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ORIGINAL PAPER

Post-Wildfire Offspring Provisioning by a Solitary Bee is Dominated by Woody Pollen Sources and Uninfluenced by Wildfire Severity

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Abstract

Bee communities often respond positively to wildfire, but little is known about their foraging behavior and pollen use in recently burned forests despite their link to demographic processes. We used palynological analysis to reconstruct how female *Osmia lignaria* – a native, solitary nesting species – provisioned pollen to offspring in post-fire areas and evaluate its influence on adult overwinter survival and body size. We placed artificial nest blocks with a standardized number of adult *O. lignaria* cocoons on 33 sites across a fire severity gradient in southwest Oregon, USA. We found that females provisioned several woody pollen species to offspring – dominated by beaked hazel (*Corylus cornuta*), salal (*Gaultheria shallon*) and California huckleberry (*Vaccinium ovatum*) – and the composition of these dominant pollen types was similar across the fire severity gradient despite strong differences in floral resource density. Nesting females provisioned male and female offspring a similar diversity of pollen types regardless of fire severity, and the number of pollen types consumed by offspring had no detectable influence on their overwinter survival or cocoon mass, a proxy for body size. Our results indicate that woody species are important food resources for *O. lignaria* in recently burned mixed conifer forests, and that management actions that promote woody species after wildfire occurs is likely to promote populations of the blue orchard bee and other solitary bee species.

Study Implications Global increases in the extent and severity of wildfires have made it imperative to understand how organisms respond to changes in key resources within post-fire areas. Native bees play a critical role in the resilience of burned forests, and our results indicate that nesting blue orchard bees fed their offspring a subset of the available floral resources across the fire severity gradient. Woody plant species dominated provisioned food items regardless of fire severity, highlighting the value of retaining woody species as bee forage in recently burned areas. Combined with our previous work, these results indicate recently burned forests can support enhanced bee reproductive output driven by the post-fire response of native woody flowering plants.

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Keywords Fire severity · Larval provisioning · Mixed conifer forest · *Osmia lignaria* · Pollen use · Overwinter survival

Fire is a key disturbance agent in many ecosystems (Pausas and Keeley 2021), and it can have especially pronounced effects in forests by causing physical restructuring and changing resource availability. For example, large reductions in canopy cover, such as that caused by high-severity fire, leads to increases in light availability, promotes flowering plants, and provides conditions favorable to insect pollinators in forests (Ulyshen et al. 2024). Indeed, such changes in structure and resources have been shown to increase the diversity and abundance of insect pollinators in a range of conifer forests (Ponisio et al. 2016; Galbraith et al. 2019a; Ulyshen et al. 2022; Gelles et al. 2022; Favorito et al. 2023). In recent decades, the size and severity of wildfires has increased due to several factors (Abatzoglou and Williams 2016; Hagmann et al. 2021; Brown et al. 2023; Parks et al. 2023; Cunningham et al. 2024), including management actions that have altered forests in ways that diverge from the structure and composition that is characteristic of natural disturbances (Heyerdahl et al. 2001; Pausas and Keeley 2021). These changes in wildfire characteristics have occurred despite conditions of reduced fuel availability (Abatzoglou et al. 2021) and are expected to continue (Flannigan et al. 2013), making it imperative to understand organismal response to fire in light of changing fire regimes.

Insect pollinators make substantial contributions to agricultural production and are a keystone group within natural ecosystems through their pollinating activities. Despite being well-studied in agricultural settings, our understanding of pollinating insects in forests is much more limited (Ulyshen et al. 2023), including how this group responds to forest management and natural disturbances (Hanula et al. 2016; Rivers et al. 2018). Recent reviews have found that insect pollinators often respond to fire via increased species richness and abundance across biomes (Carbone et al. 2019), including conifer forests (Mason et al. 2021). Nevertheless, nearly all studies evaluating forest pollinator response to fire have assessed community-scale measures, with few investigations focusing on the demographic response of insect pollinators to fire (Simanonok and Burkle 2019; Mola et al. 2020; Galbraith et al. 2021). Therefore, an improved understanding of demographic processes and their underlying drivers in post-fire areas are needed to advance bee conservation in forest ecosystems.

Nearly all bee species depend on floral resources to sustain their populations, and the amount, diversity, and quality of available floral resources is expected to influence on bee demographic processes (Roulston and Goodell 2011). Empirical studies typically find local-scale measures of floral density and/or floral richness are strongly linked with bee abundance (Potts et al. 2003; Carvell et al. 2004; Galbraith et al. 2019a). However, some studies have shown that bee abundance-floral relationships may be inconsistent depending on the floral component being evaluated (e.g., floral density vs. floral richness; Zitomer et al. 2023), and others have even found weak or non-existent relationships (Elliott 2009; Johnson et al. 2023). Moreover, bee species with ostensibly similar foraging ecologies can diverge in how they prioritize floral rewards (e.g., quantity vs. quality; Mokkapati et al. 2024). Thus, relying on bee abundance as a proxy for demographic information can be difficult, in part because abundance is an indirect measure that is a product of several distinct processes (e.g., reproduction, survival, foraging range). A more direct and preferable way to assess bee populations is by direct quantification of reproductive output; however, obtaining such information from wild bees is particularly challenging because most species nest underground (Antoine and Forrest 2021) so measuring reproductive output in this group almost always involves destructive sampling. In contrast, species that do not nest underground may provide avenues for direct assessment of the demographic drivers that underpin bee populations and how they are related to floral resources. Mason bees (*Osmia* spp.), in particular, have emerged as an excellent group for assessing the demographic response to disturbance and land use activities (Palladini and Maron 2014; Kratschmer et al. 2020), including wildfire within forests (Galbraith et al. 2021). Cavity-nesting species within this group provide an opportunity to develop a detailed understanding of floral resource use via the assessment of offspring diet (Cripps and Rust 1989a; Eckhardt et al. 2014; McAulay et al. 2021), ultimately allowing for an assessment of the relationship between floral resources and demographic outcomes.

Previously, our research with the blue orchard bee (*Osmia lignaria*) found a strong shift in offspring sex ratio across a natural gradient in wildfire severity such that nesting individuals produced more female offspring as fire severity increased (Galbraith et al. 2021). We also found that females took shorter provisioning trips and floral density was greater as fire severity increased, indicating that floral resources mediated the effects of wildfire on bee reproduction (Galbraith et al. 2021). Female bees control the sex of their eggs (Heimpel and de Boer 2008), and female offspring are larger and more expensive to produce than males in the blue orchard bee (Phillips and Klostermeyer 1978). Thus, the finding that female blue orchard bees shifted their reproductive effort towards the more expensive sex indicates that foraging habitat quality improved with increases in fire severity. Nevertheless, the mechanism(s) underlying these responses remain unknown, including whether females varied in the types of food resources they provisioned to their offspring across the fire severity gradient, and whether such differences resulted in changes to adult overwinter survival or body size.

In this study, we tested the hypothesis that the degree of fire severity – as a proxy for habitat quality – influenced the types of pollen resources nesting blue orchard bees provisioned to their offspring. It is well known that interspecific variation in pollen quality can have strong consequences for mason bee (*Osmia* spp.) populations (Roulston and Cane 2000; Vaudo et al. 2024), as survival to the adult stage can be reduced when pollen provisions are mismatched to nutritional demand during development in both the blue orchard bee (Levin and Haydak 1957) and several congeners (Sedivy et al. 2011; Bukovinszky et al. 2017; McAulay et al. 2021). Therefore, we predicted that blue orchard bees that nested in areas experiencing greater fire severity would provision their offspring with a greater number of pollen types, as pollen mixing is thought to better meet the nutritional needs of developing bees (Eckhardt et al. 2014; Filipiak 2019). Alternatively, female provisioning may be focused on a subset of food resources, rather than the diversity of all resources that are available, if those resources are nutritionally sufficient to support offspring growth and development (Filipiak 2019). If these conditions are met, females nesting in post-fire areas would be expected to provision their offspring with a similar number of pollen types, as long as the subset of resources are available across the fire severity gradient.

In the blue orchard bee, as is in other solitary bees, the amount and composition of food available to offspring during development is entirely dependent on the provisioning activities of the female. Nutritionally deficient provisions can lead to food limitation, reduced body size, and increased mortality of offspring (Torchio 1985; Bukovinsky et al. 2017). Therefore, we tested the additional hypothesis that the number of pollen types provisioned to larval bees had consequences for two measures of offspring quality: adult overwinter survival and body size. We predicted that a greater number of pollen types would be associated with increases in offspring quality, as both measures can be influenced by the composition and amount of food provisioned to developing *Osmia* bees (Levin and Haydak 1957; Torchio 1985; Sedivy et al. 2011; McAulay et al. 2021). We also explored whether male and female offspring were provisioned differentially with respect to pollen types because previous research on *Osmia bicornis* – a closely relative of the blue orchard bee – reported that sons and daughters were provisioned with different mixtures of pollen due to sex-specific physiological requirements (Filipiak 2019). Finally, we evaluated the diversity and density of floral resources around nest sites to quantify the food resources available during the blue orchard bee flight season for comparison with the food resources that females provisioned to their young. To evaluate these ideas, we used palynological analysis of fecal pellets (hereafter, frass) that were produced by larval bees within their nest cells, which provided us with the ability to reconstruct their diets and determine which floral resources were provisioned by nesting females relative to offspring sex, fire severity, and the floral resources available during nesting.

Methods

Study System and Focal Species

We conducted this research during spring 2017 in the Klamath Mountains in the greater Klamath-Siskiyou region of southwestern Oregon, USA (Fig. 1), an area which experiences hot, dry summers, wet winters, and is classified as a mixed-severity fire regime (Taylor and Skinner 1998). This region harbors > 3,500 plant species and is one of the most botanically rich forested regions in North America, with wildfire serving as a key driver of biodiversity (Whittaker 1960; Ricketts et al. 1999). In addition to a mix of overstory coniferous tree species that includes Douglas-fir (*Pseudotsuga menziesii*), Jeffery pine (*Pinus jeffreyi*), and ponderosa pine (*P. ponderosa*), hardwoods such as madrone (*Arbutus menziesii*) and tanoak (*Notholithocarpus densiflorus*) are also common in this area, with a wide diversity of understory shrubs and forbs (Whittaker 1960). The spring bloom in this region corresponds with the local

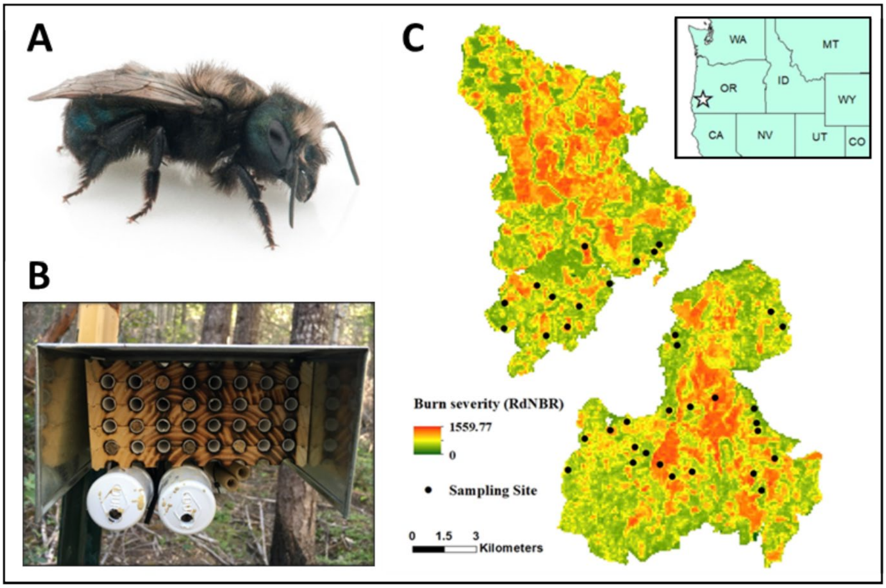

Fig. 1 **A** The blue orchard bee (*Osmia lignaria*) is a solitary, native, spring-nesting bee that uses human-provided cavities for rearing its offspring, facilitating measurement of pollen use. **B** In this study we used wooden nest blocks, each containing 32 nest chambers, lined with white paper straws and housing two white PVC containers into which pre-emergent adult cocoons were placed. Two additional reed tubes with blue orchard bee attractant can be seen under the nest block and to the right of the PVC containers. **C** Map of the Douglas Fire Complex in southwest Oregon, USA depicting location of sites where pollen use was quantified (black dots) and the broad variation in fire severity (RdNBR) across the landscape. Photo of *Osmia lignaria* by Lincoln Best, License: CC BY

blue orchard bee flight season and is dominated by woody perennial shrubs including salal (*Gaultheria shallon*), California huckleberry (*Vaccinium ovatum*), thimbleberry (*Rubus parviflorus*), and California blackberry (*R. ursinus*; Galbraith et al. 2019a).

The Douglas Fire Complex comprised the Dad's Creek Fire and the Rabbit Mountain Fire, which started in late July 2013 due to lightning ignitions and ultimately burned ~ 19,760 ha across public and private landholdings of a range of stand ages (Zald and Dunn 2018). For this study, areas that were available for sampling were constrained by a combination of land ownership and burn severity in the region. Specifically, we were restricted to working on US Department of Interior Bureau of Land Management forestlands that experienced varying levels of fire severity and had not undergone post-fire salvage logging; the majority of these sites were managed as even-aged Douglas-fir stands prior to the 2013 wildfires. Fire severity is characterized by the degree to which a location has been altered by fire disturbance through a fire's consumption of organic materials (Keeley 2009), and we used the relative differenced normalized burn ratio (RdNBR) as a measure of fire severity as derived from LANDSAT images that compared pre- and post-fire changes in vegetation (Miller and Thode 2007; Miller et al. 2009). We initially constructed four distinct fire severity categories to select sampling locations, independent of stand boundaries, that represented the entire fire severity gradient: (1) low: basal area mortality ≤ 25%; (2) moderate low: basal area mortality 26–50%; (3) moderate high: basal area mortality 51–75%; and (4) high: basal area mortality > 75%. Next, we generated randomly stratified points from each burn severity category using ArcGIS, and then selected sampling sites from the subset of points that met three distinct selection criteria; they had to (1) occur within an area that had a minimum of 6.5 ha of forest burned within a single fire severity category, (2) be > 50 m from the nearest road to avoid potential edge effects, and (3) be ≥ 1 km from other points within the same fire severity category to provide spatially independent sampling areas based on the typical foraging range of our study species (~ 500 m; Zurbuchen et al. 2010). The resulted in a sample of n = 33 sites that represented the full range of fire severity values observed within the Douglas Fire Complex.

The blue orchard bee (Fig. 1) is a solitary nesting species that is found widely throughout the United States and produces a single generation each year (Phillips and Klostermeyer 1978). This cavity-nesting species is particularly useful for research questions related to offspring provisioning and reproductive output, as they readily nest in human-provided structures and can be closely monitored without impacting natural behaviors (Spendal and Cane 2022). This species overwinters as an adult within its cocoon and emerges during spring (March–May); immediately after emergence, females mate, begin constructing their nests, and forage for provisions (Torchio and Tepedino 1980). Blue orchard bee nests are composed of a series of linearly arranged nest cells that are demarcated with mud partitions, which we refer to hereafter as a nest chamber. Within each nest cell the female deposits a provision mass that contains pollen mixed with nectar onto which she lays a single egg before sealing the cell (Phillips and Klostermeyer 1978; Torchio and Tepedino 1980). This species is a generalist forager that uses pollen from upwards of 24 plant families (Rust 1990; Haider et al. 2014), and typically mixes multiple pollen types in provisions (Williams 2003; Williams and Tepedino 2003). Within the linearly arranged nest cells in each nest chamber, female eggs are laid first in the innermost nest cells, followed by male eggs which are laid later and closer to the opening of the nest chamber (Phillips and Klostermeyer 1978; Torchio and Tepedino 1980). Female blue orchard bees are ~ 31% larger than males and they receive provisions that are ~ 37% larger (Phillips and Klostermeyer 1978), so female offspring require more parental investment than males. Shortly after hatching, blue orchard bees consume their provision as they proceed through a series of larval molts. When larvae reach the fifth instar, immediately prior to spinning a cocoon, they defecate frass randomly within the nest cell such that their fecal material represents the mixing of pollen from the entire provision that was consumed (Torchio 1989). This, coupled with pollen wall layers that are highly resistant to insect digestion (Roulston and Cane 2000), including by larval bees in the genus *Osmia* (Suarez-Cervera et al. 1994), allows frass to be used as an unbiased quantification of the food resources provides to larval bees during their development.

Experimental Design

In spring 2017, we placed two identical wooden nest blocks (Pollinator Paradise, Nampa, Idaho, USA) mounted on 1.8 m metal posts in the center of each sampling site. Both nest blocks were located 20 m from the site center, the first along a randomly selected azimuth and the second 180° from the first azimuth. Each nest block contained 32 individual nest chambers that were lined with cardboard tubes prior to placement in the field (Fig. 1). During a 1-week period (April 3–10), we seeded each nest block with 20 female and 30 male pre-emergent adults still in cocoons (i.e., 40 females and 60 males were released on each site) to allow adult bees to emerge, mate, and use nest blocks for rearing offspring. More male cocoons were provided than females to ensure mating success of females. Cocoons were purchased from a commercial dealer (Hive & Garden, West Linn, Oregon, USA) and were refrigerated at 4° C and between 60–70% relative humidity prior to being placed at nest blocks. We monitored nest blocks regularly from May 15–25 to check for emergence, and we collected nest blocks 58–65 days after deployment (June 5–9). After we retrieved nest blocks, we placed them in a shaded location where larvae completed development at ambient temperature until October 2017, at which point we used a digital x-ray imaging system (USDA-ARS Bee Identification Laboratory, Logan, Utah, USA) to quantify offspring production, identify male and female progeny (by relative size and position in nest chambers), and determine survival to the pre-emergent adult stage. After x-rays were completed, we moved bees back into cold storage at 4° C until March 2018, at which point we placed cocoons individually into 48-plate wells within a large incubator set at 20–25 °C. We checked cocoons every 1–2 days to determine the day of emergence through mid-May, after which all unhatched cocoons were presumed dead. For the subset of cocoons that were selected for pollen analysis (see below), we also measured cocoon mass, which is strongly correlated with overall body size in *Osmia* bees (Bosch and Vicens 2002), and is an outcome of the environmental conditions experienced by offspring during their development (Tepedino et al. 1984).

Quantification of Offspring Pollen Use

To quantify pollen use, we first randomly selected 3–4 nest chambers within each nest block, and then from each nest chamber randomly selected one nest cell. We purposefully constrained our choice to four types of nest cells to examine cells of both sexes and those that were constructed across time. These included (1) the nest cell containing the second female within a nest chamber (as measured from the back of the nest chamber), (2) the outermost female nest cell within a nest chamber, (3) the first male nest cell within a nest chamber, and (4) the outermost male nest cell within a nest chamber. We selected the second female nest cell because we noticed during our initial dissections that the first female nest cell was not always completely sealed, as some females opted not to put a mud plug against the wooden block when starting their initial cell. Therefore, selecting the second female nest cell allowed us to be sure that no frass was loss from the cell during its collection. If a randomly selected nest chamber did not contain a nest cell, we repeated our selection process until we selected a minimum of 3 nest cells from each site.

To collect frass samples, we first opened the cardboard nesting chamber along a pre-cut seam and pinned it to a wooden block. We then used clean fine forceps to remove all visible frass grains from selected focal nest cells and place them into gelatin capsules. We then selected 6–8 frass grains from each capsule and added them to a new microscope slide; we selected this amount because using fewer grains led to insufficient pollen on slides and using more led to clumping that prevented delineating individual pollen grains. After we placed frass onto a microscope slide, we added one drop of deionized water and then left the frass-water mixture for 5 min to allow the frass to dissolve. Next, we pulverized the frass with a precision spatula until a homogenous mixture formed and allowed this mixture to dry via evaporation for at least 10 min. We then added one drop of fuschsin acid and one drop of glycerin to the mixture, further pulverizing the mixture with the precision spatula; we undertook this final step to increase the contrast of pollen structures for digital photography (see below; Beil et al. 2008; Kratschmer et al. 2020).

For each slide, we took a new cover slip and superimposed three dots with a permanent black marker that formed a 1-cm equilateral triangle near its center before placing it onto the slide. Next, we used a Leica digital light microscope with a Leica MC120 HD digital camera (Leica Microsystems, Inc., Buffalo Grove, Illinois, USA) and Leica software (Acquire v 3.4.4 Build 9093) to take photographs at 20 × magnification in the vicinity of each of the three dots to enhance details of individual pollen grains. This resulted in three subsamples on each slide, captured as digital images, that represented the pollen consumed by each offspring. We determined the locations for each of the three photographs taken on each slide by navigating the microscope field until the permanent marker dot was just outside of view, and then took a photograph on the perimeter of each dot that allowed the maximum pollen grain count. Our goal was to capture 200 pollen grains/image; this approach ultimately yielded ca. 50–100 pollen grains/image and up to 300 pollen grains/slide. To eliminate inter-observation variation, a single observer (ARM) characterized all distinct pollen types from photos by their size and shape, measured in both polar and equatorial dimensions, and by their surface characteristics (Eltz et al. 2001). The observer then then summed the number of distinct pollen types in the three subsampling areas on each slide (hereafter, pollen richness) based on a pollen slide reference collection from the Pacific Northwest (authors, unpublished data). In addition, the observer visually estimated the relative abundance of each unique pollen type that comprised $\geq 10\%$ of the pollen total in each image in units of 5%. Pollen types representing $< 5\%$ of the total pollen count in any subsample were not included in data analysis because they were considered contaminants and not an indication of intentionally provisioned pollen (see Cane and Sipes 2006).

To estimate relative abundance for each distinct pollen type on the slide, we summed the relative proportion for each unique pollen type across all images and then standardized the relative abundance of each pollen type to 75 pollen grains (i.e., the midpoint of the range of pollen grains that was estimated across all images). We took special care when removing frass from nest cells so there was a limited amount of fresh pollen on slides; in nearly all cases, it occurred in < 1% of the sample. When fresh pollen was present, it was easy to identify by its deep coloration – typically orangish to yellowish – that contrasted markedly with pollen in frass, the latter which becomes empty after digestion and therefore has a translucent appearance. We found that exposure to digestive chemicals did not markedly alter the shape and surface characteristics of digested pollen relative to fresh pollen for most groups except for the Ericaceae, Campanulaceae, and beaked hazel, where pollen grains either collapsed or expanded greatly and flattened. Nevertheless, pollen in these groups remained recognizable and could be classified to either species or family levels.

Floral Resource Sampling

As part of our prior work studying the wild bee community response to wildfire and post-fire salvage logging (Galbraith et al. 2019a, b), we established two 50-m long transects that extended from the center of each site to quantify available floral resources during the blue orchard bee flight season (May–June 2017). Our initial observations suggested flowering plants on sites might be patchily distributed, so we implemented ordered distance sampling to quantify the density of flowering resources (Nielson et al. 2004). This approach is a point-to-object method of distance sampling that can be used to sampling floral communities and provide estimates of bloom density when flowering plants are sparsely distributed. At 10-m intervals along each transect we determined the 4th nearest flowering plant in bloom, identified it to species, and measured its distance from the transect (see Nielson et al. 2004 for details). We then summed the estimated number of open blooms for all plant species across two separate collection periods as a measure of floral density, and we summed the total number of flowering plant species recorded in bloom as a measure of flowering plant richness. We note that our floral resource data have been published previously (Galbraith et al. 2021) but are included here for context regarding how pollen provisioning varied across the fire severity gradient relative to flowering plant availability.

Statistical Analysis

For all analysis, we used the R statistical environment (v4.4.0; R Core Team 2024) to construct statistical models to test a priori hypotheses. To model pollen richness, we first used the ‘lme4’ package (v.1.1–35.5, Bates et al. 2015) to construct a linear mixed model that contained the mean number of pollen types per nest cell as the response variable, site-level fire severity (RdNBR) and offspring sex as fixed effects, site-level plant richness as a covariate, and site as a random effect. We chose to model the mean number of pollen types for each sex separately to reduce model complexity, and we chose the mean because the mean and median were strongly correlated when we examined the number of pollen types in each nest cell ($r = 0.99$). To evaluate how the abundance of pollen types varied across the fire severity gradient, we used the ‘mvabund’ package (Wang et al.

2012) to fit a single generalized linear model to each pollen type across the range of fire severity values representing each site. Specifically, we fitted a single generalized linear model to each pollen type with site-level variation in fire severity as a common set of predictor variables, and then used resampling to test for community-scale responses. This approach is an improvement over other multivariate analyses because it has increased power and can account for the mean–variance relationship that is typical of ecological community datasets (Wang et al. 2012). We used the lmerTest package (v.3.1–3; Kuznetsova et al. 2017) for assessing fixed effects for models using a normal distribution, and we evaluated model diagnostics using the autoplot function in base R for linear models and the 'simulateResiduals' function in the 'DHARMa' package for generalized linear mixed models (v.0.4.6, Hartig 2022).

To model adult overwinter survival as a function of nest cell pollen richness, we used the lme4 package to construct a generalized linear model with a quasi-binomial distribution and a logit link that contained survival as the response variable, with nest cell pollen richness and offspring sex as fixed effects. We were forced to use a quasi-binomial model because of potential overdispersion, and we were unable to incorporate random effects of nest block or study site due to issues with singularity. To model body mass as a function of nest cell pollen richness, we constructed a linear mixed model with nest cell pollen richness and offspring sex as fixed effects, and study site as a random effect; singularity also prevented us from using nest block as a random effect in conjunction with study site in this model. We used a similar approach to model body mass of fire severity, where we constructed a linear mixed model with mean body mass and offspring sex as fixed effects, and study site as a random effect; we did not use nest block as a random effect in conjunction with study site due to concerns about singularity. Prior to modeling, we calculated the mean body mass for male and female bees separately on each site.

Finally, we constructed models to assess variation in flowering plant richness and floral density (flowers/ha) across the fire severity gradient. To model flowering plant richness, we used the 'glmmTMB' package (Brooks et al. 2017) to construct a generalized linear model with a Poisson distribution and a log link that contained site-scale flowering plant richness as the response variable and site-scale RdNBR as a fixed effect with site elevation as a covariate. To model floral density, we used the lm function to construct a linear model with a normal distribution that contained log-transformed number of flowering plants/ha as the response variable with site-level fire severity (RdNBR) as a fixed effect with site elevation as a covariate. To quantify the relative composition of floral resources across the fire severity gradient, we used the 'mvabund' package as described above, except we fit a single generalized linear model to each flower plant species across the range of fire severity values representing each site. Finally, we quantified the correlation between floral density and plant species richness on each site using Pearson's correlation coefficient. Assumptions were met for all models, and for models related to fire severity we report model coefficients for a 100-unit increase in RdNBR. For generalized Poisson models we report exponentiated parameter estimates and their associated 95% confidence intervals (CIs) unless otherwise noted.

Results

Pollen Use and Offspring Fitness

We analyzed 1–5 nest cells of each sex from n = 33 sites for a total of 125 nest cells, comprising 53 male and 72 female cells across the fire severity gradient. Although we identified 19 distinctive pollen types from nest cells, only 5 types were found in > 10% of examined cells (Fig. 2). The great majority of nest cells (89.6%) contained > 1 unique pollen type, and most cells contained 3 unique pollen types (range: 1–5; Figure S1). The most commonly detected pollen type was beaked hazel (see Table 1 for scientific names), occurring in 92.8% of the nest cells examined, followed by plants in the Ericaceae family (84.8%; primarily California huckleberry and salal), big deervetch (30.4%), strawberry (12.8%), and California blackberry (10.4%). A single pollen type could not be classified to family, genus, or species (Table 1). When evaluating the relative abundance of unique pollen types, we found no evidence that the relative composition of pollen types varied across the fire severity gradient ($LRT = 23.71$, $P = 0.215$). In particular, the three most commonly encountered pollen types were largely consistent in the proportion of provisions they represented regardless of fire severity (Fig. 3).

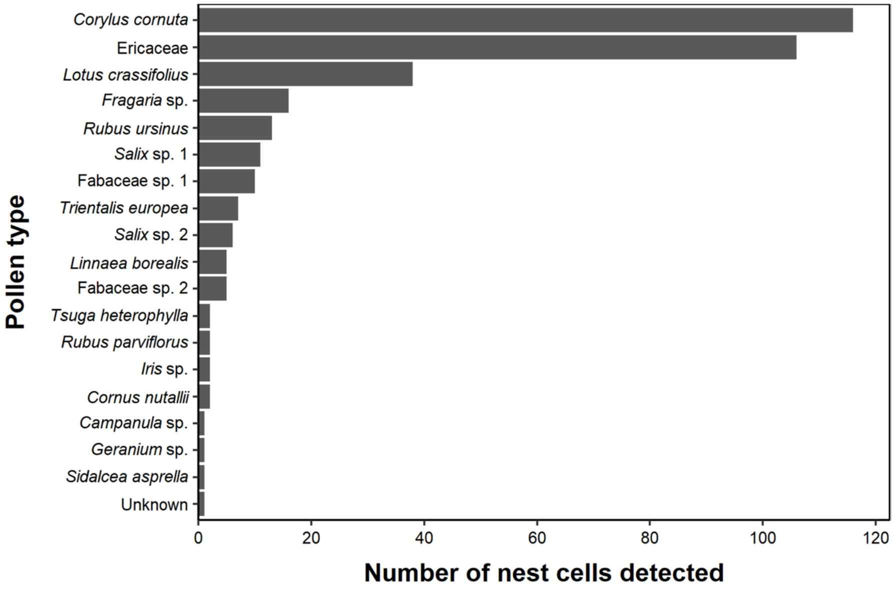

Fig. 2 Frequency of 19 unique pollen types identified by surface characteristics, size, and shape that were detected in blue orchard bee nest cells across the fire severity gradient at the Douglas Fire Complex in southwest Oregon, USA. Common names are provided in Table 1, and plants in the Ericaceae family were thought to be comprised primarily of salal (*Gaultheria shallon*) and California huckleberry (*Vaccinium ovatum*)

Table 1 Taxonomic diversity and representation of pollen types provisioned to blue orchard bee offspring in nests across a gradient in wildlife severity at the Douglas Fire Complex during spring 2017. All taxonomic information based on USDA, NRCS (2024)

Family	Taxon	Number of sites pollen detected[1]	% nest cells pollen detected[2]	Min. RdNBR[3]	Max. RdNBR[4]	Proportion of RdNBR[5]
Betulaceae	Beaked hazelnut (*Corylus cornuta*)	33	92.8%	50.27	1037.95	100%
Ericaceae	California huckleberry (*Vaccinium ovatum*), salal (*Gaultheria shallon*)	33	84.8%	50.27	1037.95	100%
Fabaceae	Big deervetch (*Lotus crassifolius*)	23	30.4%	50.27	1037.95	100%
Rosaceae	Wild strawberry (*Fragaria* sp.)	13	12.8%	60.84	1037.95	98.9%
Rosaceae	California blackberry (*Rubus ursinus*)	9	10.4%	50.27	1027.03	98.9%
Salicaceae	Willow (*Salix* sp. 1)	9	8.8%	50.27	957.27	91.8%
Fabaceae	Pea family (Fabaceae sp. 1)	8	8.0%	167.98	823.22	66.3%
Primulaceae	Arctic starflower (*Trientalis europaea*)	7	5.6%	56.57	1037.95	99.4%
Salicaceae	Willow (*Salix* sp. 2)	6	4.8%	67.75	823.22	76.5%
Caprifoliaceae	Twinflower (*Linnaea borealis*)	5	4.0%	60.84	396.84	34.0%
Fabaceae	Pea family (Fabaceae sp. 2)	4	4.0%	67.75	1037.95	98.2%
Pinaceae	Western hemlock (*Tsuga heterophylla*)	1	1.6%	764.31	764.31	—
Rosaceae	Thimbleberry (*Rubus parviflorus*)	2	1.6%	112.83	454.31	34.6%
Iridaceae	Iris (*Iris* sp.)	1	1.6%	764.31	764.31	—
Cornaceae	Pacific dogwood (*Cornus nuttallii*)	2	1.6%	167.98	251.66	8.5%
Campanulaceae	Bellflower (*Campanula* sp.)	1	0.8%	298.1	298.1	—
Geraniaceae	Geranium (*Geranium* sp.)	1	0.8%	764.31	764.31	—
Malvaceae	Dwarf checkerbloom (*Sidalcea asprella*)	1	0.8%	764.31	764.31	—
—	Unknown[6]	1	0.8%	764.31	764.31	—

[1] *Out of a total of 33 sites examined*

[2] *Out of a total of 125 nest cells examined*

[3] *Lowest level of fire severity where pollen type was detected in a nest cell*

[4] *Highest level of fire severity where pollen type was detected in a nest cell*

[5] *The degree of overlap between the fire severity levels where the pollen type was detected relative to the entire fire severity gradient*

[6] *A single pollen grain could not be classified to species, genus, or family*

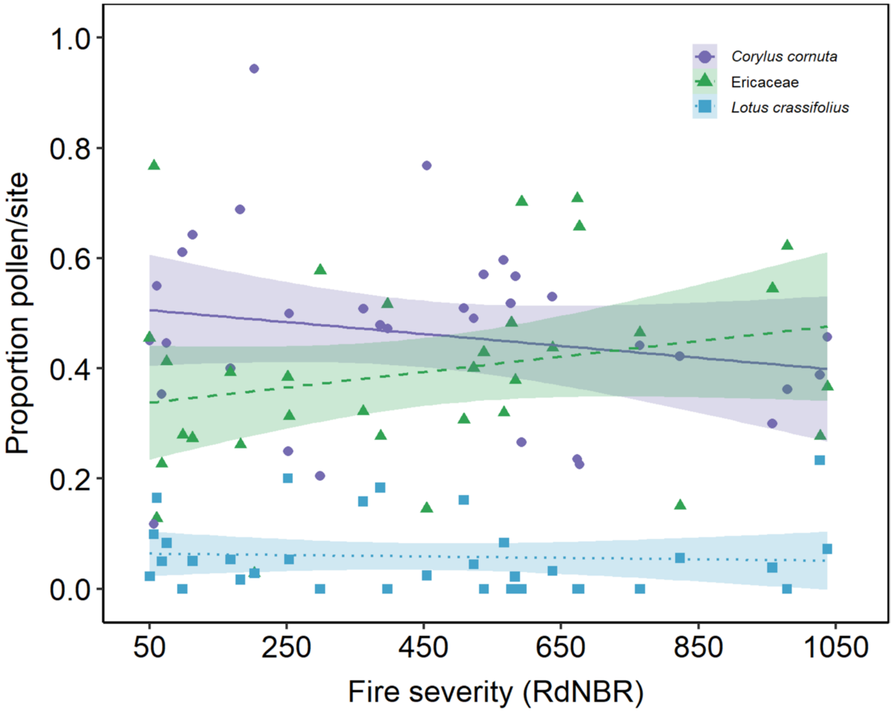

Fig. 3 Predicted relationship between fire severity and the proportion of the three most abundant pollen types recorded in blue orchard bee nest cells at the Douglas Fire Complex in southwest Oregon, USA. Observed values for beaked hazel (*Corylus cornuta*) are denoted by purple circles, plants in the Ericaceae family (i.e., primarily salal [*Gaultheria shallon*] and California huckleberry [*Vaccinium ovatum*]) are denoted by green triangles, and big deervetch (*Lotus crassifolius*) are denoted by blue squares; 95% confidence intervals are denoted by shaded areas for all three groups

When quantifying the mean number of pollen types per nest cell, we found no evidence of a relationship between fire severity ($\beta=0.01$ [95% CI: –0.05, 0.08], $z=0.42$, $P=0.678$) or offspring sex ($\beta=-0.17$ [95% CI: –0.50, 0.15], $t=-1.04$, $P=0.307$; Fig. 4). Likewise, we found no evidence that adult overwinter survival was influenced by either nest cell pollen richness ($z=0.67$, $P=0.505$) or offspring sex ($z=0.88$, $P=0.383$). Finally, we found no evidence for an effect of either nest cell pollen richness ($\beta=0.003$ [95% CI: –0.002, 0.007], $t=1.21$, $P=0.230$) or fire severity ($\beta=0.002$ [95% CI: -2.71×10^{-4}, 0.003], $t=1.67$, $P=0.107$; Figure S2) on offspring cocoon mass.

Floral Resources

We recorded 95 plant taxa representing 37 families blooming during flowering plant surveys conducted during the blue orchard bee nesting period (Table S1). Nearly half (48.4%) of these species were rare and only recorded from a single site, and only 8 taxa were found on 10 or more sites (Table S1). Of the 16 plant species that were detected on at least 20% of our sites, only 6 were recorded in nest cells as pollen despite most

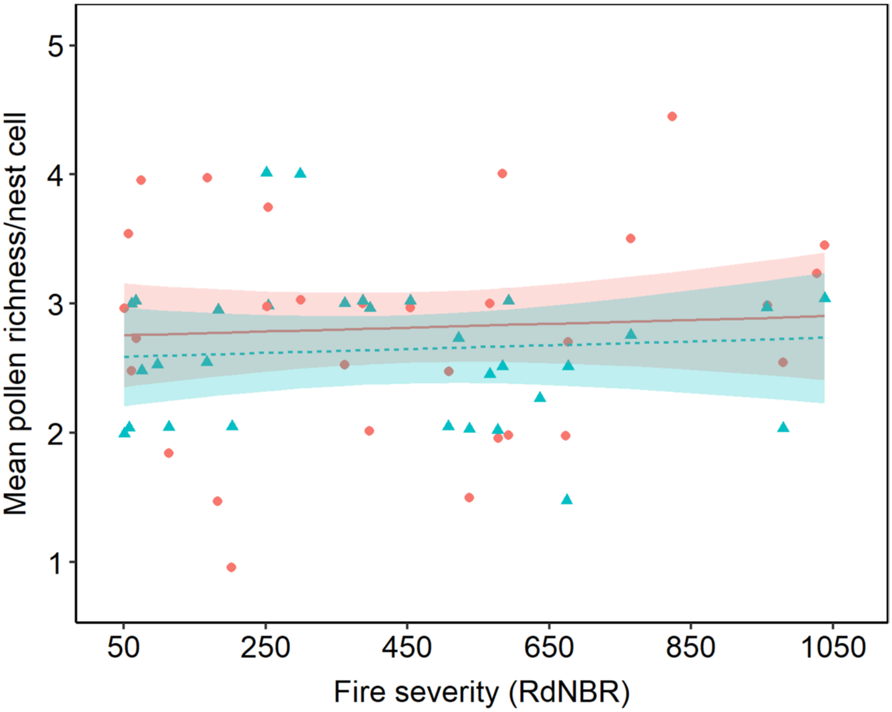

Fig. 4 Predicted relationship between fire severity and mean pollen richness for male (blue shading and blue dashed lines) and female (red shading, and red solid lines) blue orchard offspring at the Douglas Fire Complex in southwest Oregon, USA. Observed values for male offspring are denoted by blue triangles, observed values for female offspring are denoted by red circles, and 95% confidence intervals are denoted by shaded areas

species occurring across the majority of the fire severity gradient (Fig. 5). When examining the influence of fire severity on plant communities, we found no evidence of an effect of fire severity on flowering plant richness at the site scale (β=1.02 [95% CI: 0.97, 1.07], z=0.94, P=0.349; Figure S3A). In contrast, we found strong evidence of a positive influence of fire severity on floral density (β=0.45 [95% CI: 0.17, 0.74], z=3.29, P=0.003; Figure S3B), and that the composition of flowering plant species in bloom varied across the fire severity gradient (LRT=115.7, P=0.005). Finally, we found that plant richness and floral density was correlated across sites (Pearson r=0.40, P=0.021; Figure S4).

Discussion

Our study, the first to assess offspring provisioning behavior of a solitary bee across a gradient of wildfire severity, found that the number and composition of pollen types varied little relative to fire severity, and that the types of pollen that were provisioned to larval bees were a subset of the flowering plants in bloom. Previous work in non-forested ecosystems with the blue orchard bee has found it to be a

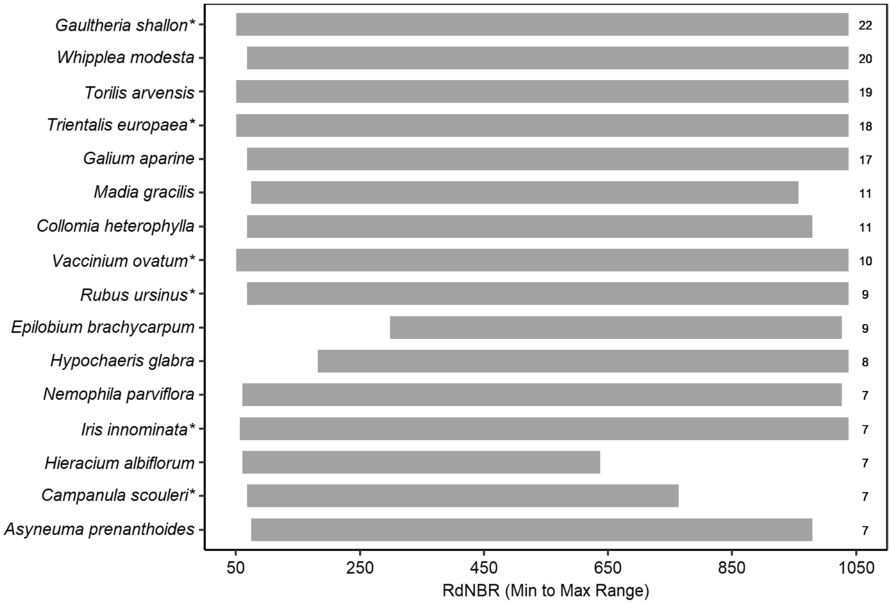

Fig. 5 The distribution of flowering plant species detected on at least 20% of sites during floral resource surveys during the blue orchard bee nesting season at the Douglas Fire Complex in southwest Oregon, USA. Bars represent the range of site-scale fire severity values where each species was detected during floral surveys. Species shown with an asterisk (*) are confirmed host plants that were used for pollen by blue orchard bees in this study; the number of sites on which each species was found is shown to the left of the bars, from a total of 33 sites sampled

facultative specialist in its pollen use, whereby females provision most nest cells with pollen from a relatively small number of flowering plants at local scales, yet dozens of genera and families are used by the species across its range (Cripps and Rust 1989b; Rust 1990; Williams and Tepedino 2003; Haider et al. 2014). This was reflected in our study, as female blue orchard bees provisioned 19 different pollen taxa, with the distribution of pollen types heavily skewed towards a small number of species, despite nearly 100 species of flowering plants blooming in the vicinity of active nests. We also found that the great majority of nest cells contained multiple pollen types, with no more than five unique pollen types in any of the nest cells we evaluated. Pollen mixing of a limited number of pollen types therefore appears to be the norm based on this and other studies of the blue orchard bee (Rust 1990; Williams and Tepedino 2003; Kraemer and Favi 2005), presumably because it increases the efficiency of harvesting pollen by provisioning females, reduces the likelihood of nutritional deficiency for offspring, or both (Eckhardt et al. 2014).

We found that male and female offspring were provisioned similarly across the fire severity gradient in terms of the richness and composition of pollen. We also found that the number of pollen types in nest cells had no detectable consequences for adult overwinter survival and body size for either sex. These findings run counter to previous work on the closely related *O. bicornis*, in which nesting females provide sex-specific pollen mixtures that correspond to the different nutritional needs of their sons and daughters (Filipiak 2019). Although examining pollen nutritional components was beyond the scope of our study, our results do indicate that pollen provisioned by nesting females was not nutritionally deficient in a way that strongly impacted larval development. They also they suggest that provisioning females were able to use a relatively small number of forage plants that were present across the fire severity gradient to obtain adequate nutrition for their offspring. These conclusions are supported by our previous work in this system where we found the majority (> 86%) of provisioned blue orchard bee nest cells survived to adulthood, and the offspring sex ratio became more biased towards the more expensive sex (i.e., females) as fire severity increased (Galbraith et al. 2021); neither of these results would be expected if provisioned pollen was limited in nutritional quality. Having access to adequate nutrition is critical for maintaining bee populations (Roulston and Cane 2000; Vaudo et al. 2015), and there is growing interest in coupling broad measures of floral resources with focused study of the pollen nutritional components and link it to different aspects of bee ecology, including foraging (Williams 2003; Mokkapati et al. 2024), reproduction (Williams and Kremen 2007; Kratschmer et al. 2020), health (Alaux et al. 2017), and even community-scale patterns of plant-bee interactions (Vaudo et al. 2020, 2024). Therefore, new investigations are needed that measure pollen use across environmental gradients, quantify nutritional components of provisioned pollen, and evaluate how pollen use influences bee offspring growth and development. This information will be especially valuable in managed forest landscapes, where it is needed to provide an improved understanding of how management actions influence the drivers of pollinator populations (Hanula et al. 2016; Rivers et al. 2018).

The most frequently provisioned pollen types recorded in this study are classified as woody shrubs, including beaked hazel and two plants in the Ericaceae, the former being present in > 92% of the nest cells we examined. Beaked hazel is noteworthy as a forage item because, as a wind-pollinated shrub, its flowers provide no nectar to insect pollinators (Fryer 2007). Wind-pollinated plants are lipid- and calorie-rich (Roulston and Cane 2000), so we speculate that beaked hazel served as a high-quality forage plant that contributed to high proportion of provisioned cells that ultimately developed into adults (Galbraith et al. 2021). Moreover, because it provides no nectar the use of beaked hazel was driven by foraging activities that targeted this species for its pollen alone, as opposed to being used for pollen secondarily during nectar foraging activities. Beaked hazel is one of the first abundant pollen sources in the spring in our region (Burgett et al. 1989) and is widely distributed throughout North America; thus, it appears to be an overlooked and important food source for the blue orchard bee and perhaps other spring-flying bee species (Hurd 1979; Rust 1974, 1990). Blooming shrubs in the heath family (Ericaceae) represented largely by two taxa – California huckleberry and salal – were the second most common pollen type we detected in nest cells and encountered > 2.5 × more often than the next most common pollen type. Although huckleberry (*Vaccinium*) is known to be used by blue orchard bees for pollen (Weistreich et al. 2023), salal has not been recorded as a food source heretofore, although other native bees have been observed foraging on it (Huffman 1992; authors, pers. obs.). All three of the aforementioned plants respond to wildfire disturbance via vegetative sprouting (Stearns 1974; Messier and

Kimmins 1991) and are likely important forage plants for the blue orchard bee and the broader bee community that occurs in post-fire mixed-conifer forest (Galbraith et al. 2019a). The remaining pollen types we detected were less frequently encountered and included taxa in families known to be used by our focal species and its congeners, such as species in the Fabaceae and Rosaceae (Hurd 1979; Rust 1990; Haider et al. 2014). As expected, provisioning females in our study avoided species in the Asteraceae family, likely because plants in this family generally provide low-quality pollen to foraging generalists like the blue orchard bee (Levin and Haydak 1957; McAulay et al. 2021).

Our study found that blue orchard bee pollen foraging was tied strongly to woody forage species, with two of the three most abundant pollen types not being documented in prior studies. This finding highlights how the floral syndrome of the blue orchard bee is based on shrubs and trees (Rust 1990) as evidenced by prior studies documenting its use of pollen from *Acer*, *Salix*, *Quercus*, *Cercis*, *Cornus*, and *Ceanothus*, among others (Rust 1974, 1990; Kraemer and Favi 2005; Haider et al. 2014). Although this may not be surprising given the blue orchard bee is classified in the *bicornis* clade of *Osmia*, a group dominated by species that often forage on woody plants (Haider et al. 2014), it does emphasize that forests may be particularly valuable for supporting blue orchard bee populations, including those that may be adjacent to crops and provide spillover pollination services (Ulyshen et al. 2023). It also suggests that forest management actions taken to promote woody forage plants in post-fire areas are likely to support more bees relative to areas where competing vegetation is targeted for reduction. For example, reducing the amount and/or extent of silvicultural herbicides is expected to promote the native floral communities upon which bees have evolved (Stokely et al. 2020, 2022). Similarly, retaining existing woody vegetation used by insect pollinators as forage should also provide benefits during the early seral period post-fire period, even if restricted to small portions of the landscape. In areas where post-fire salvage logging may be implemented, retention of dead or declining trees can benefit native bees, such as cavity-nesting species that nest in woodboring beetle exit holes in snags and declining trees (Cane et al. 2007). Undertaking actions that promote woody vegetation in recently burned forests will also benefit other elements of biodiversity, such as declining songbirds that require broadleaved hardwoods for nesting habitat (Betts et al. 2010) and other early seral organisms that are of conservation interest (Swanson et al. 2014; Kormann et al. 2021).

Conclusion

Our study expands our knowledge of how blue orchard bees use woody pollen species when nesting, and it adds to the growing body of knowledge that demonstrates that post-fire areas in forested landscapes benefit native insect pollinators (Carbone et al. 2019; Mason et al. 2021). In particular, our work shows that in areas impacted by wildfire native woody vegetation is important for supporting both bee communities (Galbraith et al. 2019a) and bee populations (Galbraith et al. 2021) during the post-fire regeneration phase. More broadly, bees play a critical role in post-fire vegetation recovery due to their pollination services that ultimately promote the ecological communities that develop after wildfire. As the extent and severity of wildfire is expected to increase in the future, the role that bees play is also likely to grow, so undertaking post-fire management actions that allow for the conservation of forest pollinators will be of increasing importance.

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Authors' contributions James W. Rivers: Conceptualization; Data curation; Formal analysis; Funding acquisition; Methodology; Project administration; Supervision; Writing – original draft; Writing – review and editing.

Nicole C. S. Bell: Data curation; Investigation; Supervision; Writing – review and editing.

Sara M. Galbraith: Conceptualization; Data curation; Investigation; Project administration; Supervision; Writing – review and editing.

Kendra R. DelToro: Data curation; Investigation; Supervision; Writing – review and editing.

Jen J-M. Hayes: Data curation; Investigation; Supervision; Writing – review and editing.

Andrew R. Moldenke: Conceptualization; Data curation; Investigation; Supervision; Writing – review and editing.

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Data availability The data underlying this article will be shared on reasonable request to the corresponding author.

Declarations

Competing interests None declared.

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