

Synergistic effects of climate and land-use change influence broad-scale avian population declines

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Abstract

Climate and land-use changes are expected to be the primary drivers of future global biodiversity loss. Although theory suggests that these factors impact species synergistically, past studies have either focused on only one in isolation or have substituted space for time, which often results in confounding between drivers. Tests of synergistic effects require congruent time series on animal populations, climate change and land-use change replicated across landscapes that span the gradient of correlations between the drivers of change. Using a unique time series of high-resolution climate (measured as temperature and precipitation) and land-use change (measured as forest change) data, we show that these drivers of global change act synergistically to influence forest bird population declines over 29 years in the Pacific Northwest of the United States. Nearly half of the species examined had declined over this time. Populations declined most in response to loss of early seral and mature forest, with responses to loss of early seral forest amplified in landscapes that had warmed over time. In addition, birds declined more in response to loss of mature forest in areas that had dried over time. Climate change did not appear to impact populations in landscapes with limited habitat loss, except when those landscapes were initially warmer than the average landscape. Our results provide some of the first empirical evidence of synergistic effects of climate and land-use change on animal population dynamics, suggesting accelerated loss of biodiversity in areas under pressure from multiple global change drivers. Furthermore, our findings suggest strong spatial variability in the impacts of climate change and highlight the need for future studies to evaluate multiple drivers simultaneously to avoid potential misattribution of effects.

KEYWORDS

Bayesian hierarchical model, Breeding Bird Survey, climate change, habitat loss, land-use change, synergistic effects

1 | INTRODUCTION

Climate and land-use change are the two greatest threats to global biodiversity (Lemoine, Bauer, Peintinger, & Böhning-Gaese, 2007; Newbold et al., 2015; Sala et al., 2000; Sohl, 2014; Wilcove, Rothstein,

Dubow, Phillips, & Losos, 1998). Although land-use change is the primary driver of contemporary biodiversity loss (Newbold et al., 2015), climate change is expected to have an increasing influence on species distributions and populations in the future (Bellard, Bertelsmeier, Leadley, Thuiller, & Courchamp, 2012; Lemoine et al., 2007; Sohl,

2014). Understanding how species respond to these environmental changes thus is critical for developing effective conservation strategies (Tingley, Estes, & Wilcove, 2013).

Although many studies have identified impacts of climate and land-use change on species, there is limited empirical evidence suggesting interactions between them, despite substantial theoretical evidence and some mesocosm-scale experiments that show these factors should act synergistically (Brook, Sodhi, & Bradshaw, 2008; Mora, Metzger, Rollo, & Myers, 2007; Oliver & Morecroft, 2014; Opdam & Wascher, 2004; Travis, 2003). For example, habitat fragmentation could decrease the capacity of species to shift their ranges in response to climate change (Opdam & Wascher, 2004), whereas habitat loss could reduce standing genetic variation thereby limiting species' capacity to adapt under a changing climate (Hoffmann & Sgrò, 2011). Furthermore, the actual processes of climate and land-use change are expected to influence each other, potentially resulting in positive feedbacks, whereby both occur at faster rates than expected in isolation (Jones, Lowe, Liddicoat, & Betts, 2009; Laurance & Williamson, 2001). Despite these lines of evidence, we still lack empirical information at broad scales on whether these two dominant drivers of global environmental change interact to impact species (Mantyka-Pringle, Martin, & Rhodes, 2012; Sirami et al., 2017). If synergistic effects are widespread, then current projections of biodiversity loss likely represent substantial underestimates (Thomas et al., 2004). Thus, developing an improved understanding of the potential for synergistic effects of climate and land-use change on populations is one of the more pressing needs for biodiversity conservation efforts.

One of the major factors that has limited assessments of interactions between climate and land-use change on animal populations is data scarcity (De Chazal & Rounsevell, 2009). Robust assessments of interactions of these factors require time series on climate, land use and species abundance at scales that capture the relationships between changes in environmental conditions and animal populations. In addition, climate and land-use changes are often correlated over space and time (Oliver & Morecroft, 2014), which poses an additional challenge to study design and inference. As a result, most studies have either assessed the impacts of only a single global change driver (Le Tortorec et al., 2017) to avoid correlation issues, or have fit static models examining the influence of multiple drivers and inferred synergistic changes by predicting into the future based on projections of climate and land-use change (i.e., models are fit to data from a single point in time and projected into the future under the assumption that contemporary patterns will hold; Heubes et al., 2013; Jetz, Wilcove, & Dobson, 2007; Sohl, 2014; Vermaat et al., 2017). Models assessing only a single driver risk incorrectly attributing impacts due to frequent confounding between climate and land cover (Oliver & Morecroft, 2014), whereas projections are necessarily speculative due to substantial uncertainty in future climate and land-use patterns and the assumption that species responses will exhibit stationarity, despite evidence to the contrary (e.g., Gutiérrez Illán et al., 2014; Yegorova, Betts, Hagar, & Puettmann, 2013).

Here, we have undertaken one of the first tests of the hypothesis that climate and land-use change have acted synergistically to influence animal population declines. We coupled a large-scale (>235,000 km²), long-term (29 years) dataset on bird population dynamics with a unique spatial dataset representing annual measures of land-use and climate at high spatial resolution. We focus on the Pacific Northwest of the United States, an area that has undergone a wide range of land-use changes. Chief among these changes is forest cover change due to the transformation of timber harvest patterns that resulted from the implementation of the Northwest Forest Plan (Adams, Hobbs, & Johnson, 2005; Hayes et al., 2005; Moeur et al., 2011; Phalan et al., 2019; Spies et al., 2007). Thus, we focus on how forest and climate change impact population dynamics of forest-associated birds.

2 | MATERIALS AND METHODS

2.1 | Bird population data

We compiled forest bird population data from 1984–2012 that were collected as part of the United States Breeding Bird Survey (BBS; Sauer, Link, Fallone, Pardieck, & Ziolkowski, 2013) within the Northwest Forest Plan Boundary (Thomas, Franklin, Gordon, & Johnson, 2006), encompassing >235,000 km² in California, Oregon and Washington (Figure 1). The BBS consists of a set of routes, each 40 km in length, along secondary roads surveyed annually by trained observers since 1966, although not all routes were surveyed every year (Sauer et al., 2013). Each route is designed to sample an individual landscape, and thus we refer to routes as landscapes. Observers stopped at 50 regularly spaced locations within each landscape and recorded the species of every bird observed during 3-min audio-visual surveys. We combined data from all stops within each landscape to quantify the total number of individuals of each species detected during each year. Observers conducted surveys during May or June of each year, providing a temporally and spatially consistent sample of bird counts. We compiled data from forest bird species of the orders Caprimulgiformes, Columbiformes, Coraciiformes, Passeriformes and Piciformes. Our final dataset included 94 species surveyed in 145 total landscapes with an average of 80 landscapes per species (range 32–99; see Appendix 1 for additional details on species selection criteria, which species were included and the number of landscapes used in models for each species). This dataset included 43 long- or medium-distance migrants, 14 short-distance migrants, 3 partial-migrants and 34 nonmigratory species as determined from comprehensive species accounts (migratory information obtained from Birds of North America; Rodewald, 2015). Landscapes sampled as part of this analysis ranged from 8 m to 1700 m in elevation at their centroid with an average of 567 m.

2.2 | Climate, land-use and land cover variables

We were interested in two broad categories of spatial data: (a) climate; and (b) habitat loss – which emerges from land-use change.

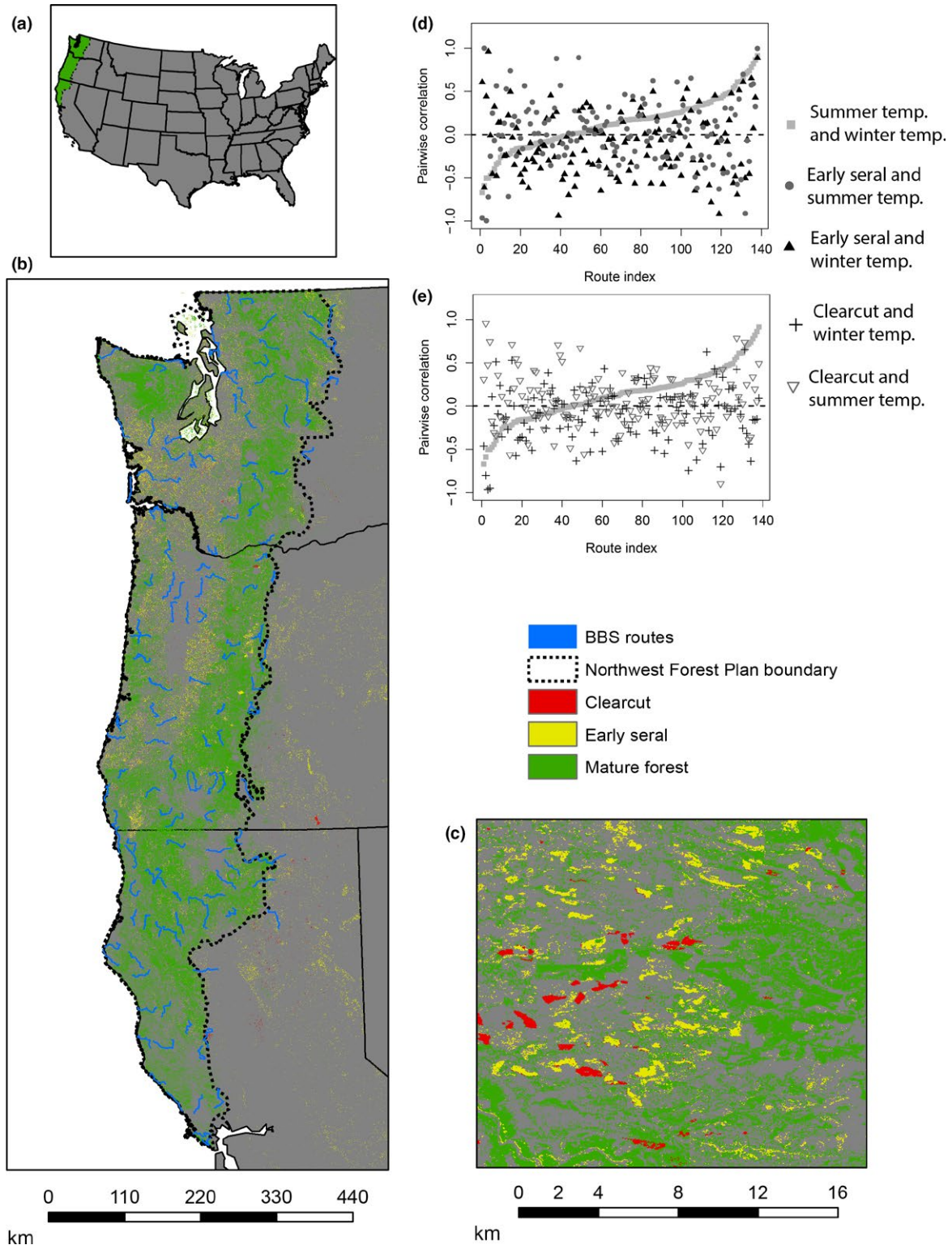


FIGURE 1 (a) Location of study area within the United States. (b) Distribution of landscapes sampled by the Breeding Bird Survey, early seral forest, clearcuts and mature forest for the year 2012 within the boundary of the Northwest Forest Plan. (c) Selected small-scale view of forest mosaic representative of the study region to show the interspersed forest types. (d) Landscape-level pairwise correlations among temperature and early seral forest variables. (e) Landscape-level pairwise correlations among temperature and clearcut variables. In both D and E, pairwise correlations were sorted by the correlation between summer and winter temperature. Panels D and E indicate that although there are correlations among covariates, there is no consistent pattern of correlations across landscapes and covariates, effectively decoupling correlations when analyzed hierarchically. Correlation plots for all other covariates can be found in Appendix 2

We used climate data generated from the Parameter Regression of Independent Slope Model (PRISM Climate Group, Oregon State University, <http://prism.oregonstate.edu>), which has been used to generate historical monthly climate data at 800 m resolution and at a continental extent. Using these data, we calculated the average daily minimum temperature of the coldest month (hereafter minimum winter temperature), the average daily maximum temperature of the warmest month (hereafter maximum summer temperature), the total precipitation in the wettest month (hereafter wet season precipitation) and the total precipitation in the driest month (hereafter dry season precipitation) for each year (1984–2012) within each landscape (these and other similar variables have been used extensively in models of climate change impacts on ecological processes; Booth, 2018, Booth, Nix, Busby, & Hutchinson, 2014, Hijmans, Cameron, Parra, Jones, & Jarvis, 2005).

The dominant land use occurring within our study region over the last 30 years has been timber harvest by clearcut, which has resulted in changes to the extent of mature forest and the conversion of natural forest to timber plantations (Hansen et al., 2013). Therefore, we chose three separate covariates that are linked to timber harvest as measures of habitat loss: (a) the area of clearcuts; (b) the area of mature forest and (c) the area of early seral forest (i.e., early successional forest). To quantify the extent of clearcuts, we used methods for detecting trends in forest disturbance discussed by Kennedy, Yang, and Cohen (2010). This method uses time series of Landsat Thematic Mapper imagery to identify forest changes, including abrupt disturbances, such as clearcuts, that are clearly delineated in a forest landscape. We classified any detected disturbance that lasted <3 years as a clearcut and quantified the proportion of each landscape clearcut in each year. More protracted disturbances are likely to be associated with insect infestations or other activities that are not related to timber harvest and impact the landscape in a different manner. We quantified the distribution of mature forest (forest with characteristics indicative of being >80 years old) using the Gradient Nearest Neighbor method (GNN; Ohmann et al., 2012). The GNN method combines satellite imagery (Landsat Thematic Mapper), mapped environmental data and ground-based vegetation measures from Forest Inventory Analysis plots to predict the composition and structure of vegetation at a 30 m resolution across our entire study area for every year since 1984. We quantified early seral forest for each year within each landscape also using the GNN methods. In addition to timber harvest, changes in forest management practices over the last 30 years have led to major shifts in the distribution of early seral forest. During this time, timber harvest on federal lands declined precipitously as management objectives shifted toward the creation and retention of late seral forest (Adams et al., 2005; Moeur et al., 2011; Spies et al., 2007). Concurrently, private industrial lands have continued to be managed for timber production, often with the use of intensive forest management practices which hastens regeneration (Hayes et al., 2005). Collectively, these management practices have led to a marked reduction in naturally regenerating forests, and a substantial change in the amount and distribution of early seral forest and particularly complex early

seral broadleaf forests (Kennedy & Spies, 2005), a trend that is projected to intensify (Spies et al., 2007). These forests provide food and cover for a range of bird species (Hagar, 2007), and their loss has led to major declines in birds associated with these forest types (Betts et al., 2010).

We note that the BBS was designed to sample a diverse array of landscapes that consequently are comprised of varying amounts of forest. As our primary focus was on forest birds, there is potential bias from treating counts from landscapes with broadly different vegetation types equivalently. To account for differences in bird abundances arising from the amount of forest within landscapes, we derived an additional variable representing the proportion of each landscape that was comprised of land with or capable of supporting >10% tree cover (see <https://lemma.forestry.oregonstate.edu/data/structure-maps> for further details) from the GNN data (Ohmann et al., 2012). Predictions of vegetation measures from the GNN method closely match forest inventory plots at coarser spatial scales (e.g., 10 km²; Ohmann et al., 2012). Thus, we calculated all variables over an area defined by a 1 km buffer on either side of each BBS route (i.e., the roads travelled by observers). This buffer size has been used in past assessments of climate impacts on bird populations using BBS data and results obtained using larger extents are highly correlated with those obtained using 1 km buffers (Gutiérrez Illán et al., 2014).

2.3 | Statistical analysis

We modeled trends in bird populations using a modified version of the hierarchical model described by Sauer and Link (2011). The BBS data have a complex nested structure, with counts within years, within landscapes for individual species. Furthermore, the data have several well-known limitations; counts tend to be overdispersed, observers have different skill levels and can change among years, and some species are more difficult to detect in an observer's first year of surveying (Sauer & Link, 2011). The model described by Sauer and Link (2011) attempts to address these limitations, while simultaneously accounting for the complex and hierarchical structure of the data. The basic form of this model is an overdispersed Poisson regression with a covariate for year, which provides inference to trends in bird abundance within each surveyed landscape. In the hierarchical framework, these landscape-level trends arise from a regional distribution, from which we can make inference to trends across the broader study area (see Appendix 2). Because these models control for, but do not correct observer bias, the models provide inference to an index of abundance, rather than to the true abundance of birds in each landscape. Additional details of this model and a formal model statement are provided in Appendix 2. We fit this model (hereafter the "trend model") to all 94 species in our dataset; thus, our results provide inference on the population trends of each species at the regional scale between 1984 and 2012, while accounting for landscape-scale variance.

To address our primary hypothesis that climate change and habitat loss interact synergistically to drive population abundances

and to control for the influence of landscape characteristics on the effects of climate change and land use, we modified our initial model in several ways (we hereafter refer to this modified model as the “covariate model”). The first modification was to allow for annual counts in each landscape to change as a function of annual measures of climate and land-use variables. This modification provides inference on how changes in climate or land use influence bird population numbers on an annual basis within a landscape (see Figure A2.7 in Appendix 2). Furthermore, to assess statistical interactions, we specified the model such that the landscape-level effect of the climate and land-use covariates depended on the rate of change of land use and climate in each landscape over the entire time series (i.e., we calculated the trend in each climate and land-use covariate over the time period a landscape was sampled and included this as a covariate influencing the landscape-level effect of annual measures of climate and/or land-use covariates; see Appendix 2). Specifically, we assessed whether the annual effect of climate varied across landscapes with different trends in each habitat loss covariate, and whether the annual effect of habitat loss varied across landscapes with different trends in each climate variable. Specifying the model in this manner allowed us to test for interactions between climate and land-use change; for example, whether the effect of annual measures of habitat loss were greater in landscapes that had experienced greater warming compared to those with less warming.

In addition to assessing the interaction between climate and land-use change, we structured the model to control for several landscape characteristics that are expected to influence how species respond to climate and land-use change. Warming is more likely to negatively impact species in areas that are initially warmer, because temperatures are more likely to exceed a species' thermal tolerance in these areas (Hitch & Leberg, 2007). Thus, we modeled the landscape-level effect of each climate covariate as a function of baseline conditions (the average summer or winter temperature or dry season or wet season precipitation over the 10 years prior to our study: 1974–1984). Likewise, there is substantial evidence that species respond most strongly to habitat loss when there is little initial habitat due to the increasing effects of fragmentation (Andren, 1994; Betts et al., 2010; Fahrig, 1998; With & King, 1999). Thus, we modeled the landscape-level effect of each habitat loss covariate as a function of the amount of the corresponding forest type (e.g., mature forest) in the first year of sampling. Lastly, recent research has suggested that old-growth forest can buffer species against climate change at fine scales (Betts, Phalan, Frey, Rousseau, & Yang, 2017; Frey, Hadley, Johnson et al., 2016); thus, we modeled the annual effects of climate as a function of the average amount of mature forest during the entire sampling period. We note that this covariate is somewhat redundant with the model assessing bird response to *annual* measures of mature forest and thus this covariate was excluded for that analysis (see Appendix 2 for more details on this model). We did not account for the potential influence of elevation on species responses to climate

and land-use change. Elevation itself is unlikely to influence bird population dynamics over the range of elevations examined, outside of its influence on climate and vegetation. Importantly, we included measures of baseline climate and land cover, which should be more relevant factors influencing bird response to climate and land use than elevation (see Appendix 3).

We standardized each covariate $\left(\frac{x_i - \bar{x}}{\sigma}\right)$ prior to fitting models, using means and standard deviations calculated across all landscapes and years to ensure that resulting coefficients were directly comparable across species and covariate types. We fit six sets of covariate models, one with each combination of the habitat loss covariates listed above combined with either the precipitation or temperature covariate. Ideally, we would have fit a single model for each species with all climate and forest change covariates; however, such a model would be highly overparameterized and at risk of being overfit. We fit all models in JAGS (Plummer, 2015a) using the “rjags” package (Plummer, 2015b), in the statistical software R (R Core Team, 2015). We ran four Markov Chain Monte Carlo (MCMC) algorithms for each model with random starting values. We ran trend model algorithms for 70,000 iterations, discarding the first 20,000 iterations as burn-in; for the covariate models, we ran algorithms for 150,000 iterations, discarding the first 50,000 as burn-in and thinning the chains to every second iteration. We assessed convergence by calculating the Gelman–Rubin diagnostic (Gelman & Rubin, 1992) and examining trace plots of the posterior distributions of every parameter. Models for three species, Brewer's Blackbird (*Euphagus cyanocephalus*), Evening Grosbeak (*Coccothraustes vespertinus*) and Cliff Swallow (*Petrochelidon pyrrhonota*), did not achieve convergence with 150,000 iterations for several of the covariate models, so we used 900,000 iterations to achieve convergence. We fit the trend model to all species. Because we were interested in the drivers of species declines we only fit the covariate models to those species predicted to be declining with probability of >0.9 between 1984 and 2012, which resulted in 40 species (see below). We assessed the influence of spatial autocorrelation on our models, with details described in Appendix 4.

2.4 | Inference across species

The above models provided inference to individual bird species, but we were also interested in making broader inference to the group of declining forest birds in order to understand the factors causing declines in bird populations. Recently developed statistical approaches provide new avenues for fitting complex hierarchical models in two stages (Hooten, Buderman, Brost, Hanks, & Ivan, 2016; Lunn, Barrett, Sweeting, & Thompson, 2013). In adapting this process to our study, the individual species models are first fit independently, and in a second stage, the posterior distributions of the species-level parameters are used as proposal distributions in a MCMC algorithm to obtain multispecies inference that robustly propagates uncertainty across levels of the model (Lunn et al.,

TABLE 1 Result of second-stage hierarchical models assessing how the interaction between climate (temperature and precipitation) and clearcuts influence forest bird counts between 1984 and 2012 within the boundary of the Northwest Forest Plan in the United States

Covariate	Median coeff.	Prop. <0	Prop.>0
Temperature model			
(a) Summer temperature			
Intercept	-0.01	0.59	0.41
Baseline summer temp	-0.06	1.00	0.00
Clearcut trend	-0.03	0.72	0.28
Mature forest	0.00	0.44	0.56
(b) Winter temperature			
Intercept	-0.02	0.64	0.36
Baseline winter temp	-0.09	1.00	0.00
Clearcut trend	0.04	0.22	0.78
Mature forest	0.04	0.00	1.00
(c) Clearcut			
Intercept	-0.01	0.97	0.03
Baseline clearcut	-0.01	0.93	0.07
Summer temp. trend	-0.01	0.57	0.43
Winter temp. trend	-0.02	0.71	0.29
Mature forest	0.00	0.36	0.64
Precipitation model			
(d) Dry season precipitation			
Intercept	0.01	0.09	0.91
Baseline dry precip	-0.004	0.82	0.19
Clearcut trend	-0.03	0.93	0.07
Mature forest	0.01	0.01	0.99
(e) Wet season precipitation			
Intercept	-0.01	0.76	0.24
Baseline wet precip	-0.02	0.99	0.01
Clearcut trend	-0.07	0.97	0.03
Mature forest	0.01	0.08	0.92
(f) Clearcut			
Intercept	-0.01	0.95	0.05
Baseline clearcut	-0.01	0.78	0.22
Dry precip trend	-0.03	0.92	0.08
Wet precip trend	-0.01	0.55	0.45
Mature forest	-0.004	0.67	0.33

For each submodel (a–f), the intercept indicates the mean effect of the climate or land cover metric (e.g., summer temp. for a) and the median coefficients (coeff.) indicate how variation in the respective covariate (all of which were standardized) influences the mean effect on bird declines. These covariate effects can be interpreted as how the covariate interacts with the respective climate or land cover metric; note, for example, that the effect of summer temperature was contingent on the temperatures measured at the beginning of the study ("baseline summer temp."; a), and that the influence of greater wet season precipitation on bird declines was stronger in areas that experienced increased clearcutting over time (e). Also reported are proportion (prop.) of posteriors <0 or >0, which are indicative of the probability that the effect is negative or positive, respectively. In model fitting, each set of covariates (e.g., intercepts and coefficients for "summer temp.") were estimated separately.

2013). We ran separate second-stage algorithms on each parameter set of interest (see Tables 1–3). We ran the second-stage algorithms for 10 million iterations, discarding the first 100,000 iterations as burn-in and thinning to every 1000th iteration. This modeling approach is similar to averaging the species-specific regional trends, but because of the hierarchical approach, we appropriately propagate the uncertainty across species into our across species estimates, thereby avoiding inappropriate deflation of uncertainty as occurs in simple averaging. These models provide inference at the level of the group of species examined on the influence of climate and land-use change. We ran four MCMC chains and assessed convergence as in the single-species models. The large degree of thinning, and large number of iterations was required, due to excessive autocorrelation in the chains, leading to very slow convergence to the posterior (Hooten et al., 2016). We fit the second-stage covariate model to species that had declined between 1984 and 2012 (i.e., probability of decline based on trend models >0.9).

For certain second-stage models, there was relatively poor mixing of the individual-level parameters, due to high autocorrelation between samples in the MCMC chain. Autocorrelation is a feature of all MCMC approaches due to the iterative nature of sampling, but the degree of autocorrelation can vary and influences the number of samples needed for convergence. In all of these models, the group-level parameters showed good mixing and convergence diagnostics indicated convergence. To test the sensitivity of the group-level parameters to poor individual-level mixing, we refit these models, excluding some species and our results were nearly identical (i.e., small changes in medians and no change in the proportion of posteriors falling on either side of 0).

3 | RESULTS

Our final dataset consisted of 610,620 observations of 94 species over 145 replicate landscapes (i.e., sampled BBS routes) across 29 years. These landscapes spanned a broad gradient of land-use and climate change (Table 4) and a gradient of correlations between land-use and climate change (Figure 1, Appendix 2). Sampling across these gradients and fitting models in a hierarchical framework allowed us to decouple the effects of these two drivers and thus directly assess synergistic effects. Trend models indicated that 64% of forest bird species (60 of 94; Figure 2; individual model outputs can be found in Appendices 1 & 4) showed some evidence of decline between 1984 and 2012 (probability of decline >0.5; Figure 2). Nearly half of all species declined with a high probability (40 species with probability of decline >0.90 compared with only 17 with probability of increase >0.9; Figure 2; Appendix 1) and thus were included in tests of the influence of land-use and climate change on declines. Migratory species comprised the majority of the declining species; 23 species were long- or medium-distance migrants (53% of long- or medium-distance migrants), one exhibiting partial migration (33% of partial-migrants), eight exhibiting short-distance migrations (57% of short-distance migrants) and another eight being nonmigratory (23% of nonmigrants). For all models, there was some degree of positive

TABLE 2 Result of second-stage hierarchical models assessing how the interaction between climate (temperature and precipitation) and early seral forest influence forest bird counts between 1984 and 2012 within the boundary of the Northwest Forest Plan in the United States

Covariate	Median coeff.	Prop. <0	Prop. >0
Temperature model			
(a) Summer temperature			
Intercept	0.00	0.53	0.47
Baseline summer temp	-0.04	0.99	0.01
Early seral trend	-0.01	0.76	0.24
Mature forest	0.01	0.18	0.82
(b) Winter temperature			
Intercept	-0.02	0.69	0.31
Baseline winter temp	-0.07	1.00	0.00
Early seral trend	-0.09	1.00	0.00
Mature forest	0.03	0.00	1.00
(c) Early seral			
Intercept	0.24	0.00	1.00
Baseline early seral	-0.11	1.00	0.00
Summer temp. trend	0.25	0.00	1.00
Winter temp. trend	-0.13	0.97	0.03
Mature forest	0.11	0.01	0.99
Precipitation model			
(d) Dry season precipitation			
Intercept	0.02	0.04	0.96
Baseline dry precip	-0.01	0.93	0.07
Early seral trend	-0.01	0.89	0.11
Mature forest	0.01	0.02	0.98
(e) Wet season precipitation			
Intercept	-0.02	0.99	0.02
Baseline wet precip	-0.01	0.85	0.15
Early seral trend	-0.01	0.91	0.09
Mature forest	0	0.5	0.54
(f) Early seral			
Intercept	0.18	0.01	0.99
Baseline Early seral	-0.17	1	0
Dry precip trend	0.06	0.06	0.94
Wet precip trend	-0.41	0.82	0.18
Mature forest	0.05	0.26	0.74

For each sub-model (a–f), the intercept indicates the mean effect of the climate or land cover metric (e.g., summer temp. for a) and the median coefficients (coeff.) indicate how variation in the respective covariate (all of which were standardized) influences the mean effect on bird declines. These covariate effects can be interpreted as how the covariate interacts with the respective climate or land cover metric; note, for example, that the influence of loss of early seral forest on bird declines was substantially stronger in areas that had experienced increased summer temperatures over time (c) and substantially weaker in areas that had more early seral forest at the onset of the study (“baseline early seral”; c and f). Also reported are proportion (prop.) of posteriors <0 or >0, which are indicative of the probability that the effect is negative or positive, respectively. In model fitting, each set of covariates (e.g., intercepts and coefficients for “summer temp.”) were estimated separately.

spatial autocorrelation in model residuals, however, for most species Moran's I was <0.3 for most years and spatial lags (Appendix 5–11). Furthermore, an assessment of autocorrelation at the level where multiple routes interacted within the model indicated low autocorrelation (Moran's I < 0.2; see Appendix 4 for further details).

Multispecies covariate models indicated that the strongest factor influencing bird abundance across all declining species within the Northwest Forest Plan Boundary was the loss of mature forest, followed by loss of early seral forest (Tables 1–3; Figure 3). Using the results of models fit to temperature and mature forest covariates (as findings were consistent across models fit with different climate covariates), we estimated that on average, a one standard deviation loss of mature forest (18% of a given landscape) equated to a 29% decline in bird population abundances, whereas a one standard deviation loss of early seral forest (~4% of a given landscape) equated to a 21% decline in bird abundance (Tables 2 & 3). Species also declined in response to clearcutting, but to a substantially lesser degree (1% decline in bird abundance with each 1 standard deviation increase in clearcut area; Table 1). Importantly, there were clear synergistic effects of climate change and habitat loss, particularly the loss of early seral forest (Figure 3): the greatest population declines in response to loss of early seral forest occurred in landscapes where summer temperatures increased the most between 1984 and 2012, with negligible declines in those that cooled (Figure 3a). In addition, we documented interactions between loss of both early seral forest and mature forest and winter temperature change. Bird population responses to loss of either forest type was weaker in landscapes where winter temperatures had increased (Figure 3b; Tables 2 & 3; Appendix 12). However, the positive effect of increasing winter temperature was insufficient to offset the effects of habitat loss in both instances (Figure 3, Table 2). Furthermore, we saw relatively strong interactions between dry season precipitation and mature forest, with birds declining the most in response to loss of mature forest in areas that had become drier and declining the least in response to loss of mature forest in areas that had become wetter (Table 3). Although there were several additional interactions between precipitation and land-use change, in all cases either the magnitude of effects was substantially weaker than the effects described above, or uncertainty was high (Tables 1–3). Thus, the above interactions appear to be the dominant ones driving bird population declines.

After accounting for land-use change, climate had variable influence on bird numbers. Importantly, we did not detect an additive effect of temperature change in the absence of habitat loss. However, birds appeared to respond to changes in precipitation, although the magnitude of responses was generally weak; models indicated that bird numbers declined more when there was less dry season precipitation or more wet season precipitation. Although temperature change did not have a strong direct influence on bird abundance across all landscapes, the effect depended strongly on the baseline temperature of the landscape. In warmer landscapes, increases in summer and winter temperatures led to declines in bird numbers, while cooling led to increases (Figure 4; Tables 1–3; Appendix 12). This effect resulted in a switch of population responses to warming from positive, in the

TABLE 3 Result of second-stage hierarchical models assessing how the interaction between climate (temperature and precipitation) and mature forest influence forest bird counts between 1984 and 2012 within the boundary of the Northwest Forest Plan in the United States

Covariate	Median coeff.	Prop. <0	Prop. >0
Temperature model			
(a) Summer temperature			
Intercept	0.01	0.43	0.57
Baseline summer temp	-0.03	0.97	0.03
Mature forest trend	0.00	0.43	0.57
(b) Winter temperature			
Intercept	-0.05	0.90	0.10
Baseline winter temp	-0.08	1.00	0.00
Mature forest trend	-0.02	0.82	0.18
(c) Mature forest			
Intercept	0.35	0.00	1.00
Baseline mature forest	-0.05	1.00	0.00
Summer temp. trend	-0.04	0.73	0.27
Winter temp. trend	-0.21	0.92	0.08
Precipitation model			
(d) Dry season precipitation			
Intercept	0.02	0.01	0.99
Baseline dry precip	0	0.7	0.3
Mature forest trend	0.01	0.06	0.95
(e) Wet season precipitation			
Intercept	-0.02	0.97	0.03
Baseline wet precip	-0.02	0.98	0.02
Mature forest trend	-0.01	0.87	0.13
(f) Mature forest			
Intercept	0.29	0	1
Baseline mature forest	-0.05	1	0
Dry precip trend	-0.15	1	0
Wet precip trend	0.38	0.25	0.75

For each submodel (a–f), the intercept indicates the mean effect of the climate or land cover metric (e.g., summer temp. for A) and the median coefficients (coeff.) indicate how variation in the respective covariate (all of which were standardized) influences the mean effect on bird declines. These covariate effects can be interpreted as how the covariate interacts with the respective climate or land cover metric; note, for example, that the influence of loss of mature forest on bird declines was reduced in areas where winter temperatures had become warmer (c) and in areas with more mature forest at the onset of the study (“baseline mature forest”; c and f), and that the influence of increased wet season precipitation on bird declines was greatest in areas that were wettest at the onset of the study (“baseline wet precip.”; e). Also reported are proportion (prop.) of posteriors <0 or >0, which are indicative of the probability that the effect is negative or positive, respectively. In model fitting, each set of covariates (e.g., intercepts and coefficients for “summer temp.”) were estimated separately.

TABLE 4 Summary statistics for trends in four climate metrics (maximum summer temperature, minimum winter temperature, total dry season precipitation and total wet season precipitation) between 1984 and 2012 within landscapes sampled by the Breeding Bird Survey within the boundaries of the Northwest Forest Plan

Climate metric	Mean annual change	Interquartile range of annual change
Maximum summer temperature	-0.012°C	-0.049–0.032
Minimum winter temperature	0.055°C	-0.006–0.075
Dry season precipitation	0 mm	-0.15–0.003
Wet season precipitation	-3.03 mm	-2.97–0.82

coolest landscapes, to negative, in the warmest landscapes. There were generally similar patterns for precipitation (greater negative responses to a drying climate in landscapes that were driest to begin with), but these effects tended to be characterized by smaller magnitude and greater uncertainty than for the effects of temperature.

In addition to the effects of baseline climate, we found that the effect of loss of both early seral and mature forest was greatest in landscapes with the least habitat at the beginning of the study (Figure 5a, b). When the initial amount of early seral or mature forest cover was higher, bird populations declined less in response to loss of either forest type. However, when the initial proportion of these land cover types was lower, bird populations declined substantially as a result of further forest loss (Figure 5b). Lastly, we detected no strong influence of the amount of old-growth within a landscape on the effect of temperature change, and only weak influence on the effect of precipitation change (Tables 1,2).

4 | DISCUSSION

4.1 | Synergistic effects of climate and land-use change

Our results indicate strong impacts of habitat loss on bird population dynamics, along with synergistic effects of habitat loss and climate change across a wide range of species and landscapes in the Pacific Northwest of the United States. Bird populations declined more rapidly in areas that lost more of both mature and early seral forest. Furthermore, declines in response to loss of early seral forest were accelerated in landscapes that warmed during the summer breeding season, whereas declines in response to loss of mature forest were accelerated in landscapes that had become drier during the dry season. Although previous work has suggested the potential for such synergistic effects, such work typically has used an approach that built distribution models using only short-term “nondynamic” data. That is, population dynamics are not modeled as a direct function of climate and land cover

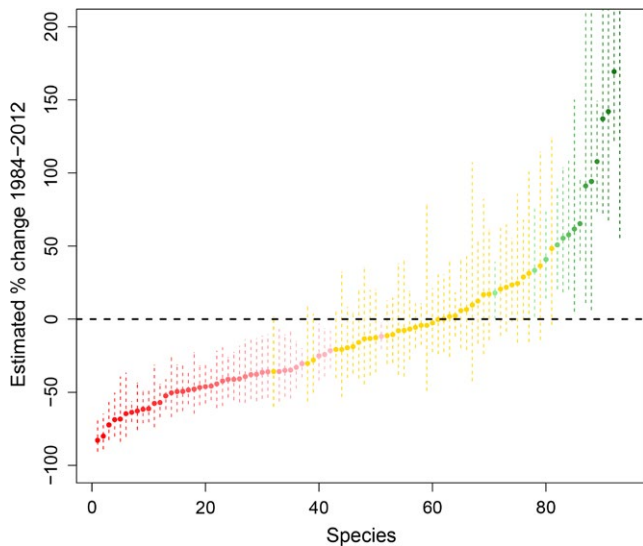


FIGURE 2 Estimated population trends for 94 forest bird species between 1984 and 2012, obtained from Bayesian hierarchical models fit to bird abundance data from the US Breeding Bird Survey. Points represent median estimates and bars span the 90% credible interval. Red shaded data points indicate species with a probability of decline >0.9 , with darker colors indicating greater probability of decline. Green shaded data points indicate species with a probability of increase >0.9 , with darker colors indicating greater probability of increase. Yellow shaded data points indicate species with a probability of decline or increase <0.9 . This figure shows that the majority of species have experienced some decline over the time period studied, with many more having a high probability of decline ($>90\%$) than a high probability of increase

changes, but rather it is assumed that if abundance in a single period is correlated with climate, land cover or their interaction, these features will constitute population drivers into the future (Heubes et al., 2013; Jetz et al., 2007; Vermaat et al., 2017). For instance, recent work suggested the potential for stronger future effects of climate change on species distributions relative to land-use change, (Sohl, 2014), but those findings were based on an assumption of future stationarity between species–environment relationships with changes in climate and land use. Thus, our study provides the first direct evidence of synergistic effects of changes in climate and land use on animal populations *over time*; this is a critical advancement, and our results suggest that projections ignoring synergisms between climate and land-use change likely underestimate negative biodiversity impacts.

Importantly, we did not document a direct effect of annual measures of temperature variables in any model except in landscapes that were initially warm (see below); temperature change, and to a lesser extent precipitation change, acted primarily through their modification of population responses to loss of early seral forest and mature forest, respectively (Figure 3). These findings, along with the strong effects of the initial amount of mature and early seral forest, indicates that habitat loss has been a stronger driver of population dynamics at a regional scale in our system, and provides support for a synergistic effect of these global change drivers (i.e., on average, climate had a relatively weak influence on bird population dynamics in the absence of land-use change). It is important to note that we would likely have misattributed or missed these impacts had we only focused on a single global change driver in isolation, or at fine spatial extents where correlations between climate and land use could not be decoupled.

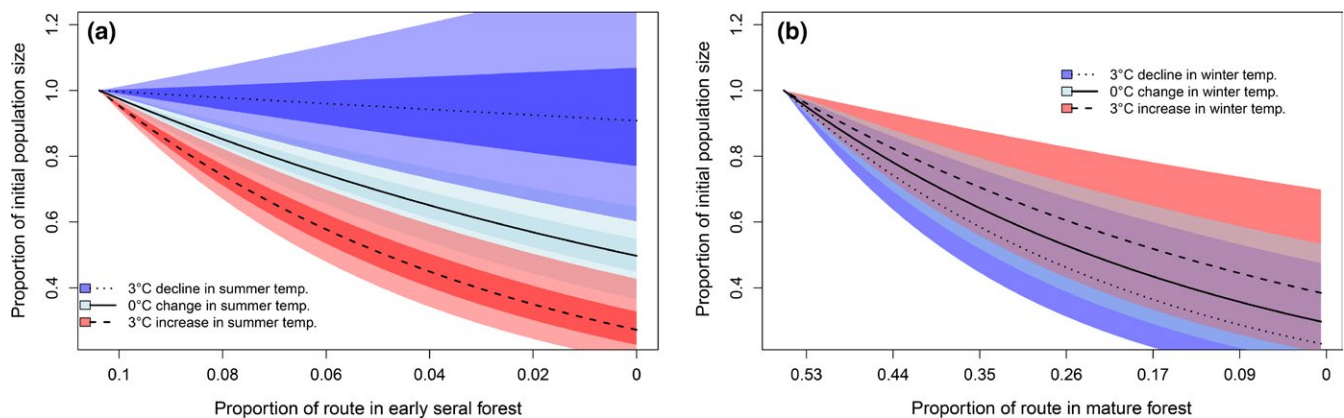


FIGURE 3 Posterior median (black lines), 95% credible intervals (darkly shaded polygons) and interquartile range (lightly shaded polygons) of predicted proportional change in bird numbers as a function of annual proportion of landscapes comprised of (a) early seral forest as related to the change in summer temperature at three different values (approximately the 90th, 50th and 10th percentiles), and (b) mature forest as related to change in winter temperature at three different values (approximately the 90th, 50th and 10th percentiles). Results were derived from second-stage Bayesian hierarchical models fit to species that were estimated to have declined between 1984 and 2012 within landscapes sampled by the Breeding Bird Survey in the Pacific Northwest of the United States. Note that the x-axes are reversed relative to convention to indicate loss of habitat moving from the left to right. Panel A shows the strong influence of warming on the effect of loss of early seral forest, with the strongest response to loss of this forest type in landscapes that had warmed the most. Panel B shows very minor effects of climate on the response to loss of mature forest, with consistently negative effects regardless of climate change within the landscape. [Colour figure can be viewed at wileyonlinelibrary.com]

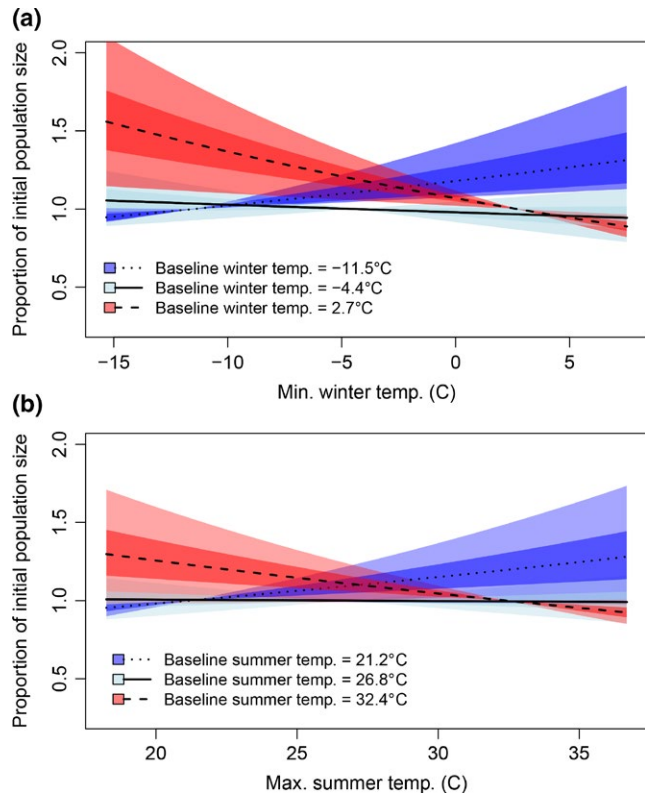


FIGURE 4 Posterior median (black lines), 95% credible intervals (darkly shaded polygons) and interquartile range (lightly shaded polygons) of predicted proportional change in bird numbers as a function of (a) minimum winter temperature at three different baseline values (90th, 50th and 10th percentiles of winter temperature), and (b) maximum summer temperature at three different baseline values (90th, 50th and 10th percentiles of summer temperature). Results were derived from second-stage Bayesian hierarchical models fit to species that were estimated to have declined between 1984 and 2012 within landscapes sampled by the Breeding Bird Survey in the Pacific Northwest of the United States. Values of plotted lines = 1 at the baseline temperature value. Baseline values refer to the average seasonal (i.e., winter or summer) temperature between 1974 and 1984. Note that populations are predicted to increase with warming if initial (i.e., baseline) temperatures along routes were cold, but populations are predicted to decrease with warming if temperatures were initially warm. Populations were predicted to be stable in response to warming at the median baseline temperature. [Colour figure can be viewed at wileyonlinelibrary.com]

The mechanisms underlying the documented declines are likely multifaceted. Large-scale losses of mature forest represent the elimination of intact landscapes, and this had clear effects on a suite of bird species. Reduced precipitation during the dry season could potentially be reducing food availability, thereby exacerbating loss of habitat. In addition, the loss of early seral forest contributed to declines. Many bird species in this region use or require early seral broadleaf forest for both breeding and foraging (Hagar, 2007), and thus its loss directly eliminates habitat for these species. Temperature change could be exacerbating these declines by favoring warm-adapted or generalist species that are better able to adapt to global change than specialists (Clavel,

Julliard, & Devictor, 2011; Julliard, Jiguet, & Couvet, 2004). Such species could be competing with, or preying upon, specialist species and those less well adapted to warmer temperatures, thereby amplifying declines. Climate change has been linked to lower food availability and subsequent declines in both migrant (Both et al., 2009; Møller, Rubolini, & Lehikoinen, 2008) and resident birds (Santisteban, Benkman, Fetz, & Smith, 2012) and it is likely that the responses to winter temperatures and wet season precipitation at least partially reflect influences on food availability. Such effects could be magnified in landscapes that have become more marginal habitat due to loss and fragmentation of various forest types.

Overall, a greater proportion of migratory species were declining than residents, but the response to climate and land-use change of migrants mirrored those of residents (Appendix 13). Thus, there appear to be clear population-level impacts of changes to the breeding habitat of these migratory species. Other factors are likely contributing to declines in these species beyond changes in climate and land-use; such factors could include processes acting during migration (e.g., collisions with manmade structures; Hüppop, Dierschke, Exo, Fredrich, & Hill, 2006, but see Arnold & Zink, 2011) or on their wintering grounds (e.g., Norris, Marra, Kyser, Sherry, & Ratcliffe, 2004; Rushing, Ryder, & Marra, 2016; Woodworth, Wheelwright, Newman, Schaub, & Norris, 2017), or that migrants are less able to adapt to changing phenology (Møller et al., 2008). Because long-term, broad-scale datasets similar to the BBS data are unavailable from the wintering grounds for many species (although eBird holds promise for future investigations; Sullivan et al., 2009), understanding the relative effects of changes on wintering and breeding grounds on migratory species will require either targeted species-specific study or the development of long-term monitoring programs on wintering grounds.

4.2 | Landscape characteristics mediate responses to climate and land-use change

Although overall patterns of bird abundance were most strongly influenced by habitat loss and the synergistic effects of climate change and habitat loss, these responses varied substantially across the BBS landscapes sampled, which has implications for conservation planning. One of the most important factors influencing the response of species to temperature change was the temperature regime of the landscape at the onset of the study (Figure 4): there was a high probability (>0.95) of lower abundance in response to warming if the minimum winter temperature was >1°C or the maximum summer temperature was >34°C. Indeed, shifts in species distributions to higher elevations and poleward due to shifting thermal niches is one of the best-known impacts of climate change (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Hitch & Leberg, 2007; Tingley, Monahan, Beissinger, & Moritz, 2009). Such responses suggest declines in population numbers at the warmer (trailing) edges of a species range (e.g., Franco et al., 2006; Zuckerman, Woods, & Porter, 2009) and the potential that overall bird numbers might not be declining if, for example, more warm-adapted species have replaced more cool-adapted species. However, most species we examined

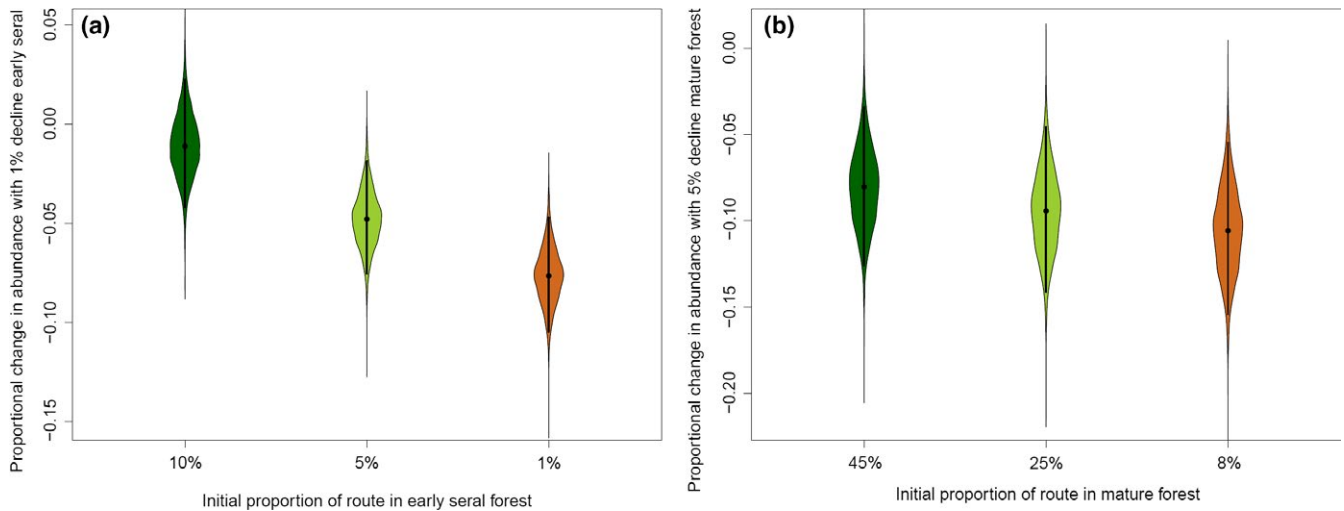


FIGURE 5 Predicted change in bird abundance resulting from a (a) 1% decline in early seral forest, and (b) 5% decline in mature forest at three different values of initial proportion of landscapes comprised of each forest type. Points represent median posterior distribution values, with bars representing 90% credible intervals. The violin plots represent the entire posterior distribution. X-axis values correspond to the mean across all landscapes $\pm 1SD$. Note the x-axes are reversed relative to conventional plots to indicate a loss of habitat moving from the left to the right. Note that the effect of habitat loss is greatest when the amount of early seral (a) or mature (b) forest is lowest at the beginning of the period [Colour figure can be viewed at wileyonlinelibrary.com]

were declining, suggesting that the overarching pattern was a general decline in bird numbers rather than a redistribution of species. Our analytical framework essentially averages population trends over landscapes distributed across elevation and latitudinal gradients; thus, any redistribution of populations via range shifts would more likely have resulted in equivocal findings, rather than the general declines we documented. Our results indicate that the observed declines are likely due to habitat loss—a reality which may also limit the capacity for populations to shift among landscapes.

Our results provide additional evidence that studies focusing solely on quantifying range-wide average population trends might falsely conclude a lack of climate effects when instead strong effects are present, but spatially variable. This finding indicates the complexity of how climate change will impact species across landscapes. Species declined in response to climate change in areas that were already warm or had experienced land-use change, but they appear to have been buffered against climate change in landscapes that were cooler or experienced less land-use change. The resulting lack of an effect of climate change in some areas highlights the notion that even though some landscapes appear resilient to climate change, land-use change can reduce this resiliency.

The amount of habitat at the onset of our study also influenced the response of birds to habitat loss. Bird abundance declined most strongly with habitat loss in areas with reduced early seral or mature forest at the outset of the study, supporting the “extinction threshold” hypothesis (Betts et al., 2010; Fahrig, 1998). Several past studies have suggested that the effects of habitat loss are particularly strong when there is little residual habitat, due to stronger effects of fragmentation (Andren, 1994; Betts, Forbes, & Diamond, 2007; Betts et al., 2010; Fahrig, 1998; With & King, 1999) but see Betts, Wolf et al. (2017). Our results support these findings and suggest

that conservation efforts are likely to be most beneficial if they focus on increasing or conserving habitat in areas with the least residual habitat.

4.3 | Limitations

Our results provide new insights into synergistic impacts of climate and land-use change on bird populations, yet there are limitations to the inferences that can be drawn from the data. First, it is possible that spatial autocorrelation influenced our model results. We investigated this possibility (see Appendix 4), suggesting limited impact at the level of our models where we would expect autocorrelation to be most influential. Methods accounting for spatial autocorrelation in hierarchical models exist (e.g., Johnson, Conn, Hooten, Ray, & Pond, 2013), but they are more complex and computationally intensive than for nonhierarchical models and we are unaware of any study that has applied them to a hierarchical model as complex as that used in our study. Nonetheless, we note that we attempted to fit such models but were unsuccessful because the models did not converge after a nearly one week of running them (see Appendix 5). In light of this computational complexity, an additional option was to simplify our approach to fit models in a nonhierarchical framework but doing so would lead to artificially deflated variance in our estimates, similar to what would result from high residual autocorrelation, subsequently inflating the risk of Type I error. Thus, we note that although our modeling approach is robust to some forms of variance, our inability to fully account for spatial autocorrelation indicates at least the potential for Type I error in our results, although it is uncertain how likely this is based on assessments presented in Appendix 4. We note that the main results discussed above were inferred from effects of large magnitude and high certainty;

therefore, we are confident that autocorrelation did not unduly impact our inference.

We examined different measures of land-use and climate change in multiple models, never including the different measures of land-use or climate (i.e., precipitation and temperature) in the same model. Although this approach does not allow us to assess marginal effects of, for example, early seral forest loss in conjunction with mature forest lost, the relatively small sample of counts within each landscape (i.e., maximum of 29 years) precluded a more highly parameterized model (Harrell, Lee, & Mark, 1996; Peduzzi, Concato, Kemper, Holford, & Feinstein, 1996). Furthermore, despite the high quality and fine resolution of our spatial data, recent work suggests that microclimatic factors (i.e., those at finer scales than can be assessed with satellite imagery) influence bird responses to climate (Betts, Phalan et al., 2017; Frey, Hadley, & Betts, 2016). Thus, other factors that were beyond the scope of our study are likely to have influenced bird population dynamics, but we restricted our focus to the factors we expected to be most influential over our study period. Although these other influences are unlikely to have greater effects than those assessed in this study, they deserve attention as avenues for future research.

Although we assessed the influence of climate and land-use change at a scale of one of the major physiographic regions of the United States, our results are only directly applicable to our specific study region, which is a constraint of any study not conducted at a global scale. If we had expanded our geographic extent we would have greatly sacrificed interpretability and specificity as we would need to develop a single land-use covariate for our entire geographic extent. Thus, we chose our spatial extent so that it was sufficiently broad to not be overly influenced by local nuances, yet fine enough that species-habitat relationships and ecological processes did not vary so much as to obscure any patterns. Lastly, although roadside surveys may not always be representative of regional patterns of bird abundance, climate and land-use change (Betts, Mitchell, Diamond, & Bêty, 2007), in this area, the patterns of climate and land-use change in the BBS landscapes mirrored those of the broader region (also see Veech, Pardieck, & Ziolkowski, 2017).

5 | CONCLUSIONS

Our findings show that the loss of both mature and early seral forests in the Pacific Northwest is associated with marked declines in populations of 40 species of birds, indicating that the maintenance of both forest types is essential for bird conservation in the region. Indeed, existing federal policy is focused around old-growth forest conservation (Thomas et al., 2006) and there have been recent calls for management that increases complex early seral forest on federal lands (Franklin & Johnson, 2012; Swanson et al., 2011). Our results indicate that management activities focused on creating early seral forest would be most beneficial in areas where temperatures have increased the most and the regions that have experienced the greatest early seral loss. Furthermore, actions promoting the maintenance and creation of both early seral and mature forest will be most

beneficial in landscapes where the amounts of these age classes have been most greatly reduced (i.e., in locations that are close to, or have surpassed habitat loss thresholds; see also Phalan et al. 2019), and where summer precipitation is expected to decline. Since the loss of mature forest exerted the greatest negative influence on bird populations, the creation of early seral forest at the expense of mature and old-growth forest in the region would likely exacerbate declines (Phalan et al., 2019). Instead, managers could consider targeting mid-aged forest in the creation of early seral forest. Furthermore, it is important to note that our inference was limited to landscapes with less than ~12% early seral forest area; we expect that there likely exists a threshold above which creation of early seral forest will cease to be beneficial.

Finally, our findings refine contemporary thinking regarding the relative impacts of climate and land-use change. Most recent work on this topic indicates that land use is the primary factor impacting species (Newbold et al., 2015), with climate change poised to become a much stronger driver in the future (Bellard et al., 2012; Lemoine et al., 2007; Sohl, 2014)⁵. Our results highlight that these factors depend strongly on local conditions and that different landscapes will experience impacts from these drivers in different and potentially synergistic ways. Such synergistic impacts may be common globally and, if so, may result in substantial underestimates of biodiversity impacts in certain regions. If broader global patterns follow those documented in our study, such underestimates are likely to occur in the areas where habitat losses are already highest; namely, areas with the most warming and least residual habitat. This possibility raises major concerns for global biodiversity conservation and highlights the need for more comprehensive understanding of how global change drivers interact. Future studies should aim to directly quantify the complex interactions between these drivers to provide more robust and targeted information for the conservation of biodiversity or run the risk of underestimating the impacts of global change.

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AUTHOR CONTRIBUTIONS

JMN, MGB and JWR conceived the study, JMN and ZW conducted analyses, JMN and MGB wrote the paper and all authors contributed to revisions.

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