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Simulated treatment effects on bird communities inform landscape-scale dry conifer forest management

Quresh S. Latif[1] | **Jeffery B. Cannon[2]** | **Eric J. Chabot[1]** | **Robert A. Sparks[1]**

[1]Bird Conservancy of the Rockies, Fort Collins, Colorado, USA

[2]The Jones Center at Ichauway, Newton, Georgia, USA

Correspondence
Quresh S. Latif
Email: quresh.latif@birdconservancy.org

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Abstract

Human land use and climate change have increased forest density and wildfire risk in dry conifer forests of western North America, threatening various ecosystem services, including habitat for wildlife. Government policy supports active management to restore historical structure and ecological function. Information on potential contributions of restoration to wildlife habitat can allow assessment of tradeoffs with other ecological benefits when prioritizing treatments. We predicted avian responses to simulated treatments representing alternative scenarios to inform landscape-scale forest management planning along the Colorado Front Range. We used data from the Integrated Monitoring in Bird Conservation Regions program to inform a hierarchical multispecies occupancy model relating species occupancy and richness with canopy cover at two spatial scales. We then simulated changes in canopy cover (remotely sensed in 2018) under three alternative scenarios, (1) a "fuels reduction" scenario representing landscape-wide 30% reduction in canopy cover, (2) a "restoration" scenario representing more nuanced, spatially variable treatments targeting historical conditions, and (3) a reference, no-change scenario. Model predictions showed areas of potential gains and losses for species richness, richness of ponderosa pine forest habitat specialists, and the ratio of specialists to generalists at two (1 km^2 and 250 m^2) spatial scales. Under both fuels reduction and restoration scenarios, we projected greater gains than losses for species richness. Surprisingly, despite restoration more explicitly targeting ecologically relevant historical conditions, fuels reduction benefited bird species richness over a greater spatial extent than restoration, particularly in the lower montane life zone. These benefits reflected generally positive species associations with moderate canopy cover promoted more consistently under the fuels reduction scenario. In practice, contemporary forest management is likely to lie somewhere between the fuels reduction and restoration scenarios represented here. Therefore, our results inform where and how active forest management can best support avian diversity. Although our study raises questions regarding the value of including landscape-scale heterogeneity as a

management objective, we do not question the value of targeting finer scale heterogeneity (i.e., stand and treatment level). Rather, our results combined with those from previous work clarify the scale at which targeting structural heterogeneity and historical reference conditions can promote particular ecosystem services.

INTRODUCTION

Anthropogenic impacts have altered dry conifer forests of western North America in ways that compromise their ecological structure and function (Brown et al., 2004). The most severely impacted forests include ponderosa pine (*Pinus ponderosa*) forests and dry mixed conifer forests (Bock & Block, 2005; Hessburg et al., 2007; Moir et al., 1997; Saab et al., 2005; Schoennagel et al., 2004). For both forest types, fire suppression and other human activities have increased vegetation density and homogenized forest structure (Agee, 1993; Covington & Moore, 1992; Schoennagel et al., 2004). These changes increase the extent and severity of wildfire and bark beetle outbreaks, raising the potential for permanent forest loss or persistent degradation, and threatening ecological function and services provided by these forests (Noss, Franklin, et al., 2006).

Forest management agencies engage in active forest management to mitigate these impacts and improve forest resilience with increasing emphasis on forest restoration to recover conditions characteristic of historical forests (Addington et al., 2018; Cannon et al., 2018; Schultz et al., 2012). Active management in dry conifer forests generally aims to reduce canopy and understory density using mechanical thinning and prescribed fire (i.e., fuels reduction), while encouraging large, fire- and drought-tolerant trees such as ponderosa pine (Agee & Skinner, 2005; Fulé et al., 2012). Forest restoration additionally encourages vegetation structures characteristic of historical forests, including relatively uneven tree distributions, more extensive canopy gaps, and greater heterogeneity at multiple spatial scales (Addington et al., 2018; Cannon et al., 2018; Churchill et al., 2013; Hessburg et al., 2007; North et al., 2009). To identify relevant historical conditions, managers must consider the particular geographic, climatic, and ecological context characterizing individual forest types and stands. Ecologists expect restoration to improve forest resilience, while also promoting a broader range of ecosystem services (Addington et al., 2018; Churchill et al., 2013; Fulé et al., 2012; Noss,

Franklin, et al., 2006). In particular, ecologists expect restoration to promote biodiversity more so than treatments focused narrowly on fuels reduction (Churchill et al., 2013; Matonis & Binkley, 2016; Reynolds et al., 2013). Wildlife has evolved under historical disturbance regimes (Bock & Block, 2005), so ecologists expect open forest conditions associated with historical disturbance regimes to align with species evolutionary histories (Hutto et al., 2008; Noss, Beier, et al., 2006). Additionally, ecologists generally expect heterogeneous landscapes to accommodate the greatest range of species representing various life histories with different responses to vegetation density and disturbance (Clarke, 2008; Fontaine & Kennedy, 2012; Kalies et al., 2010).

Key processes underlying ecological functions and services operate across broad spatial scales, necessitating coordination across forested landscapes for effective management. Several federal initiatives fund collaborative, multistakeholder frameworks for coordinating forest management across public and private lands (Cyphers & Schultz, 2019; Schultz et al., 2012; Villar & Seidl, 2014). These initiatives share goals of improving ecological function and services that transcend ownership boundaries, including water and air quality, wildlife habitat, and ecosystem resilience. Coordinating management across the wildland–urban interface is especially critical for meeting these goals. Lower elevation forests adjacent to and intermixed with human settlement are most impacted by human land use and proportionately the most privately owned (Schoennagel et al., 2009). Distributed jurisdiction of private forests across numerous landowners with independent and potentially conflicting priorities poses particular challenges for coordinating management. Managers and resource specialists need tools to evaluate and prioritize opportunities while considering landscape context to weigh landowner and programmatic objectives, and to monitor program accomplishments (Bestelmeyer et al., 2011; Schultz et al., 2012; Stevens et al., 2016).

Previous work had initiated the development of tools for spatially evaluating and prioritizing management

opportunities in dry conifer forests of the Colorado Front Range. Cannon et al. (2020) developed a framework for mapping potential benefits of forest management and applied this framework in the southern Colorado Front Range (Upper South Platte Watershed). They quantified landscape heterogeneity, fire hazard, and post-fire soil erosion hazard as a function of remotely sensed 30 m resolution forest structure data using catchments (small watersheds) as the primary analysis unit. To map opportunities for forest management, they projected changes in these ecosystem services with fuels reduction (uniform 30% reduction in canopy cover) and restoration (canopy cover distributed to target historical conditions). Cannon et al. (2020) predicted similar benefits for fire hazard and soil erosion with the two management approaches, but only restoration promoted landscape heterogeneity, which they suggested might benefit biodiversity. Consistent with the expected role of heterogeneity, Latif et al. (2020) found variable species responses to treatments, translating to a negligible effect on species richness locally, but a positive relationship of species richness with landscape-scale treatment extent.

We built upon previous work (Latif et al., 2020) to identify and map opportunities for forest management to promote and maintain avian diversity along with other potential ecological benefits. Following Cannon et al.'s (2020) framework, we simulated primary effects of management on vegetation structure and then predicted the implications for bird populations and communities. Our objectives were (1) to incorporate bird conservation into the mapping framework initiated by Cannon et al. (2020), and (2) to evaluate and compare projected implications for avian communities and ponderosa pine forest specialists of alternative management approaches of passive management, fuels reduction, or restoration. For Objective 2, we projected management implications for three metrics: (1) species richness, (2) richness of ponderosa pine forest specialists (from this point forwards specialist richness), and (3) the ratio of specialist richness to richness of generalist species unassociated with ponderosa pine forests (from this point forwards specialist–generalist ratio). This suite of community metrics allowed us to consider management implications broadly while also focusing on ponderosa pine forests, which are especially impacted by human activities, most departed from historical conditions, and therefore of particular interest to forest management and restoration. We expected open forest conditions characterized by moderate canopy cover to maximize avian species richness, and heterogeneity in canopy cover to additionally promote landscape-scale species richness. Accordingly, we expected greater gains in species richness under a restoration scenario compared with management more narrowly focused on fuels reduction.

METHODS

Study area

We simulated forest management scenarios and predicted avian responses across lower elevation dry conifer forests along the Colorado Front Range, including both public lands managed by the US Forest Service (Pike, Arapaho, and Roosevelt National Forests) and non-industrial private forests. Ponderosa pine forests, which dominate the driest sites at the lowest elevations, are historically characterized by low densities of large, uneven-aged, and patchily distributed ponderosa pine trees, interspersed with openings containing extensive components of grasses, forbs, and shrubs (Addington et al., 2018; Peet, 1981). Mixed conifer forests occupy somewhat higher elevations, higher latitudes, and more moist sites, which historically supported greater tree densities and species diversity (Addington et al., 2018, Peet, 1981). Kaufmann et al. (2006) define and delineate two life zones relevant to our study. The lower montane zone is primarily characterized by ponderosa pine forests, which are maintained historically by frequent, low-severity wildfire. The upper montane zone, while also dominated by ponderosa pine, is characterized by more extensive mixed conifer forests and greater vegetation density, which historically favored less frequent, mixed-severity wildfire (Battaglia et al., 2018), conferring greater heterogeneity at landscape scales (Malone et al., 2018). Reduced wildfire frequency and human activities (e.g., logging and grazing) have created denser stands with ingrowth of smaller trees for both forest types across both life zones. Contemporary conditions included substantial components of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), aspen (*Populus tremuloides*), and juniper (*Juniperus* spp.), with Englemann spruce (*Picea engelmannii*), blue spruce (*P. pungens*), and subalpine fir (*Abies lasiocarpa*) as secondary components at upper elevations (Kaufmann et al., 2001; Underhill et al., 2014).

Forest management simulations

We used catchments (small watersheds) from the medium resolution National Hydrography Dataset Plus (NHDPlus v2; USEPA and USGS, 2012) as the primary analysis units for forest management simulations. We included catchments in the analysis if they were (1) ≥75% forest cover (as mapped by LANDFIRE, Rollins, 2009), (2) within the upper and lower montane zones, (3) unimpacted by the 2002 Hayman fire where forest thinning is unnecessary due to widespread effects of high severity fire, and (4) ≥40.5 ha in size.
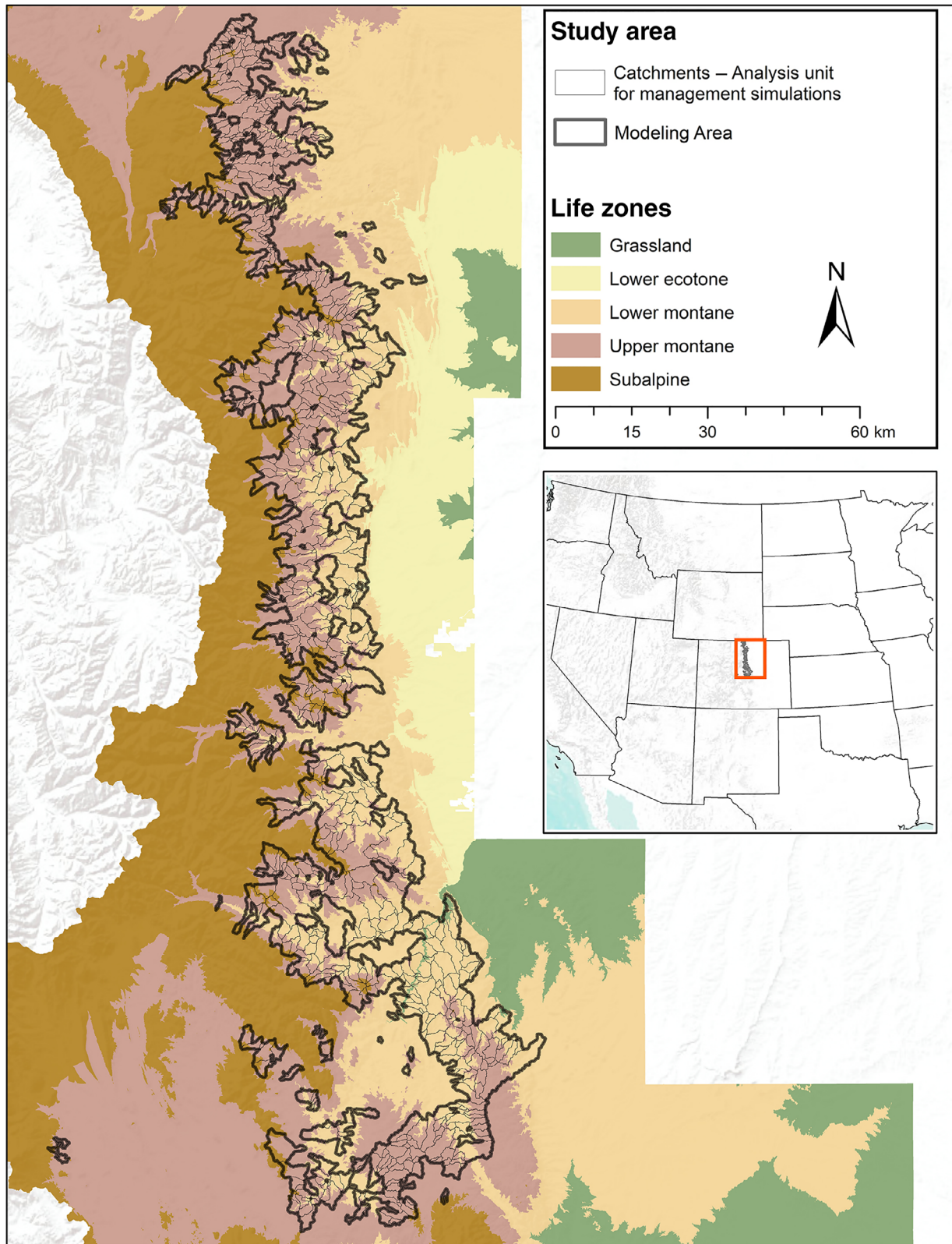
FIGURE 1 Map of study area for mapping forest management implications for birds in dry conifer forests of the Colorado Front Range (USA), including life zones and watershed catchments that provided the analysis units for management simulations

Following these criteria, we included 890 catchments in forest management simulations ranging in size from 41 to 4998 ha (mean = 463 ha; Figure 1).

We used 30 m resolution canopy cover representing conditions in 2018 to represent the baseline landscape, which we derived from LANDFIRE (Rollins, 2009). The

latest LANDFIRE imagery year before 2018 was 2014, so we adjusted 2014 values to account for forest thinning implemented in 2014–2018. Specifically, we intersected treated units with canopy cover imagery in a GIS environment and multiplied imagery values by an estimated proportion canopy cover loss for each treatment type recorded in the US Forest Service Activity Tracking System (FACTS, 2018). We adjusted canopy cover for treatment using proportion loss values reported in the literature (Fulé et al., 2012; Stephens & Moghaddas, 2005; Ziegler, 2014). Treatment areas where we adjusted canopy cover represented 18,113 acres or 2% of our study area defined by the 890 catchments included in our analysis. Additional details on CFLRP treatments (i.e., most of the treatments recorded in FACTS) and their outcomes are detailed elsewhere (Barrett et al., 2021; Cannon et al., 2018; Latif et al., 2020).

Working from the 2018 baseline, we simulated two active management scenarios, fuels reduction and restoration. For fuels reduction, we multiplied canopy cover across the entire landscape by an adjustment factor of 0.7 (i.e., a 30% reduction). For restoration, we applied an algorithm that reduced canopy cover toward historical levels, while ensuring a historically appropriate range of variability between and within topographic and elevation gradients. Specifically, we classified catchments within the study landscape based on physiographic parameters (elevation and moisture gradients), developed desired forest structure distributions by physiographic setting based on published forest reconstructions (Battaglia et al., 2018; Brown et al., 2015) and regional restoration guides (Addington et al., 2018), and simulated restoration treatments such that forest structure and variability in each catchment approached the desired conditions for the physiographic setting. We classified catchments into four physiographic settings representing combinations of upper versus lower montane life zones and wet versus dry soil moistures based on topography, and developed desired forest structure distributions for these settings. Cannon et al. (2020) provide additional details on procedure and algorithm for simulating forest restoration.

Bird surveys

The sampling design and protocol for bird surveys followed the Integrated Monitoring in Bird Conservation Regions (IMBCR) program (Pavlacky Jr. et al., 2017). Our sampling frame was the same as in Latif et al. (2020), and most bird data here overlapped their data. The sampling frame consisted of a 1-km^2 grid that included regions between 1828 and 2743 m elevation on the Arapaho and Roosevelt National Forests and between 1828 and 2896 m on the Pike National Forest (i.e., the distribution of ponderosa pine within these national forests), excluding open water and regions burned by wildfires >400 ha between 1998 and 2013 (i.e., those delineated in available remotely sensed data; MTBS, 2018). To meet objectives of previous work, sampled grid cells represented spatially balanced random samples of impact and reference strata established for effectiveness monitoring of forest restoration treatments (please refer to Latif et al., 2020). We pooled data across these strata for this study.

Primary sampling units consisted of 137 1 km^2 grid cells, each containing up to 16 points spaced 250 m apart in a 4 × 4 array (1943 points total). We surveyed 120, 120, and 106 grid cells in each of 2014, 2016, and 2018, respectively, including 95 grid cells surveyed in all 3 years and 137 grid cells surveyed in at least 1 year. This effort yielded a data set representing 346 grid-cell sampling occasions and 4184 point survey occasions. Each point survey was 6 min in duration and conducted during the breeding season (dates varied by elevation; Kingery, 1998) between 0.5 h before and 5 h after sunrise. Surveyors recorded all individual birds detected by species during this survey period, along with distances (m) to detected individuals (measured with laser range finders) and time elapsed within the survey (0–6 min) when detections were recorded (for details, please refer to Hanni et al., 2018). For the community occupancy analysis implemented here, we only included detections within 125 m of the survey point, so survey plots were effectively 125 m radius circles centered on points.

Avian community model

We analyzed avian population distributions and community structure using a multispecies, multiscale occupancy model (Dorazio et al., 2011; Mordecai et al., 2011). Detailed descriptions of the analysis model structure and fitting are provided by Latif et al. (2020) and in Appendix S1. In short, the model leveraged our nested sampling design to estimate grid-cell occupancy probability for each species (ψ), species occupancy of points within occupied grid cells during a 6-min timeframe (θ), and detectability of the species during the same 6-min timeframe (p) (Mordecai et al., 2011; Pavlacky Jr. et al., 2017). Considering the short (6-min) timeframe for estimation, point occupancy is likely to reflect variability in local abundance for species with territories $\gtrsim$4.9 ha, whereas grid-cell occupancy quantified coarser scale species distributions (Latif et al., 2016, 2020; Steenweg et al., 2018).

We used a hierarchical multispecies structure to specify species-specific parameters (ψ, θ, and p) as random variables governed by community-level hyperparameters. This model structure allowed information sharing across species, improving precision of species-specific parameters and

allowing us to derive species richness by summing occupancy probabilities across species (Dorazio et al., 2011, reviewed by Kéry & Royle, 2016). We excluded raptors, grouse, cranes, and water birds not readily detectable with our survey methods, and we only included species that breed in our study area. We augmented data to represent all potential breeders, including 100 species detected during our surveys and 28 species not detected here but detected in broader regional surveys (Data S1), to fully correct species richness estimates for imperfect detection (Dorazio et al., 2011). Therefore, species richness estimates quantified the number of relatively small, territorial, breeding landbird species present at the level of a sampling unit (100 ha grid cell or 4.9 ha survey point).

We modeled species occupancy and detection probabilities as logit–linear functions of covariates (Table 1). Occupancy relationships with four covariates relating grid cell and point occupancy with various aspects of canopy cover provided the basis for predicting avian responses to forest management. Reflecting our expectation that species would associate with intermediate levels of canopy cover, we specified a quadratic point occupancy relationship with canopy cover and specified grid-cell occupancy relationships with open forest (10%–40% canopy cover) and canopy gaps (<10% canopy cover). We derived canopy cover metrics for each year of data from 30 m resolution imagery that represented the corresponding year. For 2016 and 2018, we adjusted for forest management treatments recorded in FACTS (2018) that had been completed following the imagery year but prior to the survey year using proportion canopy cover loss values derived from the literature (Fulé et al., 2012; Stephens & Moghaddas, 2005; Ziegler, 2014). Additional covariates accounted for occupancy and detectability relationships with physiography, life zone, and survey timing (Table 1). We represented life zone using a binary indicator of whether or not the majority of survey points within a grid cell were classified as lower montane (Kaufmann et al., 2006). We scaled all covariates to mean $= 0$ and SD $= 1$ to facilitate computation and prediction. We implemented model fitting and prediction within a Bayesian framework (details in Appendix S1). We focused on reporting avian relationships with canopy cover metrics, while providing a complete summary of all model parameter estimates (e.g., detectability and other covariate relationships) in an online data repository (https://doi.org/10.5061/dryad.0zpc866zc).

Predicting avian community response to management

We applied community occupancy model predictions to evaluate implications of alternative forest management scenarios for birds. We predicted species richness by summing occupancy probabilities across all 128 species represented in the

TABLE 1 Covariates included in analyses relating avian occupancy with canopy structure along the Colorado Front Range

Covariate type	Covariate	Scale (ha)	Parameters	Description
Local canopy structure	Canopy cover	4.9	θ, p	Percent canopy cover
Landscape canopy structure	Canopy gaps	900	ψ	Percent area of neighborhood with <10% canopy cover
	Open forest	900	ψ	Percent area of neighborhood with 10%–40% canopy cover
	Open forest perimeter–area ratio	900	ψ	mean perimeter–area ratio for patches of 10%–40% canopy cover
Physiography	Heat load	100	ψ	potential direct incident solar radiation (McCune, 2007; MJ/cm^2/year; mean of point-level values for each grid cell)
	TWI	100	ψ	Topographic wetness index (Beven & Kirkby, 1979; mean of point-level values for each grid cell)
	Latitude	100	ψ	Latitude at grid-cell center
Life Zone	Lower montane	100	ψ	Majority classification of surveyed points within a grid cell as lower montane by Kaufmann et al. (2006)
Survey timing	Day of year[a]	-	p	Number of days elapsed since 1 January during survey
	Time since sunrise[a]	-	p	Number of minutes elapsed since sunrise when initiating the survey

Note: Covariates were either compiled for 1-km^2 grid cells (scale $= 100$ or 900 ha) or points nested within grid cells (scale $= 4.9$ ha). Covariates were related to grid-cell occupancy (ψ), point occupancy (θ), or detectability (p) (for complete model structure, please refer to Appendix S1). Following Latif et al. (2020), canopy cover covariates for grid-cell occupancy described 3×3 km neighborhoods (900 ha).

[a]The Canopy cover effect on point occupancy and day of year and time since sunrise effects on detectability were quadratic ($\theta \sim x + x^2$).

community model. For the remaining two metrics (specialist richness and specialist–generalist ratio), we defined ponderosa pine forest specialists using a specialization index adapted from previous work in other vegetation types (Correll et al., 2016, 2019). We quantified ponderosa pine forest specialization for a species by dividing its relative abundance (mean count per point survey) within ponderosa pine forest by the sum of ponderosa pine forest relative abundance and relative abundance in all other habitat types (0–1 range). We used all available IMBCR data for species recorded in the analyzed data set and with ≥10 detections recorded program wide to calculate this index (for programmatic extent, please refer to McLaren et al., 2021; Pavlacky Jr. et al., 2017). We identified 29 species with specialism index values ≥0.66 as ponderosa pine forest specialists (Data S1). We summed occupancy probabilities for these 29 species to derive specialist richness, and we divided specialist richness by the richness of species with specialism index values <0.5 (76 species) to derive the specialist–generalist ratio. Having relied exclusively on relative abundance within the IMBCR programmatic footprint to quantify habitat specialization, species categorized as ponderosa pine forest specialists could include regional specialists or species that experience higher fitness (albeit lower density) in other vegetation types. We verified that our specialist list included species considered iconic of ponderosa pine forests, however, and we set the specialism index threshold (0.66) to ensure inclusion of such species (e.g., Pygmy nuthatch [Kingery & Ghalambor, 2020], red crossbill [Benkman & Young, 2020], and plumbeous vireo [Goguen & Curson, 2020]).

We calculated each of the three community metrics at grid cell (1 km^2) and point (125 m radius) scales by life zone (upper vs. lower montane forest). We derived community metrics at the grid cell scale from grid-cell occupancy probabilities (ψ) and point-scale metrics from unconditional point occupancy probabilities ($\psi \times \theta$). As such, grid-cell community metrics reflected species relationships with coarse-scale canopy cover, whereas point-scale metrics integrated both coarse- and fine-scale species relationships with canopy cover. Although point metrics quantified avian communities for 250 m diameter circular plots (4.9 ha), we assigned point-level values to 250 m square cells (6.25 ha) when mapping predictions. We assumed that this slight scale mismatch did not compromise interpretation of mapped predictions for projecting and inferring local scale management implications.

We calculated differences in bird community metrics and canopy structure between passive and active management scenarios to evaluate the relationships underlying projections. We calculated differences in the means of bird community metrics and the area across which we predicted statistically definitive gains or losses in community metrics between baseline and active management scenarios. We considered a projected gain or loss to be statistically definitive in cells when the 95% credible interval for the difference in a given community metric between active management and baseline scenarios excluded zero. We evaluated the basis for projected changes in community metrics by considering them in the context of avian relationships with canopy cover and differences in canopy cover between management scenarios. Finally, we evaluated management implications for canopy heterogeneity along with its potential role in mediating bird responses. Following Cannon et al. (2020), we quantified catchment heterogeneity using the Shannon diversity index (0–1 range; Shannon, 1948) applied to catchment proportions in 10 equal-interval canopy cover bins (i.e., 0%–10%, 10%–20%, ..., and 90%–100%).

RESULTS

Forest management simulations

Simulated forest management has changed canopy cover and structure in ways that reflected the different approaches of fuels reduction and restoration (Table 2).

TABLE 2 Landscape summaries (median and 95% quantiles) for projected canopy cover metrics by life zone (upper vs. lower montane) and management scenario (reference, fuels reduction, and restoration)

Metric	Scale (ha)	Lower montane			Upper montane		
		Reference	Fuels reduction	Restoration	Reference	Fuels reduction	Restoration
Canopy gap extent	900	10 (0, 45.8)	9.7 (0.3, 44.9)	20.9 (6.3, 48.4)	7 (0, 36)	7.3 (0.2, 36.1)	9.9 (1.4, 36.7)
Open forest extent	900	33 (2, 73)	80 (32, 98)	60 (28, 77)	24 (2, 61)	78 (30, 98)	57 (21, 73)
Open forest perimeter–area ratio	900	0.07 (0.06, 0.09)	0.07 (0, 0.1)	0.08 (0.06, 0.1)	0.08 (0.06, 0.09)	0.07 (0, 0.1)	0.08 (0.06, 0.1)
Canopy cover	6.25	40.4 (9.5, 57.8)	29.1 (7.9, 40.7)	21.2 (6.7, 40.8)	42.5 (13.1, 55.9)	30.3 (10.7, 39.7)	30 (10.6, 45)
Heterogeneity	41–4998[a]	0.74 (0.56, 0.89)	0.6 (0.35, 0.79)	0.84 (0.75, 0.91)	0.71 (0.51, 0.85)	0.56 (0.28, 0.78)	0.87 (0.73, 0.95)

Note: Units are square neighborhoods centered on 1 km cells (Scale = 900), 250 m cells (scale = 6.25), or catchments (scale = 41–4998).
[a]Range of catchment sizes.

Simulated fuels reduction increased the mean extent of open forest for 900 ha grid-cell neighborhoods by 140% and 250% in lower and upper montane zones, respectively, but did not appreciably change the mean extent of canopy gaps in either life zone. Simulated restoration increased the mean extent of open forest, albeit less so than did fuels reduction (by 80% and 140%), while also increasing the mean extent of canopy gaps (by 109% and 40% in lower and upper montane zones, respectively). At a finer 4.9 ha scale, fuels reduction and restoration resulted in similar reductions in mean canopy cover in the upper montane zone (28% and 29%, respectively), whereas restoration reduced mean canopy cover more so than fuels reduction in the lower montane zone (48% and 29%, respectively). In both life zones, heterogeneity of canopy cover within catchments declined on average with fuels reduction but increased with restoration (Table 2).

Avian relationships with canopy cover

Our community model-estimated avian relationships with canopy cover that predominantly described associations with open forests and moderate canopy cover (Figure 2). At the grid-cell scale, species richness and richness of ponderosa pine forest specialists related positively with open forest conditions and negatively with canopy gaps. The specialist–generalist ratio also related positively with open forests but less definitively and non-linearly with canopy gaps, with possible but uncertain peaks at 20%–30% and 30%–40% canopy gaps in lower and upper montane zones, respectively. Grid-cell-scale community relationships reflected species occupancy relationships that were predominantly negative with canopy gaps and positive with open forest (Figure 3).

At the point scale, model estimates of specialist richness and the specialist–generalist ratio peaked at ~30%–40% canopy cover depending on life zone (Figure 2). Local species richness related more weakly with canopy cover with a possible but much less definitive peak at ~30% in the lower montane zone (Figure 2). Point-scale community-level patterns reflected species-specific relationships with canopy cover. Fifty species exhibited statistically supported occupancy relationships with canopy cover, of which 11 exhibited positive and primarily linear relationships (i.e., the 95% credible intervals for quadratic effects spanned zero), 23 exhibited primarily linear negative relationships, and 16 exhibited statistically supported quadratic relationships (Figure 3). Although two-thirds of the 34 species with primarily linear relationships declined in occupancy with increasing canopy cover, the 11 species with positive relationships also represented relatively common species (e.g., dark-eyed junco, mountain chickadee, and hermit thrush;

Figure 3). Of 16 species with supported quadratic relationships, 10 were ponderosa pine forest specialists, all of which exhibited a peak in occupancy at intermediate levels of canopy cover (Figure 4). These 10 specialist species represented the most common of ponderosa pine forest specialists, accounting for 72% of all specialist detections.

Projected avian responses to forest management

We generally projected positive responses in avian community metrics to active management, but the magnitude and spatial extent of responses varied by life zone and management approach (Figures 5–8). Although we projected gains in community metrics with both management approaches, projected gains with restoration were lower in magnitude (Figure 7) and less spatially extensive (Figures 5, 6, 8) than with fuels reduction. Projected community responses were more similar between management approaches in the upper montane zone. In the lower montane zone, restoration predominantly increased grid-scale community metrics, but these increases were less extensive than with fuels reduction (Figures 5, 6, 8). Moreover, we projected more extensive losses than gains for point-scale species richness, and losses across a similar extent as gains for point-scale specialist richness under restoration in the lower montane zone. We generally projected statistically clearer and more spatially extensive gains in community metrics at the grid cell scale compared with the point scale (except please refer to lower montane specialist–generalist ratio under the fuels reduction and lower montane species richness under restoration; Figure 8).

DISCUSSION

Projected avian community responses to simulated forest management provided insight into potential ecological implications of management along with how and where management could benefit avian conservation objectives. We corroborated our expectation that dry conifer forest birds, and especially ponderosa pine forest habitat specialists, would associate with open forests and moderate levels of canopy cover. Accordingly, we projected positive responses of avian species richness, specialist richness, and the ratio of specialists to generalists when management favored these conditions. Management aimed narrowly at fuels reduction elicited a more positive projected avian response than did restoration aimed explicitly at restoring historical conditions that included greater

landscape heterogeneity. Although inconsistent with our a priori expectation for restoration, this result does reflect the more consistent promotion of open forests and moderate canopy cover conditions under the fuels reduction scenario. Therefore, achieving historical levels of heterogeneity in canopy cover at a landscape scale via forest management may be less important than moderating canopy cover for meeting some avian conservation objectives.

Mechanisms underlying projected avian responses

Estimated species associations with moderate canopy cover and open forests are consistent with contemporary understanding of species and forest ecology. Positive occupancy relationships with open forests or moderate levels of canopy cover (from this point forwards open forest conditions) reflected the life histories of species
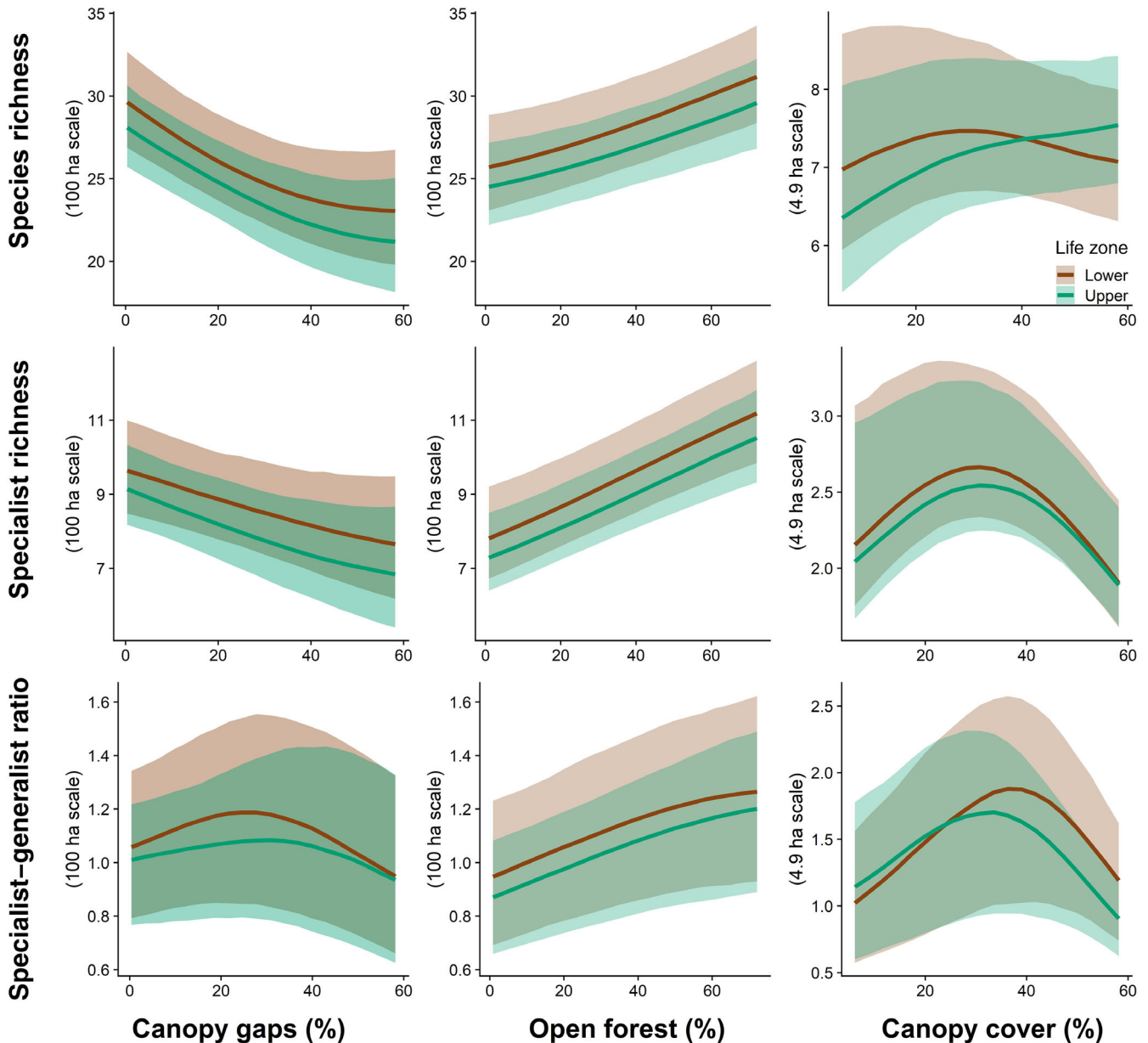
FIGURE 2 Model-estimated avian community relationships with canopy structure in dry conifer forests of the Colorado Front Range (USA). Relationships are presented for lower and upper montane forest life zones. Community metrics are species richness, richness of ponderosa pine forest specialists (specialist richness), and the ratio of specialists to species not particularly associated with ponderosa pine forests (specialist–generalist ratio). Metrics estimated at a coarser scale (100 ha) relate with coarse-scale canopy attributes (extent of canopy gaps [<10% canopy cover] and open forest [10%–40% canopy cover]), whereas finer scale community metrics (4.9 ha) were related with percent canopy cover. Relationships with a fourth canopy metric (perimeter–area ratio of open forest patches) were weakly supported by the data and therefore not shown
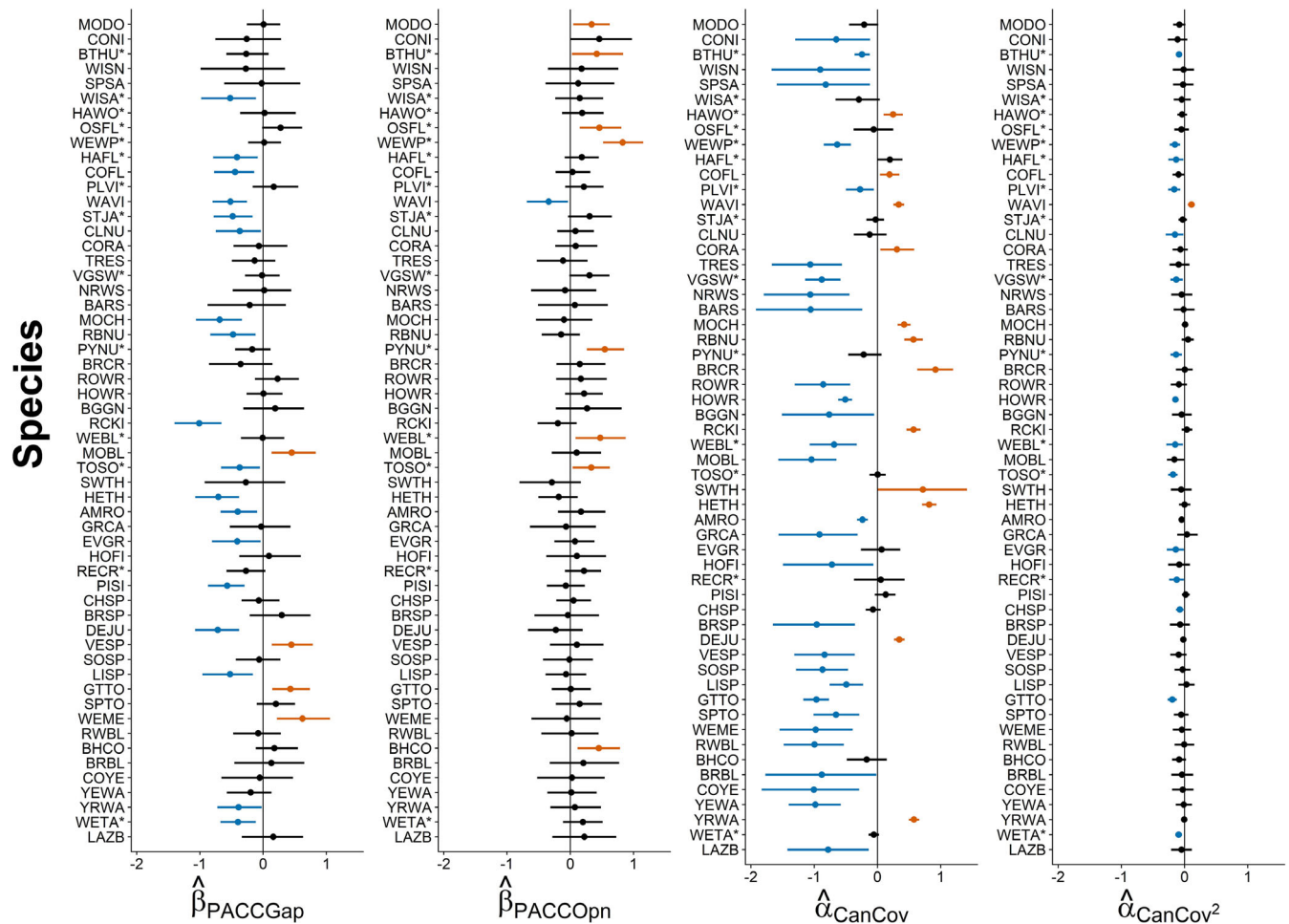
FIGURE 3 Estimated species occupancy relationships (posterior medians and 95% Bayesian credible intervals) with canopy structure metrics (defined in Table 1). Error bar colors indicate supported positive (orange) and negative (blue) relationships. For complete species names, please refer to Data S1. All covariates were scaled to mean = 0 and SD = 1 prior to analysis, and squaring was applied after scaling for CanCov^2

exhibiting these relationships. Aerial insectivores typically forage in canopy openings (e.g., Olive-sided Flycatcher and Western Wood-Pewee), species that nest or forage in the understory benefit from understory development facilitated in canopy openings (e.g., Green-tailed Towhee and Mourning Dove), and species that feed on conifer seeds may benefit from increased cone productivity on large ponderosa pine trees released from competition with smaller trees (e.g., Clark's Nutcracker, Red Crossbill, and Pygmy Nuthatch; Tomback, 2020, Benkman & Young, 2020, Kingery & Ghalambor, 2020). Many species exhibiting such relationships here also exhibited positive relationships with actual forest management implemented along the Colorado Front Range (Latif et al., 2020). Moreover, species exhibiting positive relationships with open forest conditions largely represented ponderosa pine habitat specialists, a group for which such relationships would be expected considering their evolutionary history (Hutto et al., 2008; Noss, Beier, et al., 2006).

We expected a stronger projected avian community response to restoration based on our expectation that interspecific variation in occupancy relationships with canopy cover would confer benefits of landscape heterogeneity for avian diversity. Although landscape heterogeneity did increase with simulated restoration (in contrast with fuels reduction), the projected community response to restoration contradicted our expectations. Apparently, levels of interspecific variation represented here were not enough for landscape heterogeneity to play a dominant role in determining projected management outcomes for birds. Instead, simulated restoration increased landscape-scale canopy gaps and reduced local canopy cover to levels that were less than optimal for promoting bird species and ponderosa pine specialist richness, particularly in the lower montane zone.

Our study adds to previous work for understanding forest management implications for birds. Latif et al. (2020) documented a positive empirical relationship of avian species richness with restoration treatments at a
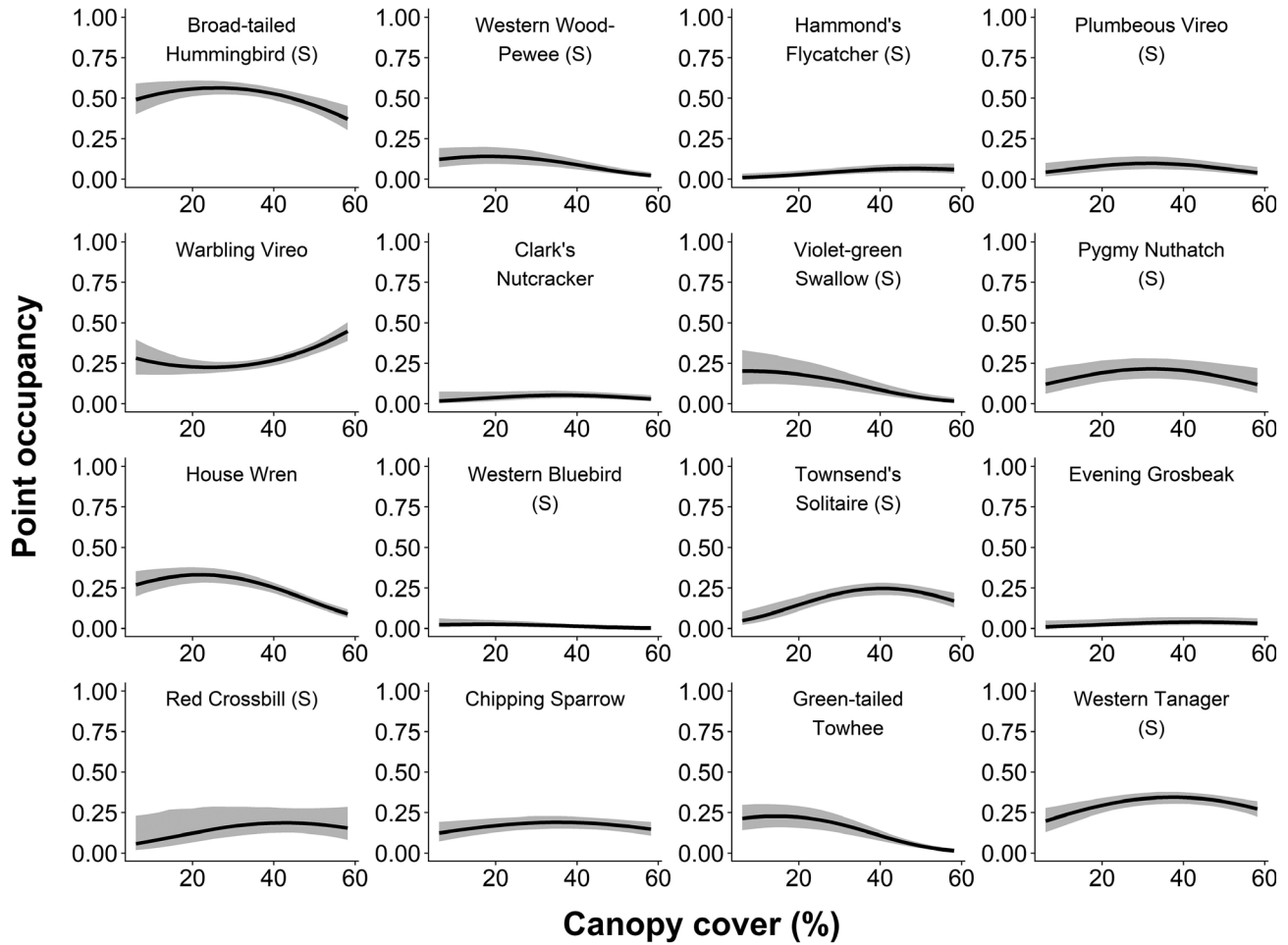
FIGURE 4 Point occupancy probabilities (posterior median and 95% credible bands) in relation to percent canopy cover for species with statistically supported quadratic (CanCov^2) relationships (please refer to Figure 3). Parenthetic "S" following species common names indicate categorization as ponderosa pine forest specialist based on a specialization index calculated from relative abundances representing regional monitoring data (please refer Predicting avian community response to management)

landscape scale, consistent with landscape heterogeneity promoting avian species richness. Our projection of relatively limited negative impacts of restoration for grid-scale avian community metrics parallels Latif et al. (2020), who found only positive and no statistically supported negative species occupancy relationships with treatment at a landscape scale. Nevertheless, our results suggest that moderation of canopy cover may outweigh landscape heterogeneity in determining avian response to active management.

Study strengths and limitations

Landscape-wide data allowed us to consider management implications for forest birds broadly. By restricting our simulations to remotely sensed attributes of vegetation structure directly targeted by forest management and clearly relevant to avian ecology, we were able to map projected bird responses with sufficient resolution to inform forest planning. Moreover, the spatially balanced and nested design used for sampling birds allowed us to project avian responses at two spatial scales, further enriching information for management. Nevertheless, restrictions imposed on our study to meet our objectives also constrained our inferences.

We lacked data explicitly representing understory vegetation, so our spatial predictions primarily inform comparison of management approaches to reducing canopy or tree density. Avian relationships with understory vegetation are implicitly represented in their relationships with canopy cover estimated by our community model (please refer to above). As such, our projections rely on correlations between canopy cover and other attributes of forest structure and composition that represent key habitat attributes for avian species. For example, our projections would not necessarily inform forest management that reduces understory vegetation
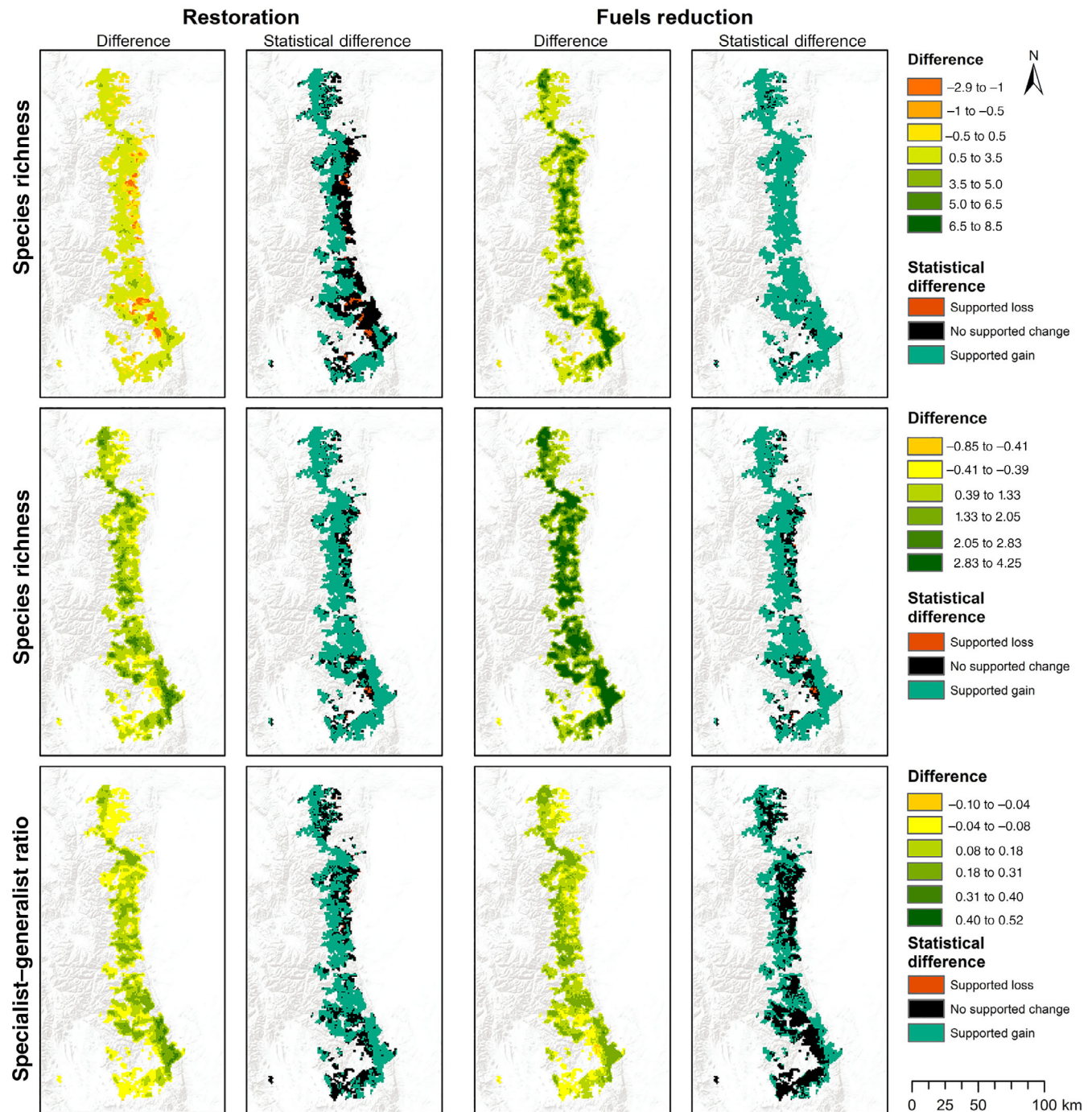
FIGURE 5 Mapped gains and losses in grid-cell scale (100 ha) avian community metrics projected for active management of dry conifer forests along the Colorado Front Range (USA). Community metrics are species richness, richness of ponderosa pine forest specialists (specialist richness), and the ratio of specialists to species not particularly associated with ponderosa pine forests (specialist–generalist ratio). Gains and losses in these metrics represent differences with the specified active management scenario (restoration or fuels reduction) relative to the baseline passive management scenario. Statistically supported differences are those where the 95% credible interval for the difference in cell-specific estimates between active and passive management excluded zero

without affecting canopy cover (e.g., some fuels reduction treatments). Additionally, large gap creation may facilitate restoration of meadows currently missing from the landscape, which could increase habitat quality and diversity in ways not necessarily captured here

(Matonis & Binkley, 2016). We accept these limitations arising from our reliance on remotely sensed canopy cover, however, in exchange for model applicability for producing maps capable of informing where to manage forests.
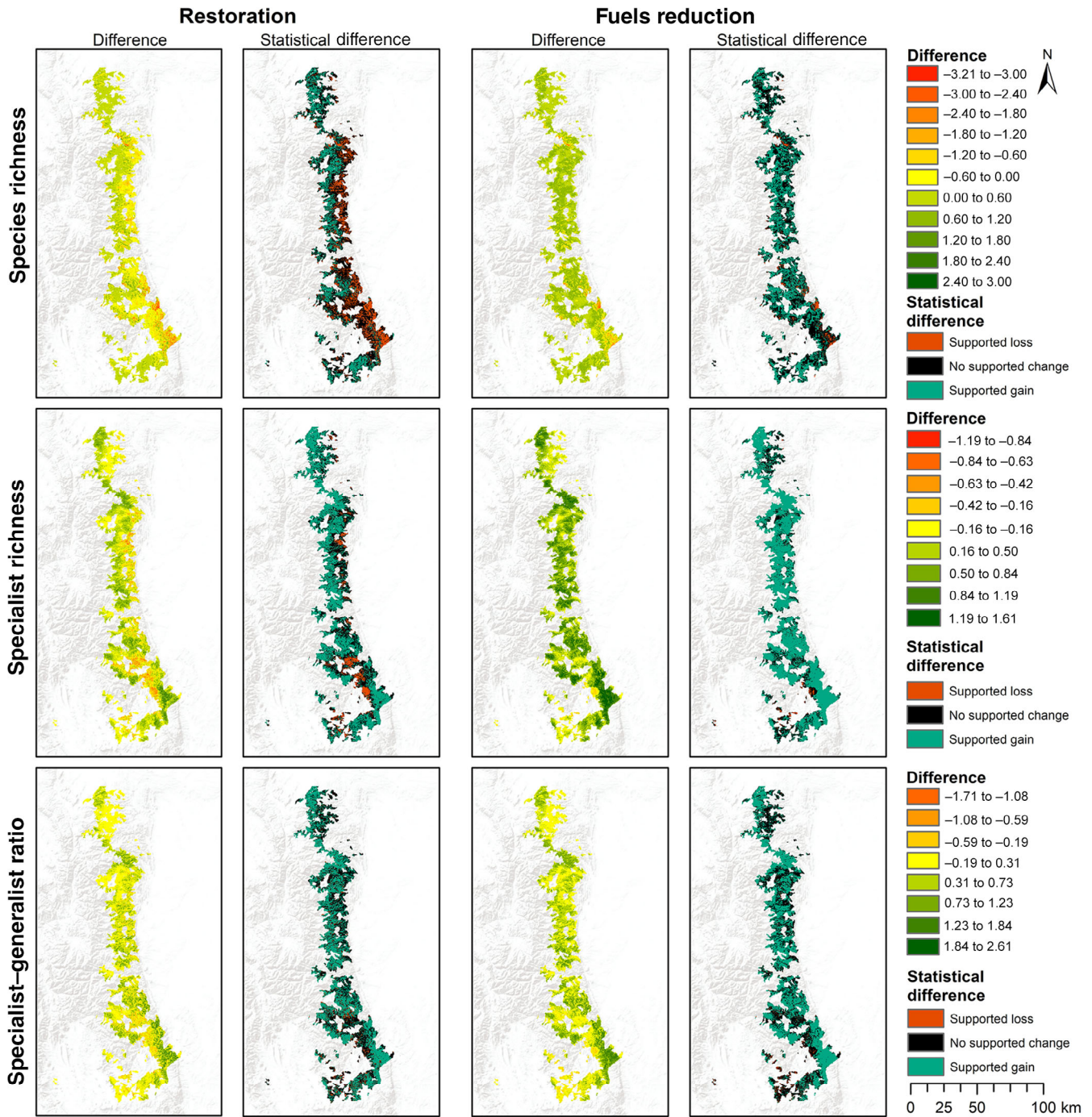
FIGURE 6 Mapped gains and losses in point scale (predicted to 6.25 ha cells) avian community metrics projected for active management of dry conifer forests along the Colorado Front Range (USA). Community metrics are species richness, richness of ponderosa pine forest specialists (specialist richness), and the ratio of specialists to species not particularly associated with ponderosa pine forests (specialist–generalist ratio). Gains and losses in these metrics represent differences in posterior median values with active management (restoration or fuels reduction) from passive management (baseline). Statistically supported differences are those where the 95% credible interval for the difference in cell-specific estimates between active and passive management excluded zero

Simulated management and projected outcomes assume treatment of entire catchments averaging approximately 463 ha in size. Although large for a single treatment, this size is within the size range of long-term planning units and therefore informs prioritization and planning at larger temporal and spatial scales (please refer to Cannon et al., 2020). Additionally, applying models for quantifying ecosystem services (e.g., our avian model and those in Cannon et al., 2020) to evaluate smaller spatial units could supplement landscape-wide
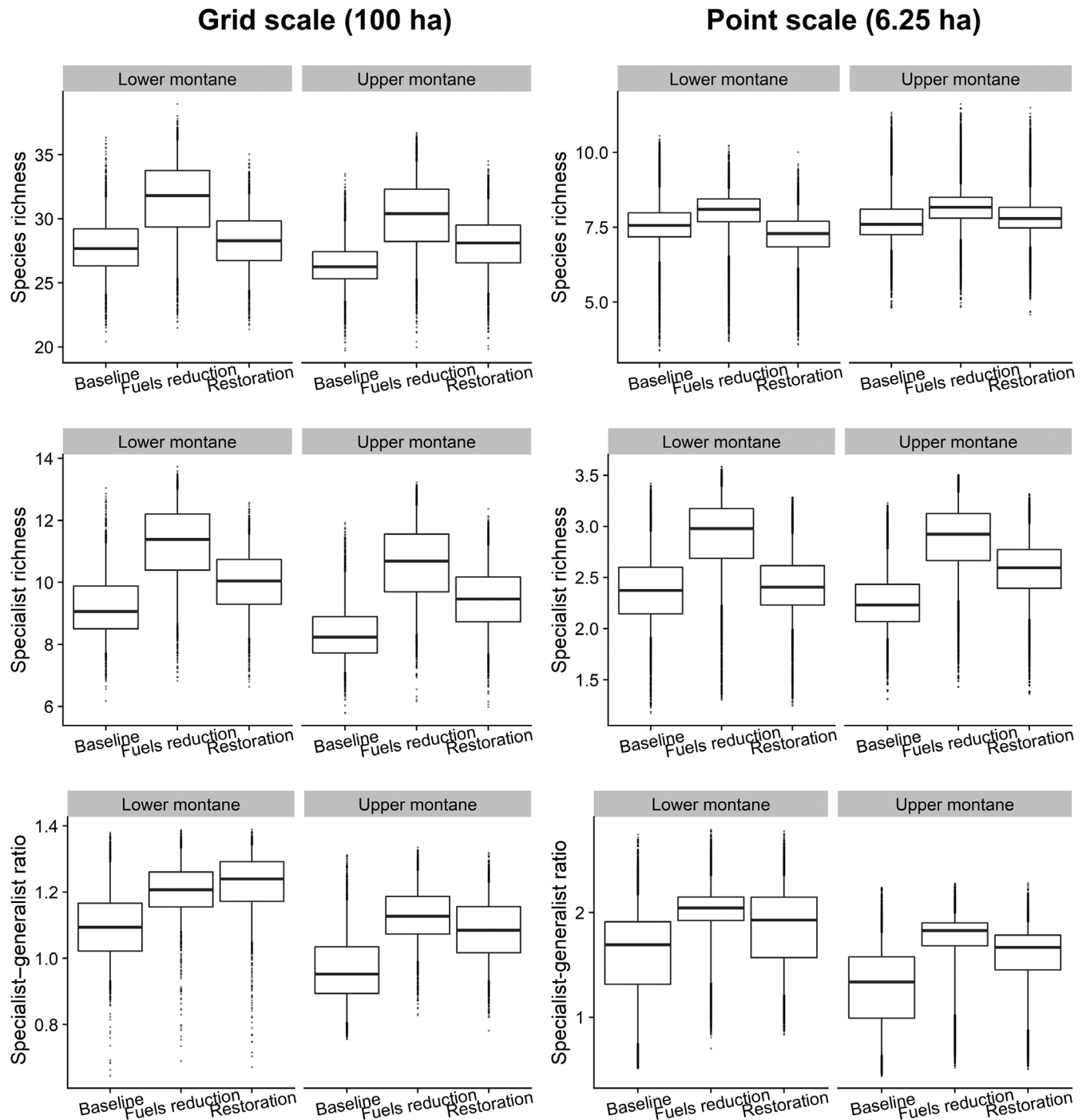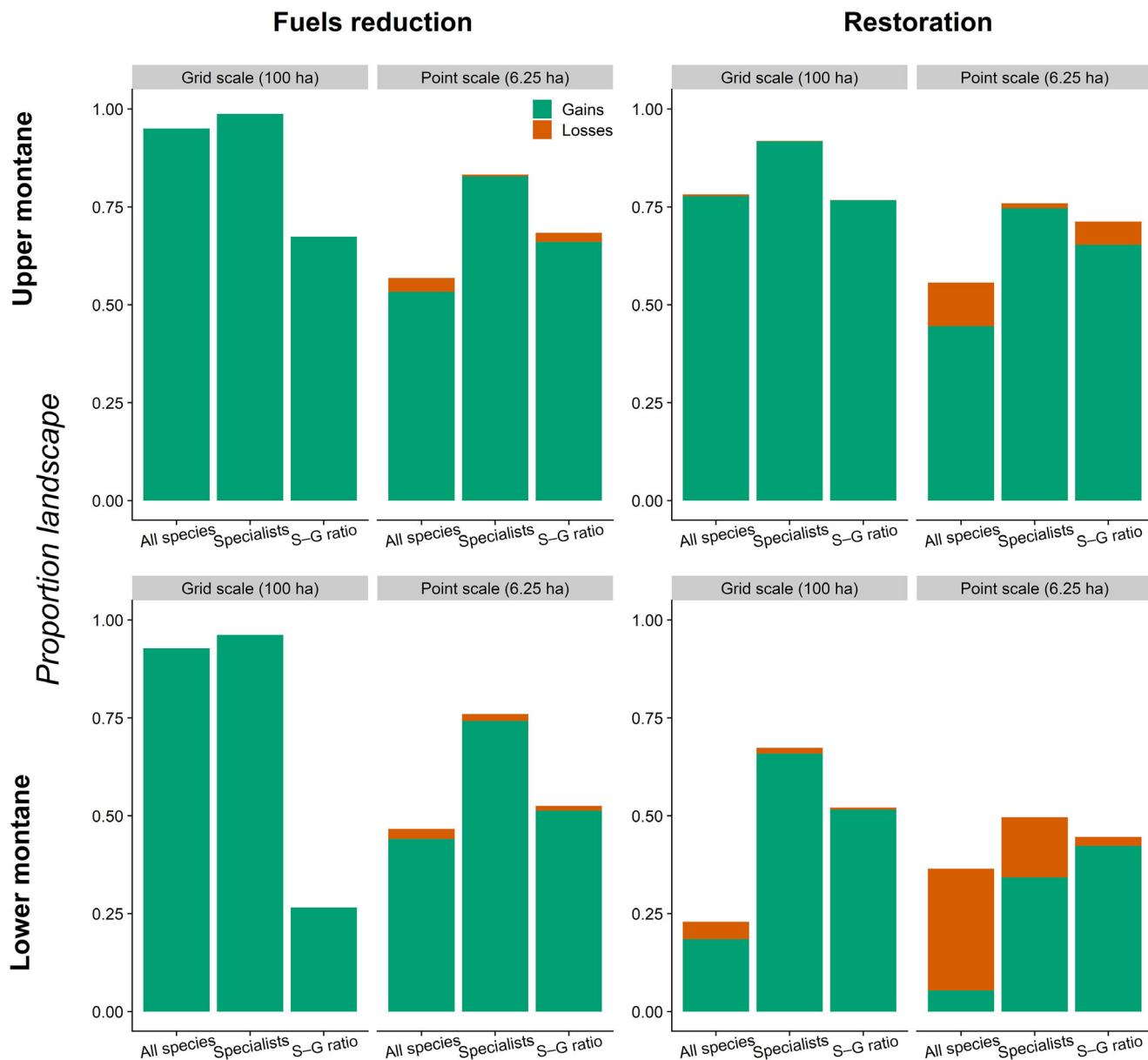
FIGURE 7 Summary of mapped predictions for avian community metrics under alternative management scenarios for Colorado Front Range dry conifer forests (USA). Community metrics are species richness, richness of ponderosa pine forest specialists (specialist richness), and the ratio of specialists to species not particularly associated with ponderosa pine forests (specialist–generalist ratio). Boxplots show the distribution of pixel-specific posterior median predictions for each metric across entire study landscape. Elements of each boxplot are median (horizontal line), 25th and 75th percentiles (box), 5th and 95th percentiles (whiskers), and pixels outside the 5th and 95th percentiles (dots). Mapping resolutions are 1 km² (100 ha) for grid-cell-scale metrics and 250 m² (6.25 ha) for point-scale metrics. Predictions are summarized by life zone (upper vs. lower montane)

analyses such as ours for informing particular planning decisions.

Our inferences regarding the role of landscape heterogeneity in mediating biological response to forest management are limited in several ways. We are restricted to

inferring richness patterns for relatively small-bodied forest birds. Previous work has established the importance of heterogeneity for apex predators with extensive breeding territories and complex habitat requirements (e.g., Goshawk; Reynolds et al., 2006). Additionally, two

FIGURE 8 Summary of predicted gains and losses in avian community metrics with active management of Colorado Front Range dry conifer forests (USA). Community metrics are species richness (All species), richness of ponderosa pine forest specialists (Specialists), and the ratio of specialists to species not particularly associated with ponderosa pine forests (specialist–generalist (S–G) ratio). Bars show the proportion of the study landscape that is predicted to increase (green) or decrease (red) at a statistically supported level (95% credible interval for the difference from baseline excludes zero). Summaries are separated by management scenario (fuels reduction vs. restoration), life zone (upper vs. lower montane forest), and scale of community metric (grid vs. point scale)

of four species exhibiting a positive relationship with canopy gaps are associated with grasslands (Western Meadowlark and Vesper Sparrow; Davis & Lanyon, 2020, Jones & Cornely, 2020). Considering the poor conservation status of grassland birds (Peterjohn & Sauer, 1999; Rosenberg et al., 2019), restoration of large canopy gaps could benefit biological conservation more so than reflected here if doing so generates habitat for additional grassland species.

Having excluded recent large wildfires from the sampling frame for avian data, our inferences are restricted to forests not impacted extensively by recent natural disturbance. Historically, natural disturbances such as fire are thought to have maintained landscape complexity in dry coniferous forests (Larson & Churchill, 2012; Ziegler et al., 2021). Implementing treatments in a manner that actually increases structural variability and landscape heterogeneity can be challenging even when explicitly

specified as management objectives (Barrett et al., 2021; Maher et al., 2019). Additionally, severity and scale limit the potential for forest management to emulate contributions of wildfire to biodiversity (Fontaine & Kennedy, 2012). Therefore, our conclusions regarding landscape heterogeneity do not necessarily apply to heterogeneity generated and maintained by natural disturbance.

Considering the 30 m resolution of remotely sensed canopy cover, our conclusions are restricted to landscape-scale structure and do not concern heterogeneity with respect to tree clumping and spacing at finer spatial scales. In principle, forest restoration targets historical levels of vegetation density and distribution at multiple spatial scales (Addington et al., 2018; Franklin et al., 2007). Despite questions we raise here regarding the value of explicitly targeting landscape heterogeneity for promoting avian diversity, we do not question the value of finer scale heterogeneity as a management target, especially for promoting desirable fine-scale fire behavior (Ritter et al., 2020), understory biodiversity (Matonis & Binkley, 2016), and tree competitive dynamics (Boyden & Binkley, 2015).

Broader implications

Our study extends the Cannon et al. (2020) mapping framework to include forest bird conservation along with wildfire-related objectives for informing dry conifer forest planning along the Colorado Front Range (for similar work in a different landscape, please refer to Stevens et al., 2016). By quantifying and summarizing opportunities for various management objectives, managers can more effectively decide where and how to implement forest management to further programmatic goals. Incorporating both government agency and private landowner priorities is especially critical to inform management of private forests, which make up 71% of the wildland–urban interface in western states, including Colorado (Schoennagel et al., 2009). The mapping framework extended here facilitates formal weighting of various priorities to identify where and how management effort could provide the greatest value. In addition to the three community metrics considered here, our extension of the Cannon et al. (2020) mapping framework allows formal consideration of various bird-related objectives, including occupancy for individual species of conservation concern or richness of any subset of species included in our analysis. Additionally, we substantially extend Cannon et al.'s (2020) mapping framework to include the northern portion of the Colorado Front Range, although assessment of wildfire-related ecosystem services remains currently restricted to the southern Front Range (i.e., the Upper South Platte Watershed).

Our results add to those of Cannon et al. (2020) concerning the value of landscape heterogeneity as an explicit target for active forest management. Cannon et al. (2020) projected similar benefits with restoration as with fuels reduction for wildfire-related ecosystem services. Therefore, restoration that explicitly targets historical levels of landscape heterogeneity does not necessarily provide any greater benefit than more narrowly focused fuels reduction for ecosystem services considered thus far in our mapping framework (i.e., wildfire hazard, soil erosion, forest bird species richness, and integrity of ponderosa pine forest bird assemblages). Forests in the upper montane zone are less departed from historical conditions, so simulated treatments in the upper montane zone tended to be relatively low intensity in our simulations. In contrast, reductions in canopy density required to achieve historical landscape structure (and represented in our simulations) within the lower montane zone would probably be impractical given contemporary regulatory and logistic constraints. In accordance with those constraints, post-treatment evaluations found that canopy cover in restoration treatments along Colorado's Front Range is higher on average than historical conditions (Cannon et al., 2018). Therefore, forest restoration in practice represents something in between the fuels reduction and restoration approaches represented in our simulations. Our results along with those of Cannon et al. (2020) suggest that failure to achieve landscape heterogeneity targets does not necessarily compromise the value of restoration for improving ecological function. Depending on their priorities, forest managers may want to focus application of restoration principles and articulation of heterogeneity targets at finer spatial scales, particularly in the lower montane life zone. We emphasize that our study does not contradict current thinking on the broad importance of heterogeneity to ecological function, but rather clarifies the scale at which targeting heterogeneity contributes to particular ecological objectives.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Quresh S. Latif served as principle investigator, secured funding, implemented avian modeling and analyses of model-based spatial predictions, and drafted the manuscript. Jeffery B. Cannon assisted with funding application, implemented management simulations, and provided input during development of the modeling approach. Eric J. Chabot and Robert A. Sparks implemented GIS-based spatial analyses, including development of both spatial layers representing avian modeling covariates and mapped products representing spatial predictions. Jeffery B. Cannon, Eric J. Chabot, and Robert A. Sparks provided editorial input during manuscript revision and peer review.

DATA AVAILABILITY STATEMENT
All scripts and data (Latif, 2021) are available in Dryad at https://doi.org/10.5061/dryad.0zpc866zc.

ORCID
Quresh S. Latif https://orcid.org/0000-0003-2925-5042
Jeffery B. Cannon https://orcid.org/0000-0002-8436-8712

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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