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Explaining the birds and the bees: deriving habitat restoration targets from multi-species occupancy models

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Abstract. Riparian corridors can be highly biodiverse but are often degraded by human activities, and are therefore frequent targets of restoration actions. Yet managers often lack clear guidance on how to conserve or restore riparian vegetation structure and composition to promote wildlife biodiversity, due to the difficulty of balancing the needs of multiple species and taxonomic groups. We used independent multi-species occupancy models to assess the response of riparian bird and bumble bee assemblages, respectively, to variation in vegetation structure and composition in montane riparian corridors. We sought to identify vegetation characteristics associated with relatively high richness across each taxonomic group to define target conditions for habitat restoration. Riparian bird occupancy increased with more willow (*Salix* spp.) cover and less overstory cover, while bumble bee occupancy increased with greater flowering plant richness, more forb cover, and less shrub cover. Relatively distinct habitat preferences of bumble bees and riparian birds emphasize the value of managing for habitat heterogeneity to promote biodiversity across multiple taxonomic groups. Multi-species modeling distills the responses of numerous species down to a single estimate of a covariate effect for an assemblage of species and can provide land managers with empirically derived targets for habitat restoration that will benefit many species.

Key words: biodiversity; bird; bombus; bumble bee; California; hierarchical model; multi-species occupancy model; occupancy modeling; riparian.

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INTRODUCTION

Riparian corridors are important conservation targets because they support diverse plant (Naiman et al. 1993) and animal (Knopf et al. 1988) communities and contribute to regional biodiversity by hosting species absent from upland areas (Sabo et al. 2005). In response to pervasive loss and degradation of riparian habitats worldwide, science-based approaches to riparian restoration (Goodwin et al. 1997) have aimed to return degraded ecosystems to historical or reference conditions (White and Walker 1997).

Defining target conditions for riparian restoration has been a challenge for land managers (van Diggelen et al. 2001). Where improving wildlife habitat is a restoration objective, a common approach is to describe habitat conditions elsewhere that support desired wildlife populations, and then replicate those conditions through habitat manipulation (Dumroese et al. 2015). Yet different wildlife species have unique habitat needs, potentially yielding an intractable number of species-specific restoration prescriptions that may not be mutually compatible (Mac Nally et al. 2002, White et al. 2013). Managers therefore must often make difficult choices about which wildlife species' needs should inform restoration design or targets for habitat management. One common approach is to tailor actions to benefit one or more focal species, in the hope that those actions will also help a much broader range of species (Lambeck 1997). However, focal species occurrence has at times proven to be a poor indicator of broader biodiversity (Andelman and Fagan 2000).

Advancements in multi-species occupancy modeling (MSOM; Iknayan et al. 2014) provide a promising tool for identifying desired post-restoration habitat conditions based on the needs of broad taxonomic groups or guilds of species (White et al. 2013), including species that are rarely observed. Most MSOM-based prescriptions for management or restoration have addressed a single, broad group such as birds (Russell et al. 2009, Zipkin et al. 2010, Jones et al. 2012, White et al. 2013) or mammalian carnivores (Burton et al. 2012, Van der Weyde et al. 2018). However, just as individual species respond to management in diverse ways, so do broad taxonomic groups (Chaudhary et al. 2016). An even more inclusive approach is therefore to build models of multiple taxonomic groups using independent MSOMs (Threlfall et al. 2017) and compare their responses to environmental variables.

Here, we provide an example of examining substantially different taxa occurring within the same habitat, by assessing how riparian bird and bumble bee assemblages respond to vegetation conditions in montane riparian corridors. We sought to identify vegetation characteristics associated with relatively high richness across each taxonomic group. We focused on riparian birds and bumble bees because both groups are likely sensitive to variation in the structure and composition of riparian vegetation, but nevertheless rely on different resources. Additionally, both taxonomic groups can be surveyed efficiently and inexpensively with a well-vetted methodology for multi-species surveys (Ralph et al. 1995, Loffland et al. 2017). Finally, we deliberately chose groups representing multiple trophic levels (i.e., invertebrate primary and vertebrate secondary consumers) under the assumption that evaluating habitat needs across ecologically disparate groups might yield restoration prescriptions with broader benefits across the ecosystem than if we considered a single trophic level (Soliveres et al. 2016). Although other studies (Söderström et al. 2001, Golet et al. 2008) have simultaneously assessed the effects of habitat covariates on multiple species of birds and insects (including bumble bees), most have not accounted for imperfect detection nor summarized the assemblage response.

We expected that the riparian bird and bumble bee assemblages would share few of the same vegetation associations because bumble bees use flowering plants for food and generally nest in ground burrows, while riparian birds use a variety of above-ground nesting substrates and are not directly tied to flowers for food. Furthermore, we predicted that on average riparian birds would have higher occupancy probability in areas with greater shrub and canopy cover because they most often use shrubs and tree canopy for nesting and foraging. We also hypothesized that on average bumble bee species would have higher occupancy probability in areas with higher flower richness indices because a greater variety of flowers likely provides a staggered blooming period that yields foraging resources over a longer period of time. Additionally, variation in flower structure among plant species likely yields access to bumble bee species with a greater variety of morphologies (e.g., species with differing tongue lengths).

METHODS

Study area

We conducted our study from May to August during 2015 and 2016 on the Plumas National Forest in the northern Sierra Nevada of California, USA (Fig. 1), at sites ranging in elevation from 1100 to 2080 m a.s.l. The Sierra Nevada region is generally warm and dry during the summer and receives most of its precipitation between October and April. We sampled riparian birds and bumble bees within riparian vegetation corridors along streams that spanned diverse vegetative and physiographic conditions embedded in a matrix of Sierran Mixed Conifer forest

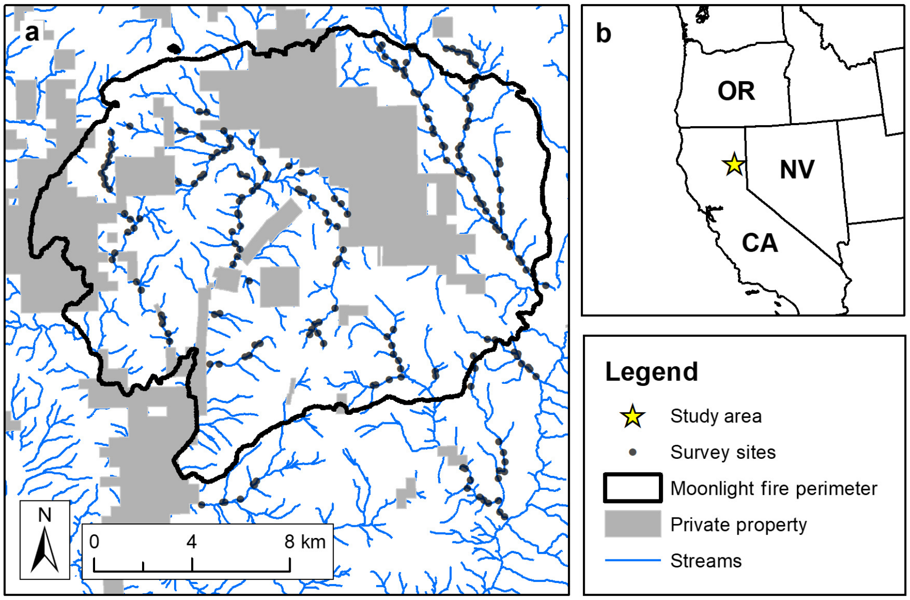

Fig. 1. Survey sites for riparian birds and bumble bees (a) within and adjacent to the Moonlight fire perimeter in the northern Sierra Nevada, California, USA, and (b) location of study area within California. State abbreviations are OR, Oregon; NV, Nevada; CA, California.

and montane chaparral (Mayer and Laudenslayer 1988). Surveyed sites were within or just outside the perimeter of the Moonlight fire, which burned 27,370 ha of forested land at mixed severity in 2007 (Micheletty et al. 2014). Heterogeneous burn severity and a decade of post-fire succession prior to our study contributed to highly diverse riparian vegetation structure and composition across survey sites (Appendix S1: Fig. S1) which we considered a benefit, although the range of vegetation characteristics in our study was likely broader than might be present at sites which have been undisturbed (i.e., unburned) for a longer period of time.

Study design

Our study encompassed 203 sites intended for sampling riparian birds and bumble bees during the summers of both 2015 and 2016. To generate this sample, we placed points every 100 m along 1st, 2nd, and 3rd Strahler order streams (Strahler 1957) on National Forest land within and near the area burned by the Moonlight fire. We used unstratified, unequal probability, generalized random tessellation stratified (GRTS) sampling (Stevens and Olsen 2004) to select sampling sites from the initial set of points with the R package spsurvey (Kincaid and Olsen 2013). This form of GRTS sampling selected sites proportional to stream reach length and Strahler order present within the study area. For each selected point, we established a survey site centered 25 m from the stream in a randomly chosen (left or right bank) direction, unless one stream bank was inaccessible, in which case we established the site on the opposite side. Although our original intention was to focus on the burned area, we also allocated a portion of our efforts to unburned stream reaches outside of the fire perimeter, to yield even greater heterogeneity in vegetation conditions at survey sites. Of the 203 sampled sites, 160 (78%) were within the fire perimeter and the rest were in adjacent areas outside the fire perimeter (Fig. 1). Bird and bumble bee surveys were conducted at the same sites.

Sampling methods

We sampled birds via 50 m radius point count surveys (Ralph et al. 1995) between 10 min before and 3.5 h after local sunrise. To maximize the number and diversity of sites sampled, we allocated our bird sampling effort to visit each site once between late May and early July in both years, rather than visiting a smaller number of sites multiple times (MacKenzie and Royle 2005). Breeding territories of landbirds are typically stable throughout the seasonal period of our study, allowing strong inferences based on a single site visit (Tingley et al. 2016, Ray et al. 2017). Each survey lasted 7 min and was divided into three consecutive time intervals: a 3-min period and then two subsequent 2-min periods. At the start of each new time period (e.g., the 2-min period after the initial 3-min period), the observer reset and only recorded any birds seen or heard during that period, regardless of any detections made during the prior period. We chose these specific time intervals to facilitate direct comparison with regional and continent-wide bird monitoring programs, as suggested by Matsuoka et al. (2014). Birds were counted out to 50 m to align reasonably closely with the spatial scale of the bumble bee surveys (20 m radius) and to ensure that a large (though variable) proportion of the habitat sampled was indeed dominated by riparian vegetation.

Between early May to mid-August in both 2015 and 2016, we conducted bumble bee surveys between 09:00 and 17:00 hours, suspending surveys during rain or cold that would suppress bumble bee activity. Most sites were surveyed twice during each season with visits typically separated by 4–6 weeks, to accommodate substantial inter-specific variation in phenology of bumble bee emergence and colony life cycle (Pyke et al. 2011). For each survey visit, we captured bumble bees within a 20 m radius of the survey site center via sweep net during a 16-min period (see Loffland et al. 2017 for detailed survey methods). Most bumble bees were captured while foraging on flowers, although a small minority (33 of 1332 captures, 3.3%) were captured in flight. Bumble bees were placed in vials, chilled in a cooler, and then photographed and identified to species immediately after the survey period. Bumble bees were released at the survey site after they warmed and became active again. Photographs were reviewed by an expert bumble bee biologist to confirm species identification when surveyors were uncertain of bumble bee species identity. Handling and collection of bumble bees were authorized under California Department of Fish and Wildlife Entity Permit SC-008645.

Vegetation survey

We described vegetation within a 20 m radius of the survey site center following methods developed by Loffland et al. (2017). During each bumble bee survey visit, we recorded the five plant species with the most abundant flowers or inflorescences, including shrubs and herbaceous plants. We recorded percent cover estimates to the nearest 1% for overstory trees, individual shrub species, all forbs combined, and all herbaceous plants combined. Herbaceous plant cover was the sum of grass, sedge, rush, forb, and fern cover. We derived indices of annual shrub and flower richness for each survey site, which we refer to as shrub richness index and flower richness index, respectively. Detailed methods for vegetation surveys and derivation of shrub and flower richness indices are provided in Appendix S2.

Riparian bird and bumble bee assemblage models

Inferences drawn from occurrence data may be biased if modeling does not account for imperfect detection (Tyre et al. 2003). We used the temporal replication in each of our surveys to build MSOMs for riparian birds and bumble bees (Dorazio and Royle 2005, Dorazio et al. 2006). These models estimate species-level parameters for occupancy and detection probability from hierarchical distributions, effectively treating species-level parameters as random effects drawn from an assemblage-wide probability distribution (Zipkin et al. 2010). Multi-species occupancy models leverage information from all modeled species to estimate the factors that strongly influence occupancy associations across an assemblage (Iknayan et al. 2014). We paired sets of environmental covariates as predictors for both models (Appendix S3: Table S1) after ensuring that all inter-covariate correlations were $<|0.7|$ (Dormann et al. 2013), and all continuous covariates for both detection and occupancy covariates were standardized (mean = 0 and standard deviation [SD] = 1). We implemented our model in a Bayesian framework, which makes it easy to use and fit models, while providing straightforward ways to propagate error from species to communities (Iknayan et al. 2014).

We built MSOMs for riparian birds and bumble bees separately. For birds, we detected 68 species within a 50 m radius of the survey sites, but we limited our analysis to 22 riparian-associated species (Appendix S3: Table S2) that are more likely to occur or are known to reach their highest densities in riparian areas, based on expert opinion and a literature review. Focusing on riparian-associated species ensured that the models would be driven by variables that matter to riparian birds, as many of the bird species we detected commonly were associated with adjacent patches of upland forest or chaparral. For bumble bees, we initially used 12 species observed but had difficulty achieving model convergence, so we omitted very rare (zero observations in either year) species, and our final model included only nine species (all species are listed in Appendix S3: Table S3).

We implemented two separate Bayesian hierarchical models that were nearly identical to those implemented by Tingley et al. (2016) for birds and Loffland et al. (2017) for bumble bees, where ybird_{ijkt} and ybee_{ijkt} are, respectively, the record of detection (1) or non-detection (0) of bird or bumble bee species i, at sampling site j, during survey k, in year t. We assumed that our data were generated as imperfect observations of a true and unobservable occurrence state zbird_{ijt} or zbee_{ijt} for birds and bumble bees, respectively, where $\text{ybird}_{ijkt} \sim \text{Bernoulli}(\text{pbird}_{ijkt} \times \text{zbird}_{ijt})$ and $\text{ybee}_{ijkt} \sim \text{Bernoulli}(\text{pbee}_{ijkt} \times \text{zbee}_{ijt})$.

The probability of detection, pbird_{ijkt}, was modeled as a function of covariates such that

$$\text{logit}(\text{pbird}_{ijkt}) = \alpha\text{bird0}_i + \alpha\text{bird1}_i \times \text{day}_{jt} + \alpha\text{bird2}_i \times \text{time}_{jt} + \alpha\text{bird3}_i \times \text{effort}_k \tag{1}$$

where day_{jt} is the ordinal day of the year, time_{jt} is the time of day when the survey began, and effort_k is a dummy variable indicating the survey period length, with a value of 1 indicating a 3-min period and 0 indicating a 2-min period. We included ordinal day because we assumed detection probability would change as the breeding season progressed (Furnas and Callas 2015). We included time of the survey visit because we assumed detection probability would be dependent on the time of day (Rollfinke and Yahner 1990). We followed Tingley et al. (2016) in assuming that detection probability would differ between the initial (longer) survey time period and the two subsequent (shorter) time periods and included effort_k to capture this variation.

The probability of detection, pbee_{ijkt} for bee species i, at sampling site j, during survey visit k, in year t, was modeled as a function of covariates such that

$$\text{logit}(\text{pbee}_{ijkt}) = \alpha\text{bee0}_i + \alpha\text{bee1}_i \times \text{day}_{jkt} + \alpha\text{bee2}_i \times \text{time}_{jkt} + \alpha\text{bee3}_i \times \text{time}^2_{jkt} \tag{2}$$

where day_{jkt} is the ordinal day of the year, time_{jkt} is the time of day when the survey was initiated, and time^2_{jkt} is time of day squared. We included ordinal day because bumble bee abundance and activity patterns typically change as the season progresses (Pyke et al. 2011) and a quadratic effect of time because bumble bee activity often peaks during the middle of the day (Peat and Goulson 2005).

The estimate of true occurrence state zbird_{ijt} and zbee_{ijt} was expected to follow a Bernoulli distribution such that $\text{zbird}_{ijt} \sim \text{Bernoulli}(\psi\text{bird}_{ijt})$ and $\text{zbee}_{ijt} \sim \text{Bernoulli}(\psi\text{bee}_{ijt})$. We modeled occupancy probability for birds, ψbird_{ijt} as a logit-linear function of covariates such that

$$\begin{aligned}\text{logit}(\psi\text{bird}_{ijt}) = {} & \beta\text{bird0}_i + \beta\text{bird1}_i \times \text{overstory}_{jt} \\ & + \beta\text{bird2}_i \times \text{shrub cover}_{jt} \\ & + \beta\text{bird3}_i \times \text{shrub richness index}_{jt} \\ & + \beta\text{bird4}_i \times \text{tobacco brush cover}_{jt} \\ & + \beta\text{bird5}_i \times \text{willow cover}_{jt} \\ & + \beta\text{bird6}_i \times \text{whitethorn cover}_{jt} \\ & + \beta\text{bird7}_i \times \text{herb cover}_{jt} \\ & + \beta\text{bird8}_i \times \text{forb cover}_{jt} \\ & + \beta\text{bird9}_i \times \text{flower richness index}_{jt} \\ & + \beta\text{bird10}_i \times \text{elevation}_j \\ & + \beta\text{bird11}_i \times \text{year}_t + \text{grid cell}_{ij}\end{aligned} \tag{3}$$

These covariates represented habitat measures that we expected would be relevant to birds and/or bumble bees (covariates defined in Appendix S3: Table S1), as we included the same covariates in models for both taxonomic groups to facilitate comparisons of parameter estimates. Tobacco brush, willow, and whitethorn cover were included because they were the shrub species with the greatest cover across all sampled plots and would likely be the target of any potential management actions. We initially inspected correlograms generated in program GeoDa (Anselin et al. 2006) and determined that there was spatial autocorrelation in the model residuals for birds out to 2.5 km and in bumble bees out to 4 km. We therefore included a normal random effect of study area region—grid cell in Eq. 3—by dividing the study area by a uniform grid comprised of 4 × 4 km cells and grouping sampling sites accordingly. When a cell had <4 sites, those sites were assigned the grouping of the nearest occupied cell. The model structure for bumble bees was identical to Eq. 3, except that the model used bee-specific parameters.

For both bird and bee models, species-specific slope and intercept parameters were drawn from hyper-distributions following the form: $\beta_i \sim \mathrm{Normal}(\mu_\beta, \sigma_\beta)$ and $\alpha_i \sim \mathrm{Normal}(\mu_\alpha, \sigma_\alpha)$, where μ and σ represent the assemblage-level (across all riparian bird or bumble bee species) mean and SD for each i species-level parameters for all β or α. We considered parameter estimates to be "significant" where the 95% Bayesian credible interval (BCI) did not include zero.

We fit the data to the separate bird and bumble bee models using JAGS ver. 3.4.0 (Plummer 2017) and the package jagsUI ver. 1.4.4 (Kellner 2016) within R ver. 3.4.1 (R Core Team 2017). For all parameters, we used vague priors (normal with mean = 0 and precision = 0.01; gamma with shape = 0.1 and rate = 0.1). We assumed model convergence when monitored parameters had Gelman-Rubin statistics <1.1 (Gelman et al. 2004). Each model was run with 3 MCMC chains. Bird and bumble bee models had a burn-in of 60,000 and 120,000 iterations, respectively, followed by a posterior draw of 20,000 thinned by 20. Model code for MSOMs is included in Appendix S4.

Inference on richness relationships

Species richness relationships for birds and bumble bees were evaluated using the full posterior of the modeled true occurrence arrays (Tingley et al. 2016, Loffland et al. 2017), with the predicted occurrence state (presence or absence) of individual bird and bumble bee species incorporating all information from parameters in the respective models. We calculated mean species richness for birds and bumble bees, $\mathrm{birdrich}_{jt}$ and $\mathrm{beerich}_{jt}$ which represent the site- and year-specific mean species richness (alpha diversity), by summing zbird_{ijt} and $\mathrm{zbee}_{ijt,}$ respectively, for each posterior sample. We considered surveys of the same sites between years to be relatively independent because both birds and bumble bees change their habitat use in accordance with yearly environmental changes, and several of the vegetation variables we assessed (generally those related to herbaceous vegetation) varied substantially between years.

To identify vegetation characteristics that supported high-richness assemblages, we binned 40 sites (10%) that had the highest model-derived riparian bird and bumble bee richness, respectively, and refer to these sites as high bird and high bee groups. We note that our binning of sites by richness is relatively arbitrary; broader or narrower binning criteria could be appropriate depending on the analysis goal. Our goal was to provide vegetation threshold values for managers that would support high-richness assemblages; summarizing site-level vegetation characteristics for the top 10% of sites for richness of each taxa provided sufficient samples for reliably estimating distributions of vegetation values at those sites.

RESULTS

We had 599 detections of 22 riparian bird species at 181 sites in 2015 and 575 detections of the same species at 201 sites in 2016 (Appendix S3: Table S2). The species with the most detections across the two-year study were as follows: MacGillivray's Warbler (*Geothlypis tolmiei*) with 207 detections (18% of observations), House Wren (*Troglodytes aedon*) with 168 detections (14% of observations), and Western Wood-Peewee (*Contopus sordidulus*) with 128 detections (11% of observations). Riparian birds exhibited only moderate interannual variation in number of detections (Appendix S3: Table S2). We captured and identified 282 bumble bees of 10 species during 398 surveys at 203 sites in 2015 and 1050 bumble bees of 11 species during 399 surveys at

200 sites in 2016 (Appendix S3: Table S3). The three most frequently captured bumble bee species across the two-year study were Vosnesensky Bumble Bee (*Bombus vosnesenskii*) with 859 captures (64% of observations), Van Dyke Bumble Bee (*Bombus vandykei*) with 141 captures (11% of observations), and Black tail Bumble Bee (*Bombus melanopygus*) with 107 captures (8% of observations). Overall and for some individual species, numbers of bumble bee captures varied greatly between the two years of the study, most notably Vosnesensky Bumble Bee, which was represented by 77 captures in 2015 and 782 captures in 2016 (Appendix S3: Table S3).

Bird and bumble bee assemblage patterns

Based on our multi-species occupancy model, riparian bird occupancy probability significantly increased with greater willow cover and less overstory cover, and birds were more likely to occupy sites in 2016 than in 2015 (Fig. 2, Table 1). Occupancy probability was not significantly affected by any remaining occupancy covariates (Fig. 2, Table 1). Detection probability was significantly greater during longer survey intervals and decreased with time of day (Table 1). Day of year had a non-significant effect on assemblage detection probability (Table 1). Plots of estimated bird species richness relative to willow cover (Fig. 3e) and overstory cover (Fig. 3a) showed similar relationships as those observed for the significant assemblage parameter estimates (Fig. 2).

Bumble bee occupancy probability was significantly affected by three covariates (Fig. 2, Table 1); bumble bee occupancy increased with greater flower richness index values, more forb cover, and less shrub cover (Figs. 2, 3). Occupancy probability was not significantly affected by any of the remaining vegetation covariates (Fig. 2, Table 1). Year had a potentially large effect on occupancy (mean = 1.54) though this effect was highly uncertain (95% BCI = −1.54 to 5.49; Table 1), undoubtedly due to large species-specific differences in annual variability. For example, captures of some species (e.g., *B. vosnesenskii* and *B. melanopygus*) increased greatly in 2016 while others (e.g., *Bombus bifarius*) declined

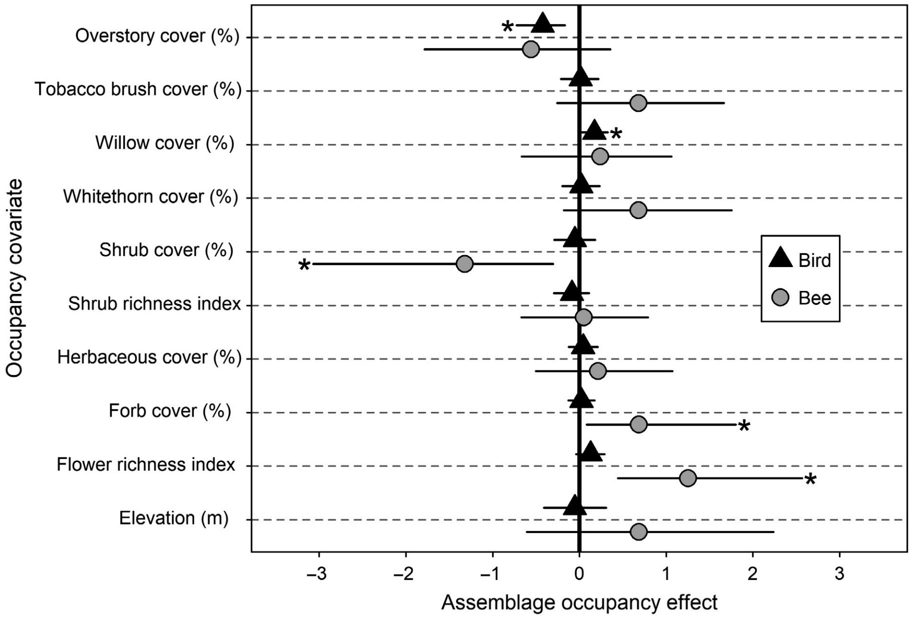

Fig. 2. Assemblage-level effects of environmental covariates on occupancy by riparian birds (Bird) and bumble bees (Bee). Covariate effects on the two taxonomic group are paired above and below dotted lines that extend to the indicated covariate on the *y*-axis. Error bars represent 95% Bayesian credible intervals (BCI). A single asterisk (*) beside a parameter estimate denotes that the 95% BCI does not cross zero for that taxonomic group. Year effect was excluded from the plot because we aimed to illustrate environmental rather than temporal effects.

Table 1. Mean parameter estimates and 95% Bayesian credible intervals (BCI) for covariates in riparian bird and bumble bee assemblage models.

	Riparian birds		Bumble bees	
Model covariates	Mean	95% BCI	Mean	95% BCI
Occupancy covariates				
Overstory cover	−0.42†	−0.72, −0.16	−0.55	−1.78, 0.36
Tobacco brush cover	0.01	−0.21, 0.22	0.68	−0.25, 1.66
Willow cover	0.17†	0.02, 0.33	0.24	−0.66, 1.06
Whitethorn cover	0.02	−0.19, 0.23	0.68	−0.18, 1.75
Shrub cover	−0.05	−0.29, 0.18	−1.32†	−3.07, −0.31
Shrub richness index	−0.08	−0.29, 0.11	0.05	−0.66, 0.79
Herbaceous cover	0.04	−0.12, 0.21	0.22	−0.50, 1.07
Forb cover	0.02	−0.12, 0.17	0.69†	0.08, 1.80
Flower richness index	0.13	−0.03, 0.29	1.25†	0.44, 2.57
Elevation	−0.05	−0.41, 0.31	0.68	−0.60, 2.24
Year	−0.47†	−0.95, −0.11	1.54	−1.54, 5.49
Detection covariates				
Day of year	0.04	−0.13, 0.22	0.15	−0.37, 0.69
Effort	0.44†	0.17, 0.70	–	–
Time of day	−0.18†	−0.36, −0.01	−0.08	−0.41, 0.23
Time of day^2	–	–	−0.06	−0.36, 0.22

Note: Covariates not included denoted with dashes.

† Estimate with BCI that does not include zero.

(Appendix S3: Table S3). Detection probability was not significantly affected by any detection covariates (Table 1).

Factors that increased riparian bird richness were distinct from factors that increased bumble bee richness. Riparian bird and bumble bee MSOMs did not share any of the same significant environmental covariates (Fig. 2, Table 1). In particular, shrub cover and flower richness index significantly affected bee occupancy, yet these parameters also significantly differed from their counterparts affecting bird occupancy (Fig. 2). Additionally, richness values for both riparian birds and bumble bees were markedly different between high bird and high bee richness site groupings (Table 2). For each of the five covariates that significantly affected riparian bird or bee occupancy, we examined distributions of vegetation values across all sites and at sites with high (top 10% of sites) species richness estimates of birds and bees, respectively (Fig. 4, Table 3). None of the sites with high bumble bee richness had flower index values <6, and, on average, sites with high bee richness had 2.18 more blooming species than all sites pooled and 1.5 more blooming species than sites with high bird richness (Table 3). Forb cover, which was also a significant positive predictor of bee occupancy but not bird occupancy, averaged 3 times greater at sites with high bee richness than at all sites pooled and twice as high as at sites with high bird richness (Fig. 4b, Table 3). Overall shrub cover, which negatively influenced bee occupancy but had no significant effect on bird occupancy, was approximately half as great at sites with high bee richness compared with all sites or sites with high bird richness and none of the high bee richness sites had values >65% (Fig. 4c, Table 3). Willow cover, which positively influenced bird occupancy but had no significant effect on bee occupancy, was rather uniformly low across all sites, including sites with high bird richness or high bee richness, but was nonetheless greatest at sites with high bird richness (Fig. 4d, Table 3). Lastly, overstory cover, which was significantly predictive of lower bird occupancy and weakly associated with lower bee occupancy, was substantially higher on average across all sites than at either sites with high bird richness or high bee richness (Fig. 4e, Table 3).

DISCUSSION

We used multi-species models for two different taxonomic groups to identify specific habitat features associated with relatively high species

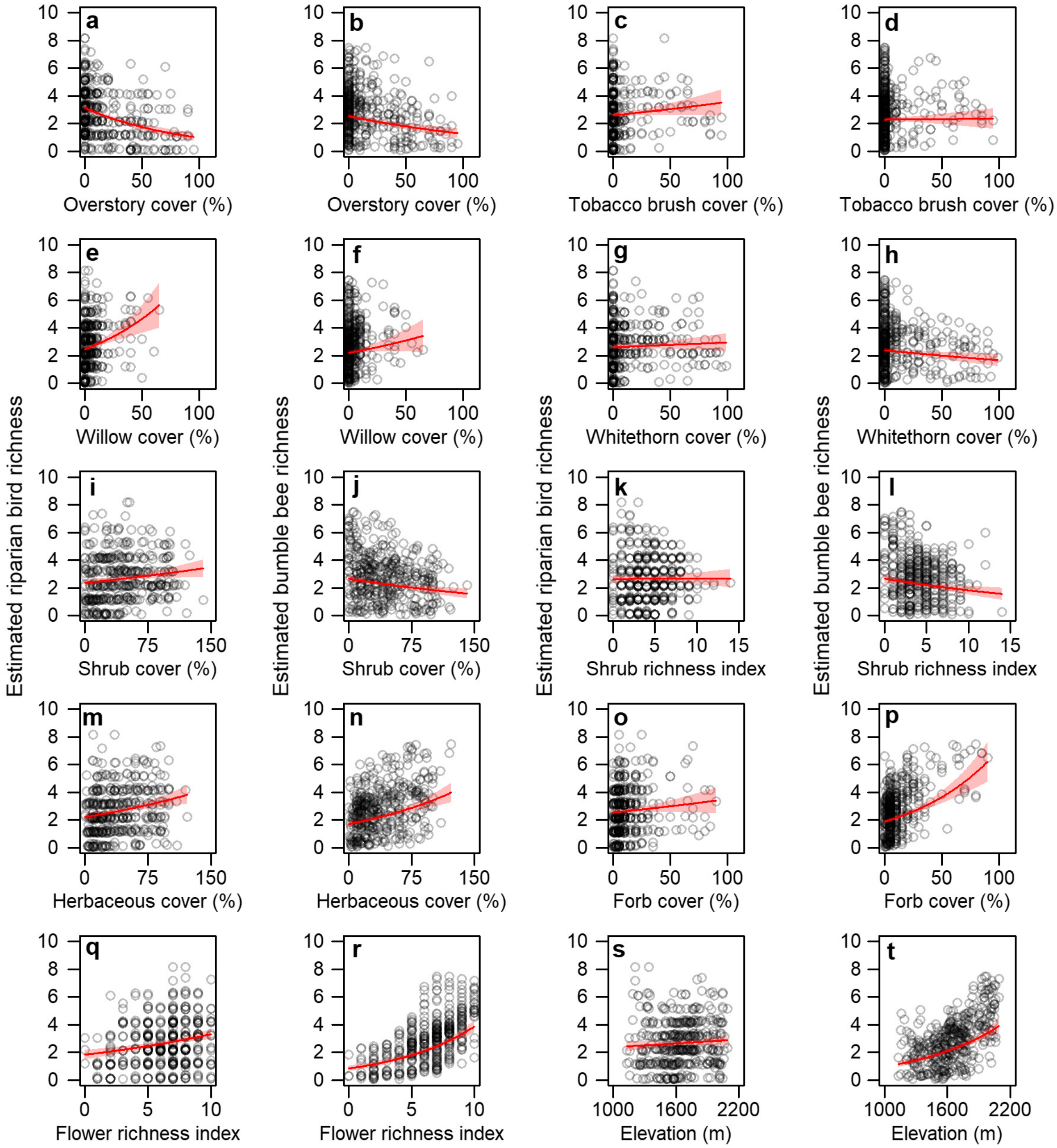

Fig. 3. Estimated species richness of riparian birds and bumble bees per site and year relative to occupancy covariates. Richness values for each taxonomic group are derived from the *z*-array (estimated true occurrence) output of the assemblage models. Solid lines illustrate the mean log-linear trend for ease of interpretation. The shaded area around each line represents 95% confidence interval for prediction.

richness within each group. The vegetation values associated with high riparian bird richness and high bumble bee richness in Table 3 can be thought of as target values for post-restoration vegetation conditions, suitable for informing the design of riparian restoration projects within our study area and, with appropriate caution, in other montane riparian areas with similar species

Table 2. Summary of estimated species richness for riparian bird and bumble bee assemblages at 40 sites (~10% of all sites) with the highest richness values for riparian birds (high bird) and bumble bees (high bee), respectively.

		Estimated richness			
Site group	Taxonomic group	1Q†	Median	Mean	3Q‡
High bird	Riparian bird	5.25	6.08	5.93	6.25
High bird	Bumble bee	1.83	3.45	3.42	4.63
High bee	Riparian bird	1.32	3.29	3.16	4.36
High bee	Bumble bee	5.52	6.10	6.16	6.69

† First quartile of data.
‡ Third quartile of data.

composition. We caution that local constraints, opportunities, or knowledge may dictate deviating from these target values, but in their absence, we believe our values can provide a useful starting point.

Riparian bird assemblage patterns

Overstory cover had a negative effect on riparian bird occupancy, which runs counter to our predictions as well as other studies that reported a positive relationship between canopy cover and riparian bird richness (Luther et al. 2008, Powell and Steidl 2015). This disparity may reflect differences in overstory tree communities between study areas because overstory at our sites was dominated by conifers rather than riparian-associated, deciduous trees. Additionally, areas with greater tree canopy cover tend to have less shrub cover due to shading (McKenzie et al. 2000) and high tree canopy cover also may limit willow cover. Some riparian bird species are more abundant in areas with greater willow cover (Ammon and Stacey 1997, Bombay et al. 2003, Baril et al. 2011), so the positive effect of willow cover on bird occupancy that we observed also may drive the negative association with overstory cover.

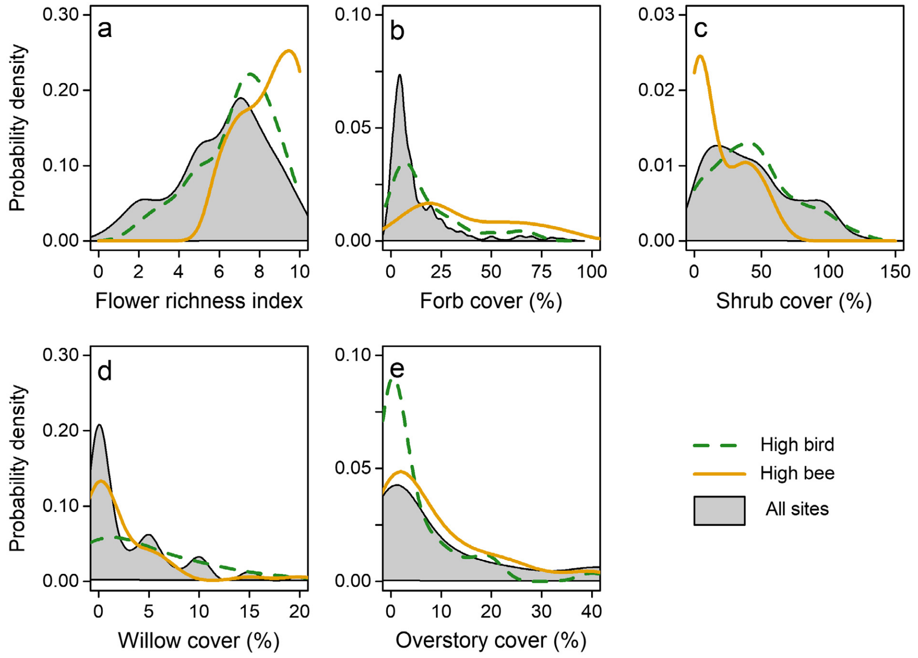

Fig. 4. Distributions of vegetation values at sites where we surveyed riparian birds and bumble bees in 2015 and 2016. The gray distribution illustrates covariate values (significant in either the bird or bee multi-species occupancy model) across all surveyed sites as a Gaussian kernel density estimate (y-axes), with bandwidth chosen automatically by the density function in the R programming language. The remaining curves represent the distribution of covariate values corresponding to 40 sites with the highest species richness estimates of birds and bees as indicated in the legend. Forb, willow, and overstory cover were truncated on the x-axis to aid in visually discerning differences in distributions; only small portions of distributions extend beyond truncation. Shrub cover extends past 100 because we measured overlapping cover of individual shrub species.

Table 3. Summary statistics for vegetation values at all sites across both years (all sites column), and sites that had high estimated richness of riparian birds (high bird richness column) and bumble bees (high bee richness column).

Occupancy covariate	Statistic	All sites	High bird richness	High bee richness
Flower richness index	1Q†	5.00	5.75	7.00
	Median	7.00	7.00	9.00
	Mean	6.20	6.88	8.38
	3Q‡	8.00	8.00	10.00
Forb cover (%)§	1Q	5.00	5.00	19.50
	Median	5.00	10.00	25.00
	Mean	12.74	18.07	36.92
	3Q	15.00	25.00	60.75
Shrub cover (%)	1Q	16.25	24.75	2.00
	Median	39.00	40.00	10.00
	Mean	43.14	43.77	19.27
	3Q	64.50	58.25	36.25
Willow cover (%)	1Q	0.00	0.00	0.00
	Median	0.50	5.00	0.50
	Mean	5.26	11.57	7.55
	3Q	5.00	11.25	5.50
Overstory cover (%)	1Q	0.00	0.00	0.00
	Median	5.00	0.00	5.00
	Mean	16.76	7.60	9.93
	3Q	25.00	8.50	15.00

Note: Only covariates that were significant (meaning Bayesian credible interval did not overlap 0) in either assemblage model (bird or bee) are reported.

† First quartile of values.

‡ Third quartile of values.

§ Percent symbol denotes percent cover.

Although we predicted that riparian bird occupancy would be positively related to shrub cover and shrub richness, we found that overall shrub cover, shrub richness, and percent cover of each of the two most abundant upland shrub species had no significant effect. The lack of importance of these variables in the bird assemblage model likely reflects our exclusion of non-riparian bird species—a model considering the entire bird assemblage present, including upland-associated bird species might yield very different results, but our interest here was more narrowly to identify target habitat characteristics that would benefit riparian species. As expected, covariates related to herbaceous vegetation also had little to no effect on riparian bird occupancy, as they were included in the model primarily to assess their importance to bumble bees.

Bumble bee assemblage patterns

The composition of the bumble bee species pool (captures of individual bumble bee species) varied strongly between years, perhaps due to the indirect effects of climate (drought in 2015) on floral resource phenology driving bumble bee abundance (Ogilvie et al. 2017). The bumble bee assemblage was most strongly affected by our flower richness index, which represented most or all flowers available during each sampling visit. Richness of bumble bees (Hines and Hendrix 2005, Hatfield and LeBuhn 2007) and other pollinators (Blaauw and Isaacs 2014) is known generally to relate positively to floral diversity, although Hegland and Boeke (2006) found floral density to be more important than floral diversity for bumble bees. Floral diversity may be important for at least three reasons: Diverse plant communities may make floral resources available longer because of temporally staggered blooming periods across species; diversity of flowering plants provides varied plant morphologies (i.e., flowers with a variety of corolla tube lengths) providing resources to bumble bees with varying tongue lengths (Inouye 1980, Harder 1985); and a more diverse flowering plant assemblage likely includes a greater number of preferred plant species for a variety of bumble bee species. We did not explicitly test these hypotheses, though bumble bee richness did increase with floral richness and the bumble bee species modeled did have varied tongue lengths (Appendix S3: Table S4).

Forb cover had a weaker effect on bumble bee richness than the flower richness index. Bumble bees are associated with greater forb cover (Scheper et al. 2013); however, if plant diversity is low, floral resources may be highly synchronized and not available throughout the nesting cycle. Our finding that greater shrub cover had a negative effect on bumble bee occupancy accords with other studies demonstrating increased bee richness (of multiple bee genera including *Bombus*) with reduced shrubs (Grundel et al. 2010, Hudson et al. 2013), although elsewhere in the Sierra Nevada *B. vosnesenskii* occurrence increased with cover of one shrub species, *Chamaebatia foliolosa* (Loffland et al. 2017). Increased shrub cover may result in decreased herbaceous cover because of shading and competitive exclusion. Bumble bees use flowering shrubs, but available information from the Sierra Nevada indicates that few shrub species are preferentially selected (Loffland et al. 2017). While none of the three dominant shrub species in our study area significantly affected bumble bee assemblage occupancy, the mean effect of each shrub was positive though highly variable, indicating that some bumble bee species in our study are positively associated with one or more shrub species, though others were not.

Taken together, results from our bee occupancy model emphasize the importance of forb cover and flowering plant diversity to bumble bees. While riparian restoration projects often feature planting willows or other shrubs to stabilize stream banks (Adhikari et al. 2013) and provide cover for wildlife (Golet et al. 2008), we suggest projects also incorporate seeding or planting efforts that establish and promote diverse, native forbs.

Divergent habitat associations and the need for heterogeneity

Evaluating preferred vegetation characteristics for both riparian birds and bumble bees yielded guidance for restoration efforts addressing a broader suite of vegetation characteristics and target conditions than consideration of either taxonomic group alone. However, riparian bird and bumble bee assemblages showed only limited overlap in their relationships to environmental variables. In some cases, restoring or managing habitat toward the means of vegetation values of one taxonomic group is unlikely to be detrimental to the other taxonomic group (e.g., striving for a flower richness index >8 will likely benefit bumble bees and seems unlikely to harm riparian birds). However, for other covariates (e.g., shrub cover, for which high bird richness was associated with a mean of nearly 44% cover, whereas high bee richness values occurred at sites averaging just over 19% cover), it may be challenging or impossible to maximize benefits for both taxonomic groups at the same locations.

The mosaic concept applied to agroecosystem management (Duelli 1997) suggests that greater environmental heterogeneity yields exploitable niches for more species. Wild bee abundance and richness are positively associated with landscape heterogeneity (Rundlöf et al. 2008, Steckel et al. 2014), and heterogeneous landscapes promote the stability of insect populations (Kindvall 1996, Oliver et al. 2010), which in turn is a critical resource for much of the riparian bird assemblage. Configurational heterogeneity provides a variety of resources and microclimates that buffer weather variability and promote diverse flora resource availability (compositional heterogeneity) across both space and time (Oliver et al. 2010). Based on these results, managers restoring multiple reaches in a similar project area should try to have heterogeneous vegetation with distinct areas along each stream reach that provides habitat beneficial to both riparian birds (e.g., willow cover) and bumble bees (e.g., floral diversity).

Although we believe our approach provides general recommendations for riparian restoration, we caution that managers also should consider the particular needs of species with distinct or unusual habitat requirements. Multi-species occupancy models can be thought of as estimating what is beneficial on average for the most species. Restoring habitat in a way that is beneficial for the assemblage may not meet the needs of some individual species, which might include the species most in need of conservation efforts. For instance, in our study area spotted sandpipers (*Actitis macularius*) typically nest on gravel bars, and tree swallows (*Tachycineta bicolor*) nest in tree cavities, but we did not include gravel or cavity availability as covariates in our models, as these habitat features are likely not important for most other riparian birds we studied. Restoration actions that fail to generate or maintain gravel bars and cavities may exclude these species from the restored assemblage. Thus, unless applied with care, an MSOM approach risks masking important species-specific habitat relationships that do not more generally favor the assemblage. With appropriate attention to limitations, however, MSOMs can be used to formulate restoration targets likely to optimize benefits across taxonomic groups with diverse life histories and resource needs, even groups that span multiple trophic levels. Land managers can use this framework to set targets for habitat restoration that are likely to yield maximally biodiverse communities.

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