Research Article

Abundance and Ecological Associations of Small Mammals

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ABSTRACT Effective conservation and management of small mammals require knowledge of the population dynamics of co-occurring species. We estimated the abundances, autocorrelations, and spatiotemporal associations of 4 small-mammal species from 2011–2016 using live-trapping mark-recapture methods on 9 sites across elevation and canopy openness gradients of a late-successional forest in the H. J. Andrews Experimental Forest, on the west slope of the Oregon Cascades. We also quantified species-specific spatial variation in adult sex ratios and body mass. We used Huggins closed capture models to estimate site- and year-specific abundances of 4 target species: Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), western red-backed voles (*Myodes californicus*), and deer mice (*Peromyscus maniculatus*). We estimated the temporal autocorrelations among site- and species-specific abundance estimates and used generalized linear mixed effects models to investigate the effects of 7 spatiotemporal covariates on species-specific mean abundance estimates. Species-specific adult sex ratios, juvenile to adult ratios, and adult body masses were not widely variable among study sites. Abundance estimates varied by as much as 4-fold among years and 6-fold among sites. Humboldt's flying squirrel abundance was temporally autocorrelated at intervals of 1 and 5 years, Townsend's chipmunk abundance was temporally autocorrelated at intervals of 1–4 years, and western red-backed vole abundance was temporally autocorrelated at 1, 4, and 5 years. Mean fall abundance estimates were associated with elevation and climate and in some cases, canopy openness and berry-producing shrubs, but the direction of the association differed among species for some covariates. Our findings could provide additional management tools for small-mammal abundance objectives, and highlight the importance of careful covariate selection in studies using indices of small-mammal abundance. © 2019 The Authors. *Journal of Wildlife Management* Published by Wiley Periodicals, Inc. on behalf of The Wildlife Society.

KEY WORDS Cascade Mountains, deer mice (*Peromyscus maniculatus*), habitat, Humboldt's flying squirrels (*Glaucomys oregonensis*), mark-recapture, Oregon, population cycle, Townsend's chipmunks (*Neotamias townsendii*), western red-backed voles (*Myodes californicus*).

There is a growing consensus that effective multi-species management and conservation requires detailed studies of the spatiotemporal dynamics of multiple co-occurring species (Mac Nally et al. 2002, Fischer et al. 2004, White et al. 2013). Such studies can provide insights into the mechanisms underlying co-occurrence (facilitation, competition, and predation) and the relative effects of management actions for co-occurring species. In addition, these studies are particularly important in undisturbed ecosystems because they establish baseline ecological associations of species and communities (Sinclair 1998). Yet, spatially replicated longitudinal studies, with repeated measures of the same population(s) over time, to evaluate these spatiotemporal dynamics are unavailable for many species, leaving a knowledge gap in many ecosystems (Krebs 2013).

In forests of the Pacific Northwest (PNW) of the United States, small mammals constitute a large proportion of the prey base for avian and mammalian predators (Fryxell et al. 1999; Bull 2000; Forsman et al. 2001, 2004; Rosenberg et al.

2003) and contribute to the maintenance of forest health through the consumption and dispersal of hypogeous fungi, berries, and seeds (Maser et al. 1978, Bowers and Dooley 1993). Much of the previous small-mammal research in the PNW has focused on the effects of forest management on small-mammal abundance or density (Holloway and Smith 2011), especially for prey species important to northern spotted owls (*Strix occidentalis caurina*) such as flying squirrels (*Glaucomys* spp.; Smith 2007). Fewer small-mammal studies have focused on multiple co-occurring species (Carey 1995, Smith and Nichols 2004, Smith 2012, Smith and Fox 2017) or quantified demographic variability and spatiotemporal abundance associations within heterogeneous old forests (Hayes et al. 1986, Rosenberg and Anthony 1993, Rosenberg et al. 1994, Smith et al. 2005, Smith 2012).

We focused our analyses on 4 common PNW species: Humboldt's flying squirrels (*Glaucomys oregonensis*), Townsend's chipmunks (*Neotamias townsendii*), deer mice (*Peromyscus maniculatus*), and western red-backed voles (*Myodes californicus*), which occur sympatrically in conifer forests of western Oregon, USA. Abundances of the target species are limited by food resources (Sullivan et al. 1983, Carey and Johnson 1995, Waters and Zabel 1995). The target species are primarily mycophagists and rely heavily on hypogeous fungi (Maser et al. 1978). In addition to fungi, Townsend's chipmunks and deer mice consume seeds and berries (Hayes et al. 1995, Tallmon et al. 2003, Lobo and Millar 2011); however, the biological effect of berry consumption remains unclear (Hayes et al. 1995, Dracup et al 2016). In addition, the target species abundances are associated with habitat features such as woody debris, which is associated with hypogeous fungi richness and biomass (Amaranthus et al. 1994); understory development and canopy openness, which may be linked to predation risk (Carey et al. 1992, Pyare and Longland 2002); and winter severity, which is thought to reduce winter survival (Aubry et al. 1991, Lehmkuhl et al. 2006). Interspecific interactions among small mammals in the PNW remains understudied, but previous studies have hypothesized that competition for limited resources could be influential to small-mammal population dynamics (Carey 1995, Weigl 2007, Smith and Fox 2017). Only a few studies have shown significant competition effects among congenerics of the target species (Smith 2012, Smith and Fox 2017).

Regular, and predictable, rises and falls of abundances (i.e., population cycling) have been observed in hardwood and conifer forests in Maine, USA, and across Canada for congenerics and conspecifics of small-mammal species in the PNW (Fryxell et al. 1998, Boonstra and Krebs 2012, Sullivan et al. 2017b). But, we lack evidence for small-mammal population cycles in the PNW despite the presence of a potential cyclical conifer seed food resource (Boutin et al. 2006, Sullivan et al. 2017b), and the historical, but declining, influence of the northern spotted owl, a resident specialist predator. Both factors have been linked with cycling small-mammal populations in other systems (Hanski et al. 1991).

The objectives of our study were to quantify age-, sex-, site-, and species-specific average body masses, juvenile to adult ratios, and adult sex ratios; estimate site- and year-specific capture probability (p), recapture probability (c), and fall abundances from 2011–2016 for the 4 target species; estimate temporal autocorrelations among each of the target species abundances; and investigate the effects of spatial and temporal covariates on the target species mean abundances (Table 1). We developed species-specific hypotheses about capture and recapture probabilities for the target species and covariates potentially related to mean abundance (Table 2). We predicted that capture and recapture probabilities would be temporally variable and would be influenced by trap availability, elevation, and habitat features that index small-mammal exposure to predation (i.e., canopy openness, shrub cover). We also predicted that mean abundances would be positively associated with positive indices of food availability (berry producing plant cover, coarse woody debris volumes, Palmer drought severity index; Amaranthus et al. 1994, Hayes et al. 1995, Tallmon et al. 2003, Zhao and Running 2010, Lobo and Millar 2011) and negatively associated with negative indices of food availability (canopy openness; Amaranthus et al. 1994); and mean abundances would be negatively associated with indices of winter severity (i.e., elevation, min. winter temp., number of days $<0°C$; Lehmkuhl et al. 2006, Boonstra and Krebs 2012). We predicted an exception to these general predictions; Townsend's chipmunks and deer mice would be positively associated with elevation and canopy openness. This exception correponds with previous associations of Townsend's chipmunk abundance with complex canopies and understory development (Carey 1995, Carey et al. 1999).

STUDY AREA

We conducted this study in the H. J. Andrews Experimental Forest (HJA), on the west slope of the Oregon Cascades, near Blue River, Oregon, 2011–2016 (Fig. 1). The HJA encompasses the 6,400-ha Lookout Creek drainage basin and is part of the Willamette National Forest. Elevations in the HJA ranged from 420–1,630 m and the terrain was mountainous. The HJA consists primarily of old relatively undisturbed temperate forests, with pockets of regenerating second-growth forest (Franklin et al. 1990). Oregon State University, Willamette National Forest, and the United States Department of Agriculture (USDA) Forest Service's Pacific Northwest Research Station jointly administer the HJA. We limited site selection to old-growth stands because our primary objective was to estimate small-mammal abundances in a late-successional forest across gradients of elevation and canopy openness.

Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and Pacific silver fir (*Abies amabilis*) vegetative communities dominated the study area (Cissel et al. 1999). These old (>400 years old) late-successional forests have high canopy cover (72–91%) and the overstory predominantly consists of large trees (>81.21 cm diameter; Schulze and Lienkaemper 2015). Understory characteristics were variable among the study sites and ranged from open

Table 1. Description and sampled range of variables considered in models of detection probability, recapture probability, and abundance for Humboldt's flying squirrels, Townsend's chipmunks, deer mice, and western red-backed voles in a late-successional forest in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016.

Variables	Description	Range
Spatial		
Elevation	Average site elevation, estimated using 2008 lidar data.	683–1,244 m
Canopy	Site percentage of 0–10 m canopy openness to >10 m canopy openness, estimated using 2008 lidar data.	9–38%
Shrub	Mean percentage cover of all woody shrubs between 0.5 m and 1.5 m in height.	10.3–58.3%
Berry	Mean percentage cover of blackberry, raspberry, and salmonberry (*Rubus* spp.), huckleberry (*Vaccinium* spp.), salal (*Gaultheria shallon*), and Oregon grape (*Mahonia aquifolium*).	12.1–51.2%
CWD[a]	Site sum of coarse woody debris volumes on 18 habitat sampling station for all CWD >10 cm in diameter.	77.3–218.2 m³
Temporal		
Year	A year-specific effect for each trapping occasion from 2011 to 2016.	2011–2016
Season	Trend from the first to the last day of the trapping in a year.	1–36
Trapping	Trend from the first to the last trapping day of each trapping occasion.	1–12 days
Julian date	Trend from the first to the last day of the project across the first 6 years of data collection.	11,269–16,323
Min. temp.	Minimum winter (1 Oct–1 Apr) daily mean temperature	−13−−3.9°C
Days below 0	The number of days in the winter with a mean daily temperature below 0°C.	11–34 days
PDSI[b]	An 18-month average index, ranging from −6 (drought) to 6 (wet), of the regional deviations from average moisture conditions and is an index of net primary productivity.	−2.7–2.3
Effort	Trap type-specific trapping effort, adjusted for stuck and sprung traps.	945–1,498.5 trap-nights
Chipmunks	The effect of year- and site-specific Townsend's chipmunk captures on trap availability of nocturnal species.	189–941 captures

[a] Coarse woody debris.
[b] Palmer's drought severity index.

understories to dense shrubs. Common understory vegetation included blackberry, raspberry, and salmonberry (*Rubus* spp.), common snowberry (*Symphoricarpos mollis*), deer fern (*Blechnum spicant*), huckleberry (*Vaccinium* spp.), Oregon grape (*Mahonia aquifolium*), oxalis (*Oxalis* spp.), salal (*Gaultheria shallon*), sword fern (*Polystichum munitum*), and vine maple (*Acer circinatum*). Twenty-two avian and mammalian predators have been documented at the HJA, including 4 species of Accipitridae, 6 species of Strigidae, and 12 carnivore species (Garman and Anthony 2001, Garman and McKee 2001). Approximately 80% of the annual precipitation occurred during the fall, winter, and spring (Oct–Apr), and primarily consists of rain at lower elevations (<1,000 m) and snow at higher elevations (>1,000 m). Spring, fall, and winter temperatures have been <6°C at 1,000 m (Bierlmaler and McKee 1989). Summer (May–Sep)

Table 2. *A priori* predictions of covariate effects on detection probability (*p*), recapture probability (*c*), and abundance (*N*) estimates for Humboldt's flying squirrels, Townsend's chipmunks, deer mice, and western red-backed voles, from live-trapping data collected in a late-successional forest in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016. We predicted positive correlations (+), negative correlations (−), or no effects (/); empty boxes indicate direction of prediction was not feasible or we did not make a prediction. We included Townsend's chipmunks as a covariate for flying squirrels because flying squirrels are nocturnal and diurnal Townsend's chipmunks would get first access to newly set traps.

	Expected results											
	Humboldt's flying squirrel			**Townsend's chipmunk**			**Western red-backed vole**			**Deer mouse**		
Covariate[a]	*p*	*c*	$\widehat{N}$	*p*	*c*	$\widehat{N}$	*p*	*c*	$\widehat{N}$	*p*	*c*	$\widehat{N}$
Spatial												
Elevation	−	+	−	−	+	+	−	+		−	+	+
Canopy	−	−	−	+	−	+	−	+		−	+	+
Shrub	+	+		+	+		+	+		+	+	
Berry		+				+						+
CWD		+				+						+
Temporal												
Julian date	+	+		+	+		/	/		/	/	
Season	−	+		+	+		+	+		+	+	
Trapping	−	+		−	+		−	+		−	+	
Effort	+	+		+	+		+	+		+	+	
Chipmunks	+	+										
Min. temp.			−			−						−
Days below 0			−			−						−
PDSI			+			+						+

[a]Spatial covariates include elevation, canopy openness percentage (Canopy), shrub cover percentage (Shrub), berry producing plant cover percentage (Berry), and coarse woody debris volume (CWD). Temporal covariates include Julian date, seasonal trend (Season), trapping session trend (Trapping), trapping effort (Effort), chipmunks (year- and site-specific Townsend's chipmunk captures), minimum winter temperature (Min. temp.), number of days below 0°C (Days below 0°C), and the Palmer drought severity index (PDSI).
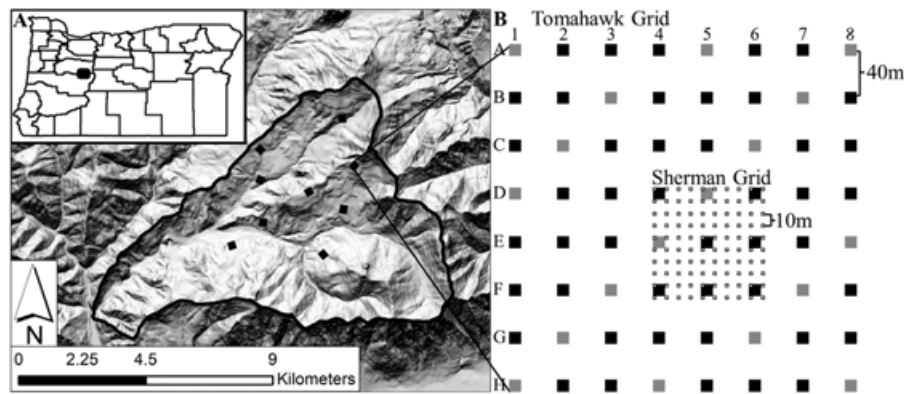
Figure 1. A) Location of the H. J. Andrews Experimental Forest, in Central Oregon, USA. We collected mark-recapture data for small mammals on 9 sites, represented by the black squares, in late-successional forests during 2011–2016. B) Each site consisted of 64 Tomahawk trapping stations arranged in an 8 × 8 array with 40-m inter-trap distances, and 100 Sherman trapping stations arranged in a 10 × 10 array with 10-m inter-trap distances. We sampled understory characteristics once during summer 2016 on 18 (light gray) of the 64 Tomahawk trapping stations.

temperatures have been >6°C at 1,000 m (Bierlmaler and McKee 1989). Mean average annual precipitation on the HJA from 1958–1996 was 2,259 mm (Swanson and Jones 2002). From 2011–2016, mean average daily temperatures and rainfall during the study period were as follows: 13.6 ± 0.31°C (SE; min. = −34.9°C, max. = 1.7°C) and 83.2 ± 43.7 mm in September, 8.6 ± 0.26°C (min. = −2.6°C, max. = 30.2°C) and 238.8 ± 75.6 mm in October, and 3.5 ± 0.24°C (min. = −6.4°C, max. = 20.9°C) and 309.7 ± 30.24 mm in November (Daly and McKee 2016).

METHODS

Trapping Design

Using Geospatial Modeling Environment, we generated 1,000 10-ha sites in late-successional forest stands across the HJA in 4 iterations that each began with a random starting point (version GME 0.7.4, Spatial Ecology, LLC., http://www.spatialecology.com, accessed 4 Aug 2011). We then classified each of these sites into 3 elevation classes (500–799 m, 800–999 m, 1,000–1,500 m, final range = 683.4–1,244.2 m) and 3 canopy openness classes (0–15%, 15–30%, 30–40%) using ArcGIS version 10.3.1, Geospatial Modelling Environment, and light detection and ranging data collected in 2008 (Spies 2016). We selected 9 of these sites to fit each unique category resulting from a cross of the 3 elevation and 3 canopy openness classes. The average inter-site distance was 2,963 m (range = 1,078–5,940 m).

At each site, we established 2 nested trapping grids to sample small mammals with a range of body sizes (Fig. 1). The larger grid (7.84 ha) consisted 64 Tomahawk trap stations arranged in an 8 × 8 array with 40 m (corrected for slope) between stations. We placed 2 Tomahawk Model 201 live traps (Tomahawk Live Trap, Hazelhurst, WI, USA) at each station. We attached 1 trap to the largest tree bole within 5 m of the trap station center, approximately 1.5 m from the ground, and placed the other on the ground (Risch and Brady 1996). If there was not a suitable tree bole within 5 m of the trap station, we placed both traps on the ground. The smaller grid (1 ha) consisted of 100 trap stations arranged in a 10 × 10 array with 10 m (corrected for slope) between stations. We placed 1 Sherman model LFATDG live trap (H. B. Sherman Traps, Tallahassee, FL, USA) at each station within 2 m of 100 Sherman trap station centers. We standardized the position of the smaller trapping grids relative to the larger trapping grid to reduce spatial sampling bias (Fig. 1). We placed both Sherman and Tomahawk traps near habitat features to increase the probability of a small mammal encountering a trap (Carey et al. 1991). To reduce trapping-related mortalities, caused by rain and cool temperatures, we set each trap in a waxed cardboard carton and supplied each a dry, cotton-stuffed nest box. We baited traps with a mixture of peanut butter, molasses, oats, and sunflower seeds (Carey et al. 1991).

We determined the site trapping order once in 2011. We prioritized high elevation sites to reduce the effect of snow and rain as fall temperatures decreased. From 2011–2016, during September, October, and November we trapped each Tomahawk grid for 3 consecutive trapping weeks, and each Sherman grid for 1 trapping week. However, in 2011 we did not trap 3 of the small Sherman grids because of logistic constraints. A trapping week consisted of 4 consecutive trap nights and we checked traps once per day.

We marked each animal with a unique ear tag and recorded individual condition, species, sex, and body mass (g). At the end of each season, we necropsied all mortalities to validate field identification of species, sex, and reproductive condition. We chose the 4 most commonly captured species as target species: Humboldt's flying squirrels, Townsend's chipmunks, deer mice, and western red-backed voles. Our live-trapping protocols were approved by Oregon State University's Institutional Animal Care and Use Committee (ACUP number 4191, 2011–2013; number 4590, 2014–2016), and were in accordance with the standard animal care principles of the American Society of Mammalogists (Sikes et al. 2016).

Development of Covariates

During summer 2016, we measured understory characteristics (i.e., shrub coverage, berry producing plant coverage,

coarse woody debris volume) at 18 Tomahawk trap stations/ site (i.e., habitat sampling stations; Fig. 1). We assumed that average site-specific understory characteristics were stable during the 6-year study because there were no major disturbances that could have changed forest structure. A single observer visually estimated site-specific understory coverage characteristics (to the nearest 5%) as the percentage of ground covered in 2-m-diameter circles, centered on each habitat sampling station. We averaged the coverage estimates from each site. We estimated site-specific coarse woody debris volumes by summing all individual log volumes (length of each log multiplied by the area at half the intersecting length) >10 cm in diameter that intersected 2 perpendicular 18 × 3-m transects centered on each habitat sampling station (Harmon and Sexton 1996). We retained only understory characteristics with ≥1 significant between-site difference in a Bonferroni-corrected separate means model ($\alpha = 0.001$) to ensure that there were statistically detectable differences between sites (pairwise Pearson's correlation coefficients in Table S1, available online in Supporting Information).

We considered 4 weather covariates: minimum winter daily air temperature (°C), maximum snow depth (mm), number of days below 0°C, and winter precipitation (mm). We obtained weather covariates from the HJA Central Meteorological Station located just east of the project's center at an elevation of 1,020 m (Daly and McKee 2016). We assumed that this location was broadly representative of the study sites for the covariates of interest. Of these covariates, we retained only minimum winter daily air temperature and the number of days below 0°C because of high correlations between maximum snow depth with the former and winter precipitation with the latter (pairwise Pearson's correlation coefficients >0.8; Table S2, available online in Supporting Information). We considered minimum winter daily air temperature an indicator of extreme winter severity and the number of days below 0°C an indicator of sustained winter severity. We considered 3 climactic covariates, Palmer's drought severity index (PDSI), the Southern Oscillation Index, and the Pacific Decadal Oscilation, but retained only PDSI because of high correlations (pairwise Pearson's correlation coefficients >0.85; Table S2). We used an 18-month average of the Oregon PDSI estimate because net primary productivity in the Northern Hemisphere has been associated with cumulative droughts >1 year (Zhao and Running 2010, Huang et al. 2016).

Analytical Methods

For each of the target species, we considered consistent site-specific divergences from the average adult sex ratio (male:female), juvenile to adult ratio (juvenile:adult), and average adult body mass (either the highest or lowest among all years) as evidence of an abnormal population structure, which might reflect differences in habitat quality (Greenberg et al. 2006, Robertson and Hutto 2006, Sollmann et al. 2015). Species-specific adult sex ratios were the number of known adult males divided by the number of

known adult females caught on each site within a year, and juvenile to adult ratios were the number of known juveniles divided by the number of known adults. We classified individuals as adults using average individual body mass and previously reported age and mass thresholds, defining adults as heavier than the following: Humboldt's flying squirrels males 100 g and females 94 g (Villa et al. 1999), Townsend's chipmunks males 68 g and females 67.5 g (Gashwiler 1976), western red-backed voles 15 g (Maser et al. 1981, Alexander and Verts 1992), deer mice 16 g (Dracup et al. 2015). We estimated mean sex-specific body mass separately for juveniles and adults using the average of all individual body masses of all captured individuals on a grid.

We estimated site-specific capture probabilities (p), recapture probabilities (c), and fall abundances of the target species with Huggins closed population mark-recapture (i.e., Huggins) models implemented in Program MARK (Huggins 1989, White and Burnham 1999). Capture probability is the probability of capturing an animal for the first time. Recapture probability is the probability of recapturing an individual. We used Akaike's Information Criterion, corrected for small sample sizes (AIC_c), and cumulative AIC_c weights (w_i) in a sequential modeling strategy to select the best supported model in each modeling step (Burnham and Anderson 2002). We selected the model with the lowest AIC_c and highest w_i as our best supported model (Burnham and Anderson 2002). In addition, we used the relative change in AIC_c (ΔAIC_c) to evaluate each model relative to the top-ranking model. We considered models within 2 AIC_c units ($\Delta AIC_c \leq 2$) of the top-ranking model competitive (Burnham and Anderson 2002). We used the degree to which the 95% confidence interval for each slope coefficient overlapped zero to evaluate the strength of evidence for single parameters, and we used the overlap of 95% confidence intervals to determine statistically significant differences between parameter estimates. In competitive models, we considered covariates with 95% confidence intervals that did not overlap zero strongly supported, covariates in competitive models with ≤10% of the 95% confidence interval overlapping zero less supported, and covariates with >10% of the 95% confidence interval overlapping zero not supported. First, we considered behavioral effects (trap attraction or trap aversion) with model structures representing variable relationships between species-specific capture and recapture probabilities. We then considered *a priori* recapture probability model structures while maintaining a time-varying model structure for capture probability. Lastly, we considered *a priori* capture probability model structures while maintaining the most supported recapture probability model structure identified in the previous step. The data were insufficient to accommodate interactions, so we considered only additive models that included, at most, 1 spatial and 1 temporal covariate. After sequential modeling, we derived abundance as a function of the number of individuals caught and the model-averaged capture probability, obtained from the capture probability sequential modeling step (Huggins 1991).

We estimated species-specific autocorrelations among grid- and year-specific abundances as a function of the separating time interval (lag). We evaluated the first 5 lags, corresponding to 1–5-year intervals, on all 9 sites and computed the species-specific range of possible correlation values if the true correlation was zero. The magnitude of correlation at each lag indicated the strength of correlation, whereas the sign indicated the direction of the correlation. We considered the magnitude of the annual lags meaningful if they exceeded the range of correlation values possible if the true correlation was zero (Kendall et al. 1998).

We used generalized linear mixed effects models (GLMM) with negative binomial error distributions to examine the relationships between each target species mean abundances and the main effects of 4 spatial and 3 temporal covariates (Table 2). Each model included 1 fixed effect and 1 random effect: spatial models included a year-specific random effect to compensate for unmodeled temporal variability and temporal models included a site-specific random effect to compensate for unmodeled spatial variability. To assess model fit, we checked each model for overdispersion by dividing the sum of the squared Pearson residuals by the residual degrees of freedom; values close to 1 suggest data without overdispersion (Bolker et al. 2009, Zurr et al. 2009).

We assessed the strength of evidence for each main effect based on the degree to which 95% confidence intervals for the estimated changes in the mean abundance (across the covariate ranges) overlapped species-specific a priori biologically meaningful values. By assessing the strength of fixed effects using each effects 95% confidence intervals and biologically meaningful values, we provided a more informative measure of each effect's strength and biological significance than hypothesis testing or retrospective power analysis alone (Steidl et al. 1997, Gerard et al. 1998, Johnson 1999). We defined biologically meaningful values as the average site-level species-specific temporal change in abundances. The biologically meaningful values were likely conservative because average temporal change in abundance also incorporated variation associated with the considered main effects and the main effects sampled range did not capture the full biological range (Sullivan et al. 2017a). We considered main effects strongly associated with mean abundance if the 95% confidence intervals for the estimated change in mean abundance across the sampled range of each covariate did not contain zero and included only values more extreme than the biologically meaningful values. We considered covariates weakly associated with mean abundance if the 95% confidence intervals for the estimated

change in mean abundance across the sampled range of each covariate did not contain zero but included values less extreme than the biologically meaningful values. The sign of the estimated change in mean abundance indicated the direction of the effects.

We used bootstrapping ($n = 5,000$) to estimate the variance for the change in mean abundance for each of the fixed effects. Individual bootstrap samples used the fitted GLMMs to estimate the difference in average abundance between the maximum and minimum values of the sampled covariates. We then estimated the 95% confidence intervals using the 0.025 and 0.975 quantiles of the bootstrapped samples.

We estimated temporal autocorrelations and fit GLMMS using R (R version 3.4.1, www.r-project.org, accessed 1 Aug 2017). We used the lme4 package version 1.1-13 to fit all GLMMs (Bates et al. 2015). We used the merTools package (merTools version 0.3.0, https://CRAN.R-project.org/package=merTools, accessed 1 Aug 2017) to conduct the bootstrap estimation.

RESULTS

From 2011–2016, we live-trapped 62,217 Tomahawk and 15,130 Sherman trap nights (adjusted for stuck and sprung traps; Nelson and Clark 1973), and captured 45,683 small mammals of 21 species (mean individuals caught/year $= 1,185$, range $= 888–1,590$). We individually marked 1,093 Humboldt's flying squirrels, 3,540 Townsend's chipmunks, 774 deer mice, and 646 western red-backed voles (Table 3). Average grid- and year-specific captures of individuals were 30.7 (range $= 4–56$) Humboldt's flying squirrels, 73.8 (range $= 25–176$) Townsend's chipmunks, 15.5 (range $= 4–42$) deer mice, and 13.1 (range $= 0–44$) western red-backed voles.

Average adult sex ratios for captured Townsend's chipmunks and deer mice favored males, whereas average adult sex ratios of western red-backed voles and Humboldt's flying squirrels were nearly equal (Table 3). We observed several site-specific departures from the mean adult sex ratios or mean juvenile to adult ratios (Table S3, available online in Supporting Information). Average sex-specific body masses did not exhibit a consistent pattern among sites (Table S3). There was no evidence of a consistent difference in temporal change of abundance between sites (Fig. 2).

Recapture probabilities of the target species were all higher than capture probabilities, and decreased during each primary trapping session (Humboldt's flying squirrels: $\beta_{Trapping} = -0.05$, 95% CI $= -0.07$ to -0.04; Townsend's

Table 3. Humboldt's flying squirrels, Townsend's chipmunks, western red-backed voles, and deer mice individuals captured from all years, and average male (M) to female (F) sex ratios, and average adult male to female sex ratios in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016.

| | Individuals captured (M:F) | | | | | | | |
Species	2011	2012	2013	2014	2015	2016	M:F ratio ($\bar{x}$)	Adult M:F ratio ($\bar{x}$)
Humboldt's flying squirrel	75:91	160:178	210:205	156:165	123:113	83:94	0.94	1.02
Townsend's chipmunk	383:279	342:275	524:399	439:250	323:233	324:242	1.40	1.56
Western red-backed vole	6:10	17:16	30:47	43:103	86:98	85:116	0.72	1.06
Deer mouse	35:9	51:42	98:77	117:78	75:49	107:50	1.92	2.05
Total	888	1,081	1,590	1,351	1,100	1,101		
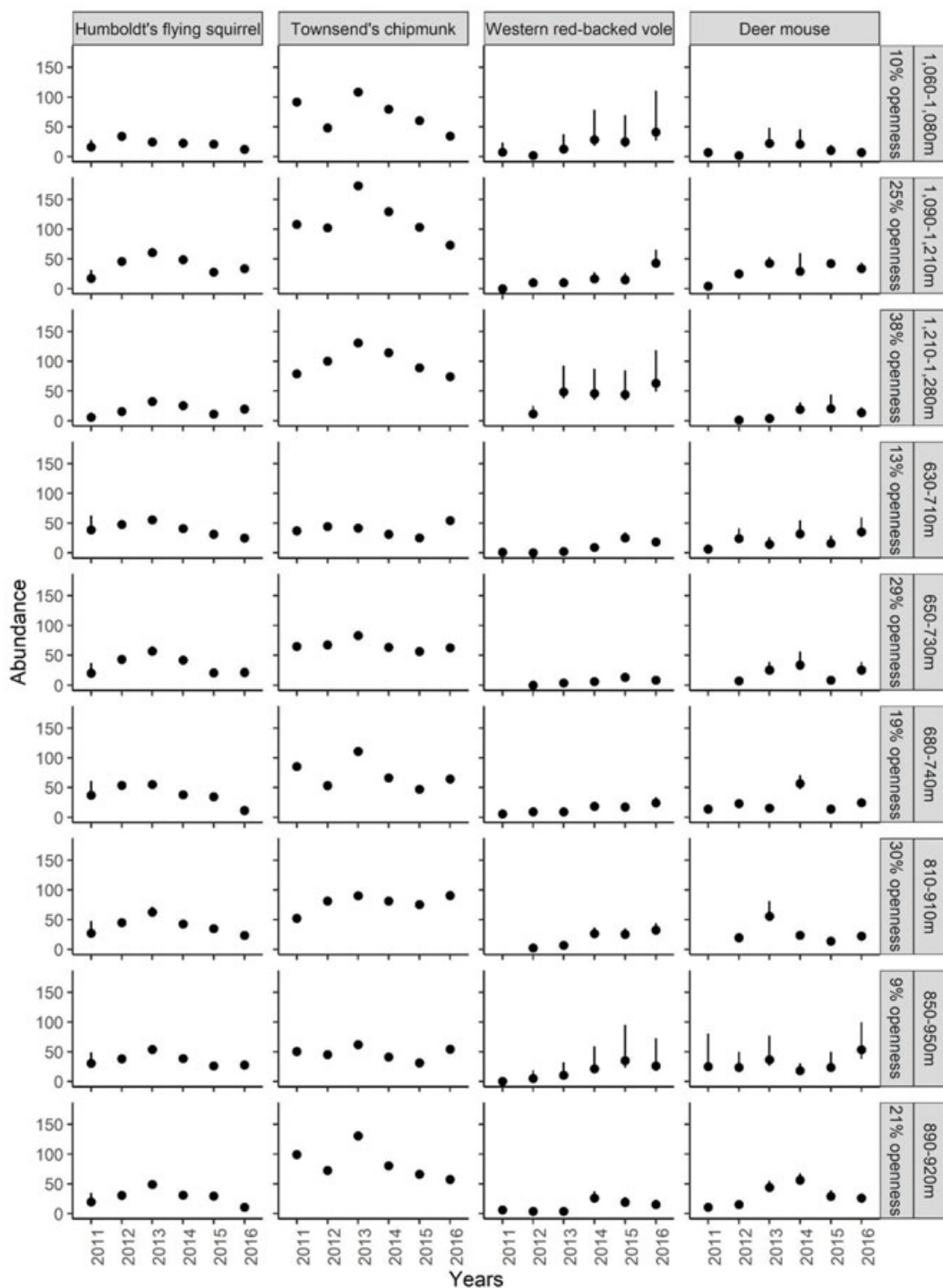
Figure 2. Site-level fall abundances from 2011–2016 of Humboldt's flying squirrels (7.84 ha), Townsend's chipmunks (7.84 ha), western red-backed voles (1 ha), and deer mice (1 ha) estimated using Huggins models and live capture data collected in a late successional forest within the H. J. Andrews Experimental Forest, Oregon, USA, during 2011–2016. Vertical bars indicate the 95% confidence intervals for the abundance estimates.

chipmunks: $\beta_{Trapping} = -0.53$, 95% CI = -0.54 to -0.52; deer mice: $\beta_{Trapping} = -0.37$, 95% CI = -0.52 to -0.22; western red-backed vole: $\beta_{Trapping} = -0.11$, 95% CI = -0.27 to 0.03; Table 4). Recapture probability for Townsend's chipmunk ($\beta_{Elevation} = -0.89$, 95% CI = -1.07 to -0.72) and western red-backed vole ($\beta_{Elevation} = -0.82$, 95% CI = -1.60 to -0.04) decreased with increases in elevation.

For Humboldt's flying squirrels and deer mice, a model including elevation was also supported, but 95% confidence intervals for the elevation slope parameter bounded zero. Capture probability of Humboldt's flying squirrels and Townsend's chipmunk differed among years (Table 5), and ranged from 15% (95% CI = 13–19%) in 2013 to 33% (95% CI = 29–38%) in 2015 for Humboldt's flying squirrels and

Table 4. Top 5 ranking models used to estimate recapture probability of Humboldt's flying squirrels, Townsend's chipmunks, western red-backed voles, and deer mice captured in a late-successional forest in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AIC_c), change in AIC_c from the top-ranking model (ΔAIC_c), AIC_c weight of evidence (w), and the number of parameters (K).

Species	Model[a]	AIC_c	ΔAIC_c	w	K
Humboldt's flying squirrel	Trapping	21,448.54	0.00	0.70	14
	Trapping + elevation	21,450.32	1.78	0.29	15
	Year	21,457.58	9.04	0.01	18
	Year + elevation	21,459.58	11.04	0.00	19
	Chipmunks	21,488.53	40.00	0.00	14
Townsend's chipmunk	Trapping + elevation	47,029.71	0.00	1.00	15
	Trapping + canopy	47,100.01	70.30	0.00	15
	Trapping	47,131.37	101.66	0.00	14
	Season + canopy	58,745.50	11,715.78	0.00	15
	Season + elevation	58,861.67	11,831.96	0.00	15
Western red-backed vole	Year + elevation	2,939.88	0.00	0.27	19
	Trapping + elevation	2,940.44	0.56	0.20	15
	Elevation	2,940.78	0.91	0.17	14
	Year	2,941.79	1.91	0.10	18
	Effort + elevation	2,942.14	2.26	0.09	15
Deer mouse	Trapping	3,652.95	0.00	0.72	14
	Trapping + elevation	3,654.88	1.93	0.27	15
	Year + shrub	3,664.13	11.17	0.00	19
	Year	3,665.22	12.26	0.00	18
	Year + elevation	3,669.24	16.29	0.00	19

[a] Model structure for initial capture probability (p) was held to a year by trapping model structure (year × trapping).

24% (95% CI = 22–27%) in 2011 to 44% (95% CI = 41–48%) in 2015 for Townsend's chipmunks. Capture probabilities of western red-backed voles and deer mice decreased during the primary trapping periods and ranged from 48% (95% CI = 33–64%) to 21% (95% CI = 5–55%) for western red-backed voles and from 37% (95% CI = 20–58%) to 19% (95% CI = 5–50%) for deer mice. Humboldt's flying squirrels ($\beta_{Canopy} = 0.19$, 95% CI = 0.03 to 0.35) and deer mice ($\beta_{Canopy} = 0.04$, 95% CI = −0.03 to 0.12) had additional positive associations between capture probability and canopy openness (Table 5). Townsend's chipmunk capture probability was positively associated with shrub cover ($\beta_{Shrub} = 0.007$, 95% CI = 0.003 to 0.01). For western red-backed voles, a model including elevation was also supported, but the 95% confidence interval for the elevation slope parameter bounded zero.

On all sites, Humboldt's flying squirrel and Townsend's chipmunk abundances increased from 2011–2013 and decreased from 2014–2015, excluding 5 sites with decreases in Townsend's chipmunk abundances from 2011–2012 (Fig. 2). Western red-backed vole abundances increased from 2011–2016 on every site (Fig. 2), except on low elevation sites. We did not observe a consistent pattern in deer mouse abundance changes (Fig. 2).

Autocorrelations among Humboldt's flying squirrel fall abundances were positive and statistically different from zero at lags of 1 and 5 years (Fig. 3). Townsend's chipmunk's autocorrelations among fall abundances were statistically different from zero, positive, and decreasing at lags of 1–4 years (Fig. 3). Autocorrelations among western red-backed vole fall abundances were statistically different from zero at 1, 2, 4, and 5 years, with positive lags at 1 and 2 years, and negative lags at 4 and 5 years (Fig. 3).

Only autocorrelations among deer mouse fall abundances with lags of 1 year were statistically different from zero (Fig. 3).

Overdispersion estimates for all GLMM mean abundance association models ranged 0.76–1.02, which did not indicate overdispersion. Humboldt's flying squirrel mean abundance was positively associated with berry-producing plant cover ($\beta_{Berry} = 1.89$, 95% CI = 1.31 to 2.56) and minimum winter temperature ($\beta_{Min. Temp.} = 0.34$, 95% CI = 0.04 to 0.65), and negatively associated with elevation ($\beta_{Elevation} = -0.81$, 95% CI = −1.23 to −0.47; Fig. 4). Mean abundance of Townsend's chipmunk was positively associated with elevation ($\beta_{Elevation} = 1.00$, 95% CI = 0.60 to 1.42), canopy openness ($\beta_{Canopy} = 2.17$, 95% CI = 1.26 to 2.99), and minimum winter temperature ($\beta_{Min. Temp.} = 0.22$, 95% CI = 0.01 to 0.43), and negatively associated with berry-producing plant cover ($\beta_{Berry} = -1.07$, 95% CI = −1.90 to −0.21). Western red-backed vole mean abundance was positively associated with elevation ($\beta_{Elevation} = 1.77$, 95% CI = 1.02 to 2.51) and canopy openness ($\beta_{Canopy} = 3.06$, 95% CI = 0.91 to 4.95), and negatively associated with berry-producing plant cover ($\beta_{Berry} = -1.78$, 95% CI = −3.39 to −0.20), minimum winter temperature ($\beta_{Min. Temp.} = -0.87$, 95% CI = −1.50 to −0.19), and PDSI ($\beta_{PDSI} = -0.45$, 95% CI = −0.54 to −0.38). Mean abundance of deer mice was positively associated with berry-producing plant cover ($\beta_{Berry} = 1.48$, 95% CI = 0.11 to 2.91), and negatively associated with minimum winter temperature ($\beta_{Min. Temp.} = -0.87$, 95% CI = −1.59 to −0.15) and PDSI ($\beta_{PDSI} = -0.14$, 95% CI = −0.24 to −0.06). Few of the effect sizes exceeded our *a priori* biological significance threshold, and there was no overlap among the target species for associations with biologically meaningful effect sizes (Fig. 4).

Table 5. Top 5 ranking models used to estimate capture probability of Humboldt's flying squirrels, Townsend's chipmunks, western red-backed voles, and deer mice captured in a late-successional forest in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016. We present model structure, Akaike's Information Criterion adjusted for sample size (AIC$_c$), change in AIC$_c$ from the top-ranking model (ΔAIC$_c$), AIC$_c$ weight of evidence (w), and the number of parameters (K).

Species	Model	AIC$_c$	ΔAIC$_c$	w	K
Humboldt's flying squirrel[a]	Year + canopy	21,484.64	0.00	0.79	10
	Year + elevation	21,487.80	3.16	0.16	10
	Year	21,490.97	6.33	0.03	9
	Year + shrub	21,492.91	8.26	0.01	10
	Julian date + canopy	21,604.13	119.49	0.00	5
Townsend's chipmunk[b]	Year + shrub	47,087.58	0.00	1.00	10
	Year + elevation	47,103.26	15.69	0.00	10
	Trapping + shrub	47,103.78	16.20	0.00	6
	Year + canopy	47,104.06	16.49	0.00	10
	Year	47,105.02	17.44	0.00	9
Western red-backed vole[c]	Trapping + elevation	2,921.40	0.00	0.38	10
	Trapping	2,922.04	0.64	0.28	9
	Trapping + shrub	2,923.85	2.46	0.11	10
	Trapping + canopy	2,923.95	2.55	0.11	10
	Effort + elevation	2,926.05	4.65	0.04	10
Deer mouse[d]	Trapping + canopy	3,632.24	0.00	0.30	5
	Trapping	3,632.92	0.68	0.21	4
	Season + canopy	3,634.56	2.32	0.09	5
	Trapping + elevation	3,634.90	2.66	0.08	5
	Trapping + shrub	3,634.93	2.68	0.08	5

[a] Model structure for recapture probability c(trapping).
[b] Model structure for recapture probability c(trapping + elevation).
[c] Model structure for recapture probability c(year + elevation).
[d] Model structure for recapture probability c(trapping).

DISCUSSION

We estimated the fall abundances, tested for temporal autocorrelations in abundance, and investigated habitat associations of 4 co-occurring small-mammal species from 2011–2016 at 9 sites within a relatively undisturbed late-successional forest. Fall abundances of the target species were considerably more variable among years than among sites, and changes in fall abundance over time varied among species. Despite sympatric exposure to spatiotemporal factors, different covariates were most associated with the mean abundance of each target species. This long-term data provides important baseline estimates of abundances and spatiotemporal associations of small mammals in a late-successional forest in the PNW, which can inform our understanding of small-mammal populations in human-modified forest cover types such as conifer plantations (Sullivan et al. 2017a).

Humboldt's flying squirrel abundance was positively and strongly autocorrelated at a lag of 5 years, suggesting that populations on our sites might exhibit population cycles at least every 5 years. This period is similar to the 4-year cyclic period suggested by Fryxell et al. (1998) for northern flying squirrels (Glaucomys sabrinus). We observed strong negative autocorrelations in western red-backed vole abundance at 4- and 5-year lags, which were similar in size, direction, and temporal patterning to previous estimates of 6- to 8-year population cycles for southern red-backed voles (Myodes gapperi) in southern British Columbia, Canada (Sullivan et al. 2017b), and in contrast to previous observations of stable western red-backed vole populations in western Oregon (Gashwiler 1970, Boonstra and Krebs 2012). The abundance autocorrelations for Townsend's chipmunks and deer mice diminished as years between estimates increased, similar to the observations of Fryxell et al. (1998). However, our population cycling inferences are weak because our time series was short but can serve as a basis for future hypothesis testing.

Abundance is not always a good indicator of habitat quality because marginal or sink habitats sometimes have high animal abundances sustained by immigration (Van Horne 1983, Robertson and Hutto 2006, Smith and Person 2007). Abundant populations existing in these habitats may be composed primarily of a subordinate sex (for species with sex-segregated habitat use patterns), or of individuals with at least one measure of individual fitness lower than in other habitats (Ecke et al. 2002, Robertson and Hutto 2006). We observed some deviations from our average population structure metrics, but these differences were variable among years, and in all instances of deviation there was no indication that individuals were less fit given the average adult body masses. These findings are consistent with Carey (1995) who reported no evidence that densities of flying squirrels and Townsend's chipmunks were a misleading indicator of habitat suitability, and suggested that differences of abundances might reflect variation in important habitat features. However, future studies should consider variation in survival and recruitment, spatiotemporal associations of age-specific estimates, and variation of ecological communities.

Much of the previous work exploring the target species abundances has focused on spatial relationships (Lehmkuhl et al. 2006, Holloway and Malcolm 2007, Holloway and
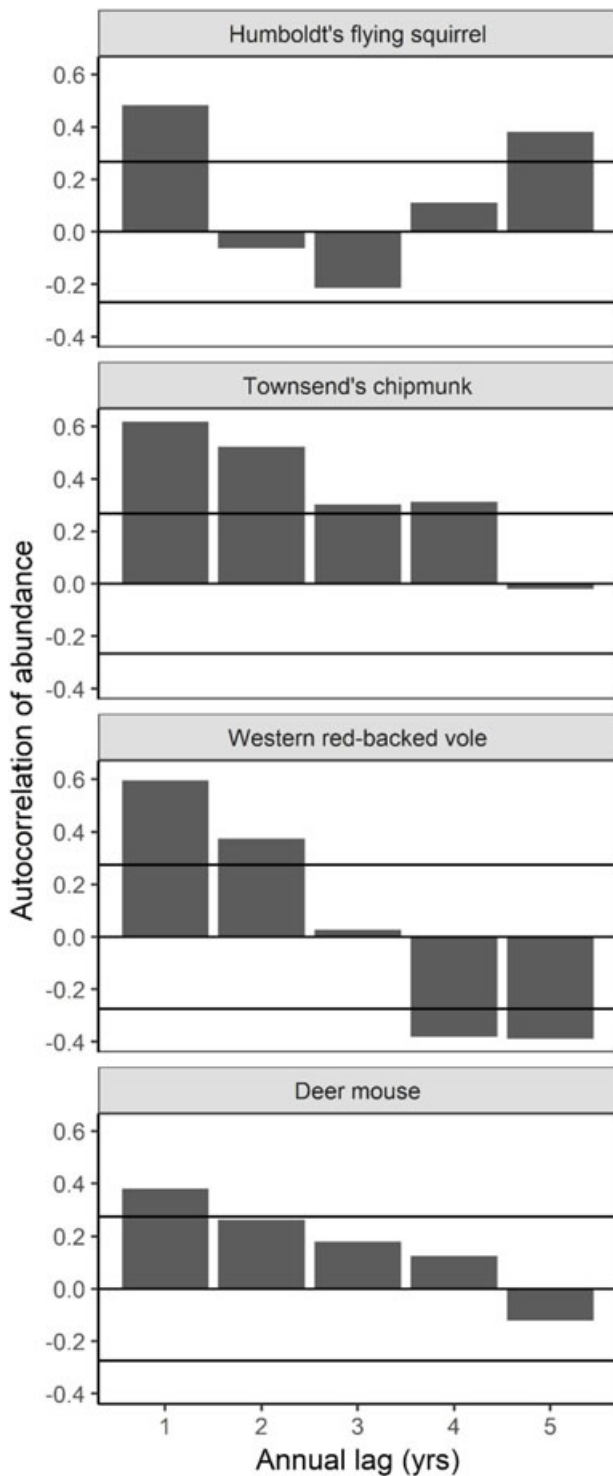
Figure 3. Intraspecific abundance temporal autocorrelations for Humboldt's flying squirrels, Townsend's chipmunks, deer mice, and western red-backed voles captured in a late-successional forest in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016. The autocorrelation for each lag represents the Pearson's correlation between annual fall abundance estimates in years as far apart as the lag. The height of bars indicates the strength of the autocorrelation and the area between the dark gray horizontal lines represents values of correlation that are not statistically different from zero.

Smith 2011, Shanley et al. 2013). Few previous studies in the PNW have examined effects of temporal covariates on small-mammal abundances (Tallmon et al. 2003, Lehmkuhl et al. 2006). We observed variation in fall abundances of these 4 species among years. Mean fall abundances of deer mice and western red-backed voles were most associated with temporal covariates, whereas fall abundances of Humboldt's flying squirrels and Townsend's chipmunks, although variable among years, were more strongly associated with spatial covariates. Temporal variation of small-mammal abundance has been understudied in the PNW, and this variation could have important influences on predators and forest dynamics linked to small-mammal populations.

We hypothesize that the positive relationship between the mean abundance of Townsend's chipmunks and elevation was related to the availability of conifer seeds, which has been associated with mean abundances of several small-mammal species (Falls et al. 2007, LaMontagne et al. 2013, Lobo 2014, Ogawa et al. 2017). Douglas-fir and western hemlock were abundant on our sites and their seed production varies annually with cyclical production peaks (Douglas-fir = 2–7 years, western hemlock = 3–4 year; Fowells 1965, Allen and Owens 1972). However, western hemlocks produce some seed every year, which might stabilize populations of seed predators on sites with relatively high western hemlock densities (Fowells 1965). On our study sites, western hemlocks were slightly more numerous on our mid- to high-elevation sites (with the exception of our highest elevation site), which could contribute to the positive association between Townsend's chipmunks mean abundance and elevation (Weldy 2018).

Our *a priori* predictions of western red-backed vole mean abundance associations were not supported. These predictions were based on previous associations with canopy closure (Doyle 1987), coarse woody debris volumes (Tallmon and Mills 1994, Thompson et al. 2009), and sensitivity to winter severity (Boonstra and Krebs 2012). For example, we predicted that western red-backed voles would be more abundant in closed canopy stands because more overstory trees might result in deeper ground litter (Rosenberg et al. 1994, Thompson et al. 2009). However, contrary to our prediction, western red-backed vole mean abundance was positively associated with canopy openness. We are unaware of any studies of western red-backed vole abundance that explored variation exclusively within old forests; instead, previous studies focused on differences between young and old forests. Thus, differences we observed from previously documented associations might imply variable species-specific associations once minimum habitat thresholds are met in late successional forests.

Mean abundances of the target species decreased during winters with more days below 0°C, which generally agreed with our prediction that winter severity would be negatively associated with abundance. Larger-bodied Humboldt's flying squirrels and Townsend's chipmunks had higher mean abundance after winters with less extreme minimum winter temperatures. The smaller-bodied western red-
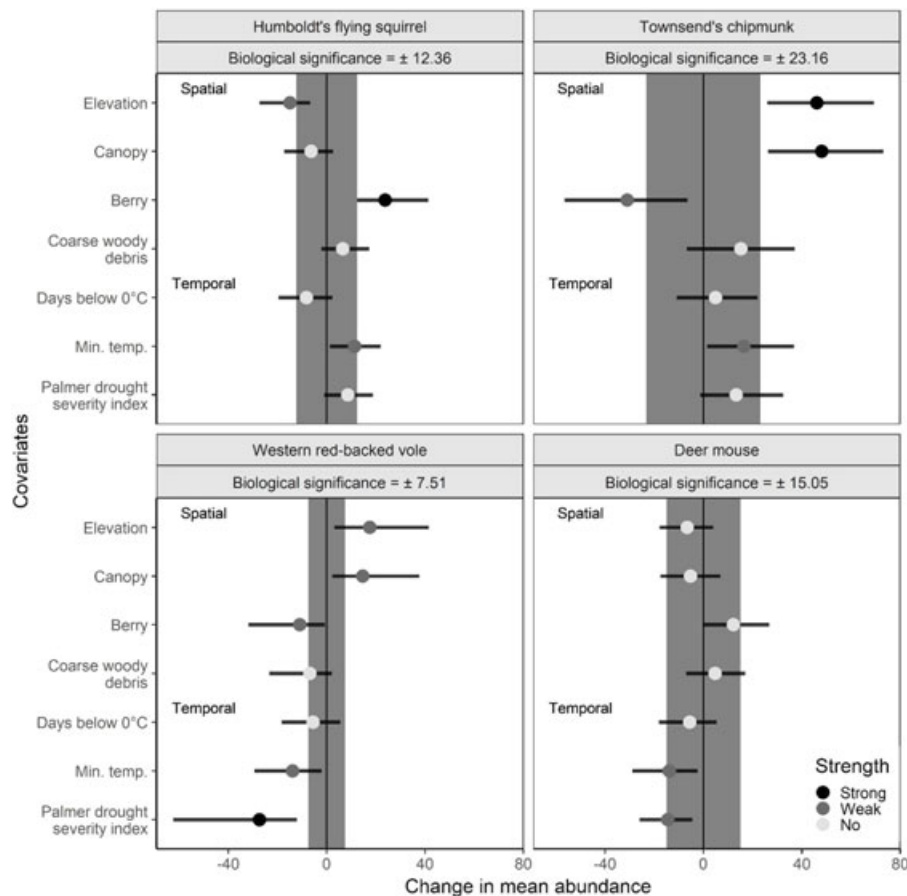
Figure 4. The estimated effect size and 95% confidence intervals on mean abundance across the sampled range of spatiotemporal covariates for Humboldt's flying squirrels, Townsend's chipmunks, deer mice, and western red-backed voles captured in a late-successional forest in the H. J. Andrews Experimental Forest, Oregon, USA, 2011–2016. The horizontal dark area indicates the range of values that do not achieve the *a priori* biological significance value, where biological significance was the average site- and species-specific temporal change in abundance. Spatial covariates include elevation, canopy openness percentage (Canopy), berry producing plant cover percentage (Berry), and coarse woody debris volume. Temporal covariates include number of days below 0°C (Days below 0°C), minimum winter temperature (Min. temp.), and the Palmer drought severity index.

backed voles and deer mice, which are both active during the winter, had lower mean abundance after the same winters. Despite differences in winter torpor strategies, both larger-bodied species appeared sensitive to extreme cold weather events (Wells-Gosling and Heaney 1984, Levesque and Tattersall 2010). Maximum winter snow depth was positively correlated with minimum winter temperature during this study, and the similarity of responses between species with similar body sizes might be associated with varying sensitivity to maximum snow depth, which can act as insulation during cold weather (Boonstra and Krebs 2012).

Prey abundance has been suggested as an influential variable affecting the population parameters or breeding ecology of multiple forest predators including the northern spotted owl (Carey and Johnson 1995, Wiens et al. 2014). However, few carnivore studies in the PNW have used prey-specific demographic estimates or surrogates for abundance (Rosenberg et al. 2003). More commonly, previous northern spotted owl demographic studies used PDSI as a surrogate variable for prey abundance (Forsman et al. 2011, Dugger et al. 2016), which likely would have been a poor predictor of prey abundance during this study because it was correlated

only with abundances of western red-backed voles and deer mice. Thus, we suggest future studies use prey-specific temporal covariates. Specifically, we suggest that minimum winter temperature would be a better overall predictor of the target species abundances but that PDSI would be a better predictor for western red-backed vole and deer mouse abundances.

Previous dietary studies of the flying squirrels in the PNW have primarily consisted of microscopic fecal pellet examinations (Maser et al. 1985, Cazares et al. 1999, Lehmkuhl et al. 2004). This methodological focus has likely influenced our understanding of flying squirrel diets and caused us to underestimate regional variation in diet (Smith 2007). We also observed a positive association between Humboldt's flying squirrel mean abundance and berry-producing plant cover. But it is unclear if this association is related to food availability, or some other mechanism such as ground cover while foraging. Thus, we suggest that future studies explore the dietary breadth of Humboldt's flying squirrels and other small mammals in the PNW using stable isotope analysis or other methods with less potential for bias towards hard-to-digest material (Trapp et al. 2017).

MANAGEMENT IMPLICATIONS

Our study indicated that managers might positively influence the abundance of Humboldt's flying squirrels by increasing the cover of berry producing plants. It is unclear, however, whether the association between flying squirrel abundance and berry producing plants was a response to food availability, additional ground cover provided by berry producing shrubs, or some other factor. Thinning treatments might increase the abundance of Townsend's chipmunks and western red-backed voles at potential detriment to flying squirrels. However, this relationship with more open canopy conditions might not hold or remain linear in young or open canopy forests.

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