Dry conifer forest restoration benefits Colorado Front Range avian communities

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Abstract. Fire suppression has increased stand density and risk of severe, stand-replacing wildfire in lower elevation dry conifer forests of western North America, threatening ecological function. The U.S. Forest Service's Collaborative Forest Landscape Restoration Program (CFLRP) aims to mitigate impacts to ecological function, while mandating effectiveness monitoring to verify restoration success. Expected benefits include improved conditions for biodiversity, but relatively few empirical studies evaluate restoration effects on biodiversity. We applied the Integrated Monitoring in Bird Conservation Regions program to survey birds in relation to CFLRP treatments along the Colorado Front Range in 2015–2017. We employed hierarchical models to analyze species occupancy and richness at 1972 points nested within 141 1-km^2 grid cells. Our objectives were to investigate (1) species occupancy relationships with treatments at local (point) and landscape (grid) spatial scales, (2) potential mechanisms for treatment relationships considering species and treatment relationships with forest structure and composition (i.e., habitat relationships), and (3) treatment and habitat relationships with species richness. The data supported positive and negative point-level treatment relationships, suggesting uneven species distributions between treated and untreated points. At the grid scale, however, we only found positive species relationships with percent area treated, and accordingly, grid-level species richness increased with treatment extent. Potential mechanisms for treatment relationships included treatments generating foraging opportunities for aerial insectivores by opening the canopy, improving conditions for ground-associated species by increasing herbaceous growth, and limiting opportunities for shrub-nesting species by reducing shrub cover. Landscape-scale patterns suggest CFLRP treatments can benefit avian communities by generating habitat for open-forest species without necessarily eliminating habitat for closed-forest species. Our results provide evidence for a commonly expected but rarely verified pattern of increased species richness with forest heterogeneity. We suggest restoration treatments will most benefit forest bird diversity by reducing canopy cover, encouraging herbaceous ground cover, limiting ladder fuel species, and encouraging shrub diversity in canopy openings, while maintaining some dense forest stands on the landscape.

Key words: bird occupancy; Collaborative Forest Landscape Restoration Program; community models; dry mixed conifer forest; environmental heterogeneity; forest management; hierarchical analysis; ponderosa pine forest; species richness; U.S. Forest Service.

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 those dominated by ponderosa pine (*Pinus pondersa*; hereafter ponderosa pine forests) and dry mixed conifer forests (Moir et al. 1997, Schoennagel et al. 2004, Bock and Block 2005, Saab et al. 2005, Hessburg

et al. 2007). Fire suppression and forest management have increased densities of smaller trees and shrubs, homogenized forest structure, and encouraged fire intolerant tree species in these forests (Covington and Moore 1992, Agee 1993, Schoennagel et al. 2004). These changes in forest composition and structure tend to increase the extent and severity of wildfire and bark beetle (*Dendroctonus ponderosae*) outbreaks, risking permanent forest loss or persistent degradation exacerbated by climate warming (Schoennagel et al. 2004, Noss et al. 2006*b*).

In recognition of these impacts, federal policy promotes active restoration largely through the Collaborative Forest Landscape Restoration Program (CFLRP), established in 2009 to promote collaboration-based,

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landscape-scale, forest management (Schultz et al. 2012, Cannon et al. 2018). Forest management aims largely to reduce canopy and understory density using mechanical thinning and/or prescribed fire (i.e., fuels reduction), while encouraging large, fire- and drought-tolerant trees like ponderosa pine (Fulé et al. 2012). Additionally, restoration targets are beginning to include historical tree mortality patterns and heterogeneity at multiple scales (Hessburg et al. 2007, North et al. 2009, Churchill et al. 2013, Addington et al. 2018, Cannon et al. 2018). Ecologists expect restoration of historical forest conditions, including more extensive open-forest conditions and greater landscape heterogeneity, to improve forest resilience and allow natural disturbance to maintain desirable forest structure (Noss et al. 2006b, Fulé et al. 2012, Churchill et al. 2013). The CFLRP requires ecological monitoring to evaluate restoration effectiveness for achieving goals of each funded project (Schultz et al. 2012, Cannon et al. 2018).

The 13 CFLRP projects implemented across the country includes one in Colorado's Front Range that supports broad-scale restoration of dry conifer forests (Underhill et al. 2014). The U.S. Forest Service administers funding for this project, and multiple stakeholders, including federal, state, and local agencies, non-governmental conservation organizations, and local industry, collaboratively develop prescriptions (Schultz et al. 2012, Underhill et al. 2014). Treatment prescriptions include local ecological and economic objectives, and have evolved from initially emphasizing fuels reduction via mechanical thinning to incorporating more prescribed fire and natural patterning of retained vegetation. Nevertheless, treatments share overarching objectives, including creating historically relevant stand conditions characteristic of low-to-mixed-severity disturbance regimes by reducing canopy cover, creating persistent openings, and encouraging heterogeneity at multiple scales (Underhill et al. 2014, Addington et al. 2018, Cannon et al. 2018). Earliest treatments along the Front Range were completed in 2006, and treatment of the entire landscape is ongoing.

Wildlife evolved under historical disturbance regimes (Bock and Block 2005), so restoration that targets historical patterns should return forests to conditions aligned with species evolutionary histories and thereby promote biodiversity (Noss et al. 2006a, Hutto et al. 2008). Additionally, restoration treatments distributed across a landscape may improve heterogeneity at a broader scale, potentially reconciling forest health and biodiversity objectives even if restoration and wildlife conservation objectives do not align for individual projects (Noss et al. 2006a). In southwestern ponderosa pine forests, avian relationships with treatments that target historical conditions are broadly positive as expected (Kalies et al. 2010), but treatment relationships are more variable in mixed conifer forests (Fontaine and Kennedy 2012). Regardless, landscape heterogeneity is thought to allow coexistence of species differentially adapted to various forest conditions (Clarke 2008, Kalies et al. 2010, Fontaine and Kennedy 2012) consistent with more general theory and evidence (Stein et al. 2014).

Although effectiveness monitoring along the Front Range focuses largely on vegetation (e.g., Cannon et al. 2018), the wildlife committee also identified birds as a monitoring focus for evaluating biodiversity conservation objectives. Birds can respond quickly to environmental change, and passive surveys can provide data on many species without specialized equipment to inform both species-specific and community-wide patterns. Additionally, by focusing on birds, observers can leverage and build upon a rich line of research for understanding species and community relationships with treatments and associated conditions (Gaines et al. 2007, Hurteau et al. 2008, Gaines et al. 2010, Kalies et al. 2010, Fontaine and Kennedy 2012, Kalies and Rosenstock 2013). Birds represent a variety of life history traits, allowing us to consider functional relationships with treatments. Positive relationships with treatments are described for aerial insectivores, species that eat conifer seeds, and species that forage and nest in understory vegetation, whereas negative relationships are described for canopy-associated foliage-gleaning insectivores, consistent with expected treatment effects on relevant resources (Gaines et al. 2007). Trait-level patterns are not necessarily consistent across studies, however (compare Gaines et al. 2007 to Kalies et al. 2010), perhaps because individual species represent multiple traits with potentially conflicting resource demands. Many researchers therefore focus instead on evaluating species-level patterns, but even these can vary across forests and treatments (compare references above). Considering this variability, ornithologists generally expect heterogeneous landscapes representing a range of disturbance and management histories to support the greatest diversity of bird species (Saab et al. 2005, Fontaine and Kennedy 2012, Latif et al. 2016b), but researchers rarely sample at landscape scales needed to verify this expectation.

Here, we analyze avian relationships with forest management treatments and related environmental features arising from the first 3 yr of monitoring in the Front Range CFLRP boundary. We surveyed nested units (points within grid cells), a subset of which intersected treatments implemented within 1–10 yr prior to bird surveys. Our objectives were to investigate (1) species occupancy relationships with treatments at two spatial scales, (2) potential mechanisms for treatment relationships involving treatment effects on bird habitat, and (3) treatment relationships with species richness along with potential mechanisms. We expected treatments to encourage conditions historically characteristic of dry conifer forests, and therefore predicted bird species would predominantly relate positively with these conditions and consequently with treatments (Kalies and Rosenstock 2013). We also expected bird species occupancy and richness to be higher in treated landscapes, because we expected treatments to

promote heterogeneity and thereby accommodate a greater range of species. Based on consistency with potential mechanisms, we evaluated the extent to which observed patterns likely reflected treatment responses vs. potentially confounding factors. Finally, we suggest how relationships from this study could inform forest management and restoration targets.

METHODS

Study area

We studied terrestrial birds in lower elevation dry conifer forests in Pike, Arapaho, and Roosevelt National Forests along the Colorado Front Range (1,832–2,895 m above sea level; Fig. 1). At lower elevations, ponderosa pine forests have been 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 maintained by frequent, low-severity wildfire (Kaufmann et al. 2001). Dry mixed-conifer forests occur at somewhat higher elevations and latitudes, where moister conditions have historically favored less frequent, mixed-severity wildfire, and greater heterogeneity in forest structure and composition at multiple scales (Underhill et al. 2014). Reduced wildfire frequency and timber harvest have created denser stands composed of smaller trees for both forest types. Current conditions include 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). Secondary tree species (those other than ponderosa pine) tend to be less fire tolerant and therefore have increased in dominance with altered fire regimes. Additionally, shrub cover has increased driven primarily by increases in tree species saplings, which are especially capable of carrying surface fires into the canopy. These conditions contribute to higher rates of crown fire exemplified by recent Front Range fire events (Graham et al. 2012, Addington et al. 2018).

Our study assessed bird distributions in relation to CFLRP treatments on Front Range National Forest lands implemented in 2006–2015. By 2015, CFLRP treatments recorded in the Forest Service Activity Tracking System (FACTS) had been implemented across 15,100 ha of forest, most of which consisted of mechanical thinning (13,100 ha) but also some prescribed fire (2,400 ha; ignores 600 ha of treatments with unknown completion dates). Overarching treatment goals included reduced crown and understory vegetation density, increased structural heterogeneity, and retention of large old drought- and fire-tolerant trees. Particular targets additionally reflected conditions naturally and historically associated with local topography and soils (Addington et al. 2018, Cannon et al. 2018). Reflecting interests of various stakeholders, CFLRP prescriptions incorporate local ecology and socioeconomic objectives, so details on individual treatments were not readily available, although managers must maintain broad restoration goals to secure funding (Addington et al. 2018, Cannon et al. 2018). Treatments achieve these goals with varying degrees of success and potential for learning from initial treatments to improve outcomes for subsequent treatments (Cannon et al. 2018). Additionally, non-CFLRP treatments, including clear cuts, mechanical thinning, and prescribed fire, were implemented across 17,000 ha (1989–2015; FACTS 2018), and at least 19 wildfires burned 115,400 ha (1984–2015; MTBS 2018) of our study area (3% and 20% of the landscape, respectively).

Bird surveys

Because treatments represented in our sample were largely complete prior to bird surveys, our study assesses bird response to CFLRP treatments relative to untreated areas of the landscape using an impact-reference design (Morrison et al. 2001). Our design leveraged sampling under the Integrated Monitoring in Bird Conservation Regions (IMBCR) program (Pavlacky et al. 2017). We defined the sampling frame by overlaying a 1-km^2 grid over the study area (Fig. 1). The sampling frame initially included regions between 1,828 and 2,743 m on the Arapaho and Roosevelt National Forests and between 1,828 and 2,896 m on the Pike National Forest. These elevation ranges reflect the distribution of ponderosa pine in these national forests. From this broader area, we excluded regions within boundaries of wildfires >400 ha between 1998 and 2013 (i.e., those delineated in available remotely sensed data; MTBS 2018) and open water. Additionally, after compiling and examining landscape metrics for sampled grid cells, we excluded cells within landscapes with extensive canopy gaps from the sampling frame (i.e., landscapes with >27% coverage of areas with <10% canopy cover; described further under *Treatment and environmental data*). The impact stratum consisted of areas within the sampling frame where CFLRP treatments had occurred or were planned but had not yet been implemented, and reference strata consisted of all other lands potentially subject to or affected by treatment. The 1-km^2 sampling units were selected from each stratum using spatially balanced random sampling (Stevens and Olsen 2004). Our sampling scheme allowed for an increasing percentage of units to intersect treatment units over time. Thus, we anticipate ultimately collecting data before and after treatment implementation in some units to allow before-after, control-impact (BACI) analysis (Popescu et al. 2012, Russell et al. 2015). As a midterm evaluation of treatment effectiveness for achieving forest health and biodiversity goals, however, intended sampling had not been fully realized at the time of this
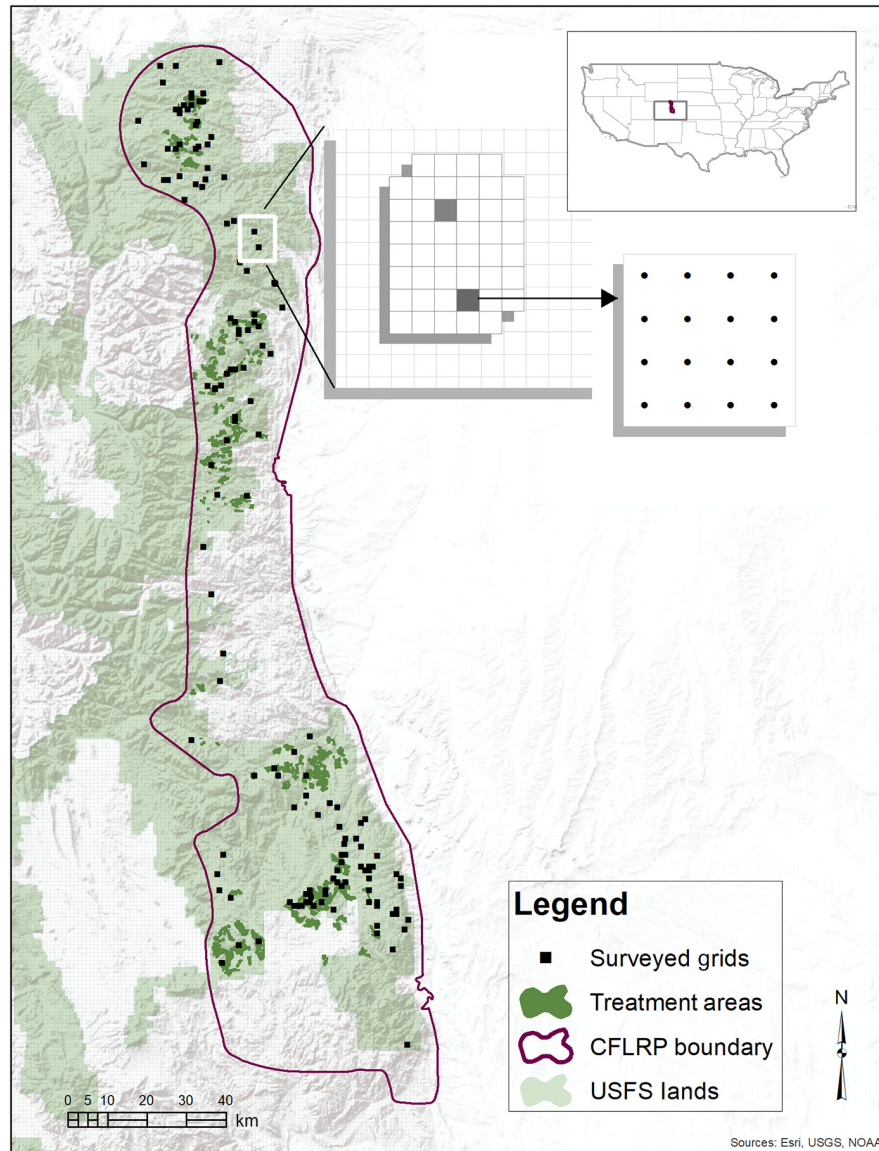
Fig. 1. Map of study area showing surveyed grids, treatment areas, Collaborative Forest Landscape Restoration Program (CFLRP) boundary and U.S. Forest Service lands. Insets show primary and secondary sampling units.

study. Our inferences therefore included the potential for confounding spatial variation inherent with impact-reference designs (Morrison et al. 2001). In particular, the reference sample potentially included meadows, riparian, extensive shrubby openings, and areas impacted previously by non-CFLRP management or small natural disturbances. Although such areas would not be subject to treatment per se, they could be affected by adjacent treatments and they represent components of the landscape targeted for restoration, so we considered their inclusion in the reference sample appropriate. In contrast, large wildfires represent conditions outside the historical range of variability that forest restoration aims to avoid.

Primary sampling units consisted of 141 1-km^2 grid cells, each containing up to 16 points spaced 250 m apart in a 4 × 4 array (1972 points total), at which field surveys were centered (Pavlacky et al. 2017). Of these, 292 points within 54 grid cells had been treated by 2016, of which a subset were surveyed every year (Table 1). We surveyed 132 grid cells in either or both 2014 and 2016 (116 cells each year). In 2015, we surveyed a smaller set of 50 grid cells as part of a separate pilot study focused on Abert's Squirrel (*Sciurus aberti*). Although selected using convenience sampling, 82% (41) of 2015 grid cells were members of spatially balanced 2014 and 2016 samples. We conducted point count surveys of 6 minutes duration during the breeding season (dates varied by

TABLE 1. Sample sizes for analyzing avian relationships with restoration treatments in ponderosa pine forests along the Colorado Front Range.

Year	Treated	Untreated
Grid level		
2014	48	68
2015	23	27
2016	46	70
All	54	87
Point level		
2014	208	1161
2015	103	477
2016	231	1337
All	292	1680

Notes: Treated points are those that intersected units treated under the Collaborative Forest Landscape Restoration Program (CFLRP). Treated grids are those within 1 km of a treated unit. Reported are the number of units surveyed in each year, and the total number surveyed across all three years.

elevation; Kingery 1998) between 0.5 h before and 5 h after sunrise. Surveyors recorded all individual birds detected by species during the survey period, along with distances (m) to detected individuals (measured with laser range finders) and time elapsed within the survey (0–6 minutes) when detections were recorded (for details, see Hanni et al. 2018).

Treatment and environmental data

We compiled three metrics quantifying CFLRP treatments (Table 2). We queried the Forest Service Activity Tracking System (FACTS 2018) to obtain spatial polygons representing units where CFLRP funded projects were implemented. We overlaid our sampling units with these polygons to quantify the extent of treatments (percTrt, Trt) and time since treatment (YST) in relation to our surveys using a Geographic Information System (ESRI 2018). Because treatments are often implemented over extended periods, we could not pinpoint within-year timing of treatment completion. We chose to consider points or units within grid neighborhoods to have been treated if the completion year in FACTS preceded the survey year. Thus, treatment metric values represented the extent of treatments contemporaneous to when bird surveys were implemented as closely as possible.

We compiled nine point-level metrics of vegetation structure from data collected following the IMBCR protocol (Table 2; Hanni et al. 2018). We measured vegetation structure using ocular estimation implemented for 50-m radius plots centered on survey points. Surveyors measured vegetation on the same day as bird surveys. Prior to surveys, we trained surveyors to ensure ocular estimates for vegetation metrics were within 10% of the trainers' estimates. Missing values included missed measurements and those that clearly exceeded realistic bounds or were inconsistent with other measurements.

We imputed missing point-level covariate values as part of Bayesian model fitting (described in occupancy model structure, Data analysis).

We compiled three metrics quantifying landscape structure within 3×3 km (900 ha) neighborhoods centered on survey grids based on remotely sensed LANDFIRE canopy cover data (Table 2; USGS 2014). We considered a 3×3 km neighborhood large enough to adequately quantify landscape composition and configuration, but small enough to be ecologically relevant to land birds (Pavlacky et al. 2015). These metrics were based on canopy cover derived from 2014 LANDFIRE imagery with values adjusted to approximate canopy cover loss with treatments implemented during survey years (2014–2016). 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 FACTS (2018). We derived proportion canopy cover loss values for each treatment type from the literature (Stephens and Moghaddas 2005, Fulé et al. 2012, Ziegler 2014). After compiling these metrics, we noticed a maximum canopy gap extent of 27% for landscapes containing treated grid cells (max PACCOpn = 27%; Table 2). We therefore excluded five grid cells from the reference sample with PACCOpn > 27%, thereby further restricting the sampling frame to focus on the landscape of interest for CFLRP treatments. For perimeter : area ratio of open forest patches (PAROpn; Table 2), we filled undefined grid cell values where there was no open forest with the mean for defined values. Slope estimates for linear covariate relationships are informed by observations with covariate values that deviate from the mean, so mean substitution ensured that observations with undefined values would not inform estimated relationships with PAROpn. Additionally, because PAROpn is undefined where PACCOpn = 0, mean substitution of undefined PAROpn values avoids inadvertently inducing a correlation between PAROpn and PACCOpn, which would unnecessarily complicate interpretation of occupancy models that include both covariates.

We compiled four metrics quantifying topography and survey timing and one more distinguishing forests at different latitudes. Additional metrics (not listed) described mean size, shape (perimeter : area ratio), and isolation of canopy gaps and open forest, relative cover of aspen in the shrub layer, and anthropogenic road density. We dropped these metrics, however, because they were correlated with other metrics ($r \geq 0.7$) or lacked statistical support (95% credible intervals for species occupancy relationships all included zero).

Framework for inference

Our inferences addressed two questions: (1) how do species occupancy and richness relate with restoration treatments (objectives 1 and 3) and (2) what were the potential mechanisms by which habitat change following

TABLE 2. Covariates included in analyses relating avian occupancy with CFLRP treatments and associated environmental attributes along the Colorado Front Range.

Feature and covariate	Abbreviation	Scale (ha)	Description
Treatment			
Treatment status	Trt	4.9	Binary indicator of whether survey point was treated (approximates whether >50% of 4.9 ha plot was treated).
Percent treatment	percTrt	314	Percent landscape treated (Treatment status = 1), where landscape is 1-km radius neighborhood centered on the grid
Years since treatment	YST	4.9	No. years since treatment
Vegetation structure			
Canopy cover	CanCov	4.9	Percent canopy cover
Canopy height	CanHt	4.9	Mean height to the top of overstory trees (m)
No. snags	NSnag	4.9	Count of snags within 50 m of survey points
Ponderosa pine canopy	PIPO	4.9	Percent of canopy provided by ponderosa pine (relative cover)
Douglas-fir canopy	PSME	4.9	Percent of canopy provided by Douglas-fir (relative cover)
Aspen canopy	POTR5	4.9	Percent of canopy provided by aspen (relative cover)
Shrub-sapling volume	ShrbVol	4.9	Cube root of volume (m^3), where volume = area covered (maximum = 7854 m^2, i.e., plot area) × average shrub height (m) for woody shrub and seedling trees species
Ladder fuel shrubs	LadFuel	4.9	Percent of shrub layer consisting of ladder fuel species, i.e., conifer, juniper, and gambell's oak saplings
Herbaceous volume	Herb	4.9	Cube root of volume (m^3), where volume = area covered by grasses and forbs (maximum = 7854 m^2, i.e., plot area) × average height (m) of grass and forbs
Landscape structure			
Extent of canopy gaps	PACCGap	900	Percent area of neighborhood with <10% LANDFIRE canopy cover
Extent of open forest	PACCOpn	900	Percent area of neighborhood with 10–40% LANDFIRE canopy cover
Perimeter : area ratio open forest	PAROpn	900	Mean perimeter-area ratio for patches of <10% LANDFIRE canopy cover
Topography			
Heat load	Heat	100	potential direct incident solar radiation (McCune 2007[2007]; MJ·cm^{-2}·yr^{-1}; mean of point-level values for each grid)
Topographic wetness index	TWI	100	Index of water retention potential based on topographic slope (Beven and Kirkby [1979]; mean of point-level values for each grid)
Forest			
Forest			Blocking variable distinguishing grids in Arapahoe-Roosevelt (1) vs. Pike (0) National Forest
Survey timing			
Day of year	DOY		No. days elapsed since January 1
Time of day[†]	Time		No. minutes elapsed since 00:00 h

Notes: Covariates were either compiled for 1-km^2 grids (scale = 100, 314, or 900 ha) or points nested within grids (scale = 4.9 ha). Two covariates for points and one for grids quantified treatments. Environmental covariates quantified vegetation structure for points and landscape structure and topography for grids. Additionally, Forest distinguished between sampling units in two national forests at the grid level.

† The effect of Time was represented as a quadratic relationship (Time + Time^2) in occupancy models.

treatment could have modulated these relationships (objectives 2 and 3). We compared the direction of observed relationships with plausible mechanisms for treatment effects on birds (Fig. 2). We also compared relationships with predictions based on species life histories and restoration targets (Tables 3, Appendix S1: Table S1). Our inferences emphasized patterns consistent with predictions and plausible mechanisms and were otherwise more cautious.

We predicted treatment–environment correlations based on treatment targets (Appendix S1: Table S1). We expected treated points to have less canopy cover, less shrub-sapling volume, less ladder fuel shrub dominance, less Douglas-fir, and more ponderosa pine. We also expected fewer small trees and more large trees at treated points, and consequently greater canopy height. We expected more extensive open forest and canopy gaps at treated grids. We had fewer predictions for years since treatment because 10 yr (time since earliest treatment) represents a limited timeframe for realizing ecological succession. Nevertheless, we evaluated these relationships as they potentially reflected evolution of treatment
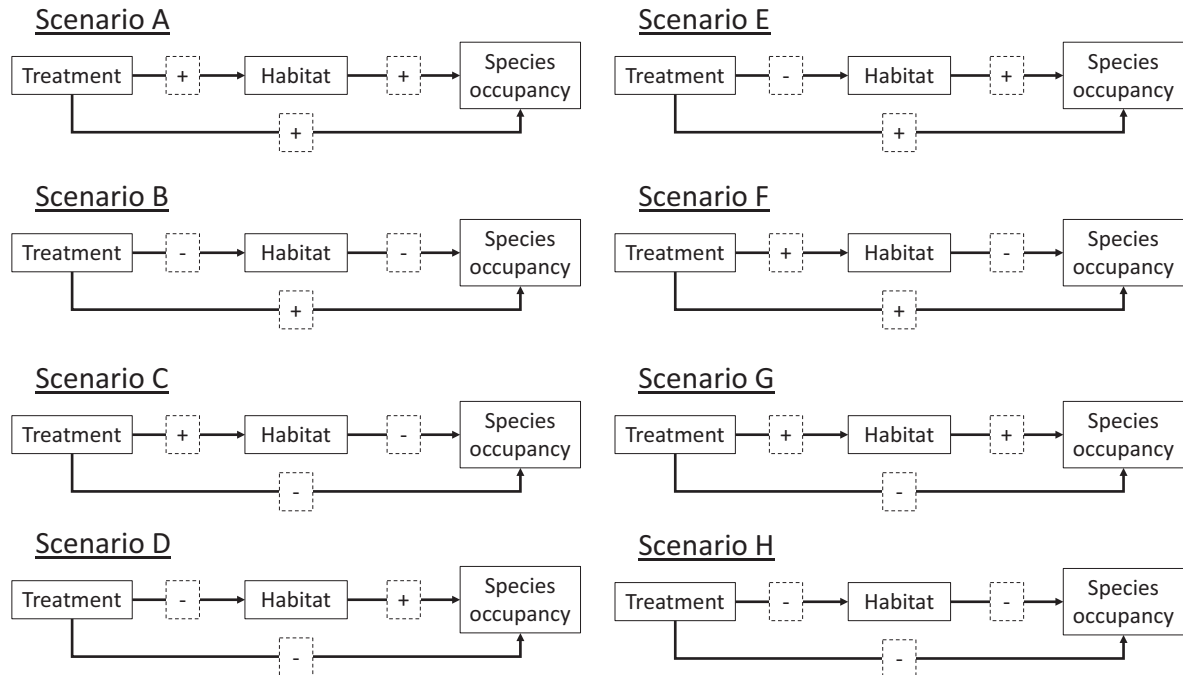
FIG. 2. Scenarios making up the framework used to infer how habitat could modulate treatment effects on species occupancy. Each scenario describes relationships (positive or negative) between a treatment metric, a habitat feature, and species occupancy. Scenarios A–D are consistent with habitat modulating a treatment effect on species occupancy. Conversely, Scenarios E–H are not consistent with habitat modulating a treatment effect.

targets, prescriptions, and effectiveness (Cannon et al. 2018).

We evaluated several predictions for species based on their life history traits (Table 3). We expected greater foraging opportunities for aerial insectivores in canopy openings with treatment, and for understory-foraging species with increased herbaceous growth. We also expected species that forage on conifer seeds to benefit from increased cone productivity for large ponderosa pine trees with reduced competition from smaller trees (Krannitz and Duralia 2004). We expected open-cup shrub- and canopy-nesting species to avoid treated points with less woody vegetation density, but we expected ground-nesting species to favor treated points with more herbaceous cover. Recognizing that these traits are not comprehensive and that species represent composites of multiple traits, we also considered literature describing treatment relationships, potential mechanisms, and other aspects of species ecology (Gaines et al. 2007, Hurteau et al. 2008, Gaines et al. 2010, Kalies et al. 2010, Kalies and Rosenstock 2013) when interpreting our results.

Data analysis

Occupancy model structure.—We analyzed avian distributions using multispecies, multiscale occupancy models (Zipkin et al. 2009, Dorazio et al. 2011, Mordecai et al.

2011). Occupancy models leverage replicate survey data to estimate species detectability (p; MacKenzie et al. 2002, 2018). Nested sampling allowed us to estimate grid occupancy probability (ψ) and occupancy of points within occupied grids (θ; Mordecai et al. 2011, Pavlacky et al. 2017). We used a removal design to represent the timing of detections within surveys, whereby 1-minute-interval encounter histories omitted intervals following the first detection for each species (Rota et al. 2009, Pavlacky et al. 2012). Thus, point occupancy estimates represented the probability of the species being present and available for detection if present at the grid. Point occupancy likely indexed local abundance for species with territories ⪆4.9 ha, whereas grid occupancy quantified coarser scale species distribution (Latif et al. 2016*a*, 2018).

We used a hierarchical multispecies structure to estimate species-specific parameters (ψ, θ, and p) as random variables governed by community level hyperparameters. The use of a common distribution among species improves precision of species-specific parameters, particularly for rare species (Zipkin et al. 2009, Dorazio et al. 2011, reviewed by Kéry and Royle 2016). Considering our interest in inferring patterns at two levels, species and community, we followed the example of numerous studies that draw species-specific parameters from a single common distribution (Dorazio et al. 2006, Kéry et al. 2009, Zipkin et al. 2009). We excluded raptors,

TABLE 3. Predicted relationships of avian occupancy with treatment and habitat covariates based on species life history traits.

Code	Description	Treatment response	Habitat relationships
Nesting			
C_P	primary cavity nesters, i.e., woodpeckers that excavate cavities	–	NSnag (+)
C_S	secondary cavity nesters, i.e., use previously excavated cavities	–	NSnag (+)
O_C	species with open-cup nests placed in the canopy	negative	PACCGap (−), PACCOpn (−), CanCov (+)
O_S	species with open-cup nests placed in woody understory vegetation, i.e., shrubs	negative	ShrubVol (+)
O_G	species with open-cup nests placed on the ground	positive	Herb (+)
Foraging			
S	woodpeckers that forage for beetle larvae in snags	–	NSnag (+)
FB	bark- and canopy-foliage-gleaning insectivores	negative	PACCGap (−), PACCOpn (−), CanCov (+)
CS	species that forage on conifer seeds	positive	CanCov(−), PIPO (+)
U	species that forage on the ground or in the understory	positive	Herb (+)
AI	aerial insectivores	positive	PACCGap (+), PACCOpn (+), CanCov (−)

Notes: Predicted habitat relationships also represent expected mechanisms for predicted treatment relationships where present. For example, open-cup nesting species are predicted to relate negatively with treatment because treatments are expected to reduce canopy cover, which is expected to reduce nesting opportunities. Dashes indicate no predicted treatment relationship. For covariate descriptions, see Table 2.

owls, grouse, cranes, and water birds not readily detectable with our survey methods. We only included species that breed in our study area, but we augmented data to include undetected potential breeders to fully correct species richness estimates for imperfect detection (Zipkin et al. 2009, Dorazio et al. 2011). The super-community of observed and potential breeders was $M = 127$ species representing all species detected in Bird Conservation Region 16 dry conifer forests (i.e., ponderosa pine, lodgepole pine, or mixed conifer forest; Hanni et al. 2018) during 2010–2017 IMBCR surveys.

We considered detection data, **y**, as representing four dimensions; $y_{ijkt} = 1$ indicated species i ($i = 1, \ldots, M$; $M = 127$) was detected at point j ($j = 1, \ldots, J$; $J = 16$) within grid k ($k = 1, \ldots, K$; $K = 146$) in year t ($t = 1, \ldots, T$; $T = 3$). A parallel array, **R**, indicated the 1-minute

interval when detections were recorded ($r_{ijkt} \in \{1, 2, \ldots, 6\}$ when $y_{ijkt} = 1$ or $r_{ijkt} = 6$ when $y_{ijkt} = 0$). We modeled data generation as

$$y_{ijkt} | u_{ijkt} \sim \text{Binomial}(r_{ijkt}, p_{ijkt} \times u_{ijkt}) \quad (1)$$

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

$$u_{ijkt} | z_{ikt} \sim \text{Bernoulli}(\theta_{ijkt} \times z_{ikt}) \quad (2)$$

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

$$z_{ikt} | w_i \sim \text{Bernoulli}(\psi_{ikt} \times w_i) \quad (3)$$

where ψ_{ikt} is the grid occupancy probability for species i given that species i belongs in the super community. Finally, we modeled whether species i belonged to the super community as $w_i \sim \text{Bernoulli}(\Omega)$ (Zipkin et al. 2009, Dorazio et al. 2011).

We modeled occupancy and detection probabilities as logit-linear functions of covariates

$$\text{logit}(p_{ijkt}) = \alpha_{0,i} + \alpha_i \times X_{jkt} \quad (4)$$

$$\text{logit}(\theta_{ijkt}) = \beta_{0,i} + b_i \times X_{jkt} \quad (5)$$

and

$$\text{logit}(\psi_{ikt}) = \delta_{0,it} + \delta_i \times X_{kt} \quad (6)$$

where $\alpha_{0,i}$, $\beta_{0,i}$, and $\delta_{0,it}$ are intercept parameters, X represent arrays of covariate values, and α_i, β_i, and δ_i are species-specific vectors containing covariate relationships. We modeled all three sets of parameters as species-specific normal random effects, and $\delta_{0,it}$ also with a fixed effect of year. We modeled detection probability (p) and point occupancy (θ) with point-level covariates, and grid occupancy (ψ) with grid-level covariates (Table 2).

We implemented analyses with different sets of covariates to address different questions (see *Framework for inference*). For Question 1, we related occupancy and detection probabilities with treatment covariates (hereafter "treatment model"). We only estimated point occupancy relationships with years since treatment within treated units (YST = 0 where Trt = 0). For Question 2, we related occupancy and detectability with environmental covariates (vegetation and landscape structure in Table 2; hereafter "habitat model"). We imputed missing values for point-level environmental covariates using Normal(μ, SD) priors, where μ and SD are the mean and standard deviation of values for neighboring points within the same grid. For Questions 1 and 2, we considered parameters describing covariate relationships

statistically supported where 95% Bayesian credible intervals (hereafter 95% BCIs) excluded zero. To assess potential mechanisms (Question 2; Fig. 2), we examined scatter plots and Pearson's correlation coefficients relating treatment with environmental metrics at corresponding scales. We included additional grid-level occupancy covariates representing topography and national forest, and survey timing covariates for detection in both treatment and habitat models. We included a quadratic term to allow non-linear relationships of detectability with survey timing ($Time + Time^2$). All continuous covariates were scaled to mean = 0 and SD = 1 to facilitate computation and prediction for both models.

Analogous to single-scale multispecies models (Dorazio et al. 2006, 2011, Zipkin et al. 2009, Kéry and Royle 2016), we informed species parameter estimates by incorporating bivariate correlation terms into community level hyper-parameters. These correlation terms related species detection ($\alpha_{0,i}$) with point occupancy ($\beta_{0,i}$; $\rho_{\theta p}$), and point occupancy ($\beta_{0,i}$) with grid occupancy ($\delta_{0,i}$; $\rho_{\psi\theta}$). These correlation terms allowed our models to approximate the general pattern of highly abundant species being both easier to detect and prevalent across the landscape (Dorazio et al. 2006, Kéry et al. 2009, Zipkin et al. 2009). As such, we expected these correlations to be positive, thereby more accurately informing occupancy and detectability for rare species, ultimately to improve estimates of species richness. We assumed a multivariate logit-scale normal distribution, where $\rho_{\psi p} = 0$ and other non-zero off-diagonal elements of the variance–covariance matrix for occupancy and detection parameters were between $\alpha_{0,i}$ and $\beta_{0,i}$ or between $\beta_{0,i}$ and $\delta_{0,i}$.

Species richness.—We inferred richness patterns represented in our models by plotting richness estimates in relation to covariates. We derived two types of richness estimates at both grid and point scales. Finite-sample estimates were partially observed at surveyed units: $\hat{N}_{\psi,obs,k} = \sum_{i=1}^{M} z_{ik}$ and $\hat{N}_{\theta,obs,jk} = \sum_{i=1}^{M} u_{ijk}$. We also derived out-of-sample predicted richness: $\hat{N}_{\psi,pred,kt} = \sum_{i=1}^{M} \psi_{ikt}$ and $\hat{N}_{\theta,pred,jk} = \sum_{i=1}^{M} \psi_{0,i} \times \theta_{ijk}$ along covariate gradients, where $\psi_{0,i}$ = predicted grid occupancy at mean covariate values. By plotting these estimates along covariate gradients, we summarized emergent richness patterns implied by model-estimated species occupancy relationships. We inferred statistical support for richness patterns from posterior median estimates and 95% BCIs for community level hyper-parameters describing mean covariate relationships for the community as a whole.

In addition to inferred richness patterns, we analyzed species richness estimates derived from the treatment model to evaluate a hypothesis for the emergent effects of treatment-mediated heterogeneity on avian community structure. Although we did not model quadratic effects of treatment extent on grid-level species occupancy, we expected landscape heterogeneity and

consequently bird species richness to peak at intermediate treatment extents (percTrt) as an emergent property of varying linear effects among species (Whittaker et al. 2001). To look for this emergent property, we used applied generalized linear regression to relate posterior species richness estimates with treatment extent

$$\log(\hat{N}_{\psi,kt}) = \Gamma_{0,t} + \Gamma_{percTrt} \times percTrt_{kt} + \Gamma_{percTrt^2} \times percTrt_{kt}^2 \tag{7}$$

where Γ represent intercept and slope regression parameters. We fitted this model to posterior estimates of N_ψ, and summarized model predictions in relation to percTrt to derive evidence relevant to our hypothesis (details in Appendix S2).

Model fitting.—We sampled posterior parameter distributions for all models using JAGS v.4 (Plummer 2003) programmed from R (Kellner 2017). We used independent noninformative priors for all parameters (for priors, see Appendix S3; model code and data available (see *Data Availability*). We ran three parallel MCMC chains of length $\geq$30,000, burn-in = 1,000, and thinning = 10 to sample posterior distributions until $n_{effective} \geq 100$ and $\hat{R} \leq 1.1$ for all parameters (Gelman and Hill 2007).

RESULTS

Surveyors detected 103 species during the study period (Appendix S4). The five most frequently detected species were Yellow-rumped Warbler, Dark-eyed Junco, Mountain Chickadee, Broad-tailed Hummingbird, and American Robin. As expected, community models estimated and accounted for positive correlations between point occupancy and detectability (posterior median [95% BCIs]: $\rho_{\theta p} = 0.68$ [0.45, 0.81] and 0.58 [0.29, 0.77] for treatment and habitat models, respectively) and between point and grid occupancy ($\rho_{\psi\theta} = 0.80$ [0.67, 0.89] and 0.81 [0.66, 0.89] for treatment and habitat models, respectively), resulting in the hyper-parameter structure intended for appropriately estimating species richness. Sampling units represented a broad range of covariate values (Appendix S5). Posterior median detectability estimates for a 6-minute survey ranged 0.18–0.99, with 45 species exhibiting statistically supported covariate relationships with detectability in one or both models (Appendix S6).

Species relationships with treatments

We found statistical support for 37 occupancy relationships with one or more treatment covariates for 28 species (Fig. 3). At the point-level, seven positive and 10 negative relationships with treatment status (Trt) were statistically supported, as well as four negative relationships with years since treatment (YST) within treated units. At the grid level, the data only definitively
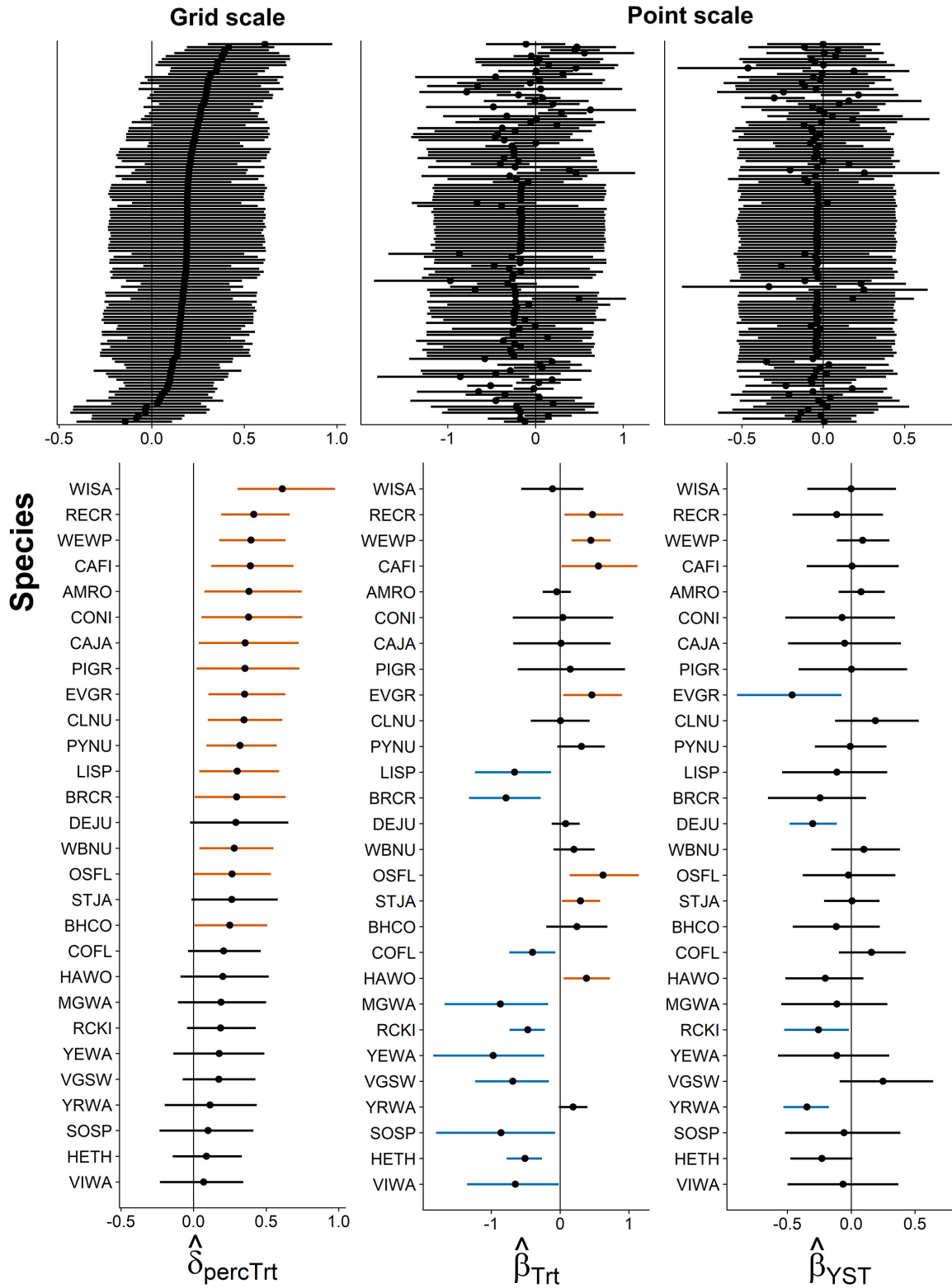
FIG. 3. Estimated occupancy relationships (posterior medians and 95% Bayesian credible intervals) with CFLRP treatment metrics (defined in Table 2). Top panels show all species (unlabeled), whereas bottom panels focus on relationships for the 28 species with at least one supported relationship (for full species names, see Table 5). In bottom panel, error bar colors indicate supported positive (orange) and negative (blue) relationships. Relationships are sorted by the relationship with grid-level percent area treated from negative to positive.

TABLE 4. Potential mechanisms for species treatment relationships.

Species	Treatment relation	Possible mechanisms
Olive-sided Flycatcher	percent treatment (+)†	More extensive open forest§
Western Wood-pewee	percent treatment (+)†	More extensive open forest§
Western Wood-pewee	treatment status (+)‡	Greater canopy dominance of ponderosa pine
Cordilleran Flycatcher	treatment status (−)‡	Greater canopy dominance of ponderosa pine and less of Douglas-fir
Steller's Jay	treatment status (+)‡	Greater canopy height
Clark's Nutcracker	percent treatment (+)†	More extensive open forest
Pygmy Nuthatch	percent treatment (+)†	More extensive open forest
Brown Creeper	treatment status (−)‡	Greater canopy dominance of ponderosa pine
Ruby-crowned Kinglet	treatment status (−)‡	Greater canopy dominance of ponderosa pine
Ruby-crowned Kinglet	years since treatment (−)‡	Greater canopy dominance of ponderosa pine
Hermit Thrush	treatment status (−)‡	Greater canopy dominance of ponderosa pine
Cassin's Finch	treatment status (+)‡	Greater canopy height
Red Crossbill	treatment status (+)‡	Greater canopy dominance of ponderosa pine and less of Douglas-fir§
Dark-eyed Junco	years since treatment (−)‡	More aspen in the canopy
Song Sparrow	treatment status (−)‡	Greater canopy height
Lincoln's Sparrow	treatment status (−)‡	Greater canopy height
Virginia Warbler	treatment status (−)‡	Reduced shrub-sapling volume
MacGillivray's Warbler	treatment status (−)‡	Reduced shrub-sapling volume
Yellow Warbler	treatment status (−)‡	Greater canopy dominance of ponderosa pine and reduced shrub-sapling volume§
Yellow-rumped Warbler	years since treatment (−)‡	Increased canopy cover and canopy dominance of ponderosa pine

Notes: Possible mechanisms describe statistically supported changes in habitat with treatment (i.e., treatment correlations with habitat covariates) capable of explaining the listed treatment relationship (for rationale, see Fig. 2).

† Grid-level treatment relationships.
‡ Point-level treatment relationships.
§ Habitat relationships consistent with species life histories listed in Table 4.

supported positive relationships with percent area treated (percTrt; 16 species).

Seven species (Olive-sided Flycatcher, Western Wood-peewee, Evening Grosbeak, Cassin's Finch, Red Cross-bill, Brown Creeper, and Lincoln's Sparrow) showed supported relationships with treatment metrics at both grid and point scales (Fig. 3, Appendix S7: Fig. S1). Grid occupancy for all seven increased with increasing percent area treated, and point occupancy for most favored treated points. Although Evening Grosbeak occupancy favored grid cells and points associated with more extensive treatment, point occupancy declined with years since treatment. Nine species only showed statistically supported relationships with grid-level percent area treated, all of which were positive (Fig. 3, Appendix S7: Fig. S2).

Ten species only showed statistically supported treatment relationships at the point level (Fig. 3, Appendix S7: Fig. S3). Occupancy for eight of these species favored untreated points, whereas the opposite was true for the remaining two. Ruby-crowned Kinglet point occupancy also declined with years since treatment.

Two species, Dark-eyed Junco and Yellow-rumped Warbler, only showed statistically supported negative relationships with years since treatment (Fig. 3,

Appendix S7: Fig. S4). Both species were widely distributed among grids, leaving little room for increases with treatment. Both species occupied recently treated and untreated points at similar rates, but older treatments less.

Habitat relationships and potential mechanisms

We found statistically supported habitat relationships for 54 species, including 25 of 28 species noted above with supported treatment relationships (Appendix S8). Grid-level occupancy relationships with landscape structure were supported for 34 species, including positive and negative relationships with all three covariates (Appendix S8: Fig. S1). Relationships with extent of canopy gaps (PACCGap) were supported for the most species and also spanned a greater range of magnitudes than relationships with open forest (PACCOpn, PAROpn). Grid-level relationships with perimeter : area ratio for open forest patches (PAROpn) were weakest and least frequently supported.

Point-level occupancy relationships with vegetation were supported for 47 species (Appendix S8: Fig. S2). We found the most statistically supported point occupancy relationships with shrub layer ladder fuel

dominance (LadFuel) and least for aspen dominance of the canopy (POTR5). Magnitudes of relationships with Douglas-fir dominance (PSME) spanned the greatest range and canopy cover (CanCov) the least range. Negative relationships were more frequently statistically supported and spanned a greater range of magnitudes than positive relationships for canopy cover (CanCov), number of snags (NSnag), and ladder fuel shrub dominance (LadFuel), whereas the opposite was true for shrub-sapling volume (ShrbVol), canopy height (CanHt), and aspen dominance (POTR5).

We found several statistically significant correlations between environmental and treatment metrics percTrt and Trt, most of which were consistent in direction with expected treatment effects (Appendix S1: Table S2, Figs. S1, S2). The extent of open forest (PACCOpn) tended to increase with increasing percent landscape treated in areas surrounding grid cells (Appendix S1: Table S2, Fig. S1). Treated points were associated with less canopy cover (CanCov), greater canopy height (CanHt), more ponderosa pine (PIPO), less Douglas-fir (PSME), and less shrub-sapling volume (ShrbVol) than untreated units, although many of these relationships were small ($|r| < 0.1$ for CanHt, PSME, and ShrbVol). Treated points also had fewer snags and more ladder fuels (LadFuel), but these differences were small and not consistent with expected treatment effects (Appendix S1: Table S2, Fig. S2). The data provided less support for remaining correlations with treatment status (PACCGap, PAROpn, POTR5, and Herb). Potentially reflecting treatment evolution, points intersecting older treatments compared to more recent treatments tended to have more canopy cover (CanCov), fewer snags (NSnag), more ponderosa pine (PIPO), and less aspen in the canopy (POTR5) compared to points in more recently treated units (Appendix S1: Table S2, Fig. S2).

Habitat relationships and environment–treatment correlations suggested potential mechanisms for 20 treatment relationships for 18 species (Table 4). For Olive-sided Flycatcher, Western Wood-peewee, Clark's Nutcracker, and Pygmy Nuthatch, grid occupancy related positively with both percent landscape treated (percTrt) and extent of open forest (PACCOpn), which in turn, were positively correlated with each other (Scenario A, Fig. 2). For Western Wood-peewee and Red Crossbill, positive point occupancy relationships with ponderosa pine dominance (PIPO) provided potential mechanisms for positive relationships with treatment status (Trt; Scenario A, Fig. 2). Negative relationships with PIPO provided potential mechanisms for negative treatment relationships (with Trt or YST) for seven species (Scenario B, Fig. 2). Positive relationships with shrub-sapling volume provided potential mechanisms for negative relationships with treatment status (Trt) for three shrub-nesting species (Virginia's Warbler, MacGillivray's Warbler, and Yellow Warbler). Relationships with canopy cover, canopy height (CanHt), and Douglas-fir dominance (PSME) provided additional potential

mechanisms for treatment status (Trt) relationships (see Cordilleran Flycatcher, Steller's Jay, Cassin's Finch, Red Crossbill, Song Sparrow, and Lincoln's Sparrow). Relationships with aspen (POTR5) and canopy cover (CanCov) provided potential mechanisms for Dark-eyed Junco and Yellow-rumped Warbler relationships, respectively, with time since treatment (YST).

Species richness

The data supported a positive relationship of grid-level species richness with percent landscape treated (percTrt), and a negative relationship of point-level richness with treatment status (Trt; Table 5). Mean richness ($N_{\psi,k}$) increased by approximately five species from grids in untreated landscapes to landscapes with ~60% area in treated units (Fig. 4). We estimated some decline in species richness at more extensively treated landscapes (60–100%; Fig. 4), although statistical support for this secondary decline was marginal (see estimate for $\Gamma_{percTrt^2}$ in Table 5). Although statistically supported (Table 5), we estimated a <1 species difference in point-level richness ($N_{\theta,jk}$) between treated and untreated points that was difficult to visually discern over other sources of variation (Fig. 4). The data did not support a species richness relationship with years since treatment (YST; Table 5).

We did not find definitive statistical support for grid-level species richness ($N_{\psi,k}$) relationships with landscape structure (i.e., 95% BCIs for community mean relationships overlapped zero), although posterior parameter distributions were predominantly positive for relationships with extent of canopy gaps (PACCGap) and canopy openings (PACCOpn; Table 5). Median predicted richness increased from grid cells in landscapes with no openings or gaps to grid cells associated with maximum gap extent (27%) or maximum open forest extent (77%) by six species (Fig. 5). We found no evidence for a grid-level richness relationship with perimeter:area ratio for open forest patches (PAROpn; Table 5).

Point-level richness ($N_{\theta,jk}$) relationships with canopy cover (negative), number of snags (negative), shrub-sapling volume (positive), ladder fuels (negative), and herbaceous volume (positive) were statistically supported (Table 5). Of these, however, changes in mean predicted richness exceeded one from minimum to maximum covariate values for only canopy cover (2.2 species), number of snags (2.2 species), and shrub-sapling volume (3.1 species; Fig. 5). Predicted species richness also appeared to increase substantially with increasing canopy height, although the increase within 3–20 m where most sampling occurred was more limited (Fig. 5).

DISCUSSION

We observed patterns largely consistent with our predictions that CFLRP treatments would benefit avian

TABLE 5. Parameter estimates relevant for assessing statistical support for species richness relationships with treatment and habitat covariates.

Model, level, and parameter	Median estimate (95% BCI)
Treatment	
Grid	
Percent treatment (Γ)†	0.1 (0.04,0.17)‡
Percent treatment^2 (Γ)†	−0.03 (−0.06,0.01)
Point	
Treatment status (mean β)	−0.16 (−0.33,−0.02)‡
Years since treatment (mean β)	−0.04 (−0.13,0.05)
Habitat	
Grid	
Extent of canopy gaps (mean δ)	0.09 (−0.04,0.22)
Extent of open forest (mean δ)	0.09 (−0.02,0.2)
Perimeter : area ratio of open forest (mean δ)	0.02 (−0.06,0.1)
Point	
Canopy cover (mean β)	−0.09 (−0.14,−0.05)‡
Canopy height (mean β)	0.02 (−0.05,0.07)
Number of snags (mean β)	−0.16 (−0.25,−0.09)‡
Ponderosa pine canopy dominance (mean β)	0.03 (−0.04,0.11)
Douglas-fir canopy dominance (mean β)	−0.05 (−0.14,0.02)
Aspen canopy dominance (mean β)	−0.01 (−0.06,0.04)
Shrub volume (mean β)	0.1 (0.05,0.15)‡
Ladder fuel shrub dominance (mean β)	−0.09 (−0.16,−0.02)‡
Herbaceous cover (mean β)	0.06 (0,0.13)‡

Notes: Symbols in parentheses refer to model formulas provided in occupancy model structure, Data analysis. Grid-level treatment relationships (Γ) are from a post hoc regression analysis (see species richness, Data analysis and Appendix S2). Remaining estimates are for community means (i.e., hyper-parameters) for covariate relationships.

† The derived posterior estimate for the intercept term for this model was $\Gamma_0 = 3.4$ (3.33,3.49).

‡ Mean covariate relationships that clearly differed from zero (95% Bayesian confidence intervals ([BCIs] excluded zero).

species richness and conservation objectives along the Colorado Front Range by increasing landscape heterogeneity. We found both positive and negative relationships with treatment status, indicating species were distributed unevenly between treated and untreated points. Grid-level species relationships with percent landscape treated were overwhelmingly positive, however, resulting in a substantial increase in species richness in treated landscapes. Thus, treated landscapes appeared to accommodate more open-forest species, without necessarily eliminating habitat for closed-forest species at treatment extents represented thus far. Although not statistically clear, estimated richness appeared to plateau or decline at the most extensively treated grids, aligning with our expectation that treatments would elevate landscape heterogeneity (the expected driver of richness) at moderate extents.

Given widespread consistency of habitat relationships with potential mechanisms for treatment relationships and species life histories, treatment relationships are likely ecologically meaningful. Positive treatment relationships and mechanisms involving reduced canopy cover and increased extent of open forest were consistent with our expectations for aerial insectivores and species that feed on conifer seeds. Occupancy patterns and potential mechanisms involving shrub-sapling volume, shrub composition, and ground cover were consistent with expectations for understory species. We also found local-scale negative treatment relationships and associations with closed-canopy conditions consistent with many species life histories, although heterogeneity was apparently sufficient to maintain these species across the landscape. Environmental features related with species occupancy and richness, and involved in suggested mechanisms for treatment relationships, represent potential foci for treatments where objectives include habitat conservation or improvement.

Potential mechanisms for treatment relationships

Consistent with our predictions, we found patterns suggesting treatments may benefit aerial insectivores by generating canopy openings, within which they forage (Gaines et al. 2007, but see Kalies et al. 2010). Extension of open forest conditions (areas with 10–40% canopy cover) could explain the expansion of Olive-sided Flycatcher and Western Wood-pewee into treated landscapes (see also Kalies et al. 2010). Several other aerial insectivores related positively with treatments (Common Nighthawk) or open-canopy conditions (Hammond's Flycatcher and Northern Rough-winged Swallow). Yellow-rumped Warbler spend a notable portion of their
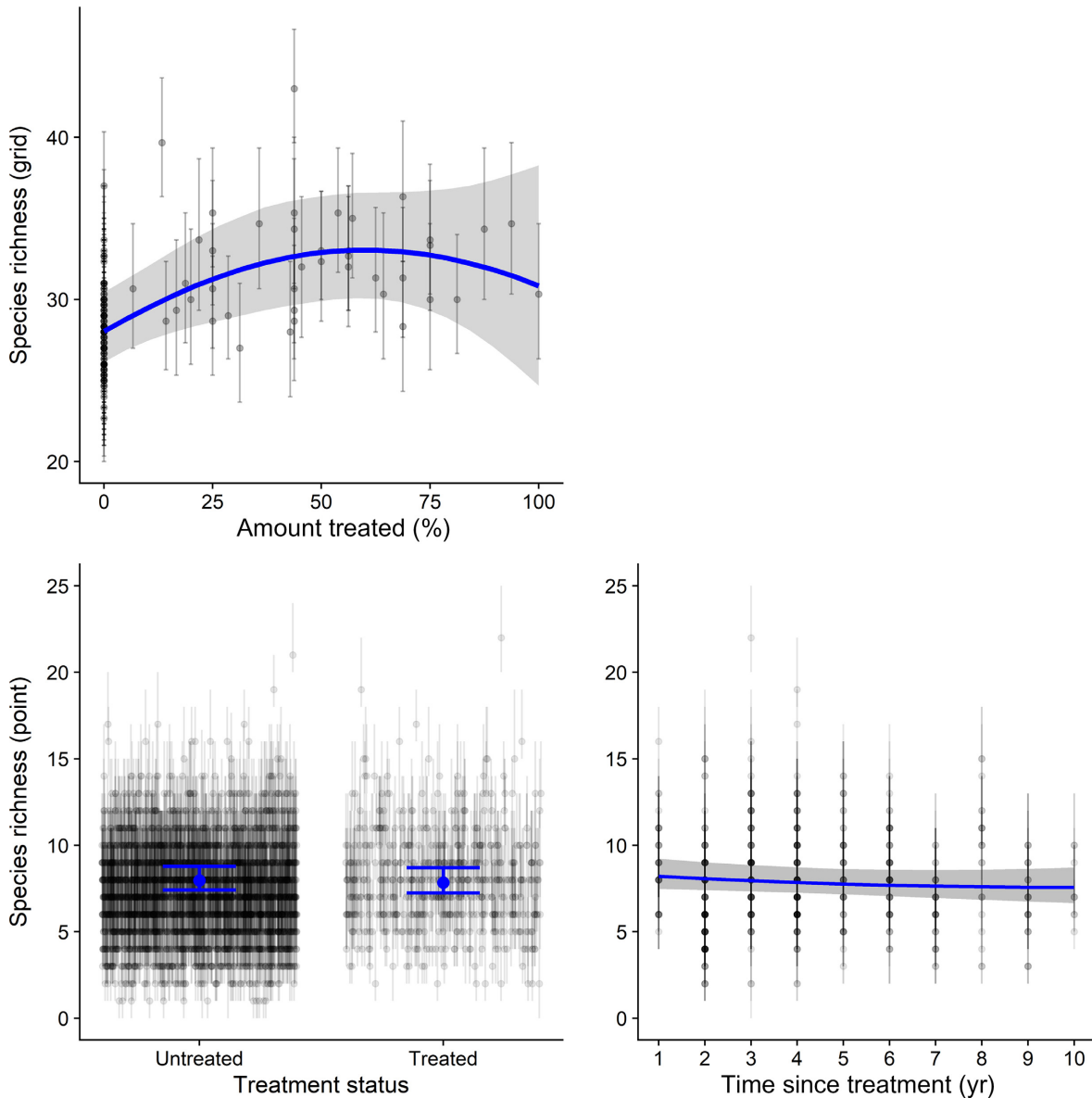
FIG. 4. Species richness in relation to treatment metrics. Estimates are posterior median with 95% Bayesian credible intervals. Points and error bars are finite-sample estimates ($\hat{N}_{\psi,obs}, \hat{N}_{\theta,obs}$) and lines with error bands ($\hat{N}_{\psi,pred}, \hat{N}_{\theta,pred}$) are predicted values.

time foraging for insects on the wing (Bemis and Rising 1998), potentially explaining their greater occurrence in recent compared with older treatments. Cordilleran Flycatcher related negatively with treatments (see also Kalies et al. 2010), for which potential mechanisms involved canopy composition rather than canopy openings.

Also consistent with our prediction several conifer-seed-eating species associated positively with treatments. Specifically, suggested mechanisms involving reduced canopy cover for Clark's Nutcracker and Pygmy Nuthatch, and more ponderosa pine for Red Crossbill, were consistent with our predictions for species that forage on conifer seeds (Tomback 1998, Kingery and

Ghalambor 2001, Benkman and Young 2019). Others describe treatment relationships or habitat relationships for Pygmy Nuthatch and Red Crossbill (Hurteau et al. 2008, Kalies and Rosenstock 2013) consistent with those predicted or reported here. Hairy Woodpecker may also forage substantially on pine seeds in the winter (Stallcup 1968).

Understory-associated species may exhibit different treatment responses depending on how particular vegetation components are affected. Treatments that effectively manage woody fuels can initially reduce shrub-sapling volume, potentially incurring negative responses by shrub-nesting species like Virginia Warbler and MacGillivray's Warbler (Olson and Martin 1999,
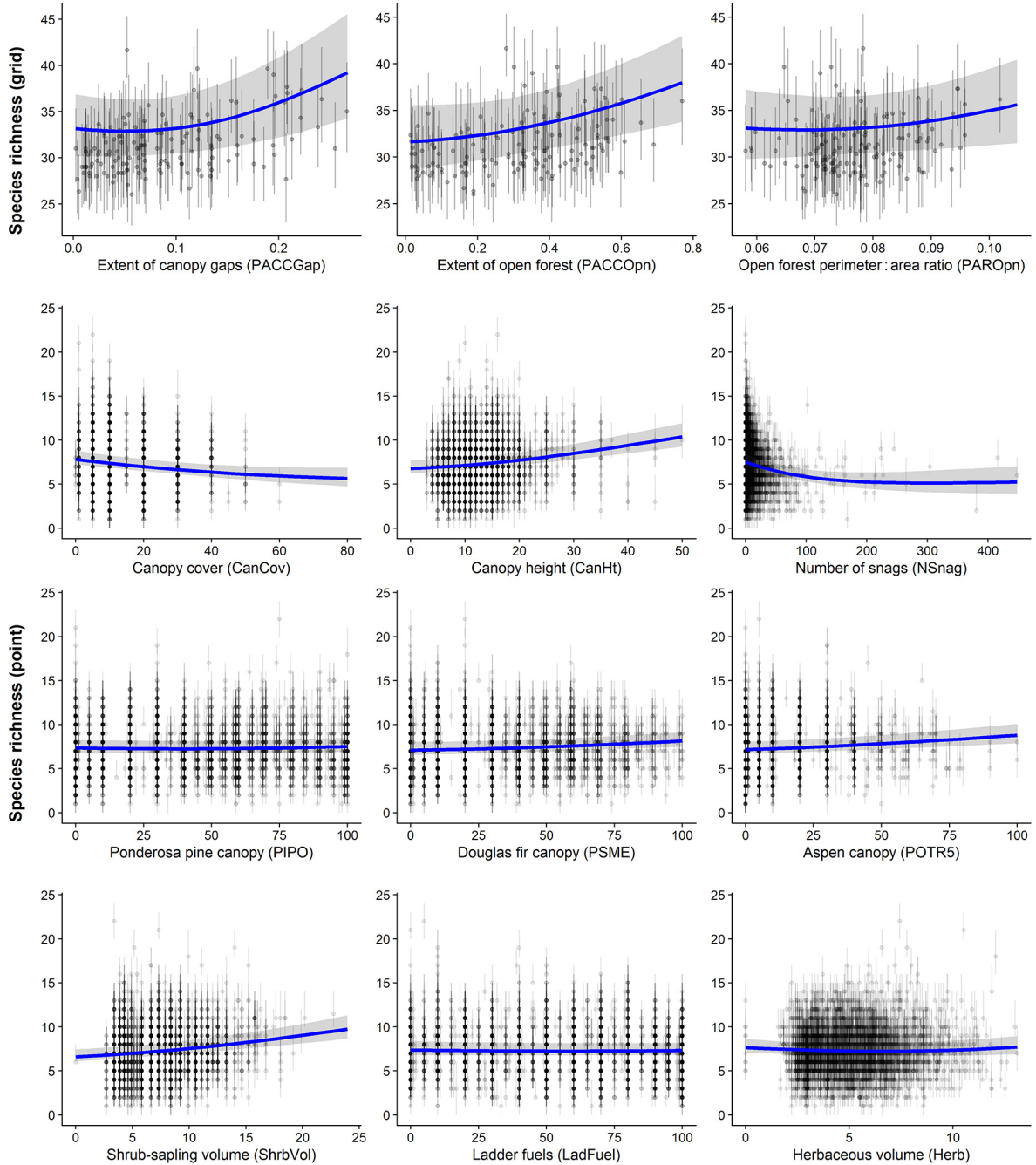
Fig. 5. Species richness in relation to habitat metrics. Estimates are posterior median with 95% Bayesian credible intervals. Points and error bars are finite-sample estimates ($\hat{N}_{\psi,\text{obs}}, \hat{N}_{\theta,\text{obs}}$) and lines with error bands ($\hat{N}_{\psi,\text{pred}}, \hat{N}_{\theta,\text{pred}}$) are predicted values.

Pitocchelli 2013). Initial negative impacts incurred by reduced shrub cover may be offset in the long term, however, with shrub regrowth in canopy openings generated by treatments. MacGillivray's Warbler, Yellow Warbler, Song Sparrow, and Lincoln's Sparrow breed in riparian vegetation (Ammon 1995, Lowther et al. 1999, Pitocchelli 2013), so their negative treatment relationships may reflect treatment avoidance of riparian rather than actual effects on upland vegetation. Treatments

that encourage broad-leafed deciduous shrubs over ladder fuels, however, could benefit these and other bird species (Hagar 2007). Greater ladder fuel dominance at treated points observed here may reflect the placement rather than effect of treatments. Treatments that reduce conifer saplings may reduce nesting opportunities for Hermit Thrush (Dellinger et al. 2012), although foraging habitat effects may explain positive treatment relationships elsewhere (Gaines et al. 2007). Positive treatment

relationships for Cassin's Finch and American Robin could reflect improved ground-foraging opportunities with understory release in canopy openings (Hahn 1996, Gaines et al. 2007, Kalies et al. 2010, Vanderhoff et al. 2016), although herbaceous growth did not correlate clearly with treatments. Numerous ground-foraging species showing positive relationships with herbaceous cover here might respond positively to treatments that clearly stimulate herbaceous growth.

Treatments may negatively impact canopy- or closed-forest-associated species by reducing canopy cover or favoring open-forest plant species. Brown Creeper and Ruby-crowned Kinglet forage in the canopy on live trees and are associated with higher elevation, closed-forest tree species (Swanson et al. 2008, Poulin et al. 2013), potentially explaining their negative treatment relationships here. Conversely, large trees targeted for retention may provide sufficient nest sites for Stellar's Jay, and open ponderosa pine forests may provide desirable conditions for this generalist forager (Kalies and Rosenstock 2013, Walker et al. 2016). Various other species associated with closed-forest conditions (e.g., avoidance of canopy gaps or open forest, or positive relationships with Douglas-fir) but nevertheless maintained or increased occupancy in treated landscapes. Forest heterogeneity was apparently sufficient to maintain these species across the landscape, and treatments may provide opportunities for species that otherwise usually occupy relatively closed forests (e.g., nesting habitat for Williamson's Sapsucker; Crockett and Hadow 1975).

Differences in occupancy of older vs. recent treatments could follow changes in treatment targets or prescriptions. Colorado Front Range CFLRP treatments have evolved from emphasizing mechanical thinning and block units to incorporating more prescribed fire and natural spatial patterning of retained vegetation (Cannon et al. 2018). Treatment correlations with canopy cover, snags, ponderosa pine, and aspen may reflect these shifts. Moreover, negative occupancy relationships with years since treatment for Evening Grosbeak, Dark-eyed Junco, Ruby-crowned Kinglet, and Yellow-rumped Warbler suggest shifts in treatment implementation that have benefited these species or at least reduced negative impacts. Alternatively, these relationships could reflect lagged treatment responses or follow successional processes, although we did not find correlations consistent with understory release. For Yellow-rumped Warbler, studies report patterns suggesting variable treatment responses, so different types of treatment (e.g., mechanical thinning, prescribed fire) could have different implications for this species (Gaines et al. 2007, Hurteau et al. 2008, Kalies et al. 2010, Fontaine and Kennedy 2012).

Species richness and composition

Effectiveness monitoring to evaluate songbird relationships with CFLRP treatments provides an example of evaluating how restoration aligns with biodiversity conservation (Noss et al. 2006a). Estimating species richness at multiple scales allowed us to evaluate scale-specific biodiversity relationships with forest restoration and ecological process (Whittaker et al. 2001, Bestelmeyer et al. 2003), ultimately informing implications for forest structure and function, and ecological integrity (USDA 2012, Wurtzebach and Schultz 2016). We found landscape-scale patterns consistent with predictions that restoring historical conditions would benefit avian diversity by returning forests to the historical range of variation with which birds have evolved (Noss et al. 2006a, Hutto et al. 2008). These patterns included increased richness with moderate-to-high treatment extent, and positive relationships of species richness with canopy gaps and open forest. These findings also corroborate the expected role of heterogeneous landscapes for promoting avian diversity in dry conifer forests, and the central role of canopy gaps and open forests as keystone structures (sensu Tews et al. 2004) in these landscapes (Saab et al. 2005, Fontaine and Kennedy 2012, Latif et al. 2016b).

Avian species richness declined locally with increasing canopy cover and understory ladder fuels, and increased with increasing shrub-sapling volume and herbaceous ground cover. These patterns agree with and add to patterns reported by others describing the importance of these features to the ecological function of canopy openings and open ponderosa pine forests (Kalies and Rosenstock 2013, Addington et al. 2018, Cannon et al. 2018). Additionally, relationships with ponderosa pine, Douglas-fir, and aspen indicate relationships of local plant with bird species composition. These local patterns suggest variability in tree species composition is important for landscape heterogeneity to support biodiversity. Although we did not find particularly strong relationships with aspen, our landscape-wide sampling may not be well suited for highlighting the importance of small isolated aspen stands. Consistent with the importance of aspen for supporting avian diversity (Griffis-Kyle and Beier 2003), statistically supported aspen relationships here were primarily positive.

Negative occupancy and richness relationships with snags here stand in contrast to others (Kalies and Rosenstock 2013) and the well-described importance of snags to many species (Saab et al. 2005, Russell et al. 2007, Latif et al. 2016b). CFLRP treatments and effectiveness monitoring avoided extensively burned forests, but smaller, older, and lower severity burns (i.e., those not represented in remotely sensed data) and bark beetle outbreaks unavoidably entered our sample. Negative snag relationships may reflect avoidance of such areas by some species, which varies with time since disturbance as snags fall and vegetative succession proceeds. Relationships observed here represent very few species with snag-associated life history traits, however (e.g., woodpeckers, secondary cavity-nesting species; except see House Wren). Restoration will likely maintain the widest range of species across the landscape by maintaining snags and minimizing disruptions to disturbance-related ecological processes.

Study strengths and limitations

Our study benefited from landscape-wide and dual-scale sampling of the IMBCR program (Pavlacky et al. 2017), allowing us to distinguish coarse- and fine-scale population and community patterns over a broad geographic extent. Meta-analyses can pool individual studies to infer general patterns (e.g., Kalies et al. 2010, Fontaine and Kennedy 2012), but inferences are necessarily restricted to spatial scales represented in synthesized studies, which to date are typically fine-scale. Considering the variability in species patterns, researchers suggest landscape heterogeneity to be important for supporting species diversity. These expectations align with general theory on the role of environmental heterogeneity as a driver of biodiversity (Stein et al. 2014). Our sampling structure allowed us to document explicitly patterns consistent with these expectations in a dry conifer forest system.

Our sampling frame includes a broad range of conditions representing forest types of interest for restoration. Within these forests, treatments targeted specific conditions and conversely avoid others. For example, CFLRP treatments would not target riparian areas, meadows, extensive shrubby openings, or areas impacted relatively recently by forest management or natural disturbance. Inclusion of such areas in our sampling frame may obscure treatment effects because species associations or avoidance of these areas can confound changes in avian distributions that occur with treatment. Nevertheless, by including these areas, the reference sample represented the landscape of interest for restoration as a whole. Thus, our study assesses CFLRP treatment effects over and above the range of variability existing across the landscape of interest, and thus informs overall assessment relevant to the future direction of the program.

Focused studies comparing effects of particular treatments could complement more general patterns reported here. Considering variability in responses to different treatments (Kalies et al. 2010, Fontaine and Kennedy 2012), varying prescriptions may most effectively promote landscape heterogeneity to support biodiversity. Our results may primarily generalize to ecosystems where restoration treatments vary in accordance with historical range of variation and relevant local constraints (Addington et al. 2018, Cannon et al. 2018).

Management implications

Monitoring effectiveness (sensu Lyons et al. 2008) of CFLRP treatments facilitates assessment of program success for meeting forest management and wildlife conservation objectives. Effectiveness monitoring also improves accountability and confidence in using large-scale forest restoration to manage wildlife resources for the public trust. Comparing impact to reference strata (Pavlacky et al. 2017) allowed us to evaluate differences in bird communities between treated and untreated forests. Our findings of increased bird species richness and the benefits for many open-forest associated bird species with treatment were consistent with the potential for treatments to restore the historical range of variation, from which the landscape as a whole has departed.

In addition to increasing species richness overall, forest restoration treatments could benefit species of conservation concern. The North American Bird Conservation Initiative identifies four species of regional conservation concern based on long-term, broad-scale population declines that occurred in our study (NABCI 2016). Three of these species (Cassin's Finch, Evening Grosbeak, and Olive-sided Flycatcher) exhibited positive treatment relationships, whereas only one (Virginia's Warbler) related negatively with treatments, and only at a local scale.

Patterns reported here could inform treatment prescriptions with objectives that include conserving or improving habitat for birds. Our results indicate treatments would generally benefit birds by reducing canopy cover and encouraging shrubby and herbaceous growth in canopy openings while limiting ladder fuels. Treatments that result in heterogeneity in canopy composition would also likely help maintain avian diversity across landscapes. Fortunately, from the perspective of bird conservation, these results are broadly consistent with restoration targets for the Colorado Front Range (Addington et al. 2018, Cannon et al. 2018).

In addition to evaluating treatments and informing prescriptions, avian monitoring could inform treatment extent. Forest managers lack information to identify how much of the landscape to treat for optimal ecological structure and function. Wildlife habitat represents a key function of interest for dry conifer forest restoration. In particular, we expect restoration treatments to promote heterogeneity needed to support the full array of species with different life histories associated with these forests. At some point, we expect treatments to reduce habitat for species associated with relatively closed forests. Consistent with this expectation, our estimates of species richness indicated a possible plateau or decline in the most extensively treated landscapes. This result highlights the potential for birds to inform how much of the landscape to treat to promote biodiversity, a core component of ecological integrity (Wurtzebach and Schultz 2016).

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2142/full

DATA AVAILABILITY

Code and data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.q573n5tfm.