessary to understand whether it directly influences the demographic responses of wild bees in field settings (Galbraith et al. 2021).

Solitary, aboveground-nesting species were the only group more abundant in younger fire-origin stands than in clearcut stands, and all nest in cavities. This group was positively associated with downed dead wood and snag abundance, suggesting that they may have been limited by nest site availability in clearcut stands. Bees are central place foragers, requiring foraging resources and nesting sites in close proximity (Westrich 1996). Surprisingly, solitary, aboveground-nesting species were just as abundant in salvage-logged as unlogged fire-origin stands, or even more so. Previous studies on bee responses to salvage logging versus fire alone in conifer forests have also failed to find differences among nesting guilds three to four years post-fire in Oregon (Galbraith et al. 2019b) or seven to eight years post-fire in Montana

(Heil and Burkle 2018). Salvage-logged stands had the highest average volumes of downed dead wood in our study due to logging slash, which may provide nest sites without the potential negative effects of standing snags. Additionally, salvage-logged stands are almost invariably near unlogged burned forests, and some bees captured while foraging in salvage-logged stands may be taking advantage of this landscape complementarity (Dunning et al. 1992). Samples of bee communities in blue vane traps sometimes reflect landscape characteristics more strongly than local foraging conditions (Rhoades et al. 2017), and bee captures in our study may reflect habitat use in many forms, including movement while scouting for forage or nest sites in a heterogeneous landscape (Zitomer et al. 2025).

Ground-nesting species comprised most of our sample, but we found no evidence that bare soil exposure explained patterns in bee community composition. This finding does not appear to be driven by our decision to combine species that nest in existing belowground cavities (i.e., *Bombus* spp.) with those that excavate their own (Fig. 6). Although ground-nesting bee abundances are often correlated with ground cover, bee species have specific and poorly known nest-site preferences that may not be consistently captured by measuring bare ground exposure (Cane 1991; Sardiñas and Kremen 2014; Harmon-Threatt 2020; Antoine and Forrest 2021). Bare soil availability was an important predictor of bee community patterns across a post-fire chronosequence of pine (*Pinus*) stands in Israel (Potts et al. 2005) but may have co-varied with other structural changes between one- and 10-years post-fire. Ground-nesting bees often prefer warmer soil surface temperatures (Wuellner 1999), and lower abundances of ground-nesting species in fire-origin stands could have to do with the cooler microclimates beneath dense vegetation and snags (Fontaine et al. 2010; Thompson et al. 2017).

The higher bee abundance and species richness that we observed in older fire-origin stands compared to older clearcut stands indicate a longer duration of early seral forest conditions in stands regenerating from natural disturbance (Figs. 2 and 4). Similarly, a study in Japan showed that bee diversity and abundance declined more quickly with post-harvest stand age in planted stands than in stands regenerating naturally (Taki et al. 2013). However, drivers of this relationship are not obvious, as we found higher abundances in fire-origin stands across species groups, despite limited floral resources. Shorter statured vegetation in older fire-origin stands may provide a more favorable microclimate and foraging landscape compared to forest harvest, as discussed above. By excluding wind-pollinated species, it is also possible that we underestimated floral resources provided by resprouting broadleaf trees that typically dominated older fire-origin stands along with tall shrubs. Recent evidence from eastern hardwood forests emphasizes the importance of overstory trees for bees (Urban-Mead et al. 2021) and wind-pollinated trees can be a substantial source of pollen for some species (Filipiak 2024). Bees have also been observed foraging on the male flowers of tanoak (Wright and Dodd 2013), one of the most common broadleaf tree species in sampled stands. Future studies should examine pollen loads on foraging bees or in larval provisions across a gradient of broadleaf tree dominance to better understand the role of canopy floral resources in this mixed-evergreen forest landscape.

Our results suggest that greater retention of downed dead wood in harvest units may help support aboveground-nesting solitary bees, a group that was underrepresented in intensively managed clearcut stands. Not only was downed dead wood more positively related to bee abundance responses than standing snags in our data, but downed dead wood retention may also be a more realistic way to improve habitat for cavity-nesting bees than snag retention. In clearcut stands, snags available for retention are often limited, the longevity of created snags is short, and snags pose operational challenges (Arnett et al. 2010; Ritchie et al. 2013). However, efforts to improve habitat conditions for wood-nesting bees in harvested stands should consider that many species rely on pre-existing cavities, including emergence holes of woodboring beetles (Sydenham et al. 2016). Activity of some woodboring beetles (e.g., Buprestidae) is higher following fire than other stand-replacing disturbances (Ray et al. 2019), which may have further influenced nest site availability between fire-origin and clearcut stands. Understanding the value of downed dead wood retention for bee habitat in harvest units would therefore benefit from an experimental approach but could be a tractable step to promote biodiversity in intensively managed forests.

Our findings provide insights for biological conservation and management of temperate forest ecosystems. Our results suggest clearcuts provide habitat for wild bee communities adapted to stand-replacing fire, except for species that nest in dead wood. However, our findings that bee habitat varies among disturbance types, time since disturbance, and nesting guilds also suggest that pollinator conservation in forest landscapes depends on more than maintaining early seral forest area. Emulating natural disturbance in forest management includes mimicking not only the local conditions generated by natural disturbance, as we have evaluated here, but also the variability in frequency and severity patterns of natural disturbance (Hunter 1993; Attiwill 1994; North and Keeton 2008). These characteristics are typically simplified in managed forests compared to natural disturbance regimes (Kuuluvainen et al. 2021), and diverse fire histories (i.e., pyrodiversity) can promote landscape-scale pollinator diversity by increasing species turnover and trait variability (Ponisio et al. 2016; Burkle et al. 2019; Ulyshen et al. 2022). However, the relatively high frequency of stand replacement also generates considerable habitat area for wild bees in intensively managed landscapes, which may compensate for differences in habitat longevity identified in this study. Ecologists are only beginning to understand how spatial and temporal heterogeneity in management might be leveraged to support biodiversity at landscape scales (Duflot et al. 2022; Harris and Betts 2023), and future work should examine the importance of this variability for wild bees.

Appendix 1—Habitat Characteristics

Table 4 Characteristics of early seral forest categories stratified by disturbance type and stand age

Age class	Disturbance type	*n*	Abiotic characteristics (mean ± sd)		
			Stand age (years)	Elevation (m)	Heat Load Index
2–5 yr	Fire	10	3.2 ± 1.2	656 ± 172	0.75 ± 0.17
	Clearcut	10	3.7 ± 0.9	710 ± 410	0.77 ± 0.17
6–9 yr	Fire	10	7.4 ± 1.2	680 ± 137	0.69 ± 0.20
	Clearcut	10	7.3 ± 1.3	689 ± 121	0.72 ± 0.15
	Salvage	11	7.5 ± 1.1	767 ± 177	0.66 ± 0.17
16–20 yr	Fire	9	18.9 ± 1.2	807 ± 442	0.74 ± 0.15
	Clearcut	9	18.2 ± 1.3	767 ± 177	0.75 ± 0.12

Heat load index ranges 0–1, with higher values representing greater topographic heat loads

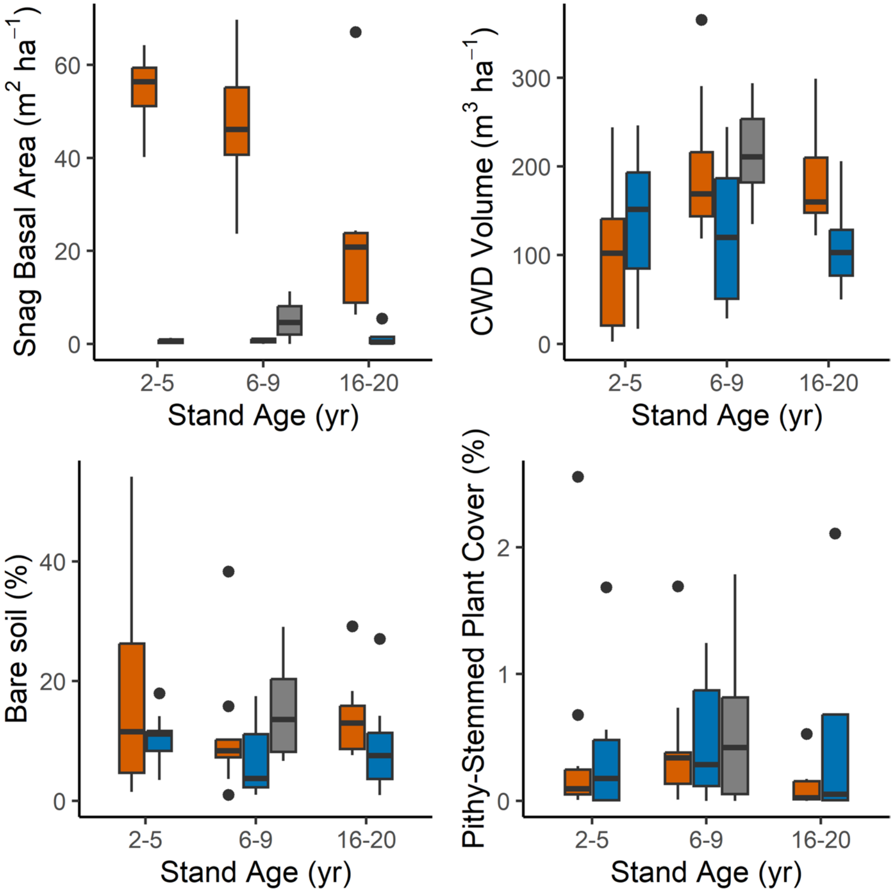
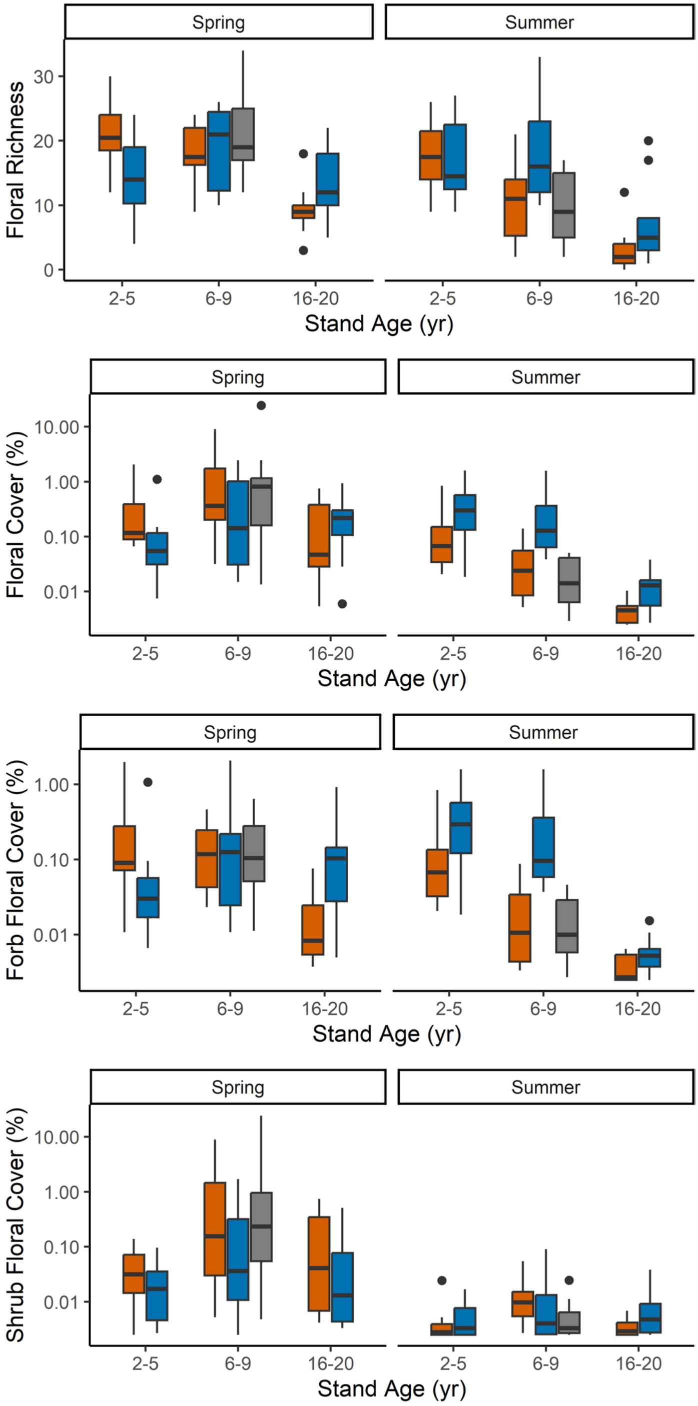


Fig. 7 Distributions of potential nesting substrates for wild bees in early seral forests generated by stand-replacing wildfire (orange), clearcut with intensive forest management (blue), or post-fire salvage logging (gray) in three different stand age classes


Spring
Summer
Floral Richness
30
20
10
0
2-5
6-9
16-20
Stand Age (yr)
Floral Cover (%)
10.00
1.00
0.10
0.01
Forb Floral Cover (%)
Shrub Floral Cover (%)

◀ **Fig. 8** Distributions of floral resource variables in early seral forests generated by stand-replacing wildfire (orange), clearcut with intensive forest management (blue), or post-fire salvage logging (gray) in three different stand age classes. Floral resources were sampled during each round of bee sampling in late spring (late May to early June) or mid-summer (mid-July to early August)

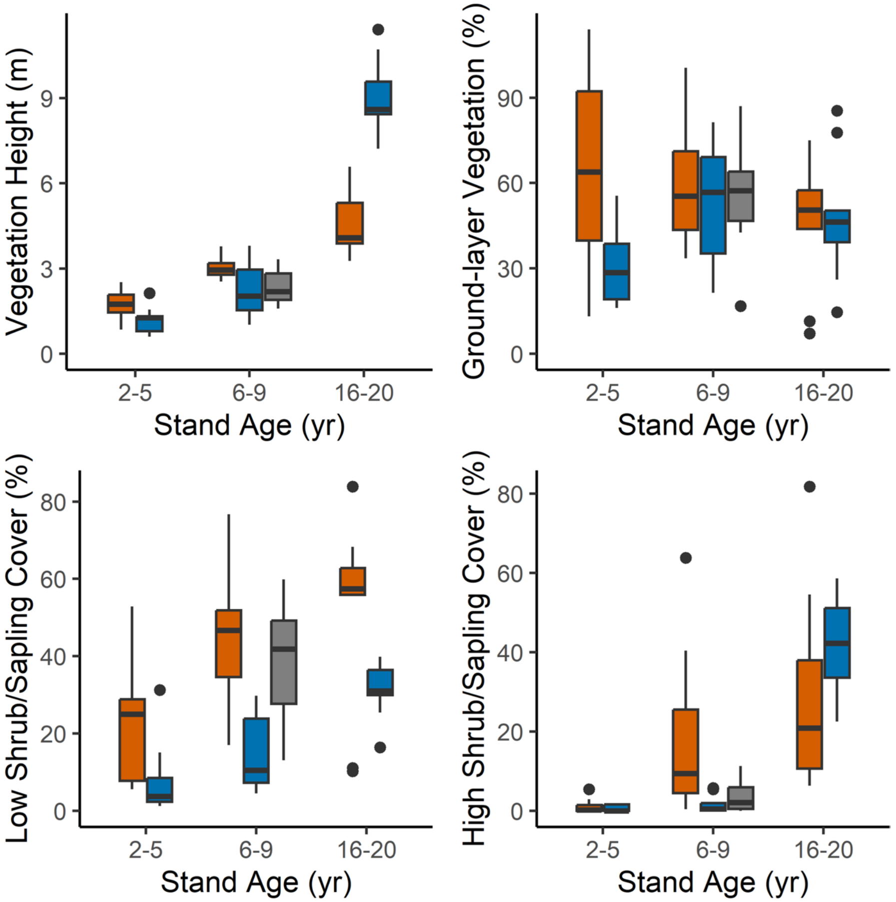


Fig. 9 Distributions of vegetation structure variables in early seral forests generated by stand-replacing wildfire (orange), clearcut with intensive forest management (blue), or post-fire salvage logging (gray) in three different stand age classes. Ground-layer vegetation represents the summed cover of all species below 0.5 m. Low shrub/sapling cover is the summed cover of all woody species, averaged between ground-layer (<0.5 m) and shrub-layer (0.5 – 2 m) strata. High shrub/sapling cover is the summed cover of all woody species in the 2 – 5 m stratum

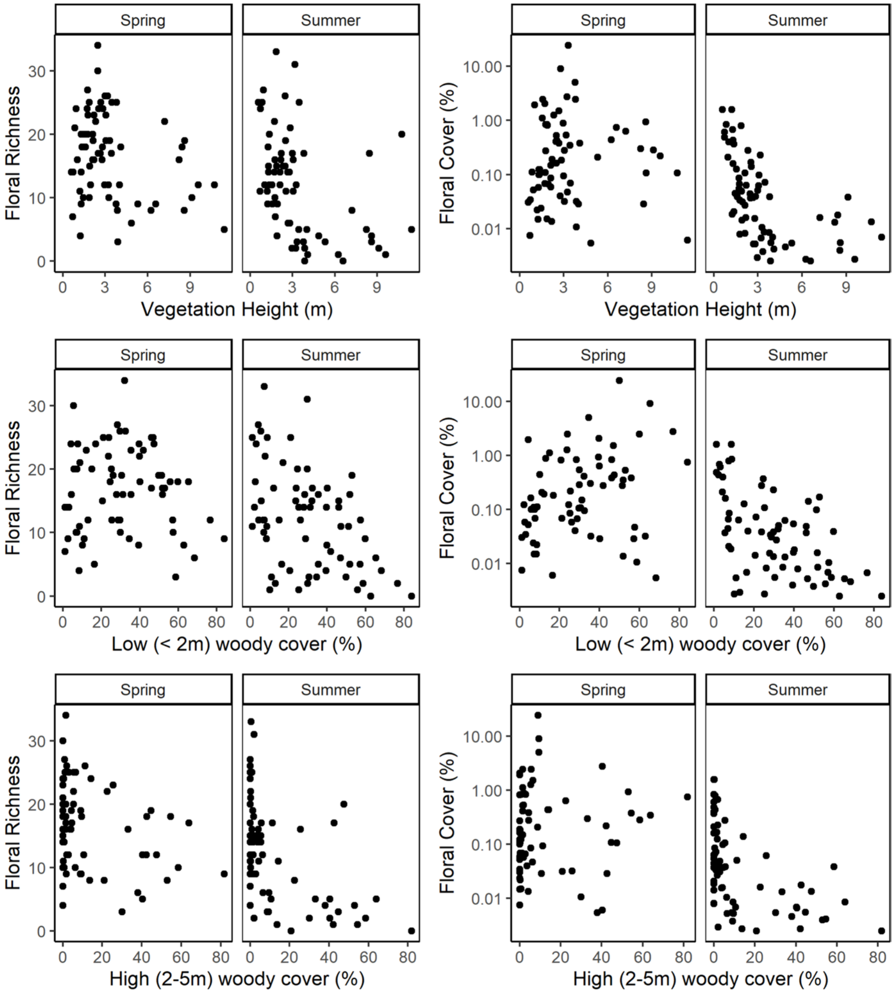


Fig. 10 Scatterplots of floral resource metrics versus vegetation structural characteristics. Note log scale for floral cover

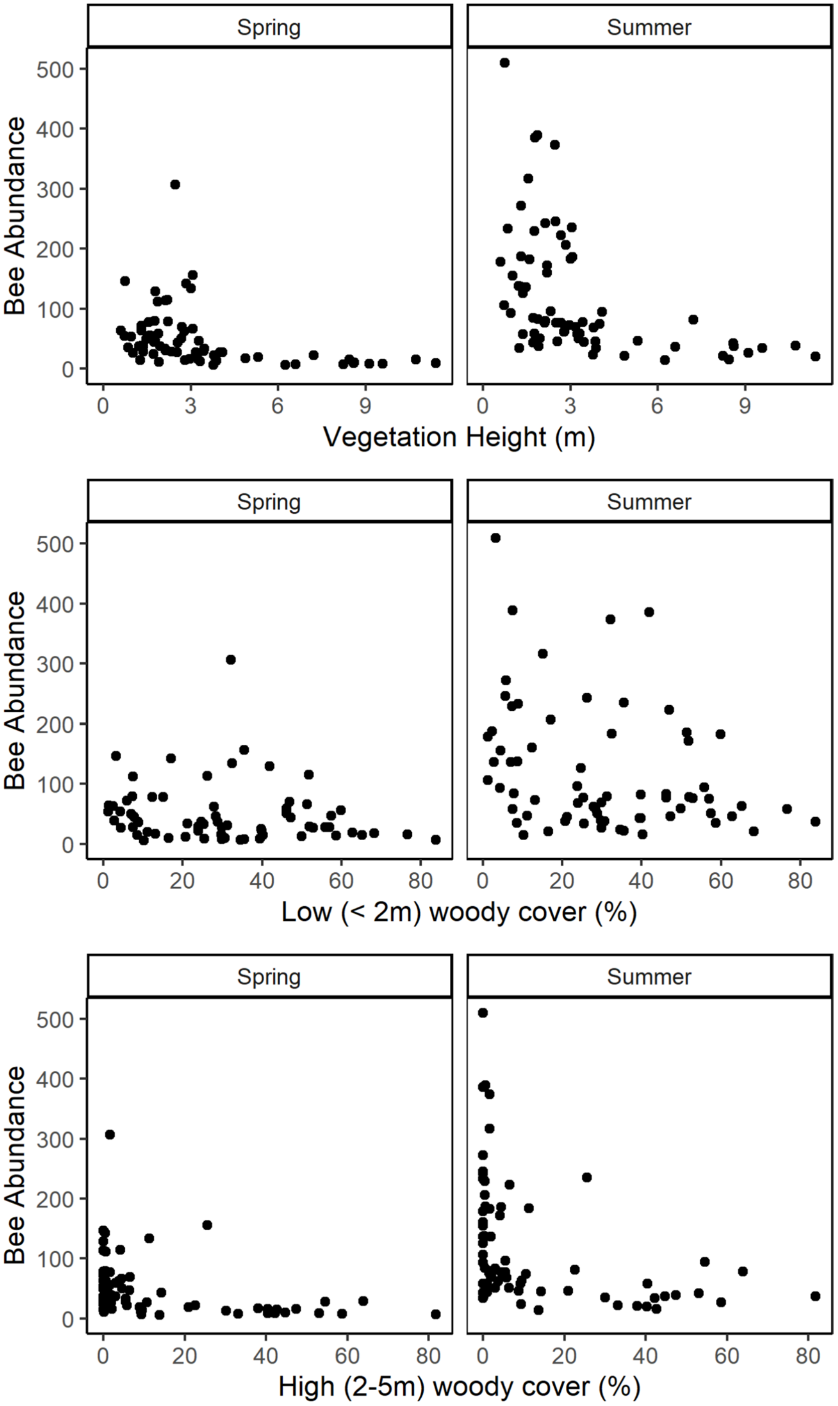


Fig. 11 Scatterplots of bee abundance (posterior median predictions for each stand) versus vegetation structural characteristics

Appendix 2—Bee Taxonomy and Life History Traits

Table 5 Species and morphospecies with at least 10 individuals and occurring in at least 10% of sampled stands. Social species include those with eusocial behavior (e.g., *Bombus* spp.) as well as primitively eusocial species (e.g., *Lasioglossum* spp.)

Species	Family	Sociality	Nest	*n*
Bombus vosnesenskii	Apidae	social [1,2]	below [1]	1456
Melissodes microstictus	Apidae	solitary [3]	below [2]	475
Xylocopa tabaniformis	Apidae	solitary [4]	above [4]	426
Melissodes communis	Apidae	solitary [3]	below [2]	312
Anthophora pacifica	Apidae	solitary [3]	below [2,5]	255
Melissodes rivalis	Apidae	solitary [3]	below [2]	204
Melissodes metenuus	Apidae	solitary [3]	below [2]	154
Bombus caliginosus	Apidae	social [1,2]	below [1]	126
Anthophora bomboides	Apidae	solitary [3]	below [2,6]	102
Apis mellifera	Apidae	social [2]	above [5]	84
Bombus mixtus	Apidae	social [1,2]	above **[1]	68
Bombus melanopygus	Apidae	social [1,2]	above **[1]	57
Melissodes lupinus	Apidae	solitary [3]	below [2]	42
Ceratina tejonensis	Apidae	solitary [2]	above [2]	41
Bombus flavifrons	Apidae	social [1,2]	below [1]	39
Bombus fervidus	Apidae	social [1,2]	above **[1]	27
Ceratina acantha	Apidae	solitary [2]	above [2]	18
Melecta pacifica	Apidae	cleptoparasitic*[2]	below [2,5]	18
Eucera cordleyi	Apidae	solitary [2,3]	below [2,3]	16
Eucera edwardsii	Apidae	solitary [2,3]	below [2,3]	16
Anthophora californica	Apidae	solitary [3]	below [2,5]	14
Hylaeus modestus	Colletidae	solitary [7]	above [7]	12
Halictus tripartitus	Halictidae	social [8]	below [9]	2205
Halictus farinosus	Halictidae	social [10]	below [9]	1268
Lasioglossum occultum	Halictidae	solitary [11]	below [2]	382
Lasioglossum mellipes	Halictidae	solitary [7]	below [2]	283
Lasioglossum nevadense	Halictidae	social [7]	below [2]	166
Lasioglossum marinense	Halictidae	social [11]	below [2]	140
Lasioglossum cordleyi	Halictidae	solitary [11]	below [2]	82
Agapostemon texanus	Halictidae	solitary [3]	below [2,12]	71
Lasioglossum puntatoventre	Halictidae	social [11]	below [2]	62
Lasioglossum egregium	Halictidae	solitary [7]	below [2]	41
Lasioglossum pacificum	Halictidae	solitary [7]	below [2]	39
Lasioglossum incompletum	Halictidae	social [11]	below [2]	30
Lasioglossum (Dialictus) sp. 3	Halictidae	social [11]	below [2]	25
Halictus ligatus	Halictidae	social [13,14]	below [6,9]	23
Lasioglossum nigrum	Halictidae	solitary [11]	below [2]	21
Halictus rubicundus	Halictidae	social [15]	below [2,9]	15
Hoplitis albifrons	Megachilidae	solitary [3,7]	above [7,16,17]	167
Osmia gabrielis	Megachilidae	solitary [3,7]	above [17]	162
Osmia densa	Megachilidae	solitary [3,7]	above [17]	134

Table 5 (continued)

Species	Family	Sociality	Nest	*n*
Osmia bella	Megachilidae	solitary [3,7]	below [17]	70
Megachile montivaga	Megachilidae	solitary [3,7]	below [19,20]	51
Osmia juxta	Megachilidae	solitary [3,7]	above [20]	48
Osmia bucephala	Megachilidae	solitary [3,7]	above [17]	42
Osmia cara	Megachilidae	solitary [3,7]	above [17]	30
Osmia coloradensis	Megachilidae	solitary [3,7]	above [17]	30
Megachile perihirta	Megachilidae	solitary [3,7]	below [19,20]	28
Osmia atrocyanea	Megachilidae	solitary [3,7]	above [17]	17
Osmia montana	Megachilidae	solitary [3,7]	above [17]	17
Osmia malina	Megachilidae	solitary [3,7]	above [17]	15

**Melecta pacifica* is a cleptoparasite on *Anthophora* spp. As the only cleptoparasitic species included in HMSC models, it was combined with the solitary group for modeling purposes. **these *Bombus* species can nest above- or belowground, and were classified as aboveground nesters to capture the potentially greater sensitivity of aboveground-nesting species to time since disturbance (Williams et al. 2010)

Table 6 Species and morphospecies with fewer than 10 individuals, or occurring in less than 10% of stands. These were excluded from HMSC models but included in species richness comparisons

Species	Family	*n*
Andrena hemileuca	Andrenidae	6
Andrena mackieae	Andrenidae	4
Andrena sp. 1	Andrenidae	3
Andrena astragali	Andrenidae	1
Andrena prunorum	Andrenidae	1
Perdita nevadensis	Andrenidae	1
Anthophora terminalis	Apidae	9
Eucera frater lata	Apidae	9
Anthophora urbana	Apidae	8
Bombus flavidus	Apidae	7
Ceratina micheneri	Apidae	7
Triepeolus subalpinus	Apidae	5
Bombus vandykei	Apidae	4
Diadasia bituberculata	Apidae	4
Melecta separata	Apidae	3
Triepeolus paenepectoralis	Apidae	3
Diadasia nigrifrons	Apidae	2
Habropoda depressa	Apidae	2
Diadasia diminuta	Apidae	1
Eucera acerba	Apidae	1
Eucera lunata	Apidae	1
Melissodes clarkiae	Apidae	1
Triepeolus sp. 1	Apidae	1
Hylaeus (Paraprosopis) sp. 1	Colletidae	1
Hylaeus mesillae	Colletidae	1
Lasioglossum titusi	Halictidae	16
Lasioglossum sisymbrii	Halictidae	8
Lasioglossum argemonis	Halictidae	7
Lasioglossum anhypops	Halictidae	6
Agapostemon virescens	Halictidae	3
Lasioglossum inconditum	Halictidae	3
Lasioglossum knereri	Halictidae	3
Lasioglossum (Dialictus) sp. 6	Halictidae	2
Lasioglossum buccale	Halictidae	2
Lasioglossum olympiae	Halictidae	2
Lasioglossum (Dialictus) sp. 2	Halictidae	1
Lasioglossum (Dialictus) sp. 8	Halictidae	1
Lasioglossum (Dialictus) sp. 9	Halictidae	1
Lasioglossum ruidosense	Halictidae	1
Lasioglossum sandhousiellum	Halictidae	1
Lasioglossum sequoiae	Halictidae	1
Lasioglossum zephyrum	Halictidae	1
Lasioglossum zonulum	Halictidae	1
Sphecodes sp. 1	Halictidae	1
Sphecodes sp. 2	Halictidae	1

Table 6 (continued)

Species	Family	*n*
Osmia (Melanosmia) sp. 1	Megachilidae	7
Hoplitis hypocrita	Megachilidae	6
Osmia proxima	Megachilidae	6
Megachile (Megachiloides) sp. 1	Megachilidae	5
Osmia enixa	Megachilidae	5
Dianthidium parvum	Megachilidae	4
Dianthidium subparvum	Megachilidae	4
Osmia albolateralis	Megachilidae	3
Osmia tersula	Megachilidae	3
Protosmia rubifloris	Megachilidae	3
Ashmeadiella cactorum	Megachilidae	2
Dianthidium ulkei	Megachilidae	2
Heriades cressoni	Megachilidae	2
Hoplitis sambuci	Megachilidae	2
Megachile fidelis	Megachilidae	2
Megachile gentilis	Megachilidae	2
Osmia (Melanosmia) sp. 5	Megachilidae	2
Osmia lignaria	Megachilidae	2
Osmia nemoris	Megachilidae	2
Anthidium illustre	Megachilidae	1
Anthidium utahense	Megachilidae	1
Ashmeadiella aridula	Megachilidae	1
Dianthidium heterulkei	Megachilidae	1
Dianthidium plenum	Megachilidae	1
Dianthidium singulare	Megachilidae	1
Hoplitis fulgida	Megachilidae	1
Megachile angelarum	Megachilidae	1
Megachile coquilletti	Megachilidae	1
Megachile melanophaea	Megachilidae	1
Megachile pugnata	Megachilidae	1
Megachile texana	Megachilidae	1
Megachile wheeleri	Megachilidae	1
Osmia (Melanosmia) sp. 3	Megachilidae	1
Osmia (Melanosmia) sp. 4	Megachilidae	1
Osmia bruneri	Megachilidae	1
Osmia inermis	Megachilidae	1
Osmia rawlinsi	Megachilidae	1
Osmia simillima	Megachilidae	1
Osmia tristella	Megachilidae	1
Stelis (Stelis) sp. 1	Megachilidae	1
Stelis (Stelis) sp. 2	Megachilidae	1
Stelis (Stelis) sp. 3	Megachilidae	1

Life History Trait References:

1. Williams, P., R. Thorp, L. Richardson, and S. Colla. 2014. *Bumble bees of North America: an identification guide*. Princeton University Press, Princeton, NJ.
2. Michener, C. D. 2007. *The bees of the world*. Second edition. The Johns Hopkins University Press, Baltimore, MD.
3. Wilson, J. S., and O. M. Carril. 2016. *The bees in your backyard*. Princeton University Press, Princeton, NJ..
4. Nininger, H. H. 1916. Studies in the life histories of two carpenter bees of California: with notes on certain parasites. *Journal of Entomology and Zoology* **8**:158–168.
5. Stephen, W. P., G. E. Bohart, and P. F. Torchio. 1969. *The biology and external morphology of bees with a synopsis of the genera of north-western America*. Oregon State University Press, Corvallis, OR.
6. 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.
7. Danforth, B. N., R. L. Minckley, J. L. Neff, and F. Fawcett. 2019. *The solitary bees: biology, evolution, conservation*. Princeton University Press, Princeton, NJ.
8. Packer, L., A. I. D. Gravel, and G. Lebuhn. 2007. Phenology and social organization of Halictus (Seladonia) tripartitus (Hymenoptera: Halictidae). *Journal of Hymenoptera Research* **16**:281–292.
9. Roberts, R. B. 1973. Bees of northwestern America: Halictus (Hymenoptera: Halictidae). Technical Bulletin 126. Agricultural Experiment Station, Oregon State University, Corvallis, Oregon.
10. Nye, W. P. 1980. Notes on the biology of Halictus (Halictus) farinosus Smith (Hymenoptera: Halictidae). Agriculture Research Results.
11. Danforth, B. N., L. Conway, and S. Ji. 2003. Phylogeny of eusocial Lasioglossum reveals multiple losses of eusociality within a primitively eusocial clade of bees (Hymenoptera: Halictidae). Systematic Biology 52:23–36.
12. Roberts, R. B. 1973. Bees of northwestern America: Agapostemon (Hymenoptera: Halictidae). Technical Bulletin 125. Agricultural Experiment Station, Oregon State University, Corvallis, Oregon.
13. Richards, M. H. 2004. Annual and social variation in foraging effort of the obligately eusocial sweat bee, Halictus ligatus (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society* **77**:484–502.
14. Packer, L., and G. Knerer. 1986. The biology of a subtropical population of Halictus ligatus Say (Hymenoptera: Halictidae): I. Phenology and social organisation. *Behavioral Ecology and Sociobiology* **18**:363–375.
15. Eickwort, G. C., J. M. Eickwort, J. Gordon, and M. A. Eickwort. 1996. Solitary behavior in a high-altitude population of the social sweat bee Halictus rubicundus (Hymenoptera: Halictidae). *Sociobiology* **38**:227–233.
16. Hurd, P. D., and C. D. Michener. 1955. *The Megachiline bees of California (Hymenoptera: Megachilidae).* University of California Press, Berkeley and Los Angeles, CA.

17. Fye, R. E. 1965. Biology of Apoidea taken in trap nests in northwestern Ontario (Hymenoptera). *Canadian Entomologist* **97**:863–877.

18. Cane, J. H., T. Griswold, Parker, and Frank D. 2007. Substrates and materials used for nesting by North American Osmia bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America* **100**:350–358.

19. Sheffield, C. S., C. Ratti, L. Packer, and T. Griswold. 2011. Leafcutter and mason bees of the genus Megachile Latreille (Hymenoptera: Megachilidae). *Canadian Journal of Arthropod Identification* **18**:1–107.

20. Hobbs, G. A., and C. E. Lilly. 1954. Ecology of species of Megachile Latreille in the mixed prairie region of southern Alberta with special reference to pollination of alfalfa. *Ecology* **35**:453–462.

21. 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.

Appendix 3— HMSC Model Fitting and Posterior Predictive Checks

Model Fitting Details

To fit each HMSC model (Hierarchical Modeling of Species Communities; Tikhonov et al. 2020; Ovaskainen and Abrego 2020), we ran five parallel MCMC chains of 15,000,000 (comparative) or 25,000,000 (explanatory) iterations with a thin rate of 5000 (comparative) or 10,000 (explanatory), and discarded the first 5,000,000 as initial burn-in. HMSC does not have built-in functionality for offset terms, so we fixed the parameter estimate for log-transformed sampling effort at unity by using a spike prior (mean = 1, sd = 0.0032), following suggestions from the developers. Otherwise, we used the default priors from HMSC.

Model Fit Evaluation

We evaluated model convergence by visually examining trace plots and based on potential scale reduction factors < 1.1 for each parameter (Gelman and Rubin 1992). We evaluated model fit in terms of explanatory power for each species using pseudo-R^2 (Ovaskainen and Abrego 2020), and conducted posterior predictive checks that evaluated the probability of our observed data under each model (Gelman et al. 2004).

We used posterior predictive checks to evaluate the fit of each model. Specifically, we calculated the probability of the observed data under the model (Gelman et al. 2004) by comparing model predicted bee abundances for each species to those observed in the dataset, within each sampling round. We also compared the total model predicted bees captured across samples in each category to the same values in the data. For each species/category, we calculated the proportion of posterior draws for which the model prediction exceeded the observation (i.e., the Bayesian p-value), with very high or very low values indicating poor model fit.

Bayesian p-values reflecting the model fit for each treatment-age category showed no indication of poor fit (Table 7). Across 53 species included in our model, the mean Bayesian p-value was 0.492 for the comparative model and 0.510 for the explanatory model. The average absolute deviations from 0.5 were 0.083 for the comparative model and 0.083 for the explanatory model. In the comparative model, two species had Bayesian p-values below 0.2 (0.111 and 0.170), and these same species had slightly better fits in the explanatory model (p-values of 0.152, 0.243, and 0.784) (Table 8).

We used Mantel tests to check for spatial autocorrelation and found no evidence of spatially structured residuals for either the comparative model (spring: r = 0.07, $p = 0.22$; summer: r = -0.10, $p = 0.90$) or explanatory model (spring: r = 0.06, $p = 0.23$; summer: r = -0.13, $p = 0.96$).

Table 7 Bayesian *p*-values representing the proportion of posterior draws for which model-predictions for the total number of sampled bees exceed the number of sampled bees in our dataset across stands in each disturbance treatment-age category

Age class	Disturbance	*n*	Bayesian *p*-value	
			Comparative model	Explanatory model
2–5 yr	Fire	10	0.508	0.554
	Clearcut	10	0.587	0.523
6–9 yr	Fire	10	0.493	0.534
	Clearcut	10	0.576	0.604
	Salvage	11	0.557	0.459
16–20 yr	Fire	9	0.524	0.534
	Clearcut	9	0.493	0.661

Table 8 Bayesian p-values for each species from both comparative and explanatory models. P-values represent the proportion of posterior draws for which model-predictions for the total number of individuals of a given species exceeds the number in our dataset across all samples. Species are sorted from most to least abundant in the sample, by family

Species	Bayesian *p*-value		Family	*n*
	Comparative model	Explanatory model		
Bombus vosnesenskii	0.4774	0.4620	Apidae	1456
Melissodes microstictus	0.5847	0.5059	Apidae	475
Xylocopa tabaniformis	0.1111	0.1521	Apidae	426
Melissodes communis	0.4489	0.3939	Apidae	312
Anthophora pacifica	0.5227	0.5910	Apidae	255
Melissodes rivalis	0.1697	0.2427	Apidae	204
Melissodes metenuus	0.2918	0.4234	Apidae	154
Bombus caliginosus	0.5231	0.5601	Apidae	126
Anthophora bomboides	0.6750	0.6256	Apidae	102
Apis mellifera	0.4771	0.5554	Apidae	84
Bombus mixtus	0.5654	0.6268	Apidae	68
Bombus melanopygus	0.4738	0.4083	Apidae	57
Melissodes lupinus	0.5007	0.5641	Apidae	42
Ceratina tejonensis	0.6325	0.6196	Apidae	41
Bombus flavifrons	0.4808	0.4860	Apidae	39
Bombus fervidus	0.5197	0.5135	Apidae	27
Ceratina acantha	0.4123	0.4201	Apidae	18
Melecta pacifica	0.4855	0.4441	Apidae	18
Eucera cordleyi	0.5171	0.4924	Apidae	16
Eucera edwardsii	0.3991	0.4378	Apidae	16
Anthophora californica	0.5405	0.5212	Apidae	14
Hylaeus modestus	0.4664	0.4912	Colletidae	12
Halictus tripartitus	0.5881	0.5429	Halictidae	2205
Halictus farinosus	0.7799	0.7836	Halictidae	1268
Lasioglossum occultum	0.5019	0.6277	Halictidae	382
Lasioglossum mellipes	0.4438	0.5048	Halictidae	283
Lasioglossum nevadense	0.5509	0.5362	Halictidae	166
Lasioglossum marinense	0.3927	0.3848	Halictidae	140
Lasioglossum cordleyi	0.5598	0.5635	Halictidae	82
Agapostemon texanus	0.4706	0.4589	Halictidae	71
Lasioglossum punctatoventre	0.5939	0.6281	Halictidae	62
Lasioglossum egregium	0.6922	0.6146	Halictidae	41
Lasioglossum pacificum	0.3921	0.4158	Halictidae	39
Lasioglossum incompletum	0.4716	0.5276	Halictidae	30
Lasioglossum (Dialictus) sp. 3	0.5424	0.4677	Halictidae	25
Halictus ligatus	0.3409	0.3952	Halictidae	23
Lasioglossum nigrum	0.4492	0.4507	Halictidae	21
Halictus rubicundus	0.4334	0.4754	Halictidae	15
Hoplitis albifrons	0.5492	0.5366	Megachilidae	167

Table 8 (continued)

Species	Bayesian p-value		Family	n
	Comparative model	Explanatory model		
Osmia gabrielis	0.6455	0.7049	Megachilidae	162
Osmia densa	0.7124	0.7410	Megachilidae	134
Osmia bella	0.4090	0.5839	Megachilidae	70
Megachile montivaga	0.4900	0.4753	Megachilidae	51
Osmia juxta	0.5404	0.6103	Megachilidae	48
Osmia bucephala	0.5685	0.6299	Megachilidae	42
Osmia cara	0.4583	0.5519	Megachilidae	30
Osmia coloradensis	0.4299	0.4366	Megachilidae	30
Megachile perihirta	0.4288	0.4342	Megachilidae	28
Osmia atrocyanea	0.4558	0.4751	Megachilidae	17
Osmia montana	0.5047	0.4879	Megachilidae	17
Osmia malina	0.4422	0.4506	Megachilidae	15

Appendix 4 — Bee Composition and Abundance Comparisons when Excluding *Bombus* spp. that Nest Above- or Belowground

Among the species in our original abundance model, three species of *Bombus* can nest above- or belowground (*B. fervidus*, *B. melanopygus*, and *B. mixtus*). We chose to categorize these species as aboveground nesters in our original analysis because aboveground nesting may make species more sensitive to time since disturbance (Williams et al. 2010). Moreover, *B. fervidus* may be nest aboveground more often than belowground (Williams et al. 2014). However, to ensure that this decision did not meaningfully affect our conclusions, we replicated our analysis of composition and abundance comparisons without these three species, which together represented 1.6% of all individual bees and 64.4% of social aboveground-nesting bees in our original analysis. The only remaining social aboveground-nesting species is *Apis mellifera*, the European honeybee. Nonetheless, excluding *Bombus* spp. did not meaningfully influence any comparisons between disturbance types, including estimates of mean relative abundance of the social aboveground-nesting guild (Table 9, Figure 13). The following paragraphs present differences in the narrative results from our manuscript, with original values crossed out (e.g., ~~123~~) alongside values from the additional model run that excludes the three *Bombus* spp.

Composition and Abundance Comparisons

Comparisons of bee abundance between disturbance types varied across stand age classes (Figure 12a). Predicted bee abundance was ~~124%~~ 127% higher (90% CI: ~~36, 255%~~ 40, 260%) for young clearcut stands and ~~74%~~ 70% higher for intermediate clearcut stands (90% CI: ~~16, 154%~~ 11, 153%) than fire-origin stands of the same age. Predicted bee abundance for salvage-logged stands, sampled only in the intermediate age class, was ~~3×~~ 3.2 × higher than for intermediate fire-origin stands (90% CI: ~~2.1, 4.7×~~ 2.1, 4.8 ×). Bee abundance declined with age of clearcut stands, but we found little evidence for this pattern in fire-origin stands (Figure 12a). Abundance was ~~83%~~ 84% lower (90% CI: ~~73, 90%~~ 73, 90%) in advanced than young clearcut stands, whereas any evidence for a decline in fire-origin stands was weak (90% CI: ~~114% decline, 20% increase~~ 108% decline, 20% increase). Consequently, estimates of bee abundance were ~~52%~~ 52% lower (90% CI: ~~21, 71%~~ 21, 72%) for advanced clearcut stands than advanced fire-origin stands.

Patterns in mean relative abundance across bee species were similar to those for overall bee abundance (Figure 12b). Mean relative abundance was ~~93%~~ 94% higher (90% CI: ~~39, 165%~~ 40, 170%) for clearcut than for fire-origin stands in the young age class and ~~38%~~ 33% higher (90% CI: ~~4, 83%~~ -2, 79%) in the intermediate age class, but ~~63%~~ 66% lower (90% CI: ~~47, 75%~~ 50, 77%) in the advanced age class. For salvage-logged stands, mean relative abundance was ~~54%~~ 50% higher (90% CI: ~~16, 107%~~ 11, 103%) than for fire-origin stands in the intermediate age class.

Comparisons of guild-level responses showed clear differences in bee community composition among disturbance × stand age combinations (Figure 13). Responses of solitary aboveground-nesting species diverged from those of the broader bee community, with higher predicted mean relative abundance for fire-origin than clearcut stands, especially in older age classes. Estimates for mean relative abundance of solitary aboveground-nesting species were ~~36%~~ 35% lower (90% CI: ~~65% lower, 16% higher~~ 64% lower, 19% higher) for clearcut than fire-origin stands in the young age class, ~~54%~~ 56% lower (90% CI: ~~24, 72%~~ 26, 74%) in the intermediate age class, and ~~83%~~ 83% lower (90% CI: ~~69, 91%~~ 69, 91%) in the advanced age class. For the remaining guilds, comparisons between clearcut and fire-origin stands generally followed broader community-level patterns (Figure 12). Bee composition in salvage-logged stands was less distinct from fire-origin stands. For example, we found no evidence for the negative response of the solitary aboveground-nesting guild (90% CI: ~~1%~~ 5% lower, ~~129%~~ 123% higher mean relative abundance in salvage-logged stands) that we observed for clearcut stands in the intermediate age class, or for the positive response of the solitary belowground-nesting guild (90% CI: ~~13%~~ 11% lower, ~~90%~~ 95% higher).

Table 9 Comparison of mean relative abundance estimates for social aboveground nesting species between original analysis and a secondary analysis excluding three species of *Bombus*. Original analysis includes four species: *Apis mellifera*, *B. flavifrons*, *B. melanopygus*, and *B. mixtus*

		Mean relative abundance (90% CI)	
Disturbance	Age class	Original analysis	Excluding *Bombus* spp.
Fire	Young	0.102 (0.066, 0.150)	0.059 (0.023, 0.131)
	Intermediate	0.101 (0.071, 0.139)	0.100 (0.054, 0.172)
	Advanced	0.065 (0.037, 0.108)	0.032 (0.009, 0.092)
Clearcut	Young	0.283 (0.209, 0.366)	0.353 (0.206, 0.521)
	Intermediate	0.203 (0.146, 0.273)	0.273 (0.161, 0.422)
	Advanced	0.052 (0.027, 0.092)	0.023 (0.006, 0.076)
Salvage	Intermediate	0.178 (0.125, 0.245)	0.115 (0.052, 0.229)

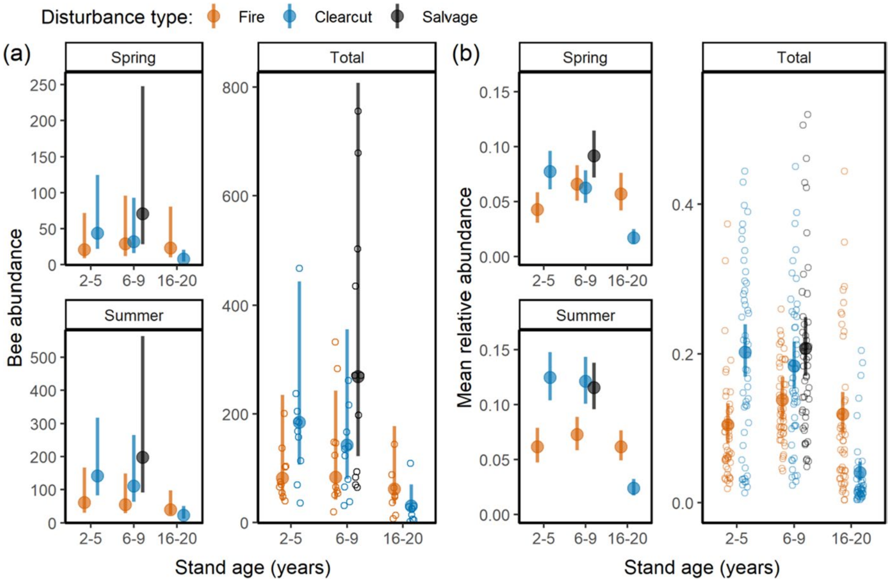


Fig. 12 Counterpart to Fig. 2 in the main manuscript, excluding *Bombus fervidus*, *B. melanopygus*, and *B. mixtus* from the social, aboveground-nesting group

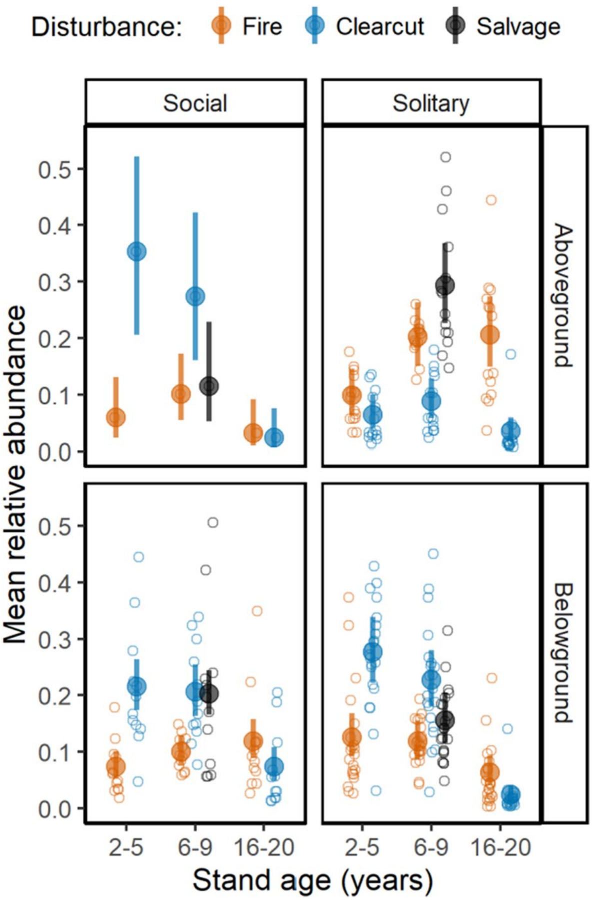


Fig. 13 Counterpart to Fig. 3 in the main manuscript, excluding *Bombus fervidus*, *B. melanopygus*, and *B. mixtus* from the social, aboveground-nesting group

Appendix 5— Bee Responses to Bare Ground and Pithy-Stemmed Plant Cover

Bee abundance responses to floral richness, floral cover, snag basal area, and downed deadwood volume are described in the main text. We also modeled bee responses to percent cover of pithy stemmed plants and bare ground as components of nesting habitat for some species. Total bee abundance was positively related to pithy-stemmed plant cover, which was primarily comprised of *Rubus leucodermis*, with a predicted 7.8-fold increase in abundance (90% CI: 3.7-, 19.3-fold) over the observed gradient of 0 – 2.5% cover (Figure 14a). However, this response varied little among functional groups with different life history strategies, suggesting it was not specific to nesting requirements. Fourth-corner coefficients did not vary among guilds (Fig. 5b), and solitary aboveground-nesting bee abundance was predicted to increase similarly to the broader community (8.5-fold; 90% CI: 3.3-, 24.8-fold). However, species known to nest in stems had some of the highest coefficient estimates (Fig. 5a, *Hoplitis albifrons* and *Ceratina tejonensis*).

Similarly, there was no indication that abundance relationships with bare ground were specific to species that nest in soil. Total bee abundance showed a weak positive relationship with bare ground, approximately doubling (111% increase) across the gradient of 1 to 54% bare ground but with considerable uncertainty (90% CI: –2, 369%; Figure 14c). The predicted increase in abundance specific to belowground-nesting species was similar but even slightly weaker (91% increase; 90% CI: –19, 473%; Figure 14d).

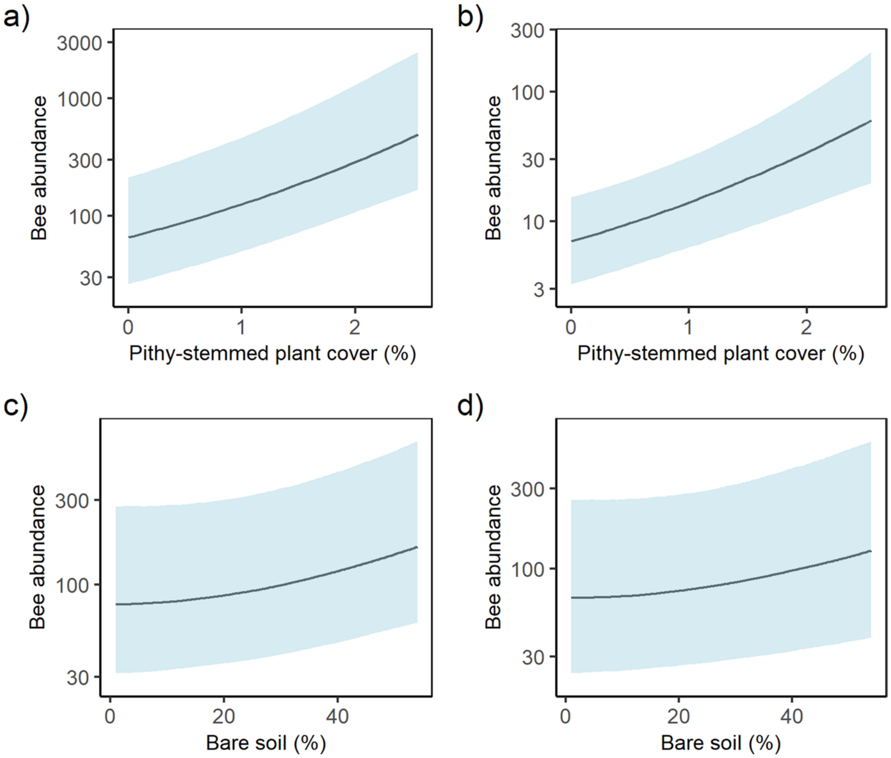


Fig. 14 Predicted bee abundance across gradients in pithy-stemmed plant cover (**a**, **b**) or bare soil (**c**, **d**). Responses are for the entire bee community (**a**, **c**), solitary aboveground-nesting species (**b**), or belowground-nesting species (**d**). Lines represent posterior median predictions and bands represent 90% credible intervals around predictions

Acknowledgements Chinook Forest Management, Manulife Investment Management, Roseburg Forest Products, and Weyerhaeuser Company provided access to sampling sites on their private land, and managers with the USDA Forest Service and USDI Bureau of Land Management facilitated access to field sites on federal land. Comments from D. Miller and D. Bell improved the clarity of the manuscript. We are grateful for the precision and persistence of field technicians who collected data: K. Burton, K. Wright, R. Rubenthaler, A. Moss, H. Payne, C. Lee, C. Kildall, J. Pow, L. Bradley, M. Sullivan, E. Tate, and S. Greenler.

Author contributions GSF—Methodology, Investigation, Data Curation, Formal Analysis, Writing – Original Draft, Visualization, Project Administration. JWR—Conceptualization, Methodology, Funding Acquisition, and Writing – Review and Editing. JV—Conceptualization, Methodology, Funding Acquisition, and Writing – Review and Editing. LRB—Investigation, Data Curation, Writing – Review and Editing. MGB—Conceptualization, Methodology, Funding Acquisition, and Writing – Review and Editing. AJK—Conceptualization, Methodology, Funding Acquisition, and Writing – Review and Editing. MES—Conceptualization, Methodology, Funding Acquisition, and Writing – Review and Editing. MAK—Conceptualization, Methodology, Funding Acquisition, Project Administration, Supervision, Resources, and Writing – Review and Editing.

Funding This work was funded by the Fish and Wildlife Habitat in Managed Forests Research Program through the Oregon Forest Research Laboratory and by the National Council for Stream and Air Improvement, Inc. MGB's work on the manuscript was supported by AFRI-2022–67019-37130.

Data availability Data and code (Frank et al. 2025) are available at Open Science Framework: https://doi.org/10.17605/OSF.IO/2FCU5. We accessioned bee voucher specimens in the Oregon State Arthropod Collection (accession record OSAC_AC_2024_02_14-001).

Declarations

Competing interests Author AJK was employed by Weyerhaeuser, one of the landowners in this study, at the time the research was conducted. Neither the landowners nor the companies that supported this work influenced the study design, data analysis, interpretation, or decision to publish.

References

Antoine, C. M., and J. R. K. Forrest. 2021. Nesting habitat of ground-nesting bees: A review. *Ecological Entomology* 46:143–59. https://doi.org/10.1111/een.12986.

Arnett, E. B., A. J. Kroll, and S. D. Duke. 2010. Avian foraging and nesting use of created snags in intensively-managed forests of western Oregon, USA. *Forest Ecology and Management* 260:1773–9. https://doi.org/10.1016/j.foreco.2010.08.021.

Attiwill, P. M. 1994. The disturbance of forest ecosystems: The ecological basis for conservative management. *Forest Ecology and Management* 63:247–300. https://doi.org/10.1016/0378-1127(94)90114-7.

Bogusch, P., L. Blažej, M. Trýzna, and P. Heneberg. 2015. Forgotten role of fires in Central European forests: Critical importance of early post-fire successional stages for bees and wasps

(Hymenoptera: Aculeata). *European Journal of Forest Research* 134:153–66. https://doi.org/10.1007/s10342-014-0840-4.

Brandeis, C., Taylor, M., Abt, K.L., Alderman, D., and U. Buehlmann. 2021. Status and trends for the U.S. forest products sector: A technical document supporting the Forest Service 2020 RPA Assessment. General Technical Report SRS-258. USDA Forest Service, Southern Research Station, Asheville, NC. https://doi.org/10.2737/SRS-GTR-258

Brown, A. M., Warton, D. I., Andrew, N. R., Binns, M., Cassis, G., and H. Gibb. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. *Methods in Ecology and Evolution* 5:344–52. https://doi.org/10.1111/2041-210X.12163.

Brown, M. L., C. D. Canham, L. Murphy, and T. M. Donovan. 2018. Timber harvest as the predominant disturbance regime in northeastern U.S. forests: Effects of harvest intensification. *Ecosphere* 9:e02062. https://doi.org/10.1002/ecs2.2062.

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* 7:1–14. https://doi.org/10.3389/fevo.2019.00252.

Cane, J. H. 1991. Soils of ground-nesting bees (Hymenoptera: Apoidea): Texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society* 64:406–13.

Cane, J. H., T. Griswold, and F. D. Parker. 2007. Substrates and materials used for nesting by North American *Osmia* bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America* 100:350–58. https://doi.org/10.1603/0013-8746(2007)100[350:SAMUFN]2.0.CO;2.

Carbone, L. M., J. Tavella, J. G. Pausas, and R. Aguilar. 2019. A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography* 28:1487–98. https://doi.org/10.1111/geb.12939.

Carrié, R., J. Ekroos, and H. G. Smith. 2018. Organic farming supports spatiotemporal stability in species richness of bumblebees and butterflies. *Biological Conservation* 227:48–55. https://doi.org/10.1016/j.biocon.2018.08.022.

Chase, M. H., J. M. Fraterrigo, B. Charles, and A. Harmon-Threatt. 2023. Wild bee response to forest management varies seasonally and is mediated by resource availability. *Forest Ecology and Management* 548:121426. https://doi.org/10.1016/j.foreco.2023.121426.

Collins, B. M., and G. B. Roller. 2013. Early forest dynamics in stand-replacing fire patches in the northern Sierra Nevada, California, USA. *Landscape Ecology* 28:1801–13. https://doi.org/10.1007/s10980-013-9923-8.

Corbet, S. A., M. Fussell, R. Ake, A. Fraser, C. Gunson, A. Savage, and K. Smith. 1993. Temperature and the pollinating activity of social bees. *Ecological Entomology* 18:17–30. https://doi.org/10.1111/j.1365-2311.1993.tb01075.x.

Crall, J. D., S. Ravi, A. M. Mountcastle, and S. A. Combes. 2015. Bumblebee flight performance in cluttered environments: Effects of obstacle orientation, body size and acceleration. *Journal of Experimental Biology* 218:2728–37. https://doi.org/10.1242/jeb.121293.

Danforth, B. N., R. L. Minckley, J. L. Neff, and F. Fawcett. 2019. *The solitary bees: biology, evolution, conservation*. Princeton, NJ: Princeton University Press. https://doi.org/10.2307/j.ctvd1c929.

DellaSala, D. A., C. T. Hanson, R. L. Hutto, D. C. Odion, and M. L. Bond. 2014. Complex early seral forests of the Sierra Nevada: What are they and how can they be managed for ecological integrity? *Natural Areas Journal* 34:310–24. https://doi.org/10.3375/043.034.0317.

Donato, D. C., J. L. Campbell, and J. F. Franklin. 2012. Multiple successional pathways and precocity in forest development: can some forests be born complex? *Journal of Vegetation Science* 23:576–84. https://doi.org/10.1111/j.1654-1103.2011.01362.x.

Duflot, R., L. Fahrig, and M. Mönkkönen. 2022. Management diversity begets biodiversity in production forest landscapes. *Biological Conservation* 268:109514. https://doi.org/10.1016/j.biocon.2022.109514.

Dunning, J. B., B. J. Danielson, H. R. Pulliam, and I. Ecology. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65:169–75. https://doi.org/10.2307/3544901.

Filipiak, Z. M., B. Denisow, E. Stawiarz, and M. Filipiak. 2022. Unravelling the dependence of a wild bee on floral diversity and composition using a feeding experiment. *Science of the Total Environment* 820:153326. https://doi.org/10.1016/j.scitotenv.2022.153326.

Filipiak, M. 2024. Plants other than animal-pollinated herbs provide wild bees with vital nutrients. *Global Ecology and Conservation* 52. https://doi.org/10.1016/j.gecco.2024.e02984.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2006. Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology* 4. https://doi.org/10.1371/journal.pbio.0040001.

Fontaine, J. B., D. C. Donato, J. L. Campbell, J. G. Martin, and B. E. Law. 2010. Effects of post-fire logging on forest surface air temperatures in the Siskiyou mountains, Oregon, USA. *Forestry* 83:477–82. https://doi.org/10.1093/forestry/cpq030.

Frank, G. S. 2023. Biodiversity responses in early seral forests of the Klamath-Siskiyou: Comparisons with birds, bees, and ground beetles among post-fire, salvage-logging, and intensive forest management environments. Dissertation, Oregon State University, Corvallis, Oregon.

Frank, G. S., L. R. Best, J. W. Rivers, M. G. Betts, J. Verschuyl, A. J. Kroll, M. E. Swanson, and M. A. Krawchuk. 2024. Occurrence records and taxonomic voucher specimens for study of wild bee communities in early seral forests generated by wildfire, post-fire salvage logging, or intensive forest management in southwest Oregon. *Catalog of the Oregon State Arthropod Collection* 8:9–14. https://doi.org/10.5399/osu/cat_osac.8.1.6082.

Frank, G. S., Rivers, J. W., Verschuyl, J., Best, L. R., Betts, M. G., Swanson, M. E., and M. A. Krawchuk. 2025. Data and code for: Comparison of early seral forest bee communities following clearcutting or wildfire depends on stand age and nesting guild. *Open Science Framework*. https://doi.org/10.17605/OSF.IO/2FCU5.

Galbraith, S. M., J. H. Cane, A. R. Moldenke, and J. W. Rivers. 2019a. Wild bee diversity increases with local fire severity in a fire-prone landscape. *Ecosphere* 10:e02668. https://doi.org/10.1002/ecs2.2668.

Galbraith, S. M., J. H. Cane, A. R. Moldenke, and J. W. Rivers. 2019b. Salvage logging reduces wild bee diversity, but not abundance, in severely burned mixed-conifer forest. *Forest Ecology and Management* 453:117622. https://doi.org/10.1016/j.foreco.2019.117622.

Galbraith, S. M., Cane, J. H., and J. W. Rivers. 2021. Wildfire severity influences offspring sex ratio in a native solitary bee. *Oecologia* 195:65–75. https://doi.org/10.1007/s00442-020-04809-3.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. *Statistical Science* 7:457–72. https://doi.org/10.1214/ss/1177011136.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. *Bayesian data analysis*. Boca Raton, FL: Chapman & Hall / CRC.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Environmental Letters* 4:379–91. https://doi.org/10.1046/j.1461-0248.2001.00230.x.

Goulson, D., M. E. Hanley, B. Darvill, J. S. Ellis, and M. E. Knight. 2005. Causes of rarity in bumblebees. *Biological Conservation* 122:1–8. https://doi.org/10.1016/j.biocon.2004.06.017.

Halofsky, J. E., D. L. Peterson, and B. J. Harvey. 2020. Changing wildfire, changing forests: The effects of climate change on fire regimes and vegetation in the Pacific Northwest, USA. *Fire Ecology* 16:4. https://doi.org/10.1186/s42408-019-0062-8.

Hanula, J. L., M. D. Ulyshen, and S. Horn. 2016. Conserving pollinators in North American forests: A review. *Natural Areas Journal* 36:427–39. https://doi.org/10.3375/043.036.0409.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr., and K. W. Cummins. 1986. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research* 15:133–302.

Harmon-Threatt, A. 2020. Influence of nesting characteristics on health of wild bee communities. *Annual Review of Entomology* 65:39–56. https://doi.org/10.1146/annurev-ento-011019-024955.

Harris, S. H., and M. G. Betts. 2023. Selecting among land sparing, sharing and Triad in a temperate rainforest depends on biodiversity and timber production targets. *Journal of Applied Ecology* 60:737–50. https://doi.org/10.1111/1365-2664.14385.

Heil, L. J., and L. A. Burkle. 2018. Recent post-wildfire salvage logging benefits local and landscape floral and bee communities. *Forest Ecology and Management* 424:267–75. https://doi.org/10.1016/j.foreco.2018.05.009.

Hemberger, J., G. Witynski, and C. Gratton. 2022. Floral resource continuity boosts bumble bee colony performance relative to variable floral resources. *Ecological Entomology* 47:703–12. https://doi.org/10.1111/een.13154.

Hunter, M. L. 1993. Natural fire regimes as spatial models for managing boreal forests. *Biological Conservation* 65:115–20. https://doi.org/10.1016/0006-3207(93)90440-C.

Joshi, N. K., T. Leslie, E. G. Rajotte, M. A. Kammerer, M. Otieno, and D. J. Biddinger. 2015. Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. *Annals of the Entomological Society of America* 108:785–99. https://doi.org/10.1093/aesa/sav057.

Kaluza, B. F., H. M. Wallace, T. A. Heard, V. Minden, A. Klein, and S. D. Leonhardt. 2018. Social bees are fitter in more biodiverse environments. *Scientific Reports* 8:1–10. https://doi.org/10.1038/s41598-018-30126-0.

Kopec, K., and L. A. Burd. 2017. Pollinators in peril: a systematic status review of North American and Hawaiian native bees. Center for Biological Diversity, Tucson, AZ.

Kormann, U. G., T. D. Stokely, J. Verschuyl, A. J. Kroll, S. Harris, D. Maguire, D. Mainwaring, J. W. Rivers, and M. G. Betts. 2021. Reconciling biodiversity with timber production and revenue via an intensive forest management experiment. *Ecological Applications* 31:1–13. https://doi.org/10.1002/eap.2441.

Krahner, A., A. C. Dietzsch, T. Jutte, J. Pistorius, and J. Everaars. 2024. Standardising bee sampling: A systematic review of pan trapping and associated floral surveys. *Ecology and Evolution* 14:e11157. https://doi.org/10.1002/ece3.11157.

Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, D. P. Vázquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A. M. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters* 10:299–314. https://doi.org/10.1111/j.1461-0248.2007.01018.x.

Kroll, A. J., A. Springford, and J. Verschuyl. 2020. Conservation and production responses vary by disturbance intensity in a long-term forest management experiment. *Ecological Applications* 30:e02148. https://doi.org/10.1002/eap.2148.

Kudo, G., T. Y. Ida, and T. Tani. 2008. Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. *Ecology* 89:321–31. https://doi.org/10.1890/06-2131.1.

Kuuluvainen, T., P. Angelstam, L. Frelich, K. Jõgiste, M. Koivula, Y. Kubota, B. Lafleur, and E. Macdonald. 2021. Natural disturbance-based forest management: Moving beyond retention and continuous-cover forestry. *Frontiers in Forests and Global Change* 4:629020. https://doi.org/10.3389/ffgc.2021.629020.

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* 17:308–20. https://doi.org/10.1016/j.baae.2016.02.001.

Lindenmayer, D., P. J. Burton, and J. F. Franklin. 2008. *Salvage logging and its ecological consequences*. Washington, D.C.: Island Press.

Mathis, C. L., D. J. McNeil, M. R. Lee, C. M. Grozinger, D. I. King, C. R. V. Otto, and J. L. Larkin. 2021. Pollinator communities vary with vegetation structure and time since management within regenerating timber harvests of the Central Appalachian Mountains. *Forest Ecology and Management* 496:119373. https://doi.org/10.1016/j.foreco.2021.119373.

Mathis, C. L., D. J. McNeil, M. Kammerer, J. L. Larkin, and M. J. Skvarla. 2024. Distance models reveal biases associated with passive trapping methods for measuring wild bee abundance. *Frontiers in Ecology and Evolution* 12:1380622. https://doi.org/10.3389/fevo.2024.1380622.

McCravy, K. W., R. K. Geroff, and J. Gibbs. 2019. Bee (Hymenoptera: Apoidea: Anthophila) functional traits in relation to sampling methodology in a restored tallgrass prairie. *Florida Entomologist* 102:134–40. https://doi.org/10.1653/024.102.0122.

Mola, J. M., and N. M. Williams. 2018. Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers. *Ecosphere* 9:e02056. https://doi.org/10.1002/ecs2.2056.

Morandin, L. A., and M. L. Winston. 2005. Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological Applications* 15:871–81. https://doi.org/10.1890/03-5271.

Neff, J. L., and B. B. Simpson. 1993. Bees, pollination systems and plant diversity. Pages 143–168 *in* J. LaSalle and I. D. Gauld, editors. Hymenoptera and Biodiversity. C. A. B. International, Wallingford, Oxon, UK.

North, M. P., and W. S. Keeton. 2008. Emulating natural disturbance regimes: An emerging approach for sustainable forest management. In *Patterns and processes in forest landscapes: Multiple use and* *sustainable management*, ed. R. Lafortezza, G. Sanesi, J. Chen, and T. Crow, 341–372. Netherlands, Dordrecht: Springer. https://doi.org/10.1007/978-1-4020-8504-8_19.

Ogilvie, J. E., and J. R. Forrest. 2017. Interactions between bee foraging and floral resource phenology shape bee populations and communities. *Current Opinion in Insect Science* 21:75–82. https://doi.org/10.1016/j.cois.2017.05.015.

Oksanen, J., G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre. and P. R. Minchin, R. B. O'Hara, P. Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. O. Hill, L. Lahti, D. McGlinn, M.-H. Ouellette, E. Ribeiro Cunha, T. Smith, A. Stier, C. J. F. Ter Braak, and J. Weedon. 2022. vegan: community ecology package. R package version 2.6–4. https://CRAN.R-project.org/package=vegan.

Ovaskainen, O., and N. Abrego. 2020. *Joint species distribution modelling: With applications in R*, 1st ed. Cambridge, UK: Cambridge University Press.

Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin, and N. Abrego. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters* 20:561–76. https://doi.org/10.1111/ele.12757.

Ponisio, L. C., K. Wilkin, L. K. M'Gonigle, K. Kulhanek, L. Cook, R. Thorp, T. Griswold, and C. Kremen. 2016. Pyrodiversity begets plant-pollinator community diversity. *Global Change Biology* 22:1794–808. https://doi.org/10.1111/gcb.13236.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, C. O'Toole, S. Roberts, and P. Willmer. 2003a. Response of plant-pollinator communities to fire: Changes in diversity, abundance and floral reward structure. *Oikos* 101:103–12. https://doi.org/10.1034/j.1600-0706.2003.12186.x.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003b. Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology* 84:2628–42. https://doi.org/10.1890/02-0136.

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. https://doi.org/10.1111/j.0307-6946.2005.00662.x.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. *Trends in Ecology and Evolution* 25:345–53. https://doi.org/10.1016/j.tree.2010.01.007.

R Core Team. 2023. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ray, C., D. R. Cluck, R. L. Wilkerson, R. B. Siegel, A. M. White, G. L. Tarbill, S. C. Sawyer, and C. A. Howell. 2019. Patterns of woodboring beetle activity following fires and bark beetle outbreaks in montane forests of California, USA. *Fire Ecology* 15:21. https://doi.org/10.1186/s42408-019-0040-1.

Reilly, M. J., C. J. Dunn, G. W. Meigs, T. A. Spies, R. E. Kennedy, J. D. Bailey, and K. Briggs. 2017. Contemporary patterns of fire extent and severity in forests of the Pacific Northwest, USA (1985–2010). *Ecosphere* 8:e01695. https://doi.org/10.1002/ecs2.1695.

Rhoades, P. R., T. Griswold, L. Waits, N. A. Bosque-Pérez, C. M. Kennedy, and S. D. Eigenbrode. 2017. Sampling technique affects detection of habitat factors influencing wild bee communities. *Journal of Insect Conservation* 21:703–14.

Rhoades, P. R., T. S. Davis, W. T. Tinkham, and C. M. Hoffman. 2018. Effects of seasonality, forest structure, and understory plant richness on bee community assemblage in a southern Rocky Mountain mixed conifer forest. *Annals of the Entomological Society of America* 111:278–84.

Ritchie, M. W., E. E. Knapp, and C. N. Skinner. 2013. Snag longevity and surface fuel accumulation following post-fire logging in a ponderosa pine dominated forest. *Forest Ecology and Management* 287:113–22. https://doi.org/10.1016/j.foreco.2012.09.001.

Rivers, J. W., and M. G. Betts. 2021. Postharvest bee diversity is high but declines rapidly with stand age in regenerating Douglas-fir forest. *Forest Science* 67:275–85. https://doi.org/10.1093/forsci/fxab002.

Rivers, J. W., S. M. Galbraith, J. H. Cane, C. B. Schultz, M. D. Ulyshen, and U.G. Kormann. 2018a. A review of research needs for pollinators in managed conifer forests. *Journal of Forestry* 116:563–72. https://doi.org/10.1093/jofore/fvy052.

Rivers, J. W., C. L. Mathis, A. R. Moldenke, and M. G. Betts. 2018b. Wild bee diversity is enhanced by experimental removal of timber harvest residue within intensively managed conifer forest. *Global Change Biology - Bioenergy* 10:766–81. https://doi.org/10.1111/gcbb.12531.

Roberts, H. P., D. I. King, and J. Milam. 2017. Factors affecting bee communities in forest openings and adjacent mature forest. *Forest Ecology and Management* 394:111–22. https://doi.org/10.1016/j.foreco.2017.03.027.

Rodríguez, A., and J. Kouki. 2015. Emulating natural disturbance in forest management enhances pollination services for dominant Vaccinium shrubs in boreal pine-dominated forests. *Forest Ecology and Management* 350:1–12. https://doi.org/10.1016/j.foreco.2015.04.029.

Rodríguez, A., and J. Kouki. 2017. Disturbance-mediated heterogeneity drives pollinator diversity in boreal managed forest ecosystems. *Ecological Applications* 27:589–602. https://doi.org/10.1002/eap.1468.

Roswell, M., J. Dushoff, and R. Winfree. 2021. A conceptual guide to measuring species diversity. *Oikos* 130:321–38. https://doi.org/10.1111/oik.07202.

Sardiñas, H. S., and C. Kremen. 2014. Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology* 15:161–8. https://doi.org/10.1016/j.baae.2014.02.004.

Sommerfeld, A., C. Senf, B. Buma, A. W. D'Amato, T. Després, I. Díaz-Hormazábal, S. Fraver, L. E. Frelich, Á. G. V. C. Gutiérrez, S. J. Hart, B. J. Harvey, H. S. He, T. Hlásny, A. Holz, T. Kitzberger, D. Kulakowski, D. Lindenmayer, A. S. Mori, J. Müller, J. Paritsis, G. L. W. Perry, S.L. Stephens, M. Svoboda, M. G. Turner, T. T. Veblen, and R. Seidl. 2018. Patterns and drivers of recent disturbances across the temperate forest biome. *Nature Communications* 9:4355. https://doi.org/10.1038/s41467-018-06788-9.

Spies, T. A., P. A. Stine, R. Gravenmier, J. W. Long, M. J. Reilly, tech. coords. 2018. Synthesis of science to inform land management within the Northwest Forest Plan area. Gen. Tech. Rep. PNW-GTR-966. Portland, OR: USDA Forest Service, Pacific Northwest Research Station. 1020 p. 3 vol.

Spiesman, B. J., A. Bennett, R. Isaacs, and C. Gratton. 2019. Harvesting effects on wild bee communities in bioenergy grasslands depend on nesting guild. *Ecological Applications* 29:e01828. https://doi.org/10.1002/eap.1828.

Stokely, T. D., U. G. Kormann, and M. G. Betts. 2020. Synergistic effects of wild ungulates and management intensification suppress native plants and promote exotics. *Forest Ecology and Management* 460:117772. https://doi.org/10.1016/j.foreco.2019.117772.

Sydenham, M. A. K., Häusler, L. D., Moe, S. R., and K. Eldegard. 2016. Inter-assemblage facilitation: The functional diversity of cavity-producing beetles drives the size diversity of cavity-nesting bees. *Ecology and Evolution* 6:412–425. https://doi.org/10.1002/ece3.1871.

Taki, H., I. Okochi, K. Okabe, T. Inoue, H. Goto, T. Matsumura, and S. Makino. 2013. Succession influences wild bees in a temperate forest landscape: The value of early successional stages in naturally regenerated and planted forests. *PLoS ONE* 8:e56678. https://doi.org/10.1371/journal.pone.0056678.

Talbert, C., and D. Marshall. 2005. Plantation productivity in the Douglas-fir region under intensive silvicultural practices: Results from research and operations. *Journal of Forestry* 103:65–70. https://doi.org/10.1093/jof/103.2.65.

Taylor, A. H., L. B. Harris, and S. A. Drury. 2021. Drivers of fire severity shift as landscapes transition to an active fire regime, Klamath Mountains, USA. *Ecosphere* 12:e03734. https://doi.org/10.1002/ecs2.3734.

Tepley, A. J., F. J. Swanson, and T. A. Spies. 2014. Post-fire tree establishment and early cohort development in conifer forests of the western Cascades of Oregon, USA. *Ecosphere* 5:80. https://doi.org/10.1890/ES14-00112.1.

Thompson, J. A., J. C. Zinnert, and D. R. Young. 2017. Immediate effects of microclimate modification enhance native shrub encroachment. *Ecosphere* 8:e01687. https://doi.org/10.1002/ecs2.1687.

Tikhonov, G., Ø. H. Opedal, N. Abrego, A. Lehikoinen, M. M. J. de Jonge, J. Oksanen, and O. Ovaskainen. 2020. Joint species distribution modelling with the r-package Hmsc. *Methods in Ecology and Evolution* 11:442–7. https://doi.org/10.1111/2041-210X.13345.

Ulyshen, M. D., Hiers, J. K., Pokswinksi, S. M., and C. Fair. 2022. Pyrodiversity promotes pollinator diversity in a fire-adapted landscape. *Frontiers in Ecology and the Environment* 20:78–83. https://doi.org/10.1002/fee.2436.

Ulyshen, M. D., K. M. Ballare, C. J. Fettig, J. W. Rivers, and J. B. Runyon. 2024. The value of forests to pollinating insects varies with forest structure, composition, and age. *Current Forestry Reports* 10:322–36. https://doi.org/10.1007/s40725-024-00224-6.

Urban-Mead, K. R., P. Muñiz, J. Gillung, A. Espinoza, R. Fordyce, M. van Dyke, S. H. McArt, and B. N. Danforth. 2021. Bees in the trees: Diverse spring fauna in temperate forest edge canopies. *Forest Ecology and Management* 482:118903. https://doi.org/10.1016/j.foreco.2020.118903.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. In *The Conservation of Bees*, eds. A. Matheson, S.L. Buchmann, C. O'Toole, P. Westrich, and I.H. Williams, 1–16. London: Academic Press.

Williams, P. H., and J. L. Osborne. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40:367–87. https://doi.org/10.1051/apido/2009025.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143:2280–91. https://doi.org/10.1016/j.biocon.2010.03.024.

Winfree, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21:213–23. https://doi.org/10.1111/j.1523-1739.2006.00574.x.

Winfree, R., R. Aguilar, D. P. Vasquez, G. LeBuhn, and M. A. Aizen. 2009. A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90:2068–76. https://doi.org/10.1890/08-1245.1.

Wright, J. W., and R. S. Dodd. 2013. Could tanoak mortality affect insect biodiversity? Evidence for insect pollination in tanoaks. *Madroño* 60:87–94. https://doi.org/10.3120/0024-9637-60.2.87.

Wright, K. W. 2018. The evolution of diet breadth in *Melissodes* bees (Apidae: Eucerini). Dissertation, The University of New Mexico, Albuquerque, New Mexico.

Wuellner, C. T. 1999. Nest site preference and success in a gregarious, ground-nesting bee *Dieunomia triangulifera*. *Ecological Entomology* 24:471–9. https://doi.org/10.1046/j.1365-2311.1999.00215.x.

Zhou, X., and J. M. Daniels. 2018. Production, prices, employment, and trade in Northwest forest industries, all quarters 2014. Resource Bulletin PNW-RB-267. USDA Forest Service, Pacific Northwest Research Station, Portland, OR. https://doi.org/10.2737/PNW-RB-267.

Zitomer, R. A., S. M. Galbraith, M. G. Betts, A. R. Moldenke, R. A. Progar, and J. W. Rivers. 2023. Bee diversity decreases rapidly with time since harvest in intensively managed conifer forests. *Ecological Applications* 33:e2855. https://doi.org/10.1002/eap.2855.

Zitomer, R. A., N. S. Pope, C. W. Epps, R. S. Crowhurst, and J. W. Rivers. 2025. Canopy cover has divergent effects on movement of closely related bumble bees in managed conifer forest landscapes. *Landscape Ecology* 40:42. https://doi.org/10.1007/s10980-024-02002-y.

Zurbuchen, A., S. Cheesman, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Long foraging distances impose high costs on offspring production in solitary bees. *Journal of Animal Ecology* 79:674–81. https://doi.org/10.1111/j.1365-2656.2010.01675.x.

Authors and Affiliations

Graham S. Frank[1] · **James W. Rivers**[2] · **Jake Verschuyl**[3] · **Lincoln R. Best**[4] · **Matthew G. Betts**[1] · **Andrew J. Kroll**[5,6] · **Mark E. Swanson**[2,7] · **Meg A. Krawchuk**[1]

✉ Graham S. Frank
graham.frank@oregonstate.edu

[1] Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR, USA

[2] Present Address: Department of Forest Engineering, Resources and Management, Oregon State University, Corvallis, OR, USA

[3] National Council for Air and Stream Improvement, Inc., Anacortes, WA, USA

[4] Department of Horticulture, Oregon State University, Corvallis, OR, USA

[5] Weyerhaeuser Company, Federal Way, Washington, WA, USA

[6] Present Address: Rocinante Consulting LLC, Corvallis, OR, USA

[7] School of the Environment, Washington State University, Pullman, WA, USA