



## Research Article

# Bumble Bee Use of Post-Fire Chaparral in the Central Sierra Nevada

HELEN L. LOFFLAND, *The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, CA 94956, USA*

JULIA S. POLASIK,<sup>2</sup> *The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, CA 94956, USA*

MORGAN W. TINGLEY, *Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269, USA*

ERIN A. ELSEY, *Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132, USA*

CHUCK LOFFLAND, *Amador Ranger District, Eldorado National Forest, USDA Forest Service, 26820 Silver Drive, Pioneer CA 95666, USA*

GRETCHEN LEBUHN, *Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132, USA*

RODNEY B. SIEGEL,<sup>1</sup> *The Institute for Bird Populations, P.O. Box 1346, Point Reyes Station, CA 94956, USA*

**ABSTRACT** Bumble bees (*Bombus* spp.) are declining across many regions in the Northern Hemisphere, leading to a need for management actions that will protect and enhance their habitats. In the Sierra Nevada of California, USA, montane chaparral is prevalent across the landscape, particularly after forest fires, and may provide important floral resources for pollinators. However post-fire montane chaparral is often targeted for removal during reforestation efforts, to reduce competition with young trees. In 2015 and 2016, we conducted non-lethal bumble bee surveys within 2 areas in the Sierra Nevada that burned in forest fires in 2004. Our goals were to describe bumble bee abundance and species richness in a post-fire landscape, to compare results from chaparral-dominated upland vegetation with results from interspersed patches of riparian vegetation, and to identify characteristics of individual chaparral stands that might make some stands more valuable to bumble bees than others. We captured 2,494 bumble bees of 12 species, and used Bayesian hierarchical modeling to determine that bumble bee abundance was substantially greater in riparian plots (modeled capture rate  $\bar{x} = 1.10 \pm 0.31$  [SD] bees/survey in 2015, and  $2.96 \pm 0.83$  bees/survey in 2016) than in upland plots ( $\bar{x} = 0.47 \pm 0.07$  bees/survey in 2015, and  $1.27 \pm 0.18$  bees/survey in 2016), which comprised a mix of chaparral shrubs and associated herbaceous plants. Modeled species richness was also greater in riparian plots, with an average mean richness of  $4.1 \pm 1.8$  bumble bee species in riparian plots versus  $2.3 \pm 1.3$  species in upland plots across the 2 years of the study. Within upland and riparian areas, plots dominated by herbaceous vegetation had greater abundance and species richness. One chaparral shrub species, bearclover (*Chamaebatia foliolosa*), was foraged on preferentially over all other shrub species and over all but 1 forb taxon, and was associated with increased occupancy probability in the Vosnesensky bumble bee (*Bombus vosnesenskii*), the most abundant bumble bee species on our study plots. A complex of closely related herbaceous species in the genus *Phacelia*, commonly associated with upland chaparral in our study area, was the plant taxon most frequently used by bumble bees, and appeared to be particularly important during mid-summer after bearclover flowers became scarce. Our findings suggest that post-fire chaparral communities are generally less intensively used by bumble bees than nearby riparian vegetation but may nevertheless provide important habitat. When chaparral removal is part of post-fire forest regeneration strategies, bumble bees will likely benefit from retention of a mosaic of upland habitat patches dominated by herbaceous vegetation and, in our study area, bearclover, which may provide foraging resources throughout the life cycle of local bumble bee colonies. Because habitat characteristics affected the occupancy of individual bumble bee species differently, managers should consider foraging preferences of target bumble bee species when making land management decisions. © 2017 The Wildlife Society.

**KEY WORDS** bearclover, *Bombus*, bumble bee, *Chamaebatia foliolosa*, chaparral, *Cirsium*, *Hackelia*, *Phacelia*, pollinator, post-fire, Sierra Nevada.

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<sup>1</sup>E-mail: rsiegel@birdpop.org

<sup>2</sup>Current address: Wyoming Game and Fish Department, 528 S Adams St Laramie, WY 82070, USA.

Bumble bees (*Bombus* spp.) provide vital ecosystem services as pollinators of native plant species and agricultural crops (Kearns and Inouye 1997). However, many bumble bee species are declining across the Northern Hemisphere because of factors that are often inter-related and include habitat loss and fragmentation (Goulson et al. 2008, Koh et al. 2016), agricultural practices (Carvell 2002, Williams

and Osborne 2009, Dicks et al. 2016), altered fire regimes (Taylor and Catling 2011), disease (Cameron et al. 2011, Koch and Strange 2012), and climate change (Potts et al. 2010, Kerr et al. 2015, Miller-Struttman et al. 2015). With declines of bumble bees attributed in part to habitat loss (Goulson et al. 2008, Koh et al. 2016), understanding how habitat characteristics influence bumble bee abundance and diversity may help guide land management efforts towards improving habitat for bumble bees and other pollinators (Goulson et al. 2011).

Bumble bees are commonly associated with meadows and other riparian vegetation, which typically provide diverse floral resources for foraging (Kremen et al. 2004, Hatfield and LeBuhn 2007, Elliot 2009). In contrast, patterns of bumble bee diversity and abundance in upland habitats such as montane chaparral have not been well described. Although the value of chaparral for overall biodiversity in montane landscapes is well established (Lawrence 1966, Raphael et al. 1987, Quinn and Keeley 2006, Humple and Burnett 2010) it remains unclear how important montane chaparral and other upland plant communities are for bumble bees, and what characteristics may make some areas more valuable to bumble bees than others.

Private and public land managers often target montane chaparral for suppression or removal to aid with forest regeneration and to reduce fire risk (McGinnis et al. 2010). Chaparral that develops in forest openings created by fire or timber harvest is often selectively treated to reduce competition with naturally occurring or planted conifer seedlings (McDonald and Everest 1996, McDonald et al. 2004) in areas where reforestation is a management priority. Treatment methods to reduce or remove unwanted vegetation include prescribed fire, broadcast spraying of herbicides to kill all herbaceous and shrub cover within conifer plantations (or in preparation for conifer planting), targeted herbicide application to shrub species (generally manzanita [*Arctostaphylos* spp.], ceanothus [*Ceanothus* spp.], or bearlover [*Chamaebatia foliolosa*]) or noxious weeds (e.g., cheatgrass [*Bromus tectorum*], bull thistle [*Cirsium vulgare*], Klamath weed [*Hypericum perforatum*], yellow star thistle [*Centaurea solstitialis*]) that leaves other shrubs and herbaceous vegetation intact, hand-grubbing to remove the above-ground portion of target shrub species using hand tools, and tilling and mastication using heavy equipment to excavate or grind and shred all vegetation regardless of species (McDonald et al. 2004).

Recent increases in forest fire activity across the montane west (Westerling et al. 2006, Miller et al. 2009, Dennison et al. 2014) have stimulated a concomitant increase in post-fire forest restoration efforts, but existing information is generally insufficient to help land managers ensure those efforts are likely to benefit bumble bees and other pollinators. Research in some temperate regions suggests forest fire may yield enhanced habitat for bumble bees and other pollinators (Campbell et al. 2007, Bogusch et al. 2014), but observed effects of fire on pollinators in Mediterranean climates have been mixed (Ne'eman et al. 2000, Moretti et al. 2009). In the Sierra Nevada Mountains of California, USA, fire-mediated

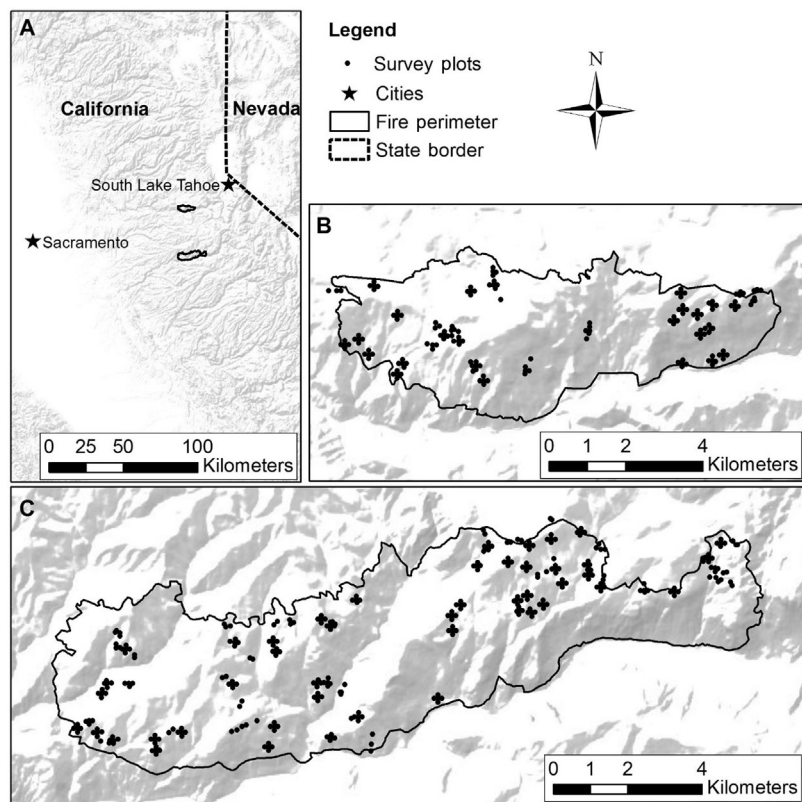
increases in floral resources provided by stands of blooming chaparral shrubs and associated herbaceous vegetation may be important for bumble bees, including species that are declining, such as the western bumble bee (*Bombus occidentalis*; Cameron et al. 2011). Assessing the value of upland vegetation for bumble bees, comparing its usage with that of interspersed riparian areas, and identifying characteristics that make some chaparral stands more valuable for retention as bumble bee habitat than others, could help land managers incorporate bumble bee habitat needs into reforestation efforts, which commonly involve suppression or removal of chaparral through chemical or mechanical methods.

Our goal was to gain a better understanding of bumble bee use of post-fire upland habitat, especially montane chaparral, in the Sierra Nevada by identifying habitat characteristics that influence bumble bee abundance and diversity within such areas. We hypothesized that upland areas dominated by montane chaparral might support a relatively high abundance and diversity of bumble bees, though perhaps not as high as riparian areas, where floral diversity may be greater, and that chaparral plant species may vary substantially in their importance to bumble bees.

## STUDY AREA

This study took place from May to August 2015 and 2016 on Eldorado National Forest in the central Sierra Nevada of California (Fig. 1), at sites ranging in elevation from 1,000 m to 2,120 m. The Sierra Nevada has a Mediterranean climate with warm, dry summers and precipitation falling mainly during the late fall, winter, and spring. The study area comprised lands managed by the United States Department of Agriculture [USDA] Forest Service within the footprints of 2 mixed-severity forest fires, the Fred's and Power fires, which burned approximately 3,116 ha and 6,877 ha, respectively, in 2004 (USDA Forest Service 2014). The fire areas are situated at similar elevations on relatively steep south-facing slopes along parallel river drainages (South Fork American River, North Fork Mokelumne River) and are separated from one another by 28 km. Eleven and 12 years after the fires, much of the burned areas, which had been largely forested with mature stands and plantations of varying age prior to the fire, were dominated by herbaceous vegetation and chaparral shrub species, particularly bearlover, mountain whitethorn (*Ceanothus cordulatus*), deerbrush (*Ceanothus integerrimus*), and greenleaf manzanita (*Arctostaphylos patula*). Areas that burned at lower severity retained varying amounts of live forest cover, which was dominated by ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), and black oak (*Quercus kelloggii*). Riparian vegetation, comprised of a mix of deciduous shrubs (particularly willow [*Salix* spp.], alder [*Alnus* spp.], and dogwood [*Cornus* spp.]), forbs, and sedges [*Carex* spp.], occurred along perennial and ephemeral streams, and was generally sparsely distributed along narrow corridors <10 m wide. Even the largest riparian patches were generally <50 m wide and covered <2 ha.

Subsequent to the fires, both sites have undergone varying degrees of salvage logging, conifer replanting, and mechanical



**Figure 1.** Location of the Fred's and Power fires in the central Sierra Nevada, California, USA (A), and distribution of individual bumble bee survey plots (2015–2016) on the Fred's fire (B) and the Power fire (C).

and chemical treatment of plantations. At the Fred's fire the majority of the pre-fire timberlands that were situated on slopes gentle enough to access were salvage logged and replanted after the fire. Post-planting silvicultural treatments within plantations have included mechanical and chemical treatment of competing vegetation. At the Power fire, approximately half of the accessible pre-fire timberlands were salvage logged and replanted, and mechanical or hand treatment of competing vegetation has occurred, but chemical treatment has not.

## METHODS

### Bumble Bee and Vegetation Surveys

We surveyed bumble bees within 20-m-radius plots located throughout the areas burned by the Fred's and Power fires on Eldorado National Forest (Fig. 1). For efficiency during surveys, most plots were clustered in groups of 5, with a central plot and 4 satellite plots centered 100 m from the mid-point of the central plot in each cardinal direction. We determined locations for the 5-plot clusters using a random design stratified by 3 elevation bands (<1,372 m, 1,373 m–1,676 m, >1,676 m) with the centers of plot clusters located a minimum of 275 m apart. Although adjacent plots and even clusters of plots could easily have been within the foraging radius of individual bumble bees (Elliot 2009), our aim was to look at relatively fine-scale habitat selection. We also used a stratified random sampling strategy to deliberately place additional plots in riparian areas, which were relatively

rare at our study sites and were not well represented in our initial, habitat-blind random sample. We used 2012 imagery from the National Agriculture Imagery Program (NAIP) to map riparian patches >0.4 ha, and then placed as many plots within each patch as would fit using 100-m spacing. Because of the small size of riparian patches within the study area,  $\leq 3$  plots were delineated within any single riparian patch. In all instances, we selected plot coordinates based on existing geospatial land cover information using ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA, USA).

We deliberately delineated more plot clusters (from the initial random sampling and the riparian-only sampling) than we could likely survey, and then surveyed as many as time permitted, choosing plot clusters in random order within each of the 3 elevation zones. We surveyed most plots twice during each field season, once between 20 May and 26 July, and then again between 9 July and 15 August; however, 41 plots were in an area that became inaccessible to us during the second half of the 2015 field season because of law enforcement activities, and we therefore surveyed them only once that year. Because we thus had extra survey capacity, we surveyed 16 accessible plots a third time between 11 August and 20 August that year. We visited plots in the lower elevation zones earlier in each survey window than plots in the higher elevation zones to account for earlier bloom and bumble bee emergence cycles at lower elevations. This timing ensured that  $\geq 1$  visit would coincide with the expected period of peak colony size for each species.

When field visits revealed that survey plots overlapped roads or were situated on terrain that was too steep to survey or was inaccessible for other reasons, we adjusted the center point location by  $\leq 20$  m from the intended location. During each visit, we surveyed each plot for bumble bees over a 16-minute survey period, with 95% of surveys conducted between 0900 and 1600 hours. During that period a single observer would visually scan and walk throughout the plot. When the surveyor encountered a bumble bee within the 20-m-radius plot, they captured the bumble bee in a sweep net and suspended the survey until they transferred the bumble bee to a numbered vial, which they placed in a cooler to chill. The surveyor also recorded the plant species on which the bumble bee was caught (or noted if the bumble bee was caught in flight). The timed survey resumed after the surveyor processed the bumble bee. At the end of the 16-minute survey period (counting only active survey time), the survey was complete. The surveyor then removed the chilled bees from the cooler and photographed them from various angles using a digital camera (PowerShot ELPH135; Canon<sup>®</sup>, Tokyo, Japan). The surveyor also recorded the species of each bumble bee and the characteristics used to identify it to species (i.e., cheek length, face color, terga color, number of terga, corbicular presence) and caste (queen, worker, drone). When the bumble bee warmed up and became active again, the surveyor released it, generally after just a few minutes outside the cooler. In addition to our photo voucher system, we collected and pinned  $\leq 10$  individuals of each species, excluding queens. Voucher specimens are housed at the Bohart Museum of Entomology, University of California, Davis, Davis, California, USA. Our photo voucher system allowed us to limit the number of specimens collected relative to traditional entomological survey techniques, a substantial benefit given the documented declines in some bumble bee species. The photos also permitted subsequent review of species and caste determinations made by the field crew. Handling and collection of bumble bees was authorized under California Department of Fish and Wildlife Entity Permit SC-008645.

Within the 20-m-radius survey plot, we recorded ocular percent cover estimates to the closest 1% for overstory (by species), shrubs (by species), understory (by category: grasses, forbs, sedges or rushes, ferns), and abiotic ground cover components (standing water, flowing water, bare soil or rock, gravel bar, leaf litter). We also identified the 5 flowering plant species with the most solitary flowers or inflorescences blooming in the plot on the day of the survey. In 2 instances where apparent hybridization or plant similarity made identification to species difficult, we combined multiple species into species complexes for analysis. We combined varileaf phacelia (*Phacelia heterophylla*), silverleaf phacelia (*P. hastata*), and rock phacelia (*P. egeana*) and analyzed the group as a single phacelia complex, and combined velvety stickseed (*Hackelia velutina*) and Sierra stickseed (*H. nervosa*) as a single stickseed complex. Regardless of whether individual plots had been selected by the initial random sample or the subsequent augmentation to add additional riparian plots, we designated individual plots as riparian if the field visits revealed

they contained any standing or flowing water or if they had a  $\geq 10\%$  cover of riparian shrubs, trees, sedges, and rushes combined; we designated all other plots as upland.

### Statistical Analyses

**Bumble bee abundance.**—To assess bumble bee abundance, we modeled the average number of bumble bee captures/plot (grouping across species) as a Poisson-distributed variable ( $\lambda$ ) in a Bayesian framework. We included a normally distributed random effect (cluster) to account for the clustering of most plots into groups of 5. We modeled  $\lambda$  as log-linearly related to 6 fixed effects: whether a plot was upland (upland), whether the plot was in a cluster of mixed vegetation (i.e., containing  $\geq 1$  upland plots and  $\geq 1$  riparian plots) plots (mixed), an interaction between whether a plot was upland and whether it was in a mixed cluster, the ordinal day of the year (jday), a year effect (yr), and the plot elevation (elev), such that:

$$\begin{aligned} \log(\lambda_{jk}) = & \gamma_0 + \text{cluster}_j + \gamma_1 \text{upland}_j \\ & + \gamma_2 \text{mixed}_j + \gamma_3 \text{mixed}_j \text{upland}_j + \gamma_4 \text{jday}_{jk} \\ & + \gamma_5 \text{yr}_j + \gamma_6 \text{elev}_j \end{aligned}$$

for the  $k$ th visit to site  $j$ . We included the interaction term because *post hoc* data exploration indicated that bee abundance was lower in riparian plots within mixed clusters versus entirely riparian clusters. We hypothesize that this difference could be due to mixed clusters typically sampling smaller or less dense riparian patches than clusters where all the plots were riparian, although we acknowledge other causes may exist.

We fit the data to the model using JAGS (JAGS version 4.0.0, <http://mcmc-jags.sourceforge.net>, accessed 1 Jan 2016) within R (R version 3.2.1, [www.r-project.org](http://www.r-project.org), accessed 10 Dec 2015). We used vague priors (normal:  $\mu = 0$ ,  $\sigma = 100$ ) for all parameters. We ran 3 Markov chain Monte Carlo (MCMC) chains with a burn-in of 5,000, followed by a posterior draw of 15,000 thinned by 20, yielding a posterior sample of 2,250 draws across all chains. We assumed convergence when the Gelman–Rubin statistic of all monitored parameters calculated across both chains was  $< 1.1$  (Gelman et al. 2004). Inference from the fitted model was based on evaluation of 95% Bayesian credible intervals (BCI) of each coefficient  $\gamma_i$ . We considered significant any results where 95% credible intervals did not include zero.

**Bumble bee species richness patterns.**—When analyzing community patterns it is critical to account for potentially missed species (Gotelli and Colwell 2001). We capitalized on temporally replicated surveys for bumble bees at the same plots within each of the 2 field seasons to build a community occupancy model (Dorazio and Royle 2005, Dorazio et al. 2006, Iknayan et al. 2014) within a hierarchical Bayesian framework. Such models have previously demonstrated the robust capacity to estimate the effects of environmental variables (Ruiz-Gutiérrez et al. 2010), management treatments (Zipkin et al. 2010), and temporal turnover (Tingley and Beissinger 2013) on species assemblages while accounting for the biases of imperfect detection.

Community occupancy models have 2 major assumptions relevant to this study. First, to calculate the probability of detection for each species, the models assume that individual plots are closed to immigration or emigration of species across replicate surveys (MacKenzie et al. 2002). This assumption can be relaxed by interpreting models as predicting usage rather than occupancy (MacKenzie 2005), and closure violations can, in some instances, be subsumed into variance explained by temporally dynamic covariates of detection (Rota et al. 2009). In our study, although closure would be violated for individual bees, because occupancy focuses on the occurrence of species at sites, not individuals at sites, and because bumble bee colonies are active throughout a season (queens and then subsequent broods of workers forage from early spring through fall, and drones pursue mates) and fixed in space throughout a season (the location of the nest is static and defines maximum foraging distance), the closure assumption is likely valid for species within our plots. Second, community occupancy models are hierarchical in that they assume species-level parameters are drawn from hyper-distributions governed by community-level parameters. For this model assumption to be valid, species-level traits must be adequately approximated by a chosen probability distribution, typically the normal distribution. Although, the cases when such an assumption could be invalid are poorly explored in the ecological literature (but see Pacifici et al. 2014 for advice on choice of hierarchical groupings), given that all species in our system are congeneric, we think this hierarchical assumption is appropriate. Additionally we timed our 3-month survey season each year to overlap with expected peak colony size for bumble bee species present within our study area, which ranged from mid-June to early August (Koch et al. 2012, Williams et al. 2014).

We developed a Bayesian hierarchical model, where  $y_{i,j,k}$  is a Bernoulli random variable that indicates if species  $i$  was detected ( $y_{i,j,k} = 1$ ) or not detected ( $y_{i,j,k} = 0$ ) at sampling point  $j$  during survey visit  $k$ . We treated sampling points surveyed in separate years as independent, for 990 sampling points: 495 visited in each of 2015 and 2016. We used a mixture model specification to describe the data-generating process in terms of probability distributions, such that  $y_{i,j,k} \sim \text{Bernoulli}(p_{i,j,k} \cdot z_{i,j})$ , where  $z_{i,j}$  is a latent variable (i.e., imperfectly observed) used to indicate true occurrence of species  $i$  at point  $j$ , modeled as  $z_{i,j} \sim \text{Bernoulli}(\psi_{i,j})$ . The probability of detecting species  $i$  at point  $j$  during sampling visit  $k$  is defined as  $p_{i,j,k}$ . We assume that a detection ( $y_{i,j,k} = 1$ ) represents a true occurrence ( $z_{i,j} = 1$ ) but that a non-detection ( $y_{i,j,k} = 0$ ) could be the outcome of either a true absence ( $z_{i,j} = 0$  with probability  $1 - \psi_{i,j}$ ) or a true presence ( $z_{i,j} = 1$  with probability  $1 - p_{i,j,k}$ ).

We modeled detectability as a function of 3 covariates:

$$\text{logit}(p_{i,j,k}) = \alpha_0 + \alpha_1 \text{day}_{j,k} + \alpha_2 \text{time}_{j,k} + \alpha_3 \text{time}_{j,k}^2$$

where  $\text{day}_{j,k}$  is the day of the year, and  $\text{time}_{j,k}$  is the time of day at which the survey started. We included a quadratic effect on time of day because we conducted surveys

throughout daylight hours and we expected bees to be most active in the middle of the day (Peat and Goulson 2005, Hatfield and LeBuhn 2007).

We modeled the occurrence probability for each species at each plot,  $\psi_{i,j}$ , using the logit link function and *a priori* covariates such that:

$$\begin{aligned} \text{logit}(\psi_{i,j}) = & \beta_0 + \text{cluster}_{i,j} + \beta_1 \text{upland}_j + \beta_2 \text{elev}_j \\ & + \beta_3 \text{shrub}_j + \beta_4 \text{overstory}_j + \beta_5 \text{herb}_j \\ & + \beta_6 \text{whitethorn}_j + \beta_7 \text{bearclover}_j + \beta_8 \text{deerbrush}_j \\ & + \beta_9 \text{manzanita}_j + \beta_{10} \text{year}_j \end{aligned}$$

where  $\beta_0$  is a species-specific intercept,  $\text{cluster}_{i,j}$  is a random effect to account for spatial pseudoreplication of sampling points within clusters, and  $\beta_1 - \beta_{10}$  are the effects of environmental covariates on species  $i$ : whether the plot was upland (vs. riparian), the elevation, and the percent cover of shrubs (all species pooled), total overstory (% cover), all herbaceous plant categories pooled (herb; % cover), species-specific cover for mountain whitethorn, bearclover, deerbrush, and greenleaf manzanita, and the effect of survey year. We included percent cover of the 4 shrub species as distinct variables because they were the most abundant chaparral shrub species in our study area (and therefore most likely to be treated during future reforestation efforts), and anecdotal observations indicated potential disparity in the presence of foraging bumble bees on the 4 species. We standardized all continuous occupancy and detectability covariates to a mean of 0 and a standard deviation of 1.

We hypothesized that for individual species, covariate parameters would be drawn from community-level hyper-distributions, providing inference on covariate relationships common to the entire community of bumble bees. For the community-level hyper-distributions, we defined each species-level covariate parameter ( $\beta_0 - \beta_{10}$  and  $\alpha_0 - \alpha_3$ ) as being pulled from a normal distribution following the form:

$$\beta_i \sim \text{Normal}(\mu_\beta, \sigma_\beta)$$

where  $\mu_\beta$  and  $\sigma_\beta$  are hyper-parameters representing the community-level mean and standard deviation, respectively, for each of  $i$  species-level parameters for  $\beta_i$ . We gave hyper-parameters vague (i.e., locally flat) priors ( $\mu$ : normal priors with  $\mu = 0$  and  $\sigma = 100$ ;  $\tau$ : gamma priors with shape and rate parameters of 0.01).

We fit the model and assessed convergence as previously described. Because the species richness model was larger than the abundance model, we ran 3 MCMC chains composed of an adaptation period of 1,000 with a burn-in of 60,000, followed by a posterior draw of 15,000 thinned by 100, yielding a posterior sample of 450 draws across all chains. Inference from the fitted model was based on evaluation of 95% BCI of community hyper-parameters (e.g.,  $\mu_{\beta_0}$ ), species-specific parameters (e.g.,  $\beta_7$ ), and posterior estimates of true plot-specific species richness derived from the  $z_{i,j}$  matrix. We considered significant any results where 95% credible intervals did not include zero,

and weak any non-significant results where the posterior distribution was nevertheless strongly skewed positive or negative.

*Foraging use versus availability of blooming plant species.*— We evaluated bumble bee foraging use versus availability for each plant species (or complex of species) following the method of Neu et al. (1974). We chose this method because we did not track plant usage by individual bumble bees nor did we have exhaustive inventories of all plant species within each plot. The method described by Neu et al. (1974) relies on a chi-squared goodness-of-fit test of the distribution of available plant species versus used plant species, where available is a stand-in for expected frequency (i.e., the null hypothesis is that bees will forage on plants at rates proportional to their frequency on the landscape). Following a significant chi-squared test, a Bonferroni Z-statistic (Allredge and Ratti 1992) is used to test for specific plant species that are used significantly more or less frequently.

The definitions used for use and availability are key to interpreting such an analysis (Hall et al. 1997). We defined usage as the proportion of all bee captures that occurred on a given plant species (Allredge and Ratti 1992). We defined availability as the proportion of times that we identified each plant species as one of the 5 flowering plant species with the most solitary flowers or inflorescences across all plots and surveys. We limited our analysis to only those plant species that had  $\geq 1$  bee capture, thus differentiating between high use and low use within the community of plants that are actually foraged on by bees in our study area (Johnson 1980). Consequently, our analysis revealed plant species that were preferentially used by bumble bees, species that were avoided by bumble bees, and species that were used in proportion to their availability. For the 4 most frequently (and preferentially) used plant species, we plotted frequency of use against date and frequency of plant presence in the top 5 blooming species against date to examine changing patterns in availability to and use by bumble bees during the study period.

## RESULTS

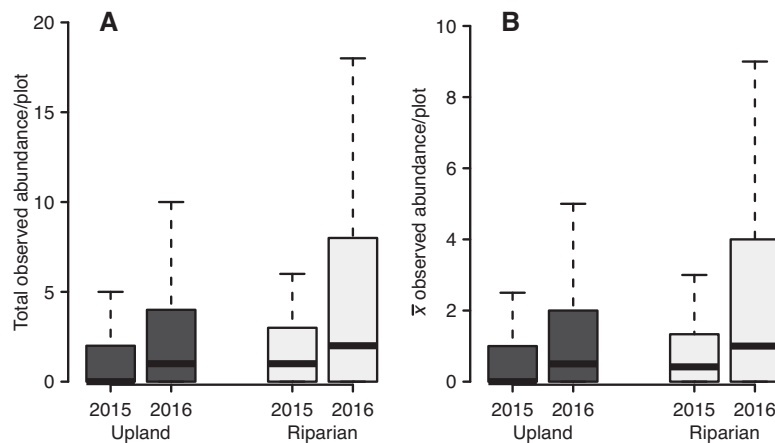
We captured and identified 676 bumble bees of 12 species during 965 surveys on 495 plots in 2015, and 1,818 bumble bees of 11 species during 987 surveys on 495 plots in 2016 (413 upland plots and 82 riparian plots; Table 1). The Vosnesensky bumble bee (*Bombus vosnesenskii*; 1,733 captures, 69% of all bees captured), van Dyke bumble bee (*B. vandykei*; 299 captures, 12% of all bees captured), and black tail bumble bee (*B. melanopygus*; 236 captures, 10% of all bees captured) were the most frequently encountered species. The remaining species encountered, in decreasing order of captures were the fuzzy-horned bumble bee (*B. mixtus*), California bumble bee (*B. californicus*), yellow head bumble bee (*B. flavifrons*), indiscriminate cuckoo bumble bee (*B. insularis*), two form bumble bee (*B. bifarius*), Fernald cuckoo bumble bee (*B. fernaldae*), red-belted bumble bee (*B. rufocinctus*), white-shouldered bumble bee (*B. appositus*), and forest bumble bee (*B. sylvicola*; Table 1).

Vegetation structure varied greatly across plots, with average values of  $17 \pm 22.4\%$  (SD) overstory cover from trees,  $41 \pm 31.3\%$  shrub cover, and  $43\% \pm 35.5\%$  herbaceous cover. Of 135 clusters of plots, 97 (72%) consisted of plots ( $n = 332$  plots) entirely of a single plot type (i.e., all upland or all riparian). The remaining 38 clusters (28%;  $n = 163$  plots) comprised a mixture of riparian and upland plots. Counts of raw bumble bee abundance within plots indicated moderate differences in the number of bumble bees in upland versus riparian plots, although riparian plots had substantially higher variance (Fig. 2). Our Poisson regression model of plot abundance revealed higher capture rates of bumble bees in riparian plots than upland plots ( $\gamma_1, -0.814 \pm 0.311$ , 95% BCI =  $-1.399$  to  $-0.198$ ). Mixed plot-type clusters had lower abundance than clusters comprised of entirely riparian or entirely upland plots (95% BCI on  $\gamma_2 = -1.884$  to  $-0.526$ ), and within these mixed clusters, riparian plots had lower bee abundance than upland plots (95% BCI on  $\gamma_3 = 0.410$ – $1.671$ ). Elevation had no effect on abundance (95% BCI on  $\gamma_6 = -0.207$ – $0.190$ ) but strong positive effects of survey year (95% BCI on  $\gamma_5 = 0.901$ – $1.076$ ) and day of

**Table 1.** The number of individual bumble bees per year of each species and caste detected, and the number and percent of riparian and upland plots with detections in the central Sierra Nevada, California, USA.

Species	No. individuals detected						No. and % plots with detections							
	Workers		Drones		Queens		Riparian			Upland				
	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016	2015	2016		
Black tail bumble bee	1	109	9	113	1	3	3	4%	21	17%	7	3%	75	18%
California bumble bee	7	12	4	10	5	11	5	7%	6	5%	9	4%	20	5%
Fernald cuckoo bumble bee <sup>a</sup>	NA	NA	3	6	0	0	2	3%	1	1%	1	0%	4	1%
Forest bumble bee	2	0	0	0	0	0	1	1%	0	0%	0	0%	0	0%
Fuzzy-horned bumble bee	17	56	1	1	1	2	3	4%	10	8%	6	3%	23	6%
Indiscriminate cuckoo bumble bee <sup>a</sup>	NA	NA	15	13	1	0	9	12%	4	3%	5	2%	7	2%
Red-belted bumble bee	1	1	2	0	1	0	0	0%	0	0%	3	1%	1	0%
Two form bumble bee	1	6	0	2	0	0	0	0%	4	3%	1	0%	1	0%
Van Dyke bumble bee	60	135	39	37	10	18	12	16%	18	14%	15	20%	64	16%
Vosnesensky bumble bee	315	924	159	297	5	33	31	41%	52	41%	143	63%	200	49%
White-shouldered bumble bee	1	0	0	0	1	0	2	3%	0	0%	0	0%	0	0%
Yellow head bumble bee	7	5	5	23	2	1	7	9%	10	8%	6	3%	12	3%

<sup>a</sup> Cuckoo species have only drones and queens; therefore, workers column is not applicable (NA).



**Figure 2.** Total observed abundance (A) and mean observed abundance per survey (B) of bumble bees per plot over 2–3 surveys per year in the central Sierra Nevada, California, USA, 2015–2016. Abundances are separated by upland versus riparian and survey year. Boxplots show mean value (horizontal line), central 50% quantile (box), and range (whiskers).

year (95% BCI on  $\gamma_4 = 0.090$ – $0.160$ ) were evident. For unmixed clusters, the modeled mean rate of bumble bee capture was  $1.10 \pm 0.31$  bees/survey on riparian plots and  $0.47 \pm 0.07$  bees/survey on upland plots in 2015, and  $2.96 \pm 0.83$  bees/survey on riparian plots and  $1.27 \pm 0.18$  bees/survey on upland plots in 2016. For plots in mixed clusters, the 2015 estimated capture rate for upland plots was nearly the same as in purely upland clusters, at  $0.41 \pm 0.08$  bees/survey ( $1.10 \pm 0.22$  in 2016) but was much lower for riparian areas, at  $0.32 \pm 0.07$  bees/survey ( $0.86 \pm 0.17$  in 2016).

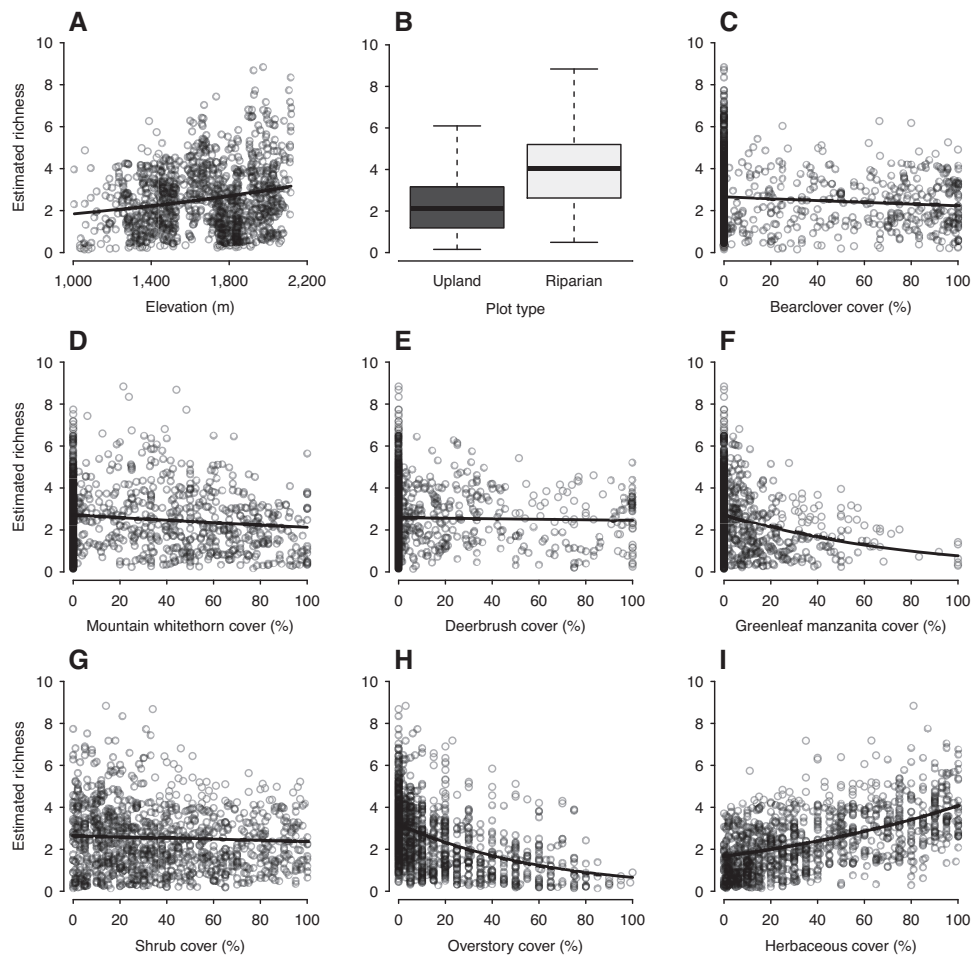
We detected 11 bumble bee species on riparian plots and 10 species on upland plots but only 9 species on both plot types; the white-shouldered bumble bee and forest bumble bee were unique to riparian plots (both found in 2015 only) and the red-belted bumble bee was unique to upland plots. However only a small number of individuals of these 3 species were captured, precluding determination that they were strictly associated with riparian or upland plant communities. Pooling captures across all species and years, 67% ( $n = 1,660$ ) of the captured bees were workers, 30% ( $n = 739$ ) were drones, and 4% ( $n = 95$ ) were queens (Table 1). We recorded members of all castes (queens, workers, drones) for 8 of the 12 species, indicating that the sampling period captured much of the colony activity for most species (Table 1). The 4 species for which 1 or more castes were not represented all had sample sizes  $< 10$  individuals, generally with captures recorded well inside our sampling period (with the exception of the forest bumble bee, which was represented only by 2 individuals during the last week of survey in 2015), so we do not believe we missed the appropriate activity window but rather that these species were simply uncommon within our study area.

### Bumble Bee Species Richness Patterns

Our hierarchical community model of bumble bee species richness identified multiple important covariates of occupancy across the entire bumble bee community. Herbaceous cover had a strongly positive (95% BCI =  $0.41$ – $1.48$ )

community-wide effect, and total overstory had a weakly negative effect (95% BCI =  $-1.21$  to  $0.002$ ), whereas total shrub cover (95% BCI =  $-0.53$  to  $0.36$ ) had no community-wide effect. These community-wide relationships were evident in model-estimated richness patterns for surveyed plots (Fig. 3). Of the 4 *a priori* selected chaparral shrub species, only greenleaf manzanita had a strong community-wide effect of reducing bumble bee species occurrence (95% BCI =  $-1.19$  to  $-0.22$ ), although mountain whitethorn also had a weak negative effect on bee species occurrence (95% BCI =  $-0.93$  to  $0.03$ ). Deerbrush and bearclover had highly uncertain effects (95% BCI on deerbrush =  $-0.46$  to  $0.44$ ; bearclover =  $-0.57$  to  $0.62$ ). Upland plots had strongly negative community-wide effects on species occurrence (95% BCI =  $-1.92$  to  $-0.34$ ), as did low elevation plots (95% BCI =  $0.25$ – $1.80$ ). We estimated an average mean richness of  $2.3 \pm 1.3$  bumble bee species in upland plots and  $4.1 \pm 1.8$  species in riparian plots (Fig. 3). Unlike our abundance results, there was only a weak community-wide effect of survey year (95% BCI =  $-0.11$  to  $2.71$ ). Detectability of bumble bees was unaffected by time of day (95% BCI on  $\mu_{a2} = -0.19$  to  $0.22$ ,  $\mu_{a3} = -0.17$  to  $0.12$ ) and day of year (95% BCI on  $\mu_{a1} = -0.19$  to  $0.34$ ).

In addition to community-level inference, we found that several environmental covariates significantly affected probability of occurrence for particular bumble bee species (Table 2). Probability of occurrence increased significantly with elevation for 6 species (Fig. 4A). Although no bumble bee species had a significant relationship to total shrub cover (Fig. 4G), 7 species had a significant positive relationship to herbaceous cover (Fig. 4I). Three species significantly declined with overstory cover (California bumble bee, van Dyke bumble bee, Vosnesensky bumble bee; Fig. 4H). No species showed strong independent relationships to deerbrush (Fig. 4E) or mountain whitethorn (Fig. 4D), but Vosnesensky bumble bee, the most abundant species on our plots, increased significantly with increasing bearclover cover (Fig. 4C). Four species showed strong negative relationships to greenleaf manzanita (van Dyke bumble bee, California



**Figure 3.** Mean estimated bumble bee species richness per plot in the central Sierra Nevada, California, USA, 2015–2016, in relationship to elevation (A), plot type (B), bearclover cover (C), mountain whitethorn cover (D), deerbrush cover (E), greenleaf manzanita cover (F), shrub cover (G), overstory cover (H), and herbaceous cover (I). Cover estimates exceeded 100% when multiple species of a vegetation class were overlapping in a plot, although plot axes are cropped at 100% for consistency. Solid lines illustrate mean log-linear trend lines for ease of interpretation.

bumble bee, yellow head bumble bee, black tail bumble bee; Fig. 4F). Five species (two form bumble bee, yellow head bumble bee, indiscriminate cuckoo bumble bee, black tail bumble bee, fuzzy-horned bumble bee) had higher occupancy in riparian plots than upland plots (Fig. 4B).

### Foraging Use versus Availability of Blooming Plant Taxa

Pooling observations across all bumble bee species and castes, we observed bumble bees foraging on 106 plant species and 2 species complexes, each of which was identified as one of the 5 flowering plant species with the most solitary flowers or inflorescences blooming during at least 1 plot survey. Although we recorded only the top 5 flowering plant species during each visit, there were <5 species blooming at 57% of plot visits, indicating that our methods described the majority of plants available to foraging bees. Bumble bees foraged on 11 plant taxa significantly more than expected based on their availability across plots and years, and foraged on 36 plant taxa significantly less than expected (Table 3). Bearclover was the most frequently used shrub species (and the second most frequently used plant species overall), accounting for 17% ( $n = 390$ ) of all bumble bee captures,

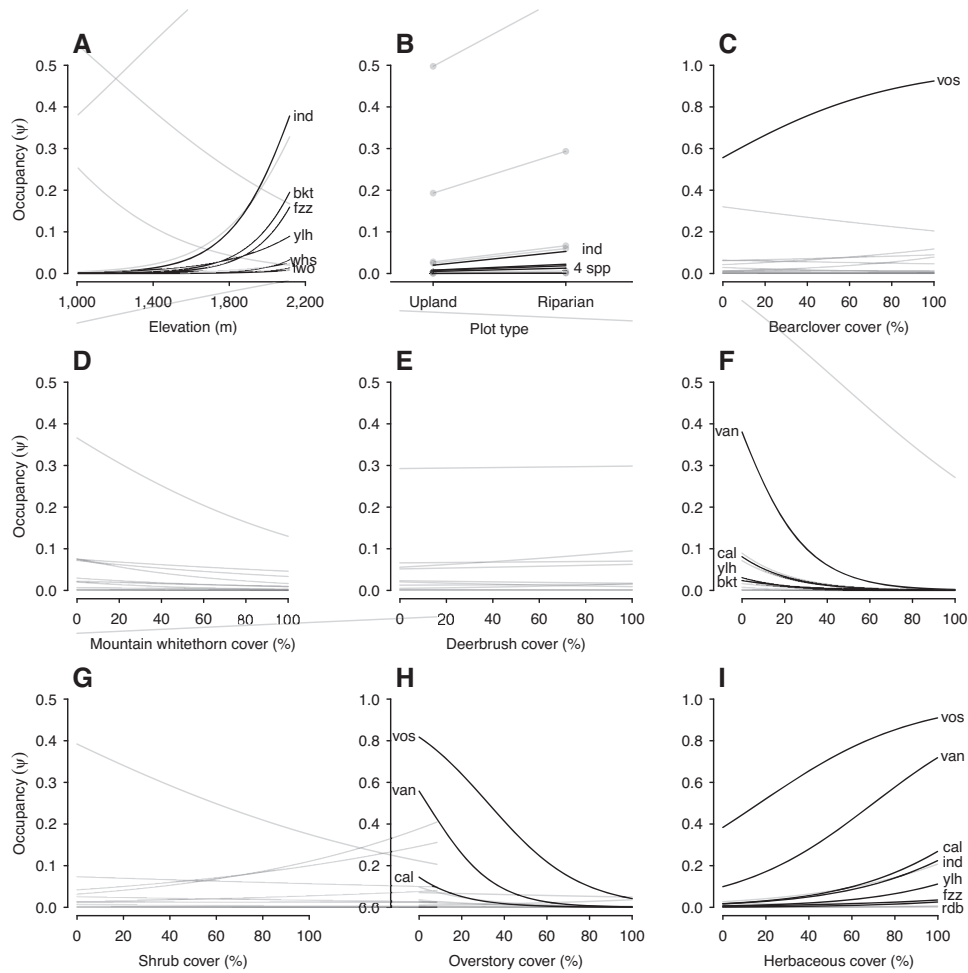
with 6 species represented; despite being the most available blooming plant, bearclover was used significantly more than would be expected based on its availability (Fig. 5). Mountain whitethorn was the third most available plant species but was rarely used by bumble bees, accounting for only 0.8% ( $n = 17$ ) of all bumble bee captures, with 4 species represented. Deerbrush was another abundant shrub that was rarely used by bumble bees, accounting for only 0.3% ( $n = 7$ ) of all bumble bee captures, with just 2 species represented. We never caught bees foraging on greenleaf manzanita flowers, a common shrub species on our plots that largely bloomed prior to our survey period.

Among herbaceous species, the phacelia complex was very highly preferred by bumble bees for foraging relative to its availability and accounted for 20% ( $n = 455$ ) of all bumble bee captures, with 6 species represented (Fig. 5). A non-native plant species, bull thistle, was the third most frequently used plant species, and was used more than expected based on its availability, accounting for 8% ( $n = 182$ ) of all bumble bee captures, with 6 species represented. The stickseed complex was also preferred and made up 7% ( $n = 151$ ) of all bumble bee captures, with 6



**Table 2.** Posterior mean parameter values for each fixed-effect covariate by bumble bee species in the central Sierra Nevada, California, USA, 2015–2016. We assumed parameters for each species came from a normal distribution with common mean and variance for each covariate. The sign of the estimate indicates whether the relationship with the covariate was positive or negative. The covariates are upland plot type (upland), elevation (elev), herbaceous cover (herb), overstory cover (over), shrub cover (shrub), mountain whitethorn cover (wthrn), bearlover cover (bclov), deerbrush cover (drbsh), greenleaf manzanita cover (glman), and year (yr). Asterisks represent 95% Bayesian credible intervals that did not cross zero.

Species	Upland	Elev	Herb	Over	Shrub	Wthrn	Bclov	Drbsh	Glman	Yr
Black tail bumble bee	-0.93*	1.49*	0.14	-0.36	0.22	-0.25	0.65	-0.23	-0.57*	4.38*
California bumble bee	-0.92	-0.66	1.08*	-1.26*	0.29	-0.25	-0.12	0.16	-0.72*	1.64*
Fernald cuckoo bumble bee	-0.91	1.12	0.8	-0.09	-0.09	-0.16	0.14	0.02	-0.71	1.2
Forest bumble bee	-1.09	1.21	0.82	-0.67	-0.06	-0.25	0.09	-0.01	-0.58	0.3
Fuzzy-horned bumble bee	-0.96*	1.56*	0.63*	0.29	-0.01	-0.59	0.04	0.04	-0.56	2.31*
Indiscriminate cuckoo bumble bee	-1.01*	1.39*	1.01*	-0.85	0.42	-0.49	0.37	0.06	-0.72	-0.15
Red-belted bumble bee	-0.55	0.85	0.94*	-0.13	-0.16	-0.32	-0.18	0.34	-0.78	0.09
Two form bumble bee	-1.16*	1.81*	0.67	-0.16	-0.42	-0.72	-0.14	-0.12	-0.75	1.78
Van Dyke bumble bee	-0.55	-0.42	1.12*	-1.43*	-0.35	-0.42	-0.21	0.01	-0.87*	1.29*
Vosnesensky bumble bee	-0.71	0.47	0.99*	-1.03*	0.04	0.15	0.78*	-0.03	-0.28	1.56*
White-shouldered bumble bee	-1.17	1.76*	0.83	-0.44	0.05	-0.5	0.04	-0.03	-0.68	-0.51
Yellow head bumble bee	-1.04*	0.86*	1.05*	-0.62	-0.12	-0.38	-0.45	-0.09	-0.75*	1.74*



**Figure 4.** Modeled occupancy for each of the 12 bumble bee species detected in the central Sierra Nevada, California, USA, 2015–2016, in relationship to elevation (A), plot type (B), bearlover cover (C), mountain whitethorn cover (D), deerbrush cover (E), greenleaf manzanita cover (F), shrub cover (G), overstory cover (H), and herbaceous cover (I). Lines represent the relationship for each bumble bee species and are black and labeled for significant relationships: white-shouldered bumble bee (wsh), California bumble bee (cal), yellow head bumble bee (ylh), indiscriminate cuckoo bumble bee (ind), fuzzy-horned bumble bee (fzz), red-belted bumble bee (rdb), two form bumble bee (two), van Dyke bumble bee (van), and Vosnesensky bumble bee (vos); lines in gray represent non-significant relationships. The 4 unnamed species in panel B are two form bumble bee (two), yellow head bumble bee (ylh), black tail bumble bee (bkt), and fuzzy-horned bumble bee (fzz).

**Table 3.** Floral species usage and availability for plant species that were used by bumble bees significantly less or significantly more for foraging than expected based on their availability in the central Sierra Nevada, California, USA, 2015–2016. Usage is defined as the proportion of all bumble bee captures on a given plant species. Availability is defined as the proportion of times that each plant species was identified as one of the 5 flowering plant species with the most solitary flowers or inflorescences blooming in a plot on the day of a survey. Class indicates whether a species was used more than expected (1) or less than expected (–1) based on availability. Plants are organized from highest to lowest usage by bumble bees.

Common name	Scientific name	Usage	Availability	Class
Phacelia complex	<i>Phacelia hastata</i> , <i>P. heterophylla</i> , <i>P. egena</i>	0.203	0.062	1
Bearclover	<i>Chamaebatia foliolosa</i> <sup>b</sup>	0.174	0.097	1
Bull thistle	<i>Cirsium vulgare</i> <sup>a</sup>	0.081	0.026	1
Stickseed complex	<i>Hackelia nervosa</i> , <i>H. velutina</i>	0.067	0.029	1
Sneezeweed	<i>Helenium bigelovii</i>	0.044	0.007	1
Parish's yampah	<i>Perideridia parishii</i>	0.038	0.012	1
Brewer's monardella	<i>Monardella breweri</i>	0.033	0.008	1
Swamp onion	<i>Allium validum</i>	0.029	0.002	1
Canada goldenrod	<i>Solidago canadensis</i>	0.026	0.008	1
Pennyroyal	<i>Monardella odoratissima</i>	0.023	0.007	1
Diamond clarkia	<i>Clarkia rhomboidea</i>	0.014	0.042	–1
Hedge nettle	<i>Stachys ajugoides</i>	0.011	0.003	1
Nude buckwheat	<i>Eriogonum nudum</i>	0.011	0.043	–1
Sierra Nevada pea	<i>Lathyrus nevadensis</i>	0.010	0.019	–1
Blue gilia	<i>Gilia capitata</i>	0.009	0.045	–1
Mountain whitethorn	<i>Ceanothus cordulatus</i> <sup>b</sup>	0.008	0.061	–1
Meadow lotus	<i>Hosackia oblongifolia</i>	0.007	0.025	–1
Deerbrush	<i>Ceanothus integerrimus</i> <sup>b</sup>	0.003	0.032	–1
Elegant clarkia	<i>Clarkia unguiculata</i>	0.003	0.008	–1
Purple nightshade	<i>Solanum xanti</i>	0.002	0.015	–1
Silverleaf lupine	<i>Lupinus obtusilobus</i>	0.002	0.005	–1
Woolly sunflower	<i>Eriophyllum lanatum</i>	0.001	0.051	–1
Woolly mullein	<i>Verbascum thapsus</i> <sup>a</sup>	0.001	0.029	–1
Lemon scented tarweed	<i>Madia citriodora</i>	0.001	0.023	–1
Seep-spring monkeyflower	<i>Mimulus guttatus</i>	0.001	0.021	–1
Western buttercup	<i>Ranunculus occidentalis</i>	0.001	0.018	–1
Hartweg's iris	<i>Iris hartwegii</i>	0.001	0.012	–1
Western morning-glory	<i>Calystegia occidentalis</i>	0.001	0.011	–1
Gay penstemon	<i>Penstemon laetus</i>	0.001	0.010	–1
Sticky cinquefoil	<i>Potentilla glandulosa</i>	0.001	0.010	–1
Thimbleberry	<i>Rubus parviflorus</i> <sup>b</sup>	0.001	0.006	–1
Unidentified lupine	<i>Lupinus spp.</i>	0.001	0.004	–1
Torrey's monkeyflower	<i>Mimulus torreyi</i>	0.000	0.031	–1
Fivespot	<i>Nemophila maculata</i>	0.000	0.007	–1
Western wallflower	<i>Erysium capitatum</i>	0.000	0.007	–1
Crimson columbine	<i>Aquilegia formosa</i>	0.000	0.007	–1
Scarlet monkeyflower	<i>Mimulus cardinalis</i>	0.000	0.006	–1
Cudweed	<i>Pseudognaphalium beneolens</i>	0.000	0.006	–1
Sierra lessingia	<i>Lessingia leptoclada</i>	0.000	0.003	–1
Wandering daisy	<i>Erigeron glacialis</i>	0.000	0.003	–1
Anderson's thistle	<i>Cirsium andersonii</i>	0.000	0.003	–1
Harvest brodiaea	<i>Brodiaea elegans</i>	0.000	0.003	–1
Corn lily	<i>Veratrum californicum</i>	0.000	0.003	–1
Slender cinquefoil	<i>Potentilla gracilis</i>	0.000	0.003	–1
Arrowleaf groundsel	<i>Senecio triangularis</i>	0.000	0.002	–1
Single-stemmed groundsel	<i>Senecio integerrimus</i>	0.000	0.002	–1
Pacific bleeding heart	<i>Dicentra formosa</i>	0.000	0.002	–1

<sup>a</sup> Non-native plant species for California.

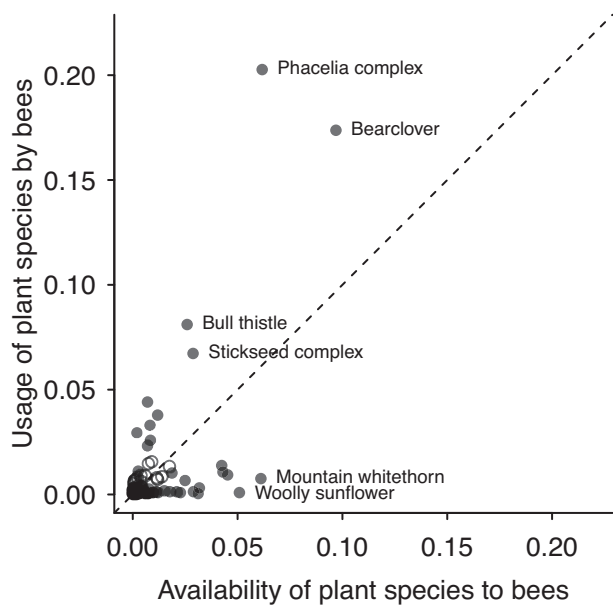
<sup>b</sup> Woody plant species.

species represented. The phacelia and stickseed complexes and bull thistle, although sometimes found in riparian zones, occur broadly across drier upland communities within our study area, as do 2 of the remaining preferred plant species: Brewer's monardella (*Monardella breweri*), and pennyroyal (*Monardella odoratissima*). The 5 remaining plant species that were significantly preferred occur primarily in riparian settings: sneezeweed (*Helenium bigelovii*), Parish's yampah (*Perideridia parishii*), swamp onion (*Allium validum*), Canada goldenrod (*Solidago canadensis*), and hedge nettle (*Stachys albens*). Of the herbaceous plants that were used significantly

less than expected based on their availability, the 4 most abundant were woolly sunflower (*Eriophyllum lanatum*), blue gilia (*Gilia capitata*), nude buckwheat (*Eriogonum nudum*), and diamond clarkia (*Clarkia rhomboidea*).

## DISCUSSION

Previous research has demonstrated the importance of meadows and other riparian habitats to bumble bees in montane ecosystems (Hatfield and LeBuhn 2007), but our findings indicate that upland communities, particularly where dominated by herbaceous vegetation that includes



**Figure 5.** Usage versus availability of 70 plant species or species complexes in the central Sierra Nevada, California, USA, 2015–2016, on which bumble bees were observed foraging. The dashed line represents a 1:1 line separating species that were preferentially used by bumble bees (above the line) from those that were used less than expected based on availability (below the line). Filled dots represent plant species that were used significantly more or less than expected based on Bonferonni-corrected tests (Neu et al. 1974, Alldredge and Ratti 1992).

favored forbs such as the phacelia complex and shrubs such as bearclover, may also be beneficial to some bumble bee species. Additionally, our finding that riparian plots in mixed clusters had relatively few bees indicates that small, isolated patches of riparian vegetation may be less intensively used by bumble bees than larger, continuous areas of either riparian vegetation or chaparral. At the landscape level, chaparral and associated herbaceous vegetation in upland areas may even provide north-south connectivity for bumble bees between major riparian systems that tend to cluster along east-west river corridors in the region (Lozier et al. 2013).

We found 12 bumble bee species across all surveys in our relatively restricted study areas, accounting for 46% of the estimated 26 bumble bee species in California and 60% of the estimated 20 bumble bee species in the Sierra Nevada (Thorp et al. 1983). The majority of the individual bumble bees we captured were of 3 species: Vosnesenky bumble bee and black tail bumble bee, both considered common species in the west by Koch et al. (2012), and van Dyke bumble bee, categorized as uncommon by Koch et al. (2012). Four additional species were represented with between 29 and 78 captures, and the remaining 5 species were represented by fewer than 10 captures each. Of these 9 less frequently captured species, 3 have a status of uncommon in the west (California bumble bee, Fernald cuckoo bumble bee, and forest bumble bee), and the rest are considered common or very common (Koch et al. 2012).

Some of the coarse-scale habitat characteristics that we found to be associated with bumble bee abundance and diversity on our plots are consistent with previous research in other post-fire ecosystems, which also reported negative

relationships with post-fire overstory tree cover (Winfree et al. 2007, Grundel et al. 2010). Our related finding of a positive association between herbaceous cover after fire and bumble bee species richness is consistent with other findings on bees (Moretti et al. 2009), insects in general, and the floral resources on which they rely (Ne’eman and Dafni 1999, Ne’eman et al. 2000, Campbell et al. 2007). Taken together, these broad-scale findings support retention of forest openings dominated by herbaceous vegetation and chaparral as bumble bee habitat, even in areas where the primary management goal may be forest regeneration. Indeed, in our study areas, estimated pre-European fire return intervals (<https://www.fs.fed.us/r5/rsl/clearinghouse/r5gis/frid/>, accessed 06 Mar 2017) average just 16 years, suggesting that prior to the fire suppression era, frequent fires maintained a dynamic matrix of forest and open areas by intermittently removing overstory trees and chaparral shrubs from portions of the landscape (Van de Water and Safford 2011). Mimicking the landscape-level effects of the past fire regime through thoughtful retention of patches of herbaceous vegetation and chaparral would likely benefit bumble bees (Nyoka 2010, Strahan et al. 2015, Hanula et al. 2016).

Understanding fine-scale relationships that allow some plants to be used by bumble bees more than others can help guide more nuanced land management decisions that can support bumble bee conservation. Particularly useful for developing bumble bee-friendly reforestation practices was our finding that one chaparral shrub species, bearclover, was much more heavily used by bumble bees than others. Bearclover was used as a foraging resource by 6 bumble bee species in our study, was positively associated with bumble bee species richness, and for Vosnesenky bumble bee (the most common bumble bee species in our study area) was a better predictor of occupancy than was herbaceous cover. Our findings suggest that within montane chaparral, bearclover is a primary floral resource whose presence may largely support foraging bumble bees in the early summer.

Four bumble bee species declined significantly as greenleaf manzanita increased, despite the fact that overall shrub cover did not drive species richness or abundance. We suspect that greenleaf manzanita may have a negative influence on occupancy for 3 reasons: the bloom period for this species is generally restricted to the early spring, prior to our sampling; greenleaf manzanita tends to occur on relatively exposed ridgetop settings, which may be inherently less inviting to bumble bees; and unlike mountain whitethorn, deerbrush, and bearclover, manzanita does not fix nitrogen in the surrounding soil. It is possible that this latter factor results in less lush and diverse herbaceous communities (and therefore nectar and pollen resources) in comparison to areas with nitrogen fixing shrubs (Delwiche et al. 1965, Heisey et al. 1980).

Among herbaceous plants, we observed a complex of 3 closely related perennial forbs, silverleaf phacelia, rock phacelia, and varileaf phacelia to be highly preferred by bumble bees (more so than any other species or species complex in our study) and used significantly more often than would be expected based on relative availability. These and other species in the *Phacelia* genus, are frequent upland

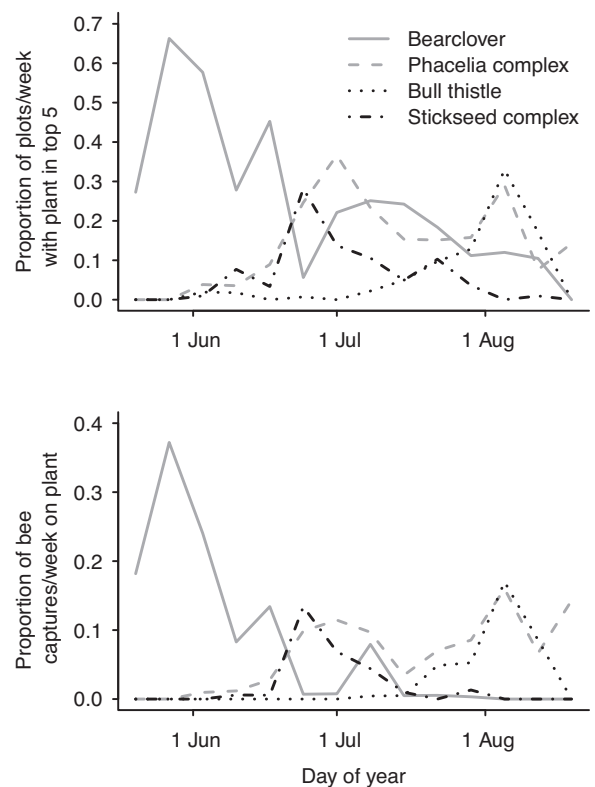
associates after forest fire (Quinn and Keeley 2006). Our finding that bumble bees foraged preferentially on the phacelia complex is consistent with other research that has shown a strong affinity of bumble bees for plants in the *Phacelia* genus (Thorp et al. 1983).

The third most frequently used plant species in our study was the non-native bull thistle, which we observed to be used by 6 bumble bee species. Both native and non-native thistles are well documented as forage species for bumble bees (Thorp et al. 1983, Williams et al. 2014). Non-native plants have previously been reported to support bee communities across multiple bee genera (Tepedino et al. 2008), and could potentially play a role in bumble bee conservation efforts but only under careful consideration for possible deleterious consequences on other ecosystem components or processes (Schlaepfer et al. 2011).

In our study, bearclover and the phacelia complex together accounted for 38% of all bumble bee foraging captures. Adding in the next 2 most frequently used taxa (stickseed complex, and bull thistle) accounted for 52% of all foraging captures we recorded. The timing of bloom period and bumble bee use for these 4 primary forage plants varied substantially. Bearclover bloomed heavily during April through early June in our study area, with limited re-bloom later in the summer. Stickseed complex peaked in late June and phacelia complex bloomed through June and July, as bearclover flowers became more scarce (Fig. 6A). As the stickseed complex and bearclover bloom period waned in July, bull thistle increased and then peaked in August. As this shift in flower availability occurred, we stopped detecting bees foraging on bearclover and increasingly detected them on the phacelia and stickseed complexes, and then later on bull thistle (Fig. 6B). The temporal stratification in blooming by these 4 species highlights the value of heterogeneous upland habitat at a spatial scale that ensures a variety of forage species within average foraging distances for bumble bees (usually 100–1,000 m; Elliot 2009).

Bumble bees are unable to move their colonies within a season, so the availability of pollen and nectar within the foraging radius of individual nests directly affects the size and success of bumble bee colonies and populations (Elliot 2009, Roulston and Goodell 2011). For an area to sustain multiple broods per year within a bumble bee colony, it must be rich in pollen and nectar from early spring when foundress queens prepare their nest stores, to midsummer when workers emerge to forage for subsequent broods, and finally into late summer and fall, when new queens emerge and increase their caloric intake to prepare for overwintering (Williams et al. 2014). Even in an otherwise forested areas, bumble bees may thrive if those areas also include a mosaic of open areas where preferred herbaceous plants and shrubs provide needed floral resources throughout the life-cycle of a colony.

Our findings provide land managers interested in bumble bee conservation with a rationale for retaining forest openings when reforesting burned areas, and also for prioritizing chaparral stands dominated by bearclover over stands dominated by whitethorn, deerbrush, or greenleaf manzanita when selecting chaparral for retention within the central Sierra



**Figure 6.** (A) The weekly proportion of plots in the central Sierra Nevada, California, USA, with bearclover, members of the phacelia complex, bull thistle, or members of the stickseed complex among the top 5 blooming plant species (A), and the weekly proportion of bumble bee captures on those same plant taxa (B), throughout the 2015 and 2016 field seasons.

Nevada. Moreover, among bearclover-dominated stands, managers should emphasize retention of stands intermixed with abundant herbaceous vegetation, especially when proximal to riparian areas, where floral resources (and bumble bee communities) are likely to be more diverse and persist throughout a longer total blooming season. Suppression or removal of chaparral shrub species other than bearclover in our study area is unlikely to reduce foraging resources for bumble bees, at least in the short-term before conifer forest is reestablished and may suppress herbaceous growth. Indeed, treatment of chaparral through chemical or mechanical means may result in greater herbaceous species cover and richness within the treated landscape relative to untreated areas (McDonald and Everest 1996, McGinnis et al. 2010, Bohlman et al. 2016), potentially yielding longer overall blooming phenology across the entire spring and summer when compared to mature monotypic stands of chaparral shrubs. Yet chaparral shrub species in upland areas may provide other benefits to bumble bees regardless of whether bees forage on them, as well-distributed shrubs of all species may provide valuable shade for bumble bee thermoregulatory needs during the hottest months (Heinrich 2004), especially when conifer seedlings are still small and cast little shade.

In addition, we recorded anecdotal observations of other insect pollinators foraging on mountain whitethorn and deerbrush in abundance, and previous research in California has shown the importance of ceanothus and manzanita for

multiple genera of bees (Thorp et al. 1983, Potts et al. 2003), suggesting that land managers interested in meeting the needs of all native pollinators should not discount the possible importance of these shrub species.

In our study the phacelia complex, bearclover, stickseed complex, and bull thistle were most heavily used by bumble bees, but we did not assess plant species usage prior to or after our late May–mid–August field season, when early-blooming (e.g., manzanita) or late-blooming plant species (e.g., California fuchsia [*Epilobium canum*]) may have played a greater role. Plant species preferred by bumble bees may vary considerably within and between species and across the Sierra Nevada according to elevation, latitude, and perhaps other factors. Although our findings provide a preliminary rationale for management decisions in the central Sierra Nevada, multi-year research across a broader variety of vegetation communities throughout the larger Sierra Nevada region is needed to more fully understand bumble bee habitat needs.

## MANAGEMENT IMPLICATIONS

Post-fire chaparral communities within the Sierra Nevada are often suppressed or removed to facilitate reforestation efforts. Where post-fire forest reforestation is pursued, forest managers should strive to maintain or include forest canopy gaps where preferred herbaceous plants and chaparral shrubs with diverse blooming phenology may thrive and provide floral resources for bumble bees and other pollinators. When vegetation control or removal does occur, in our study area, bumble bees will benefit the most if herbaceous patches of vegetation are retained (especially species preferentially used by bumble bees, such as the phacelia and stickseed complexes), along with chaparral stands dominated by bearclover. Because habitat characteristics affect the occupancy of individual bumble bee species differently, managers should consider foraging preferences of target bumble bee species when making land management decisions if such information is available, but retaining mosaics of herbaceous vegetation and chaparral shrubs will likely maximize post-fire bumble bee foraging resources across time and space. Any chemical or hand treatments in post-fire tree plantations should be applied narrowly to unwanted shrub species only, such that the disturbance to non-target vegetation is minimized. Furthermore, managers should consider planting or seeding such areas with forb species that are used frequently by bumble bees. Where mechanical or chemical treatment of herbaceous or chaparral plant species used by bumble bees does occur, bumble bees would likely benefit if it is delayed until autumn, or at least after the local peak bloom period. For noxious weed abatement (especially noxious forbs known to provide bumble bee forage) that may require herbicide treatment early in the season, we recommend replanting or seeding with native plants with similar bloom phenology to replace foraging resources that are lost.

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## LITERATURE CITED

- Allredge, J. R., and J. T. Ratti. 1992. Further comparison of some statistical techniques for analysis of resource selection. *Journal of Wildlife Management* 56:1–9.
- Bogusch, P., L. Blažej, M. Trýzna, and P. Heneberg. 2014. Forgotten role of fires in Central European forests: critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). *European Journal of Forest Research* 134:1–14.
- Bohman, G. N., M. North, and H. D. Safford. 2016. Shrub removal in reforested post-fire areas increases native plant species richness. *Forest Ecology and Management* 374:195–210.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences* 108:662–667.
- Campbell, J. W., J. L. Hanula, and T. A. Waldrop. 2007. Effects of prescribed fire and fire surrogates on floral visiting insects of the Blue Ridge province in North Carolina. *Biological Conservation* 134:393–404.
- Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* 103:33–49.
- Delwiche, C. C., P. J. Zinke, and C. M. Johnson. 1965. Nitrogen fixation by *Ceanothus*. *Plant Physiology* 40:1045–1047.
- Dennison, P. E., S. C. Brewer, J. D. Arnold, and M. A. Moritz. 2014. Large wildfire trends in the western United States, 1984–2011. *Geophysical Research Letters* 41:2928–2933.
- Dicks, L. V., B. Viana, R. Bommarco, B. Brosi, R. Hill, A. V. Lopes, C. Pires, H. Taki, M. del Coro Arizmendi, S. A. Cunningham, L. Galetto, and S. G. Potts. 2016. Ten policies for pollinators. *Science* 315:975–976.
- Dorazio, R. M., and J. A. Royle. 2005. Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association* 100:389–398.
- Dorazio, R. M., J. A. Royle, B. Soderstrom, and A. Glimskar. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. *Ecology* 87:842–854.
- Elliott, S. E. 2009. Subalpine bumble bee foraging distances and densities in relation to flower availability. *Environmental Entomology* 38:748–756.
- Gelman, A., J. Carlin, H. Stern, and D. Rubin. 2004. *Bayesian data analysis*, second edition. Chapman and Hall, London, England.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4:379–391.
- Goulson, D., G. C. Lye, and B. Darvill. 2008. Decline and conservation of bumble bees. *Annual Review of Entomology* 53:191–208.
- Goulson D., P. Reyner, B. Dawson, and B. Darvill. 2011. Translating research into action: bumblebee conservation as a case study. *Journal of Applied Ecology* 48:3–8.
- Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications* 20:1678–1692.
- Hall, L. S., P. R. Krausman, and M. L. Morrison. 1997. The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin* 25:173–182.
- Hanula, J. L., M. D. Ulyshen, and S. Horn. 2016. Conserving pollinators in North American forests: a review. *Natural Areas Journal* 36:427–439.
- Hatfield, R. G., and G. LeBuhn. 2007. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae) in montane meadows. *Biological Conservation* 139:150–158.
- Heinrich, B. 2004. *Bumblebee economics*. Harvard University Press, Cambridge, Massachusetts, USA.
- Heisey, R. M., C. C. Delwiche, R. A. Virginia, A. F. Wrona, and B. A. Bryan. 1980. A new nitrogen-fixing nonlegume: *Cbamaebatia foliolosa* (Rosaceae). *American Journal of Botany* 67:429–431.
- Humble, D. L., and R. D. Burnett. 2010. Nesting ecology of yellow warblers (*Dendroica petechia*) in montane chaparral habitat in the northern Sierra Nevada. *Western North American Naturalist* 70:355–363.

- Iknayan, K. J., M. W. Tingley, B. J. Furnas, and S. R. Beissinger. 2014. Detecting diversity: emerging methods to estimate species diversity. *Trends in Ecology and Evolution* 29:97–106.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluation resource preference. *Ecology* 61:65–71.
- Kearns, C. A., and D. W. Inouye. 1997. Pollinators, flowering plants, and conservation biology. *Bioscience* 47:297–307.
- Kerr, J. T., A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, D. L. Wagner, L. F. Gall, D. S. Sikes, and A. Pantoja. 2015. Climate change impacts on bumble bees converge across continents. *Science* 349:177–180.
- Koch, J. B., and J. P. Strange. 2012. The status of *Bombus occidentalis* and *B. moderatus* in Alaska with special focus on *Nosema bombi* incidence. *Northwest Science* 86:212–220.
- Koch, J. B., J. P. Strange, and P. Williams. 2012. Bumble bees of the Western United States. USDA Forest Service Research Notes Publication FS-972, Washington, D.C., USA.
- Koh, I., E. V. Lonsdorf, N. M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T. H. Ricketts. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences* 113:140–145.
- Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters* 7:1109–1119.
- Lawrence, G. E. 1966. Ecology of vertebrate animals in relation to chaparral fire in the Sierra Nevada foothills. *Ecology* 47:278–291.
- Lozier, J. D., J. P. Strange, and J. B. Koch. 2013. Landscape heterogeneity predicts gene flow in a widespread polymorphic bumble bee, *Bombus bifarius* (Hymenoptera: Apidae). *Conservation Genetics* 14:1099–1110.
- MacKenzie, D. I. 2005. Was it there? Dealing with imperfect detection for species presence/absence data. *Australian and New Zealand Journal of Statistics* 47:65–74.
- MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. A. Royle, and C. A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255.
- McDonald, P. M., and G. A. Everest. 1996. Response of young ponderosa pines, shrubs, and grasses to two release treatments. USDA Forest Service Research Note PSW-RN-419, Albany, California, USA.
- McDonald, P. M., G. O. Fiddler, and D. A. Potter. 2004. Ecology and manipulation of bearclover (*Chamaebatia foliolosa*) in northern and central California: The status of our knowledge. USDA Forest Service General Technical Report PSW-GTR-190, Albany, California, USA.
- McGinnis, T. W., J. E. Keeley, S. L. Stephens, and G. B. Roller. 2010. Fuel buildup and potential fire behavior after stand-replacing fires, logging fire-killed trees and herbicide shrub removal in Sierra Nevada forests. *Forest Ecology and Management* 260:22–35.
- Miller, J. D., H. D. Safford, M. Crimmins, and A. E. Thode. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems* 12:16–32.
- Miller-Struttman, N. E., J. C. Geib, J. D. Franklin, P. G. Kevan, R. M. Holdo, D. Ebert-May, A. M. Lynn, J. A. Kettenbach, E. Hedrick, and C. Galen. 2015. Functional mismatch in bumble bee pollination mutualism under climate change. *Science* 349:1541–1544.
- Moretti, M., F. De Bello, S. P. M. Roberts, and S. G. Potts. 2009. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology* 78:98–108.
- Ne'eman, G., and A. Dafni. 1999. Fire, bees, and seed production in a Mediterranean key species *Salvia fruticosa* Miller (*Lamiaceae*). *Israel Journal of Plant Sciences* 41:157–163.
- Ne'eman, G., A. Dafni, and S. G. Potts. 2000. The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecology* 146:97–104.
- Neu, C. W., C. R. Byerts, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541–545.
- Nyoka, S. E. 2010. Can restoration management improve habitat for insect pollinators in ponderosa pine forests of the American southwest? *Ecological Restoration* 28:280–290.
- Pacifici, K., E. F. Zipkin, J. A. Collazo, J. I. Irizarry, and A. DeWan. 2014. Guidelines for *a priori* grouping of species in hierarchical community models. *Ecology and Evolution* 4:877–888.
- Peat, J., and D. Goulson. 2005. Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris*. *Behavioral Ecology and Sociobiology* 58:152–156.
- Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: trends, impacts, and drivers. *Trends in Ecology and Evolution* 25:345–353.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, C. O'Toole, S. Roberts, and P. Willmer. 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance, and floral reward structure. *Oikos* 101:103–112.
- Quinn, R. D., and S. G. Keeley. 2006. Introduction to California chaparral. University of California Press, Berkeley, USA.
- Raphael, M. G., M. L. Morrison, and M. P. Yoder-Williams. 1987. Breeding bird populations during twenty-five years of postfire succession in the Sierra Nevada. *Condor* 89:614–626.
- Rota, C. T., R. J. Fletcher Jr., R. M. Dorazio, and M. G. Betts. 2009. Occupancy estimation and the closure assumption. *Journal of Applied Ecology* 46:1173–1181.
- Roulston, T. H., and K. Goodell. 2011. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* 56:293–312.
- Ruiz-Gutiérrez, V., E. F. Zipkin, and A. A. Dhondt. 2010. Occupancy dynamics in a tropical bird community: unexpectedly high forest use by birds classified as non-forest species. *Journal of Applied Ecology* 47:621–630.
- Schlaepfer, M. A., D. F. Sax, and J. D. Olden. 2011. The potential conservation value of non-native species. *Conservation Biology* 25:428–437.
- Strahan, R. T., M. T. Stoddard, J. D. Springer, and D. W. Huffman. 2015. Increasing weight of evidence that thinning and burning treatments help restore understory plant communities in ponderosa pine forests. *Forest Ecology and Management* 35:208–220.
- Taylor, A. N., and P. M. Catling. 2011. Bees and butterflies in burned and unburned alvar woodland: evidence for the importance of postfire succession to insect pollinator diversity in an imperiled ecosystem. *Canadian Field-Naturalist* 125:297–306.
- Tepedino, V. J., B. A. Bradley, and T. L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. *Natural Areas Journal* 28:44–50.
- Thorp, R. W., D. S. Horning, and L. L. Dunning. 1983. Bumble bees and cuckoo bumble bees of California (Hymenoptera: Apidae). *Bulletin of the California Insect Survey* 23:1–79.
- Tingley, M. W., and S. R. Beissinger. 2013. Cryptic loss of montane avian richness and high community turnover over 100 years. *Ecology* 94:598–609.
- U.S. Department of Agriculture [USDA] Forest Service. 2014. Region 5 Vegetation Burn Severity—2014 Version 3. Pacific Southwest Region National Forests, McClellan, California, USA. <http://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=stelprdb5327833> Accessed 15 Mar 2015
- Van de Water, K. M., and H. D. Safford. 2011. A summary of fire frequency estimates for California vegetation before Euro-American settlement. *Fire Ecology* 7:26–58.
- Westerling, A. L., H. G. Hidalgo, D. R. Cayan, and T. W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940–943.
- Williams, P. H., and J. L. Osborne. 2009. Bumblebee vulnerability and conservation world-wide. *Apidologie* 40:367–387.
- Williams, P. H., R. W. Thorp, L. L. Richardson, and S. R. Colla. 2014. Bumble bees of North America. Princeton University Press, Princeton, New Jersey, USA.
- Winfrey, R., T. Griswold, and C. Kremen. 2007. Effect of human disturbance on bee communities in a forested ecosystem. *Conservation Biology* 21:213–223.
- Zipkin, E. F., J. A. Royle, D. K. Dawson, and S. Bates. 2010. Multi-species occurrence models to evaluate the effects of conservation and management actions. *Biological Conservation* 143:479–484.

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