*Article*

# Fire and Mechanical Forest Management Treatments Support Different Portions of the Bird Community in Fire-Suppressed Forests

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**Abstract:** Silvicultural treatments, fire, and insect outbreaks are the primary disturbance events currently affecting forests in the Sierra Nevada Mountains of California, a region where plants and wildlife are highly adapted to a frequent-fire disturbance regime that has been suppressed for decades. Although the effects of both fire and silviculture on wildlife have been studied by many, there are few studies that directly compare their long-term effects on wildlife communities. We conducted avian point counts from 2010 to 2019 at 1987 in situ field survey locations across eight national forests and collected fire and silvicultural treatment data from 1987 to 2016, resulting in a 20-year post-disturbance chronosequence. We evaluated two categories of fire severity in comparison to silvicultural management (largely pre-commercial and commercial thinning treatments) as well as undisturbed locations to model their influences on abundances of 71 breeding bird species. More species (48% of the community) reached peak abundance at moderate-high-severity-fire locations than at low-severity fire (8%), silvicultural management (16%), or undisturbed (13%) locations. Total community abundance was highest in undisturbed dense forests as well as in the first few years after silvicultural management and lowest in the first few years after moderate-high-severity fire, then abundance in all types of disturbed habitats was similar by 10 years after disturbance. Even though the total community abundance was relatively low in moderate-high-severity-fire habitats, species diversity was the highest. Moderate-high-severity fire supported a unique portion of the avian community, while low-severity fire and silvicultural management were relatively similar. We conclude that a significant portion of the bird community in the Sierra Nevada region is dependent on moderate-high-severity fire and thus recommend that a prescribed and managed wildfire program that incorporates a variety of fire effects will best maintain biodiversity in this region.

**Keywords:** fire; forest management; fuel treatment; disturbance; birds; Sierra Nevada

## 1. Introduction

The management of multi-use forests is a vital component of global biodiversity conservation, long-term carbon storage, economic well-being, recreation, and ecosystem sustainability [1,2]. Forest ecosystems worldwide face numerous current and emerging threats [3,4]. Among these threats is alteration of natural disturbance regimes, which may reduce forest resilience to climate change and other emerging threats [5–8].

Fire is the fundamental disturbance process in seasonally dry conifer forests of western North America [9,10]. The suppression of fire over the past century has had profound effects by altering the vegetative composition and structure across the region [11,12]. Though the frequency of fires has increased sharply since the mid-1980s [13], and is likely to remain higher than during the latter half of the 20th century [14], average fire return intervals are still far longer today than pre-suppression and the area burned is far smaller [15–18]. In the Sierra Nevada Mountains of California (Figure 1), the reduced presence of fire combined with past silvicultural activities (e.g., 20th-century tree harvest and reforestation)

has led to a decrease in large trees, higher densities of smaller-size trees [19–21], and more homogeneous forests with reduced shade-intolerant plant assemblages [22–26]. This disturbance deficit has likely resulted in profound effects on the wildlife community composition and structure, e.g., [27,28].
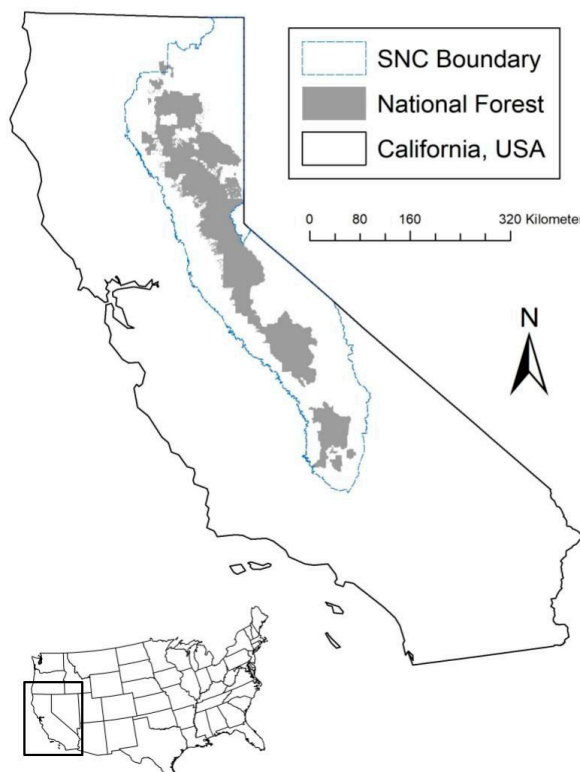


**Figure 1.** Study area in the Sierra Nevada Mountains of California, USA. The Sierra Nevada Conservancy (SNC, https://sierranevada.ca.gov/) boundary indicates the extent of the study region, and the shaded area indicates locations within the ownership boundaries of USDA Forest Service national forest lands.

Natural disturbance regimes are recognized as fundamental to the maintenance of avian communities in North America [29]. There is a growing body of evidence supporting the importance of burned landscapes to fire-prone forest bird communities in western North America, e.g., [27,30,31]. The magnitude of vegetation change resulting from all types of disturbances has a primary role in setting the post-disturbance successional trajectory and has been shown to be important in fires as measured by severity [30,32]. Fire severity is typically measured as an index of the amount of change in the vegetation visible to satellites, which is the tallest vegetation layer in a stand [33]. Typically, in forested stands, when a fire consumes canopy vegetation, it will burn lower vegetation layers as well, while low-severity fire often consumes understory and ground vegetation but leaves the overstory intact. Mechanical fuel reduction treatments can differ in the amount of vegetation removed in different vertical strata, though in dry fire-prone western forests, they generally target vegetation removal from multiple layers, including the canopy, subcanopy, and understory [34]. While the negative effects of fires are well known, there are also many benefits to ecosystems that have evolved with fire [35,36]. Increased habitat heterogeneity promulgated by fire can promote higher biodiversity [31]. Additionally, it is clear that the early-seral forest habitat created by high-severity fire provides a habitat for a number of wildlife species [37], with many associated with, and in some cases dependent on, particular combinations of severity and time since the fire [27,28,38,39].

While fire has been suppressed over the past century, mechanical timber harvest has replaced fire as the primary disturbance in these forests. Mimicking natural disturbances

such as fire through forest silvicultural management has been advocated as a practical alternative to conserve biodiversity in fire-adapted forests [40,41]. With the challenges of re-introducing fire to its historic extent in western North American forests, forest management policies have promoted emulation silviculture, a strategy that attempts to use mechanical timber harvest to mimic the structural legacy of natural fire [42–45]. Within these forests, effects of managing landscapes for reduced fuel loads has been shown to have relatively small effects on the existing bird community composition [46–49]. However, the main benefit of disturbance, in a disturbance starved system, may not be to maintain the status quo but rather to provide a habitat for those species most closely tied to conditions created by the natural disturbance regime [50].

Much of the management activity in Sierra Nevada forests today is targeted toward reducing the severity of fires by reducing fuel loads to provide more opportunities for future fire containment and suppression [51–53]. Fuels treatments generally aim to reduce surface and ladder fuels, as well as overall stand density, targeting small- to medium-size trees and understory vegetation for removal to promote slower rates of fire spread and lower severity [54,55]. Following both fires and forest management, the vegetation structure and composition can respond in a variety of ways, including increased herbaceous and shrub cover, tree recruitment, and changes in ephemeral structural components such as snags [56,57].

There are considerable efforts at state and federal levels to restore fire-prone, disturbance-starved forests in California and across the U.S. Restoration of these forests is likely to require employment of a broad range of tools, including mechanical treatments, prescribed fire, and wildland fire [58–60]. As such, there is a corresponding need to understand how wildlife species respond to these different potential restoration treatments [35]. There is evidence that fire sets in motion successional processes that may or may not be similar to the successional process following silvicultural activities [61,62], and may result in disparate responses of wildlife [63,64]. A better understanding of the similarities and differences in avian responses to fire and mechanical treatments can help guide a balanced approach to forest management over space and time to maintain natural levels of biodiversity in these natural disturbance-starved systems.

In this study, we evaluated the effects of fire and silvicultural disturbances on the avian community in actively managed national forests of the Sierra Nevada over a 20-year post-disturbance time period. We sought to understand how the most common disturbances and a suite of other factors influence the abundances of avian species. We used data from an extensive avian-monitoring program [65] to evaluate total bird abundance, diversity, and the abundance of 71 individual species across the first two decades following mechanical timber harvest, prescribed and low-severity fire, and moderate- and high-severity fire. We also assessed the dissimilarity between avian assemblages within each of these categories to assess the differences in the overall community composition among these land categories.

## 2. Materials and Methods

### 2.1. Study Location

Our study was performed within the Sierra Nevada and southern Cascade Mountains in California, U.S. (Figure 1). We sampled birds within 8 national forest management units that encompass nearly 3 million hectares, including Sequoia, Sierra, Stanislaus, Eldorado, Tahoe, Plumas, and Lassen National Forests and the Lake Tahoe Basin Management Unit. Our study area was defined as all upland forest and montane chaparral that is available for management within the national forest boundaries [65]. No specific permits were required to conduct this work, either by the land manager or by the wildlife agency, and the coordinates of all study locations are available online [66]. This study did not involve any threatened or endangered species.

The climate is Mediterranean, with the majority of precipitation occurring from November to March and falling primarily as snow at the higher elevations and rain elsewhere. Precipitation generally increases with elevation. The study area consists pre-

dominantly of Sierra mixed-conifer and true-fir cover types with smaller amounts of montane chaparral and hardwood-dominated habitat. Within the conifer forests, ponderosa pine (*Pinus ponderosa*) is dominant at lower elevations; mixed-conifer forests comprising ponderosa pine, white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), Douglas fir (*Pseudotsuga menzeisii*), and incense cedar (*Calocedrus decurrens*) are dominant at intermediate elevations and often intermixed with several hardwood species (e.g., *Quercus* spp.); and white fir, red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), and lodgepole pine (*Pinus contorta*) are dominant at higher elevations.

*2.2. Site Selection*

Field data were assembled from a bioregional monitoring project designed to monitor trends in upland forest birds inhabiting actively managed national forest lands. Survey locations were selected using a generalized random tessellation stratified (GRTS) sampling protocol [67,68]. The set of potential survey locations was built from a tessellation generated in ArcGIS (ver. 9.2; Environmental Systems Research Institute, Redlands, CA, USA), consisting of a grid of 1 km$^2$; cells with a random origin covering the entire study area. To more accurately represent the areas available to silvicultural management, we limited the study area to locations within 1 km of accessible roads and slopes less than 35%. We overlaid a vegetation layer of 35 different California Wildlife Habitat Relationship (CWHR) land cover types (https://map.dfg.ca.gov/metadata/ds1327.html) and eliminated habitat types such as grassland, sagebrush, riparian, foothill chaparral, oak woodland, subalpine, barren, and juniper that were not subject to typical silvicultural treatments. Sample locations ranged in elevation from 1003 to 2871 m and latitudes from 35.3906° to 41.2931°. At each survey location, we established two transects in adjacent 1 km grid cells. Transects were made up of four point count stations at 250 m in the cardinal directions from a fifth station in the center. This resulted in a sample of 1987 stations on 398 transects distributed as 199 spatially balanced pairs.

We then assigned a history of fire and management at each point count station location. To do this we overlaid the points on the Forest Service Activities Tracking System (FACTS [69]) to identify the subsample of stations that had been mechanically treated, as well as a fire severity assessment map [33,70], to identify the subsample of stations that have burned. We identified all stations within GIS polygons labeled with FACTS activity codes that indicated that a silvicultural treatment had occurred through mechanical means (records were available from 1995 through 2016). The FACTS polygons that we included in our sample were labeled with activity codes indicating that thinning treatments were conducted using mechanical machinery (e.g., tractors, skidders, harvesters, feller-bunchers, yarders, skylines, or helicopters). These activities included pre-commercial thin or tree release and weed (49% of treatments), commercial thinning (39%), insect and disease control (11%), clearcuts (1%), and wildlife habitat improvements (<1%). A small number of survey stations were burned or mechanically treated after 2016 when FACTS data were not available, and these locations were removed from all analyses.

In the 1990s, forest management strategies in the western U.S. underwent a transition from a focus on economic production and fire suppression to a focus on fuel reduction for fire resilience [34]. Prior to the early 1990s, clearcutting and overstory removals in addition to salvage and sanitation harvests were common silvicultural activities. In 1993, guidelines designed to protect the California spotted owl habitat implemented restrictions on removing large trees (>76 cm DBH) and maintenance of canopy cover of over 40% [71]. Typical mechanical treatments at our study sites during the study period (since 1995 when the FACTS database records began) consisted of several fuel reduction or stand improvement treatments, often, but not always, including removal of merchantable overstory trees. Fuel reductions and pre-commercial thinning treatments were focused on removing ladder fuels (shrubs, small trees, some overstory), while leaving the largest trees (e.g., shaded fuel break). The removal of these understory fuels left behind stands that were more likely to

retain canopy structures when fires occurred. Post-treatment surface fuels were frequently piled and burned, and occasionally sites were treated with low-severity broadcast burning.

We recorded the year in which the silvicultural activity was reported as completed in the FACTS database, and since activities did not occur uniformly within the FACTS GIS polygons (and occasionally we found details within the database were not accurate), we verified that changes in vegetation occurred by comparing records to time-stamped aerial imagery in Google Earth. The mechanical treatment activities were easily visible in the imagery, and if no changes to the forest structure at a given survey station were visible near the dates reported in FACTS, then we did not include that station in the mechanically treated subsample. If we could verify that visible changes to the vegetation were present and consistent with the FACTS database, then we assumed those management activities had occurred as described in the database and we included that station in the mechanical treatment subsample. If the vegetation changes occurred more than 100 m from the survey station location, we did not include that station in the mechanical treatment subsample. If a station received multiple treatments prior to bird surveys, we started the time since treatment count from the last treatment event, and if treated during survey years (2010–2019), we restarted the time since treatment count from that year. Similarly, we identified all stations within a fire perimeter and sampled the vegetation burn severity (assessed as canopy cover % change) at each location and grouped all stations that were burned with less than 25% canopy cover change as low-severity fire and over 25% as moderate-high-severity fire, again verifying all locations identified as burned with aerial imagery in Google Earth. All locations that were mechanically treated (salvage logging or fuels or other vegetation removals) following a fire were removed from analyses. We also removed all data from the year in which a fire or treatment occurred (i.e., time since disturbance cannot be less than 1). All locations with no FACTS or fire disturbance history were included in the undisturbed subsample. We also noted whether each station was located within a clearcut visible on aerial photographs going back to 1980 and included those data in the bird abundance models to account for recent silvicultural treatment history beyond the records contained in the FACTS database that could profoundly influence the avian community decades later. Sample sizes varied by treatment category: moderate-high-severity fire = 217 point count stations on 56 transects, 1144 location-year sampling units; low-severity fire = 197 point count stations on 70 transects, 1094 location-year sampling units; mechanical treatment: 275 point count stations on 99 transects, 1584 location-year sampling units; and undisturbed: 1542 point count stations on 350 transects, 11,391 location-year sampling units. The sample was dominated by the undisturbed treatment class, a very small portion of which may have been burned or mechanically treated locations that were not captured by the treatment tracking data we used or that we were unable to verify with aerial imagery.

### 2.3. Field Surveys

We used standardized five-minute unlimited-distance point count surveys [72,73] to sample the avian community during the peak of the breeding season. At each survey station, we recorded all birds detected (visually or audibly) and estimated their distance to the nearest 1 m from the observer. We visited each station up to twice between 1 May and 15 July in 2010 through 2017, and in 2019. Our field survey project received reduced funding starting in 2017, and we only surveyed half the full sample in 2017 and 2019 and no locations in 2018. The average number of visits per station was 11.9 across the nine years of surveys, or 1.6 surveys per year per point count station. We completed counts within four hours of sunrise and did not survey during inclement weather. Prior to conducting point counts, all observers completed an intensive two-week training program and passed a double-observer field test of bird identification. At each station, we characterized the vegetation within 50 m of the survey plot center using visual estimates of the percentage of the plot that was covered by trees and shrubs (shrub cover includes all understory woody vegetation species), counted standing snags >10 cm diameter, and measured structural characteristics, including the live-tree basal area using a 10-factor key from at least three

locations within the survey plot [65]. These relevé vegetation surveys were conducted up to three times at each point count station across the 10-year time span of bird surveys. We used the vegetation measurements to characterize the progression of vegetation change over time within each treatment type and used violin plots [74] to show changes over time within each treatment category, including the mean values of each subsample.

### 2.4. Bird Abundance Analyses

We recorded a total of 148 species over nine years of surveys on these sites, but for these analyses, we removed species such as raptors, waterfowl, nocturnal species, detections not identified to species, and non-breeding migrants for which our point count methodology generated an inappropriate sample [72]. We further removed all species with fewer than 99 individuals detected within 100 m of observers across all survey events. The remaining 78 species were included in hierarchical distance models to estimate abundance at each location-year sampling unit using the distsamp function in the Unmarked package [75] with statistical package R version 3.3.1 [76]. Seven of the 78 species had models that fit the data overall but had one or more parameters (described below) with very large standard errors, so we dropped those species from result summaries, leaving a final total of 71 species for which we show results. These 71 species represented 98% of all individuals detected in this dataset. See Supplementary Table S1 for a list of species included in the analyses, common and scientific names, four-letter American Ornithologigal Society codes, total number of detections, foraging and nesting guilds, and nest types.

To characterize the responses of a large group of species to an unbalanced sample of a wide variety of vegetation disturbances over a long time period, we took the approach of fitting abundance models to establish covariate relationships and then used simplified summaries of vegetation and environmental conditions to project abundances for each species over time in each disturbance type. We chose this approach so that we could directly compare the effects of those disturbances, while reducing the influence of habitat variation and unbalanced sample sizes in the different disturbance types. To construct the abundance models, we used a stacked-years data structure such that each site-by-year combination was treated as an independent sampling unit [77,78]. Although the abundance at a point count location in a given year is not fully independent from the abundance at the same point in other years, this data structure treats the abundance state at each point as completely open to colonization or extinction between years, which may mimic actual ecological processes of rapidly changing conditions following disturbance better than assuming closed populations across years. It also makes parameterizing the vegetation and blocking variables in the model more straightforward than modeling yearly site extinction and colonization processes directly. These benefits come at the cost of potentially underestimating the error in some model parameter coefficients. However, because we are primarily interested in estimating abundances rather than testing hypotheses about covariate influences, we feel that this data structure is warranted and does not bias our conclusions. To maintain a representative number of sampling units within each yearly time-since-disturbance category, we capped both burned and mechanical treatment subsamples at 20 years since disturbance for model-fitting data since sample sizes were substantially smaller beyond that time period (even though our disturbance history records included up to 30 years for fires and up to 23 years for FACTS). Finally, we removed all data from the year in which disturbances occurred (=0 years post-disturbance) from the model-fitting data, and additionally we did not summarize projected abundances for 1 or 20 years post-disturbance in order to remove some extreme values at the ends of the time range for some species.

For each species, we fit a single set of model covariates (described below). In addition to field measurements of the vegetation structure, we included several other variables to account for geography, climate, and topography. We sampled elevation, aspect, and slope at each station center from the Sierra Nevada Regional Digital Elevation Model [79]. We included three additional variables to account for the influence of a widespread drought

throughout the region from 2012 to 2015. Two of these were weather-related variables, and another represented the amount of tree mortality as a result of drought-induced beetle infestations [78]. The climatic water deficit (CWD, a measure of water stress based on evapotranspiration, solar radiation, and air temperature) and a temperature index that characterizes the average June maximum temperature compared to a 2009 baseline were sampled using the California basin characterization model (270 m resolution, [80–82]). Tree mortality was calculated using an index [83] based on the normalized difference wetness index (NDWI, [84]) using freely available LANDSAT imagery in Google Earth Engine (see [78] for further details on these methods).

The detection process was modeled using a multinomial function:

$$Multinomial(N_i, \pi_{i,j}) = \alpha 0_i + \alpha_{slope}{}^*X1_i + \alpha_{liveBA}{}^*X2_i + \alpha_{shrub}{}^*X3_i$$

where detection probability varies by location $i$ in distance class $j$ with slope ($\alpha\_slope$), live-tree basal area ($\alpha\_liveBA$), and percentage shrub cover ($\alpha\_shrub$) included as covariates in the half-normal (with scale parameter $\sigma$) detection function.

Abundance at location $i$ was modeled as a Poisson function assuming closure within each year and including an offset for the number of visits:

$$N_i \sim Poisson(\lambda_i) = \beta 0_i + \beta_{elev}{}^*X1_i + \beta_{elev}{}^2{}^*X2_i + \beta_{lat}{}^*X3_i + \beta_{elev^*lat}{}^*X4_i + \beta_{south}{}^*X5_i +$$
$$\beta_{CWD}{}^*X6_i + \beta_{mort}{}^*X7_i + \beta_{CWD^*lat}{}^*X8_i + \beta_{shrub}{}^*X9_i + \beta_{tree}{}^*X10_i + \beta_{snags}{}^*X11_i +$$
$$\beta_{clearcut}{}^*X12_i + \beta_{MHSF^*YSF}{}^*X13_i + \beta_{LSF^*YSF}{}^*X14_i + \beta_{MT^*YSM}{}^*X14_i + \beta_{MHSF^*YSF}{}^2{}^*X16_i +$$
$$\beta_{LSF^*YSF}{}^2 + \beta_{MT^*YSM}{}^2{}^*X18_i + offset(log(visits))$$

Covariates in the abundance portion of the model included variables to account for the highly variable landscape and topography, namely elevation ($\beta_{elev}$), quadratic of elevation ($\beta_{elev}{}^2$), latitude ($\beta_{lat}$), interaction between elevation and latitude ($\beta_{elev^*lat}$), and southness (i.e., aspect represented as a proportion of south-facing ($\beta_{south}$). We also included the vegetation structure covariates shrub cover ($\beta_{shrub}$), tree cover ($\beta_{tree}$), snag density ($\beta_{snags}$), and a binary variable indicating whether each location was within a ~1980–1995 clearcut patch ($\beta_{clearcut}$) to account for recent profound silvicultural management that preceded the FACTS data. Three variables to account for recent drought conditions were also incorporated, climatic water deficit ($\beta_{CWD}$), temperature index ($\beta_{temp}$), mortality ($\beta_{mort}$), plus an interaction between climatic water deficit and latitude ($\beta_{CWD^*lat}$). Finally, the model included variables designed to quantify the influence of the three treatment types (MHSF = moderate-high-severity fire, LSF = low-severity fire, and MT = mechanical treatment) that we described above and to allow for the influence of those treatments on each species to vary over time. For these variables, we included the interaction between a treatment-type binary variable (=1 where the treatment or fire occurred and =0 elsewhere) and the number of years since fire (YSF) or mechanical treatment (YSM) occurred. Treatment was modeled as a linear variable proportional to time since treatment ($\beta_{MHSF^*YSF}$), ($\beta_{LSF^*YSF}$), and ($\beta_{MT^*YSM}$), as well as their quadratic effects to account for non-linear associations (e.g., to fit species with the highest or lowest abundances at intermediate values of time, or abundances that plateau at intermediate values).

All continuous-scale covariates, including time since disturbance, were standardized (mean = 0.0, standard deviation = 1.0) prior to calculating the squared terms (thus the quadratic terms have high values for both high and low elevations and low values for elevations near the mean). We examined the degree of collinearity between vegetation, topography, and climatic variables using the vif function in the R package HH [85] to calculate variance inflation factors (VIF) and found no evidence of a high degree of collinearity (all VIF < 3.0). Since the live-tree basal area was moderately correlated with both tree cover ($R = 0.57$) and shrub cover ($R = 0.38$), we only included the live-tree basal area as a detection covariate. We selected the live-tree basal area for the detection model because we felt it was the most proximate vegetation feature that influences the observers' ability to hear bird vocalizations and visually detect individuals.

To evaluate the differences in abundance for each species between characteristic undisturbed, burned, or mechanically treated locations, we used the fitted models to predict abundance within each treatment category across a broad range of time since disturbance (2–19 years) with a set of characteristic covariate values derived from averages across time within each disturbance type (see Figure 2 for a summary of field measurements and Figure A1 for summarized vegetation covariate values used in predicted abundance models). Covariates for these predictions included overall mean values (set to zero for standardized variables) for latitude, elevation, slope, southness, live-tree basal area, mortality, CWD, and temperature index. For the vegetation covariates, we used the mean yearly value for each of tree cover, shrub cover, and snag density within each disturbance type to represent the characteristic vegetation conditions and reflect typical changes over time (Figure A1), and we chose three sets of covariate values that represent three common undisturbed forest conditions: (1) undisturbed dense forest (high tree cover, low shrub cover, low snags); (2) undisturbed open forest (low tree cover, low shrub cover, low snags); and (3) undisturbed shrub-dominant montane chaparral (low tree cover, high shrub cover, low snags). From the predicted abundances of each species at each time/disturbance-type combination, we compared the estimates at 2–6 years, 7–12 years, and 13–19 years post-disturbance to the predicted, 5%, and 95% confidence interval values for each of the undisturbed types using a *t*-test (two-tailed, unequal variance) to assess the differences in abundance between habitats. From those comparisons, we evaluated whether each species reached its highest abundance within one of the disturbance/time categories or one of the undisturbed habitat types. As a general summary of community-level adaptations to disturbance types, we assessed whether each species was consistently more or less abundant in each of the disturbance categories across the entire time range in comparison to the undisturbed types and summed the number of species that are more abundant (+), less abundant (-), or not different in abundance (0) in each of the disturbance types (Table S1). We report the summed total abundance of all species across time since disturbance for each disturbance type in comparison to the three undisturbed types and also calculate the inverse Simpson's diversity metric with the R package Vegan [86], also known as Simpson's dominance, which is an index that increases intuitively as diversity increases and reflects the effective number of species present in a sample [87].

Finally, we quantified the dissimilarity of the bird communities within the treatment and time categories using the anosim function [86], which provided a comprehensive statistical test of the pairwise dissimilarity between each of the disturbance and undisturbed types and highlighted the species that contribute to those dissimilarities. We plotted the average pairwise dissimilarity for groups of points including the undisturbed types as well as the entire range of time across the three disturbance types, and repeated the same analysis after splitting the disturbance types into groups of time of 2–6 years, 7–12 years, and 13–19 years since the disturbance event. We also identified the species that had the largest similarity contrasts (contribution to total dissimilarity ≥ 0.002 and abundance at least 50% larger in one group compared to another) to show which species contribute most to differences in community composition between habitat types.
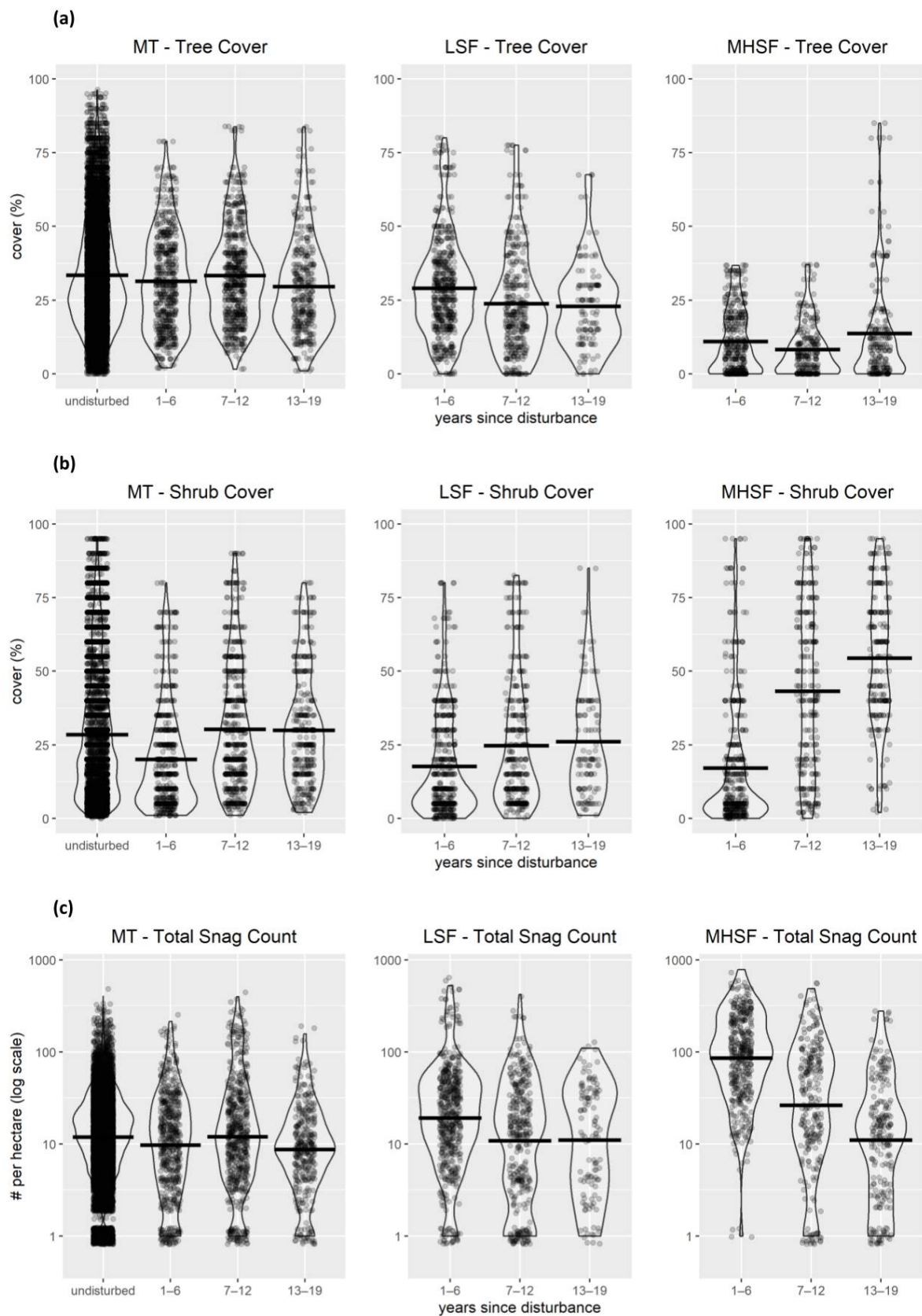
**(a)**



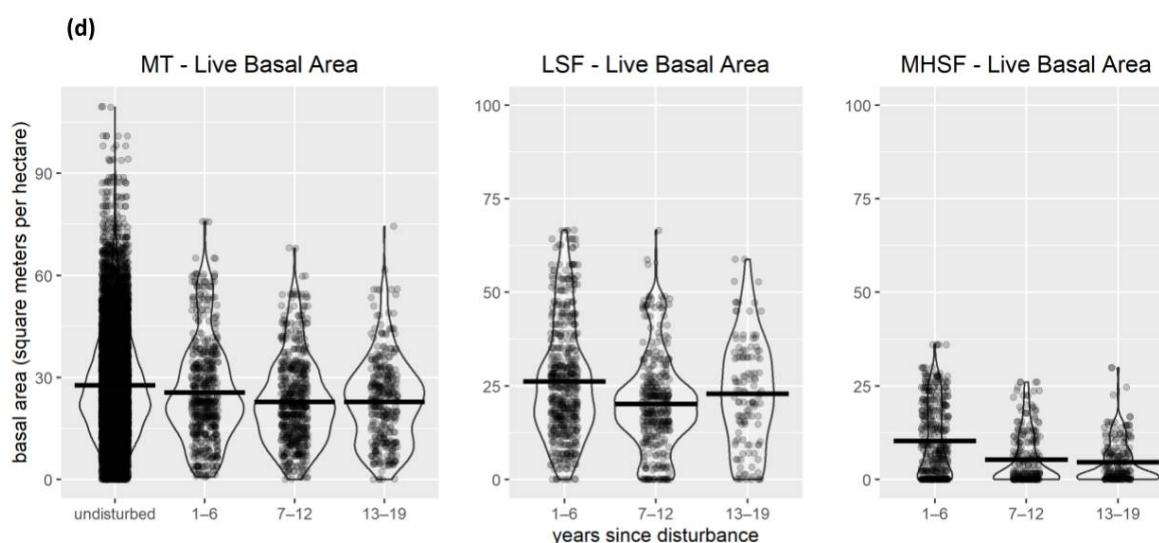**(b)**



**(c)**



**Figure 2.** *Cont.*

**(d)**



**Figure 2.** Vegetation measurements at field survey locations within each disturbance type, and summarized across three time periods, in comparison to all undisturbed locations. Vegetation measures (also used as covariates in abundance models) include (**a**) shrub cover, (**b**) tree cover, (**c**) snag density, and (**d**) basal area. Violin plots show mean values as a bold horizontal line. MHSF = moderate-high-severity fire; LSF = low-severity fire; MT = mechanical treatment; UO = undisturbed open forest; US = undisturbed shrub; UD = undisturbed dense forest.

## 3. Results

### 3.1. Vegetation Changes Following Disturbance

Although there was variability within disturbance categories, each disturbance type resulted in characteristic patterns of vegetation change and recovery over time (Figure 2). The mean tree cover within mechanical treatment locations was similar to undisturbed locations and stayed similar for 19 years after treatments (Figure 2a). Initially following disturbance, the tree cover in low-severity fire locations was similar to mechanical treatment locations but declined modestly in the later period. In the first 12 years following moderate-high-severity fire, the tree cover was much lower and only began to increase after 13 years. The shrub cover reduced in the first 6 years following mechanical treatment, but over 19 years, there was little difference compared to undisturbed locations (Figure 2b). The shrub cover was lower immediately after low-severity fire and moderate-high-severity fire and increased over time, but the increase was more rapid and reached a much higher level after moderate-high-severity fire. Snags were somewhat rare in undisturbed, mechanical treatment, and low-severity fire locations and more abundant in moderate-high-severity fire locations through the first 12 years but then decreased rapidly such that 13–19 years post-disturbance, the snag density was similar to undisturbed levels (Figure 2c). The live-tree basal area was lower following moderate-high-severity fire but declined only slightly following mechanical treatment and low-severity fire and was similar overall to undisturbed locations (Figure 2d).

### 3.2. Bird Abundance and Response to Disturbance

Patterns of total bird abundance varied between disturbance types and over time (Figure 3). Immediately following disturbance, bird abundance was the highest in mechanical treatment but then steadily declined over time, such that by the end of the time period, it supported the second-lowest total abundance. In contrast, abundance in moderate-high-severity fire locations was far lower immediately following disturbance compared to undisturbed or the other two disturbance types. However, it increased rapidly in the two decades following disturbance such that it equaled the undisturbed levels and was higher than the other two disturbance types. Low-severity fire locations were initially similar in abundance to the undisturbed types but declined over time to the lowest value overall.
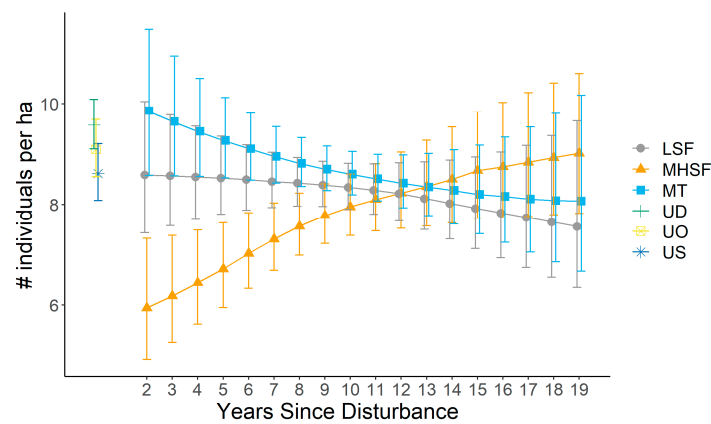
**Figure 3.** Total abundance (sum of all individuals across all species) over time. Abundance estimates were generated for each species within each disturbance type projected from characteristic vegetation values for tree cover, shrub cover, and snags (Figure A1), while holding all other model parameters constant. Error bars show the sum of 5% and 95% CIs for each species' abundance estimate. MHSF = moderate-high-severity fire; LSF = low-severity fire; MT = mechanical treatment; UO = undisturbed open forest; US = undisturbed shrub; UD = undisturbed dense forest.

A different pattern emerges when considering diversity among the different disturbance types (Figure 4). Moderate-high-severity fire locations had far higher diversity for the first 13 years post-disturbance, peaking in year 13, but then precipitously declined, such that the other two disturbance types supported equal or higher diversity by 19 years post-disturbance. This decrease in diversity coincided with a large increase in the total bird abundance, which was driven by a relatively small number of primarily shrub-associated species (e.g., sparrows). Low-severity fire locations initially had much lower diversity than moderate-high-severity fire locations but increased over time such that by 19 years post-disturbance, low-severity fire areas supported the highest bird diversity. Diversity in mechanical treatment locations was initially the lowest of all disturbance types but increased modestly across time. Diversity was higher in all three disturbance types across all time periods than the two undisturbed forest types but generally lower than in the shrub-dominated undisturbed type. Undisturbed shrub had far higher diversity than the undisturbed forest types and was similar to moderate-high-severity fire locations overall.
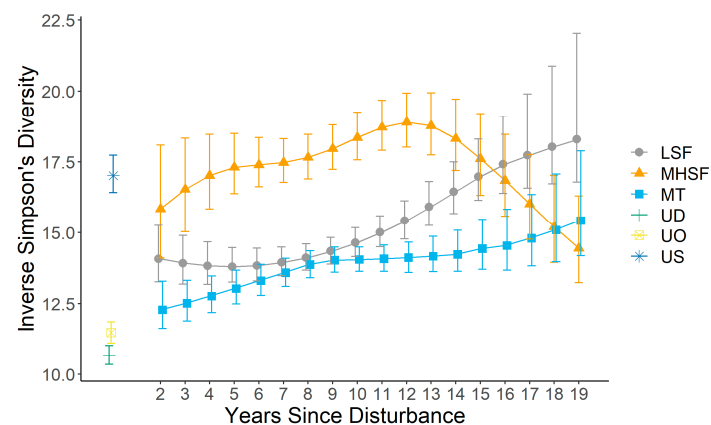


**Figure 4.** Inverse Simpson's diversity calculated from modeled species abundance estimates projected over time. Modeled abundance estimates were generated for each species within each disturbance type projected from characteristic vegetation values for tree cover, shrub cover, and snags (Figure A1), while holding all other model parameters constant. Error bars show the diversity of 5% and 95% CIs for species' abundance estimates. MHSF = moderate-high-severity fire; LSF = low-severity fire; MT = mechanical treatment; UO = undisturbed open forest; US = undisturbed shrub; UD = undisturbed dense forest.

The species' responses to disturbances that contribute to these patterns were highly varied, but some broad patterns did emerge (Table S2). There were 21/71 species that declined following moderate-high-severity fire in comparison to their abundance in undisturbed locations. These species were largely associated with mature forests and were among the most abundant species in our study area (e.g., red-breasted nuthatch, yellow-rumped warbler, hermit warbler). However, the majority of the community (38/71) had higher abundances following moderate-high-severity fire, including 10 species that were more than twice as abundant in moderate-high-severity fire locations than any other disturbance or undisturbed type. Most of these moderate-high-severity fire-dependent species were among the rarer species in the community, such as yellow warbler, lazuli bunting, mountain and western bluebird, house wren, and black-backed woodpecker. All of the species that were far more abundant in moderate-high-severity fire locations are either shrub or snag associates (Tables S1 and S2). Most species in the community were also largely tolerant of low-severity fire and mechanical treatment, with 50/71 species having little to no difference in abundance in either of these disturbance types compared to undisturbed, and 16/71 in both disturbance types having higher abundance. Nine of the ten most abundant species in our study area were not significantly different in abundance following low-severity fire or mechanical treatment compared to undisturbed locations.

In comparing the time and disturbance-type combinations at which each species was predicted to reach its maximum abundance, we again found much variation and a few general patterns. There were relatively few species that had the highest abundances in undisturbed types (13/71) in comparison to the disturbance types (Table S2). More species (34/71) were predicted to reach peak abundance in moderate-high-severity fire than in mechanical treatment (16/71) or low-severity fire (8/71) locations. In addition, the species that reached peak abundance in moderate-high-severity fire locations tended to be among the moderate and less abundant species, while those that peaked in mechanical treatment locations tended to be among the most abundant. Species were also mostly predicted to occur at peak abundance in either extreme of the timescale, with those peaking in mechanical treatment locations somewhat evenly split among the early and late time periods and those in moderate-high-severity fire locations generally peaking during the later time period (13–19 years since disturbance; 22/34 species).

When we considered life history traits, such as nest substrate and foraging strategy, of these species, some clear patterns emerged. Of the ground- and shrub-nesting species, the majority (22/32) reached peak abundance in moderate-high-severity fire locations, with the rest were evenly spread among the other conditions. Ten of the nineteen cavity-nesting species reached the highest abundance in moderate-high-severity fire locations, with two others in low-severity fire locations, three in mechanical treatment locations, and four in undisturbed habitats. Of the 28 tree-nesting species, 10 reached peak abundance in mechanical treatment locations, 7 in moderate-high-severity fire (generally earlier post-disturbance), 6 in undisturbed dense forest, and 5 in low-severity fire locations. Among foraging strategies, two of the three bark-drilling woodpeckers reached peak abundance in moderate-high-severity fire locations; bark gleaners were spread evenly among the other conditions. Of the 25 omnivore and seed-consuming species, 15 reached peak abundance in moderate-high-severity fire locations. Fourteen of the thirty-three foliage, ground, and aerial insectivores reached peak abundance in moderate-high-severity fire locations, with 4 in low-severity fire, 6 in mechanical treatment, and 9 in undisturbed habitats.

### 3.3. Community Similarity

Similarity analysis revealed that moderate-high-severity fire locations provide habitats for a unique component of the bird community, having the largest dissimilarities in species composition in comparison to other disturbance types, with undisturbed dense forest being the next largest, and low-severity fire, mechanical treatment, undisturbed shrub, and undisturbed open forest locations having comparable and smaller dissimilarities on average (Figure 5 and Table S2). The smallest dissimilarity was between undisturbed

open forest and undisturbed dense forest, followed by low-severity fire and mechanical treatment locations. Comparing the bird communities between groups of points defined by both time and disturbance categories showed that the most unique bird communities were found early (2–6 years) after moderate-high-severity fire and especially after 13–19 years (Figure 5). The smallest dissimilarities occurred between habitats in the 7–12 years' time period, especially for low-severity fire and mechanical treatment locations.
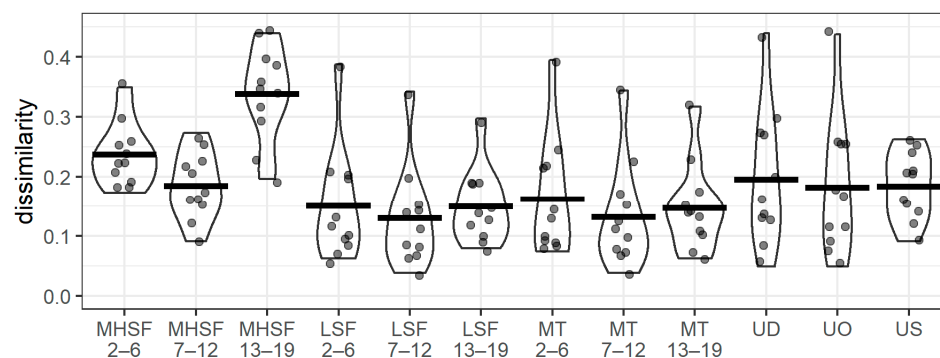


**Figure 5.** Dissimilarity across all pairwise combinations of disturbance/time categories and disturbed habitat types (total pairwise comparisons, *n* = 11). Horizontal bars show group means. MHSF = moderate-high-severity fire; LSF = low-severity fire; MT = mechanical treatment; UO = undisturbed open forest; US = undisturbed shrub; UD = undisturbed dense forest. Numbers indicate ranges of years since disturbance.

The species that accounted for the largest portion of each dissimilarity comparison included a group of mature forest-associated species (golden-crowned kinglet, yellow-rumped warbler, red-breasted nuthatch, Hammond's flycatcher, and hermit warbler, among others; see Table S3). These mature forest species were more abundant in undisturbed dense forest and undisturbed open forest in comparison to moderate-high-severity fire, and also in undisturbed dense forest in comparison to undisturbed shrub habitats. A group of shrub and open habitat species also appeared to be driving the dissimilarity between moderate-high-severity fire and undisturbed shrub locations in comparison to undisturbed dense forest, undisturbed open forest, and mechanical treatment locations (fox sparrow, house wren, yellow warbler, and green-tailed towhee, among others). There were no species with strong contributions to dissimilarity between low-severity fire and mechanical treatment or between undisturbed dense forest and undisturbed open forest locations.

## 4. Discussion

Following a century of fire suppression, the concomitant natural disturbance deficit in many frequent-fire forests, recent large increases in area burned at high severity, and renewed calls for increasing forest resilience, it is important to understand the broader ecological effects of different disturbance agents that could potentially be used to restore these forests. We found large differences in the composition and abundance of the avian community among disturbance types across the first 20 years following disturbance. The conditions that supported the highest abundance and diversity of avian species varied across the post-disturbance period. Overall, far more species reached peak abundance following some form of disturbance than in forests that had not been disturbed in the past 20 years. In this current state of homogenized, smaller-diameter, and overly dense forest stands created through decades of intensive logging and fire suppression within this region [88,89], the importance of disturbance to the avian community is very apparent. However, the relatively low dissimilarity between mechanical treatment areas, low-severity fire areas, and undisturbed forests suggest that from an avian community perspective, these disturbances do not bring about ecologically meaningful changes to the system. Our findings do highlight the unique contribution that moderate-high-severity fire has in

sustaining avian diversity in this ecosystem as it exists today, and we suggest that a diverse and abundant avian community can be sustained through a combination of disturbance agents with moderate- to high-severity fire as a critical component.

### 4.1. The Importance of Fire

Moderate-high-severity fire resulted in the highest diversity of birds in the 20-year post-disturbance period and also had the greatest dissimilarity in species composition compared to other disturbances or undisturbed conditions. Coupled with the fact that almost half of the species we evaluated reached their highest abundances in moderate-high-severity fire locations, and most of those were among the rarer species in the community, these findings suggest that this type of fire is an important driver of avian diversity today in this ecosystem. These results reinforce the conclusion that pyrodiversity in the Sierra Nevada is important to avian diversity [27,31].

The group of bird species contributing to the uniqueness of moderate-high-severity fire habitats include many species associated with shrubs. The strong increase in shrub cover over time following moderate-high-severity fire and its influence on birds has been shown in other studies [64,90]. While much of the focus on post-high-severity fire habitats to date has been on snag-dependent wildlife, its importance to the diverse shrub-nesting community should be appreciated when managing these areas in the decades following fire [57]. Shrub abatement, through mastication or herbicide treatments, is a common refor-estation practice post-fire [91]; but our results indicate that retaining shrub habitats in these areas appears to be vital to supporting the diversity of the shrub-nesting and foraging bird community (Point Blue unpublished data). Shrubs, as well as herbaceous grasses and forbs, also produce the fruit and seeds necessary for the omnivore and seed-consuming foraging guilds, with 62% of those species showing peak abundance in moderate-high-severity fire locations. These broad-leaf-dominated habitats in conifer-dominated landscapes are important to many bird species [92].

The large increase in snags is unique to moderate-high-severity fire and likely explains the association of these habitats with increased abundance of two bark-drilling insectivores (hairy and black-backed woodpeckers) who feed primarily on wood-boring beetle larvae that specialize on fire-killed trees. Among the snag-nesting guild overall, however, we did not find that primary and secondary cavity nesters were consistently more abundant in moderate-high-severity fire locations in comparison to other disturbed and undisturbed conditions, despite the vastly higher abundance of snags. This result may indicate that foraging resources created through disturbances are a more direct influence on the cavity-nesting avian community than nesting resources. Cavity-nesting birds in western dry conifer forests can be burned-forest or green-forest specialists; some will nest in high-severity-burned forest, while foraging in green forest (e.g., white-headed woodpecker) or shrub fields created by high-severity fire (e.g., house wren [93,94]). Thus, the juxtaposition of burned and green forest may be more important to snag-dependent species than simply the number of snags [95,96]. No common mechanical silvicultural techniques used in the Sierra Nevada create snags, and artificial snag creation is unlikely to promote insect activity commensurate with beetle- or fire-killed trees [97]. Prescribed fire treatments may also fail to promote habitat quality for snag-dependent wildlife [98], and mechanical treatments, including those typical in this study, often result in reduced snag densities [99].

The importance of vegetation structural diversity for birds in western North American forests is well established [100–102]. Variable canopy cover and understory regeneration in moderate-severity fires promote this type of high structural diversity, and while certain silvicultural treatments may be able to mimic these structural conditions, the recent prescriptions used by the USDA Forest Service in the Sierra Nevada (as represented within our mechanically treated subsample) do not appear to do so. While natural events other than fire (such as insect mortality) can lead to large numbers of snags and more open forest conditions, we found that, at least in the short term, beetle-driven mortality does not illicit a similar avian community as moderate-high-severity fire [78]. This is likely due, at least in

part, to differences in food resources [98]. A more nuanced analysis is needed to explore the similarities and differences in the avian community response to fire compared to insect mortality, but we suspect that, like other studies have shown, species responses will be highly idiosyncratic [103].

As low-severity fire is the treatment type largely recommended by forest ecologists to restore function and process to Sierra Nevada forests, it is important to evaluate the implications of extensive and increased reliance on prescribed fire as a management tool on avian biodiversity. Low-severity fire had the fewest species that reached peak abundance among all the disturbance types and fewer also than the undisturbed types. Abundance was high initially but declined over time, and while diversity increased over time, it was among the lowest overall. Our study also showed that the species composition in low-severity fire locations was largely similar to undisturbed forests. Many studies across dry western conifer forests show a neutral response to low-severity prescribed fire for a large majority of bird species, e.g., [63,104–106]. These burns often take place in fire-suppressed forests dominated by dense conifer stands, largely leaving the canopy trees alive but burning understory vegetation. Thus, the species present before burns are likely to be those associated with dense fire-suppressed forests. Low-severity fire applied in this forest type may not be able to restore the patchy mosaic of tree clumps and open areas required by many of the rarer understory and snag-associated species we found to be more abundant in moderate-high-severity fire locations. Incorporating high-severity fire into prescribed fire treatments to better emulate the heterogeneity found within mixed-severity fire could help maintain avian diversity.

*4.2. Managing Disturbances over Time*

The habitats for a variety of wildlife species that develop following fire differ in terms of quantity, quality, and distribution, depending on how those fires burn and the forest conditions that were present prior to the fire [32,38,107–110]. The area burned and conditions of the fires that occur over time determine how much of these important habitats are present across the landscape [111], and due to the long history of fire suppression in the Sierra Nevada, post-fire habitats are vastly underrepresented today in comparison to the conditions in which most species that inhabit western forests are likely adapted [112].

The vast majority of studies of the effects of managing western forests using traditional silvicultural approaches compared to a mixed-severity fire regime on wildlife communities have only included relatively short time frames (reviewed in [63]), and thus the dynamic nature of post-disturbance habitats and their value to wildlife communities after five years following disturbances is not well understood (but see [27,39,109]). Our results support the idea that post-fire habitats carry importance through at least the first two decades following disturbance rather than just during the initial post-fire period that is often the focus of management and conservation debate. Indeed, short-term studies of post-fire habitats may undervalue these long-term post-fire habitats to birds and other wildlife. The temporal variation in species abundances following each of the disturbances we investigated imply that there will be both opportunities for promoting biodiversity and challenges for revising forest management guidelines, including how to optimize the intervals at which to re-enter with the next treatment. Thus, the dynamic nature of post-disturbance communities should be considered in planning the management of these areas [27]. The timing and type of disturbance may be critical to ensuring resilience through ecological memory [7].

*4.3. Disturbance in a Disturbance-Starved System*

A frequently stated objective for mechanical fuel reductions is to mimic the effects of natural disturbance in forested ecosystems [63,113], and our results imply that the current suite of forest management techniques used in the Sierra Nevada mimics the effects of low-severity fire only. It has been shown in other regions as well that mechanical silvicultural treatments are rarely able to mimic natural processes [2]. A meta-analysis of wildlife species responses to fuel treatments in comparison to fire revealed that it is common for species to

respond similarly in the short term (up to five years) to low-moderate-severity fire and fuel treatments [63]. Since the species composition within undisturbed forest habitats is largely similar to mechanically treated and low-severity-fire habitats in our analyses, increasing the area influenced by fire, adding complexity to the end results of silvicultural treatments [6], and increasing burn severity in prescribed fire could all help to support native species that do not respond positively to other forms of disturbance in landscapes dominated by fire-suppressed forests.

The results of this study should be considered in the context that the entire study area had been subjected to a century of extensive logging and fire suppression, and our undisturbed dataset reflects a wide variety of long-term (30+ years) post-disturbance conditions, as primary forest is only a small fraction of the Sierra Nevada landscape [114]. This legacy may partly explain the low dissimilarity in the bird community between low-severity fire, mechanical treatment, and undisturbed forest types. Even with a large increase in the area burning in the Sierra Nevada across the timespan of our study [14], the majority of the landscape (75% of our sampling stations) was defined as undisturbed, whereas the natural disturbance regime for the vast majority of our sampling stations would have included fire return intervals of 5–15 years [11,112]. A lack of disturbance has long been recognized as leading to declines in forest birds in eastern North American forests [56,115]. Our baseline for avian community composition in the Sierra Nevada may be quite different than what one would have encountered prior to the forced removal of indigenous peoples (i.e., European colonization). The undisturbed forest types had high total bird abundance but were dominated by about 10 mature forest and generalist species that peaked in abundance in these conditions and are among the most abundant species in our dataset and ubiquitous across the region. In contrast, a number of species that reached their greatest abundance in moderate-high-severity fire locations were among the least common species encountered in our dataset.

With this disturbance deficit, our results suggest that low-severity fire and mechanical treatment (as practiced over the last 20 years) are of insufficient consequence to provide habitats for the full range of species that occupy this ecosystem. Thus, without a dramatic decrease in fire return intervals, mechanical treatments that more closely mimic the structural changes created by mixed-severity fire, including more clumps and gaps [45], may be warranted. One study in our region found that silvicultural treatments that removed a significant portion of the overstory and stimulated an understory shrub response post-treatment resulted in an avian community, at least for shrub-associated species, more similar to the moderate-high-severity fire community we found in this study [116]. Similarly, prescribed fires that include some areas that burn at moderate and high severity could be beneficial to the avian community. Low-severity fire alone may best be applied as a maintenance treatment in stands that already closely resemble the natural conditions under a more active disturbance regime (e.g., after mechanical treatment or wildfire). With the large disturbance deficit built up over the past century, preparing the landscape for fire, and then allowing far more wildfires to burn, appears necessary to pay down this deficit [39,117].

Given that we continue to find that fire is such an ecologically important component of western North American forests, the appropriate amount and spatial arrangement of moderate-high-severity fire to promote and retain over time should be considered at the watershed scale, rather than, for example, simply meeting target area quantities across larger regions. We suspect that achieving targets for moderate-high-severity fire in a small number of very large, very high severity fires would be less ecologically beneficial than if those acres were spread out more evenly across the entire region [96]. Thus, while we might attempt to reduce the number and extent of large very high severity fires we can simultaneously promote an increase in moderate-high-severity fire acres spread across the entire region in smaller patches. Without this approach it will be difficult to ensure that these habitats are provided at an appropriate scale and spatial arrangement to maintain the wildlife populations that depend upon them [118]. Additional studies on

this topic are warranted as we embark on programs to treat large landscapes across these forested ecosystems.

*4.4. Analysis Assumptions and Unmodeled Influences on Avian Abundance*

Though there was large variability in vegetation conditions within each disturbed habitat type as well as in the undisturbed subsample, we still found that the disturbance types had strong effects on avian species abundances. There is a vast difference in post-fire conditions between moderate and very high burn severity within the moderate-high-severity fire subsample, as well as potentially large differences in the effects of prescribed versus low-severity wildfire within the low-severity fire subsample. This variation within subsamples represents the wide variety of potential post-disturbance vegetation successional trajectories that are influenced partly by factors that we accounted for in models (fire severity, topography, latitude, climate, recent clearcut history) as well as factors that we did not account for (e.g., pre-fire habitat structure and composition, long-term disturbance legacy, landscape scale processes, the specific types of silvicultural treatments used in the mechanical treatment subsample). In the mechanical treatment subsample, we also had to assume that the time since disturbance was reset by the time since the most recent management activity. Without a more nuanced analysis to evaluate the effect of multiple treatments, we do not yet understand whether particular combinations of multiple treatment events at the same location could have strong interactive effects for certain bird species. Furthermore, by combining all forest habitat types together (e.g., yellow pine and true fir forest) and modeling abundance based only on topographical, climate, and vegetation structure variables, we make the assumption that the time-since-disturbance effect within different habitat types is consistent. Further studies to explore the potential for more detailed associations between bird species and particular habitat components and composition would be warranted.

Mechanical silvicultural treatments also did not occur on a random sample of the landscape but rather were targeted toward overstocked locations in need of thinning, locations that were highly productive for maximizing the board feet of timber, areas that were not difficult to access, and strategic locations for fire containment [58,59]. Since the end result of mechanical treatment is typically to bring those stands back to a more open forest condition that would also be typical of a frequent low-severity fire disturbance regime [119], the potential spatial disparity in the distribution of disturbance regimes across the landscape (e.g., mechanical treatment and low-severity fire on flatter slopes and nearer to human settlements, and moderate-high-severity fire on steeper slopes and more remote areas) has unknown consequences for wildlife. We have shown, for example, that the allocation of management areas can have strong indirect effects on the bird community [77], and thus an analysis of the correlation between the spatial distribution of biodiversity and the spatial distribution of disturbance history across the landscape would be informative. While we tried to control for some of this potential bias in the conditions in which each disturbance tended to occur, it is likely these effects are influencing the magnitude and patterns of response we observed. Given that managers have some ability to structure the spatial distribution of disturbance across the landscape, it could be beneficial to use optimization methods (e.g., [120,121]) to build spatial targets of landscape disturbances to mimic important historical conditions and maintain needed levels of important habitats as we progress into an uncertain climate future.

To control for uneven sampling, we fit these models and then projected abundances onto hypothetical data to isolate the individual influences of the disturbance types, not only from other co-varying factors, but also from unbalanced sampling across the subsamples themselves. We think this was warranted in order to clearly show the effects of each disturbance type on the avian community, and since this monitoring program was designed as a representative sample of the entire landscape without regard to fire or management activities, we feel that it is an effective illustration of the differences between those disturbance effects. The rather weak correlations between bird species' foraging and nesting

characteristics points to the complexity of bird life histories and the myriad influences on their population abundances and distributions. The lack of clear patterns between these broad avian species life history characteristics and many of the post-disturbance habitats we investigated also indicates that the one post-disturbance habitat type that did show strong influence on more species than any of the other types, moderate-high-severity fire, is a uniquely important component of the landscape. This analysis is also based on a space-for-time substitution, so it is possible that some older mechanical treatment, low-severity fire, or even moderate-high-severity fire locations were subjected to slightly different management techniques or the patterns of burn severity were not consistent across time in such a way that could potentially bias results. In fact, we do have evidence that the spatial patterns of burn severity have been changing [122] and could result in lower diversity within recent large fires [96]. Again, a more nuanced analysis would be useful to investigate these processes in more detail.

## 5. Conclusions

Decades of fire suppression along with other management prescriptions have resulted in a more homogeneous forest structure and composition than that with which the Sierra Nevada wildlife community has evolved. Besides the creation of important snag and shrub resources, fires set in motion a rapid successional process that lasts for decades and has strong effects on wildlife communities. Evidence from this study of the bird community in the Sierra Nevada indicates that mechanical silvicultural treatments and low-severity fire, given the altered conditions that exist today, cannot produce the full range of effects created through a natural mixed-severity fire regime. We suggest instead that mechanical treatments, low-severity fire, and mixed-severity fire be seen as complementary tools to manage seasonally dry fire-prone forests to restore a diverse avian community.

## Appendix A



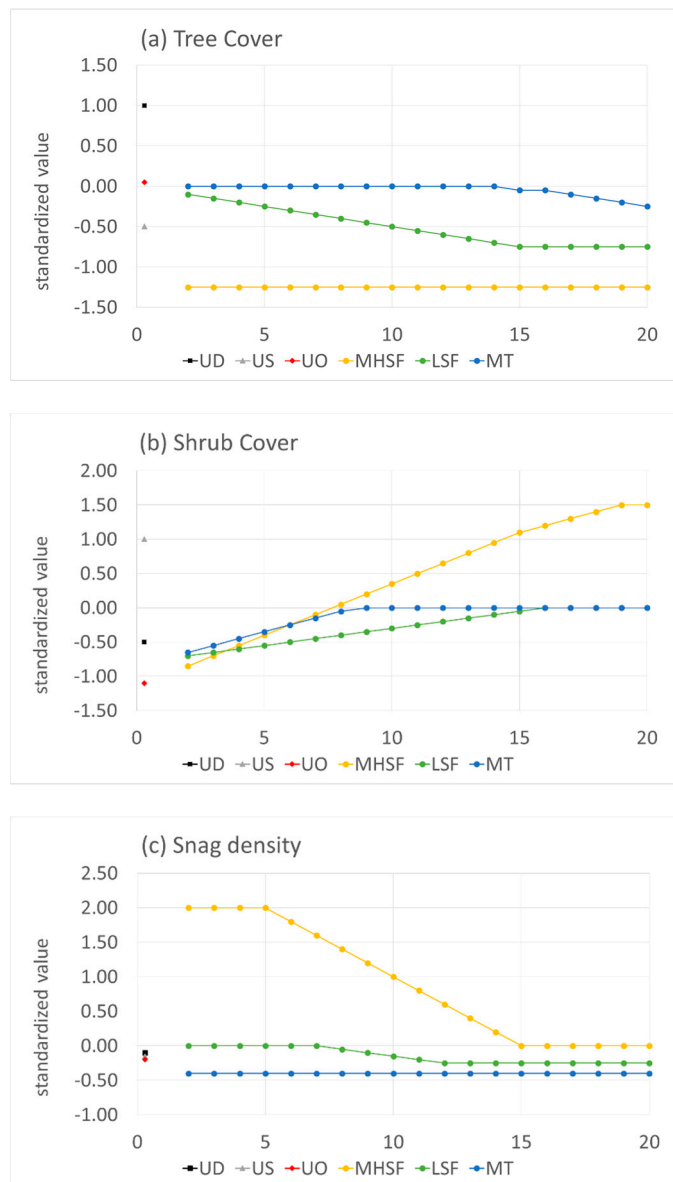**Figure A1.** Vegetation values: (**a**) tree cover, (**b**) shrub cover, and (**c**) snag density used for modeling predicted abundance over time in each disturbance type. Scales of each figure are in standardized units (mean = 0.0, standard deviation = 1.0). Predicted abundances for each species were based on these measurements, time from 2 to 19 years, and average values (standardized value = 0.0) for all other covariates.

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