Forest Ecology and Management 534 (2023) 120883

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Habitat characteristics structuring bee communities in a forest-shrubland ecotone

Will Glenny [a,*], Justin B. Runyon [b], Laura A. Burkle [a]

[a] Montana State University, Department of Ecology, Bozeman, MT 59717, United States
[b] USDA Forest Service, Rocky Mountain Research Station, Bozeman, MT 59717, United States

ARTICLE INFO

Keywords:
Pollinator
Ecotone
Conifer encroachment
Management

ABSTRACT

The relationship between bee community composition and habitat characteristics at local scales may inform management decisions and conservation strategies for species of conservation concern. Ecotones are transition zones between two adjacent habitats that can potentially support abundant and diverse bee communities by providing complementary habitat characteristics within the foraging distance of most bee species. In a forest-shrubland ecotone, we evaluated the relationships between multiple habitat characteristics and the taxonomic and functional diversity of bee communities. Early in the growing season, floral abundance was positively associated with bee abundance but negatively associated with bee richness and functional diversity, indicating that large floral displays increase specialization of common bee species. The abundance of trees within the ecotone was positively associated with coarse woody debris (CWD), and in turn CWD had a positive association with bee richness and functional diversity early in the growing season and positive association with functional richness later in the growing season. Ecological processes within the ecotone that convert trees into CWD may provide resources for aboveground cavity nesting bee species. Late in the growing season soil composition was associated with bee functional diversity. The functional richness of bee communities also had a positive association with the specialization of bee-flower interaction networks, indicating that bee communities with more functional groups contain more specialist bee species. Studies that disentangle the effects of specific habitat characteristics on bee community composition will help identify management strategies that are consistent with bee conservation in ecotone environments.

1. Introduction

Wild bees are critical for the reproduction of forbs that serve as valuable habitat and food for species of conservation concern and that form the foundation for healthy ecosystems (Wratten et al., 2012; Dumroese et al., 2016). Recent declines of bee populations globally have increased the need to understand how habitat characteristics structure local bee communities in order to apply land management actions that are compatible with healthy bee communities (Vanbergen and the Insect Pollinators Initiative, 2013). In particular, both food and nesting resources may be important to support these species across distinct life history stages (Winfree, 2010; Roulston and Goodell, 2011; Glenny et al., 2022). However, it remains unclear how the presence and abundance of food and nesting resources are linked to the composition of bee communities at local scales. Resolving the relationships between habitat characteristics and the composition of bee communities at local scales is important to inform restoration actions capable of meeting predefined goals for bee communities (Glenny et al., 2022).

Heterogenous habitat patches with complementary floral and nesting resources are likely to support bee species with distinct life histories at a landscape scale. Complementary resources at a landscape level reduce the need for bees to disperse long distances in search of resources (Jha and Kremen, 2013), increase the resilience of bees against food shortages (Mandelik et al., 2012; Mallinger et al., 2016; Ponisio et al., 2016), provide a diversity of species-specific nesting materials (Roulston and Goodell, 2011; Harmon-Threatt, 2020), and support more bee species at a landscape level (Steffan-Dewenter et al., 2002; Tscharntke et al., 2005). Specifically, ecotones are the transition zone between two habitat types that may provide complementary resources for bees by supplying both foraging and nesting resources across a relatively small spatial scale (Wiens et al., 1985; Cadenasso et al., 2003; Ries et al., 2004). For instance, across a landscape in the northern Rocky

* Corresponding author at: Montana State University Department of Ecology, Lewis Hall 310, United States.
E-mail address: willglenny@gmail.com (W. Glenny).

https://doi.org/10.1016/j.foreco.2023.120883
Received 17 December 2022; Received in revised form 15 February 2023; Accepted 17 February 2023
Available online 6 March 2023

Mountains, bumble bee abundance was greatest along the forest-grassland habitat edge where forests provided nesting resources and open grasslands supported more food resources (Clake et al., 2022). Management actions that alter the presence and abundance of habitat characteristics at local scales within ecotones could significantly influence the structure and function of plant and pollinator communities.

The transition from forest to grassland/shrublands is among the most well-studied ecotones due to the ecological consequences of conifer encroachment on habitat suitability for biotic communities (Heyerdahl et al., 2006; Davies et al., 2011). Climate change, fire exclusion, and intensive grazing are altering disturbance regimes that once excluded conifers from establishing in adjacent habitats (Heyerdahl et al., 2006; Davies et al., 2011). Conifer encroachment into adjacent shrub ecosystems has been observed to decrease shrub and herbaceous cover by competing for light and soil resources (Bates et al., 2000; Davies et al., 2011; Bates and Davies, 2017), increase the size and severity of wildfires (Romme et al., 2009; Engber et al., 2011), and provide perches for predators of the potentially endangered sage grouse (*Centrocerus urophasianus)* (Connelly et al., 2000; Manzer and Hannon, 2005; Severson et al., 2017). Consequently, coniferous plant species within forest-shrubland ecotones may alter the presence and abundance of habitat characteristics that structure pollinator communities at local scales.

Habitat characteristics at local scales may recruit bee species with specific combinations of functional traits and reflect trait-environment relationships that structure bee communities (Keddy, 1992; Cornwell and Ackerly, 2009; HilleRisLambers et al., 2012). Disturbances, management actions, climate change, and land use change alter the abundance of bee species from functional groups defined by sociality, body size, diet breadth, phenology, and preferred nesting substrates (Williams et al., 2010; Rader et al., 2014; Forrest et al., 2015; Warzecha et al., 2016; Grass et al., 2021), potentially due to changes in habitat availability. For instance, wildfire increased the abundance of coarse woody debris and cavity nesting bee species (Gelles et al., 2022) and thinned forested sites maintained higher levels of cavity nesting solitary bee species than clear cut sites (Fortuin and Gandhi, 2021), but coarse woody debris did not affect the abundance or success of cavity nesting bees in post-wildfire coniferous forests (Heil and Burkle, 2018; Simanonok and Burkle, 2019). Additionally, habitat characteristics that alter the functional composition of local bee communities potentially alter interaction patterns between bee and flower communities (Devictor et al., 2010; Junker et al., 2019). Habitat characteristics that recruit species that occupy a unique functional niche may increase the specialization of bee communities because pollinators with unique traits interact with fewer floral partners (Junker et al., 2013; Kaiser-Bunbury and Blüthgen, 2015) and habitat characteristics that increase the abundance of bee species from similar functional groups (Moretti et al., 2009; Blüthgen and Klein, 2011) may increase competition and resource partitioning. Resolving the effects of habitat characteristics on the functional diversity of bees in local communities may strengthen our understanding of bee-habitat relationships and bee-flower interactions to inform conservation and restoration decisions (Bartomeus et al., 2018).

We investigated the effects of habitat characteristics within a forest-sagebrush ecotone on the taxonomic and functional diversity of bee communities and bee-flower interaction network structure across sites along a forest and sagebrush ecotone in southwest Montana, USA (Fig. 1). We hypothesized that the abundance of trees within the ecotone would have direct effects on habitat characteristics that alter the availability of food and nesting resources for bees. Specifically, the abundance of trees within the ecotone would be negatively associated with floral resources by competing with understory plant communities for water and light resources (Bates et al., 2000; Davies et al., 2011) and reduce bee abundance and richness, but positively associated with nesting resources if trees are converted into coarse woody debris (CWD) or decompose into litter and duff and increase bee abundance and richness (Simanonok and Burkle, 2019; Foote et al., 2020; Harmon-Threatt, 2020). Trait-environment relationships may alter the functional diversity of bee communities and bee-flower interaction network

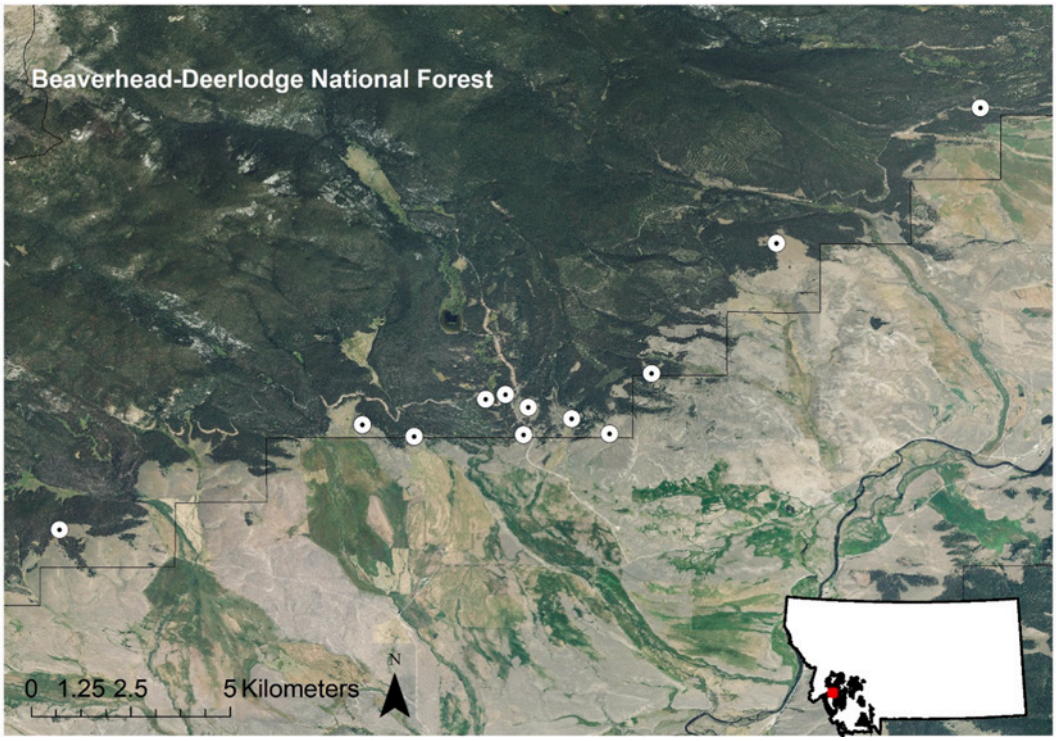

Fig. 1. Map of the study area. Sites (white circles) were distributed along the boundary of the Beaverhead-Deerlodge National Forest (solid line). The inset map provides a reference for the location of the study area (red square) within the Beaverhead-Deerlodge National Forest (black polygons) in southwest Montana. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

structure at local scales. We hypothesized that there would be a positive association between the quantity of a particular habitat characteristic and the abundance of bees within the guild that utilizes that resource, like CWD volume and aboveground cavity nesting bee species, leading to increases in functional richness and diversity of bee communities at local scales. Furthermore, we hypothesized that higher functional diversity of bees would increase the specialization and modularity of bee-flower networks. This hypothesized relationship could result from bee communities that contain more species which occupy a unique functional niche and form more specialized relationships with groups of flower species (Junker et al., 2019).

2. Methods

2.1. Site selection

This study took place in the Beaverhead-Deerlodge National Forest in the Big Hole Valley of southwest, Montana. The study area is characterized as a high elevation sagebrush basin (elevation > 2000 m above sea level) surrounded by sub-alpine forests. The study area is north of the Big Hole River along the transition zone between shrubland and forest (Fig. 1). The dominant shrub is mountain big sagebrush (*Artemisia tridendata* ssp. *vaseyana*), and forests are dominated by lodgepole pine (*Pinus contorta*) with scattered Douglas-fir (*Pseudotsuga menzeisii*) and ponderosa pine (*Pinus ponderosa*). The expansion of conifers (primarily lodgepole pine) into sagebrush has occurred in this area for at least 150 years likely due to fire suppression, domestic livestock grazing, and climate change (Heyerdahl et al., 2006; Davies et al., 2011).

Along a 20-km section of this forest-shrubland ecotone, 14 sites were randomly placed at locations that a.) contained both shrub and tree species, b.) conifer cover was < 10%, c.) slope < 30%, and were d.) separated by at least 110 m. These criteria ensured that sites were not located in pure forest or sagebrush habitat types, but randomly within the ecotone to describe habitat characteristics that are representative of this ecosystem. We selected twelve of these sites that were spaced the furthest apart for this study to ensure spatial correlation did not influence habitat characteristics (Supplemental Methods). The average pairwise distance between sites was 5,286 m and ranged from 366 to 19,354 m. At each site, a circular plot (55 m radius) was established. Within the plot boundaries, we measured food and nesting resources for bees and observed bee-flower interactions (methods below).

2.2. Habitat characteristics related to bee communities

2.2.1. Tree abundance within the ecotone

We estimated total tree abundance within the ecotone by counting the number of individuals of all conifer species (*Pinus ponderosa, Pinus contorta, Pseudotsuga menziesii,* and *Juniperus communis*), including seedlings and saplings, that occurred within the site boundaries (Grundel et al., 2010) (Supplemental Methods). To understand how the abundance of trees within the ecotone may influence the amount of light that is available for flowers and bees at the forest floor, canopy openness was measured by taking photographs from the center of the plot and at three locations evenly spaced apart on the plot boundary using a fish-eye lens attachment for a cell phone and analyzed using the Gap Light Analyzer (Frazer et al., 1999; Simanonok and Burkle, 2019) (Supplemental Methods). Canopy openness was estimated as the percentage of each photograph that was not obscured by trees and then calculating the mean for each site.

2.2.2. Habitat characteristics for belowground nesting bees

At each site, we measured the below ground soil composition, the depth of litter and duff, and the amount of bare ground to understand how variation in different components of soil structure may affect habitat characteristics for ground nesting bee species. Three 55 m transects, directed 120-degrees apart were established and the soil surface cover was recorded at each meter along each transect using the line-point intercept method (Floyd and Anderson, 1987; Herrick, 2005). At each site, the total number of occurrences of bare ground was divided by the total number of soil surface measurements (n = 150) to estimate the percent bare ground. Below ground soil composition was measured by collecting a soil core every 10 m along each transect using a 33″ soil probe (AMS, American Falls, ID, USA). All soil cores from a site (n = 15) were combined to create a composite sample. Soil texture and nutrients may influence bee nesting substrates and flowering communities. Each soil composite was analyzed for pH, the concentrations of phosphorous (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) ions, cation exchange capacity (CEC), percent organic matter (OM), and percent sand, silt, and clay by AgVise laboratories (Northwood, ND, USA) (Supplemental Methods). Directly adjacent to each soil core, litter and duff depth were measured by cutting a cross section of the soil with a hatchet and measuring the vertical depth (cm) from the soil surface to the interface with mineral soil (Brown, 1974). The average depth of all litter and duff measurements at each site (n = 15) was calculated.

2.2.3. Habitat characteristics for aboveground nesting bees

We measured the volume of CWD at each site to understand how the availability of potential nesting resources structures the taxonomic and functional diversity of bee communities. To estimate the volume of CWD at each site (m^3/m^2), we measured the diameter of each piece of wood that was greater than 2.5 cm in diameter, more than 50 cm in length, and fell within 1 m on either side of the transects (Heil and Burkle, 2018; Simanonok and Burkle, 2019) (Supplemental Methods). The volume of CWD was estimated for each transect using the following equation from (Harmon and Sexton, 1996): $9.869 \times \sum(\frac{d^2}{8} \times l)$ where d is the diameter for each piece of wood and L is the length of the transect (55 m). The volume of CWD was then averaged across all transects at a site to estimate the amount of nesting resources available to aboveground nesting bee species within the plot.

2.3. Pollinator observations

To investigate the potential associations between habitat characteristics, bee community composition, and network structure, bee-flower interactions were observed at each site once per week for two weeks in the summer of 2018 (25–28 June; 23–26 July) and once per week for nine weeks in the summer of 2019 (6 June – 1 August). Observations in 2019 began following snowmelt in early June and ended when plants produced seed in August, spanning the duration of the growing season to account for seasonal variation of bee communities. Three sites were sampled per day (Supplemental Methods). Observations were conducted between 0900 and 1700 h and under sunny and calm conditions (Gibson et al., 2011). Due to unanticipated weather events and differences in site accessibility, the total number of observation periods at each site varied between nine and 11 times.

During each observation period at a site, two observers captured flower-visiting bees for one hour (two total hours of observation) (Supplemental Methods). We recorded the flower species from which each bee was captured (Lesica et al., 2012). Captured specimens were kept and identified to the lowest taxonomic level in the lab (typically to species or morphospecies), using published keys for bees within the region (Reese et al., 2018) and with the help of expert taxonomists. Because males of many species could not be confidently matched to females, males were excluded from the analysis to ensure fair comparisons of community composition between sites.

To understand the effects of habitat characteristics on the taxonomic and functional structure of bee communities while accounting for seasonal variation in bee community composition, we used hierarchical clustering analysis to identify natural breaks in the bee community composition across the growing season (Burkle and Alarcón, 2011; Burkle and Runyon, 2019) and aggregated the results of observation

periods within a phenological group at each site. We applied a Ward's hierarchical clustering analysis to a species abundance matrix of bee specimens caught during each day of sampling (Supplemental Fig. 1). The resulting dendrogram was cut at a height of 1.75 to create two categories of bee communities, each with a similar number of observation dates (n = 23 early and n = 20 late) and with an equivalent total branch length. Categories generally corresponded with observation periods conducted early in the growing season (beginning of June to mid-July) and late in the growing season (mid-July to mid-August). Aggregating the results of observation periods at a larger temporal scale was warranted given that a compressed growing season within this system results in fewer natural breaks in the bee community and relatively few bee-flower interactions were observed during an observation period. Therefore, we were able to analyze the bee community composition at each site given a reliable sample size and at an ecologically relevant timescale.

Mean bee abundance and richness were estimated at each site within each phenological group to ensure bee abundance was not biased by the number of observation periods conducted. Within each phenological group, the total number of specimens caught at a site was divided by the number of observation periods to calculate mean bee abundance. Similarly, we used rarefaction to estimate the expected species richness at each site. Within a phenological group, rarefied species richness estimates were based on the sample size from the site with the fewest number of specimens caught (early n = 9, late n = 29) (Supplemental Fig. 2).

2.4. Estimating the abundance of floral resources for bees

Within each site, we estimated the mean floral density per observation period within the early or late periods of the growing season to quantify the floral resources available to bees. The floral density was estimated by counting the number of pollen-receptive inflorescences across all plant species in each plot (Supplemental Methods). At each site within a period of the growing season, we calculated the floral density per observation period. Mean floral density was log-transformed to reduce the influence of species with large floral displays and meet the assumptions of statistical tests.

2.5. Functional traits

For all bee species, we compiled information on four life history traits related to species-habitat associations, including nesting location, mean body size, sociality, and diet breadth (Supplemental Table 1). Nesting location was categorized as belowground, belowground-cavity, aboveground-cavity, parasitic-belowground, and parasitic-aboveground to capture the full range of nesting behaviors of bees in the study region. Sociality was categorized as eusocial, social, solitary, parasitic-social, or parasitic-solitary. Any species that was identified as primitively social, nesting in aggregations, or can display polymorphism in sociality, was categorized as 'social' to increase interpretability. Categorical traits were assigned to each species through a literature review of (Harmon-Threatt, 2020), (Michener, 2007), and (Durney, 2018). Body size (mm) was measured for each bee as the intertegular distance (ITD) using a dissecting microscope and ocular micrometer (Leica, Wetzlar, Germany). Intertegular distance was averaged for each bee species across all sites because individuals of the same species rarely occurred with adequate sample size at multiple sites. Diet breadth was estimated for each species as the total number of plant species a bee species was observed to visit across all sites over the course of the study and was log-transformed for normality (Supplemental Table 1).

Within each period of the growing season, we estimated the functional dispersion ('Fdis' in the package 'FD'; (Laliberté and Legendre, 2010) and functional richness ('Fric' in the package 'FD'; (Laliberté and Legendre, 2010) of bee communities at each site to calculate multidimensional measures of trait diversity (Supplemental Methods).

2.6. Analytical methods

There was only a single measurement for each habitat characteristic at a site, so to reduce the effects of pseudoreplication the subsequent analysis was conducted independently on early and late periods of the growing season.

2.6.1. Direct and indirect effects of conifer abundance on habitat characteristics and bee communities

We used piecewise structural equation modelling (PSEM) to disentangle the direct and indirect effects of multiple correlated habitat characteristics on bee community composition and functional diversity (Lefcheck, 2016). Piecewise SEM decomposes a network of interrelated response and explanatory variables into a series of component multiple linear regression models, which are combined and evaluated to generate inferences on the entire system. Component models were therefore constructed using explanatory and response variables that meet the traditional assumptions of ordinary least square (OLS) regression (Lefcheck, 2016). We checked the distribution and collinearity of each explanatory variable and excluded any variables that did not meet the assumptions of OLS regression (Supplemental Methods).

To reduce the dimensionality of multiple correlated measurements from the soil composites, a principal components analysis (PCA) was used to create a single measurement of belowground soil composition (Buckles and Harmon-Threatt, 2019). A PCA was performed on the log-transformed measurements of OM, pH, P, K, Ca, Mg, CEC, sand, silt, and clay ('rda' in the R package 'vegan') and results were scaled to best represent relationships between belowground soil components (Supplemental Fig. 3). The first principal component explained 79.4% of the total variation from the individual components of soil composition and was therefore used as a single covariate that explains most of the variation in below ground soil structure at each site.

In total, we fit seven component models to create a hypothesized diagram that explains the direct and indirect effects of habitat characteristics on the structure of bee communities (Table 1). To assess the overall fit of the PSEM, we used Shipley's test of d-separation, which tests if the overall fit of the model would be improved by including additional missing links among variables in the data set. To facilitate comparisons across variables measured on different scales, model coefficients were standardized by the ratio of the standard deviation of the explanatory variable to the standard deviation of the response variable (Lefcheck, 2016). The strength and direction of relationships between variables are therefore interpreted by the magnitude and sign of the standardized coefficient.

Table 1
Component models used in a piecewise structural equation model. Each component model was an ordinary least squares regression based on a Gaussian distribution.

Response	Predictors
Mean CWD volume	Trees in the ecotone
Below ground soil composition	Trees in the ecotone, mean CWD volume
Average floral abundance	Trees in the ecotone, below ground soil composition, mean CWD volume
Bee richness	Trees in the ecotone, below ground soil composition, mean CWD volume, average floral abundance
Average bee abundance	Trees in the ecotone, below ground soil composition, mean CWD volume, average floral abundance
Functional dispersion	Trees in the ecotone, below ground soil composition, mean CWD volume, average floral abundance, bee richness
Functional richness	Trees in the ecotone, below ground soil composition, mean CWD volume, average floral abundance, bee richness

2.6.2. Drivers of bee community composition and functional diversity

We used a distance-based redundancy analysis (DBRDA) to explain how habitat characteristics influence bee community composition (McArdle and Anderson, 2001). We calculated the dissimilarity of bee communities between sites by applying a Bray-Curtis index to the bee species abundance matrix and included mean CWD, conifer abundance, belowground soil composition, and mean floral abundance as main effects to predict bee community composition at each site. The DBRDA was followed by an analysis of variance (ANOVA) to detect habitat characteristics which could significantly affect pollinator community composition.

Habitat characteristics at local scales may serve as a filter that selects for species with a particular set of traits to persist in a community (Keddy, 1992). Therefore, we investigated the relationship between habitat characteristics and the abundance and occurrence of species from functional groups to understand the effects of habitat characteristics on bee community structure using the RLQ method combined with fourth corner analysis (Dray et al., 2014) (Supplemental Methods).

We used a beta regression (Cribari-Neto and Zeileis, 2010) to quantify the relationship between the proportion of cavity nesting bees in a community to mean CWD volume. The proportion of cavity nesting bees for each site was calculated by dividing the total number of cavity nesting bees caught by the total number of bees caught across all observation periods. Consequently, the proportion of cavity nesting bees at a site is a fractional outcome which assumes a value between zero and one and requires a generalized linear modelling approach that assumes a beta-distributed dependent variable (Cribari-Neto and Zeileis, 2010). Estimates of the slope coefficient were exponentiated to interpret the results on the odds scale.

2.6.3. Effects of functional richness and dispersion on bee-flower network organization

Using the results of observation periods (Supplemental Table 2), we constructed bee-flower interaction networks to understand how differences in functional richness and dispersion of bee communities is related to modularity and interaction specialization. Within each period of the growing season, at each site, bee-flower observations were aggregated across observation periods to create a single interaction network based on the frequency of visits observed between flower and bee species (observed network). For each observed network, we estimated complementary specialization (H_2'; (Blüthgen et al., 2006) and modularity (Q; (Dormann and Strauss, 2014) as indicators of resource partitioning among bees. Specialization estimates how strongly bee interactions deviate from a random sample of flower species in the community and ranges between 0 (generalist) and 1 (specialist) (Blüthgen et al., 2006) (Supplemental Methods). Additionally, Q estimates the likelihood that the observed bee-flower interaction network contains subunits of interacting species and has a modular structure (Olesen et al., 2007; Dormann and Strauss, 2014). Levels of modularity was calculated using the Beckett method (Beckett, 2016) and range from 0 to 1, with greater values indicating a higher likelihood that the data reflect a modular organization (Dormann and Strauss, 2014). Modularity estimates from observed networks were standardized against 100 null networks using the delta method (Dormann, 2020) (Supplemental Methods). A measure of sampling intensity was used to weight ordinary least squares regression to scale residuals in proportion to how well we sampled the network (Schleuning et al., 2012) and account for the effects of network size on modularity and specialization (Supplemental Methods).

2.7. Statistical software used

All analyses were performed in the statistical software 'R' version 4.1.1 (R Core Team 2020). Hierarchal clustering analysis was performed using the 'cluster' package version 2.1.2 (Maechler et al., 2012) and 'fpc' package version 2.2–10 (Hennig, 2010), piecewise structural equation modelling used the 'piecewiseSEM' package version 2.1.2 (Lefcheck, 2016), multivariate analyses were conducted using the 'vegan' package version 2.5–7 (Oksanen et al., 2007), network analyses were conducted using the 'bipartite' package version 2.16 (Dormann et al., 2008), functional trait analysis was conducted using the 'FD' package version 1.0–12 (Laliberté and Legendre, 2010), beta-regression was performed using the 'betareg' package version 3.1–4 (Cribari-Neto and Zeileis, 2010), and RLQ and fourth corner analyses were performed using the 'ade4′ package version 1.7–18 (Dray and Dufour, 2007).

3. Results

Tree and floral abundance varied across sites, but the percent bare ground and canopy openness were consistently high (Table 2). As a result of consistently high levels of bare ground, the depth of litter and duff material was shallow across sites (Table 2). Dead and downed coniferous plant species contributed most of the CWD volume at each site. Consequently, sites within the forest-sagebrush ecotone generally resembled shrublands, with coniferous trees in the ecotone that increased CWD (Fig. 2).

There was a total of 117 observation periods (early n = 61, late n = 56), resulting from 236 person-hours of bee-flower observations (early = 117 h, late = 119 h). We collected 1549 female bees (early n = 604, late n = 945), representing 149 species (Supplemental Table 3). Across all sites and periods in the growing season the average number of bees caught per observation period ranged from 1.4 to 48.0 (median = 13.8) and the predicted number of species that may occur at a plot given equal sampling effort ranged from 6.3 to 20.3 (median = 8.0). Species belonging to the genus *Bombus* were the most frequently collected (n = 465 individuals), followed by *Osmia* (n = 376) and *Lasioglossum* (n = 234).

3.1. Below ground soil composition

Soil PC1 explained 79.43% of the variation in below ground soil composition. Micronutrients and pH were consistent across all sites, but phosphorous concentration ranged between 6 and 58 ppm and had the greatest influence on the PCA axis 1 (scaled loading score = 1.25). The texture of soils across study sites were characterized mostly as sand and loam. Clay content had the second strongest influence on the PCA axis 1 (scaled loading score = −0.88), and soil texture ranged from 3 to 27% clay content (Supplemental Fig. 3).

3.2. Direct and indirect effects of habitat characteristics on bee communities

3.2.1. Early season observation periods

The hypothesized SEM model did not differ significantly from the data (Fisher C-score = 3.80, df = 6, p-value = 0.70), suggesting all

Table 2
Summary statistics for habitat characteristics across sites. The median, minimum, and maximum values for each habitat characteristic are reported as the untransformed value measured across all sites and observation periods. The area sampled was consistent at each site, so the values reported are standardized per site.

Habitat Characteristic	Units	Median	Minimum	Maximum
Trees in the ecotone	Count per plot	78.5	9	374
Mean canopy openness	% open	98.59	78.54	100.00
Mean floral abundance (early)	Count per plot	38,171	3816	135,603
Mean floral abundance (late)	Count per plot	75,744	7821	321,844
Mean coarse woody debris volume	m^3/m^2	22.825	0.638	129.968
Bare ground	%	86	49.33	98.67
Mean litter and duff depth	cm	0.4	0.01	1.19

Fig. 2. Photos from sites within this study depicting the range of tree abundance from low (left) to high (right). Sites typically resembled shrubland ecosystems with trees (mostly coniferous seedlings and saplings) distributed at low densities and high levels of canopy openness.

relevant links between response and predictor variables are considered. The model was most effective describing bee richness ($R = 0.80$), bee functional richness ($R = 0.73$) and bee functional diversity ($R = 0.72$) and was least effective describing mean floral abundance ($R = 0.16$) (Fig. 3).

There were seven significant relationships of interest ($p < 0.05$). Specifically, the abundance of trees in the ecotone had a positive association with CWD volume (standardized path coefficient = 0.80) (Fig. 3). The volume of CWD had a positive association with mean rarefied richness (standardized path coefficient = 0.93) and functional diversity of bee communities (standardized path coefficient = 1.94) (Fig. 3). The mean floral abundance was positively associated with bee abundance (standardized path coefficient = 0.84) but negatively associated with mean rarefied richness (standardized path coefficient = −0.62) and functional diversity of bee communities (standardized path coefficient = −0.97). Additionally, mean rarefied richness was negatively associated with the functional diversity of bee communities (standardized path coefficient = −1.53). The complete model output is reported in (Supplemental Table 4).

3.2.2. Late season observation periods

The hypothesized SEM model did not differ significantly from the data (Fisher C-score = 6.48, df = 6, p-value = 0.37), suggesting all relevant links between response and predictor variables are considered. The model was most effective describing bee functional diversity ($R = 0.94$), bee functional richness ($R = 0.92$) and mean rarefied richness ($R = 0.84$) and was least effective describing soil composition ($R = 0.31$) (Fig. 3).

There were seven significant relationships of interest ($p < 0.05$). Specifically, trees in the ecotone were positively associated with CWD volume (standardized path coefficient = 0.80) (Fig. 3). The volume of CWD had a positive association with the functional richness of bee communities (standardized path coefficient = 0.57) (Fig. 3). The mean floral abundance had a positive association with the functional richness of bee communities (standardized path coefficient = 0.80) but a negative association with mean rarefied richness (standardized path coefficient = -0.49). The mean rarefied richness of bee communities was positively associated with the functional richness (standardized path coefficient = 0.72) and functional diversity (standardized path coefficient = 0.93) of bee communities (Fig. 3). Additionally, the soil composition was positively associated with the functional diversity of bee communities (standardized path coefficient = 0.70). The complete model output is reported in (Supplemental Table 4).

3.3. Coarse woody debris as nesting resources for bees

There was no association between floral abundance, CWD volume, below ground soil composition, or the abundance of trees in the ecotone and bee community composition during early or late periods of the growing season (Table 3). However, in both periods of the growing season the proportion of cavity-nesting bees caught from a site was strongly correlated with CWD volume (Fig. 4). Specifically, within early season bee communities, the odds increase by 1.40 that bee communities will contain more aboveground nesting bee species (SE = 1.15, z-value = 2.35, p-value < 0.001) and within late season bee communities the odds increase by 1.58 (SE = 1.15, z = value = 3.32, p-value < 0.001) for every one-fold increase in CWD volume. Results from the RLQ and fourth corner analysis indicate no associations between bee traits and habitat characteristics (Supplemental Fig. 4).

3.4. Effects of bee community structure on bee-flower network organization

We found evidence for a positive relationship between functional richness and specialization among bee-flower networks sampled during observation periods late in the growing season (Table 4).

4. Discussion

Our study indicates that habitat characteristics within the ecotone have direct and indirect effects on the taxonomic and functional diversity of bee communities and that the functional richness of bee communities is associated with the specialization of bee-flower networks. Tree abundance within the ecotone had a positive association with CWD volume, and CWD volume in turn had a positive association with bee richness and functional dispersion among early season bee communities and functional richness among late season bee communities. Disturbances that convert trees within the ecotone into CWD could increase nesting sites for aboveground nesting species (Simanonok and Burkle, 2019; Foote et al., 2020). Coarse woody debris may in turn be important during times of the growing season when aboveground nesting species are abundant and recruit bee species with unique functional traits into local communities. Additionally, floral abundance had a positive effect on bee abundance but a negative effect on functional diversity early in the growing season, and negative effects on bee richness throughout the growing season. Large floral displays composed of a few plant species may increase specialization of bee species with common functional traits, like bumble bees, and result in large local communities that are dominated by a common species (Heinrich, 1976). Furthermore, we found that there was a positive association between functional richness and network-level specialization late in the growing season. Local communities that contain more functional groups may also include specialist bee species that have a narrow dietary niche, but the relationship between functional diversity and bee-flower network structure remains poorly studied. Trait-environment relationships may inform land management actions to achieve predefined end goals for the

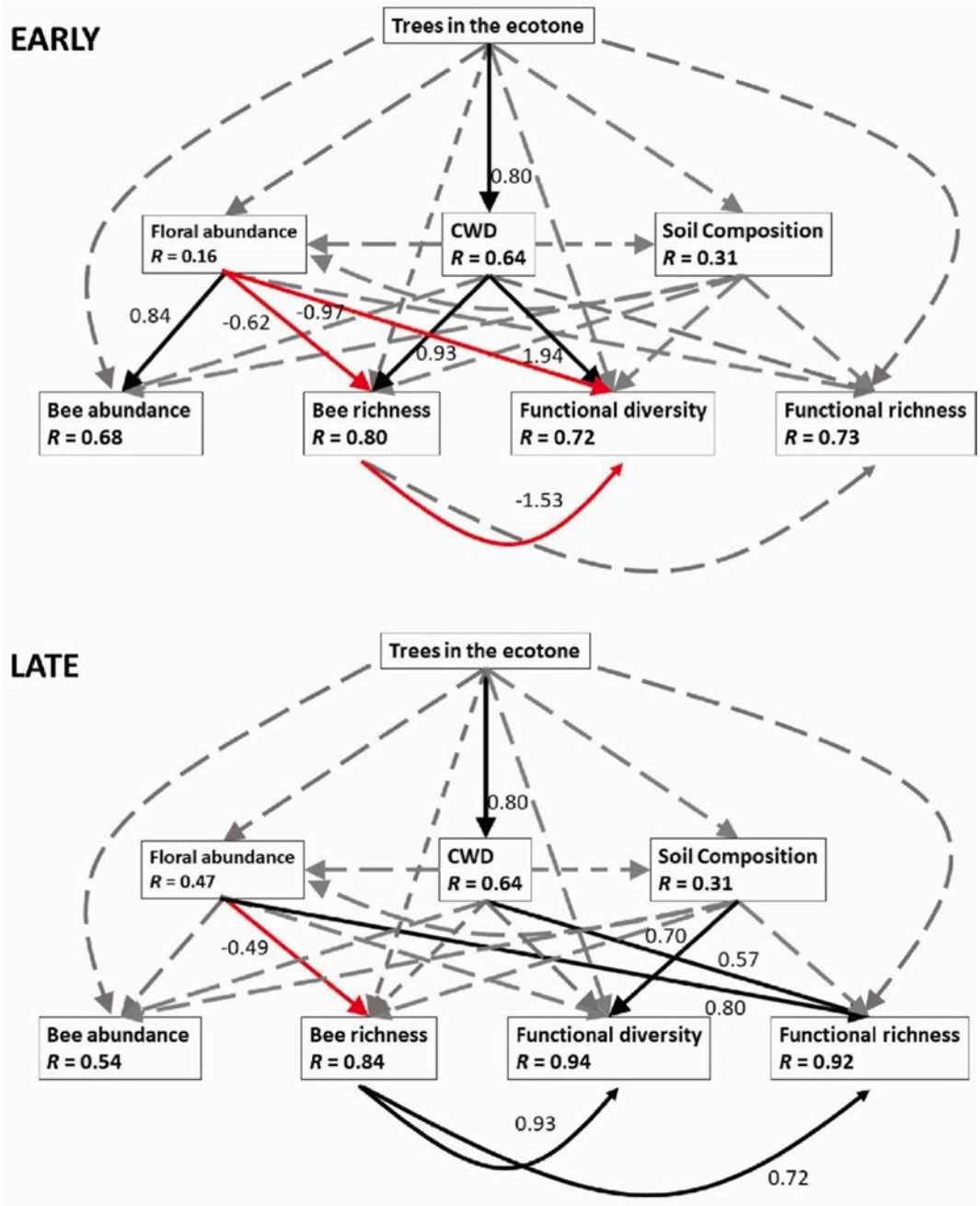

Fig. 3. Piecewise structural equation model testing for direct and indirect effects of habitat characteristics on bee community and functional diversity across early and late season observation periods. Dashed arrows represent relationships between predictor and response variables (boxes) with little statistical support ($p > 0.05$), while solid arrows (red = negative, black = positive) depict relationships with strong statistical support. The standardized path coefficient is reported for relationships with strong statistical support and pseudo-r-squared values are reported for each predictor and response variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

restoration of bee communities in semi-natural ecosystems.

Floral abundance had a positive or negative association with the taxonomic and functional diversity of bee communities and potentially reflects the effects of food resources on the foraging behaviors of bees that are active at different times in the growing season. Early in the growing season the positive association of floral abundance on bee abundance, but negative association with bee richness and functional diversity potentially, indicates that large floral displays dominated by a few plant species increase the specialization of common and abundant bee species within local communities. This result was surprising given that bee richness is known to track floral resources (Potts et al., 2003; Moretti et al., 2009; Taki et al., 2013; LaManna et al., 2021). Within this ecosystem, bumble bees are common, share functional traits, and can specialize on large floral displays of a preferred resource (Heinrich, 1976). Large floral displays of a preferred plant species could therefore recruit more individuals of the same bumble bee species into local communities and reduce functional diversity. Additionally, we aggregated estimates of floral abundance across each observation period in a phenological group and estimates of floral abundance that are aggregated across larger temporal scales are positively associated with bumble bee abundance (Guezen and Forrest, 2021). Later in the growing season when bee communities are the most diverse, the positive association between floral abundance and functional richness could indicate that food resources reduce the strength of habitat filters and increase the

Table 3
Results from an Analysis of Variance on a distance-based Redundancy Analysis testing for the effects of habitat characteristics on bee community composition at sites during early and late periods of the growing season.

Phenological group	Covariate	Df	Sum of Squares	F-stat	p-value
Early	Floral abundance	1	0.25	0.89	0.61
	Trees in the ecotone	1	0.30	1.10	0.32
	Below ground soil composition	1	0.31	1.11	0.35
	CWD	1	0.40	1.46	0.08
	Residual	7	1.94		
Late	Floral abundance	1	0.19	0.65	0.80
	Trees in the ecotone	1	0.14	0.48	0.95
	Below ground soil composition	1	0.14	0.46	0.96
	CWD	1	0.16	0.54	0.90
	Residual	7	2.07		

number of functional groups present within local bee communities (HilleRisLambers et al., 2012). Flower species with diverse morphologies and phenophases may be particularly important to benefit bee species with different activity periods and foraging behaviors throughout the growing season (Havens and Vitt, 2016; Ogilvie and Forrest, 2017).

The abundance of trees within the ecotone had a positive association with CWD volume, which in turn may increase the functional diversity and richness of bee communities by providing nesting resources for bee species from unique functional groups. Trees within the ecotone may be converted into downed woody debris through disturbances like wildfire, wind, or management actions (Harmon et al., 1986), increasing the amount of CWD along habitat boundaries. The availability of CWD may be particularly important for aboveground nesting bee species within systems dominated by shrubs and grasses, and where fire suppression and intensive grazing regimes have removed processes that convert standing woody biomass into dead and downed debris (Heyerdahl et al., 2006; Davies et al., 2011). This observation is supported by the positive association between the volume of CWD and the proportion of bees that are cavity nesting species among early and late season observation periods, which is consistent with studies from a Mediterranean shrubland following wildfire (Potts et al., 2003; Peralta et al., 2017). Additionally, within this system, *Osmia* species are active early in the growing season and are aboveground cavity nesters that require CWD for nesting substrates (Michener, 2007; Danforth et al., 2019). It could therefore be the case that the positive association between CWD volume and functional diversity and functional richness early in the growing season is a result of *Osmia* species that have a unique set of functional traits and are recruited to local communities by the availability of nesting sites. Coarse woody debris volume was also positively associated with the functional richness of bee communities among late season observation periods. Nesting resources may reduce the strength of habitat filters during times of high bee diversity and increase the number of functional groups present within local communities (HilleRisLambers et al., 2012). Nesting resources may be equally important as food resources when

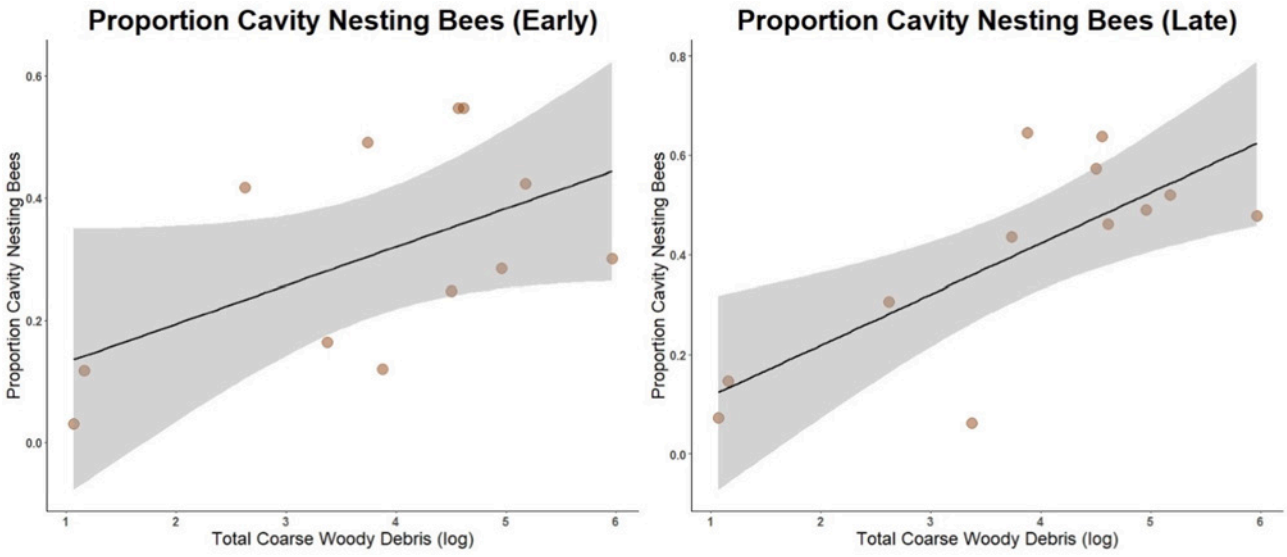

Fig. 4. The proportion of cavity nesting bees increased as the volume of coarse woody debris increases in early and late periods of the growing season.

Table 4
Model outputs from separate linear models investigating the relationship between functional richness and dispersion, with bee-flower interaction network modularity and specialization (H2′) during early and late periods of the growing season. Asterisks denote where specialization could not be estimated for a network with too few observations.

Phenological group	Response	Covariate	Estimate	Std.error	t-value	d.f.	p-value
Early	Modularity	Functional Richness	1.07	1.80	0.60	9	0.57
		Functional Dispersion	0.30	0.53	0.56	9	0.59
	Specialization	Functional Richness	−1.67	3.57	−0.47	8*	0.65
		Functional Dispersion	0.40	1.05	0.38	8*	0.96
Late	Modularity	Functional Richness	1.17	1.14	1.02	9	0.33
		Functional Dispersion	0.31	0.19	1.64	9	0.14
	Specialization	Functional Richness	5.36	1.84	2.92	9	**0.02**
		Functional Dispersion	0.30	0.31	0.96	9	0.36

considering restoration and conservation actions for bee communities in semi-natural ecosystems.

Soil composition was associated with the functional diversity of late-season bee communities indicating that that soil texture and nutrients potentially influence the abundance of species with unique traits in local communities. Clay and phosphorous had the strongest influence on the gradient of soil composition. Clay retains water and potentially selects for large-bodied bees that are strong enough to excavate these soils (Cane, 1991; Harmon-Threatt, 2020; Antoine and Forrest, 2021). Additionally, phosphorous rich soils may increase the floral display and nectar abundance of some plant species resulting in attractive plants for more bee species (Vaudo et al., 2022). Future work may investigate associations between soil characteristics and bee and vegetation communities to understand the direct and indirect effects of soils on bees.

Depending on the period of the growing season there was a positive or negative association between bee richness and functional diversity, indicating that bee species added to local communities either had redundant or complementary functional traits. Environmental filters may be strong early in the growing season and constrain local communities to include bee species which share traits. For instance, low flower availability and unpredictable weather events early in the growing season may favor species that overwinter as adults and constrain bee communities to species with adaptations for early season conditions (Osorio-Canadas et al., 2018). By contrast, environmental filters may weaken later in the growing season when floral abundance is greatest and increase the abundance of bee species with unique traits within local communities. However, there was no effect of habitat characteristics on individual traits at any point in the growing season. It could be the case that foraging bees are temporarily present at local sites when habitat characteristics have a stronger effect on resident species. Future studies may investigate the relationship between habitat characteristics and bee nesting success to describe the effect of resource availability on species ecological performance (Simanonok and Burkle, 2019).

While relationships between functional diversity and bee-flower network specialization or modularity were rare, a positive association between functional richness and specialization among bee communities sampled later in the growing season indicates that local bee communities with more functional groups may also contain more specialized bee species. Contrary to our hypothesis, we did not observe a relationship between functional dispersion and richness or modularity. This finding contrasts with a positive relationship between functional dispersion and modularity observed in hummingbird-flower networks in South America (Maglianesi et al., 2015; Maruyama et al., 2018). Studies conducted at a macroecological scale encompass large environmental gradients which may be required to produce filtering effects that are strong enough to influence the modularity of bee-flower networks. A better understanding of the spatial and temporal scales required to structure bee and flower communities are needed before the relationship between functional diversity and network organization can be resolved.

4.1. Management implications for bee conservation

Management actions that remove conifers while increasing floral and nesting resources for bee species may be necessary to achieve management goals and support bees in semi-natural ecosystems. While the abundance of trees within the ecotone seem to indirectly benefit the taxonomic richness, functional diversity, and functional richness of local bee communities by increasing CWD volume, trees that establish within the ecotone and grow into mature individuals could eventually increase canopy cover and outcompete flowering plants at the forest floor for light and water resources (Roberts et al., 2017). Various management actions are applied to remove conifers that have encroached into grassland/shrublands (Miller, 2005) and may emulate natural disturbances to increase the availability of food and nesting resources that structure bee communities at local and landscape scales (Rodríguez and Kouki, 2015, 2017; Glenny et al., 2022). For instance, prescribed burning and thinning can increase bee abundance and richness by creating early seral stage habitats with abundant floral communities, coarse woody debris, and bare ground (Rodríguez and Kouki, 2015; Decker and Harmon-Threatt, 2019; Moylett et al., 2020). Conifer removal actions may also increase slash left on sites and suppress regeneration of understory plant species (Tardós et al., 2019) and cover nesting locations for ground nesting bees (Rivers et al., 2018), and burning of slash piles can destroy floral communities, sterilize seed banks in soils, and consume CWD (Mott et al., 2021). Coarse woody debris may provide persistent nesting resources for bees as it decays over hundreds of years within this ecosystem (Harmon et al., 1986). Consequently, conifer removal strategies have potentially mixed effects on bee communities depending on how they affect habitat characteristics (Owen et al., 2009; Ross et al., 2012; Mott et al., 2021). Future studies that apply conifer removal treatments and compare the effects on habitat characteristics and bee communities are required to identify management actions that are consistent with pollinator conservation. Additionally, studies that survey habitat characteristics, bee communities, and bee-flower interactions across shrublands with increasing basal area or distance from the forest edge may be important to understand the future effects of conifer encroachment and the need for conifer removal actions to conserve bee communities. Understanding the specific habitat requirements of bee species may be important to design management actions that support bee species that play important functional roles within ecosystems and ensure continued pollination services to plant communities.

CRediT authorship contribution statement

Will Glenny: Conceptualization, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Project administration. **Justin B. Runyon:** Conceptualization, Investigation, Resources, Writing – review & editing, Supervision, Funding acquisition. **Laura A. Burkle:** Conceptualization, Investigation, Resources, Writing – review & editing, Supervision, Funding acquisition.

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.

Data availability

Data will be made available on request.

Acknowledgments

The authors thank J. Salix, A. Freeman, T. Hall, J. Dufficy and M. Kessler for field assistance, T. Griswold, S. Burrows, E. Reese, and C. Delphia for assistance with bee identifications, M. Lavin for plant identifications, and M. Simanonok for helpful discussions. Funding was provided by the USDA Forest Service Beaverhead-Deerlodge National Forest and the Northern Region Native Plant Program. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.120883.

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