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ORIGINAL PAPER

Blooming Plant and Bee Communities in an Inland Pacific Northwestern Forest Vary by Forest Type, Season, and Environmental Factors

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Abstract

Native bees are diverse and efficient pollinators that have been studied in many forested regions of the United States. However, such studies are rare in the inland Pacific Northwest. To address this gap, we examined 1) how blooming plant and bee communities differed between two forest types (warm-dry and cool-moist) in spring and summer and 2) how a suite of environmental conditions influenced these communities each season. We collected 4,469 bees from 122 species/morphospecies over two years. Bees were typically twice as abundant in warm-dry versus cool-moist forests. In addition, bloom and bee species composition in each forest type and season were distinct. Canopy density was negatively related to bloom responses in spring and summer. Heat load had a positive effect on bees in both seasons. Surprisingly, the presence of elk was positively associated with bee responses in summer. Groundcover and bloom availability effects on bees varied seasonally. Blooming plant and native bee communities of inland Pacific Northwest forests vary over relatively small spatiotemporal scales, implying that forest type and season are important considerations when planning management actions for achieving pollinator conservation goals in these forests. Our study broadly suggests that various common forest management practices that influence canopy coverage (e.g., fuel reduction thinning, restoration) and large herbivore densities will likely influence blooming plants and bees. In many cases, forest management may operate synergistically with native bee conservation. Still, a high priority for future research is understanding how blooming plant and bee communities respond directly to management actions.

Keywords Forest pollinators · Community ecology · Biodiversity · Conservation · Entomology

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Introduction

Forests provide habitat for wildlife, including native bees, which are essential pollinators in most terrestrial ecosystems and contribute substantially to biodiversity (Hanula et al. 2016; Orr et al. 2021; Ulyshen et al. 2023). Forests are increasingly recognized as valuable bee habitats and are a high priority research area (Winfree et al. 2006; Rhoades et al. 2018; Rivers et al. 2018b; Ulyshen et al. 2023, 2024). Native bees have been studied in many forests in the United States (Hanula et al. 2016), including southeast pine plantations (e.g., Loy et al. 2020), deciduous forests of the Midwest and east coast (e.g., Grundel et al. 2010; Roberts et al. 2017; Chase et al. 2023), and pine forests in the Rocky Mountains (e.g., Gelles et al. 2022; Davies et al. 2023). In the Pacific Northwest (PNW), forests are widespread (Halpern and Spies 1995; Bansal et al. 2017) and recent studies have investigated native bees in these forests (Galbraith et al. 2019; Rivers and Betts 2021; Zitomer et al. 2023). However, most PNW forest pollinator studies have been conducted west of the Cascades and have focused on early successional forests, leaving a paucity of information regarding forests of the inland PNW. Differences between western and inland PNW forests may limit the applicability of research results from western PNW landscapes to inland regions (Halpern and Spies 1995; Bansal et al. 2017).

Native bees are diverse, with approximately 3,000 species in the western United States (Carril and Wilson 2023), and an estimated 700 species in Oregon (Best et al. 2021). Bee community species composition varies seasonally (Kimoto et al. 2012; DeBano et al. 2016), with some species active early in the season, and others active later. All bees rely on pollen, nectar, and/or floral oils for nest-provisions and adult nutrition, with species varying from pollen specialists to generalists (Michener 2007). Blooming plants also vary seasonally, and their availability is often positively related to bee abundance and richness (Hyjazie and Sargent 2022). In addition to floral resources, bees need nesting substrates. In North America, most bees are ground-nesting, although other species nest in cavities, stems, or bunchgrass (Harmon-Threatt 2020), and differences in nesting substrate availability can affect bee community composition (Potts et al. 2005; Grundel et al. 2010; Sardiñas and Kremen 2014). In forests, variation in environmental conditions can influence bees directly (e.g., through effects on temperature and moisture) or by affecting the availability of forage plants and nesting resources.

Inland Northwest forests tend to be drier, experience more extreme temperatures, and have a shorter fire return interval than western PNW forests (Daubenmire 1969; Juran 2017; Reilly et al. 2017). Although many forests west of the Cascades are dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) (Bansal et al. 2017), inland Northwest forests are often dominated by ponderosa pine (*Pinus ponderosa*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), grand fir (*Abies grandis*), Engelmann spruce (*Picea engelmannii*) and Douglas-fir (Long et al. 2009). These differences influence plant communities, including floral resources available to pollinators (Daubenmire 1969). Habitat heterogeneity (e.g., variation in canopy

density, temperature, moisture) also occurs within these larger forest types, and stands within a forest type may differ from each other. For example, inland PNW forests vary at small scales (Ohmann and Spies 1998) and numerous classification systems attempt to capture this variability (e.g., Johnson and Clausnitzer 1992; Powell et al. 2007) including systems that use a "temperature-moisture" approach. In this approach, some forest stands experience cooler, wetter conditions and others are warmer and drier (e.g., "plant association groups" sensu Strickler 1965; Powell 2007). Thus, describing how broad regional (inland vs western PNW) and localized (within the inland PNW) patterns influence blooming plants and bees across multiple seasons is a crucial step for inland PNW forest pollinator conservation.

In addition to describing spatial and temporal patterns in blooming plant and bee communities in inland PNW forests, identifying environmental factors that influence them is a high priority. Environmental variables can affect bees indirectly by altering floral and nesting resources or directly by affecting bees themselves. For example, topography and canopy density influence site characteristics such as water balance and solar radiation, which can affect plants that provide food and nesting resources (Anderson et al. 1969; Weiss et al. 1988; Dahlgren et al. 2007; Murphy et al. 2020; Ulyshen et al. 2024). These factors may also impact bees directly through effects on microclimate that influence thermoregulation (Willmer and Stone 1997; Doherty et al. 2021). In addition, seasonal differences in temperature and precipitation can interact with environmental factors that affect bees. For example, in spring, north-facing slopes may not warm adequately for some bee species, while in summer, those sites may remain cool and moist, allowing for higher abundance of blooms.

Other factors, such as native ungulate activity (e.g., elk, *Cervus canadensis*), likely affect bees through their impact on food and nesting resources. For example, ungulates can alter understory plant structure (Steward et al. 2009; Averett et al. 2017), which can affect nesting (e.g., stems) and floral resource availability. Although ungulates can reduce floral abundance by directly consuming or trampling plants (Gómez 2005), their activity can also increase bloom abundance of some plants by stimulating flowering (Paige and Whitman 1987). In the PNW, the consumption of flowers by deer (*Odocoileus* spp.) and elk appears to negatively affect native bees by reducing flowers of species preferred by bees (Beckett et al. 2022; DeBano et al. In Press).

Although some studies have examined how environmental variables affect blooming plants and native bees in the inland Northwest, these studies focused on open habitats (e.g., DeBano et al. 2016; DeBano et al. In Press; Roof et al. 2018; Mitchell et al. 2023) and except for Oja (2020), have not described communities in inland PNW forests. To our knowledge, no studies have examined how seasonality and environmental variables affect blooming plant and bee communities in forested areas in the inland PNW. We conducted analyses to address larger scale questions pertaining to forest type and season and additional analyses on smaller-scale variation, providing insights into the mechanisms within forest types that structure bee and blooming plant communities in forests of the inland PNW. Specifically, the goals of our study were to:

1. Describe blooming plant and bee communities and how they vary seasonally and between two inland PNW forest types (warm-dry vs. cool-moist).
2. Investigate relationships between environmental factors and blooming plant and bee communities in spring and summer.

Although forests across the PNW were primarily managed for timber prior to the Northwest Forest Plan, implemented in 1994 (Gaines et al. 2022), many are now managed for additional objectives, including wildlife habitat. Pollinator conservation is a recent area of interest in forest management (DeBano et al. 2016; Hanula et al. 2016) and understanding factors that influence bloom and bee communities is a key step in developing sustainable, regionally-specific forest management plans that incorporate pollinator health (Ulyshen et al. 2024).

Methods

Study Area and Design

We conducted this research in the northeast (NE) study area of the USDA Forest Service Starkey Experimental Forest and Range (Starkey) in 2020 and 2021 (Fig. 1). Starkey has supported forest and rangeland management research since the 1940s (Skovlin 1991; Rowland et al. 1997), and riparian blooming plant and bee communities here have been extensively studied (DeBano et al. 2016; Roof et al. 2018; Arstingstall et al. 2021; Mitchell et al. 2022, 2023). Starkey is located in Union County,

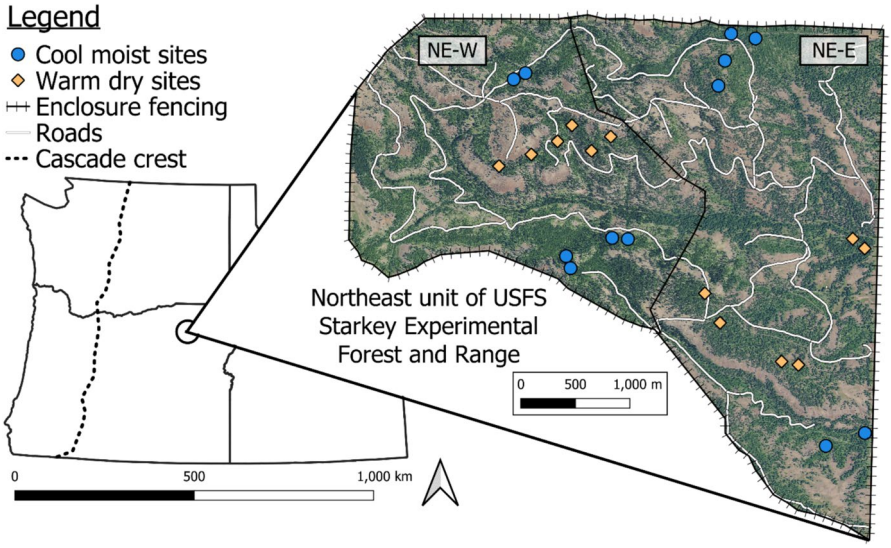

Fig. 1 Map of study area, sampling by forest type, and location of Starkey Experimental Forest and Range in the Pacific Northwest. Each site was sampled twice in 2020 and 2021. The Northeast study area of Starkey is divided by a cross fence to maintain elk populations at two densities

Oregon (45° 14' N, 118° 31' W), and experiences warm, dry summers and cool, wet winters. December is the coldest month (average daily minimum, maximum: −4.2 ° C, 3.7 ° C) and July is the warmest (average daily minimum, maximum: 12.5 ° C, 30.1 ° C) (NOAA 2021). On average, Starkey receives 44.2 cm of precipitation annually, mostly between October and May (NOAA 2021). Four primary plant communities occur in the NE study area, including xeric grasslands, previously logged forests, cool-moist forests (typically north-facing, grand fir dominated), and warm-dry forests (typically south- and east-facing, ponderosa pine dominated) (Stewart et al. 2011). The NE study area of Starkey varies in elevation from 1,140 m to 1,360 m. For a more thorough description of the forests in the NE study area at Starkey, see Ruprecht et al. (2023) and Stewart et al. (2011).

Our study area was surrounded by 2.4 m-tall, game-proof fencing, forming a two-enclosure system (Rowland et al. 1997; Fig. 1). Each spring, elk are released in each enclosure, and although exact numbers vary year-to-year, the eastern enclosure (NE east, 8.4 km^2) was stocked with more elk than the western enclosure (NE west, 6.1 km^2) in 2020 and 2021. In 2020, 16 of 54 (30%) cow elk were fitted with Global Positioning System (GPS) collars in NE east, and 8 of 20 (40%) cow elk in NE west. In 2021, 24 of 48 (50%) cow elk were fit with collars in NE east, and 13 of 16 (81%) cow elk in NE west.

Since our study was the first phase of a longer-term project, we selected 24 sampling sites based on a thinning operation scheduled to occur after our study concluded (Fig. 1). This resulted in 12 paired sites, with one of each pair inside the perimeter of the targeted stand and one adjacent. The average distance between sites was 1,970 m and the average distance between sites within a pair was 213 m. Six pairs were located in NE east and six in NE west (Fig. 1). Within each enclosure, we stratified sites by forest type, with three pairs in warm-dry forest plant association groups (Powell et al. 2007) and three in cool-moist forests (Fig. 1). To sample environmental predictors, blooming plants, and bees, we established an array of five parallel 0.3 m × 20 m belt transects separated by 15 m (Figure S1).

Environmental Variables

We measured environmental variables, including groundcover, canopy density, topography, and an estimate of elk activity at all 24 sites. We sampled groundcover in two seasons, spring (late May – early June) and summer (late June – early July) in 2020 and 2021 using 15 0.6 m × 0.6 m quadrats at the center and ends of each of the five transects (Figure S1). For each quadrat, we estimated the percent cover (estimated to nearest 1%) of litter, small woody debris (< 6 cm diameter), large woody debris (> 6 cm diameter), tree trunks, forbs, grasses, shrubs, bare ground, biological soil crust, bone, animal scat, rocks, and stumps, summed to 100%. We assumed that tree-needle density remained relatively constant between sample periods and measured canopy density once yearly at the same 15 points using a spherical crown densiometer (Lemmon 1957). Groundcover and canopy density measurements were averaged at the site level. Aspect and slope were extracted from a digital elevation model (Goulden et al. 2016)

and used with latitude to calculate a heat load index (estimate of incident solar radiation and warming) for each site. We used the heat load index described in McCune and Keon (2002) as follows:

$$HLI = 0.339 + 0.808 * \cos(L) * \cos(S) - 0.196 * \sin(L) * \sin(S) - 0.489 * \cos\left(\left|\pi - \left|A - \left(\frac{5\pi}{4}\right)\right|\right|\right) * \sin(S)$$

where HLI = heat load index, L = latitude, S = slope, and A = aspect, with L, S, and A in radians.

We estimated potential site-specific elk herbivory pressure, hereafter "elk pressure," with elk detection data using locations obtained from the GPS collars on elk within the two enclosures (Fig. 1). Wisdom et al. (1993) provide details on the capture and handling of elk. All animal capture and handling adhered to current protocols approved by the USDA Forest Service, Starkey Experimental Forest Institutional Animal Care and Use Committee (IACUC No. 92-F-0004) and followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes and Animal Care and Use Committee of the American Society of Mammalogists, 2016). Although the NE east enclosure was stocked with more elk than NE west, elk distributions are heterogeneous, and a wide range of use occurs in each enclosure (Kie et al. 2005; Ruprecht et al. 2023). Since the proportion of collared elk varied between the two enclosures and study years, we estimated site-specific elk pressure each year and season as follows:

$$EHP = \frac{Collar\ fixes_{i,t}}{Collar\ fixes_{e,t}} * \#\ of\ Elk_e$$

where elk herbivory pressure (EHP) = total number of collar fixes within 100 m of site (i) up until the date that site (i) 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.

Plant Sampling

Concurrent with groundcover sampling, we sampled blooming plant communities by counting all blooming stems along belt transects in each site (Figure S1). Such counts are a common way to quantify available floral resources (e.g., Kimoto et al. 2012; DeBano et al. 2016; Roof et al. 2018; Mitchell et al. 2023). We identified all blooming stems to species except for some lupines and wild rose. Lupines were identified as largeleaf lupine (*Lupinus burkei*), sulphur lupine (*Lupinus sulphureus*), or other purple lupines (*Lupinus* spp.), a category that included several similar, challenging to differentiate species. We recorded wild roses as *Rosa* spp. due to challenges with field identification. We followed

common and scientific naming conventions used in the USDA NRCS PLANTS Database (http://plants.usda.gov).

Bee Sampling

Concurrent with blooming plant surveys, we sampled native bee communities using two common passive trapping methods: pan traps and vane traps (Rhoades et al. 2017). At every site, we used an array of 15 240-ml pan traps deployed in five groups of three (one each: fluorescent-blue, fluorescent-yellow, and white) at the center of each transect (Figure S1). These traps were pooled upon collection. In the center of the middle transect, we suspended one vane trap (fluorescent-blue vanes and fluorescent-yellow collection bucket) filled with 250–300 ml of slightly soapy water from a post ~1.5 m above the ground. Traps were deployed on days when weather forecasts called for partly to fully sunny skies and daytime highs above 10 ^{o} C, though springtime conditions are often unpredictable in this region. Because traps were deployed across all sites as rapidly as possible (usually within 24 h), all sites experienced similar weather conditions. We left all traps in the field for 48 h and counted the number of disturbed traps (e.g., tipped by animals) upon collection. Sites were resampled when >9 pan traps were disturbed or when the vane trap was found empty due to disturbance. See Kuhlman and Burrows (2017) for identification methods and complete list of keys used. Pan and vane specimens were pooled for all analyses.

Statistical Methods

Patterns in Environmental Variables, Blooming Plants, and Bees by Forest Type and Season

We described patterns in environmental variables, bloom responses, and bee responses at the 24 sites relative to forest types in spring and summer with means (averaged across sites and years) and 90% confidence intervals. We combined individual groundcover classes into larger, more biologically meaningful categories. The wood groundcover class was a combination of small and large woody debris, stumps, and litter classes and was included as an approximation of available nesting substrates for wood and stem nesting bees (e.g., pithy stems in litter). The forb and shrub groundcover classes were combined to approximate a site's ability to produce blooms. We examined three blooming plant responses: abundance, richness, and diversity, and three bee responses: abundance, richness, and diversity. Bloom abundance was the sum of blooming stems on all transects in a site and bloom richness was the number of blooming taxa encountered along all transects at a site. Bloom and bee diversity were estimated using Hill-Shannon diversity estimated at equal sample coverage (Chao et al. 2014) and hereafter are referred to as "diversity." Bee abundance was the total number of bees caught in pan and vane traps at a site. We estimated bee richness using Chao1 species richness estimation, which estimates total species richness at a site given the occurrence of species

in a dataset and the occurrence of those species in a site (Chao et al. 2014). Hill-Shannon diversity estimated at equal sample coverage and Chao1 bee richness were calculated using the iNEXT package in R (Hsieh et al. 2024). We evaluated spring and summer separately, resulting in 12 total models.

We evaluated variation in community composition of blooming plants and bees relative to forest type and season using nonmetric multidimensional scaling (NMDS) ordinations in which sample units (unique site by season combinations, e.g., site #1, Spring 2020) were plotted in plant and bee species spaces (McCune and Mefford 2018). We used abundance of blooms (counts per species per site) and bees (counts per species per site) in ordinations. Prior to multivariate analyses, we removed all species from the datasets that occurred in <5 sample units, resulting in a plant matrix with 45 plant species in 96 sample units and a bee matrix with 73 bee species in 96 sample units. Removing rare species is one approach to control for sampling effort and reduce noise from rare species when comparing community assemblages (McCune et al. 2002; Sgarbi et al. 2020). For both plant and bee ordinations, we used the following settings: Sorenson's distance measure, a maximum of 500 iterations, randomized starting coordinates, step length of 0.2, 250 runs with real- and randomized-data, and penalties for ties. We evaluated statistical differences in community composition between year, forest type, and season using multi-response permutation procedures (MRPP) with Sorenson's distance measure (Biondini et al. 1985), which evaluates the probability of a grouping by chance and measures within group homogeneity, or an A-value (McCune et al. 2002). We conducted indicator species analyses (Dufrêne and Legendre 1997) to identify taxa most closely associated with each forest type in spring and summer. Indicator species analyses calculate an indicator value ranging from 0 (no indication) to 1 (perfect indication) for species in groups of sites (McCune et al. 2002). We used PC-ORD (McCune and Mefford 2018) for all NMDS, MRPP, and indicator species analyses.

Modeling Effects of Environmental Variables on Blooming Plant and Bee Responses

We analyzed the effects of environmental variables on the three blooming plant and three bee responses using generalized linear mixed effects models. We evaluated blooming plant responses using:

$$\text{Response} \sim \text{EHP} + \text{HLI} + \text{CD} + (1|\text{Block}/\text{Site})$$

and bee responses using:

$$\text{Response} \sim \text{EHP} + \text{HLI} + \text{CD} + \text{BA} + \text{BR} + \text{FS} + \text{WD} + \text{BG} + (1|\text{Block}/\text{Site})$$

where EHP = elk herbivory pressure, HLI = heat load index, CD = canopy density, BA = bloom abundance, BR = bloom richness, FS = forb + shrub cover, WD = wood, and BG = bare ground.

We included the random effect of 1|Block/Site to account for the spatial nesting of paired sites in blocks and for repeated sampling across years. We evaluated seasons separately because bloom and bee communities in Starkey are known to vary between seasons (e.g., DeBano et al. 2016; Mitchell et al. 2023). We assessed

collinearity between predictors prior to analysis to ensure no pair of predictors exhibited an |r|> 0.7 (Dormann et al. 2013) (Figure S2). We also examined the variance inflation factor (VIF) of predictors for each model to ensure no predictors had a VIF > 3 (Zuur et al. 2009).

We used the glmmTMB package in R (Brooks et al. 2017) and relative maximum likelihood for all generalized linear mixed model analyses. Except for bloom abundance, bloom richness, and bee abundance, models were fit with normal distributions. We used a normal distribution for bee richness models since Chao1 richness estimation results in positive and continuous values. We initially fit bloom abundance, bloom richness, and bee abundance models with Poisson distributions, but bloom and bee abundance models were over-dispersed, so we refit these models with negative binomial distributions. Model assumptions were checked and met for all models. Model fit was evaluated using simulated residuals estimated with the DHARMa package (Hartig 2022) and by examining plots of fitted- versus predicted-values.

Results

General Results

During our study we counted 17,341 blooms on 101 plant species (Table S1) and collected 4,469 bees from 122 species or morphospecies (Table S2). We collected 2,205 bees in vane traps and 2,264 bees in pan traps. Of the 4,469 bees collected, 4,360 were identified to species or morphospecies and the remaining 109 to genus or subgenus, most of which were *Lasioglossum* (40), *Osmia* (25), *Andrena* (13), *Hylaeus* (11), or *Bombus* (9). The most common bee genera across our study were *Lasioglossum* (43% of all specimens), *Osmia* (15%), *Halictus* (13%), *Bombus* (10%) and *Andrena* (7%). Of the 122 taxa collected, 41 were represented by just one or two specimens across the dataset. The five most commonly collected species included *Halictus farinosus* (350 specimens), *Lasioglossum trizonatum* (329 specimens), *L. cooleyi* (278 specimens), *L. punctatoventre* (168 specimens), and *Hoplitis fulgida* (158 specimens). See Table S2 for more details. Elk habitat use, as quantified with GPS collar locations, was spatially heterogeneous during our study (Fig. 2). Cumulative use increased from spring to summer in both years, primarily in the same areas (i.e., use was concentrated in "hot spots") (Fig. 2). Patterns of elk use were also generally similar from year to year in summer, but less so in spring (Fig. 2).

Differences Between Forest Types and Seasons

Four of six environmental variables differed significantly between forest types (Table 1). Warm-dry forests had higher heat load index values and more bare ground, but less woody debris and lower canopy density than cool-moist sites (Table 1). Forb/shrub cover and elk pressure were similar between forest types in both seasons (Table 1).

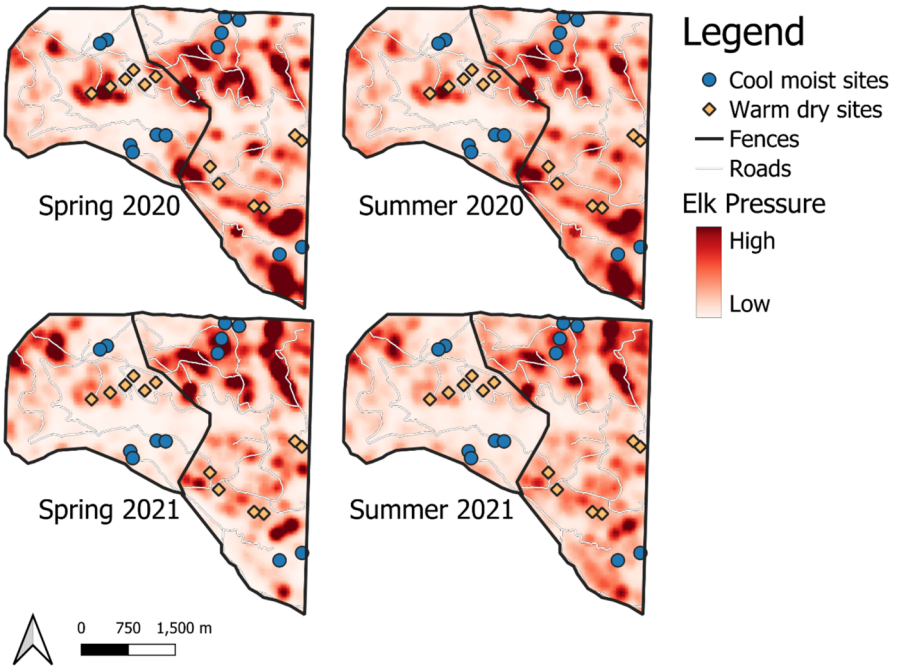

Fig. 2 Heat map of cumulative elk pressure across the Northeast (NE) study area within the Starkey Experimental Forest and Range for the four sampling periods. Heat map values were derived from GPS collar locations from late March (2020) or late April (2021) through the first sampling date for each sampling period. Sample sites categorized by forest type

Bloom abundance, richness, and diversity were similar between forest types (Table 1). However, the community composition of blooming plants showed strong patterns of variation relative to forest type and season (Fig. 3). The plant ordination converged on a 3-dimensional solution with a final stress of 16.4 and an A-value (goodness of fit) of 0.27, where axis 1 explained 33% of the variation in the data, axis 2 explained 14%, and axis 3 explained 11%. In the ordination, spring sites were negatively, and summer sites positively associated with axis 1. Warm-dry sites were negatively, and cool-moist sites positively associated with axis 2. MRPP analyses showed that plant communities differed significantly by season ($A = 0.08$, $p < 0.001$) and forest type ($A = 0.02$, $p < 0.001$), but not by year ($A = -0.001$, $p = 0.64$). Indicator species analyses revealed several plant species were significant indicators of each season/forest type grouping. In spring five native perennials and one native annual species were indicators of cool-moist forests, whereas four native perennials, two native annual, and one introduced annual species were associated with warm-dry forests (Table 2). In summer, five native perennial species were significant indicators of cool-moist sites, and six native perennials were indicators of warm-dry forests (Table 2).

Bee abundance, estimated species richness, and diversity were consistently higher in warm-dry versus cool-moist sites; however, the magnitude of difference varied by season, with generally larger effects in spring (Fig. 4). In both seasons,

Table 1 Differences in environmental and blooming plant metrics between warm-dry and cool-moist forest types. Values are means (averaged across sites and years) ±90% confidence intervals. Contrasts between warm-dry and cool-moist forests with non-overlapping 90% confidence intervals are bolded

		Spring		Summer	
Variable Type	Response	Warm-dry	Cool-moist	Warm-dry	Cool-moist
Environmental variables	Wood (% groundcover)	**50 ± 2.8**	**59 ± 2.6**	**44 ± 2.8**	**52 ± 3.2**
	Forb/shrub (% groundcover)	26 ± 3.6	25 ± 2.1	29 ± 4.2	29 ± 2.5
	Bare ground (% groundcover)	**0.49 ± 0.21**	**0.06 ± 0.05**	**0.75 ± 0.38**	**0.13 ± 0.07**
	Canopy density* (% canopy cover)	**51 ± 1.7**	**57 ± 1.2**	–	–
	Heat load index*	**0.90 ± 0.01**	**0.81 ± 0.02**	–	–
	Elk pressure (# of elk)	0.11 ± 0.03	0.09 ± 0.04	0.13 ± 0.02	0.11 ± 0.04
Bloom Responses	Abundance (# of blooming stems)	227 ± 45	261 ± 78	112 ± 29	121 ± 31
	Richness (# of blooming species)	10 ± 1.1	10 ± 1.1	8.9 ± 0.91	9.6 ± 1.2
	Diversity	1.5 ± 0.13	1.4 ± 0.11	1.4 ± 0.15	1.4 ± 0.16

*Only measured once per year

bee abundance and diversity were significantly higher in warm-dry forests compared to cool-moist forests (Fig. 4). Estimated bee richness was generally higher in warm-dry forests, but the difference was not statistically significant in spring or summer. Bee communities also differed by season and forest type (Fig. 5). The ordination converged on a 3-dimensional solution with a final stress of 20.1 and an A value of 0.27, where axis 1 explained 32% of the variation in the data, axis 2 explained 25%, and axis 3 explained 13%. Bee communities differed significantly by year ($A = 0.03$, $p < 0.001$), season ($A = 0.07$, $p < 0.001$) and forest type ($A = 0.02$, $p < 0.001$). In spring, there were no significant indicator bee species of cool-moist forests, whereas 18 taxa were indicators of warm-dry forests (Table 3). These were primarily ground-nesting species, about half of which were solitary (Table 3). In summer, significant indicators of cool-moist sites included two solitary and one eusocial species, although eight solitary and one eusocial species were indicators of warm-dry forests (Table 3). Most indicator species were medium to large-sized, polylectic species (Table 3).

Environmental Variable Effects on Blooms and Bees

The effects of canopy density, heat load index, and elk pressure on blooming plant abundance, species richness, and diversity varied with season (Fig. 6; Table S3).

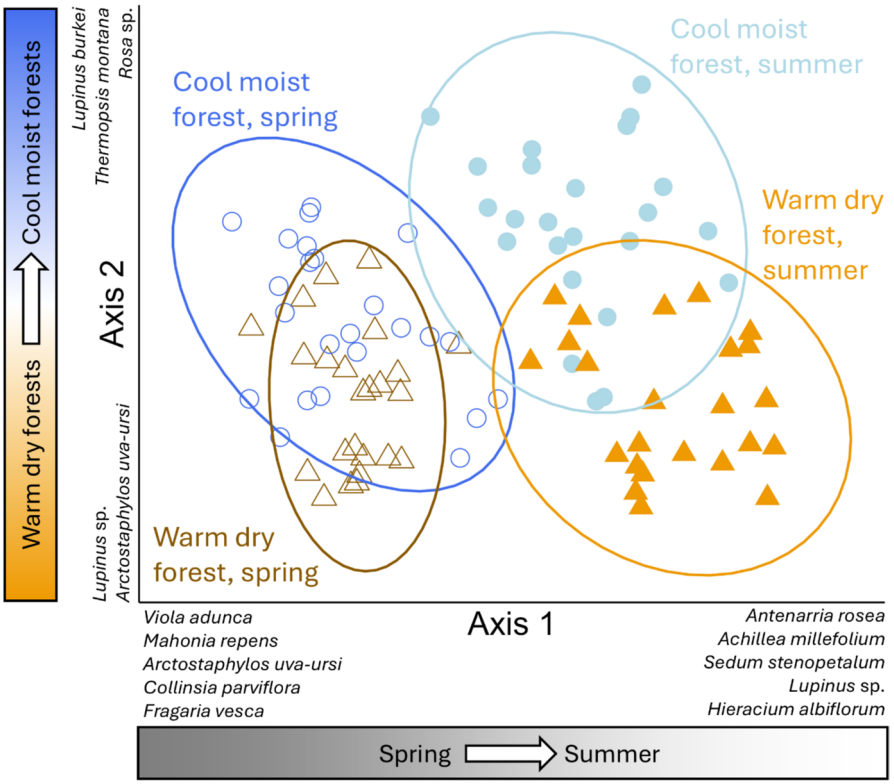

Fig. 3 Differences in blooming plant community composition relative to season and forest type. NMDS ordination plots show sample units in blooming plant community space. Open symbols represent sites sampled in spring and filled symbols represent sites sampled in summer. Blue circles represent cool moist forest sites and orange/brown triangles represent warm dry forest sites. Axis 1 explained 32.7% of the variation in the data, axis 2 explained 13.9%, and axis 3 (not shown) explained 10.6%

In spring, abundance was negatively associated with canopy density, richness was negatively associated with heat load index and canopy density, and diversity was negatively associated with elk pressure and canopy density. In summer, canopy density was negatively associated with bee abundance, but no other predictors were significant (Fig. 6; Table S3).

The effect of environmental variables on bee abundance, estimated richness, and diversity differed by season (Fig. 7; Table S4). In spring, abundance was positively associated with heat load index and negatively associated with forb/shrub and wood cover (Fig. 7). The negative effect of wood cover on bee abundance was greater than the effects of heat load index or forb/shrub cover (Fig. 7). Bee species richness was negatively associated with wood cover (Fig. 7). No predictors were significant in the spring diversity model.

The effect of environmental variables on bees in summer differed from spring, and summer models generally included more significant predictors (Fig. 7; Table S4). In summer, bee abundance was positively associated with elk pressure,

Table 2 Plant indicator species with life history traits for each forest type by season. Only species with indicator values of > 20 are shown

Season and Forest Type	Species	Family	Indicator value	*P*-value
Spring – Cool-moist	Hookedspur violet (*Viola adunca*)	Violaceae	65	0.0002
	Woodland strawberry (*Fragaria vesca*)	Rosaceae	52	0.002
	Creeping barberry (*Mahonia repens*)*	Berberidaceae	47	0.0002
	Smallflower miterwort (*Mitella stauropetala*)	Saxifragaceae	33	0.003
	Heartleaf springbeauty (*Claytonia cordifolia*)$^{+}$	Portulacaceae	21	0.004
	Sagebrush violet (*Viola vallicola*)	Violaceae	21	0.004
Spring – Warm-dry	Kinnikinnick (*Arctostaphylos uva-ursi*)*	Ericaceae	76	0.0002
	Virginia strawberry (*Fragaria virginiana*)	Rosaceae	60	0.0002
	Darkthroat shooting star (*Dodecatheon pulchellum*)	Primulaceae	47	0.0002
	Slender phlox (*Microsteris gracilis*)$^{+}$	Polemoniaceae	46	0.0002
	Maiden blue eyed Mary (*Collinsia parviflora*)$^{+}$	Scrophulariaceae	44	0.001
	Elegant mariposa lily (*Calochortus elegans*)	Liliaceae	33	0.01
	Spring draba (*Draba verna*) $^{I,+}$	Brassicaceae	21	0.03
Summer – Cool-moist	Largeleaf lupine (*Lupinus burkei*)	Fabaceae	67	0.0002
	Wild rose (*Rosa* sp.)*	Rosaceae	62	0.0002
	Slender goldenbanner (*Thermopsis montana*)	Fabaceae	59	0.0002
	Western columbine (*Aqualegia formosa*)	Ranunculaceae	29	0.001
	Longtube twinflower (*Linnaea borealis*)	Caprifoliaceae	22	0.005
Summer – Warm-dry	Other purple lupines (*Lupinus* sp.)	Fabaceae	78	0.0002
	Rosy pussytoes (*Antennaria rosea*)	Asteraceae	62	0.0002
	Common yarrow (*Achillea millefolium*)	Asteraceae	51	0.0002
	Yellow penstemon (*Penstemon confertus*)	Scrophulariaceae	44	0.0002
	Wormleaf stonecrop (*Sedum stenopetalum*)	Crassulaceae	31	0.0004
	White hawkweed (*Hieracium albiflorum*)	Asteraceae	26	0.006

All plants are native perennial forbs unless otherwise noted. All common names and natural history information obtained from USDA Plants Database

^{I} Introduced, * Shrub, $^{+}$ Annual

wood cover, and bare ground and negatively correlated with bloom richness. Bare ground had the greatest effect on abundance (Fig. 7). The positive effect of woody debris cover on bee abundance in summer was not as large as the negative effect in spring (Fig. 7). Summer richness was positively associated with elk pressure, heat load index, and wood cover. Elk pressure had the largest effect (Fig. 7). Heat load index was the only predictor that was significantly correlated with bee diversity in the summer (Fig. 7).

Discussion

Forests are increasingly recognized as important bee habitat (Ulyshen et al. 2024); findings from our study support this, with > 100 bee species identified over a relatively small spatiotemporal scale. Our study is the first to describe seasonal variation in blooming plant and native bee communities in inland PNW forests and examine how environmental variables influence these communities across seasons. Blooming plant and bee communities in this region demonstrate strong spatiotemporal variability, with distinct blooming plant and bee communities associated with spring and summer and with cool-moist and warm-dry forest types. In addition, we identified environmental variables that were most important in influencing blooming plants and bees in spring and summer, including canopy density for blooming plants and wood and bare groundcover, heat load index, and elk pressure for bees.

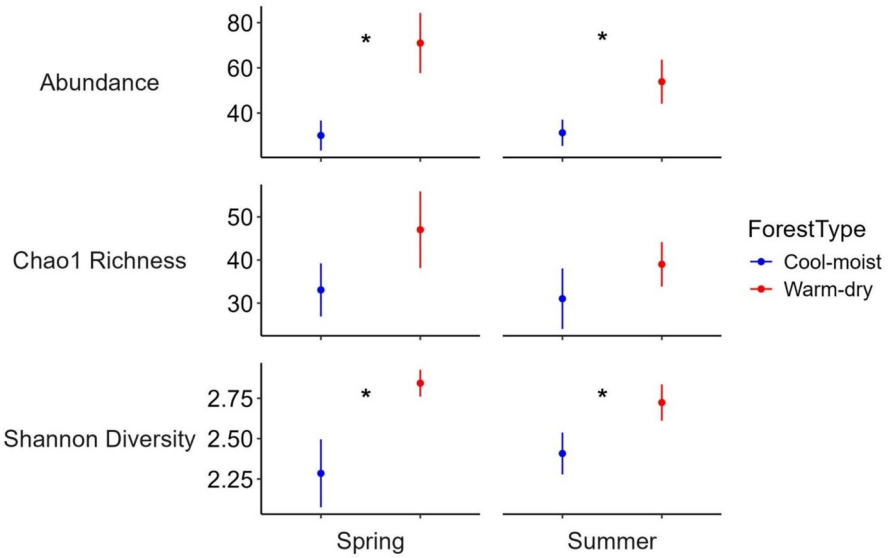

Fig. 4 Arithmetic mean bee responses and 90% confidence intervals by forest type. Asterisks indicate plots where 90% confidence intervals do not overlap

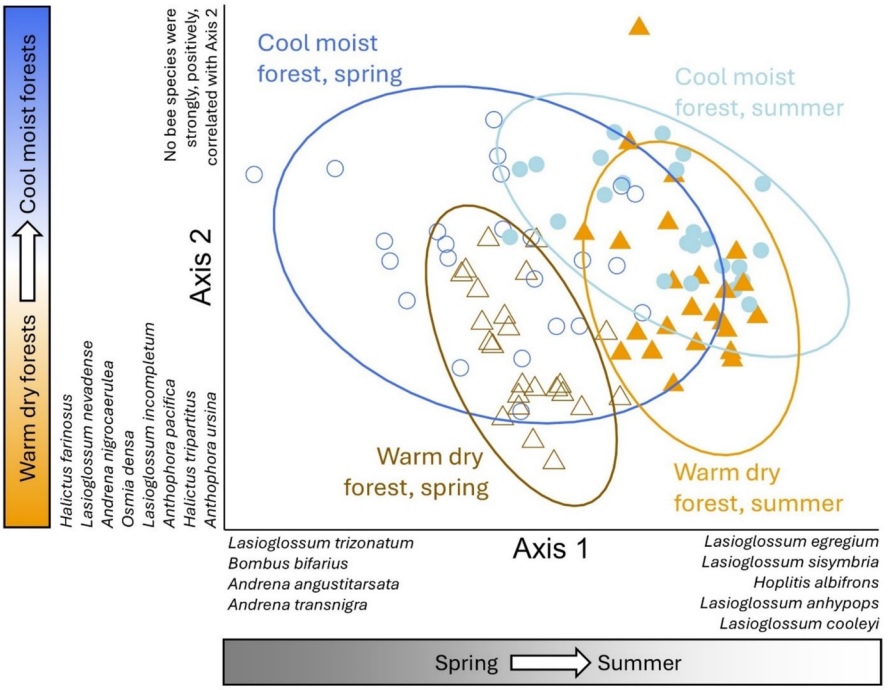

Fig. 5 Differences in native bee community composition relative to season and forest type. NMDS ordination plots show sample units in bee community space. Open symbols represent sites sampled in spring and filled symbols represent sites sampled in summer. Blue circles represent cool moist forest sites and orange/brown colored triangles represent warm dry forest sites. Axis 1 explained 31.5% of the variation in the data, axis 2 explained 25.2%, and axis 3 (not shown) explained 13.2%

Forest Types and Season

In our study area, blooming plant and bee communities differed between forest types (warm-dry and cool-moist) and seasons (Figs. 3, 4). Observed differences likely stem from environmental variables that were correlated with forest type. For example, warm-dry forests had less dense canopies, higher heat load index values, more bare ground, and less woody debris than cool-moist forests (Table 1). Sites in warm-dry forests also had a higher abundance and diversity of bees collected in spring and summer. Although blooming plant communities did not differ significantly between years, bee communities did, suggesting that bee communities in this region exhibit higher interannual variability than blooming plant communities. Conditions of warm-dry forests may favor bee communities. For example, warm-dry forests tended to be located on aspects and slopes that had higher heat load index values, likely resulting in warmer, drier site conditions that may be more hospitable for bees, especially in spring, when ambient temperature may be limiting. Globally, bees tend to be most diverse in xeric habitats (Orr et al. 2021). Other factors like the prevalence

Table 3 Bee indicator species and life history traits for each forest type by season. Only species with indicator values of > 25 are shown

Season and Forest Type	Species	Family	Soc	Nes	Lec	SI	IV	*P*
Spring – Cool-moist	No significant indicator species	-	-	-	-	-	-	-
Spring – Warm-dry	*Lasioglossum (Hemihalictus)* sp. 2	Halictidae	?	?	?	?	70	0.0002
	Anthophora pacifica	Apidae	S	G	P	L	67	0.0002
	Andrena nigrocaerulea	Andrenidae	S	G	P	M	63	0.0002
	Halictus farinosus	Halictidae	E	G	P	M	57	0.0002
	Andrena microchlora	Andrenidae	S	G	P	S	52	0.0002
	Osmia densa	Megachilidae	S	AW	P	M	47	0.0002
	Lasioglossum olympiae	Halictidae	S	G	P	M	46	0.0004
	Bombus bifarius	Apidae	E	B	P	L	44	0.0002
	Andrena nigrihirta	Andrenidae	S	G	P	M	41	0.0002
	Lasioglossum trizonatum	Halictidae	S	G	P	S	40	0.001
	Andrena transnigra	Andrenidae	S	G	P	M	36	0.0002
	Lasioglossum (Hemihalictus) sp. 1	Halictidae	?	?	?	?	34	0.0008
	Halictus tripartitus	Halictidae	E	G	P	S	34	0.003
	Lasioglossum reasbeckae	Halictidae	?	G	?	P	31	0.002
	Bombus flavifrons	Apidae	E	B	P	L	27	0.11
	Lasioglossum nevadense	Halictidae	?	G	P	P	26	0.06
	Lasioglossum sedi	Halictidae	?	G	?	P	26	0.002
	Anthophora ursina	Apidae	S	G	P	L	26	0.003
Summer – Cool-moist	*Lasioglossum egregium*	Halictidae	S	G	P	S	36	0.001
	Bombus mixtus	Apidae	E	B	P	L	27	0.10
	Osmia bucephala	Megachilidae	S	AW	P	L	26	0.02
Summer – Warm-dry	*Hoplitis albifrons*	Megachilidae	S	ACS	P	M	55	0.0002
	Lasioglossum cooleyi	Halictidae	E	G	P	S	54	0.0002
	Lasioglossum punctatoventre	Halictidae	?	G	P	P	47	0.0004
	Lasioglossum sisymbrii	Halictidae	S	G	P	S	37	0.0004
	Lasioglossum anhypops	Halictidae	S	G	P	M	35	0.002
	Agapostemon angelicus/texanus	Halictidae	S	G	P	M	32	0.0004
	Osmia albolateralis	Megachilidae	S	ACS	?	S	29	0.01
	Hoplitis fulgida	Megachilidae	S	ACSW	P	M	29	0.03
	Diadasia nigrifrons	Apidae	S	G	O	M	27	0.0004

"Soc" = sociality ("E" = eusocial; "S" = solitary); "Nes" = nesting ("A" = above ground; " "C" = cavities; "B" = both above ground and below ground cavity nester, "G" = ground nester; "S" = stems; "W" = wood;); "Lec" = lecty ("O" = "oligolectic"; "P" = polylectic), "SI" = size (based on female length, with "P" = petite (≤ 5 mm), "S" = small (> 5 mm but ≤ 10 mm), "M" > 10 mm but ≤ 15 mm), and "L" > 15 mm); "IV" – indicator value, "?" denotes unknown value. See Supplementary Material for life history references

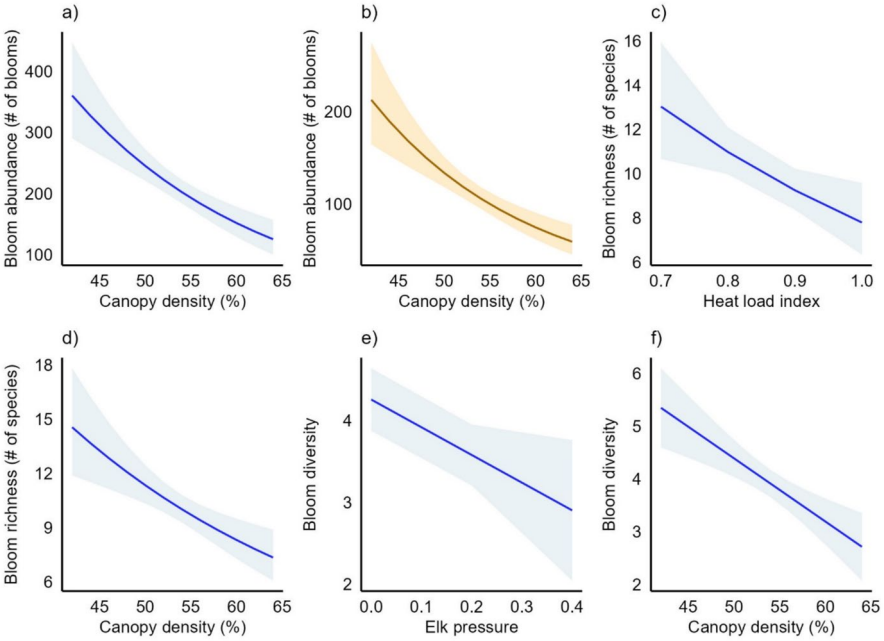

Fig. 6 Estimated relationships between significant model coefficients and bloom abundance, richness, and diversity. Blue plots indicate spring and orange plots indicate summer. Solid lines are fitted relationships and colored bands are 90% confidence intervals for spring (**a**) and summer (**b**) bloom abundance versus canopy density; spring bloom richness versus heat load index (**c**) and canopy density (**d**); and spring bloom diversity versus elk pressure (**e**) and canopy density (**f**)

of bare ground in warm dry sites may also make for more favorable nesting conditions for many bees, since most species in North America are ground-nesting (Harmon-Threatt 2020).

Modeling Effects of Environmental Variables

Blooming Plants

Because blooming plants are crucial food resources for native bees (Michener 2007), we modeled their responses to heat load index, elk pressure, and canopy density. We found a negative relationship between heat load index and spring bloom richness, a result consistent with other studies showing that southwest-facing slopes (slopes with higher heat load indices) are generally associated with fewer blooms (Lindh 2005). The topographic characteristics associated with a higher heat load index are also typically associated with drier soil conditions (Geroy et al. 2011), which could result in fewer blooms since lower moisture is generally correlated with lower bloom abundance and richness (Phillips et al. 2018; Davies et al. 2023). The negative association of elk pressure with spring bloom diversity is also not surprising, because elk

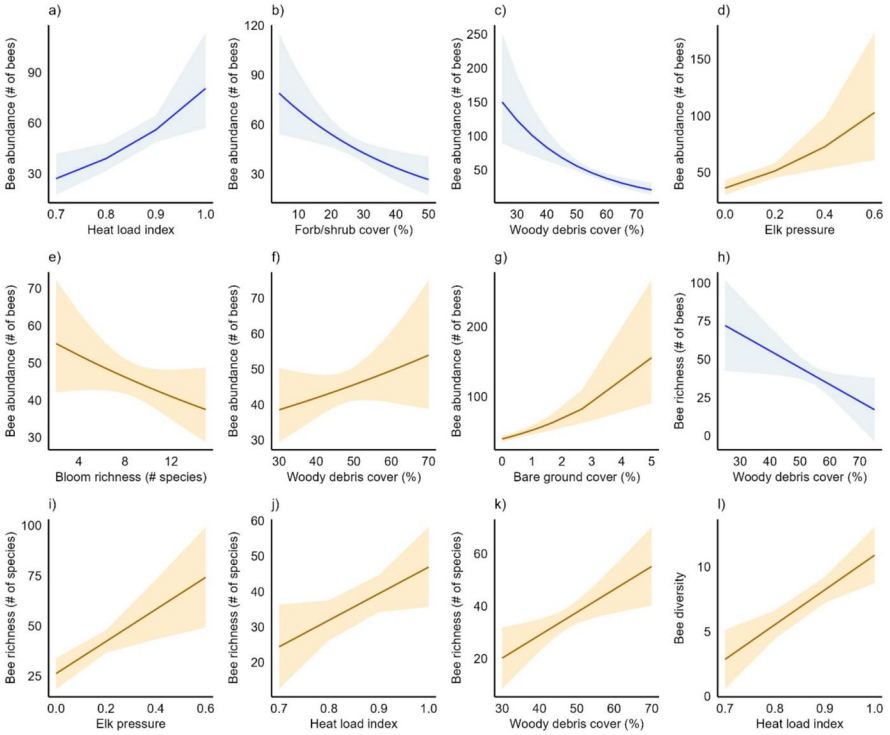

Fig. 7 Estimated relationships between significant model coefficients and bee abundance, richness, and diversity. Blue plots indicate spring and orange plots indicate summer. Solid lines are fitted relationship and colored bands are 90% confidence intervals for spring bee abundance versus heat load index (**a**), forb/shrub cover (**b**), and woody debris cover (**c**); summer bee abundance versus elk pressure (**d**), bloom richness, (**e**), woody debris cover (**f**), and bare groundcover (**g**); spring bee richness versus woody debris (**h**); summer bee richness versus elk pressure (**i**), heat load index (**j**), and woody debris cover (**k**); and summer bee diversity versus heat load index (**l**)

herbivory may decrease the abundance of species they prefer (DeBano et al. 2016; DeBano et al. In Press). This may lower the evenness of the community, resulting in decreased diversity without necessarily reducing richness or overall abundance. The negative effect of canopy density on spring blooms is consistent with numerous other studies showing a negative relationship of canopy density with bloom abundance, richness, and diversity (Lindh 2005; Ares et al. 2010; Neill and Puettmann 2013; Ulyshen et al. 2024). Canopy density was the only variable measure that affected bloom responses in summer, when it was negatively associated with bloom abundance.

Native Bees

We examined the effects of eight environmental variables on native bees in spring and summer. Although few studies have examined responses of forest

bee communities to environmental variables across seasons, a recent study by Chase et al. (2023) investigated spring and summer responses of bees to forest management in a deciduous system and like us, found bee responses varied by season. In their system, bee abundance was correlated with bloom abundance in spring, and bloom abundance, canopy cover, and nesting substrate availability were important predictors of bee abundance in summer. In contrast, we did not identify a significant relationship between bloom and bee abundance or any effect of canopy cover on bees. Instead, we found heat load index affected bees consistently in spring and summer, while the effects of elk pressure and various nesting substrates on bees varied between seasons. Because their study was conducted in deciduous forests, it is not surprising that Chase et al. (2023) found that canopy cover played a more important, seasonally dependent role compared to our results in coniferous forests, where canopy cover does not change substantially between seasons.

Heat load index affected bees similarly regardless of season, being positively associated with abundance in spring and with richness and diversity in summer. Since bee diversity in North America is primarily driven by small, ground-nesting bees (Harmon-Threat 2020), warmer sites may harbor a higher abundance, richness and diversity of bees as many small bees may be thermally restricted than larger bees (Peters et al. 2016; Bishop and Armbruster 1999).

In contrast, we found some variables were important in spring, but not summer. For example forb/shrub cover was negatively associated with bee abundance, a result consistent with previous work (Hanula et al. 2015). Forb/shrub cover may cool the underlying ground, potentially making these spots less viable nesting habitats, particularly in spring, when temperatures may be more limiting for the ground-nesting bees that were common indicator species in spring (Table 3). In the summer, forb/shrub cover did not significantly affect bees, perhaps indicating that the microclimatic effects of these plants are ameliorated later in the season.

Other variables influenced bees in summer, but not spring. The positive association of elk pressure in summer was unexpected given that other work has found that ungulate herbivory decreases floral resources that bees rely on (e.g., Beckett et al. 2022; DeBano et al. In Press). We hypothesize that this pattern reflects shared habitat or forage preferences of bees and elk (DeBano et al. 2016, DeBano et al. In Press) rather than a causal relationship.

Bare ground was also positively associated with bee abundance in summer, a finding consistent with other studies (Hopwood 2008; Rivers et al. 2018a) and not surprising given most bee species in North America (Harmon-Threatt 2020), and over 50% of the bees collected in our study, were ground-nesting (Table 3, Table S2). The negative association between bee abundance and bloom richness in summer is not necessarily unexpected given that even forb communities with few blooming species can attract large numbers of common bees if, for example, species that are present provide high floral rewards. However, this pattern may also be due to trapping efficiency being influenced by floral diversity since higher richness of flowers may result in traps becoming less attractive (relative to available blooms) to bees (e.g., Kuhlman et al. 2021).

Unlike other environmental variables, woody debris cover was negatively associated with some bee metrics in spring and positively related to them in summer. These seasonal differences may be influenced by bee species turnover as summer communities had a larger proportion of indicator species that were cavity nesters compared to spring (Table 3). Past studies have found variable effects of woody debris on forest bee communities (e.g., Rivers et al. 2018a; Gelles et al. 2022; Chase et al. 2023). Unlike Rivers et al. (2018a), decreased bee abundance at sites with more woody debris in spring in our study was not driven by its inverse relationship with bare ground (which was not significantly related to bee metrics in spring).

Surprisingly, we did not find any significant effect of canopy density on bee communities. In other forested systems, researchers have repeatedly found that canopy density is negatively associated with bee abundance and richness (e.g., Grundel 2008; Chase et al. 2023; Ulyshen et al. 2024), including in other PNW forests (e.g., Rivers and Betts 2021) and in similar semi-arid conifer forests (e.g., Rhoades et al. 2018; Gelles et al. 2022; Davies et al. 2023). One explanation is that the forests in our study area have low enough average canopy density that the magnitude of variation encompassed by this study was not ecologically significant enough to influence bees either directly or indirectly (through effects on floral resources).

Comparisons to other Temperate Forests

Temperate forests are widely distributed across North American and can harbor abundant and species-rich communities of native bees (e.g., Grundel et al. 2010; Chase et al. 2023; Ulyshen et al. 2023), including species that prefer forested habitats (e.g., Smith et al. 2021). The Pacific Northwest region is no exception, as a body of work from PNW forests west of the Cascades demonstrates (e.g., Rivers et al. 2018a; Galbraith et al. 2019; Best et al. 2021).

Interestingly, the bee and blooming plant communities in the inland forests we examined were substantially different from those found in western PNW forests. For example, very few of the dominant spring-blooming plants observed in our study (Table S1) were common or even present in western PNW forest-pollinator and plant studies (e.g., Lindh 2005; Galbraith et al. 2019; Zitomer et al. 2023). Similarly, the composition of bee communities in our study differs from western PNW studies that used similar sampling methods (Table S2). For example, in contrast to bee communities in our study, western PNW communities were not as strongly dominated by *Lasioglossum*, *Osmia*, or *Andrena*, and often included genera that we did not detect, or were rare in our study (Rivers et al. 2018a; Galbraith et al. 2019; Zitomer et al. 2023).

Another relevant contrast between our study and western PNW forest-pollinator studies is that those studies have focused primarily on recently burned (e.g., Galbraith et al. 2019) or recently logged (e.g. Rivers et al. 2018a) early seral forests. In contrast, the youngest forests in our study were 28 years old (Ruprecht et al. 2023) and the oldest had not been harvested since the early 1930's (Skovlin 1991). Our study suggests that inland PNW forests can support diverse bee communities much longer than western PNW forests, which have limited utility as pollinator habitat

after canopy closure often occurring after 10–12 years (Zitomer et al. 2023; Frank et al. 2025). Our finding of abundant, species-rich assemblages of bees in comparatively old forests, suggests that inland PNW forests likely support bee communities in early and late seral forests alike, thus increasing the conservation-value of these forests.

Management Implications and Conclusions

Our study shows the importance of understanding spatial and temporal variability in native bee communities of PNW forests and the value of seasonal examinations of the relationships between environmental variables and bees. Our results suggest that warm-dry forest types may provide important habitat for native bee conservation in inland PNW forests, as these vegetation types generally support a more diverse and abundant collections of native bees than do cool-moist forests in this area. Surprisingly, although less canopy cover was associated with more floral resources, we did not find a concomitant response of bee communities, suggesting that forest thinning (e.g., for fuels management goals) may not have the same positive effects on bees as seen in other regions (Neill and Puettman 2013; Davies et al. 2023). However, forest thinning may also influence certain groundcover metrics, like woody debris cover, so it is still unclear how thinning may indirectly influence bees in this region. Our study also implies that elk and bees may benefit from similar habitats, suggesting that management actions that target improving elk foraging habitat may coincidentally improve habitat for native bees, which frequently co-occurred in sites used by elk in our study area. Finally, our work adds to existing evidence from statewide surveys (Best et al. 2021) that bee communities are heterogeneously distributed through time and space and locality-specific research will be key for effective pollinator conservation in the PNW region.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s44392-025-00043-y.

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Author Contributions SM, SD, and MR conceived of and designed the study; MR and SD were responsible for funding acquisition; SM and SD collected the data, SB identified all bee specimens; SM, SD, and RN performed data analysis; SM led manuscript preparation and writing; SD contributed to writing the original draft, and all authors contributed substantially to additional drafts and edits of the paper and approved the final manuscript for publication.

Data Availability Data and code used in analyses is available upon request.

Declarations

Competing interests Authors declare no competing interests.

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