Species Traits Predict Local Population Change Above and Beyond Regional Trend

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Abstract

Why do some populations persist in the face of environmental change while others decline? We tested the extent to which variation in local population change across species is attributable to three species traits: (i) habitat selectivity, (ii) temperature niche position, and (iii) degree of insectivory, with the null hypothesis that local trends are simply a reflection of broader regional trends. We modeled population change for 60 bird species on 806 route-years from 2000-2025 using the North Carolina Mini Breeding Bird Survey (NCMBBS), a long-term population survey of uniquely high spatial resolution, in a Bayesian hierarchical framework. Unlike previous studies, our studied species are all competing in the same landscape and experiencing the same changes in habitat and climate over time, allowing us to isolate the effects of species traits on ‘winners’ and ‘losers’ in a local landscape. We found that more species in the study area are in decline (56.7%) than are increasing (26.7%) or stable (16.7%). Local

population change was positively related to regional trends, though local population change was generally more extreme. Above and beyond the influence of regional population trend, temperature niche position and habitat selectivity also predicted which species ‘win’ and ‘lose’, with species at the warm edge of their temperature niches and habitat specialists both more likely to decline. There was a weak positive effect of diet percent insectivory, but this likely reflects that grassland species, often not obligate insectivores, are in steeper decline rather than that insectivory provides a population benefit. We extend the frameworks set up in larger, but coarser scale, studies to show these species traits indeed shape avian populations and communities at the local level, above and beyond how they shape populations regionally.

Key Words: birds, breeding bird survey, North Carolina, piedmont, population trends, scale, species traits, winners and losers

Lay Summary

In our changing world, why do some bird species thrive while others decline? We hypothesized that species traits would predict population change for 60 species from 2000-2025 on the North Carolina Mini Breeding Bird Survey. We tested whether population change could be predicted by (i) how many habitats the species uses, (ii) how warm the study area was relative to temperatures throughout their breeding range, (iii) how much their diet relies on insects, and (iv) species population change at the broader regional scale. If species traits were not important for predicting population change, only (iv) the regional trend would be predictive. We found more species in the

study are in decline (56.7%) than are increasing (26.7%) or stable (16.7%). Habitat specialists and species for whom the study area was warmer were more likely to decline. There was little to no effect of insect reliance. Results emphasize that species traits affect local bird population trends beyond what is captured by regional trends, highlighting how ecological dynamics vary across species' ranges.

Introduction

Birds are faced with a wide array of challenges, chiefly among them urbanization and habitat loss, shifting spring phenology, and climate change. Between 1970-2017, the overall population of North American birds declined by 29% (Rosenberg et al. 2019). And yet despite widespread declines in many species, some species may indeed be global change winners. Hawks and raptors have increased after recovery from DDT (Bierregaard et al. 2014, Nygård et al. 2019), and habitat protection and management has facilitated population increases for many waterfowl species (Rosenberg et al. 2019). Understanding the attributes of a species that help explain why some populations are able to persist or even increase in the face of global environmental change while others decline is a critical goal of conservation biology.

Various studies have found relationships between avian population trends and species traits (Sullivan et al. 2015, Mason et al. 2019, Morelli et al. 2020, Stevens et al. 2024). With global change we may expect specialist species to be replaced by generalists who can better withstand environmental variation (Wilson & Yoshimura 1994, Clavel et al. 2011). Bird species with negative population trends tend to be more specialized across an array of ecological traits compared to species with positive

population trends (Morelli et al. 2020), and specialization in habitat and diet may play the largest roles in driving this relationship (Salido et al. 2012). Habitat specialists tend to respond more negatively to landscape disturbances (Devictor et al. 2008) and may therefore be most vulnerable to global change, across habitat types (Sullivan et al. 2015) and eco-regions (Stevens et al. 2024). Wider diet niche breadths and lower diet specialization have been found to be positively correlated with avian population trends in both the UK (Salido et al. 2012) and North America (DiCecco & Hurlbert 2022). Widespread insect declines (Wagner 2020) and increasing phenological mismatch with caterpillars (Visser at al. 2006, Burgess et al. 2018, Belitz et al. 2025), may negatively impact the populations of insectivorous birds more than omnivorous birds with widespread diets (Salido et al. 2012).

Habitat- and diet-related traits are typically characterized at the species level, and have often been used to explain species-wide responses in overall population trend, geographic range size, or urban tolerance (e.g. Di Cecco & Hurlbert 2022, Neate-Clegg et al. 2023). However, population trends within a species can be geographically variable–the same species may be a ‘winner’ in one part of its range and yet a ‘loser’ in another (Stanley et al. 2014). Most North American bird species exhibit spatial variation in population trends across their ranges, and aggregating to the regional scale can obfuscate where populations are doing poorly and why (Johnston et al. 2025). Climate, in particular, varies across a species' geographic range, as does the extent to which climate has been changing. Warming generally has negative impacts on both survival and fitness across taxa (Cunningham et al. 2021, Jørgensen et al. 2022), but its effects are context dependent. Populations on the warmer edges of a species range are more

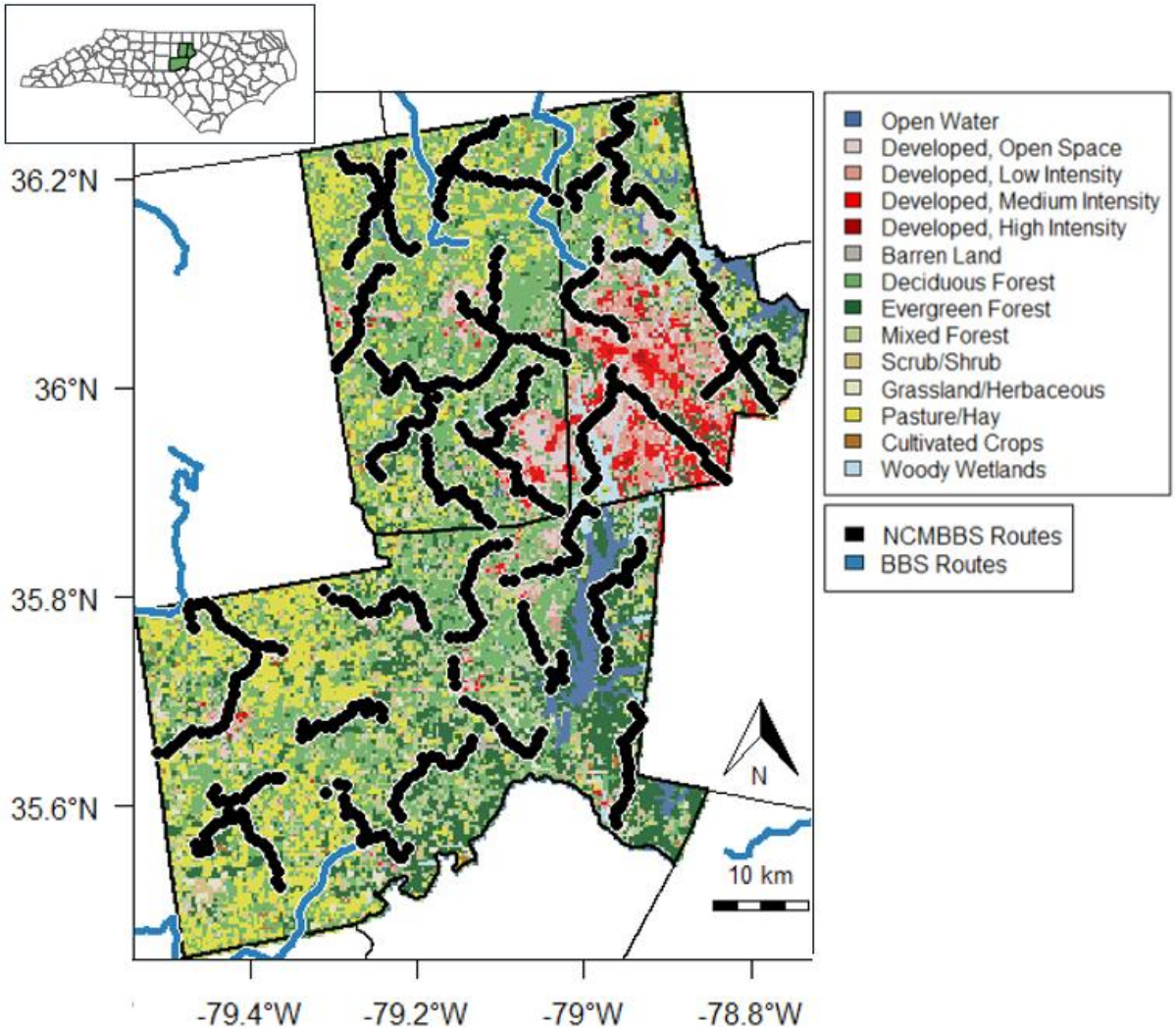
93 likely to decline (Chen et al. 2011), while populations on colder edges may actually
94 experience population increases and expand with increased warming (Rushing et al.
95 2020). Temperature niche position, the temperature of a locality relative to the range of
96 temperatures experienced by a species across its range, is an example of a location-
97 specific species trait that may be more useful than species-level traits for explaining
98 local trends (Manthey et al. 2015).
99 Together, these studies suggest that multiple trait axes may be important for
100 predicting population change. However, most assessments of population trends, and
101 the role that traits play in these processes, are typically approached at a range-wide or
102 regional scale (Sullivan et al. 2015, Mason et al. 2019, Morelli et al. 2020, Stevens et al.
103 2024). Local trends at fine spatial scales are more likely to capture important ecological
104 dynamics that might otherwise be averaged out over large regions. As for comparing
105 trends across species, within a given continent-wide analysis those species are often
106 not occupying and competing within the same landscapes as they would in a more
107 local-scale study, even though their ranges might overlap to varying degrees. Whether
108 species' traits that have been implicated at larger scales can also explain local-scale
109 trends remains largely unknown.
110 Here, we make use of a unique dataset of local population trends, the North
111 Carolina Mini Breeding Bird Survey (NCMBBS, Goulden et al. *in press*), to evaluate the
112 influence of species traits on local winners and losers while controlling for local
113 conditions and known regional population change. The null expectation is that local
114 winners and losers are simply a reflection of larger regional population trends. However,
115 relative to regional trends, we hypothesize that more negative local population trends

should be apparent for (i) habitat specialists that can only utilize a subset of habitat types (ii) insect specialists which are more vulnerable to insect declines and potential phenological mismatch, and (iii) species on the warm edge of their temperature niche.

Methods

Avian Population Data

The North Carolina Mini Breeding-Bird Survey (NCMBBS) is an ongoing community science project in which volunteers have conducted annual breeding season surveys along 34 systematic routes in central North Carolina since 1999 (Goulden et al. *in press*). Survey routes are 9.5 miles long and consist of 20 stops, with three-minute point counts conducted every half mile. Compared to national monitoring efforts (Sauer et al., 2017), the NCMBBS's closely spaced routes provide thorough coverage of a relatively small area, with a 6-fold higher spatial resolution in terms of kilometers of survey route per square kilometer.



131

132 Figure 1. Map of the study area in central North Carolina. North Carolina Mini Breeding
133 Bird Survey routes (NCMBBS) are shown in black atop National Land Cover Database data.
134 North American Breeding Bird Survey (BBS) routes are shown in blue.

135 Alt text: Map showing the distribution of North Carolina Mini Breeding Bird Survey routes
136 across the study area.

137 We used data starting from 2000 when at least two-thirds of the routes had been
138 sampled, as routes were gradually added to the project from 1999-2001. Filtering for
139 bird species observed for at least 9 years on 5 survey routes provided 61 species
140 suitable for analysis. This filter excludes species that are seen too sparsely in time or on

too few routes to have confidence drawing conclusions about their local trends. These may be species that are poorly sampled by roadside surveys (e.g. owls, hawks, waterbirds), species which experienced the majority of their declines before the surveys began, or species which have only recently expanded into the region. We additionally excluded one species, *Antrostomus vociferus* (Eastern Whip-poor-will), as the underlying data to calculate its habitat selectivity was not available. This left 60 species suitable for analysis on 34 routes over 26 years (806 route-years).

Observer Effects

The effects of observer skill can impact the outcome of population predictions (Link and Sauer 2011, Johnston et al. 2017). To account for this impact, we calculated observer quality for each observer as:

(Eq. 1) $$\text{observer quality}_{[obs_f]} = \text{mean}\left(\frac{N_{[r,y,obs_f]} - \text{mean}(N_{[r,obs_a]})}{\text{mean}(N_{[r,obs_a]})}\right)$$

where N represents the number of species observed, r is the route, y is the year, obs_f is the focal observer, and obs_a represents all other observers. We calculated the number of species seen by the focal observer on a given route year, subtract from that the mean number of species seen on that route by all other observers, and then divided by the route mean for all other observers (Eq. 1). This allowed us to determine for a given route, year, observer combination how many more or fewer species were seen compared to when the focal observer is absent. Because some observers conduct surveys on multiple survey routes that may have different underlying bird diversity, for

each focal observer we then average all their route, year scores to end with an observer quality metric that distinguishes when a given observer tends to identify more or fewer species compared to route averages. An observer who sees the average number of species on their routes receives a score of 0, while negative values indicate observing fewer species than average and positive values are better than average**.** When there has been only one observer across the survey history of a route, we assign them an observer score of 0. Observers who identify more species are likely more skilled surveyors and will detect more of each species as well as have higher detection of rare species (Kelling et al. 2015, Johnston et al. 2017).

More than one observer may be present on a NCMBBS route (Goulden et al, *in press*) so observer quality for each survey was assigned based on the highest observer quality score among observers present in a given year, so long as that focal observer had completed more than one survey. For 82% (28/34) of the routes on the NCMBBS, the same focal observers have surveyed for more than 10 years, which increases consistency in observer skill and confidence in our population trend estimates. We included observer quality in the model as described below and, as expected, found that observer quality had a small positive effect on counts (β_{obs} = 0.190$\pm$0.005).

Species Traits

Regional trends for all species were calculated from the North American Breeding Bird Survey (BBS) using the USGS Regional Trend Analysis Form (Hostetler et al. 2025, https://eesc.usgs.gov/mbr/bbs2025/tf.html) for the Piedmont Bird Conservation Region, which encompasses the NCMBBS and extends northeast from

Alabama to New Jersey. The Piedmont region covers 164 BBS routes. Regional trends available on the analysis form website at the time of collection (June 2026) could be calculated to include data until 2024, so we calculated trends from 2000 to 2024 to best match the NCMBBS.

The methods for calculating breeding habitat selectivity come from DiCecco & Hurlbert (2022). Habitat selectivity was derived from associating eBird species occupancy rasters (Strimas-Mackey et al. 2021) with 30-m National Land Cover Database (NLCD, USGS 2024) habitat characteristics, and characterizes the degree to which a bird species is found primarily in one habitat versus a variety of habitats during the breeding season. Higher values indicate that the species is a habitat specialist, while lower values mean the species is a habitat generalist**.**

For temperature niche position, we calculated the z-score of the study area temperature relative to the distribution of warmest-quarter mean temperatures using WorldClim (Fick & Hijmans 2017) across each species' breeding range. We calculated this climate variable for the warmest-quarter of the year as that aligns with the breeding distribution of these species and when they are surveyed by the NCMBBS. This provides a measure of how much colder (negative values) or warmer (positive values) the study site in North Carolina is compared to the mean breeding season temperature of a species.

We used the Avian Diet Database (Hurlbert et al. 2021) to calculate percent insectivory as the average percent of the diet that is estimated to be arthropods by weight or volume. Diet data for some bird species come only from one particular source (Martin et al. 1961) which simply distinguishes between "plant" and "animal" diet

209 portions. With the exception of species in the families Corvidae and Turdidae we
210 assumed this animal diet was primarily arthropods. We used only spring, summer, and
211 fall diet data when available (49 species) and included winter diet data when not (5
212 species). When a species was not represented in the diet database, we used the mean
213 percent arthropods by weight or volume for the species' family, again using first only
214 spring, summer, and fall diet data (5 species), or winter when unavailable (1 species).
215 Correlation between species' percent arthropod diet and family mean percent arthropod
216 diet was high (r = 0.72).
217
218 *Statistical Analyses*
219 Counts were modeled in a hierarchical Bayesian framework, based on Sauer and
220 Link (2011), which accounts for the nested structure of the data and reduces error by
221 allowing for variance at multiple levels. Counts for species on the NCMBBS were
222 modeled using a negative binomial distribution to account for overdispersion,
223
224 (Eq. 2) $$C \sim \text{negative binomial}(\mu, \theta)$$
225 (Eq. 3) $$\mu = \alpha + \alpha_{[sp,rt]} + \beta_{[sp]} \times \text{year} + \beta_{\text{obs}} \times \text{observer quality}$$
226 (Eq. 4) $$\theta \sim \text{gamma}(2,1)$$
227 (Eq. 5) $$\alpha \sim \text{normal}(0,2)$$
228
229 where the intercept for counts is modeled as a universal intercept (α) with a
230 normal(0,2) prior and the negative binomial overdispersion parameter (θ) was given a
231 gamma(2,1) prior (Eq. 2-5). To the universal intercept we added a random intercept for

each species, route combination ($\alpha_{[sp,rt]}$), capturing the route-specific abundance for each species, with a normal(0,1) prior (Eq. 6).

(Eq. 6) $$\alpha_{[sp,rt]} \sim \text{normal}(0,1)$$

The effect of change over time (year) was modeled as a species-specific slope (β_{sp}). We calculated one effect of observer quality (β_{obs}) across all routes and species, to account for variation that different observers introduce, and use a normal(0, 0.5) prior (Eq. 7).

(Eq. 7) $$\beta_{\text{obs}} \sim \text{normal}(0,0.5)$$

Second-level predictors in the Bayesian hierarchical model characterize variation between rather than within species. The effects of species' traits (temperature niche position, percent insectivory, habitat selectivity, and regional trend) are added as predictors in the calculation of the species' local population trends (β_{sp}), effectively propagating uncertainty in a single model. Trends were modeled as a function of the intercept ($\gamma_\beta \sim \text{normal}(0.2)$) plus slopes ($\kappa$) for each species trait, with process variance represented by σ_β (Eq. 8-10).

(Eq. 8)
$$\beta_{[sp]} \sim (\gamma_\beta + \kappa_{\text{temp.niche}} \times \text{Temperature Niche Position}_{[sp]} + \kappa_{\text{perc.insect}} \times \text{Percent Insectivory}_{[sp]} + \kappa_{\text{hab.select}} \times \text{Habitat Selectivity}_{[sp]} + \kappa_{\text{regional.trend}} \times \text{Modeled Regional Trend}_{[sp]},$$

$$\sigma_\beta)$$

(Eq. 9) $$\kappa \sim \text{normal}(0,1)$$

(Eq. 10) $$\sigma_\beta \sim \text{half} - \text{normal}(0,0.5)$$

Gamma (γ_β) represents the population trend for the average species at mean species traits. All traits were scaled so the average species had a trait value of 0, both to improve model fit and for ease of interpretation of relative trait effects. The priors for κ for each trait were set as a normal(0,1) distribution, while variance was given a half-normal(0,0.5) prior. All estimated VIF scores were between 1 and 1.2, suggesting that multicollinearity is not an issue in this model. We ultimately removed *C. virginianus* (Northern Bobwhite) from the trait analysis, as the Bobwhite is declining at twice the rate of any other species, is ecologically distinct as the only galliform, and was an outlier with high Cook's distance. Inclusion of the Northern Bobwhite weakens the effects of temperature niche position and habitat selectivity, while strengthening the effect of percent insectivory (Supplemental Figure S3).

Rather than estimating the effect of regional trend with a point-estimate mean, we explicitly incorporated the uncertainty within the regional trend estimate in our model. Failure to account for uncertainty in predictors in a linear model leads to estimates biased towards zero (Fuller 2009). To do so, we modeled the observed regional trend (Hostetler et al. 2025) for a given species ($\text{BBS Regional Trend}_{[sp]}$) with a normal distribution with a mean given by the latent, true regional trend ($\text{Modeled Regional Trend}_{[sp]}$), and standard deviation given by the known uncertainty in the BBS trend given by the USGS Regional Trend Analysis Form ($\text{BBS}\sigma_{[sp]}$) (Eq. 11).

The in-model regional trend is then given by a normal distribution with hyperparameters mu ($\mu_{\text{regional.trend}}$), with a normal(0,1.5) prior, and sigma ($\sigma_{\text{regional.trend}}$), with a half-normal(0,0.5) prior (Eq. 12-14).

(Eq. 11) $$\text{BBS Regional Trend}_{[sp]} \sim \text{normal}\left(\text{Modeled Regional Trend}_{[sp]}, \text{BBS } \sigma_{[sp]}\right)$$

(Eq. 12) $$\text{Modeled Regional Trend}_{[sp]} \sim \text{normal}\left(\mu_{\text{regional.trend}}, \sigma_{\text{regional.trend}}\right)$$

(Eq. 13) $$\mu_{\text{regional.trend}} \sim \text{normal}(0,1.5)$$

(Eq. 14) $$\sigma_{\text{regional.trend}} \sim \text{half-normal}(0,0.5)$$

We implemented the model in Stan using the R package *rstan* (Stan Development Team, 2024) and estimated via MCMC with four chains, each run for 10,000 iterations with a warm-up of 2,000 iterations. We assessed convergence based on Rhat ≤ 1.01 and n.eff > 400 for all parameters. No divergences were present. For classifying population trends we use whether the 87% credible interval crosses zero to distinguish if populations are increasing, decreasing, or stable. However, for estimating the influence of species traits we are more conservative and assess effect sizes based on the 95% credible interval.

We additionally tested for phylogenetic independence in the residuals of β_{sp} using the R package *phytools* (version 2.5.2, Revell 2024). Across 100 simulated phylogenetic trees, created using the package *rtrees* (Daijiang 2023), the average Pagel's λ was close to zero (λ = 0.062, p-value = 0.98), therefore we did not incorporate a phylogenetic component into our model (Pagel 1999).

Results

We examined a total of 60 species, representing a survey effort counting 195,196 birds across 806 route-years. Thirty-four species (56.7%) have experienced a decline over the 26 survey years (2000-2025, Figure 1, 87% credible intervals do not cross zero). In contrast, 16 species (26.7%) populations have increased, and 10 species (16.7%) were considered to be stable (87% credible intervals crossed 0).

The species in sharpest population decline was *C. virginianus*, whose populations are declining by -13.42 $\pm$0.95 (posterior mean $\pm$ posterior sd) percent per year, followed by *Passer domesticus* (House Sparrow, -8.68 $\pm$ 0.73) and *Quiscalus quiscula* (Common Grackle, -6.61 $\pm$0.35). The three species experiencing the highest population growth in the study area are *Corvus ossifragus* (Fish Crow, 5.16 $\pm$0.52), *Vireo griseus* (White-eyed Vireo, 5.05 $\pm$0.52), and *Setophaga dominica* (Yellow-throated Warbler, 4.67 $\pm$0.59).

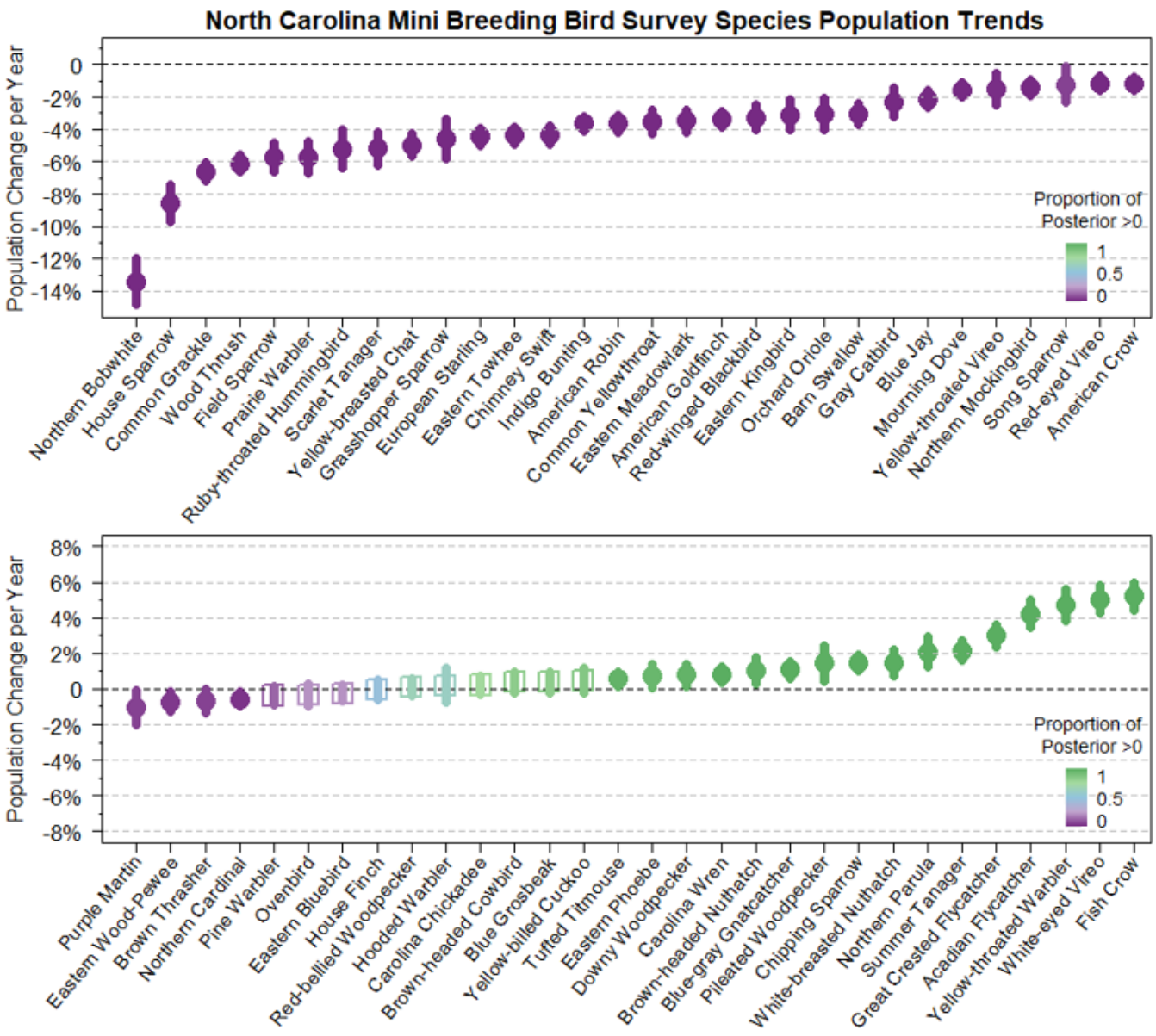


Figure 1. Local population trend estimates for 60 bird species from the North Carolina Mini Breeding Bird Survey (2000-2025), ranked by mean trend estimate in percent change per year. Bars represent 87% credible intervals and are colored based on the proportion of the posterior that is greater than 0. Species coded as stable (87% credible interval crosses zero) have open square symbols.

Alt Text: Graph depicting population trend estimates with mean and 87% credible intervals, showing more birds are declining than are increasing or stable.

Regional trend was the strongest predictor of local trends and had a strong positive relationship with NCMBBS population trends ($\kappa_{regional.trend}$ = 0.025±0.003, Figure 2, Supplemental Figure S1.). For 83.1% of species, local population trend estimates were more extreme than regional trends (Figure 2; Supplemental Table S1). There were four species whose regional and local trend directions entirely disagreed. *Polioptila caerulea* (Blue-gray Gnatcatchers) increased on the NCMBBS despite declining regionally, and *Cardinalis cardinalis* (Northern Cardinal), *Spinus tristis* (American Goldfinch), and *Vireo flavifrons* (Yellow-throated Vireo) declined locally while increasing throughout the Piedmont.

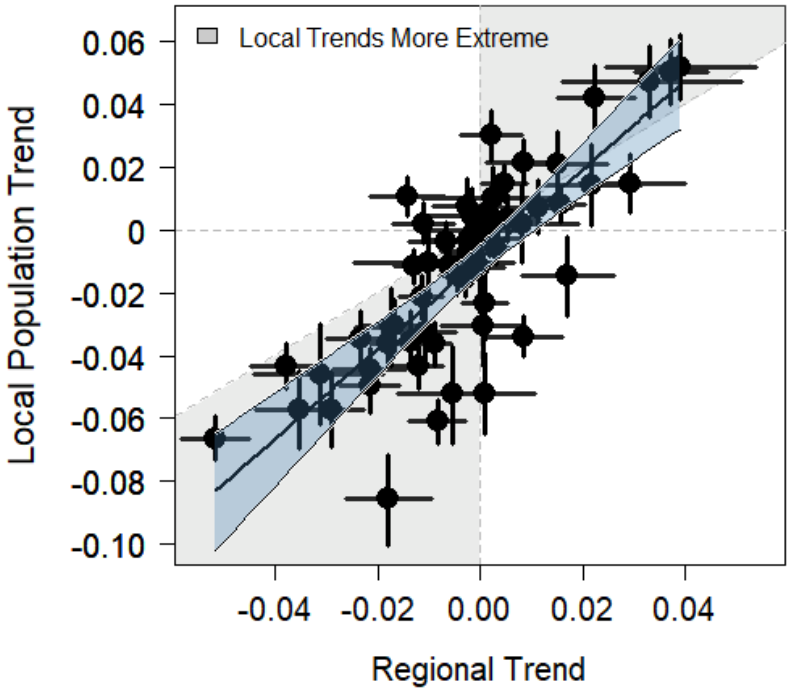


Figure 2. Linear effect of Regional Trend on Local Species Population Change. Shaded area represents area above/below the 1:1 line where species trends are more extreme locally

than regionally (83.4% of species). Error bars represent one posterior standard deviation. The Piedmont regional trends are shown here unscaled for ease of interpretation but were centered and scaled for the analysis. For comparison of the effect size of scaled regional trend with other species traits see Supplemental Figure S1.

Alt Text: Graph depicting the tight relationship between local population trends and regional trends, with 95% credible interval.

Above and beyond the influence of the regional trend, temperature niche position had a moderate negative impact on local population trends (-0.0063 ± 0.0026), with species for whom NC is the warmer edge of their temperature niche more likely to have declined. Habitat selectivity also had a negative impact (-0.0058 ± 0.0024), with species with specialized habitat requirements more likely to have declined. Percent insectivory had a weak positive effect (0.0045 ± 0.0025, 95% CI [-0.0037, +0.0092]) (Figure 3).

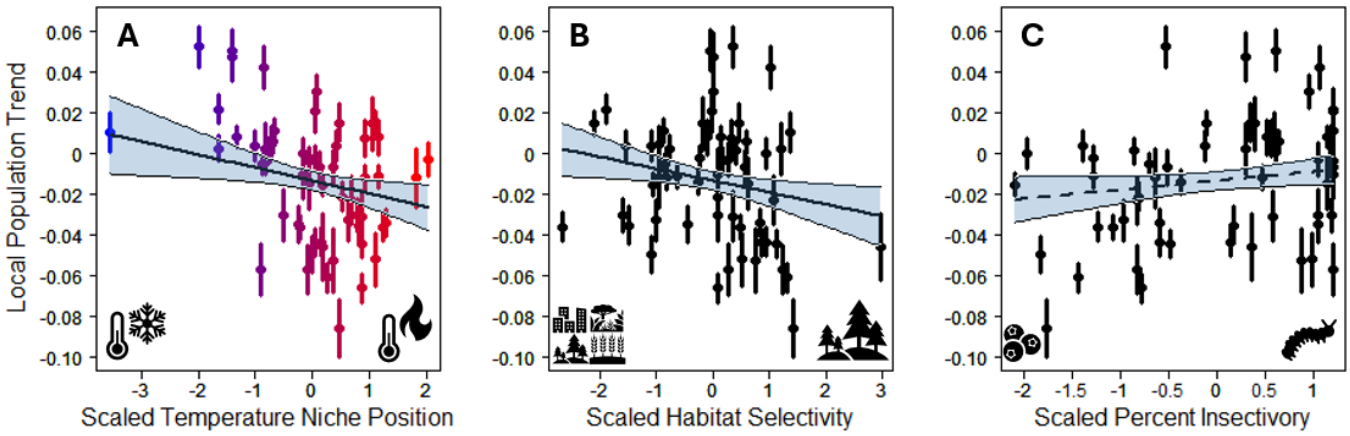


Figure 3. Linear Effect of Species Traits on Local Species Population Change. Temperature niche position (A) and habitat selectivity (B) both have moderate negative effects on species population trends, with species with more selective habitat requirements and for

which the study site is warmer than their average breeding range temperature more likely to be in decline. Percent insectivory (C) had a weak, positive effect (0.0045±0.0025, 95% CI crosses 0).

Alt Text: Graphs with panels labeled from a to c depicting the relationships between temperature niche position, habitat selectivity, and percent insectivory to local population trend.

The effect of regional trend was roughly 4 times greater than the effect of temperature niche position or habitat selectivity. When regional trend is removed from the model, all effects of species traits were stronger, including a stronger positive effect of percent insectivory (Supplemental Figure S2). Pairwise correlations among species traits and regional trend were generally weak (Supplemental Table S2).

Discussion

In central North Carolina, more than half (56.7%) of the local bird species are declining. As expected, local population trends were strongly predicted by broader regional trends throughout the entire Piedmont ecoregion. This makes intuitive sense both because the trends of local populations statistically contribute to regional trend estimates, and also because the same pressures that species face locally, due to climate change, land use change, and phenological mismatch, also operate at the regional scale. However, we also find that, even after accounting for regional population trends, species traits help inform which species are winners or losers. Species that are habitat specialists declined more steeply than generalists, consistent with prior work (Devictor et al. 2008, Sullivan et al. 2015, Stevens et al. 2024). Similarly, species for whom the study area represents the warm edge of their temperature niche were more

likely to decline, supporting previous findings examining temperature niche position across species ranges (Chen et al. 2011).

These two traits — habitat breadth and temperature niche position — are not strongly correlated with one another or with regional trend, indicating that their effects are likely independent. Additionally, the greater effect size of temperature niche compared to habitat selectivity supports the inclusion of traits that are defined relative to a particular locality or landscape. Together, our results suggest that while local population change is strongly linked to broader regional dynamics, species traits explain additional variation in who wins and who loses even at fine spatial scales.

While the relationship between species traits and population trends has been quantified directly at the regional or continental scale (e.g. Salido et al. 2012, Mason et al. 2019, Di Cecco & Hurlbert 2022), there are three primary advantages to the local-scale perspective that we take here. First, results demonstrate that local population trends were consistently more extreme than regional trends. Traits explain the excess variation in these trends beyond what is captured at the regional scale. Secondly, contrasts between local and regional population change can be informative. We found four species, including Northern Cardinal*,* whose local and regional trends were in opposition. Johnston et al (2025) found that many species are declining in areas where they are most abundant. Although Northern Cardinals in our study area are only declining at the gradual rate of -0.56% per year, they are the most abundant species in our survey. Locally, even this highly-abundant, urban-adapted species is suffering population loss over time. Finally, and more fundamentally, when scaling to the regional level, there is no longer the guarantee that these “winners” and “losers” are competing

with one another in the same landscape, experiencing the same habitat changes, and subject to the same climatic changes. A key advantage of the NCMBBS is that all 60 species are coexisting within the same landscape during the 25-year study period. This design allows us to isolate the influence of species traits on the populations of birds in a local area more cleanly than a geographically broad analysis could.

Only 16.7% of the studied central North Carolina bird species appear to have increasing populations. For the most part, these are species with low-to-average habitat selectivity (e.g. Chipping Sparrow (*S. passerina)*, Summer Tanager (*Piranga rubra*), and White-eyed Vireo (*V. griseus)*), and who are on the colder edge of their temperature niche in central North Carolina (e.g. Brown-headed Nuthatch (*Sitta pusilla*), Summer Tanager (*P. rubra)*, Yellow-throated Warbler (*S. dominica)*). Many of these species are also experiencing range expansions, including Fish Crow, which has been gradually expanding inland from coasts into the survey region (McGowan 2020, Prachand & Escalante 2026), and Summer Tanager and White-eyed Vireo, who have always occurred throughout North Carolina but whose populations have expanded northwards (Hitch & Leberg 2006), likely also shifting their centroid of abundance as they track their climatic niche (Manthey et al. 2015). With continuing climatic change, we should expect birds with southern distributions to experience population growth in this area of North Carolina, with more success if they are also habitat generalists. This finding supports the conclusions of previous studies addressing temperature niche, climate, and population change (Manthey et al. 2015, DiCecco & Hurlbert et al. 2022).

The weak positive effect of a more insectivorous diet runs counter to expectation in light of widespread insect declines (Wagner 2020), the close link between

insectivorous birds and their food availability (Tallamy & Shriver 2021), and potentially increasing phenological mismatch (Visser at al. 2006, Burgess et al. 2018, Belitz et al. 2025). Stevens et al (2024) similarly found a weak positive effect of insect dependence while examining population change in bird species across eco-regions, which they ultimately attribute to the influence of strong population growth in waterfowl with low reliance on insects. Similarly, we believe that interpreting the positive direction of this weak effect requires consideration of the ecological diversity within the 60 studied species. Even after the exclusion of *C. virginianus*, the species in next sharpest decline are *P. domesticus* (House Sparrow) and *Q. quiscula* (Common Grackle), which are not declining due to any fault of a non-insect focused diet but rather range-wide changes in habitat availability due to changes in farming practices throughout eastern North America (Lowther & Cink 2020, Peer & Bollinger 2020). At the continental scale, the steepest declines in North American bird populations have occurred among grassland birds (Rosenberg et al. 2019), many of which rely on seeds and omnivorous diets as adults, and these species are declining in our study. Of the species highly dependent on insects, their population trends on the NCMBBS run the full gamut of population changes. Therefore, it appears our diet categorization is more effectively capturing that grassland birds, which consume a higher percentage of non-insect foods, are more likely to decline than other species – not that insectivorous birds receive a population benefit from their consumption of insects. A clear future direction should explore how fine-scale habitat changes in the local environment of the NCMBBS has shaped population trends across these species.

Our findings highlight the interconnected effects of species traits across scales, and demonstrate that habitat selectivity and temperature niche position influence local species population trends. While the regional scale is useful for assessing large-scale declines, it masks important variation occurring at more local scales. Regional dynamics are ultimately the manifestation of a set of local-scale dynamics. Beyond what is captured within this larger regional envelope, traits capture the variation in species responses to ongoing change, helping us to understand how species will respond into the future, including expected winners and losers.

Acknowledgements

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Data Availability: All data and code associated with the article can be found at Zenodo [doi pending] or GitHub [https://github.com/IJBG/ncmbbs-trends-by-traits].

Literature Cited

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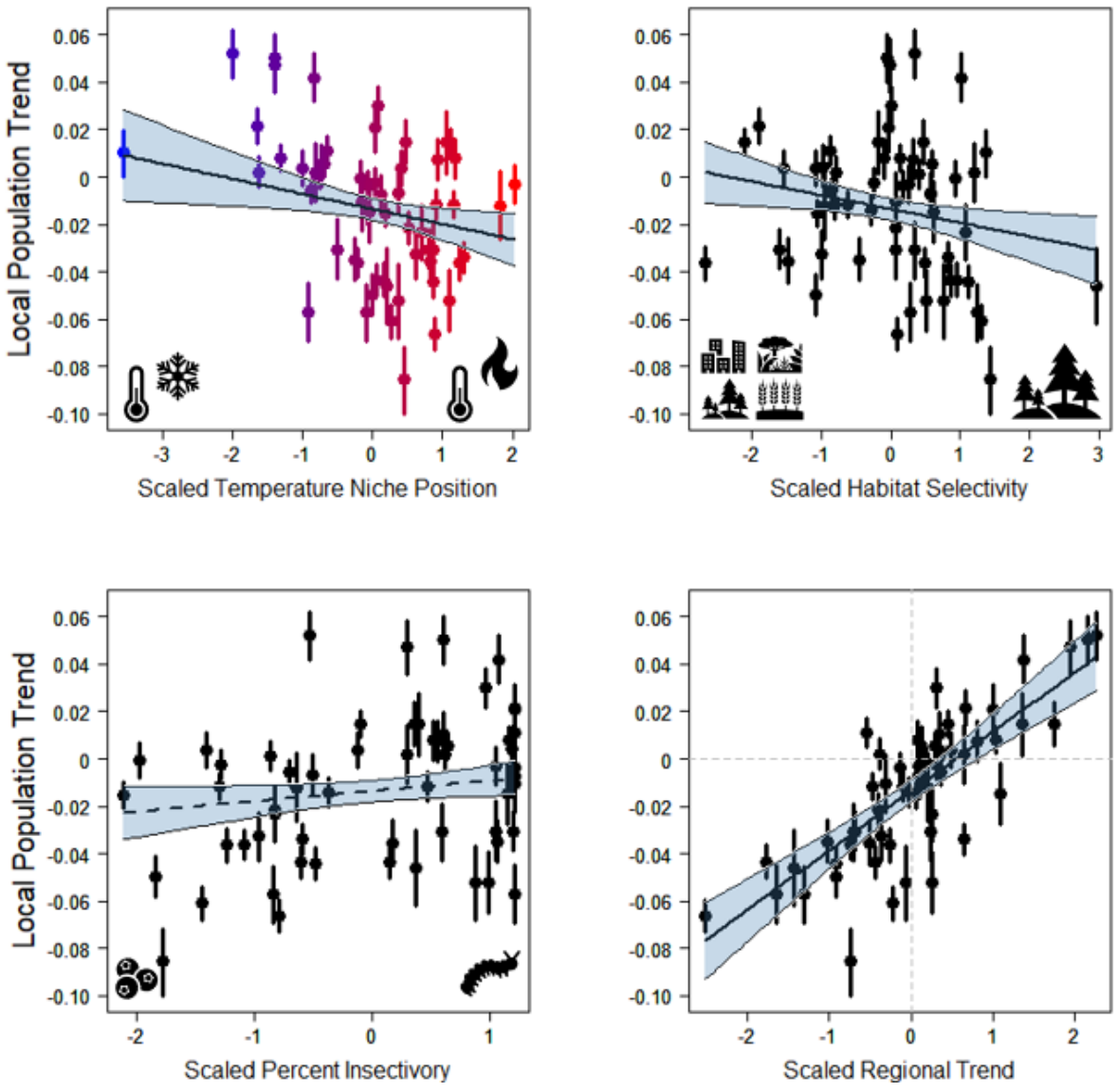
Supplementals:

Supplemental Figure 1.

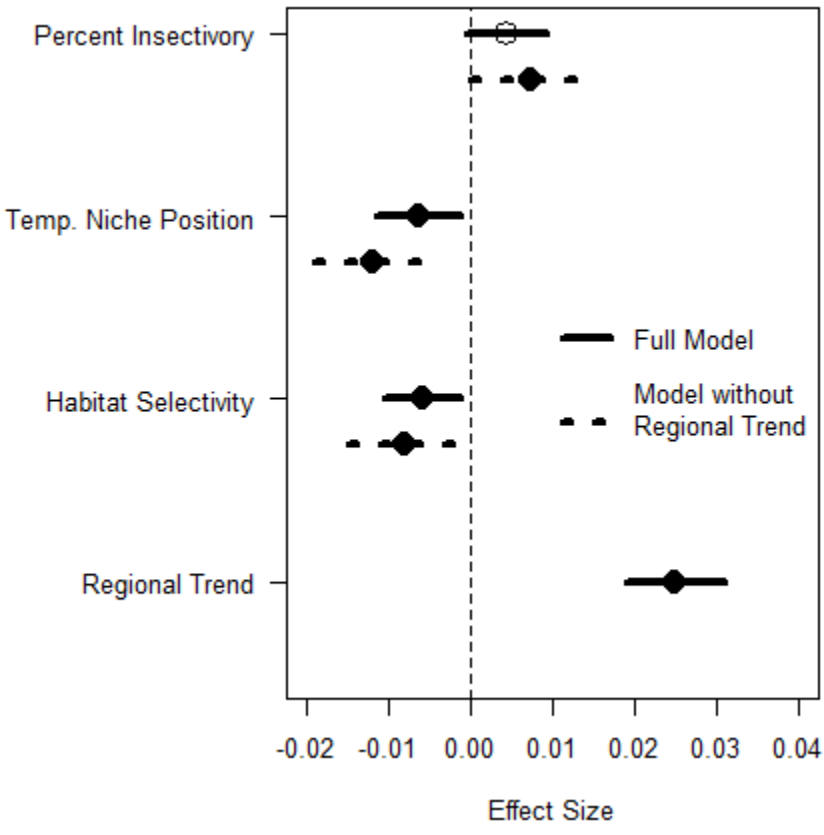


Supplemental Figure S1. Linear Effect of Species Traits on Species Population Change. Dashed lines represent effects that are unsupported at the 95% credible interval. Piedmont regional trend is the strongest predictor of population trends, with how species are doing regionally strongly positively related to local population change (0.025±0.0031). Habitat selectivity and temperature niche position both have moderate negative effects on species population trends (H.S.: 0.0058±0.0024, T.N.P.:

608 0.0063±0.0026), with species with more significant habitat requirements and those for
609 whom the study site is warmer than their average breeding range temperature more
610 likely to be in decline. Percent insectivory had a weak, unsupported positive effect
611 (0.0045±0.0025, 95% CI crosses 0).

612 Alt Text: Graphs with panels labeled from a to d depicting the relationships
613 between temperature niche position, habitat selectivity, percent insectivory, and regional
614 trend to local population trend.

615



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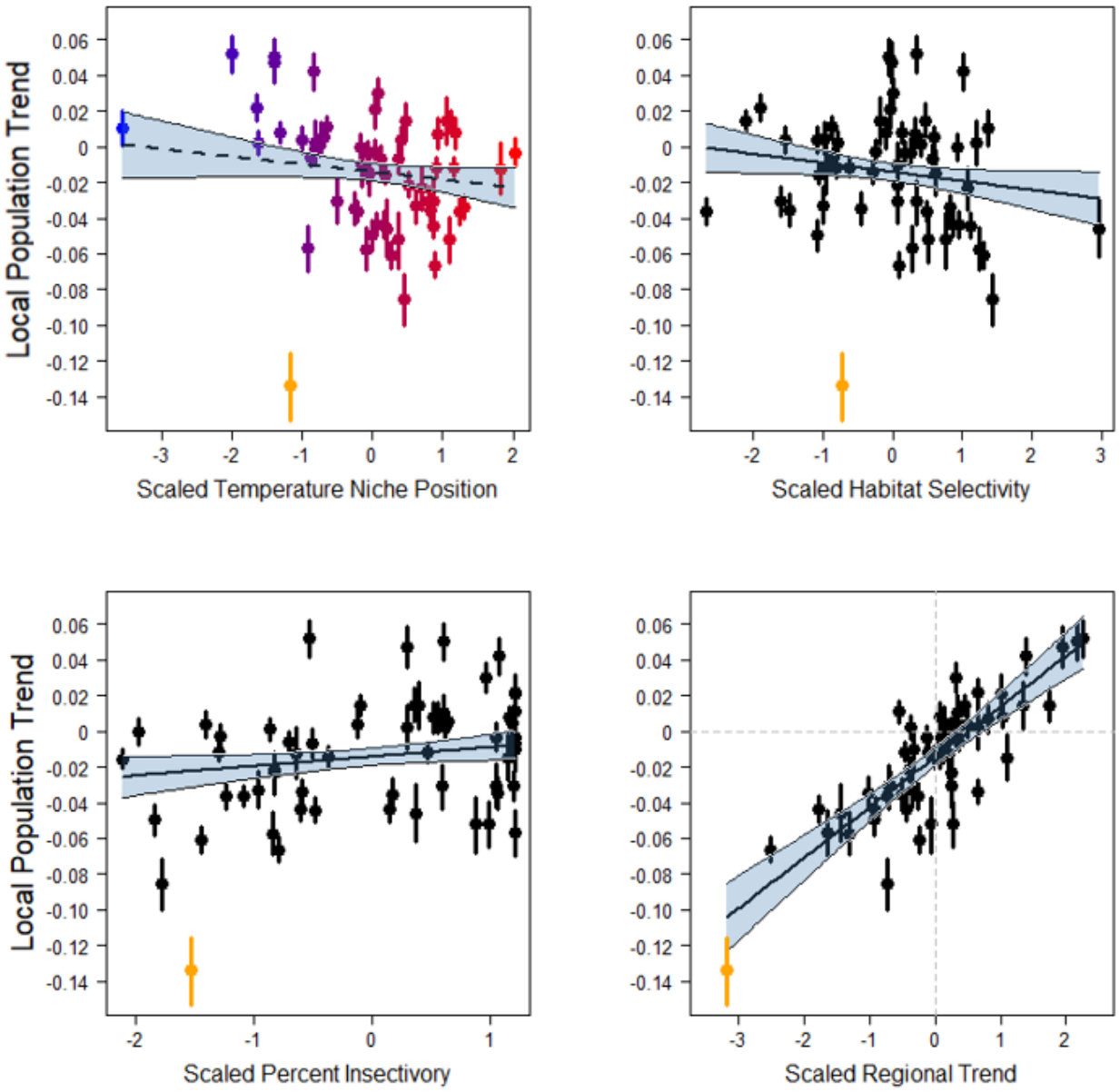
618 Supplemental Figure S2. Species trend estimates across models with and
619 without the inclusion of regional trend. Solid lines represent the full model with all

species traits, while dotted lines represent models without regional trend. Filled circles indicate 95% credible intervals that do not cross zero. In the full model, percent insectivory has an unsupported small positive effect (0.0045 +- 0.0025), while regional trend (0.025 +- 0.0031), temperature niche position (-0.0063 +- 0.0026), and habitat selectivity (-0.0058 +- 0.0024) effects are all supported. In the model without regional trend, percent insectivory has supported weak positive effect (0.0073 +- 0.0037), while temperature niche position (-0.012 +- 0.0036) and habitat selectivity (-0.0079 +- 0.0036)'s effects become more strongly negative.

Alt Text: Graph plotting the credible intervals of the effects of species traits in the main model as well as a supplemental model without regional trend.



Supplemental Figure S3. Linear Effect of Species Traits on Species Population Change, with Bobwhite included. In our main model, one species, the Northern Bobwhite, was removed from analysis as an outlier. The model shown in this figure includes the Northern Bobwhite, highlighted in yellow. Inclusion of the Bobwhite weakens the relationships between temperature niche position and habitat selectivity with local population trends, while strengthening percent insectivory's relationship with

local population trends. Dashed lines represent effects that are unsupported at the 95% credible interval.

Alt Text: Graphs with panels labeled from a to d depicting the relationships species traits and local population trend from a supplemental model that includes the species C. virginianus, Northern Bobwhite.

Supplemental Table S1. Summary of species population trend estimates, credible intervals, and species traits, available as a .csv

Supplemental Table S2. Correlation between scaled species traits. No traits were strongly correlated.

	Regional Trend	Percent Insectivory	Temperature Niche Position
Percent Insectivory	0.26		
Temperature Niche Position	-0.19	-0.18	
Habitat Selectivity	-0.04	0.04	-0.10

Supplemental Table S3. Summary of the effects of species traits in the main model as well as in a supplementary model without regional trend included, available as a .csv