

Fuels reduction thinning positively influences native bees, but not blooming plants, in a mixed coniferous forest

Scott R. Mitchell^{a,*}, Sandra J. DeBano^a, Mary M. Rowland^b, Skyler Burrows^c

^a Oregon State University, Department of Fisheries, Wildlife, and Conservation Sciences, Hermiston Agricultural Research and Extension Center, Hermiston, OR 97838, United States

^b USDA Forest Service, Pacific Northwest Research Station, La Grande, OR 97850, United States

^c US National Pollinating Insects Collection, Department of Wildland Resources, Utah State University, UT 84322, United States

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ABSTRACT

Progressively more intense and frequent forest fires in western North America have led to higher demand for active fuels management activities. The most common method to manage fuel loads in western forests is fuels reduction thinning. Concurrently, growing evidence highlights the importance of forests as valuable habitat for native bees. However, the effects of fuels reduction thinning on bees are not well understood in the Pacific Northwest (PNW), United States. We examined how thinning affected native blooming plant and bee communities by conducting a before-after, control-impact (BACI) study across four years (2020–2023) and 24 sites in a northeastern Oregon coniferous forest. We sampled bees using passive traps and hand nets, counted blooming plants along transects, measured groundcover and bare ground, and estimated elk (*Cervus canadensis*) herbivory from GPS collars twice per year. Throughout our study we counted 42,209 blooms of 101 species and collected 11,880 bees of 166 species. Thinning decreased canopy cover and increased woody debris. Thinning also increased, though not significantly, elk herbivory. Although blooming plants were not significantly affected by thinning, bee abundance, richness, and diversity increased in thinned sites. Thinning also changed bee community composition, with increases in wood and soil nesting bees but no change in cavity nester abundance. Blooming plant responses may have been moderated by increased elk herbivory in thinned sites. Our findings suggest fuels reduction thinning in PNW forests may have positive effects on native bees, with bee responses apparently initially driven by changes in nesting habitat rather than in floral resources.

1. Introduction

Although fires are a natural component of many forested ecosystems, modern forest conditions have exacerbated the severity and frequency of forest fires, creating significant challenges for forest management (Dodge, 1972; Ellis et al., 2021; Jones et al., 2022; Kreider et al., 2024). In the western United States, shifting forest and climatic conditions have resulted in increasingly destructive fires that have caused significant loss of timber resources, property, and human lives (Steel et al., 2014; Thomas et al., 2017; Radeloff et al., 2023; Wasserman and Mueller, 2023). In response, land managers have taken steps to reduce the risk of catastrophic fires by imposing restrictions on activities (e.g., burn bans) or by actively managing accumulated fuel loads in forests (Urza et al., 2023; Brodie et al., 2024; Edgeley et al., 2025). Since natural ignitions

(e.g., lightning) are common in western forests and not all fire-starts can be prevented (Kalashnikov et al., 2023), fuels management is an appealing option that can prevent fires from becoming large and destructive (e.g., Pollet and Omi, 2002; Fulé et al., 2012; Johnston et al., 2021; Brodie et al., 2024).

The primary means of controlling or reducing unhealthy fuel loading in forests is through thinning, prescribed burns, or a combination of thinning and burning (Brodie et al., 2024; Davis et al., 2024). Thinning can be used to reduce stand density and remove mid-canopy trees that can act as ladder fuels, while prescribed burns can help remove dense understory vegetation and fine fuels on forest floors (Peterson et al., 2025). Although the combination of thinning and burning is likely the most effective method to reduce wildfire risk, it is also the most challenging and expensive to implement (Urza et al., 2023; Davis et al.,

* Corresponding author.

E-mail addresses: scott.mitchell@oregonstate.edu (S.R. Mitchell), sandy.debano@oregonstate.edu (S.J. DeBano), mary.rowland@usda.gov (M.M. Rowland), skyler.burrows@usu.edu (S. Burrows).

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2024; Barker et al., 2025); thus, thinning alone is more widely applied across the western United States (Quinn-Davidson and Varner, 2012; Kolden, 2019). Fuels reduction thinning not only reduces wildfire risk (e.g., Pollet and Omi, 2002; Fulé et al., 2012; Johnston et al., 2021; Brodie et al., 2024) but can broadly influence forest ecosystems and have conservation implications for forest-dwelling animals, including pollinators. The need to understand how forest management influences pollinator communities has been identified as a salient knowledge gap (Rivers et al., 2018; Rivers and Ulyshen, 2025).

Native bees are often considered the most effective pollinator in many ecosystems (Ballantyne et al., 2015; Ollerton, 2017). In North America, there are around 5000 species of native bees (Ascher and Pickering, 2024), all of whom rely on pollen or nectar resources (Michener, 2007). Although most of these species nest below ground in soil, others nest in pre-existing cavities (e.g., abandoned rodent nests, hollow logs) or in excavated or existing holes in wood (Harmon-Threatt, 2020). Approximately 60% of North American bee species live in western states (Carril and Wilson, 2023) and hundreds of species inhabit forests (Hanula et al., 2016), making western forests high priority landscapes for native bee conservation (Ulyshen et al., 2023).

Many forests support diverse bee communities (e.g., Rhoades et al., 2018; Rivers et al., 2018; Ulyshen et al., 2023, 2024; Mitchell et al., 2025), with the abundance of floral resources and diverse mix of available nesting substrates (soil, cavities, and woody debris) likely contributing to their diversity (Ulyshen et al., 2023). However, variation in physical characteristics within and among forests can affect the availability of floral and nesting resources for bees. For instance, several studies have found that forest canopy cover is negatively correlated with bloom abundance and richness (Lindh et al., 2005; Neill and Puettmann, 2013; Mitchell et al., 2025). With fewer floral resources under denser canopies, numerous studies have found negative associations between bee abundance and richness and canopy cover (e.g., Chase et al., 2023; Ulyshen et al., 2024; Rivers and Betts, 2021; Rhoades et al., 2018). In addition, the availability of nesting substrates like bare ground and coarse woody debris can vary in forests (e.g., Gelles et al., 2022), even across small spatial scales (Mitchell et al., 2025). Recent work has shown that the relationship between these variables and native bee communities can depend on the plant association group or forest type (Mitchell et al., 2025). Fuels reduction treatments directly alter some of these characteristics (e.g., canopy cover) and likely affect bloom and bee communities, which may respond in distinct ways in different forest types.

The response of bees to fuels reduction treatments depends in part on the kind of treatment applied, the forest type, and the specific bee communities. Multiple studies have investigated the effect of fuels reduction treatments on bees in different North American forests (e.g., Odanaka et al., 2019; Chase et al., 2023; Davies et al., 2023; Cole et al., 2025). However, to our knowledge, only three studies have examined bee responses to fuels reduction treatments in western North American forests (Gelles et al., 2022; Davies et al., 2023; Cole et al., 2025), even though these forests are high priority areas for future treatment (Woolsey et al., 2024). Two of these studies were conducted in ponderosa pine (*Pinus ponderosa*) forests in Colorado (Gelles et al., 2022; Davies et al., 2023), and one in mixed-conifer forests in northern California (Cole et al., 2025), leaving a major research gap for how fuels reduction thinning affects bee communities in the Pacific Northwest (PNW), an area of far greater timber production than California (Crandall et al., 2025).

Despite a lack of research on the effects of fuels reduction thinning on native bees in many western regions, including the PNW, studies investigating commercial thinning or the effects of environmental variables (e.g., canopy cover) can help inform hypotheses on how thinning affects floral resources, nesting habitat, and bee communities. Because blooming plants in the forest understory are often limited by light (Chazdon and Pearcy, 1991), increases in light availability that result from canopy thinning are generally expected to produce more blooms

(Lindh, 2005), which should benefit bees. For instance, studies in Colorado (Davies et al., 2023) and California (Cole et al., 2025) found that fuels reduction sites (thinned or thinned and burned) had more blooms than untreated sites. However, another Colorado study found that thinning did not significantly increase bloom abundance or richness (Gelles et al., 2022), suggesting some ambiguity in how blooming plants responded to treatment. Thinning may also affect environmental factors other than canopy cover that can, in turn, affect bloom abundance. One example is patterns of native ungulate movement and herbivory. Ungulates may change their use of thinned or logged forests stands due to increased nutritional resources in these sites, including flowering plants (Ruprecht et al., 2023; Manlick et al., 2025). Elk (*Cervus canadensis*), in particular, can decrease the bloom abundance of some plant species that are important forage for bees (Roof et al., 2018; DeBano et al., 2016, 2025; Glenny et al., In Review).

Forest thinning also may influence bees through effects on nesting substrate availability. Approaches that do not remove residual logs from thinned sites (e.g., lop and scatter thinning) can deposit large amounts of coarse woody debris on the forest floor (Piqué and Doménech, 2018), potentially increasing the availability of nesting habitat for wood-nesting bees. Several studies have found that woody debris is positively associated with bee richness or diversity, which could be due to increased availability of diverse nesting substrates (Fortuin and Gandhi, 2021; Gelles et al., 2022; Chase et al., 2023). Thinning may also alter the availability of, or the microhabitats around, bare ground, potentially impacting ground-nesting bees. However, effects of thinning on bare ground remain unclear, with some studies finding increased bare ground following thinning (Davies et al., 2023) and others finding no response (Chase et al., 2023).

Bee communities are predicted to respond to changes in floral resources and nesting habitat. For example, bees may be more abundant and species-rich in forests with thinner canopies. In general, this pattern has been observed (reviewed in Ulyshen et al., 2024), indicating that thinning could improve habitat for bees by simply reducing canopy cover (Payne et al., 2024). In addition, several studies examining clearcutting or commercial thinning in the western PNW suggest that bees are most abundant and diverse in recently harvested forests but decline rapidly as canopy closure occurs (Zitomer et al., 2023; Brown et al., 2025). Research in other regions also suggests that fuels reduction treatments may be positively correlated with bee abundance and richness (Campbell et al., 2018; Odanaka et al., 2019; Chase et al., 2023; Davies et al., 2023; Favorito et al., 2023; Cole et al., 2025); however many of these studies were conducted in very different forest types (e.g., loblolly pine (*Pinus taeda*), temperate deciduous forests) or only examined a subset of the bee community (Cole et al., 2025).

Two studies that did examine thinning in western forests showed conflicting responses: one found that bee abundance, richness, and diversity were greater in thinned stands (Davies et al., 2023), while the other found that thinning alone (without additional burning) did not enhance pollinator abundance or richness (Gelles et al., 2022). Notably, the first study found concomitant effects on floral abundance (Davies et al., 2023). In contrast, the study that did not detect an effect on bees (Gelles et al., 2022) also found no effect of thinning on floral abundance. Together, these findings highlight the potential importance of floral resources in modulating bee responses to thinning. Given that both Gelles et al. (2022) and Davies et al. (2023) examined forests in Colorado, it is unclear if changes in floral resource availability resulting from thinning would drive bee responses in PNW forests, or if other factors such as nesting substrate availability or quality play a role.

Given the lack of research in the PNW and the sometimes-contradictory results of studies in other regions about how thinning affects bee communities, floral resources, and nesting habitat, it is unclear how PNW bee communities, especially in drier inland forests, located in the eastern portion of the region, will respond to fuels reduction thinning. To address this research gap, we used a four year (2020–2023) before-after, control-impact (BACI) study to examine the

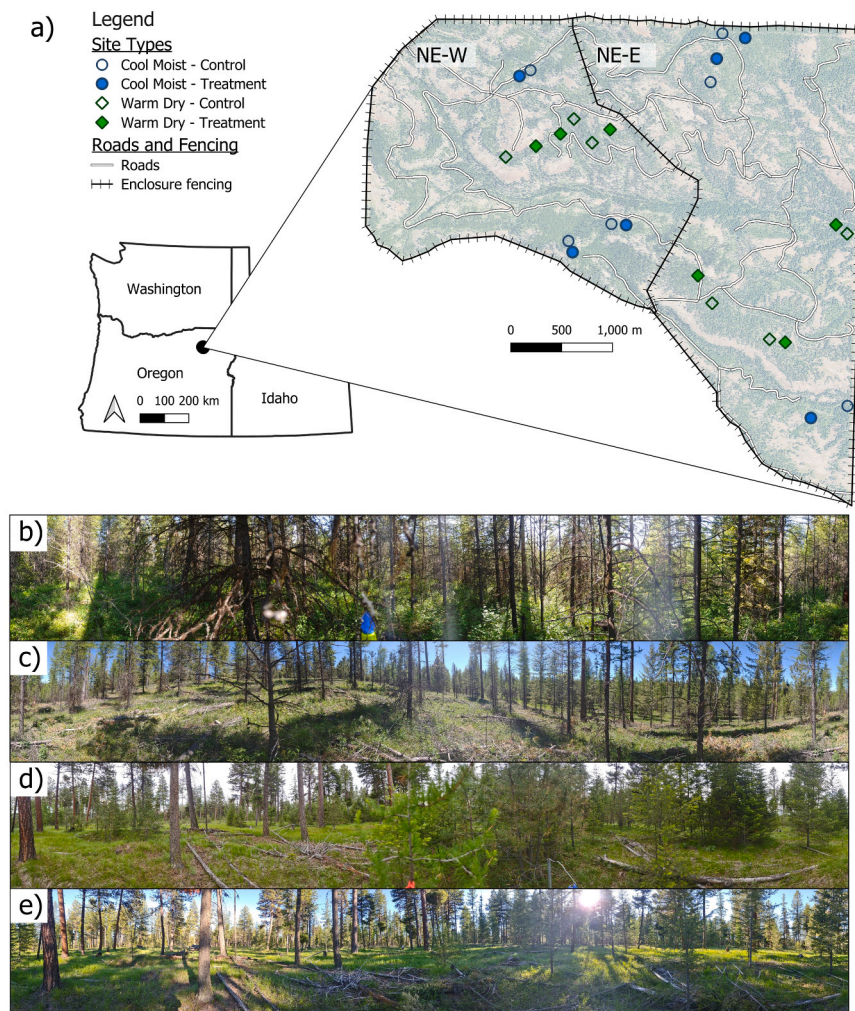


Fig. 1. The USDA Forest Service Starkey Experimental Forest and Range (Starkey); a) inset map of the Pacific Northwestern States of the United States with enlarged, detailed map of the NE study region of Starkey; b) cool moist forest site pre-thinning treatment; and c) the same cool moist site following the thinning treatment; d) warm dry forest site pre-thinning treatment and e) the same warm dry site following thinning treatment.

effects of fuels reduction thinning on nesting habitat, blooming plants, and native bee communities in an inland PNW forest. Our objectives were to:

1. Describe how environmental factors (canopy cover, woody debris, bare ground, and elk herbivory) change in response to lop and scatter thinning.
2. Evaluate how bloom and bee abundance, richness, diversity, and community composition shift in response to lop and scatter thinning.
3. Evaluate how the availability of nesting resources and nesting guilds of bees respond to lop and scatter thinning.

In relation to our first objective, we assumed that the removal of overstory trees in thinned sites would reduce canopy cover and the scattering of downed wood from thinning would increase woody debris and reduce bare ground. We hypothesized that elk would increase their use of thinned sites because of increased accessibility to understory foraging resources. For our second objective, we hypothesized that bloom abundance, richness, and diversity would increase in thinned sites due to increased light. We also predicted that community composition of blooming plants would change with thinning due to species-specific responses to increased light availability (e.g., shade-dependent species would produce fewer blooms). We hypothesized that bee abundance, richness, and diversity would be higher in thinned sites, because more open canopies would enhance bloom availability, thereby

increasing floral resources for a variety of bees. For our third objective, we hypothesized that thinning would increase in woody debris and decrease bare ground as thinned trees were scattered on the ground. We hypothesized a concomitant response in the abundance of wood nesting bees, which could be nest site limited in control sites.

2. Methods

2.1. Study area

We conducted our study in the 14.5 km² northeastern portion (NE) of the USDA Forest Service Starkey Experimental Forest and Range (Starkey) from 2020 to 2023 (Fig. 1a). Starkey has been used extensively for wildlife, forest, and rangeland management research since the 1940s (Skovlin, 1991; Rowland et al., 1997) and more recently to study blooming plant and bee communities both in riparian meadows (DeBano et al., 2016, 2025; Roof et al., 2018; Arstingstall et al., 2021; Mitchell et al., 2022, 2023) and forested systems (Oja, 2020; Mitchell et al., 2025). Located in Union County, Oregon, United States (45.29970° N, 118.53766° W), the climate is typical of this region, with cool, wet winters and warm, dry summers. Based on 30-year average climate models (1990–2020), Starkey receives 44.2 cm of precipitation each year and is warmest in July (average daily minimum, maximum: 12.5 °C, 20.1 °C) and coldest in December (average daily minimum, maximum: −4.2 °C, 3.7 °C) (NOAA, 2021). Most of Starkey, including

the NE area, is enclosed with 2.4-m high ungulate-proof fencing to allow experimental manipulation of numbers of deer (*Odocoileus* spp.) and elk, both common wild ungulates in this ecoregion (Rowland et al., 1997). The NE area varies in elevation from 1140 m to 1360 m and is home to four primary plant communities, including xeric grasslands, previously logged forests, cool moist forests (Fig. 1b, c) dominated by grand fir (*Abies grandis*), and warm dry forests (Fig. 1d, e) dominated by ponderosa pine (Stewart et al., 2011). Our treatment sites were located in units that were salvage-logged in 1992, a harvest that removed approximately 7 million board feet of Douglas-fir (*Pseudotsuga menziesii*) and grand fir previously killed by bark beetles and drought (Ruprecht et al., 2023). Control sites were not as badly affected by beetle kill and were not salvage logged. See Stewart et al. (2011) and Ruprecht et al. (2023) for more detailed descriptions of the forests and land use history in these sites.

Portions of the NE study area were thinned in fall 2021 to reduce wildfire hazard by reducing tree density and ladder fuels. This pre-commercial thinning included several stipulations, e.g., retaining all shrubs (unless impeding with removal of trees), no removal of trees with a diameter > 23 cm, and specific criteria for tree density and average spacing, depending on the cut unit. Desired density ranged from 295 to 432 trees/hectare across all cut units. Several treatments were applied, all by hand (i.e., no mechanized logging equipment used), with “lop and scatter” being the most common. This method entails cutting all trees meeting the unit criteria for preferred species, with slash piles no higher than 60 cm and with any trees over 3 m long and 5 cm in diameter cut to lengths not to exceed 2.4 m.

For our study, we established 12 pairs of sites in NE, for a total of 24 sites (Fig. 1). One site from each pair was thinned, using a lop and scatter method, after the second year of sampling in 2021 (“treatment”), and one site was not thinned (“control”). Sites were further allocated between forest plant association groups, with six pairs in warm dry and six pairs in cool moist forests (Powell et al., 2007). The average distance between sites within a pair was 213 m, the average nearest neighbor between pairs was 631 m, and the average distance between pairs was 1970 m (Fig. 1a). Sites were sampled in spring (late May and early June) and summer (late June and early July) of each year, resulting in a total of eight sampling periods across four years (pre-treatment: 2020–2021, post treatment: 2022–2023).

2.2. Environmental variables

To understand how thinning influenced physical aspects of the environment, including nesting habitat, we assessed canopy cover and ground cover in each site. Canopy cover and ground cover were measured at 15 points in each site. The 15 points were arranged with one point in the center and one point on each end of five, 20-m plant sampling transects (described below) that were spaced 15 m from each other (Figure S1). Canopy cover was measured according to the methods in Mitchell et al. (2025) using a spherical crown densiometer (Lemmon, 1957). Ground cover was measured in the aforementioned 15 points using a 0.6-m x 0.6-m quadrat at each point, where we estimated percent cover (to the nearest 1%) of: litter, small woody debris (<6 cm diameter), large woody debris (≥6 cm diameter), slash (small and large woody debris generated by thinning), tree trunks, forbs, grasses, shrubs, bare ground, biological soil crusts, bone, animal scat, rocks, and stumps. Ground cover values summed to 100% within each point and averaged across the whole site. We measured ground cover composition once in spring and once in summer for each of the study years. Canopy cover was only measured once per year (spring sample period) as tree-needle and branch density were assumed to be relatively constant in the conifer-dominated forests that we sampled. Elk GPS collar fixes from within 100 m of each site were used to estimate elk herbivory pressure of each site. Since the study area is surrounded by fencing that prevents elk movement in or out of the forest, a known number of elk reside within the forest (see Mitchell et al. 2025 for additional details). Since the

number of elk in the study area and the proportion of collared individuals varied from year to year, elk herbivory pressure was standardized across all sites using the following equation:

$$EHP = \frac{\text{Collar fixes}_{i,t}}{\text{Collar fixes}_{e,t}} * \#ofElk_e$$

where elk herbivory pressure (EHP) = total collar fixes within 100 m of center of the site (i) until that site was sampled at time (t) divided by the total number of collar fixes within the enclosure (e) in which site (i) was located until time (t) multiplied by the total number of elk in the enclosure (Elk_e) that year.

2.3. Plant sampling

Concurrent with ground cover sampling we counted blooming stems along five 0.3-m x 20-m transects in each site, a commonly used method for assessing floral resources in other pollinator studies in the region (e.g., Kimoto et al., 2012; DeBano et al., 2016, 2025; Roof et al., 2018; Mitchell et al., 2023, 2025). Transects were placed parallel to each other and were separated by 15 m. Except for lupines (*Lupinus* spp.), roses (*Rosa* spp.), and hawksbeard (*Crepis* spp.), all blooms were identified to species. Lupines were identified as largeleaf lupine (*L. burkei*), sulphur lupine (*L. sulphureus*), and other purple lupines (*Lupinus* spp.). Roses were identified to genus and were either Nootka rose (*R. nutkana*), Wood's rose (*R. woodsii*), or a hybrid. Hawksbeards were identified to genus and were either tapertip hawksbeard (*Crepis acuminata*) or limestone hawksbeard (*C. intermedia*). We used scientific and common names described in the USDA NRCS Plants Database (<https://plants.usda.gov>).

2.4. Bee sampling

Concurrent with plant sampling, we sampled bee communities using pan traps and vane traps (Rhoades et al., 2017). We used 15 240-ml pan traps (5 each: fluorescent blue, fluorescent yellow, and white) and one vane trap (fluorescent blue vanes and fluorescent yellow collection bucket) at each site. Pan traps were deployed in 5 groups of 3 (one of each color, spaced ~0.5 m apart in an equilateral triangle) at the center of each plant transect and filled with ~200 ml of slightly soapy water. The vane trap was attached to the top of a 1.5-m post in the center of the middle transect and filled with 250–300 ml of slightly soapy water. Both trap types were deployed for approximately 48 h, and exact deployment times were recorded and used to calculate total trap-hours for each trap type. Upon collection, we pooled all pan trap contents from a site and counted the number of tipped traps. Sites were resampled when > 9 pan traps (60%) were disturbed or when the vane trap was found empty due to disturbance.

In the last 5 sample periods (summer 2021, spring and summer 2022, spring and summer 2023), we also conducted timed hand-netting of bees at each site to 1) understand which blooming species were visited by bees in our study area, and 2) improve our understanding of how the effects of thinning on blooming plants may influence bee foraging resources. During timed hand net sessions, we systematically walked through sites netting bees visiting reproductive parts of flowers (e.g., anthers). The duration of netting periods varied from 10 to 40 min and was recorded at the end of a netting session. Handling time was excluded from hand net sampling duration. All bees were pinned and identified according to the methods and keys listed in Kuhlman and Burrows (2017). Representative specimens of each species in this study and in Mitchell et al. (2025) are vouchered in the National Pollinating Insects Collection at the USDA Agricultural Research Service's Pollinating Insects Research Unit in Logan, Utah, USA (accession #NPIC-00113).

2.5. Response variables

We evaluated the effects of thinning on canopy cover, bare ground,

and total woody debris cover (small woody debris, large woody debris, and slash combined) to understand how bee nesting substrates may be affected by thinning. Bare ground and total woody debris were selected from all other groundcover variables as these were predicted to be the best proxies of two important bee nesting habitats (soil and wood, respectively). The blooming plant responses evaluated included bloom abundance, bloom richness, and estimated Hill-Shannon species diversity (Chao et al., 2014). The bee response variables included bee abundance in vane traps, bee abundance in pan traps, total bee species richness (vane and pan traps combined), and Hill-Shannon diversity (vane and pan traps combined). We also conducted a literature search to describe the simplified nesting guilds (soil, wood, or cavity) of the bee species collected. We used these traits for additional analyses of the abundance of each nesting guild as separate response variable.

2.6. Statistical methods

Using a BACI framework, we analyzed the effect of thinning using generalized linear mixed effects models (e.g., Radinger et al., 2023), an approach suggested as a more flexible alternative to other methods of BACI analysis. This allows for different underlying distributions that better fit different data types, incorporating offsets to account for uneven sampling effort (e.g., variable trap hours due to trap disturbance), and the inclusion of more complex random effect terms (Pardini et al., 2018). Using this approach, we evaluated the effects of thinning on environmental variables (canopy cover, total woody debris cover, elk herbivory pressure, and bare ground) and on bee and bloom variables (abundance, richness, and Hill-Shannon diversity). All models were fit with the following model structure:

Response $\sim$ Forest Type * Treatment Type * Time Period + (1|Block/Site) + (1|Year/Season)

where treatment type, time period, and forest types were categorical variables defined as: treatment type (“treatment” or “control”), time period (“before” or “after” the application of the treatment), and forest type (“warm dry” or “cool moist”). In the notation above, the three-way interaction between these three categorical terms is explicitly included, but all lower-order two-way interactions are also included. To address our objectives, we only interpreted the three-way interaction and the two-way interaction between treatment type and time period. A statistically significant interaction between treatment type and time period indicates an effect of thinning on our response variables and is essential to detecting a BACI treatment effect (e.g., Radinger et al., 2023). We included the three-way interaction between forest type, treatment type, and time period to evaluate if the effects of thinning varied by forest type. We included the 1|Block/Site random effect term to account for the spatial nesting of paired sites (treatment and control) within experimental blocks and to account for resampling the same sites across seasons and years. We included the 1|Year/Season random effect term to account for temporal nesting of seasons within years and to account for inter- and intra-annual variability in bee and bloom communities.

For overall bee abundance, we analyzed bee abundance in vane and pan traps separately in order to incorporate a log-offset term in the model to account for variable sampling effort (trap-hours), which primarily arose from trap disturbances. To analyze the abundance of different nesting guilds, we combined vane and pan trap data and did not use an offset term. Pan and vane traps were combined for these analyses due to overall low abundance of some guilds at some sites. We analyzed richness and Hill-Shannon diversity with trap types combined. Since vane and pan traps likely attract slightly different species (Rhoades et al., 2017), combining trap types for richness and diversity measures should provide a more complete estimate of bee richness and diversity. We used the iNEXT package in R (Hsieh et al., 2016) to estimate bee and bloom species richness and diversity at equal sampling coverage using H0 for richness and H1 for diversity (Hsieh et al., 2016; Roswell et al., 2021). We ran all GLMM models using the glmmTMB package in R (Brooks et al., 2017) using relative maximum likelihood for

all models. We initially fit all abundance models (bloom abundance, vane trap bee abundance, pan trap bee abundance, wood nester abundance, soil nester abundance, and cavity nester abundance) using a negative binomial distribution with a log link function. Since H0 and H1 richness and diversity estimates result in positive continuous values, and our data were well approximated by a normal distribution, we fit all richness and diversity models using a normal distribution. Model assumptions were checked and met for all models. We evaluated model fit using simulated residuals estimated with the DHARMA package (Hartig, 2022), by plotting fitted versus predicted values, and calculating marginal and conditional pseudo R^2 values using the MuMIn package (Bartoń 2024). For the models fit with a negative binomial distribution and a log link function, we reported R^2 values calculated using the trigamma function, as recommended by the authors of the MuMIn package (Bartoń 2024). We interpreted significance at $\alpha = 0.10$ for all statistical models.

2.7. Multivariate methods

To determine whether thinning had a significant effect on community composition of blooms and bees, we performed a two-factor PERMANOVA test (Anderson, 2001) with treatment type (control or treatment) and time period (before or after) as the factors, using a Sørensen (Bray-Curtis) distance measure. This approach tests for the main effect of treatment type and time period as well as the interaction between treatment type and time period. We used the interaction term to determine if the application of thinning significantly influenced bloom and bee community composition in treated sites. We also conducted indicator species analyses (Dufrene and Legendre, 1997) on spring and summer bloom and bee communities to understand which blooming plant and bee species may benefit from thinning versus those that may perform best in undisturbed site conditions. We used treatment by time combinations as the grouping factor, resulting in four groups (control-before, treatment-before, control-after, and treatment-after). Indicator species analyses generate an indicator value that ranges from 0 to 1 for species in groups of sites. PERMANOVA and indicator species analyses were conducted in PC-ORD on matrices of sampling units (a unique site by month combination) by species where cells were the abundance of a given species in a given sampling unit (McCune and Meffod., 2018). Last, to better interpret how changes to blooming plant communities may affect bees and understand which plants are important to bees, we used hand net data to create plant-pollinator networks in the bipartite package (Dormann et al., 2008).

3. Results

3.1. General results

Across the four study years, we counted 42,209 blooms from 101 taxa. The 10 most abundant blooming species were *Collinsia parviflora*, *Viola adunca*, *Myosotis stricta*, *Calochortus elegans*, *Fragaria vesca*, *Arc-tostaphylos uva-ursi*, *Vaccinium scoparium*, *Sedum stenopetalum*, *Madia glomerata*, and *Draba verna*. See Table S1 for a list of blooming plant species by year and treatment type.

We collected 11,880 bees from 166 species or morphospecies across all trapping methods, including 5948 bees of 132 species or morphospecies in pan traps and 4249 bees from 108 species or morphospecies in vane traps. In total, we conducted 65.25 h of hand netting during which we collected 963 bees from 99 different species or morphospecies foraging on 65 different plant species. Of the 166 species collected in the study, 69 were collected in all three capture methods, 36 were collected by at least 2 capture methods, 29 were only captured in pan traps, 22 were only captured in blue vane traps, and 10 were only captured in hand nets. See Table S2 for more details on pan trap bees, Table S3 for vane trap bees, and Table S4 for hand net bees.

Of the 156 bee species or morphospecies collected in pan and vane

Table 1

Generalized linear mixed effects model (GLMM) results for the main effects of treatment type (treatment or control), time period (before or after treatment) and the interaction of treatment type and time period (BACI effect – the effect of thinning), the last column is a three way interaction between treatment type, time period, and forest type (cool-moist or warm-dry), with marginal R-squared ($R^2_{\text{marg.}}$) and conditional R-squared ($R^2_{\text{cond.}}$). Significant terms are bolded.

Category	Variable	Treatment Type		Time Period		BACI Interaction		BACI Interaction with Forest Type		Pseudo- R^2	
		z-value	p-value	z-value	p-value	z-value	p-value	z-value	p-value	$R^2_{\text{marg.}}$	$R^2_{\text{cond.}}$
Site variables	Canopy cover	2.0	0.04	1.9	0.06	-7.3	> 0.001	1.9	0.06	0.52	0.82
	Woody debris	-4.0	> 0.001	1.5	0.12	6.5	> 0.001	0.88	0.38	0.58	0.73
	Elk herbivory	0.41	0.68	-1.6	0.10	1.5	0.12	-0.23	0.82	0.07	0.63
	Bare ground	0.14	0.89	0.72	0.47	-0.28	0.78	0.24	0.81	0.11	0.43
Blooming plant variables	Abundance	2.0	0.04	0.23	0.81	-0.90	0.37	-0.35	0.73	0.11	0.51
	Richness	0.42	0.68	-0.77	0.44	-0.36	0.72	-0.19	0.85	0.03	0.41
	Hill-Shannon	0.049	0.96	0.27	0.79	-0.46	0.65	0.82	0.41	0.02	0.44
	Vane abundance	-1.9	0.05	-0.70	0.48	2.8	0.006	-1.6	0.11	0.12	0.43
Bee variables	Pan abundance	-0.50	0.62	-0.096	0.92	2.91	0.004	-0.84	0.40	0.18	0.74
	Richness	-0.077	0.94	-1.1	0.26	2.3	0.02	-1.66	0.097	0.08	0.22
	Hill-Shannon	-0.049	0.96	-1.1	0.27	2.24	0.03	-1.59	0.11	0.07	0.21
	Wood nesters	0.13	0.89	-0.96	0.34	1.90	0.06	-1.75	0.08	0.09	0.30
Nesting guild abundance	Soil nesters	-1.09	0.28	-0.90	0.37	1.63	0.10	-1.1	0.26	0.03	0.44
	Cavity nesters	-2.2	0.03	-0.33	0.74	-0.003	0.99	-0.14	0.89	0.09	0.54

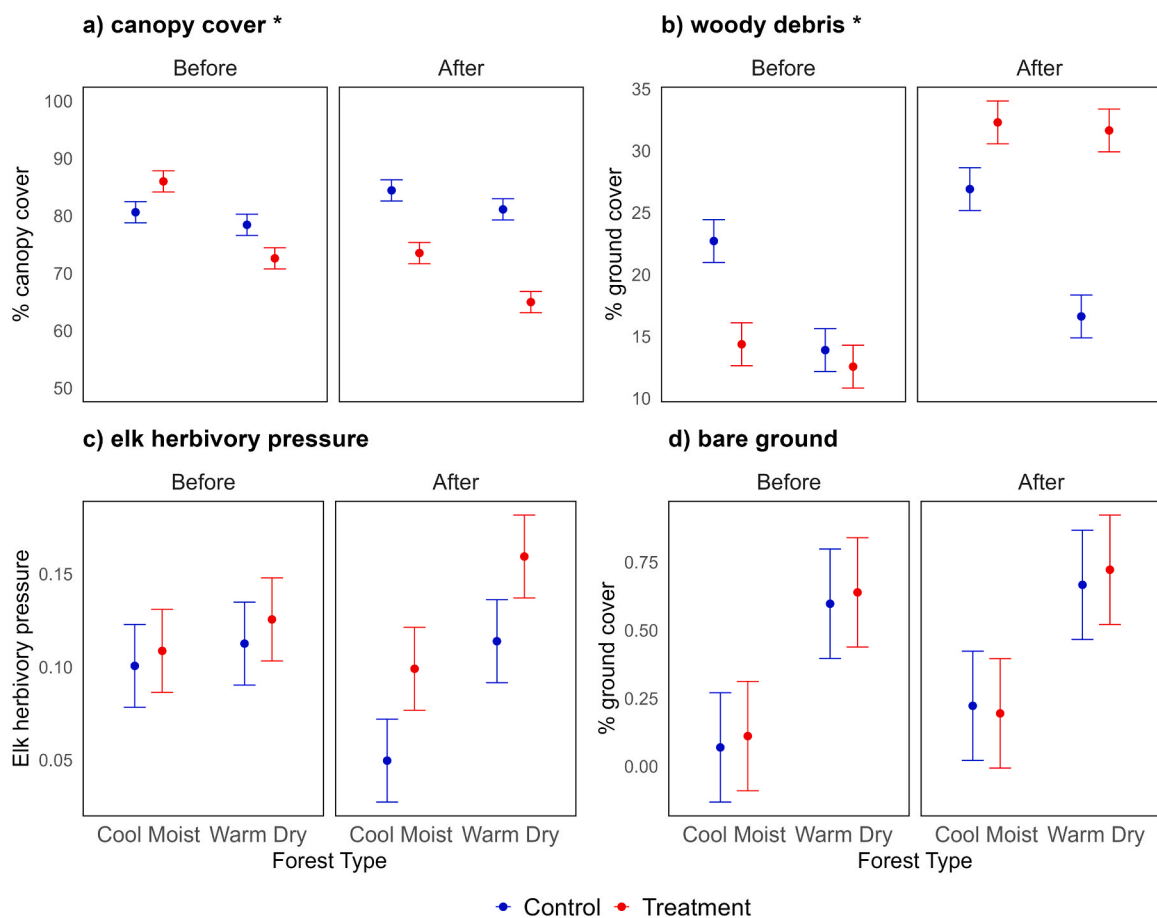


Fig. 2. Environmental responses to thinning: a) canopy cover, b) percent of ground cover as woody debris, c) elk herbivory pressure, and d) percent of ground cover as bare ground. Plots show estimated marginal means and 90% confidence intervals. Significant BACI effect of thinning is indicated by an asterisk.

traps, 57 species or morphospecies represented 95% of individuals collected. Of these 57 species, we were able to determine or infer nesting habits for 50 species, representing 87% of all specimens collected. Of these 50 species, we determined that 33 were soil or soil surface nesting (6595 individuals), 11 were wood nesting (1435 individuals), and 6 were cavity nesting (869 individuals). See Table S5 for details about nesting characteristics.

3.2. Environmental responses to thinning

As expected, canopy cover was significantly lower in treatment sites relative to control sites after thinning, and the magnitude of the effect depended on forest type, with a larger reduction in canopy cover in cool moist forests compared to dry forests (Table 1, Fig. 2a). Thinning also increased the amount of large woody debris in treatment sites relative to control sites (Table 1, Fig. 2b). Although elk pressure increased in sites after thinning, the effect was not statistically significant (Table 1,

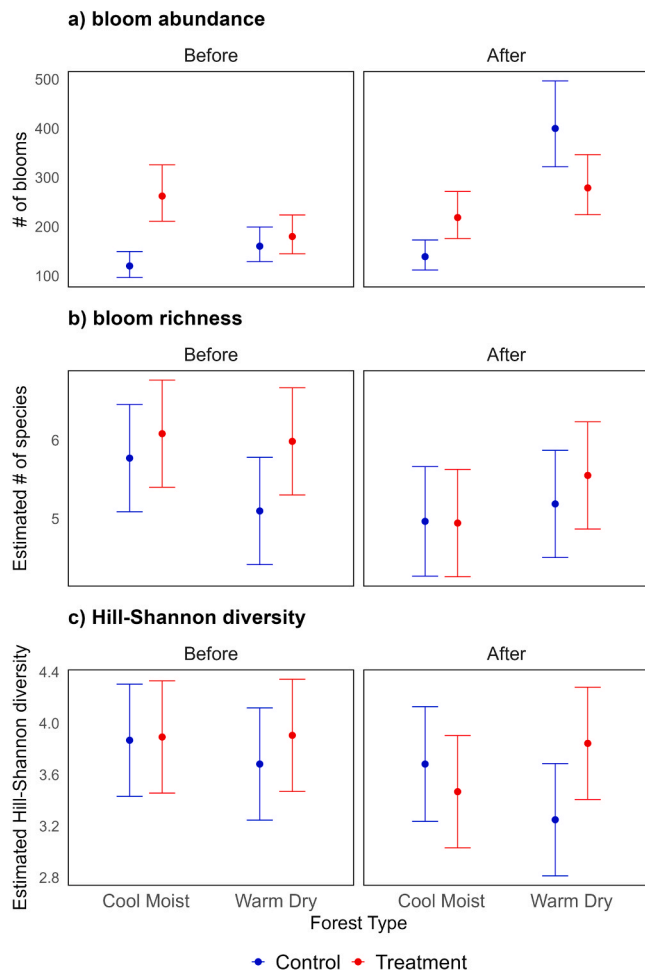


Fig. 3. Bloom responses to thinning by forest type: a) bloom abundance, b) bloom richness, and c) Hill-Shannon bloom diversity. Plots show estimated marginal means and 90% confidence intervals.

Table 2

Plant indicator species for each group associated with the before-after control-impact design. Species with an indicator value (IV) of 20 or greater and a p-value of less than 0.10 are included in this table.

Season-Time Combination	Treatment Group	Species	IV	P
Spring, Before Thinning	Control	<i>Calochortus elegans</i>	30.3	0.003
		<i>Lupinus sp.</i>	24.6	0.003
	Treatment	<i>Fragaria vesca</i>	64.7	0.0002
		<i>Mahonia repens</i>	44.3	0.0008
		<i>Fragaria virginiana</i>	43.8	0.0006
		<i>Thermopsis montana</i>	41.8	0.0002
Spring, After Thinning	Control	<i>Erythronium grandiflorum</i>	39	0.003
		<i>Dodecatheon pulchellum</i>	35.1	0.006
		<i>Myosotis stricta</i>	23.8	0.04
		<i>Claytonia lanceolata</i>	21.1	0.002
	Treatment	<i>Arctostaphylos uva-ursi</i>	38.6	0.01
		<i>Taraxacum officinale</i>	38.2	0.001
Summer, Before Thinning	Control	<i>Sedum stenopetalum</i>	29.2	0.002
	Treatment	<i>Achillea millefolium</i>	31.1	0.02
		<i>Thermopsis montana</i>	29.3	0.01
		<i>Lupinus sp.</i>	26.6	0.04
		<i>Rosa sp.</i>	23.7	0.05
		<i>Madia glomerata</i>	22.3	0.03
Summer, After Thinning	Control	<i>Calochortus elegans</i>	56.1	0.0002
		<i>Collinsia parviflora</i>	31.2	0.04
		<i>Microseris nutans</i>	30	0.05
	Treatment	<i>Myosotis stricta</i>	21.6	0.04

Fig. 2c). The amount of bare ground did not change in response to thinning; however, bare ground generally occurred at very low levels across the study (Table 1, Fig. 2d).

3.3. Blooming plant responses to thinning

Bloom abundance was, on average, higher in treatment sites than control sites, regardless of time period (i.e., before or after application of thinning), but thinning did not increase bloom abundance in treatment sites relative to control sites (Table 1, Fig. 3a). The sampling coverage used for richness and diversity estimates of blooming plants was 90% and blooming plant richness (Fig. 3b) and Hill-Shannon diversity (Fig. 3c) were also not affected by thinning (Table 1, Fig. 3b and c).

We identified significant indicator species for control and treatment sites before and after thinning in spring and summer. Indicator species for control sites (two in spring and one in summer) and treatment sites (four in spring and five in summer) before thinning was implemented suggest baseline differences in community composition existed in these sites before treatment. After thinning, two spring blooming species and one summer species were associated with treatment sites (Table 2). Although blooming plant community composition differed by treatment type (PERMANOVA, $F_{1, 188} = 3.1$, $p = 0.0002$) and time (PERMANOVA, $F_{1, 188} = 3.4$, $p = 0.0002$), the lack of a significant interaction between treatment type and time (PERMANOVA, $F_{1, 188} = 0.8$, $p = 0.7$) indicates no effect of thinning on plant community composition.

3.4. Bee responses to thinning

Thinning increased the number of bees collected in both vane traps and pan traps with some indication that this effect varied by forest type for vane traps, but not for pan traps (Table 1, Fig. 4a,b). The sampling coverage of bees used for richness and diversity estimation was 37%. Thinning increased bee species richness but this effect depended on forest type, with bee species richness increasing in cool moist, but not warm dry forests (Table 1, Fig. 4c). Although we did not observe a statistically significant interaction between forest type and the BACI effect for Hill-Shannon diversity ($p = 0.11$), the effect was much more pronounced in cool moist forests than in warm dry forests (Table 1, Fig. 4c, d). In addition, some nesting guilds of bees responded to thinning. Wood nesting bees increased in abundance in treatment sites after thinning, but only in cool moist forests (Table 1, Fig. 5a). Soil nesting bees, the most common bees in our sites, also became more abundant in treatment sites in both forest types after thinning (Table 1, Fig. 5b). Cavity nesting bees did not respond to thinning but were more abundant in control sites in cool moist forests both before and after thinning (Table 1, Fig. 5c).

Indicator species analysis revealed six soil nesting bee species and one wood nesting species that were strongly associated with thinned, spring sites, and six soil nesting, and three wood nesting bee species strongly associated with thinned, summer sites (Table 3). Control sites generally had more indicator species before thinning was applied and treatment sites had more indicator species after thinning than did control sites (Table 3). Bee community composition differed by treatment type (PERMANOVA, $F_{1, 188} = 1.7$, $p = 0.04$) and time (PERMANOVA, $F_{1, 188} = 8.4$, $p = 0.0002$) and by the interaction of treatment type and time (PERMANOVA, $F_{1, 188} = 1.6$, $p = 0.04$), suggesting that thinning altered bee community composition.

3.5. Blooming plant and bee interactions

In spring bee-plant networks, we found that *Arctostaphylos uva-ursi* was visited by a higher abundance of bees than other plants and that *Bombus bifarius* was the most commonly collected flower visitor (Fig. 6). Interestingly, both *A. uva-ursi* and *B. bifarius* were significant indicators of thinned sites as determined by plant transect and bee trapping data (Tables 2 and 3). In summer bee-plant networks, *Calochortus elegans* and

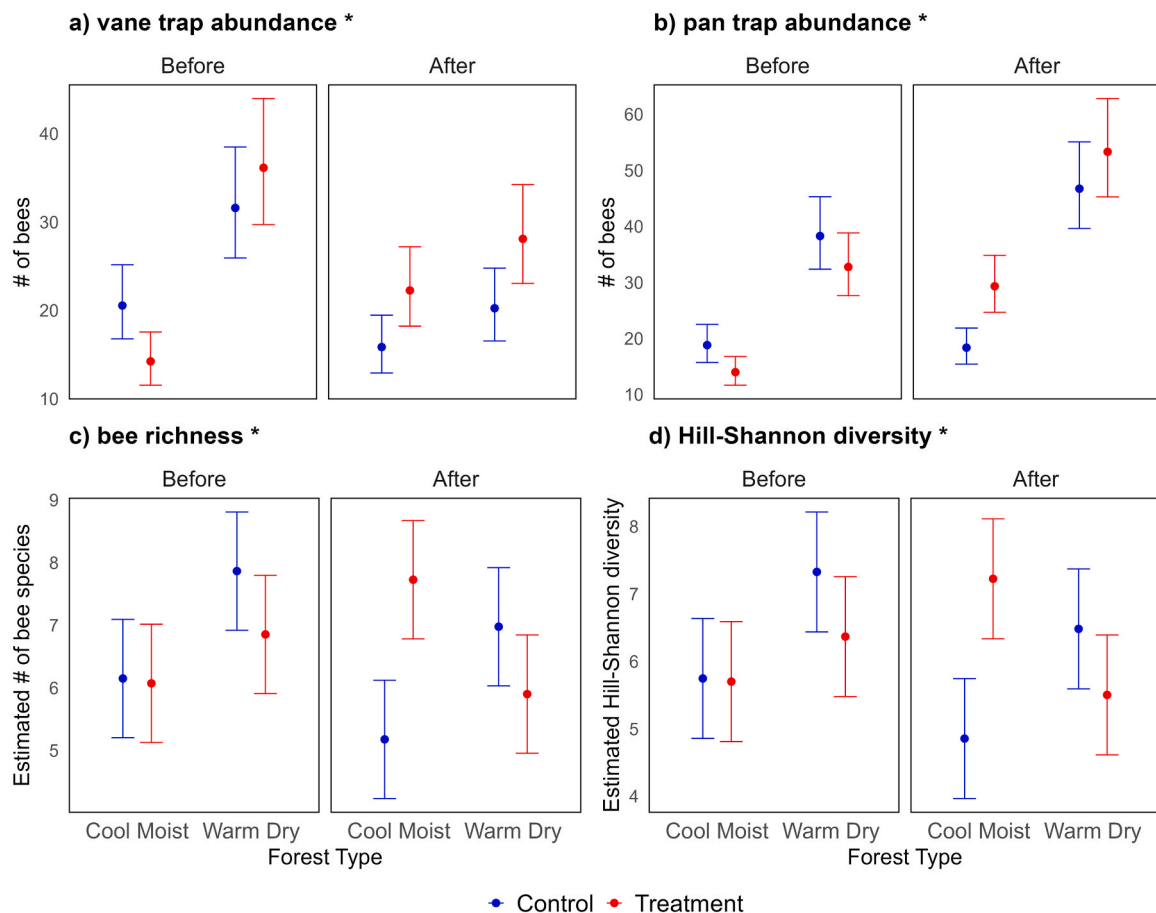


Fig. 4. Bee responses to thinning by forest type: a) abundance of bees in vane traps, b) abundance of bees in pan traps, c) bee richness, and d) Hill-Shannon bee diversity. Plots show estimated marginal means and 90% confidence intervals. Significant BACI effect of thinning is indicated by an asterisk.

purple lupines (*Lupinus burkei* and *L. spp.*) were the most visited plants and the most common bees collected in hand nets were *B. flavifrons* and *B. mixtus* (Fig. 6). *C. elegans* was a significant indicator of control sites before thinning in spring and control sites after thinning in summer (Table 2). In summer, we collected 10 or more bees of several significant indicators of thinned sites, including *Dufourea dilatipes*, *Halictus rubicundus*, *Osmia atrocyanea*, *O. densa*, and *O. juxta* (Table 3).

4. Discussion

Our study used a before-after, control-impact (BACI) experimental design with specific manipulative treatments allowing us to draw robust, causal conclusions about the effects of thinning. Finally, our study examined how the effect of thinning differs between forest types across small spatial scales. Our study demonstrated that fuels reduction thinning in PNW forests strongly influenced bee communities, and that some bee responses differed by forest type, with effects only observed in cool moist but not warm dry forests. We also found that thinning decreased canopy cover, increased woody debris and did not influence bare ground availability. In contrast, blooming plants were unaffected by thinning. We postulate that the response of bees to thinning may be mediated by effects on nesting habitat or other environmental variables (e.g., canopy density), rather than by changes in abundance or species richness of blooms.

4.1. Thinning and environmental variables

We found that thinning altered canopy cover and woody debris. In addition, we found some evidence that thinning was associated with

higher levels of elk herbivory. These environmental variables are known to play a role in shaping bee communities in these forests, primarily through their effects on floral resources and nesting habitat availability (Mitchell et al., 2025).

Consistent with our predictions and other studies (e.g., Davies et al., 2023; Favorito et al., 2023), we found that thinning decreased canopy cover. However, the magnitude of the effect depended on forest type, with greater reductions in canopy cover in cool moist forests relative to warm dry forests. This is likely due to higher canopy cover in cool moist forests than warm dry forests prior to treatment (Fig. 2a; Mitchell et al., 2025). Given the prior history of logging in treatment sites within NE in the 1990s (Stewart et al., 2011; Ruprecht et al., 2023), these results suggest that overstory trees grow more rapidly in cool moist forests.

We also observed an increase of woody debris in response to thinning that was similar between forest types (Fig. 2). The thinning approach used in our study area was lop and scatter, in which fallen trees are cut into chunks and roughly spread across the understory – a practice which directly increases the amount of large woody debris on the ground. Other forms of thinning might not result in similar increases in woody debris. For instance, lop and scatter thinning produces more woody debris than do thin plus burn or thin plus mastication treatments (Piqué and Doménech, 2018; Urza et al., 2023). In our study, we did not find a significant effect of thinning on bare ground, even though we had hypothesized that lop and scatter thinning would reduce bare ground. This is likely because bare ground was present at very low levels prior to thinning, meaning the probability that scattered debris from thinning would cover existing bare ground was low. The type of thinning approach adopted is likely to influence how ground cover responds. For instance, bare ground is expected to increase in treatments where debris

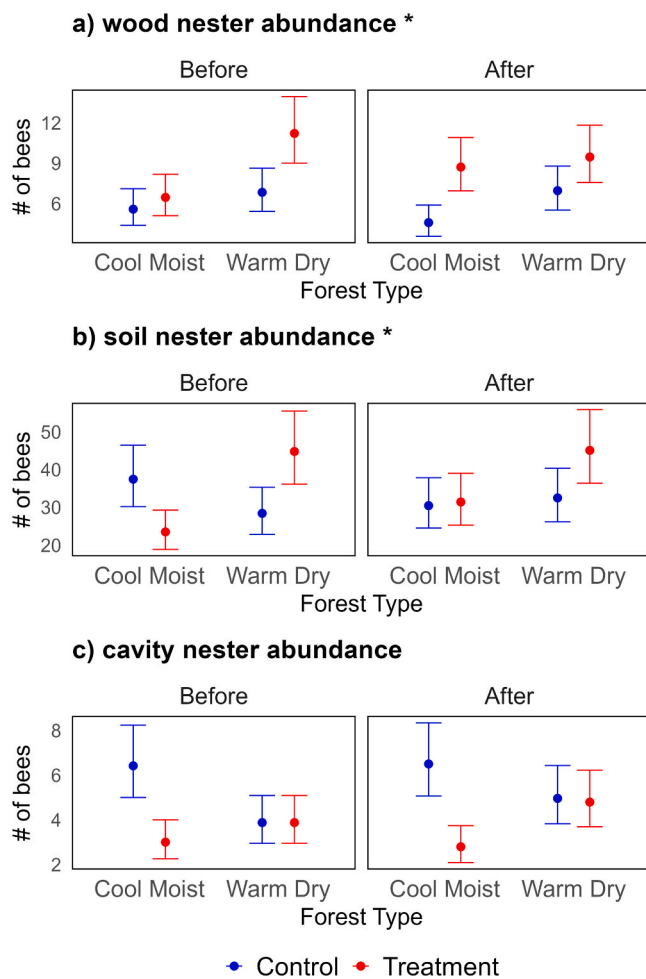


Fig. 5. Abundance of bee nesting guild (pan and vane traps combined, top 87% of bees included) in response to thinning: a) wood nesting, b) soil nesting, and c) cavity nesting bees in cool moist and warm dry forests. Plots show estimated marginal means and 90% confidence intervals. Significant BACI effect of thinning is indicated by an asterisk.

from thinning is burned (Goodwin et al., 2018), and pile burning may have long-lasting effects on bare ground, where intensely heated soils under burn piles remain bare for years (Barefoot et al., 2019). Changes to ground cover composition, particularly bare ground and coarse woody debris, may mediate the positive effects of thinning on bee communities (discussed below), as these are two important nesting substrates for many native bees.

While not significant, we also noted that elk changed their movement patterns in response to thinning during our sampling period (Fig. 2); however, this effect may depend on overall elk density (Ruprecht et al., 2023). After thinning, elk tended to spend more time in thinned sites relative to control sites in both warm dry and cool moist forests. Elk consume some of the same plants that bees forage upon (DeBano et al., 2016) and thus can reduce the abundance of blooms of those species, with cascading effects on bee species richness (DeBano et al., 2025; Glenn et al., In Review). Therefore, changes in elk habitat selection patterns resulting from thinning could influence plant communities that bees depend upon. Our study highlights the importance of continued research that focuses on how thinning affects the larger animal community, including native ungulates, to better understand the influence of this common management approach on trophic webs involving native pollinators.

4.2. Thinning and blooming plant communities

Contrary to our hypotheses, we did not detect significant effects of thinning on bloom abundance, richness, diversity, or community composition. Although we found that bloom communities differed between treatment and control sites and that these communities varied across time, there was no significant interaction between treatment type and time. Thus, thinning treatments alone did not influence blooming plant communities. Given that many other studies have detected overall positive effects of thinning on floral resources (e.g., Campbell et al., 2018; Chase et al., 2023a; Davies et al., 2023; Favorito et al., 2023; Cole et al., 2025), this lack of affect in our study system was surprising. One possible explanation is that lop and scatter thinning produces a significant amount of woody debris, including fine materials (e.g., pine needles), that may initially cover small understory plants, thereby reducing their ability to produce blooms. When these fine materials eventually degrade, blooming understory plants may then be able to take advantage of the higher light availability associated with thinned canopies. Unlike our study, which was performed during the first two years post-treatment, most studies that have demonstrated positive effects of thinning on floral resources conducted sampling more than two years after treatment applications (e.g., Lindh, 2005; Neill and Puettmann, 2013; Davies et al., 2023; Cole et al., 2025). If monitoring were continued beyond two years post-treatment in our study system, bloom responses may become more evident as thinning debris degrades. This highlights the importance of longer-term monitoring on the effects of thinning on blooming plants in this system. The lack of bloom response may also be related to elk herbivory, given that elk tended to spend more time in thinned sites than control sites after treatment.

4.3. Bee responses to thinning

Contrary to blooming plants, we found that bee community responses were consistent with our hypotheses, i.e., that thinning changed bee community composition and increased the abundance, species richness, and diversity of bees; however, these effects were more frequently detected and pronounced in cool moist forest types. In general, this finding agrees with expectations that forested systems with less dense overstory canopies provide better habitat for bees (Hanula et al., 2016; Ulyshen et al., 2024). Similar patterns have been observed across a wide range of North American forests, including studies in eastern deciduous forests (Campbell et al., 2018), southern loblolly pine forests (Favorito et al., 2023), and even in western conifer forests (Davies et al., 2023; Cole et al., 2025). While the pattern remains consistent across North American forests, many studies found concomitant positive associations with thinning and blooming plants (Campbell et al., 2018; Chase et al., 2023; Davies et al., 2023; Favorito et al., 2023; Cole et al., 2025), which we did not find, suggesting that floral resource availability is not the only way that bees benefit from fuels reduction thinning. Other variables that forest thinning can affect include the availability of nesting substrates and temperature.

One limitation of existing trapping methods is that trap efficiency may be influenced by the visibility or brightness of traps (Baird and Dacke, 2016) or the quality of surrounding habitat (e.g., Kuhlman et al., 2021; Westerberg et al., 2021; Krahner et al., 2024). To address these limitations, various authors have suggested using multiple trapping methods, each of which may have different biases (e.g., Prendergast et al., 2020; Saunders et al., 2021), as we have done. Typically, trap efficiency issues should primarily affect abundance response, not richness estimates that account for sample coverage, or community composition. Since we found significant responses in all three measures of bee communities, we expect that the responses we are seeing are not due to trapping limitations.

Thinning can increase the amount of dead wood on forest floors (Piqué and Doménech, 2018) and can alter soil microclimates, potentially protecting soils from extreme temperatures (Golden and

Table 3

Bee indicator species by season and treatment group. Species with an indicator value (IV) of 20 or greater and a p-value of less than 0.10 are included in this table.

Season-Time Combination	Treatment Group	Species	IV	P	Nesting guild
Spring, Before Thinning	Control	<i>Lasioglossum olympiae</i>	30.2	0.01	Soil
		<i>Lasioglossum (Hemihalictus) sp. 1</i>	28.5	0.006	Unknown
		<i>Dufourea dilatipes</i>	24.2	0.004	Soil
		<i>Osmia tristella</i>	22.7	0.007	Wood
		<i>Andrena nivalis</i>	20.6	0.03	Soil
	Treatment	<i>Halictus farinosus</i>	28.7	0.1	Soil
		<i>Lasioglossum egregium</i>	23.6	0.008	Soil
		<i>Bombus bifarius</i>	37.2	0.005	Cavity
		<i>Melecta pacifica</i>	27.5	0.004	Parasite
		<i>Osmia juxta</i>	34.9	0.002	Wood
Spring, After Thinning	Control	<i>Lasioglossum cooleyi</i>	34.8	0.005	Soil
		<i>Andrena nigrihirta</i>	33.6	0.01	Soil
		<i>Halictus rubicundus</i>	32.4	0.02	Soil
		<i>Andrena sp.</i>	30	0.002	Soil
		<i>Lasioglossum nevadense</i>	29.7	0.03	Soil
	Treatment	<i>Lasioglossum punctatoventre</i>	21.5	0.05	Soil
		<i>Hoplitis fulgida</i>	34.4	0.001	Wood
		<i>Lasioglossum egregium</i>	30.2	0.02	Soil
		<i>Osmia tristella</i>	27.3	0.005	Wood
		<i>Osmia bella</i>	24.6	0.002	Soil
Summer, Before Thinning	Control	<i>Bombus mixtus</i>	39.2	0.0006	Cavity
		<i>Hoplitis albifrons</i>	35.1	0.001	Wood
		<i>Osmia bucephala</i>	23.7	0.06	Wood
		<i>Lasioglossum trizonatum</i>	35.3	0.002	Soil
		<i>Andrena sp.</i>	20	0.005	Soil
	Treatment	<i>Andrena nigrocaerulea</i>	41.4	0.0002	Soil
		<i>Halictus farinosus</i>	39.9	0.0006	Soil
		<i>Osmia densa</i>	39.3	0.0006	Wood
		<i>Osmia juxta</i>	38.8	0.0002	Wood
		<i>Halictus rubicundus</i>	37.5	0.005	Soil
Summer, After Thinning	Control	<i>Dufourea dilatipes</i>	30.3	0.004	Soil
		<i>Osmia atrocyanea</i>	25.8	0.04	Wood
		<i>Halictus tripartitus</i>	24	0.1	Soil
		<i>Andrena prunorum</i>	22.3	0.02	Soil
	Treatment				

Hutchinson, 2015; Swanson et al., 2023). Prior pollinator studies have found that thinning can increase the availability of woody debris (Fortuin and Gandhi, 2021; Chase et al., 2023) and bare ground (Davies et al., 2023; Favorito et al., 2023), suggesting that thinning could influence various nesting guilds of bees differently. We observed that wood and soil nesting bees were more abundant in thinned sites, possibly due to changes in the availability of nesting substrates or the conditions of existing substrates. In contrast, we did not see higher abundance of cavity nesting bees in thinned sites. This suggests that thinning may improve habitats for wood and soil nesting bees, but not predictably for cavity nesting bees. This finding is supported by our indicator species analyses which showed that all indicator species of post-treatment thinned sites were either soil or wood nesting bees.

The increase in wood-nesting bee abundance in response to thinning depended on forest type and was only evident in cool moist forests (Fig. 5). This may be due to the fact that in cool moist forests, before thinning, woody debris was much lower in treatment sites relative to control sites, while in warm dry forests, the amount of woody debris present in treatment and control sites before thinning was similar. This may have amplified the before/after difference in cool moist forests. At least one other study found that wood nesting bees increased with volume of woody debris (Fortuin and Gandhi, 2021) and several suggested that increased woody debris availability was likely an important factor driving community composition following thinning (Chase et al., 2023; Favorito et al., 2023).

We also saw more soil nesting bees in thinned sites but did not find statistical support that this effect depended on forest type. This result was surprising given that bare ground was unaffected by thinning treatments. However, although thinning may not increase the amount of exposed soil surface, it may improve soil nesting conditions in other ways, such as through temperature-mediated effects. For example, temperature can influence the ability of bees to fly (e.g., Corbet et al.,

1993; Stone, 1994; Wilmer and Stone, 2004) and can alter larval and pupal development (Antoine and Forrest, 2021) and affect emergence timing (Cane, 2021). Forest thinning can increase soil temperatures (Ma et al., 2010; Zhang et al., 2018), which can affect ground nesting bees. Forest thinning is also associated with higher air temperatures (Ma et al., 2010), which can influence bee communities more broadly, but may have outsized effects on smaller bees. Many ground nesting bees are small, and both increased air and soil temperatures may be associated with the higher abundance of soil nesting bees we observed in thinned sites. In our study system, bee abundance, richness, and diversity were positively associated with an index for heat load based on slope, aspect, and latitude (Mitchell et al., 2025), suggesting that higher temperatures resulting from thinning may positively influence bees by increasing soil and air temperatures relative to control sites.

Cavity nesting bee abundance remained relatively unchanged by thinning, suggesting that these bees neither benefit nor are harmed, by thinning. In our study, cavity nesting bees were entirely represented by bumble bees (Table S3). Bumble bees are large-bodied and capable of flying long distances and are thus less likely to be affected by localized habitat changes than smaller bees (Coutinho et al., 2018). As large, hairy bees, bumble bees are also less likely to be influenced by temperature-mediated changes, as they are more tolerant of cooler temperatures (Peters et al., 2016).

4.4. Interactions between plants and bees

Indicator species analyses paired with plant-pollinator networks provide further support to our conclusion that changes in nesting habitat, rather than floral resources, are driving bee responses to thinning in this system. For instance, several indicator species for thinned sites were wood nesting species, including *Osmia atrocyanea*, *O. densa*, and *O. juxta* that likely benefited from increased availability of woody

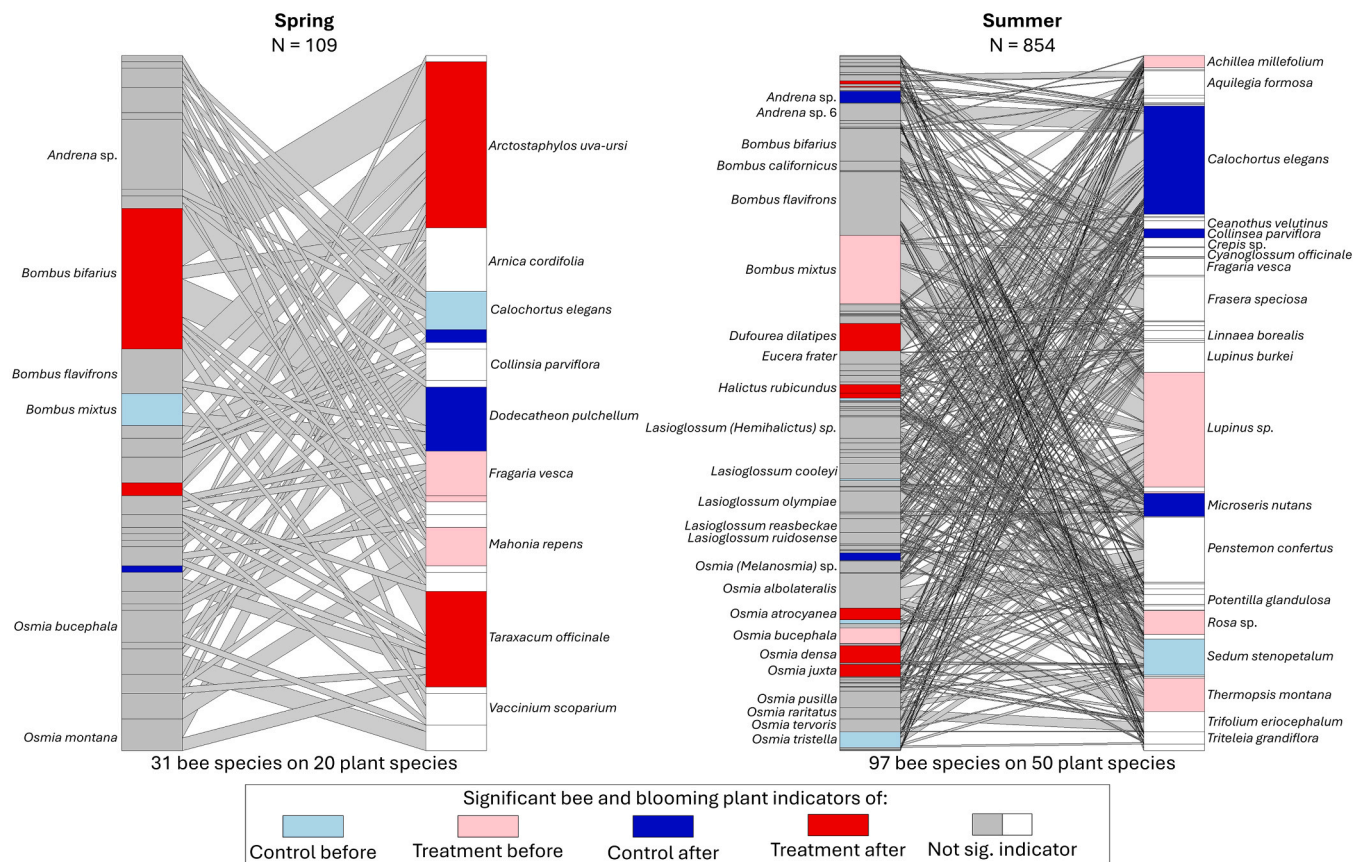


Fig. 6. Bipartite networks of bees and plants in spring and summer: plots derived from hand netting efforts in the spring (16.25 h of netting) and summer (49 h of netting). In the spring plot, named species are represented by at least 5 individuals and in the summer plot species are named if at least 10 individuals were collected. Color coding is determined by indicator species analyses performed on transect data (blooming plants) and on bees collected with passive trapping (see [Tables 1 and 2](#)).

debris. All three species are generalist foragers, and we collected all at relatively high rates on a wide variety of plant species. For example, *O. densa* was collected on 11 different plant species ([Table S4](#)). Generalist foragers are less likely to be impacted by decreases in any particular blooming species in thinned sites.

Another bee species that was an indicator of thinned sites and collected in handnet sampling was *Dufourea dilatipes*. Unlike the three *Osmia* species, *D. dilatipes* is an apparent specialist, with almost all individuals collected on *Calochortus elegans*, a small perennial lily that is an indicator of control sites. Although *C. elegans* was present in all site types, it was less abundant in treatment sites after thinning, relative to control sites ([Table S1](#)). In contrast, *D. dilatipes* increased in treatment sites, particularly in the second year after thinning. These opposite trends in abundance for this bee and its primary floral associate suggest that *D. dilatipes* was not limited by floral resources in thinned sites and its increase in those sites may be due to other physical changes associated with thinning. *D. dilatipes* is a soil nesting bee and decreased canopy cover and increased woody debris may have resulted in changes to soil conditions that improved nesting habitat for this species ([Golden and Hutchinson, 2015](#); [Swanson et al., 2023](#)).

5. Conclusions

Overall, we found that fuels reduction thinning significantly increased bee abundance, richness, and diversity, with some groups of bees, such as soil and wood nesters, benefiting from thinning more than others. These increases appeared to be moderated by environmental conditions (e.g., canopy cover and nesting substrate), rather than by bloom availability. We did not detect effects of thinning on blooming

plants, potentially because of the lop and scatter process, which may cover blooming plants on the forest floor in the first few years after treatment. In addition, increased elk use of thinned sites may have partially offset positive effects of thinning on blooms that would have otherwise been observed. Further studies of bee responses to various debris management strategies (e.g., lop and scatter, mastication, burning) and of how ungulates respond to thinning are a high priority.

Our study also illustrates the power of using a BACI experimental design, which allowed us to draw robust conclusions and infer causal relationships between measured responses and thinning. We know of no other study on thinning effects on bee and bloom communities that used a BACI design; rather, most studies rely on a space-for-time approach. Space-for-time methods work well in ecology since more complex experimental designs (like BACI) are logistically challenging, expensive, and time-consuming to implement. However, space-for-time studies are less robust in terms of inferences about causal relationships because pre-treatment conditions are unknown. Complex site histories may result in persistent differences between treatment and control sites that are often unrelated to the current treatments being implemented. Taken as a whole, our study suggests managing pollinators and wildfire hazard can be complementary activities, with fuels reduction thinning likely to improve habitat for bees.

CRedit authorship contribution statement

Skyler Burrows: Writing – review & editing, Resources, Methodology, Data curation. **Sandra J. DeBano:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Mary M.**

Rowland: Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Scott R. Mitchell:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2026.123896](https://doi.org/10.1016/j.foreco.2026.123896).

Data availability

Data will be made available on request.

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