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RESEARCH ARTICLE

Forest microclimate and composition mediate long-term trends of breeding bird populations

Hankyu Kim[1,2] | Brenda C. McComb[1,3] | Sarah J. K. Frey[1,3] | David M. Bell[4] | Matthew G. Betts[1,3]

[1]Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, Oregon, USA

[2]Department of Forest and Wildlife Ecology, College of Agricultural and Life Sciences, University of Wisconsin-Madison, Madison, Wisconsin, USA

[3]Forest Biodiversity Research Network, College of Forestry, Oregon State University, Corvallis, Oregon, USA

[4]Pacific Northwest Research Station, USDA Forest Service, Corvallis, Oregon, USA

Correspondence
Hankyu Kim, Department of Forest and Wildlife Ecology, College of Agricultural and Life Sciences, University of Wisconsin-Madison, Madison, WI, USA.
Email: hankyu.kim@wisc.edu

Matthew G. Betts, Department of Forest Ecosystems and Society, College of Forestry, Oregon State University, Corvallis, OR, USA.
Email: matthew.betts@oregonstate.edu

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Abstract

Climate change is contributing to biodiversity redistributions and species declines. However, cooler microclimate conditions provided by old-growth forest structures compared with surrounding open or younger forests have been hypothesized to provide thermal refugia for species that are sensitive to climate warming and dampen the negative effects of warming on population trends of animals (i.e., the *microclimate buffering hypothesis*). In addition to thermal refugia, the compositional and structural diversity of old-growth forest vegetation itself may provide resources to species that are less available in forests with simpler structure (i.e., the *insurance hypothesis*). We used 8 years of breeding bird abundance data from a forested watershed, accompanied with sub-canopy temperature data, and ground- and LiDAR-based vegetation data to test these hypotheses and identify factors influencing bird population changes from 2011 to 2018. After accounting for imperfect detection, we found that for 5 of 20 bird species analyzed, abundance trends tended to be less negative or neutral at sites with cooler microclimates, which supports the *microclimate buffering hypothesis*. Negative effects of warming on two species were also reduced in locations with greater forest compositional diversity supporting the *insurance hypothesis*. We provide the first empirical evidence that complex forest structure and vegetation diversity confer microclimatic advantages to some animal populations in the face of climate change. Conservation of old-growth forests, or their characteristics in managed forests, could help slow the negative effects of climate warming on some breeding bird populations via microclimate buffering and possibly insurance effects.

KEYWORDS
biodiversity conservation, climate refugia, forest ecosystem, global warming, H.J. Andrews Experimental Forest, long-term ecological research, old-growth forests, redundancy hypothesis

1 | INTRODUCTION

Recent climate change has elevated global temperatures in past decades and is expected to continue at an unprecedented rate (IPCC, 2021). Climate change is well known to increase extinction risk (Maclean & Wilson, 2011; Román-Palacios & Wiens, 2020). And it is potentially associated with several factors, such as increasing temperatures that can induce thermal stress (Albright et al., 2017; Conradie et al., 2019; McKechnie & Wolf, 2010), changes in species interactions, phenological patterns (Blois et al., 2013; Kharouba et al., 2018; Renner & Zohner, 2018) and population trajectories (Both et al., 2010; Martay et al., 2017).

Although temporal variation in temperatures is usually driven by broad-scale climatic regimes, spatial variation in temperatures is influenced by fine-scale spatial variation in topography and vegetation (De Frenne et al., 2019; Geiger et al., 2009; Wolf et al., 2021). Such fine-scale spatial variation of temperatures that creates microclimate for organisms could provide thermal refugia when broad-scale climate becomes stressful during extreme thermal events (Ashcroft, 2010; Lenoir et al., 2017; Suggitt et al., 2018). Forest vegetation structures are well known to buffer below-canopy temperatures from warmer free air temperatures above or outside of the canopy providing cooler microclimates (De Frenne et al., 2019). The forest structure typical of old growth, such as greater canopy heights, biomass, and vertical vegetation structure, may provide more stable microclimates during the growing season, thereby providing thermal refugia for forest-associated organisms (Frey et al., 2016; Wolf et al., 2021). In the Pacific Northwest of the United States, Betts et al. (2018) suggested that the area of old-growth forest at landscape scales can potentially mitigate the negative effects of warming macroclimates on breeding bird population trends, especially for those species known to be associated with cooler temperatures. They hypothesized that a primary mechanism could be the microclimate buffering effects of old-growth forests.

Unfortunately, long-term, fine-scale microclimate data that is concurrently collected with data on animal populations is extremely rare. Thus, past studies investigating climate change effects on animal populations and distributions have typically used coarse spatial resolution climatic data (800 m–55 km; Fick & Hijmans, 2017; Harris et al., 2014), but individual organisms typically experience microclimate at fine spatial scales (e.g., under forest canopies, in complex topographies; Dobrowski, 2011; Lembrechts et al., 2019). To accurately assess the effects of microclimate on individual animals it is critical to ensure that the spatial scale of the climate data matches the behavior and physiology of the organisms of interest (Ashcroft, 2010; Dobrowski, 2011; Lembrechts et al., 2019).

Increased thermal stress (Conradie et al., 2019; Pollock et al., 2021; van de Ven et al., 2020) and phenological mismatches between peak of food availability and energetic requirements for breeding (Both & Visser, 2001; Jones & Cresswell, 2010; Mayor et al., 2017; Renner & Zohner, 2018) are two well-known stressors for breeding birds under a warming climate. By providing cooler microclimates, old-growth forest structure may have the capacity to dampen population declines of forest birds from climate warming. This *microclimate buffering hypothesis* predicts that population trends of species will be less negative, or even positive, in certain microclimates depending on each species' or populations' physiological limits (Figure 1a). Studies on birds have revealed associations

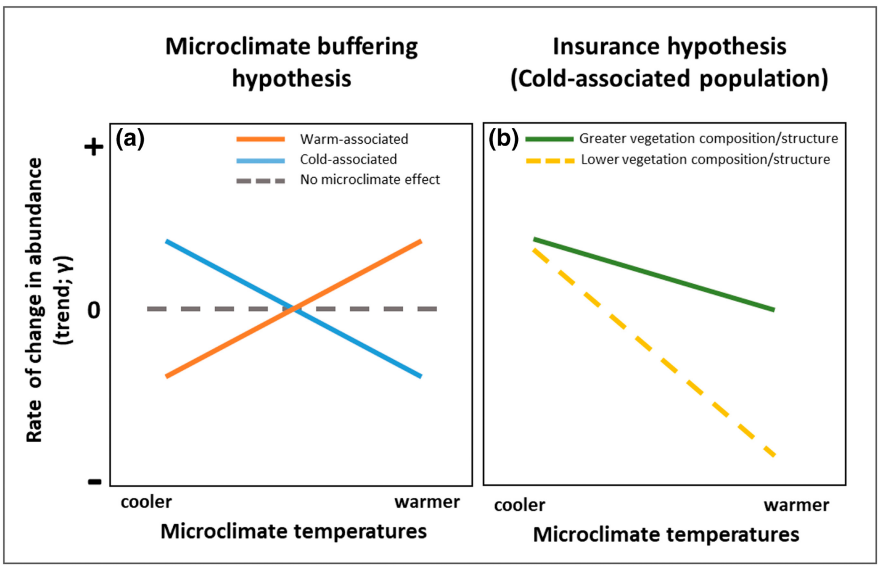

FIGURE 1 Conceptual diagram for (a) microclimate buffering hypothesis and (b) insurance hypothesis. Panel (a) shows that if a population of a species is associated with cooler temperatures, the rate of change in abundance will be lower in the warmer microclimates, and vice versa. Populations with no obvious association with the thermal environment may show no relationship. Panel (b) demonstrates the insurance effect on bird population trends, due to forest vegetation composition and/or structure. We tested hypotheses with simplified linear relationships, but the relationships between microclimate and trends may not be linear in the real world. Species–temperature associations shown here illustrate the potential patterns and we do not assume a-priori which species are cold-or-warm associated in our study.

between microclimatic conditions and species distributions (Champlin et al., 2009; Jähnig et al., 2020; Massimino et al., 2020; Srinivasan et al., 2018). Yet, existing research mostly focuses on the distributions of animals over the short term, and thus are of limited use in testing the degree to which population trends are affected by microclimate.

Among various disturbances on ecosystems from climate change, phenological mismatches between prey availability and peak energy requirements of breeding birds can be caused by differential responses to the global warming among plants, arthropod prey and birds (Renner & Zohner, 2018). If plants leaf out and arthropods emerge earlier in warm microclimates, there is the risk that migratory birds will mistime breeding with the peak of food availability, with negative fitness consequences (Both et al., 2006; Renner & Zohner, 2018). Because leaf-out phenology varies by plant species (Ward et al., 2018), forests with higher plant diversity often have a protracted period of insect availability (Shutt et al., 2019). Additionally, complex forest structure can support a more diverse arthropod prey community than simple-structured forests (Halaj et al., 1998; Schowalter, 1995, 2011; Yi & Moldenke, 2005). Old-growth forests in the Pacific Northwest of the United States also typically have higher compositional (species and other resource components such as coarse woody debris and snags) and structural diversity than young, managed forests (Franklin et al., 2018; Franklin & Spies, 1991; Halpern & Spies, 1995). Together, these diversified resources can potentially provide a broader temporal window of food availability during the peak of energy need for the breeding bird when climate-change driven disturbance occurs (Figure 1b). Forest microclimate can influence food resources, such that food resources may be less abundant in areas with warm microclimates. However, under the biodiversity insurance hypothesis (Loreau et al., 2003; Naeem & Li, 1997; Yachi & Loreau, 1999), structurally and compositionally diverse forests could provide wider a window of food availability under warming conditions, and offset the negative effects warming on bird abundances (Figure 1b). This *insurance hypothesis* has been extensively tested and synthesized (Balvanera et al., 2006; Loreau & Mazancourt, 2013); however, most studies have used small-scale field experiments or in vitro experiments on aquatic organisms, terrestrial invertebrates and plants (Pires et al., 2018), rather than on free-ranging terrestrial taxa such as birds (but see; Catano et al., 2020).

Using long-term bird population data from the Oregon Cascade Mountains, we investigated whether old-growth forests can mitigate climate-change effects on breeding bird populations by (a) buffering breeding season microclimates (Figure 1a) and/or (b) providing insurance as a result of structural and/or compositional diversity when there are negative effects of microclimate conditions (Figure 1b). Under the insurance hypothesis, we predicted that forests with either higher compositional or structural diversity would be less likely to exhibit negative bird population trends under warming conditions than forests that are simpler in composition and structure. These hypotheses are not mutually exclusive, but our methods and data enabled us to test independent effects of each hypothesis on long-term bird population trends.

2 | MATERIALS AND METHODS

2.1 | Study area

This study took place at H.J. Andrews Experimental Forest (HJA) (44.23°N, 122.188°W) in the Western Cascade Mountains of Oregon, USA (Figure 2a). The HJA (6400 ha) is dominated by Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) at the lower elevations, and Pacific silver fir (*Abies amabilis*), noble fir (*Abies procera*) and mountain hemlock (*Tsuga mertensiana*) at the higher elevations. Red alder (*Alnus rubra*), bigleaf maple (*Acer macrophyllum*) and black cottonwood (*Populus trichocarpa*) occur most frequently in the valley bottoms. Elevation ranges from 407 to 1632 m (Figure 2b). About a quarter of the HJA forest consists of stands that were harvested and replanted with Douglas-fir approximately 25–70 years ago; the remaining 75% is old-growth where no or minimal forest management (harvesting or thinning) has occurred (Bell et al., 2017; Lienkaemper & H. J. Andrews LTER, 2015; Figure 2c–e). Second-growth forests in our study area are now closed-canopy coniferous forest, and some have experienced minor disturbance events (e.g., ice damage, windthrow, experimental thinning) resulting in shrubs and additional tree species growing intermixed with Douglas-fir. Annual precipitation ranges from 1660 to 2810 mm and occurs mostly from November to March. We selected bird and microclimate sampling locations (points; $n = 184$) using a hybrid systematic and stratified sampling design (Figure 2b,c; see Frey et al., 2016 for details). We stratified points across gradients in elevation (460–1558 m; see Figure S6), vegetation structure (45–50 year-old plantations, $n = 66$; primary forest, $n = 118$) and distance from roads (points on the routes on roadside, $n = 60$; off-road transects, $n = 124$). Some locations in the landscape were impossible to access safely due to extreme topography so were excluded from sampling.

2.2 | Bird, microclimate, vegetation, and topography data

From 2009 to 2018 we conducted 10-min avian point count surveys between 5:00 and 10:30 a.m. at 184 points during the breeding season from May to July (Figure 2b). Surveyors visited each point at least once per year; up to six times from 2009 to 2013 and 1–4 times from 2014 to 2018. We grouped adjacent points into routes that consisted of 8–15 points, and randomly assigned observers to each route. Routes were surveyed in random order for each replication of the annual survey. To reduce potential biases due to observers and time of day, routes were visited in reverse order on every other visit. Prior to data collection, we provided 2–6 weeks of training on bird identification, distance estimation, and survey protocol to all observers. During the counts, observers recorded all birds heard and seen. Observers recorded bird species, sex (male, female, unknown), type of detection (song, call, visual, drumming), estimated distance in three distance bins (<50, 50–100, and >100 m), and time of detection

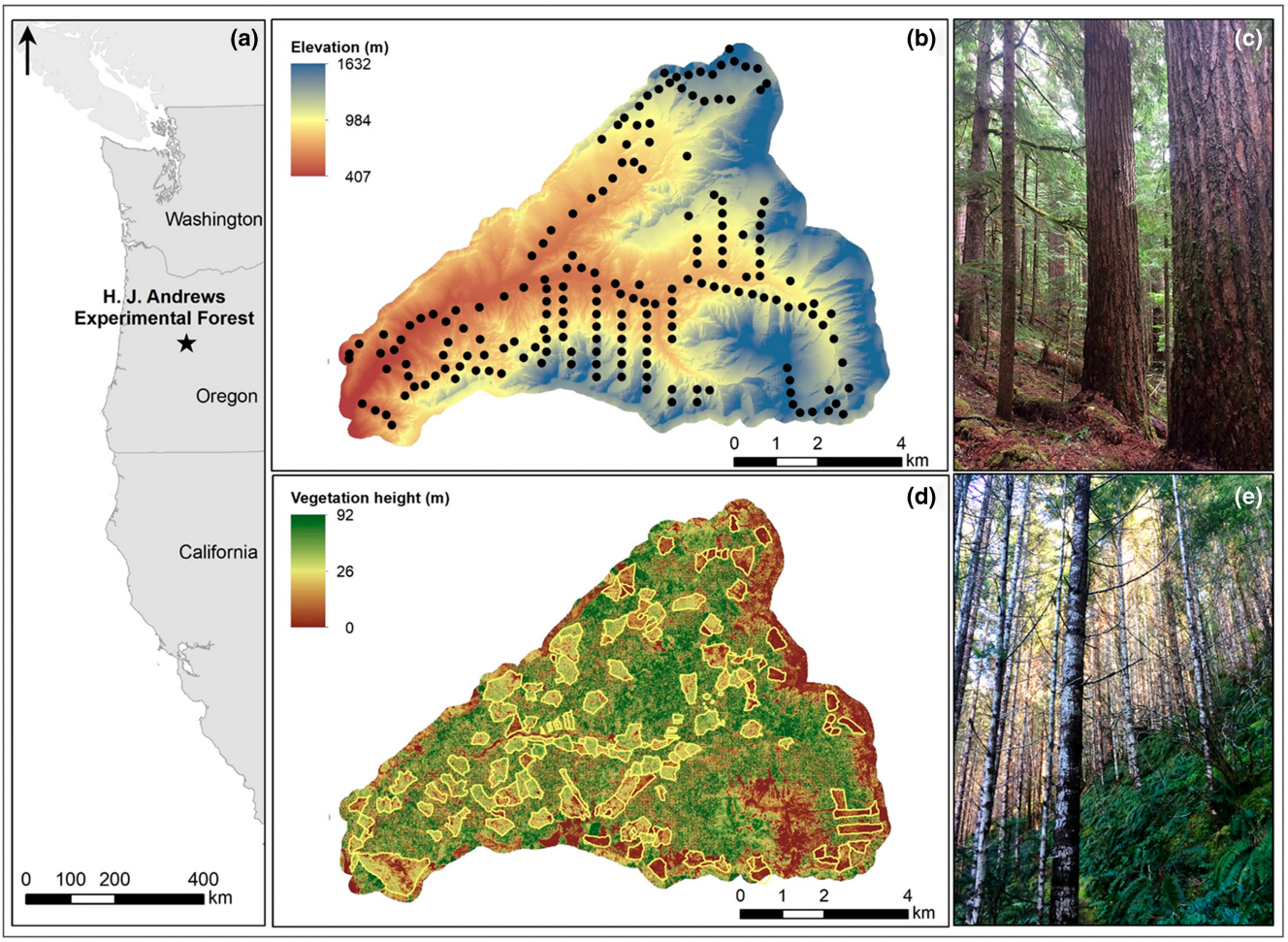

FIGURE 2 Study area map and photographs of typical vegetation in the study area. (a) Location of the study area, H.J. Andrews Experimental Forest in Oregon. (b) Sampling locations (points; black circles) and altitudinal gradient of the watershed. (c) Vegetation height and stands with harvest history (yellow boundaries). (d) Typical old-growth Douglas-fir-Western hemlock forest and (e) Douglas-fir second-growth plantation in H.J. Andrews Experimental Forest.

for each detection event to the nearest minute. For each point count survey, we recorded observation-level covariates; weather (0–7, clear sky without cloud to pouring rain and snow), start time, wind speed (0–7, Beaufort Scale), stream noise (0–7, from absolute silence to noise that prohibits hearing anything close by), date, and snow cover. We ceased avian point count surveys during heavy rain or windy conditions that interfered with bird singing behavior, observers' ability to detect birds, and the safety of observers.

At each point count station, we deployed a HOBO Pendant® Temperature/Light Data Logger (Onset Computer Corporation) at 1.5 m above the ground facing south, with a radiation shield made with halved white PVC pipe (see Frey et al., 2016 for details). We set data loggers to record temperature every 20 min. We filtered and removed temperature data to exclude erroneous readings and readings from periods when the loggers were under snow. Data from 1 to 4 loggers each year were lost due to animal damage or malfunction and those data were imputed from the remaining data (Wolf et al., 2021).

In 2018, we sampled vegetation composition and structure at each point count station. We established 25-m diameter vegetation plots, such that the centroid of each plot was 5 m from the point count station in a random direction. Understory woody vegetation species and cover were measured in each circular plot. We split the circular plot into quarters and measured cover of vegetation 0–2 m in height within each subplot. Each species' vegetation cover was measured as area covered by a plant species from above. Observers were trained for visual estimation of vegetation cover in the unit of 1.2-m^2 squares (approximately 1% of each sub-plot) using folding rulers. Some shrubs of different species were overlapping each other slightly and measured separately; hence some plots had shrub covers that can exceed 100%. Standing live and dead trees were sampled using a 10-factor wedge prism (English unit) from the center of each vegetation plot (variable radius plot or point sampling Burkhart et al., 2019). This method tallies trees that are counted through the prism, which are calibrated to refract light so that the only trees counted are in certain size classes within a certain distance that can be interpreted as a basal area of 2.296 m^2/ha. We measured each live and dead trees >6 cm in diameter at breast height (DBH), and calculated tree species richness, average tree DBH, the coefficient of variation (CV) in DBH, and basal area of trees around the center point of each plot. In addition, we measured diameter and length of

logs and aboveground stumps >6 cm in diameter at one end within the vegetation plot and used these measurements to calculate total volume of the coarse woody debris (m^3) per plot. We used the highest hit surface model and elevation surface model from a LiDAR flight in 2016 (Oregon Lidar Consortium, 2016) to extract canopy cover above 12 m (Parker & Brown, 2000; Shaw et al., 2002), maximum tree height, canopy height CV, and average canopy height from 100 m-radius plots centered on each bird point count point. We estimated elevation using a digital elevation model from the same LiDAR flight (Oregon Lidar Consortium, 2016). We extracted LiDAR-based forest characteristics from each plot, using the r package 'raster'. The LiDAR flight collected data between May 28 and June 21 in 2016, using a Leica ALS80 sensor and yielded >8 points per square meters (Oregon Lidar Consortium, 2016).

2.3 | Data processing and selection of metrics

We included all birds that were detected by sight or sound within a 50-m radius of count points across four surveys per year. Only species with >2% of visits across all 184 points were included, resulting in a total of 23 species. We summarized temperature data from data loggers into monthly averages of daily mean, maximum and minimum temperatures for May and June. We used May and June temperatures to reflect the period when birds are present during the breeding season, which also overlaps with the timing of vegetation growth of most trees and shrubs in the study area (Ward et al., 2018). We then combined mean monthly daily temperatures for May and June into a single variable per each year and site using a principal component analysis (PCA) with the first axis (75.56% of the total variability explained) as a composite index of breeding season climate (tempPC1; Figure S1; Table S1). The use of principal components enabled a more parsimonious approach to testing the effects of climate on annual abundance changes; this subverted the need to fit multiple individual climate variables as covariates in separate models which could inflate the risk of type 1 error. This index represents under-canopy breeding season microclimate variation across the sampling sites in the watershed and across multiple years. We also used PCA to reduce multidimensional forest vegetation characteristics into two main indices. Variables in this PCA comprised: understory woody species richness, understory woody species cover (summed over all woody species), tree species richness, total woody species richness, total live tree basal area, snag basal area, deciduous tree basal area, average DBH, DBH CV, coarse woody debris volume per hectare, maximum tree height, average canopy height, canopy height CV, and canopy cover (Table S2). We reduced these vegetation metrics from LiDAR-driven models and ground vegetation surveys to two dimensions on the first and second principal component axis (vegPC1 and vegPC2; Table S2). The first principal component, vegPC1, explained 28.05% of the total variance and was positively related to forests with tall trees, with greater canopy cover and trees with greater DBH on average, and less understory shrub species richness and cover (Figure 3). The second principal component, vegPC2 explained 16.63% of the total variation, and was negatively related to tree species richness, snag basal area, canopy height CV and average DBH, while positively related to deciduous tree species basal area and canopy cover (Figure 3). For both microclimate and vegetation data, we used the PCA approach to reduce dimensions of the complex nature of both variables, while capturing the variation of those across the space and time (microclimate only) of the sampling points in our study and maintaining interpretability of those composite indices using eigenvectors. It has been argued that principal components can be difficult to interpret biologically but is an important and commonly used approach in ecology (Jollife & Cadima, 2016). Nevertheless, as an additional test, we standardized and summed seven variables that reflected forest composition (understory plant richness, total plant richness, tree richness, variation in DBH, total basal area of snags, total volume of coarse woody debris on ground, variation in canopy height) and seven variables, representing structural measures (canopy cover, mean canopy height, maximum tree height, total basal area, average DBH, variation in DBH, variation in canopy height). We then replaced our principal component variable for vegetation composition and structure with these variables; results were qualitatively similar to the analysis using principal component–driven covariates (Figure S8; Table S4). Although forest structure is an important driver of microclimate in our system (Frey et al., 2016; Wolf et al., 2021), elevation and microtopography also exert considerable influences on microclimate. This lack of strong correlation between forest structure variable (vegPC1) and temperatures across all of our sites ($r = -.079$, across all years) enabled us to test the independent effects of forest structure and microclimates on bird population trends. Finally, we extracted the elevation of each sampling location from the digital elevation model based on the 2016 LiDAR data.

2.4 | Modeling population abundance dynamics and its drivers with N-mixture models

We used a modified Dail–Madsen model (dynamic N-mixture model) for modeling population trends as a rate of change in abundance, while accounting for imperfect detection of individual birds (Dail & Madsen, 2011). Dynamic N-mixture models estimate initial abundance of a population, detection probability and their dynamic processes in the subsequent primary periods in a multi-level hierarchical model structure (specific model structure in our study is described below).

In our study, the initial abundance was modeled as Poisson or zero-inflated Poisson (ZIP) distribution of expected value (latent variable) of initial abundance λ_i at each i site for the first period:

$$N_{i,1} \sim \text{Poisson}\left(\lambda_i\right),$$

$$N_{i,1} \sim \text{ZIP}\left(\lambda_i\right).$$

And the observation process:

$$C_{i,j,t} \sim \text{Binomial}\left(N_{i,t}, p\right).$$

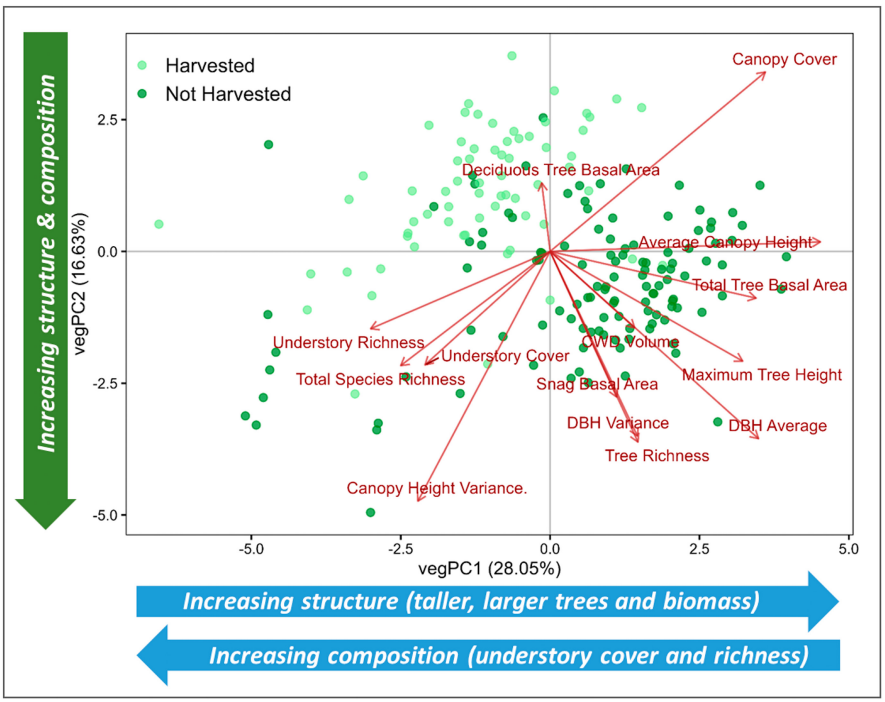

FIGURE 3 PCA bi-plot for principal component 1 and principal component 2. Distribution of sample plots on the first and second principal component axes (dots), showing plots located in stands with harvest history (light green) and no harvest history (old-growth; dark green). Vegetation variable loadings for each covariate on the two principal component scores (vegPC1, vegPC2) are shown as vectors with labels. Note that higher vegPC1 is positively related to higher average canopy height, total tree basal area, maximum tree height, average diameter at breast height (DBH) and canopy cover. On the contrary, lower vegPC1 is positively related to higher understory plant richness, cover and total species richness. On the second axis, higher vegPC2 is related to higher canopy cover and low canopy height variation, and basal area of deciduous tree species. Deciduous tree species basal area was not related to total tree basal area, as they are relatively rare in our coniferous forest. Lower vegPC2 is positively related to understory, tree and total species richness, snag basal area and coarse woody debris (CWD) volume, and high variation in canopy height.

Count (observation; *C*) of number of birds at given site *i*, on primary period (year) *t*, and secondary period (replicated visits) *j* has a binomial probability for the abundance of birds at a site at a given year, for the detection probability *p*.

As our interest was to directly assess trend and drivers of trend, we estimated annual rates of change (trend; γ) across the years (2011–2018).

$$N_{i,t} = N_{i,t-1} \times \gamma.$$

We used a maximum likelihood approach to estimate these model parameters (λ, p, γ) under this hierarchical model structure in our study.

Detection probability *p* was modeled as a function of observation-level covariates (stream noise, time of survey, day of year of the survey, wind speed, weather, and a quadratic term for the day of year of the survey; detection probability sub-model).

$$\begin{aligned}\text{logit}(p) = {} & \beta_0 + \beta_1 \times \text{stream} + \beta_2 \times \text{noise} + \beta_3 \times \text{time of survey} \\ & + \beta_3 \times \text{wind speed} + \beta_5 \times \text{day of year} + \beta_6 \times \text{day of year}^2.\end{aligned}$$

And the initial latent abundance (λ) was modeled as a function of vegPC1, vegPC2, elevation, and the quadratic term of elevation (initial abundance sub-model).

$$\begin{aligned}\log(\lambda) = {} & \beta_7 + \beta_8 \times \text{vegPC1} + \beta_9 \times \text{vegPC2} \\ & + \beta_{10} \times \text{elevation} + \beta_{11} \times \text{elevation}^2.\end{aligned}$$

Lastly, the annual rate of change (trend sub-model) in bird abundance was modeled as a function of microclimate, vegPC1, vegPC2, and two-way interactions between microclimate and each vegetation variable.

$$\begin{aligned}\log(\gamma) = {} & \beta_{12} + \beta_{13} \times \text{vegPC1} + \beta_{14} \times \text{vegPC2} + \beta_{15} \times \text{microclimate} \\ & + \beta_{16} \times \text{vegPC2} \times \text{microclimate} + \beta_{17} \times \text{vegPC1} \times \text{microclimate}\end{aligned}$$

The *microclimate buffering hypothesis* predicts that ambient microclimate indices should affect the rate of change in bird abundance (trend; γ); for the population of a species in the study area that have negative associations to warmer breeding season temperatures, warmer microclimates should show the greatest abundance declines, but cooler 'microrefugia' sites should show reduced or no declines (Figure 1a). The *insurance hypothesis* predicts that vegetation indices would mediate the effect of microclimate on the rate of change in bird abundances (Figure 1b). Both vegPC1 and vegPC2 are associated with compositional and structural diversity of the forest vegetation (Figure 3), so if trends in species' populations are a function of the interaction between either of these vegetation indices (vegPC1, vegPC2) and microclimate (tempPC1) then we would detect support for the *insurance hypothesis*. To test if our covariates explain variations in population trends of birds, and thus support our hypotheses, we used likelihood ratio tests between the null model

(intercept-only trend sub-model and detection and initial abundance sub-model with all covariates) and the hypothesis model (model with all covariates as described above in all sub-models) for each species to test our hypotheses. We used a significance level of 0.1 as a criterion for statistical support, to reduce the potential risk of type 2 error.

We first selected the appropriate mixing statistical distribution for abundance (Poisson or ZIP distributions) using Akaike's information criteria. Then we checked for model identifiability, by comparing the negative log-likelihood as the *K* increases toward 400. *K* is a nuisance parameter that sets the maximum value set for estimating abundance in maximum likelihood space, to make the fitting process efficient (Kéry & Royle, 2020). To reduce computation time and ensure that the fitted models were within the boundary of parameter space, we chose the lowest value of *K* that showed a stabilized minimum negative log-likelihood (Kéry, 2018; Kéry & Royle, 2020). To choose the distribution for abundance and *K* values, we set covariates for initial abundance and detection probability models as above, but we used an intercept-only model for the trend sub-model. Among the 23 selected species, we were able to identify 20 species' models for which log-likelihood and initial abundance estimates converged as *K* increased to 400 (Figures S2 and S3, Table 1).

3 | RESULTS

Seven of 20 species declined over the 8-year study, while nine species increased; we did not detect trends for four species (Figure 4). We found support for either the *microclimate buffering* or the *insurance* effect for six species (likelihood ratio test $p < .1$; Table 1, species shown in Figure 5). Trends of abundance of the five species declined at greater rates in warmer locations than in cooler areas, while one species among the six showed abundance increases in relatively warm locations (Figure 5). These findings indicate that microclimates within forested landscapes do provide refugia for these species. Among these six species, for Wilson's warbler (*Cardellina pusilla*), red crossbill (*Loxia curvirostra*), hermit warbler (*Setophaga occidentalis*), and chestnut-backed chickadee's (*Poecile rufescens*) average conditions across the watershed were associated with declining population trends. Two other species, varied thrush (*Ixoreus naevius*) and Swainson's thrush (*Catharus ustulatus*) increased. Varied thrush abundance increased in the study site, and this species' trend was positively related to warmer microclimates.

We only found statistical support for the *insurance hypothesis* in two species, Wilson's warbler and red crossbill (Figure 5). For these two species, higher compositional diversity (lower vegPC2, Figure 3) reduced the negative effects of warmer microclimates on the abundance trends (Figure 5).

Few species showed evidence for additive main effect of vegetation (either vegPC1 or vegPC2). Swainson's thrush, red crossbill, and varied thrush had more positive trends in areas with higher structural complexity (higher vegPC1). Wilson's warbler trends were negatively related to greater vegPC2 index, with less diversity in plants and canopy height (Figure 5). Detection probability, initial abundance and trend estimates and their covariate coefficient estimates are provided in Figures S4–S6. Golden-crowned kinglet, chestnut-backed chickadee, hermit warbler, pacific-slope flycatcher and dark-eyed junco were the five most abundant species in the first year (2011), followed by Swainson's thrush, Pacific wren and brown creeper (Figure S4).

TABLE 1 Likelihood ratio test results for dynamic N-mixture models for each species. Rows in bold indicate that there was at least one predictor with statistical support, suggesting evidence for either microclimate or insurance effects (i.e., "alternate model"). Degrees of freedom for obtaining *p*-values in chi-squared distribution is five for all models. Model coefficients and confidence intervals are reported in Figure 5, and S4–S6

	Log-likelihoods			
Species (4-letter code)	Alternate model	Null model	χ^2	*p*
Dark-eyed Junco (DEJU)	1624.001	1626.710	5.419	.367
Hermit Thrush (HETH)	1023.926	1026.577	5.302	.380
McGillivray's Warbler (MGWA)	429.041	433.039	7.996	.156
Pacific-slope Flycatcher (PSFL)	2614.799	2618.604	7.609	.179
Swainson's Thrush (SWTH)	**2149.351**	**2157.229**	**15.756**	**.008**
Brown Creeper (BRCR)	1449.444	1451.532	4.177	.524
Black-throated Gray Warbler (BTYW)	406.988	408.443	2.911	.714
Chestnut-backed Chickadee (CBCH)	**3100.569**	**3112.302**	**23.467**	**.000**
Golden-crowned Kinglet (GCKI)	2185.889	2188.837	5.897	.316
Hammond's Flycatcher (HAFL)	1079.661	1082.645	5.969	.309
Hairy Woodpecker (HAWO)	616.140	617.267	2.253	.813
Hermit Warbler (HEWA)	**2657.323**	**2667.529**	**20.413**	**.001**
Pacific Wren (PAWR)	2354.839	2359.178	8.679	.123
Red-breasted Nuthatch (RBNU)	1412.863	1415.516	5.306	.380
Red-breasted Sapsucker (RBSA)	394.573	397.677	6.208	.287
Red Crossbill (RECR)	**1131.424**	**1185.751**	**108.655**	**.000**
Varied Thrush (VATH)	**814.967**	**819.632**	**9.331**	**.097**
Western Tanager (WETA)	484.902	488.083	6.360	.273
Wilson's Warbler (WIWA)	**582.306**	**588.793**	**12.974**	**.024**
Yellow-rumped Warbler (YRWA)	315.669	317.555	3.773	.583

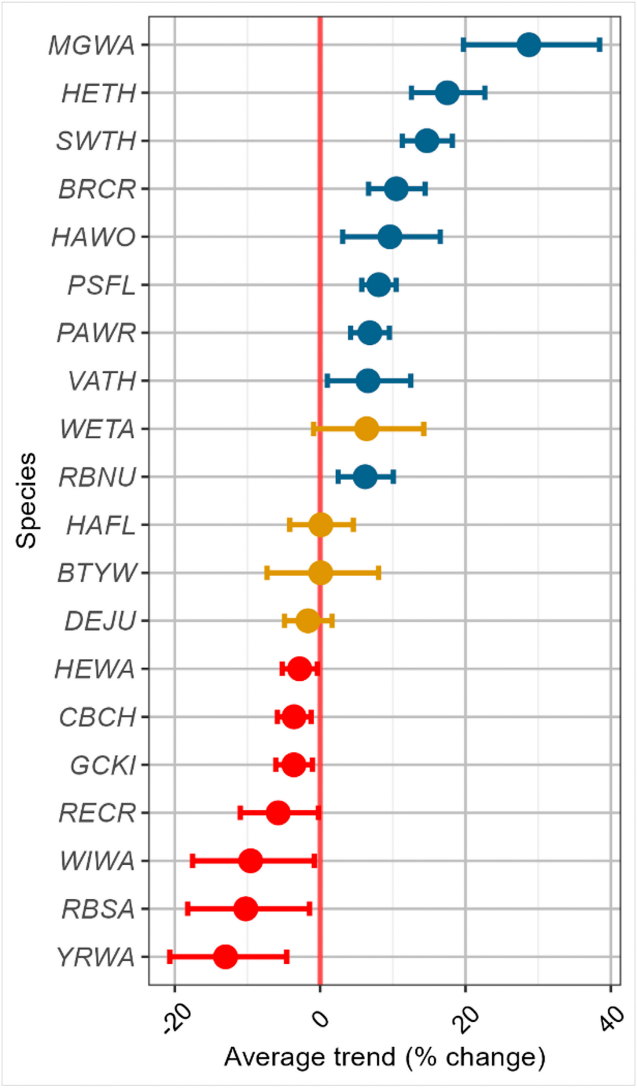

FIGURE 4 Average population trend (% change in abundance) of 20 species between 2011–2018. Please see Table 1 for the alphabetical codes for the species names.

4 | DISCUSSION

Microclimates are critical for understanding how biodiversity responds to macroclimatic change but are still often overlooked when it comes to understanding and predicting biotic responses to global change (Zellweger et al. 2020). We used a long-term empirical microclimate dataset paired with concurrent bird population surveys to test whether microclimatic refugia—conferred by topography and old-growth structure—has the potential to buffer populations from climate change. We found support for microclimate buffering hypothesis for 6 out of 20 species. In particular, declining species that are sensitive to warm conditions (Wilson's warbler, hermit warbler, chestnut-backed chickadee) seemed to benefit the most from such refugia effects. In addition, old and diverse forests seem to further contribute to less negative or even neutral population trends for some species.

Overall, we found that populations of seven species declined over our eight-year study, in comparison with nine that exhibited increases, and four with no detectable trend (Figure 4). These local population trends are consistent with regional population trends in Oregon for yellow-rumped warblers (*Setophaga coronata*), Wilson's warblers, golden-crowned kinglets, and hermit warblers, based on Breeding Bird Survey data (1993–2019; Sauer et al., 2020). Among the declining species, hermit warbler, golden-crowned kinglet and chestnut-backed chickadee are some of the most common songbird species in the watershed (31% of total individual detections in this study, combined). Considering their prevalence and their ecological function as secondary consumers, declines in these common taxa are potentially concerning for maintaining ecological functions and providing ecological services (e.g., insect regulation; Campbell et al., 1983; Harris et al., 2020).

Importantly, rates of bird population declines were not evenly distributed across the microclimate gradient in the watershed. Population trends of five species were strongly negatively related to warmer microclimates (Figure 5), supporting the *microclimate buffering hypothesis* (Figure 1a). For these five species, population trends were more negative in warmer locations, while negative population trends were dampened in cool microclimates (Figure 5). During the breeding season, below-canopy microclimates tend to be much cooler in old-growth forests (up to 2.5°C; Frey et al., 2016), at higher elevations, and in locations with concave micro-topographies (Frey et al., 2016; Rupp et al., 2020; Wolf et al., 2021). Consequently, our results support the idea that forests with complex structure and composition could buffer negative effects of warming—particularly if they are located at high elevations and in complex terrain.

If the relationship between species' trends and microclimate are due to species' innate physiological limits, rather than driven by ecological processes such as food availability and migration timing, it may be worth noting that some of these species' geographical range distributions (Swainson's Thrush, Red Crossbill, Wilson's Warbler, Chestnut-backed Chickadee) are positioned northward relative to the study site. However, Varied Thrush's (which seemed to increase in abundance in warming sites) has a breeding range that is much further north to Alaska, and our study site is in the southern portion of its range. Whether such variation is due to stronger interaction effects between local climate and ecological interactions, or variations in physiological limits among local sub-populations needs further investigation (Ralston et al., 2016; Williams et al., 2022).

The positive response to warmer microclimates of varied thrush was somewhat unexpected, as our study site is on the southern portion of the species' entire breeding range. Given their ground-foraging behavior and short distance migration, we could hypothesize that these species may be benefited by early snow-free ground conditions in these warmer patches and colonize these openings more quickly than other ground foragers that migrate from longer distances. Future research on phenology of snow melt, plants, and avian response could help to disentange these relationships.

Although bird community composition is broadly similar between old-growth and old plantations of our study landscape (Figure S7), we acknowledge that habitat quality differences could exist between these types. Because plantations and old-growth stands are spatially

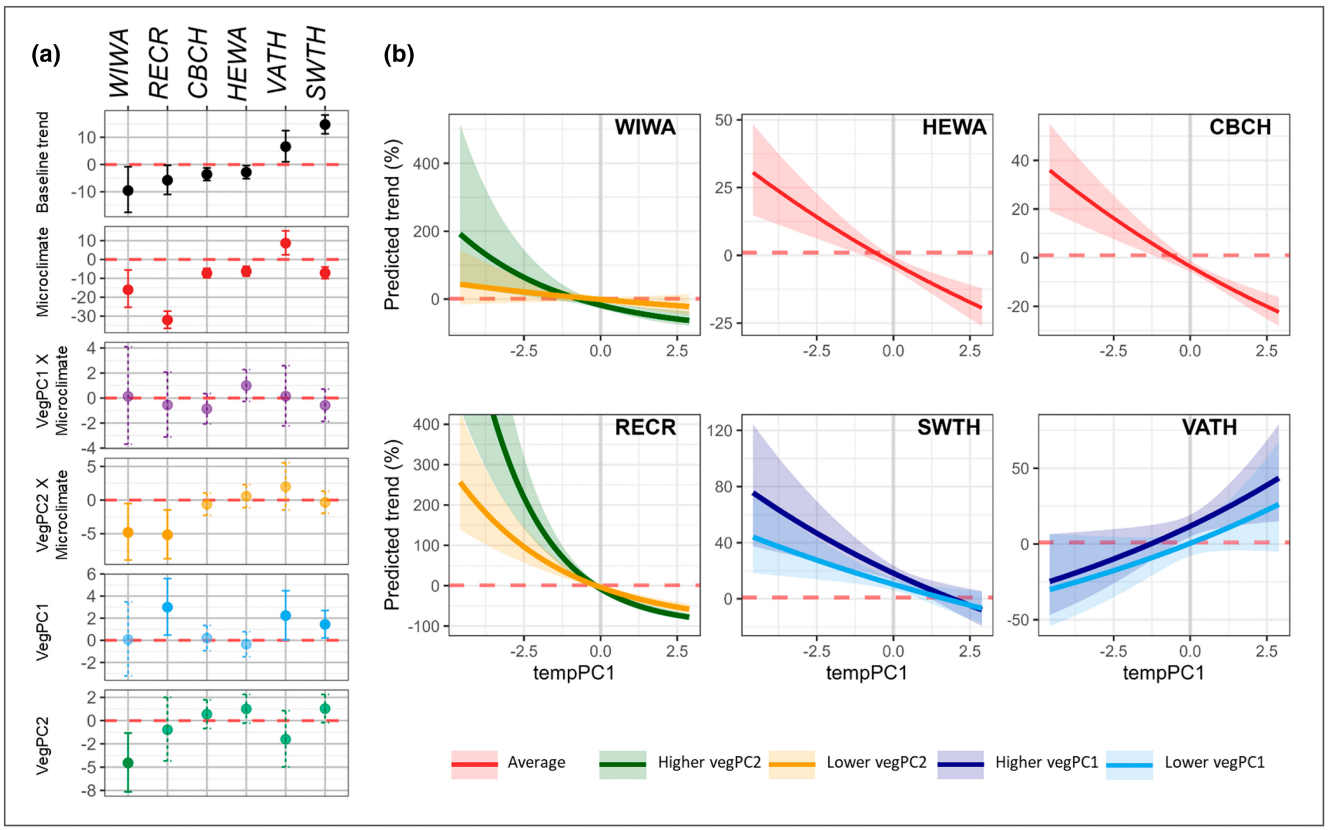

FIGURE 5 (a) Estimated standardized covariate effects on population trend models of six species that support the hypotheses. The *Y*-axis indicates the percent change in population trends per unit change in each covariate, and the dotted red horizontal line indicates no change. (b) Fitted trend estimates of models with 90% confidence intervals, predicting trend (% change in abundance) as function of microclimate temperature (tempPC1), and its interaction with vegetation (vegPC2) for Wilson's warbler (WIWA) and red crossbill (RECR). Swainson's thrush (SWTH) and varied thrush (VATH) plots show additive main effects of vegPC1 on trends. Covariates that are not presented in this panel are held at their mean values.

interspersed (Figure 2), it is possible that birds living in plantations could behaviorally buffer themselves by occasionally moving into old growth (for instance on hot days). Similarly, at a population level, high-quality old-growth stands may serve as sources in a source-sink dynamic (Betts et al., 2022; Hagan et al., 1996; Morelli et al., 2020), spilling-over individuals to neighboring stands. We did not test for such effects here, but we note that such 'spillover' or adjacency effects would render our results more conservative with respect to the effect of forest structure and microclimate on population trends.

Current and projected future warming during the spring breeding period in the Pacific Northwest (Abatzoglou et al., 2014; IPCC, 2021; Weiskopf et al., 2020) suggests that declining population trends for four species (Wilson's and hermit warblers, red crossbill and chestnut-backed chickadee) may continue. Under rapid climate change, past clearcutting of old-growth forests in the Pacific Northwest (Krankina et al., 2014; Strittholt et al., 2006) and current intensive management of forests combine to limit the availability of microclimatic refugia needed to reduce the negative impacts of global warming on bird populations. Retaining old-growth forests, and managing second-growth to have greater complexity could provide critical microclimatic refugia for these species across the region, which could mitigate declines in sub-populations within a larger metapopulation context (Hannah et al., 2014; Hanski, 1998; Morelli et al., 2020).

Although we did not test the direct mechanisms for negative impacts of warming on bird population trends, previous research on avian physiology and ecology suggests potential mechanisms that explain the relationships between microclimate, vegetation and bird population trends that we observed. First, thermal stress from warming temperatures increases metabolic rates; it becomes energetically costly for birds to thermoregulate via physiological and behavioral modifications (Conradie et al., 2019; Gerson et al., 2019; McKechnie & Wolf, 2019; van de Ven et al., 2020). Such costs can be especially detrimental for breeding birds that need to meet high energetic requirements of reproduction. All four declining species are small passerine species and may have high-energy requirements during the breeding season (Cucco & Malacarne, 1997; Nagy & Holmes, 2005). Energy expenditure may amplify when thermal optima are exceeded during the mid-breeding season (Grémillet et al., 2012; O'Connor et al., 2021; Wolf & Walsberg, 1996).

A second potential mechanism affecting trends in bird populations is limitation in food availability during an energetically demanding period. Warmer microclimates would advance leaf-out and arthropod emergence, well before timing of the peak requirements

during the nesting season (match-mismatch; Cushing, 1990). This may be most detrimental for long-distance migrants such as Hermit Warblers that seem to have limited phenotypic plasticity for spring arrival dates (Mayor et al., 2017; Robinson et al., 2019). Nonetheless, reduced fitness and a reduced probability of double brooding may result from an increasing mismatch between resource availability and resource needs for some species (Reed et al., 2013). These potential phenological mismatches will vary spatially, leading to locations on a landscape where both availability of resources and suitable microclimates may increase individual fitness but reduce it in others (Burgess et al., 2018; Jeong et al., 2020; Kwon et al., 2019; Shutt et al., 2019). Thus, how these mismatches are manifested over subpopulations or entire geographic ranges is not clear.

At least two species in our study demonstrated statistical interactions that support the *insurance hypothesis* (Figures 1b and 5b). For the two species, Wilson's warblers and red crossbills, a decrease in vegPC2 (increase in forest vegetation compositional diversity; Figure 2) reduced negative effects of a warming microclimate. Conifer cone crop is a necessary food resource for red crossbills, and warmer, drier microclimates can cause cones to shed seeds earlier making them unusable for breeding adults and recently fledged young birds (Benkman & Young, 2020). Having various species of conifers available could offer an extended period of seed availability as they can vary in response to the microclimate. It is also worth noting that crossbills can breed across most of the year when cone crop is available even in very early spring or in winter, and our timing of the survey may only capture post-breeding flock of the birds in this region. Similarly, Wilson's warblers can potentially benefit from more diverse understory plant species and cover, protracting the leaf-out period and food availability under warmer spring conditions. Wilson's warblers selectively forage on lepidopteran larvae on deciduous shrub species (Hagar et al., 2007); high canopy cover diversity could influence understory vegetation and associated arthropod prey sources as temperatures increase. To test these mechanisms, future studies should focus on investigating population trends, and individual fitness and diet use during phenological matching and mismatching across microclimatic gradients.

In a meta-analysis of 466 studies across various systems, insurance effects were stronger from in vitro experiments that controlled biodiversity more strictly, compared with experiments conducted in field plots (Balvanera et al., 2006). In our study, the ability of vegetation to mediate microclimate effects on population trends was detected for only two species in our study. This may be due to a strong microclimatic effect or because some bird species cannot subsidize food from even increased compositional and structural diversity. Alternatively, the range of plant compositional diversity across the microclimatic gradient was not sufficient to detect an interaction effect. Finally, unexplained non-breeding season drivers such as changes in habitat availability and quality, as well as climate change stressors in the non-breeding periods may have played a greater role than breeding season microclimate on influencing population trends; mortality during non-breeding periods is also a significant driver of population dynamics in migratory species (Sillett & Holmes, 2002).

5 | CONCLUSION

Our findings indicate that old-growth forest characteristics can provide climate refugia for some species over an 8-year period. In a recent study, Rosenberg et al. (2019) reported that western forest birds have declined by 29.5% from 1970 to 2018. Although the mechanisms of these mass declines in western forests are still unclear, recent research suggests that old-growth forest associated species are in decline despite current conservation policy measures (Phalan et al., 2019). In addition, climate-change driven spring and summer warming in the Pacific Northwest seems to be deteriorating breeding habitat of forest birds in the region (Betts et al., 2018; Northrup et al., 2019). It is an open question whether climatic buffering can be maintained as regional temperatures continue to rise, and changes to forest structure and composition continue due to land-use change and/or from climate change (Chmura et al., 2011; Coops & Waring, 2011). Wolf et al. (2021) found that microclimate buffering effects of forests are consistent across years, but microclimatic conditions were still coupled with the annual fluctuations of regional climate (macroclimate). Under current projections of global climate warming (IPCC, 2021), buffered microclimates under a forest canopy may be cooler than the surroundings but may still warm at similar rates to 'hot spots' under current conditions. However, microclimatic refugia provided by old-growth and complex forests may provide time to enable species to adapt to a warming climate (Hannah et al., 2014; Morelli et al., 2020).

AUTHOR CONTRIBUTIONS

Matthew G. Betts, Hankyu Kim, Sarah J. K. Frey, Brenda C. McComb, and David M. Bell contributed to the conceptualization and design of the project, editorial input and wrote parts of the manuscript. Matthew G. Betts and Sarah J. K. Frey installed the design of the long-term data collection. Hankyu Kim, Sarah J. K. Frey, and David M. Bell contributed to the data collection, curation, and processing for the analysis. Hankyu Kim conducted statistical analysis and prepared the initial draft of the manuscript.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Raw bird point count data (SA024) and microclimate data (MS045) are available at the H.J. Andrews LTER database (http://andlter.forestry.oregonstate.edu/data). LiDAR data is available at the Oregon Department of Geology and Mineral Industries Oregon Lidar Consortium website (Quad name: Carpenter Mountain, Mackenzie River and Blue River; https://www.oregongeology.org/lidar). Code used for the anlaysis is available at Zenodo data repository (https://doi.org/10.5281/zenodo.6979125).

ORCID

Hankyu Kim https://orcid.org/0000-0001-8682-8535
Brenda C. McComb https://orcid.org/0000-0001-7013-3640
Sarah J. K. Frey https://orcid.org/0000-0002-4343-0700
David M. Bell https://orcid.org/0000-0002-2673-5836
Matthew G. Betts https://orcid.org/0000-0002-7100-2551

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