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Bee diversity decreases rapidly with time since harvest in intensively managed conifer forests

Rachel A. Zitomer[1] | Sara M. Galbraith[2] | Matthew G. Betts[1] |
Andrew R. Moldenke[3] | Robert A. Progar[4] | James W. Rivers[2]

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

[2]Department of Forest Engineering, Resources & Management, Oregon State University, Corvallis, Oregon, USA

[3]Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon, USA

[4]USDA Forest Service, Sustainable Forest Management Research, Washington, District of Columbia, USA

Correspondence
James W. Rivers
Email: jim.rivers@oregonstate.edu

Present address
Sara M. Galbraith, Center for Environmental Management of Military Lands, Colorado State University, Fort Collins, Colorado, USA.

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Abstract

Despite widespread concerns about the anthropogenic drivers of global pollinator declines, little information is available about the impacts of land management practices on wild bees outside of agricultural systems, including in forests managed intensively for wood production. We assessed changes in wild bee communities with time since harvest in 60 intensively managed Douglas-fir (*Pseudotsuga menziesii*) stands across a gradient in stand ages spanning a typical harvest rotation. We measured bee abundance, species richness, and alpha and beta diversity, as well as habitat characteristics (i.e., floral resources, nesting substrates, understory vegetation, and early seral forest in the surrounding landscape) during the spring and summer of 2018 and 2019. We found that bee abundance and species richness declined rapidly with stand age, decreasing by 61% and 48%, respectively, for every 5 years since timber harvest. Asymptotic estimates of Shannon and Simpson diversity were highest in stands 6–10 years post-harvest and lowest after the forest canopy had closed, ~11 years post-harvest. Bee communities in older stands were nested subsets of bee communities found in younger stands, indicating that changes were due to species loss rather than turnover as the stands aged. Bee abundance—but not species richness—was positively associated with floral resource density, and neither metric was associated with floral richness. The amount of early seral forest in the surrounding landscape seemed to enhance bee species richness in older, closed-canopy stands, but otherwise had little effect. Changes in the relative abundance of bee species did not relate to bee functional characteristics such as sociality, diet breadth, or nesting substrate. Our study demonstrates that Douglas-fir plantations develop diverse communities of wild bees shortly after harvest, but those communities erode rapidly over time as forest canopies close. Therefore, stand-scale management activities that prolong the precanopy closure period and enhance floral resources during the initial stage of stand regeneration will provide the greatest opportunity to enhance bee diversity in landscapes dominated by intensively managed conifer forests.

KEYWORDS
bees, early seral forest, forest biodiversity, intensive forest management, pollinator, timber plantation

INTRODUCTION

Animal pollinators mediate the reproduction of nearly 90% of flowering plant species worldwide (Ollerton et al., 2011) and thus play a critical role in maintaining wild plants and agricultural crops in addition to supporting trophic food webs in natural ecosystems (Kearns et al., 1998; Porto et al., 2020). Wild bees are the most important pollinator group in nearly all temperate terrestrial systems (Ollerton, 2017; Ollerton et al., 2011; Willmer et al., 2017; Winfree, Williams, et al., 2007), and widespread declines in this group (Burkle et al., 2013; Potts et al., 2010) have prompted concerns about the consequences for ecosystem function and human food security (Allen-Wardell et al., 1998; Potts et al., 2010). Understanding their habitat requirements and response to anthropogenic activities is therefore critical for the effective conservation of wild bees and the pollination services they provide to agricultural and natural systems.

At the local scale, the abundance and diversity of wild bee communities are typically associated with the availability of foraging resources (Hyjazie & Sargent, 2022) and nesting substrates (Harmon-Threatt, 2020; Roulston & Goodell, 2011). Pollen and nectar are the primary food resources for bees and thus floral density can be an important regulator of wild bee communities (Hyjazie & Sargent, 2022; Roulston & Goodell, 2011). More species-rich plant communities provide a greater variety of floral rewards, enabling both specialist and generalist species to obtain adequate nutrition, and increase the continuity of resources throughout the flight season (Hyjazie & Sargent, 2022; Mallinger et al., 2016). The availability of nest substrates primarily affects community composition via shifts in the relative abundance of nesting guilds (Harmon-Threatt, 2020). Species' responses to disturbances such as agricultural tilling and fire vary depending on nesting ecology (Moretti et al., 2009; Williams et al., 2010). Direct measures of nest substrates, such as exposed soil, cavities, and dead wood, in natural ecosystems have also been shown to influence the abundance of ground-nesting, cavity-nesting, and wood-nesting guilds, respectively (Potts et al., 2005; Urban-Mead et al., 2021; Westerfelt et al., 2018). These patterns indicate that nest-site limitation can occur across groups with diverse nesting requirements in both agricultural and natural settings.

In addition to local-scale processes, patterns of diversity and composition of wild bee communities have been associated with the amount and heterogeneity of land cover types in the broader landscape (Kennedy et al., 2013). Importantly, these relationships are context dependent (Winfree, 2010). Bees may not experience the negative effects of small or isolated habitat patches if the surrounding matrix provides complementary or supplementary resources (Bänsch et al., 2021; Mallinger et al., 2016). In other cases, resources provided by small patches may be sufficient to support bees (Matteson et al., 2008; Tscharntke et al., 2002) or mitigate the negative effects of undesirable landscape conditions. For example, the improvement of local habitat quality via organic farming practices can offset the negative impacts of landscape homogeneity in some agricultural systems (Murray et al., 2012; Rundlöf et al., 2008). Therefore, the impacts of landscape-scale factors on wild bee communities often depend on the characteristics of both the landscape and the local environment.

When considering drivers of bee diversity, the habitat characteristics that support the greatest alpha (i.e., site-level) diversity may be associated with lower beta diversity (i.e., variation in community composition among sites; Ponisio et al., 2016; Heil & Burkle, 2018). Beta diversity results from both species turnover, which implies environmental or spatiotemporal filtering of communities, and nestedness, which reflects a process of species loss in which communities with few species are subsets of more species-rich communities (Baselga, 2010). Thus, there is a need to quantify patterns of species richness and community composition at spatial scales using multiple metrics to understand which land management practices and scales of planning are likely to result in the loss or promotion of overall biodiversity.

Although the responses of wild bees to land use change—especially agricultural intensification—have been well studied, little attention has been paid to bee communities within forest ecosystems, particularly temperate conifer forests intensively managed for wood production (Krishnan et al., 2020; Rivers, Mathis, et al., 2018). This is surprising given that such forests cover >48 million ha in the western USA alone (Oswalt et al., 2018) and play an important role in housing biodiversity and supporting ecosystem services (Brockerhoff et al., 2008; Kormann et al., 2021). Wild forest bees play an important role in structuring and promoting diversity in understory plant communities within these ecosystems (Hanula et al., 2016), and are likely to contribute economically valuable pollination services to adjacent agricultural areas (Bailey et al., 2014; Kennedy et al., 2013; Sõber et al., 2020). Although the body of research on bees in forests continues to grow, gaps remain in basic information needed by scientists, managers, and policymakers who seek to promote wild bee conservation and maintain pollination services in managed forests (Hanula et al., 2016; Rivers, Mathis, et al., 2018).

Nonequilibrium theories, such as the intermediate disturbance hypothesis, have often been used to predict patterns in forest succession and biodiversity across time (Grime, 1973; Huston, 1979). In temperate coniferous

forests, intermediate levels of disturbance that remove dominant tree species promote floristic diversity by allowing the co-existence of less shade-tolerant plant species until canopy closure is re-established (Swanson et al., 2011, 2014). The value of forests as a habitat for bees is therefore thought to be determined largely by the time since disturbance and the subsequent pace of tree regeneration (Mathis et al., 2021; Rivers & Betts, 2021). The early seral period is truncated by fast-rotation forestry practices that accelerate canopy re-establishment (Harris & Betts, 2021). In intensively managed plantations, these practices typically include (1) the removal of woody debris and residual vegetation, which increases the availability of light, nutrients, and soil moisture for crop trees; (2) planting nursery-grown seedlings, which typically hastens early growth and increases the density of commercial tree species; and (3) herbicide application to suppress competing vegetation (Adams et al., 2005; Kormann et al., 2021). Such measures are implemented to maximize the growth of crop trees, yet simplify the composition and successional pathway of plant communities, limiting the longevity of the early seral period when animal-pollinated plants are most dominant (Brockerhoff et al., 2008; Stephens & Wagner, 2007; Stokely et al., 2022).

Bee communities respond strongly and rapidly to the increased abundance and diversity of floral resources in early seral forests produced by timber harvest (Cartar, 2005; Rivers & Betts, 2021; Rubene et al., 2015), but how they change over time as forests regenerate is poorly understood. Previous investigations of bee communities in regenerating forests have often targeted a specific subset of bee species such as bumble bees (Cartar, 2005) or forest specialists (Smith et al., 2021), and most have focused on a relatively short period following harvest (Cartar, 2005; Mathis et al., 2021; Rivers & Betts, 2021; Rodríguez & Kouki, 2017; Rubene et al., 2015). Only a single study (Taki et al., 2013) has quantified change with time since harvest across a full rotation and this study did not examine the influence of landscape context on forest bee communities or quantify compositional changes in these communities with time since harvest. Research that fills this knowledge gap is critical to enable forest managers to select appropriately timed, effective conservation actions that target wild bee communities and enhance the pollination services they provide (Hanula et al., 2016; Rivers, Galbraith, et al., 2018).

In this study, we used a space-for-time substitution to evaluate the response of bee communities across a gradient in time since harvest while also considering the local availability of critical resources (i.e., food and nesting substrates) and the extent of early seral forest in the surrounding landscape. We conducted this investigation in the Oregon Coast Range, a globally important timber region and a leading producer of softwood lumber in the USA (Adams & Latta, 2007; Oregon Forest Resources Institute, 2021), and undertook our work in intensively managed Douglas-fir (*Pseudotsuga menziesii*) plantations, the dominant commercial tree species in this region. We hypothesized that bee diversity is influenced by time since harvest because canopy closure occurs rapidly in such forests and marks a transition from an open environment with favorable thermal conditions and plentiful floral resources to a darker, cooler, closed environment with scarce floral resources (Hanula et al., 2016). We tested four specific predictions of this hypothesis: (1) bee abundance, species richness, and diversity are negatively related to time since harvest (hereafter, stand age); (2) bee abundance and species richness are positively related to local floral resource availability; (3) extent of early seral forest within the surrounding landscape positively affects bee abundance and species richness in young stands, but this effect attenuates with stand age as local habitat suitability deteriorates; and (4) species loss, rather than turnover, leads to the dissimilarity of bee communities within older stands relative to those in younger stands. Finally, we quantified changes in bee community composition and functional traits across biotic and abiotic environmental gradients associated with species-specific habitat suitability to assess how these characteristics modified community responses to stand age.

METHODS

Study area

We conducted our study during 2018–2019 in the central portion of the Oregon Coast Range (Figure 1a). This area is a low-elevation mountainous region bordered by the Pacific Ocean on the west and the Willamette Valley on the east that experiences a temperate, Mediterranean climate and high primary productivity (Franklin & Dyrness, 1988). Precipitation typically ranges from 150 to 300 cm per year and occurs primarily between November and May as rain, with mostly dry weather during the summer months (Franklin & Dyrness, 1988). This area falls within the western hemlock (*Tsuga heterophylla*) climax vegetation zone (Franklin & Dyrness, 1988) and is dominated by commercially grown Douglas-fir that is distributed across the landscape in a patchwork mosaic of even-aged stands interspersed with mixed-age federal forest lands (Franklin & Forman, 1987). Minor conifer species include western hemlock, western redcedar (*Thuja plicata*), and Sitka spruce (*Picea sitchensis*). Hardwood species such as bigleaf maple (*Acer macrophyllum*) and red
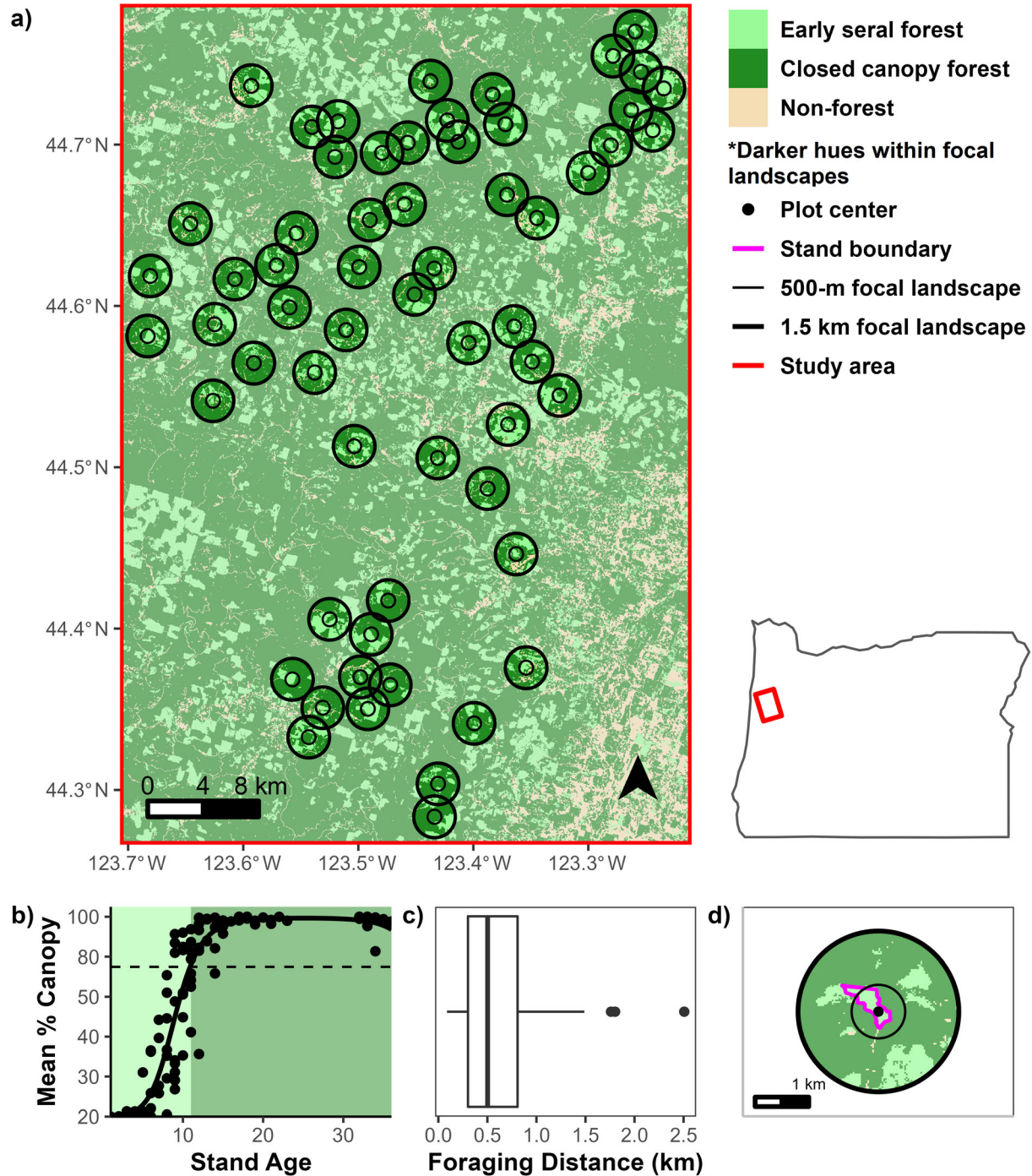
FIGURE 1 Study area and land cover variable designation. (a) Study area in the Oregon Coast Range with $n = 60$ sampled Douglas-fir stands; location of study area is shown within the state of Oregon at the bottom right. (b) Plot of average canopy cover for each stand plotted against stand age used to classify forest cover as early seral or closed canopy. Fitted line represents mean canopy cover as a function of stand age first and second order polynomial terms using a binomial generalized linear model. The dashed horizontal line represents the mean canopy cover (75%) used to delineate the closed-canopy forest condition. Shading shows forest age ranges classified as early seral or closed canopy. (c) Distribution of estimated foraging distances for all bee species sampled used to select focal landscape radii: 500 m represents the median value and 1.5 km represents the upper fence of the distribution. (d) Exemplary map of a single study site with focal landscape radii around the stand center where sampling was conducted.

alder (*Alnus rubra*) are scattered throughout the landscape, especially on the periphery of commercial forest stands and in riparian areas (Franklin & Dyrness, 1988).

Nonforest land cover types, such as developed land, pastureland, shrub scrub, and wetlands, were limited to ~6% of our study area (Dewitz, 2019).

Study design

We selected 60 commercial harvest units (hereafter, stands) that were harvested via clear-cutting 1–35 years prior to the start of sampling in 2018. We selected this age range to represent the full gradient of forest regeneration, from harvest to the end of a typical timber rotation, in commercial Douglas-fir forests in this region. We selected stands from lists provided by the Oregon Department of Forestry and three private landowners (Starker Forests, Weyerhaeuser, and Manulife Investment Management) to represent a range of typical forest management practices used in the region. We selected stands from across the age gradient within each landowner to avoid confounding differences in age with differences in management. After selecting stands for sampling, we recalculated their ages using remote sensing techniques (Appendix S1: Section S1) because we found that age determination was not standardized across ownership. Stand centroids were separated by ≥2000 m (average nearest neighbor distance 3056 m) to minimize spatial autocorrelation among sampling sites; stands averaged 20.8 ha (range: 7.7–39.5 ha) and 305 m above sea level (masl; range: 97–630 m).

At the centroid of each stand, we established a sampling plot with three 20×3 m belt transects radiating from the plot center for floral surveys and hand-netting and a 33-m line transect that extended from the plot center along each belt transect for nest substrate surveys. We randomly selected an azimuth for placement of the first transect and established the other two transects 120° and 240° from it to maximize coverage and avoid placement bias. We established 3-m radius fixed-area subplots at the end of each line transect for vegetation surveys.

Field sampling

Between mid-late May and mid-late July in 2018 and 2019, we collected insect pollinators and surveyed floral resources in three sampling rounds that covered the majority of the flight season of wild bees in western Oregon (Rivers & Betts, 2021; Rivers, Mathis, et al., 2018). The first sampling round occurred during the bloom of early-flowering plants (e.g., *Gaultheria shallon*, *Mahonia aquifolium*, and *Rubus ursinus*) and the final sampling round occurred at the end of the blooming period for most late-flowering plants (e.g., *Anaphalis margaritacea*, *Rubus bifrons*, and *Cirsium* spp.) in the region. We sampled bees using a combination of passive and active sampling methods because our goal was to characterize the entire bee community and using multiple sampling approaches is thought to reduce bias when assessing bee diversity (Cane et al., 2000; Joshi et al., 2015; Packer & Darla-West, 2021; Rhoades et al., 2017). We visited

each stand twice during each sampling round, first to conduct hand-netting and floral surveys and then to implement passive trapping. After completing all bee sampling and floral surveys, we collected data on vegetation structure and ground cover (2018 only) and nest cavity availability (2019 only) to assess habitat elements thought to influence bee community composition.

During our first visit in each round, we netted flower-visiting insects in each belt transect for 30 min during favorable weather conditions (i.e., no precipitation, wind speeds <3.5 m/s, and ambient temperature ≥16°C) between 08:00 h and 16:00 h. We did not count time spent handling insects toward the time allotted for netting. To assess floral resource availability, we estimated the number of open blooms of all insect-visited plant species within each belt transect by counting the number of plant stems in bloom and multiplying by the average number of blooms we observed on up to 10 stems per species. We counted inflorescences for *Daucus carota*, *Toxicodendron diversilobum*, and *Trifolium repens*, and head inflorescences of species in the Asteraceae because accurate counts of individual flowers were difficult to make in the field. This likely imposed little bias on estimates of floral resource availability for pollinators because where many tiny flowers are densely packed into inflorescences, pollinators typically handle multiple flowers on the same inflorescence during a visit, treating the inflorescence as a single floral unit (Ramírez, 2003). We divided the total number of blooms by the total transect area (m^2) to obtain a single measure of floral density for each site during each sampling round.

During our second visit in each round, we passively sampled pollinators using nine bowl traps (three each in fluorescent yellow, fluorescent blue, and white; New Horizons Supported Services, Marlboro, MD) and two blue vane traps (BVTs) with yellow collection jars (SpringStar Inc. [now Banfield Bio Inc.], Woodinville, WA). We positioned bowl traps of alternating colors at equal intervals along the three belt transects on wire holders so that they were ~20 cm from the ground in areas with low or no vegetation. Where necessary, we clipped vegetation within a 30 cm radius of bowl traps to ensure that they were unobstructed. We mounted each BVT to a 1.8 m high metal T-post with a black plastic electric fence insulator, positioned opposite each other 20 m from the plot center. We placed the first BVT post using a randomly selected azimuth to avoid placement bias. We partially filled all traps with ~5 cm of soapy water and placed them out for 48 h per sampling round. We did not collect bees earlier in the flight season (March–April) to minimize the capture of foundress bumble bee (*Bombus* spp.) queens, which could reduce bumble bee abundance and species richness via negative

impacts on colony establishment and survival (Packer & Darla-West, 2021).

For vegetation surveys, we recorded visual estimates of cover for each species of tree, shrub, and fern, for all forbs combined, and for all graminoids combined in each subplot. We estimated cover to the nearest 5%; if a feature was present but the cover was deemed <2.5% we assigned a value of 1% in subsequent calculations. We classified broadleaf shrub and tree species according to designations used in prior work in intensively managed Douglas-fir stands in our study area (Harris & Betts, 2021; Kormann et al., 2021). To estimate broadleaf cover for each stand, we summed cover for all broadleaf species in each subplot, then averaged broadleaf cover across all three subplots. We measured the height of each species or group in each vegetation plot using a 3 m stick. To estimate understory vegetation height for each stand, we weighted the height of each understory species/group by their estimated cover for each subplot, then averaged across all three subplots. We estimated canopy cover using a convex densiometer at seven locations (the plot center and the middle and end points of each of the three belt transects) over which we calculated an average.

To evaluate nest-site availability for ground-nesting and cavity-nesting bee species at each site, we estimated exposed soil cover and the number of potential nest cavities in woody debris, respectively. To get a single measure of exposed soil cover for each stand, we measured the extent of exposed soil (i.e., mineral soil/pebbles <5 cm diameter) every 1 m along the three 33-m line transects using a GRS densitometer (Forestry Suppliers, Inc., Jackson, MS), summed together all measures for each transect, and then averaged across transects. To estimate the number of potential nest cavities, we counted the number of beetle holes >1 mm in diameter in a 1 m section of exposed wood on every piece of woody debris (log, snag, or stump >5 cm in diameter) centered on the intersection with the 33-m line transect and summed the total number of holes counted in all transects for each stand. Access issues due to forest management activities prevented field data collection at $n = 10$ sites during one or more sampling visits (5.0% of netting and floral surveys, 3.8% of trapping surveys, and 3.3% of potential nest cavity or vegetation measures). One BVT was knocked down during sampling at two sites and all BVTs and bowl traps were knocked down at one site (1.7% of trap sampling bouts), but missing data were not biased by stand age.

Species identification and trait assignment

Bee specimens were identified by an experienced taxonomist (L. R. Best, Oregon State University; Appendix S1: Section S2). Specimens were identified to species level unless no keys or reference collections were available for the group, in which case specimens were categorized into morphospecies. Taxonomic voucher specimens are housed at the Oregon State Arthropod Collection, Corvallis Oregon (Zitomer, Galbraith, Betts, Moldenke, et al., 2023). For all species/morphospecies with female specimens captured, we used LAS EZ software with a Leica dissecting microscope (Leica Microsystems, Buffalo Grove, IL) to measure intertegular distance (ITD) as an index of overall body size (Cane, 1987). For each species, we calculated the average of three replicate ITD measurements per individual for up to 10 female specimens, then averaged across individuals to obtain a species-level measure. We then estimated the typical foraging distance for each species using the allometric equation for the typical homing distance in Greenleaf et al., 2007; (Appendix S1: Equation S1). In addition to body size, we compiled information from published literature on six additional functional traits related to bee life history and resource requirements: sociality, nest substrate, nest location, nest construction, lecty (e.g., diet breadth), and peak foraging period (Appendix S1: Section S3; Table S1). We selected these traits because they have been previously shown to predict bee species responses to disturbance and landscape composition and configuration (Williams et al., 2010).

Landscape context and topographical variables

To quantify landscape context, we considered focal landscapes to be the area surrounding a sampling site and defined by the scale(s) at which bees are expected to be influenced by the surrounding landscape (Fahrig, 2013). We selected focal landscapes of two sizes around each plot center using forest age rasters (Appendix S1: Section S1) to represent the foraging ranges of near- and far-foraging bee species based on the distribution of predicted foraging distances of all bee species captured in our study. We selected a focal landscape radius of 500 m based on the median predicted foraging distance for all species captured in the study to represent near-foraging species and a 1.5 km radius to match the upper fence (third quartile × 1.5 interquartile range) of the distribution (Figure 1c) to represent the foraging distance of larger, wider-ranging species. We then reclassified forests as either early seral or closed canopy using the predicted mean age at which canopy cover reached 75% in our sampled stands (i.e., 11 years post-harvest; Figure 1b) as the threshold value between classes, consistent with the delineation of closed-canopy forest used in other studies in the region (Cohen & Spies, 1992; Harris & Betts, 2021). Thus, we classified forest <11 years post-harvest as early seral and forest ≥11 years post-harvest as closed canopy. We chose this threshold

because we hypothesized that canopy closure represented a transition to lower quality habitat for insect pollinators via a reduction in understory temperature, light, and floral resources (Hanula et al., 2016). We then calculated the percent cover of early seral forest within each focal landscape using the *grainchanger* package (Graham et al., 2019) in R (v4.1.1; R Core Team, 2020).

In addition to delineating age classes, we also used a digital elevation model raster (Farr et al., 2007) to estimate elevation (masl) and heat load index (HLI) for each site, both of which can influence the composition of pollinator and plant communities in mountainous ecosystems (McCabe et al., 2019; Simanonok & Burkle, 2014). HLI is a continuous index, which combines slope, aspect, and latitude to predict potential direct radiation (McCune & Keon, 2002; Theobald et al., 2015), which may influence plant blooming (Neill & Puettmann, 2013) and thermal suitability of local habitat for bees (Corbet et al., 1993; Potts & Willmer, 1997). Of note, HLI reflects only potential thermal differences related to topography, but not vegetation or canopy cover, the latter of which are expected to change throughout forest regeneration and have consequences for forest bee communities (Hanula et al., 2015; Rivers & Betts, 2021; Taki et al., 2013).

Hill numbers

To characterize changes in bee diversity with stand age, we constructed sample size- and sample coverage-based rarefaction and extrapolation curves (Chao & Jost, 2012) and calculated observed and estimated Hill numbers for bee communities in three early seral stand age classes: young (1–5 years post-harvest), intermediate (6–10 years post-harvest) and mature (≥11 years post-harvest) using species counts aggregated across all years and sampling rounds with the *iNEXT* package (v 2.0.20; Hsieh et al., 2020). Hill numbers represent the effective number of species for species richness ($q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$; Chao et al., 2014). We repeated these analyses to compare sample completeness and diversity measures between years of the study, aggregating species counts across sampling rounds and age classes. We used combined counts from all sampling methods to calculate bee abundance, species richness, and diversity measures here and in all other analyses.

Bee abundance and species richness responses

To test our hypotheses about the relationships of bee abundance and species richness to stand age, floral resource availability, and extent of early seral forest in the focal landscapes, we fitted a negative binomial generalized linear mixed model (GLMM) to model each response variable—bee abundance and species richness—as a function of those environmental variables using the *glmmTMB* package (v1.0.2.1; Brooks et al., 2017). We chose to use negative binomial models because Poisson GLMMs fitted with the same variable structure were overdispersed. For the abundance model, we used a negative binomial GLMM with a log link. For the species richness model, we used a zero-inflated negative binomial GLMM with a logit link and allowed dispersion parameters to vary with fixed effects. These adjustments accounted for heteroscedasticity and corrected mild under dispersion in residual plots of the negative binomial GLMM we initially fitted. We assessed model fit and dispersion using deviance residual plots and evaluated spatial autocorrelation of model residuals using the *DHARMa* package (v0.4.6, Hartig, 2022) and checked for collinearity among fixed effect variables using variance inflation factors with the *performance* package (v0.9.0; Lüdecke et al., 2021).

In each model, we included the fixed effects terms stand age (continuous variable), floral richness, log(floral density), and percent early seral forest cover in the 500-m and 1.5-km radius focal landscapes. We also included interaction terms between stand age and percent early seral forest for both focal landscape radii because we expected the effects of landscape variables to depend on local stand age. Finally, we included HLI, elevation, sampling round, and year as fixed effect covariates, and site and year × sampling round as random effect terms. We scaled and centered all continuous variables except log(floral density) to improve model fit and reduce the correlation between main effects and their interactions (Harrison, Donaldson, et al., 2018), then back-transformed model coefficients and predictions for interpretability using the *emmeans* package (v1.7.1-1; Lenth et al., 2018).

For both fixed effect interaction terms in each model, we estimated the slope of the relationship between the response variable and percent early seral forest in the focal landscape with stand age fixed at the midpoints of the age ranges used to define the three age classes in our diversity analyses (i.e., 2.5, 7.5, and 25 years post-harvest), with all other variables held at their mean values. We used likelihood ratio tests to assess the contributions of fixed effect variables of interest to each model by comparing full models to models reduced by one fixed effect term at a time (i.e., our full and reduced models had the same random effect structure) and computed confidence intervals for main fixed effects terms using the *broom.mixed* package (v0.2.9; Bolker & Robinson, 2022).

Partitioning beta diversity

To quantify the extent to which dissimilarity in bee communities across the stand age gradient was driven by species replacement and/or species loss, we computed three beta diversity indices in the *betapart* package (v1.5.4; Baselga & Orme, 2012): Simpson pairwise dissimilarity measure (β_{sim}), a measure of species turnover (i.e., replacement); nestedness-resultant pairwise dissimilarity (β_{nes}), a measure of community nestedness (i.e., species loss); and Sorenson pairwise dissimilarity measure (β_{sor}), a measure of overall beta diversity which is the sum of the other two measures (Baselga, 2010). We fitted negative exponential distance decay functions to describe the change in pairwise community dissimilarity with increasing differences in pairwise stand age for each dissimilarity index using the "decay.model" function (Baselga & Orme, 2012). We also used Mantel permutation tests ($n = 999$ permutations) to compute Pearson correlations for each relationship. We used species counts aggregated across all years and sampling rounds for all beta diversity analyses.

Bee and floral community composition

We used nonmetric multidimensional scaling (NMDS) implemented using the *vegan* package (v2.5-7; Oksanen et al., 2020) to visualize changes in bee community composition across habitat gradients and functional traits associated with community response using Bray–Curtis distance measures. For all ordinations we used species counts aggregated across all sampling years and rounds. We removed $n = 7$ stands where no species were detected because dissimilarity measures between communities lacking species are not meaningful (McCune & Grace, 2002; Ricotta & Podani, 2017). We also removed rare species that occurred in <3% of stands (59 species total) from analysis and applied a generalized log transformation to species abundance measures to enhance the detection of relationships between community composition and environmental gradients following the data adjustment protocol recommended by McCune and Grace (2002). We used stressplots to determine whether the fit was sufficient for plotting (<0.2), then used the "envfit" function (Oksanen et al., 2020) to determine relationships of environmental and species trait variables with ordination axes using fitted vectors. The direction and length of vectors correspond to the strength of variable correlation with NMDS axes.

Environmental variables fitted as vectors to ordinations included: percent early seral forest cover within 500-m and 1.5-km radius focal landscapes in 2018, stand age in 2018, floral richness, floral density, broadleaf cover, mean understory vegetation height, slope, HLI, elevation, and exposed soil cover. We applied a square root transformation to the mean understory vegetation height variable and a log transformation to the nesting cavity and floral density variables to reduce skew and improve linear fit with NMDS axes (McCune & Grace, 2002). We plotted environmental and species trait variables with $R^2 > 0.1$ onto ordination plots as vectors for numeric variables and as class centroids for categorical variables. We repeated this ordination process without trait variable fitting for bee genera, removing four genera that occurred in <3% of stands. We displayed the 25% of the remaining genera that were most strongly correlated with ordination axes using the "ordiselect" function in the *goeveg* package (v0.4.2; Goral & Schellenberg, 2021). We conducted ordinations of flower species and genera to visualize changes in floral resource composition across habitat gradients using the same protocol as for bee community ordinations (Appendix S1: Sections S4 and S5).

RESULTS

Over the course of the study, we collected, in total, 12,427 bees representing five families, 24 genera and 148 species/morphospecies. Approximately 4× more bees and 30% more species were collected in 2018 than in 2019 despite nearly identical sampling efforts that took place at the same time of year. The majority of bees collected were polylectic, solitary, soil-nesting species, but several of the most abundant species were classified as eusocial. The most commonly collected genera, in decreasing order of abundance, were *Bombus* ($n = 5054$ individuals), *Halictus* ($n = 2411$), *Lasioglossum* ($n = 2170$), and *Melissodes* ($n = 973$); these four genera represented ~85% of all bees captured (Appendix S2: Figure S1). The most commonly encountered species, *Bombus vosnesenskii*, comprised ~29% ($n = 3656$) of all bees captured.

Relationships of bee abundance, species richness, and diversity to stand age

We found strong evidence that bee abundance and bee species richness were related to stand age (bee abundance: $\chi^2_{df=1} = 46.73$, $p < 0.001$; bee species richness: $\chi^2_{df=1} = 41.81$, $p < 0.001$). For every 5-year increase in stand age, mean bee abundance decreased by 61.0% (95% CI: −69.8%, −49.6%) (Table 1; Figure 2a) and mean bee species richness decreased by 48.3% (95% CI: −57.5%, −37.2%; Table 1; Figure 2d) when all other variables were held at their mean values. In our comparisons of bee

TABLE 1 Mean bee responses to environmental variables of interest estimated for the reference class (first sampling round in 2018) with all other continuous model variables held at their mean value using generalized linear mixed models.

Response variable	Environmental variable	Increment	Estimated percent change in response variable (95% CI)[a]	χ^2	p-value
Bee abundance	Stand age	5 years	−61.0 (−69.8, −49.6)	46.73	<0.001
	Floral richness	One species	3.1 (−0.5, 6.9)	2.77	0.096
	Floral density	Doubling	19.3 (5.8, 34.5)	8.60	0.003
	% Early seral forest (500 m): Stand age	+10 percentage points early seral forest		1.58	0.209
	% Early seral forest (1.5 km): Stand age	+10 percentage points early seral forest		1.46	0.227
Bee species richness	Stand age	5 years	−48.3 (−57.5, −37.2)	41.813	<0.001
	Floral richness	One species	1.6 (−0.9, 4.2)	1.55	0.213
	Floral density	Doubling	7.7 (−2.3, 18.7)	2.22	0.137
	% Early seral forest (500 m): Stand age	+10 percentage points early seral forest		0.02	0.886
	% Early seral forest (1.5 km): Stand age	+10 percentage points early seral forest		7.36	0.007

Note: χ^2 statistics and p-values come from drop-in-deviance tests.

[a]Expressed as percent change in the mean value of the response variable for the specified increment of increase in the environmental variable when all other variables are held at their mean value.
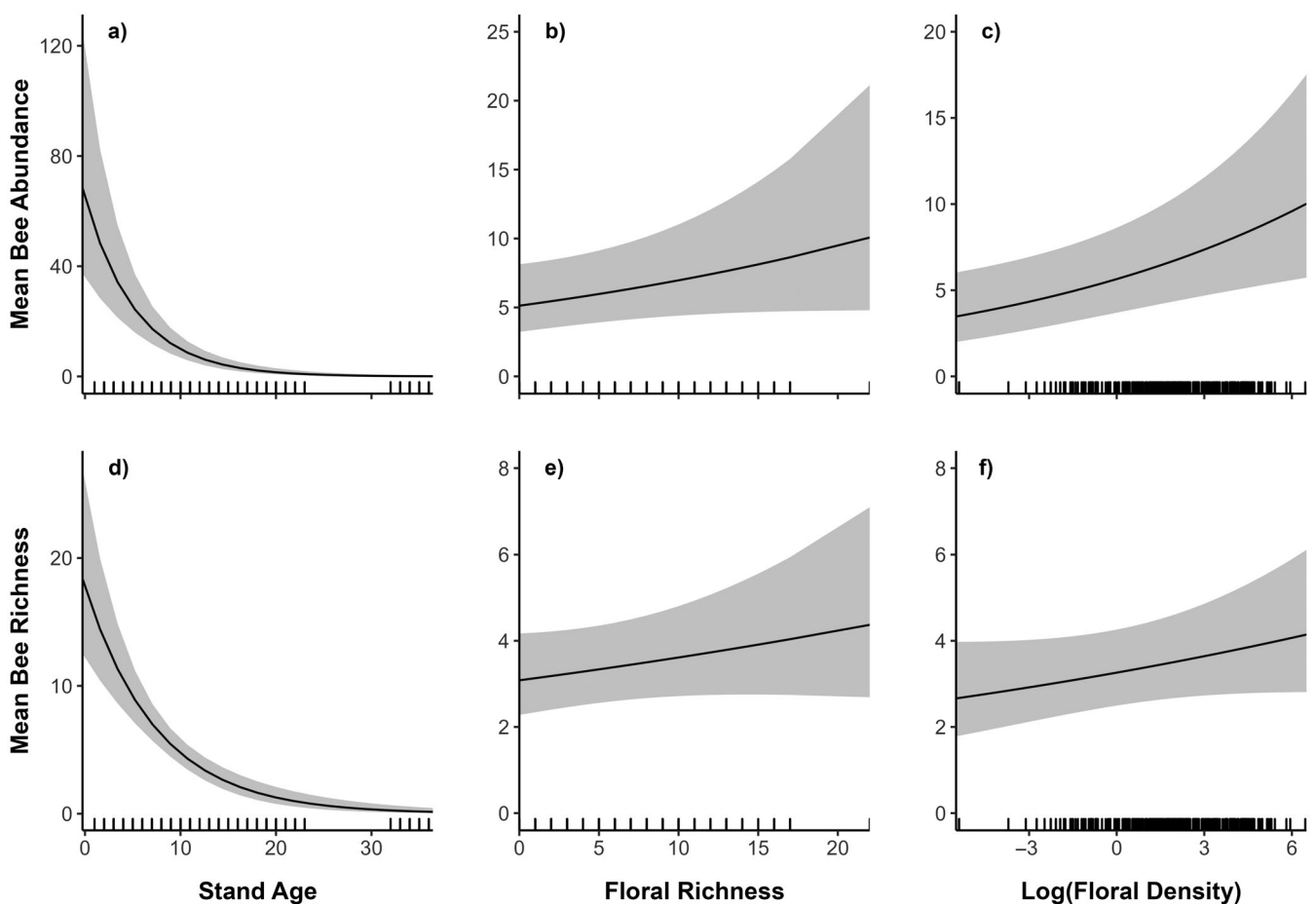

FIGURE 2 Plots of modeled mean bee abundance (top row; a–c) and mean bee species richness (bottom row; d–f) versus local predictor variables: stand age (left; a, d), flower richness (middle; b, e), and log(floral density) (right; c, f) with all other fixed effect terms held at their mean values and random effects excluded. All plots show predictions for the reference classes for year (2018) and sample round (1). In each plot, the estimated relationship is shown as a solid line with the 95% CI shown as a ribbon. Rug plots on the x axis show observed values of predictor variables.

diversity measures among stand age classes, observed and estimated species richness were greatest in the young age class and lowest in the mature age class. For estimated species richness, the 95% CI of the intermediate age class overlapped with those of both the young and mature age whereas the 95% CIs of the young and mature classes did not overlap (Table 2). Both Shannon and Simpson diversity, which give greater weight to common and dominant species, respectively, were highest in the intermediate age class and lowest in the mature age class, although 95% CIs for both measures overlapped between the young and mature age classes (Table 2).

Extrapolated species richness curves increased slowly beyond the reference sample size (Figure 3a) and extrapolated Shannon and Simpson diversity curves were asymptotic after the reference sample size for all three age classes (Figure 3b,c). Sample coverage was high for all age classes and diversity measures (Figure 3d–f), indicating that sampling completeness was adequate to make comparisons among age classes. Sample coverage for the young age class was estimated at 99.6% (reference sample size = 8832 individuals), 98.9% for intermediate stands (reference sample size = 3124 individuals), and 94.7% for the mature age class (reference sample size = 471 individuals).

Although observed and estimated species richness was greater in 2018 than in 2019, 95% CIs for estimated bee species richness overlapped between years. Observed and estimated Shannon and Simpson diversity were higher in 2019 than in 2018 (Table 2). Despite the large difference in bee abundance sampled in the 2 years, sample coverage was similar, estimated at 99.7% for 2018 (reference sample size = 9966 individuals) and 98.7% for 2019 (reference sample size = 2461 individuals).

Relationships of bee abundance and species richness to floral resources

We detected a relationship between bee abundance and floral density ($\chi^2_{df=1} = 8.60$, $p = 0.003$), but not between bee species richness and floral density ($\chi^2_{df=1} = 2.22$, $p = 0.137$). A doubling in floral density was associated with an estimated 19.3% (95% CI: 5.8%, 34.5%) increase in mean bee abundance (Table 1; Figure 2c) and an estimated 7.7% increase (95% CI: −2.3%, 18.7%) in bee species richness (Table 1; Figure 2f). We found no evidence that floral richness was related to bee abundance or bee species richness (abundance: $\chi^2_{df=1} = 2.77$, $p = 0.096$; species richness: $\chi^2_{df=1} = 1.55$, $p = 0.213$). A 1−species increase in floral richness was associated with an estimated 3.1% increase (95% CI: −0.5%, 6.9%) in mean bee abundance (Table 1; Figure 2b) and an estimated 1.6% increase (95% CI: −0.9%, 4.2%) in mean bee species richness (Table 1; Figure 2e).

TABLE 2 Observed and estimated (asymptotic) diversity estimates for bee communities in managed Douglas-fir forests in the Oregon Coast Range.

Group	Diversity measure	Hill no.	Observed diversity	Estimated diversity (95% CI)
Stand Age Class				
Young (1–5 years)	Species richness	$q = 0$	124	284.0 (182.1, 564.6)
	Shannon diversity	$q = 1$	19.7	19.9 (19.7, 20.6)
	Simpson diversity	$q = 2$	8.3	8.3 (8.3, 8.7)
Intermediate (6–10 years)	Species richness	$q = 0$	107	161.0 (129.8, 243.7)
	Shannon diversity	$q = 1$	21.9	22.5 (21.9, 23.6)
	Simpson diversity	$q = 2$	10.1	10.2 (10.1, 10.9)
Mature (≥11 years)	Species richness	$q = 0$	58	89.2 (69.6, 142.1)
	Shannon diversity	$q = 1$	17.1	17.1 (17.1, 21.8)
	Simpson diversity	$q = 2$	8.3	8.5 (8.3, 9.8)
Year				
2018	Species richness	$q = 0$	133	165.0 (146.6, 208.5)
	Shannon diversity	$q = 1$	18.8	18.2 (18.1, 18.9)
	Simpson diversity	$q = 2$	7.0	7.0 (7.0, 7.2)
2019	Species richness	$q = 0$	102	147.4 (120.7, 212.0)
	Shannon diversity	$q = 1$	29.1	30.1 (29.1, 31.5)
	Simpson diversity	$q = 2$	19.4	19.5 (19.4, 20.5)

Note: Diversity measures for the three stand age classes were calculated from summed species counts across three sampling rounds in 2018 and 2019 and diversity measures for each year were calculated from species counts summed across all stand ages.
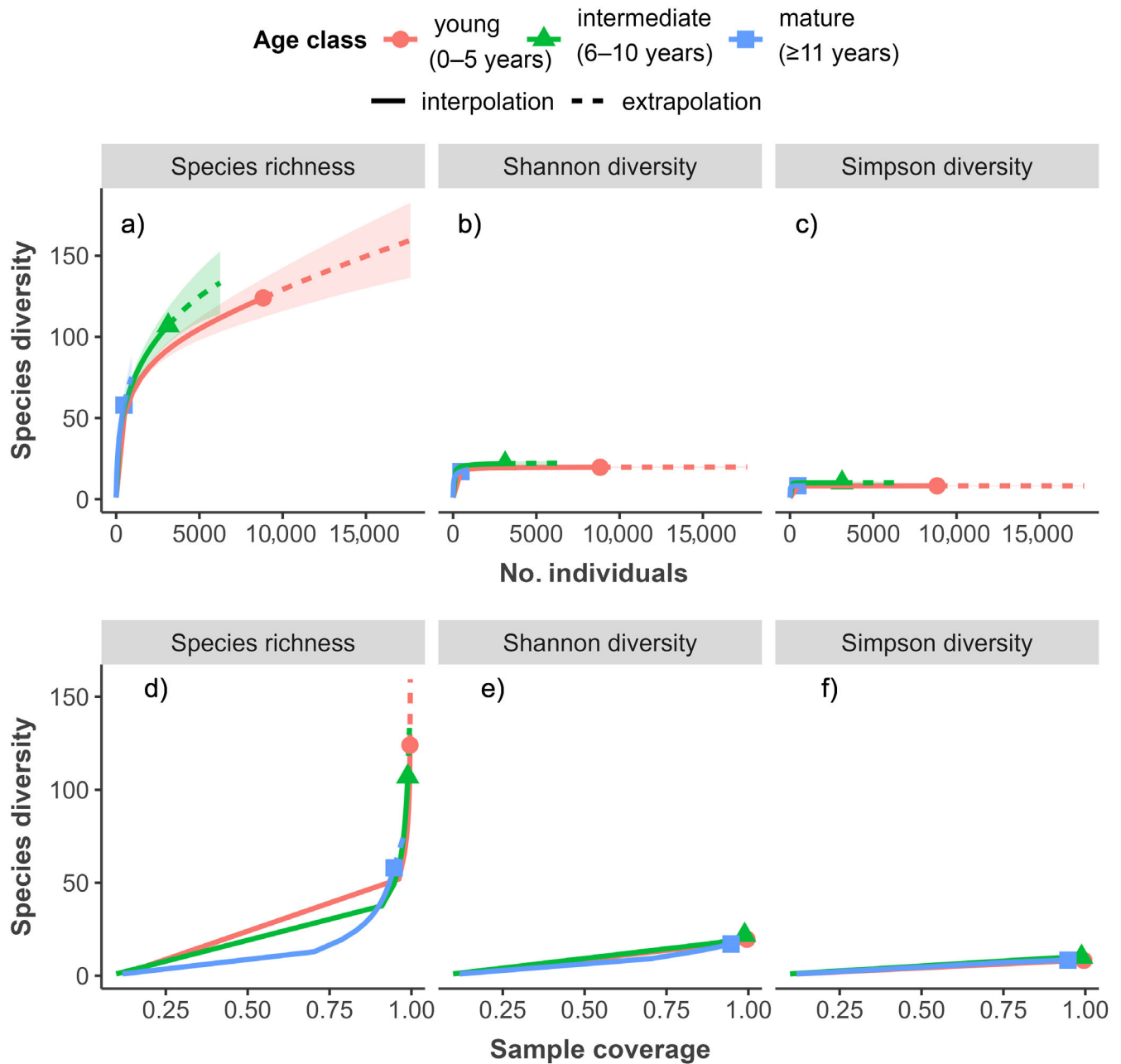
FIGURE 3 Sample-size-based (top; a–c) and sample coverage-based (bottom; d–f) rarefaction and extrapolation curves for wild bee communities in three stand age classes using three diversity orders. Curves were extrapolated to two times the reference sample size. Left-hand plots show species richness ($q = 0$), middle plots show Shannon diversity ($q = 1$), and right-hand plots show Simpson diversity ($q = 2$). Reference sample sizes (number of individuals sampled) are represented by filled symbols, solid lines represent rarefaction curves, dashed lines represent extrapolation curves, and shaded regions represent 95% CIs.

Relationships of bee abundance and species richness to early seral forest extent

We found no evidence that the relationship between bee abundance and the extent of early seral forest in the focal landscape was mediated by stand age (500-m radius focal landscape × stand age: $\chi^2_{df=1} = 1.58$, $p = 0.209$; 1.5-km radius focal landscape × stand age:

$\chi^2_{df=1} = 1.46$, $p = 0.227$). In contrast, we did find evidence that the relationship between bee species richness and extent of early seral forest in the focal landscape was influenced by stand age at the 1.5-km radius ($\chi^2_{df=1} = 7.36$, $p = 0.007$), but not at the 500-m radius ($\chi^2_{df=1} = 0.02$, $p = 0.886$). Estimated values for these relationships calculated from GLMMs are provided in Table 3 and visualized in Figure 4.

TABLE 3 Mean bee responses to interactions between percent early seral forest within a 500 m and 1.5 km radius focal landscape and stand age with stand age fixed at three ages (2.5, 7.5, and 25 years post-harvest) estimated for the first sampling round in 2018 with all other continuous model variables held at their mean value using generalized linear mixed models.

Response variable	Focal landscape radius	Stand age (year)	Estimated percent change in response variable (95% CI)[a]
Bee abundance	500 m	2.5	−1.9 (−21.7, 22.8)
		7.5	−8.3 (−22.9, 9.0)
		25	−27.4 (−48.9, 3.0)
Bee abundance	1.5 km	2.5	−94.2 (−99.9, 291.3)
		7.5	−82.7 (−99.2, 358.0)
		25	820.3 (−98.3, 4045.7)
Bee species richness	500 m	2.5	2.1 (−7.6, 13.0)
		7.5	1.3 (−7.1, 10.6)
		25	−1.3 (−24.3, 28.6)
Bee species richness	1.5 km	2.5	−14.3 (−33.2, 10.1)
		7.5	2.2 (−15.8, 23.9)
		25	88.6 (20.9, 294)

[a]Percent change in the mean value of the response variable for a 10-point increase in percent early seral forest within the focal landscape radius.
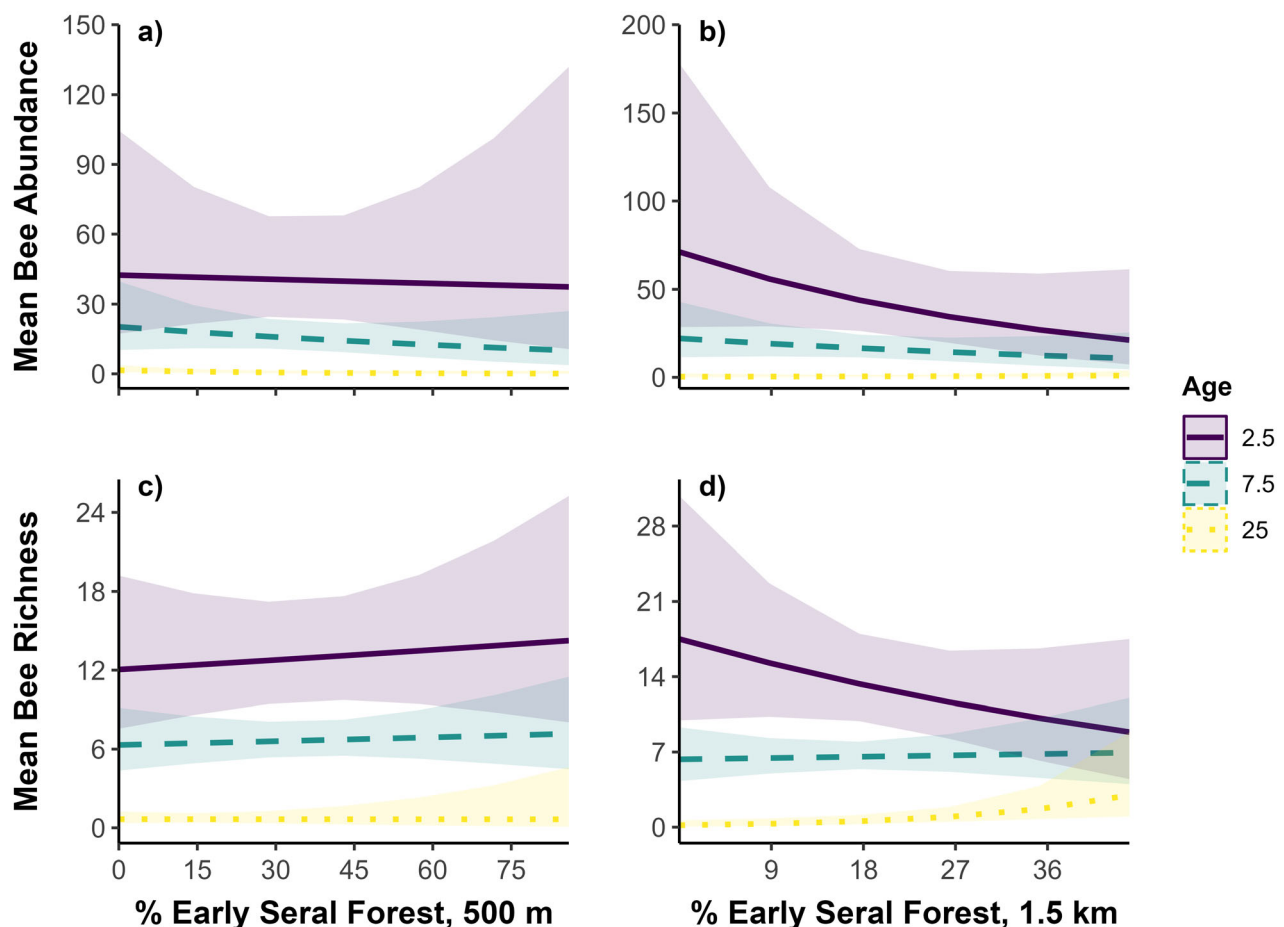

FIGURE 4 Plots of modeled mean bee abundance (top row; a, b) and mean bee species richness (bottom row; c, d) versus percent early seral forest in the surrounding 500 m radius (left) and 1.5 km radius (right) focal landscapes estimated for three stand age values. All other continuous fixed effect terms are held at their mean values and categorical terms are held at their reference classes (year 2018, sample round 1), with random effects excluded. Predicted relationships for each stand age are shown as lines with 95% CIs as ribbons.

Partitioning changes in beta diversity across the stand age gradient

Overall, pairwise community dissimilarity (β_{sor}) among stands increased with pairwise stand age difference (intercept = 0.438, slope = 0.080; Figure 5a). Partitioning this relationship into turnover and nestedness components revealed that dissimilarity resulting from turnover was greater between stands of the same age (β_{sim} intercept = 0.300; Figure 5b) than dissimilarity resulting from nestedness (β_{nes} intercept = 0.167; Figure 5c). However, dissimilarity resulting from nestedness (i.e., species loss) was responsible for nearly all the change in pairwise community dissimilarity among stands as stand age difference increased (β_{nes} slope = 0.038 [Figure 5c] vs. β_{sim} slope = 0.0001 [Figure 5b]). Across all stands, turnover was responsible for a greater proportion of beta diversity than nestedness (β_{sim} = 0.853, β_{nes} = 0.093). This, along with the higher intercept value for β_{sim} in the pairwise decay function, indicated that bee community assemblages differed primarily due to species turnover between stands of similar ages and that bee assemblages in older stands typically comprised a subset of species found in younger stands.

Community composition

NMDS ordinations of sites in species and genera space produced stable (stress <0.2) two-dimensional solutions for both bees (Figure 6) and flowers (Appendix S2: Figure S2). For bee community ordinations, the environmental variables that were most strongly correlated with NMDS axes were stand age (bee genera: R^2 = 0.74, $p \leq 0.001$; bee species: R^2 = 0.55, $p \leq 0.001$), log(floral density) (bee genera: R^2 = 0.65, $p < 0.001$; bee species: R^2 = 0.61, $p \leq 0.001$), floral richness (bee genera: R^2 = 0.60, $p \leq 0.001$; bee species: R^2 = 0.48, $p \leq 0.001$), and percent early seral forest cover in the 500-m radius focal landscape (bee genera: R^2 = 0.34, $p \leq 0.001$; bee species: R^2 = 0.25, $p = 0.002$). Broadleaf cover was correlated with NMDS axes in ordinations with genera (R^2 = 0.13, $p = 0.025$), but not with species. Stand age and broadleaf cover increased in the opposite orientation of all other fitted environmental vectors (Figure 6). None of the bee species traits we considered (i.e., sociality, nest substrate, nest construction, nest location, lecty, foraging distance, or peak foraging period) were correlated with NMDS axes with $R^2 > 0.1$.

We observed similar relationships of environmental variables with NMDS axes in ordinations with flower taxa (Appendix S2: Figure S2). Stand age was the variable most strongly correlated with NMDS axes for ordinations
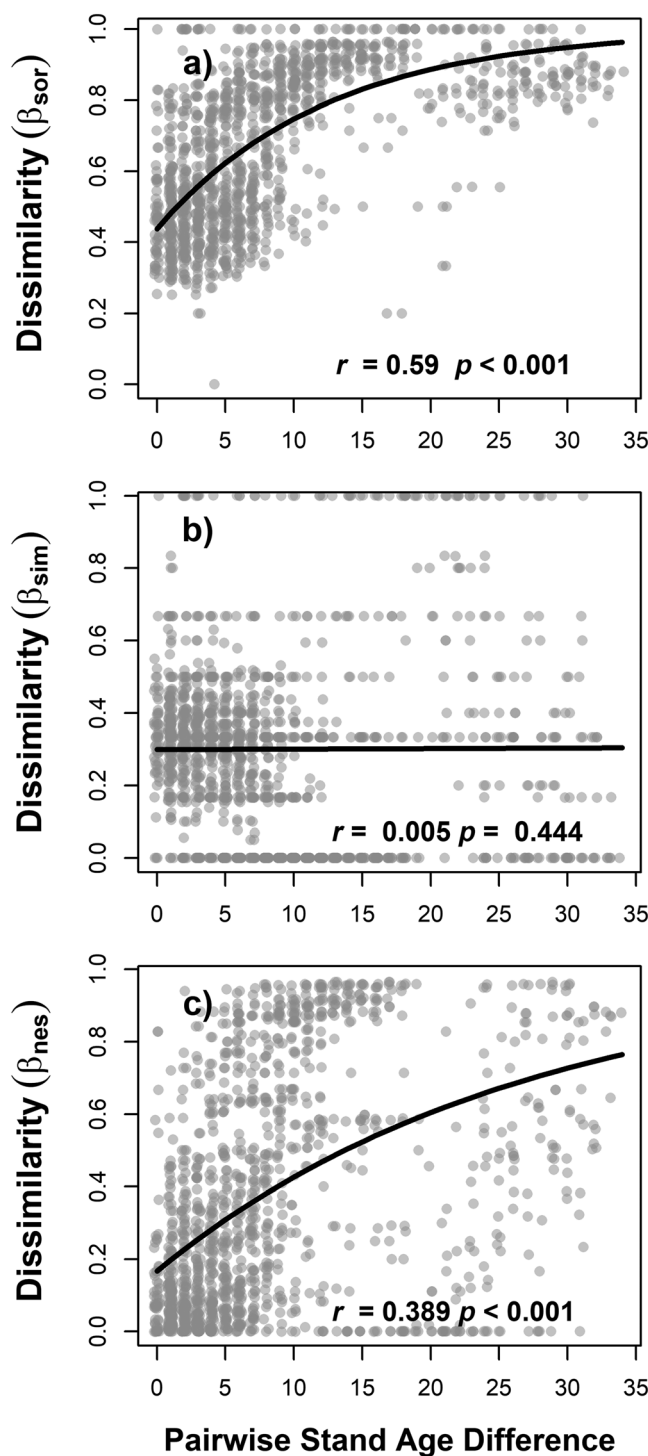

FIGURE 5 Relationships between pairwise beta diversity measures versus pairwise stand age differences for native bee communities in n = 60 managed Douglas-fir forest stands in the Oregon Coast Range. (a) Sorenson pairwise dissimilarity (β_{sor}) shows overall beta-dissimilarity. (b) Simpson pairwise dissimilarity (β_{sim}) shows turnover-resultant dissimilarity. (c) Nestedness-resultant pairwise dissimilarity (β_{nes}) shows dissimilarity resulting from nestedness of less species-rich assemblages within more species-rich ones. Pearson correlation coefficients (r) and p-values are shown.
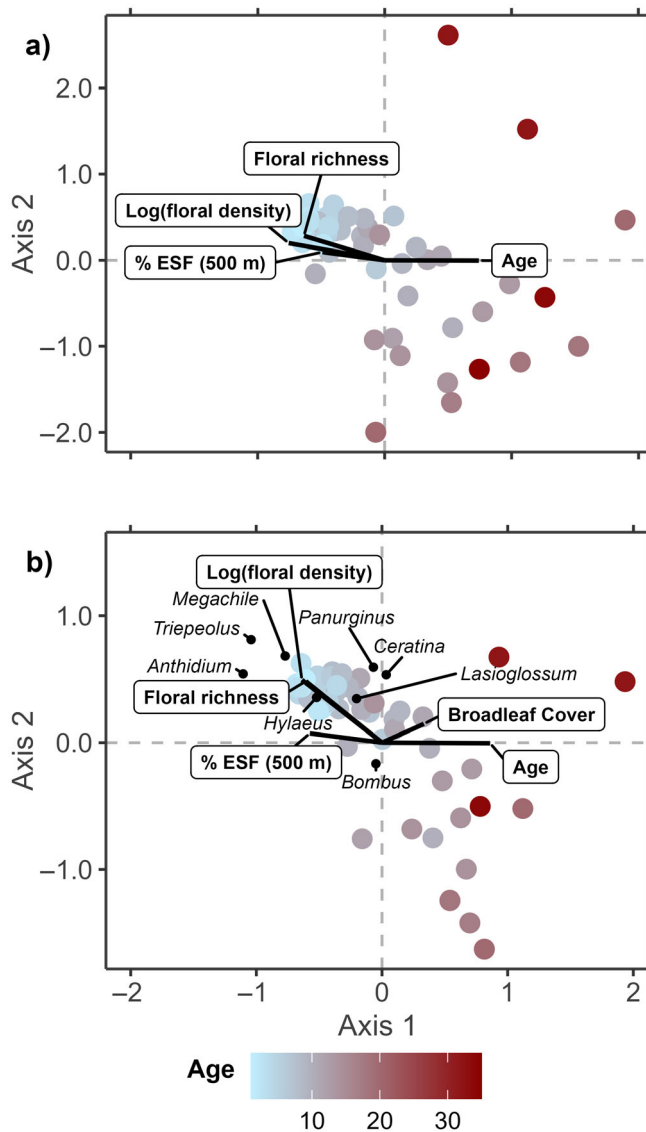
FIGURE 6 Nonmetric multidimensional scaling (NMDS) ordination plots display sampled stands (colored by stand age) in taxa space, with the first axis rotated to load stand age. Environmental variables linearly correlated with NMDS axes with $R^2 > 0.1$ are displayed by vectors, which show the direction and strength of the linear relationship; percent early seral forest cover within the 500-m radius focal landscape is abbreviated as % ESF (500 m). (a) Ordination of wild bee species. (b) Ordination of wild bee genera, with the genera most strongly correlated with NMDS axes annotated.

with both genera and species (flower genera: $R^2 = 0.44$, $p < 0.001$; flower species: $R^2 = 0.47$, $p \leq 0.001$) followed by percent early seral forest in the 500-m radius focal landscape (flower genera: $R^2 = 0.23$, $p = 0.002$; flower species: $R^2 = 0.22$, $p \leq 0.001$). Percent early seral forest in the 1.5-km radius focal landscape was correlated with NMDS axes in ordinations with flower species ($R^2 = 0.20$, $p = 0.004$), but not with genera. Broadleaf

cover was weakly correlated with NMDS axes in ordinations with flower genera ($R^2 = 0.11$, $p = 0.050$), but not with species. Plant growth form and native status were weakly correlated with NMDS axes in ordinations with flower species (growth form: $R^2 = 0.15$, $p < 0.001$; native status: $R^2 = 0.11$, $p \leq 0.001$). Forbs were associated with slightly younger stands than shrubs and exotic species were associated with slightly younger stands than native species (Appendix S2: Figure S2a).

DISCUSSION

We found diverse bee communities in early seral timber plantations prior to canopy closure, adding to a growing body of research demonstrating that managed coniferous forests can support a large number of wild bees during the early seral period (Galbraith et al., 2019a, 2019b; Heil & Burkle, 2018; Rhoades et al., 2018; Rivers & Betts, 2021; Rivers, Mathis, et al., 2018). Bee abundance and species richness were strongly related to stand age and declined across a relatively short period as the forest canopy closed. These findings complement previous work that has found negative relationships between stand age (Taki et al., 2013) or other correlates of stand regeneration (e.g., canopy cover, tree basal area) and local pollinator abundance and species richness (Grundel et al., 2010; Hanula et al., 2015; McCabe et al., 2019; Odanaka & Rehan, 2020; Rhoades et al., 2018).

Bee communities in young and intermediate-aged stands had similar estimated species richness values, but communities in intermediate-aged stands were composed of relatively more common and dominant species, and estimated species richness and diversity measures in mature stands were substantially lower. Although species turnover accounted for the majority of beta diversity among stands of similar ages, species that were lost as stands aged were rarely replaced, so assemblages in older stands typically comprised subsets of species found in younger stands. Closed-canopy stands did not support additional bee species or appear to benefit any taxonomic or functional groups. This aspect of our findings diverges from those of several studies conducted in eastern deciduous forests, where some bee species are associated with mature forests (Harrison, Gibbs, & Winfree, 2018; Smith et al., 2021; Winfree, Griswold, & Kremen, 2007). In such forests, light transmittance to the understory in spring is high prior to leaf out of deciduous trees, supporting ephemeral spring flowers and early-emerging bees (Harrison, Gibbs, & Winfree, 2018; Urban-Mead et al., 2021). In contrast, canopy cover in intensively managed coniferous forests changes little throughout the growing season as nearly all overstory trees are evergreen, and it

limits understory light and flowering plants throughout the entire flight season. Therefore, canopy cover seems to strongly influence bee communities in both hardwood and conifer forests, but the temporal dynamics of canopy cover differ between forest types.

Canopy closure occurred ~11 years post-harvest in our study, similar to estimates from another recent study conducted in this region (Harris & Betts, 2021), reinforcing the conclusion that the temporal window for occupancy of bees and other groups that require early seral forest conditions is especially short in intensively managed stands (Betts et al., 2010; Swanson et al., 2011). The length of this temporal window is contingent on the pace of regeneration to canopy closure and influenced by intensive management practices. In less intensively managed forests, time to canopy closure following a stand-replacing disturbance typically takes much longer than we observed in our study. For example, canopy closure occurred an average of 23 years post-harvest in secondary conifer forests following clear-cutting on federal lands in the Oregon Coast Range (Yang et al., 2005). In naturally regenerating Douglas-fir forests in the Coast Range and Western Cascades, succession to canopy closure is estimated to require at least 40 years, but it may take >100 years (Freund et al., 2014; Tappeiner et al., 1997; Tepley et al., 2014) and may never be achieved in some low productivity conditions (Franklin et al., 2002). Therefore, under less intensive management, the duration of habitat availability for wild bees and other species that require preclosure conditions may be ≥2× longer than observed in our study (Harris & Betts, 2021). Less intensively managed forests also support the greater diversity of tree species and could potentially continue to provide resources after canopy closure via the pollen and nectar from deciduous trees (Mola et al., 2021; Urban-Mead et al., 2021). Therefore, additional research in conifer forests that experience less intensive management than those in our study will prove useful for broadening our understanding of how longer early seral periods may influence bee community dynamics and their pollination services.

We predicted that stand age would influence bee abundance and species richness, in large part due to its indirect effects on floral resource availability. Although floral density decreased with stand age, the negative relationships between stand age and bee abundance and species richness were not entirely explained by floral resource availability. Previous studies have demonstrated a reduction in the effectiveness of pan traps as floral resource availability increases (Baum & Wallen, 2011; Cane et al., 2000), which may have had a muting effect on the relationships we observed with bee communities. However, this effect was likely minor in our study, given that we used a combination of sampling techniques to minimize the biases arising from any single method (Packer & Darla-West, 2021; Rhoades et al., 2017). Notably, we captured 12.1× more bees and 12.6× more bee species in young stands with low floral density than in mature stands with similar floral density. This observation bolsters the conclusion that more bees were present in younger forests and that factors other than floral resources and sampling methods contributed to this pattern.

One possibility is that the abiotic characteristics of young early seral stands produced a more favorable microclimate for bees than did older forests. This notion is supported by findings of previous studies of flower-visiting insect communities across climate and canopy cover gradients that bees were the dominant pollinator group in drier and more open conditions whereas flies dominated communities in wetter, closed-canopy environments (Devoto et al., 2005; McCabe et al., 2019). Several studies have suggested that soil and cavity-nesting bees preferentially establish nests in warm, sun-exposed sites (Everaars et al., 2011; Mayr et al., 2020; Potts et al., 2005; Wuellner, 1999). We did not find evidence that nest-site availability was correlated with shifts in bee community composition or functional characteristics related to nesting requirements. However, it is possible that bee communities were influenced by the thermal suitability of nest sites that corresponded to conditions in young, open stands. It is also worth noting that bumble bees, the most dominant group in our study, generally nest in larger cavities than the ones we counted, including abandoned rodent or bird nests (Williams et al., 2014). Future studies that quantify these features may be able to provide additional insight into nest-site limitation for this important group.

The extent of early seral forest in the surrounding landscape had weak effects on bee communities that varied with the age of the stand sampled. Neither abundance nor species richness of wild bees in young and intermediate age were influenced by early seral forest extent in the focal landscape. This is surprising, as most solitary bees and some social bees are thought to have relatively limited movement capacity (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007; Knight et al., 2005; Zurbuchen et al., 2010) and dispersal limitation appears to filter bee communities in other patchy landscapes (Bommarco et al., 2010; Jauker et al., 2009; Sydenham et al., 2017). The lack of differentiation in functional characteristics of communities could be due to the dominance of far-dispersing species such as bumble bees (Kendall et al., 2022; Pope & Jha, 2018). It is also possible that early seral forest in the surrounding landscape had relatively limited effects on bee communities in young stands

because movement between early seral forest patches was facilitated by landscape features that were used as corridors (Hanula et al., 2016). For example, secondary roads are prominent landscape features in managed forest landscapes (Forman & Alexander, 1998) that can provide foraging and nesting habitats (Hanula et al., 2016; Lee et al., 2021; Wojcik & Buchmann, 2012) and act as navigational landmarks (Brebner et al., 2021; Kheradmand & Nieh, 2019). Further study is needed to understand the value of secondary roads to wild bees in managed forests and the extent to which they contribute to the connectivity of bee populations in early seral forest.

Although it is possible that lethal sampling could have impacted the bee communities we sampled, we find this unlikely for at least two reasons. First, the extent of sampling in our study was less intensive than a previous study investigating this topic, which found bee community structure to be resilient to repeated lethal sampling conducted every 2 weeks across a 5-year sampling period (Gezon et al., 2015). Second, sampling of bee communities using similar approaches has not led to reductions in bee abundance or diversity in previous multiyear studies in temperate conifer forests (Galbraith et al., 2019a, 2019b; Rivers, Galbraith, et al., 2018). Thus, we have no reason to believe that our sampling approach was sufficient to lead to changes in the local bee community. Instead, we hypothesize that interannual variation in temperature, precipitation, and timing of weather events influenced the pattern we observed. Year-to-year fluctuations of the magnitude observed in this study are common in insect populations, and may be particularly pronounced in social species (Turley et al., 2022). Previous studies have attributed these patterns to variation in weather (Graham et al., 2021; Kammerer et al., 2021; Ogilvie & Forrest, 2017; Thomson, 2016). The early spring of 2019 was unusually warm in our study region, with pronounced temperature spikes in April, followed by a cold and rainy period in late May, and notably cooler and wetter conditions through the end of summer relative to the preceding year. These weather patterns probably affected floral density in the late spring and summer of 2019 and may have disrupted the continuity of floral resource availability during a critical period in bumble bee colony growth (Ogilvie & Forrest, 2017), causing particularly strong declines in this group in the second year of our study.

Our results suggest that in intensively managed forest landscapes, stand-level activities that promote floral resources within the first several years following harvest are most likely to be effective in supporting wild bee communities. Recent work has shown that a moderate reduction in herbicide application in the initial years following harvest increases floral resource and pollinator species richness in early seral conifer plantations (Stokely et al., 2022) and may mitigate the undesirable impacts of ungulate herbivory and introduced plant species (Stokely et al., 2018, 2020). Associated revenue trade-offs may be low in some economic scenarios (Kormann et al., 2021) allowing "win–win" outcomes for timber production and biodiversity conservation. Including native bee-pollinated plant species in seed mixes used for roadside and log landing revegetation and erosion control may also supplement and potentially fill phenological and nutritional gaps in floral resources of early seral plant communities (Lee et al., 2021; Wojcik & Buchmann, 2012). In cases in which biodiversity conservation is a primary goal of conifer forest management, approaches that prolong the precanopy closure period are likely to be particularly effective for promoting wild bee communities. Uneven-aged silvicultural methods, such as group selection approaches that create small-scale canopy openings, have similarly been shown to promote pollinator communities in mixed-aged hardwood forests (Proctor et al., 2012; Roberts et al., 2017) and may have similar benefits in western conifer forests. Importantly, many of these interventions are also expected to benefit other early seral-associated groups, including several that have experienced long-term population declines (Betts et al., 2010; Hagar, 2007; Swanson et al., 2014).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Original and processed data (Zitomer, Galbraith, Betts, Progar, & Rivers, 2023) are available on Dryad at https://doi.org/10.5061/dryad.pzgmsbcq9. Voucher materials (Zitomer, Galbraith, Betts, Moldenke, et al., 2023) are

available in the Oregon State Arthropod Collection (osac. oregonstate.edu) under accession no. OSAC_AC_2023_ 01_09-001-01. Forest disturbance spatial layers from Clary, 2020. National Land Cover Database imagery from Dewitz, 2019. Digital elevation model raster from Farr et al., 2007. Additional data sets and literature sources used for species trait determination are described in Appendix S1: Table S1.

ORCID

Rachel A. Zitomer https://orcid.org/0000-0002-1888-1817
Sara M. Galbraith https://orcid.org/0000-0002-5138-3297
Matthew G. Betts https://orcid.org/0000-0002-7100-2551
James W. Rivers https://orcid.org/0000-0001-5041-6002

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.