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RESEARCH ARTICLE

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Wildfire reveals transient changes to individual traits and population responses of a native bumble bee *Bombus vosnesenskii*

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Abstract

1. Fire-induced changes in the abundance and distribution of organisms, especially plants, can alter resource landscapes for mobile consumers driving bottom-up effects on their population sizes, morphologies and reproductive potential. We expect these impacts to be most striking for obligate visitors of plants, like bees and other pollinators, but these impacts can be difficult to interpret due to the limited information provided by forager counts in the absence of survival or fitness proxies.
2. Increased bumble bee worker abundance is often coincident with the pulses of flowers that follow recent fire. However, it is unknown if observed postfire activity is due to underlying population growth or a stable pool of colonies recruiting more foragers to abundant resource patches. This distinction is necessary for determining the net impact of disturbance on bumble bees: are there population-wide responses or do just a few colonies reap the rewards?
3. We estimated colony abundance before and after fire in burned and unburned areas using a genetic mark–recapture framework. We paired colony abundance estimates with measures of body size, counts of queens, and estimates of foraging and dispersal to assess changes in worker size, reproductive output, and landscape-scale movements.
4. Higher floral abundance following fire not only increased forager abundance but also the number of colonies from which those foragers came. Importantly, despite a larger population size, we also observed increased mean worker size. Two years following fire, queen abundance was higher in both burned and unburned sites, potentially due to the dispersal of queens from burned into unburned areas. The effects of fire were transient; within two growing seasons, worker abundance was substantially reduced across the entire sampling area and body sizes were similar between burned and unburned sites.
5. Our results reveal how disturbance can temporarily release populations from resource limitation, boosting the genetic diversity, body size, and reproductive output of populations. Given that the effects of fire on bumble bees acted indirectly through pulsed resource availability, it is likely our results are generalizable to

other situations, such as habitat restorations, where resource density is enhanced within the landscape.

KEYWORDS
bees, disturbance, fire, genetic mark–recapture, pollinators, resource limitation

1 | INTRODUCTION

Ecological disturbance is a key driver of population dynamics, distribution and diversity (Sousa, 1984; Turner, 2010). The impacts of disturbance on sessile organisms, mainly plants, are well studied with documented effects on growth, reproductive output or nutritional content, among other factors (Pyke, 2017; Sousa, 1984). These disturbance-mediated effects on plant communities likely have strong bottom-up effects on higher trophic levels. However, it can be difficult to study the impacts of disturbance on highly mobile consumers, especially beyond measures of presence/absence alone. To fully understand the role of disturbance and resource shifts in altering animal populations, we must distinguish between situations when animals simply reoccupy disturbed landscapes versus ones in which they have increased survival or reproduction.

Fire is the most common disturbance in many terrestrial ecosystems worldwide (Bowman et al., 2009). It often profoundly affects the abundance, diversity and distribution of populations and communities (Bond & Van Wilgen, 1996). The response of organisms to fire depends in part on the severity, frequency and intensity of the burn, as well as the adaptations of species to fire regimes (Keeley, Pausas, Rundel, Bond, & Bradstock, 2011). With warmer and drier climates, increased frequency of more severe fires (McKenzie & Littell, 2017), and expanded use of fire as a restoration tool (Brown & Smith, 2000), the relative importance of fire in shaping resource landscapes is likely to increase. Fire has been shown to directly or indirectly alter animal community composition and many animals are adapted to respond to fires in a variety of ways (reviewed in Pausas & Parr, 2018). Organisms may also be adapted to certain successional stages and alter their patterns of movement to follow their preferred habitat types (Nimmo et al., 2019). Given the ubiquity of fire-stimulated flowering (Pyke, 2017), we expect the effects of fire on obligate flower visitors, like bees and other pollinators, to be especially strong and offer general insight to the bottom-up effects of disturbance on consumers.

Our understanding of bees' response to fire mostly comes from counts of individual foragers on flowers or in traps placed across a variable mosaic of burns (Reviewed in: Carbone, Tavella, Pausas, & Aguilar, 2019; Nicholson & Egan, 2019). As such, the documented effects of fire on bee abundance and diversity tend to reflect the conditions within the postfire plant community—when flowering plant species are more abundant or diverse, pollinator communities respond in kind. The heterogeneous landscapes created by fire, whether by spatial variation in severity (Galbraith, Cane, Moldenke, & Rivers, 2019; Ponisio et al., 2016) or time since fire (Potts, Vulliamy, Dafni, Ne'eman, O'Toole, et al., 2003), provide diverse foraging and nesting habitats (Grundel et al., 2010). Although forager-based assessments of abundance and diversity may be a reasonable proxy for some aspects of solitary species, it could poorly capture responses of social taxa because an abundance of workers on flowers may simply reflect a situation in which a few colonies aggregate on concentrated resources. Whether the altered resource environments created by fire affect population size (i.e. colony abundance), survivorship or reproduction across a landscape remains unclear.

Bumble bees offer a particularly tractable system to study how post-fire resource pulses affect mobile consumers across levels—from individuals to colonies and populations. Following fire, bumble bee workers are more abundant in a variety of different ecosystems and regions (Galbraith et al., 2019; Mola & Williams, 2018; Smith DiCarlo, DeBano, & Burrows, 2019). However, it is difficult to distinguish between aggregation and population-wide effects due to the production of non-reproductive foragers. Positive correlations between forager abundance and floral density may not necessarily reflect increased population sizes (Roulston & Goodell, 2011) because large numbers of workers can be produced even if queen production is not increased (Westphal, Steffan-Dewenter, & Tscharntke, 2009; Williams, Regetz, & Kremen, 2012). In the absence of genetic data, a scenario in which many foragers are observed from a single colony is indistinguishable from a scenario in which many foragers are observed from numerous colonies. Furthermore, if many colonies successfully establish, but there are insufficient resources for the higher colony density, they may produce small workers or fail to produce reproductive individuals.

Because bumble bees are highly mobile organisms, our understanding of disturbance-mediated changes in colony abundance, body size or reproduction must be informed by their movement patterns, although this is often not done. Bumble bees are central place foragers with queens choosing nest locations in the early spring and workers subsequently foraging from these fixed locations (Figure 1). The high mobility of bumble bee foragers promotes the use of multiple habitat types (Redhead et al., 2016), and in the case of heterogeneous fires, provides them access to a mosaic of burned and unburned patches. If colonies in undisturbed habitats are flying to forage in disturbed habitats, any differences in the conditions between those habitats may be obscured since all colonies, regardless of location, have access to approximately the same resources. Additionally, when colonies produce reproductives at the end of the season, it is critical to consider the dispersal potential of those individuals. If colonies in disturbed areas produce more queens than those in undisturbed areas, the effects of

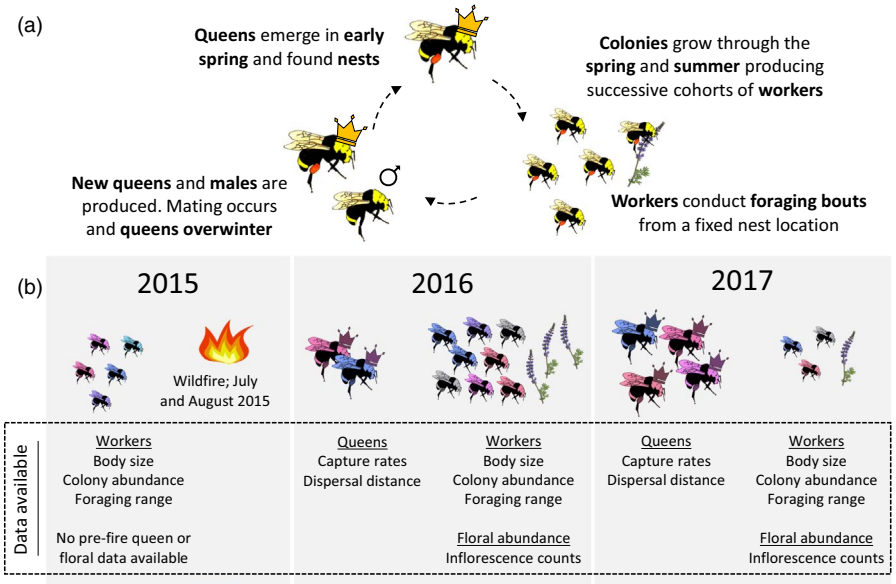

FIGURE 1 Conceptual figure of bumble bee life cycle (a) and data available before and after fire (b). (b) Pre-fire (2015), worker data are available with effort proportional to perceived floral abundance. Body size data are available for lethally captured specimens (see text for details). Pre-fire queen data or site-level floral abundance is unavailable. Post-fire, in 2016 and 2017, we collected data on queen abundance and dispersal distance (from sibling assignment; see text for details). In 2016, workers were collected during two visits to each site. Inflorescence counts were taken at each site, allowing for the regression of response variables against site-level floral abundance. *In 2017, a poor flowering year meant many sites never had workers, so we collected workers from the nearest flowering patch to the original sites (see text for details and justification). In general, we observed few differences between sites before fire, followed by a stark difference after fire with a larger population of bigger workers, represented here as more individuals from more colonies (more colours). The effects of fire lasted through queen season in 2017 where many queens were observed. Few workers and flowers were observed 2 years after fire. *Bombus vosnesenskii* drawing provided with permission from Maureen Page

increased reproduction could spillover from the disturbed into undisturbed areas if dispersal distances are relatively long and dispersal is common. Understanding the movement of highly mobile organisms within disturbed areas provides the necessary context to interpret how patterns of abundance and condition may arise after disturbance.

We used a genetic mark–recapture approach to investigate how wildfire affects bumble bee population abundance and reproductive output. We collected samples before and after fire in burned and unburned sites to estimate changes in colony abundance, body size and reproductive output. We used these data to distinguish between a scenario in which there is simply an increase in bumble bee activity density versus one in which a larger and more fecund population is transiently produced. Specifically, we determined (a) whether bumble bee colony abundance was higher in burned sites compared to pre-fire or unburned sites, (b) if forager body size changed in response to fire or floral abundance, (c) if reproductive output, as measured by queen abundance, changed in the years following fire and (d) how forager and queen movements helped explain the observed response of the population to fire.

2 | MATERIALS AND METHODS

2.1 | Study area and sites

The study was conducted at the University of California McLaughlin Reserve (38°52′25.74″N, 122°25′56.25″W) in the springs of 2015, 2016 and 2017 (Figure 1). The focal sites were spring-flowering grasslands surrounded by a mix of chaparral and oak-woodland. Forb species bloom over a short period (typically March–May) in the study area and are quickly overgrown by a mix of native and non-native grasses. The region has a relatively infrequent fire return interval (*c.* 15–75 years). These fires produce short-term positive effects on forb species richness and abundance in the grasslands (Mola & Williams, 2018; Safford & Harrison, 2004).

We established five sites prior to fire in 2015 as part of a pilot study to estimate bumble bee foraging distance and colony abundance. In July and August 2015, two wildfires burned through half of the study area on the reserve (Figure S1). We revisited the original five sites (two burned, three unburned) and six others (three burned, three unburned) after the unexpected opportunity to study wildfire in 2016 and 2017 (for a total of five burned, six unburned sites). Given the timing of the fires, the dry vegetation within the grasslands was rapidly consumed. Mean fire severity (RdNBR), as estimated from the Monitoring Trends in Burn Severity database was >600 (high severity) within all burned sites (https://www.mtbs.gov/; Figure S1). The additional sites were chosen in consultation with reserve managers (C. Koehler and P. Aigner, pers. comm.) and represent areas of known pre-fire bumble bee activity to match the characteristic of the pre-fire sites, as well as to ensure many workers could be captured, increase the detection of colonies across multiple sites and reduce the number of individuals without siblings in the dataset (Carvell et al., 2012). Our sampled areas therefore represent 'good'

bumble bee habitat and not randomly chosen patches. Because of the spatial arrangement of our original sites and the way fire burned through the area, our burned and unburned sites are spatially clustered (Figure S1). We compare burned and unburned sites within year as well as the original five to their pre-fire status, allowing us to address some of the complications associated with clustered sampling. For example, potential differences in precipitation across the study area (Appendix S2) were consistent before and after the fire suggesting that any new differences in bee responses post-fire were likely fire-induced rather than due to such abiotic factors. Sites differed in size according to natural boundaries such as water, woodland or a substantial change in vegetation cover, but site area alone was not predictive of the number of individual bees captured (Pearson's $r = 0.060$, $df = 9$, $p = 0.860$) or floral abundance (Pearson's $r = 0.156$, $df = 9$, $p = 0.646$).

2.2 | Field collections

2.2.1 | Worker collections

We captured *Bombus vosnesenskii* workers from flowers before and after fire within burned and unburned areas. Although *B. melanopygus* and *B. californicus* also occur sporadically at the reserve (less than ~5% of all *Bombus* individuals; J.M. Mola, pers. obser.), *B. vosnesenskii* was chosen as the focal species to ensure collections of workers would yield a sufficiently large dataset to estimate sibship and colony abundance. Our collections in 2015 were not with the intention of studying fire and workers were lethally or non-lethally collected during multiple visits to each site with effort roughly proportional to observed abundance among the original five sites. The non-lethal method used tarsal clipping following Holehouse, Hammond, and Bourke (2003). Following fire, in 2016, JMM collected foragers systematically during two rounds at each site. Bees were netted for 2 hr or until 24 individuals had been captured, whichever occurred first. In 2017, we attempted to systematically collect workers at all sites again, but a poor flowering year resulted in low captures at our focal sites regardless of burn category. As such, we captured workers at the nearest location possible within the appropriate burn category (<500 m), keeping overall effort and approach standardized as was done in 2016. All captures in 2016 and 2017 were lethal to ensure body sizes could be reliably measured in the laboratory. We recorded the spatial coordinates of each captured individual using a GPS device. Collections of workers occurred on days with full or partial sun and sustained winds below 5 m/s from all areas at a site with open flowers. Collection dates varied slightly between years reflecting variation in bumble bee activity and bloom, but occurred between April and June, a critical period for colony growth within our study region (Crone & Williams, 2016). Occasionally, we encountered individual bumble bees opportunistically outside of our sites and captured them because they may be siblings of other individuals in the dataset. These additional individuals (in total only six workers in 2015 and one queen in 2017) are included in analyses grouped by year and/or burn category, but are excluded from site-level analyses. All tarsal clips or whole specimens were stored in 95% ethanol and kept in a −20°C freezer until laboratory analysis. All subsequent molecular laboratory methods are described in Appendix S3.

2.2.2 | Worker body size

To determine if forager body size changed in response to fire and floral abundance, we measured all whole specimens available before and after fire. Body size was estimated by measuring the intertegular span (ITS) of all whole specimens in the laboratory using digital calipers. Each measurement was taken by one research assistant blind to the specimen's origin to minimize observer bias. To analyse the effect of fire on worker body size, we fit a linear model of ITS as a function of burn category, year and their interaction. We then fit a linear mixed-effects model with ITS as a function of $\log_{10}$ floral abundance, burn category and their interaction with site as a random effect to determine if changes in body size were related to floral abundance.

2.2.3 | Queen collections

We non-lethally captured queens of *B. vosnesenskii* following fire to track changes in reproductive output (i.e. queen abundance) and measure dispersal distances. We collected queens at or near our focal sites with effort evenly distributed between burned and unburned areas. No queen count data are available prior to fire and we were unable to obtain reliable estimates of queen ITS in the field. In both years following fire, queens were netted during timed sampling events, placed into vials on ice until non-lethal tarsal samples were taken (as described above for non-lethal worker collections), and released. For each queen captured, we indicated whether she was nest searching or foraging to determine whether burning may improve nest site availability. To determine whether queen abundance differed between years and with fire, we fit a linear mixed model of queen captures per minute as a function of burn category, year and their interaction with site as a random effect. Non-lethal tarsal samples were stored in 95% ethanol in −20°C until further analysis to aid in the estimation of queen dispersal distance (*described below*). Additionally, in 2017, queens were given a site-specific paint mark on the thorax to determine individual dispersal distances. Recaptured queens were not clipped a second time.

2.2.4 | Site-level floral abundance

For each site after fire, and on the same day as bumble bee collections, we estimated the total inflorescence abundance for each plant species visited by *B. vosnesenskii* within a 50 m radius of the approximate site centre (see Mola & Williams, 2018 for further details). The 50 m radius was chosen as it more reliably captures the patchy distribution of plants in our focal sites compared to

transects or quadrats. Inflorescence abundance was recorded in $\log_{10}$ bins following Williams et al. (2012), reflecting the magnitude over which bumble bees are likely to respond to changes in resource abundance. For consistency, one observer (JMM) conducted all estimates. For each species, we estimated the $\log_{10}$ inflorescence abundance and summed these estimates across all plant species to get the site-level $\log_{10}$ floral abundance used in analyses. Although we do not have pre-fire site-level floral abundance, we previously determined that floral density, abundance and longevity were increased in burned compared to unburned sites post-fire and that median floral density of patches used by bumble bees increased by 36% in burned sites compared to pre-fire (Mola & Williams, 2018). Such findings are reinforced by another study of the same fires at McLaughlin Reserve (LoPresti et al., 2018).

2.3 | Statistical analysis

2.3.1 | Sibship assignment

Individuals were assigned to colonies using COLONY version 2 (Wang, 2004) on called genotypes (DNA extraction, library preparation and genotype calling details provided in Appendix S3). We constrained analysis of sibships by running COLONY separately for each year (i.e. all specimens from 2015, 2016 and 2017 separately). Because queens are full-sibs of workers from the previous year (Lepais et al., 2010; Mola & Williams, 2019), we ran additional analysis of queen sibship with workers from the previous year included (i.e. queens from 2016 with workers from 2015 and queens from 2017 with workers from 2016). For each group, we selected three sets of 5,000 anonymous SNPs to be used in COLONY. The 5,000 SNPs were selected randomly from all markers that had a minor allele frequency greater than 0.05, occurred at least 1,000 bp from the next nearest selected SNP, and were in Hardy–Weinberg Equilibrium as calculated from allele frequencies. We ran COLONY assuming monogamous breeding for both sexes (Owen & Whidden, 2013) and with the full pairwise-likelihood score setting. We conducted five runs of COLONY on medium length for each of the three SNP sets used. Only sibships present in all three COLONY outputs were retained for subsequent analysis, ensuring high confidence in our colony assignments.

2.3.2 | Colony abundance

First, we estimated broad-scale changes in colony abundance across burn category and year, by dividing our COLONY output into six treatments (burned/unburned × workers from 2015, 2016 and 2017). We obtained the maximum-likelihood estimate of population size and 95% CI within each treatment from 1,000 bootstrap runs in the R package CapWire (Pennell, Stansbury, Waits, & Miller, 2013), which estimates population size using a two-innate rates model that assumes heterogeneity of capture probability and is appropriate for estimates of bumble bee nest abundance (Goulson et al., 2010).

Second, we determined the relationship between site-level colony abundance and site-level floral abundance using post-fire data from 2016. Following Geib, Strange, and Galen (2015), we divided the number of unique colonies (N_{nr}) from each collecting event (site-day combination), as estimated from COLONY, by the total number of individuals successfully genotyped (N_g) from that collecting event. We multiplied $N_g \times N_i$ to yield a standardized estimate of the number of detected nests (N_{ns}). If all individuals from a collection event were successfully genotyped, then $N_{ns} = N_{nr}$. Next, we estimated 'effective colony number' (N_c) during each collection event as $N_c = 1.5 \times N_{ns}$, based on the Crozier model for effective population size of eusocial haplodiploid organisms (Crozier, 1979; Geib et al., 2015). Lastly, we divided the effective colony number (N_c) by the sampling area of each site to standardize colony abundance by site area, which we termed site-level colony density (N_c/0.01 km^2). We modelled the relationship between site-level colony density and flower availability by fitting a linear mixed-effects model of site-level colony density (N_c/0.01 km^2) as a function of $\log_{10}$ floral abundance, burn category and their interaction with site as a random effect to account for multiple visits to the same collection location.

2.3.3 | Colony foraging distance and space use

We compared foraging distances before and after fire as well as colonies use of burned and unburned areas by estimating colony locations and specific foraging distances in each condition. We first calculated the centroid of all individuals assigned to the same colony (siblings) and used it as our best estimate of colony location. We then took the mean of the distances between each sibling and the colony's centroid (Carvell et al., 2012; Jha & Kremen, 2013; Redhead et al., 2016). Although this is likely a crude estimate of any individual colony's location and range, it represents a reliable way to get estimates of foraging range from many colonies and conduct relative comparisons between colonies or repeated collections within a common landscape (Mola & Williams, 2019; Pope & Jha, 2017). Because foraging could occur across the burn perimeter, all foraging distance estimates are made with all captures before fire (2015) and all captures after fire (2016) regardless of burn category or site. Differences in mean colony-specific foraging distance were compared using a Wilcoxon Rank-Sum test.

To understand how frequently colonies foraged in both burned and unburned areas, and to determine whether we can treat the burned and unburned areas as relatively independent units for estimating landscape-scale colony abundance, we compared the observed number of colonies foraging within both burn categories to a null expectation. We counted the observed number of colonies foraging within both burned and unburned sites by extracting the locations of all siblings within a given colony and counting any colonies with siblings found in both burn categories. To obtain the null expectation, we randomly reassigned individuals to colonies 1,000

times by shuffling colony membership to preserve the number and size distribution of colonies but randomize individual identity. For each iteration, we totalled the number of colonies detected within at least one burned and unburned site. If the number of observed colonies is less than expected from the null distribution, then it suggests colonies forage predominantly within one burn category (i.e. burned or unburned).

2.3.4 | Queen dispersal

To estimate the dispersal distances of queens within our study landscape, we calculated the separation distance between sibling queens collected within the same year, or between queens and their sister-workers from the previous year (Lepais et al., 2010; Mola & Williams, 2019). For each pair of queens belonging to the same colony, we calculated the linear distance between individuals. Due to the low number of queens with siblings in the dataset, we present these results simply as raw estimates with no associated statistical analysis.

2.3.5 | Statistical software and packages

All analyses were performed in R version 3.6.0 (R Core Team, 2016). Mixed-effects models were fit using the package LMER4 (Bates, Sarkar, Bates, & Matrix, 2007) and posthoc Tukey pairwise significance tests were conducted using function *glht* within the MULTCOMP package (Hothorn et al., 2016). We fit full models with all relevant predictors as well as model subsets and then selected the best model using an AICc framework using the *aictab* function in the AICCMODAVG package (Mazerolle, 2019). To obtain *p* values of mixed models, we conducted likelihood ratio tests of the selected model against a null model with the focal effect(s) removed.

3 | RESULTS

3.1 | Colony abundance

In total, we captured 268, 302 and 71 workers in 2015, 2016 and 2017, respectively (Appendix S4). In the first year after fire, just over twice as many bees were captured in burned sites compared to unburned sites ($burned_n$ = 204, $unburned_n$ = 98; Table 1). Despite strong search effort and abundant queens in 2017 (*see below*), workers were uncommon in the grasslands, probably because forb numbers were lower across the whole study area that year. Workers from 2017 are excluded from further genetic analyses because only two individuals were determined to be full-sibs (Table 1).

Based on the maximum likelihood estimate of colony abundance from CapWire, burned sites supported over 3× the number of colonies compared to before fire (2015 vs. 2016), but colony abundances at unburned sites did not change from 2015 to 2016 (Figure 2a; Table 1). Before fire, we detected 191 unique colonies, with 38.8% of colonies represented by two or more sibling workers. After fire, in 2016, we detected 260 colonies, with only 20.9% of colonies detected multiple times, despite capturing more bees overall (Table 1). The uncertainty in estimated numbers at burned sites following fire increased as detections of full-sibs became rarer with a larger population size. Before fire, our detected colony abundance represented ~31% of the total CapWire estimated number of colonies. After fire, we detected only ~18% of the total estimated colony number (Table 1).

Site-level colony density (N_c/0.01 km^2) was strongly positively predicted by site-level floral abundance ($\beta \pm SD$: 1.812 ± 0.419, R^2_m = 0.271, R^2_c = 0.870, χ^2 = 12.266, $p < 0.001$; Figure 2b). The model containing only floral abundance was most probable (Table S3). Given that most individuals captured at a site did not belong to a sibling group, the number of individuals captured at a site strongly correlated with the estimated number of colonies within that site ($N_i \sim N_c$/0.01 km^2; Pearson's r = 0.637, df = 20, p = 0.001).

TABLE 1 Captures of workers and estimated colony abundance across burn category and year

Year	Burn category	Total captures	Total genotyped	Unique colonies[a]	Colony abundance[b]	Proportion detected[c]
2015	ALL	268	255	191	619 (564–905)	0.31
	Burned	174	169	129	491 (419–815)	0.26
	Unburned	94	86	69	228 (184–417)	0.30
2016	ALL	302	296	260	1,420 (1,177–2,192)	0.18
	Burned	204	199	184	1,600 (1,143–3,321)	0.12
	Unburned	98	97	82	344 (268–676)	0.23
2017[d]	ALL	71	56	55	—	—
	Burned	46	39	38	—	—
	Unburned	25	17	17	—	—

[a]Value within a burn category may not match the combined total as some colonies have workers in both categories.

[b]CapWire maximum likelihood estimate and 95% confidence interval.

[c]Calculated as unique colonies/maximum likelihood colony abundance.

[d]Only one sibling pair was detected in 2017 so CapWire estimates are unobtainable.

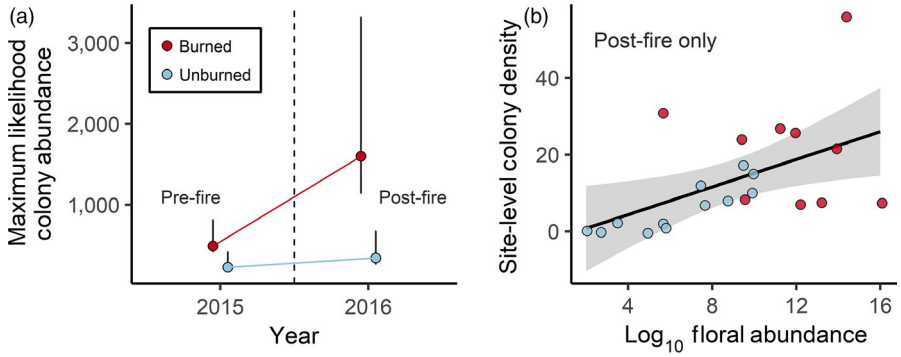

FIGURE 2 Change in colony abundance across year and burn category. (a) CapWire estimate of colony abundance from all captures within each burn category and year. Vertical bars represent 95% CI from 1,000 bootstrap estimates. Fire occurred July/August 2015, dashed vertical line is for visual clarity between pre- and post-fire period. (b) Site-level colony density (N_c/0.01 km^2) as a function of Log_{10} floral abundance. Best-fit line (black) and 95% CI (grey shading) represent the output of a linear model of fixed effects. Points are horizontally jittered for visual clarity

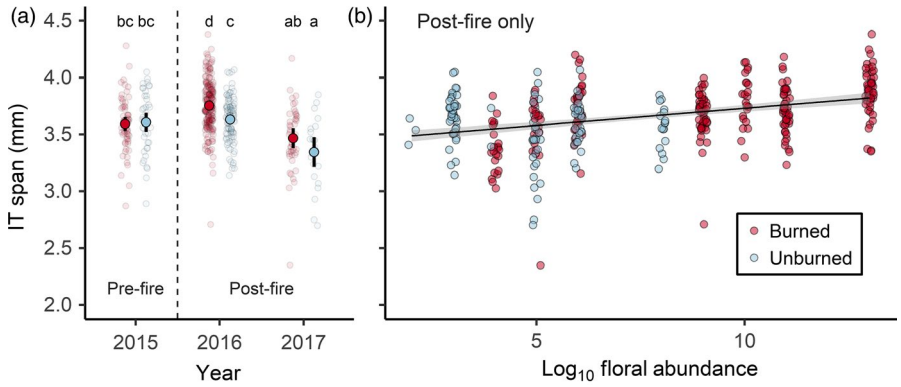

FIGURE 3 Worker size differed between burn category, year and in response to site-level floral abundance. (a) ITS as a function of year and burn category. Solid points and error bars represent the mean and 95% CI, respectively. Dashed vertical line is for visual clarity between pre- and post-fire period. Letters represent differences of $p < 0.05$ from a Tukey HSD Post hoc test. (b) ITS as a function of site-level floral abundance post-fire. Pre-fire (2015) floral abundance data are not available. Line represents linear fit with 95% CI. Points are horizontally jittered for visual clarity

TABLE 2 Queen captures with recorded and relative effort. Relative effort is standardized by dividing all recorded effort by the largest value (760 min) to ensure our differences in captures are not due to differences in effort

Year	Burn category	Years post-fire	Recorded effort (min)	Captures	Relative effort	Relative captures
2016	Burned	1	760	38	1.00	38.00
2016	Unburned	1	740	39	1.03	40.17
2017	Burned	2	726	202	1.05	211.46
2017	Unburned	2	740	128	1.03	131.84

3.2 | Worker body size

Body size was not significantly different in burned and unburned sites before fire (Figure 3a, $t = 0.323$, $p = 0.999$), but workers from burned sites were significantly larger the first year following fire (Figure 3a, $t = -4.52$, $p < 0.001$). Forager body sizes were then smaller at both burned and unburned sites in 2017, and although mean ITS remained ~4% higher in burned sites than in unburned sites, this difference was not statistically significant ($t = -2.31$, $p = 0.018$). Differences in body size were strongly positively correlated with increased site-level floral abundance ($\beta \pm SD$: 0.027 ± 0.005, $R^2_m = 0.141$, $R^2_c = 0.254$, $\chi^2 = 26.58$, $p < 0.001$; Figure 3b). The most probable model of body size and floral abundance did not include burn category (Table S4), but all the sites with the highest floral abundance were in burned areas.

3.3 | Queen abundance

In the first growing season following fire, 2016, we captured approximately the same number of queens in burned and unburned areas (Table 2). Queen capture rate increased in the second year following fire (2017) across both burned and unburned areas,

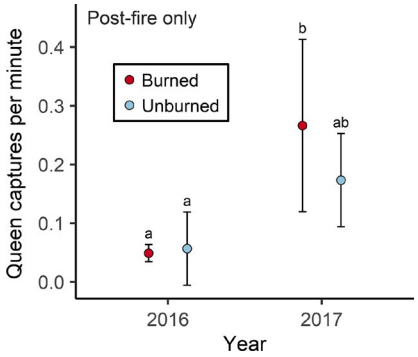

FIGURE 4 Queen capture rate as a function of burn category and year. Two seasons following fire queen abundance increased regardless of burn category, likely because the effect of fire is realized over the entirety of the reserve with queens dispersing between burned/unburned areas (Table 3). Letters represent differences of $p < 0.05$ from a Tukey HSD Post hoc test

with total captures in burned areas growing more dramatically (Figure 4; Table 2). The best fit model included year alone, although the additive and full models were similar (ΔAICc = 1.3, Table S5). There were no significant differences in the proportion of queens nest searching in burned versus unburned areas in either 2016 (burned = 5 nest searching, 32 foraging; unburned = 1 nest searching, 37 foraging; $\chi^2 = 1.71$, $p = 0.19$) or 2017 (burned = 25 nest searching, 177 foraging; unburned = 17 nest searching, 111 foraging; $\chi^2 = 0.005$, $p = 0.94$).

3.4 | Foraging distance, space use and dispersal distance

Mean colony-specific foraging distance was 594 m in 2015 (Figure 5a, $N = 35$, $SD = 915$ m, range: 0.5–3266 m) and 927 m in

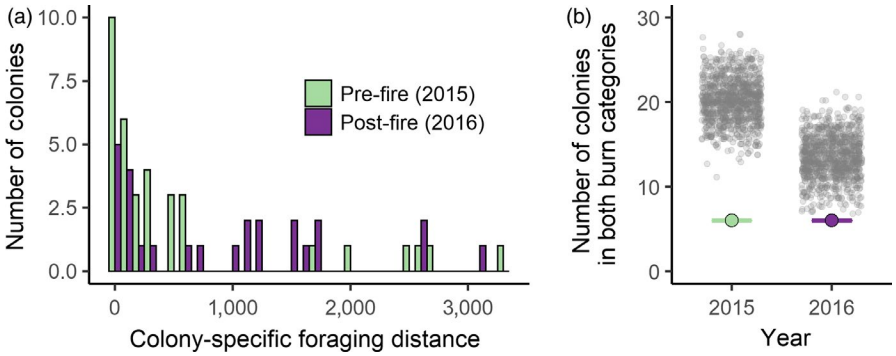

FIGURE 5 Colony-specific foraging distances and colony separation across burn perimeter. (a) Frequency of mean colony-specific foraging distance in bins of 100 m. (b) Number of colonies observed at both burned and unburned sites (coloured point and line) compared to 1,000 random draws (grey circles)

TABLE 3 Dispersal distances between worker–queen pairs, queen–queen pairs and recaptured (paint marked) queens

Relationship	Movement direction	No. colonies	Separation in metres
Worker 2015 → Queen 2016 (Sibship)	Unburned → Burned	1	8,103
	Unburned → Unburned	–	–
	Burned → Unburned	–	–
	Burned → Burned	–	–
Worker 2016 → Queen 2017 (Sibship)	Unburned → Burned	2	5,311, (7,708, 8,028, 6,243)[a]
	Unburned → Unburned	1	85
	Burned → Unburned	–	–
	Burned → Burned	1	133
Queen 2016 → Queen 2016 (Sibship)	Mixed	–	–
	Unburned only	1	666
	Burned only	–	–
Queen 2017 → Queen 2017 (Sibship)	Mixed	1	(656, 5,687, 5,434)[a]
	Unburned only	3	21, 48, 764
	Burned only	4	(325, 1,840, 2,144), (2,120, 933, 2,958)[a], 2,238, 2,987
Queen recaptures 2017 (Paint Tagged)	Mixed	–	–
	Unburned only	2	600, 500
	Burned only	4	0,0,0[b], 3,000

[a]Separation distances in parentheses are pairwise distances between individuals within one colony.

[b]Zeros are queens recaptured at the same site.

2016 (Figure 5a, $N = 26$, $SD = 910$, range: 5–3,080 m), although this difference was not statistically significant ($W = 351$, $p = 0.132$).

Workers from the same colonies were detected within both burn categories less than expected by chance alone (Figure 5b, Mean [range] of shuffled expectation 2015: 20.2 [11–28]; 2016: 13.4 [7–21]; observed 2015: 6, 2016: 6; $p < 0.001$), and all colonies detected in both burn categories had only one sibling detected in the minority category (e.g. three siblings in unburned sites and one in burned).

We detected seven queens who were from the same colony of workers from the previous year (Table 3). These queens were separated from their worker-siblings by distances of 85–8,103 m (Table 3). We detected 15 pairs of sister queens within the same year similarly with dispersal distances of 21–5,687 m. We paint-marked 327 queens in 2017, and re-observed 6 of them at distances ranging from 0 (same site) to ~3,000 m.

4 | DISCUSSION

Our study reinforces two core ideas related to fire and more generally to disturbance impacts. First, the resource-rich environments released by fire can drive bottom-up effects on consumers. We demonstrate how fire-driven impacts on resource abundance have strong population-level effects by increasing the population density, morphology and reproductive capacity of a highly mobile consumer. Second, although previous studies have observed increased bumble bee worker abundance shortly after fire (Galbraith et al., 2019; Mola & Williams, 2018; Smith DiCarlo et al., 2019), we demonstrate this response is not the result of a few dominant colonies, but of transient changes in population size (i.e. colony abundance). Given that the observed effects were all strongly predicted by site-level floral abundance, we expect these results to extend to other scenarios in which floral abundance is restored to high levels or changes rapidly within the landscape.

4.1 | Colony abundance

After fire, not only were there more workers of *B. vosnesenskii* in the burned sites but also those workers came from nearly threefold more colonies than before fire. Counts of foragers on flowers alone may simply reflect aggregation of foragers from a few colonies to an abundant resource patch and not increased population size (Roulston & Goodell, 2011), or may reflect true increases in population sizes (Geib et al., 2015). Genetic mark–recapture revealed that more abundant foragers also reflected substantially more colonies detected after fire (Figure 2a). These effects are strongly correlated with increased floral abundance in burned sites (Figure 2b). We conclude that the increased forager abundance following fire is not just associated with a few colonies, but instead reflects an increase in the number of colonies the landscape is able to support with increased resource density.

4.2 | Worker body size

The observed increase in worker body size at burned sites post-fire (Figure 3) suggests that increased colony abundance in burned areas does not come at the expense of producing smaller workers. Other studies have shown that post-fire landscapes are differentially colonized by larger bodied insect species (LoPresti et al., 2018; Ne'eman, Dafni, & Potss, 2000). Our study complements these cross-taxon comparisons by documenting within-species changes in forager size in response to fire (Figure 3a). The strong relationship between floral abundance and forager body size (Figure 3b) suggests that post-fire resource pulses provide the means for colonies to produce larger workers. Larger bumble bee workers contribute more resources to the colony (Kerr, Crone, & Williams, 2019) and field observation and experimental studies show that queen production and colony mass are positively predicted by larger mean worker size (Herrmann, Haddad, & Levey, 2018; Malfi, Crone, & Williams, 2019). The result is also consistent with a recent manipulative field experiment using *B. vosnesenskii*, which found food supplementation increased mean worker ITS by ~6% (Malfi et al., 2019). Although it is possible that the observed differences in body size are due to site selection by larger foragers, knowledge from studies with captive colonies and the foraging distances observed within our study support the conclusion that the pattern is most parsimoniously driven by increased resource abundance.

4.3 | Foraging distance and space use

Although our ability to estimate foraging distance was somewhat limited by the low number of full-sib pairs, especially after fire, it is clear siblings were most commonly detected in one burn category or the other (Figure 5). Given that colonies were observed in a single burn category more than expected by random (Figure 5b), colonies should be most strongly influenced by the local resource availability within their respective burn category. Although some colonies had separation distances that exceeded 2 km and a few colonies used both burned and unburned sites, it seems unlikely that colonies within our study system commonly do so. If they did, we should have observed increased body sizes across all sites in 2016 (Figure 3a), since colonies established within unburned areas would also have been commonly foraging on the resource-rich burned areas and therefore producing workers of equivalent size. However, given the long foraging distances of *B. vosnesenskii* observed in our study and in other studies across a variety of habitats (Jha & Kremen, 2013; Mola, Miller, O'Rourke, & Williams, 2020a; Rao & Strange, 2012), it is likely that in other scenarios colonies would benefit from access to a diverse range of successional stages.

4.4 | Queen abundance and dispersal

Queen abundance was strikingly higher in the second year following fire within both burned and unburned sites. We captured over

threefold as many queens in unburned sites and over fivefold as many in burned sites (Table 2), although there was large variability between collection events (Figure 4). The delayed response of queen abundance follows logically from the timing of reproductive production in the bumble bee life cycle (Figure 1), and mirrors expected time lags in bee abundance following years in which colonies are highly productive (Crone, 2013; Ogilvie et al., 2017; Potts, Vulliamy, Dafni, Ne'eman, & Willmer, 2003). Although the effect was stronger in burned sites, queen abundance increased in unburned areas as well, suggesting either that queens produced by colonies within burned areas in 2016 spilled over into unburned areas the following year or that queen production increased within unburned sites as well. Given that queens were observed to have dispersed up to 8 km (Table 3), and the lack of increased colony abundance or body size in unburned areas in 2016, the hypothesis of spillover seems most likely. Roughly, the same proportion of queens were observed nest searching regardless of burn status. That said, most queens at all sites were already foraging (Appendix S4), presumably having already finished nest searching. As such, we are unable to rule out the possibility that reduced groundcover from burning improves nest site availability. Elucidating the impact of burning on queen nest searching and early foraging would provide a better picture of how fire interacts with bumble bee nest availability and establishment. Collection of queens in 2018 resulted in only 24 captures, despite a focused search effort by six people over 2 days (J.M. Mola, unpubl. data), suggesting the effects of fire on queen abundance within our system were transient.

4.5 | Transient effects of fire

The effects of fire on floral resources and bee populations appear short-lived in our system. Although we observed many foundress queens in early spring 2017 (Figure 4), we observed very few workers in either burned or unburned grasslands (Table 1). We speculate the low worker abundance was due to a later flowering period than previous years combined with a sustained period of hot, dry days which caused early floral senescence. However, we did not directly measure the relationship between precipitation and floral phenology. We cannot rule out the possibility that in the absence of these weather patterns we would have observed sustained effects of fire. However, we can confidently conclude that we no longer observed strong differences in bumble bee body size or abundance between the burned and unburned sites. These factors were reduced across the reserve regardless of burn category. Our results are consistent with other studies in grasslands that show relatively short-lived effects of fire as grasses quickly recolonize and overtake forbs (Brown & Smith, 2000; Harrison, Inouye, & Safford, 2003). Similar outcomes to burning would be likely if restoration efforts targeted the removal of invasive grasses, as is done in some areas of the study region. In other landscapes where the effects of fire on vegetation persist, such as conifer forests, it seems probable that the effects for bees would remain for several more years (Brown & Smith, 2000; Brown, York, Christie, & McCarthy, 2017).

4.6 | Application to species of conservation concern

Our study focuses on a common species, *B. vosnesenskii*, but there is great interest in how fire may affect species of conservation concern (e.g. *B. affinis*; Jepsen, Evans, Thorp, Hatfield, & Black, 2013). A critical distinction for at-risk species would be whether increased colony abundance was due to in situ survival, recolonization of the burned area by adjacent populations or some combination of both. Determining the relative weight of these pathways would be critical for rare species where nearby source populations may not exist to recolonize a burned area in the event of mass mortality. In our study, we are unable to distinguish between survival and recolonization. Prior studies suggest that burning is unlikely to kill ground-nesting solitary bees (Cane & Neff, 2011). However, bumble bees predominantly nest in underground open cavities and recent observations of overwintering queens of *B. vosnesenskii* along the California coast have found queens overwintering in a presumably flammable duff layer (Williams et al., 2019). Understanding the nesting and overwintering substrates for target species and their relative fire risk given the timing or intensity of fire would be a necessary first step before determining the vulnerability of bumble bee populations to fire management.

5 | CONCLUSIONS

Disturbances like wildfire can have large transient effects on ecosystems, with impacts realized among trophic levels and spatial scales. Our results leverage a unique situation where genetic data and morphological measurements before and after fire help reveal an otherwise difficult-to-observe process in a highly mobile insect species. We find striking increases in colony abundance, forager size and queen production in early postfire landscapes. These effects are short-lived in this system, but the colony responses we observed demonstrate a rapid response to disturbance and provide a clear example of floral resource limitation within a bumble bee population. Whether changing patterns of the scale and frequency of wildfire can result in enduring effects of disturbance on bumble bees remains an open question. The effects of wildfire observed here are largely positive on this abundant taxon, but careful consideration of how resource landscapes respond to fire will be necessary for predicting or evaluating the response of other organisms, especially rare ones, to disturbance.

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AUTHORS' CONTRIBUTIONS

J.M.M. and N.M.W. designed the project; J.M.M. collected the field data; S.M.O. performed DNA extractions and library prep; J.M.M. analysed the sequence data under careful guidance from M.R.M.; J.M.M. wrote the initial draft of the manuscript; N.M.W. and J.M.M. rewrote the manuscript together. All authors provided feedback and edits to the final draft of the manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.25338/B8VS52 (Mola, Miller, O'Rourke, & Williams, 2020b). Genetic data are available as BAM files in the NCBI Short Read Archive (accession no. PRJNA627406 & PRJNA627450).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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