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Trends in Passerine Abundance in Denali National Park and Preserve, Alaska from 1995–2025

A singing fox sparrow.
NPS / JARED HUGHEY

Trends in Passerine Abundance in Denali National Park and Preserve, Alaska from 1995–2025

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Abstract

Here, we assess trends in the relative abundance of six forest-adapted and six shrub-adapted passerines from point count data collected along the Denali Park Road from 1995–2025. We found pervasive, positive trends among forest-adapted passerines, suggesting conifer expansion as a primary driver of changes in abundance within this assemblage. We found weaker evidence of changes in abundance among shrub-adapted passerines with only fox sparrow and savannah sparrow showing strong evidence of declines. Notably, we found no evidence of increasing abundance in this assemblage despite the observed expansion of deciduous shrubs within our sampling frame. This is consistent with previous work in Denali showing a weak response by shrub-adapted passerines to shrub expansion, possibly due to suboptimal structural characteristics of the expanding shrub cover, such as shorter height and a relatively diffuse distribution. Trends for forest-adapted passerines in Denali differed strongly from those estimated at the broader Bird Conservation Region (BCR) scale from North American Breeding Bird Survey (BBS) data, likely reflecting differences in the vegetation gradients captured by the two sampling frames. Where the BCR-level trends were stable, the trends in Denali were strongly negative (American robin) or positive (Swainson’s thrush and varied thrush). Where the BCR-level trends were strongly negative, the trends in Denali were strongly positive (dark-eyed junco, ruby-crowned kinglet, and yellow-rumped warbler). The BBS effort in Alaska is concentrated in below-treeline areas within the central boreal belt whereas our sampling frame along the Denali Park Road traverses both treeline and shrubline, making its passerine trends more susceptible to the effects of expanding trees and shrubs.

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Introduction

In 1992, Alaska Bird Observatory biologists began conducting bird surveys along the Denali Park Road. This effort was supported by the prototype version of the National Park Service's Inventory and Monitoring Program and later incorporated into the Central Alaska Network's monitoring program. For those initiating these surveys, the park road was a means for accessing the boreal-tundra landscape, and they could not have fully anticipated its importance as an elevational transect. The park road traverses both treeline and alpine shrubline and, consequently, is uniquely situated for understanding vegetation-driven shifts in bird distribution. The expansion of woody vegetation (erect shrubs and trees) is one of the more widespread and conspicuous phenomena affecting boreal-tundra regions under a warming climate. Upslope advances in treeline and shrubline (Harsch et al. 2009; Myers-Smith and Hik 2018) and colonization by tall shrubs along riparian corridors and on hillslopes are evident across the circumpolar Arctic (Myers-Smith et al. 2011; Tape et al. 2006) and Subarctic (Brodie et al. 2019; Frost et al. 2023; Stueve et al. 2011; Roland et al. 2013, 2016).

Such conspicuous vegetation change prompted Mizel et al. (2023) to assess the separate roles of shrub and conifer expansion on passerine abundance along the Denali Park Road. They found that forest- and shrub-adapted passerines showed contrasting and nonintuitive responses. While forest-adapted species were most sensitive to shrub and conifer expansion above initial treeline (i.e., its position in 1995), shrub-adapted species were most sensitive to shrub and conifer infilling below initial treeline. Specifically, shrub-adapted passerines responded weakly to shrub expansion above initial treeline but showed strong negative responses to conifer expansion below initial treeline. The latter process was also evidenced by upslope shifts in the elevational optima of shrub-adapted passerines (i.e., where their abundance peaked) that coincided with the leading edge of increasing conifer cover. These results suggest that tree and shrub encroachment below treeline, mainly in the form of conifer infilling, may be pushing the elevational optima of shrub-adapted passerines upslope rather than these species following the pull of modest shrub expansion above treeline.

This mechanistic understanding of changes in abundance is critical for placing local-scale trends in a broader context. Nevertheless, resource managers also require estimates of trends or interval-specific summaries of population change (Link and Sauer 1998). Here, we estimate trends in the relative abundance of six forest-adapted and six shrub-adapted passerines from point count data collected along the Denali Park Road from 1995–2025. We expected forest-adapted passerines to show stable to increasing abundance based on prior work documenting their positive response to conifer expansion in Denali (Mizel et al. 2023). We expected shrub-adapted passerines to show declining trends based on their observed negative response to treeline advance and conifer infilling (Mizel et al. 2023).

Methods

Passerine Count Data

Our study area along the Denali Park Road (hereafter, park road) traverses upland coniferous forest, sparsely canopied woodland at treeline, dense riparian and upland shrublands, open shrublands within passes and near shrubline, and alpine habitats including *Dryas*, mixed dwarf shrub tundra, and fellfield.

Alaska Bird Observatory biologists established three roadside survey routes, comprising a total of 156 point count stations with 0.8 km spacing along the park road. From 1995–2025, trained observers from the Alaska Bird Observatory (1995–2000) and the National Park Service (2001–2025) conducted surveys during mid-April to early July. In 20 of the 31 survey years, we followed a repeat visit protocol wherein points were each surveyed an average of 5.3 times. The remaining years generally followed a single visit protocol.

During each 3-minute point count survey, all birds seen or heard within 400 m during the count period were recorded. We only used detections of singing males for analysis and restricted analyses to the twelve most abundant species (six shrub-adapted and six forest-adapted species; Table 1) to ensure sufficient data for model fitting. The species-specific data were structured as a series of counts made at site $j = 1, 2, \ldots J$, during repeat survey $k = 1, 2, \ldots K$, in year $t = 1, 2, \ldots T$.

Table 1. Posterior medians for the trend coefficients on the zero-inflation probability θ_2 and the Poisson mean ζ for passerines in Denali (1995–2025). Only models for forest-adapted species were zero-inflated. The forest-adapted species are listed first followed by the shrub-adapted species beginning with fox sparrow.

	θ_2			**ζ**		
Species	**median**	***q2.5***	***q97.5***	**median**	***q2.5***	***q97.5***
American robin	−1.33 ^{A}	−1.54 ^{A}	−1.15 ^{A}	0.14	−0.01	0.29
Dark-eyed junco	−0.68 ^{A}	−1.19 ^{A}	−0.33 ^{A}	0.08	−0.14	0.32
Varied thrush	−1.42 ^{A}	−1.84 ^{A}	−1.09 ^{A}	0.17	−0.01	0.35
Yellow-rumped warbler	−0.61 ^{A}	−0.89 ^{A}	−0.35 ^{A}	0.25	0.06	0.44
Swainson’s thrush	−0.70 ^{A}	−1.08 ^{A}	−0.38 ^{A}	0.04	−0.20	0.29
Ruby-crowned kinglet	0.62 ^{A}	0.29 ^{A}	1.01 ^{A}	−0.20 ^{A}	−0.32 ^{A}	−0.08 ^{A}
Fox sparrow	–	–	–	−0.22 ^{A}	−0.38 ^{A}	−0.04 ^{A}
Savannah sparrow	–	–	–	−0.15 ^{A}	−0.30 ^{A}	0.00 ^{A}
Wilson’s warbler	–	–	–	−0.10	−0.25	0.07
Orange-crowned warbler	–	–	–	−0.06	−0.20	0.08
American tree sparrow	–	–	–	−0.07	−0.17	0.03
White-crowned sparrow	–	–	–	0.01	−0.10	0.12

^{A} The 95% credible interval (or the values spanning the lower (q2.5) and upper (q97.5) quantiles) does not overlap 0, also shown shaded gray.

Shrub-Adapted Passerine Models

We modeled the relative abundance of shrub-adapted passerines using overdispersed Poisson regression. The log-transform of mean abundance λ_{jt} was:

$$\log(\lambda_{jt}) = \beta_0 + \mathrm{X}_j'\boldsymbol{\beta} + \mathrm{Z}_{jkt}'\boldsymbol{\alpha} + \zeta year_t + \delta_t + \eta_j + \omega_g + \varepsilon_{jt}$$

where β_0 is an intercept, $\boldsymbol{\beta}$ and $\boldsymbol{\alpha}$ are vectors of coefficients, X'_j and Z'_{jkt} are matrices of habitat and availability covariates, respectively, ζ is a trend term, δ_t are mean-zero, normal random variables for each year, η_j accommodates spatial correlation, ω_g are mean-zero normal random variables for each observer, $g = 1, 2, \dots 26$, and ε_{jt} are mean-zero normal random variables for each site-year. The η_j are multivariate normal realizations of a spatial Gaussian process with a variance-covariance matrix defined by an exponentiated quadratic function of the inter-point distances with marginal standard deviation τ and the length-scale ρ.

The availability covariates included the linear and quadratic effects of time since sunrise and the linear, quadratic, and cubic effects of Julian date. With the exception of savannah sparrow (*Passerculus sandwichensis*), the habitat effects included the combined cover of willow (*Salix* spp.) and alder (*Alnus* spp.) shrubs, the cover of dwarf birch (*Betula nana*), the interaction of the previous two variables, and a binary variable which was 1 when tree cover was < 8% and was 0 otherwise. These effects were intended to capture the known positive response of tall shrub-adapted passerines to both willow and alder shrub cover and a weak response to dwarf birch cover (Mizel 2025). In contrast, savannah sparrow shows higher densities at intermediate deciduous shrub cover (Mizel 2025). Thus, for savannah sparrow, we specified an effect for the presence–absence of tree cover < 8% and the linear and quadratic effects of the combined cover of willow and dwarf birch shrubs.

The tree and shrub cover covariates were extracted from the raster maps of Nawrocki (2021) using the mean values within a 200-m buffer around each point. These maps represent percentage cover (circum–2020) at a 10-m resolution and are the result of applying hierarchical statistical learning models that integrated environmental, multi-season spectral, and surface texture covariates.

Forest-Adapted Passerine Models

Only 66 of the 156 points had >5% tree cover within a 200-m radius according to the Nawrocki (2021) raster maps, resulting in an excessive number of zero counts for forest-adapted passerines under a Poisson distribution. Thus, we modeled the relative abundance of forest-adapted passerines using zero-inflated Poisson regression, which is a mixture of Poisson and Bernoulli probability mass functions. The latter component has parameter θ which is the probability of observing a count with a Poisson distribution. We specified a model for its logit-transform:

$$logit(\theta_{jt}) = \theta_0 + \theta_1 tree\ cover_j + \theta_2 year_t$$

where θ_0 is the intercept, θ_1 is the effect of coniferous and deciduous tree cover (Nawrocki 2021), and θ_2 is a trend term.

The model for the log-transform of the Poisson mean parameter λ was the same as the one used for shrub-adapted passerines with two exceptions. We only estimated one habitat effect (tree cover) and the η_j were mean-zero, normal random variables rather than outcomes of a spatial Gaussian process. The latter simplification was made due to the lower abundance of forest-adapted passerines and their restricted distribution in our sampling frame, both of which resulted in limited information for estimating the Gaussian process kernel.

Model Summary and Implementation

Inferences about changes in abundance over time were based on whether the 95% credible intervals (CI) for trend terms included 0. The zero-inflated Poisson models used for forest-adapted passerines included trend terms on both the zero-inflation probability θ and the Poisson mean λ. Thus, we made inferences about changes in abundance based on whether either or both trend terms had 95% CIs that did not include 0. In contrast, the overdispersed Poisson models used for shrub-adapted passerines included a single trend term from which we could make our inferences.

We also compared trends in Denali to those estimated from the North American Breeding Bird Survey (BBS) in the Northwestern Interior Forest Bird Conservation Region (BCR 4) between 1995–2022 (Sauer et al. 2020). The BBS summarizes changes in abundance at the BCR-level using the geometric mean of proportional change (hereafter, the interval-specific trend), which we calculated for our $T = 31$-year dataset as:

$$B = 100 \times \left(\left(\frac{n_T}{n_1} \right)^{1/(T-1)} - 1 \right)$$

where

$$n_t = \exp\left(\beta_0 + \zeta year_t + \delta_t + 0.5\tau^2 + 0.5\sigma_\varepsilon^2\right)$$

and

$$n_t = \left(1 - \frac{exp(\theta_0 + \theta_2 year_t)}{(1 + exp(\theta_0 + \theta_2 year_t))}\right) \times \exp\left(\beta_0 + \zeta year_t + \delta_t + 0.5\sigma_\eta^2 + 0.5\sigma_\varepsilon^2\right)$$

for shrub- and forest-adapted passerines, respectively.

We fit models in a Bayesian framework using Stan (Stan Development Team 2025) via R (R Core Development Team 2025) and the package cmdstanR (Gabry et al. 2025). We used a non-centered parameterization (Papaspiliopoulos et al. 2007) for efficient exploration of the posterior. We specified weakly informative priors for all regression parameters (e.g., *Normal*(0,1)) and *Half–t*(3,0,1) for the hierarchical standard deviation parameters. We assessed convergence by examining trace and scatter plots of posterior draws and by determining that $\hat{R}$ values were ≤ 1.01 for all parameters (Gelman and Rubin 1992). Continuous covariates were scaled to have mean = 0 and standard deviation = 1 to improve convergence properties. Code and data for running models are available at https://irma.nps.gov/DataStore/Reference/Profile/2317800 (Mizel 2026).

Results

Trend Coefficients

Except for a decline in American robin (*Turdus migratorius*) abundance, forest-adapted species showed positive trends (Table 1; Figure 1). These trends were largely driven by changes in the zero-inflation probability θ. That is, among forest-adapted species except American robin, the trend coefficients on θ, but not those on λ, had 95% CIs that did not overlap 0 (Table 1). For American robin, the 95% CIs for both trend coefficients did not include 0 (Table 1). The evidence for changes in the abundance of shrub-adapted passerines was weaker with only fox sparrow (*Passerella iliaca*) and savannah sparrow showing evidence of declines (Table 1; Figure 2).

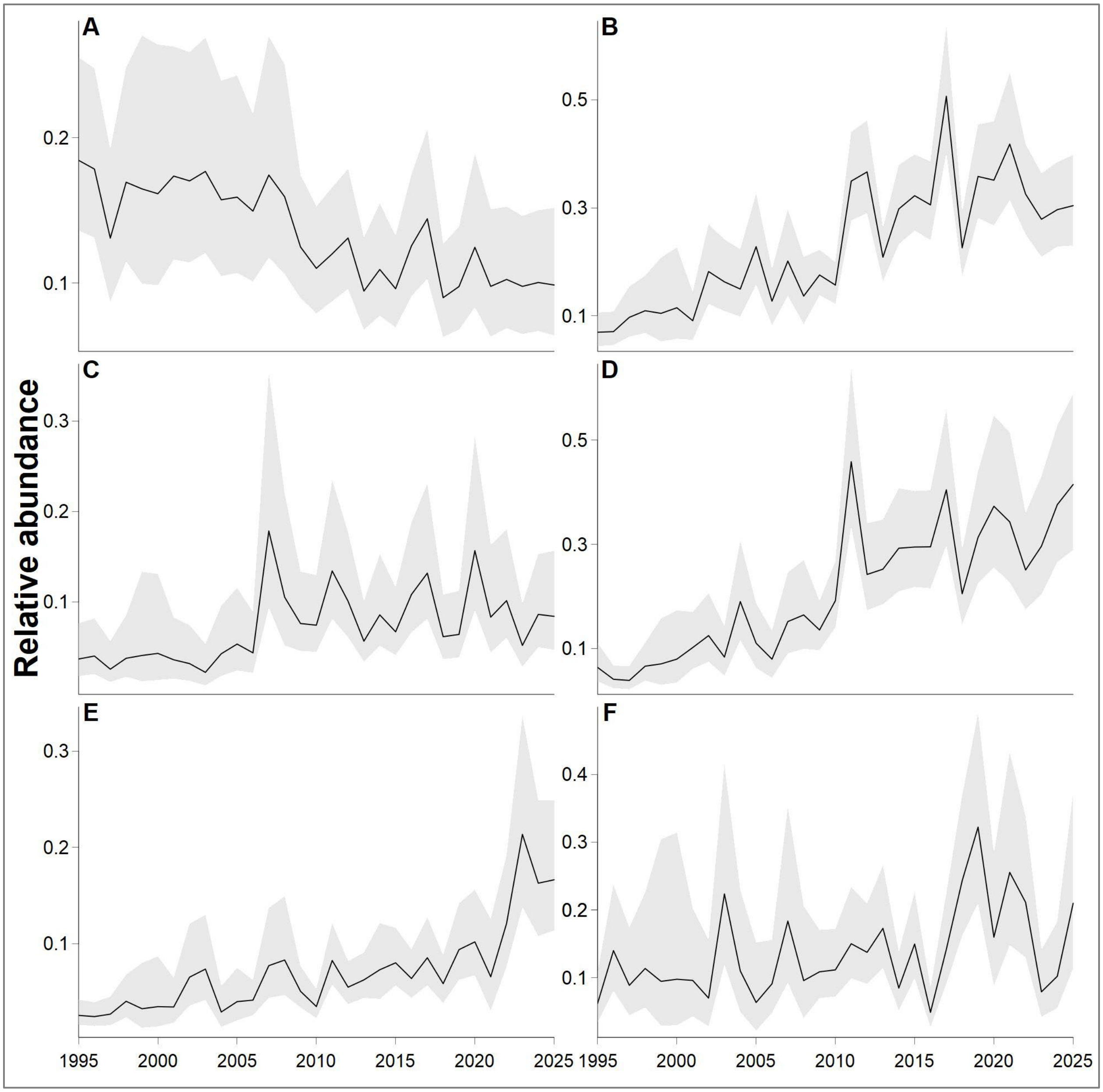

Figure 1. Mean abundance of forest-adapted species from 1995–2025. The black line is the posterior median and the shaded region is the 95% CI. Species include: A) American robin, B) dark-eyed junco, C) varied thrush, D) yellow-rumped (myrtle) warbler, E) Swainson's thrush, and F) ruby-crowned kinglet.

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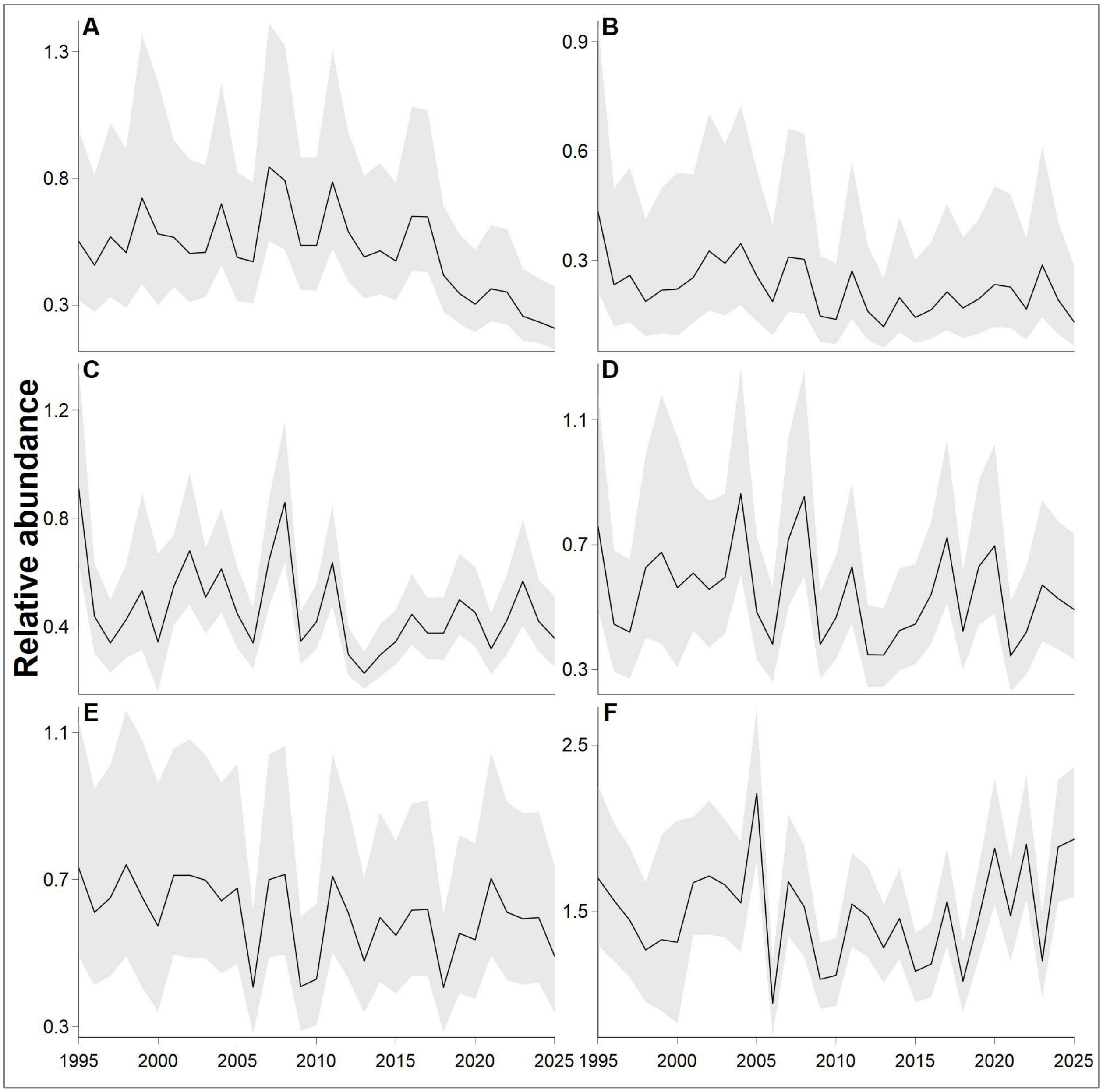

Figure 2. Mean abundance of shrub-adapted species from 1995–2025. The black line is the posterior median and the shaded region is the 95% CI. Species include: A) fox sparrow, B) savannah sparrow, C) Wilson's warbler, D) orange-crowned warbler, E) American tree sparrow, and F) white-crowned sparrow. *NPS / JEREMY MIZEL*

Comparisons with the BBS Using the Interval-Specific Trends

Among forest-adapted passerines, the interval-specific trends (i.e., the geometric means of proportional change) in Denali differed strongly from those estimated at the BCR-level (Table 2). Specifically, three species (dark-eyed junco (*Junco hyemalis*), ruby-crowned kinglet (*Corthylio calendula*), and yellow-rumped warbler (*Setophaga coronata*)) had strong positive trends in Denali as opposed to strong negative trends at the BCR-level. The remaining forest-adapted species (varied thrush (*Ixoreus naevius*), Swainson's thrush (*Catharus ustulatus*), and American robin) had strong positive or negative trends in Denali but showed weak evidence of change at the BCR-level.

Table 2. Interval-specific trend estimates (the posterior median of the geometric mean of proportional changes in abundance) for Denali (1995–2025) and BCR 4 (Northwestern Interior Forest; 1995–2022). The latter was extracted from Sauer et al. (2020). The forest-adapted species are listed first followed by the shrub-adapted species beginning with fox sparrow.

	Denali			**BCR 4**		
Species	**median**	***q2.5***	***q97.5***	**median**	***q2.5***	***q97.5***
American robin	−2.06 A	−3.54 A	−0.68 A	−0.24	−0.71	0.24
Dark-eyed junco	5.02 A	3.32 A	6.80 A	−1.09 A	−1.69 A	−0.50 A
Varied thrush	2.80 A	0.26 A	5.50 A	−1.77	−2.93	0.06
Yellow-rumped warbler	6.45 A	4.25 A	8.67 A	−0.94 A	−1.61 A	−0.30 A
Swainson's thrush	6.44 A	4.63 A	8.31 A	0.04	−0.41	0.48
Ruby-crowned kinglet	4.13 A	1.58 A	6.76 A	−1.79 A	−2.75 A	−0.79 A
Fox sparrow	−3.17 A	−4.99 A	−1.36 A	−0.14	−0.97	0.63
Savannah sparrow	−3.90 A	−5.45 A	−2.39 A	−3.52 A	−4.56 A	−2.42 A
Wilson's warbler	−3.07 A	−4.54 A	−1.66 A	−1.55 A	−2.54 A	−0.12 A
Orange-crowned warbler	−1.44 A	−2.83 A	−0.02 A	−1.81 A	−2.64 A	−0.87 A
American tree sparrow	−1.32 A	−2.34 A	−0.32 A	0.20	−1.46	2.46
White-crowned sparrow	0.42	−0.58	1.43	−1.52 A	−2.19 A	−0.85 A

A The 95% credible interval (or the values spanning the lower (*q*2.5) and upper (*q*97.5) quantiles) do not overlap 0, also shown shaded gray.

Within Denali, the interval-specific trends were strongly negative for shrub-adapted passerines except white-crowned sparrow (*Zonotrichia leucophrys*) which contrasted with the much weaker evidence of changes from the trend coefficient estimates (Table 2). Inferences from the interval-specific trends likely differed from those provided by trend coefficients as the former included the stochastic year effects from the first and last years of the interval. Notably, several shrub-adapted passerines showed stochastically high abundance in the first survey year which, in turn, made the interval-specific trends more likely to be strongly negative (Figure 2, C–D).

Nonetheless, the interval-specific trends for shrub-adapted passerines were relatively similar between Denali and the BCR-level (Table 2). Specifically, three species (savannah sparrow, Wilson's warbler (*Cardellina pusilla*), and orange-crowned warbler (*Leiothlypis celata*)) had negative trends at both scales. However, the remaining three species (fox sparrow, white-crowned sparrow (*Zonotrichia leucophrys*), and American tree sparrow (*Spizelloides arborea*)) showed negative trends at one scale (Denali or BCR 4) while being stable at the other (Table 2).

Discussion

Here, we found pervasive, positive trends among forest-adapted passerines in Denali over a 31-year period, suggesting conifer expansion as a primary driver of change in abundance within this assemblage. Further, these positive trends were primarily driven by decreases in the zero-inflation probability (as opposed to changes in the Poisson mean), likely reflecting slow conifer recruitment inducing incremental increases in the probability of presence of forest-adapted passerines (Mizel et al. 2016). The only exception to this pattern was the declining abundance of American robin. American robin differs from other forest-adapted passerines in Denali by virtue of having a bimodal distribution with peaks in abundance both below and above treeline (Mizel et al. 2016). Mizel et al. (2016) documented decreasing American robin occupancy probability at higher elevations in Denali over time while low elevation occupancy was relatively stable. Thus, the negative trend in American robin abundance observed here likely reflects decreased abundance above treeline, although the mechanism remains unknown.

We found weaker evidence of changes in abundance among shrub-adapted passerines with only fox sparrow and savannah sparrow showing strong evidence of declines on the basis of trend coefficient estimates. We also found no evidence of increasing abundance in this assemblage despite the observed expansion of deciduous shrubs within our sampling frame (Brodie et al. 2019). This is consistent with previous work in Denali showing a weak response by shrub-adapted passerines to what is modest shrub expansion (Mizel et al. 2023). Mizel et al. (2023) and Mizel (2024) suggested that such a weak response may reflect structural characteristics of the expanding shrub cover, such as shorter height and a more diffuse distribution, that are not preferred by tall shrub-adapted passerines. The observed weak response to shrub expansion could also reflect floristic characteristics of expanding shrub cover, namely a predominance of dwarf birch which sees considerably less passerine use than willow and alder shrubs (Mizel 2025).

Trends for forest-adapted passerines in Denali differed strongly from those estimated at the BCR-level. Among half of the forest-adapted species that we considered, the BCR-level trends were stable while those estimated for Denali were either strongly negative or positive. Among the remaining forest-adapted species that we considered, the BCR-level trends were consistently negative while the trends estimated for Denali were consistently positive. In contrast, Handel and Sauer (2017) found weak evidence of opposing trend directions between the BBS (BCR 4) and a statewide off-road monitoring effort (the Alaska Landbird Monitoring Survey; ALMS). This likely reflects the greater alignment of the ALMS and BBS efforts in terms of primarily sampling in below-treeline areas within Alaska’s central boreal belt rather than the near- and above-treeline habitat that predominates within the Denali Park Road corridor. Thus, Denali’s passerine monitoring is well-positioned to provide valuable context to regional scale trends that may not capture distributional change.

Spatially variable vegetation change is well documented throughout the circumpolar North (Epstein et al. 2013; Myers-Smith et al. 2011; Ropars and Boudreau 2012; Sturm et al. 2001; Tape et al. 2006), suggesting that passerine trends within these regions are likely to show similar spatial heterogeneity. The below-treeline emphasis of BBS sampling in Alaska coupled with the estimation of simple trends alone (i.e., absent the effects of the local environment) may mask distributional shifts into more poorly sampled areas (i.e., near- and above-treeline). Thus, directly addressing the effects of the local environment in models (e.g., time-varying conifer and deciduous shrub cover; Mizel et al. 2023) may increase the interpretability of their results for conservation.

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