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SPECIAL FEATURE: SCIENCE FOR OUR NATIONAL PARKS' SECOND CENTURY

Recent stability of resident and migratory landbird populations in National Parks of the Pacific Northwest

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Abstract. Monitoring species in National Parks facilitates inference regarding effects of climate change on population dynamics because parks are relatively unaffected by other forms of anthropogenic disturbance. Even at early points in a monitoring program, identifying climate covariates of population density can suggest vulnerabilities to future change. Monitoring landbird populations in parks during the breeding season brings the added benefit of allowing a comparative approach to inference across a large suite of species with diverse requirements. For example, comparing resident and migratory species that vary in exposure to non-park habitats can reveal the relative importance of park effects, such as those related to local climate. We monitored landbirds using breeding-season point-count data collected during 2005–2014 in three wilderness areas of the Pacific Northwest (Mount Rainier, North Cascades, and Olympic National Parks). For 39 species, we estimated recent trends in population density while accounting for individual detection probability using Bayesian hierarchical *N*-mixture models. Our analyses integrated several recent developments in *N*-mixture modeling, incorporating interval and distance sampling to estimate distinct components of detection probability while also accommodating count intervals of varying duration, annual variation in the length and number of point-count transects, spatial autocorrelation, random effects, and covariates of detection and density. As covariates of density, we considered metrics of precipitation and temperature hypothesized to affect breeding success. We also considered effects of park and elevational stratum on trend. Regardless of model structure, we estimated stable or increasing densities during 2005–2014 for most populations. Mean trends across species were positive for migrants in every park and for residents in one park. A recent snowfall deficit in this region might have contributed to the positive trend, because population density varied inversely with precipitation-as-snow for both migrants and residents. Densities varied directly but much more weakly with mean spring temperature. Our approach exemplifies an analytical framework for estimating trends from point-count data, and for assessing the role of climatic and other spatiotemporal variables in driving those trends. Understanding population trends and the factors that drive them is critical for adaptive management and resource stewardship in the context of climate change.

Key words: avian trends; Bayesian hierarchical models; climate change; detection probability; monitoring; Mount Rainier National Park; North Cascades National Park Service Complex; Olympic National Park; point-count analysis; population density; Special Feature: Science for Our National Parks' Second Century.

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INTRODUCTION

Several aspects of terrestrial ecosystem change can be inferred efficiently by monitoring landbirds, which occupy relatively high trophic positions and provide important ecological functions such as seed dispersal and insect control. Landbird populations have thus been identified as "vital signs" by the U.S. National Park Service (NPS), because their abundance can indicate park resource conditions and signal the effects of ecological stressors (Fancy et al. 2009). Vital signs monitoring in montane parks is especially urgent because mountain habitats are among those most immediately susceptible to effects of climate change (IPCC 2013, 2014). Monitoring in montane wilderness areas also facilitates inference regarding effects of climate on population dynamics, because populations are less affected by other forms of anthropogenic disturbance while using these remote and relatively roadless areas.

The Pacific Northwest harbors the largest complex of designated wilderness in the contiguous United States, including three montane parks: Olympic National Park (OLYM), Mount Rainier National Park (MORA), and North Cascades National Park Service Complex (NOCA). These parks, which provide refuge for landbirds dependent on late-successional forest conditions and subalpine habitats, also serve as reference sites for assessing the effects of land-use and land-cover changes on bird populations throughout the region (Silsbee and Peterson 1991, Simons et al. 1999, Siegel et al. 2012). Vital signs monitoring in these parks is coordinated under the North Coast and Cascades Network Inventory and Monitoring Program (Weber et al. 2009) and includes breeding-season point-counts targeting the large suite of landbirds breeding in these mountain habitats (Siegel et al. 2007).

Recent methods applied to point-count data allow for modeling various components of the detection process while simultaneously analyzing individual detections, population state, and demographic trends (Royle 2004, Alldredge et al. 2007, Nichols et al. 2009, Dail and Madsen 2011, Schmidt et al. 2013, Amundson et al. 2014, Kéry and Royle 2016). Given within-season replication of counts, such as multiple count intervals during a single visit to a point-count station, individual detection histories can be used within a closed-population framework to account for detection probability when modeling population size (Alldredge et al. 2007) or occupancy (Saracco et al. 2011). Trends in occupancy or population size can be modeled using detection histories within and across seasons (Royle 2004, MacKenzie et al. 2006, Kéry et al. 2009). Time- and distance-to-detection data recorded during point-counts can be used to exploit a combined time-removal and distance-sampling method for modeling population status while accounting for both the availability and perceptibility of individual birds (Amundson et al. 2014), where availability (Will the bird sing?) and perceptibility (Will we hear it?) are distinct components of detection probability (Alldredge 2004). Methods also exist to allow for multiple count intervals that differ in length (Farnsworth et al. 2002), an important feature of many point-count protocols. Most of these methods are based on "N-mixture" models (Royle 2004) that link a Poisson model of true N (abundance at a site) with a binomial model of observed N (count at a site), such that a mixture of binomial models, each with a potentially distinct sample size N, determines model likelihood. N-mixture models provide a hierarchical extension of generalized linear models, allowing us to model parameters at each level, for example, counts as a function of survey conditions and abundance as a function of environment (Kéry and Royle 2016). We used this model-based method for assessing trends in order to account for uncertainty in the detection and state processes simultaneously and at multiple spatial scales (point, transect, park) while allowing for random effects (observer effects on detection, year effects on abundance) and the potential for species presence at points with zero detections (according to the binomial model of counts).

We collected ten years (2005–2014) of breeding-season point-count data from the three montane parks using 204 permanent transects stratified by elevation. Each point-count along a transect included data on distance- and time-to-detection, as well as multiple count intervals, with sequential count intervals differing in length. To analyze data with these features, we extended the spatial model of Amundson et al. (2014) to (1) estimate temporal trends in population density from our time series and (2) allow for count intervals varying in length according to the method of Farnsworth et al. (2002). The extended model provides a particularly flexible approach for estimating spatiotemporal trends using point-count data. Implemented in a Bayesian framework and using Markov chain Monte Carlo methods for parameter estimation, this approach also allows parameter summaries at multiple scales and conveniently estimates any missing data (Kéry and Royle 2016). To summarize, this model incorporates interval and distance sampling to estimate distinct components of detection probability and accommodates other common features of point-count data, including count intervals of varying duration, annual variation in the number of point-counts, spatial autocorrelation, random effects, and covariates of detection and density.

To explore potential effects of climate on these species, we used mean spring temperature (MST) and annual precipitation-as-snow (PAS) as candidate covariates of population density. Winters with heavy snow accumulation in mountains of the western United States have been associated with reduced breeding bird abundance in subalpine forests (Raphael and White 1984, DeSante 1990). We hypothesized that years of heavy snow and cooler spring temperatures could delay initiation of breeding and result in food scarcity early in the nesting season (Hahn et al. 2004, Pereyra 2011, Mathewson et al. 2012), leading to lower recruitment and lagged effects of lower breeding bird abundance in the subsequent year (DeSante 1990). We expected the effects of persistent spring snow cover to be least favorable for migratory, ground-nesting, and insectivorous species. Our analysis featured a selection of migratory and resident species appropriate for evaluating the potentially varied effects of observed trends in climate, and informing management options with respect to landbird ecology.

METHODS

Survey design

We conducted point-counts in three wilderness parks: MORA, NOCA, and OLYM (Fig. 1). These parks span elevations 0–4400 m above sea level and contain areas dominated by large tracts of late-successional, coniferous, and broadleaf forest, as well as subalpine and alpine plant communities. Habitats and bird species assemblages are somewhat heterogeneous across each of the parks, with the most marked differences occurring between eastern and western slopes of NOCA (Altman 2000, Siegel et al. 2012).

Surveys were conducted along point-count transects using methods detailed in Siegel et al. (2007). Due to safety and logistical issues encountered in these large, rugged parks, transects originated along park trails or, occasionally, park roads, and extended 1–2 km into the surrounding habitat. Although this design limited our area of inference, a buffer of just 1 km around trails and roads includes a substantial portion of each park: 57% of the total land area in MORA, 31% in NOCA, and 39% in OLYM. The sampling frame consisted of potential transect "origins" spaced every 50 m along maintained trails and roads in each park. Potential origins were screened using data from a Geographic Information System to eliminate busy stretches of road as well as steep or waterfront areas where off-trail sampling would not be possible. To ensure adequate sampling across elevations, origins were binned by elevational stratum as "low" (<650 m above sea level), "middle" (650–1350 m), or "high" (>1350 m), with one exception: The boundary between low and middle elevations in MORA was set at 800 m, because almost none of this park lies below 650 m.

From the large sampling frame of potential transect origins in each park (n = 1094 to 9771 depending on stratum and park), a set of spatially dispersed origins were selected using the Generalized Random-Tessellation Stratified (GRTS) sampling method (Stevens and Olsen 2004) with reverse hierarchical ordering. The GRTS sample within each park was further stratified according to an augmented, serially alternating panel design (Urquhart et al. 1998) consisting of one set of transects to be surveyed annually (the annual panel) and five sets surveyed every five years (the alternating panels). This design

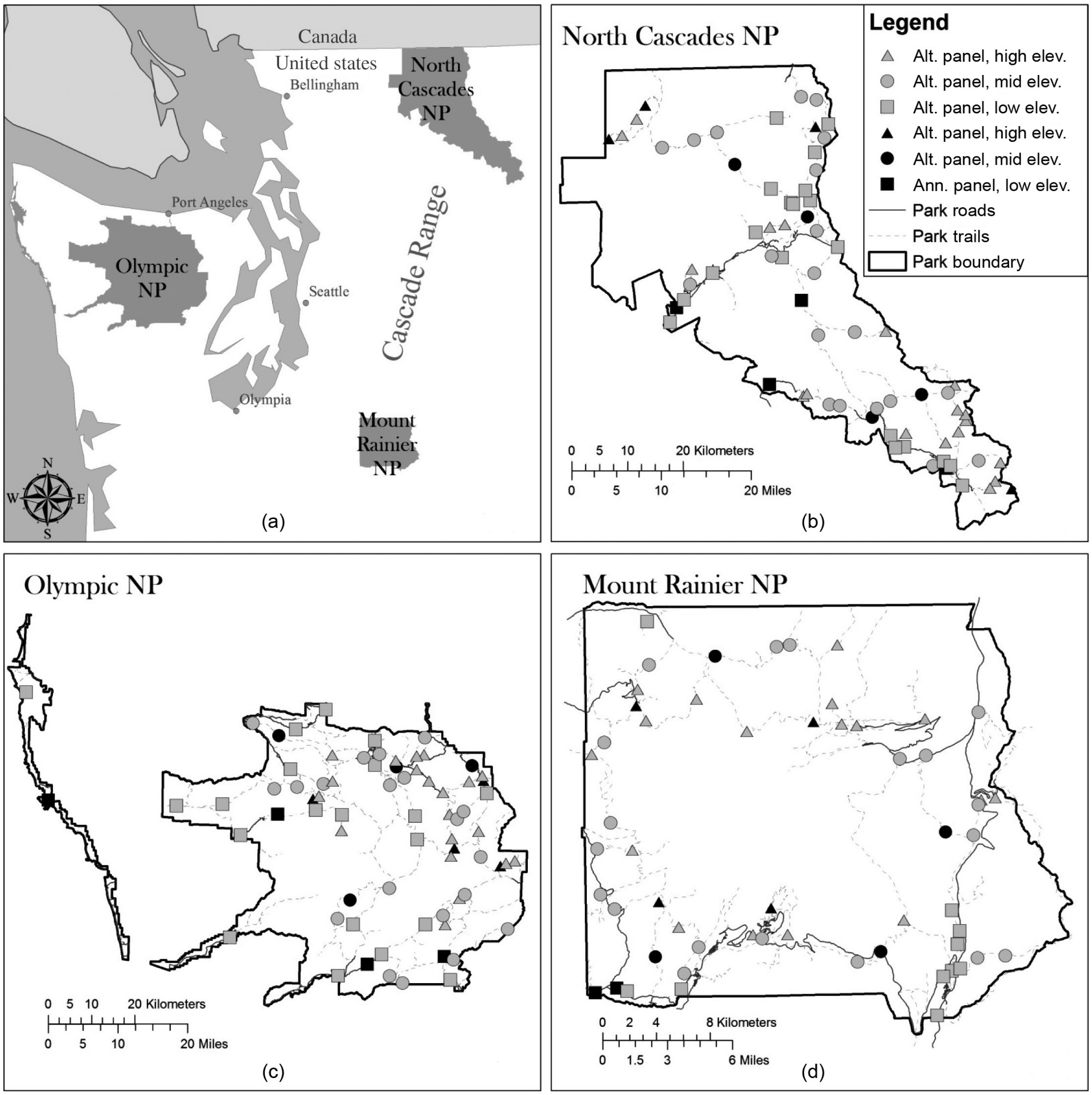

Fig. 1. National Park (NP) locations (a) and the "origin" or midpoint of each surveyed transect in each park (b–d). Each transect originated on a trail or road and extended away from the trail or road up to 2 km from its origin.

allowed for sampling two panels per year (the annual panel and one alternating panel), providing substantial year-to-year continuity as well as good representation of diverse habitats and regions in each park (Breidt and Fuller 1999, Urquhart and Kincaid 1999, McDonald 2003). Each of the six panels in a park included transects representing the three elevational strata (Table 1). In NOCA and OLYM, each panel included four transects from each elevation, for a total of 12 transects per panel and 72 transects per park. In MORA, where low-elevation habitat was more limited, each panel included two fewer transects from low elevations, for a total of 10 transects per panel and 60 at the park level.

Ideally, each permanent transect stretched perpendicularly across a trail or road, intersecting the origin and linking a set of permanent

Table 1. Number of point-count transects and their distribution among parks, elevational strata, and survey panel types.

Park	MORA†		NOCA‡		OLYM§	
Panel type¶	Annual	Alternating††	Annual	Alternating	Annual	Alternating
Low-elevation‡‡	2	10	4	20	4	20
Mid-elevation	4	20	4	20	4	20
High-elevation	4	20	4	20	4	20
Total transects§§	10	50	12	60	12	60

† Mount Rainier National Park.

‡ North Cascades National Park Service Complex.

§ Olympic National Park.

¶ Transects in annual panels are surveyed every year and those in alternating panels are surveyed once in every five years of monitoring.

†† One-fifth of the alternating panels are surveyed in a given sampling year; for example, each year in MORA we sample one alternating panel containing two low-, four mid-, and four high-elevation transect.

‡‡ "Low-elevation" is <650 m above sea level (asl) for NOCA and OLYM and <800 m asl for MORA; "Mid-elevation" extends to 1350 m; and "High-elevation" is >1350 m (excluding >2500 m in MORA and >2029 in NOCA; see Table 2).

§§ Each transect links a unique set of at least eight point-count stations located at 200-m intervals. The number of point-count stations surveyed along a transect in a given year can vary, but is usually >8 if conditions permit.

point-count stations (hereafter, "points") spaced at 200-m intervals beginning 100 m on either side of the origin. When cliffs, impassable streams, or other obstacles were encountered, pre-defined rules were used to redirect transects (Siegel et al. 2007). Where off-trail travel was impossible, transects continued along trails until a departure was feasible. Depending on terrain and annually varying circumstances affecting point access, the number of points sampled along each transect ranged from 8 to 25.

The annual panel of transects in each park has been surveyed each year since 2005, and the first survey of alternating panels occurred during 2007–2011. Thus, our current trend estimates were based on 136 transects that have been surveyed multiple times (34 transects in the annual panel plus 102 transects in alternating panels that were surveyed for the second time during 2012–2014).

Data collection

Each year a crew leader and 5–7 others participated in a three-week training session led by personnel from The Institute for Bird Populations and NPS. In addition to field methodology (e.g., locating points), training included identification of all bird species by sight and sound, as well as practice in estimating distance to birds. Before collecting data, crew members were required to pass an examination demonstrating proficient bird identification skills.

Data collection was timed to coincide with the breeding season, and especially with the peak in singing for most species. To avoid counting birds still engaged in migration, surveys began no earlier than 23 May at NOCA and OLYM and no earlier than 1 June at the higher-elevation park, MORA. Lower elevations in each park were sampled earlier in the season than higher elevations, to better track peak breeding season by elevation. All surveys were completed by 31 July.

In accordance with other NPS bird monitoring protocols (Coonan et al. 2001, Peitz et al. 2003, Siegel et al. 2010), each point-count included a five-minute survey period conducted in two intervals (minutes 0–3 and 3–5 comprised intervals 1 and 2, respectively). A third interval of two minutes (minutes 5–7) was added in 2011 to facilitate estimation of detection probability using time-of-detection methods (Alldredge et al. 2007). Species and distance from observer were recorded for each bird or flock (Reynolds et al. 1980, Fancy 1997, Nelson and Fancy 1999, Rosenstock et al. 2002), except for a small number of individuals classified as "flyovers" with no apparent connection to the surveyed habitat. Species traits (residency, nesting, and dietary habits) were assigned in accordance with Rodewald (2015), with special attention to trait variants specific to populations in the Pacific Northwest.

Population model structure

We used a Bayesian hierarchical framework (Fig. 2) to fit models of detectability and abundance for each of 39 focal species commonly

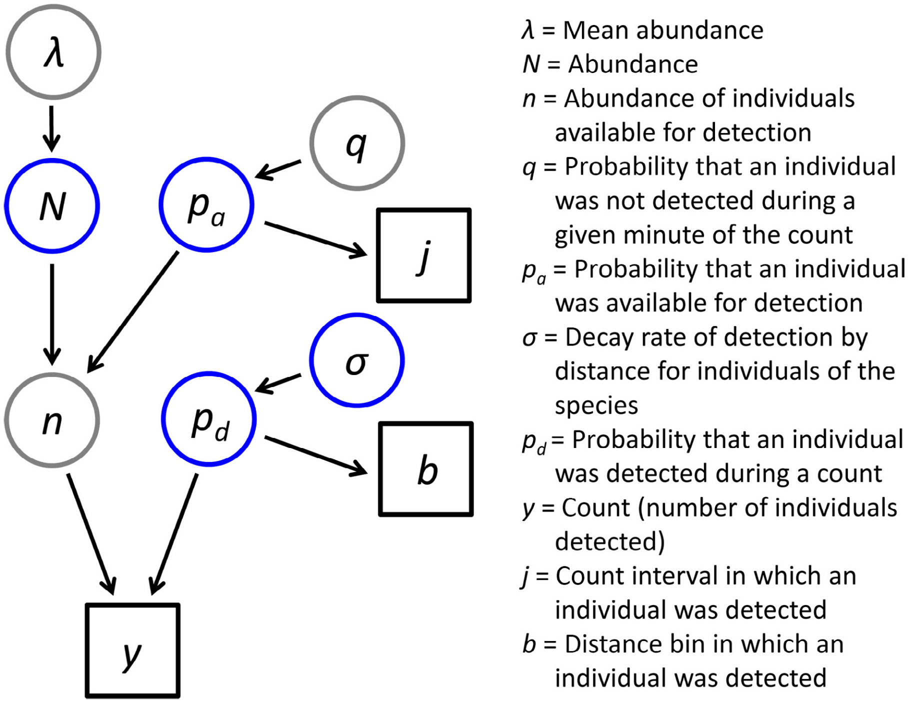

Fig. 2. Graphical representation of directional relationships between data (squares) and estimated parameters (circles) in the models presented here. Focal parameters appear in dark blue circles. Actual bird abundance (N) was modeled as a Poisson-distributed function of mean abundance (λ) and its covariates. The per-minute rate of detection failure (q) and its covariates informed availability for detection (p_a), which in turn influenced the interval (j) in which each bird was detected and the estimated number of birds available for detection (n). Finally, the decay rate of detection by distance (σ) and its covariates controlled distance-based perceptibility (p_d) and the observed detection-distance bin (b), as well as the number of available birds counted (y).

detected in these parks. Following Amundson et al. (2014), our three-level hierarchical model allowed estimation of (1) components of individual detection, including probabilities of individual availability (p_a) and perceptibility leading to detection (p_d); (2) point-year counts as a function of p_a and p_d; and (3) spatiotemporal trends in abundance, including effects of local climate.

Level 1: Individual observations.—Building on Amundson et al. (2014), we developed an observation model for each focal species under the assumption that individual birds were imperfectly observed. Detectability at a given point (for k in 1, …, K points) and year (for t in 1, …, T years) was characterized in terms of a bird's availability for detection ($p_{a,kt}$) and its distance-mediated perceptibility to the observer ($p_{d,kt}$). Following Farnsworth et al. (2002), we used time-removal data from each count interval $j = 1, \ldots, J$ to model interval-specific probabilities of availability, $\pi_{a,kt}$, corrected for unequal interval lengths. Assuming birds of a given species were equally detectable (an assumption relaxed below), and defining $q_{kt} = (1 - \pi_{a,kt})$ as the probability of failing to detect a bird that was present in a given minute, detection probability varied among our three count intervals $j = [1, 2, 3]$ as

$$\begin{aligned}\pi_{a,kt1} &= 1 - q_{kt}^3,\\ \pi_{a,kt2} &= q_{kt}^3(1 - q_{kt}^2), \text{and}\\ \pi_{a,kt3} &= q_{kt}^5(1 - q_{kt}^2).\end{aligned}$$

For a three-minute count interval, q_{kt}^3 was the probability that a bird was not detected during that interval. Birds not detected in the first three minutes could be detected in the next two minutes with probability $(1 - q_{kt}^2)$, etc. The probability that a bird was never detected across all three intervals (seven minutes) was q_{kt}^7, and $1 - q_{kt}^7 = p_{a,kt} = \sum_j \pi_{a,ktj}$. Conditioning $\pi_{a,ktj}$ on $p_{a,kt}, \pi^c_{a,ktj} = \pi_{a,ktj}|p_{a,kt} = \pi_{a,ktj}/p_{a,kt} = \pi_{a,ktj}/\sum_j \pi_{a,ktj}$. By defining $p_{a,kt}$ in terms of $1 - q_{kt}$, we were able to account for unequal interval lengths when modeling bird availability for detection as a function of date, time, or other point- and/or year-specific covariates, x_{kt}, as $\mathrm{logit}(q_{kt}) = \beta_0 + \sum_x \beta_x x_{kt}$.

Distance-mediated perceptibility, p_d, was estimated using observed detection distances. To reduce effects of heterogeneity among observers in the ability to detect birds at a distance, we aggregated the data for each species across all point-years and dropped ~10% of the farthest observations of each species, resulting in a species-specific truncation radius. Detection distances were then sorted into five bins of variable width, equalizing the number of individual detections in each bin (Amundson et al. 2014). The truncation radius was reduced if necessary to obtain independence across detections between detection interval and detection-distance bin, as determined by analysis of variance ($\alpha = 0.05$). We modeled the probability that a bird was detected in distance bin $b = 1, \ldots, 5$ within the truncation radius of point k and year t, as $p_{d,kt} = \sum_b \pi_{d,ktb}$, where $\pi_{d,ktb}$ was the probability of detection in bin b. Conditioning $\pi_{d,ktb}$ on $p_{d,kt}$, $\pi_{d,}{}^{c}{}_{ktb} = \pi_{d,ktb}\ |p_{d,kt} = \pi_{d,ktb}/p_{d,kt} = \pi_{d,ktb}/\sum_b \pi_{d,ktb}$. We modeled detection frequency by distance bin using the half-normal distribution (Buckland et al. 2001, Royle et al. 2004, Farnsworth et al. 2005, Amundson et al. 2014) as

$$\pi_{d,ktb} = \exp(-r_b^2/2\sigma_{kt}^2)(2r_b\delta_b/r_{\max}^2),$$

where r_b = radius of bin b, σ_{kt} = rate of decay in detections by distance, δ_b = width of bin b, and $r_{\max}$ = truncation radius. We explored fitting the shape parameter of the detection function as a constant, specified as $\log(\sigma_{kt}) = \log(\sigma_0)$, or as a function of covariates varying in space and time (observer, ambient noise level, group size), specified as $\log(\sigma_{kt}) = \log(\sigma_0) + \sum_x \beta_x x_{kt}$.

Level 2: Counts.—In our count model for the focal species, each point- and year-specific total count, y_{kt}, was related to a specific population size, N_{kt}, through the processes of availability and perceptibility (Amundson et al. 2014). The number of individuals available was modeled as $n_{kt} \sim \mathrm{Binomial}(N_{kt},\ p_{a,kt})$, while the number of available individuals perceived was modeled as $y_{kt} \sim \mathrm{Binomial}(n_{kt}, p_{d,kt})$.

Level 3: Population density.—We modeled population size, N_{kt}, as a Poisson random variable with mean λ_{kt}. Mean population size was a log-linear function of point- and year-specific fixed and random effects, such as

$$\log(\lambda_{kt}) = \beta_0 + \beta_1 t + \mathrm{year}_t + \mathrm{transect}_k, \quad (1)$$

which included a "regional" trend with year t that was not differentiated by park or elevational stratum, as well as random effects of year and transect to account for temporal and spatial clustering of surveys. Adding park-specific trends and covariates, we explored models of the form

$$\begin{aligned}\log(\lambda_{kt}) = {} & \mathrm{park}_{p[k]} + \mathrm{year}_t + \mathrm{park}_{p[k]}:\mathrm{year}_t \\ & + \beta_{p[k]}t + \mathrm{transect}_k + \sum_x \beta_x x_{kt},\end{aligned} \quad (2)$$

where the intercept $\mathrm{park}_{p[k]}$ and slope $\beta_{p[k]}$ could vary across the $p = 1, \ldots, P = 3$ parks, and the park and random year effects could interact. Covariates x_{kt} were elevation or metrics of climate.

We also considered a model that might reveal evidence for elevational shifts in abundance over time, by fitting stratum-specific trends as

$$\log(\lambda_{kt}) = \mathrm{stratum}_{l[k]} + \beta_l t + \mathrm{year}_t + \mathrm{transect}_k, \quad (3)$$

where $l = [1, 2, 3]$ indexed the high-, mid-, and low-elevation strata in our study design.

For each species, we reported mean population density (number per hectare) across the sampled plots, accounting for variation among species in effective plot size (truncation radius) as $\mathrm{mean}(N_{kt})/[\pi r_{\max}^2/10{,}000]$. Using results from the stratum-specific model 3, we also extrapolated N to the stratum level as $N_{lt} = (1/\mathrm{effort}_{lt}) \sum_{l[k]} N_{kt}$, where effort_{lt} was the sampling density or the effective area surveyed (sum of effective plot sizes) in stratum l and year t divided by the total area of stratum l. Although we remain cautious about extrapolating N beyond our sampling frame, our goal was to illustrate potential effects of sampling density on trend estimates. Our strata contained similar numbers of point-count stations (Table 1) but differed in area (Table 2) and, consequently, in sampling density.

Table 2. Approximate area (in hectares) of each park and elevational stratum in this study.

Park	MORA†	NOCA	OLYM†	Stratum totals
Low-elevation	3811	30,164	111,124	145,099
Mid-elevation	29,602	102,908	175,751	308,261
High-elevation	55,684	142,376	81,341	279,401
Park totals	89,097	275,448	368,216	732,761

Note: MORA, Mount Rainier National Park; NOCA, North Cascades National Park Service Complex; OLYM, Olympic National Park.

† Excluding the largely glaciated areas above 2500 m in MORA and above 2029 m in NOCA.

After extrapolating population size to the stratum scale, it might be possible for trends in larger populations/strata to swamp those in smaller populations/strata. To explore this possibility, we compared trends estimated using model 1 with weighted-average trends estimated using model 3, where each stratum l weight was the geometric mean estimate of annual values N_{lt}.

Climate

We explored effects of temperature and precipitation on breeding bird dynamics using annual data and 1971–2000 normals from ClimateNA (http://www.climatewna.com/), accessed on 2 June 2016. ClimateNA uses bilinear interpolation and local elevation adjustment to downscale monthly, gridded climate data as scale-independent point data (Wang et al. 2016), providing climate metrics directly estimated for each point along our transects. Elevation adjustments were based on empirical lapse rates, improving prediction accuracy on average 0–17% (depending on the climate variable) relative to 800-m gridded data, and with improvements above average in mountainous areas (Wang et al. 2016).

To characterize spring conditions, we selected MST (the average daily temperature from 1 March through 31 May) and annual precipitation-as-snow (PAS, millimeters of snow falling between 1 August and 31 July). Specifically, we calculated MST and PAS as anomalies, relative to 1971–2000 normals, for use as predictors of population size, under the expectation that increased snowfall would have negative effects, and increased temperature would have positive effects, on breeding and recruitment. For surveys in year t, lag-1 MST was the mean temperature anomaly from 1 March to 31 May of year $t - 1$, and lag-1 PAS was the snowfall anomaly from 1 August of year $t - 2$ to 31 July of year $t - 1$. We considered both additive and interaction effects of these anomalies and, because the correlation between MST and PAS was moderate (Kendall's $\tau = -0.45$), we also considered a model based on PAS and "residual MST," the residuals of a linear regression of MST anomalies on PAS anomalies (Graham 2003).

Parameter estimation

Continuous covariates were standardized (mean = 0, SD = 1) to facilitate convergence of parameter estimates and interpretation of relative effects. Years 2005–2014 were coded as 1–10. Models were fitted using JAGS version 3.3.2 (Plummer 2003) called remotely from R version 3.2.2 (R Core Team 2015). We assumed random effects were normally distributed with mean μ and precision τ (τ = 1/variance). We used vague normal priors with mean 0 and variance 100 for fixed effects and hyperparameters (μ), a uniform prior bounded at 0 and 200 for the intercept of perceptibility (σ_0), and uniform priors bounded at 0 and 10 for variances at the scale of σ. For each fitted parameter, we drew posterior estimates from 3 Markov chains of 70,000–100,000 samples each, after thinning by 1 in 30 to 1 in 50 and discarding the first 20,000-50,000 samples. We assessed the convergence of each parameter estimate using the Gelman-Rubin potential scale reduction parameter, R-hat, which indicates adequate convergence at values of up to 1.2 (Kéry and Schaub 2012).

To assess goodness-of-fit for our sub-models of species availability and perceptibility, we used Bayesian P-values generated from posterior predictive distributions, assuming good fit for P near 0.5 and inadequate fit for $P < 0.1$ or $P > 0.9$. We also estimated sub-model fit using a lack-of-fit (LOF) ratio or $\hat{c}$ (sensu Kéry and Royle 2016:253), often used in a quasi-likelihood framework to adjust (inflate) the standard errors of parameter estimates. Our LOF ratio was the chi-square discrepancy between observed and expected (modeled) response values divided by the chi-square discrepancy between expected and predicted (simulated) response values. In other words, if y_i, $\hat{y}_i$, and y_i^*, respectively, were observed, expected, and simulated response values for each point-count i, then our LOF ratio was $\sum_i X_i^{\text{obs}} / \sum_i X_i^{\text{pred}}$, where $X_i^{\text{obs}} = (y_i - \hat{y}_i)^2 / (\hat{y}_i + 0.5)$, and $X_i^{\text{pred}} = (y_i^* - \hat{y}_i)^2 / (\hat{y}_i + 0.5)$. Distinct assessments of fit were possible for the two components of detectability due to the distinct data being used to inform each sub-model (Fig. 2; Amundson et al. 2014).

We assessed support for each covariate of abundance, availability, or perceptibility using the 95% credible interval (CI) for the estimate of its associated coefficient; the covariate was supported when this 95% CI did not contain zero. Mean parameter estimates across species-trait groups were quantified using Bayesian meta-analysis (sensu Kéry and Royle 2016:680–683), a two-step hierarchical analysis to account for uncertainty in parameter estimates for individual species (Sauer and Link 2002).

RESULTS

We conducted a total of 8404 point-count surveys at 3177 distinct survey point locations across the three parks during 2005–2014, resulting in the detection of 121 landbird species. For 43 of these species, we detected more than 200 individuals, averaging at least 6–7 individuals detected per park-year. We selected 39 of these 43 species for our analyses, omitting four species (Pine Siskin, Red Crossbill, Evening Grosbeak, and Vaux's Swift) that were often detected in flocks and thus did not conform to the assumptions of the models explored here. These 39 species exhibit a variety of nesting and dietary traits that might affect species response to climate, and they include 15 "residents" that overwinter in the Pacific Northwest (Table 3).

Detection probability

Most detections occurred within the first survey interval, leading to estimates of p_a (the probability that individuals were available for detection) that were consistently high across species (Table 4): mean ± SE for $p_a = 0.88 \pm 0.02$. In these often forested landscapes, however, detection frequency declined rapidly with distance from the observer (Table 4): mean ± SE for $\sigma_{kt} = 46.81 \pm 2.83$ and for $r_{\max} = 109.59 \pm 7.52$. These patterns led to lower estimates of p_d (distance-based perceptibility) relative to p_a: mean ± SE for $p_d = 0.36 \pm 0.01$.

For every species modeled, the simplest (intercept-only) model of availability was adequate, as Bayesian P-values were near 0.5 without estimating effects of covariates on p_a (Fig. 3). Similarly, the simplest model of distance-based perceptibility (with σ constant across point-years) was adequate for approximately three-quarters of our focal species. For the remaining approximately one-quarter of these species, the Bayesian P-value associated with p_d indicated poor fit and was not appreciably improved by modeling random effects of observer, day, or transect. Nevertheless, the LOF ratio was adequate (near 1.0) for most species, regardless of perceptibility (Fig. 3). Because LOF was low (<1.1) in every case, we report results based on the simplest models of p_a and p_d, and we have not attempted to adjust the bounds on our parameter estimates.

Trends in population density

Fitting a model without park or climate effects (model 1), we estimated that all but one species were either stable or increasing across the sampled points in these three parks during 2005–2014 (Fig. 3). The simplest detection model appeared adequate for the one declining species (Mountain Chickadee) as well as for all five of the increasing species (Warbling Vireo, Yellow-rumped Warbler, Townsend's Warbler, Western Tanager, and Cassin's Finch).

Fitting a park-structured model (model 2), again without climate effects, had little effect on the proportion of declining populations observed (Fig. 4). This model suggested park-level declines across the sampled points in at least six species (Northern Flicker, Olive-sided Flycatcher, Clark's Nutcracker, Mountain Chickadee, Red-breasted Nuthatch, and Dark-eyed Junco). However, at least two of these species (Olive-sided Flycatcher and Dark-eyed Junco) also increased in density across samples in one of these parks, suggesting spatial rather than temporal fluctuations over this period. No species declined in all three parks, but two species appeared to increase in all three parks (Yellow-rumped and Townsend's Warblers), and at least 16 species appeared to increase in one or two parks without notable declines elsewhere (Red-breasted Sapsucker, Warbling Vireo, Gray Jay, Chestnut-backed Chickadee, Swainson's Thrush, Hermit Thrush, American Robin, Varied Thrush, American Pipit,

Table 3. Landbird species commonly detected† in our point-counts during 2005–2014.

Species code	Common name	Scientific name	Migrant	Main diet	Nesting habit
SOGR	Sooty Grouse	*Dendragapus fuliginosus*	No	Plants	Ground
RUHU	Rufous Hummingbird	*Selasphorus rufus*	Yes	Nectar	Tree
RBSA	Red-breasted Sapsucker	*Sphyrapicus ruber*	No	Insects	Cavity
HAWO	Hairy Woodpecker	*Picoides villosus*	No	Insects	Cavity
NOFL	Northern Flicker	*Colaptes auratus*	No	Insects	Cavity
OSFL	Olive-sided Flycatcher	*Contopus cooperi*	Yes	Insects	Tree
WEWP	Western Wood-Pewee	*Contopus sordidulus*	Yes	Insects	Tree
HAFL	Hammond's Flycatcher	*Empidonax hammondii*	Yes	Insects	Tree
PSFL	Pacific-slope Flycatcher	*Empidonax difficilis*	Yes	Insects	Tree
CAVI	Cassin's Vireo	*Vireo cassinii*	Yes	Insects	Tree
WAVI	Warbling Vireo	*Vireo gilvus*	Yes	Insects	Tree
GRAJ	Gray Jay	*Perisoreus canadensis*	No	Varied	Tree
STJA	Steller's Jay	*Cyanocitta stelleri*	No	Varied	Tree
CLNU	Clark's Nutcracker	*Nucifraga columbiana*	No	Varied	Tree
MOCH	Mountain Chickadee	*Poecile gambeli*	No	Insects	Cavity
CBCH	Chestnut-backed Chickadee	*Poecile rufescens*	No	Insects	Cavity
RBNU	Red-breasted Nuthatch	*Sitta canadensis*	No	Insects	Cavity
BRCR	Brown Creeper	*Certhia americana*	No	Insects	Tree
PAWR	Pacific Wren	*Troglodytes pacificus*	No	Insects	Cavity
GCKI	Golden-crowned Kinglet	*Regulus satrapa*	No	Insects	Tree
SWTH	Swainson's Thrush	*Catharus ustulatus*	Yes	Insects	Shrub
HETH	Hermit Thrush	*Catharus guttatus*	Yes	Insects	Ground
AMRO	American Robin	*Turdus migratorius*	Yes‡	Insects	Tree
VATH	Varied Thrush	*Ixoreus naevius*	No	Insects	Tree
AMPI	American Pipit	*Anthus rubescens*	Yes	Insects	Ground
NAWA	Nashville Warbler	*Oreothlypis ruficapilla*	Yes	Insects	Ground
YEWA	Yellow Warbler	*Setophaga petechia*	Yes	Insects	Shrub
YRWA	Yellow-rumped Warbler	*Setophaga coronata*	Yes	Insects	Tree
BTYW	Black-throated Gray Warbler	*Setophaga nigrescens*	Yes	Insects	Tree
TOWA	Townsend's Warbler	*Setophaga townsendi*	Yes	Insects	Tree
MGWA	MacGillivray's Warbler	*Geothlypis tolmiei*	Yes	Insects	Shrub
WIWA	Wilson's Warbler	*Cardellina pusilla*	Yes	Insects	Ground
WETA	Western Tanager	*Piranga ludoviciana*	Yes	Insects	Tree
CHSP	Chipping Sparrow	*Spizella passerina*	Yes	Seeds	Shrub
FOSP	Fox Sparrow	*Passerella iliaca*	Yes‡	Insects	Ground
SOSP	Song Sparrow	*Melospiza melodia*	No	Insects	Shrub
DEJU	Dark-eyed Junco	*Junco hyemalis*	Yes‡	Seeds	Ground
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*	Yes	Insects	Tree
CAFI	Cassin's Finch	*Haemorhous cassinii*	Yes	Seeds	Tree

† Four commonly detected species were omitted due to pronounced flocking behavior not suited to the models explored here (Pine Siskin, Red Crossbill, Evening Grosbeak, and Vaux's Swift).

‡ Species that may commonly remain resident over winter at lower elevations in Olympic National Park.

Nashville Warbler, Black-throated Gray Warbler, McGillivray's Warbler, Western Tanager, Fox Sparrow, Song Sparrow, and Cassin's Finch).

Given an adequate number of detections in the region, our park-structured model could be used to estimate park-specific trends even for species rarely or never detected in one or two parks. In practice, however, the park-structured model appeared to overestimate the initial abundance of a species in parks where it was rarely or never observed. Therefore, in Fig. 4 we do not report the trend estimate for a species in any park where it was "rare," that is, where its average annual count was <2.

After excluding species where they were rare, estimates of mean population density derived from (1) unstructured "regional" models and (2) park-structured models were highly correlated (Kendall's $\tau = 0.971$, $z = 8.69$, $P \ll 0.001$). However, for temporal trends in population

Table 4. Sample size and posterior point-estimates (means) for several parameters from our regional model (model 1 in the text) of each landbird species in Table 3.

Species code	Raw count	p_a†	Censored (%)‡	$r_{\max}$§	σ_{kt}¶	p_d††	Population density‡‡
SOGR	720	0.97	24.68	169	80.30	0.41	0.02
RUHU	695	0.79	10.00	28	9.75	0.24	1.84
RBSA	212	0.73	9.22	88	33.73	0.29	0.04
HAWO	402	0.75	9.90	91	39.09	0.35	0.07
NOFL	408	0.83	9.92	209	79.83	0.28	0.01
OSFL	758	0.93	14.70	216	80.32	0.27	0.02
WEWP	321	0.97	9.87	125	59.30	0.41	0.02
HAFL	1721	0.96	9.84	64	30.37	0.41	0.38
PSFL	2464	0.97	9.68	73	33.68	0.39	0.46
CAVI	279	0.89	10.04	92	42.73	0.40	0.04
WAVI	1188	0.96	22.30	82	44.30	0.49	0.12
GRAJ	765	0.84	10.00	117	45.14	0.29	0.08
STJA	426	0.85	10.02	125	59.52	0.41	0.03
CLNU	249	0.28	9.72	215	90.32	0.34	0.01
MOCH	393	0.93	9.82	91	36.76	0.31	0.02
CBCH	3588	0.93	16.07	39	22.07	0.52	1.79
RBNU	2324	0.93	9.93	130	49.76	0.29	0.20
BRCR	981	0.90	9.62	59	24.73	0.34	0.32
PAWR	4580	0.97	16.94	79	38.06	0.42	0.66
GCKI	2793	0.94	10.00	43	20.31	0.41	1.52
SWTH	2499	0.95	10.00	111	48.30	0.36	0.22
HETH	2661	0.97	9.78	193	71.59	0.27	0.10
AMRO	2189	0.89	9.55	115	44.70	0.29	0.20
VATH	5338	0.98	9.79	187	73.87	0.30	0.17
AMPI	329	0.90	9.65	118	41.01	0.24	0.04
NAWA	404	0.72	10.03	94	41.05	0.36	0.07
YEWA	904	0.96	9.51	83	33.16	0.31	0.14
YRWA	1864	0.93	9.93	92	44.30	0.42	0.22
BTYW	349	0.94	9.51	89	43.27	0.42	0.05
TOWA	3263	0.97	27.43	68	46.97	0.63	0.45
MGWA	702	0.93	9.72	90	36.98	0.32	0.11
WIWA	461	0.95	9.73	83	36.07	0.36	0.06
WETA	1795	0.95	9.99	112	51.53	0.39	0.16
CHSP	686	0.89	9.67	98	41.21	0.34	0.11
FOSP	285	0.89	9.96	170	57.51	0.22	0.02
SOSP	256	0.58	9.54	115	51.21	0.37	0.02
DEJU	5900	0.94	9.58	93	36.71	0.30	0.94
BHGR	338	0.87	9.85	123	58.41	0.41	0.02
CAFI	234	0.61	9.96	105	47.79	0.38	0.03

† Mean estimated probability that the species is available for detection.
‡ Percent of (distal) detections censored to ensure independence between detection distance and detection interval.
§ Maximum detection distance (in meters) determined by censoring‡ detections.
¶ Mean estimated rate of decay for the half-normal distance function.
†† Mean estimated probability that the species is detected when available for detection.
‡‡ Mean estimated population size per hectare across all plots surveyed.

density, there was little correspondence between park-specific and regional estimates in two of the three parks (Appendix S1: Fig. S1). Also, temporal trends in this region were not related to mean population density across all points (Kendall's $\tau = 0.023$, $z = 0.206$, $P = 0.837$; Appendix S1: Fig. S2). Mean population density (birds/ha) within the species' detection radius of each point-count station ranged from 0.01 to 1.84 (mean ± SE = 0.28 ± 0.07) across species, after censoring 9–27% (mean ± SE = 11.42% ± 0.69%) of the most distant detections of each species to ensure independence between detection interval and detection distance.

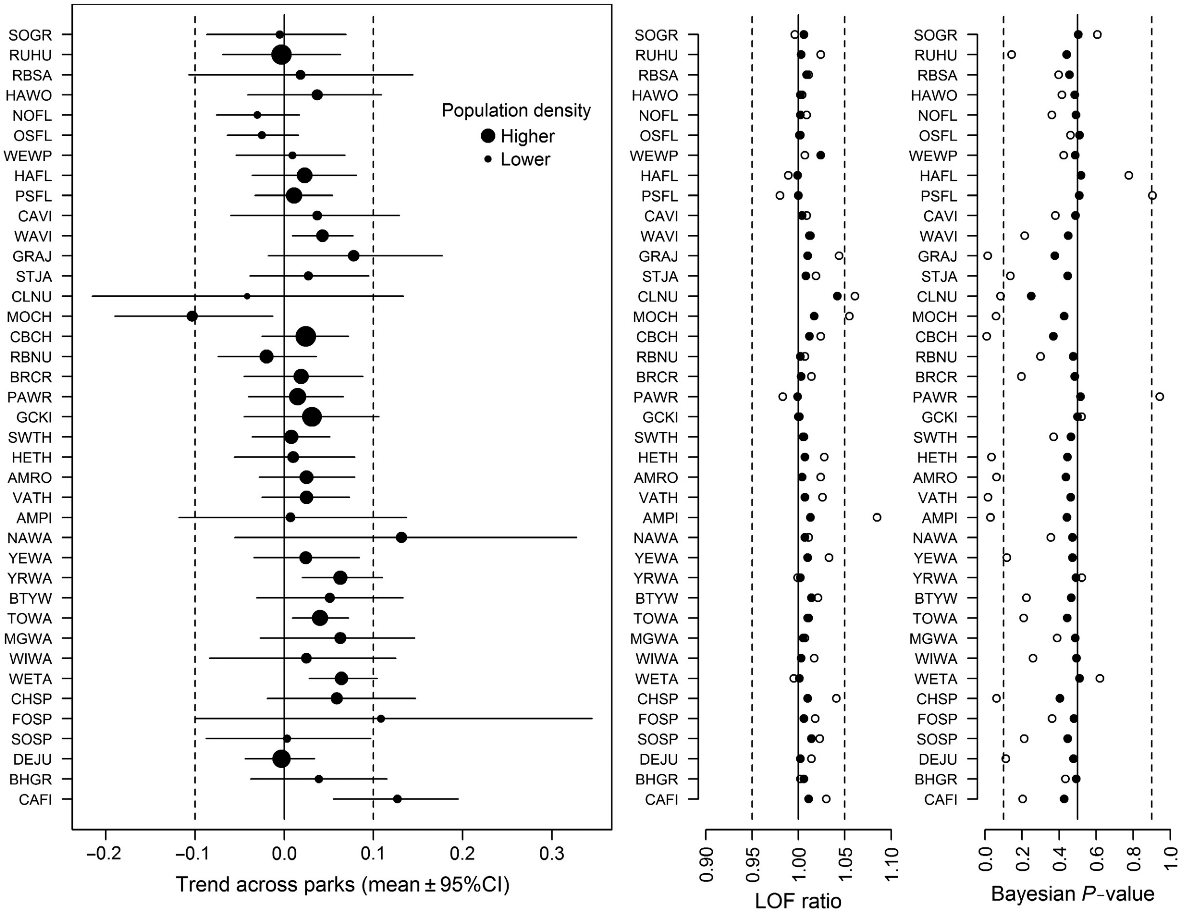

Fig. 3. Trends in population density for 39 landbird species during 2005–2014, estimated from point-counts in Mount Rainier, North Cascades, and Olympic National Parks (using model 1 in the text). Species codes on the *y*-axis are defined in Table 3. In the left-hand panel, fitted coefficients along the *x*-axis summarize the log-linear effect of year (coded as 1–10) on mean population density, dot sizes indicate the relative density estimated for each species, and horizontal lines represent 95% CIs (Bayesian credible intervals). Lack-of-fit (LOF) ratios (center panel) and Bayesian *P*-values (right-hand panel) are shown for sub-models of species availability (filled dots) and detection (open dots). Lack-of-fit ratios nearer to 1.0 and Bayesian *P*-values nearer to 0.5 indicate models with better fit. Dashed vertical lines are provided for visual reference.

Results from the stratum-specific model (3) also suggested very few declining trends (Fig. 5; Appendix S1: Table S1). Only four declining trends were supported: one in the highest stratum (Mountain Chickadee), two in the mid-elevation stratum (Mountain Chickadee and Western Wood-Pewee), and one in the lowest stratum (Olive-sided Flycatcher). In contrast, 15 positive trends were supported: three in the highest stratum (Cassin's Finch, Nashville Warbler, and Varied Thrush), seven in the mid-elevation stratum (American Pipit, Fox Sparrow, Hermit Thrush, Townsend's Warbler, Warbling Vireo, Western Tanager, and Yellow-rumped Warbler), and five in the lowest stratum (Chestnut-backed Chickadee, Townsend's Warbler, Western Tanager, Western Wood-Pewee, and Yellow-rumped Warbler). Any other trends apparent in Fig. 5 were not supported; for example, the 95% CI on each trend estimate overlapped zero for Steller's Jay, Song Sparrow, and Black-headed Grosbeak. Importantly, our overall trend estimate for each species was not affected by stratum-level sampling effort (Fig. 6). Of the six trending species

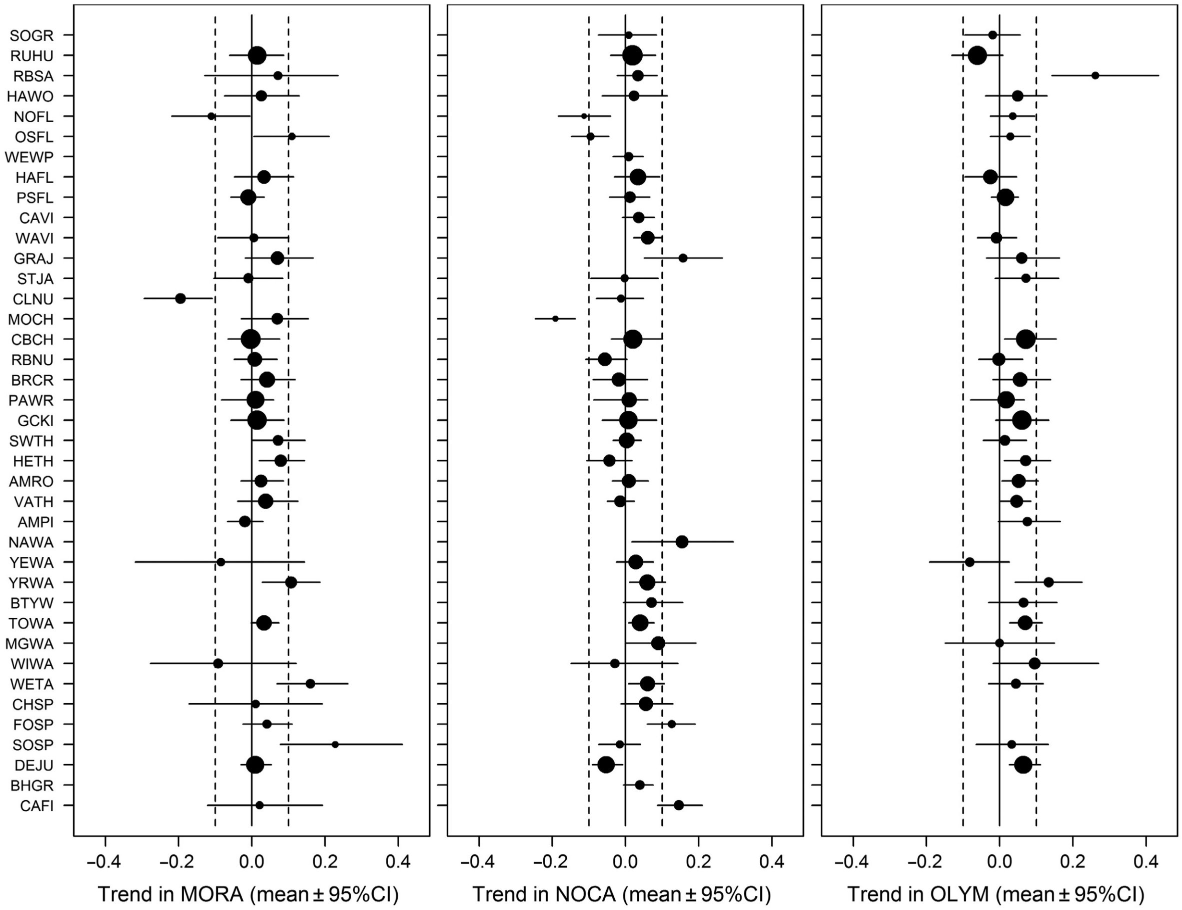

Fig. 4. Trends in population density (±95% credible intervals) for each species as in Fig. 3, estimated (using model 2) separately for Mount Rainier (MORA), North Cascades (NOCA) and Olympic (OLYM) National Parks. Estimates have been omitted where species were rarely detected. Species codes are defined in Table 3.

identified in Fig. 3, Townsend's Warbler was the only species with 95% CIs that overlapped zero after adjusting for stratum-level sampling effort (Fig. 6), and that overlap was slight (Appendix S1: Table S1). Population densities often differed dramatically between elevational strata (Fig. 5; Appendix S1: Fig. S3). The direction of stratum-specific trends was generally congruent within species (except for the Olive-sided Flycatcher), but dynamics varied widely among species (Appendix S1: Fig. S3).

Climate

Precipitation-as-snow and MST across our points varied substantially among years during the study period (Appendix S1: Fig. S4). Median PAS appeared lowest at points in NOCA (Appendix S1: Fig. S5), but there was no significant difference among parks in either PAS (ANOVA, $F_{2,27} = 0.222$, $P = 0.802$) or MST (ANOVA, $F_{2,27} = 0.043$, $P = 0.958$) after averaging climate metrics across points by year.

Lagged precipitation-as-snow generally had a negative effect on population densities of the focal species. Fig. 7 displays this inverse relationship between population density and lagged PAS for the Dark-eyed Junco, the most abundant species in our analysis, with strong and opposing population trends between parks (Fig. 4). The fitted coefficient of the lag-1 PAS anomaly was clearly negative for at least six species and positive for none (Fig. 8). In contrast, effects of lagged MST were less directional across species and weaker or less supported within species. Effects of the lag-1

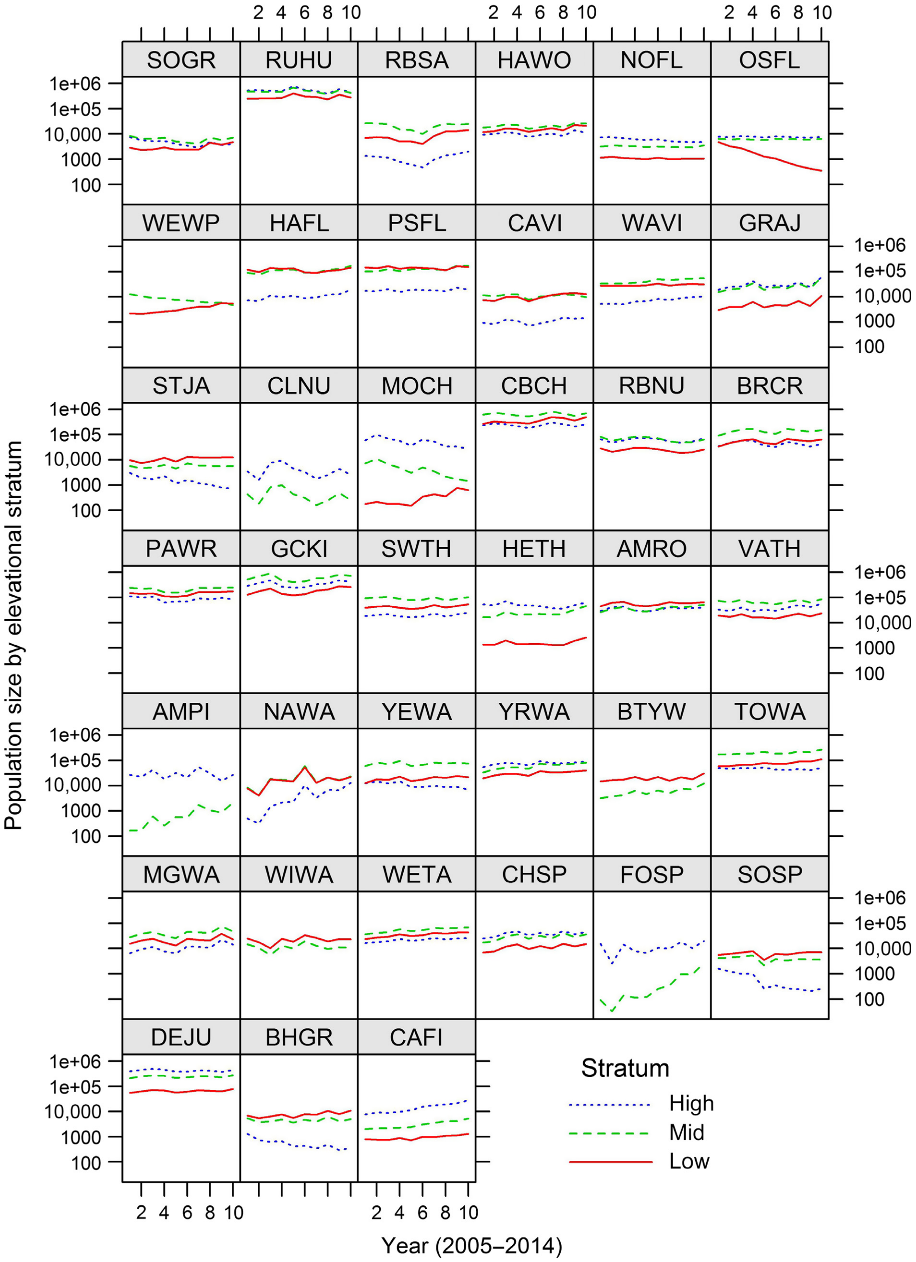

Fig. 5. Annual estimates of population size by elevational stratum. Species codes are defined in Table 3.

residual MST anomaly were positive for only two species (Gray Jay and Swainson's Thrush) and negative for none (Fig. 8). We found no support for interacting effects of PAS and MST, and only Swainson's Thrush showed clear effects of both PAS and MST.

Trends in population density were similar between models with and without climate effects (Kendall's $\tau = 0.827$, $z = 12.763$, $P \ll 0.001$; Appendix S1: Fig. S6). After accounting for effects of climate, year was still an important source of variance in point-estimates of population density across species, with positive year effects in 2007 and 2008 (95% CIs > 0) relative to negative year effects in 2006 and 2009 (95% CIs < 0). A park effect was also evident after

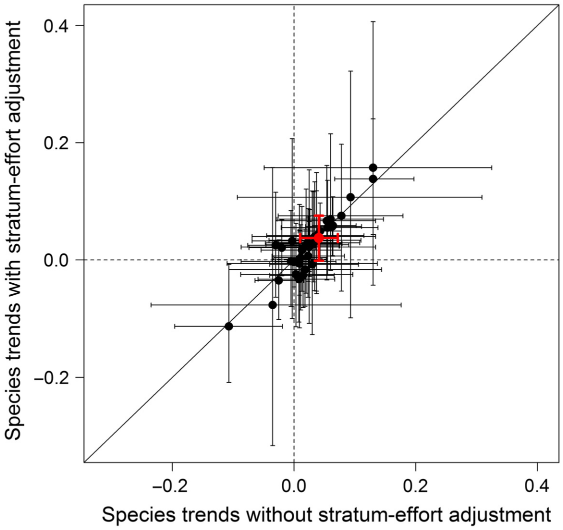

Fig. 6. Effects of sampling effort at the stratum level on estimates of population trend for each focal species. Trend estimates are summarized by means (dots) and 95% credible intervals (bars), and one trend (in red) represents the single species for which differences in stratum-level sampling effort might affect inference: The otherwise positive trend estimate for Townsend's Warbler overlapped zero (slightly) only after adjusting for stratum-level sampling effort.

accounting for climate, and the highest point-estimates of landbird density occurred in NOCA.

Species traits

Posterior estimates of trend and effects of climate did not vary consistently by any of the species traits defined in Table 3, although we identified several suggestive relationships. We graphed parameter point-estimates by species group (Appendix S2) and determined mean effects within groups using Bayesian meta-analysis. Here, we report the 95% credible intervals for mean effects by species group, beginning with our meta-analysis of results grouped by migration habit. For long-distance migrants, the mean trend in sampled population density was positive (shaded 95% CI > 0) in every park; for residents, the mean trend was positive only in OLYM (Appendix S2: Fig. S1a–c). The mean effect of precipitation-as-snow was negative for both resident and migrant species (Appendix S2: Fig. S1d; 95% CI < 0). There was no clear effect of MST on migrant population densities in sampled plots (95% CI = [−0.027, 0.066]), but results from fits to resident population densities (95% CI = [−0.008, 0.117]) tended to be positive (Appendix S2: Fig. S1e). The fit of our climate-based models was similar for migrants and residents (Appendix S2: Fig. S1f), and migration habit did not influence the fit of models for species availability or detection (Appendix S2: Fig. S1g–j); availability and detection fits were similar for migrants and residents both in climate-based models with park-structured trends (Appendix S2: Fig. S1g–h) and in regional models without climate covariates (Appendix S2: Fig. S1i–j). Three species (American Robin, Fox Sparrow, and Dark-eyed Junco) that typically migrate during the non-breeding season appear to reside year-round in or near one of these parks (OLYM; Table 3). However, re-classifying these three species as residents for this analysis had no important effect on results.

Preferred diets included insects (*n* = 31), seeds (*n* = 3), plants (*n* = 1), nectar (*n* = 1), and omnivory (*n* = 3). Neither trend nor response to climate varied appreciably with diet, regardless of how diets were grouped (Appendix S2: Fig. S1k–n), although we note that seedeaters might have trended more positively than other species (Appendix S2: Fig. S1k). Because 31 of our 39 focal species preferred to eat insects, there was little power to detect effects of diet on our results.

Preferred nest locations included ground, shrub, cavity, and tree (Appendix S2: Fig. S1o–r). Although our point-estimates for the effects of climate were somewhat more negative for ground-nesting birds (Appendix S2: Fig. S1q–r), this pattern was not supported by mean group effects derived via meta-analysis (Appendix S2: Fig. S1s–t). By grouping all non-ground-nesters, we avoided a strong correspondence between nesting and residency resulting from the fact that all cavity-nesters in this dataset were residents. There was no correspondence between nesting and diet or diet and residency among these 39 species.

DISCUSSION

Our landbird monitoring program fills a need unmet by other regional and national monitoring efforts, such as the Breeding Bird Survey (BBS; Droege 1990). Mountain parks in the Pacific Northwest are sparsely sampled by the BBS

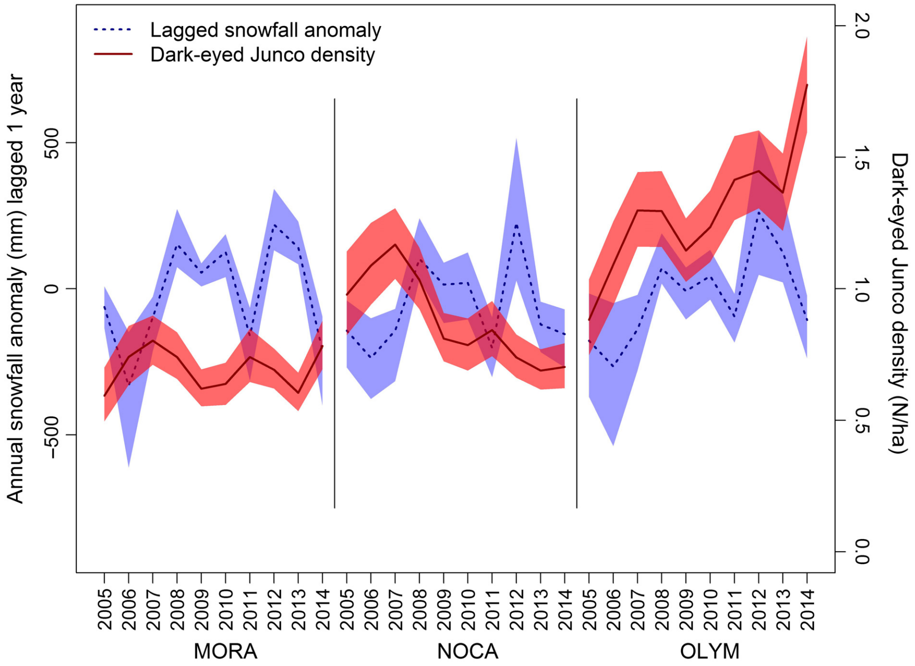

Fig. 7. Annual snowfall anomalies (dashed line) through 31 July of year $t - 1$, and estimates of population density for the Dark-eyed Junco (solid line) derived from point-counts conducted during the summer of year t. Snowfall anomaly was defined as precipitation-as-snow (PAS) in year $t - 1$ divided by mean PAS for 1971–2000, averaged over all plots (point-count stations) in this study. Population density was estimated as number per hectare effectively surveyed at each plot according to the truncation radius for this species (Table 4), averaged over all plots within a park. Shaded areas represent 95% credible intervals for snowfall (blue) and population size (red). MORA, Mount Rainier; NOCA, North Cascades; and OLYM, Olympic National Park.

(Altman and Bart 2001), and BBS data are collected exclusively at roadsides, limiting their value for extending inferences to areas not adjacent to roads (O'Connor 1992, DeSante and George 1994, Sauer 2000). By focusing on mountain parks, our survey design provides data appropriate for addressing management issues in more remote areas and at a finer resolution than typically addressed by the BBS (Sauer and Cooper 2000, Hutto and Young 2002).

Species trends and relationship to recent climate

Our results suggest predominantly stable trends in the population density of landbirds breeding in mountain parks of the Pacific Northwest during 2005–2014. This result is in keeping with broad trends estimated from BBS data, which suggest that breeding birds in forests of the western United States have experienced stasis over the past few decades (Sauer and Link 2011). Our analysis also suggests that many species have responded positively to lower snowfall in recent years, in keeping with the hypothesis that a large fraction of bird species breeding in the United States have been affected positively by recent climate change (Stephens et al. 2016). In corroboration, Butchart et al. (2010) reported a positive trend in the terrestrial Wild Bird Index during the 2000s, reversing two decades of decline in that index.

Precipitation at breeding sites, but not temperature, helped to explain population trends in these parks. Illán et al. (2014) also showed that metrics of precipitation were more predictive than metrics of temperature for forecasting (and hindcasting) a large group of landbird species using BBS data from 1970 to 1974 and 1998 to 2002. Specifically, December precipitation and January temperature were most explanatory in that study. We restricted our exploration of climate to a small set of potential covariates, including metrics of precipitation and temperature

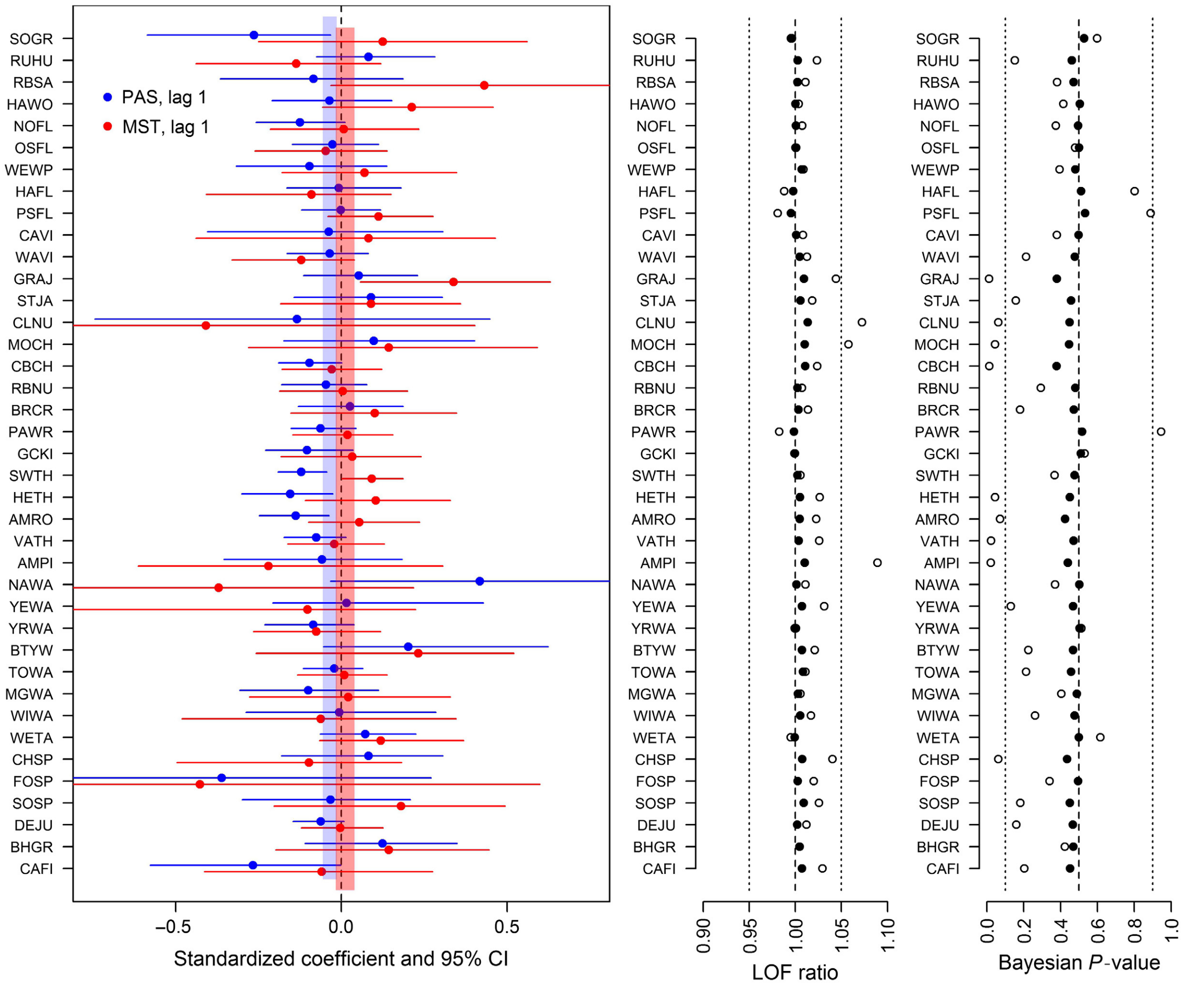

Fig. 8. Summary of climatic effects in hierarchical models of species-specific landbird population density. The left-hand panel summarizes fitted coefficients for fixed effects of lagged precipitation-as-snow (blue) and lagged mean spring temperature (red) on mean population density, log(λ); dots (means) and horizontal lines (95% credible intervals) depict species-specific relationships, while shaded vertical strips depict the mean ± SE of all fitted coefficients of snowfall (blue) and temperature (red). Central and right-hand panels are as in Fig. 3.

expected a priori to affect landbirds in these mountain parks. While our results lend support to the growing consensus that precipitation is playing a strong role in the contemporary dynamics of bird distributions in western North America (Tingley et al. 2012, Illán et al. 2014), it is important to note the relatively minor role of climate in explaining these recent population trends in the Pacific Northwest. This result may be due to the short time series analyzed here and the apparent lack of trends in climate across our sampling points over the past ten years (Appendix S1: Fig. S4).

Relatively weak effects of climate in breeding habitats might be due to more important effects of climate in non-breeding habitats. Nott et al. (2002) reported effects of El Niño/Southern Oscillation and North Atlantic Oscillation events on the dynamics of 10 of 34 landbird species, using data generated from banding studies. Identifying where migrants spend the winter is important when estimating the effects of these events, which are known to vary spatially. Although our analyses should be extended to the non-breeding season when sufficient data are available, we note that resident and migrant trends were largely similar in the current study, suggesting that non-park habitats did not dominate dynamics during this period.

Although effects of climate were weak and dominated by precipitation in this study, MST might have had disproportionate effects on resident species. We expected a positive effect of temperature on resident density, and our results nearly supported one (Appendix S2: Fig. S1e). Warmer springs should facilitate earlier breeding, and residents should be more likely to respond to local variation in spring temperatures on the breeding grounds. Migrant response should be constrained by the timing of migration, which is tied to environmental cues that may be fixed (e.g., day length) or that may be experienced in locations far removed from breeding sites.

We also found little evidence for upslope range shifts across the sampled region: No species increased at higher elevations while declining at lower elevations (Fig. 5). The Olive-sided Flycatcher was the only species to exhibit a strong decline at lower elevations. Although this decline did not appear to be offset by an equivalent increase at higher elevations, this species did increase in MORA (Fig. 4), where there was more high-elevation habitat; recall that there was so little low-elevation habitat in MORA that the boundary between low and middle elevations was set higher (800 m) than in other parks (650 m).

Our meta-analysis suggested declines only in resident species, but few residents were in decline and residency did not appear to explain the population trends and effects of climate we observed. Diet and nesting habit explained even less than residency. Tingley and Beissinger (2013) also reported a lack of correspondence between species traits and patterns of loss in breeding birds of the Sierra Nevada, after exploring a number of taxonomic and life-history affinities. Furthermore, climate does not stand out as the likely driver of species trends in the western United States. Tingley et al. (2012) suggest divergent responses to climate among species in the Sierra Nevada, and our results suggest only weak climatic effects over the past decade. For migrants, trends could have been mediated by climate or other processes operating in non-breeding habitats. After accounting for effects of climate, we found that 2007 and 2008 were relatively "good" years for most species (resident and migrant alike). These years are thus good candidates for analysis of non-breeding habitats and other processes that might affect population dynamics.

It is also worth considering the potential for continuing declines in snowfall and increasingly warmer spring temperatures to enhance the trends we observed. Although the positive trends we observed may have been mediated by a warmer, drier climate, it is unlikely that an increasingly warmer, drier climate would continue to enhance population densities indefinitely. Dramatic declines in snowfall and increasing temperatures are projected for the Pacific Northwest by 2040, and these changes are expected to be especially severe in the three parks studied here (Littell et al. 2009). Given these projections, we might expect landbird densities to stabilize or decline in the future due to climate-mediated stress at some trophic level(s) in this system.

Model fit and flexibility

Our model extends the flexible framework of Amundson et al. (2014) to accommodate count intervals of varying length as in Farnsworth et al. (2002), and to use counts repeated through time to estimate population trends (Appendix S3). The large amount of missing data in our dataset helps to exemplify how this modeling framework can accommodate spatial and temporal variability in survey effort, an important component of many point-count surveys. Our survey effort at each point varied among years due to variation inherent in an alternating panel design (with two out of every six panels surveyed annually) and annual variation in circumstances affecting the number of points surveyed along each transect. Although this variation resulted in missing data for the vast majority of points modeled each year, missing data are conveniently estimated in this Bayesian framework (Kéry and Royle 2016).

Hierarchical models can reduce bias associated with imperfect detection that would otherwise compromise parameter estimates. However, an important assumption of many distance-sampling models is perfect detection at zero distance. This assumption may not hold in avian point-count studies due to observer effects on bird behavior or because birds may be concealed in the forest canopy overhead; in our study, canopy layers can extend 75 m above the observer. Fortunately, the assumption of perfect detection at zero distance is obviated in models that combine distance sampling with the time-removal method to model availability (Farnsworth et al. 2005, Amundson et al. 2014).

Assumptions that continue to require attention in *N*-mixture models include (1) random placement of survey points with respect to the population's distribution; (2) detection of individuals prior to any movement; (3) accurate estimation of distance-to-detection; (4) accurate identification of species and unique individuals; (5) independence between probabilities of individual availability and perceptibility; (6) closure, defined as lack of birth, death, immigration, and emigration during each survey season; and (7) presence of the entire breeding population during each survey season. Observer training and careful design of survey protocols and analyses can help meet these assumptions (Amundson et al. 2014). For example, after censoring 10% of detections—those at the greatest distances (Kéry and Royle 2016)—we found little evidence of rounding error in estimates of dispersal distance. Still, analysis of variance sometimes indicated significant dependence between distance- and time-to-detection, suggesting violation of (5). In these cases, we censored up to 27% (mean = 11%) of detections to avoid significant dependence between detection interval and distance. For several species, we explored the effect of censoring rate on estimates of population density; in agreement with Amundson et al. (2014), we found little effect. However, assumptions 2, 6, and 7 may be more difficult to meet (Alldredge et al. 2007, Simons et al. 2009, Hoekman and Lindberg 2012, Schmidt et al. 2013, Mizel et al. 2017). The timing of arrival on the breeding grounds can vary importantly across the breeding season, and this source of variation cannot be modeled directly in studies based on a single visit to each point during the season. Thus, trends in abundance can be confounded with trends in arrival date (Mizel et al. 2017). Although we found little support for an effect of day on availability, availability was generally quite high among our focal species, such that there was little remnant variance for covariates to explain. Our estimates of perceptibility were lower, however, and model fit was poor for this component of detection in at least 11 of 39 focal species. For these species, exploring random effects of observer, day, or transect on perceptibility rarely improved the detection model. Further modeling of the covariates of perceptibility might be needed to characterize spatial or temporal variation in detection rates affecting estimates of population density for these species. Short of this, we explored different approaches to binning detections by distance, again without effect. For example, substituting five fixed-width bins for the five variable-width bins used in the current analysis had no appreciable effect on parameter estimates or model fit. This result was perhaps surprising because our variable-width bins usually offered superior fits to the half-normal distribution, compared with fixed-width binning.

Our estimates of population density, regional trend, climate effects, year effects, and the parameters controlling components of detection (σ, $r_{\max}$) were robust to variations in model structure; for example, regional trends were similar across models 1 and 3, and park-specific trends were similar across models with and without climate effects. We also expected low bias and high precision in our parameter estimates, given our survey design. Bias and precision in parameter estimates from point-count studies are influenced by joint effects of mean species abundance, detection probability, the number of points surveyed, and the number of counts within a season at a point (here, the number of count intervals during the single annual visit to a point). Lower values for any of these quantities lead to higher bias and lower precision (Yamaura et al. 2016). As in many avian point-count studies, both detectability and mean population density were low for many species in our study. However, the number of points surveyed and effective number of counts per point in our study were high enough to ensure low bias and high precision in our parameter estimates, according to simulations by Yamaura et al. (2016). Nevertheless, some bias in reporting on trends across species is introduced by focusing on species common enough to support parameter estimation. This approach is perhaps unavoidable and is at least justified if the more common species have larger effects on ecosystem structure and function (Gaston and Fuller 2008, Stephens et al. 2016).

Continuing to advance methods in hierarchical modeling of population and community processes will improve our ability to extract meaningful parameter estimates from diverse datasets

(Tingley and Beissinger 2013). Combining data on detection distance and time increases the flexibility and utility of models designed to estimate abundance (Amundson et al. 2014). Collecting data on detection distance and time is straightforward for point-counts and should be more broadly encouraged by the ecological research community (Twedt 2015).

Northwestern parks as a resource for bird conservation

Our analysis revealed important spatial variation in landbird trends among parks, with many species exhibiting a decline in one park offset by an increase elsewhere (Fig. 3). Differences in climate among parks might explain some of this variation. For example, the relatively negative snowfall anomaly at NOCA might explain the tendency for migrants to increase in that park. Spatiotemporal differences in habitat quality among parks might also contribute to the recent stability of these species, as might the interaction between habitat and climate. For some montane species, these parks might collectively support part of a metapopulation with local dynamics that are sufficiently independent to generate regional stability (Hanski and Gilpin 1997). If so, these parks may function as a network of habitats that vary from year to year in their importance as breeding habitat and potential refugia for particular species (Hejl et al. 1988, Blandón et al. 2016, Duarte et al. 2016). An example might be the Dark-eyed Junco, with opposing trends in two parks (Fig. 4) but stability within each elevational stratum (Appendix S1: Table S1, Fig. S3). As annual conditions change, a network of protected areas might provide dynamic refugia for landbird species.

Our results might also shed light on competing hypotheses of range shift in response to climate change. Species are expected to move into higher terrain and more temperate climates in response to warming temperatures (Chen et al. 2011, but see Tingley et al. 2012). Perhaps some migrants have shifted their use of breeding habitats toward these mountain parks, resulting in the positive trends we observed. If migrants are increasing their use of mountain parks at the expense of other habitats, our breeding-season surveys might infer population stability or increase in spite of losses due to, for example, degradation of the winter habitats that migrants use. However, increased use of mountain parks seems unlikely given that we failed to find evidence for increased use of higher-elevation habitats within these parks.

Although we have begun to address the potential for elevational shifts in habitat use that might confound trend estimates, it is more difficult to address shifts in arrival time (Mizel et al. 2017) using single-visit studies (Schmidt et al. 2013). Our results at least suggest that processes related to population loss have not dominated dynamics in the montane Pacific Northwest. However, it is at least conceivable that trends in climate or other factors have influenced arrival date and, in turn, detection probability in ways that have countered our ability to detect declines in abundance. Although we observed no trends in PAS or MST, two metrics of breeding-season climate, it will be important to investigate other potentially influential aspects of climate that these populations encounter throughout the year.

While the climatic variation that we considered appears to have been largely beneficial to the landbird populations we studied, climatic and other stressors will likely increase over time and challenge national park resources (National Park System Advisory Board Science Committee 2012, Monahan and Fisichelli 2014). Mountainous regions with steep and complex terrain, such as those we sampled, can function as climate refugia and can be harnessed in contemporary plans for critical habitat management and species conservation in the face of climate change (Morelli et al. 2016). Using robust estimators that incorporate effects of climate can contribute meaningfully to efforts to conserve the complex ecological communities that represent our natural resources.

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Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1902/full