BEHAVIORAL ECOLOGY –ORIGINAL RESEARCH

Wildfire severity influences offspring sex ratio in a native solitary bee

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Abstract

Although ecological disturbances can have a strong influence on pollinators through changes in habitat, virtually no studies have quantified how characteristics of wildfire influence the demography of essential pollinators. Nevertheless, evaluating this topic is critical for understanding how wildfire is linked to pollinator population dynamics, particularly given recent changes in wildfire frequency and severity in many regions of the world. In this study, we measured the demographic response of the blue orchard bee (*Osmia lignaria*) across a natural gradient of wildfire severity to assess how variation in wildfire characteristics influenced reproductive output, offspring sex ratio, and offspring mass. We placed nest blocks with a standardized number and sex ratio of pre-emergent adult bees across the wildfire gradient, finding some evidence for a positive but highly variable relationship between reproductive output and fire severity surrounding the nest site at both local (100 m) and landscape (750 m) scales. In addition, the production of female offspring was > 10% greater at nest sites experiencing the greatest landscape-scale fire severity relative to the lowest-severity areas. The finding that blue orchard bees biased offspring production towards the more expensive offspring sex with increasing fire severity shows a functional response to changes in habitat quality through increased density of flowering plants. Our findings indicate that burned mixed-conifer forest provides forage for the blue orchard bee across a severity gradient, and that the increase in floral resources that follows high-severity fire leads females to shift resource allocation to the more costly sex when nesting.

Keywords Solitary bee · Fire severity · Mixed-conifer forest · *Osmia lignaria* · RdNBR · Vital rates

Introduction

Disturbances play an integral role in shaping global biodiversity patterns (Pickett and White 1985; Hobbs and Huennecke 1992). Many ecosystems are adapted to routine disturbances, which maintain biodiversity via increases in habitat

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heterogeneity and changes in the composition of component species (Huston 1979; Hobbs and Huennecke 1992). However, altered disturbance regimes can lead to more extreme changes to ecosystem structure and function (Turner 2010; Johnstone et al. 2016). In fire-prone landscapes, variation in species-level responses to wildfire serves to maintain ecosystem structure and function, but anthropogenic drivers of change (i.e., elevated temperatures and decades of fire suppression) have led to alterations in the frequency (Westerling et al. 2006), severity (Flannigan et al. 2013; van Mangem et al. 2013), and timing (Westerling et al. 2006; Flannigan et al. 2013; Jolly et al. 2015) of wildfire events. These trends are predicted to continue in the coming decades, especially in the northern hemisphere (Westerling et al. 2006; Flannigan et al. 2013; Dennison et al. 2014), thus influencing the persistence of organisms that are adapted to historical wildfire patterns (Swetnam 1999; Stevens-Rumann et al. 2018; He et al. 2019; Pausas 2019).

Pollinators generally benefit from canopy-reducing disturbances in forest ecosystems (Hanula et al. 2016), but their response to wildfire differs between pollinator guilds

and within different geographic regions (Brown et al. 2017; Koltz et al. 2018; Carbone et al. 2019). In fire-adapted ecosystems, flowering plant abundance typically increases for several years following a wildfire, providing food resources that enhance the abundance and diversity of wild bees (Potts et al. 2003; Potts et al. 2005; Bogusch et al. 2014; Mola and Williams 2018; Burkle et al. 2019). Even within fire-adapted systems, wildfire characteristics such as severity (i.e., ecological changes that are incurred from a wildfire; Keeley 2009) can have a strong influence on post-wildfire pollinator communities at multiple spatial scales (Ponisio et al. 2016; Galbraith et al. 2019a; Lazarina et al. 2019). Nevertheless, nearly all studies on the impact of wildfire on wild pollinators have focused on community-level measures (Brown et al. 2017). Furthermore, relatively few studies have examined pollinator population dynamics in forest ecosystems, despite the need to understand how pollinators respond to forest disturbances and the management activities that often follow such events (Rivers et al. 2018; Galbraith et al. 2019b). As such, our understanding of the demographic response of pollinators to forest wildfire and its characteristics remains unexamined despite its importance for understanding pollinator population change through time.

The lone paper that has quantified the influence of forest wildfire characteristics on the demographic response of solitary bees found no evidence that fire severity influenced bee nest success (Simanonok and Burkle 2019). Of note, that study relied on natural colonization of artificial nesting blocks and was potentially confounded by changes in the availability of foraging habitat and nesting cavities that arise from mixed-severity wildfire, as wildfire can both create and remove dead wood (Donato et al. 2016) used by cavity-nesting bees. Although the study provided an important step towards understanding native bee reproduction in post-fire habitat, additional work is needed to understand how fire characteristics in other systems influence bee vital rates and related behaviors, such as foraging and offspring provisioning.

In this study, we quantified bee vital rates using artificial nesting blocks at which we released a standardized number of pre-emergent adults of the native blue orchard bee (*Osmia lignaria*), then quantified reproductive activity. Solitary bees, which are typically central place foragers, can reproduce successfully only if they collect enough pollen and nectar within a reasonable distance from their nest. Furthermore, the quality of habitat influences offspring quality; in *Osmia lignaria* and similar species, foraging females invest in larger progeny with a greater proportion of females when more resources are available (Kim 1999; Ulbrich and Seidelmann 2001; Ivanov 2006; Peterson and Roitberg 2006; Seidelmann et al. 2010). Thus, our approach allowed for using nesting bees as a bioassay to evaluate fire-mediated changes in habitat quality while avoiding the potential

confound between changes in nest site availability that often accompanies wildfire severity. Quantifying bee reproduction in artificial nest blocks is a powerful way to evaluate how local and landscape composition influence reproductive output on native bees (Williams and Kremen 2007; Palladini and Maron 2014; Fliszkiewicz et al. 2015), although the method has been used relatively sparingly to date.

The primary hypothesis we tested in our study was that wildfire severity would be positively related to the number of offspring produced because floral resources (i.e., flowering forbs and shrubs) are positively related to fire severity in the years following wildfire in our study system (Galbraith et al. 2019a). Specifically, we examined how bee reproductive output responded to fire severity at the local scale (100-m radius around nest site) and landscape scale (750 m radius around nest site), as bees can forage across both scales when provisioning offspring (Rust 1990; Williams and Tepedino 2003). In addition to enhancing the quantity of young produced, females may exhibit variation in the quality of their offspring across environmental gradients in space and time, so we also tested the hypothesis that females nesting in high-severity fire areas produce relatively more females, the larger offspring sex that requires greater parental investment on a per-individual basis, and larger offspring overall (Phillips and Klostermeyer 1978; Torchio and Tepedino 1980). Because female solitary bees forage alone, longer foraging trips are expected to lead to greater energetic expenditure and/or increase the risk of brood loss (Goodell 2003; Roulston and Goodell 2011), both of which is expected to limit the number of offspring females produce. Thus, we also quantified how foraging trip duration varied relative to wildfire severity and tested the hypotheses that foraging trip duration would be inversely related to fire severity. Likewise, foraging in solitary bees can be constrained by cold temperatures, and the blue orchard bee has a spring flight season that can limit foraging activities when air temperatures are cool (Vicens and Bosch 2000; Forrest and Chisholm 2017). Thus, we also considered how ambient temperature varied across the fire severity gradient (Ferrez et al. 2011).

Methods

Study system and focal bee species

We studied bee breeding biology within recently burned mixed-conifer forest in the Klamath-Siskiyou ecoregion of southwestern Oregon, USA (Fig. 1) from April-June 2017. This is a steeply mountainous area that is characterized by a mixed-severity fire regime (Taylor and Skinner 2003) which, paired with a Mediterranean climate with a long growing season, supports high plant diversity (Whittaker 1960). Much of the region is forested with a mix of conifers such as

Fig. 1 Top: Map of a subset of sampling sites to illustrate the mixed-severity fire mosaic with a 100-m and 750-m radius buffer around the nest site. Map is color-coded by fire severity categories (dark green = unburned, light green = low, yellow = moderate low, orange = moderate high, red = high), which were used to guide initial plot selection, but not analysis. Bottom left: photo shows a wooden nest block mounted with two PVC emergence tubes. Bottom right: example X-ray image of blue orchard bee nests, with labels beneath the corresponding cells that identify the nest contents (lower right)
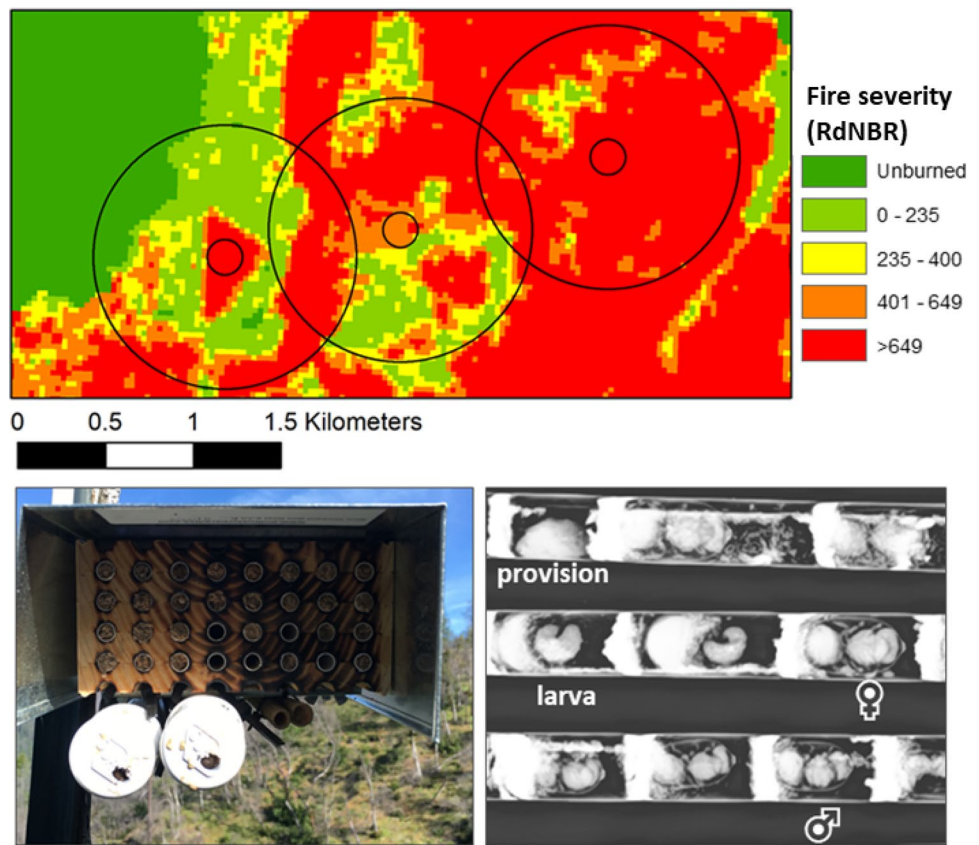
Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and Jeffrey pine (*Pinus jeffreyi)*, with scattered hardwood species such as tanoak (*Lithocarpus densiflorus*). Spring flowering plant communities are dominated by trees (e.g., *Arbutus menziesii*), ericaceous shrubs (e.g., *Arcostaphylos* spp., *Gaultheria shallon, Vaccinium ovatum*), and some flowering herbaceous perennials (e.g., *Whipplea modesta*; Whittaker 1960).

Our study was part of a broader effort to understand the influence of fire severity on wild bee communities (Galbraith et al. 2019a, b) within the Dad's Creek Fire and Rabbit Mountain Fire, which together comprised the majority of the ~ 19,600 ha Douglas Fire Complex. These lightning-ignited fires burned on forest managed by private industry and the Bureau of Land Management (BLM) in late July-late August 2013 (Zald and Dunn 2018). Forest stands were typically managed as even-aged Douglas-fir stands before the fire, with some snags and live trees left after harvest for wildlife habitat. We selected study sites managed by the BLM that represented the full gradient of fire severity in our study area (Galbraith et al. 2019a). None of the stands used in our study of bee demography include areas that were subjected to post-fire salvage logging.

We selected the blue orchard bee as our focal species because (1) it is native to our study region, and

the subspecies used in our experiment (*Osmia lignaria propinqua*) is common to western North America (Rust 1974); (2) it is commercially available in large quantities because it is used for orchard pollination; (3) its relatively large size and foraging range allows for testing the relative contribution of habitat conditions at both local and landscape scales (Williams and Tepedino 2003; Williams and Kremen 2007; Palladini and Maron 2014; Fliszkiewicz et al. 2015); and (4) it has a breeding ecology that is well studied because of its use of human-provided nesting structures (Bosch and Kemp 2001). This species nests in a variety of pre-existing cavities (Rust 1974) where it creates linear nests consisting of a series of brood cells separated by mud wall partitions. Upon emerging in the early spring, females mate and then begin foraging to provision fresh pollen and nectar into brood cells (Torchio 1989). Once a provision mass is completed, the female lays a single fertilized (female) or unfertilized (male) egg. After hatching, offspring consume the provision and develop within their nest cells throughout the summer, producing a cocoon by fall in which to overwinter as pre-emergent adults (Bosch and Kemp 2000). Female offspring require a greater foraging investment because they are larger and develop on a larger provision (an average of 35 pollen loads versus the 31 needed for male offspring; Phillips and Klostermeyer 1978).

Experimental design

We used the relative difference normalized burn ratio (hereafter RdNBR; Miller and Thode 2007) obtained from the 2014 Monitoring Trends in Fire severity database (MTBS 2014) to determine fire severity within the Douglas Complex. We randomly selected 34 spatially independent stands to place nest blocks which encompassed the fire severity continuum within the Douglas Complex (RdNBR range = 50–1037). We constrained stand selection to locations with a minimum patch size of 6.5 ha of forest within the same fire severity category to minimize variation in fire severity within the vicinity of nest sites. Fire severity categories were based on established relationships between RdNBR and basal area mortality (i.e., low [< 25%], moderate-low [25–49%], moderate-high [50–75%], and high severity [> 75%]; see Reilly et al. 2017). For nests in the same fire severity category, we established sites at least 1 km apart to allow for spatial independence based on the expected foraging range by our study species (Rust 1990; Zurbuchen et al. 2010). To minimize roadside influence and edge effects, all nest sites were located > 50 m from the nearest secondary road (mean distance = 158 m). Nest sites represented the variation in elevation (425–1020 m) and aspect (40°–172° from north) of burned areas within the Douglas Complex.

We sourced pre-emergent adult bees for the study that were propagated in western Oregon. We received the bees in natal cocoons in late January 2017, keeping them chilled until moving them to field sites during April 3–10, 2017. On each stand, we placed two 1.8 m T-posts on which to attach nest blocks; each was located 20 m from the stand center, with the first post placed at a random azimuth from the center and the second post placed 180° from the original azimuth. On each post, we mounted a commercially available nest block facing southeast that contained 32 nest tunnels (http://pollinatorparadise.com/; Fig. 1) and lined each tunnel with a cardboard straw. At each nest block, we divided 30 male and 20 female bee cocoons into 2 emergence tubes, each of which consisted of a capped 10 cm long, 2.5 cm diameter PVC tube with an exit hole drilled in one end facing southeast; bees were kept chilled in capped emergence tubes until arrival at each nest site.

Quantification of bee foraging activity and use of floral resources

Once female foraging began in > 50% of the blocks (which occurred 41–49 days post-deployment), we surveyed the number of nest tunnels that were completed (i.e., mud-capped) or active (i.e., contained evidence of pollen and/or an in-progress nest cell) as an index of 'mid-season' nesting activity. We filmed female provisioning trips at 1–2 nest blocks in a randomly selected subset of study sites (n = 16)

across the fire severity gradient. We recorded all videos between 11:00–16:00 for a minimum of 30 min/block during a 2.5 week period (8–25 May 2017) that coincided with the period of maximum foraging activity. To film, we placed a digital camcorder on a tripod approximately 1.5 m from the entrance holes of the nest block so that all nest entrances were visible and filled the viewfinder completely. We collected video data when ambient temperature exceeded 15.5° C to increase the likelihood that we would record bee activity given this species is typically active above this threshold (Torchio 1985).

To transcribe videos, we calculated the length of a foraging trip as the elapsed time from when a female left a nest tunnel to when a female returned to the same tunnel. We also recorded whether females returning from trips had pollen clearly visible on the scopa because this species takes separate trips to gather mud for nest cell divisions (Bosch and Kemp 2001) and we were evaluating foraging trip duration only. When quantifying foraging behavior, we assumed that any female departing from and returning to a single nest was the same individual (Tepedino and Torchio 1994).

Quantification of bee demographic measures

We collected nest blocks after nesting activity had ceased (58–65 days after deployment) and transported them to an open air, non-insulated shed where they were stored at ambient temperature until offspring had developed into adults (September 2017), at which point we transferred the nests to a cooler maintained at 3–5 °C to simulate overwintering (Bosch and Kemp 2001). In October 2017, we used X-radiography to diagnose the contents of each cardboard straw, including the number and sex of offspring (Fig. 1; Stephen and Underraga 1976). We determined sex ratio from the X-ray images (i.e., cocoon size, shape, and location in the nest tunnel), dissecting cocoons and visually confirming bee sex when it was not easily determined via images. We then overwintered the offspring until spring 2018, when we quantified the mass of overwintering adults in cocoons by randomly selecting up to four occupied nest tunnels in each nest block and weighing each cocoon and contents with an electronic balance to the nearest 0.1 mg.

Quantification of environmental covariates

We quantified available floral resources and canopy cover during the period that bees were active (May and June 2017) along transects that extended 50 m from each nest block. We estimated canopy cover every 10 m along the floral resource transect using a spherical densitometer. At each of these same locations, we assessed flowering plant density using ordered distance sampling, which is efficient for estimating plant density in areas with sparse bloom (Nielson et al. 2004;

Galbraith et al. 2019a, b). We identified and measured the distance to the 4th nearest plant that was in flower at each of these ten points per site (Nielson et al. 2004). We monitored air temperature at blocks using iButtons (iButtonLink, LLC, Whitewater, WI), which we attached to the shaded bottom of one randomly selected nesting block per site. iButtons recorded air temperature to the nearest 0.5° C every 5 min until we collected the nesting blocks, after which we calculated the average daily maximum temperature (i.e., daily maximum temperature, averaged over the course of the study) at each nest block.

Statistical analysis

We evaluated how fire severity was related to our response variables of interest at the site level using linear models ('lm' package in the R statistical environment) and negative binomial generalized linear models ('glm.nb' in package 'MASS'; R version 3.4.2; R Core Team 2013). We selected variables for the models based on a priori hypotheses and then evaluated for potential correlation among covariates. In the case that variables correlated > 0.5, we removed the covariate from the model that we considered less ecologically relevant. For all models, we evaluated model fit by checking for any unexpected correlation in the distribution of residuals when plotted against each covariate. We also confirmed that residuals were not over-dispersed in models with a negative binomial distribution by checking that the squared residuals/DF < 1. We present model-estimated marginal means and their 95% confidence intervals (CIs) on the original scale (i.e., back-transforming where relevant), with model covariates set to their mean values.

To test our hypothesis that reproductive output would be positively related to fire severity, we first summed the total number of nest cells provisioned by foraging females (i.e., "nest cells") and the number of offspring that appeared as adults on the images (i.e., "adult offspring") for both nesting blocks at each site. We then constructed generalized linear models measuring the relationship between final offspring variables (i.e., nest cells or adult offspring) and either local fire severity (i.e., average RdNBR within a 100 m radius from the plot center) or landscape fire severity (i.e., average RdNBR within a 750 m radius from the plot center). Bears (*Ursus americanus*) had damaged or removed some of the nesting blocks, so the final models included an offset variable to account for sampling effort. The final models included reproductive output response variables as count data, modelled with a negative binomial error distribution and a log 'link', with elevation as a covariate and the log-transformed number of blocks as an offset variable.

To test our hypothesis that fire severity would be positively related to offspring output and body size, we constructed linear models with the proportion of female offspring (i.e., the number of females divided by number of offspring on each site), or the average offspring body mass at the site level as response variables. Both models included either local or landscape fire severity as main effect variables and elevation as a covariate, but the offspring mass model included an additional covariate for offspring sex to account for sexual dimorphism within the species. To assess the influence of fire severity on foraging trip duration, we calculated the average pollen-foraging trip duration at the site level as the response variable. For this linear model, the only predictor variable was fire severity on the local scale because of modest sample sizes.

To quantify the relationship between fire severity and habitat conditions at the nest site, we modeled habitat variables (i.e., canopy cover, flower density, and maximum air temperature) against local fire severity. Although canopy cover is an established function of fire severity (Miller and Thode 2007), our goal was to quantify the strength of this relationship in our study. The linear model included percent canopy cover as the dependent variable, with local fire severity, elevation, and aspect as explanatory variables. To measure the influence of fire severity on floral resource density surrounding the nest site, we used a linear model with natural log-transformed flowering plants per hectare as the dependent variable and local fire severity as the main effect variable. We averaged plant densities on each site, and we included elevation and aspect as covariates in the model. We generated separate models for the average flowering plant density in May and the average flowering plant density across the full season when bees were active (both the May and June sampling periods). To test our hypothesis that air temperatures would be positively related to fire severity at the sites, we modelled the average daily maximum temperature (°C) as the dependent variable, with local fire severity and elevation as explanatory variables. Due to unexpected gaps in the temperature data, we could only include a subset of sites ($n = 19$) and dates (day of year 90–125 and 145–175, where January 1 = 1). We calculated the weekly relative maximum temperature rankings among all sites and evaluated the Pearson correlation coefficient of the initial ranking versus the average ranking. A correlation coefficient close to 1 ($R = 0.92$, $p < 0.001$; Supplementary Materials S1) indicated that the relative differences in maximum temperature among sites remained consistent over time, so we used this data as a representative sample of temperature among sites. Model residuals indicated a quadratic fit, with a squared term for the fire severity variable.

Results

Bee reproductive output and foraging behavior

Of the 68 nest blocks we deployed, 6 were damaged and could not be used; thus, results presented here are based

on 62 nest blocks from $n = 32$ study sites. Across all sites, female bees constructed 12,080 nest cells; 10,492 adult offspring were produced from these cells, with 13.1% ($n = 1588$) of nest cells failing to yield developed offspring. Reproductive output averaged 169 adult offspring produced per nest block (range 23–276), or approximately 5 offspring per nest tunnel. Of the cells that did not develop into adults, the great majority 85.3% ($n = 1355$) contained either a provision or provision with a visible egg, with 2.8% ($n = 45$) of mortality occurring during the larval stage and 11.8% ($n = 188$) occurring in the pupal stage. The proportion of nest cells that did not develop to adults was positively correlated with local fire severity ($R^2 = 0.40$, $p = 0.023$), but not landscape scale fire severity ($R^2 = -0.06$, $p = 0.756$).

We found some evidence for a positive relationship between the number of initiated nest cells and local fire severity, with a 0.4% (95% CI -0.002, 0.081) increase in provisioned cells for every 100-unit increase in fire severity (Fig. 2a; Table 1). Similarly, we found evidence for a positive relationship between the number of initiated nest cells and local fire severity, with 6% (95% CI: -0.003, 0.121) more offspring per 100-unit increase in fire severity (Fig. 2b; Table 1). However, the variability among sites was high at both scales. Similarly, we found some evidence for a positive influence of both local and landscape fire severity on the number of adult offspring, but data ranged from almost no change across the fire severity gradient to a strong positive trend (Fig. 2c, d; Table 1).

Although the relationship between the proportion of female offspring produced and local- fire severity was weakly negative, showing a 0.7% decrease for every 100-unit increase in mean fire severity (95% C.I. -0.019, 0.004; Fig. 2e; Table 1), the trend was again highly variable. However, there was less variability in the response at the landscape scale, for which we observed a 2% average increase in the proportion of female offspring for every 100-unit increase in landscape-scale fire severity (95% C.I. 0.007, 0.039; Fig. 2f; Table 1). This equated to > 10% more females produced, on average, at nest sites whose surrounding landscape experienced the most severe fire, relative to nest sites in the least severely burned landscapes. The average mass of female progeny (107.9 mg; 95% CI 95.1, 120.7) and male progeny (73.5 mg; 95% CI 54.6, 92.4) was consistent across the fire severity gradient at the local scale, with limited evidence for a positive relationship between offspring mass and landscape scale fire severity (Table 1).

In video footage, we observed 1070 round-trip foraging visits by female bees. We visually confirmed pollen foraging (i.e., viewed completed female trips with pollen on scopae) for 327 of these trips. Visible pollen foraging occurred at 15 of the 25 nest blocks for which we obtained video, representing only $n = 9$ sites. These sites covered most of the local fire severity gradient in our study area (local RdNBR range

57.75–754.26), but only a small range of the landscape scale fire severity (landscape RdNBR range: 44.92–413.34). The mean recorded foraging trip duration was 8.8 min, with the average length of trips per site ranging from 5.6 to 14.9 min. Within this limited sample, the average trip duration was 0.7 min (i.e., 42 s) shorter for every 100-unit increase in local fire severity, but variation was high (95% C.I. -1.88, 0.32; Fig. 3). On average, bees had initiated nests in 22 of the nest tunnels provided between the 2 blocks (range 0–64) mid-season (May 2017). No clear patterns emerged related to the number of initiated nest tunnels mid-season and fire severity at either the local or landscape scales (Fig. 4a, b).

Fire severity and habitat conditions

Fire severity influenced habitat conditions at nesting block sites. In our study sites, we found an average 8.4% (95% CI -0.114, -0.054) reduction in mean canopy cover for each 100-unit increase in fire severity. The density of flowering plants during the time period when blocks were out was also positively related to fire severity; on average, density of plants flowering during the bee nesting season increased 5× for every 100-unit increase in fire severity (95% CI 0.33, 0.67; Fig. 5a). The relationship between fire severity and flowering plant density held when we assessed the density of flowering plants in May only ($\beta = 0.005$, 95% CI 0.003, 0.007). Average maximum air temperature at the nest sites exhibited quadratic relationship with fire severity, and initially increased 1.3 °C for every 100-unit increase in fire severity (95% CI 0.36, 2.22; Fig. 5b). The relationship between mean maximum air temperature and fire severity reversed slightly for the most severely burned sites ($\beta = -0.001$, 95% CI -0.002, -0.0001).

Discussion

Predicting the long-term impacts of shifting disturbance regimes on biodiversity requires an understanding of how vital rates of component species vary in response to disturbance events (Folke et al. 2004; Driscoll et al. 2010; Turner 2010; Johnstone et al. 2016). In this study, we found evidence for a modest positive relationship between local and landscape scale fire severity and both the number of provisioned nest cells and the number of adult offspring produced by blue orchard bees, with high variability among sites. These results were unlikely to be confounded by natural colonization, as we observed very few other species using the blocks and did not collect blue orchard bees in the sites during the year leading up to this study (Galbraith et al. 2019a, b). The proportion of female offspring also increased with fire severity at the landscape level, with > 10% more females in nest blocks placed in the most severely burned landscapes.
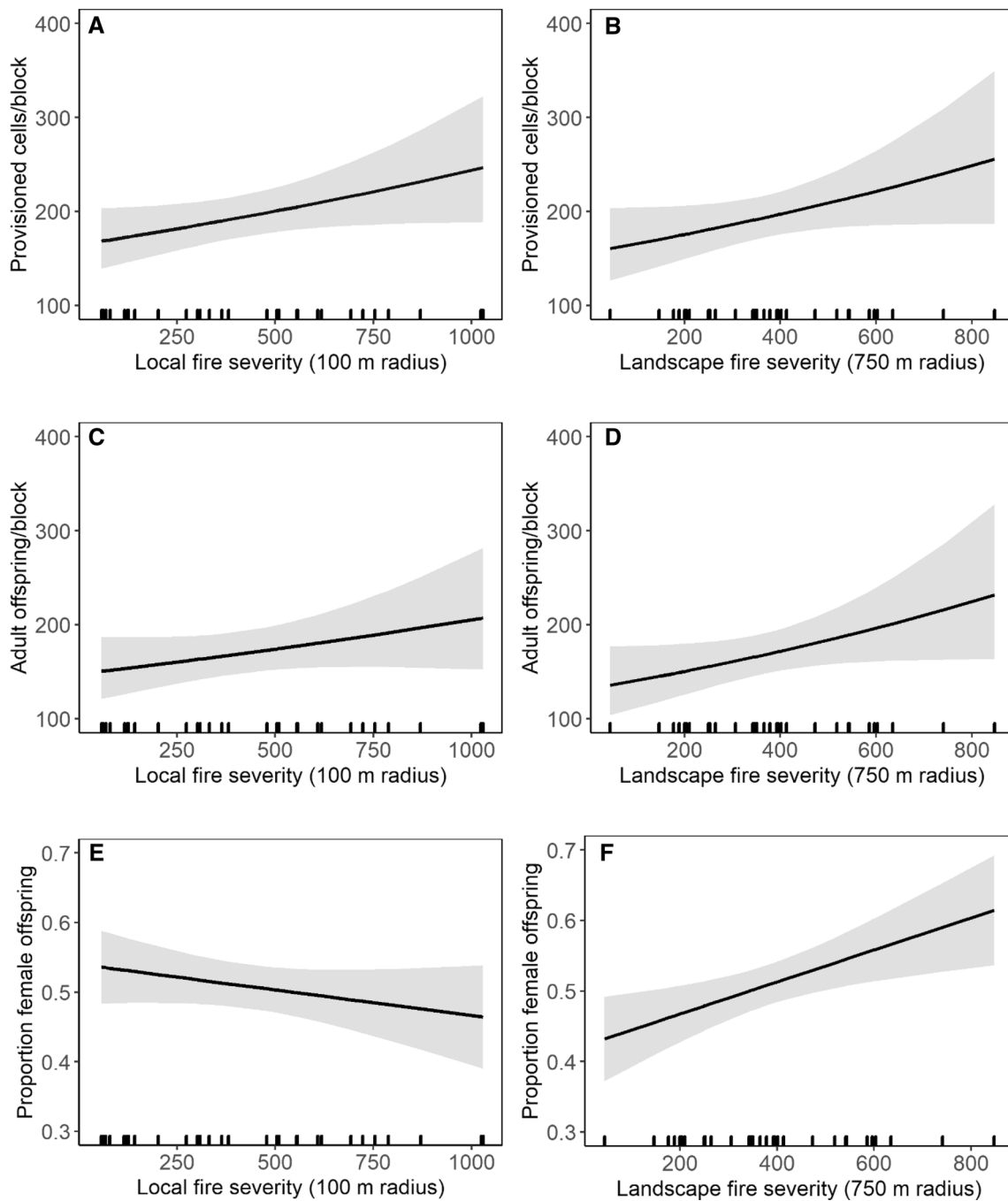
Fig. 2 Predicted relationship between fire severity and reproductive output measures. For all figures, lines represent marginal mean and a 95% CI (shaded region); rugplot shows fire severity value of each study site. Marginal means are calculated with elevation held at its mean (all figures) and offset by sampling effort (**a**–**d**)

Overall, bee offspring production was sizable in nesting blocks; more than a third of the nesting blocks had all of their nesting tunnels completely filled, and some blocks had additional nests cells constructed within other cavities on our nest structures, although those additional cells were not considered in our analysis. Furthermore, most provisioned nest cells (86.9%) developed into adult offspring, a survival rate equaling or exceeding values observed in other studies across a range of managed and unmanaged habitats (e.g., Rust 1990; Palladini and Maron 2014; Boyle et al. 2020). Thus, our results adds to the limited research showing that post-wildfire conifer forest supports native bee reproduction.

With a sex ratio at near-unity across sites, and a greater proportion of females at the high end of the fire severity

Table 1 Marginal means and 95% confidence intervals for reproductive response variables displayed for the two habitat models: local and landscape-scale mean fire severity (i.e., mean RdNBR at either a 100 or 750 m radius around the nest site)

Response variable	Local fire severity (RdNBR, 100 m)			Landscape fire severity (RdNBR, 750 m)		
	Estimate (β)	95% CI	p	Estimate (β)	95% CI	p
Nest cells	100.004	99.998, 100.081	0.052	100.058	99.997, 100.121	0.062
Adult offspring	100.033	99.986, 100.061	0.157	100.067	99.999, 100.137	0.054
Proportion female offspring	− 0.007	− 0.019, 0.004	0.232	0.023	0.007, 0.039	0.007
Progeny mass (mg)	− 0. 014	− 0.118, 0.091	0.795	0.163	− 0.010, 0.335	0.064

All models include elevation as a covariate. Estimates and 95% CIs are provided for a 100-unit increase in mean fire severity. Results for nest cells and adult offspring have been back-transformed to an odds scale
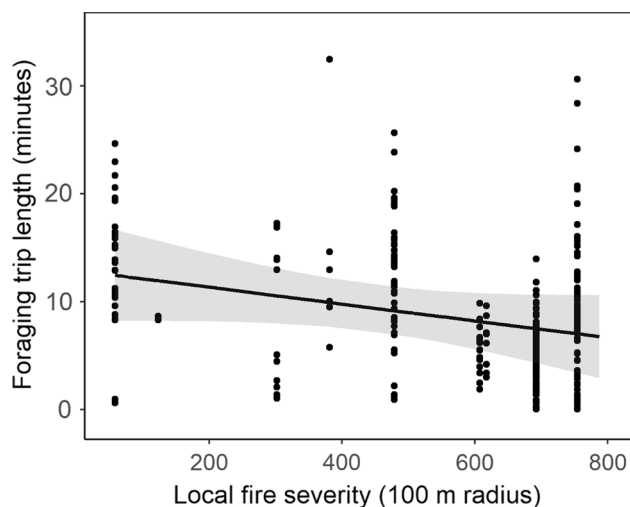

Fig. 3 Relationship between fire severity and the mean duration of foraging trips. Line represents marginal means with a 95% confidence interval (shaded region) overlaid with a scatterplot of the length of each of the recorded pollen foraging trips included in the model

gradient, our study also had more female progeny than is typically observed in this species (Tepedino and Torchio 1982). The female-biased offspring production we documented appears to be the product of abundant floral resources that matched bee activity (Torchio and Tepedino 1980). The relatively greater proportion females in areas surrounded by a more severely burned landscape indicates an investment in more of this larger, more costly sex due to resource availability (Kim 1999; Ulbrich and Seidelmann 2001; Ivanov 2006; Peterson and Roitberg 2006; Seidelmann et al. 2010). Foraging females may also have invested in more female offspring in more severely burned landscapes because they were able to forage more efficiently; they tend to produce more male offspring as they age (Torchio and Tepedino 1980). Blue orchard bees can forage > 600 m from nest sites (Rust 1990) with a homing ability of > 1 km (Guedot et al. 2009), and they are known to combine near- and long-distance foraging trips to access preferred nectar or pollen resources (Williams
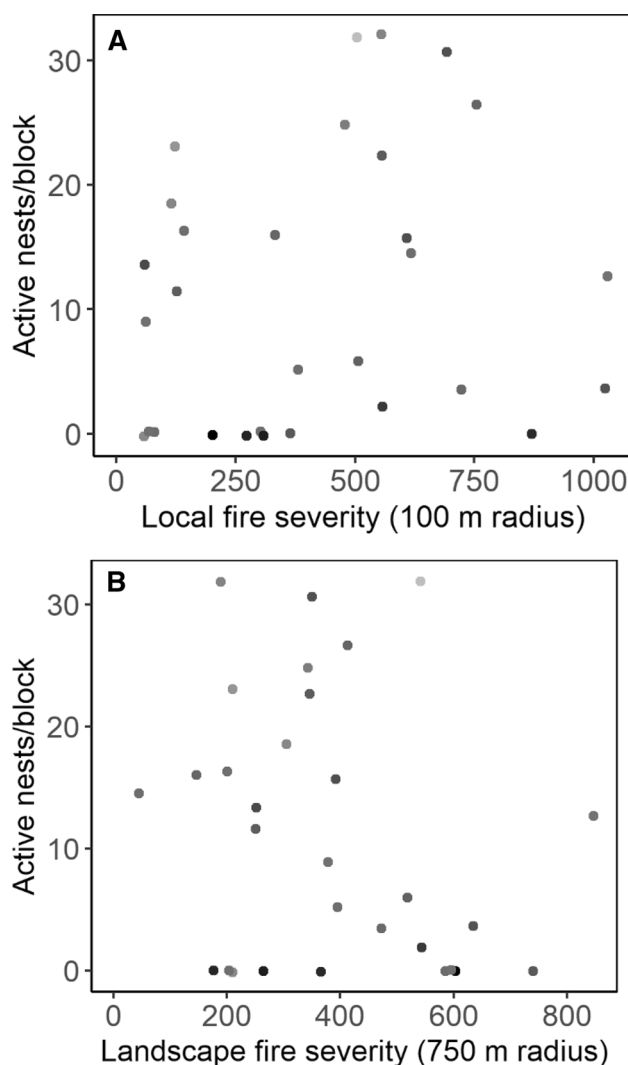
Fig. 4 Scatterplot of the number of active nest tunnels per block during May 2017 (i.e., the mid-point of the study season) plotted against fire severity as the **a** local- and **b** landscape-scale around nest sites. Lighter data points indicate lower elevation, with darker points showing higher elevation
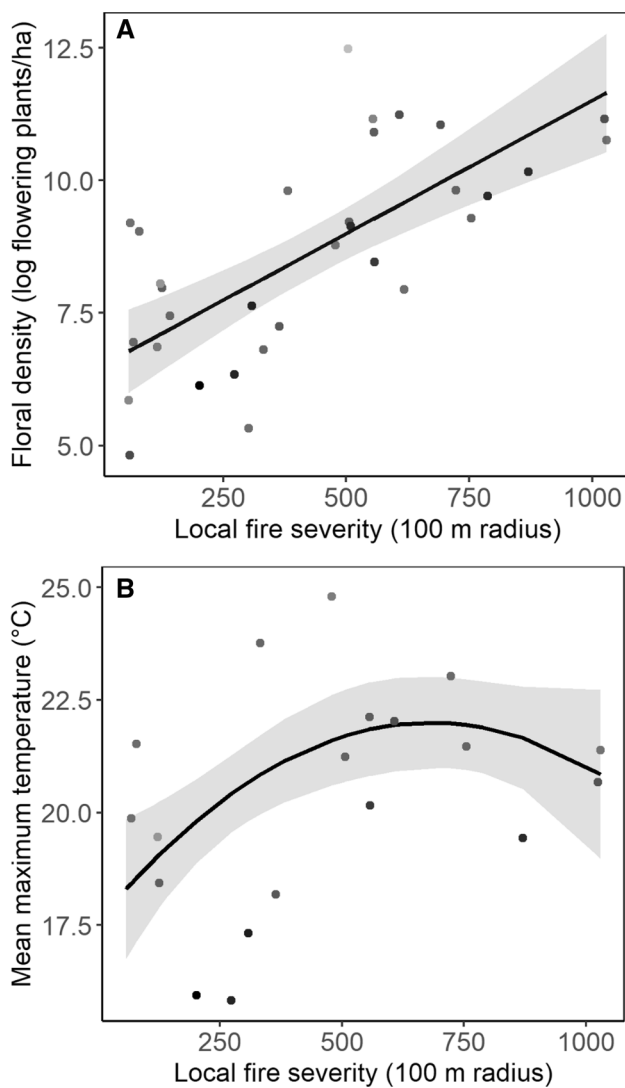
Fig. 5 Relationship of fire severity and **a** flowering plant density, and **b** mean maximum daily temperature. Models show marginal means and 95% confidence intervals with covariates held at their mean values, overlaid with scatterplots of the observed data. Points represent raw data, shaded by elevation, with high elevation shown as darker points and low elevation shown as lighter points

and Tepedino 2003). Therefore, it is perhaps not surprising that landscape-scale fire severity was an important component bee habitat quality in our system. However, it is less clear why the same trend in sex ratios was not observed as fire severity increased in the area immediately surrounding the nest. We hypothesize it is due to need for bees to undertake the near- and long-distance foraging flights; the most common flowering species observed in sites (i.e., *Collomia heterophylla, Acmispon parviflorus,* and *Madia exigua*) have small flowers, likely offering relatively few pollen and nectar resources. We speculate that foraging females may have been taking longer foraging trips to seek out resource-rich *Rubus, Vaccinium, Ceanothus,* and

Phacelia species, for example, on sites throughout the burn area, although this hypothesis remains to be tested.

Alternatively, there may be negative impacts of local fire severity on the conditions immediately surrounding the nest which led to the greater proportion of offspring failing to develop into adults and a marginally smaller proportion of females in the nest blocks. More severely burned sites had greater flower density, which appears to be due to reduced canopy cover in severely burned forest patches, particularly in lower-elevation sites. However, nest blocks in the most severely burned forest patches also had a lower chance of developing to the adult stage. Previous research suggests a trade-off between offspring production and survival in this species, largely due to greater parasitoid presence (Palladini and Maron 2014). Although we were unable to identify parasitoids in our nest images, most of the nest cells that did not develop to adults contained only the provision or provision and egg, suggesting that parasitoids were not the main cause of offspring death. Survival may have been more directly related to abiotic conditions, especially more extreme temperatures at the nest site. Conifers can provide an insulating effect on air temperature, particularly at high elevations (Ferrez et al. 2011) and we observed an initial positive relationship between fire severity and maximum air temperature in our sites, although there was a slight decline in maximum temperature at the most severely burned sites. Warmer temperatures may have benefitted female foraging, but temperature extremes may have also reduced offspring survival, disproportionately impacting females if the extremes occurred early in the season. Future research should focus on the interaction between abiotic and biotic conditions in contributing to post-fire habitat quality for bees, especially because this study focused only on the success of bees when introduced in artificial nest blocks, and the spatial availability of aboveground nesting substrates will also change due to forest fire (Galbraith et al. 2019a; Simanonok and Burkle 2019).

Our findings provide complementary evidence to our previous research in the region, wherein fire severity proved to be a strong driver of bee abundance and richness in the same sites, as measured by passive trapping. Traps collected substantially more bees in the most severely burned relative to the less severely burned sites, with almost no bees or flowering plants detected where canopies remained intact after the fire (Galbraith et al. 2019a). Both of these studies highlight the role of wildfire severity in shaping pollinator habitat in forest landscapes, especially during the few years following the burn, when the greatest impacts from wildfire are generally observed (Carbone et al. 2019). Our study also complements approaches that focus on forager density after fire (e.g., Mola and Williams 2018) or natural nesting activity after fire (e.g., Love and Cane 2016; Buckles and Harmon-Threatt et al. 2019), which show the distribution of resources

after the disturbance, but do not typically connect foraging or nesting to bee vital rates, as we have done here. The findings of these distinct, yet complimentary datasets highlights the value of using multiple methods that go beyond only passive trapping to better understand the complex influence of environmental changes on pollinators.

Based on the results of this study, we conclude that wildfire severity influences bee sex ratios via changes to both biotic and abiotic habitat conditions. Because bees pollinate many of the flowering plants that structure terrestrial habitats and food chains, a better understanding of how heterogeneous forest fires influence reproductive outputs of resident bee communities is an essential component of understanding the implications of shifting fire regimes on biodiversity and how post-fire landscape management actions could be beneficial or detrimental to native bees. Approaches like ours, which provide a more complete process-based understanding of how populations respond to disturbance events, hold potential for helping us predict the complex responses of ecologically important groups of organisms as disturbance regimes shift worldwide. Our study illustrates how forest fire influences bee reproductive output by demonstrating how mixed-severity wildfire creates a patchwork of flowering communities and abiotic conditions that affect bee offspring quality at large spatial scales in conifer forest.

Author contribution statement All authors contributed to conceiving and designing the experiments. SMG performed the experiments and analyzed the data. All authors contributed to writing the manuscript.

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