Avian multi-scale habitat relationships for the Four-Forest Restoration Initiative:

Final Report

May 2020

Bird Conservancy of the Rockies
14500 Lark Bunting Lane
Brighton, CO 80603
303-659-4348
www.birdconservancy.org

Tech. Report # SC-4FRI-05
Challenge Cost Share Supplemental Agreement 15-CS-11030420-011

Bird Conservancy of the Rockies

Connecting people, birds and land

Mission: Conserving birds and their habitats through science, education and land stewardship

Vision: Native bird populations are sustained in healthy ecosystems

Bird Conservancy of the Rockies conserves birds and their habitats through an integrated approach of science, education, and land stewardship. Our work radiates from the Rockies to the Great Plains, Mexico and beyond. Our mission is advanced through sound science, achieved through empowering people, realized through stewardship, and sustained through partnerships. Together, we are improving native bird populations, the land, and the lives of people.

Core Values:

1. **Science** provides the foundation for effective bird conservation.
2. **Education** is critical to the success of bird conservation.
3. **Stewardship** of birds and their habitats is a shared responsibility.

Goals:

1. Guide conservation action where it is needed most by conducting scientifically rigorous monitoring and research on birds and their habitats within the context of their full annual cycle.
2. Inspire conservation action in people by developing relationships through community outreach and science-based, experiential education programs.
3. Contribute to bird population viability and help sustain working lands by partnering with landowners and managers to enhance wildlife habitat.
4. Promote conservation and inform land management decisions by disseminating scientific knowledge and developing tools and recommendations.

Suggested Citation:
Latif, Q. S. and D. C. Pavlacky, Jr. 2020. Avian multi-scale habitat relationships for the Four-Forest Restoration Initiative: Final report. Bird Conservancy of the Rockies. Brighton, Colorado, USA.

Cover Photo:
Kaibab National Forest by Chris White.

Contact Information:
Quresh Latif
Quresh.latif@birdconservancy.org
Bird Conservancy of the Rockies
14500 Lark Bunting Lane
Brighton, CO 80603
970-482-1707

Executive Summary

Effectiveness monitoring critically informs broad-scale restoration and management of southwestern frequent-fire ponderosa pine-dominated forests. Forest restoration targets vegetation structure and consists primarily of timber harvest, mechanical thinning, and prescribed fire to restore historical ecological function arising from frequent, low-severity wildfire. Managers expect improved ecological function to benefit wildlife, making wildlife an important focus for effectiveness monitoring.

The Four-Forest Restoration Initiative (4FRI) leverages ongoing long-term monitoring under the Integrated Monitoring in Bird Conservation Regions (IMBCR) program to implement effectiveness monitoring focusing on birds. Using 10 years of monitoring data, we analyzed avian species and community relationships with vegetation structure and composition to support hypothesis-driven effectiveness monitoring. Our objectives were to 1) evaluate multi-scale habitat relationships for site occupancy and species richness of songbirds in ponderosa pine woodlands of the Coconino and Kaibab National Forests, 2) estimate multi-scale habitat relationships with species occupancy and community dynamics (e.g., colonization, extirpation, turnover, and changes in species richness), and 3) evaluate habitat relationships for the abundance of selected songbird species of management interest. To meet these objectives, we applied Bayesian hierarchical occupancy and abundance models to estimate relationships of species occupancy, richness, abundance, occupancy dynamics, and population trends with vegetation attributes relevant to forest restoration. We additionally evaluated strength of evidence for estimated relationships by comparing them to *a priori* hypotheses reflecting current knowledge of avian species life history and ecology.

Estimated habitat relationships with occupancy and abundance were consistent with most (132 of 172) *a priori* hypotheses for 60 species, providing relatively strong evidence upon which to base hypotheses for treatment effects. For example, available evidence suggested landscapes with extensive ponderosa pine forest provide high quality habitat for Western Wood-Pewee, Stellar's Jay, White-breasted Nuthatch, Pygmy Nuthatch, Brown Creeper, Dark-eyed Junco, Yellow-rumped Warbler and Red-faced Warbler. In contrast, landscapes with extensive canopy gaps appear to provide limited quality habitat for Acorn Woodpecker, Gray Flycatcher, Plumbeous Vireo, Stellar's Jay, White-breasted Nuthatch, Mountain Chickadee, Hermit Thrush, Ruby-crowned Kinglet, Olive Warbler, Red-faced Warbler, and Western Tanager. After controlling for landscape-level patterns, local-scale habitat relationships suggested broad value in forest restoration that maintains tall mature trees for numerous species and species richness. By following a hypothetico-deductive approach, we provide reliable knowledge representing the best available science for informing management decisions. We provide guidelines for applying this knowledge towards hypothesis-driven effectiveness monitoring of restoration and management of southwestern frequent-fire ponderosa pine forests.

Acknowledgements

We thank Dan Kipervaser with the US Forest Service Four Forest Restoration Initiative for funding this project and providing logistical support. We thank Josh Bahling and John Souther for their continued support of this project. We also thank the 4FRI Multi-party Monitoring Board and 4FRI Multi-party Monitoring Board Wildlife Subcommittee, especially Bryce Esch (NAU ERI), Hannah Griscom (AZ Game & Fish), Jamie Sanderlin (US Forest Service, RMRS), Shaula Hedwall (USFWS), Julia Camp (US Forest Service), Ariel Leonard (US Forest Service), Valerie Stein Foster (US Forest Service), Mark Bellis (US Forest Service), and Justin Schofer (US Forest Service), for their involvement in guiding this project and providing input along the way. Finally, we thank the field technicians who collected avian and vegetation point count data. We thank Chris White (Bird Conservancy) for his leadership throughout this project, including during sampling design, field implementation, analysis, and writing.

Table of Contents

Introduction

The USDA Forest Service (USFS) develops land management plans to maintain and restore ecosystem sustainability, including ecological integrity, viable wildlife populations, and diversity of plant and animal communities (USDA 2012). Human activities, including grazing, logging, and fire suppression, have substantially altered the structure and function of frequent-fire forests of the southwestern United States (Moore et al. 1999, Allen et al. 2002). Changes include loss of large fire-resistant ponderosa pine (Pinus ponderosa) trees and increased density of smaller fire-intolerant tree species and understory vegetation. These changes have increased the risk of uncharacteristically severe wildfire, with potential for permanent forest degradation and loss. The USFS currently engages in broad-scale landscape-wide restoration efforts with Collaborative Forest Landscape Restoration Projects (CFLRPs) aimed at mitigating these changes primarily using timber harvest, mechanical thinning, and prescribed fire (Schultz et al. 2012). In particular, the Four-Forest Restoration Initiative (4FRI) aims to restore the structure, pattern, composition, and health of fire-adapted ponderosa pine (Pinus ponderosa) ecosystems, reduce fuels and the risk of unnaturally severe wildfires, and provide for wildlife and plant diversity in four national forests (Kaibab, Coconino, Apache-Sitgreaves, and Tonto National Forests; Schultz et al. 2012).

Federal funding sources support and mandate effectiveness monitoring in conjunction with broad-scale forest restoration (Colavito 2016). Effectiveness monitoring plays an important role in making state-dependent decisions, evaluating the success of management objectives and contributing to adaptive management cycles (Lyons et al. 2008). Monitoring often focuses on vegetation characteristics directly targeted by restoration treatments, but supporting and maintaining wildlife communities are important ecological functions provided by forests. If treatments effectively restore desirable function, practitioners expect to improve conditions for various wildlife species. Predicting species responses to ponderosa pine restoration provides a framework for linking restoration ecology with biodiversity conservation (Noss et al. 2006). Empirical studies are beginning to verify expectations for the positive effects of ponderosa pine restoration on wildlife communities (Kalies et al. 2010, Latif et al. In Press). Meaningful evaluation of forest restoration therefore would ideally include an understanding of the historical disturbance regime and monitoring treatment effects on wildlife. Accordingly, 4FRI includes avian monitoring implemented in conjunction with Integrated Monitoring in Bird Conservation Regions (IMBCR; Pavlacky et al. 2017, Latif et al. In Press) in relation to planned treatments in its effectiveness monitoring program.

Monitoring under IMBCR follows a spatially balanced stratified sampling design (Stevens and Olsen 2004) allowing analysts to combine data subsets appropriate for estimating avian population or community parameters at various scales for particular objectives. Surveys of 4FRI task orders for pre-treatment avian monitoring were conducted in 2015–2018. The 4FRI wildlife subcommittee (hereafter wildlife subcommittee) initially intended to use forest-wide IMBCR background data to serve as control data in a before-after-control-impact (BACI; Morrison et al. 2008) evaluation of treatment effects. Background monitoring was discontinued after 2017, and while before-after designs are still possible, background sampling in adjacent National Forests concurrent with sampling 4FRI treatments is necessary for the control-impact aspect of the BACI design (Morrison et al. 2008). Before-after treatment and lag effects can be estimated upon completion of post-treatment surveys within task orders.

The USFS, in collaboration with the wildlife subcommittee, entered into a master partnership agreement with Bird Conservancy to implement a preliminary analysis of available pre-treatment task order and forest-wide IMBCR data, the results of which are detailed in this report. We analyzed broad-scale habitat relationships to provide context and inform predictions for future treatment effects analyses. We also reviewed the literature and integrated our results with published information within a hypothesis-driven framework (*sensu* Sells et al. 2018) to maximize rigor for inferring habitat relationships. The wildlife subcommittee members and Bird Conservancy staff identified three objectives for this analysis:

1. Evaluate multi-scale habitat relationships for site occupancy and species richness of songbirds in ponderosa pine woodlands of the Coconino and Kaibab National Forests along gradients of stand and landscape structure.

2. Estimate multi-scale habitat relationships with species occupancy and community dynamics (e.g., colonization, extirpation, turnover, and changes in species richness) for songbirds over time in ponderosa pine woodlands of the Coconino and Kaibab National Forests along gradients of stand and landscape structure.

3. Evaluate habitat relationships for the abundance of selected songbird species of management interest in ponderosa pine woodlands of the Coconino and Kaibab National Forests. Abundance can exhibit patterns not apparent for occupancy, so this objective supplements objectives 1 and 2 for select species with sufficient data.

Following fulfillment of these objectives, we discuss how habitat relationships inferred here could inform treatment prescriptions and hypothesis-driven effectiveness monitoring of forest restoration.

Methods

Sampling

Avian data were collected in the Coconino and Kaibab National Forests between 2009 and 2017 (Pavlacky et al. 2017, White and Latif 2020) and 4FRI task orders between 2015 and 2018 (Figure 1). Sampling units were 1-km^2 grid cells consisting of 16 survey points separated by 250 m and located ≥125 m from the grid cell boundary (Pavlacky et al. 2017). Surveyors visited a spatially balanced sample (*sensu* Stevens and Olsen 2004) of grid cells within National Forest strata and a finite sample within selected task orders during each year of monitoring. At each point within each grid cell, surveyors recorded all bird species seen or heard during a six minute survey period (White and Latif 2020). Over the entire 2009–2018 study period represented in this analysis, we surveyed 999 points within 85 task order grid cells and 1,222 points within 81 background grid cells, totaling 2,221 points within 166 grid cells (Table 1). Sixty percent of the 166 grid cells (primarily background cells) were surveyed in > 1 year, yielding 463 grid surveys and 5738 point surveys across the 10-year (2009–2018) study period.

Table 1. Sampling effort contributing to analysis of habitat relationships. Primary sampling units are 1-km^2 grid cells and secondary units are 150-m radius circular point-centered plots, with 6–16 points (mean [SD] = 13.4 [2.9]) spaced evenly 250 m apart nested within grid cells. Task order sampling units represented areas targeted for forest restoration treatments, whereas background units represented a broader landscape within national forest boundaries. Most task order sampling units were surveyed only once each (i.e., different task orders surveyed each year), whereas background units were surveyed repeatedly across years, although not every unit was surveyed in every year.

Year	**Task order**		**Background**	
	***n* points**	***n* grids**	***n* points**	***n* grids**
2009	0	0	365	30
2010	0	0	563	45
2011	0	0	481	44
2012	0	0	391	30
2013	0	0	478	37
2014	0	0	832	56
2015	419	30	434	32
2016	382	37	472	43
2017	152	16	469	34
2018	300	29	0	0
All	999	85	1,222	81

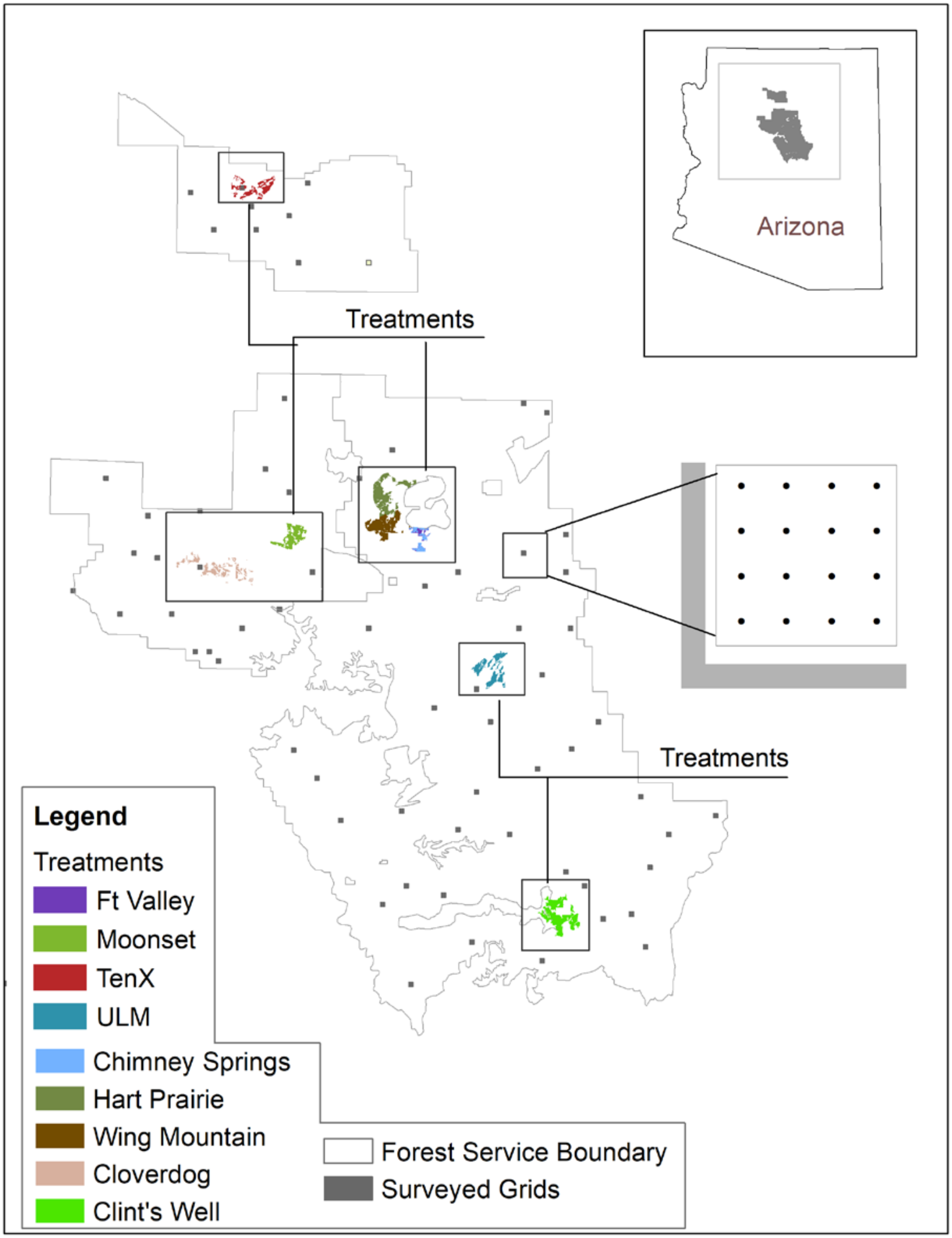

Figure 1. Distribution of background sampling units and four task orders (Ft. Valley is Fort Valley) encompassing the study area for analysis of multi-scale avian habitat relationships. Each primary sampling unit for bird surveys consists of a 1km^2 grid cell containing a 4×4 array of evenly spaced survey points.

Covariates

We included 17 covariates in models quantifying habitat relationships with avian occupancy and abundance (Table 2). Habitat covariates quantified vegetation structure and composition for forest stands (150m radius [7ha] or 50m radius [4.9 ha] circular neighborhoods centered on survey points) and landscapes (1km radius [314 ha] circular neighborhoods centered on grid cells). We derived landscape covariates from remotely sensed data sources describing canopy cover (USDA Forest Service 2019a) and the extent of ponderosa pine dominated forest (LANDFIRE 2019). Landscape covariates describing canopy cover quantified the extent and variability in size of canopy gaps (<10% canopy cover) and open forest (10–40% canopy cover). We excluded an additional two landscape covariates describing the mean size of gaps and open forest patches and one covariate describing the density of edge between gaps, open forest, and closed forest due to the high correlations ($r > 0.7$) of these with other covariates. Prior to deriving covariates based on canopy cover, we adjusted raw canopy cover values to account for wildfires that had occurred between 2011 (the imagery year for canopy cover) and each year birds were surveyed. For wildfires that occurred after 2011 but before a given bird-survey year, we multiplied canopy cover by percent canopy mortality derived from remotely sensed data within wildfire perimeters (MTBS 2019 or USDA Forest Service 2019b). We treated all canopy cover values for 2009 and 2010 as missing within perimeters of wildfires that occurred after these survey years but before 2011. Landscape mosaics described by vegetation composition and configuration are important for managing landscapes for wildlife conservation objectives (Lindenmayer et al. 2008). The 314 ha neighborhoods used for landscape covariates were sufficiently large to quantify landscape composition and configuration but small enough to be ecologically relevant to songbirds. We compiled two stand-level covariates quantifying canopy cover and coverage of ponderosa pine-dominated forest from remotely sensed data sources (7 ha) and eight stand-scale covariates from rapid assessment vegetation data (4.9 ha) collected at survey points (Table 1; Pavlacky et al. 2017, Hanni et al. 2018). Four of the stand covariates were specifically identified as informative for management by the wildlife committee, and the remaining six were demonstrated as potentially informative in a previous analysis (Latif et al. In Press). Two additional covariates represented the timing of surveys for quantifying potential heterogeneity in detection probabilities (Table 2).

Table 2. Covariates used for analyzing multi-scale habitat relationships of songbirds in the Coconino and Kaibab National Forests, Arizona, 2009–2017. Data sources are National Land Cover Database (NLCD), LANDFIRE, and IMBCR field measurements.

Scale	Covariate (abbrev.)	Resolution (ha)	Description	Data source
Landscape (grid cell)	Canopy gaps (percGap)[a]	314	Percent area of neighborhood with < 10% canopy cover	NLCD
	Open forest (percOpen)[a]	314	Percent area of neighborhood with 10-40% canopy cover	NLCD
	Ponderosa pine forest (PIPO1km)[a]	314	Percent area of neighborhood with ponderosa pine forest cover (categorized by EVC in LANDFIRE)	LANDFIRE

Scale	Covariate (abbrev.)	Resolution (ha)	Description	Data source
	Variation in gap size (CVGap)[a,b]	314	Coefficient of variation for size of patches within neighborhood with <10% canopy cover	NLCD
	Variation in open forest patch size (CVOpen)[a]	314	Coefficient of variation for size of patches within neighborhood with 10-40% canopy cover	NLCD
Stand (point)	Canopy cover (CanCov)[a,c]	7	Percent canopy cover	NLCD
	Canopy height (CanHt)	4.9	Mean height to the top of overstory trees (m)	IMBCR
	Number of snags (NumSnags)[a]	4.9	Count of snags within 50 m of survey points	IMBCR
	Ponderosa pine forest (PIPO150m)[a]	7	Percent area of neighborhood with ponderosa pine forest cover (categorized by EVC in LANDFIRE)	LANDFIRE
	Gambel oak canopy (QUGA)	4.9	Percent of canopy provided by Gambel oak (relative cover)	IMBCR
	Shrub-sapling height (ShrubHt)[a]	4.9	mean height of woody vegetation (within 0.25-3m) within a 50m radius of the survey point (zero for points without shrubs)	IMBCR
	Shrub-sapling cover (ShrubCov)	4.9	percent cover of woody vegetation (within 0.25-3m) within a 50m radius of the survey point	IMBCR
	Shrub-sapling volume (ShrubVol)[c]	4.9	Cube root of volume (m^3), where volume = area covered (max = 7854 m^2, i.e., plot area) × average shrub height (m) for woody shrub and seedling trees species	IMBCR
	Ladder fuels (Ladder)	4.9	Percent of shrub-sapling layer (0.25-3m) consisting of ladder fuel species, i.e., conifer, juniper, and Gambel oak saplings	IMBCR
	Herbaceous volume (HerbVol)	4.9	Cube root of volume (m^3), where volume = area covered by grasses and forbes (max = 7854 m^2, i.e., plot area) × average height (m) of grass and forbes	IMBCR

Scale	Covariate (abbrev.)	Resolution (ha)	Description	Data source
Survey	Day of year (DOY)[c]	--	Number of days elapsed since January 1	IMBCR
	Time since sunrise (Time)[c]	--	Number of minutes elapsed since sunrise	IMBCR

[a] Identified by wildlife subcommittee as particularly informative for management

[b] This covariate was only included in abundance models. For community occupancy models, we failed to achieve convergence within a reasonable timeframe for parameters describing relationships with this covariate, suggesting data limitations for supporting estimation.

[c] These served as covariates of detection probability. Canopy cover was a covariate of detection probability along with occupancy or abundance.

Inference framework

To maximally inform future treatment effects analysis, we inferred habitat relationships within a hypothetico-deductive framework (Sells et al. 2018). We developed *a priori* hypotheses for habitat relationships based on species life histories and published literature describing species ecology. We first grouped species by life history and hypothesized relationships based on group membership (Table 3). We then synthesized group-level hypotheses with species-specific ecological literature to develop hypotheses for individual species (Appendices A, B). Recognizing that life history groups are not comprehensive and that species represent composites of multiple traits, we placed greater weight on species-specific ecology described in the literature where relevant information was available when developing species hypotheses. Additionally, we generally hypothesized that species richness would be greater and species turnover would be less (i.e., greater community stability) in landscapes and forest stands with low to intermediate canopy cover dominated by ponderosa pine, large trees (represented in this study by a tall average canopy), and low shrub volume (cover and height) because such conditions represent pre-settlement conditions and disturbance regimes under which birds in frequent-fire forests evolved (Kalies and Rosenstock 2013, Latif et al. 2016, Sanderlin et al. 2016).

Where our results were consistent with *a priori* hypotheses, we drew relatively strong inference of habitat relationships, whereas we exercised caution where estimated relationships were inconsistent with hypotheses or inconsistent across available literature. Additionally, we identified relatively large-magnitude (hereafter strong) covariate relationships (described further in *Data analysis*) to further inform inference. When translating habitat relationships inferred into hypotheses for treatment effects, we would expect the largest treatment effects in so far as treatments alter conditions with which we have estimated strong relationships that are also consistent with clear *a priori* hypothesis.

Table 3. Species life history groups and predicted relationships with habitat features and forest restoration treatments, along with expected mechanisms for hypothesized treatment relationships.

Trait	Code	Description	Hypothesized habitat relationships
Nesting	C_P	Primary cavity nesters, i.e., woodpeckers that excavate cavities	snags (+)

Trait	Code	Description	Hypothesized habitat relationships
	C_S	Secondary cavity nesters, i.e., use previously excavated cavities	snags (+)
	O_C	Species with open cup nests placed in the canopy	canopy cover (+)
	O_S	Species with open cup nests placed in woody understory vegetation, i.e., shrubs	canopy cover (-), shrub density (+)
	O_G	Species with open cup nests placed on the ground	canopy cover (-), herbaceous cover (+)
	OT	Other includes species that nest on cliffs, on anthropogenic structures, or in various substrates that are not easily categorized.	--
Foraging	Sn	Woodpeckers that forage for beetle larvae in snags	snags (+)
	CI	Insectivores that forage on live trees, including bark- and canopy foliage-gleaning species	canopy cover (+)
	CS	Conifer seed-eating species	canopy cover (-), canopy height (+), ponderosa pine (+)
	Gr	Species that forage on the ground or on herbaceous vegetation, including herbivores and insectivores.	canopy cover (-), herbaceous cover (+)
	Sh	Species that forage on shrubs or in the shrub layer, including herbivores and insectivores.	canopy cover (-), shrub density (+), ladder fuels (-), deciduous shrubs (+)
	Fl	Hummingbirds, which forage for nectar from flowers.	canopy cover (-), shrub density (+), ladder fuels (-), herbaceous cover (+)
	AI	Aerial insectivores	canopy cover (-), shrub density (+), ladder fuels (-)
	Gn	Generalist forager; foraging behavior varies with available resources, and includes more than two of modes described above.	--

Data Analysis

We modeled habitat relationships with two population metrics, occupancy and abundance. For objectives 1 and 2, we used a dynamic multi-species hierarchical framework to model species occupancy, occupancy dynamics, and emergent community-level patterns (Dorazio et al. 2010; model structure detailed in Appendix C). We extended community models (Dorazio et al. 2006, Iknayan et al. 2014) to estimate occupancy at multiple scales (Mordecai et al. 2011, Pavlacky et al. 2012), mirroring our hierarchical sampling design (Pavlacky et al. 2017). Community models include individual occupancy models for each species, while sharing information across species to inform estimates for species with sparse data to better inform species richness estimates corrected for imperfect detection.

For quantifying species and community dynamics (objective 2), we estimated initial occupancy, subsequent occupancy change (colonization and extirpation; i.e., colonization and local extinction in MacKenzie et al. 2003, Royle and Kéry 2007), and covariates with both. For this analysis, we excluded raptors, owls, grouse, cranes, and water birds not readily detectable with our survey methods. We also only included species that breed in our study area and excluded detections flagged as likely representing migrants (Hanni et al. 2018). We followed the multi-scale parameterization developed by Green et al. (2019), whereby we modeled colonization and extirpation rates at a landscape scale (grid cell level), and conditioned local scale (point level) occupancy on the occupancy status of the landscape unit. Initially, we attempted to fit time-specific parameters for local extinction and colonization to model hypotheses for non-equilibrium dynamics of the species (MacKenzie et al. 2006, Dorazio et al. 2010), but we were unable to achieve convergence with this model within a feasible timeframe. We therefore simplified our model by assuming colonization and extirpation rates were static across years, while allowing variation across species and environmental conditions described by covariates (see also Green et al. 2019). Constraining extirpation and colonization across time allowed us to model equilibrium dynamics for the species (MacKenzie et al. 2006: 208-212). From colonization and extirpation rates, we derived species turnover as the proportion of occupied sites that were previously unoccupied by a species and community turnover as the mean of species turnover rates (see formulae in Appendix C). We considered covariate relationships with turnover to infer how population and community stability varied with environmental conditions. Having modeled colonization and extirpation rates as static processes, we can identify an equilibrium state at which the model predicts occupancy and richness to remain constant until the system is perturbed such as expected with environmental change. We compared covariate relationships with occupancy, richness and turnover for initial versus equilibrium states. We considered relationships that differed between initial versus equilibrium states to be potentially unstable or ephemeral, and thus inferred potential differences in short- versus long-term responses to treatment.

For objective 3, we analyzed habitat relationships with abundance and population trend for 20 focal species of management concern for which we had sufficient data to support hierarchical distance-sampling models (Royle et al. 2004, Hostetter et al. 2019; model structure detailed in Appendix D ; for focal species significance, see Table 4). Abundance models included parameters quantifying population trend and habitat relationships with trend. We applied these models within a Bayesian framework, providing greater flexibility in model structure, such as point-level density estimates and random effects to account for non-independence among points. We implemented posterior predictive model checking (*sensu*; Gelman and Hill 2007) to assess goodness-of-fit for each focal species (Table 4). When presenting results, we flagged species for which we found evidence for lack of model fit. We recommend caution when interpreting abundance estimates and predictions from models flagged as poorly fitted as they fail to quantify substantial portions of variation in the observed data.

We examined 95% Bayesian credible intervals (BCIs) to infer statistical support for covariate relationships and to identify strong relationships. We considered a relationship statistically supported if the corresponding BCI excluded zero. Additionally, we considered a covariate relationship with occupancy, occupancy dynamics, or abundance to be strong if the corresponding BCI had an upper limit < -0.1 or a lower limit > 0.1 (i.e., strong negative or strong positive relationships, respectively). We identified covariate relationships with abundance trends as strong if the BCI fell entirely below -0.02 or above 0.02. Although the cutoffs for these designations of strong relationships were somewhat arbitrary, we wanted to recognize the potential for relationships to be statistically supported but not necessarily ecologically meaningful. We were especially concerned with the potential for statistically supported but non-meaningful relationships at the point level where our sample sizes were large and statistical power was therefore high for clearly characterizing relationships as non-zero. We therefore supplemented information on statistical support by highlighting relatively strong relationships with the caveat that the ecological significance of a given relationship can only be ultimately determined in the context of particular applications or questions. We inferred statistical support for any apparent species richness relationships with covariates if BCIs for hyper-parameters quantifying mean covariate relationships across species did not include zero.

Table 4. Abundance of focal species and model goodness-of-fit. The table lists 20 focal species designated by the 4FRI wildlife subcommittee for modeling environmental relationships with abundance and abundance trends. These species were selected from those with sufficient data to inform hierarchical abundance models to represent a range of life history traits and additionally for their significance to management. For each species, we assessed model goodness-of-fit (GOF) by calculating and comparing deviance (-2×log-likelihood) for observed data versus simulated data drawn from the posterior predictive distribution (Gelman and Hill 2007[1]). We considered GOF $p > 0.95$ or $p < 0.05$ as providing evidence for lack of model fit (marked with asterisks). Estimates from abundance models suggested to be poorly fitted should be interpreted with caution.

Focal species	Life history		National Forest focal species	Additional management significance	GOF *p*
	Foraging	Nesting			
Grace's Warbler	CI	O_C	Kaibab, Coconino	Management indicator for clumps of mature ponderosa pine/pine-oak forests, yellow pine, and open parklike forests	0.06
Western Tanager	CI	O_C			0.01*
Mountain Chickadee	CI	C_S			0.20
Stellar's Jay	Gn	O_C			0.62
Hermit Thrush	Sh, Gr	O_S		Potential sensitivity to restoration treatments	0.31
Western Bluebird	Gr	C_S	Kaibab	Management indicator for understory development within openings in ponderosa pine stands	0.94
Dark-eyed Junco	Gr	O_G			0.19
Chipping Sparrow	Gr	O_S			0.63
Mourning Dove	Gr	O_S			0.10
Brown-headed Cowbird	Gr	OT		Obligate brood parasite with potential to negatively impact conservation status of many species	0.67
White-breasted Nuthatch	CI	C_S			0.00*

Focal species	Life history		National Forest focal species	Additional management significance	GOF *p*
	Foraging	Nesting			
Pygmy Nuthatch	CI	C_S	Coconino	Management indicator for relatively large (>18 inches diameter at breast height) snags	0.66
Brown Creeper	CI	C_S			0.33
House Wren	Gr	C_S			0.10
Western Wood-Pewee	AI	O_C			0.00*
Violet-green Swallow	AI	C_S		Potential sensitivity to restoration treatments	0.98*
Cordilleran Flycatcher	AI	C_S			0.02*
Broad-tailed Hummingbird	FI	O_C		Potential sensitivity to restoration treatments	0.04
Hairy Woodpecker	Sn	C_P		Represents woodpeckers, which are of management concern	0.18
Northern Flicker	Gn	C_P		Represents woodpeckers, which are of management concern	0.06

[1] Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/ hierarchical models. Cambridge University Press, New York, NY.

Results

During the study period, we recorded detections for 119 species. The five most commonly detected species were Pygmy Nuthatch, Dark-eyed Junco, Mountain Chickadee, White-breasted Nuthatch, and Grace's Warbler (Appendix A).

Species occupancy, occupancy dynamics, and richness

We found statistically supported occupancy relationships with covariates for 70 species. At the grid-cell level, we found statistical support for 49 covariate relationships with components of occupancy (initial occupancy, colonization, or extirpation) for 36 species (Figure 2). At the point level, we found statistical support for 211 covariate relationships with point occupancy for 68 species (Figure 3). Posterior median detectability estimates for a 6-min survey ranged 0.25–0.99 across species, with 49 species exhibiting statistically supported covariate relationships with detectability (Appendix E).

The data supported 28 relationships with extent of canopy gaps (percGap) for 27 species (Figure 2). Initial occupancy for 5 species related positively, colonization for 12 species related negatively and extirpation for 11 species related positively with canopy gaps. Furthermore, turnover increased notably with increasing canopy gap extent for seven species (Gray Flycatcher, Hairy Woodpecker, House Wren, Violet-green Swallow, White-breasted Nuthatch, Western Tanager, and Yellow-rumped Warbler; Appendix F). Thus, most species with supported relationships with canopy gaps showed reduced colonization or increased extirpation in grid cells with extensive gaps, often implying lower occupancy or greater turnover (i.e., less stable populations) in these cells (except American Crow, Horned Lark, Lark Sparrow, and Western Meadowlark; Appendix F). Colonization for five species – Warbling Vireo, House Wren, Hermit Thrush, Olive Warbler, and Red Crossbill – related negatively with extent of open forest (percOpen). Additionally, colonization for American Robin related positively and for Lesser Goldfinch negatively with variability in the size of open forest patches (CVOpen). Fourteen species exhibited statistically supported grid-cell occupancy relationships with percent ponderosa pine forest (PIPO1km). For eight of these species (Western Wood-Pewee, Steller's Jay, White-breasted Nuthatch, Pygmy Nuthatch, Brown Creeper, Dark-eyed Junco, Yellow-rumped Warbler, and Red-faced Warbler), colonization related positively, whereas the remaining six species (Common Raven, Juniper Titmouse, Bewick's Wren, House Finch, Spotted Towhee, and Virginia Warbler) exhibited functionally negative relationships (either negative for colonization or positive for extirpation) with percent ponderosa pine forest (PIPO1km).

At the point level, we found statistically supported relationships with canopy cover (CanCov) for 41 species (Figure 3). We found similar numbers of positive relationships (19) as negative relationships (22). We found similarly numerous (41) relationships with canopy height (CanHt), although the direction of these were more frequently positive (31) than negative (10). We found supported relationships with ponderosa pine forest (PIPO150m) for 33 species, of which more were negative (22) than positive (11). We found fewer and weaker relationships with other covariates: 15 with snags (NumSnags), 19 with Gambel oak (QUGA), 24 with shrub cover (ShrubCov), 12 with shrub height (ShrubHt), 9 with ladder fuels (Ladder), and 17 with herbaceous volume (Herb).

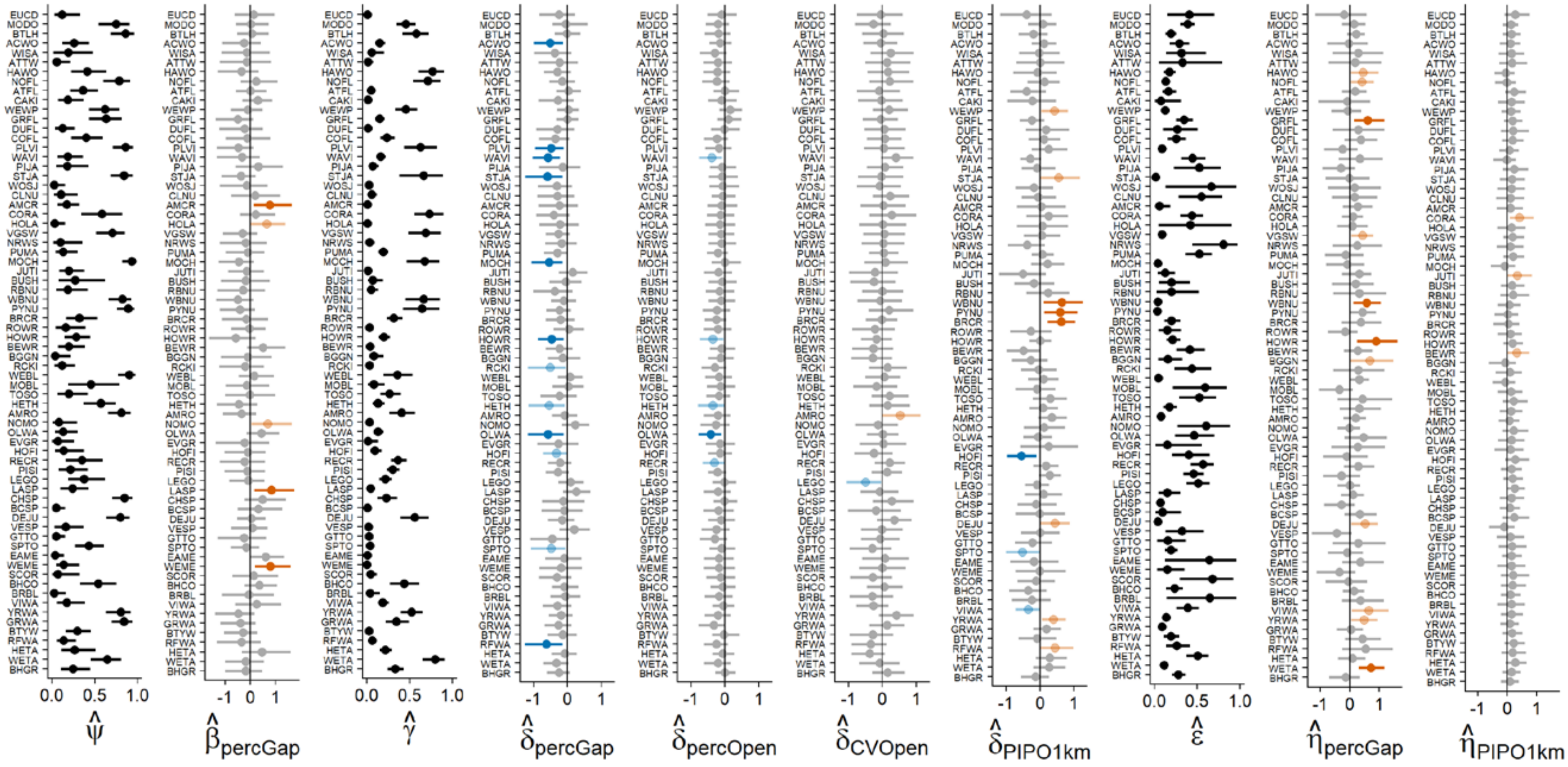

Figure 2. Estimated covariate relationships (posterior medians and 95% BCIs) with grid-level occupancy for 70 species exhibiting at least one statistically supported relationship at either grid- or point-levels (species codes defined in Appendix A). First, third, and eighth panels show initial occupancy (ψ), colonization (γ), and extirpation (ε) rates at mean covariate conditions, followed by covariate relationships with each (β, δ, and η, respectively; for complete covariate names and descriptions, see Table 2). Only covariate relationships statistically supported for at least one species are shown. Colors indicate supported positive (red) and negative (blue) relationships, with darker colors indicating strong relationships ($|\beta|$, $|\delta|$, or $|\eta| > 0.1$).

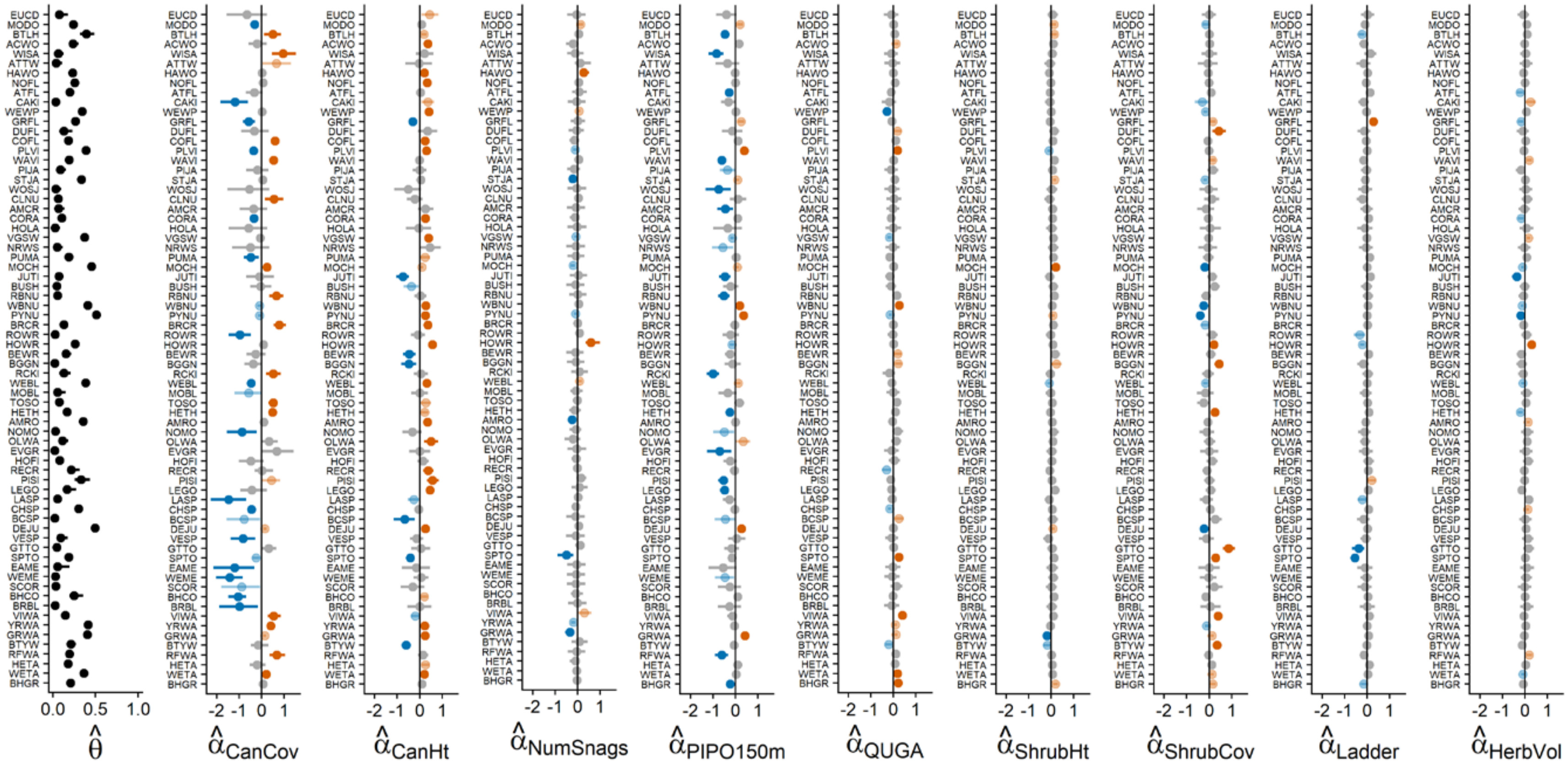

Figure 3. Estimated covariate relationships (posterior medians and 95% BCIs) with point-level occupancy for 70 species exhibiting at least one statistically supported relationship at either grid- or point-levels (species codes defined in Appendix A). The first panel shows point-level occupancy (θ) at mean covariate conditions, and the rest are covariate relationships (α; for complete covariate names and descriptions, see Table 2). Colors indicate supported positive (red) and negative (blue) relationships, with darker colors indicating strong relationships (|α| > 0.1).

We found several apparent covariate relationships with species richness. The data supported negative and positive community-level means for grid-level colonization (posterior median [95% BCI]: $\bar{\delta}_{percGap}$ = -0.22 [-0.34, -0.11]) and extirpation ($\bar{\varepsilon}_{percGap}$ = 0.17 [0.01, 0.32]) relationships with extent of canopy gaps, respectively. Reflecting these relationships, we found a decline in (posterior median) predicted species richness of nine in grid cells with extensive canopy gaps when approaching equilibrium, whereas we estimated no such decline in cells without canopy gaps (Figure 4). We also found support for a negative relationship of mean colonization with extent of open forest ($\bar{\delta}_{percOpen}$ = -0.16 [-0.26, -0.05]). Accordingly, model-predicted species richness increased when approaching equilibrium by six species for grid cells with no open forest but did not for cells with 100% open forest (Figure 4). We found support for an initially strong positive relationship of species richness with variability in open forest patch size ($\bar{\beta}_{CVOpen}$ = 0.28 [0.03, 0.53]), although this relationship diminished when approaching equilibrium (Figure 4). An initial positive relationship with PIPO1km flipped in direction to a negative relationship when approaching equilibrium, largely reflecting greater extirpation rates in grid cells with extensive ponderosa pine forest ($\bar{\varepsilon}_{PIPO1km}$ = 0.15 [0.04, 0.26], Figure 4). Mean turnover did not vary much in relation to any grid-level covariates either initially or at equilibrium (Figure 4). Point-level species richness increased with increasing canopy height ($\bar{\alpha}_{CanHt}$ = 0.08 [-0.01, 0.16]; Figure 5). Mean relationships for point-level occupancy differed from zero for other covariates ($\bar{\alpha}_{CanCov}$ = -0.15 [-0.3, -0.2]; $\bar{\alpha}_{PIPO150m}$ = -0.19 [-0.27, -0.1]), but predicted species richness did appear to vary meaningfully in relation to these covariates (Figure 5).

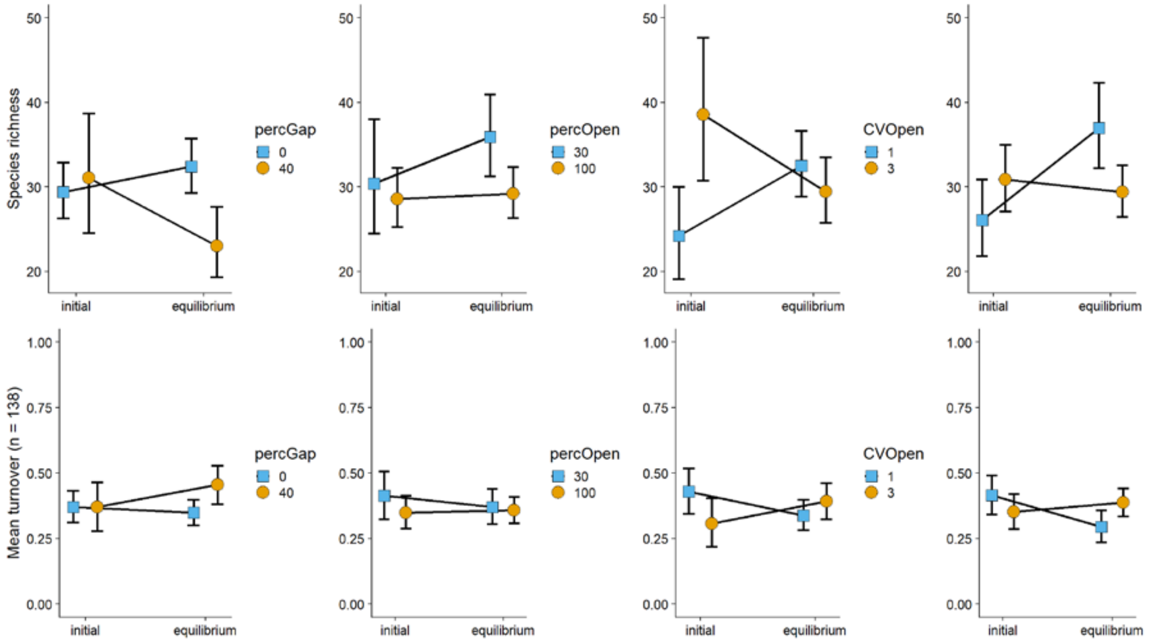

Figure 4. Posterior median predictions (points) and 95% Bayesian credible intervals (error bars) for grid-level species richness (top row) and community-level turnover (mean across species, bottom row). Plotted predictions show trajectories as we move from the initial year of study towards equilibrium assuming average colonization and extirpation rates estimated during the 10-year study period. Estimates for minimum and maximum values are represented for each covariate (percent canopy gaps [percGap], percent open forest [percOpen], coefficient of variation in open forest patch size [CVOpen], and percent ponderosa pine-dominated forest [PIPO1km]) are represented by blue squares and orange circles, respectively.

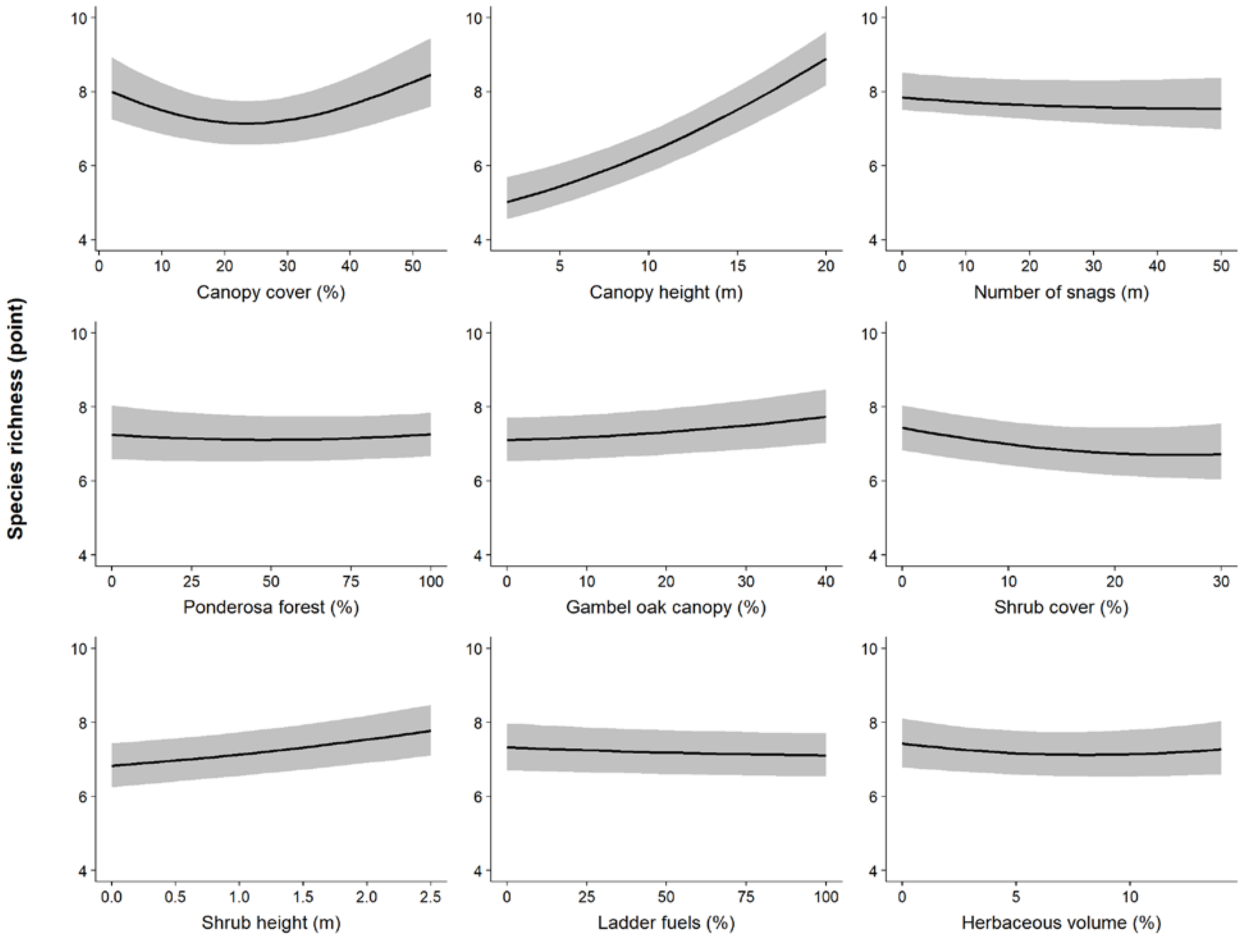

Figure 5. Predicted point level species richness in relation to covariates. Lines and error bands are posterior median and 95% Bayesian credible intervals, respectively.

Abundance and trends for focal species

At the grid-level, we found statistical support for 10 habitat relationships with landscape-scale abundance for 8 focal species, support for overall population trends for 10 species, and support for 10 habitat relationships with abundance trend for 7 species (Figure 6). At the point level, we found 56 statistically supported habitat relationships with local abundance, including at least one relationship for each focal species (Figure 7). Models for most species fit the data reasonably well in that we did not find clear evidence for overall lack of fit (Table 4). Nevertheless, models fitted poorly for White-breasted Nuthatch, Western Wood-Pewee, Violet-green Swallow, and Cordilleran Flycatcher, suggesting abundance estimates for these four species should be interpreted with caution.

Five species exhibited supported grid-level abundance relationships with canopy gaps (percGap; Figure 6). Abundance for Cordilleran Flycatcher, House Wren, and Violet-green Swallow related negatively with gaps. Dark-eyed Junco exhibited a positive abundance trend but primarily in grid cells with less extensive gaps (Appendix G). A strong positive abundance trend in grid cells with extensive canopy gaps made up for an initial negative relationship with canopy gaps for Hairy Woodpecker. Furthermore, considering the negative relationship of trend with CVGap, Hairy Woodpecker abundance trended upward primarily in grid cells with consistently large gaps. Mountain Chickadee exhibited a positive abundance trend that was especially pronounced in grid cells with extensive open forest. Brown Creeper were less abundant with more open forest, although we estimated abundance with limited precision in grid cells with less extensive open forest. Abundance or abundance trends for Dark-eyed Junco, Mourning Dove, Violet-green Swallow, and Pygmy Nuthatch related positively with canopy heterogeneity (CVGap or CVOpen) in contrast with Hairy Woodpecker. Western bluebird, Northern Flicker, and Mourning Dove exhibited positive grid-level relationships for abundance or abundance trends with extent of ponderosa pine forest (PIPO1km). Chipping Sparrow exhibited a negative trend in grid cells with extensive ponderosa pine forest, and Broad-tailed Hummingbird exhibited a positive trend in cells with less ponderosa forest. A positive trend in grid cells with extensive ponderosa forest eliminated an initial negative relationship with ponderosa pine forest for Brown Creeper.

Point-level abundance related positively with canopy cover for six focal species and negatively for five focal species (Figure 7). A negative point-level abundance relationship was consistent with positive grid-level relationships with canopy gaps for Cordilleran Flycatcher (see above). In contrast, a negative point-level abundance relationship for Violet-green Swallow was not consistent with the negative grid-level relationship with canopy gaps. Supported relationships for 12 focal species with canopy height were all positive. Supported point-level abundance relationships with ponderosa pine forest (PIPO150m) were positive for five focal species and negative for one species – Broad-tailed Hummingbird. Furthermore, this negative relationship was not consistent with the positive grid-level relationship of trend with ponderosa pine forest (see above). Focal species relationships with snags (NumSnags) were more frequently negative (four species) than positive (Hairy Woodpecker). We found two positive focal species relationships with Gambel oak (Western Tanager and White-breasted Nuthatch) and two negative (Chipping Sparrow and Violet-green Swallow). Focal species relationships with shrub cover and height were primarily positive (seven species) except for Grace’s Warbler. The two relationships with ladder fuels (Ladder) were negative (House Wren and Broad-tailed Hummingbird). Focal species relationships with herbaceous volume were primarily positive (seven species; *contra* one species – Hermit Thrush).

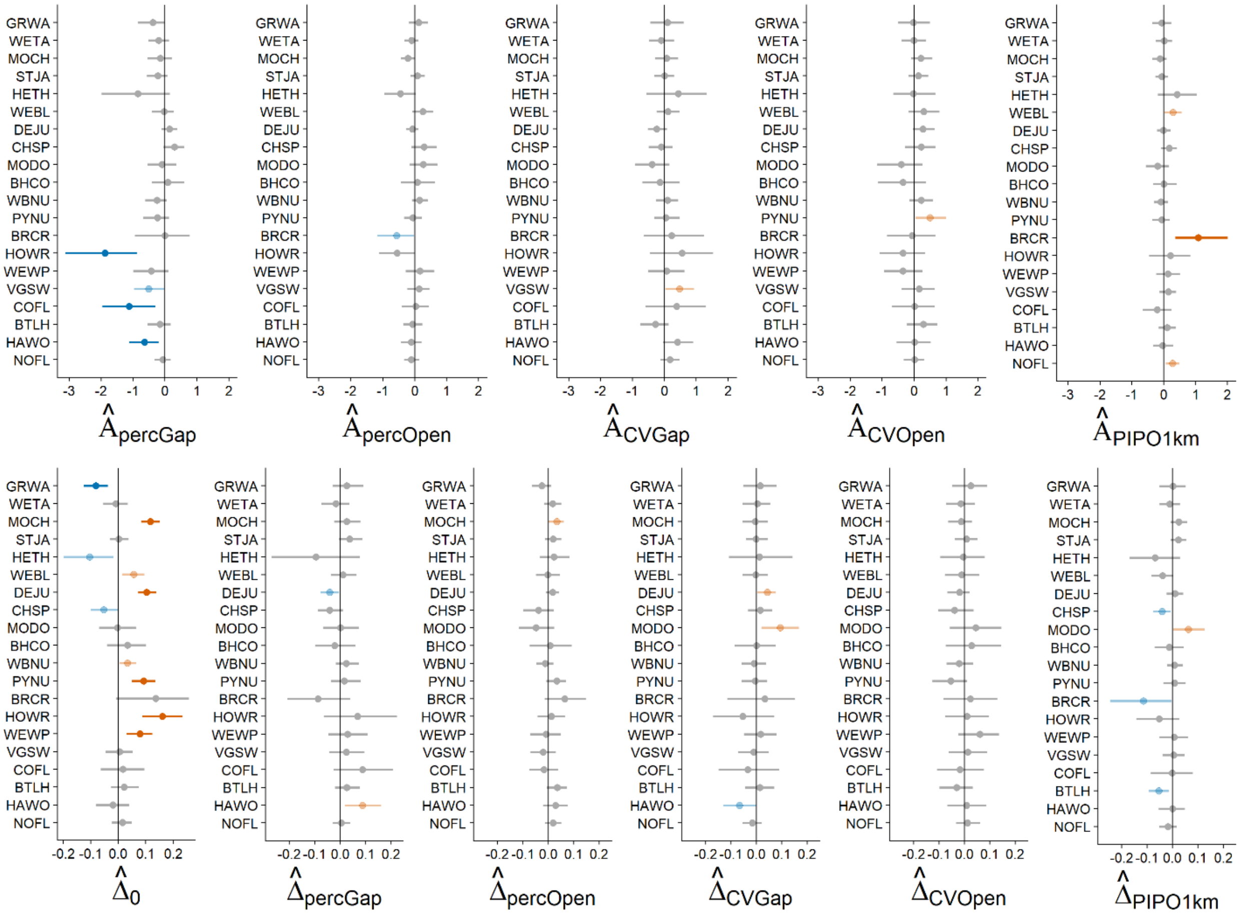

Figure 6. Grid-cell level (landscape scale) habitat relationships with abundance (top) and population trend (bottom) for 20 focal species. Focal species are Grace's Warbler (GRWA), Western Tanager (WETA), Mountain Chickadee (MOCH), Steller's Jay (STJA), Hermit Thrush (HETH), Western Bluebird (WEBL), Dark-eyed Junco (DEJU), Chipping Sparrow (CHSP), Mourning Dove (MODO), Brown-headed Cowbird (BHCO), White-breasted Nuthatch (WBNU), Pygmy Nuthatch (PYNU), Brown Creeper (BRCR), House Wren (HOWR), Western Wood-Pewee (WEWP), Violet-green Swallow (VGSW), Cordilleran Flycatcher (COFL), Broad-tailed Hummingbird (BTLH), Hairy Woodpecker (HAWO), and Northern Flicker (NOFL). Relationships are with percent area with canopy gaps (<10% canopy cover; percGap), percent area with open forest (10-40% canopy cover; percOpen), coefficient of variation in gaps (CVGap) or open forest patches (CVOpen), and percent ponderosa pine-dominated forest (PIPO1km). Population trends (Δ_0) are linear relationships with year (1–10) at mean covariate conditions, and habitat relationships with trend describe how trends changed with covariates. Dots and lines are posterior median and 95% Bayesian credible intervals. Colors indicate supported positive (red) and negative (blue) relationships, with darker colors indicating strong relationships (lower 95% credible limit for $|A| > 0.1$, $|\Delta_0| > 0.1$, or $|\Delta_{[covariate]}| > 0.02$).

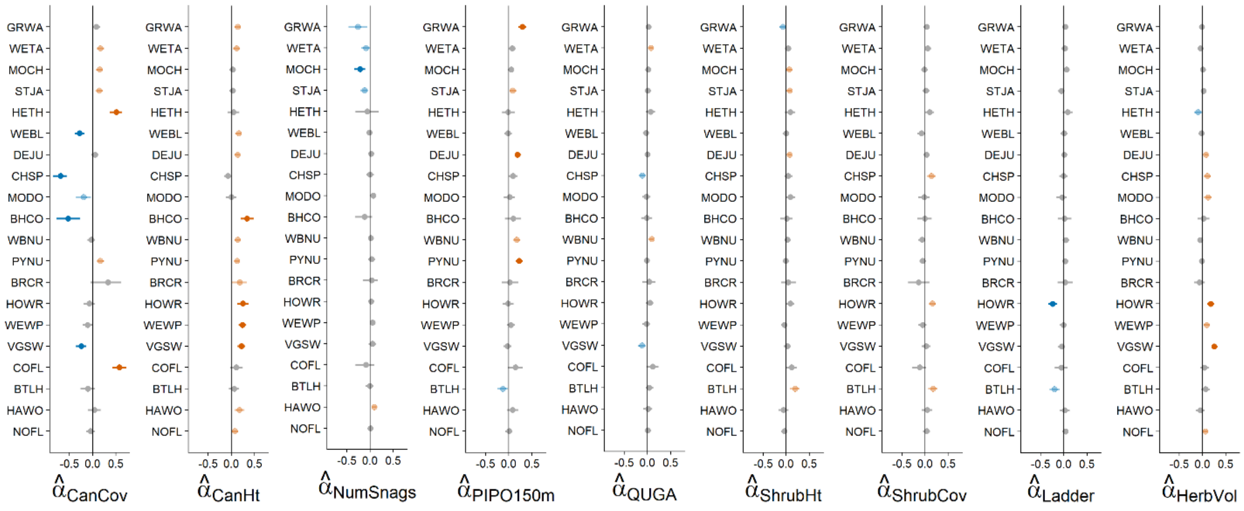

Figure 7. Point level habitat relationships with local abundance for 20 focal species. Focal species are Grace's Warbler (GRWA), Western Tanager (WETA), Mountain Chickadee (MOCH), Steller's Jay (STJA), Hermit Thrush (HETH), Western Bluebird (WEBL), Dark-eyed Junco (DEJU), Chipping Sparrow (CHSP), Mourning Dove (MODO), Brown-headed Cowbird (BHCO), White-breasted Nuthatch (WBNU), Pygmy Nuthatch (PYNU), Brown Creeper (BRCR), House Wren (HOWR), Western Wood-Pewee (WEWP), Violet-green Swallow (VGSW), Cordilleran Flycatcher (COFL), Broad-tailed Hummingbird (BTLH), Hairy Woodpecker (HAWO), Northern Flicker (NOFL). Relationships are with percent canopy cover (CanCov), canopy height (CanHt), number of snags (NumSnags), percent area with ponderosa pine-dominated forest (PIPO150m), canopy dominance of Gambel oak (QUGA), shrub height (ShrubHt), percent shrub cover (ShrubCov), shrub dominance of ladder fuels (Ladder), and herbaceous volume (HerbVol). Dots and lines are posterior median and 95% Bayesian credible intervals. Colors indicate supported positive (red) and negative (blue) relationships, with darker colors indicating strong relationships (lower 95% credible limit for $|\alpha| > 0.1$).

Consistency of relationships with a priori hypotheses

Habitat relationships estimated for species occupancy, occupancy dynamics, focal species abundance, or abundance trends provided evidence for evaluating 172 *a priori* hypotheses reflecting species life history traits or species ecological literature (Table 5). The data supported 132 hypotheses for 60 species and contradicted 27 hypotheses for 22 species. We considered evidence for the remaining 13 hypotheses (12 species) mixed either because relationships estimated in our study were inconsistent across scales, or because relationships reported in the literature were inconsistent. In 61 additional cases for 41 species, statistically supported relationships estimated here were not anticipated based on life history traits or ecological literature, suggesting potential novel hypotheses.

Covariate relationships for species richness and mean turnover were mostly inconsistent with our community-level *a priori* hypotheses. Lower species richness in grid cells with extensive canopy gaps, open forest conditions, and ponderosa pine-dominated forest especially later in the study somewhat contradicted our hypotheses. Nevertheless, inconsistency of these relationships initially versus at equilibrium and the lack of any meaningful covariate relationships with mean turnover provided relatively weak evidence for evaluating community-level hypotheses. At the point-level, the positive relationship of species richness with canopy height provided some support for our hypothesis that species richness would be greater in forest stands dominated by large trees. Nevertheless, we failed to identify meaningful relationships of species richness with canopy cover, ponderosa pine forest, or shrub volume for evaluating our community-level hypotheses.

Table 5. Strength of evidence for statistically supported habitat relationships with focal species abundance or occupancy within a hypothetico-deductive framework. Supported and contradicted relationships are those where statistically supported relationship(s) were consistent with or opposite *a priori* hypotheses. Strongly supported or contradicted relationships are those with at least one strong-magnitude relationship (see text for definition) or the same relationship measured at two different spatial scales. We considered evidence mixed if we found relationships that both supported and contradicted the hypothesis for different population parameters, or if relationships reported in the literature are not consistent. We considered relationships novel if they were not hypothesized in either direction prior to considering our results. For complete variable names and descriptions, see Table 2.

Species	**Habitat feature (hypothesized relationship)**	**Empirical evidence**		
		Overall	**Abundance**	**Occupancy**
Eurasian Collared-Dove	Canopy height (none)	novel		CanHt+
Mourning Dove	Canopy cover (-)	strongly supported	percGap+ on trend; CanCov-	CanCov--
	Snags (none)	novel		NumSnag+
	Ponderosa pine forest (none)	novel	PIPO1km+ on trend	PIPO150m+
	Shrub cover and height (+)	mixed		ShrubHt+, ShrubCov-
	Herbaceous volume (+)	supported	Herb+	
Broad-tailed Hummingbird	Canopy cover (-)	strongly contradicted		CanCov++
	Canopy height (+)	supported		CanHt+
	Ponderosa pine forest (+)	mixed	PIPO150m+, but PIPO1km- on trend	PIPO150m+
	Shrub cover and height (none)	novel	ShrubHt+, ShrubCov+	ShrubHt+
	Ladder fuels (-)	supported	Ladder-	Ladder-
Acorn Woodpecker	Canopy cover (unclear)	novel		percGap- for colonization
	Canopy height (+)	supported		CanHt++
	Gambel oak (+)	supported		QUGA+
Williamson's Sapsucker	Canopy cover (unclear)	novel		CanCov++
	Ponderosa pine forest (none)	novel		PIPO150m--

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
Hairy Woodpecker	Canopy cover (-)	mixed	percGap- initially, but percGap+ for trend	percGap+ for extirpation and turnover
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Snags (+)	strongly supported	NumSnags+	NumSnag++
	Canopy heterogeneity (none)	novel	CVGap- for trend	
American Three-toed Woodpecker	Canopy cover (+)	supported		CanCov+
Northern Flicker	Canopy cover (-)	contradicted		percGap+ for extirpation and turnover
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Ponderosa pine forest (none)	novel	PIPO1km+	
	Herbaceous volume (none)	novel	Herb+	
Western Wood-Peweea	Canopy height (none)	novel	CanHt++	CanHt++
	Snags (none)	novel		NumSnag+
	Ponderosa pine forest (none)	novel		PIPO1km+ for colonization
	Gambel oak (none)	novel		QUGA--
	Shrub cover and height (+)	contradicted		ShrubCov-
	Herbaceous volume (none)	novel	Herb+	

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
Gray Flycatcher	Canopy cover (-)	strongly supported		CanCov--, but percGap++ for extirpation and turnover and percGap- for occupancy
	Canopy height (-)	strongly supported		CanHt--
	Ponderosa pine forest (none)	novel		PIPO150m+
	Shrub cover and height (+)	supported		ShrubCov+
	Ladder fuels (-)	strongly contradicted		Ladder++
	Herbaceous volume (-)	supported		Herb-
Dusky Flycatcher	Gambel oak (+)	supported		QUGA+
	Shrub cover and height (+)	supported		ShrubCov++
Cordilleran Flycatchera	Canopy cover (-local, + landscape)	mixed	CanCov++, but percGap-	CanCov++
	Canopy height (none)	novel		CanHt++
Ash-throated Flycatcher	Ponderosa pine forest (-)	strongly supported		PIPO150m--
	Herbaceous volume (+)	contradicted		Herb-
Cassin's Kingbird	Canopy cover (-)	strongly supported		CanCov--
	Canopy height (+)	supported		CanHt+
	Shrub cover and height (+)	contradicted		ShrubCov-
	Herbaceous volume (none)	novel		Herb+

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
Plumbeous Vireo	Canopy cover (-)	mixed		CanCov--, but percGap-- for colonization, although occupancy was nevertheless generally stable (low turnover)
	Canopy height (+)	strongly supported		CanHt++
	Snags (-)	supported		NumSnag-
	Ponderosa pine forest (+)	strongly supported		PIPO150m++
	Gambel oak (+)	strongly supported		QUGA++
	Shrub cover and height (none)	novel		ShrubHt-
Warbling Vireo	Canopy cover (+)	strongly supported		CanCov+; percGap-- and percOpen- for colonization
	Ponderosa pine forest (-)	strongly supported		PIPO150m--
	Shrub cover and height (+)	supported		ShrubCov+
	Herbaceous volume (none)	novel		Herb+
Pinyon Jay	Ponderosa pine forest (-)	supported		PIPO150m-
Steller's Jay	Canopy cover (+)	strongly supported	CanCov+	percGap-- for colonization
	Snags (-)	strongly supported		NumSnags--
	Ponderosa pine forest (none)	novel	PIPO150m+	PIPO150m+, PIPO1km+ for colonization

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
	Shrub cover and height (none)	novel	ShrubHt+	ShrubHt+, ShrubCov-
Woodhouse's Scrub-Jay	Ponderosa pine forest (-)	strongly supported		PIPO150m--
Clark's Nutcracker	Canopy cover (-)	strongly contradicted		CanCov++
American Crow	Canopy cover (+)	contradicted		percGap+ for initial occupancy, although relationship diminished over time
	Ponderosa pine forest (none)	novel		PIPO150m--
Common Raven	Canopy cover (+)	strongly contradicted		CanCov--
	Canopy height (+)	strongly supported		CanHt++
	Ponderosa pine forest (none)	novel		PIPO1km+ for extirpation (and consequently turnover)
	Herbaceous volume (none)	novel		Herb-
Horned Lark	Canopy cover (-)	supported		percGap+, but relationship diminished over time
Purple Martin	Canopy cover (negtive)	strongly supported		CanCov--
	Canopy height (+)	supported		CanHt+
Violet-green Swallow[a]	Canopy cover (-)	mixed	CanCov--, but percGap-	percGap+ for extirpation (and turnover, - for occupancy)
	Canopy height (+)	strongly supported	CanHt++	CanHt++

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
	Snags (+)	contradicted		NumSnags-
	Ponderosa pine forest (+)	contradicted		PIPO150m-
	Gambel oak (none)	novel	QUGA-	QUGA-
	Canopy heterogeneity (none)	novel	CVGap+	
	Herbaceous volume (+)	strongly supported	Herb++	Herb+
Northern Rough-winged Swallow	Ponderosa pine forest (none)	novel		PIPO150m-
Mountain Chickadee	Canopy cover (+)	supported	CanCov+, although percOpen+ for trend	CanCov++, and percGap-- for colonization
	Canopy height (+)	supported		CanHt+
	Snags (+)	strongly contradicted	NumSnags--	NumSnags-
	Ponderosa pine forest (none)	novel		PIPO150m+
	Shrub cover and height (none)	novel	ShrubHt+	ShrubHt+, ShrubCov-
	Herbaceous volume (none)	novel		Herb-
Juniper Titmouse	Canopy height (-)	strongly supported		CanHt--
	Ponderosa pine forest (-)	strongly supported		PIPO150m--, and PIPO1km++ for extirpation
	Herbaceous volume (none)	novel		Herb--
Bushtit	Canopy height (-)	supported		CanHt-
Red-breasted Nuthatch	Canopy cover (+)	strongly supported		CanCov++

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
	Ponderosa pine forest (-)	strongly supported		PIPO150m--
White-breasted Nuthatch[a]	Canopy cover (-)	mixed		CanCov-, but percGap+ for extirpation and turnover
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Ponderosa pine forest (+)	strongly supported	PIPO150m+	PIPO150m++, and PIPO1km++ for colonization
	Gambel oak (none)	novel	QUGA+	QUGA++
	Shrub cover and height (none)	novel		ShrubCov--
	Herbaceous volume (-)	supported		Herb-
Pygmy Nuthatch	Canopy cover (-)	mixed	CanCov+	CanCov-
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Snags (+)	contradicted		NumSnags-
	Ponderosa pine forest (+)	strongly supported	PIPO150m++	PIPO150m++ and PIPO1km++ for colonization
	Gambel oak (none)	novel		QUGA-
	Canopy heterogeneity (none)	novel	CVOpen+	
	Shrub cover and height (-)	mixed		ShrubHt+, ShrubCov-
	Herbaceous volume (-)	strongly supported		Herb--
Brown Creeper	Canopy cover (+)	strongly supported	percOpen-	CanCov++
	Canopy height (+)	strongly supported	CanHt+	CanHt++

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
	Ponderosa pine forest (+)	strongly supported	PIPO1km+ for trend	PIPO1km++ for colonization
	Shrub cover and height (none)	novel		ShrubCov-
Rock Wren	Canopy cover (-)	strongly supported		CanCov--
	Ladder fuels (none)	novel		Ladder-
House Wren	Canopy cover (-)	mixed	percGap--	CanCov-, but percGap- and percOpen- for colonization, and percGap+ for extirpation
	Canopy height (-)	strongly contradicted	CanHt++	CanHt++
	Snags (+)	strongly supported		NumSnags++
	Ponderosa pine forest (+)	contradicted		PIPO150m-
	Shrub cover and height (+)	strongly supported	ShrubCov+	ShrubCov++
	Ladder fuels (-)	strongly supported	Ladder--	Ladder-
	Herbaceous volume (+)	strongly supported	Herb++	Herb++
Bewick's Wren	Canopy height (-)	strongly supported		CanHt--
	Ponderosa pine forest (-)	supported		PIPO1km+ for extirpation and turnover
	Gambel oak (+)	supported		QUGA+

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
Blue-gray Gnatcatcher	Canopy cover (unclear)	novel		percGap+ for extirpation and turnover (smaller increase in occupancy with gaps)
	Canopy height (-)	strongly supported		CanHt--
	Gambel oak (+)	supported		QUGA+
	Shrub cover and height (+)	strongly supported		ShrubHt+, ShrubCov++
Ruby-crowned Kinglet	Canopy cover (+)	strongly supported		CanCov++ and percGap- for colonization
	Ponderosa pine forest (-)	strongly supported		PIPO150m--
Western Bluebird	Canopy cover (-)	strongly supported	CanCov--	CanCov--
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Ponderosa pine forest (none)		PIPO1km+	PIPO150m+
	Snags (+)	supported		NumSnag+
	Shrub cover and height (-)	strongly supported		ShrubHt-, ShrubCov-
	Herbaceous volume (-)	supported		Herb-
Mountain Bluebird	Canopy cover (-)	supported		CanCov-
Townsend's Solitaire	Canopy cover (-)	strongly contradicted		CanCov++
	Canopy height (none)	novel		CanHt+
Hermit Thrush	Canopy cover (+)	strongly supported	CanCov++	CanCov++, and percGap- and percOpen- for colonization

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
	Canopy height (+)	supported		CanHt+
	Ponderosa pine forest (-)	strongly supported		PIPO150m--
	Shrub cover and height (+)	strongly supported		ShrubCov++
	Herbaceous volume (-)	supported		Herb-
American Robin	Canopy heterogeneity (none)	novel		CVOpen+ for colonization
	Canopy height (none)	novel		CanHt++
	Snags (-)	strongly supported		Snags--
	Herb (+)	supported		Herb+
Northern Mockingbird	Canopy cover (-)	strongly supported		CanCov-- and percGap+, although latter diminished over time
	Ponderosa pine forest (none)	novel		PIPO150m-
Olive Warbler	Canopy cover (-)	strongly contradicted		percGap-- and percOpen-- for colonization (occupancy favored closed forest in later years)
	Canopy height (+)	strongly supported		CanHt++
	Ponderosa pine forest (+)	supported		PIPO150m+
Evening Grosbeak	Ponderosa pine forest (+)	contradicted		PIPO150m--
House Finch	Canopy cover (-)	contradicted		percGap- for colonization

Species	**Habitat feature (hypothesized relationship)**	**Empirical evidence**		
		Overall	**Abundance**	**Occupancy**
	Ponderosa pine forest (-)	strongly supported		PIPO1km-- for colonization
Red Crossbill	Canopy cover (-)	contradicted		percOpen- for colonization
	Canopy height (+)	strongly supported		CanHt++
	Gambel oak (none)	novel		QUGA-
Pine Siskin	Canopy cover (-)	contradicted		CanCov+
	Canopy height (+)	strongly supported		CanHt++
	Ponderosa pine forest (+)	strongly contradicted		PIPO150m--
	Ladder fuels (+)	supported		Ladder+
Lesser Goldfinch	Canopy heterogeneity (none)	novel		CVOpen- for colonization (occupancy shifts from favoring positive to negative CVOpen during the study)
	Canopy height (none)	novel		CanHt++
	Ponderosa pine forest (-)	strongly supported		PIPO150m--
Green-tailed Towhee	Shrub cover and height (+)	strongly supported		ShrubCov++
	Ladder fuels (-)	strongly supported		Ladder--
Spotted Towhee	Canopy cover (-)	mixed		CanCov-, but percGap- for colonization
	Canopy height (-)	strongly supported		CanHt--
	Snags (-)	strongly supported		NumSnags--

Species	**Habitat feature (hypothesized relationship)**	**Empirical evidence**		
		Overall	**Abundance**	**Occupancy**
	Ponderosa pine forest (-)	supported		PIPO1km- for colonization, resulting in occupancy reduction over time with extensive ponderosa forest
	Gambel oak (+)	strongly supported		QUGA++
	Shrub cover and height (+)	strongly supported		ShrubCov++
	Ladder fuels (-)	strongly supported		Ladder--
Chipping Sparrow	Canopy cover (-)	strongly supported	CanCov--	CanCov--
	Ponderosa pine forest (-)	supported	PIPO1km- for trend	
	Gambel oak (none)	novel	QUGA-	QUGA-
	Shrub cover and height (+)	supported	ShrubCov+	
	Herbaceous volume (+)	supported	Herb+	Herb+
Black-chinned Sparrow	Canopy cover (-)	supported		CanCov-
	Canopy height (-)	supported		CanHt--
	Ponderosa pine forest (-)	supported		PIPO150m-
	Gambel oak (+)	supported		QUGA+
Vesper Sparrow	Canopy cover (-)	strongly supported		CanCov--
Lark Sparrow	Canopy cover (-)	strongly supported		CanCov-- and percGap++
	Canopy height (-)	supported		CanHt-
	Ladder fuels (none)	novel		Ladder-

Species	**Habitat feature (hypothesized relationship)**	**Empirical evidence**		
		Overall	**Abundance**	**Occupancy**
Dark-eyed Junco	Canopy cover (-)	strongly contradicted	percGap- for trend (positive trend with less extensive canopy gaps)	CanCov+ and percGap+ for extirpation (less occupancy in later years and more turnover with extensive canopy gaps)
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Ponderosa pine forest (none)	novel	PIPO150m+	PIPO150m+ and PIPO1km+ for colonization
	Canopy heterogeneity (none)	novel	CVGap+ for trend	
	Shrub cover and height (none)	novel	ShrubHt+	ShrubHt+, ShrubCov--
	Herbaceous volume (-)	contradicted	Herb+	
Eastern Meadowlark	Canopy cover (-)	strongly supported		CanCov--
Western Meadowlark	Canopy cover (-)	strongly supported		CanCov-- and percGap++ for occupancy
	Ponderosa pine forest (none)	novel		PIPO150m-
Scott's Oriole	Canopy cover (none)	novel		CanCov-
Brown-headed Cowbird	Canopy cover (-)	strongly supported	CanCov--	CanCov--
	Canopy height (none)	novel	CanHt++	CanHt+
Brewer's Blackbird	Canopy cover (-)	strongly supported		CanCov--
Virginia's Warbler	Canopy cover (-)	strongly contradicted		CanCov++ and percGap+ for extirpation

Species	**Habitat feature (hypothesized relationship)**	**Empirical evidence**		
		Overall	**Abundance**	**Occupancy**
	Canopy height (-)	supported		CanHt-
	Snags (none)	novel		NumSnags+
	Ponderosa pine forest (-)	supported		PIPO1km- for colonization
	Gambel oak (+)	strongly supported		QUGA++
	Shrub cover and height (+)	strongly supported		ShrubCov++
Yellow-rumped Warbler	Canopy cover (unclear)	novel		CanCov++ and percGap+ for extirpation
	Canopy height (+)	strongly supported		CanHt++
	Snags (unclear)	novel		NumSnags-
	Ponderosa pine forest (-)	contradicted		PIPO1km+ for colonization
	Gambel oak (none)	novel		QUGA+
	Shrub cover and height (+)	contradicted		ShrubCov-
Grace's Warbler	Canopy cover (+)	supported		CanCov+
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Ponderosa pine forest (+)	strongly supported	PIPO150m++	PIPO150m++
	Snags (none)	novel	NumSnags-	NumSnags--
	Shrub density or height (+)	mixed	ShrubHt-	ShrubHt--, ShrubCov+
	Gambel oak (+)	supported		QUGA+
Black-throated Gray Warbler	Canopy height (-)	strongly supported		CanHt--
	Gambel oak (none)	novel		QUGA-
	Shrub cover and height (+)	mixed		ShrubHt-, ShrubCov++

Species	Habitat feature (hypothesized relationship)	Empirical evidence		
		Overall	Abundance	Occupancy
Red-faced Warbler	Canopy cover (+)	strongly supported		CanCov++ and percGap-- for colonization
	Ponderosa pine forest (-)	strongly supported		PIPO150m--
	Herbaceous volume (+)	supported		Herb+
Hepatic Tanager	Canopy height (+)	supported		CanHt+
Western Tanager[a]	Canopy cover (+)	strongly supported	CanCov+	CanCov++ and percGap++ for extirpation (and turnover)
	Canopy height (+)	strongly supported	CanHt+	CanHt++
	Gambel oak (+)	strongly supported	QUGA+	QUGA++
	Shrub cover and height (+)	supported		ShrubCov+
	Herbaceous volume (-)	supported		Herb-
Black-headed Grosbeak	Ponderosa pine forest (-)	strongly supported		PIPO150m--
	Gambel oak (+)	strongly supported		QUGA++
	Shrub cover and height (+)	supported		ShrubHt+, ShrubCov+
	Ladder fuels (none)	novel		Ladder-

[a] Due to evidence for lack of fit, abundance models and estimates for these species should be interpreted with caution.

Discussion

Our analysis quantifies multi-scale habitat relationships capable of informing forest management. We have quantified numerous species-specific and community-wide occupancy relationships with environmental features potentially affected by forest management and restoration. Additionally, we have quantified environmental relationships for abundance and population trends for 20 focal species of particular interest to forest management and representing a broad suite of life history traits relevant to evaluating ecological function. Finally, we have evaluated *a priori* hypotheses for habitat relationships in light of empirical relationships reported here to allow inference within a hypothesis-driven framework. Statistically supported habitat relationships that are consistent with species' life histories and *a priori* hypotheses based on our understanding of species ecology will be most reliable for informing management. Novel habitat relationships found in our study but not elsewhere or that contradict the literature would ideally be investigated further before applying them to inform management or develop predictions for restoration treatments.

Habitat relationships with multiple population parameters can inform a more complete understanding of potential population responses to environmental change than can relationships for any one parameter alone. Monitoring both abundance and occupancy is important for a comprehensive understanding of the status of wildlife populations, including population size and geographic distribution (Jones 2011). Although occupancy and abundance are related and usually correlated (Noon et al. 2012), each represents a different aspect of a species distribution capable of responding differently to habitat variation or change. For example, site occupancy is related to the aspect of a population involving the extent of occurrence and geographic area occupied, whereas abundance is related to density and population size (MacKenzie and Nichols 2004). Regardless, density or occupancy alone can mislead inference of habitat quality (Van Horne 1983, but see Bock and Jones 2004), whereas habitat relationships with explicit dynamic processes (e.g., colonization and extirpation) can support stronger inference (MacKenzie et al. 2006, Green et al. 2019). Greater colonization rates suggest landscapes with extensive ponderosa pine forest provide high quality habitat for Western Wood-Pewee, Stellar's Jay, White-breasted Nuthatch, Pygmy Nuthatch, Brown Creeper, Dark-eyed Junco, Yellow-rumped Warbler and Red-faced Warbler. Lower colonization and greater extirpation in landscapes with extensive canopy gaps suggest potential for large-scale disturbance (e.g., wildfire) or clearcutting to limit or reduce habitat quality for Acorn Woodpecker, Gray Flycatcher, Plumbeous Vireo, Stellar's Jay, White-breasted Nuthatch, Mountain Chickadee, Hermit Thrush, Ruby-crowned Kinglet, Olive Warbler, Red-faced Warbler, and Western Tanager (forest restoration is not expected to substantially extend canopy gaps).

Despite the particular value of colonization and extirpation for understanding habitat quality, species life history and other parameters can provide additional context. Turnover may relate more strongly with a given habitat feature, thereby indicating variation in population stability and habitat quality, than occupancy (e.g., Common Raven relationships with ponderosa pine forest). Relationships for population trends or occupancy dynamics can suggest ways in which species may respond to habitat change gradually or ephemerally (e.g., see relationships for Warbling Vireo, Horned Lark, and American Crow). Occupancy dynamics for Hairy Woodpecker and House Wren suggest landscapes with extensive canopy gaps provide relatively poor habitat quality for these species. Nevertheless, canopy gaps containing numerous snags left by recent large-scale disturbance can represent high-quality habitat for woodpeckers and secondary cavity-nesting birds, including these species (Saab et al. 2007, Saab et al. 2011, Latif et al. 2016). Despite its ephemerality, which could perhaps stimulate movement and thereby affect occupancy dynamics, such habitat may be important for population persistence (Saab and Vierling 2001, Wightman et al. 2010). Recent disturbance history may help explain the positive abundance trend for Hairy Woodpecker in landscapes with extensive gaps.

After controlling for landscape-level patterns, covariate relationships with local-scale (point-level) occupancy suggested broad value in forest restoration that maintains tall mature trees for numerous species and species richness. Forest restoration treatments that reduce canopy cover may additionally increase Western Bluebird occupancy. Reductions in canopy cover would not necessarily diminish the value of restoration for Plumbeous Vireo, White-breasted Nuthatch, and Pygmy Nuthatch as long as tall trees are maintained. Treatments that reduce sapling and shrub cover while maintaining mature trees could especially boost populations for Western Wood-Pewee, Mountain Chickadee, White-breasted Nuthatch, Pygmy Nuthatch, Brown Creeper, Western Bluebird and Dark-eyed Junco.

Relationships measured at multiple spatial scales or with different aspects of a habitat feature can more fully inform its ecological value. After accounting for positive landscape-scale relationships with canopy cover (i.e., negative with canopy gaps or open forest), Plumbeous Vireo, Violet-green Swallow, White-breasted Nuthatch, House Wren, and Spotted Towhee all exhibited negative relationships with canopy cover locally. Thus, relatively small local openings within forested landscapes may provide the best habitat for these species. Broad-tailed Hummingbird populations may reach greatest densities in relatively small patches of ponderosa pine forest within diverse landscapes or those dominated by other tree species. A tall shrub-sapling layer interspersed with openings may provide the best habitat for Mourning Dove, whereas a shorter but extensive shrub-sapling layer may be best for Black-throated Gray Warbler.

We largely failed to corroborate our *a priori* hypotheses for species richness and community stability. Negative relationships of species richness with canopy gaps, open forest, and extent of ponderosa pine at equilibrium contradicted our hypotheses, although these relationships may be transient considering they were not present initially. Mean turnover was largely invariant along covariate gradients, suggesting landscape-level conditions measured here do not influence overall community stability. Variability in open forest patch size may positively influence species richness, although we only observed this relationship initially. Additionally, this relationship was not anticipated based on *a priori* understanding of the system (i.e., did not corroborate any *a priori* hypotheses), so we recommend further investigation before widespread application for management. At a local scale, we did corroborate an expected value of large trees (represented here by tall average canopy heights) for promoting species richness (see also Kalies and Rosenstock 2013). Nevertheless, we may need to analyze species richness and community dynamics for ponderosa pine forest specialists or other more ecologically meaningful species groups to fully realize community-level habitat relationships relevant to management.

Study limitations

Due to limitations in computing speed and power, we analyzed species occupancy and richness using an equilibrium model with limited capacity to evaluate year-specific or trends in dynamics over time. Because we ignored inter-annual variation in occupancy dynamics and only allowed variability in relation to covariates, our community occupancy model assumes processes governing changes in occupancy are approaching equilibrium over time (*sensu* MacKenzie et al. 2006:pp 208-212). In contrast, populations and communities experiencing stochastic environmental variation, as well as increasing or decreasing trajectories over time, are expected to be governed by non-equilibrium dynamics (MacKenzie et al. 2006, Royle and Kéry 2007). Nevertheless, our model may allow comparison of habitat relationships when the system is in flux versus relatively stable by comparing patterns early versus late in the study, respectively. For example, predicted relationships for initial occupancy may represent potential patterns soon after treatments are implemented, whereas predicted relationships for equilibrium occupancy may suggest longer term average patterns expected if post-treatment conditions are maintained. Abundance models for the 20 focal species do estimate inter-annual variability, but we only represented covariate relationships with overall abundance and trend rather than relationships with annual fluctuations. Thus, our models strictly estimate overall trajectories within the 10-year study period represented in our data. Models that more explicitly represent inter-annual dynamics and habitat relationships with these dynamics may be needed to predict system responses to forest restoration or other changes in habitat.

Available environmental data may also limit our ability to observe important relationships. Our covariates by no means quantify all habitat features potentially governing species distributions or those relevant to forest management (e.g., ponderosa pine density, size distributions, and basal area). Following input from the wildlife committee, we designated 10% and 40% as canopy cover thresholds for delineating canopy gaps and open forest (see also Latif et al. In Press). Closer consideration could suggest alternative thresholds with greater potential for revealing relationships with open forest conditions. Although our sampling specifically targeted birds, we were restricted in the range of spatial scales at which we could measure habitat relationships. Broad community-wide data are inevitably restricted in resolution for representing habitat relationships at the particular scales and with particular features most relevant to individual species. In addition, we investigated linear effects of local canopy cover and landscape composition, but quadratic responses to canopy cover (Kalies and Rosenstock 2013) and non-linear threshold responses to landscape composition (Lindenmayer et al. 2008) may be more in line with predictions for historical range of variability. We therefore cannot overemphasize the need for multiple studies and for considering all available scientific literature to reliably manage with the best available science.

Potential applications for forest management and monitoring

By following a hypothetico-deductive approach, we have provided reliable knowledge (*sensu* Sells et al. 2018) representing the best available science for informing management decisions in southwestern frequent-fire ponderosa pine forests with avian habitat objectives. Rather than taking statistically supported patterns at face value, we considered species life history and current understanding of species ecology to evaluate the reliability of observed relationships. Strong-magnitude and clearly supported relationship that corroborate *a priori* hypotheses represent the most reliable information for informing forest management. Additionally, considering the inevitable limitations of any one study (discussed above), relationships consistently described by multiple studies but not necessarily corroborated or contradicted here may nevertheless represent reliable knowledge especially if consistent with an understanding of species ecology. In contrast, we suggest treating relationships not consistently reported across studies or novel relationships not anticipated in *a priori* hypotheses with skepticism. Ideally, focused study investigating mechanisms underlying such relationships would precede their application towards informing management. Regardless, integrating forest restoration with supported predictions within a structured decision making framework (*sensu* Schwartz et al. 2018) may represent the best approach for including bird habitat objectives while recognizing uncertainties in our understanding of species ecology.

Literature Cited

Allen, C. D., M. Savge, D. A. S. Falk, Kieran F., T. W. Swetnam, T. Schulke, P. Stacey, P. Morgan, M. Hoffman, and Klingel. 2002. Ecological restoration of southwestern Ponderosa pine ecosystem: A broad perspective. Ecological Applications **12**:1418-1433.

Bock, C. E., and Z. F. Jones. 2004. Avian habitat evaluation: should counting birds count? Frontiers in Ecology and the Environment **2**:403-410.

Colavito, M. M. 2016. The role of science in the collaborative forest landscape restoration program. Journal of Forestry **115**:34-42.

Dorazio, R. M., M. Kéry, J. A. Royle, and M. Plattner. 2010. Models for inference in dynamic metacommunity systems. Ecology **91**:2466-2475.

Dorazio, R. M., J. A. Royle, B. Söderström, and A. Glimskär. 2006. Estimating species richness and accumulation by modeling species occurrence and detectability. Ecology **87**:842-854.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/ hierarchical models. Cambridge University Press, New York, NY.

Green, A. W., D. C. Pavlacky Jr., and T. L. George. 2019. A dynamic multi-scale occupancy model to estimate temporal dynamics and hierarchical habitat use for nomadic species. Ecology and Evolution **9**:793-803.

Hanni, D. J., C. M. White, N. J. V. Lanen, J. J. Birek, J. M. Berven, and M. F. McLaren. 2018. Integrated Monitoring in Bird Conservation Regions (IMBCR): Field protocol for spatially-balanced sampling of land bird populations. Unpublished report. Bird Conservancy of the Rockies, Brighton, Colorado, USA.

Hostetter, N. J., B. Gardner, T. S. Sillett, K. H. Pollock, and T. R. Simons. 2019. An integrated model decomposing the components of detection probability and abundance in unmarked populations. Ecosphere **10**:e02586.

Iknayan, K. J., M. W. Tingley, B. J. Furnas, and S. R. Beissinger. 2014. Detecting diversity: emerging methods to estimate species diversity. Trends in Ecology & Evolution **29**:97-106.

Jones, J. P. G. 2011. Monitoring species abundance and distribution at the landscape scale. Journal of Applied Ecology **48**:9-13.

Kalies, E. L., C. L. Chambers, and W. W. Covington. 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: A meta-analysis. Forest Ecology and Management **259**:333-342.

Kalies, E. L., and S. S. Rosenstock. 2013. Stand structure and breeding birds: Implications for restoring ponderosa pine forests. The Journal of Wildlife Management **77**:1157-1165.

LANDFIRE. 2019. Existing Vegetation Type Layer, LANDFIRE 2.0.0. U.S. Department of the Interior, Geological Survey. Accessed July 31, 2019.

Latif, Q. S., J. S. Sanderlin, V. A. Saab, W. M. Block, and J. G. Dudley. 2016. Avian relationships with wildfire at two dry forest locations with different historical fire regimes. Ecosphere **7**:e01346.

Latif, Q. S., R. L. Truex, R. A. Sparks, and D. C. Pavlacky. In Press. Dry conifer forest restoration benefits Colorado Front Range avian communities. Ecological Applications. DOI:10.1002/eap.2142.

Lindenmayer, D., R. J. Hobbs, R. Montague-Drake, J. Alexandra, A. Bennett, M. Burgman, P. Cale, A. Calhoun, V. Cramer, P. Cullen, D. Driscoll, L. Fahrig, J. Fischer, J. Franklin, Y. Haila, M. Hunter, P. Gibbons, S. Lake, G. Luck, C. MacGregor, S. McIntyre, R. M. Nally, A. Manning, J. Miller, H. Mooney, R. Noss, H. Possingham, D. Saunders, F. Schmiegelow, M. Scott, D. Simberloff, T. Sisk, G. Tabor, B. Walker, J. Wiens, J. Woinarski, and E. Zavaleta. 2008. A checklist for ecological management of landscapes for conservation. Ecology Letters **11**:78-91.

Lyons, J. E., M. C. Runge, H. P. Laskowski, and W. L. Kendall. 2008. Monitoring in the context of structured decision-making and adaptive management. The Journal of Wildlife Management **72**:1683-1692.

MacKenzie, D. I., and J. D. Nichols. 2004. Occupancy as a surrogate for abundance estimation. Animal Biodiversity and Conservation **27**:461-467.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology **84**:2200-2207.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Baily, and J. E. Hines. 2006. Occupancy estimation and modeling. Elsevier Inc.

Monitoring Trends in Burn Severity (MTBS). 2019. Monitoring Trends in Burn Severity. https://www.mtbs.gov/viewer/index.html. Accessed in 2019.

Moore, M. M., W. W. Covington, and P. Z. Fule. 1999. Reference conditions and ecological restoration: A southwestern ponderosa pine perspective. Ecological Applications **9**:1266-1277.

Mordecai, R. S., B. J. Mattsson, C. J. Tzilkowski, and R. J. Cooper. 2011. Addressing challenges when studying mobile or episodic species: hierarchical Bayes estimation of occupancy and use. Journal of Applied Ecology **48**:56-66.

Morrison, M. L., W. M. Block, M. D. Strickland, B. A. Collier, and M. J. Peterson. 2008. Wildlife study design. Springer, New York, New York, USA.

Noon, B. R., L. L. Bailey, T. D. Sisk, and K. S. McKelvey. 2012. Efficient Species-Level Monitoring at the Landscape Scale. Conservation Biology **26**:432-441.

Noss, R. F., P. Beier, W. Wallace Covington, R. Edward Grumbine, D. B. Lindenmayer, J. W. Prather, F. Schmiegelow, T. D. Sisk, and D. J. Vosick. 2006. Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. Restoration Ecology **14**:4-10.

Pavlacky, D. C., J. A. Blakesley, G. C. White, D. J. Hanni, and P. M. Lukacs. 2012. Hierarchical multi-scale occupancy estimation for monitoring wildlife populations. The Journal of Wildlife Management **76**:154-162.

Pavlacky, D. C., Jr., P. M. Lukacs, J. A. Blakesley, R. C. Skorkowsky, D. S. Klute, B. A. Hahn, V. J. Dreitz, T. L. George, and D. J. Hanni. 2017. A statistically rigorous sampling design to integrate avian monitoring and management within Bird Conservation Regions. PLoS One **12**.

Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology **85**:1591-1597.

Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology **88**:1813-1823.

Saab, V. A., R. E. Russell, and J. G. Dudley. 2007. Nest densities of cavity-nesting birds in relation to postfire salvage logging and time since wildfire. Condor **109**:97-108.

Saab, V. A., R. E. Russell, J. J. Rotella, and J. G. Dudley. 2011. Modeling nest survival of cavity-nesting birds in relation to postfire salvage logging. Journal of Wildlife Management **75**:794-804.

Saab, V. A., and K. T. Vierling. 2001. Reproductive success of Lewis's Woodpecker in burned pine and cottonwood riparian forests. The Condor **103**:491-501.

Sanderlin, J. S., W. M. Block, and B. E. Strohmeyer. 2016. Long-term post-wildfire correlates with avian community dynamics in ponderosa pine forests. *in* Ralston, Barbara E., ed. Proceedings of the 12th Biennial Conference of Research on the Colorado River Plateau. Scientific Investigations Report 2015-5180. Reston, VA: US Geological Survey. p. 89-101. Pages 89-101.

Schultz, C. A., T. Jedd, and R. D. Beam. 2012. The Collaborative Forest Landscape Restoration Program: a history and overview of the first projects. Journal of Forestry **110**:381-391.

Schwartz, M. W., C. N. Cook, R. L. Pressey, A. S. Pullin, M. C. Runge, N. Salafsky, W. J. Sutherland, and M. A. Williamson. 2018. Decision Support Frameworks and Tools for Conservation. Conservation Letters **11**:e12385.

Sells, S. N., S. B. Bassing, K. J. Barker, S. C. Forshee, A. C. Keever, J. W. Goerz, and M. S. Mitchell. 2018. Increased scientific rigor will improve reliability of research and effectiveness of management. The Journal of Wildlife Management **82**:485-494.

Stevens, D. L., and A. R. Olsen. 2004. Spatially balanced sampling of natural resources. Journal of the American Statistical Association **99**:262-278.

USDA. 2012. United States Department of Agriculture (USDA). 2012. National Forest System land management planning. Federal Register 77:21162 - 21276.

USDA Forest Service. 2019a. NLCD 2011 Tree Canopy Cover (CONUS). Salt Lake City, UT. Accessed July 31, 2019.

USDA Forest Service (USFS). 2019b. Rapid assessment of vegetation conditions after wildfire (RAVG). Washington, DC: U.S. Department of Agriculture, Forest Service. https://www.fs.fed.us/postfirevegcondition/ index.shtml. Accessed 2019.

Van Horne, B. 1983. Density as a misleading indicator of habitat quality. Journal of Wildlife Management **47**:893-901.

White, C. M and Q.S. Latif. 2020. Four Forest Restoration Initiative Bird Surveys: 2018 Field Season Report. Bird Conservancy of the Rockies. Brighton, Colorado, USA.

Wightman, C. S., V. A. Saab, C. Forristal, K. Mellen-McLean, and A. Markus. 2010. White-headed Woodpecker nesting ecology after wildfire. Journal of Wildlife Management **74**:1098-1106.

Appendix A.

Species detection summaries ("Detections" = number of point surveys the species was recorded; "Sum of counts" = sum of all raw counts of the species where detected) and life history traits. Complete names and descriptions of life history traits appear in Table 3.

Species (Taxonomic name)	**Code**	**Detections (max = 5738)**	**Sum of counts**	**Traits**	
				Foraging	**Nesting**
Rock Pigeon (*Columbia livia*)	ROPI	1	1	Gn	OT
Band-tailed Pigeon (*Patagioenas fasciata*)	BTPI	28	32	Gn	O_C
Eurasian Collared-Dove (*Streptopelia decaocto*)	EUCD	34	52	Gr	O_C
White-winged Dove (*Zenaida asiatica*)	WWDO	5	6	Gn	O_C
Mourning Dove (*Zenaida macroura*)	MODO	629	766	Gr	O_S
Greater Roadrunner (*Geococcyx californianus*)	GRRO	6	6	Gn	O_C, O_S
Common Nighthawk (*Chordeiles minor*)	CONI	52	58	AI	O_G
White-throated Swift (*Aeronautes saxatalis*)	WTSW	11	26	AI	OT
Black-chinned Hummingbird (*Archilochus alexandri*)	BCHU	28	30	Fl	O_C
Anna's Hummingbird (*Calypte anna*)	ANHU	18	21	Fl	O_S
Broad-tailed Hummingbird (*Selasphorus platycercus*)	BTLH	851	906	Fl	O_C
Killdeer (*Charadrius vociferus*)	KILL	5	6	Gr	O_G
Spotted Sandpiper (*Actitis macularius*)	SPSA	1	1	Gr	O_G
Lewis's Woodpecker (*Melanerpes lewis*)	LEWO	7	7	AI	C_S
Acorn Woodpecker (*Melanerpes formicivorus*)	ACWO	387	515	AI, CI	C_P
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	WISA	86	102	CI	C_P
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	RNSA	2	3	CI, AI	C_P

Species (Taxonomic name)	**Code**	**Detections (max = 5738)**	**Sum of counts**	**Traits**	
				Foraging	**Nesting**
American Three-toed Woodpecker (*Picoides dorsalis*)	ATTW	14	17	Sn	C_P
Downy Woodpecker (*Dryobates pubescens*)	DOWO	33	36	Sn, Cl	C_P
Ladder-backed Woodpecker (*Dryobates scalaris*)	LBWO	6	7	Cl, Sh	C_P
Hairy Woodpecker (*Dryobates villosus*)	HAWO	772	863	Sn	C_P
Northern Flicker (*Colaptes auratus*)	NOFL	991	1135	Gn	C_P
Ash-throated Flycatcher (*Myiarchus cinerascens*)	ATFL	375	446	Gr, Sh	C_S
Cassin's Kingbird (*Tyrannus vociferans*)	CAKI	66	95	AI	O_C
Western Kingbird (*Tyrannus verticalis*)	WEKI	5	6	AI	O_C, O_S
Olive-sided Flycatcher (Contopus cooperi)	OSFL	46	55	AI	O_C
Greater Pewee (*Contopus pertinax*)	GRPE	1	1	AI	O_C
Western Wood-Pewee (*Contopus sordidulus*)	WEWP	1427	1832	AI	O_C
Hammond's Flycatcher (*Empidonax hammondii*)	HAFL	2	2	AI	O_C
Gray Flycatcher (*Empidonax wrightii*)	GRFL	676	825	AI	O_C
Dusky Flycatcher (*Empidonax oberholseri*)	DUFL	56	67	AI	O_S
Cordilleran Flycatcher (*Empidonax occidentalis*)	COFL	586	660	AI	C_S
Black Phoebe (*Sayornis nigricans*)	BLPH	5	7	AI	OT
Say's Phoebe (*Sayornis saya*)	SAPH	9	11	AI	OT
Gray Vireo (*Vireo vicinior*)	GRVI	44	49	Sh	O_C
Hutton's Vireo (*Vireo huttoni*)	HUVI	8	8	Cl	O_C
Plumbeous Vireo (*Vireo plumbeus*)	PLVI	1952	2435	Cl	O_C
Warbling Vireo (*Vireo gilvus*)	WAVI	417	649	Cl	O_C
Pinyon Jay (*Gymnorhinus cyanocephalus*)	PIJA	84	226	CS	O_C

Species (Taxonomic name)	**Code**	**Detections (max = 5738)**	**Sum of counts**	**Traits**	
				Foraging	**Nesting**
Steller's Jay (*Cyanocitta stelleri*)	STJA	1557	2144	Gn	O_C
Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*)	WOSJ	15	18	Gn	O_S
Clark's Nutcracker (*Nucifraga columbiana*)	CLNU	46	60	CS	O_C
American Crow (*Corvus brachyrhynchos*)	AMCR	42	56	Gn	O_C
Common Raven (*Corvus corax*)	CORA	335	456	Gn	O_C
Horned Lark (*Eremophila alpestris*)	HOLA	6	9	Gr	O_G
Tree Swallow (*Tachycineta bicolor*)	TRES	1	1	AI	C_S
Violet-green Swallow (*Tachycineta thalassina*)	VGSW	1417	2425	AI	C_S
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	NRWS	15	23	AI	OT
Purple Martin (*Progne subis*)	PUMA	227	358	AI	C_S
Barn Swallow (*Hirundo rustica*)	BARS	8	13	AI	OT
Cliff Swallow (*Petrochelidon pyrrhonota*)	CLSW	1	4	AI	OT
Mountain Chickadee (*Poecile gambeli*)	MOCH	2231	3109	CI	C_S
Bridled Titmouse (*Baeolophus wollweberi*)	BRTI	1	2	CI	C_S
Juniper Titmouse (*Baeolophus ridgwayi*)	JUTI	218	277	CI	C_S
Bushtit (*Psaltriparus minimus*)	BUSH	76	123	CI, Sh	OT[a]
Red-breasted Nuthatch (*Sitta canadensis*)	RBNU	110	130	CI	C_S
White-breasted Nuthatch (*Sitta carolinensis*)	WBNU	1974	2380	CI	C_S
Pygmy Nuthatch (*Sitta pygmaea*)	PYNU	2497	4227	CI	C_S
Brown Creeper (*Certhia americana*)	BRCR	408	448	CI	C_S
Rock Wren (*Salpinctes obsoletus*)	ROWR	93	115	Gr	OT
Canyon Wren (*Catherpes mexicanus*)	CANW	6	6	Gr	OT

Species (Taxonomic name)	Code	Detections (max = 5738)	Sum of counts	Traits	
				Foraging	Nesting
House Wren (*Troglodytes aedon*)	HOWR	829	1208	Gr	C_S
Bewick's Wren (*Thryomanes bewickii*)	BEWR	200	251	Sh	C_S
Cactus Wren (*Campylorhynchus brunneicapillus*)	CACW	1	1	Gn	OT
Blue-gray Gnatcatcher (*Polioptila caerulea*)	BGGN	85	95	CI, Sh	O_C, O_S
Golden-crowned Kinglet (*Regulus satrapa*)	GCKI	5	6	CI	O_C
Ruby-crowned Kinglet (*Regulus calendula*)	RCKI	145	222	CI	O_C
Western Bluebird (*Sialia mexicana*)	WEBL	1563	2338	Gr	C_S
Mountain Bluebird (*Sialia currucoides*)	MOBL	41	63	AI	C_S
Townsend's Solitaire (*Myadestes townsendi*)	TOSO	189	213	AI	O_G
Hermit Thrush (*Catharus guttatus*)	HETH	543	708	Sh, Gr	O_S
American Robin (*Turdus migratorius*)	AMRO	1488	2128	Gr	O_C
Crissal Thrasher (*Toxostoma crissale*)	CRTH	3	3	Gr	O_S
Northern Mockingbird (*Mimus polyglottos*)	NOMO	59	88	Gr	O_S
European Starling (*Sturnus vulgaris*)	EUST	4	5	Gr	C_S
Phainopepla (*Phainopepla nitens*)	PHAI	20	37	Gn	O_C, O_S
Olive Warbler (*Peucedramus taeniatus*)	OLWA	132	149	CI	O_C
House Sparrow (*Passer domesticus*)	HOSP	2	2	Gr	O_S
Evening Grosbeak (*Coccothraustes vespertinus*)	EVGR	16	23	Gn	O_C
House Finch (*Haemorhous mexicanus*)	HOFI	82	100	Gn	O_C
Cassin's Finch (*Haemorhous cassinii*)	CAFI	31	39	Gn[b]	O_C
Red Crossbill (*Loxia curvirostra*)	RECR	301	808	CS	O_C

Species (Taxonomic name)	**Code**	**Detections (max = 5738)**	**Sum of counts**	**Traits**	
				Foraging	**Nesting**
Pine Siskin (*Spinus pinus*)	PISI	364	564	CS	O_C
Lesser Goldfinch (*Spinus psaltria*)	LEGO	259	382	Gr	O_C
Black-throated Sparrow (*Amphispiza bilineata*)	BTSP	5	5	Gr	O_S
Lark Sparrow (*Chondestes grammacus*)	LASP	213	333	Gr	O_G
Chipping Sparrow (*Spizella passerina*)	CHSP	1353	1809	Gr	O_S
Black-chinned Sparrow (*Spizella atrogularis*)	BCSP	73	96	Sh, Gr	O_S
Brewer's Sparrow (*Spizella breweri*)	BRSP	1	1	Sh, Gr	O_S
Dark-eyed Junco (*Junco hyemalis*)	DEJU	2469	3667	Gr	O_G
Vesper Sparrow (*Pooecetes gramineus*)	VESP	96	142	Gr	O_G
Canyon Towhee (*Melozone fusca*)	CANT	1	1	Gr	O_S
Rufous-crowned Sparrow (*Aimophila ruficeps*)	RCSP	42	51	Gr	O_G
Green-tailed Towhee (*Pipilo chlorurus*)	GTTO	96	126	Sh, Gr	O_S
Spotted Towhee (*Pipilo maculatus*)	SPTO	576	879	Gr	O_G
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	YHBL	1	1	Gn	OT
Eastern Meadowlark (*Sturnella magna*)	EAME	11	32	Gr	O_G
Western Meadowlark (*Sturnella neglecta*)	WEME	86	130	Gr	O_G
Bullock's Oriole (*Icterus bullockii*)	BUOR	10	10	CI	OT[c]
Scott's Oriole (*Icterus parisorum*)	SCOR	26	31	Gn[d]	OT[a]
Red-winged Blackbird (*Agelaius phoeniceus*)	RWBL	4	8	Gn	O_S
Brown-headed Cowbird (*Molothrus ater*)	BHCO	553	664	Gr	OT[e]
Brewer's Blackbird (*Euphagus cyanocephalus*)	BRBL	11	19	Gr	O_S
Great-tailed Grackle (*Quiscalus mexicanus*)	GTGR	1	1	Gr	OT

Species (Taxonomic name)	**Code**	**Detections (max = 5738)**	**Sum of counts**	**Traits**	
				Foraging	**Nesting**
Orange-crowned Warbler (*Oreothlypis celata*)	OCWA	5	5	CI	O_G
Virginia's Warbler (*Oreothlypis virginiae*)	VIWA	320	400	Sh	O_S
MacGillivray's Warbler (*Geothlypis tolmiei*)	MGWA	22	25	CI	O_S
Common Yellowthroat (*Geothlypis trichas*)	COYE	3	3	Sh, Gr	O_S, O_G
Yellow Warbler (*Setophaga petechia*)	YEWA	1	1	Gr	O_S
Yellow-rumped Warbler (*Setophaga coronata*)	YRWA	1788	2564	CI	O_C
Grace's Warbler (*Setophaga graciae*)	GRWA	1968	3057	CI	O_C
Black-throated Gray Warbler (*Setophaga nigrescens*)	BTYW	384	539	CI, Sh	O_C
Red-faced Warbler (*Cardellina rubrifrons*)	RFWA	293	412	CI	O_G
Painted Redstart (*Myioborus pictus*)	PARE	6	7	CI	O_G
Hepatic Tanager (*Piranga flava*)	HETA	287	351	Gn	O_C
Western Tanager (*Piranga ludoviciana*)	WETA	1745	2182	CI	O_C
Black-headed Grosbeak (*Pheucticus melanocephalus*)	BHGR	579	680	Gn	O_C, O_S
Blue Grosbeak (*Passerina caerulea*)	BLGR	6	7	Gn	O_C
Lazuli Bunting (*Passerina amoena*)	LAZB	5	5	Gn	O_S

[a] Builds pendulum nest in shrubs. Use of shrubs as primary substrate may confer similar relationships to restoration as opencup shrub nesters, but pendulum nests may be less exposed to predation.

[b] Mupltiple foraging modes are described in the literature, including foraging in the canopy and on the ground. Ponderosa pine seeds are explicitly listed as a major food item, so forest restoration is expected to benefit Cassin's Finch to the extent that ponderosa pine are maintained and seed productivity is encouraged.

[c] Builds pendulum nest in the canopy. Use of canopy as primary substrate may confer similar relationships to restoration as open-cup canopy nesters, but pendulum nests may be less exposed to predation.

[d] Primarily feeds on arthropods and nectar. Arthropods are captured from a variety of sources, including on the ground, herbaceous vegetation, and shrubs.

[e] Obligate brood parasite. Hosts predominantly represent a variety of open-cup nesting species.

Appendix B.

Species-specific *a priori* hypotheses for habitat relationships. For each species and habitat feature, we hypothesized a positive (+) or negative (-) relationship based on life history and available species-specific ecological literature. Where there was conflict, species-specific ecology trumped life history considerations for these hypotheses, although we did not review literature for many species with insufficient data to meaningfully evaluate hypotheses (i.e., <20 detections and no statistically supported relationships). We predicted “unknown” (Un) where different sources in the literature provided conflicting information relevant to a given relationship. Superscripts indicate whether the prediction is based on nesting (N) or foraging (F) life history, or the literature (L, L1, L2, or L3). If the basis for a hypothesis was the literature, we explain under “Rationale and references” (see footnotes for references) wherein explanations link to specific hypotheses via L or L# superscripts. Species for which we had no definitive hypotheses were excluded from this table.

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
Band-tailed Pigeon (*Patagioenas fasciata*)	$+^{N}$									
Eurasian Collared-Dove (*Streptopelia decaocto*)	$+^{N}$	$+^{L}$							$+^{F}$	[L]Associated with riparian gallery forest[BNA]
White-winged Dove (*Zenaida asiatica*)	$+^{N}$									
Mourning Dove (*Zenaida macroura*)	$-^{N,L1}$					$-^{L2}$	$+^{N}$		$+^{F}$	[L1]Associated with open habitats[BNA], and positive relation with wildfire[1]; [L2]Negative relationship

Species (Taxonomic name)	**Predictions**									
	Canopy cover^{a}	**Canopy height^{b}**	**Snags**	**Ponderosa pine^{a,c}**	**Gambel oak^{c}**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels^{c,d}**	**Herbaceous volume**	**Rationale and references**
										with perimeter-area ratio of open forest[2]
Greater Roadrunner (*Geococcyx californianus*)							$+^{N}$			
Common Nighthawk (*Chordeiles minor*)	$-^{N,F,L}$						$+^{F}$	$-^{F}$	$+^{N}$	Nesting habitat includes open and disturbed forests[BNA], and related positively with wildfire[3]
White-throated Swift (*Aeronautes saxatalis*)	$-^{F}$						$+^{F}$	$-^{F}$		
Black-chinned Hummingbird (*Archilochus alexandri*)	$-^{F}$									
Anna's Hummingbird (*Calypte anna*)	$-^{N,F}$						$+^{N,F}$	$+^{F}$	$+^{F}$	
Broad-tailed Hummingbird (*Selasphorus platycercus*)	$-^{F,L1}$	$+^{L2}$		$+^{L2}$				$-^{L2}$	$+^{L2}$	^{L1}Positive relation with canopy gap extent[2], and positive relations with wildfire[1,3,4]; ^{L2}Associated with open ponderosa

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										pine woodland with widely spaced mature trees[BNA]; [L3]Negative relations with Douglas fir and ladder fuels, and positive relation with herbaceous cover[2]
Killdeer (*Charadrius vociferus*)	-[N,F]								+[N,F]	
Spotted Sandpiper (*Actitis macularius*)	-[N,F]								+[N,F]	
Lewis's Woodpecker (*Melanerpes lewis*)	-[F]		+[N]				+[F]	-[F]		
Acorn Woodpecker (*Melanerpes formicivorus*)	Un[F,L1]	+[L2]	+[N]	+[L2]	+[L2]		+[F]	-[F]		[L1]Inconsistent relationships with fire[3,4]; [L2]Strong association with oak, including forests characterized by large widely spaced ponderosa pine with oak understory[BNA]

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
Williamson's Sapsucker (*Sphyrapicus thyroideus*)	Un^{L}		+^{N}							Positive landscape-scale relation with restoration treatments elsewhere, *but* negative relations with canopy gaps[2], selective harvest[3], and high-severity fire[4]
Red-naped Sapsucker (*Sphyrapicus nuchalis*)			+^{N}				+^{F}	-^{F}		
American Three-toed Woodpecker (*Picoides dorsalis*)	+^{L}		+^{N}							Associated with higher elevation mature spruce-fir forest with relatively dense canopies[BNA]
Downy Woodpecker (*Dryobates pubescens*)	-^{L}	-^{L}	+^{N}							Associated with open habitats characterized by small trees and low canopy height[BNA]
Ladder-backed Woodpecker (*Picoides scalaris*)	+^{F}		+^{N}				+^{F}	-^{F}		
Hairy Woodpecker	-^{L}	+^{L}	+^{N}	+^{L}						Associated with mature open pine forests and woodlands[BNA], and

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
(*Dryobates villosus*)										positive relation with wildfire[1,4]
Northern Flicker (*Colaptes auratus*)	-^{L1}	+^{L1}	+^{N,L2}	-^{L2}						^{L1}Associated with low canopy cover and tall trees along mature forest edges, in open woodland and savanna, and in burned forest[1,BNA]; ^{L2}Negative relations with medium-sized ponderosa pine densities and positive relation with snags[5]
Ash-throated Flycatcher (*Myiarchus cinerascens*)	-^{F,L}		+^{N}	-^{L}			+^{F}	-^{F}	+^{F}	Associated with open habitats, including woodlands, shrublands, and riparian. Associated pinyon-juniper rather than ponderosa pine woodland[BNA]
Cassin's Kingbird (*Tyrannus vociferans*)	-^{F,L1}	+^{L2}					+^{F}	-^{F}		^{L1}Nests and forages in open areas[BNA]; ^{L2}associated with riparian gallary forest with tall canopy[BNA]

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
Western Kingbird (*Tyrannus verticalis*)	$-^{F}$						$+^{F}$			
Olive-sided Flycatcher (Contopus cooperi)	$-^{F,L1}$						$+^{F}$	$+^{L2}$		[L1]Positive relations with forest openings, edges, and wildfire[1,2,3,4,6,BNA], and negative relation with canopy cover[6]; [L2]Positive relation with ladder fuels[2]
Greater Pewee (*Contopus pertinax*)	$-^{F}$						$+^{F}$	$-^{F}$		
Western Wood-Pewee (*Contopus sordidulus*)	$-^{F,L}$						$+^{F}$	$-^{F}$		Associated with open forests and edges[2,BNA]
Hammond's Flycatcher (*Empidonax hammondii*)	$-^{F,L}$	$+^{L}$		$+^{L}$			$+^{F,L}$	$-^{F}$		Positive relationships with open forest, canopy height, ponderosa pine, and shrub volume[2]
Gray Flycatcher (*Empidonax wrightii*)	$-^{F,L}$	$-^{L}$					$+^{F}$	$-^{F}$	$-^{L}$	Associated with open woodlands and other open habitats, including pinyon-juniper woodland with low

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
										canopy height. Favors shrubby habitats with low ground cover[BNA]
Dusky Flycatcher (*Empidonax oberholseri*)	$-^{F,N}$			$+^{L1}$		$+^{L2}$	$+^{N,F,L2}$	$-^{F,L2}$		[L1]Associated with brushy lower elevation habitats characterized by Gambell oak and juniper[BNA]. [L2]Positive relations with perimeter-area ratio for open forest patches and shrub volume, and negative relation with ladder fuels[2]
Cordilleran Flycatcher (*Empidonax occidentalis*)	$+,-^{F,L1}$		$-^{L2}$	$-^{L2}$			$+^{F}$	$-^{F,L2}$		[L1]Associated with openings within relatively dense forest, so potential for negative local relationship coupled with positive landscape relationship with canopy cover[BNA] [L2]Negative relations with snags, ponderosa pine, and ladder fuels[2]

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
Black Phoebe (*Sayornis nigricans*)	-[F]						+[F]	-[F]		
Say's Phoebe (*Sayornis saya*)	-[F]						+[F]	-[F]		
Gray Vireo (*Vireo vicinior*)	-[F]						+[F]	-[F]		
Hutton's Vireo (*Vireo huttoni*)	+[N,F]									
Plumbeous Vireo (*Vireo plumbeus*)	-[L]	+[L]	-[L]	+[L]	+[L]	-[L]				Associated with open ponderosa pine forest and oak understory[BNA]; positive relations with canopy gaps and openings, ponderosa pine, and canopy height[2,5]; negative relations with perimeter-area ratio of open forest and snags[2,5]
Warbling Vireo (*Vireo gilvus*)	+[L1]		-[L2]	-[L2]			+[L1]			[L1]Associated with dense-canopy riparian deciduous forests (e.g., *Populus* spp.) containing dense willow shrub cover[BNA]; negative

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										relation with extent of open forest documented[2]; [L2]Negative relations with snags and ponderosa pine[2]
Pinyon Jay (*Gymnorhinus cyanocephalus*)	$-^{F}$			$-^{L}$						Although inhabits ponderosa pine, associated more with pinyon-juniper forest[BNA]
Steller's Jay (*Cyanocitta stelleri*)	$+^{N,L1}$	$+^{L1}$	$-^{L1}$			$+^{L2}$			$-^{L1}$	[L1]Negative relations with canopy gaps, snags, and herbaceous cover[2,5]; positive relations with canopy height and large ponderosa pine trees[2,5]; [L2]associated with forest fragmentation and edges[BNA]
Woodhouse's Scrub-Jay (*Aphelocoma woodhouseii*)	$-^{N}$			$-^{L}$			$+^{N}$			Associated more with pinyon-juniper rather than ponderosa pine woodland.[BNA]
Clark's Nutcracker	$-^{F,L}$			$+^{F}$						Associated with open habitats[BNA], and positive relation with open

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
(*Nucifraga columbiana*)										forest, *although* negative relation with canopy gaps[2]
American Crow (*Corvus brachyrhynchos*)	$+^{N,L}$									Negative relation with canopy gaps[2], *although* associated with open habitats with scattered trees[BNA]
Common Raven (*Corvus corax*)	$+^{N}$	$+^{L}$								Positive relation with canopy height reported[2]
Horned Lark (*Eremophila alpestris*)	$-^{N,F}$								$+^{N,F}$	
Tree Swallow (*Tachycineta bicolor*)	$-^{F}$		$+^{N}$				$+^{F}$	$-^{F}$		
Violet-green Swallow (*Tachycineta thalassina*)	$-^{F,L}$	$+^{L}$	$+^{N}$	$+^{L}$			$-^{L}$	$-^{F,L}$	$+^{L}$	Associated with open woodlands[BNA]; positive relations with canopy gaps, open forest, large ponderosa pine, and herbaceous cover reported, and negative relations with shrub volume, ladder fuels,

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										and medium ponderosa pine reported[2,5]
Northern Rough-winged Swallow (*Stelgidopteryx serripennis*)	-[F,L]						+[F]	-[F]		Positive relation with canopy gaps reported[2]
Purple Martin (*Progne subis*)	-[F]	+[L]	+[N]				+[F]	-[F]		Associated with tall riparian gallery forest[BNA]
Barn Swallow (*Hirundo rustica*)	-[F]						+[F]	-[F]		
Cliff Swallow (*Petrochelidon pyrrhonota*)	-[F]						+[F]	-[F]		
Mountain Chickadee (*Poecile gambeli*)	+[F]	+[L]	+[N]							Associated with mature forest, i.e., tall trees[BNA]
Bridled Titmouse (*Baeolophus wollweberi*)	+[F]		+[N]							
Juniper Titmouse (*Baeolophus ridgwayi*)	-[L]	-[L]	+[N]	-[L]						Associated with open woodland, especially pinyon-juniper woodlands with relatively short canopy

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										compared to ponderosa pine[BNA]
Bushtit (*Psaltriparus minimus*)	-[L]	-[L]		-[L]			+[F,L]			Associated with open woodland with shrubby understory. Especially associated with pinyon-juniper woodland, and therefore short canopy compared to ponderosa pine[BNA]
Red-breasted Nuthatch (*Sitta canadensis*)	+[F,L]	+[L]	+[N]	-[L]				+[L]	-[L]	Associated with mature coniferous forests with high canopies and large trees, but less so pure ponderosa pine stands[BNA]; negative relations with canopy gaps, ponderosa pine, and herbaceous cover, and positive relation with ladder fuels and canopy cover reported[2,7]
White-breasted Nuthatch (*Sitta carolinensis*)	-[L]	+[L]	+[N,L]	+[L]					-[L]	Associated with forest and woodland openings and edges[BNA]; positive relations with canopy height, ponderosa pine,

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										and snags, and negative relation with herbaceous cover reported[2,5]
Pygmy Nuthatch (*Sitta pygmaea*)	-[L]	+[L]	+[N,L]	+[L]			-[L]	+[L]	-[L]	Strongly associated with mature ponderosa pine forest, characterized by frequent low-severity wildfire, and consequently sparse shrub layer[BNA]; positive relations with canopy gaps and open forest reported, *although* positive relation with local canopy cover also reported[2]; positive relations with canopy height, large ponderosa pine, and ladder fuels, and negative relations with herbaceous cover reported[2,5]; positive relation with snags reported[5] and snags are key habitat component[BNA], *although*

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
										negative relation also reported[2]
Brown Creeper (*Certhia americana*)	+[F,L]	+[L]	+[N,L]	+[L]					-[L]	Associated with late-successional and old growth forest with high canopy coverage, and large trees and snags. Prevalent in dense ponderosa pine forest[BNA]; positive relation with canopy height, and negative relations with ponderosa pine and herbaceous cover reported[2]
Rock Wren (*Salpinctes obsoletus*)	-[F]								+[F]	

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
Canyon Wren (*Catherpes mexicanus*)	$-^{F}$								$+^{F}$	
House Wren (*Troglodytes aedon*)	$-^{F,L}$	$-^{L}$	$+^{N,L}$	$+^{L}$			$+^{L}$	$-^{L}$	$+^{F,L}$	Associated with open ponderosa pine and forest edges, absent from mature forest, and assocated with snags[BNA]; negative relations with canopy cover, canopy height, and ladder fuels, and positive relations with snags, ponderosa pine, shrub volume, and herbaceous cover reported[2]
Bewick's Wren (*Thryomanes bewickii*)	$-^{F,L}$	$-^{L}$	$+^{N}$	$-^{L}$	$+^{L}$		$+^{F,L}$	$-^{F}$		Associated with open shrubby habitats. Especially associated with pinyon-juniper (*contra* pondersa pine) woodland, with low canopy and a Gambell oak component[BNA]
Blue-gray Gnatcatcher	$\mathrm{Un}^{N,F}$	$-^{L}$		$-^{L}$	$+^{L}$		$-^{L}$	$-^{F}$		Understory species associated with open shrubby habitats;

Species (Taxonomic name)	**Predictions**									
	Canopy cover^{a}	**Canopy height**^{b}	**Snags**	**Ponderosa pine**^{a,c}	**Gambel oak**^{c}	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**^{c,d}	**Herbaceous volume**	**Rationale and references**
(*Polioptila caerulea*)										especially associated with pinyon-juniper (*contra* pondersa pine) woodland, with low canopy and a Gambell oak component^{BNA}
Golden-crowned Kinglet (*Regulus satrapa*)	+^{N,F}									
Ruby-crowned Kinglet (*Regulus calendula*)	+^{N,F,L}	+^{L}	-^{L}	-^{L}				+^{L}		Negative relations with canopy gaps, snags, and ponderosa pine, and positive relations with canopy height and ladder fuels reported[2]
Western Bluebird (*Sialia mexicana*)	-^{F,L}	+^{L}	+^{N,L}	+^{L}			-^{L}		-^{L}	Associated with open ponderosa pine woodlands with edges, widely spaced mature trees, and snags with open grassy understory^{BNA}; Negative relations with canopy cover and herbaceous volume, and positive

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										relation with canopy gaps reported.[2,6,7]
Mountain Bluebird (*Sialia currucoides*)	$-^{F,L}$		$+^{N}$				$+^{F}$	$-^{F}$	$+^{L}$	Associated with open habitats containing short grasses and short vegetation, and absent from dense forest with high canopy cover[BNA]
Townsend's Solitaire (*Myadestes townsendi*)	$-^{N,F,L}$		$+^{L}$	$+^{L}$			$+^{F,L}$	$-^{F}$	$-^{L}$	Favors open forest stands[BNA]; positive relations with snags, ponderosa pine, and shrub volume, and negative relation with herbaceous cover reported[2]
Hermit Thrush (*Catharus guttatus*)	$+^{L1}$	$+^{L2}$	$-^{L2}$	$-^{L2}$		$+^{L2}$	$+^{N,F}$	$-^{F}$	$-^{L2}$	[L1]Associated with old growth closed-canopy conifer forest[BNA], and negative associations with landscape-scale extent of canopy gaps and open forest, *but* negatively related with canopy cover locally[2]; [L2]Positive relations with

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										perimeter-area ratio of open forest and canopy height, and negative relations with snags, ponderosa pine, and herbaceous cover reported[2]
American Robin (*Turdus migratorius*)	$+^{N,L}$		$-^{L}$				$+^{L}$		$+^{F}$	Favors early successional forest[BNA]; negative relations with canopy cover and snags, and positive relation with shrub volume reported[2]
Crissal Thrasher (*Toxostoma crissale*)	$-^{N,F}$						$+^{N}$		$+^{F}$	
Northern Mockingbird (*Mimus polyglottos*)	$-^{N,F}$			$-^{L}$			$+^{N}$		$+^{F}$	Associated with non-forest habitats rather than ponderosa pine woodland[BNA]
European Starling (*Sturnus vulgaris*)	$-^{F}$		$+^{N}$						$+^{F}$	

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
Phainopepla (*Phainopepla nitens*)							+[N]			
Olive Warbler (*Peucedramus taeniatus*)	-[L]	+[L]		+[L]						Strongly associated with open ponderosa pine forest with mature trees[BNA]
House Sparrow (*Passer domesticus*)										
Evening Grosbeak (*Coccothraustes vespertinus*)	+[N,L]	-[L]		+[L]			+[L]			Negative relations with canopy gaps and canopy height, and positive relation with shrub volume reported[2]; associated with ponderosa pine in Arizona[BNA]
House Finch (*Haemorhous mexicanus*)	-[L]			-[L]						Associated with open coniferous forests, avoids dense stands, and common along forest edges; associated more with pinyon-juniper rather than

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
										ponderosa pine woodland[BNA]
Cassin's Finch (*Haemorhous cassinii*)	-[L]	+[L]								Negative relation with canopy cover[7] and positive relation with canopy height reported[2]
Red Crossbill (*Loxia curvirostra*)	-[F,L1]	+[L2]		+[F,L3]				+[L3]	-[L3]	[L1]Avoids dense forest stands[BNA], *although* negative relation with canopy gaps repoted[2]; [L2]associated with mature forest with tall trees[BNA]; [L3]positive relations with ponderosa pine and ladder fuels, and negative relation with herbaceous cover reported[2,5]
Pine Siskin (*Spinus pinus*)	-[F,L]	+[L]		+[F,L]				+[L]	-[L]	Associated with mature open ponderosa pine forests[BNA]; negative relations with canopy gaps and herbaceous cover, and positive relations with

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
										ponderosa pine and ladder fuels[2]
Lesser Goldfinch (*Spinus psaltria*)	$-^{L}$			$-^{L}$			$+^{L}$	$-^{L}$	$+^{F}$	Associated with a variety of open and shrubby habitats; not associated with ponderosa pine forest[BNA]; negative relation with ladder fuels reported[2]
Black-throated Sparrow (*Amphispiza bilineata*)	$-^{N,F}$						$+^{N}$		$+^{F}$	
Lark Sparrow (*Chondestes grammacus*)	$-^{N,F,L}$	$-^{L}$					$-^{L}$		$+^{N,F,L}$	Associated with open habitats with grassy or herbaceous cover and containing or adjoining scattered trees or shrubs[BNA]
Chipping Sparrow (*Spizella passerina*)	$-^{N,F,L}$	$-^{L}$	$-^{L}$	$+^{L}$			$+^{N,L}$		$+^{F,L}$	Prefers open coniferous forests and woodlands, breeding shrubby edges of openings[BNA]; negative relations with canopy

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	**Canopy height[b]**	**Snags**	**Ponderosa pine[a,c]**	**Gambel oak[c]**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels[c,d]**	**Herbaceous volume**	**Rationale and references**
										cover, large ponderosa pine trees, and snags, and positive relations with ponderosa pine dominance and herbaceous cover reported[2,5,7]
Black-chinned Sparrow (*Spizella atrogularis*)	$-^{N,F}$	$-^{L}$		$-^{L}$	$+^{L}$		$+^{N,F}$	$-^{F}$	$+^{F}$	Associated with shrublands, including those containing Gambell oak[BNA]
Brewer's Sparrow (*Spizella breweri*)	$-^{N,F}$						$+^{N,F}$	$-^{F}$	$+^{F}$	
Dark-eyed Junco (*Junco hyemalis*)	$-^{N,F}$	$+^{L}$	$+^{L}$					$+^{L}$	$-^{L}$	Negative relations with canopy gaps, ponderosa pine (absolute) cover, and herbaceous cover, and positive relations with canopy height, ladder fuels, and snags reported[2,5]
Vesper Sparrow (*Pooecetes gramineus*)	$-^{N,F,L}$						$-^{L}$		$+^{N,F}$	Associated with open habitats with sparse, patchy herbaceous vegetation, low-to-moderate shrub cover,

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height[b]**	**Snags**	**Ponderosa pine[a,c]**	**Gambel oak[c]**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels[c,d]**	**Herbaceous volume**	**Rationale and references**
										and tall forbes[BNA]; positive relation with extent of canopy caps reported[2]
Canyon Towhee (*Melozone fusca*)	$-^{N,F}$						$+^{N}$		$+^{F}$	
Rufous-crowned Sparrow (*Aimophila ruficeps*)	$-^{N,F}$								$+^{N,F}$	
Green-tailed Towhee (*Pipilo chlorurus*)	$-^{N,F,L}$		$-^{L}$	$+^{L}$			$+^{N,F,L}$	$-^{F,L}$	$+^{F,L}$	Associated with shrubby habitats and avoids forest[BNA]; positive relations with canopy gaps, ponderosa pine, shrub volume, and herbaceous cover, and negative relations with canopy cover, snags, and ladder fuels reported[2]
Spotted Towhee (*Pipilo maculatus*)	$-^{N,F,L}$	$-^{L}$	$-^{L}$	$-^{L}$				$-^{L}$	$+^{N,F,L}$	Associated with variety of broad-leaf shrubby habitats, including with Gambell oak; not a forest species, so not

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										expected to associate with ponderosa pine[BNA]; negative relations with snags and ladder fuels, and positive relation with herbaceous cover reported[2]
Eastern Meadowlark (*Sturnella magna*)	$-^{N,F}$			$-^{L}$					$+^{N,F}$	Associated with grassland habitats, not ponderosa pine woodland[BNA]
Western Meadowlark (*Sturnella neglecta*)	$-^{N,F,L}$			$-^{L}$					$+^{N,F,L}$	Associated with grassland habitats, not ponderosa pine woodland[BNA]
Bullock's Oriole (*Icterus bullockii*)	$+^{F}$									
Red-winged Blackbird (*Agelaius phoeniceus*)	$-^{N}$						$+^{N}$			
Brown-headed Cowbird (*Molothrus ater*)	$-^{F,L}$		$-^{L}$						$+^{F}$	Prefers open habitats and woodland edges[BNA]; negative relations with canopy cover and snags, and positive relation

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height[b]**	**Snags**	**Ponderosa pine[a,c]**	**Gambel oak[c]**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels[c,d]**	**Herbaceous volume**	**Rationale and references**
										with canopy gaps reported[2,7]
Brewer's Blackbird (*Euphagus cyanocephalus*)	$-^{N,F}$						$+^{N}$		$+^{F}$	
Great-tailed Grackle (*Quiscalus mexicanus*)	$-^{F}$								$+^{F}$	
Orange-crowned Warbler (*Oreothlypis celata*)	$+^{N,F}$								$+^{N}$	
Virginia's Warbler (*Oreothlypis virginiae*)	$-^{N,F}$	$-^{L}$		$-^{L}$	$+^{L}$		$+^{N,F,L}$	$-^{F}$		Associated with forests containing large amounts of scrubby habitat, including Gambell oak; associated more with shorter canopy pinyon-juniper rather than ponderosa pine woodland[BNA]; positive relation with shrub volume reported[2]

Species (Taxonomic name)	**Predictions**									
	Canopy cover^{a}	**Canopy height^{b}**	**Snags**	**Ponderosa pine^{a,c}**	**Gambel oak^{c}**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels^{c,d}**	**Herbaceous volume**	**Rationale and references**
MacGillivray's Warbler (*Geothlypis tolmiei*)	$+^{F}$		$-^{L}$				$+^{N,L}$	$-^{L}$	$+^{L}$	Positive relations with shrub volume and herbaceous cover, and negative relations with sangs and ladder fuels[2]
Common Yellowthroat (*Geothlypis trichas*)	$-^{N,F}$						$+^{N,F}$	$-^{F}$	$+^{N,F}$	
Yellow Warbler (*Setophaga petechia*)	$-^{N,F,L}$			$-^{L}$			$+^{N,L}$	$-^{L}$	$+^{F}$	Positive relations with extent of canopy gaps and shrub volume, and negative relations with canopy cover, ponderosa pine dominance, and ladder fuels[2]
Yellow-rumped Warbler (*Setophaga coronata*)	Un^{N,F,L}	$+^{L}$	Un^{L}	$-^{L}$			$+^{L}$	$+^{L}$	Un^{L}	Associated with mature coniferous forest, where less common in early successional stands[BNA], *but* negative relations with canopy cover reported[3]. Negative relations with ponderosa pine dominance; positive

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height[b]**	**Snags**	**Ponderosa pine[a,c]**	**Gambel oak[c]**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels[c,d]**	**Herbaceous volume**	**Rationale and references**
										relations with canopy height, shrub volume, ladder fuel dominance, and snags; and mixed relationships with herbaceous cover and snags reported[2,5]
Grace's Warbler (*Setophaga graciae*)	+[N,F]	+[L]		+[L]	+[L]		+[L]			Associated with pine forest with shrubs and Gambell oak in the understory, and thought to have declined with lower prevalence of large ponderosa pine[BNA]; positive relation with density of large ponderosa pine trees reported[5]
Black-throated Gray Warbler (*Setophaga nigrescens*)	+[N,F,L]	-[L]					+[F,L]	-[F]		Associated with open coniferous forests with brushy undergrowth. Associated more with shorter canopy pinyon-juniper rather than ponderosa pine woodland[BNA]

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	**Canopy height[b]**	**Snags**	**Ponderosa pine[a,c]**	**Gambel oak[c]**	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels[c,d]**	**Herbaceous volume**	**Rationale and references**
Red-faced Warbler (*Cardellina rubrifrons*)	+[F]			-[L]					+[N]	Associated more with higher elevation forests rather than ponderosa pine[BNA]
Painted Redstart (*Myioborus pictus*)	+[F]								+[N]	
Hepatic Tanager (*Piranga flava*)	-[L]	+[L]								Associated with mature open forest[BNA]
Western Tanager (*Piranga ludoviciana*)	+[N,F,L]	+[L]		+[L]	+[L]		+[L]	-[L]	-[L]	Associated with open coniferous woodlands with tall canopy, larger trees, and shrub component[BNA], *although* negative relation with density of large ponderosa pine reported[5]; Gambell oak listed as habitat component[BNA]; positive relations with canopy height and ponderosa pine dominance, and negative relations with ladder fuels and

Species (Taxonomic name)	**Predictions**									
	Canopy cover[a]	**Canopy height**[b]	**Snags**	**Ponderosa pine**[a,c]	**Gambel oak**[c]	**Canopy heterogeneity (landscape)**	**Shrub cover and height**	**Ladder fuels**[c,d]	**Herbaceous volume**	**Rationale and references**
										herbaceous cover reported[2]
Black-headed Grosbeak (*Pheucticus melanocephalus*)	+[N,L]	+[L]	-[L]	-[L]			+[N,L]	-[L]	-[L]	Well developed understory and large trees are key habitat components. Gambell oak also listed as habitat component. Associated more with riparian rather than ponderosa pine forest[BNA]; within ponderosa pine forest, however, positive relations with absolute ponderosa pine canopy cover, and negative relations with snag density, ladder fuel dominance, density of medium ponderosa pine, and herbaceous cover reported[2,5]

Species (Taxonomic name)	Predictions									
	Canopy cover[a]	Canopy height[b]	Snags	Ponderosa pine[a,c]	Gambel oak[c]	Canopy heterogeneity (landscape)	Shrub cover and height	Ladder fuels[c,d]	Herbaceous volume	Rationale and references
Blue Grosbeak (*Passerina caerulea*)	+[N]									
Lazuli Bunting (*Passerina amoena*)	-[L]						+[N]			

---

[a] Predictions applied at both stand and landscape scales

[b] Canopy height is a proxy for tree size, which is expected to increase with treatments that thin small trees.

[c] Predictions are for relationships with species dominance rather than absolute cover.

[d] Ladder fuels are defined here as conifer, juniper, and Gambel oak saplings in the shrub layer (0.25–3m height).

[BNA] Species-specific account in Birds of North America online (now rolled into Birds of the World) retrieved in 2020 from https://birdsoftheworld.org/bow/home.

[1] Bock, C. E., and W. M. Block. 2005. Fire and birds in the southwestern United States. Studies in Avian Biology 30:14-32.

[2] Latif, Q. S., R. L. Truex, R. A. Sparks, and D. C. Pavlacky. In Press. Dry conifer forest restoration benefits Colorado Front Range avian communities. Ecological Applications.

[3] Kalies, E. L., C. L. Chambers, and W. W. Covington. 2010. Wildlife responses to thinning and burning treatments in southwestern conifer forests: A meta-analysis. Forest Ecology and Management 259:333-342.

[4] Fontaine, J. B., and P. L. Kennedy. 2012. Meta-analysis of avian and small-mammal response to fire severity and fire surrogate treatments in U.S. fire-prone forests. Ecological Applications 22:1547-1561.

[5] Kalies, E. L., and S. S. Rosenstock. 2013. Stand structure and breeding birds: Implications for restoring ponderosa pine forests. The Journal of Wildlife Management 77:1157-1165.

[6] Gaines, W., M. Haggard, J. Begley, J. Lehmkuhl, and A. Lyons. 2010. Short-term effects of thinning and burning restoration treatments on avian community composition, density, and nest survival in the eastern Cascades dry forests, Washington. Forest Science 56:88-99.

[7] Gaines, W. L., M. Haggard, J. F. Lehmkuhl, A. L. Lyons, and R. J. Harrod. 2007. Short-Term Response of Land Birds to Ponderosa Pine Restoration. Restoration Ecology 15:670-678.

Appendix C.

Community model for analyzing habitat relationships with species occupancy, occupancy dynamics, and species richness.

We analyzed bird occupancy using a model that incorporates multiscale dynamics (Green et al. 2019) implemented within a hierarchical multispecies framework (Dorazio et al. 2010). We considered detection data, **y**, as representing four dimensions; $y_{ijkt} = 1$ indicated species i ($i = 1, \ldots, M$; $M = 138$) was detected at point j ($j = 1, \ldots, J$; $J = 16$) within grid k ($k = 1, \ldots, K$; $K = 163$) in year t ($t = 1, \ldots, T$; $T = 10$). To inform detectability estimation following removal sampling (Rota et al. 2009), we compiled a parallel array, **R**, whose elements indicate time to detection or the end of the survey ($r_{ijkt} \in \{1,2, \ldots, 6\}$ when $y_{ijkt} = 1$, or $r_{ijkt} = 6$ when $y_{ijkt} = 0$). We modeled data generation as

$$y_{ijkt} | u_{ijkt} \sim Binomial\left(r_{ijkt}, p_{ijkt} \times u_{ijkt}\right),$$

where p_{ijkt} is the probability of detecting species i during a one-minute interval given occupancy of point j in grid k and year t. We modeled point occupancy as

$$u_{ijkt} | z_{ikt} \sim Bernoulli\left(\theta_{ijkt} \times z_{ikt}\right),$$

where θ_{ijkt} is the point occupancy probability for species i given grid k is occupied in year t. We modeled grid occupancy during the initial year of the study as

$$z_{ik1} | w_i \sim Bernoulli(\psi_{0ik} \times w_i),$$

where ψ_{0ik} is the initial grid occupancy probability in year 1 for species i given that species i belongs in the super community. We modeled grid occupancy in subsequent years ($t = 2, 3, \ldots, 10$) as

$$z_{ikt} | w_i \sim Bernoulli \begin{Bmatrix} \left[1 - \varepsilon_{ik(t-1)}\right] \times w_i & z_{ik(t-1)} = 1 \\ \gamma_{ik(t-1)} \times w_i & z_{ik(t-1)} = 0 \end{Bmatrix},$$

where γ_{ikt} and ε_{ikt} are grid-level colonization and extirpation probabilities for species i, respectively, given that species i belongs to the super community. Finally, we modeled whether species i belonged to the super community as $w_i \sim Bernoulli(\Omega)$ (Dorazio et al. 2010).

We modeled occupancy and its dynamics as logit-linear functions of covariates:

$$logit\left(p_{ijkt}\right) = \mathbf{x}_{\boldsymbol{jkt}} \boldsymbol{\zeta}_{\boldsymbol{i}}$$

$$logit\left(\theta_{ijkt}\right) = \mathbf{x}_{\boldsymbol{jkt}} \boldsymbol{\alpha}_{\boldsymbol{i}},$$

$$logit(\psi_{0ik}) = \mathbf{x}_{\boldsymbol{kt}} \boldsymbol{\beta}_{\boldsymbol{i}},$$

$$logit(\gamma_{ik}) = \mathbf{x}_{\boldsymbol{kt}} \boldsymbol{\delta}_{\boldsymbol{i}},$$

$$logit(\varepsilon_{ik}) = \mathbf{x}_{\boldsymbol{kt}} \boldsymbol{\eta}_{\boldsymbol{i}},$$

where $\mathbf{x}_{jkt}$ and $\mathbf{x}_{kt}$ are point- and grid-specific covariate vectors, respectively, and $\boldsymbol{\zeta}_i$, $\boldsymbol{\alpha}_i$, $\boldsymbol{\beta}_i$, $\boldsymbol{\delta}_i$, and $\boldsymbol{\eta}_i$ are species-specific vectors whose elements are logit-linear regression parameters. We modeled all regression parameters as species-specific normal random effects.

We derived several additional parameters describing species occupancy, species richness, and their dynamics. We quantified grid-level species richness for a given year *t* as the sum of all grid-cell occupancy probabilities across species multiplied by the probability of a species occurring in the study area (i.e., probability of belonging to the super community):

$$\widehat{N}_t = \sum_{i=1}^{M=138} \psi_{it} \times \Omega.$$

Similarly, we quantified point-level richness by summing point-level occupancy probabilities across species multiplied by the probability of species occurrence in the study area:

$$\widehat{N}_t = \sum_{i=1}^{M=138} \theta_{ijkt} \times \psi_{it} \times \Omega.$$

Because we sum occupancy probabilities rather than occupancy states (i.e., z_i, u_i), species richness here represents predicted richness for a hypothetical unit rather than estimated richness at sampled units (i.e., contrast with Latif et al. 2016, Sanderlin et al. 2016). Species turnover is the proportion of occupied sites that were previously unoccupied by species *i*. We estimated species turnover for a given year *t* as

$$\tau_{it} = \frac{\gamma_i \times (1-\psi_{it})}{\gamma_i \times (1-\psi_{it}) + (1-\varepsilon_i) \times \psi_{it}}.$$

We then calculated community-level turnover as the average turnover across species:

$$\widehat{T} = \frac{\sum_{i=1}^{M=138} \bar{\tau}_i}{M}.$$

We compared species richness and turnover for initial versus equilibrium states by plugging in either initial or equilibrium occupancy, respectively, into the corresponding formula. We estimated initial occupancy (ψ_{0ik}) following equations listed above, and equilibrium occupancy as a function of colonization and extirpation:

$$\psi_{(eq)ik} = \frac{\gamma_{ik}}{\gamma_{ik} + \varepsilon_i}.$$

Our derivations follow Royle and Kery (2007) as closely as possible, with adjustments to reflect our exclusion of inter-annual variability of occupancy dynamics.

References

Dorazio, R. M., M. Kéry, J. A. Royle, and M. Plattner. 2010. Models for inference in dynamic metacommunity systems. Ecology 91:2466-2475.

Green, A. W., D. C. Pavlacky Jr., and T. L. George. 2019. A dynamic multi-scale occupancy model to estimate temporal dynamics and hierarchical habitat use for nomadic species. Ecology and Evolution 9:793-803.

Latif, Q. S., J. S. Sanderlin, V. A. Saab, W. M. Block, and J. G. Dudley. 2016. Avian relationships with wildfire at two dry forest locations with different historical fire regimes. Ecosphere 7:e01346.

Rota, C. T., R. J. Fletcher Jr, R. M. Dorazio, and M. G. Betts. 2009. Occupancy estimation and the closure assumption. Journal of Applied Ecology 46:1173-1181.

Royle, J. A., and M. Kéry. 2007. A Bayesian state-space formulation of dynamic occupancy models. Ecology 88:1813-1823.

Sanderlin, J. S., W. M. Block, and B. E. Strohmeyer. 2016. Long-term post-wildfire correlates with avian community dynamics in ponderosa pine forests. in Ralston, Barbara E., ed. Proceedings of the 12th Biennial Conference of Research on the Colorado River Plateau. Scientific Investigations Report 2015-5180. Reston, VA: US Geological Survey. p. 89-101. Pages 89-101.

Appendix D.

Species-specific models for analyzing habitat relationships with abundance and population trends for focal species.

We analyzed population density and abundance separately for individual species using a hierarchical distance sampling framework (Royle 2004, Royle et al. 2004, Buckland et al. 2015, Kéry and Royle 2016). We analyzed abundance patterns for focal species identified by the wildlife subcommittee. For each species, we excluded the furthest 5% of detections from analysis and then classified remaining detections into 10 equal-width distance bins.

We modeled the number of individuals detected at point *j* in grid *k*, year *t*, and distance bin *d* (y_{jktd}) as multinomially distributed conditional on the total number detected (n_{jkt}),

$$y_{jktd}|n_{jkt} \sim Multinomial\left(n_{jkt}, \boldsymbol{\pi_{jkt}}\right),$$

where $\boldsymbol{\pi_{jkt}}$ is a multinomial probability vector of length $D = 10$, the number of distance bins. Each element of $\boldsymbol{\pi_{jkt}}$ is the product of the probability of detecting an individual in a given distance class (g_{jktd}) and the proportionate area (A_d; $\pi_{jktd} = g_{jktd} \times A_d$). Detection probability declined with distance for bin *d* following a hazard function:

$$g_{jktd} = 1 - exp\left(-\left(dist_d/a_{jkt}\right)^b\right),$$

where *a* and *b* are estimated parameters governing a hazard function. The total number of individuals detected during a point survey (n_{jkt}) depended on abundance at point *j* in grid *k* and year *t*,

$$\left[n_{jkt}|N_{jkt}\right] \sim Binomial\left(N_{jkt}, p_{jkt}\right),$$

where p_{jkt} is the overall probability of detecting an individual integrated across all distance bins ($p_{jkt} = \sum_{d=1}^{D} g_{jktd}$). Detectability varied with covariates and among years by modeling a_{jkt} (decline with distance) as

$$log\left(a_{jkt}\right) = \mathbf{w_{jkt}}\boldsymbol{\zeta} + \zeta_{dev,t},$$

where $\mathbf{w_{jkt}}$ is a vector of point-level covariate values, $\boldsymbol{\zeta}$ is a vector of regression slope parameters, and $\zeta_{dev,t}$ quantifies deviations from mean detectability in each year *t*. We modeled $\zeta_{dev,t}$ as a year-specific normal random effect.

We modeled point-level local abundance in year 1 using a zero-inflated Poisson distribution,

$$\left[N_{jkt}\right] \sim Poisson\left(\lambda_{jkt} \times u_{jk} \times z_k\right),$$

where u_{jk} and z_k are binomial state parameters describing species occupancy of points and grids, respectively, modeled as $u_{jk}|z_k \sim Bernoulli(\theta \times z_k)$ and $z_k \sim Bernoulli(\psi)$.

We modeled variability in local abundance using a log-linear model:

$$log\left(\lambda_{jkt}\right) = \alpha_{0,kt} + \mathbf{w_{jkt}}\boldsymbol{\alpha},$$

where $\alpha_{0,kt}$ is the intercept at grid cell k in year t, $\mathbf{w}_{\mathbf{jkt}}$ is a vector point-level covariate values, and $\boldsymbol{\alpha}$ is a vector of regression slope parameters. We modeled variability in focal species abundance among grid cells and years by modeling variability in the intercept as

$$\alpha_{0,kt} = A_{0,k} + A_{dev,kt} + \mathbf{x}_{\boldsymbol{kt}}\boldsymbol{A} + \delta_{kt} \times t,$$

where $A_{0,k}$ is a log-normal grid-specific intercept, $A_{dev,kt}$ is the year-specific deviation from the grid-level mean ($A_{dev,kt} \sim Normal[0, \sigma_t]$), $\mathbf{x}_{\boldsymbol{kt}}$ and $\boldsymbol{A}$ are grid-level covariate values and regression parameters, and δ_{kt} is a grid- and year-specific trend parameter. The trend parameter varied as a function of grid-level covariates:

$$\delta_{kt} = \mathbf{x}_{\boldsymbol{kt}}\boldsymbol{\Delta}.$$

References

Buckland, S. T., E. A. Rexstad, T. A. Marques, and C. S. Oedekoven. 2015. Distance sampling: methods and applications. Springer International Publishing, Switzerland.

Kéry, M., and J. A. Royle. 2016. Applied hierarchical modeling in ecology. Elsevier, Inc.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108-115.

Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. Ecology 85:1591-1597.

Appendix E.

Data supplement – we provide a zip file ("Data_supplement.zip") containing 1) R scripts for data compilation, analysis, results summaries, and plots, 2) data contained in R workspaces needed to run scripts, and 3) two Excel files ("Abundance_model_estimates.xlsx" and "Occupancy_model_estimates.xlsx") containing all model parameter estimates.

Appendix F.

Grid-scale occupancy relationships for 36 species with at least one statistically supported relationship.

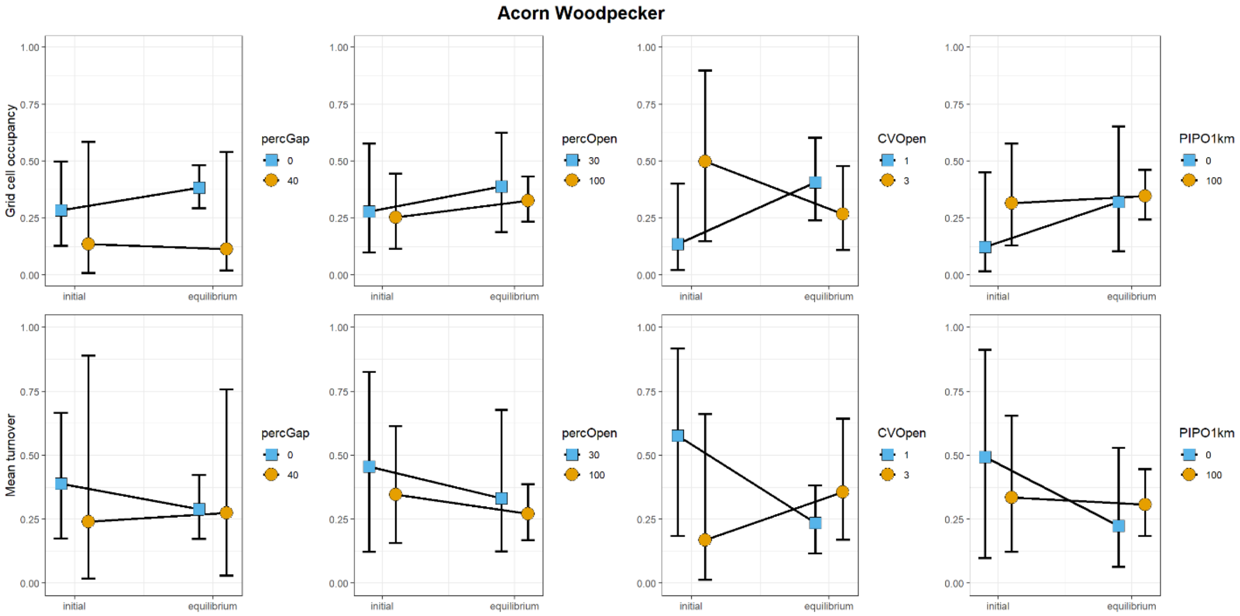

Figure F1. Grid-level occupancy relationships for Acorn Woodpecker.

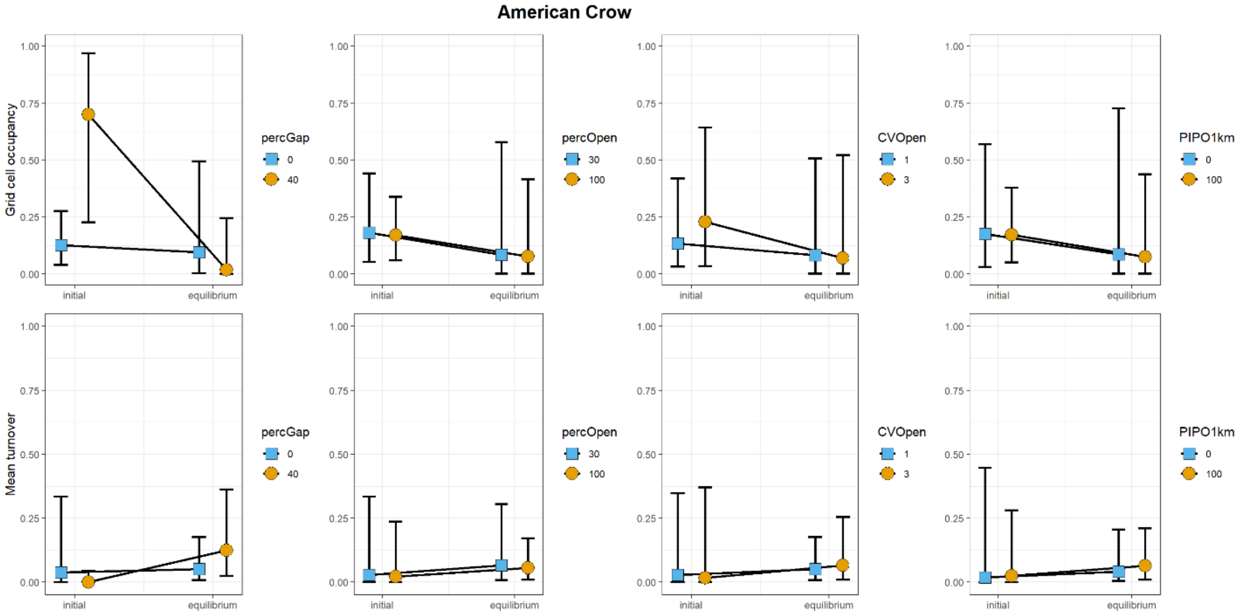

Figure F2. Grid-level occupancy relationships for American Crow.

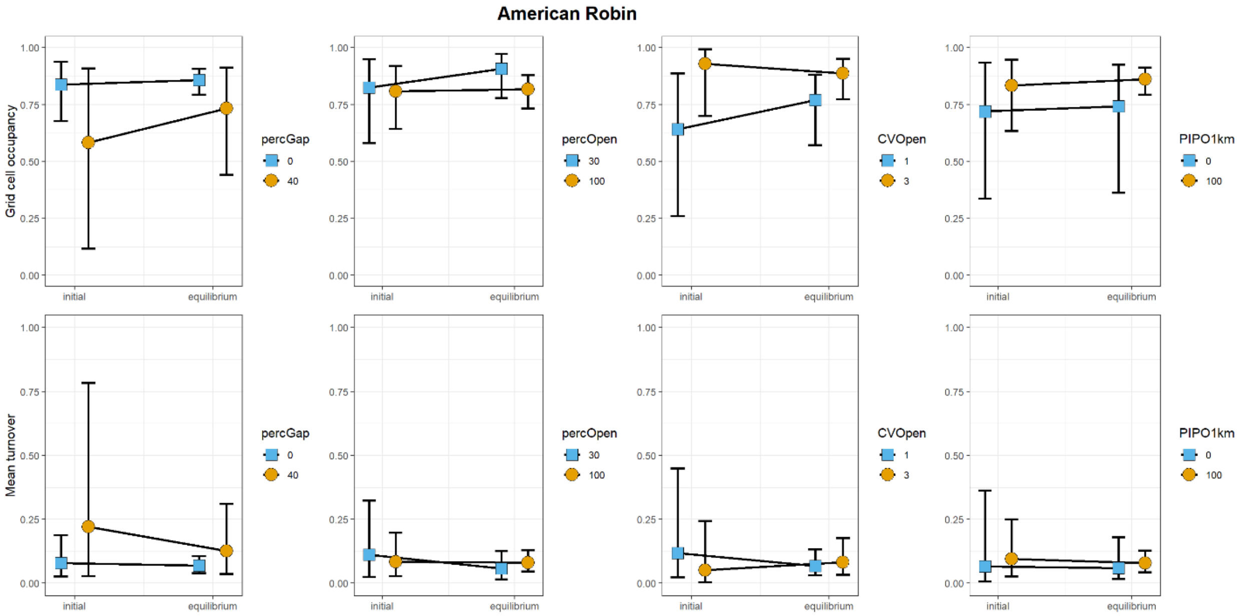

Figure F3. Grid-level occupancy relationships for American Robin.

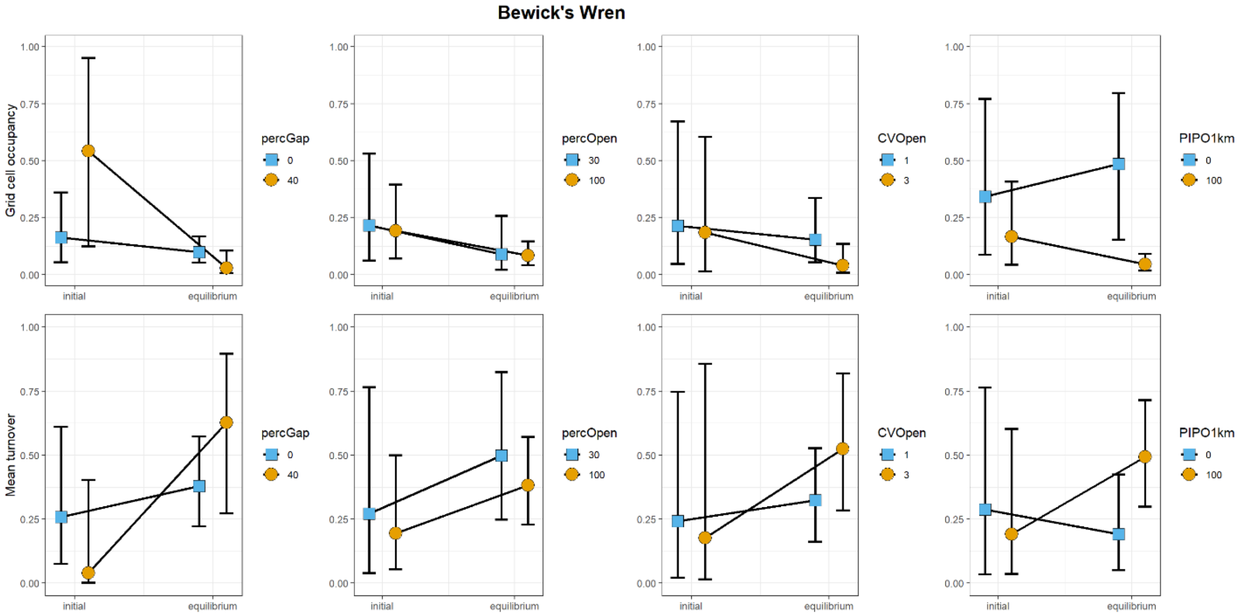

Figure F4. Grid-level occupancy relationships for Bewick's Wren.

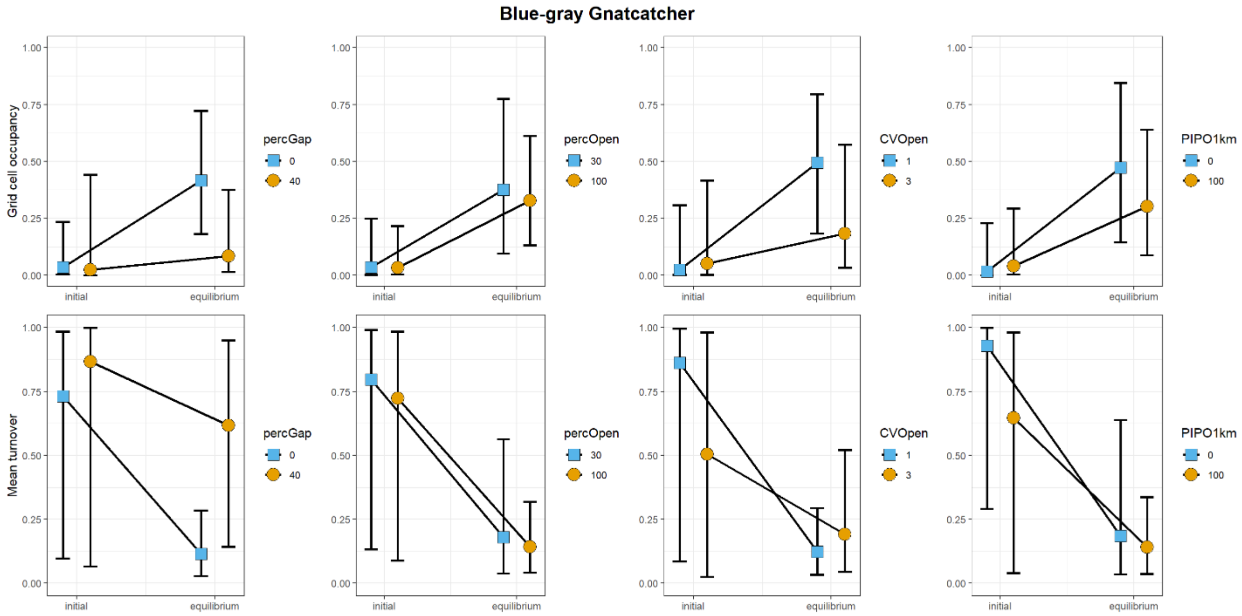

Figure F5. Grid-level occupancy relationships for Blue-gray Gnatcatcher.

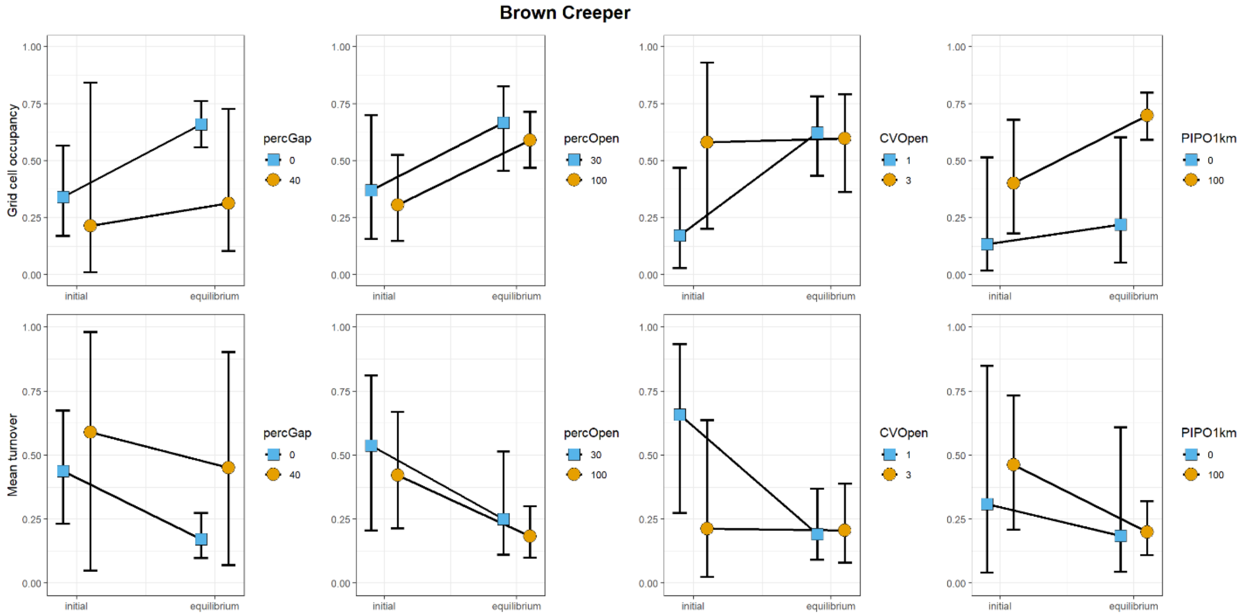

Figure F6. Grid-level occupancy relationships for Brown Creeper.

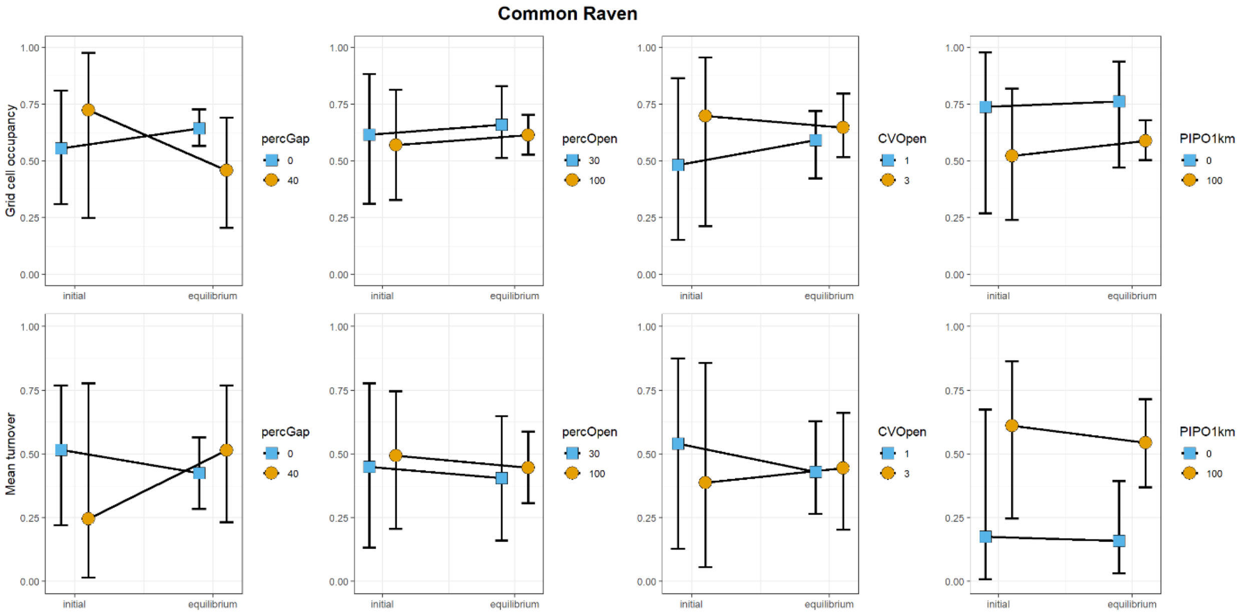

Figure F7. Grid-level occupancy relationships for Common Raven.

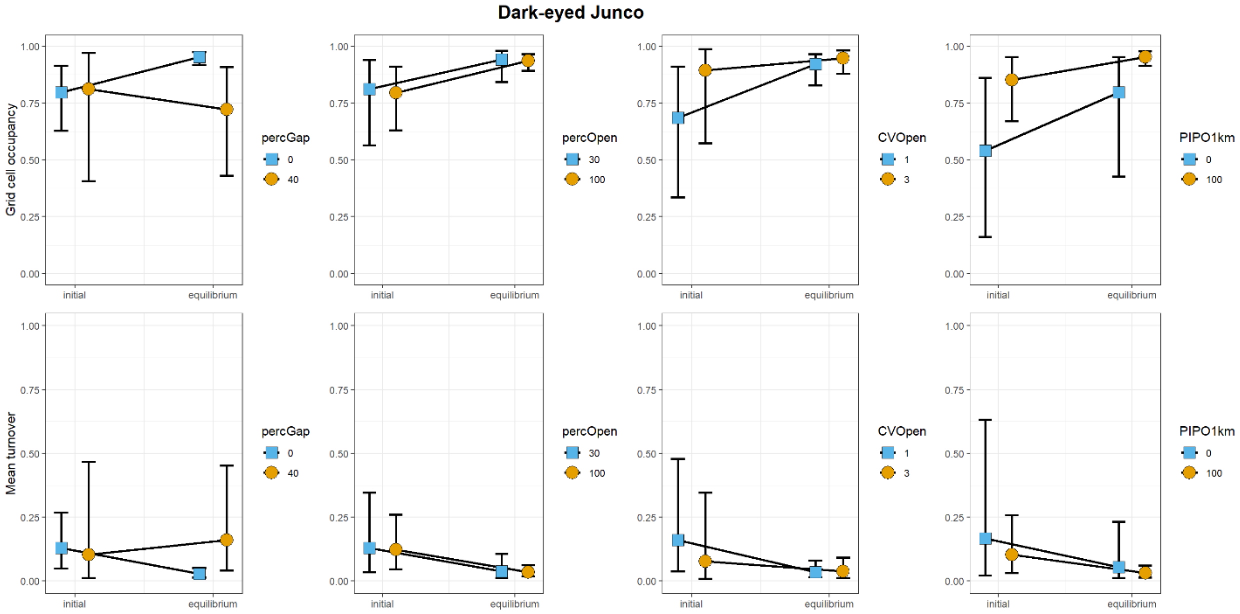

Figure F8. Grid-level occupancy relationships for Dark-eyed Junco.

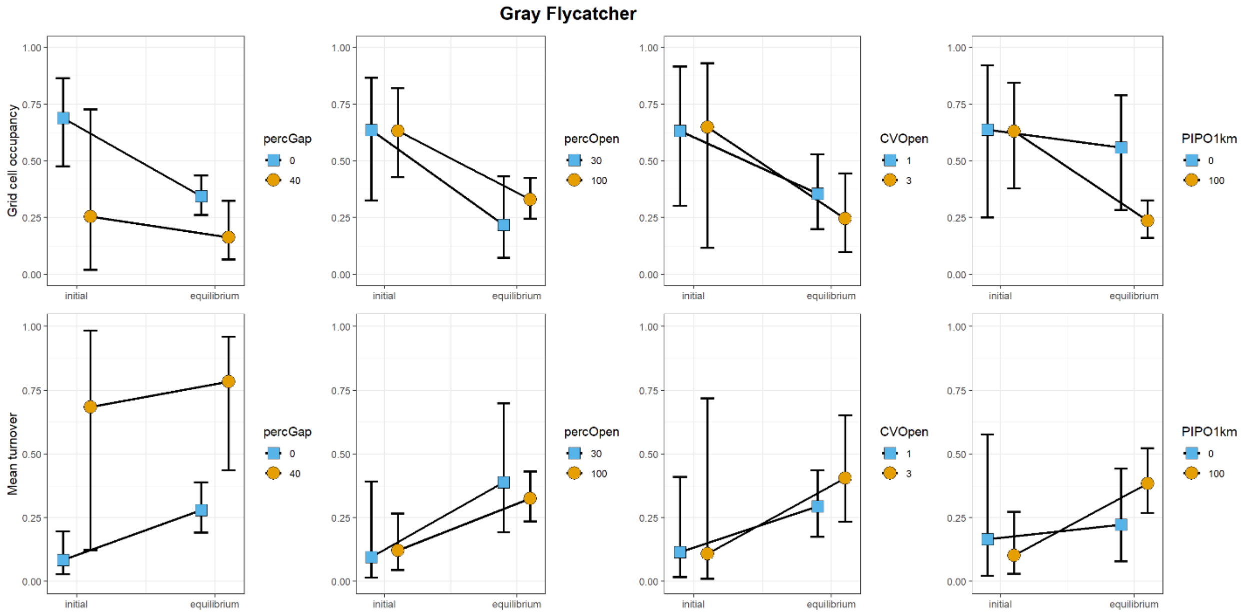

Figure F9. Grid-level occupancy relationships for Gray Flycatcher.

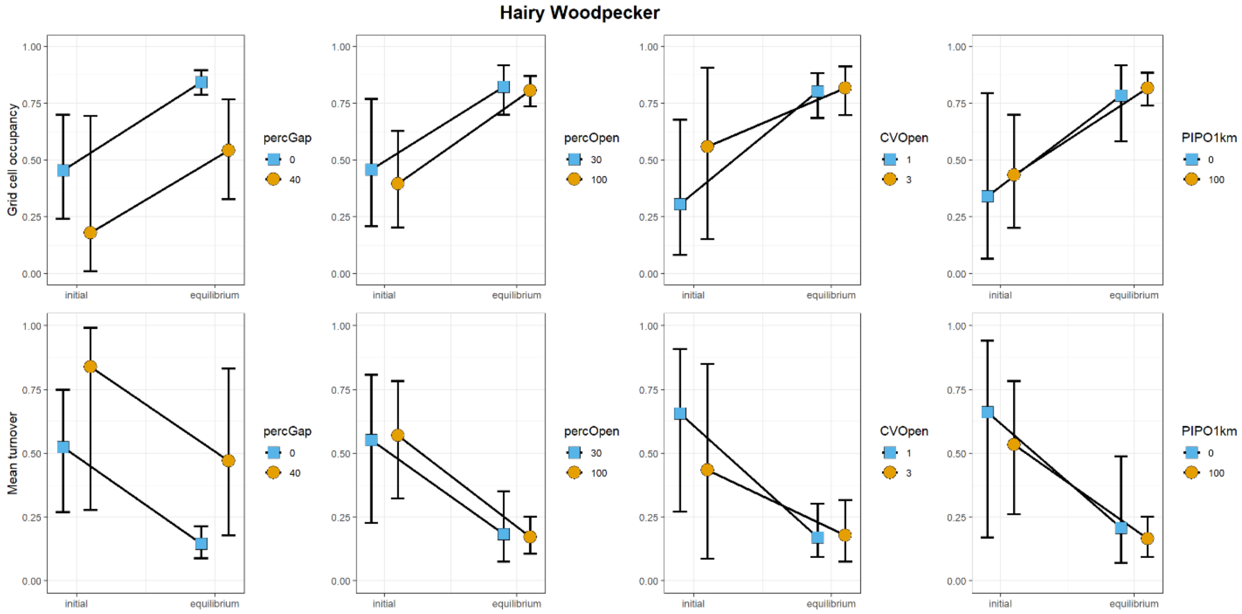

Figure F10. Grid-level occupancy relationships for Hairy Woodpecker.

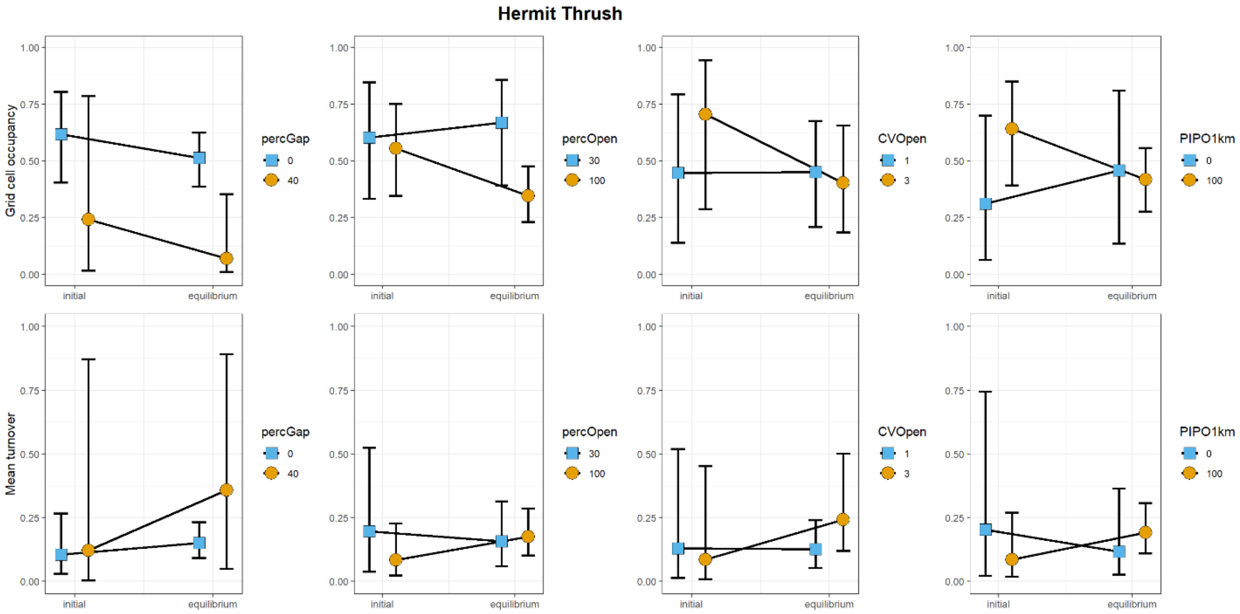

Figure F11. Grid-level occupancy relationships for Hermit Thrush.

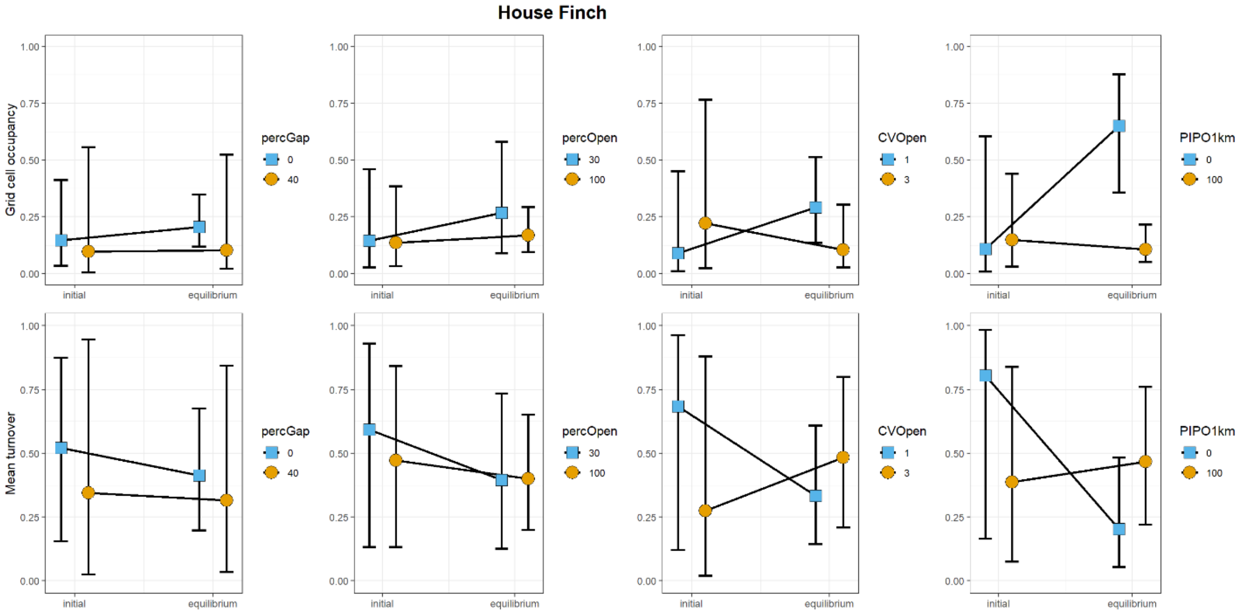

Figure F12. Grid-level occupancy relationships for House Finch.

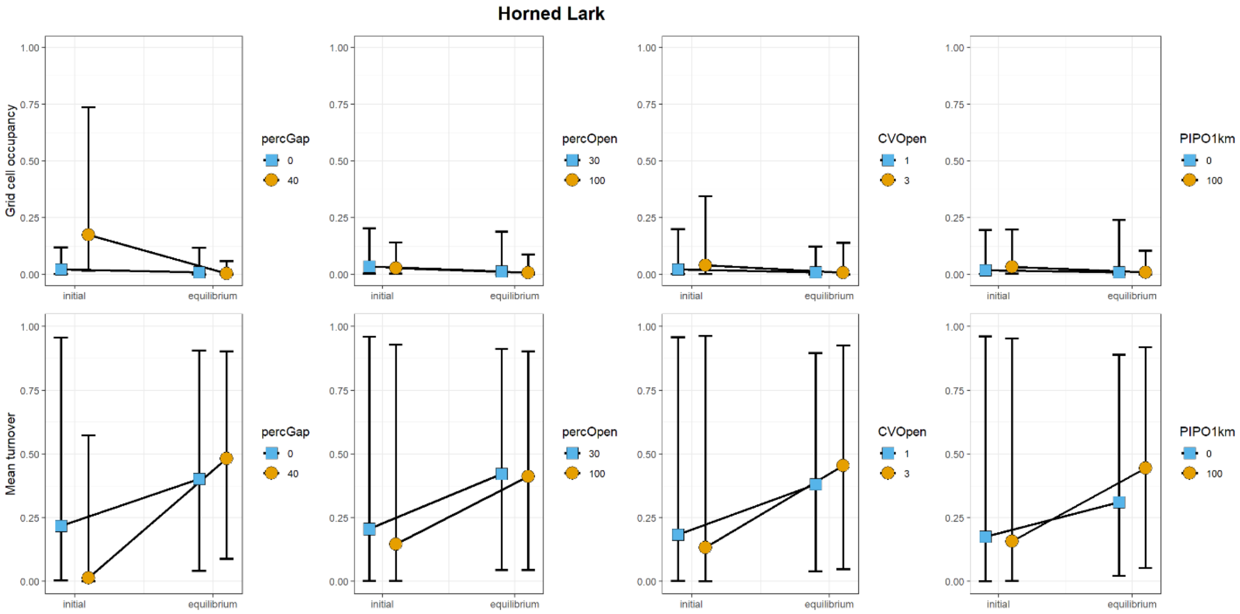

Figure F13. Grid-level occupancy relationships for Horned Lark.

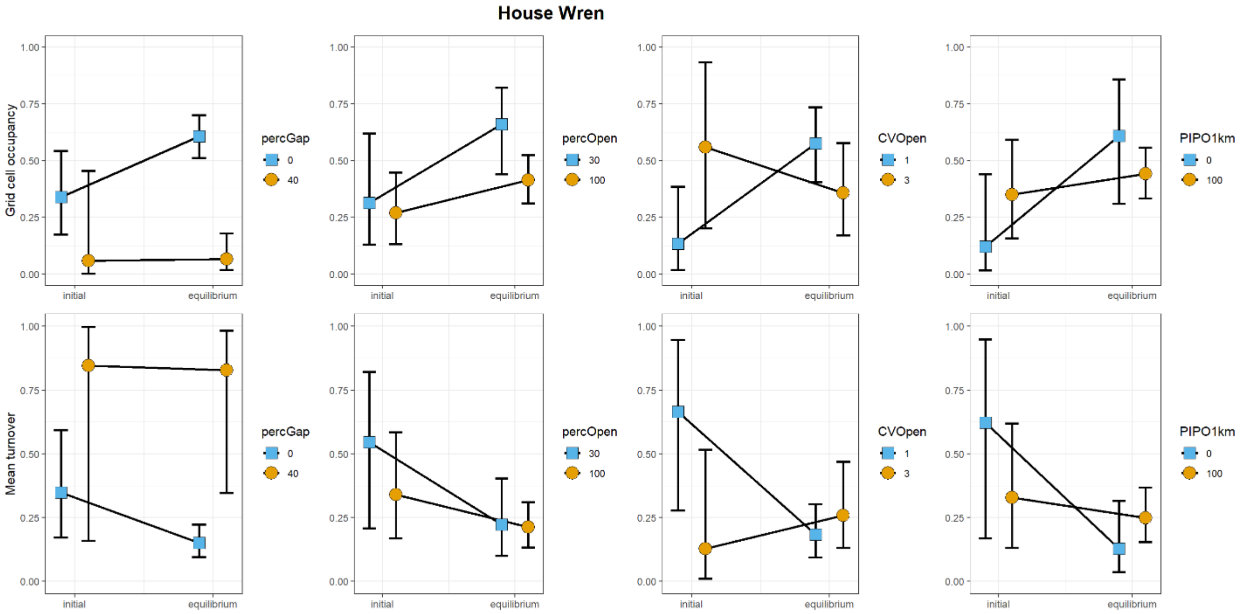

Figure F14. Grid-level occupancy relationships for House Wren.

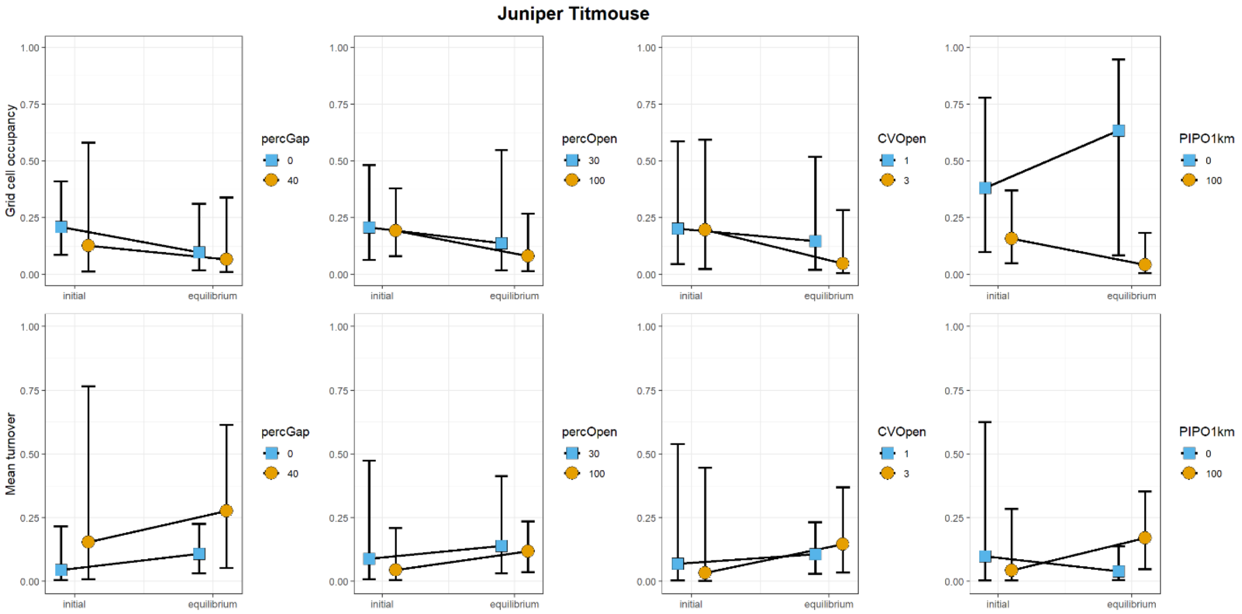

Figure F15. Grid-level occupancy relationships for Juniper Titmouse.

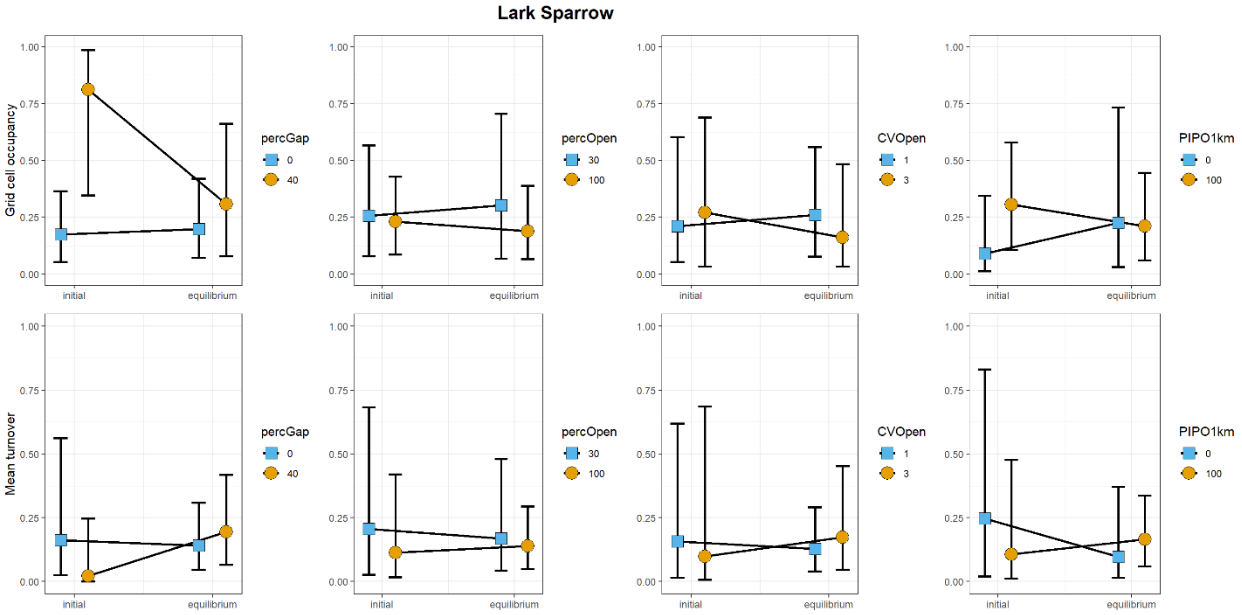

Figure F16. Grid-level occupancy relationships for Lark Sparrow.

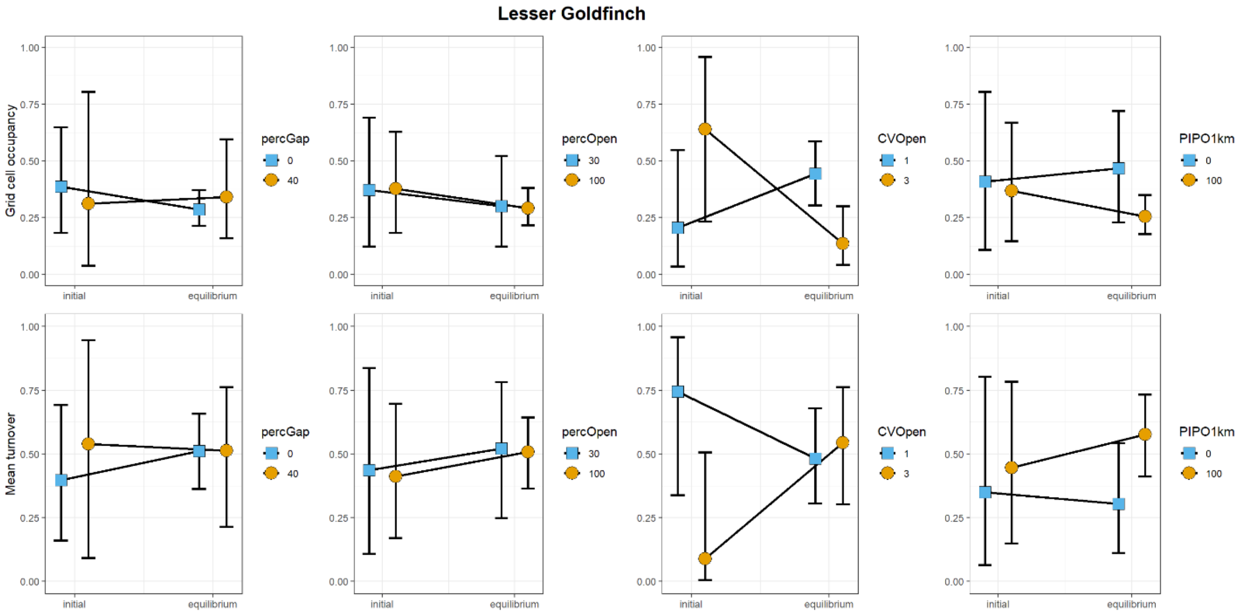

Figure F17. Grid-level occupancy relationships for Lesser Goldfinch.

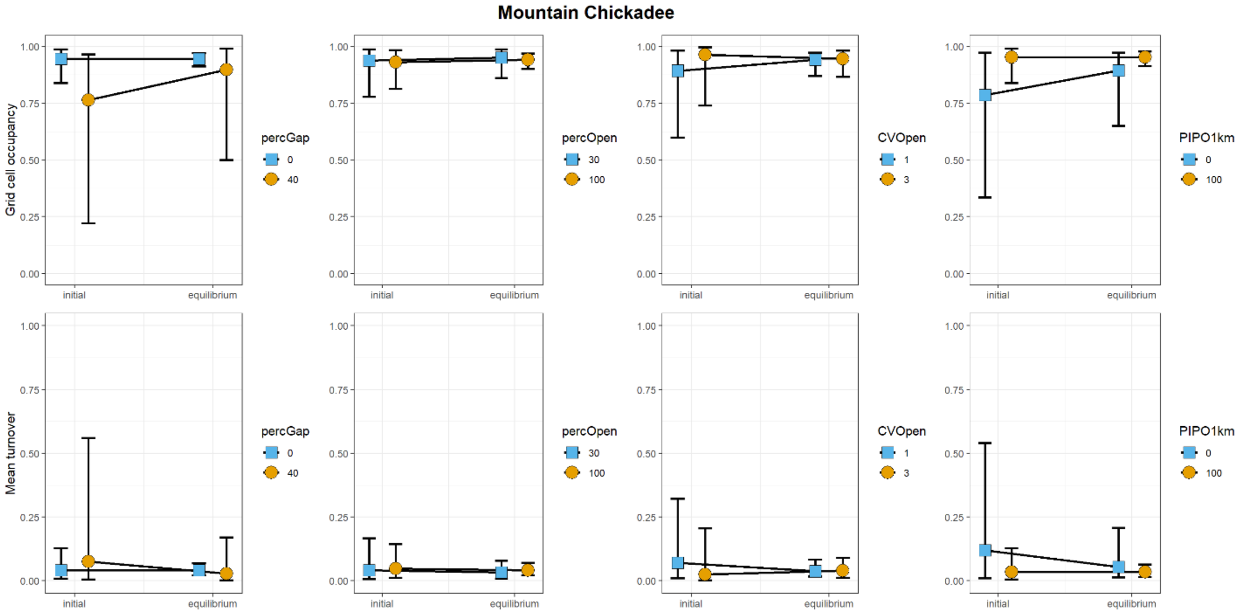

Figure F18. Grid-level occupancy relationships for Mountain Chickadee.

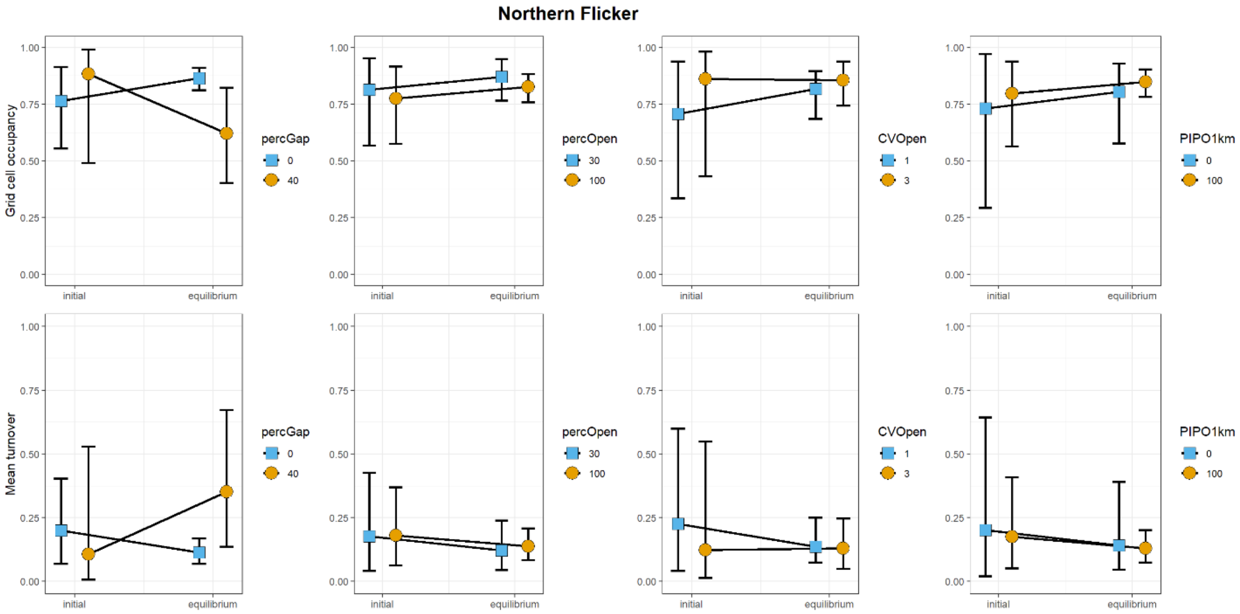

Figure F19. Grid-level occupancy relationships for Northern Flicker.

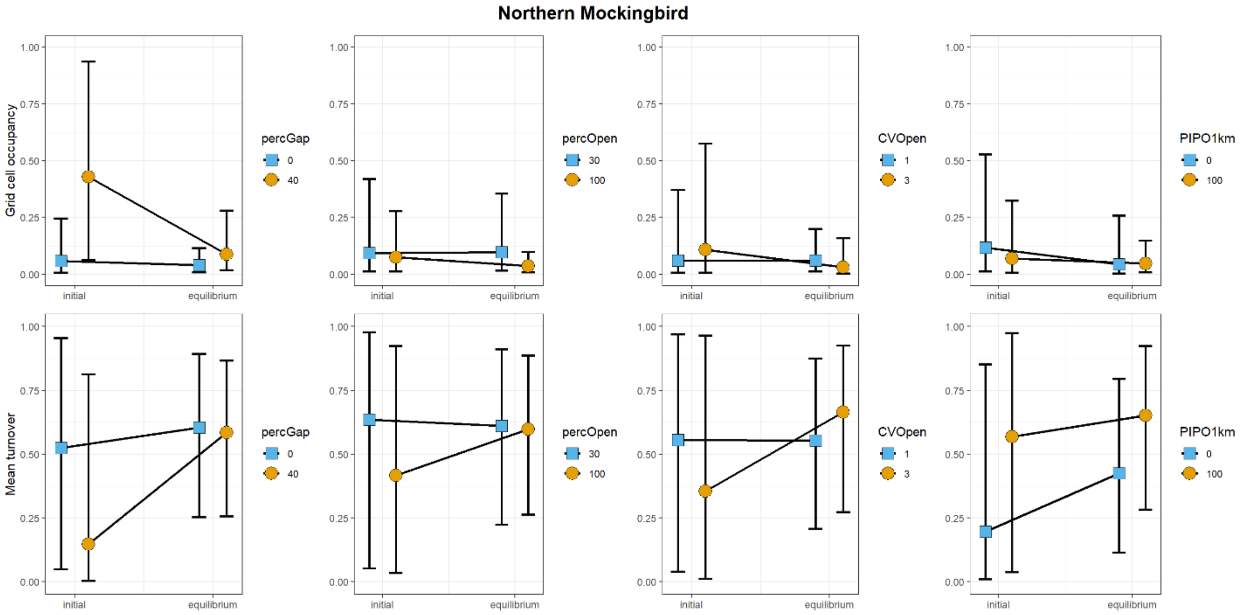

Figure F20. Grid-level occupancy relationships for Northern Mockingbird.

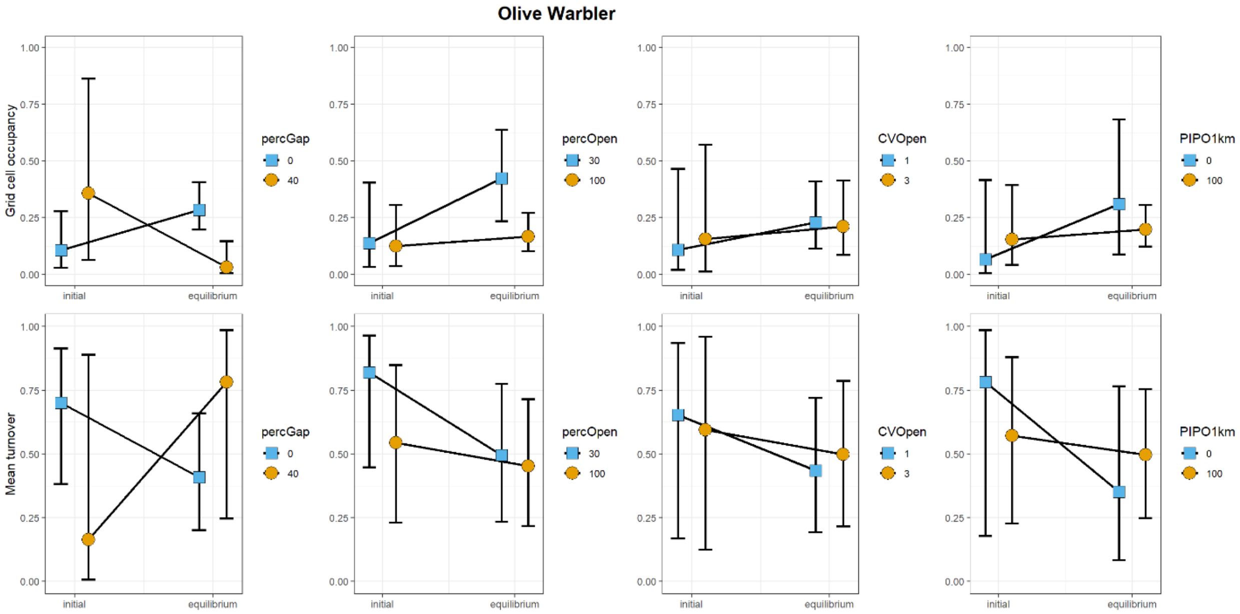

Figure F21. Grid-level occupancy relationships for Olive Warbler.

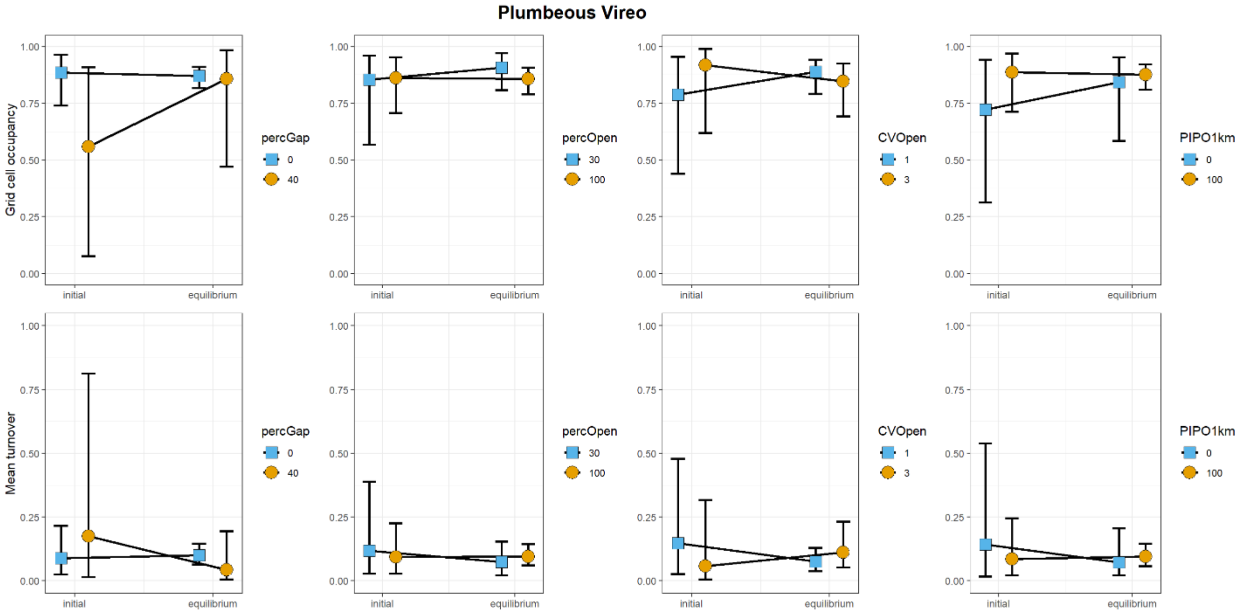

Figure F22. Grid-level occupancy relationships for Plumbeous Vireo.

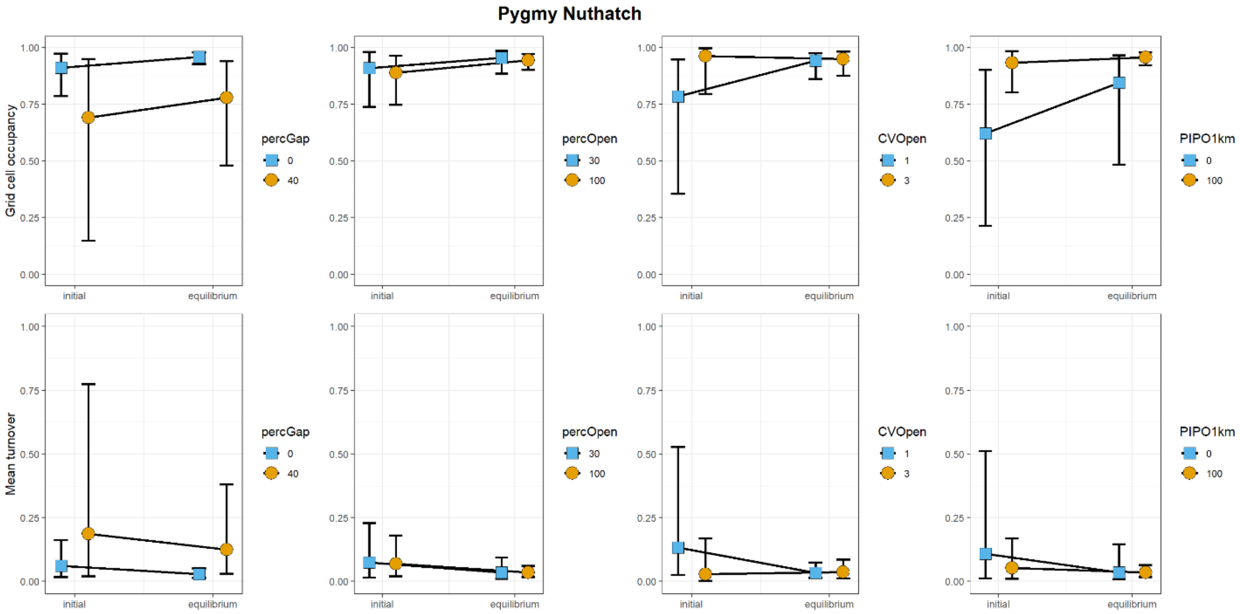

Figure F23. Grid-level occupancy relationships for Pygmy Nuthatch.

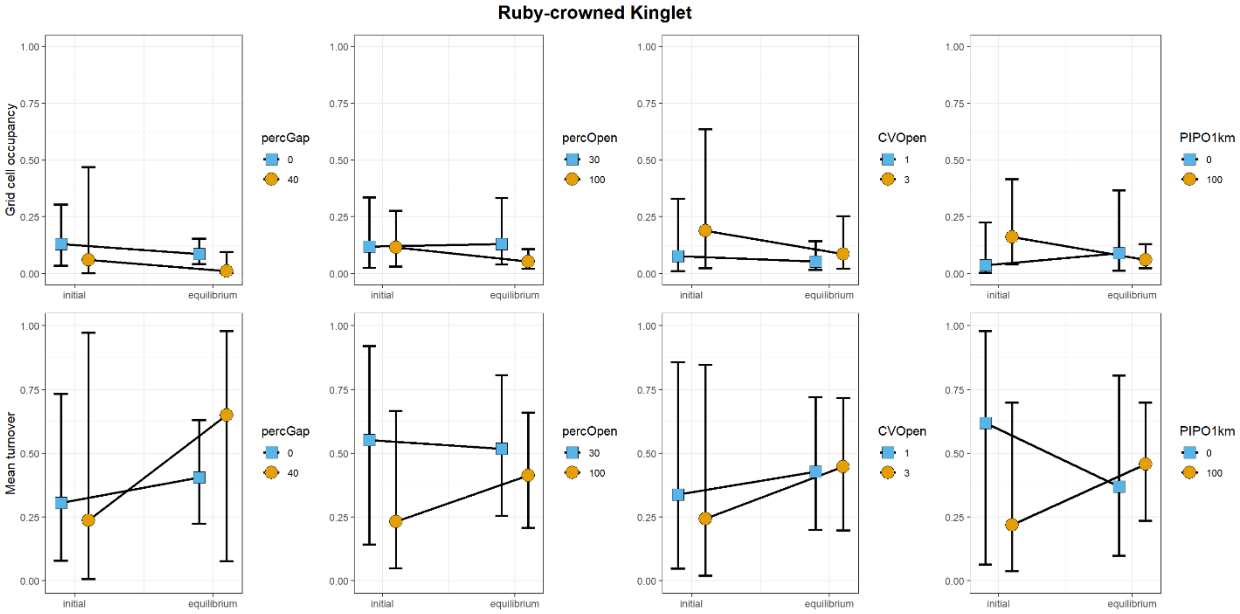

Figure F24. Grid-level occupancy relationships for Ruby-crowned Kinglet.

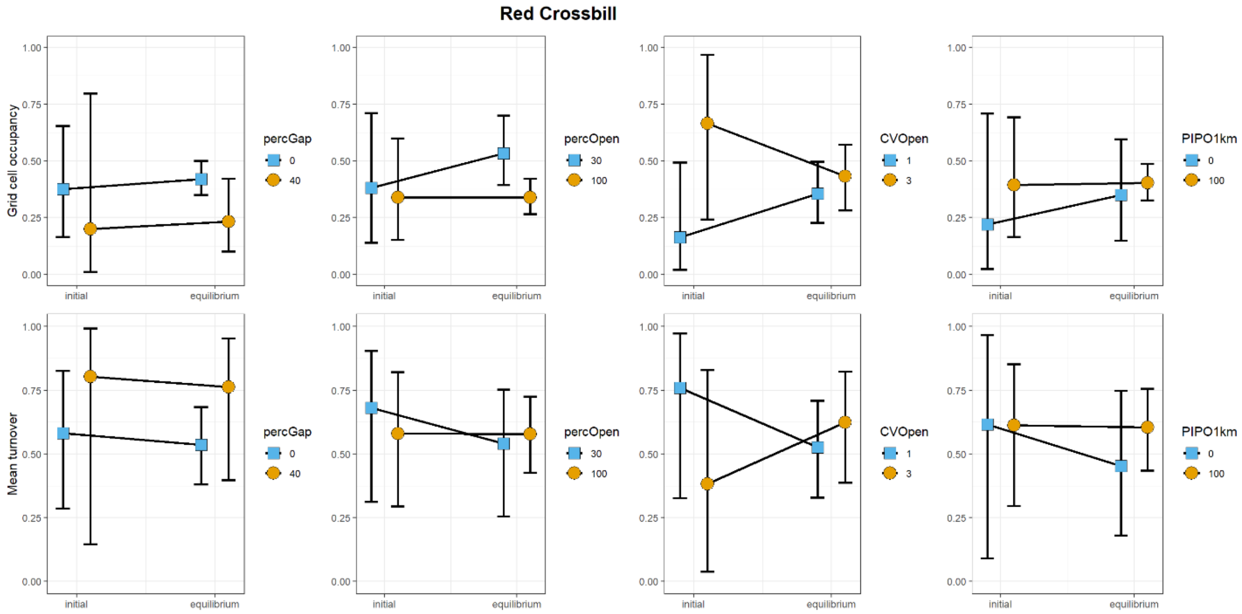

Figure F25. Grid-level occupancy relationships for Red Crossbill.

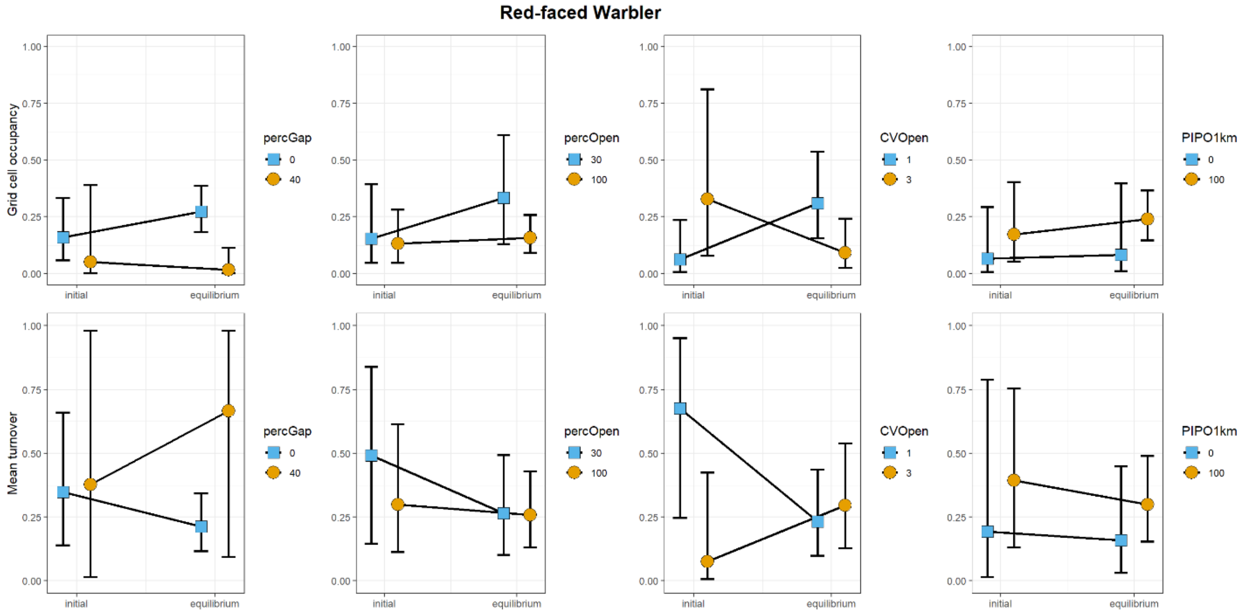

Figure F26. Grid-level occupancy relationships for Red-faced Warbler.

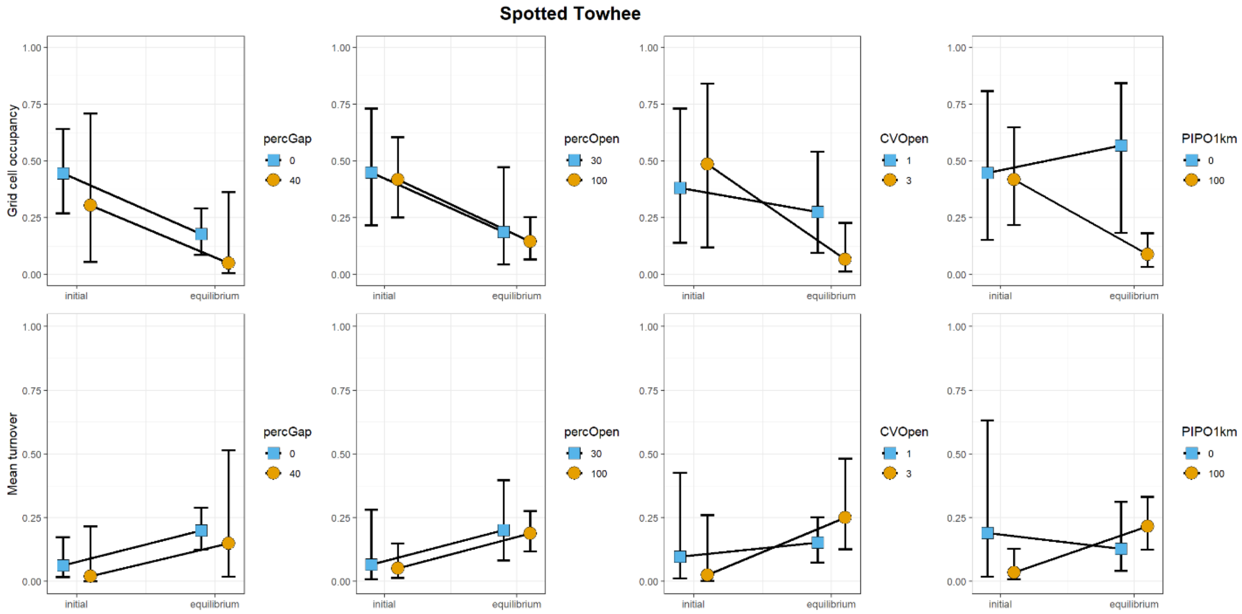

Figure F27. Grid-level occupancy relationships for Spotted Towhee.

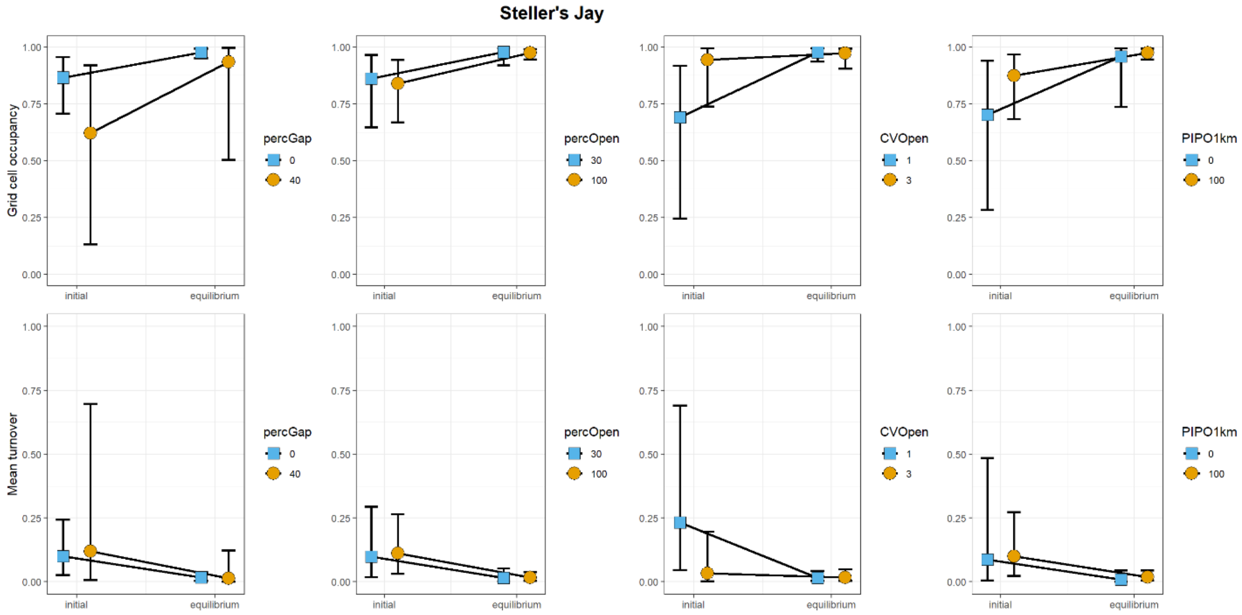

Figure F28. Grid-level occupancy relationships for Steller’s Jay.

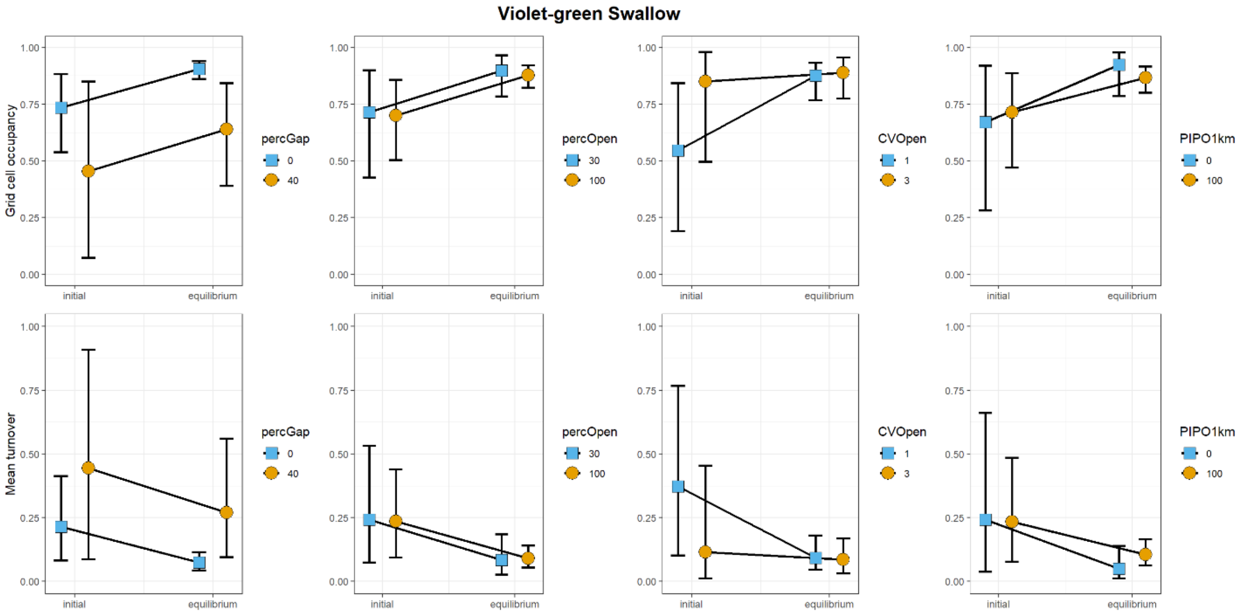

Figure F29. Grid-level occupancy relationships for Violet-green Swallow.

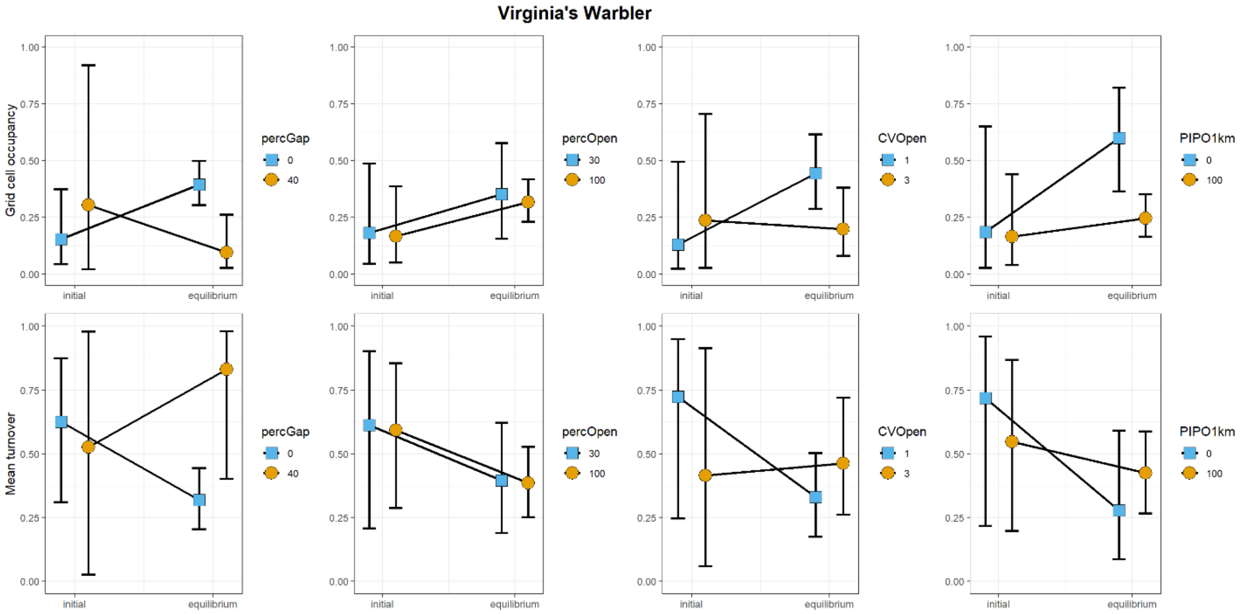

Figure F30. Grid-level occupancy relationships for Virginia’s Warbler.

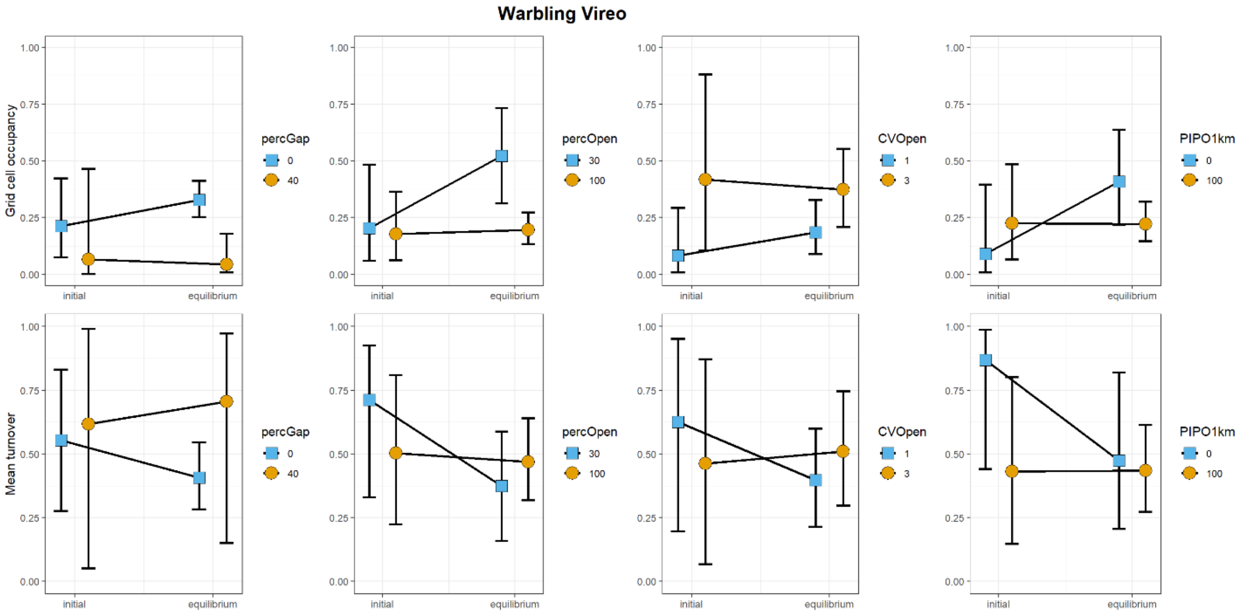

Figure F31. Grid-level occupancy relationships for Warbling Vireo.

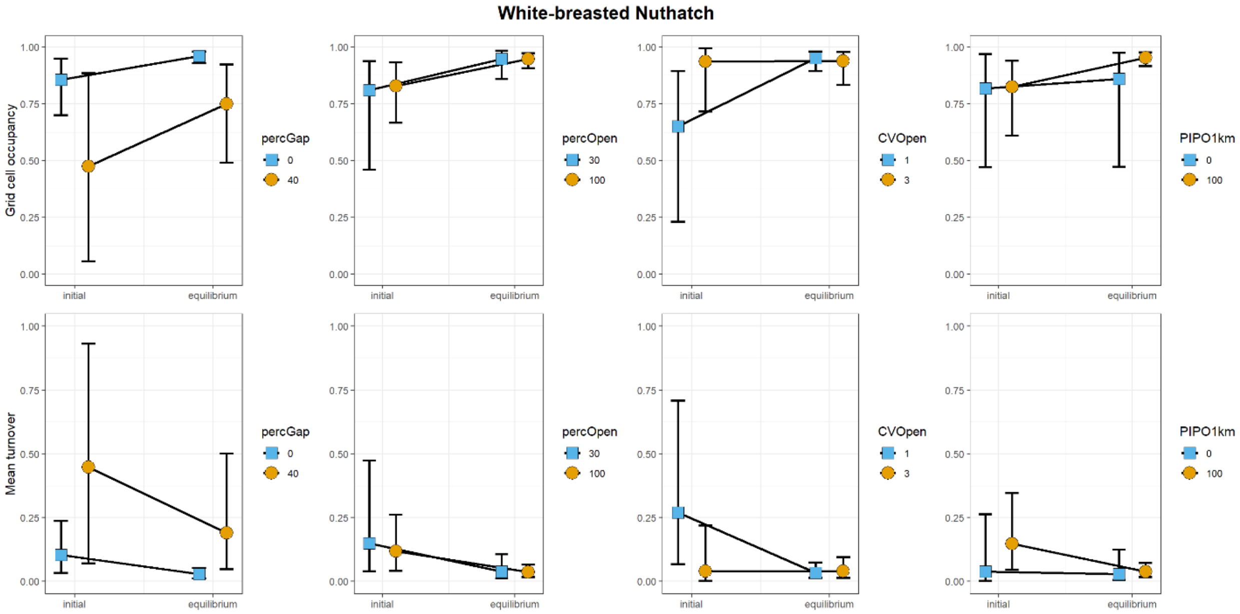

Figure F32. Grid-level occupancy relationships for White-breasted Nuthatch.

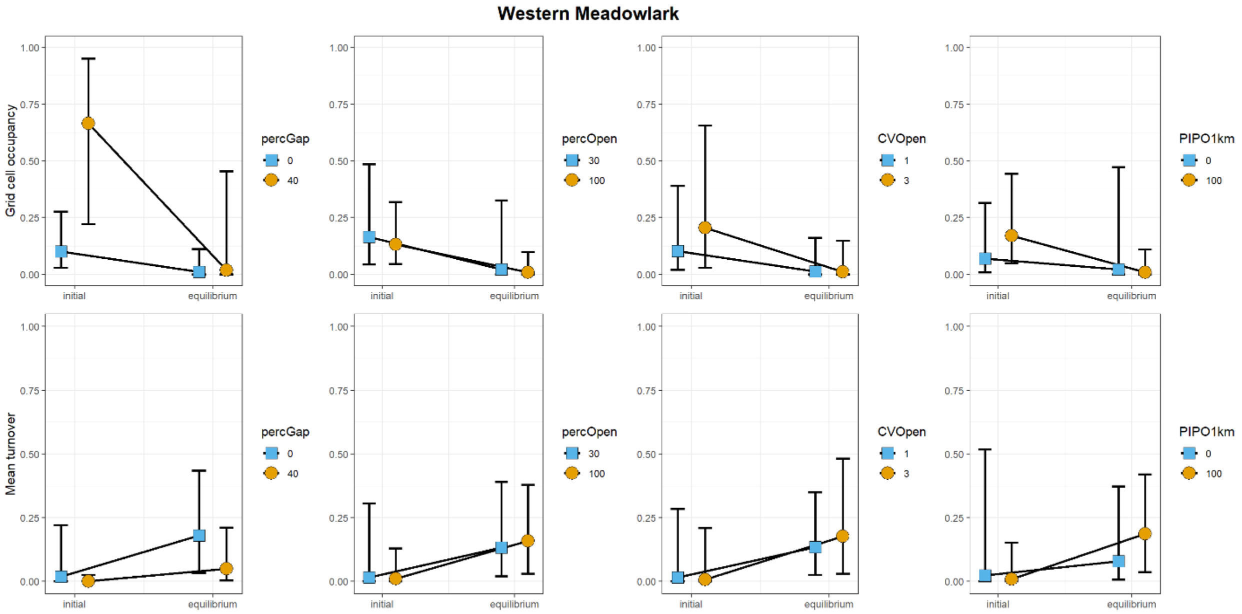

Figure F33. Grid-level occupancy relationships for Western Meadowlark.

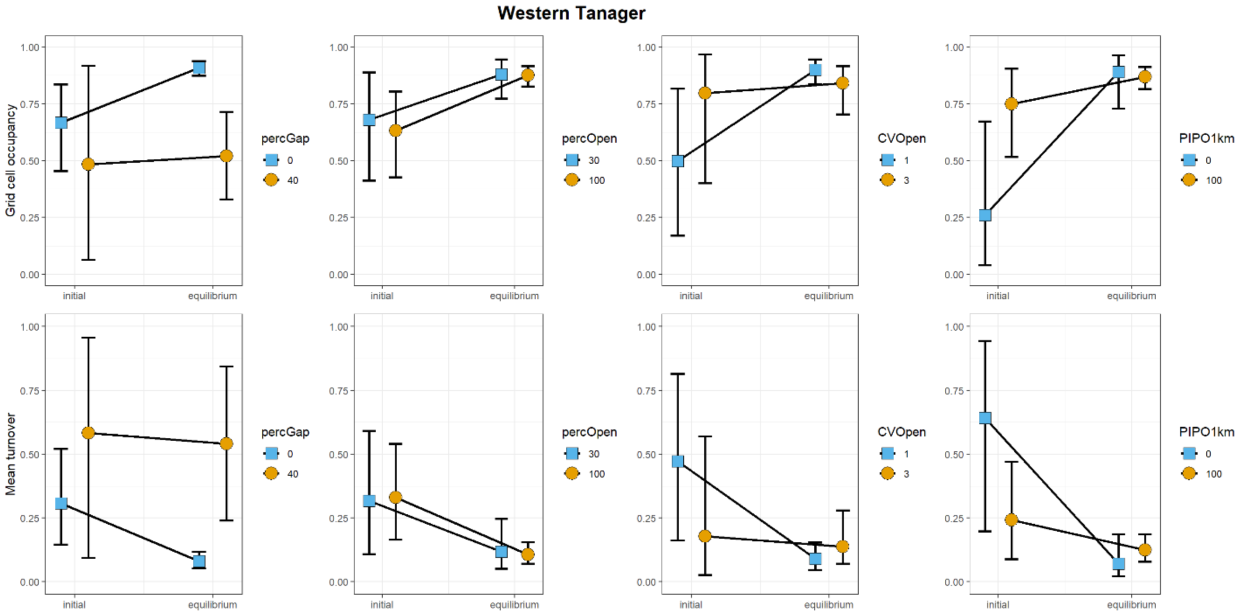

Figure F34. Grid-level occupancy relationships for Western Tanager.

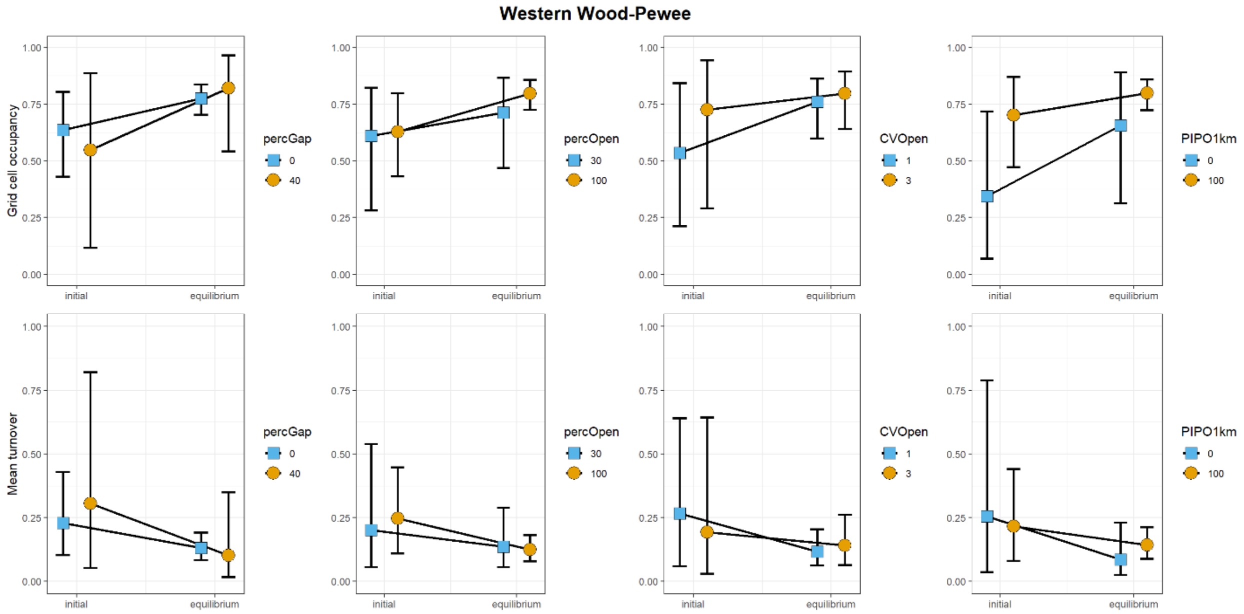

Figure F35. Grid-level occupancy relationships for Western Wood-Pewee.

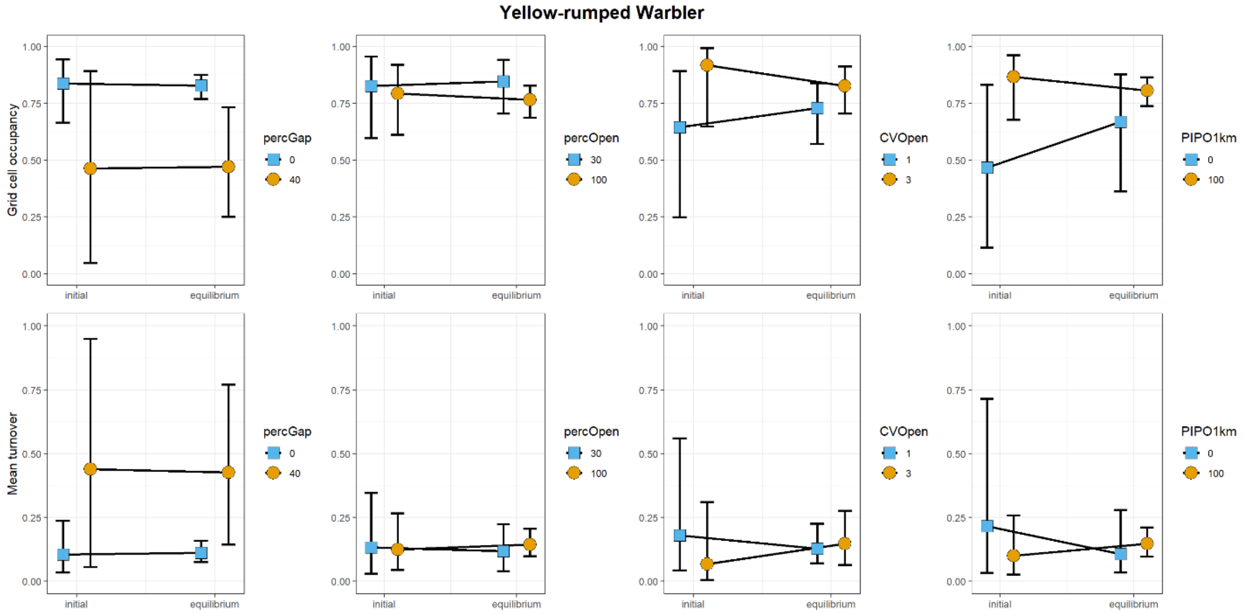

Figure F36. Grid-level occupancy relationships for Yellow-rumped Warbler.

Appendix G.

Abundance relationships for 20 focal species.

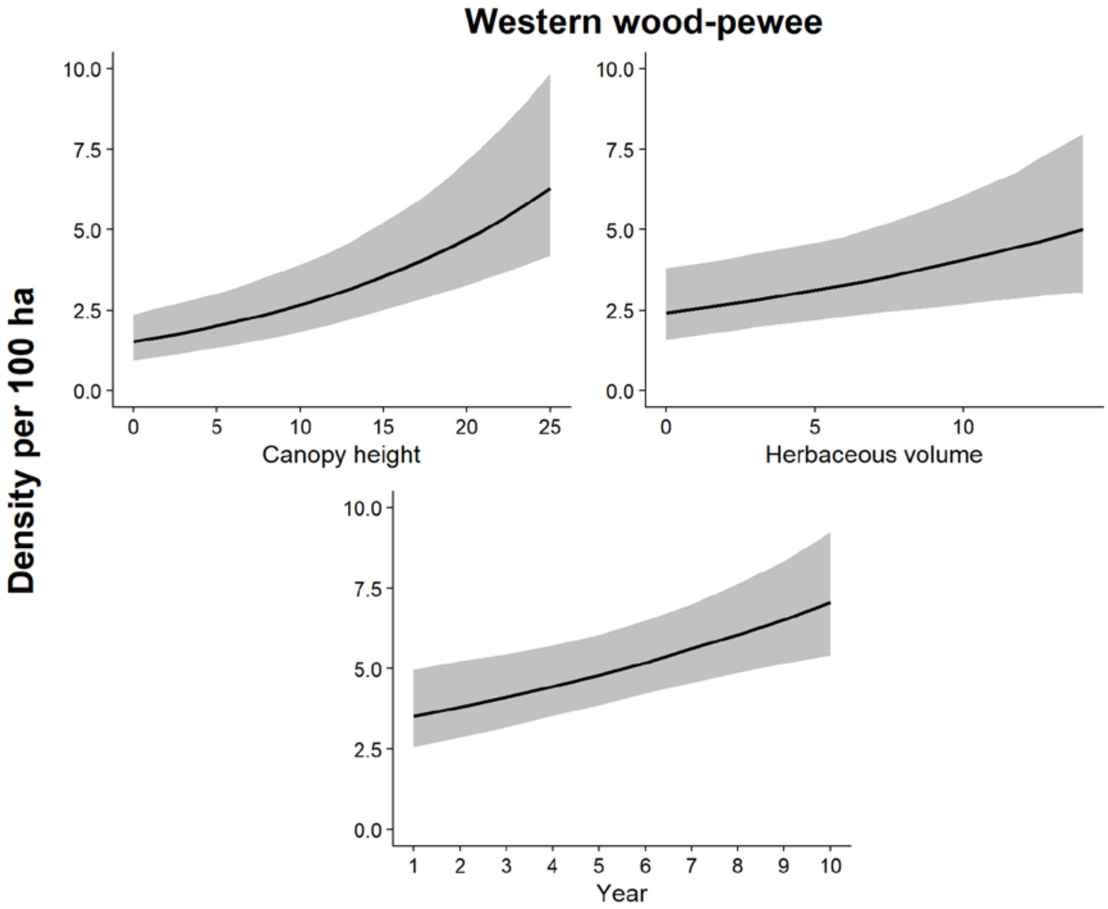

Figure G1. Abundance relationships for Western Wood-Pewee

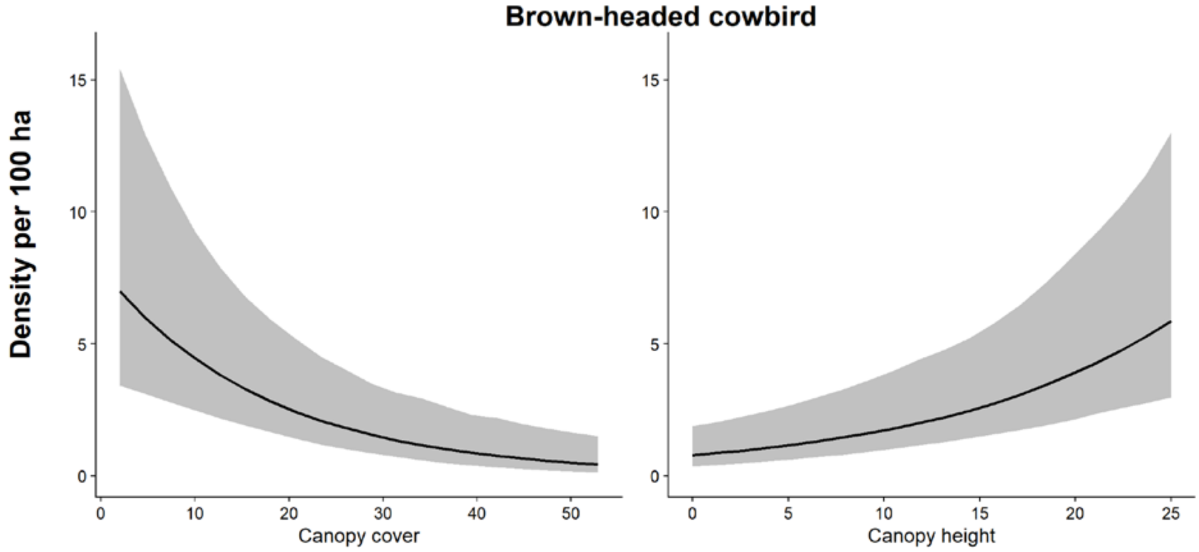

Figure G2. Abundance relationships for Brown-headed Cowbird

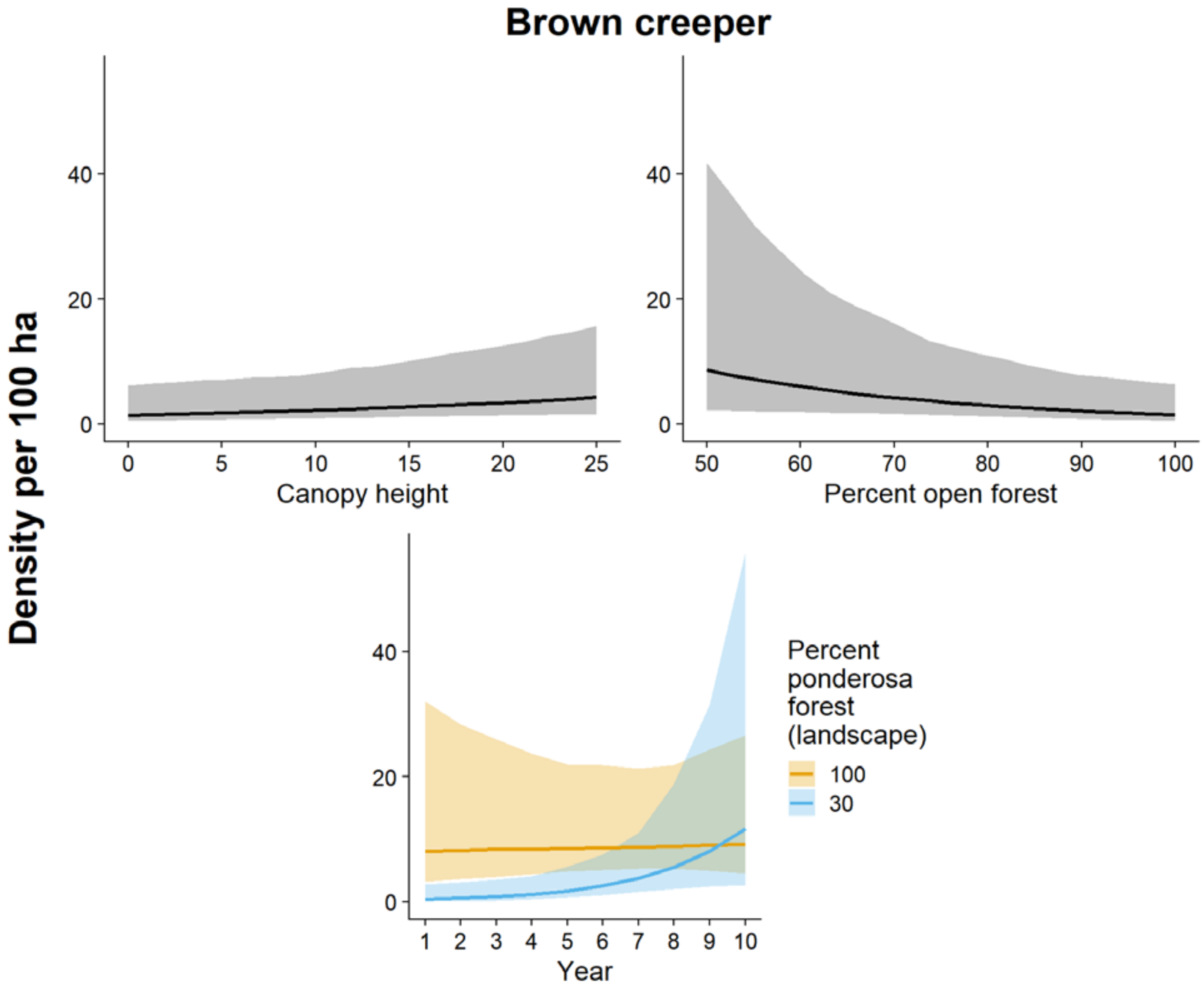

Figure G3. Abundance relationships for Brown Creeper

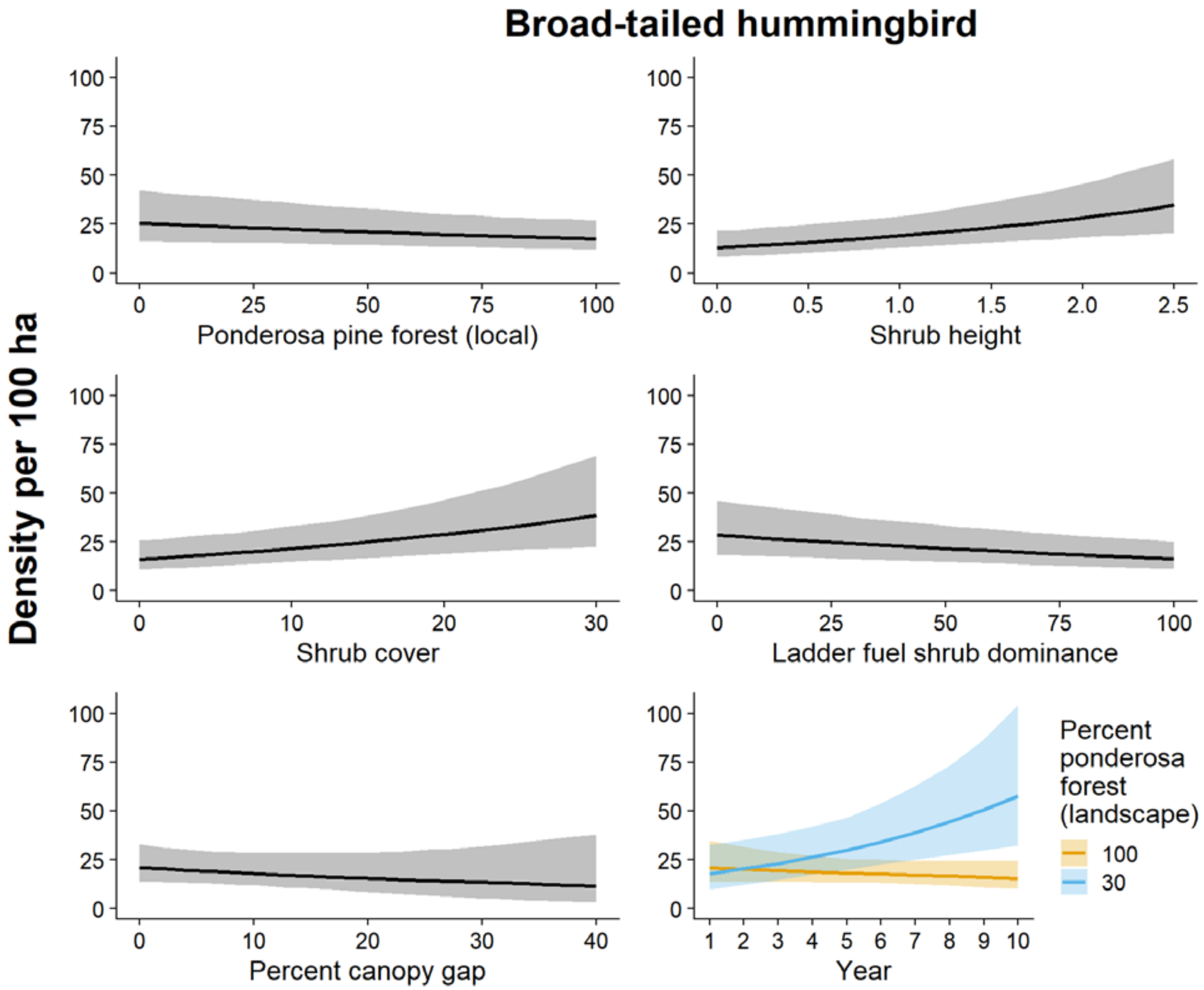

Figure G4. Abundance relationships for Broad-tailed Hummingbird

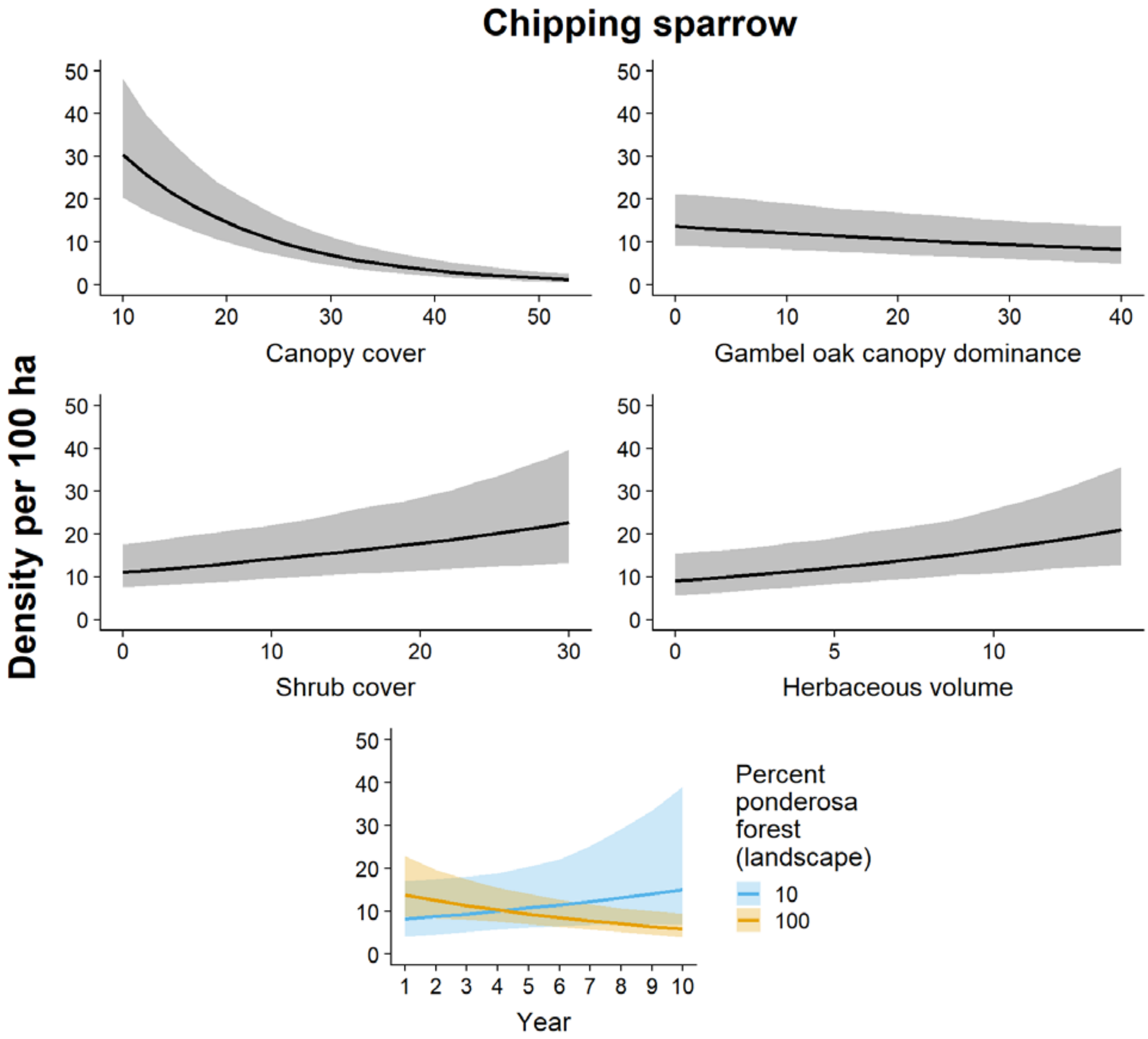

Figure G5. Abundance relationships for Chipping Sparrow.

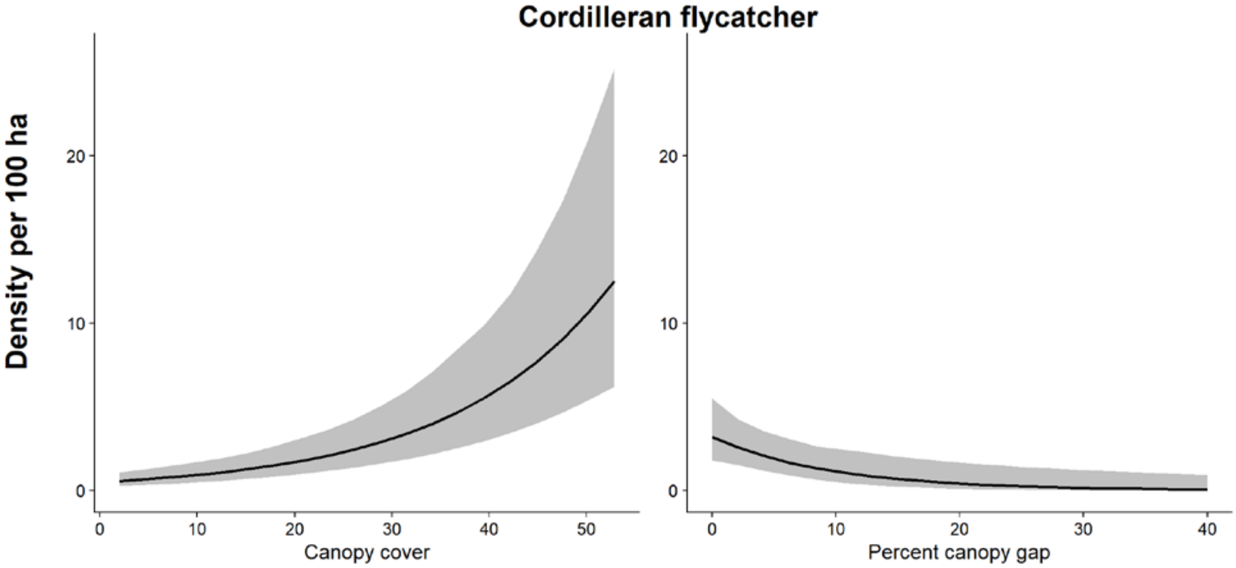

Figure G6. Abundance relationships for Cordilleran Flycatcher

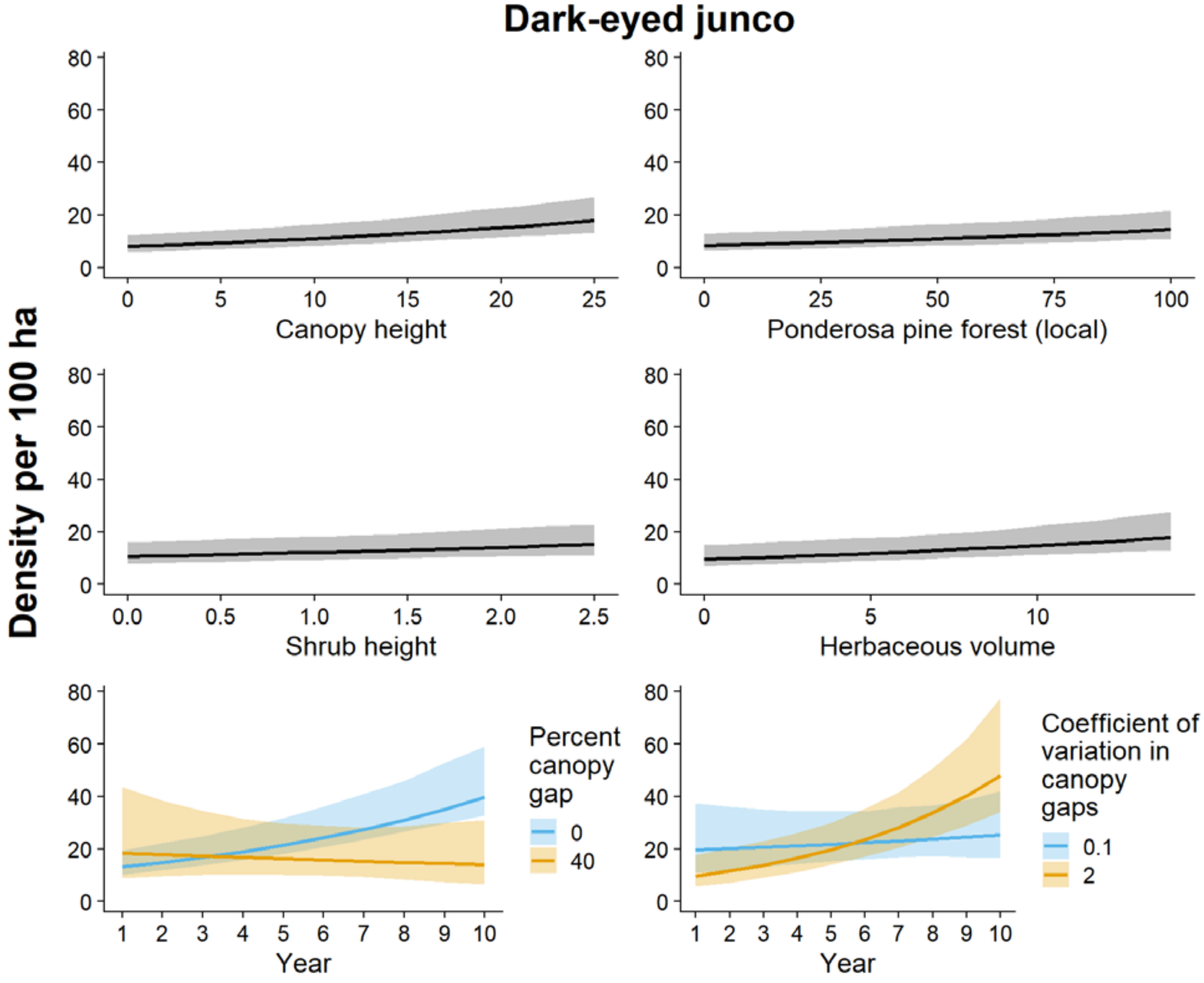

Figure G7. Abundance relationships for Dark-eyed Junco

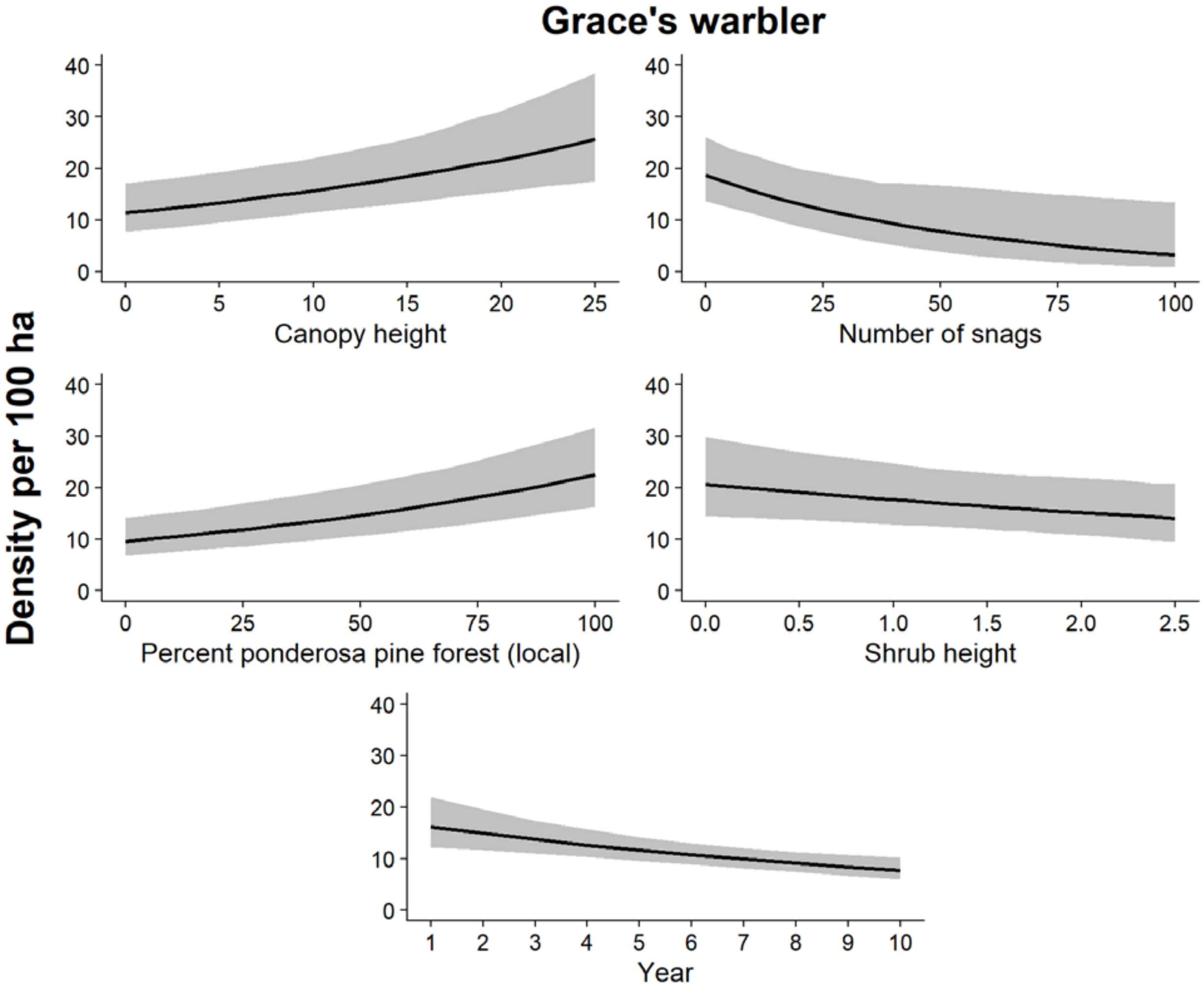

Figure G8. Abundance relationships for Grace’s Warbler.

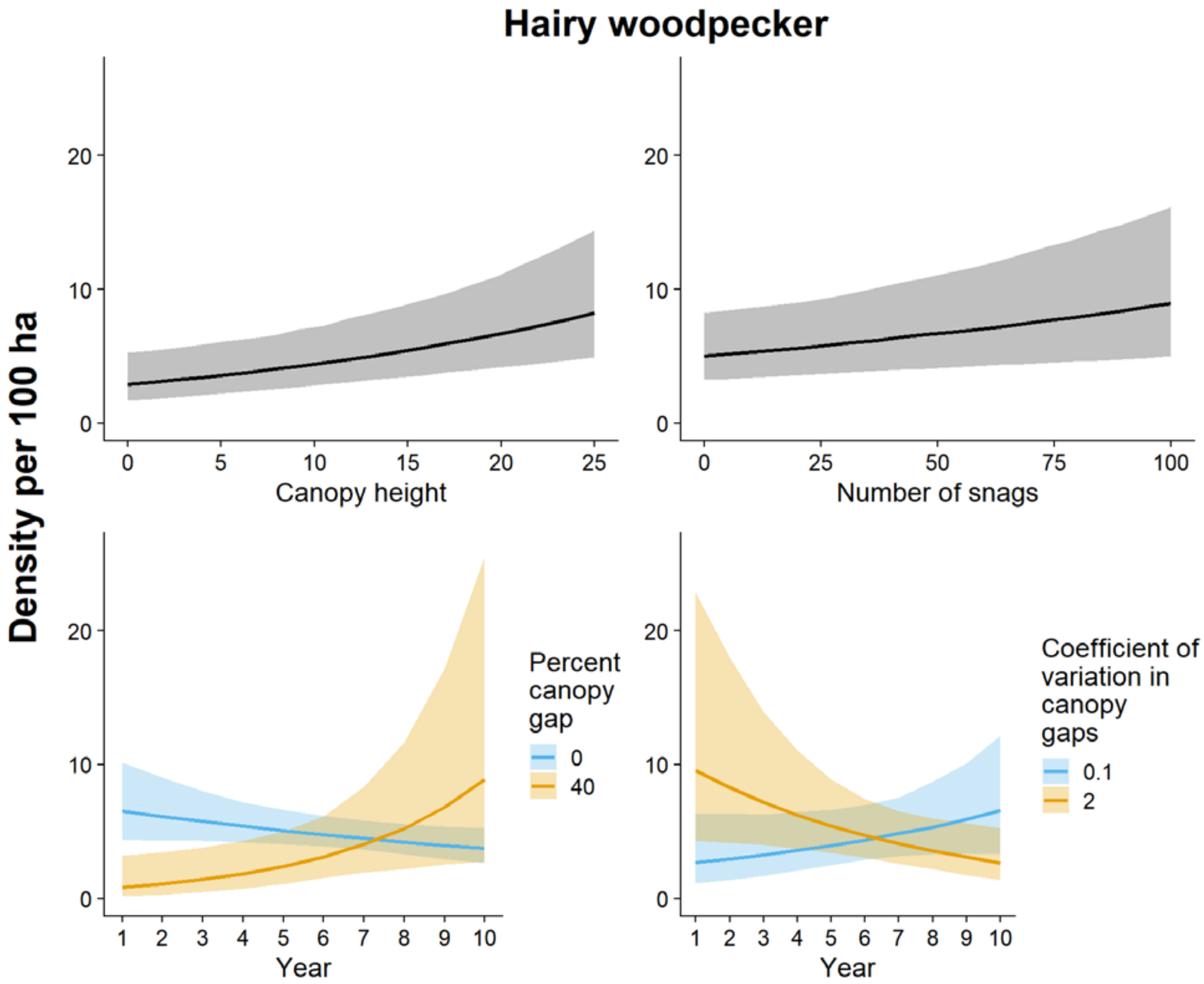

Figure G9. Abundance relationships for Hairy Woodpecker.

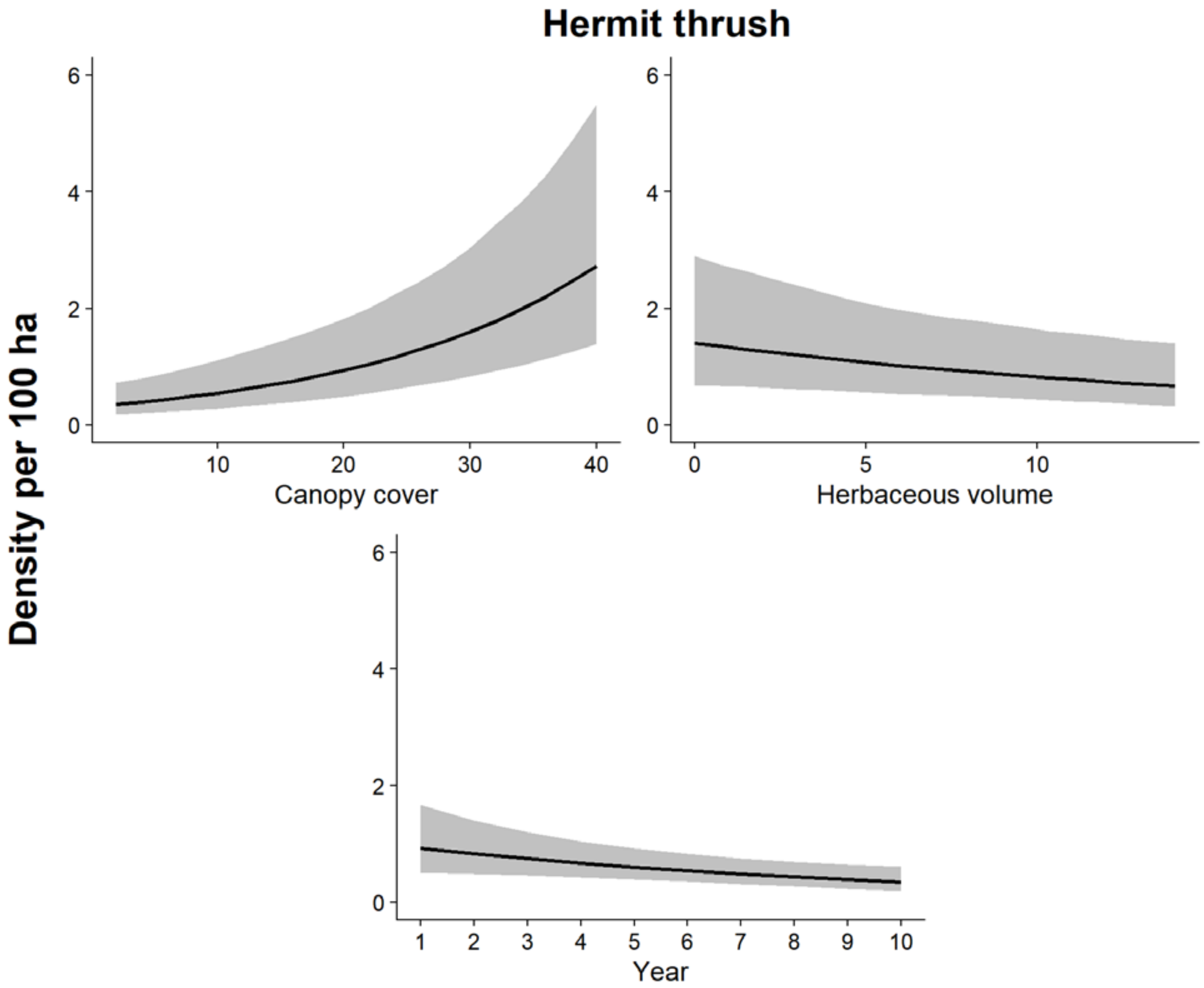

Figure G10. Abundance relationships for Hermit Thrush.

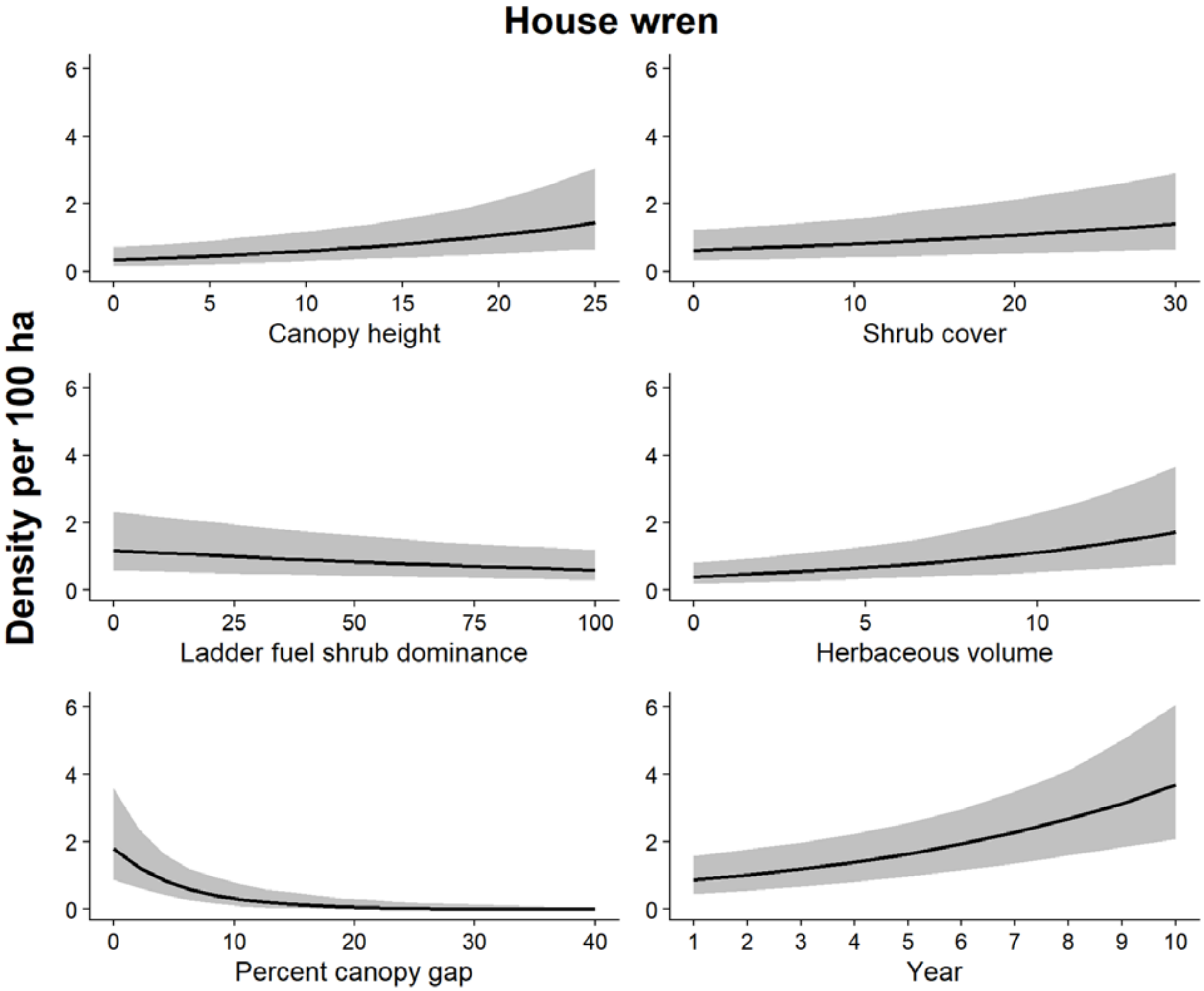

Figure G11. Abundance relationships for House Wren.

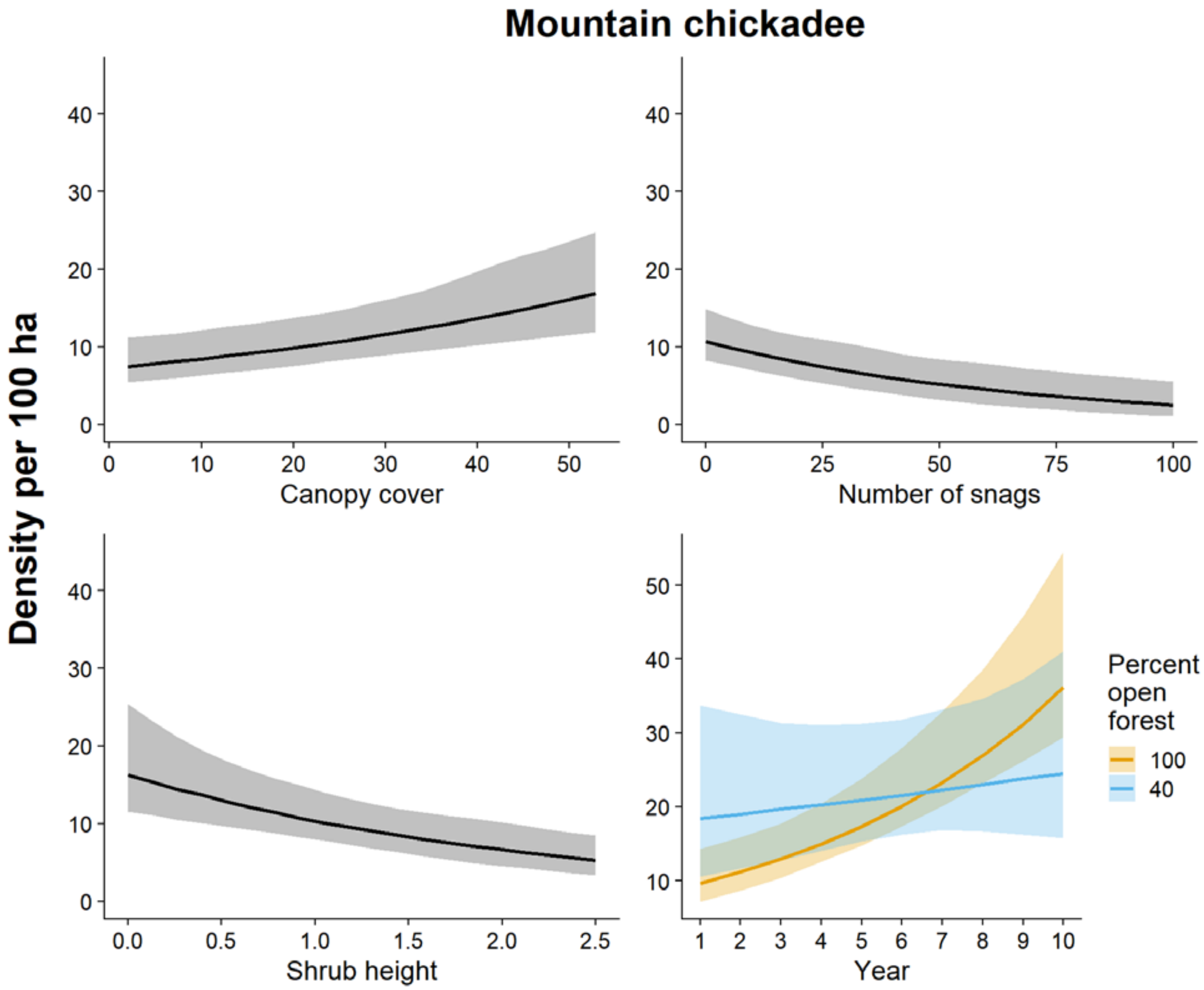

Figure G12. Abundance relationships for Mountain Chickadee.

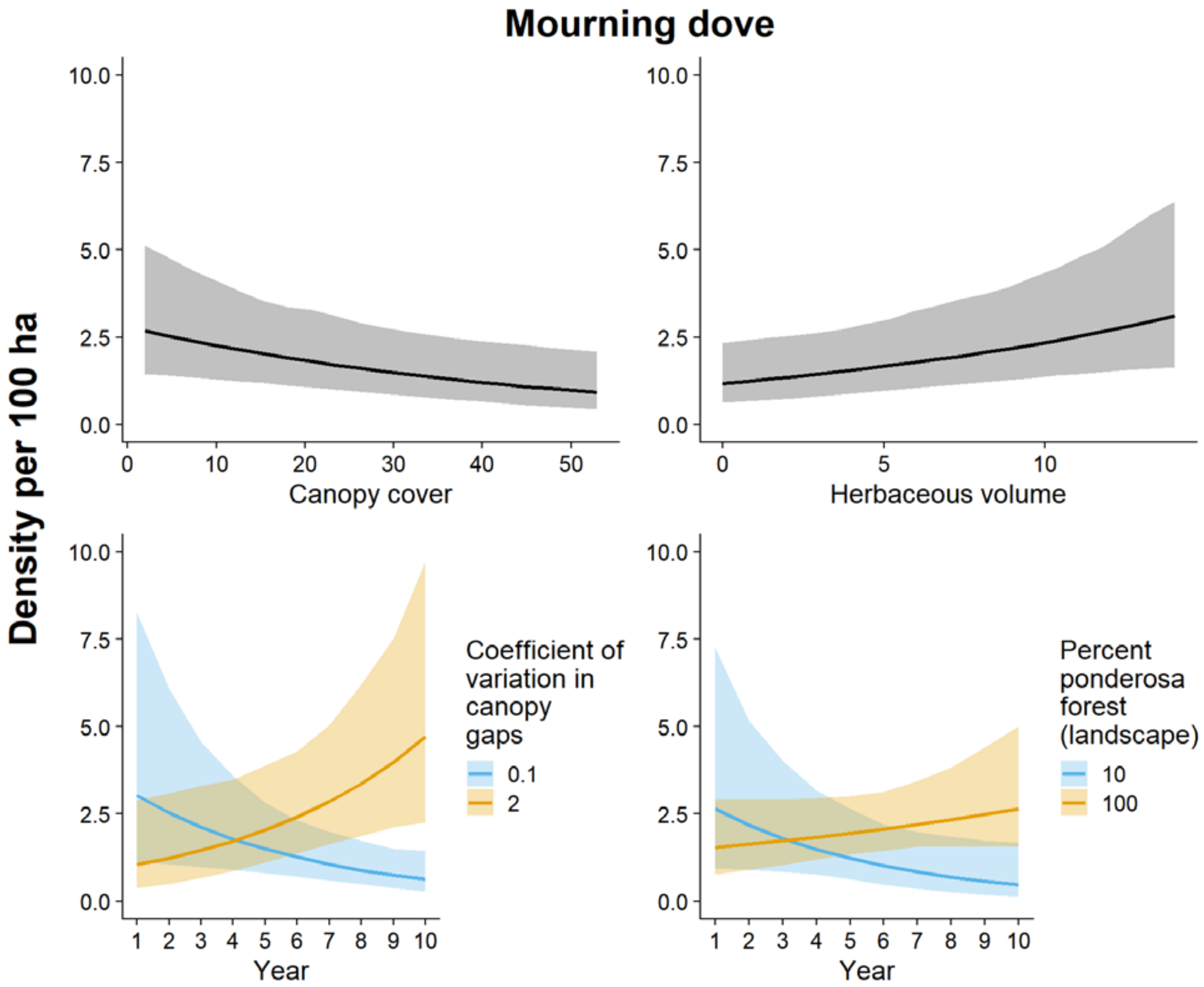

Figure G14. Abundance relationships for Mourning Dove.

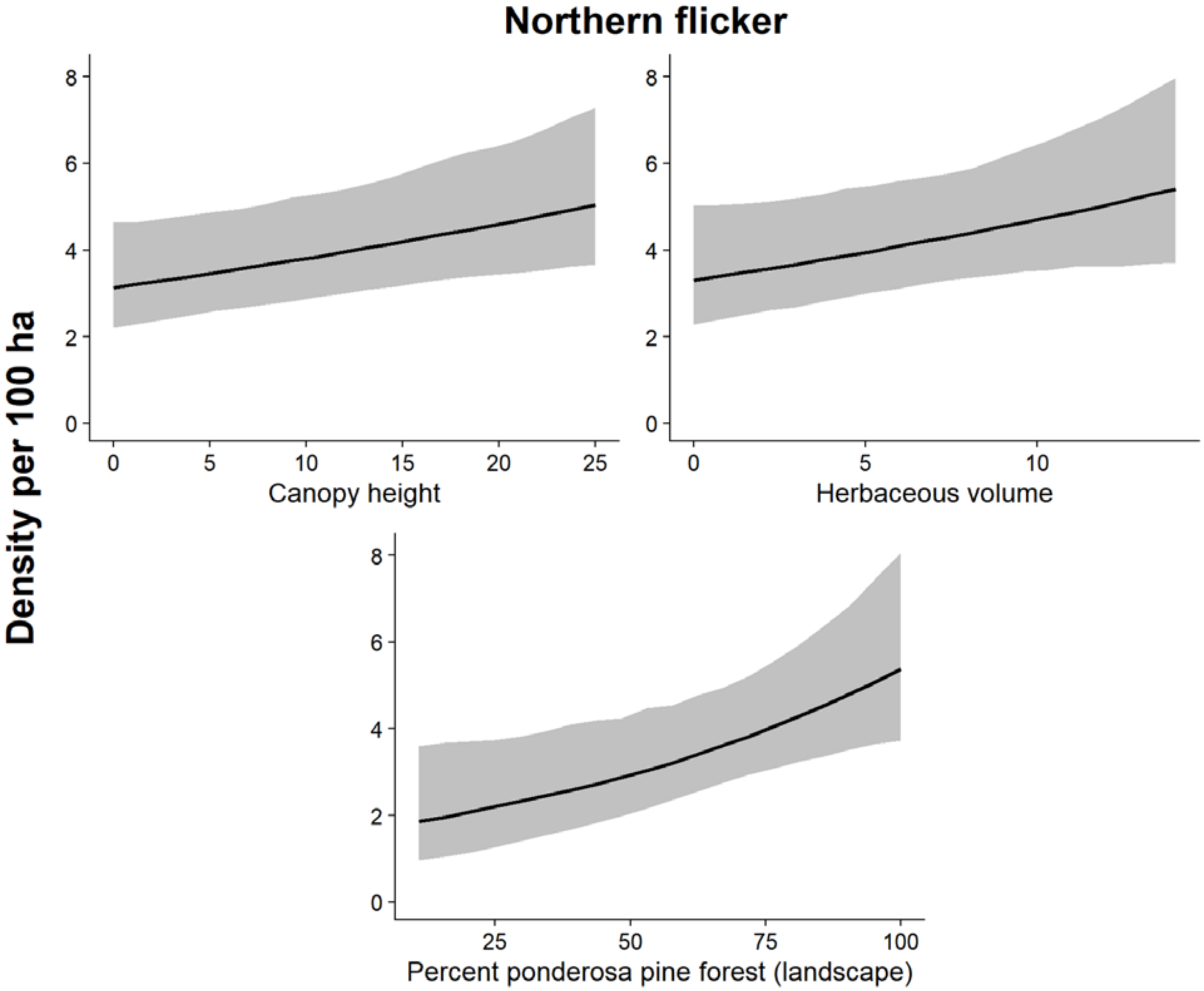

Figure G14. Abundance relationships for Northern Flicker.

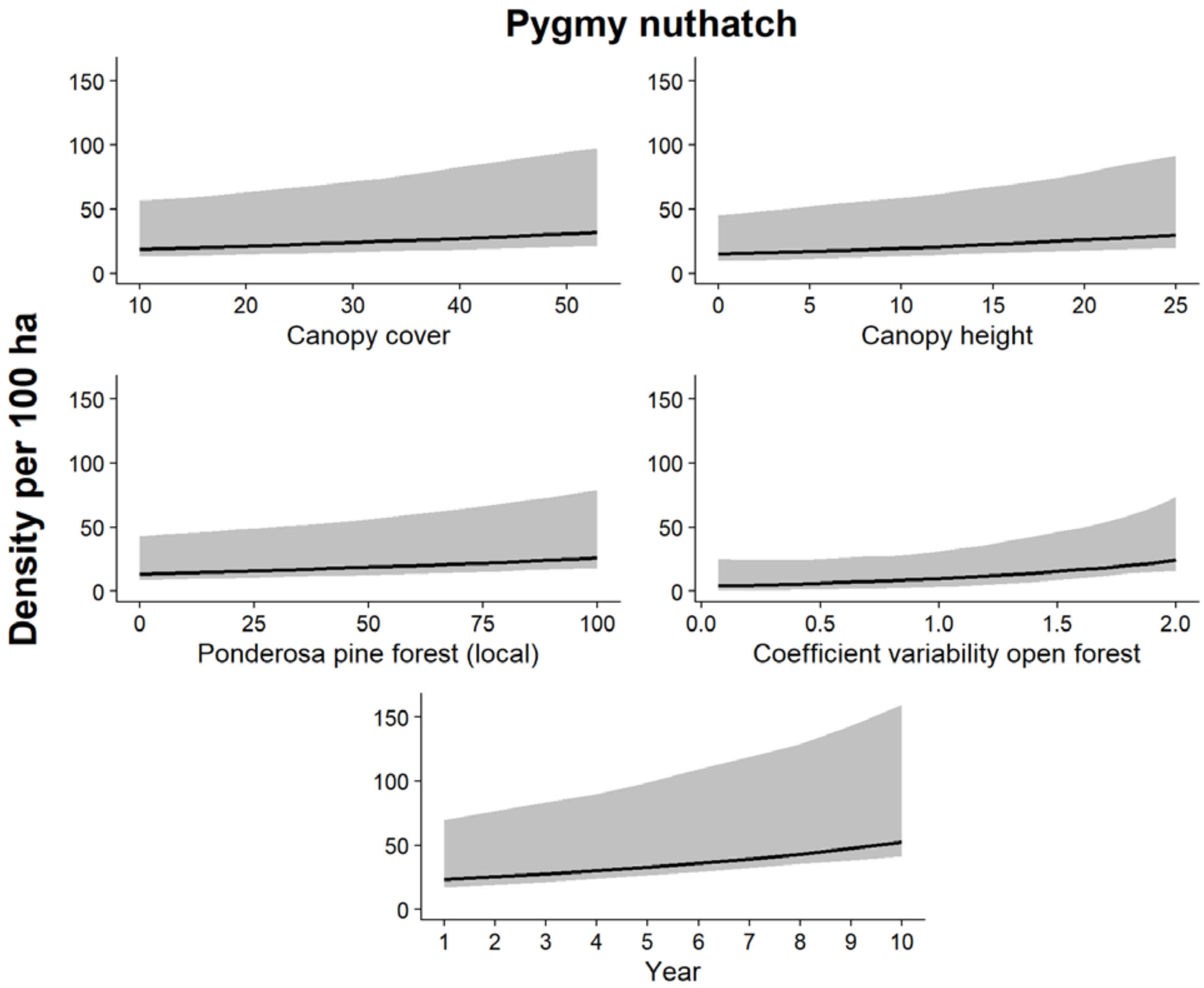

Figure G15. Abundance relationships for Pygmy Nuthatch

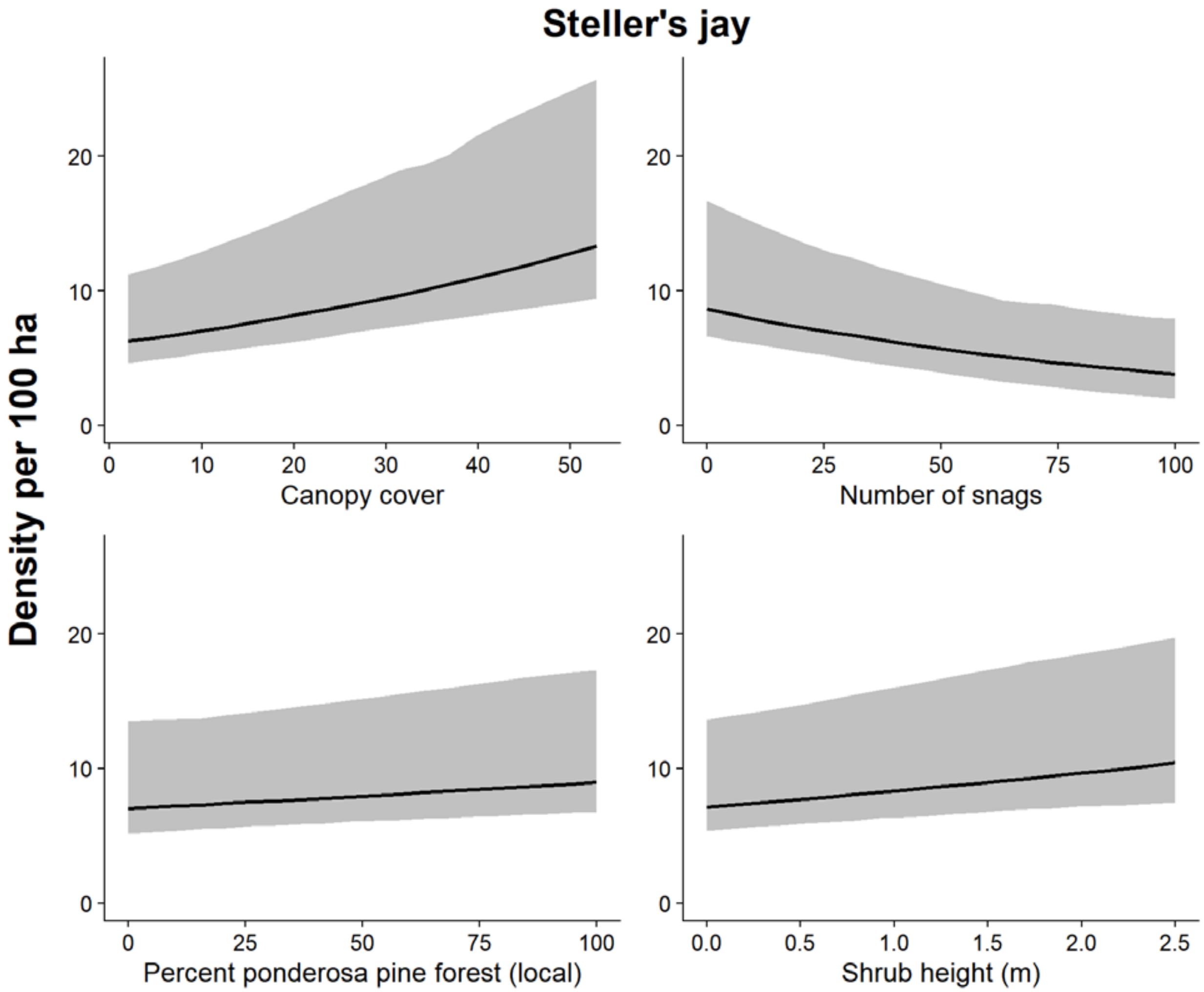

Figure G16. Abundance relationships for Steller's Jay.

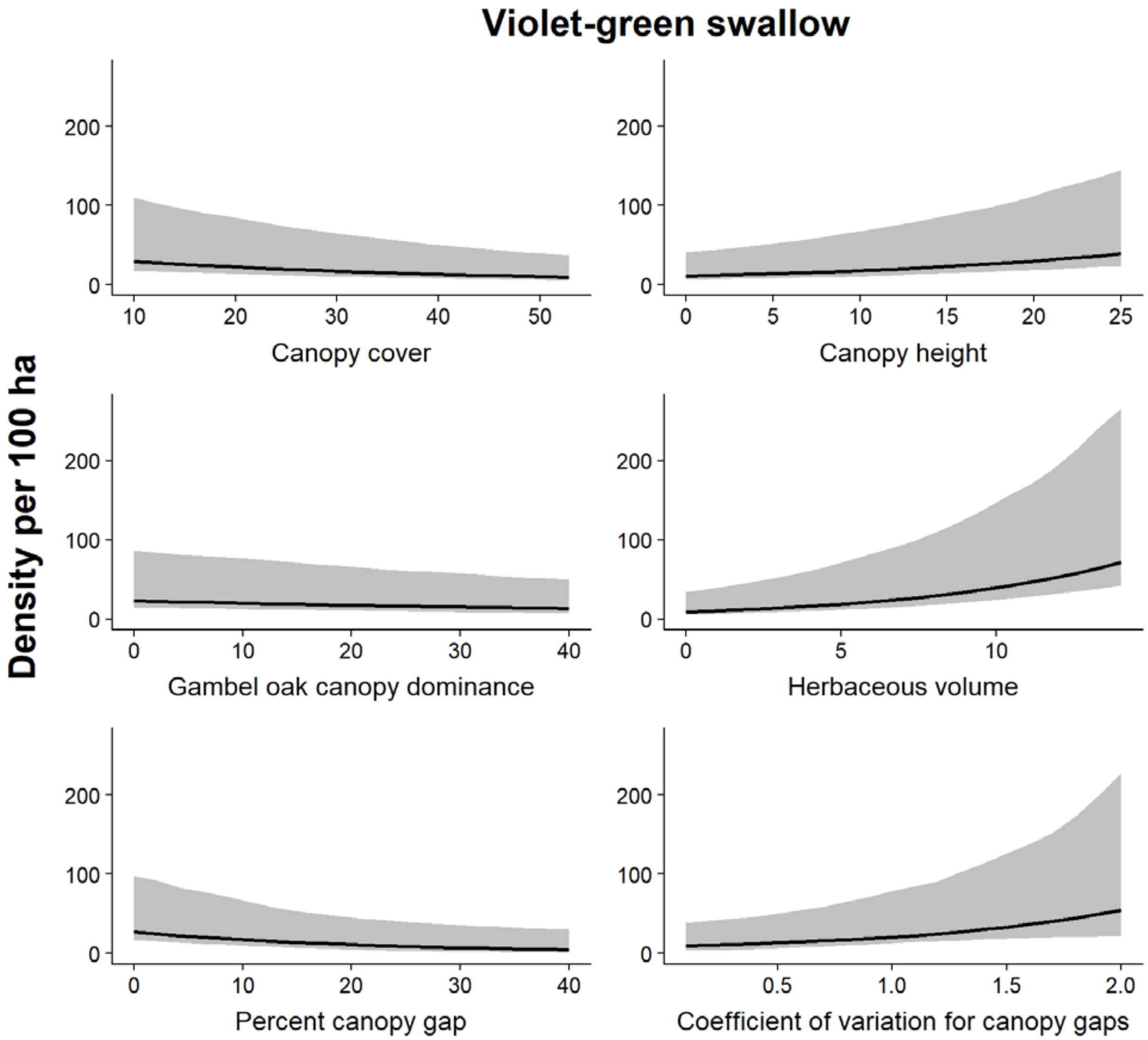

Figure G17. Abundance relationships for Violet-green Swallow.

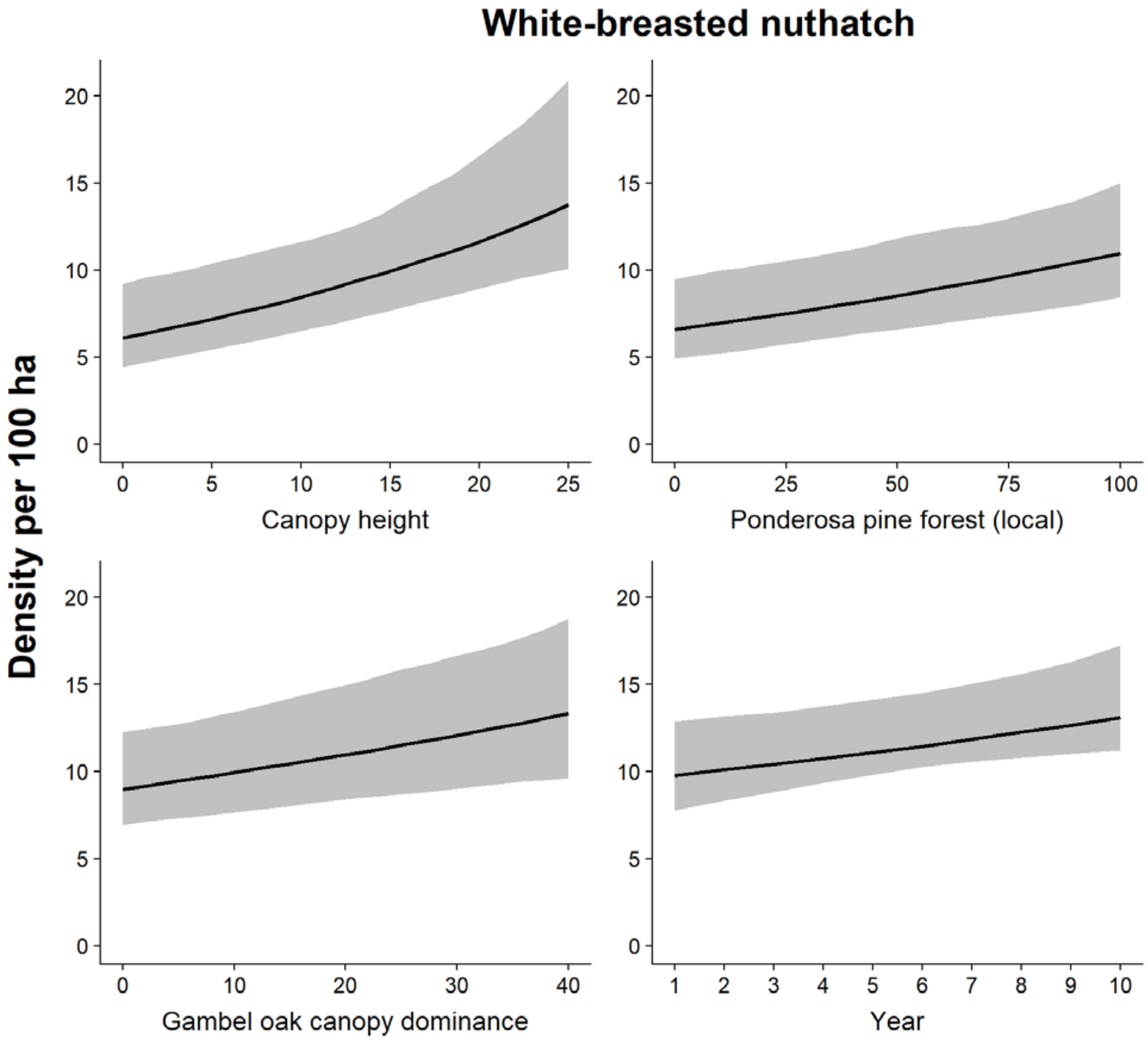

Figure G18. Abundance relationships for White-breasted Nuthatch.

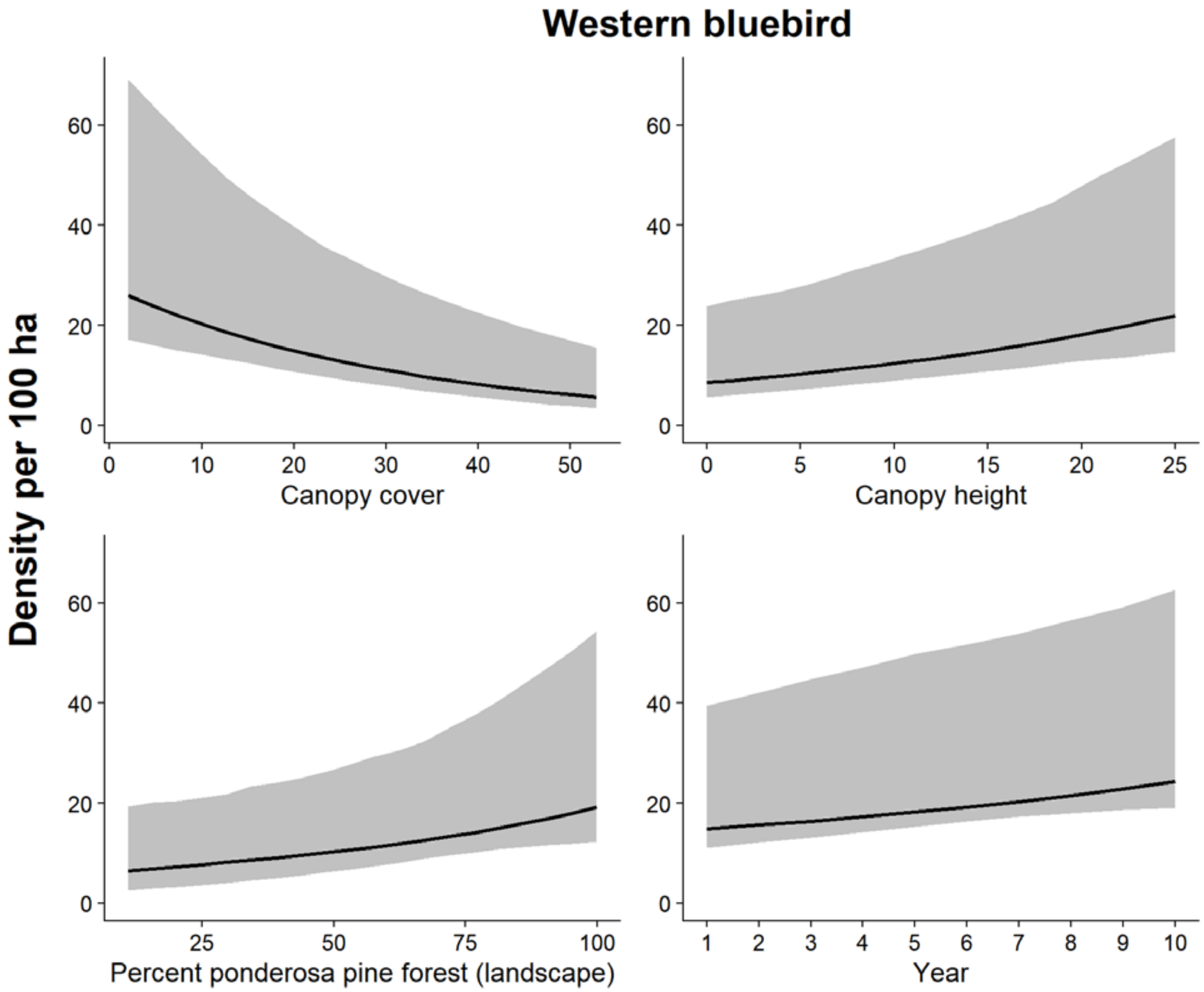

Figure G19. Abundance relationships for Western Bluebird

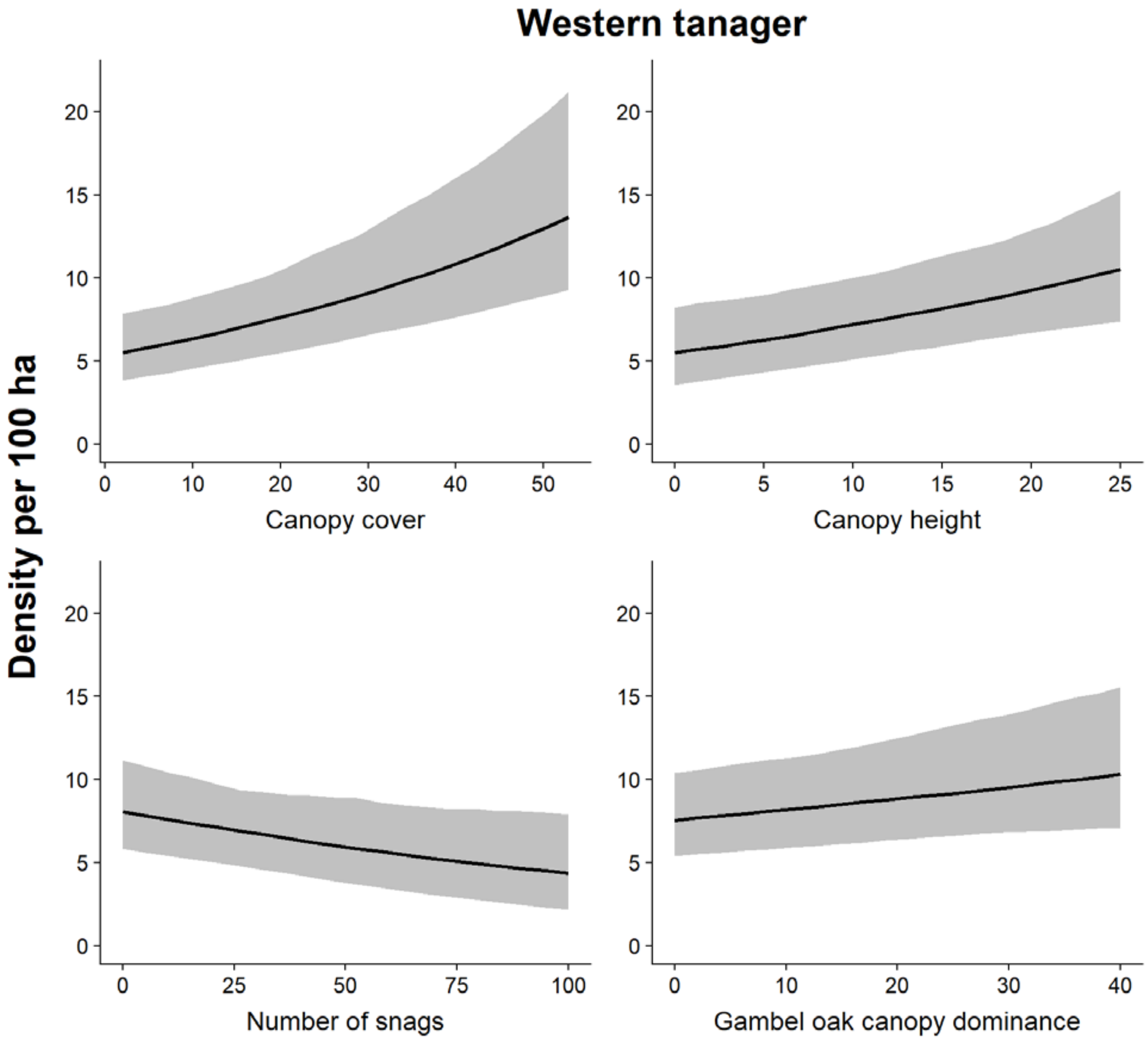

Figure G20. Abundance relationships for Western Tanager