Recent drought and tree mortality effects on the avian community in southern Sierra Nevada: a glimpse of the future?

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Abstract. Birds respond rapidly to changes in both habitat and climate conditions and thus are good indicators of the ecological effects of a changing climate, which may include warmer temperatures, changing habitat conditions, and increased frequency and magnitude of extreme events like drought. We investigated how a widespread tree mortality event concurrent with a severe drought influenced the avian community of the Sierra Nevada mountain range in California. We assessed and compared the separate effects of climate stresses and altered habitat conditions on the avian community and used this information to evaluate the changes that are likely to occur in the near future. We built tree mortality maps from freely available Landsat imagery with Google Earth Engine. We analyzed avian point counts from 2010 to 2016 in the southern Sierra Nevada, to model temperature, water deficit, and tree mortality effects on the abundances of 45 bird species, and then used these models to project abundances into the future based on three climate projections. A large portion of the avian community, 47%, had a positive relationship with temperature increase, compared to 20% that responded negatively. More species (36%) declined with drier conditions than increased (29%). More species declined in response to high tree mortality (36%) than increased (9%). A preponderance of species adapted to colder temperatures (higher elevation) had negative responses to high tree mortality and water deficit, but positive responses to increasing temperature. We projected the highest total bird abundances in the future under the warmest climate scenario that we considered, but habitat modification (e.g., tree mortality) and water deficit could offset the positive influence of temperature for many species. As other studies have shown, climate warming may lead to substantial but idiosyncratic effects on wildlife species that could result in community composition shifts. We conclude that future climate conditions may not have a universally negative effect on biodiversity in the Sierra Nevada, but probable vegetation changes and increased likelihood of extreme events such as drought should be incorporated into climate-smart forest and wildlife management decisions.

Key words: bark beetle; birds; climate change; climatic water deficit; Dendroctonus; distance sampling; drought; forest; Google Earth Engine; Normalized Difference Wetness Index; occupancy model; Sierra Nevada.

INTRODUCTION

The complex interactions between physical climate change and its effects on habitat conditions make predicting impacts to wildlife communities challenging (Bellard et al. 2012). Modeling species' vulnerabilities to shifting climate conditions while also incorporating climate-driven habitat changes can help address the challenges of managing wildlife and their habitats for the future (Huang et al. 2017). Modeling species' responses to future conditions can help quantify the uncertainty inherent in species vulnerability rather than ignoring the future or relying on the educated guesses of experts

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(Wiens et al. 2009). As changes in wildlife populations in response to climate change are realized, a variety of ecological consequences may result. These consequences could include differing levels of competition and predation within novel communities (Stralberg et al. 2009), and homogenization of communities (Gaüzère et al. 2015), both of which are likely to involve increased extirpations and extinctions (Moritz and Agudo 2013).

Climate can have a strong influence on the distribution and community composition of wildlife because of dynamic population processes, biotic interactions, and range shifts as a function of the bioenergetic adaptations of each species (Lawler et al. 2009, Tingley et al. 2009, Blois et al. 2013). Studies on this topic differ in whether they draw inference from correlative analyses that identify equilibrium patterns, or mechanistic responses to the influences of climate (Wiens et al. 2009). Regardless of whether studies use correlative or mechanistic analyses, it is possible to infer from those species-climate associations to assess the future vulnerability of species by modeling their responses to projections of future conditions. Though it is often assumed that species distributions will shift across elevation or latitude to track their climate niches, studies of birds are varied and do not necessarily follow patterns shown by vegetation, mammals, butterflies, or other organisms (Tingley et al. 2012, Roth et al. 2014, Bowler et al. 2015).

Studies that seek to predict species distributions given a changing climate have revealed that a complex assortment of mechanisms lead to individualistic responses that do not necessarily follow common notions about biogeographical shifts (Rapacciuolo et al. 2014). In montane areas where elevation begets far higher spatial heterogeneity in vegetation and wildlife communities than along latitudinal gradients, the reshuffling of species composition may occur rapidly as climate warming and precipitation changes accelerate in the future (La Sorte and Jetz 2010a). Birds are capable of rapidly adjusting breeding locations in response to environmental conditions (Purcell 2002), but the magnitude and direction of these changes can be idiosyncratic (La Sorte and Jetz 2010b, Gaüzère et al. 2017). Attempts to predict these changes using climate envelope models assume that species-climate relationships will hold constant over time and species will relocate to wherever their existing climate envelope will exist in the future, regardless of changes in physical habitat characteristics. However, besides direct climate effects on wildlife, there are also strong indirect effects, such as altered vegetation productivity and composition that have the potential to further induce reshuffling of wildlife communities (LeBrun et al. 2017).

While drought stress generally reduces forest vegetation productivity and tree seedling recruitment (Van Mantgem and Stephenson 2007), the effects of drought on avian abundance and species richness vary depending on ecosystem characteristics. For example, in dry ecoregions species richness decreases with drought, while in montane ecoregions it increases, particularly for nonmigrants (Albright et al. 2010). However, studies of the effects of environmental and vegetation changes together are rare, mainly because of the large difference in detail and scale between typical sources of habitat and climate data, making it difficult to evaluate the mechanisms that drive wildlife distributions (La Sorte and Jetz 2010a). New data sources that comprehensively scale down regional climate predictions to a local level are now readily available (Flint and Flint 2014), and make local-scale studies of both climate and vegetation change possible.

To gain greater insight into the potential effects of climate change and climate-driven changes in habitat on avian communities, we measured the responses of the avian community to the combined effects of drought and associated tree mortality in the Sierra Nevada Mountains of California. From 2013 to 2016 California experienced a severe drought following several years of near normal precipitation and a far above average snowpack in the Sierra Nevada mountain range in 2011. This drought, combined with record-high winter temperatures, created conditions where pine trees were not equipped to employ their natural defenses against bark beetles (Dendroctonus spp., Negrón and Fettig 2014). As a result, many pine trees succumbed to these stresses and widespread mortality occurred, increasing in magnitude and area each year from 2014 to 2016 (USFS 2017a). While the drought led to widespread forest die-off (Asner et al. 2016), the locations where mortality occurred resulted from a more nuanced combination of water stress, physiography, and the patchy distribution of bark beetles (Young et al. 2017).

Because birds in the lower and mid-elevation forests of the Sierra Nevada have evolved with frequent disturbances (Skinner and Chang 1996, Hutto et al. 2008, DellaSala et al. 2014), and are mobile and able to exploit irruptive resources, we postulated that species would respond rapidly to changes such as vegetation mortality, temperature increases, and reduced precipitation that resulted from the drought. Furthermore, the drought may be an analog of the effects of longer-term climate changes that will likely include increased temperatures and reduced precipitation. Thus, species' responses to the drought may be used to infer the mechanistic influences of climate and vegetation productivity on the avian community into the future.

Using records from an extensive avian monitoring program, we evaluated abundances of 45 bird species from upland forested areas across four national forests in the southern Sierra Nevada where bark beetleinduced tree mortality was most prevalent. We evaluated changes in the abundance of individual bird species in relation to climatic water deficit (CWD), difference in average breeding season daily high temperature from a pre-drought baseline, and a satellite imagery-derived index of tree mortality during the drought. We then used these results to model those effects into the future under three different climate scenarios. We evaluated patterns of response based on numerous guilds including nesting, feeding, habitat specificity, and temperature associations.

MATERIALS AND METHODS

Study location

Our study occurred in the lower and mid-elevation conifer forest of the Sequoia, Sierra, Stanislaus, and Eldorado National Forests of the Sierra Nevada in California. Within this study region, the dominant habitat types were Sierra mixed conifer, true fir, ponderosa pine, chaparral, and several hardwood (primarily *Quercus* spp.) dominated types (Mayer and Laudenslayer 1988). Ponderosa pine (*Pinus ponderosa*) forests were dominant at lower elevations; mixed conifer forests, composed of ponderosa pine, white fir (*Abies concolor*), sugar pine (*P. lambertiana*), Douglas fir (*Pseudotsuga menzeisii*), and incense cedar (*Calocedrus decurrens*) were dominant at intermediate elevations; and white fir, red fir (*A. magnifica*), Jeffrey pine (*P. jeffreyi*), and lodgepole pine (*P. contorta*) were dominant at higher elevations.

Site selection

We employed data from a bioregional monitoring project designed to monitor trends in upland forest birds within the actively managed national forests of the Sierra Nevada (Roberts et al. 2011, Fogg et al. 2014). This monitoring project was targeted toward areas available to silvicultural management and potential sampling locations were therefore limited to within 1 km of accessible roads and with slopes <35%. We did not include non-forest and non-montane California Wildlife Habitat Relationship (Mayer and Laudenslayer 1988) land cover types (e.g., annual grassland, barren, montane chaparral, montane riparian, wet meadow).

We limited our analysis to a subset of the total available survey locations. We removed every location that was affected by fire or silvicultural management activities from 2009 to 2016, so that any apparent changes in total plant biomass and water content across time would primarily represent the effects of plant vigor or senescence, and beetle-induced mortality. To limit the analysis to locations that were potentially affected by both tree mortality and drought we removed all survey locations that did not have at least 10% of the total tree cover attributed to sugar or ponderosa pine, the two species most impacted by the bark beetle outbreak. Our final data set resulting from all stratifications described above included 184 survey locations, covering elevations ranging from 1,070 to 2,370 m and latitudes from 35.39° to 38.98°.

Survey protocol

We used standardized five-minute unlimited-distance point count surveys (Ralph et al. 1993, 1995) to sample the avian community during the peak of the breeding season. At each survey location, we recorded all birds detected within a 5-minute period and estimated distance of first detection to the nearest 1 m from the observer. We visited each location up to twice per year between 10 May and 5 July, with an average number of visits per location per year of 1.6. We completed counts within 4.5 h of sunrise and did not survey during inclement weather or other conditions that would substantially reduce detection probability.

Model covariates

We included a set of covariates in the models to account for the separate effects of habitat, climate, tree mortality, and physiography on bird abundance. To account for the effects of habitat, we visually estimated the proportion of area covered by trees (including live and dead trees) and shrubs within 50 m of the survey location. We measured structural characteristics including diameter of the largest trees with a measuring tape, and basal area (a measure of woody cross-sectional area in standing trees) using a 10-factor key from at least three locations within 50 m of the survey location. Vegetation surveys were conducted between one and three times at each survey location across the entire study period. Where multiple surveys were available, we averaged measurements to return a single covariate value across all years for each location. To characterize topography, we sampled (with bilinear interpolation) elevation, aspect, and slope at each survey location from the Sierra Nevada Regional Digital Elevation Model (data available online).²

Measuring tree mortality represented a significant challenge. There were no existing data sources that mapped mortality on a continuous scale and at a fine enough spatial resolution to inform our bird abundance models. The U.S. Forest Service Aerial Detection Surveys (ADS, USFS 2017*b*) completed a near comprehensive survey of our study area, but the maps are coarse both spatially (large vector polygons) and in terms of assessment precision (coarse visual estimates of dead trees per acre), and thus are not capable of representing the amount of mortality at a scale relevant to individual bird territories (1–3 ha). Consequently we decided to employ remote sensing to attempt to quantify mortality at a fine scale.

To measure tree mortality at a similar resolution to our field vegetation (50 m radius), we created maps of Normalized Difference Wetness Index (NDWI, Gao 1996) from archival Landsat 5TM, 7ETM+, and 8OLI satellite imagery (30 m resolution) using the Google Earth Engine API (Google Earth Engine Team 2015). Normalized Difference Wetness Index is a satellitederived index using the near-infrared (NIR) and shortwave infrared (SWIR1) spectral band values to calculate a proxy measurement for plant water content, and has been shown to return consistent results even across different sensors (Li et al. 2013). Values of NDWI increase in proportion to the amount that green vegetation and vegetation water content contribute to the radiance values of a pixel. Thus it reflects not only the forest canopy vegetation, but any sub-canopy and ground vegetation visible to the satellite. Despite the potential for subcanopy vegetation cover to substantially influence the signal, Potter (2016) showed that NDWI, as well as the normalized difference vegetation index (NDVI), is sensitive to tree mortality. Normalized Difference Wetness Index has been used in a variety of geographies to assess water stress of vegetation, and has been shown to effectively indicate tree mortality in the Sierra Nevada during

² www.ice.ucdavis.edu/snep/dataset.asp?dataset=318

the drought we investigated (Van Gunst et al. 2016, Byer and Jin 2017).

We created spatially comprehensive NDWI raster images for each year from 2009 through 2016 using Google Earth Engine to build summer seasonal median images from Landsat imagery covering the 3-month summer dry period for each year. This resulted in up to five image dates in each composite. Landsat 5 TM images were composited for 2009 through 2011, Landsat 7 ETM+ in 2012, and Landsat 8 OLI for 2013–2016. To avoid snow cover and to sample peak vegetation growth and greenness, we used different image date ranges for the relatively wet years of 2009-2010 (15 May-15 August), high snow year of 2011 (1 June-1 September), and very dry years of 2012-2016 (1 May-1 August). We used the Landsat simple composite algorithm in the Google Earth Engine API to convert images to TOA reflectance and return the median of the least cloudy pixels from all images that fell within each date range (images *available online*).³ This composite resulted in highly consistent images that represented the vegetation cover for each pixel across the bird breeding season and were corrected for clouds and other nuisance effects on the images. We calculated NDWI by calculating the normalized difference of the NIR and SWIR1 bands of the composited imagery for each individual year (Gao 1996). We then sampled the yearly NDWI maps at each of our bird survey locations using the average of all image pixels centered within a 50 m radius (see Data S1 for code).

Following a similar logic to methods in Van Gunst et al. (2016), we calculated an index of tree mortality as the difference in NDWI between a reference year prior to the beginning of our bird survey data and the mortality outbreak (2009) and the year surveyed. Yearly calculations were as follows: mortality index 2016 = NDWI2009 - NDWI 2016, mortality index 2015 = NDWI2009 - NDWI 2015, and so on. We consider this metric a proportional index of the amount of tree mortality. Since the satellite imagery records reflectance of 30-m pixels, and pixels may not be completely covered by canopy trees, the mortality index not only reflects tree mortality but also includes some unquantified and variable amount of shrub and ground cover vegetation water stress. However, the understory cover consists largely of shrubs (32% average cover), grass (4%), fern (2%), and forbs and other ground-level vegetation (13%) that are not subject to beetle mortality. Furthermore our field crews did not report that shrub and ground-level vegetation was visually affected by the drought conditions, even during the late summer (August). Thus the median value compositing of imagery across the summer should effectively remove nuisance effects like snow and clouds, with minimal influence from seasonal vegetation senescence that could affect the NDWI values.

Since we had not designed our long-term bioregional monitoring study for investigating tree mortality, we did

not record the progression of apparent mortality during our field visits while the mortality was actively increasing (2012-2015). Starting in 2016 during our bird survey visits, multiple observers estimated the proportion area within 100 m of each survey location that was covered by dead trees. We subsequently verified the field estimates with aerial photography in Google Earth with a field of view of approximately 500 m on a high resolution 19-inch computer screen, and compared the apparent coverage of dead trees (brown and red coloration rather than green) from July or August 2016 images relative to earlier image dates. These data were used to corroborate our satellite-derived index of mortality by plotting against the 2016 index values and calculating a linear fit (R^2) . Our field estimates are coarse visual estimates and only apply to a single year (2016), thus they are not sufficient on their own to be included as covariates in models of bird abundance.

To evaluate the effects of climate on bird abundance, we calculated two metrics from down-scaled California Basin Characterization Model (270 m resolution; Flint et al. 2013, 2014, Flint and Flint 2014) climate and hydrology model data sets. Water-year average CWD and average June high temperature were sampled from these GIS layers at each bird survey location with the R package raster (R Core Team 2013, Hijmans et al. 2016). We chose to sample June average high temperature because it coincides with our breeding season surveys and should be more representative of proximal temperature effects on the breeding bird populations than yearly average high temperature, which would typically occur in July or August. Our interest in temperature was in how it influenced abundance on a yearly basis, and thus we needed a metric to portray the departure from a baseline value. Like the mortality index, we calculated the temperature index for each year at each survey location as the difference of the average June high temperature for a given year from the average June high temperature of the reference baseline year in 2009. For the mortality index, a baseline close in time to our field survey data was necessary to avoid potential vegetation structural changes that could add noise to the NDWI calculations, whereas for the temperature index the choice of baseline should not affect the information provided by index values at all, so we chose 2009 as a baseline year to be consistent with the mortality index.

Climatic water deficit effectively integrates the combined effects of solar radiation, evapotranspiration, and air temperature on watershed conditions given available soil moisture derived from precipitation. It estimates the amount of additional water that would have evaporated or transpired had it been available in the soil. We included CWD across the entire water year (Flint et al. 2013) rather than as a difference calculation like the temperature index as it reflects a hydrological process that occurs over a longer time period. The water stress, temperature, and mortality index calculations were designed so that larger positive values indicated larger effects of

³ https://developers.google.com/earth-engine/landsat

the drought-induced changes (i.e., drier soil, higher temperatures, or dryer and less green vegetation).

There is some correlation among the mortality, water deficit, and temperature indices due to the mechanistic relationship between temperature and water stress, and combined with topography they both also influence tree mortality (CWD/temperature index R = 0.55, CWD/ mortality index R = 0.44, temperature index/mortality R = 0.40). However, we examined the degree of collinearity between all variables using the vif function in the R package HH (Heiberger 2017), and found that all VIF < 3.0 (VIF > 4.0 is generally considered problem-atic collinearity; Garson 2012).

Analysis

We restricted our analyses to a subset of the bird species detected. We removed from our analyses all species not effectively sampled by our field methods including all waterfowl, nocturnal species, and non-breeding migrants (Ralph et al. 1993, 1995). We further restricted our analysis to species with at least 50 detections to avoid fitting models for overly sparse data. This resulted in a final list of 45 species accounting for the vast majority of the avian community (95% of all individuals detected). Counts and estimated distance at first detection were included in hierarchical distance models to account for detectability and estimate abundance per hectare (56 m radius circular area) for each of the 45 species at each survey location each year using the distsamp function in the R package Unmarked (Fiske and Chandler 2011; see Data S1 for code).

We used a "stacked years" data structure such that each site-by-year combination was treated as an independent sample unit (Burnett and Roberts 2015; J. A. Royle, personal communication). Although the abundance at a site in a given year is not fully independent from the abundance at the same site in another year, this data structure treats the occupancy state at each site as completely open to colonization or extinction between years. We felt this more accurately reflected the dynamic nature of these occupancy patterns during a period of rapid change in habitat conditions. This approach avoids the high computational demand of explicitly parameterizing population demographics in a more complex modeling framework while allowing the fit of variables that vary over time, with the trade-off of potentially underestimated errors in some model parameter coefficients. We summed the survey detections from multiple visits to the same site within the same year and used an offset (logtransformed visit count) to account for the differences in survey effort.

We selected a best fit (lowest Akaike's information criterion [AIC]) model for each species from among three global models fit with different detection functions: hazard, half-normal, and uniform. The detection portion of the models included tree basal area, shrub cover, and slope as covariates. The abundance portion of the model included elevation (with quadratic term), aspect, tree cover (with quadratic term), shrub cover (with quadratic term), percentage of pine composition of tree cover, and maximum tree DBH, to account for vegetation conditions. The abundance portion of the models also included the temperature, CWD, and tree mortality indices, as well as interaction terms for temperature and CWD with elevation, and tree mortality with tree cover. All continuous covariates were standardized by subtracting the mean across all observations and dividing by the standard deviation. A year covariate was explored for both the abundance and detection portions of the model, but it was highly collinear with the three indices so not appropriate in the abundance model, and it did not improve AIC in the detection portion of the model so we chose to remove it. We fit such a complex model to ensure that we removed as much variation as possible from factors that might mask the climate and tree mortality effects.

The model coefficients of primary interest were the temperature, water deficit, and tree mortality indices, and by including these indices as separate covariates, we partitioned the ecological effects of those distinct processes on each species' abundance. For each species, we calculated the index effect by dividing the squared coefficient by its standard error (approximating the chisquared test statistic with large sample size; Kleinbaum and Nizam 2008) and keeping the original sign. This statistic allows for a more direct comparison of the effect of each variable on abundance. We plotted these values and 95% profile likelihood confidence intervals and considered all effects for which confidence intervals did not include zero as significant. We then assessed patterns by counting the number of significant positive and negative effects across all 45 species. We assessed several ecological characteristics of species to identify whether there were consistent positive or negative associations with the temperature, water deficit, and mortality indices. We assessed nesting location, nest type, and foraging strategy (referenced from Saab et al. 2014), migration status and habitat specialization (referenced from Gardali et al. [2012], adjusted to correct for Sierra specific populations of each species), and species temperature index (STI; Devictor et al. 2008) across all species to determine any associations with the temperature, water deficit, and mortality indices. Species temperature index was calculated as the abundance-weighted average value of the 30-yr (1981-2010) average maximum temperature (Flint and Flint 2014) for all detections for each species in the data set. This index is highly correlated with the average abundance-weighted elevation for each species (R = 0.97), and reflects whether species are associated with high temperatures (low elevations) vs. low temperatures (high elevations).

We calculated the difference in total species abundance (average sum of all estimated species abundances at each survey location within a given year) to evaluate which species saw consistent increases or declines during the drought and assessed significance of the difference in means of abundance pre-drought (2010–2012) from drought years (2013–2016) with a *t* test (two-tailed, unequal variance). We report the species with significant differences (P < 0.05). Similarly, we summed species presence at each location (where predicted abundance > 0.5) as an estimate of species richness per survey location and compared pre-drought with drought year values.

Finally, we used the models to predict the future abundance of each species from 2021 to 2050 under three different climate models representing a range of probable futures under high emissions scenarios. Climate models project statewide changes of between +1°C and +6°C in temperature and between -20% and +40% change in precipitation compared to the 1951-1980 averages (Flint and Flint 2014). We sampled yearly projected June average high temperature and water-year CWD values from 2021 to 2050 from the moderately warmer (GFDL-B1, minimal changes in precipitation and ~2.5°C increase in temperature), warm and wet (CNRM-RCP85, 40% increase in precipitation and ~5°C increase in temperature), and warmest and dry (MIROC-RCP85, 20% decrease in precipitation and ~5.5°C increase in temperature) scenarios. A portion of the temperature index values in the warmest and dry scenario, and to a lesser degree the warm and wet scenario, exceeded the range of temperature index values from which we fit models, and thus we truncated those values at the maximum observed temperature index value (6.97) in our 2010-2016 data set to avoid fitting data outside of the range of the training data. This resulted in changing temperature index values for the warmest and dry scenario at 33% of the sample, which, prior to truncating, had an average of 9.02 and ranged up to 12.84. For the warm and wet scenario data set, we truncated 7% of thetemperature index values, which, prior to truncating, had an average of 7.47 and ranged up to 8.89. We also altered the habitat covariates at each survey location by reducing tree cover by amounts equal to the 2016 field-estimated mortality, and increasing shrub cover by 50% of the estimated mortality based on the assumption that shrubs will increase as a result of increased canopy openings (Nagel and Taylor 2005). We kept the mortality index estimates at 2016 values and all other covariates the same as the model fitting data set in order to assess the relative influence that the future climate conditions have on the bird community. We report total bird abundance for years 2021-2050 and evaluate the difference between our field data (2010-2016) estimates and future climate scenario estimates with a t test to assess significant differences (P < 0.05) in means for each species and report the species that increase or decline under each climate scenario.

RESULTS

The historic drought led to higher temperatures, water deficit, and mortality compared to pre-drought years (Fig. 1). The reference year (2009) was relatively cool

compared to long-term averages, with an average of 19.6°C across our survey locations, compared with 21.8 during 1981–2008. For any given year, the average June high temperature in this study area was highly correlated with elevation ($R \sim 0.9$). The range of temperature index values for our 2010-2016 data set was -1.98°C to +6.97°C, with an average of +3.40 across all years. The range of CWD values for our 2010-2016 data set was 124.6 to 1,137.8 mm, with an average of 706.0 mm. At our field sites, CWD (Fig. 1a) was lowest following the high-snowpack year in 2011 (mean = 499.5 mm), and was high from 2012 to 2015 (792.9 mm) until dropping during the near normal water year of 2016 (696.6 mm). Similarly, June average high temperature, as well as the temperature index (Fig. 1b, c), was lowest in 2011 $(\text{mean} = 20.4^{\circ}\text{C})$ and highest during the drought years of 2013-2015 (25.2°C), and remained high in 2016 (25.4°C). The mortality index (Fig. 1d) indicates that vegetation water content increased in 2010 and 2011 (mean index = -0.03), but then drying occurred each year starting in 2012 resulting in mean mortality index = 0.05 in 2016. The 2016 mortality index values revealed a good fit with our field estimates of mortality $(r^2 = 0.636, \text{ Fig. 2})$. The linear fit indicated that a mortality index value of 0.1 corresponded to 40% mortality field estimate (percentage of 100 m radius circle covered by dead trees). The average mortality across all survey locations from our 2016 field estimates was 17%, and one-half of the survey locations (n = 94, 51%) had <10%coverage by dead trees. Average total tree cover (live or dead) across all survey locations in this data set was 36.7% (range 10-76%), while shrub cover was 32.4% (range 3-90%). When adjusted relative to existing tree cover, average mortality at each survey station was 38.7%. Yearly average tree cover estimates (which included dead trees) decreased from 38.6% in 2010 to 33.4% in 2016.

The climate conditions during the recent drought in California led to much higher temperatures and CWD when compared to 1981–2010 values (Fig. 3). The range of CWD values that our survey locations experienced during the drought nearly encompassed future climate predictions (Fig. 3). Average temperatures from 2010 to 2016 were approximately 2°C higher than the 1981–2010 average and were similar to future predictions under both the warm and wet scenario and the moderately warmer scenario; however, the warmest and dry scenario eclipsed what we observed during the drought (almost 5°C warmer than the 1981–2010 average).

The majority of species showed mixed responses to the three indices (Fig. 4, Table 1). More species were affected by temperature and CWD than tree mortality as evidenced by the number of significant effects and their magnitude (Fig. 4). More species had positive effects for temperature index (21) than negative (9), while more species had a negative response to CWD (17) than positive (13). Most (24) of the species that responded to CWD also had a response to the



FIG. 1. (a) Water deficit, (b) June average maximum temperature, (c) temperature index, and (d) mortality index values at each survey location for the time period included in this study. The temperature and mortality indices are calculated as the difference of the given year from the reference baseline year in 2009. The drought years of 2012-2015 result in high climatic water deficit and temperature anomalies relative to pre-drought years and the baseline year (2009). Climatic water deficit drops in 2016 but temperature remains high. Mortality index increases each year from a low in 2011. Box plots show median values with thick horizontal lines, upper and lower quartiles as box top and bottom, and 95% confidence intervals. Each point is one survey location (n = 184).

temperature index but in the opposite direction, while only one responded to both effects in the same direction (Olive-sided Flycatcher, both positive). Most coldadapted (low STI) species abundances declined with high CWD and mortality, but increased with high temperature. Warm-adapted (high STI) species responses to temperature index were mixed, but generally the effect of CWD was positive. More species (16) had a negative response to tree mortality than positive (three), including all of the nine most abundant cold-adapted species. The three species that responded positively to mortality (White-breasted Nuthatch, Brown Creeper, and Western Wood-Pewee) are associated with dead conifer trees (snags) in our study area.

Only two species had at least one negative effect from among the three indices with no positive effects (Mountain Chickadee and American Robin) and only one species showed a decline in abundance during the drought (American Robin). There were five species with at least one positive effect from among the three indices and no negative effects (Hammond's Flycatcher, Steller's Jay, Spotted Towhee, Lesser Goldfinch, and Wrentit). Eight of the 45 species increased in abundance during the drought (Nashville Warbler, Golden-crowned Kinglet, Western Wood-Pewee, MacGillivray's Warbler, Hammond's Flycatcher, Wrentit, Yellow Warbler, and Dusky Flycatcher). Thus, the majority of species in this community have mixed or neutral responses to the combined effects of drought and tree die-off, but species that were negatively impacted were far fewer than species that responded positively. We were unable to identify any strong relationships between the magnitude or sign of species' temperature, water deficit, or mortality index effects and species' ecological characteristics, including



FIG. 2. Verification of satellite-imagery-derived mortality index by plotting against field estimates of percentage of area covered by dead trees. Field estimates were only gathered during survey location visits in 2016, so the comparison is for a single year only. The linear fit ($r^2 = 0.64$) is shown with 95% confidence interval (dotted lines). Each point is one survey location (n = 184).

foraging behavior, nesting location, or nest type (Table 1).

Total community abundance increased each year of the drought from a low of 20.1 individuals per survey location in 2011 to a high of 23.6 individuals in 2016. Species richness followed a similar pattern to abundance, rising from a low of 10.6 species per survey location in 2011 to a high of 13.1 in 2015 and 12.9 in 2016. The abundance and species richness increases were driven more by locations where there was low or no tree mortality. Comparing pre-drought (2010–2012) to drought (2013–2016) at locations with low mortality (5% or less according to our field estimates), abundance increased by 2.9 individuals per survey location vs. 0.5 individuals where there was high mortality (25% or more of the tree cover within 100 m of the survey location was dead). Species richness was less affected by mortality, as it increased by 1.6 species per survey location at low mortality sites and 1.3 species at high mortality sites.

Given that temperature was the most common positive influence on species abundance, we found that total community abundance varied in accordance with the temperature projections of the three future climate scenarios (Fig. 5). The warm and wet scenario estimates (mean = 22.7) were similar to what we observed during the drought years (22.4), while the warmest and dry scenario estimates were higher (24.1), though the variance among years was far higher than what we observed in the 2010–2016 field data. The predicted total community abundance in the moderate scenario (20.7) was nearly the same as what we observed in our field data prior to the drought (20.6), though again the variance among years was much larger. All three future scenario models resulted in some yearly values of total community abundance higher than observed field data, as well as some lower values.

Abundance of both generalists and species known to be more associated with particular habitat types ("associates") increased during the drought in comparison to pre-drought years (Fig. 6a). The abundance of habitat



FIG. 3. (a) June average maximum temperature and (b) climatic water deficit (CWD) averaged across all field survey locations in each year for three time periods: historical (1981–2010), field data set (2010–2016), and future (2021–2050 BCM projections). The future projections were sampled from three scenarios: warm and wet (CNRM-RCP85), warmest and dry (MIROC-RCP85), and moderately warmer (GFDL-B1). The range of CWD values in the field data time period (2010–2016) encapsulates nearly the entire range of future projected climate conditions through 2050, however even higher temperatures are projected under the warmest and dry and warm and wet models than were observed in the current data set. Box plots show median values with thick horizon-tal lines, upper and lower quartiles as box top and bottom, and 95% confidence intervals, each point is one yearly average across all survey locations.



FIG. 4. Dot plot showing individual species effects of water deficit, temperature, and tree mortality indices, with horizontal lines indicating 95% profile likelihood confidence intervals. Magnitude of the effect is determined by distance from the vertical line at zero on the *x*-axis (approximating a chi-squared test statistic). Species ordered by species temperature index (STI) with low STI at the top. For scientific names of species, see Table 1. Nonsignificant effects are not plotted. Ten species had no significant effects and are not shown.

associates was predicted to be higher during both the warm and wet (10.9), and the warmest and dry (11.6) future scenarios, and remain relatively stable under the moderate scenario (9.5) in comparison to the predrought (8.9) and drought years (9.8). Generalists were predicted to remain relatively stable under the three future scenarios (warm and wet = 11.7, warmest and dry = 12.5, moderate = 11.2) in comparison to the predrought (11.9) and drought (12.5) averages. As with total abundance estimates, there was far more variation among yearly abundance estimates under the future scenarios than what we observed in our field data. Abundance within migration groups was similar between the warm and wet and warmest and dry scenarios (Fig. 6b), and lower on average across all three groups under the moderate scenario. Residents' abundance increased on average across all three scenarios (warm and wet = 5.5, warmest and dry = 5.8, moderate = 5.3, in comparison to pre-drought = 4.2 and drought = 4.5), while short-distance migrants were predicted to decrease (warm and wet = 7.7, warmest and dry = 8.0, moderate = 7.3, in comparison to pre-drought = 8.7 and drought = 9.1). Long-distance migrants were predicted to increase in comparison to pre-drought (7.7) and drought (8.8) under the warm and wet (9.5), and warmest and dry (11.3) scenarios, and remain relatively similar under the moderate scenario (8.1).

	7	ŗ	Veg.	Nest			Hab.	Mig.	CWD	Temp.	Mort.	
Species	Scientific name	Forage	Lyr.	type	Elevation	STI	Spec.	type	index	index	index	Future abundance
Green-tailed Towhee	Pipilo chlorurus	MO	HS	0	2,023	23.92	2	0	NS	SN	NS	NS
Fox Sparrow	Passerella iliaca	GI	ΗS	0	2,014	23.99	2	0	+	Ι	Ι	+ (warm/wet, warmest/dry)
Red-breasted Sapsucker	Sphyrapicus ruber	MO	CA	Cp	2,013	24.21	2	0	NS	SN	SN	I
Dusky Flycatcher	Empidonax oberholseri	AI	SH	0	1,953	24.32	0	ю	I	+	Ι	+ (warm/wet, warmest/dry)
Mountain Chickadee	Poecile gambeli	FI	CA	Cs	1,985	24.38	1	1	I	SN	I	1
White-headed Woodpecker	Picoides albolarvatus	MO	CA	Cp	1,932	24.51	1	1	I	+	Ι	NS
Golden-crowned Kinglet	Regulus satrapa	FI	CA	0	1,913	24.53	7	1	I	+	I	- (moderate)
Olive-sided Flycatcher	Contopus cooperi	AI	HS	0	1,950	24.60	7	б	+	+	I	NS
Pine Siskin	Spinus pinus	SC	CA	0	1,872	24.64	1	0	Ι	+	Ι	NS
Yellow-rumped Warbler	Setophaga coronata	FI	CA	0	1,897	24.65	1	ы	Ι	+	Ι	+ (warmest/dry)
Hermit Thrush	Catharus guttatus	GI	ΗS	0	1,921	24.65	1	ы	NS	+	Ι	+
Towsend's Solitaire	My a destes towns endi	AI	GR	0	1,918	24.69	2	0	Ι	+	SN	+ (warm/wet, warmest/dry)
Macgillivray's Warbler	Geothlypis tolmiei	FI	ΗS	0	1,879	24.78	2	б	Ι	+	SN	+
Cassin's Finch	Haemorhous cassinii	MO	CA	0	1,946	24.79	2	1	NS	SN	SN	- (moderate)
Yellow Warbler	Setophaga petechia	FI	HS	0	1,914	24.85	7	ю	NS	SN	NS	+ (warm/wet, warmest/dry)
Red-breasted Nuthatch	Sitta canadensis	BG	CA	Cp	1,869	25.05	1	1	I	+	Ι	- (moderate)
Hammond's Flycatcher	Empidonax hammondii	AI	CA	0	1,882	25.27	2	ю	NS	+	SN	+ (warmest/dry)
Warbling Vireo	Vireo gilvus	FI	CA	0	1,837	25.27	1	ю	I	+	NS	- (moderate)
White-breasted Nuthatch	Sitta carolinensis	BG	CA	Cs	1,839	25.32	7	1	+	I	+	NS
Steller's Jay	Cyanocitta stelleri	MO	CA	0	2,026	25.44	1	1	+	SN	SN	NS
Western Tanager	Piranga ludoviciana	FI	CA	0	1,848	25.52	1	б	I	+	SZ	- (moderate, warm/wet)
Hermit Warbler	Setophaga occidentalis	FI	CA	0	1,804	25.53	7	3	I	+	I	– (moderate)
Mountain Quail	Oreortyx pictus	SC	GR	0	1,787	25.57	1	1	NS	NS	NS	NS
Brown Creeper	Certhia americana	BG	CA	Cs	1,804	25.63	1	1	I	+	+	NS
Dark-eyed Junco	Junco hyemalis	MO	GR	0	1,775	25.77	1	7	NS	SN	SN	I
Band-tailed Pigeon	Patagioenas fasciata	SC	CA	0	1,783	25.81	7	7	+	I	SN	NS
American Robin	Turdus migratorius	GI	CA	0	1,772	25.83	1	7	NS	I	I	I
Northern Flicker	Colaptes auratus	MO	CA	Cp	1,752	25.92	1	1	NS	SN	NS	I
Nashville Warbler	Leiothlypis ruficapilla	FI	GR	0	1,707	26.15	7	ю	I	+	+	+ (warmest/dry)
Western Wood-Pewee	Contopus sordidulus	AI	CA	0	1,756	26.22	1	ю	+	I	+	NS
Hairy Woodpecker	Leuconotopicus villosus	BD	CA	Cp	1,732	26.32	1	1	NS	SN	NS	+
Purple Finch	Haemorhous purpureus	SC	CA	0	1,759	26.33	1	1	+	NS	I	- (moderate, warm/wet)
Cassin's Vireo	Vireo cassinii	FI	CA	0	1,660	26.56	1	Э	I	+	I	- (moderate)
Chipping Sparrow	Spizella passerina	MO	ΗS	0	1,676	26.58	7	7	+	NS	I	I
Black-throated Gray Warbler	Setophaga nigrescens	FI	CA	0	1,567	27.45	7	ю	NS	+	I	+
Spotted Towhee	Pipilo maculatus	OM	GR	0	1,516	27.49	1	7	NS	+	NS	+ (warm/wet, warmest/dry)
Mourning Dove	Zenaida macroura	MO	SH	0	1,622	27.66	7	1	+	I	NS	NS

Species	Scientific name	Forage	Veg. Lyr.	Nest type	Elevation	ITZ	Hab. Spec.	Mig. type	CWD index	Temp. index	Mort. index	Future abundance
Acorn Woodpecker	Melanerpes formicivorus	BD	CA	Cp	1,585	27.88	ю	-	+	I	NS	NS
Lazuli Bunting	Passerina amoena	MO	HS	0	1,485	27.96	7	ю	I	+	NS	+ (warm/wet, warmest/dry
Black-headed Grosbeak	Pheucticus melanocephalus	FI	CA	0	1,434	28.11	2	3	+	I	NS	+
Bushtit	Psaltriparus minimus	FI	HS	0	1,424	28.37	1	1	NS	SN	NS	NS
Lesser Goldfinch	Spinus psaltria	MO	HS	0	1,420	28.51	1	2	+	SN	NS	- (moderate, warm/wet)
Wrentit	Chamaea fasciata	FI	HS	0	1,372	28.70	2	1	NS	+	NS	+
Brown-headed Cowbird	Molothrus ater	MO	ΝA	Р	1,356	28.83	1	7	+	I	NS	1
Hutton's Vireo	Vireo huttoni	FI	CA	0	1,256	29.58	7	1	NS	NS	NS	+ (warm/wet, warmest/dry
Notes: CWD, climatic wate	r deficit; STI, species temperatu	tre index. Sh	secies ar	e ordered	1 by STI, with	lowest at	the top.	Model c	oefficients	s with 95%	6 confiden	ce intervals that do not inter

TABLE 1. (Continued)

insectivores (AI), bark-drilling insectivores (BD), bark-gleaning insectivores (BG), foliage insectivores (FI), ground insectivores (GI), carnivores (CA), nectarivores (NE), seed consumers sect zero are shown as positive (+) or negative (-), otherwise non-significant (NS). Difference in mean yearly species abundance from field data (2010-2016) under three different climate models over a 30-yr time span (2021–2050) are shown as +, -, or NS (not significant) assessed from t test comparisons (+ or - determined by P < 0.05). Foraging types (Forage): aerial Nest types: cavity (Cp, primary excavator and Cs, secondary non-excavator) or open cup (O). Elevation and STI calculated as abundance-weighted averages across all detections within this data set. Habitat specialization (Hab. Spec: 1, generalist; 2, habitat associated; 3, habitat specialist) and migration status (Mig. type: 1, resident; 2, short-distance migrant; 3, long-distance migrant) were referenced from Gardali et al. (2012) and adjusted to more closely match southern Sierra Nevada populations. The three futures represent a warm and wet (CNRM-RCP85), warmest and dry (MIROC-RCP85), and moderately warm and minimally (SC), or omnivores (OM). Nesting vegetation layers (Veg. Lyr.); ground (GR), shrub (SH), or canopy (CA). different precipitation scenario (GFDL-B1). There were more species that differed (P < 0.05) in abundance from 2021 to 2050 under the future scenario models than in our field data comparison of pre-drought with drought years (likely because of larger sample size increasing power of the *t* test). Species with lower future abundance across all three climate scenarios included Dark-eyed Junco, American Robin, Red-breasted Sapsucker, Brown-headed Cowbird, Mountain Chickadee, Chipping Sparrow, and Northern Flicker (Table 1). Those with higher abundance included Black-throated Gray Warbler, Hermit Thrush, Hairy Woodpecker, Black-headed Grosbeak, Wrentit, and MacGillivray's Warbler.

DISCUSSION

As climate conditions change, wildlife species will have to alter their geographic distributions to track suitable climate conditions, adapt to new conditions within their current ranges, or go extinct (Moritz and Agudo 2013). Given that some combination of those three outcomes will occur across all species at any given location, and since changes in habitat will lag behind the changes in climate (Stralberg et al. 2015), we are likely to encounter previously unrecorded community compositions (Stralberg et al. 2009). These changes will likely occur in a disorderly fashion as climate tolerance thresholds are reached by different species at different times, and iterative large-scale disturbances reset vegetation succession processes in some locations, all of which may be exacerbated by extreme climate events.

Our results support other findings that bird communities quickly respond to ecological changes including both climate and habitat changes. Abundance and distribution fluctuations in response to climate change could result from movements of individuals (especially juveniles) across different elevations and latitude, into different habitats (favoring habitat generalists, Davey et al. 2012), and also from changes in productivity at different elevations or temperatures (Nott et al. 2002). It is unclear from our data which of these processes is leading to the increased community abundance we observed during the drought. Given that abundance increased more in locations with low tree mortality than high mortality, there could be some directional dispersal as a direct result of the tree die-off event. However, a more nuanced analysis would be needed to fully address this question. Our finding of increased overall abundance in response to higher temperatures fits our understanding of the montane conifer avian community in that the warmer temperatures extend the breeding period for many species by giving them a warmer early spring, which likely decreases energetic demands and increases insect prey. Our results also suggest that the avian community in these habitats may be resilient to multi-year droughts and some amount of future temperature and precipitation changes. Among the species included in this data set, we found that the warm-adapted species tended to



FIG. 5. Future predicted abundances under three different climate models in comparison to pre-drought (2010–2012) and drought (2013–2016) field data estimates. We predicted each species' abundance over a 30-yr time span (2021–2050) based on projected future climate conditions under three different scenarios: warm and wet (CNRM-RCP85), warmest and dry (MIROC-RCP85), and moderately warmer (GFDL-B1). Box plots show median values as thick horizontal lines, upper and lower quartiles as box top and bottom, and 95% confidence intervals. Each point is one yearly average abundance of all species per survey location.

respond positively to water stress at these locations, with mixed responses to temperature. On the western slope of the Sierra Nevada, elevation and precipitation are positively correlated, so it is to be expected that warmadapted (i.e., lower elevation) species would be better adapted to drier conditions and could outcompete species associated with lower temperatures. Even though the cold-adapted species almost universally responded positively to higher temperatures, they were sensitive to water stress and tree mortality. Thus, under future climate scenarios where warmer and wetter conditions prevail, we expect that the cold-adapted species abundances will increase in locations where habitat change (e.g., tree mortality) is minimal. Under the warmest and dry future, the opposing influences of temperature and water deficit will have less certain results on the warmadapted species.

Our results indicate that a preponderance of habitat generalists will benefit from the projected climate changes, while the outcomes of bird species associated with particular habitat features are more varied. Other large-scale studies have found that montane bird



FIG. 6. Future abundances under three different climate models by (a) habitat association and (b) migration guilds. We predicted each species' abundance over a 30-yr time span (2021–2050) based on projected future climate conditions under three different scenarios: warm and wet (CNRM-RCP85), warmest and dry (MIROC-RCP85), and moderately warmer (GFDL-B1). Box plots show median values with thick horizontal lines, upper and lower quartiles as box top and bottom, and 95% confidence intervals. Each point is one yearly average abundance of all species per survey location.

communities can be resilient to climate changes (Albright et al. 2010), but there is ample evidence that many species' ranges will be reduced (La Sorte and Jetz 2010a) and that functional diversity may decline (Gaüzère et al. 2015). In addition, contrary to studies showing that climate warming negatively impacts long-distance migrants disproportionately in comparison to residents and shortdistance migrants (Albright et al. 2010), we found that long-distance migrants increased during the drought and were projected to remain at similar abundance under the two climate scenarios with the most warming. Residents were projected to increase and short-distance migrants to decrease under the two warm scenarios. The lowest abundances across the board were predicted to occur in the moderate scenario.

It is important to consider that our projections did not predict out to the full extent of warming under the most extreme scenario. The range of temperatures we observed during the drought were eclipsed by two of the three future climate projection scenarios we assessed. Thus, we were not able to predict the influence that temperatures beyond what we observed and included in the model fitting data set would have on species' abundances. There very well may be thresholds beyond the temperature range that we assessed for many species with positive associations with the temperature index at which abundance declines. We also did not incorporate temporal lag effects, and it is possible that more than the four years of sustained high temperature or high water deficit that we observed in our data set could result in lowered population viability due to exposure to those conditions beyond the timeframe of our study. The data used to build our models covers a period of time spanning a transition from a cool and wet period to a very warm and dry drought period. Therefore, without a warm and wet period to inform the models and the fit of those variables for these species, our results could be erroneous if there is an influential interaction between those variables for which we did not account. Furthermore, although we did model an interaction between elevation and the temperature and water deficit indices, this may not fully account for species that may track specific habitat and climate conditions in the future, and that these conditions may be distributed differently than they are today (Elsen and Tingley 2015).

Our assumption that bird abundance at field sites is independent between years ignores any potential site fidelity, which could slow site-level colonization and extinction, as well as other mechanisms that could lead to spatial autocorrelation at survey locations, and thus potentially underestimates the standard errors of model covariates that vary across time at survey locations, including all three indices. But, birds are highly vagile and have been shown to be fit best with models that do not assume closure across short time periods (Rota et al. 2009). Furthermore, since we rely on detection distances to calculate the detectability function for each species the assumption of closure across survey periods does not apply. Several other sources of error resulting from the imperfect detectability of birds at our field sites could influence our abundance estimates (Iknayan et al. 2014), which we have taken careful measures to account for in our survey design by using only highly trained field observers and surveying within consistent seasonal, time, and weather constraints.

Tree mortality is expected to continue if not accelerate as temperatures increase and drought stress becomes more commonplace (Bentz et al. 2010). Both low elevation and high elevation forest types in the Sierra Nevada are susceptible to drought-induced mortality (Hurteau et al. 2007). While pine species at lower elevations, such as ponderosa and sugar pine, have evolved to be strongly drought tolerant (Maherali et al. 2004), they are still susceptible to mortality, especially when drought stress is combined with the presence of bark beetles such as mountain and western pine beetles (Dendroctonus spp.). High elevation forest types also experience episodic mortality as a result of extreme environmental conditions resulting from both abnormally high and low winter snowpack (DeClerck et al. 2005) and bark beetle infestations, and thus further habitat changes are likely to occur if temperature and water deficit increases in the future.

The temperature and water deficit indices had more influence on species in this community than the tree mortality index, suggesting that climate effects over this time frame were more influential on birds in this region than tree mortality and vegetation productivity. However, the magnitude of vegetation changes observed during the study period was relatively small (<5% change in tree cover). Even after four years of drought and beetle mortality, the ponderosa and sugar pines that were hardest hit in this mortality event showed minimal structural decay, still retaining the vast majority of needles with little to no loss of branches. Thus, despite over 38% of existing tree cover experiencing beetle mortality, the inevitable changes in tree cover, shrub cover, and other structural characteristics had not yet taken place.

Stephens et al. (2014) found relatively small effects to the avian community in the Northern Sierra Nevada as a result of mechanical fuel treatments resulting in moderate reductions in tree cover, suggesting that the forest avian community is tolerant of modest changes in forest structure. A century of timber harvest, reforestation, and fire suppression has led to far more homogenous and dense forest conditions than were present in these forests prior to European colonization (Parsons and DeBenedetti 1979, Minnich et al. 1995, Mallek et al. 2013). Despite the eventual widespread loss of trees and subsequent increase in shrubs, these stands may still be within the natural range of live conifer tree cover that the bird community has adapted to exploit. The total number of species affected by mortality (45%) was somewhat smaller than the number affected by temperature (67%) and CWD (67%), but that should not distract from the finding that 36% of the avian community was

negatively affected by tree mortality. The preponderance of cold-adapted species that decline in response to tree mortality and water deficit implies a significant loss of habitat for those species in our study area, and if droughts occur again in the future it could offset any benefits for those species that may result from higher temperatures, as has been shown in nearby desert regions (Iknayan and Beissinger 2018).

Bark-drilling woodpeckers and primary cavity excavators have been shown to respond positively to beetleinduced mortality (Saab et al. 2014). However, for this group, including: Red-breasted Sapsucker, White-headed Woodpecker, Red-breasted Nuthatch, Hairy Woodpecker, Northern Flicker, and Acorn Woodpecker, we found none with a positive response to the mortality index, while two (White-headed Woodpecker and Redbreasted Nuthatch) were negative. In addition, one-half of the species in this group were predicted to decline in the future. Saab et al. (2014) also found positive responses from shrub-nesting and secondary cavity-nesting species following beetle mortality, but given that our sites have not progressed through the loss of canopy cover to promote higher shrub cover, or additional nest cavity availability for secondary cavity nesters, we did not find the same associations. However, given our assumption of increased shrub cover in future abundance projections, we did find that more than one-half of shrub-nesting species (7 of 13 total) were predicted to increase and only two to decrease. Furthermore, our assumption that mortality will remain at 2016 values in the future abundance projections, and thus that no more mortality events will occur over that timeframe, is unlikely. We expect that there will be more bark beetle mortality in the future, and that these events will create additional changes to forest structure that will be meaningful to the avian community.

Several recent studies have shown that bird and other wildlife species distributions changed dramatically over regional scales as a result of climate warming (Devictor et al. 2008, Gaüzère et al. 2015). Our findings suggest that cold temperature adapted species will increase in this study area. Rather than shifting upslope in response to warmer and drier conditions, we predicted they will increase even at the lower and warmer end of their elevational distributions, consistent with the findings of Albright et al. (2010). Tingley et al. (2012) presented several results that are comparable to what we observed in our study. First, the opposing influences of temperature and precipitation on many species was shown both in our mechanistic analysis, as well as their correlative distribution analysis. Additionally, they found that low elevation species were more commonly influenced by precipitation, while high-elevation birds were more influenced by temperature, which also matches our results. When exploring the effects within migration groups, they found that residents and short-distance migrants are more likely to shift ranges in response to climate, and we too found that abundance changes in response to projected

future climate were strongest in those groups, but in different directions (positive in residents, negative in short-distance migrants). Since we did not directly track distributions in this study, a more thorough analysis is warranted to address whether there are likely to be substantial changes to species' distributions in this region as the climate warms and to more fully understand the mechanisms that lead to those changes.

The ready availability of imagery, standardized processing code, and computing power of the free Google Earth Engine online application made this study feasible, and allowed us to incorporate estimates of mortality that are far more precise and spatially detailed than other available data including the USFS ADS assessment (USFS 2017b). Although the mortality index we employed in this study is highly correlated with the amount of mortality that we observed by the end of the drought, this index is largely a comprehensive measure of vegetation vigor that represents the water content in all leaves, not just trees, and for that reason it may not have been as tightly linked to the observable tree mortality as we had originally intended. However, this measure is likely to be highly informative of important vegetation processes in the same way as numerous other studies that have used similar vegetation indices like NDVI (Gottschalk et al. 2005). Thus, there is some unquantified noise in our measure of the tree mortality influence on abundance. Also, the negative values for this index in 2010-2012 indicating higher vegetation water content have influence on the fit of that variable and may have obscured the simple effect of tree mortality that we expected to find. Identifying other metrics of wide spread habitat change will be important for monitoring and predicting future biodiversity responses to climate change.

CONCLUSION

How wildlife respond to climate change is likely to be complex. Studies that use extreme climate anomalies that manifest conditions analogous to those predicted in the future may provide a powerful tool to project the effect of climate change on wildlife communities. However, we suggest caution that these results are just one possible response of these species to projected future conditions based on a single drought during the short time span of this study, and there may be other important drivers that could influence wildlife communities in the future. Thus, any results from this study that could inform management actions should be considered a first step in the adaptive management framework that includes regular monitoring and updating of management plans and strategies. Total avian community abundance in our study area increased throughout the drought period and our model results projected similarly high abundances in response to warmer future climate conditions. However, many of the species that appear to benefit from increased temperatures are also sensitive to high water deficit and tree mortality. Thus, their positive response to increasing temperatures in the future could be offset by drought or habitat change. The full effects of the recent drought and tree mortality event are still unfolding, understanding the mechanisms that lead to changes in abundance may help predict how these species will respond to the interaction between mortalitydriven habitat disturbances and climatic changes, and can inform climate-smart conservation and management actions to enhance resiliency and adaptive capacity of species and their habitats. While beetle mortality resulted in a rather substantial reduction in the live tree cover in our study area, the short-term effects on the avian community were rather modest. Our results show that abundant and diverse bird assemblages still inhabit the forest stands affected by mortality, and therefore managers should consider this potentially important biodiversity when developing management responses like salvage logging and reforestation. A particularly informative extension of this analysis would be to implement the future projections of bird habitat in a spatially explicit context, allowing researchers and managers to evaluate how multiple disturbance processes including climate change, fire, timber harvest, fuels treatments, and beetle mortality combine to influence habitat quality and connectivity over time under multiple future climate and management scenarios.

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SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1848/full

DATA AVAILABILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.rm2n805