



Small mammal relative abundance within riparian ecosystems of the Blue Mountains

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ARTICLE INFO

Keywords:

Abundance

Forest ecology

Community ecology

Microhabitat

Oregon

Riparian ecology

Riparian restoration

Small mammals

ABSTRACT

There is a growing interest and investment in restoring riparian areas in the Pacific Northwest to protect biodiversity and water quality, and to restore quality habitat for threatened fish species. However, these management activities change vegetation conditions and potentially impact terrestrial species in these ecosystems. Our objective was to estimate associations between small mammals and 4 broad cover types—conifers, shrubs, grasses, and forbs—in riparian areas within the Blue Mountains of northeast Oregon, USA. We estimated abundances and spatial association for 10 small mammal species using a multispecies hierarchical abundance model and mark-recapture data collected on 36 sites from 2014 to 2017. We predicted that forest-associated species would be more abundant with greater conifer cover, that increases in shrub cover would favor most species, and that increases in grass and forb cover would favor grassland-associated species. Yellow-pine chipmunks (*Tamias amoenus*) were positively associated with conifer cover, while long-tailed voles (*Microtus longicaudus*) and montane voles (*Microtus montanus*) were negatively associated with conifer cover. Associations with shrub cover were positive for bushy-tailed woodrats (*Neotoma cinerea*), deer mice (*Peromyscus maniculatus*), and yellow-pine chipmunks, but negative for montane voles. Bushy-tailed woodrats and montane voles were negatively associated with grass cover. This study is the first to characterize the riparian small mammal communities in this region and provides insights on the effects of restoration activities on riparian ecosystems in dry interior forests and grasslands. We suggest that riparian plantings, a ubiquitous restoration practice, will increase the relative abundances for some, but not all, small mammal species. We also demonstrate use of a new multi-species abundance model that can be a powerful tool for analyzing mark-recapture data because it allowed us to extend the scope of our analysis to data poor species by pooling information with data rich species.

1. Introduction

Riparian areas are critical transition zones between aquatic and terrestrial ecosystems. The gradient of streamside vegetation along healthy streams promotes biodiversity and can help regulate water flow and stream temperature (Richardson et al., 2007; González et al., 2017). However, long-term human disturbance (e.g., roads, splash dams, railroad logging; Jones et al., 2001; Roni et al., 2002; Olson et al., 2007), grazing by domestic livestock (Beschta et al., 2013; Batchelor et al., 2015; Kaweck et al., 2018), and occasionally excessive herbivory by native ungulates, including Rocky Mountain elk (*Cervus canadensis*

nelsoni) and mule deer (*Odocoileus hemionus*; Schoenecker et al., 2004; Averett et al., 2017), have collectively degraded riparian areas (Case and Kauffman, 1997; Pollock et al., 2007).

Major efforts have been undertaken to restore riparian areas (Kauffman et al., 2004; Blumm and DeRoy, 2019), with estimated costs of more than \$1 billion annually in the USA (Bernhardt et al. 2005). In the Pacific Northwest, much of riparian restoration focus has been on improving spawning and brood-rearing habitats for threatened Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*O. mykiss*) within the Columbia River basin, the largest watershed in the region (Monzyk et al., 2009; Jonasson et al., 2016; Justice et al., 2017).

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<https://doi.org/10.1016/j.foreco.2021.119899>

Received 13 August 2021; Received in revised form 21 November 2021; Accepted 23 November 2021

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Commonly used restoration strategies include depositing streamside woody vegetation and planting native trees to stabilize banks and provide shade to lower water temperatures during summer, installing fencing to limit domestic livestock grazing, and augmenting streams with large woody debris to enhance pool development (Averett et al., 2017; Honea et al., 2009; Justice et al., 2017; Torgersen et al., 1999; Wing and Skaugset, 2002). Multiple studies have documented the benefits of the influx of salmon-derived nutrients to streams after habitat restoration (Helfield and Naiman, 2001; Gende et al., 2002; Holtgrieve et al., 2009; Shakeri et al., 2018). However, much less is known about the effect of these riparian restoration strategies on terrestrial wildlife communities, especially in the mixed-coniferous forests of eastern Oregon.

The structural complexity of vegetation in riparian areas promotes a diverse assemblage of small mammal species (Kaufman et al., 2001; Anthony et al., 2003; Hamilton et al., 2015). Some small mammal species help regulate invertebrate populations, while others influence patterns of vegetation by consuming the fruits, seeds, roots, stems, and leaves of vascular plants (Grant et al., 1982; Endress et al., 2016). Small mammals are also important mechanisms for dispersal of seeds and spores, including those of ectomycorrhizal fungi that are critical to nutrient and water uptake for many coniferous trees and shrubs (Stephens and Rowe et al., 2020; Trappe and Claridge 2005). Several species serve as ecological engineers by digging underground burrows that can help promote forb germination and reduce the density of the grass canopy, furthermore these burrows can be subsequently used by reptiles and pollinating insects (Dickman et al., 1999; Regosin et al., 2003; Rothermel and Luhring, 2005; Ross et al., 2020). These specialized relationships among small mammals and plants play a critical role in the maintenance of healthy riparian and forest ecosystems.

The relatively small spatial scales at which small mammals complete their life cycles, coupled with their comparatively short generation times, make them a useful index for quantifying and predicting the impacts of ecological changes within the ecosystem (Moser and Witmer, 2000). Although many small mammal species persist in a broad range of habitats within their geographical ranges, they can also respond to changes in vegetation at relatively discrete spatial and temporal scales, including scales typical of management projects (Bowman et al., 2002; Jenkins et al., 2007; McCaffery et al. 2020). Although habitat associations for many small mammal species are generally understood in the Pacific Northwest (e.g., Johnson and O'Neil, 2001), there is need for better understanding of relationships between small mammals and fine-scale vegetation composition to elucidate effects of restoration activities that include modifications to broad vegetation cover types, i.e., trees, shrubs, forbs, and grasses.

Our primary goal for this study was to quantify associations among small mammal abundance and vegetation cover types in restored riparian areas across a watershed in the Blue Mountains of northeastern Oregon, USA and then to use this site-specific information to develop hypotheses about potential changes in abundance and distribution of small mammals on our study sites that may result from riparian plantings of trees and shrubs and the maturation of those plantings over time. Our specific objectives were to (1) estimate summer abundances for 10 small mammal species from 2014 to 2017 across a gradient of upland grassland and forested riparian ecosystems, and (2) investigate the relationships among species-specific abundances and four vegetation cover types (conifer trees, shrubs, forbs, and grasses). We developed three general hypotheses to characterize our expectations about associations of small mammals to different cover types and species-specific predictions:

- (1) *We predicted that as conifer cover increased, the relative abundance of forest-associated small mammal species would increase.* In xeric ecosystems, bushy-tailed woodrat (*Neotoma cinerea*), golden-mantled ground squirrels (*Callospermophilus lateralis*), northern flying squirrels (*Glaucomys sabrinus*), and yellow-pine chipmunks

(*Neotamias amoenus*), are associated with coniferous, or mixed conifer-deciduous forests and forest edges (Bartels and Thompson, 1993; Johnston and Anthony, 2008; Kuhn and Vander Wall, 2008; Lehmkuhl et al., 2006; Meyer et al., 2007; Ritchie et al., 2009; Shick et al., 2006; Sutton, 1993; Vander Wall and Jenkins, 2011). Therefore, we expected these forest adapted species to be positively associated with conifer cover. In contrast, the abundances of deer mice (*Peromyscus maniculatus*), long-tailed voles (*Microtus longicaudus*), montane voles (*M. montanus*), vagrant shrews (*Sorex vagrans*), and western jumping mice (*Zapus princeps*), species that are often negatively associated with increased conifer cover, would decrease (Sullivan et al., 2000; Gillihan and Foresman, 2004; Zwolak, 2009; Anich and Hadly, 2013; Borchert et al., 2014).

- (2) *We predicted the relative abundance of most small mammals would increase with increased shrub cover.* Some small mammal studies in xeric ecosystems found positive responses to shrub cover presumably because of the cooler microclimate, diverse forage opportunities, and protection from avian predators (Converse et al., 2006; Johnston and Anthony, 2008; Gray et al., 2019). Therefore, we expected that generalist and forest adapted small mammal species, such as deer mice and yellow-pine chipmunks, would have positive associations with increasing shrub cover (Arnan et al., 2014; Coppeto et al., 2006; Muñoz et al., 2009; Parsons et al., 2013; Smith and Maguire, 2004; Vander Wall, 1994).
- (3) *We predicted a greater relative abundance of grassland associated species and insectivores with increasing cover of grasses and forbs.* Five species, Columbian ground squirrels (*Urocitellus columbianus*), long-tailed vole, montane vole, vagrant shrew, and western jumping mouse, are associated with open grassy meadows and riparian zones with forbs (Gillihan and Foresman, 2004; Randall and Johnson, 1979; Sullivan et al., 2000; Weddell, 1991). Therefore, we expected these species to have a positive association with the relative coverage of grasses and forbs because these plants supply important food resources (Gillihan and Foresman, 2004; Hart et al., 2004; Martin and McComb, 2002; Randall and Johnson, 1979).

2. Methods

2.1. Study area

Our study area was located within the Wallowa-Whitman National Forest in the Upper Grande Ronde River watershed in the Blue Mountains, Oregon, USA (Fig. 1). The watershed consisted of dry mixed coniferous forests, dry and wet meadows, and riparian corridors. Conifer forests were dominated by either ponderosa pine (*Pinus ponderosa*) or a mix of lodgepole pine (*P. contorta*), Douglas-fir (*Pseudotsuga menziesii*), and grand-fir (*Abies grandis*). Riparian meadows contained a diverse variety of deciduous shrubs, including black hawthorn (*Crataegus douglasii*), grey alder (*Alnus incana*) and willow (*Salix* spp.), and forbs, including cinquefoils (*Potentilla* spp.), Virginia strawberry (*Fragaria virginiana*), and corn lily (*Veratrum californicum*). Dry meadow grasslands consisted of varying mixes of both native and non-native grasses. Dominant native grasses included pinegrass (*Calamagrostis rubescens*) and blue wildrye (*Elymus glaucus*), and dominant non-native grasses included meadow foxtail (*Alopecurus pratensis*) and Kentucky bluegrass (*Poa pratensis*). The elevation of sites varied from 1100 to 1500 m. Mean seasonal temperature 2014–2017 ranged from 2 °C in the winter to 14 °C in the summer, with 63 cm of average annual precipitation mostly in the form of snow (PRISM Climate Group 2020).

2.2. Site selection

We placed 36 sampling grids within nine reaches and six major drainages of the Upper Grande Ronde River within the study area

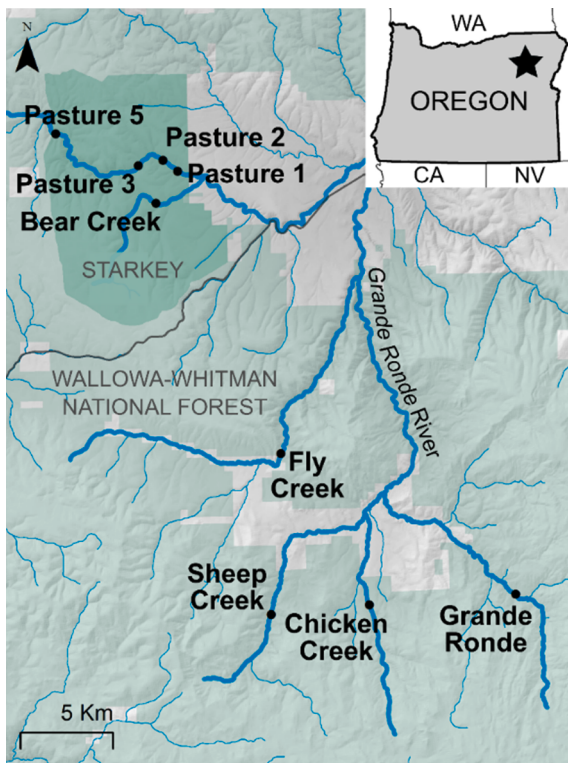


Fig. 1. Map of study area in the Upper Grande Ronde River watershed, Oregon, USA. Black points represent each of the nine reaches studied.

(Fig. 1). The Meadow Creek drainage was split into four reaches (Pastures 1, 2, 3, and 5) as part of previous and ongoing long-term forestry and rangeland management experiments within the Starkey Experimental Forest (Averett et al., 2017). We placed four 5×5 (15-m spacing between trap stations; 0.81 ha area including buffer) trapping grids within each reach. Grids were located entirely within the riparian floodplain when possible, either spanning or adjacent to the stream. Adjacent toe-slopes were also included within the grid if the floodplain was narrower than the grid dimensions. Trapping grids within a reach were 130 m apart (range 40–560 m) on average, except two adjacent grids in Pasture 3 (grids 5 and 6) which were 16 m apart because we were constrained by ungulate exclosure fencing, a stream, or a steep toe slope. We subjectively located grids to represent wide variations in the relative amounts of four vegetation cover types (conifer forest, riparian shrubs, grass, forbs) found within each reach, with the exception of Pasture 2, 3, and 5 where grid locations were pre-determined by ungulate exclosure fencing (Averett et al., 2017).

Various management activities had occurred associated with riparian restoration, timber management, and ungulate (cattle, deer, and elk) management across the study sites (Appendix 1; Rowland et al., 1997; [USFS] US Department of Agriculture, 2012; DeBano et al., 2016; Averett et al., 2017). Typical of the region, logging near our sites created a patchwork of stand ages, but no timber harvest or fuels management activities had occurred on forested portions of our grids for several decades (Skovlin 1991). Likewise, no recent wildfire or prescribed burning had taken place on study sites. Planting of trees and shrubs and limited in-stream coarse woody debris augmentations occurred in recent years at several sites (Appendix 1). Commonly planted species included ponderosa pine, black cottonwood (*Populus trichocarpa*), black hawthorn, golden currant (*Ribes aureum*), narrowleaf willow (*Salix exigua*), and Geyer's willow (*S. geyeriana*; Averett et al., 2017). Minimal growth of plantings across all sites occurred during the years of our data collection, and planted shrubs constituted only a small fraction of the total riparian shrub cover (Averett et al., 2017), so we considered the effects of these

management activities on the vegetation occurring in these four reaches to be minimal for the purposes of this study.

2.3. Vegetation cover types

In the summer of 2016, we mapped each trapping grid (with an additional 15-m buffer around grid edges) into discrete vegetation patches using trapping stations within each grid as reference points. Patches were visually distinguished from each other by a >25% change in one or more of the four cover types as observed from the ground. Estimated coverage for each cover type within a patch was then quantified using a modified octave scale to account for rare, but potentially important cover types (e.g., Gauch, 1982): 0, <1%, 1–5%, 6–10%, 11–25%, 26–50%, 51–75%, and 76–100%. Additionally, we estimated the percentage (continuous scale of 0–100% in 10% increments) of each cover type that was native and non-native. We multiplied the percent of each cover type by the total area of a patch to estimate the area of the cover type within each patch. This was repeated for every patch, and the area of each cover type was then summed across patches to derive a grid-level area estimate of cover.

2.4. Small mammal trap surveys

At each of the 25 stations within each grid, we placed two traps, one Sherman trap (H.B. Sherman Traps, Tallahassee, FL, USA) and one Tomahawk 201 trap (Tomahawk Live Trap, Hazelhurst, WI, USA) on the ground within 2 m of station center. Each trap was covered with a waxed cardboard carton and placed a plastic nest-box insulated with polyester batting inside to reduce trapping-related mortalities from exposure to weather. We baited traps with a mixture of almond butter, oats, and molasses. Traps were opened for four nights each during two consecutive weeks (400 trap nights total per grid per year). We collected mark-recapture data from June through August during 2014–2017 at Pasture 1, 2, 3, and 5, and during 2015–2017 on the remaining reaches.

We recorded species, age, sex, mass (g), and reproductive condition of all captured small mammals, except snowshoe hares (*Lepus americanus*) and striped skunks (*Mephitis mephitis*) which were released without further processing. All squirrels, chipmunks, woodrats, mice, voles, and weasels were marked with uniquely identifying ear tags (model #1005–1; National Band and Tag Co., Newport, KY). All individuals were released at the location of capture. Our project was approved by the Starkey Institutional Animal Care and Use Committee (#92-F-0004) and protocols were in accordance with standard animal care guidelines of the American Society of Mammalogists (Sikes et al., 2016).

2.5. Data analysis

We calculated minimum number known alive (MNKA) for each species, which is the sum of the number of unique animals captured. We then estimated abundance, spatial associations of abundance, overall site suitability, and capture probability using a multispecies hierarchical abundance model for species with > 50 MNKA across all sampling periods. This model assumes populations are closed during primary trapping occasions, marks are not lost, and that heterogeneity in capture probability is appropriately modeled (Huggins, 1991, 1989). The model estimated abundance conditional on the number of unique individuals captured for each site $\times$ year combination and the probability of capturing each individual once within that specific primary occasion, and estimated capture probability using individual encounter histories for marked individuals. We estimated grid- and primary-trapping-occasion abundance for 10 species on 36 grids each trapped for at least three years. We also evaluated the number of occasions where individuals were captured in more than one grid as a measure of grid interdependence, since some grids were in close proximity to each other.

We used a standard observation model for capture-recapture data

($y_{s,i,k,t}$) to estimate capture probability $p_{s,i,k,t}$ for individual i , of species s , during primary occasion k , and secondary occasion t , as a Bernoulli distributed random variable.

$$y_{s,i,k,t} \sim \text{Bernoulli}(p_{s,i,k,t})$$

We modeled variation in p on the logit scale as a function of a species-specific random intercept, a species-specific behavioral response to previous capture, and a reach- and species- level zero-centered random effect ($p_{s,r}$). We included the species-level random intercept (α_1) to account for species-specific variation in mean detection probability, where hyperparameter μ_{species} is the mean capture probability across species, and σ_{species} is the variation in mean capture probability across species. The species-specific behavioral response (α_2) is the effect of recapture on capture probability, $\text{Recapture}_{s,i,t}$ was 1 if an individual was previously captured within a primary sampling occasion and 0 otherwise, where hyperparameter $\mu_{\text{recapture}}$ is the mean effect of recapture on capture probability, and $\sigma_{\text{recapture}}$ is the variation in the effect of recapture across species. We included a reach (r) and species-specific α_3 to account for unmeasured species-specific spatial variation in detection probability.

$$\text{logit}(p_{s,r}) = \alpha_1 + \alpha_2 * \text{Recapture}_{s,i,t} + \alpha_3_{s,r}$$

$$\alpha_1 \sim \text{Normal}(\mu_{\text{species}}, \sigma_{\text{species}})$$

$$\alpha_2 \sim \text{Normal}(\mu_{\text{recapture}}, \sigma_{\text{recapture}})$$

$$\alpha_3_{s,r} \sim \text{Normal}(0, \sigma_{\text{species,reach}})$$

We derived the probability of first capture $p_{s,r}^{1st}$ for individuals of each species and reach.

$$\text{logit}(p_{s,r}^{1st}) = \alpha_1 + \alpha_3_{s,r}$$

From $p_{s,r}^{1st}$ we then calculated the probability ($p_{s,r}^*$) that individuals of each species in each reach, was captured at least once during t secondary occasions.

$$p_{s,r}^* = 1 - \prod_{t=1}^t (1 - p_{s,r}^{1st})$$

Species-, grid-, and primary trapping occasion-specific abundances ($N_{s,g,k}$) were estimated assuming a binomial process model conditional on MNKA for each species, grid, and primary trapping occasion ($\text{MNKA}_{s,g,k}$) and $p_{s,r}^*$.

$$\text{MNKA}_{s,g,k} \sim \text{Binomial}(p_{s,r}^*, N_{s,g,k})$$

where g is a subset of r . We assumed that abundances for each species and class ($N_{s,g,k}$) were Poisson distributed with mean $\lambda_{s,g,k}$ (Converse and Royle, 2012). We modeled the effects of four grid-level covariates and a grid- and species-specific random intercept on mean abundance on the log scale. However, we used a zero-inflation term (I_s) to account for variation in overall species-specific site suitability (ϕ_s) across primary occasions due to the number of primary occasions where we did not capture any individuals of a species.

$$I_s \sim \text{Bernoulli}(\phi_s)$$

$$N_{s,g,k} | I_s \sim \text{Poisson}(\lambda_{s,g,k} * I_s)$$

$$\log(\lambda_{s,g,k}) = \beta_0 + \beta_1 * \text{Shrub}_g + \beta_2 * \text{Conifer}_g + \beta_3 * \text{Forb}_g + \beta_4 * \text{Grass}_g$$

$$\beta_{s,g,k} \sim \text{Normal}(\mu_{\text{abundance}}, \sigma_{\text{abundance}})$$

$$\beta_1 : \beta_4 \sim \text{Normal}(\mu_{\text{predictor}}, \sigma_{\text{predictor}})$$

We estimated hyperparameters of the random effect distributions

using noninformative priors. We considered three sets of priors for model parameters α and β , where α indicates the set of parameters for $p_{s,r}$ and β indicates the set of parameters for $\lambda_{s,g,k}$.

We evaluated goodness-of-fit for our model using a posterior predictive check approach (Gelman et al. 2013) to estimate a Bayesian p -value (Meng, 1994). We first simulated new realizations of the $\text{MNKA}_{s,g,k}$ data from the posterior distributions for $p_{s,r}^*$ and $N_{s,g,k}$. We then calculated Freeman-Tukey (Freeman and Tukey, 1950) test statistics for the observed and simulated datasets. The Bayesian p -value was derived as the proportion of times the test statistic for the simulated data was higher than the test statistic for the observed data. Perfect agreement between the observed and simulated data occurs when the Bayesian p -value equals 0.5, and a Bayesian p -value near zero or one indicates a lack of fit.

We performed a post-hoc analysis to consider changes in species-specific responses to grid-level coverage of non-native and native grasses because most non-native plant species were from this cover type and grasses could be identified reliably during our vegetation surveys. We refit the inferential model twice replacing the grass covariate with the coverages of non-native and native grasses. We then contrasted changes in the magnitude, direction, and precision of the mean coefficient estimates relative to the total grass covariate.

We fit the model using JAGS software version 4.3.0 (Plummer, 2003) through the jagsUI package version 1.5.1 (Kellner, 2019) in R version 3.6.1 (R Core Team, 2019). Data and an R script for the final model are provided in Appendix 2. Each model was run with three independent chains consisting of a 20,000-iteration adaptation period, a 50,000-iteration burn-in period, and a 50,000-iteration sampling period to estimate the posterior distribution. To improve convergence, continuous predictor variables were scaled by subtracting the mean and dividing by the standard deviation. We assessed model convergence by visual examination of trace plots and we computed the Brooks–Gelman–Rubin convergence diagnostic ($\hat{R}$; Brooks and Gelman, 1998). We describe parameter posterior distributions by their mean and 95% credible interval (hereafter CI) and assessed the strength of individual effects based on the degree to which the CI for the estimate overlapped zero. We considered covariates with a CI that did not overlap zero strong, covariates with < 10% of the CI overlapping zero weak, and covariates with > 10% of the CI overlapping zero to have no effect.

3. Results

3.1. Small mammal community

We captured 9131 small mammals of 20 species during 44,611 trap nights (21991 Tomahawk and 22,620 Sherman trap nights) from 2014 to 2017. Ten species had sufficient numbers of captures (≥ 50) for further analysis (Table 1). We captured the following species infrequently and excluded them from analysis: long-tailed weasels (*Mustela*

Table 1

Total minimum number known alive (MNKA; and number of recaptures) for ten common small mammal species live-trapped at 36 grids. Each grid was surveyed for two weeks during summer from 2014 to 2017 in the Upper Grande Ronde River watershed, Oregon, U.S.A.

Common name	MNKA (no. recaptures)
Bushy-tailed woodrat	275 (169)
Columbian ground squirrel	64 (31)
Deer mouse	1218 (415)
Golden-mantled ground squirrel	117 (67)
Long-tailed vole	422 (69)
Montane vole	1285 (196)
Northern flying squirrel	114 (36)
Vagrant shrew	185
Western jumping mouse	379 (107)
Yellow-pine chipmunk	1545 (665)

fenata; $n = 7$), mink (*Neovison vison*; $n = 2$), Pacific shrews (*Sorex pacificus*; $n = 2$), northern pocket gophers (*Thomomys talpoides*; $n = 12$), southern red-backed voles (*Myodes gapperi*; $n = 14$), red squirrels (*Tamiasciurus hudsonicus*; $n = 42$), water voles (*Microtus richardsoni*; $n = 6$), and short-tailed weasel (*Mustela erminea*; $n = 2$).

3.2. Model assessment

Posterior distributions for all parameters were similar for all three prior set specifications. Thus, we report inferences from model results obtained using prior set 1. Visual inspection of trace plots and estimates of the Brooks–Gelman–Rubin convergence diagnostic indicated convergence ($R < 1.03$) was obtained for all monitored parameter estimates. The Bayesian p-value estimated from the posterior predictive checks was 0.43 indicating adequate fit for all models. This suggests that both candidate models were capable of generating data consistent with the observed data.

3.3. Capture probability

Recapture probabilities (c) were lower than initial capture probabilities for all species except bushy-tailed woodrats, and the ranges of mean estimates for the two probabilities overlapped for yellow-pine chipmunks and golden-mantled ground squirrels. Recapture probabilities overall were consistent within a species ($\sigma_{\text{recapture}} = 1.57$, CI: 0.86–2.85). Vagrant shrews ($\bar{c}$ range: 0.0035–0.004) were least likely to be recaptured, primarily due to their high mortality. Recapture probability increased in likelihood as follows: long-tailed voles ($\bar{c}$ range: 0.058–0.065), montane voles ($\bar{c}$ range: 0.070–0.090), western jumping mice ($\bar{c}$ range: 0.085–0.103), northern flying squirrels ($\bar{c}$ range: 0.095–0.111), deer mice ($\bar{c}$ range: 0.116–0.170), Columbian ground squirrels ($\bar{c}$ range: 0.150–0.191), yellow-pine chipmunks ($\bar{c}$ range: 0.161–0.225), golden-mantled ground squirrel ($\bar{c}$ range: 0.227–0.289), and bushy-tailed woodrats ($\bar{c}$ range: 0.302–0.391). Capture probabilities varied among species ($\sigma_{\text{species}} = 5.01$, CI: 0.24–9.75) and among species and reaches ($\sigma_{\text{species,reach}} = 4.99$, CI: 0.25–9.75). Capture probability ranged from 0.171 (CI: 0.125–0.223 for northern flying squirrels at Pasture 2 during 2014–2017) to 0.310 (CI: 0.277–0.344 for bushy-tailed woodrats at all Bear Creek from 2015 to 2017).

The overall probability of an individual being captured at least once during a primary occasion was high for all of our species, as follows: vagrant shrews ($\bar{p}^*$ range: 0.815–0.870), long-tailed voles ($\bar{p}^*$ range: 0.813–0.848), montane voles ($\bar{p}^*$ range: 0.779–0.856), western jumping mice ($\bar{p}^*$ range: 0.820–0.877), northern flying squirrels ($\bar{p}^*$ range: 0.772–0.825), deer mice ($\bar{p}^*$ range: 0.849–0.939), Columbian ground squirrels ($\bar{p}^*$ range: 0.873–0.931), yellow-pine chipmunks ($\bar{p}^*$ range: 0.797–0.900), golden-mantled ground squirrel ($\bar{p}^*$ range: 0.838–0.913), and bushy-tailed woodrats ($\bar{p}^*$ range: 0.876–0.948). Number of individuals captured in more than one grid relative to total number of captures was low (bushy-tailed woodrat: 2.1%, Columbian ground squirrel: 2.3%, deer mouse: 1.3%, golden-mantled ground squirrel: 5.3%, long-tailed vole: 0%, montane vole: 0.1%, northern flying squirrel: 3.0%, western jumping mouse: 2.1%, yellow-pine chipmunk: 2.3%).

3.4. Relative abundances and site suitability

Overall site suitability across all grids ranged from 0.239 (CI: 0.163–0.326) for Columbian ground squirrels to 0.987 (CI: 0.953–0.999) for deer mice (Fig. 2). Across all four years of trapping, we captured deer mice most frequently (94% of grids; 113 out of 120 grid-year combinations) and Columbian ground squirrels least often (21% of grids; 25 out of 120 grid-year-combinations). Abundance across grids and years varied within species, with some grids having consistently higher abundances for some species (Fig. 3 and Fig. 4).

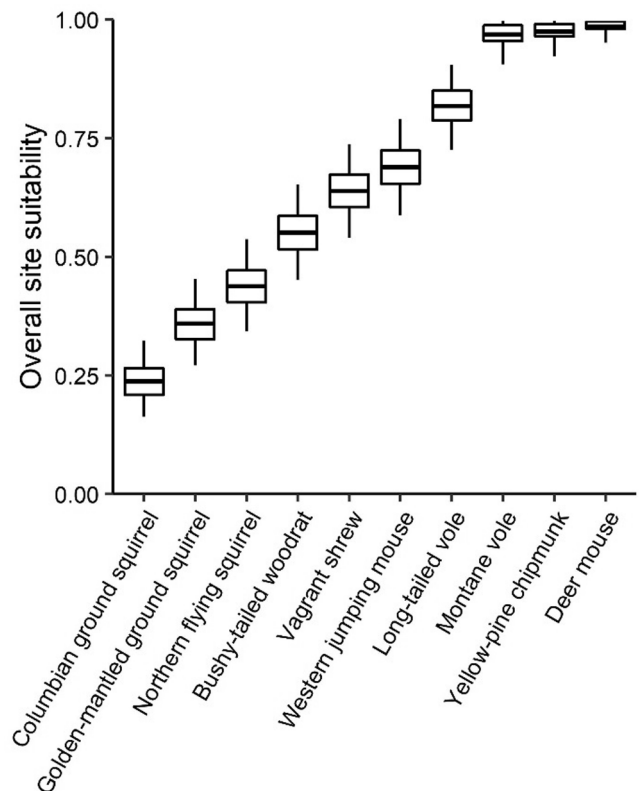


Fig. 2. Overall site suitability estimates for 10 small mammal species live-trapped on 36 grids from 2014 to 2017 in the Upper Grande Ronde River watershed, Oregon, USA.

3.5. Cover type associations

The relative proportions of cover types varied across reaches (Fig. 5). Within-reach variation was lowest for Pasture 2 and highest for Chicken Creek.

Cover type varied across grids. For example, conifer cover ranged from 0% (Grid 5) to 68% (Grid 28); shrub cover ranged from 0% (Grid 25) to 41% (Grid 32); forb cover ranged from 0.07% (Grid 23) to 58% (Grid 5); and grass cover ranged from 0.10% (Grid 28) to 69% (Grid 2) (Fig. 5). We found strong associations between abundance and vegetation cover types for five species (Fig. 6). Both bushy-tailed woodrats and montane voles were negatively associated with grass. There were strong positive associations with shrubs for bushy-tailed woodrats, deer mice, and yellow-pine chipmunks, and a negative association for montane voles. There was a strong positive association with conifers for yellow-pine chipmunks, and a strong negative association with conifers for both vole species. We found no strong association with forbs for any species (Fig. 6). In our post-hoc parameterizations of non-native and native grass cover, we observed some sensitivity in mean grass covariate effect and coverage estimates through changes in the direction, magnitude and precision of coefficient estimates. But strong species-specific coefficient estimates from the first grass parameterization were smaller in magnitude than for the alternative grass parameterizations (Appendix 3).

4. Discussion

Here we provide the first estimates of summer relative abundances for a community of small mammals occupying restored riparian areas in the Blue Mountains physiographic province. Our findings highlight several associations between small mammal species and vegetation cover types that are often the broad focus of riparian restoration

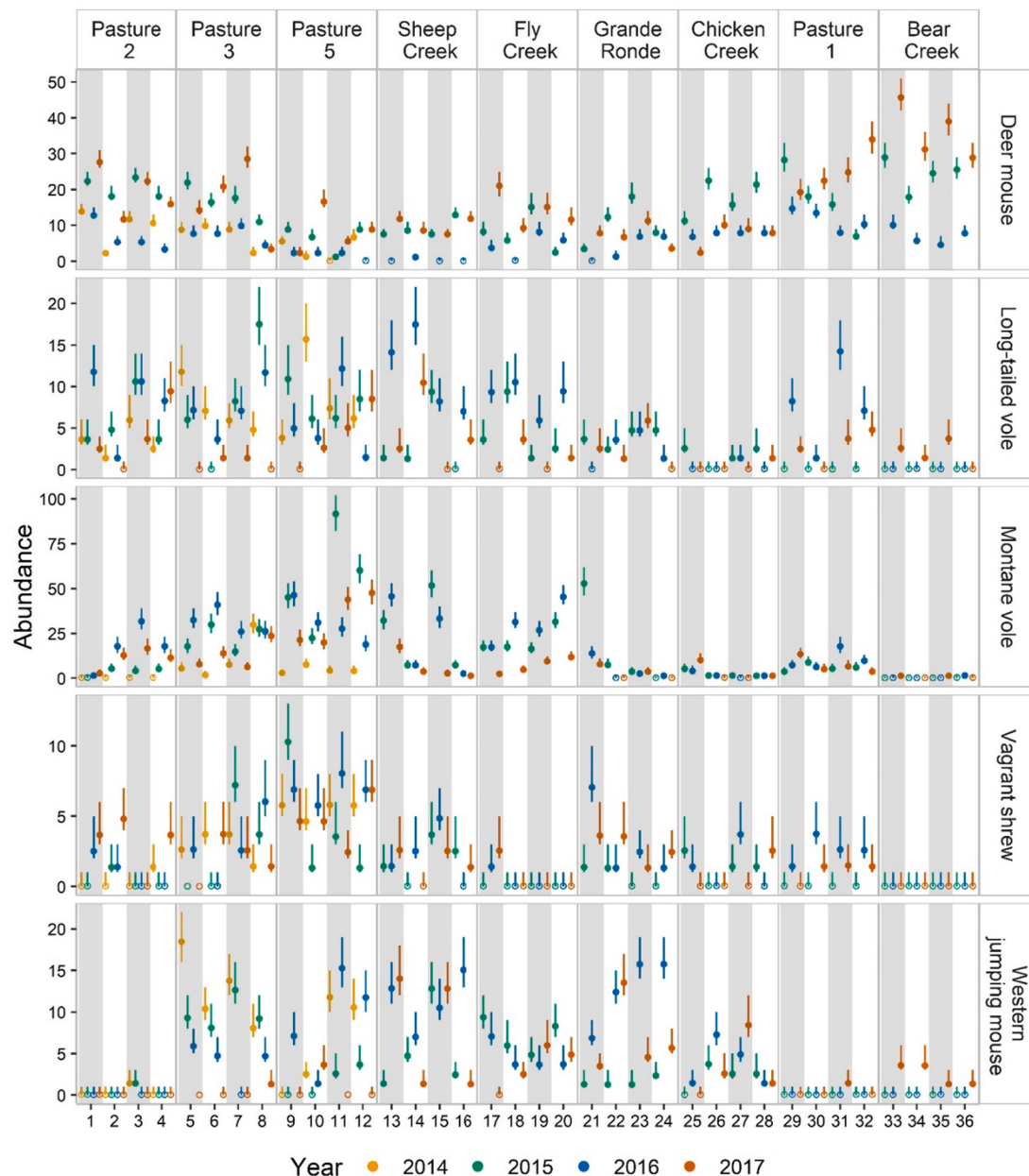


Fig. 3. Grid-level abundance estimates of mice, voles, and shrews estimated using a multispecies hierarchical abundance model and live-trapping mark-recapture data recorded 2014–2017 in the Upper Grande Ronde River watershed, Oregon, USA. X-axis numbering represents individual trapping grids. Solid points represent mean abundance estimates, open points represent abundance estimates that contain zero in the 95 % CI. Vertical bars depict the 95% credible intervals, which incorporate uncertainty due to site suitability. Shading is for grid-level delineation.

treatments. This was a retrospective study, and our results should be viewed within the constraints of hypothesis generating and exploratory studies. By grouping plants into four cover types (forbs, grass, shrubs, trees), effects associated with interactions between and among cover types may have been undetected. We also did not assess effects that individual plant species or the structural arrangement of those species may have in supporting habitat for the species captured during this study. Additionally, we did not measure other extrinsic factors (e.g., species-specific food resources, animal behaviors, soil type, home range size) that may influence species-habitat relationships. However, our results show several associations between small mammal species and cover types that may be useful for predicting changes in small mammal abundances at a relatively small (e.g., 1-ha) scale associated with common restoration and other management activities within riparian areas.

We expected that relative abundances of forest-associated small mammals would be greater with higher levels of conifer cover. This prediction was supported for yellow-pine chipmunks which had a strong positive association with both conifer and shrub cover. This is consistent with previous research that found yellow-pine chipmunks dispersing and caching ponderosa pine and Douglas-fir seeds, in addition to other seeds and berries from endemic shrubs such as antelope bitterbrush (*Purshia tridentata*; Vander Wall, 1994; Smith and Maguire, 2004; Kuhn and Vander Wall, 2008; Vander Wall and Jenkins, 2011). We did not find any strong association with conifer cover for northern flying squirrels, bushy-tailed woodrats, or golden-mantled ground squirrels. Flying squirrels are forest obligates, but conifer cover was <50% for most of our grids, and our grid size was much smaller than reported home ranges for individual flying squirrels. Thus, low abundances and low capture probabilities, relative to previous findings, may be partly

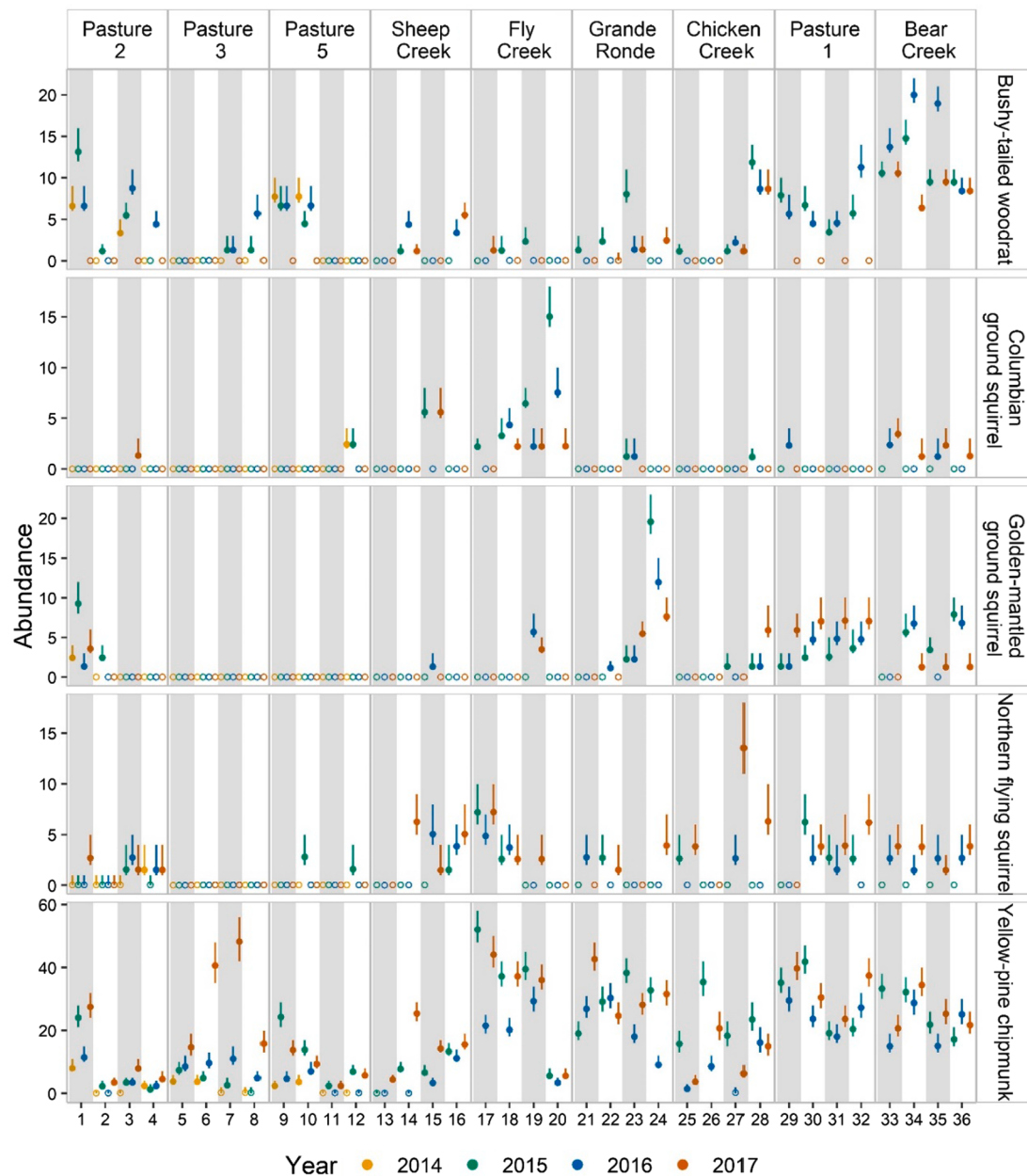


Fig. 4. Grid-level abundance estimates of squirrels, chipmunks, and woodrats estimated using a multispecies hierarchical abundance model and live-trapping mark-recapture data recorded 2014–2017 in the Upper Grande Ronde River watershed, Oregon, USA. X-axis numbering represents individual trapping grids. Solid points represent mean abundance estimates, open points represent abundance estimates that contain zero in the 95% CI. Vertical bars depict the 95% credible intervals, which incorporate uncertainty due to overall site suitability. Shading is for grid-level delineation.

due to a small grid size (relative to individual home ranges of flying squirrels) and poor overall site suitability which limited our ability to detect strong associations with conifer cover. We captured most bushy-tailed woodrats in forested areas with either a robust shrub component combined with a sparse overstory canopy, or in high stem-density forest with little understory. For golden-mantled ground squirrels, trees appear to be an overall component of habitat but percent conifer cover alone would not necessarily capture the non-forest component of ground squirrel habitat such as meadows, or any associations with vegetation complexity or structure.

Conversely, we expected that as conifer cover increased, the relative abundances of grassland associated species would decrease. This prediction was supported for two species, long-tailed voles and montane voles, both of which had strong negative associations with conifer cover. These two vole species are known to occupy open canopy, grassland

habitats and primarily consume grasses, sedges, and forbs, but they have also been observed to opportunistically forage on conifer seedlings and saplings (Smolen and Keller, 1987; Sullivan et al., 2001). We suggest further research is needed to explore the extent that voles forage into forest edges and open canopy forests, because young conifers, including those planted as part of riparian restoration efforts, may be vulnerable to girdling and tree damage caused by voles (e.g., Sullivan et al., 2001).

We expected that the abundance of most small mammal species would be positively associated with shrub cover. This prediction was supported for woodrats, chipmunks, and deer mice. However, a strong negative relationship was found between shrubs and montane voles. Our data are consistent with other studies that link woodrat habitat, in part, to woody shrubs and dense understory (Carey et al., 1999; Gray et al., 2019; Johnston and Anthony, 2008; Lehmkuhl et al. 2008; Smith, 1997). Our study also supports other research findings that deer mice are

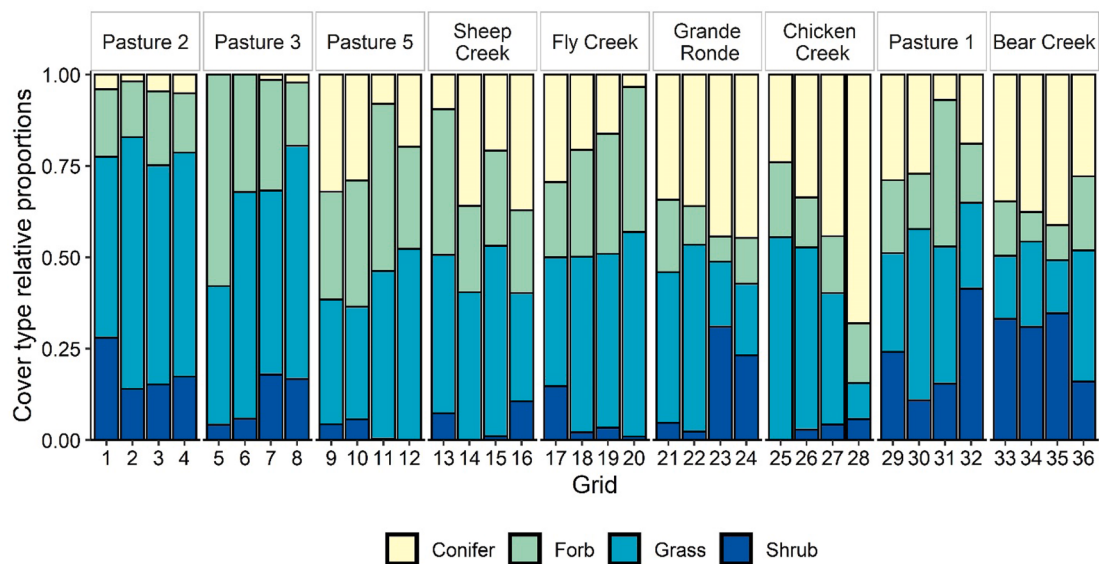


Fig. 5. Summary of the relative proportions of four vegetation cover types on 36 grids within nine stream reaches in the Upper Grande Ronde River watershed, Oregon, USA.

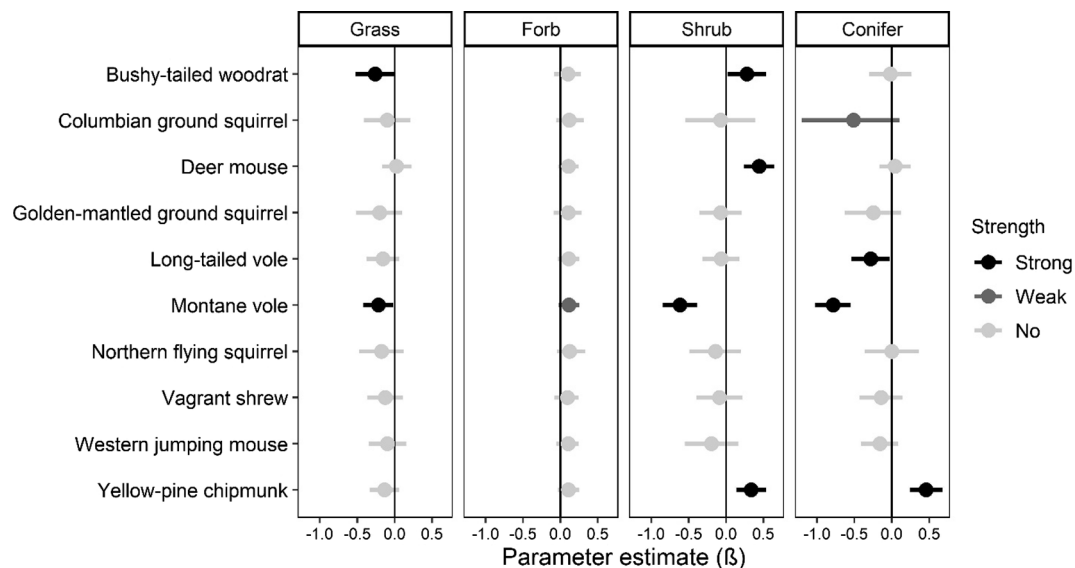


Fig. 6. Estimated coefficient estimates (β ; log-scale) and 95% credible intervals for species-specific vegetation cover type associations with abundance for 10 small mammal species captured during the summer 2014–2017 in the Upper Grande Ronde River watershed, Oregon, USA. Covariate strength of the cover type effect was interpreted as a strong (black), weak (dark grey), or no (light grey) association.

positively associated with shrub cover (Ceradini and Chalfoun, 2017a; Doyle, 1990; Gray et al., 2019; Hamilton et al., 2015; Johnston and Anthony, 2008). Some studies have failed to find consistent vegetation associations for deer mice, but this may be due to the ability of deer mice to adapt quickly to changes in resource availability and competition across diverse cover types (Smith and Maguire, 2004; Stapp and Van Horne, 1997). The strong negative association of montane voles with shrub cover, coupled with their strong negative association with conifer cover, further suggests a strong preference for meadows dominated by grasses and forbs by montane voles in the Upper Grande Ronde River watershed. Montane voles may exclude long-tailed voles from grassy meadows as the two vole species rarely co-occur in the same patches and this competition may help explain the lack of any observed relationship between forbs, grass, and shrubs and long-tailed voles (Anich and Hadly, 2013; Parmenter and MacMahon, 1983; Randall and Johnson, 1979; Sera and Early, 2003). Related research on the effects of heterospecific

densities for other small mammal species highlight the gap in knowledge on how deterministic processes, rather than vegetation structure, influence abundance (Le Borgne et al., 2018; Denomme-Brown et al., 2021).

We expected the abundances of montane and long-tailed voles, western jumping mice, Columbian ground squirrels, and vagrant shrews to be positively associated with grass and forb cover. However, we found a strong negative relationship between montane voles and grass, a weak positive relationship between montane voles and forbs, and no other associations for other grassland species captured. Most small mammals found in grass- or forb-dominated ecosystems have dietary needs that are specific to individual grass and forb species, either due to their physiology or due to the palatability, digestibility, energetics, seasonality, or nutrient content of individual forb and grass species (Peters 2007; Poe et al., 2019). Therefore, cover types as we measured them may perform poorly for generalizing fine-scale vegetation needs for

these species. For example, montane voles likely specialize in specific forbs, and not all forbs would necessarily be palatable for voles.

Other habitat variables not evaluated during this study could account for why we did not observe strong cover type relationships for some species. For example, we did not evaluate the suitability of soil for burrowing which could help explain why we found no associations between forbs and ground squirrels. Species like Columbian ground squirrels form colonies and require soil suitable for building underground burrow systems (Elliott and Flinders, 1991). Grids in some reaches were comprised of rocky cobble shallow soil or were saturated with water for much of the year and may not have been suitable for colonization by ground squirrels, even though forb cover in these grids was similar in extent to grids that did support ground squirrels. Likewise, captures of vagrant shrews were relatively low and heterogeneous across grids compared to some other species, suggesting that they may be operating at scales much finer than our grid-level vegetation assessment could detect. Moreover, their reliance on insects and other invertebrates may not be well correlated with our cover types. We also found no clear relationships between cover types and jumping mice, which are primarily granivores but feed on a wide variety of grasses, forbs and shrubs (Hart et al. 2004). In addition to cuing into food resources across more than one cover type, they may have been cuing into different food resources throughout the summer that may have been different, for example, in June compared to August.

Our post-hoc analysis found estimates of species-specific cover type associations might be sensitive to coverage of non-native grasses and we encourage future studies to explore the relationships among mammal abundance and non-native grasses more thoroughly. With increasing establishment of non-native grasses, the diversity and abundance of native grasses have declined in many Pacific Northwest grasslands (Bradley et al., 2018; Kerns et al., 2020). For our study sites, these non-native grasses included cheatgrass (*Bromus tectorum*), ventenata (*Venttenata dubia*) and meadow foxtail (*Alopecurus pratensis*), the latter having been intentionally planted in prior livestock forage experiments in some grids (e.g., Grid 502 at Starkey). With the expansion and establishment of many non-native grass species, further research is needed on the species-specific relationships between grasses and the potential to support native herbivorous small mammal populations (Bricker et al., 2010; Callaway and Maron, 2006; Halpern and Underwood, 2006; Ceradini and Chalfoun, 2017b).

In the future, we expect the various restoration plantings (primarily trees and shrubs) that have occurred prior to our study should result in improved habitat for many small mammal species as these plantings mature, but the spacing and extent of these plantings may have different effects. With the possible exception of yellow-pine chipmunks, we do not anticipate any major changes in abundances due to conifer planting because they are typically planted at a relatively low density, compared to hardwood trees and shrubs, in restoration projects to improve conditions for fish (providing some shade and an eventual source of in-stream woody debris), in contrast to densities more typical for forest restoration. For example, widely dispersed conifers are not likely to result in higher abundances of flying squirrels and bushy-tailed woodrats, because these species appear to need adequate protective cover from predators provided by multi-layered mature forest or high-stem density younger forest (Wilson and Forsman 2013). However, planting of conifer trees could be used to improve connectivity across riparian areas to adjacent forest for these species. We hypothesize that planted shrubs (e.g., black hawthorn, golden currant, and willow) will have the earliest and the greatest impacts to the small mammal community, with increases in yellow-pine chipmunk, bushy-tailed woodrat, and deer mouse abundance. Montane vole abundance will likely decline as shrub cover increases, while long-tailed voles may not respond strongly to an increased cover and volume of shrubs over time.

There may be opportunities to help diversify the small mammal community by planting native forbs and grasses in areas dominated by non-native grasses. A detailed list of plant species consumed by each

small mammal is lacking, suggesting the need for more detailed diet studies for many of the species we found. In the meantime, a prudent approach might be to consider planting a diverse array of native grasses and forbs appropriate for the soil, moisture, and light conditions at each site. Such efforts with forbs may also improve conditions for the diverse pollinator community occupying these riparian areas (DeBano et al. 2017; Roof et al. 2018).

The multi-species abundance model formulation presented here is a powerful, relatively new tool for analyzing mark-recapture data. By sharing information across spatially or temporally stratified datasets investigators can increase the precision of estimates through partial pooling (e.g. Bowden et al., 2003; Converse et al., 2006) and expand the scope of analysis into strata where data might be too sparse to estimate independently (Converse and Royle 2012; Sollman et al., 2015; Duarte et al. 2017). Similarly, by extending the framework for joint analysis of stratified mark-recapture data for single species to a multispecies framework, we were able to extend the scope of our analysis to data poor species by pooling information with data rich species (Zipkin et al., 2009, 2010). These are particularly important benefits when analyzing small mammal mark-recapture datasets, which are typically characterized by stratified sampling designs that simultaneously capture multiple species with low capture probabilities. During analysis these datasets are often reduced to a subset of the total captured species that has suitably high numbers of individual captures and recaptures. For example, Weldy et al. (2019) reported analysis for the four most commonly captured species from a total of 21 captured species, because data for the remaining 17 species were too sparse to independently estimate capture probability. In contrast, we were able to obtain reasonably precise estimates of group-specific abundance for 10 of 20 captured species, including Columbian ground squirrels, bushy-tailed woodrats, northern flying squirrels, and western jumping mice which are largely understudied in this region, by using our contemporary modelling framework.

5. Conclusions

Our stand-level findings suggest that there will be changes over time to the small mammal community in response to riparian restoration which may influence the roles that each species play, including serving as important prey for diverse avian and mammalian predators. Our data could be used to inform riparian planting prescriptions, especially if a goal of the plantings is to diversify small mammal species, intentionally favor some species at the exclusion of others, or promote the abundance of one or more species without losing species diversity. Our data can also be used as baseline conditions to periodically monitor changes to the small mammal community occurring across our 36 sites as a result of plantings, changes in ungulate herbivore levels (both domestic and wild), or other management activities planned for the reaches we evaluated in this study. We suggest that riparian restoration efforts continue to consider consequences of plantings and other stream modifications to the diverse fauna associated with riparian areas, even if the primary focus is salmonid rehabilitation, as an integrated approach may lead to a more comprehensive understanding of the linkages, trophic dynamics, and ecosystem processes and services within riparian areas that could benefit all the species using these disproportionately diverse ecosystems.

CRedit authorship contribution statement

Lindsay S. Millward: Software, Validation, Formal analysis, Data curation, Writing – original draft. **Todd M. Wilson:** Conceptualization, Methodology, Investigation, Writing – original draft, Supervision, Project administration, Funding acquisition. **Matt J. Weldy:** Methodology, Software, Formal analysis, Writing – original draft. **Mary M. Rowland:** Conceptualization, Resources, Writing – review & editing, Funding acquisition. **Adam Duarte:** Software, Methodology, Writing – review & editing. **Damon B. Lesmeister:** Methodology, Writing –

review & editing, Supervision. **William J. Ripple:** Conceptualization, Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Mike Wisdom, Mark Penninger, and Joshua Chapman for

facilitating funding and providing logistical support for this project. Field technicians included Amanda Bintliff, Emily Burkhart, Erin Halcomb, Kate Hopwood, DeAnne Jacobsma, Mikayla Kelly, and Veronica Stevens. Kent Coe was instrumental in assisting with vegetation surveys. We thank Sydney Andersen and McKenna Marshall for assisting with data proofing and processing. Funding was provided by the US Forest Service Pacific Northwest Research Station, US Forest Service Region 6 Regional Office, the Wallowa-Whitman National Forest, and Oregon State University. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the US Government of any product or service.

Appendix 1

Summary of riparian tree and shrub plantings (completion year), ungulate grazing (during study period), and other recent riparian management activities (completion year) for grids that were live-trapped for small mammals during the summers of 2014–2017 in the Upper Grande Ronde River watershed, Oregon.

Grid #	Reach	Restoration Planting	Ungulate Grazing				Other Recent Management Activities (year)
			Deer	Elk	Cattle	Sheep	
1	Meadow Creek – Pasture 2	2013	x	x			Wood and boulder placement in stream (2012)
2	Meadow Creek – Pasture 2	2013	x	x			Wood and boulder placement in stream (2012)
3	Meadow Creek – Pasture 2	2013					Wood and boulder placement in stream (2012); ungulate exclosures (2012)
4	Meadow Creek – Pasture 2	2013					Wood and boulder placement in stream (2012); ungulate exclosures (2012)
5	Meadow Creek – Pasture 3	2013					Wood and boulder placement in stream (2012); ungulate exclosures (2012)
6	Meadow Creek – Pasture 3	2013					Wood and boulder placement in stream (2012); ungulate exclosures (2012)
7	Meadow Creek – Pasture 3	2013	x	x			Wood and boulder placement in stream (2012)
8	Meadow Creek – Pasture 3	2013	x	x			Wood and boulder placement in stream (2012)
9	Meadow Creek – Pasture 5	2014	x	x			Wood and boulder placement in stream (2013)
10	Meadow Creek – Pasture 5	2014	x	x			Wood and boulder placement in stream (2013)
11	Meadow Creek – Pasture 5	2014					Wood and boulder placement in stream (2013); ungulate exclosure (2014)
12	Meadow Creek – Pasture 5	2014					Wood and boulder placement in stream (2013); ungulate exclosure (2014)
13	Sheep Creek	2014	x	x			Wood placement in stream (2014)
14	Sheep Creek	2014	x	x			Wood placement in stream (2014)
15	Sheep Creek	2014	x	x			Wood placement in stream (2014)
16	Sheep Creek	2014	x	x			Wood placement in stream (2014)
17	Fly Creek	2010	x	x	x	x	Wood placement in stream (2009)
18	Fly Creek	2010	x	x	x	x	Wood placement in stream (2009)
19	Fly Creek	2010	x	x	x	x	Wood placement in stream (2009)
20	Fly Creek	2010	x	x	x	x	Wood placement in stream (2009)
21	Chicken Creek	2015	x	x			Wood placement in stream (2014)
22	Chicken Creek	2015	x	x			Wood placement in stream (2014)
23	Chicken Creek	No	x	x			None
24	Chicken Creek	No	x	x			None
25	Upper Grande Ronde	2011	x	x			Mine tailing and road rehabilitation (2009); wood placement in stream (2010)
26	Upper Grande Ronde	2011	x	x			Mine tailing and road rehabilitation (2009); wood placement in stream (2010)
27	Upper Grande Ronde	2011	x	x			Mine tailing and road rehabilitation (2009); wood placement in stream (2010)
28	Upper Grande Ronde	2011	x	x			Mine tailing and road rehabilitation (2009); wood placement in stream (2010)
29	Meadow Creek – Pasture 1	2013	x	x			Wood and boulder placement in stream (2012)
30	Meadow Creek – Pasture 1	2013	x	x			Wood and boulder placement in stream (2012)
31	Meadow Creek – Pasture 1	2013	x	x			Wood and boulder placement in stream (2012)
32	Meadow Creek – Pasture 1	2013	x	x			Wood and boulder placement in stream (2012)
33	Bear Creek	2011	x	x	x		Wood placement and road removal (2010)
34	Bear Creek	2011	x	x	x		Wood placement and road removal (2010))
35	Bear Creek	2011	x	x	x		Wood placement and road removal (2010)
36	Bear Creek	2011	x	x	x		Wood placement and road removal (2010)

Appendix 2

JAGS code for the multispecies hierarchical abundance model, conditional on first capture, which links site- species- and time-specific counts of marked individuals with individual mark-recapture encounter histories. The code is annotated with brief descriptions of model components. Parameter indexing in the code is different than in the text.

```

library(jagsUI)
data <- list(
  y = y,
  #beta_Ind = c(1,1,1,1,0,0,0,0,0),
  beta_Ind = beta_Ind,
  iX = iX,
  X = X,
  MNKA = MNKA,
  RECAP = RECAP,
  n_sp = 10,
  n_yr = 4,
  n_b = 4,
  n_stratum = 120,
  n_block = 9,
  M = M
)
cat("
  model {
    #Priors

    hyper[1,1] ~ dnorm(0, 0.000001) # prior set 1
    #hyper[1,1] ~ dunif(-10,10) # prior set 2
    #hyper[1,1] ~ dnorm(0, 0.001) # prior set 3
    hyper[1,2] ~ dunif(0, 10) # SD hyperparameter for sigma_stratum
    hyper[1,3] <- hyper[1,2]*hyper[1,2] # Var hyperparameter for var_stratum
    hyper[1,4] <- 1/(hyper[1,2]*hyper[1,2])# Tau hyperparameter for tau_stratum

    hyper[2,1] ~ dnorm(0, 0.368) # prior set 1
    #hyper[2,1] ~ dbeta(0.5,0.5) # prior set 2
    #hyper[2,1] ~ dnorm(0, 0.5) # prior set 3
    hyper[2,2] ~ dunif(0, 10) # SD hyperparameter for random intercepts
    hyper[2,3] <- hyper[1,2]*hyper[1,2] # Var hyperparameter for slopes
    hyper[2,4] <- 1/(hyper[1,2]*hyper[1,2]) # Tau hyperparameter

    hyper[3,1] ~ dnorm(0, 0.368) # prior set 1
    #hyper[3,1] ~ dbeta(0.5,0.5) # prior set 2
    #hyper[3,1] ~ dnorm(0, 0.5) # prior set 3
    hyper[3,2] ~ dunif(0, 100) # SD hyperparameter for slopes
    hyper[3,3] <- hyper[3,2]*hyper[3,2] # Var hyperparameter for slopes
    hyper[3,4] <- 1/(hyper[3,2]*hyper[3,2]) # Tau hyperparameter for slopes

    for(h in 4:8){
      hyper[h,1] ~ dnorm(0, 0.000001) # prior set 1
      #hyper[h,1] ~ dunif(-10,10) # prior set 2
      #hyper[h,1] ~ dnorm(0, 0.001) # prior set 3
      hyper[h,2] ~ dunif(0, 100) # SD hyperparameter for slopes
      hyper[h,3] <- hyper[h,2]*hyper[h,2] # Var hyperparameter for slopes
      hyper[h,4] <- 1/(hyper[h,2]*hyper[h,2]) # Tau hyperparameter for slopes
    }
    hyper[9,1] <- 0
    hyper[9,2] ~ dunif(0,10)
    hyper[9,3] <- hyper[7,2]*hyper[7,2]
    hyper[9,4] <- 1/(hyper[7,2]*hyper[7,2])

    for(sp in 1:n_sp){
      phi[sp] ~ dunif(0,1)
      theta[sp] <- 1-phi[sp]
      ltheta[sp] <- logit(phi[sp])

      alpha[sp] ~ dnorm(hyper[2,1], hyper[2,4])
      alpha2[sp] ~ dnorm(hyper[3,1], hyper[3,4])# Random slopes
      #beta_0[sp] ~ dnorm(hyper[1,1],hyper[1,4])
      beta1[sp] ~ dnorm(hyper[4,1], hyper[4,4]) # Random slopes
      beta2[sp] ~ dnorm(hyper[5,1], hyper[5,4]) # Random slopes
      beta3[sp] ~ dnorm(hyper[6,1], hyper[6,4]) # Random slopes
      beta4[sp] ~ dnorm(hyper[7,1], hyper[7,4]) # Random slopes

      for(s in 1:n_stratum){
        beta_0[s,sp] ~ dnorm(hyper[1,1],hyper[1,4])
      } #s
      for(j in 1:n_block) {

```

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```

    alpha[sp] ~ dnorm(hyper[2,1], hyper[2,4])
    rep_p[j,sp] ~ dnorm(hyper[9,1],hyper[9,4]) #random effect random p
  } #b
} #sp

#Likelihood
for(sp in 1:n_sp){
  for(s in 1:n_stratum){
    a[s,sp] ~ dbern(phi[sp])
    p1c[s,sp] <- min(0.999,max(0.001,(1-prod(psyun[s,sp])))) #probability that animal is caught once
    MNKA[s,sp] ~ dbin(p1c[s,sp],Ns[s,sp]) #binomial likelihood for abundance
    Ns[s,sp] ~ dpois(lambda[s,sp]*a[s,sp])
    # RE Shrub Conifer Forbs Grass
    log(lambda[s,sp]) <- beta_0[X[s,1],sp] + beta1[sp]*X[s,2] + beta2[sp]*X[s,3] + beta3[sp]*X[s,5] + beta4[sp]
  } #s
} #sp
for(sp in 1:n_sp){
  for(i in 1:M[sp]){
    for(t in 1:8){
      logit(p[i,t,sp]) <- alpha[sp] + alpha2[sp]*RECAP[i,t,sp] + rep_p[iX[i,sp],sp]
      y[i,t,sp] ~ dbern(p[i,t,sp])
    } #t
  } #i
} #sp
for(sp in 1:n_sp){
  for(s in 1:n_stratum){
    for(t in 1:8){
      logit(psy[s,t,sp]) <- alpha[sp] + rep_p[X[s,21],sp]
      psyun[s,t,sp] <- (1-psy[s,t,sp])
    } #t
  } #s
} #sp

#Derived Parameters
for(sp in 1:n_sp){
  for(s in 1:n_stratum){
    logit(realp[s,sp]) <- alpha[sp] + rep_p[X[s,21],sp]
    logit(realc[s,sp]) <- alpha[sp] + alpha2[sp] + rep_p[X[s,21],sp]
    n.pred[s,sp] ~ dbin(p1c[s,sp],Ns[s,sp])
    ex[s,sp] <- p1c[s,sp]*lambda[s,sp]*a[s,sp]
    resid[s,sp] <- pow(pow(MNKA[s,sp],0.5)-pow(ex[s,sp],0.5),2)
    resid.pred[s,sp] <- pow(pow(n.pred[s,sp],0.5)-pow(ex[s,sp],0.5),2)
  } #s
} #sp
fit <- sum(resid[1:120,1:10])
fit.pred <- sum(resid.pred[1:120,1:10])
}
",fill = TRUE,file="mod.txt")

parameters <- c('fit','fit.pred','beta1','beta2','beta3','beta4','alpha2','phi','hyper','Ns','p1c','realp','realc')
inits <- function() {
  list(
    p0 = runif(1),
    Ns = MNKA,
    a = ZIP
  )
}

ni <- 100,000 ; nt <- 1 ; nb <- 50,000 ; nc <- 3 ; na <- 20,000
modX1_Base <- jags(data, inits, parameters, "mod.txt", n.chains = nc, n.thin = nt, n.iter = ni, n.burnin = nb, n.adapt =
na)

```

Appendix 3

Estimated coefficients (log-scale) and associated 95% credible intervals for each species from the first grass cover model parameterization and both post-hoc alternative grass parameterizations (native and non-native grass).

Species	Covariate	Mean	Credible Interval	
			2.5%	97.5%
Golden-mantled ground squirrel	Non-native Grass	-0.164	-0.464	0.130
	Native Grass	-0.059	-0.340	0.219
Northern flying squirrel	Non-native	-0.143	-0.433	0.150
	Native	-0.060	-0.306	0.185
Long-tailed vole	Non-native	-0.128	-0.355	0.098
	Native	-0.094	-0.329	0.138
Montane vole	Non-native	-0.152	-0.361	0.055
	Native	-0.204	-0.420	0.007
Bushy-tailed woodrat	Non-native	-0.213	-0.481	0.045
	Native	-0.085	-0.307	0.135
Deer mouse	Non-native	0.008	-0.191	0.215
	Native	0.017	-0.166	0.202
Vagrant shrew	Non-native	-0.130	-0.373	0.112
	Native	0.005	-0.241	0.252
Yellow-pine chipmunk	Non-native	-0.190	-0.400	0.018
	Native	0.106	-0.081	0.299
Columbian ground squirrel	Non-native	-0.078	-0.380	0.230
	Native	-0.079	-0.393	0.228
Western jumping mouse	Non-native	-0.102	-0.362	0.152
	Native	-0.006	-0.230	0.225

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