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Short-term effects of post-fire salvage logging intensity and activity on breeding birds in the Sierra Nevada Mountains, USA

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Abstract

Background: Salvage logging of fire-killed trees in western US conifer forests has been shown to negatively affect many wildlife species, but there are few quantitative studies from the Sierra Nevada, CA. Salvage intensity (i.e., the proportion of fire-killed trees removed during logging activities) has also rarely been measured; instead, most studies track the presence/absence of salvage activities. We explored the effects of post-fire salvage on the breeding bird community following the 2012 Chips and 2013 Rim fires using a before-after control-impact sample design, and modeled species responses to salvage including a test of whether species responded to salvage intensity or the presence of salvage activities as a whole.

Results: Salvage operations removed an average of 71% of the snag basal area in the Chips Fire and 64% in the Rim Fire within 50 m of our salvaged survey locations. Bird species responses to salvage in both fires were largely non-significant or negative (Chips: 11 negative, 4 positive, 19 non-significant; Rim: 13 negative, 4 positive, 20 non-significant). Statistical support for the salvage intensity vs. salvage activity models was split evenly among all species. Positive salvage responders in both fires included species adapted to open habitats and seed consumers, while a wide variety of species, including woodpeckers, species associated with open and dense mature forest, and some shrub nesters, responded negatively to salvage. We also evaluated five salvage prescription scenarios based on snag basal area, salvage intensity, and area treated to determine whether any combination could minimize the negative effects on the salvage-sensitive species yet retain the same salvage yield. The scenarios with the smallest area targeted with high-intensity salvage saw the smallest declines in abundance and diversity, but nearly all scenarios reduced both measures.

Conclusions: No combinations of salvage intensity and distribution from among the scenarios we explored were able to fully mitigate the negative effect on the bird community; however, the magnitude of declines in abundance and diversity was smaller than expected, and the majority of the species analyzed had a non-significant response. We recommend targeting salvage activities in the Sierra Nevada to those locations where snags pose a safety issue or where reforestation is most needed to conserve this fire-adapted bird community.

Keywords: Sierra Nevada, Wildfire, Snags, Salvage logging, Post-fire habitat, Conifer forest, Distance sampling, Birds, Wildlife community

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Resumen

Antecedentes: La tala rasa de árboles muertos por incendios en bosques del oeste de los EEUU han mostrado que afectan negativamente muchas especies de aves, aunque hay muy pocos estudios cuantitativos en la Sierra Nevada de California. La intensidad de la tala rasa (i.e. la proporción de árboles muertos por el fuego y removidos luego de la tala) ha sido raramente medida, mientras que la mayoría de los estudios detectan la presencia o ausencia de actividades de tala rasa. Exploramos los efectos de una tala rasa post fuego sobre anidamiento de comunidades de aves en los incendios de Chips (2012) y Rim (2013) usando un diseño de muestreo de control de impacto a priori y a posteriori, y modelamos la respuesta de las especies a la tala rasa incluyendo un test sobre cómo las especies respondieron a la intensidad de la tala o a la presencia de actividades de tala rasa como un todo.

Resultados: Las operaciones de tala rasa removieron en promedio el 71% del área basal de los árboles muertos en pie en el incendio de Chips, y del 64% en el de Rim, en un radio de 50 m dentro de las ubicaciones del muestreo de la tala. Las respuestas de las especies de aves en ambos incendios fueron en su mayoría no significativas o negativas (Chips: 11 negativas, 4 positivas, 19 no-significativas; Rim: 13 negativas, 4 positivas y 20 no-significativas). El valor estadístico para los modelos de tala rasa intensiva vs, modelos de actividad de tala como un todo fue igualmente repartido entre todas las especies. Las especies que respondieron positivamente a la tala rasa en ambos incendios incluyeron especies adaptadas a espacios abiertos y consumidores de semillas, mientras que una amplia variedad de especies incluyendo pájaros carpinteros, especies asociadas con bosques abiertos y maduros y algunas que anidan en arbustos, respondieron negativamente a la tala rasa. También evaluamos cinco escenarios de prescripciones basados en el área basal de árboles muertos en pie, la intensidad de la tala, y el área tratada, para determinar si alguna combinación minimizaba los efectos de la tala en especies sensibles y a su vez mantenía el mismo rendimiento de la tala. Los escenarios con menores áreas en los que se practicaba una alta intensidad de tala mostraron las menores declinaciones en abundancia y diversidad, aunque casi todos los escenarios redujeron ambas medidas.

Conclusiones: Ninguna combinación de intensidad de tala y distribución de entre todos los escenarios explorados fueron capaces de mitigar totalmente el efecto negativo en la comunidad de aves; por supuesto la magnitud de las declinaciones en abundancia y diversidad fue menor a la esperada, y la mayoría de las especies analizadas mostraron una respuesta no significativa. Recomendamos que las actividades de tala rasa en la Sierra Nevada se concentren en aquellos lugares donde los árboles muertos en pie se tengan en consideración o donde la reforestación sea muy necesaria para conservar esta comunidad de aves adaptada al fuego.

Background

Wildfire, the primary disturbance agent in conifer forests of western North America, has been increasingly recognized as an irreplaceable component of ecosystem form and function (North 2012; Roberts et al. 2021; Safford et al. 2021). Mixed-severity fire catalyzes a cascade of successional processes that can reshuffle community structure and composition (Agee 1993; Brawn et al. 2001; Smucker et al. 2005). The high density of standing dead trees (snags) and the structurally and floristically diverse understory characteristic of areas affected by high-severity fires support unique biological communities compared to an unburned forest (Hutto et al. 2016; Roberts et al. 2021). As such, complex early seral forest is recognized as important to the maintenance of biodiversity in disturbance-dependent forested ecosystems (Donato et al. 2009; Tingley et al. 2016a; Loffland et al. 2017; Tailie et al. 2018; Steel et al. 2019).

Salvage logging is a common post-fire management practice in areas burned at moderate to high severity. Salvage logging objectives include capturing the economic value of fire-killed trees, preparing the site for

reforestation, removing hazardous trees, and reducing fuel loads that may lead to future extreme fire behavior (Beschta et al. 2004; Long et al. 2014; Coppoletta et al. 2016). These post-fire management actions can have decades-long legacies that influence vegetation structure and composition (Lindenmayer and Noss 2006; Lindenmayer et al. 2008; Swanson et al. 2010). Salvage logging can also directly or indirectly affect many aspects of post-fire wildlife habitat, including snag density, and vegetation succession (Donato et al. 2006; Russell et al. 2006; Shatford et al. 2007) and as a result can influence the presence and abundance of many wildlife species for decades following harvest (summarized in Thorn et al. 2017).

The effects of salvage logging on biotic communities have been well-studied; however, gaps remain in our understanding. An apparent gap within the post-fire salvage literature is the way salvage is characterized in evaluations: most often as a binary effect (salvaged or unsalvaged). The few studies describing salvage intensity (e.g., Haggard and Gaines 2001, Koivula and Schmiegelow 2007, Cahall and Hayes 2009, Saab et al.

2007) did not quantify snag volume before and after timber removal at both unlogged and logged salvage areas to control for pre-fire forest structure. Only one study exists that measured basal area removed before and after salvage treatments (Fontaine 2007). Making inferences in relation to snag retention and salvage prescriptions may be difficult without characterizing what attracted a particular species to a burned stand before salvage operations. In addition, while several studies have evaluated the effects of post-fire salvage logging on birds in western conifer forests (e.g., Haggard and Gaines 2001, Hutto and Gallo 2006, Saab et al. 2007, Cahall and Hayes 2009, Rost et al. 2013), most have focused on a narrow subset of the bird community. As the annual area burned and the proportion burned at high severity increase (Steel et al. 2018), it is also important to evaluate more comprehensively how the bird community responds to salvage logging, in particular mature forest species (Lee et al. 2013; Zmihorski et al. 2019). The majority of post-fire salvage logging studies have also focused on single fires, and thus, the resulting burn patterns, fire size, landscape context, and post-fire management directives may be unique to that particular fire (Rost et al. 2013). Salvage prescriptions are often not well-defined or described (Leverkus et al. 2018) which may make it difficult for land managers to apply mitigations to achieve desired conditions and balance tradeoffs. In the Sierra Nevada Mountains of California, there are few published studies that assess the effects of salvage logging on wildlife and these are generally limited to single species (Hanson and North 2008; Tarbill et al. 2018). Yet the applicability of results from other regions may be limited, as the biotic interactions, local adaptation, and behavioral rules governing habitat associations can give rise to spatial variability in wildlife-habitat relationships (Araujo and Luoto 2007; Morrison 2012; Aarts et al. 2013)

To better assess the effects of salvage on a large subset of the breeding bird community and more accurately measure salvage intensity, we implemented a before-after control-impact (BACI) sampling design to evaluate changes in abundance following salvage treatments for 41 bird species at two fire areas in the Sierra Nevada, with the goal of identifying how the intensity of salvage influences the abundance of a broad range of avian species. We modeled how changes in the basal area of

standing dead trees following salvage logging treatments affect bird abundance. We then used our model predictions to evaluate several salvage logging scenarios that varied in intensity and extent to compare their potential impacts on the bird community to help inform approaches that may minimize negative impacts to the avian community.

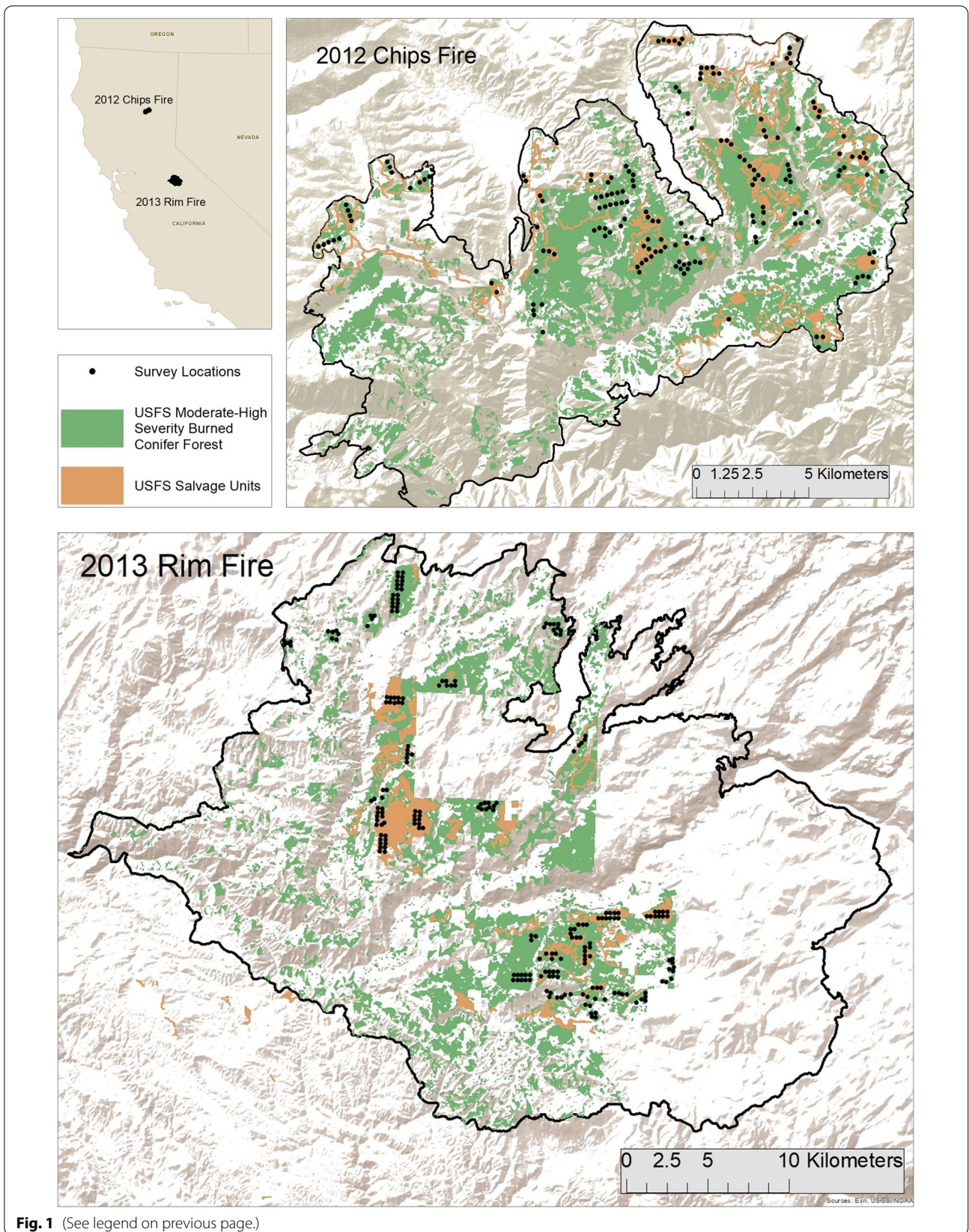
Methods

Study area

Our study took place within two wildfires in the central and northern Sierra Nevada Mountains, CA, USA (Fig. 1). The Chips Fire ignited on July 29, 2012, and burned 30,890 ha on the Plumas and Lassen National Forests. The Rim Fire ignited on August 17, 2013, and burned 104,131 ha on the Stanislaus National Forest and Yosemite National Park. Both fires also burned substantial areas of private lands. Burn severity was measured with a relative differenced normalized burn ratio (RdNBR), a satellite imagery-based measure of burn severity that accounts for the biasing effect of the pre-fire vegetation conditions (Miller and Thode 2007; Miller et al. 2009). High-severity fire (with >75% of trees killed) occurred across 30% of the Rim Fire area, compared to 22% of the Chips Fire. High-severity patches varied in size within and between the fires, with many patches in the Rim Fire over 1000 ha, compared to typically smaller patches under 500 ha in Chips Fire. Pre-fire vegetation in both fires was typical of Sierra Nevada west-slope mixed conifer forest. Common tree species include ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), Douglas fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), red fir (*A. magnifica*), and black oak (*Quercus kelloggii*). Pre-fire understory vegetation cover was characterized by a sparse to moderate shrub layer including *Ceanothus* and *Manzanita* spp. Pre-fire forests in the Chips Fire were more fir-dominated within the areas we sampled and had been fire-suppressed for at least the previous 100 years (Safford and Van de Water 2014). Pre-fire forests in the Rim Fire were characterized by younger pine-oak forest with a more active fire history in the last 30 years. The climate in the area is Mediterranean with warm, dry summers and cool, wet winters. Elevation of survey locations ranged from 1224 to 1903 m (mean = 1530 m) in the Chips Fire and 1146 to 1952 m (mean = 1427 m) in

(See figure on next page.)

Fig. 1 Locations of the 2012 Chips and 2013 Rim fires in the Sierra Nevada, CA, USA. Bird survey locations (black dots) were placed within salvage logging units (Chips = 87 locations; Rim = 106 locations) and outside of units (Chips = 87 locations; Rim = 109 locations) overlaid on areas that burned at moderate to high severity on US Forest Service land in both fires. Locations were surveyed for birds and vegetation 1 year before and 1–2 years after salvage treatments



the Rim Fire. Annual precipitation averaged 75–150 cm with more precipitation in the Chips Fire and more precipitation falling as snow vs. rain as elevation increased across these topographically diverse areas.

Sampling design

We established survey locations within proposed salvage units and then determined the slope, aspect, elevation, pre-fire tree density and size class, forest type, and burn severity of that sample. We selected control locations that closely matched the range and frequency of the salvage sample habitat conditions to minimize differences between the salvaged and control samples. In the Chips Fire, we utilized survey locations from an existing monitoring program (Stephens et al. 2014; Burnett and Roberts 2015) and included additional locations in proposed salvage units. In the Rim Fire, due to the larger fire area and area salvaged, we established new locations using a Generalized Random Tessellation Stratified method (GRTS, Stevens and Olsen 2004). The final sample consisted of 106 salvaged and 109 control locations in the Rim Fire and 87 salvaged and 87 control locations in the Chips Fire (Table 1; see the Appendix for a detailed sampling design).

Salvage treatments

Salvage treatments differed substantially in the 2012 Chips and 2013 Rim fires, with areal extent of the salvage activities, timing of the activities, and snag retention being the most consistent differences. In the

Chips Fire, the Plumas and Lassen National Forests salvaged 1330 ha compared to 3388 ha that the Stanislaus National Forest salvaged in the Rim Fire (12% of burned moderate-high-severity fire on US Forest Service land in the Chips Fire compared to 16% in the Rim Fire). Logging occurred using primarily tractor-based methods with some helicopter and skyline logging in the Chips Fire (USDA Forest Service 2013 and 2014). Salvage unit size was smaller in the Chips than in the Rim Fire (averaging 9 vs. 17 ha) as well as contiguously salvaged area when considering private land (500 ha in the Chips compared to 2000 ha in the Rim Fire; Fig. 1). Salvage occurred in the Chips Fire in fall 2013 and was completed by the end of winter 2013–2014. In contrast, salvage operations took longer in the Rim Fire, beginning in fall 2014, continued through 2015, and were completed that winter. In both fires, no harvesting occurred within 4.5 m of streams and all trees with green foliage were retrained. The Chips Fire followed a prescription that retained 13% of each unit where all snags were left standing. In the remaining matrix, few or no merchantable trees were left standing. In the Rim Fire, operators retained nine conifer snags per ha, as well as all hardwood snags. Snags were generally retained in clumps in both fires; however, considerable non-merchantable material (conifer snags < 30 cm dbh) was left standing in the Rim Fire, in contrast to the Chips Fire where it was removed. These differences are apparent in photos taken before and after treatments (Fig. 2).

Table 1 Characteristics of salvage and control survey locations in the Chips and Rim fires in the Sierra Nevada, CA, USA. Burn severity is expressed as the relativized difference in normal burn ratio (RdNBR), and elevation is expressed in meters; mean ± standard deviation with the range in parentheses is shown. All other metrics are percentages

		Chips Fire		Rim Fire	
		Salvage (N = 87)	Control (N = 87)	Salvage (N = 106)	Control (N = 109)
Pre-fire habitat type (%)	Sierra mixed conifer	91	80	65	68
	Ponderosa pine	0	1	15	27
	Montane hardwood conifer	0	3	17	5
	White fir	9	16	0	0
	Lodgepole pine	0	0	3	0
Pre-fire tree size class (%)	Class 3 (15–28 cm dbh)	10	18	4	14
	Class 4 (29–61 cm dbh)	45	37	77	71
	Class 5 (>62 cm dbh)	45	45	19	15
Pre-fire tree density class (%)	Sparse (10–24%)	2	6	0	0
	Open (25–39%)	27	16	0	0
	Moderate (40–59%)	51	46	11	12
	Dense (60–100%)	20	32	89	88
Burn severity (RdNBR) (range)		764 ± 193 (299–1068)	632 ± 243 (301–1061)	887 ± 204 (382–1227)	811 ± 210 (424–1169)
Average elevation (m) (range)		1550 ± 130 (1277–1845)	1504 ± 172 (1224–1903)	1380 ± 130 (1146–1620)	1475 ± 186 (1151–1952)



Fig. 2 The Chips Fire before (upper left) and after (upper right) salvage; note snag retention patch in the top right corner. The Rim Fire before (lower left) and after (lower right) salvage with overall higher retention of small-diameter conifer and oak snags

Survey methods

Surveyors conducted 5-min exact-distance point counts at each survey location and recorded all bird species seen or heard (Ralph et al. 1995). With the aid of rangefinders, surveyors estimated the exact distance to the initial detected location of each individual bird. Counts began around local sunrise, were completed within 4 h, and did not occur in inclement weather. Surveyors received 2 weeks of training to identify and estimate distances to birds and passed a double-observer field test. Most points were visited twice during the peak of the breeding season from mid-May through the end of June. In both fires, we collected 1 year of pre-salvage bird survey data the year after the fires (2013 in Chips, 2014 in Rim). In the Chips Fire, we collected post-salvage bird data in 2014 and 2015 (2–3 years post-fire). Because salvage was ongoing during 2015 in the Rim Fire, we collected post-salvage data in 2016 and 2017 (3–4 years post-fire). In Rim, all 106 salvage and 109 control locations were visited in 2014 and 2016; in 2017, we visited a subset of locations that were salvaged in 2015 to acquire a second year of post-treatment data, in addition to a subset of control locations.

Vegetation data were collected at all survey locations for both fires the year after the fire burned and before any post-fire management occurred (2013 in Chips, 2014 in Rim). We then repeated the vegetation surveys in 2015 in the Chips Fire and in 2016 or 2017 in the Rim Fire, after

all salvage activities took place. We measured vegetation characteristics within a 50-m radius plot centered at each point count location following a modified version of the relevé protocol, outlined in Ralph et al. (1993). We visually estimated shrub cover and height, herbaceous cover, and measured basal area of live trees and snags using a 10-factor basal area angle gauge at the plot center and at the four cardinal directions 35 m from the plot center which we used to calculate both an average and variability (standard deviation). Shrub height and cover and basal area of both live and dead trees can change drastically in relation to time since fire and post-fire management (i.e., shrubs grow rapidly post-fire and snags begin to fall, while salvage operations can disrupt shrub growth and remove snags). To describe vegetation conditions as accurately as possible for each sampling unit, we calculated vegetation covariates at each location in each year. However, we were not able to conduct field vegetation surveys every year. When bird and vegetation survey data were available for the same year, we used the measurement from that year, but when vegetation survey data were not available for the same year as bird surveys (largely in the control untreated subsample), we calculated the values of vegetation covariates for the years in which vegetation surveys did not take place by assuming a constant rate of change between surveys. For treated locations, we calculated salvage intensity by dividing the post-salvage snag basal area value by the

pre-salvage value to determine the proportion of the snag basal area that was removed during salvage activities in addition to any natural loss or gain and then subtracted that value from 1.0.

Data analysis

We estimated bird density with hierarchical distance sampling models using the “distamp” function in the R package unmarked, version 0.12-2 (Fiske and Chandler 2011; R Core Team 2014). This modeling framework allowed us to estimate the density of each species, corrected for variation in detection probability as a function of distance from the observer, and we treated each survey location-year combination as an independent sampling unit (Sollmann et al. 2015). We modeled all species that had a minimum of 50 point-level detections within 125 m of the observer (Table 2; see Table 4 for all species detected, including unmodeled species).

or were inestimable) and had the lowest Akaike’s Information Criterion (AIC) value. To model intensity, we included a time variable indicating pre- or post-salvage, along with a variable (range 0.0–1.0) defined as the proportion of available snags that were removed during salvage activities. All locations received a value of 0.0 for the salvage intensity variable before salvage, and control locations retained the 0.0 after salvage, even though our surveys did show that some background loss of snag basal area occurred (mean = 0.12 m²/ha in Chips and 0.35 m²/ha in Rim). We modeled salvage activity as a binary variable using a three-level factor blocking covariate depicting both time and treatment (levels: pre-treatment, post-salvage-treated, post-salvage-control). Abundance at location *i* is modeled as a Poisson function assuming closure within each year and including an offset for the number of visits. We included model covariates for habitat and topography conditions in addition to salvage timing and intensity or activity:

Equation 1 — the treatment intensity model:

$$\begin{aligned} \text{Poisson}(\lambda_i) = & \beta_0i + \beta_{\text{elev}} * X1_i + \beta_{\text{slope}} * X2_i + \beta_{\text{south}} * X3_i + \beta_{\text{slope}*\text{south}} * X4_i \\ & + \beta_{\text{liveBA}} * X5 + \beta_{\text{shrub}} * X6_i + \beta_{\text{PreTrtSnagBA}} * X7_i + \beta_{\text{snagSD}} * X8_i \\ & + \beta_{\text{snagRemove}} * X9_i + \text{offset}(\log(\text{visits})) \end{aligned} \quad (1)$$

Equation 2 — the treatment activity model:

$$\begin{aligned} \text{Poisson}(\lambda_i) = & \beta_0i + \beta_{\text{elev}} * X1_i + \beta_{\text{slope}} * X2_i + \beta_{\text{south}} * X3_i + \beta_{\text{slope}*\text{south}} * X4_i \\ & + \beta_{\text{liveBA}} * X5 + \beta_{\text{shrub}} * X6_i + \beta_{\text{PreTrtSnagBA}} * X7_i + \beta_{\text{snagSD}} * X8_i \\ & + \beta_{\text{PreTrt}} * X9_i + \beta_{\text{PostControl}} * X10_i + \beta_{\text{PostTrt}} * X11_i \\ & + \text{offset}(\log(\text{visits})) \end{aligned} \quad (2)$$

We modeled the detection process using a multinomial function:

$$\text{multinomial}(N_i, \pi_{i,j}) = \alpha_0i + \alpha_{\text{liveBA}} * X1_i + \alpha_{\text{shrubht}} * X2_i$$

where detection probability varies by location *i* in distance class *j* with live tree basal area (α_{liveBA}), and shrub height (α_{shrubht}) included as covariates in the half-normal (with scale parameter σ) detection function. We hypothesized that one of two mechanisms for the influence of salvage logging on species abundance might be more appropriate for each species: (1) species may be sensitive to all salvage activities regardless of local salvage intensity (Eq. 1, the salvage activity model) and (2) salvage response may best be characterized by the continuous local salvage intensity variable (Eq. 2, the salvage intensity model). We fit two models for each species to evaluate whether quantifying salvage treatments as a continuous variable (intensity) or as a binary variable (salvaged vs. unsalvaged) better described the effect on each species and selected the best model that fit all parameters well (95% confidence intervals of parameter estimates within a range of –10 to +10

Covariates in the abundance portion of the model included variables to account for the heterogenous landscape and topography, namely elevation (β_{elev}), slope (β_{slope}), southness (i.e., aspect represented as proportion of south-facing (β_{south})), and the interaction between slope and southness ($\beta_{\text{slope}*\text{south}}$). Vegetation structure covariates shrub cover (β_{shrub}), pre-treatment snag basal area ($\beta_{\text{PreTrtSnagBA}}$), snag variability (measured as the standard deviation of five BA measurements per plot, β_{snagSD}), and either the proportion of snags removed via salvage (the treatment intensity model) ($\beta_{\text{snagRemove}}$) or a three-level factor variable ($\beta_{\text{PreTrt}}, \beta_{\text{PostControl}}, \beta_{\text{PostTrt}}$).

We were able to fit models for 34 species in the Chips Fire and 37 species in the Rim Fire, 41 species total (Table 2).

We examined model coefficients and 95% confidence intervals for the salvage intensity and activity variables to assess the direction and significance of each species’ response to salvage, assuming when confidence intervals did not overlap zero that the responses were significant. To assess the combined effect of the two post-salvage

Table 2 Common name, scientific name, and 4-letter abbreviation of bird species for which we modeled the effects of salvage logging in the Sierra Nevada, CA, USA. Response to salvage intensity or activity is shown with significantly positive (+), negative (−), neutral (0), or not analyzed (NA)

Common name	Scientific name	4-letter abbreviation	Chips Fire	Rim Fire
Acorn woodpecker	<i>Melanerpes formicivorus</i>	ACWO	NA	+
American robin	<i>Turdus migratorious</i>	AMRO	−	0
Anna's hummingbird	<i>Calypte anna</i>	ANHU	NA	0
Black-backed woodpecker	<i>Picoides arcticus</i>	BBWO	−	NA
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	BHGR	−	0
Brown creeper	<i>Certhia americana</i>	BRCR	−	−
Black-throated gray warbler	<i>Setophaga nigrescens</i>	BTYW	NA	−
Cassin's finch	<i>Haemorhous cassinii</i>	CAFI	+	0
Cassin's vireo	<i>Vireo cassinii</i>	CAVI	0	−
Chipping sparrow	<i>Spizella passerina</i>	CHSP	0	0
Dark-eyed junco	<i>Junco hyemalis</i>	DEJU	0	0
Dusky flycatcher	<i>Empidonax oberholseri</i>	DUFL	0	0
Fox sparrow	<i>Passerella iliaca</i>	FOSP	0	+
Hammond's flycatcher	<i>Empidonax hammondii</i>	HAFL	−	0
Hairy woodpecker	<i>Leuconotopicus villosus</i>	HAWO	0	−
Hermit warbler	<i>Setophaga occidentalis</i>	HEWA	0	−
House wren	<i>Troglodytes aedon</i>	HOWR	0	−
Lawrence's goldfinch	<i>Spinus lawrencei</i>	LAGO	NA	0
Lazuli bunting	<i>Passerina amoena</i>	LAZB	−	0
Lesser goldfinch	<i>Spinus psaltria</i>	LEGO	NA	+
MacGillivray's warbler	<i>Geothlypis tolmiei</i>	MGWA	−	0
Mountain bluebird	<i>Sialia currucoides</i>	MOBL	+	NA
Mountain chickadee	<i>Poecile gambeli</i>	MOCH	−	−
Mourning dove	<i>Zenaidura macroura</i>	MODO	NA	0
Nashville warbler	<i>Leiostyris alpestris</i>	NAWA	0	−
Northern flicker	<i>Colaptes auratus</i>	NOFL	0	0
Olive-sided flycatcher	<i>Contopus cooperi</i>	OSFL	0	−
Pine siskin	<i>Carduelis pinus</i>	PISI	+	NA
Purple finch	<i>Haemorhous purpureus</i>	PUFI	0	−
Red-breasted nuthatch	<i>Sitta Canadensis</i>	RBNU	−	−
Red-breasted sapsucker	<i>Sphyrapicus ruber</i>	RBSA	0	NA
Spotted towhee	<i>Pipilo maculatus</i>	SPTO	0	0
Steller's jay	<i>Cyanocitta stelleri</i>	STJA	−	0
Townsend's solitaire	<i>Myadestes townsendi</i>	TOSO	0	0
Warbling vireo	<i>Vireo gilvus</i>	WAVI	NA	0
White-breasted nuthatch	<i>Sitta carolinensis</i>	WBNU	NA	0
Western bluebird	<i>Sialia mexicana</i>	WEBL	+	+
Western tanager	<i>Piranga ludoviciana</i>	WETA	−	0
Western wood-pewee	<i>Contopus sordidulus</i>	WEWP	0	0
White-headed woodpecker	<i>Picoides albolarvatus</i>	WHWO	0	0
Yellow-rumped warbler	<i>Setophaga coronata</i>	YRWA	0	−

levels of the salvage activity variable, we used the difference between the post-salvage-control and post-salvage-treated coefficients, with average magnitudes of the 95% confidence intervals from the two coefficients,

as a summary of the treatment effect. We grouped species into “salvage sensitive” species that had a significant negative salvage response in either fire or “salvage neutral or positive” species that had non-significant

responses in both fires or a significant positive response in either fire.

Salvage scenario modeling

Finally, we used fitted models to simulate the relative impact of five hypothetical salvage logging scenarios in comparison to doing no salvage at all. We predicted abundances for each species across a set of hypothetical locations in the post-treatment period with average values (0.0 on the standardized scale) for all model covariates except pre-treatment basal area, and the treatment intensity or activity variables. We varied pre-treatment snag basal area across a range of values ($n = 60$) to mimic the distribution of observed snag basal area values for each fire and varied treatment intensity and activity to depict a variety of salvage prescriptions. We calculated the amount of snag basal area removed to match the same amount that we recorded as removed in each fire. Thus, in the scenarios where higher intensity salvage occurred, fewer locations were treated, but where salvage intensity was limited to a lower value a larger proportion of the locations would have to be treated to match the target total basal area removed. In this analysis, it is thus implicit that all salvage scenarios are otherwise similar in salvage techniques (e.g., trees are removed in similar spatial patterns, unit size, snag sizes retained, etc.). We chose the set of scenarios (Table 3) to be representative of our understanding of the range of potential decisions that might be made in actual practice on National Forests or other public lands. Scenarios also varied in targeting locations with

high pre-treatment snag basal area, to a randomized selection of locations, and to a set of locations that mimic the observed patterns in salvage intensity from each study area fire. We assessed the relative differences of scenarios by evaluating the total abundance across all species within the “salvage sensitive” and “salvage neutral and positive” species groups, as well as the diversity of the entire community measured with the inverse Simpson metric using the R package *Vegan* (Oksanen et al. 2018). We plotted these results with violin plots showing the mean values in addition to each individual salvage scenario data point.

Results

Vegetation changes

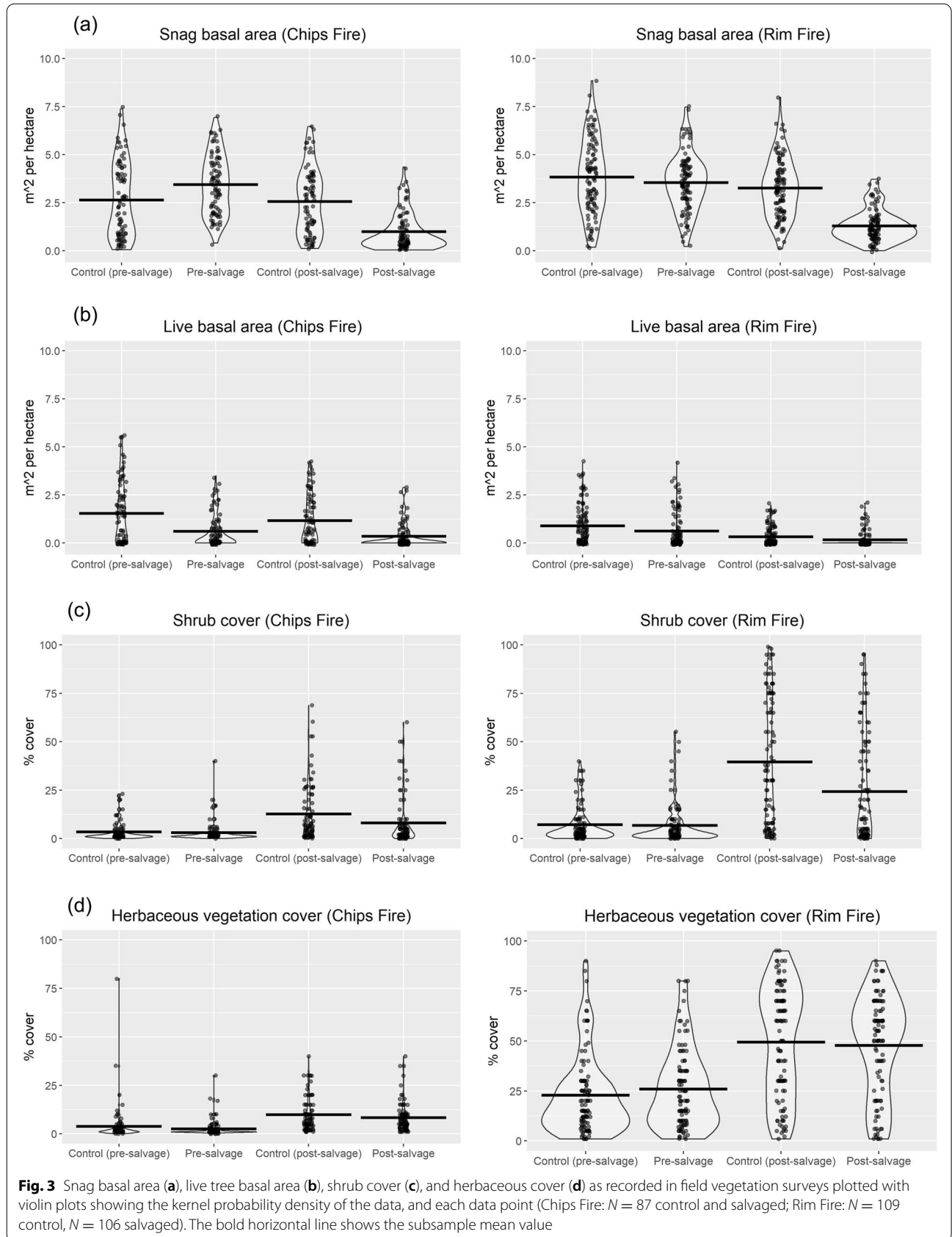
The pre-treatment snag basal area was lower on average in the Chips Fire ($3.0 \text{ m}^2 \text{ ha}^{-1}$) compared to the Rim Fire ($3.69 \text{ m}^2 \text{ ha}^{-1}$), and the pre-treatment live tree basal area was higher (Chips = $1.08 \text{ m}^2 \text{ ha}^{-1}$, Rim = $0.76 \text{ m}^2 \text{ ha}^{-1}$, Fig. 3a, b). Salvage treatments resulted in 71% of the snag basal area removed at treated locations in the Chips Fire and 64% in the Rim Fire, with a range of 0–100% snags reduced (0% at two and six locations in Chips and Rim fires, respectively, where a small number of snags were harvested combined with delayed mortality from live trees ultimately increased the amount of snags post-treatment). Shrub cover and height increased over time after both fires, but the increase was larger overall in the Rim Fire, and both fires had a large amount of variability (Fig. 3c). In the Chips Fire, shrub cover was low pre-salvage and increased modestly in both treated and control locations (from 3.2% and 3.6% at treated and control locations to 8.2% and 12.7%, respectively). In the Rim Fire, shrub cover increased substantially from pre- to post-treatment periods at all locations (from 6.8% and 7.2% at treated and control locations to 23.5% and 36.1%, respectively). Shrubs rapidly increased in height following the fires; the average height of the top quartile of foliage post-salvage was 1.0 m at treated locations and 1.3 m at control locations in Chips, while in Rim the shrub height was 1.5 m at treated locations and 1.7 m at control locations. Herbaceous cover (all non-woody understory plants) differed substantially between fires but was similar at control and salvage points (Fig. 3d). The Chips Fire averaged 4 and 3% pre-salvage at control and treated locations (compared to 23 and 26% in the Rim Fire) and increased to 10 and 8%, respectively, following salvage treatments (compared to 49 and 48% in the Rim Fire).

Bird response to salvage

Support for the salvage intensity and salvage activity models was split evenly among all species, but within the

Table 3 Salvage scenarios were chosen to represent different hypothetical prescriptions for salvaging a representative selection of locations that mimic the measured pre-fire snag basal area from each fire. Scenarios varied in salvage intensity and proportion of area treated; the number of locations salvaged was limited to the minimum needed to achieve a total basal area that matched the observed total basal area removed in each fire

Salvage scenario strategy	Salvage intensity	Proportion of total area treated	
		Chips	Rim
No salvage	0%	0%	0%
Target high snag basal area locations	90%	23%	22%
Target high snag basal area locations	50%	52%	48%
Salvage locations at random	90%	40%	35%
Salvage locations at random	50%	70%	65%
Mimic real data (land manager input)	0–100% (average 64% in Rim, 71% in Chips)	50%	50%



Chips Fire, more species had lower AIC in the salvage activity model (20) than the salvage intensity model (14), and the Rim models were opposite with fewer salvage activity models selected (15) than salvage intensity (22, Fig. 4). For approximately half of all species, we detected significant salvage effects in at least one fire. More species had negative responses to salvage (11 in Chips, 13 in Rim) than positive (4 in Chips and 4 in Rim). Species that responded positively to salvage included some open habitat species, such as western and mountain bluebirds (*Sialia mexicana*, *S. currucoides*), and some seed consumers including pine siskin (*Carduelis pinus*), Cassin's finch (*Haemorhous cassinii*), and lesser goldfinch (*Spinus psaltria*). A wide variety of species with various life histories responded negatively to salvage including black-backed woodpecker (*Picoides arcticus*), hairy woodpecker (*Leuconotopicus villosus*), and both shrub- and edge-associated species (e.g., lazuli bunting [*Passerina amoena*], MacGillivray's warbler [*Geothlypis*

tolmiei], olive-sided flycatcher [*Contopus cooperi*], and house wren [*Troglodytes aedon*]) and green forest-associated species (e.g., mountain chickadee [*Poecile gambeli*], red-breasted nuthatch [*Sitta canadensis*], brown creeper [*Certhia americana*], western tanager [*Piranga ludoviciana*], hermit warbler [*Setophaga occidentalis*], yellow-rumped warbler [*S. coronata*], and Cassin's vireo [*Vireo cassinii*]).

Of the 30 species for which we were able to fit models in both fires, 22 showed a similar response to salvage (where the sign of the coefficient was the same regardless of the statistical significance for both fires; Fig. 4). Five of the eight species with different responses had non-significant positive responses to salvage in the Chips Fire but a significant negative response in Rim (Cassin's vireo, house wren, olive-sided flycatcher, purple finch [*H. purpureus*], yellow-rumped warbler), and two species (American robin [*Turdus migratorius*] and lazuli bunting) had significant negative salvage responses

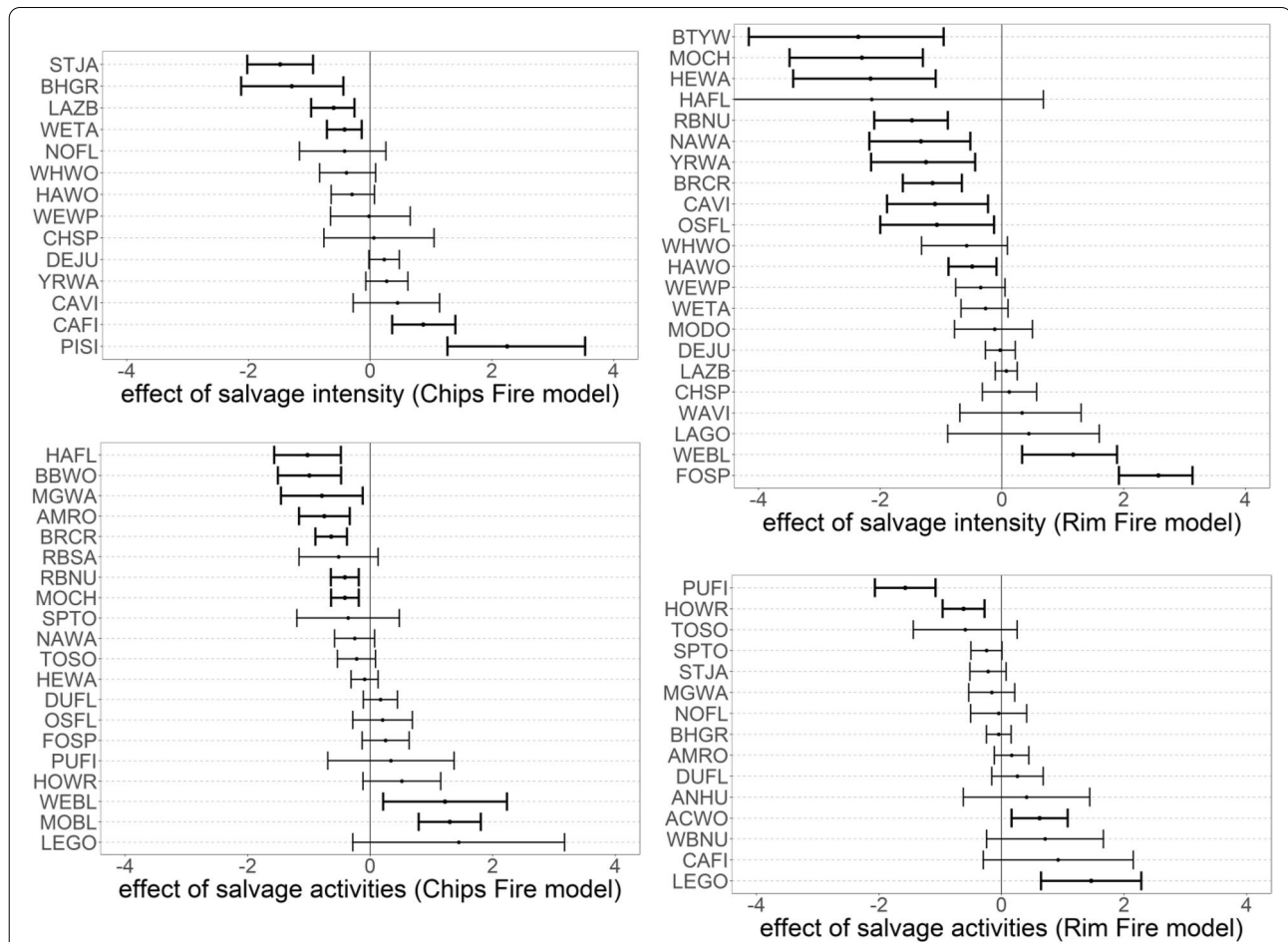


Fig. 4 Salvage effect coefficients for Chips and Rim fires from fitted models. Each species was modeled with either a salvage intensity model (continuous variable representing the proportion of snags removed) or a salvage activity model (binary variable representing salvaged or control). Error bars show 95% confidence intervals. Significant effects are shown with bold error bars

in Chips but non-significant positive responses in Rim. There were no species with opposite and significant responses to salvage intensity or activity between the two fires.

Testing scenarios of intensity and area salvaged

Projected bird abundances and diversity showed that none of the strategies for arranging the salvage activities or intensity completely mitigated the negative effects of salvage (Figs. 5 and 6). For both abundance and diversity, the scenarios that prescribed a larger proportion of locations to be salvaged resulted in the largest reductions in salvage-sensitive species in comparison to no salvage. Across both fires, the salvage-sensitive species ($N = 20$) had a far higher total abundance than the salvage-neutral and positive species ($N = 21$). The abundance of salvage-sensitive species was reduced in every salvage scenario in comparison to the no salvage scenario, though these reductions were partially offset by increases in the

salvage-neutral and positive species (Fig. 5). Targeting the high snag basal area stands for salvage did not have as large a negative effect on the bird community compared to scenarios that applied a lighter salvage prescription across a larger area. Other scenarios resulted in average abundance declines ranging from 8 to 28% in comparison to the no salvage scenario (Fig. 5). These declines in salvage-sensitive species were partially offset by smaller increases in salvage-neutral and positive species abundance. Diversity was also reduced in nearly every scenario, with effects of salvage in Rim stronger than in Chips (Fig. 6). Other scenarios resulted in diversity values of 90–95% of the no salvage scenario in Rim and 97–102% in Chips (Fig. 6).

Across all the salvage scenarios in both fires, the species that declined the most in comparison to the no salvage scenario (abundances 16–32% lower) included Hammond’s flycatcher, black-backed woodpecker, mountain chickadee, brown creeper, red-breasted nuthatch,

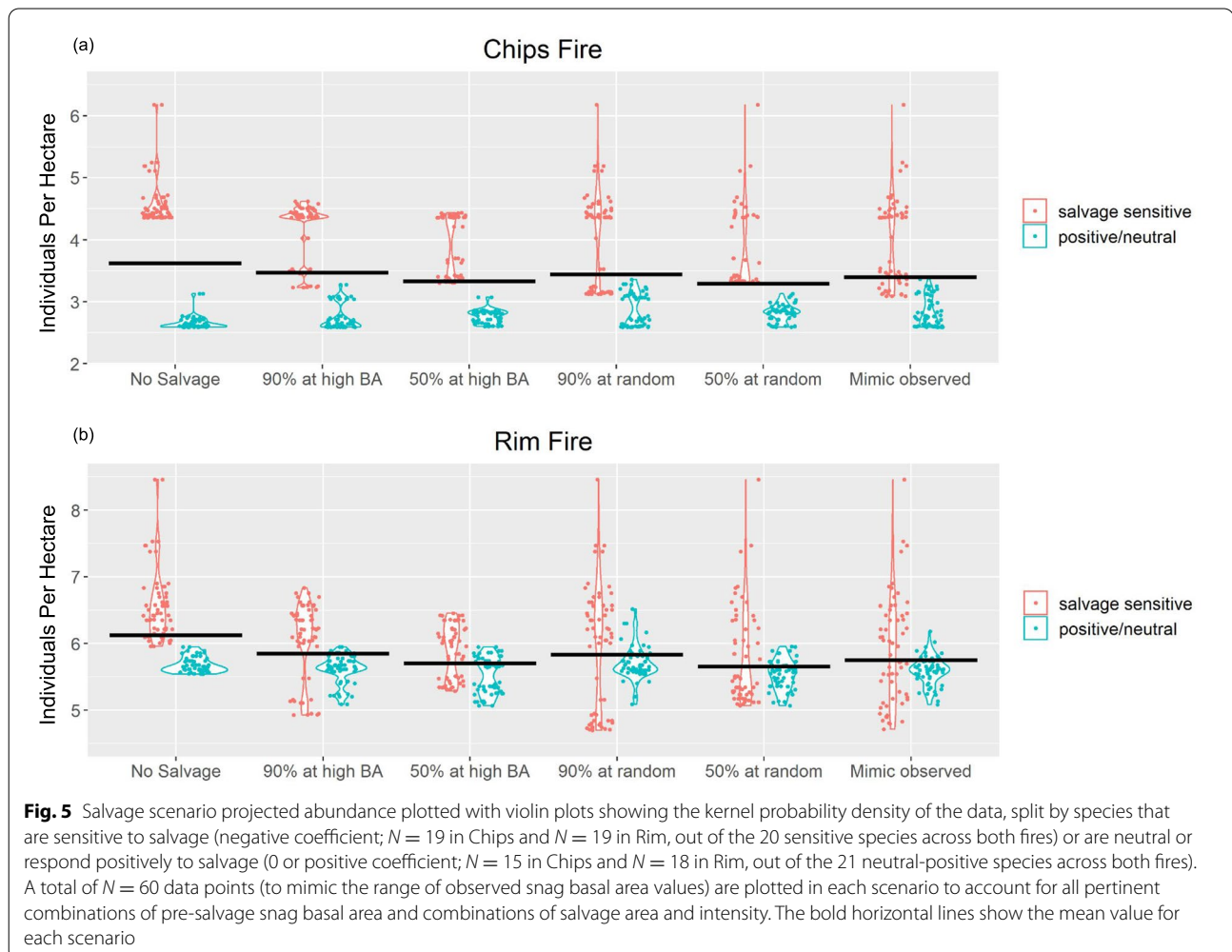
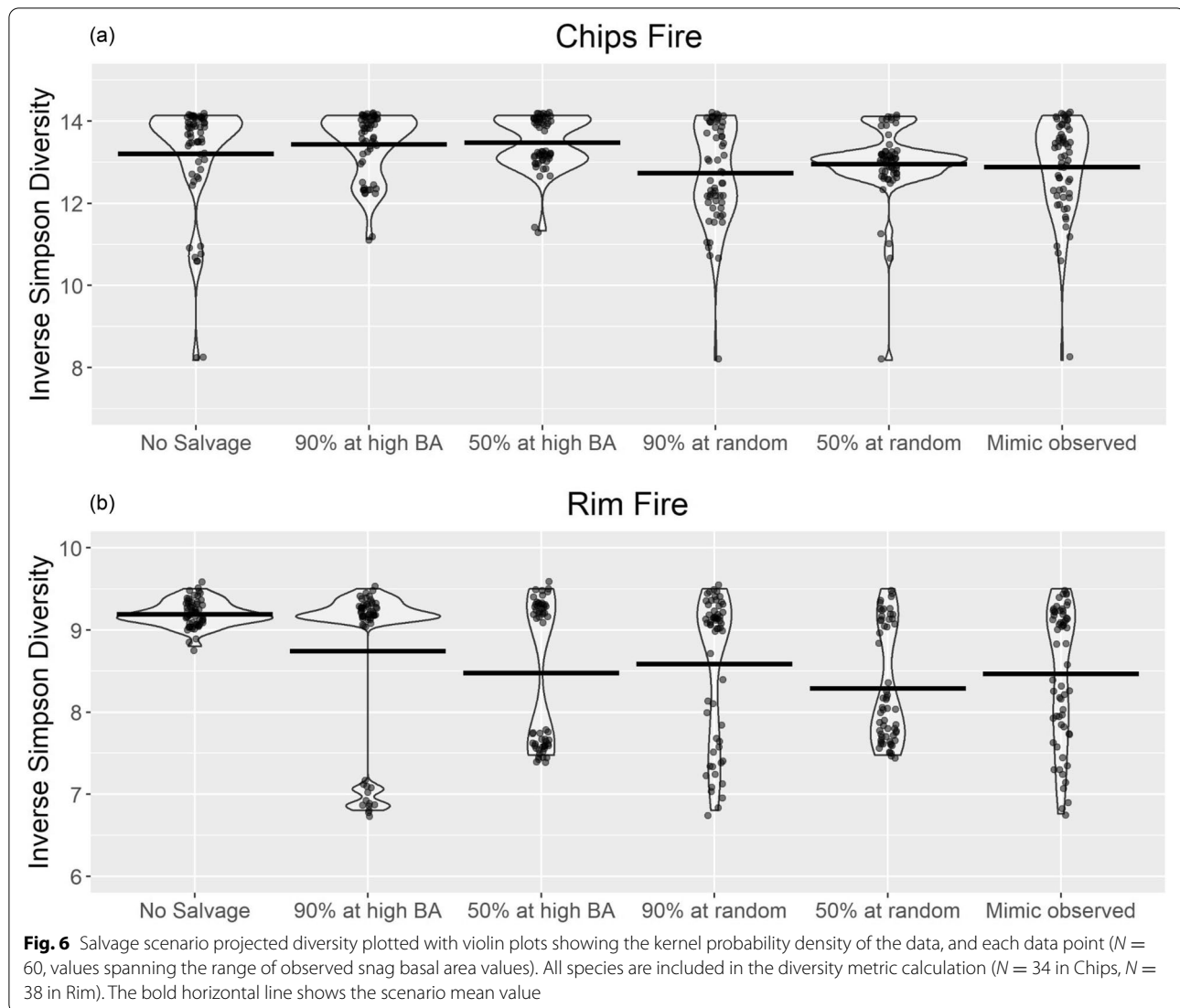


Fig. 5 Salvage scenario projected abundance plotted with violin plots showing the kernel probability density of the data, split by species that are sensitive to salvage (negative coefficient; $N = 19$ in Chips and $N = 19$ in Rim, out of the 20 sensitive species across both fires) or are neutral or respond positively to salvage (0 or positive coefficient; $N = 15$ in Chips and $N = 18$ in Rim, out of the 21 neutral-positive species across both fires). A total of $N = 60$ data points (to mimic the range of observed snag basal area values) are plotted in each scenario to account for all pertinent combinations of pre-salvage snag basal area and combinations of salvage area and intensity. The bold horizontal lines show the mean value for each scenario



black-throated gray warbler (*Setophaga nigrescens*), hermit warbler, Steller's jay (*Cyanocitta stelleri*), and Townsend's solitaire (*Myadestes townsendi*). But the reductions in abundance for these species were offset by increases in abundance (54–138% higher) for several species including Cassin's finch, western bluebird, fox sparrow, mountain bluebird, pine siskin, and lesser goldfinch, though these species tended to be relatively rare overall.

Discussion

The majority of the post-fire bird community did not benefit from salvage logging; however, snag retention strategies likely avoided more severe negative effects. By modeling salvage intensity, our study shows that increasing retention in salvage treatments, especially in the Rim Fire, can lessen declines in fire-adapted species. Woodpeckers, some secondary cavity nesters, and

sparsely forested and mature forest species did respond negatively to salvage, while generally seed-eaters, some shrub nesters, and grassland species (e.g., bluebirds) responded positively. Our results mirror those that others have found for birds in coniferous forests across North America, showing largely negative effects, many of which focused on cavity nesters (Kotliar et al. 2002, Morissette et al. 2002, Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Cahall and Hayes 2009, Kronland and Restani 2011), but also open-cup nesters and mature forest birds (Morissette et al. 2002; Cahall and Hayes 2009). Quantifying salvage intensity also allowed for modeling a variety of potential salvage scenario alternatives. These did not offer a clear strategy to offset these negative effects, although the scenarios that limited the area treated by intensively salvaging a relatively small portion of the burned forest generally minimized

the negative effects on the bird community. However, the magnitude in the decline of abundance and diversity in the salvage scenarios was less than expected compared to other studies in western North America (as cited above). Strategies that included reducing area salvaged across the fires, avoiding riparian areas, and retaining snags and live trees likely may have mitigated a steeper decline.

While results for most species were consistent across fires, especially the mature forest species, there were some differences that suggest post-fire salvage decisions can be tailored to protect certain species. Differences in salvage activities between fires included smaller salvage units and smaller overall area salvaged in the Chips Fire, whereas the Rim Fire was salvaged over a longer period, larger salvage units, and larger overall area salvaged. Despite the differences in total area salvaged, however, the proportion of conifer forest that burned at moderate-high severity was very similar between the fires, which implies that any species that responded differently between the fires did so because of factors such as the salvage techniques, landscape or spatial pattern effects, elevation or latitude differences, and post-fire vegetation response (Webster and Halpern 2010; Crotteau et al. 2013). Vegetation growth, especially of herbaceous plants and shrubs, was extremely robust within the Rim Fire footprint. In addition to overall higher snag retention, we suspect that the strong vegetation response provided additional nesting and foraging opportunities and explains the overall higher bird abundance in Rim compared to Chips. It may also be a sign of a more active fire history in the Rim Fire landscape producing soil and seed bank conditions that were conducive to the strong post-fire vegetation response and revealing the potential through ecological memory to produce a relatively stronger post-fire recovery (Fontaine et al. 2009; Johnstone et al. 2016). We had a 1-year lag in completing post-salvage surveys in the Rim Fire due to ongoing logging, which also allowed for vegetation to respond after salvage activities.

More species were sensitive to salvage intensity (rather than the presence or absence of salvage activities) in the Rim Fire compared to the Chips Fire, suggesting that snag retention may have been more important in Rim due to larger salvage units and contiguous area salvaged. In the Chips Fire, designing smaller salvage units may have benefited edge species such as olive-sided flycatcher and western wood-pewee (*Contopus sordidulus*) which responded negatively in the Rim Fire (marginally for the latter species) but neutral in the Chips Fire. These species may have found appropriate habitat on the edges of salvage units, as

Fontaine (2007) also documented in the 2002 Biscuit Fire. Smaller salvage units also may help explain why some mature forest species, such as yellow-rumped warbler and Cassin's vireo had negative responses to salvage in Rim Fire but had a neutral response in the Chips Fire. The Chips Fire was also located at a higher elevation and 250 km north of the Rim Fire, with proportionally more mature forest dominated by fir and lesser amounts of the smaller size class pine-oak forest and plantations present in the Rim Fire, which may have led to a more muted shrub response and the absence of re-sprouting oaks. The higher cover of shrubs and oaks in the Rim Fire may also explain why some species associated with these habitat attributes responded negatively to salvage in the Chips Fire but were non-significant in the Rim Fire (e.g., black-headed grosbeak [*Phaeothicus melanocephalus*], lazuli bunting, MacGillivray's warbler).

Despite the differences in landscape context and salvage activities across the two fires, the effects of salvage logging on species that utilize recent fire-killed trees were consistently negative. Hairy woodpecker, black-backed woodpecker, and white-headed woodpecker (marginally significant) responded negatively to salvage, matching the results from other studies in western coniferous forests (Kotliar et al. 2002, Hutto and Gallo 2006, Koivula and Schmiegelow 2007, Hanson and North 2008, Cahall and Hayes 2009, Kronland and Restani 2011). Acorn woodpecker (*Melanerpes formicivorus*) was the only cavity-excavator with a significant positive response to salvage, likely responding to open conditions for fly-catching, their primary breeding-season foraging strategy (Koenig et al. 2019). Black-backed woodpecker is a species of management interest in the Sierra Nevada burned forests; thus, their significant negative response to salvage activities will likely be a driver of post-fire management decisions. Whether this pattern is consistent across all fires is unclear, especially with varying salvage logging prescriptions (Tarbill et al. 2018). In contrast to studies from the Rockies and boreal forest, previous work from the Sierra Nevada has shown that black-backed woodpeckers avoid the interiors of large high-severity patches (White et al. 2019; Campos et al. 2020) and place nests close to low-severity and unburned forest edges (Stillman et al. 2019). With their sensitivity to salvage and preference for high snag basal area and landscape fire heterogeneity, salvage prescriptions can be designed to conserve the most high-value habitat for the species, including areas at higher elevation (Tingley et al. 2016b), as well as smaller high-severity patches embedded in landscapes with lower severity effects (Campos et al. 2020).

In both fires, many mature and open forest bird species that utilize the tree canopy for foraging and nesting (e.g., Steller's jay, Cassin's vireo, mountain chickadee, red-breasted nuthatch, brown creeper, yellow-rumped warbler, hermit warbler, western tanager) had a negative salvage effect but persisted within the unsalvaged stands. Burned forest is typically not the primary habitat for mature conifer forest species (Taillie et al. 2018); however, with fires increasing in frequency, severity, and size in the Sierra (Westerling et al. 2006; Miller and Safford 2012; Steel et al. 2015), our study documents that many of these green-forest associates can persist in unsalvaged areas that burn at moderate to high severity. The California spotted owl (*Strix occidentalis*), a mature forest specialist, can persist in mixed-severity burned areas especially when high-severity patch sizes are relatively small and areas are not heavily salvaged logged (Lee et al. 2013; Kramer et al. 2021).

Like woodpeckers and mature forest species, some early seral forest-associated species showed consistent responses to salvage in these two fires. For example, shrub species, including dusky flycatcher (*Empidonax oberholseri*) and fox sparrow, showed a similar neutral to positive response to salvage in both fires. Shrub-nesting birds have been shown to respond positively to post-fire salvage in other studies (Fontaine 2007; Cahall and Hayes 2009). Historically, many of these species may have occupied chaparral habitat that repeatedly burned at high severity and thus would not have contained a large number of snags or downed wood (Coppoletta et al. 2016). A few species were notable in having somewhat divergent responses, although these were not statistically significant, such as house wren (negative response in Rim but neutral in Chips) and MacGillivray's warbler and lazuli bunting (negative in Chips, neutral in Rim). The large differences in shrub response between the fires (both inside and outside of salvage) may explain these divergent responses. These species were all far more abundant in the Rim Fire.

Salvage scenario modeling from both fires showed differences in how the salvage-sensitive and neutral or positive species responded. One clear pattern across both fires was that the scenarios that minimize the area targeted for salvage activities tended to maximize bird abundance while maintaining diversity at levels similar to the no salvage scenario. Total bird abundance in the Rim Fire was much larger overall than in the Chips Fire, but also within each fire the salvage-sensitive species were more abundant than the salvage-neutral and positive species. In both fires, salvage-sensitive species exhibited larger declines in abundance than the increases from the salvage-neutral and positive species. While the

scenario that minimized area treated by more intensively removing snags from the highest snag density areas maximized bird abundance and diversity, it is notable that the highest snag basal area locations generally also had the highest abundance and diversity estimates. Thus, the salvage strategies that target these locations may disturb the highest bird diversity locations within the fires and potentially areas with the highest density of species of management concern such as the black-backed woodpecker.

Caveats and limitations

To control for uneven sampling and other unmodeled influences on species abundances, we fit models separately to each fire and then projected abundances onto hypothetical data to isolate the unique effects that salvage activities in each fire had on this group of species. We feel this was warranted to elucidate the effects of different salvage activities and strategies in each fire on the species most common in burned forests, some of which are reliant on this habitat type. In addition, some species were rare before or after the salvage treatments which limited our ability to fit models; thus, we may have had a low statistical power to fully evaluate the effects on species that are sensitive to salvage treatments. Utilizing a multi-species occupancy model (Dorazio et al. 2010) would also increase the power to potentially detect an effect in rare species (Burnett and Roberts 2015). Another limitation is that we did not characterize the spatial distribution of salvage treatments, specifically prescriptions like snag retention patches versus more dispersed snag removals versus other potential patterns. We attempted to track these spatial effects by including the variability in snag basal area in the models, but this measure may not be an adequate quantification of the spatial effects (it was not a strong predictor for a large proportion of the community). Delineating retention areas and measuring occurrence in relation to distance from those areas would further clarify how and where snag retention is most needed. In addition, our analysis summarizes the effects of salvage and snag removal intensity over a short term, only 1–2 years post-salvage and 3–4 years post-fire. Long-term effects on the bird community may be different as salvaged areas are replanted, shrub competition is controlled, and snags begin to fall. Habitat quality for the bird community could either be enhanced by management or the negative effects we found could cascade through longer time periods leading to suppressed biodiversity over the decades following salvage treatments. We recommend monitoring salvaged and unsalvaged areas long term to better understand these patterns.

Our findings should be interpreted within the context of the intensity of salvage logging that occurred in these fires. Large portions of these fires were left unsalvaged, salvage units were relatively small, and snags and any tree with live green foliage were retained within the units. If salvage had been near complete removal of snags and green trees that may die across all moderate- and high-severity burned areas (more typical of some private timber lands in the Sierra Nevada), effects may have been different. Our sampling locations occurred across a wide range of salvage intensity and given a larger portion of the community were found to respond to salvage intensity rather than the presence/absence of salvage activities, one might expect greater intensities of salvage would have stronger effects on these species. Also, as larger portions of the landscape are salvaged, those species associated with edges of salvage units (e.g., olive-sided flycatcher) or those able to seek refugia in the adjacent unsalvaged areas may have stronger negative effects.

Conclusions

Our study has demonstrated largely negative to neutral effects of post-fire salvage logging for the bird community in the Sierra Nevada, corroborating evidence from across multiple western conifer ecosystems. The overall magnitude of negative effects we demonstrated in the salvage scenarios was less than we expected compared to other studies in conifer forests that found more substantial reductions in bird abundance and diversity metrics. Land management agencies have taken significant steps towards mitigating negative effects (e.g., increased snag retention, avoiding riparian areas, and incorporating protections for special status species). When planning post-fire salvage, managers should consider targeting logging to specific conditions where the benefits outweigh the costs of interventions (Long et al. 2014). These conditions can include protecting life and property from falling snags and creating defensible space for future fire in the wildland-urban interface. Forest ecologists have also recommended targeting interiors of large high-severity patches for salvage and reforestation to avoid type conversion to shrub and hardwood communities (Crotteau et al. 2013; Welch et al. 2016). Indeed, these areas may be less important for supporting high bird diversity in the Sierra Nevada due to low pyrodiversity (Steel et al. 2021). We recommend that managers should take an innovative approach to post-fire areas by salvaging as small an area as possible and setting aside early seral reserves for salvage-sensitive species (Hutto et al. 2016; Lindenmayer et al. 2018), especially for those species that are most closely tied to snag forests.

Appendix

Supplemental information for sampling design, data analysis, and habitat covariate results

Sampling design for Chips and Rim fires

In the Chips Fire, we began with 195 survey locations from an existing monitoring program (Stephens et al. 2014; Burnett and Roberts 2015). These locations were originally selected by randomly choosing three starting points within subwatersheds and then establishing 11 additional points spaced 250 m apart in a random direction. Additional locations were selected to fit within the boundaries of proposed timber removal treatments which generally had a linear shape. Thirty of these 195 locations fell within salvage unit boundaries. To achieve a balanced sample and coverage within the Chips Fire, we placed an additional 110 survey locations in nearly all the proposed salvage units to maximize the sample. We also added an additional 30 control locations adjacent to existing control locations that were accessible (slopes <35%) that, when combined with the above survey locations, fell within the range of conditions in proposed salvage units. All site selection was carried out in a GIS and all survey locations were spaced at least 250 m apart. All control sample locations were at least 250 m outside of a treatment unit.

Our Rim Fire sampling strategy differed from the Chips Fire to account for far more burned and salvaged area. We stratified the potential sampling area using proposed salvage unit boundaries (provided by Stanislaus National Forest), pre-fire forest type, cover and density classes (USDA Forest Service 2004), topography (Sierra Nevada Ecosystem Project (SNEP) 1999), and burn severity. To create a grid of potential survey locations, we used the Military Grid Reference System (100-m resolution), clipped it to the proposed salvage polygons, and removed all areas with slopes greater than 30%. We generated a list of spatially balanced random transect starting locations using a Generalized Random Tessellation Stratified method (GRTS, Stevens and Olsen 2004) in the proposed salvage areas. Up to 10 survey locations were established every 250 m within 20 salvaged subsample transects, and each location was at least 100 m from the salvage polygon boundary. We purposely oversampled in proposed salvage areas expecting some areas would not receive treatments. To create a control subsample, we only included areas >250 m outside of proposed salvage units, elevations above 867 m, slopes <30%, conifer pre-fire forest types, dense, moderate, and open density classes, and weighted the GRTS selection to match the frequency of burn severity in our salvaged

subsample. GRTS was then used to select nine control transects with 10 points each.

As a final step for both fires, we dropped all potential control locations with RdNBR (relativized difference in normal burn ratio) values less than the minimum of the salvaged subsample value in each fire (Chips = 298, Rim = 382). We also excluded from the control subsamples all survey locations in both fires with > 5% of the area within a 250-m radius of the location in a roadside or private land salvage logging unit to avoid the presence of these activities and their influence on bird abundance. Sample sizes were further reduced in both fires as less area was salvaged than proposed and, in the case of the Chips Fire, due to an overabundance of potential control locations falling outside of the salvage habitat parameters. The final sample consisted of 106 salvaged and 109 control locations in the Rim Fire and 87 salvaged and 87 control locations in the Chips Fire.

Data analysis and modeling

In addition to the variables accounting for time and treatment, we included continuous variables for average pre-salvage snag basal area (constant across years at each location) to account for differences in pre-salvage snag volume, the standard deviation of snag basal area (to account for an uneven distribution of snags within the survey plot, and varied across years), live tree basal area (varied across years), percent shrub cover (varied across years), and additional covariates to quantify the effects of topographic conditions (constant across years) sampled from the Sierra Nevada Regional Digital Elevation Model. The topographic variables included elevation, slope, aspect (converted to southness = 1.0 for directly south-facing, 0.5 for east and west, and 0.0 for north), and an interaction between slope and aspect. We evaluated the degree of collinearity between all variables using the variance inflation factor (VIF; Heiberger 2018) and detected no evidence for a high degree of collinearity (VIF < 3). All continuous covariates except salvage intensity were standardized before model fitting.

Our modeling approach assumed an open population of individuals at each location (unlimited immigration and emigration) but avoided the high computational demand of including population demographic parameters in a distance sampling framework by treating each survey location-year combination as an independent sampling unit (Sollmann et al. 2015). We acknowledge that this assumption may potentially underestimate error in some model parameter coefficients, but such bias would largely be limited to those parameters that do not vary with time, and this data structure may be

more appropriate than models assuming a closed population or limited dispersal in an area of rapid habitat changes such as the post-disturbance early seral habitats in our study area. We initially attempted to model the response to salvage by combining data from both fires; however, we found the model fit was poor, which we assume indicates that some covariates have inconsistent effects between the two fires. Thus, we modeled bird abundances in Chips and Rim fires separately. We modeled all species that had a minimum of 50 point-level detections within 125 m of the observer (see Table 4 for all species detected, including unmodeled species).

Bird response to habitat covariates

Fitted models showed additional patterns of association with habitat variables, generally meeting expected characteristics of open habitat versus forest birds (Fig. 7a–d in the Appendix). Pre-treatment basal area tended to have a negative influence on broad-leaf-associated species such as Nashville warbler (*Leiothlypis ruficapilla*) and fox sparrow (*Passerella iliaca*) and a positive effect on forest- and snag-associated birds such as Hammond's flycatcher (*Empidonax oberholseri*), brown creeper, white-headed woodpecker (*Picoides albolarvatus*), and black-backed woodpecker; these effects were significant for more than one-third of the community (14/34 in Chips, 15/37 in Rim; Fig. 7a). In contrast, snag basal area variability was significant for only a small proportion of the community (6/34 in Chips, 5/37 in Rim) and there was little congruence in the direction of association with this variable in species across both fires (Fig. 7b). Live tree basal area was a significant effect for a large proportion of the community (22/34 in Chips and 17/37 in Rim), and the direction of these effects fit our assumptions about early seral habitat species such as western bluebird and lazuli bunting avoiding sites with high live tree basal area, while forest associates such as hermit warbler and red-breasted nuthatch were positively associated (Fig. 7c). Forest birds such as yellow-rumped warbler and red-breasted nuthatch avoided high shrub cover, while fox sparrow and spotted towhee (*Pipilo maculatus*) had a positive association, and the effects were significant for approximately one-third of the community (10/34 in Chips, 12/37 in Rim; Fig. 7d). The number of significant positive and negative associations across all four of these habitat covariates tended to be evenly distributed across species in both fires, except for the live tree basal area in the Rim Fire models which had a larger number of significant positive effects (13) than negative (4).

Table 4 All species detected regardless of distance from the observer in the Chips and Rim fires during the 2013–2017 breeding bird surveys. An “X” denotes whether a species was detected in either or both fires

Common name	Scientific name	4-letter code	Chips Fire	Rim Fire
Acorn woodpecker	<i>Melanerpes formicivorus</i>	ACWO		X
American goldfinch	<i>Spinus tristis</i>	AMGO	X	X
American kestrel	<i>Falco sparverius</i>	AMKE	X	X
American robin	<i>Turdus migratorius</i>	AMRO	X	X
Anna’s hummingbird	<i>Calypte anna</i>	ANHU	X	X
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	ATFL		X
Bald eagle	<i>Haliaeetus leucocephalus</i>	BAEA	X	
Black-backed woodpecker	<i>Picoides arcticus</i>	BBWO	X	X
Black-chinned sparrow	<i>Spizella atrogularis</i>	BCSP		X
Bell’s sparrow	<i>Artemisospiza belli</i>	BESP		X
Bewick’s wren	<i>Thryomanes bewickii</i>	BEWR	X	X
Blue-gray gnatcatcher	<i>Poliophtila caerulea</i>	BGGN	X	X
Brown-headed cowbird	<i>Molothrus ater</i>	BHCO	X	X
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	BHGR	X	X
Black phoebe	<i>Sayornis nigricans</i>	BLPH		X
Brewer’s blackbird	<i>Euphagus cyanocephalus</i>	BRBL	X	X
Brown creeper	<i>Certhia americana</i>	BRCR	X	X
Band-tailed pigeon	<i>Patagioenas fasciata</i>	BTPI	X	X
Black-throated gray warbler	<i>Setophaga nigrescens</i>	BTYW	X	X
Bullock’s oriole	<i>Icterus bullockii</i>	BUOR	X	X
Bushtit	<i>Psaltirparus minimus</i>	BUSH		X
Cassin’s finch	<i>Haemorhous cassinii</i>	CAFI	X	X
Canada goose	<i>Branta canadensis</i>	CAGO	X	
Calliope hummingbird	<i>Selasphorus calliope</i>	CAHU	X	X
California towhee	<i>Melospiza crissalis</i>	CALT		X
Canyon wren	<i>Catherpes mexicanus</i>	CANW	X	X
California quail	<i>Callipepla californica</i>	CAQU	X	X
California scrub-jay	<i>Aphelocoma californica</i>	CASJ		X
Cassin’s vireo	<i>Vireo cassinii</i>	CAVI	X	X
Cedar waxwing	<i>Bombycilla cedrorum</i>	CEDW		X
Chipping sparrow	<i>Spizella passerina</i>	CHSP	X	X
Cliff swallow	<i>Petrochelidon pyrrhonota</i>	CLSW	X	
Cooper’s hawk	<i>Accipiter cooperii</i>	COHA	X	X
Common loon	<i>Gavia immer</i>	COLO	X	
Common nighthawk	<i>Chordeiles minor</i>	CONI	X	X
Common raven	<i>Corvus corax</i>	CORA	X	X
Dark-eyed junco	<i>Junco hyemalis</i>	DEJU	X	X
Downy woodpecker	<i>Dryobates pubescens</i>	DOWO	X	X
Dusky flycatcher	<i>Empidonax oberholseri</i>	DUFL	X	X
Eurasian collared dove	<i>Streptopelia decaocto</i>	ECDO		X
European starling	<i>Sturnus vulgaris</i>	EUST		X
Evening grosbeak	<i>Hesperiphona vespertina</i>	EVGR	X	X
Fox sparrow	<i>Passerella iliaca</i>	FOSP	X	X
Great blue heron	<i>Ardea herodias</i>	GBHE	X	
Golden-crowned kinglet	<i>Regulus satrapa</i>	GCKI	X	X
Green-tailed towhee	<i>Pipilo chlorurus</i>	GTTO	X	X
Hammond’s flycatcher	<i>Empidonax hammondi</i>	HAFI	X	X
Hairy woodpecker	<i>Leuconotopicus villosus</i>	HAWO	X	X

Table 4 (continued)

Common name	Scientific name	4-letter code	Chips Fire	Rim Fire
Hermit thrush	<i>Catharus guttatus</i>	HETH	X	X
Hermit warbler	<i>Setophaga occidentalis</i>	HEWA	X	X
House finch	<i>Haemorhous mexicanus</i>	HOFI		X
House wren	<i>Troglodytes aedon</i>	HOWR	X	X
Hutton's vireo	<i>Vireo huttoni</i>	HUVI	X	X
Indigo bunting	<i>Passerina cyanea</i>	INBU		X
Killdeer	<i>Charadrius vociferus</i>	KILL	X	
Lawrence's goldfinch	<i>Spinus lawrencei</i>	LAGO	X	X
Lark sparrow	<i>Chondestes grammacus</i>	LASP		X
Lazuli bunting	<i>Passerina amoena</i>	LAZB	X	X
Lesser goldfinch	<i>Spinus psaltria</i>	LEGO	X	X
Lewis's woodpecker	<i>Melanerpes lewis</i>	LEWO	X	
Lincoln's sparrow	<i>Melospiza lincolni</i>	LISP	X	X
Mallard	<i>Anas platyrhynchos</i>	MALL	X	X
MacGillivray's warbler	<i>Geothlypis tolmiei</i>	MGWA	X	X
Mountain bluebird	<i>Sialia currucoides</i>	MOBL	X	X
Mountain chickadee	<i>Poecile gambeli</i>	MOCH	X	X
Mourning dove	<i>Zenaidura macroura</i>	MODO	X	X
Mountain quail	<i>Oreortyx pictus</i>	MOUQ	X	X
Nashville warbler	<i>Leiothlypis ruficapilla</i>	NAWA	X	X
Northern flicker	<i>Colaptes auratus</i>	NOFL	X	X
Northern pygmy-owl	<i>Glaucidium gnoma</i>	NOPO	X	X
Orange-crowned qarbler	<i>Leiothlypis celata</i>	OCWA	X	X
Olive-sided flycatcher	<i>Contopus cooperi</i>	OSFL	X	X
Osprey	<i>Pandion haliaetus</i>	OSPR	X	X
Pacific wren	<i>Troglodytes pacificus</i>	PAWR	X	X
Peregrine falcon	<i>Falco peregrinus</i>	PEFA		X
Pine grosbeak	<i>Pinicola enucleator</i>	PIGR		X
Pine siskin	<i>Carduelis pinus</i>	PISI	X	X
Pileated woodpecker	<i>Dryocopus pileatus</i>	PIWO	X	X
Pacific-slope flycatcher	<i>Empidonax difficilis</i>	PSFL	X	X
Purple finch	<i>Haemorhous purpureus</i>	PUFI	X	X
Pygmy nuthatch	<i>Sitta pygmaea</i>	PYNU	X	X
Red-breasted nuthatch	<i>Sitta Canadensis</i>	RBNU	X	X
Red-breasted sapsucker	<i>Sphyrapicus ruber</i>	RBSA	X	X
Rufous-crowned sparrow	<i>Aimophila ruficeps</i>	RCSP		X
Red crossbill	<i>Loxia curvirostra</i>	RECR	X	X
Rock wren	<i>Salpinctes obsoletus</i>	ROWR	X	X
Red-shouldered hawk	<i>Buteo lineatus</i>	RSHA		X
Red-tailed hawk	<i>Buteo jamaicensis</i>	RTHA	X	X
Rufous hummingbird	<i>Selasphorus rufus</i>	RUHU	X	
Red-winged blackbird	<i>Agelaius phoeniceus</i>	RWBL	X	X
Sandhill crane	<i>Antigona canadensis</i>	SACR	X	
Sooty grouse	<i>Dendragapus fuliginosus</i>	SOGR	X	
Song sparrow	<i>Melospiza melodia</i>	SOSP	X	X
Spotted owl	<i>Strix occidentalis</i>	SPOW	X	
Spotted towhee	<i>Pipilo maculatus</i>	SPTO	X	X
Sharp-shinned hawk	<i>Accipiter striatus</i>	SSHA	X	X
Steller's jay	<i>Cyanocitta stelleri</i>	STJA	X	X

Table 4 (continued)

Common name	Scientific name	4-letter code	Chips Fire	Rim Fire
Townsend's solitaire	<i>Myadestes townsendi</i>	TOSO	X	X
Townsend's warbler	<i>Setophaga townsendi</i>	TOWA	X	X
Tree swallow	<i>Tachycineta bicolor</i>	TRES	X	
Turkey vulture	<i>Cathartes aura</i>	TUVU	X	X
Violet-green swallow	<i>Tachycineta thalassina</i>	VGSW		X
Warbling vireo	<i>Vireo gilvus</i>	WAVI	X	X
White-breasted nuthatch	<i>Sitta carolinensis</i>	WBNU	X	X
White-crowned sparrow	<i>Zonotrichia leucophrys</i>	WCSP		X
Western bluebird	<i>Sialia mexicana</i>	WEBL	X	X
Western grebe	<i>Aechmophorus occidentalis</i>	WEGR	X	
Western tanager	<i>Piranga ludoviciana</i>	WETA	X	X
Western wood-pewee	<i>Contopus sordidulus</i>	WEWP	X	X
White-headed woodpecker	<i>Picoides albolarvatus</i>	WHWO	X	X
Williamson's sapsucker	<i>Sphyrapicus thyroideus</i>	WISA	X	
Wilson's warbler	<i>Cardellina pusilla</i>	WIWA	X	X
Wrentit	<i>Chamaea fasciata</i>	WREN		X
White-throated swift	<i>Aeronautes saxatalis</i>	WTSW		X
Yellow warbler	<i>Setophaga petechia</i>	YEWA	X	X
Yellow-rumped warbler	<i>Setophaga coronata</i>	YRWA	X	X

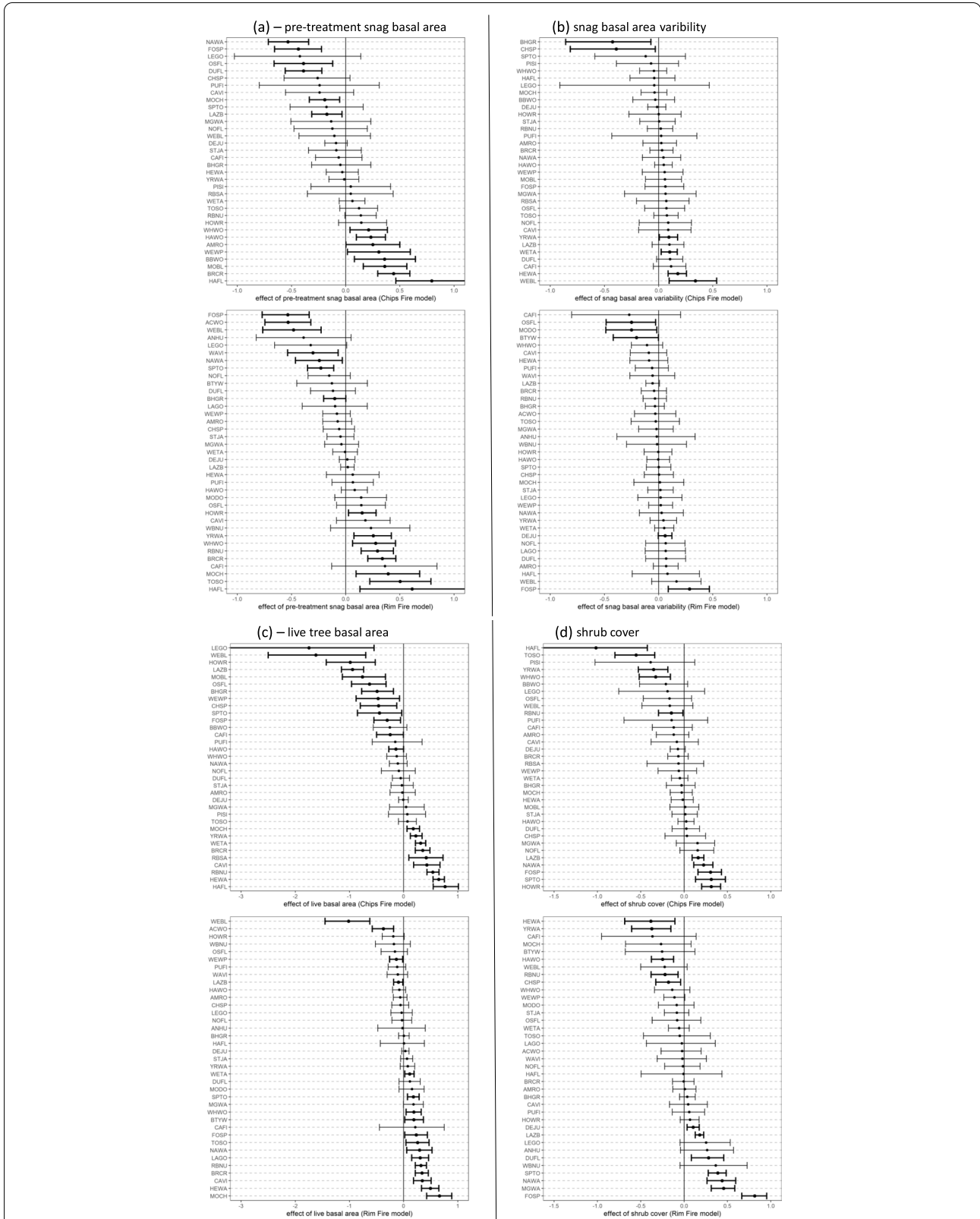


Fig. 7 Modeled habitat covariate effect coefficients for Chips and Rim Fire models. Each species was modeled with a set of covariates including elevation (not shown), latitude (not shown), slope (not shown), aspect (not shown), **a** pre-treatment snag basal area, **b** snag basal area standard deviation, **c** live tree basal area, and **d** shrub cover. Error bars show 95% confidence intervals

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Authors' contributions

All authors contributed to the conceptualization, methodology, writing, review, editing, project administration, funding acquisition, resources, and supervision. LJR conducted the formal analysis and visualization. All authors have read and agreed to the published version of the manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

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Competing interests

The authors declare that they have no competing interests.

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