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OXFORD

Species-specific ecological traits, phylogeny, and geography underpin vulnerability to population declines for North American birds

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ABSTRACT

Species declines and extinctions characterize the Anthropocene. Determining species vulnerability to decline, and where and how to mitigate threats, are paramount for effective conservation. We hypothesized that species with shared ecological traits also share threats, and therefore may experience similar population trends. Here, we used a Bayesian modeling framework to test whether phylogeny, geography, and 22 ecological traits predict regional population trends for 380 North American bird species. Groups like blackbirds, warblers, and shorebirds, as well as species occupying Bird Conservation Regions at more extreme latitudes in North America, exhibited negative population trends; whereas groups such as ducks, raptors, and waders, as well as species occupying more inland Bird Conservation Regions, exhibited positive trends. Specifically, we found that in addition to phylogeny and breeding geography, multiple ecological traits contributed to explaining variation in regional population trends for North American birds. Furthermore, we found that regional trends and the relative effects of migration distance, phylogeny, and geography differ between shorebirds, songbirds, and waterbirds. Our work provides evidence that multiple ecological traits correlate with North American bird population trends, but that the individual effects of these ecological traits in predicting population trends often vary between different groups of birds. Moreover, our results reinforce the notion that variation in avian population trends is controlled by more than phylogeny and geography, where closely related species within one region can show unique population trends due to differences in their ecological traits. We recommend that regional conservation plans, i.e. one-size-fits-all plans, be implemented only for bird groups with population trends under strong phylogenetic or geographic controls. We underscore the need to develop species-specific research and management strategies for other groups, like songbirds, that exhibit high variation in their population trends and are influenced by multiple ecological traits.

Keywords: Bayesian modeling, Bird Conservation Region, Breeding Bird Survey, migration distance, North America, ecological traits

How to Cite

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LAY SUMMARY

- A common hypothesis for explaining variation in avian population trends is that species which share traits also share similar population trajectories.
- We sought to test this hypothesis by analyzing how breeding population trends for 380 North American bird species related to traits describing a species' life history or ecological niche at any stage of their annual life cycle.
- Our analysis revealed that not only phylogeny and geography, but multiple ecological traits, and particularly migration distance, contributed to explaining variation in bird population trends. While groups like songbirds exhibited high interspecific variation in population trends, other groups like ducks exhibited similar population trends.
- Order-specific analyses highlighted the relative effects of ecological traits, phylogeny, and geography on influencing trends, with geography having a strong effect on shorebirds while songbirds appeared to be most impacted by increasing migration distance.
- We found that (1) average regional population trends were most negative for blackbirds, sparrows, warblers, and shorebirds, and most positive for ducks, raptors, and waders, and (2) average regional population trends were more negative in Bird Conservation Regions at more extreme latitudes in North America.
- Our results emphasize the need for species-specific research and management strategies to recover North American bird populations.

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Los rasgos ecológicos, la filogenia, y la geografía sustentan la vulnerabilidad a la disminución de aves norteamericanos

RESUMEN

Las disminuciones y extinciones de especies caracterizan el Antropoceno. Determinar la vulnerabilidad de las especies a las disminuciones y dónde y cómo mitigar las amenazas es fundamental para conservar especies eficientemente. Una hipótesis para identificar las causas de las disminuciones es que las especies con características ecológicas compartidas también comparten amenazas y, por lo tanto, experimentan tendencias de población similares. Aquí, usamos un marco de modelo bayesiano para probar si la filogenia, la geografía, y 22 rasgos ecológicos predicen las tendencias regionales de población para 380 especies de aves norteamericanas. Descubrimos que, además de la filogenia y la geografía, la dependencia de los insectos, la distancia de migración, el tamaño de la población, la masa corporal, la amplitud de hábitats ocupadas, la amplitud de la dieta, el tamaño de la nidada, el periodo de la incubación, el periodo del polluelo, y el nivel del forraje contribuyeron a explicar la variación en las tendencias regionales de población de las aves norteamericanas. Además, encontramos que las tendencias regionales y los efectos relativos de la dependencia de los insectos, la filogenia, y la geografía son diferentes en respeto a los principales grupos de aves. Las tendencias regionales de población variaron con grupos filogenéticos y regiones geográficas. Especies principalmente de las familias Icteridae, Parulidae, y Charadriidae, además de especies ocupando regiones de latitudes extremas en Norteamérica demostraron tendencias de población negativas, mientras que especies de patos y rapaces, además de especies ocupando regiones del interior de Norteamérica demostraron tendencias de población positivas. Nuestro trabajo ofrece evidencia de que varios rasgos ecológicos se correlacionan con las tendencias de la población de aves norteamericanas, pero también que los efectos individuos de cada rasgo en predecir las tendencias poblaciones faltan de poder. Además, nuestros resultados refuerzan la noción de que la variación en las tendencias de la población de aves está controlada por algo más que la filogenia y las regiones biogeográficas, donde las especies relacionadas dentro de una región pueden sufrir tendencias de población diferentes debido a las diferencias en sus características ecológicas. Recomendamos expandir las estrategias de conservación actuales para incluir más énfasis en la protección de especies específicas.

Palabras clave: los rasgos ecológicos, América del Norte, modelado bayesiano, Bird Conservation Region, Breeding Bird Survey, la distancia de migración

INTRODUCTION

The sixth mass extinction characterizes the Anthropocene (Lewis and Maslin 2015). Humans continue to alter terrestrial, marine, and atmospheric systems at unprecedented rates (Ellis 2011). The consequences of global change manifest across scales, from dramatic alterations to microrefugia on a local scale to widespread biodiversity loss at a global scale (McCarty 2001). This pattern holds true across taxa, with recent studies exposing precipitous declines for amphibians (Becker et al. 2007), fish (Christensen et al. 2014), birds (Rosenberg et al. 2019, Burns et al. 2021), and insects (van Klink et al. 2020, Wagner et al. 2021. However, while widespread patterns of population loss due to global change become clearer, different species' relative vulnerability to decline often remains unknown.

One hypothesis for understanding vulnerability to population decline is that species with shared life-history traits and/or niches also share demographic fates. Specifically, two closely related species occupying similar environmental space are hypothesized to be exposed to similar limiting factors and therefore experience similar population trends (Harvey and Pagel 1991). Collectively, we define these characteristics as "ecological traits," which describe a species' life history or ecological niche at any stage of their annual life cycle. These traits include demographic variables and vital rates as well as environmental associations, resource use strategies, reproduction strategies, and movement ecology, encompassing a range of spatial scales. Ecological traits are, in some cases, what make species more or less vulnerable to anthropogenic threats. For example, predation by cats may be the actual factor limiting a species' population (Loss et al. 2015), but the ecological traits intrinsic to the species will determine their vulnerability and exposure to these threats.

Ecologists have long hypothesized that shared ecological traits may result in similar population trends (Harvey and Pagel 1991, Ackerly and Donoghue 1995, Harvey et al. 1995). This hypothesis is often implicit to many current bird conservation strategies and management plans across state and federal agencies, joint ventures, and other organizations who manage at the regional or habitat level rather than on a species-by-species basis (e.g., habitat and landscape-level conservation plans; see Underwood 2011). The "ecological correlates of declines" hypothesis has been examined and discussed both in theory across ecological and evolutionary scales and in practice with an applied focus across a variety of taxonomic groups (Fisher and Owens 2004). Broadly, species' population trends and/or extinction risk assort non-randomly across phylogeny (Fisher and Owens 2004). Therefore, we generally expect related species to show similar demographic responses to the same environmental conditions given they inherit the majority of the traits that dictate their life history and habitat use from a shared common ancestor (Fisher and Owens 2004). Many studies have sought to explain population trends or extinction risk for different taxonomic groups using this logic (Coulthard et al. 2019). For example, Lips et al. (2003) found that aquatic habitats, restricted elevational ranges, and larger body size predicted amphibian declines in Central America, and Bartomeus et al. (2013) identified that large body size and narrow diet breadth explained bee species declines in the northeastern USA. Within North American birds, Thomas et al. (2006) found that Arctic-breeding shorebirds that migrated over continental North America were more at risk of population declines compared to shorebirds that used other migratory routes, and Soykan et al. (2016) demonstrated indirect relationships between 9 life-history traits and winter population trends for 228 North American bird species using Christmas Bird Count (CBC) data. Finally, Rosenberg et al. (2019) found that North American grassland and forest birds have undergone the steepest declines in abundance since 1970. Overall, these studies have been limited by either the use of simplified quantitative methods (e.g., using binary response variables for population trends; Lips et al. 2003), or a lack in available, detailed data across larger geographic scopes (e.g., limited trait data; Rosenberg et al. 2019).

North American birds have been monitored and studied extensively through structured long-term surveys (e.g., CBC, Breeding Bird Survey [BBS]; Soykan et al. 2016, Ziolkowski et al. 2023), citizen-science initiatives (e.g., eBird), and taxa-specific monitoring programs (e.g., International Shorebird Survey; Manomet 2019). These efforts have generated a wealth of long-term data, making birds an excellent candidate group to test the hypothesis that shared ecological traits result in similar population trends (Neate-Clegg et al. 2020). In particular, BBS data facilitated pinpointing continental and regional trends for individual bird species, enabling researchers to uncover events like the unprecedented loss of three billion birds in North America since 1970 (Rosenberg et al. 2019). With advances in quantitative techniques like Bayesian modeling, we can now use these data to search for correlates of the ongoing and widespread declines of North American bird populations.

Beyond global drivers of environmental change like habitat alteration and climate change, most specific drivers of decline for North American bird species remain unknown. Moreover, we even lack information on the relative vulnerability of different species to the drivers of global change, further hampering effective conservation efforts to reverse population declines. One hypothesis proposed to predict species vulnerability to decline is centered around insect loss, suggesting that birds that depend on insects throughout multiple stages of their annual cycle (e.g., aerial insectivores) are already declining (Rioux Paquette et al. 2014) or expected to decline more than species with broader diets due to widespread declines of insect populations (Nebel et al. 2010, but see Spiller and Dettmers 2019). An alternative hypothesis for understanding bird vulnerability to population declines focuses on biogeography, positing that threats are not spatially homogeneous such that groups of species may be more or less vulnerable depending on the biomes within geographies they inhabit during the breeding and/or nonbreeding season (With et al. 2008). In addition to documenting the loss of North American avifauna, Rosenberg et al. (2019) uncovered evidence for multiple explanations of vulnerability to decline, finding that net changes in bird abundance differed notably by taxonomic group and major biomes.

In this study, we integrated ecological traits (e.g., body size, diet, etc.), geography (i.e., Bird Conservation Regions [BCR]), and phylogenetic relationships in a single statistical framework to determine whether ecological traits explain variation in estimated regional trends in annual abundance for 380 North American bird species. We used BCRs to control for geographic variation in intraspecific population trends across species' breeding ranges. BCRs are ecologically distinct regions that support distinct bird communities, ecosystems, and land cover regimes (BSC and NABCI 2014), thus making them a biologically relevant representation of geography in our analysis. We hypothesized that models including other ecological traits—such as body mass, insect dependence, and migration distance—would better explain variation in regional population trends for North American bird species than a model only considering phylogeny and geography, following evidence from previous studies (Soykan et al. 2016). Specifically, we predicted that regional population trends would increase with increasing average body mass, given the success of existing conservation programs in North America for large-bodied bird species such as raptors and waterfowl. Many of these species suffered steep declines before 1970 and their populations are likely still rebounding after the implementation of conservation policies during the mid-to-late 20th century (Rosenberg et al. 2019). Furthermore, we predicted that regional population trends would decrease for bird species with higher insect dependence across the annual cycle, given evidence of global declines in insect populations (Goulson 2019, van Klink et al. 2020) that have been hypothesized to have adversely affected insectivorous birds (Spiller and Dettmers 2019, Tallamy and Shriver 2021). Finally, we expected regional population trends to be more negative with increasing annual migration distance given the mounting evidence of widespread losses among long-distance migrants in North America (Robbins et al. 1989, Soykan et al. 2016, Rosenberg et al. 2019).

To test these predictions, we compiled an avian ecological trait database with over 200 traits, isolated 22 unique ecological traits, and analyzed the relationship between ecological traits and regional population trends for 380 species of North American birds with sufficient BBS data, a subset of the 529 species considered by Rosenberg et al. (2019). By combining comprehensive results on species trends with an equally comprehensive compilation of ecological traits within a common statistical framework, we isolated and tested specific predictions of potential correlates of avian population trends. We then dove further and repeated the analysis on specific orders of birds to further disentangle the role of ecological traits in predicting regional population trends, and how phylogeny and geography may modulate those effects for some groups of birds. Understanding differences in vulnerability to population decline across the diverse North American avifauna will be a critical step in developing effective, targeted conservation strategies for reversing species-specific declines.

Methods

Data

We compiled multiple datasets on avian ecological traits from leading bird conservation initiatives to form a comprehensive dataset on North American birds. We gathered the bulk of the trait variables considered in our analysis from the Partners in Flight's (PIF) Avian Conservation Assessment Database maintained by the Bird Conservancy of the Rockies (Partners in Flight 2021)and the Global Avian Trait Database (BirdBase) maintained by the Şekercioğlu Lab at the University of Utah (Şekercioğlu et al. 2004, Şekercioğlu et al. 2019). We supplemented these databases with smaller, unpublished datasets focusing on insect dependence and spatial distributions of North American birds. Combined, the master dataset had over 200 trait variables. We did not consider specific anthropogenic threats or proxies for these threats such as exposure to cats, habitat loss, or climate change, all of which are thought to drive declines for many bird species (Loss et al. 2015). Such threats are fundamentally distinct from the ecological traits we considered for this study. While threats are extrinsic forces that often have no direct relationship with a species (e.g., cats existing around human development), ecological traits represent any intrinsic characteristic of a species relating to its life history or environmental space that determine its vulnerability to natural and anthropogenic threats. We filtered out many trait variables to minimize repetition, pseudo-replication, and correlation among variables. Specifically, we removed continuous trait variables with a correlation coefficient of $r > 0.4$ (i.e., restrictive threshold for correlation between variables in ecological modeling; Dormann et al. 2013), trait variables that were calculated based on the values of another variable in the dataset (i.e., pseudo-replication), and categorial trait variables that used similar categories but offered the same information as other categorical variables (i.e., repetition). After this filtering, our final dataset retained 22 traits that we used as predictor variables in our analysis (Table 1). The response variable in our analysis was the estimated regional trends in annual abundance from BBS data for each species from 1970 to 2017, which we describe below.

We estimated regional trends in annual abundance for each BCR for each species using BBS data to explicitly account for variation in population trends due to geography. We reasoned that separating trends by BCR inherently captures the spatial, intraspecific variation in population trend estimates due to geographical differences rather than attempting to approximate those effects on continental trends using biomes or other human classifications of biogeography. Additionally, we reasoned that BCR-level trends would be useful for capturing intraspecific variation in population trends (e.g., a species might have substantially different population trends within the core of its range versus the fringes; Wilson et al. 2018). Under this framework, trends for species with low variation among BCRs will be better explained by ecological traits, whereas trends for species with high variation among BCRs will be better explained by geography.

BBS data are the result of thousands of bird surveys conducted since 1970 along predefined routes in the USA and Canada, and thus carry biases that must be accounted for or at least acknowledged when using them to estimate population trends. One of the primary criticisms of BBS data are that they are collected from road-side surveys. Bird communities along roadsides often differ from those in undisturbed areas, and differences in the level of activity along different roads can further change the presence or detectability of certain bird species (Griffith et al. 2010). Furthermore, BBS data are collected by trained observers albeit with inevitably unequal levels of experience and confidence in identifying birds (Campbell and Francis 2011). Even assuming constant observer error, species detectability may also change over time. Though modern modeling techniques can deal with some issues associated with BBS data (e.g., using random effects to account for route-level and observer effects), they do not account for the limitations described above, which can sometimes lead to incorrect trend estimates (Janousek et al. 2019). Despite these drawbacks, BBS data are unparalleled in their coverage of bird communities throughout North America over the last 50 years.

We estimated regional trends in annual abundance from BBS data (1970-2017) using a two-step modeling process. First, we modeled BCR-level trends from raw BBS data using the standard methodology (i.e., hierarchical general additive model) described in Smith and Edwards (2021) that explicitly accounts for variation in observer error, survey effort, and spatial heterogeneity associated with the distribution of BBS survey routes. However, trend estimates from this first model exhibited higher uncertainty for some species than others due to differences in BBS data availability among species. To correct for uncertainty across the trend estimates based on differences in data availability, we calculated revised trend estimates using a second hierarchical general additive model with a shrinkage estimator that explicitly corrects for uncertainty in the original estimates following a protocol similar to that utilized in Rosenberg et al. (2019). Although Rosenberg et al. (2019) adjusted annual indices of abundance by shrinking them towards means for shared major breeding and nonbreeding biomes, we instead focused on the rate of annual abundance change by BCR region. The principle of the two approaches is the same. Using a hierarchical model and shrinkage estimator, population trend estimates with higher uncertainty shrink towards the mean population trend for each BCR. Under this framework, revised regional population trend estimates for species with ample survey data show little change from the original estimates, whereas revised population trend estimates for species lacking data are more conservative than the original estimates and are less likely to skew subsequent analyses. We chose to shrink estimated regional population trends towards the means of shared BCR regions rather than breeding and nonbreeding biomes as we included biome categories as ecological traits in our analysis. More details on the hierarchical models described here and how they are implemented are provided in the supplementary materials for Rosenberg et al. (2019). Due to the data constraints with BBS data and phylogenetic tree data (see below), we derived revised regional population trend estimates for 380 species in North America and analyzed ecological correlates of population trends for these species. Our species pool is a subset of the 529 species considered in Rosenberg et al. (2019) for which regional trends in annual abundance could be estimated using BBS data from 1970 to 2017 and for which phylogenetic data were available. We note that our species pool is inherently biased towards terrestrial North American birds given that BBS data is not available for many coastal and pelagic species (i.e., seabirds).

Analysis

We examined the relationship between regional population trends for 380 North American bird species and different combinations of 22 ecological trait variables using Bayesian varying intercept models (Table 2). We chose to use a Bayesian modeling framework for our goal of identifying ecological correlates of bird declines as it allowed us the flexibility to include error terms for each regional population trend estimate, predictor variables of multiple data types, and our need to account for phylogenetic and geographic dependencies among species. Our general model structure was as follows:

$$\text{regional trend}\,|\text{error} \sim \text{traits} + (1|\,\text{geography}) + (1|\text{phylogeny})$$

where regional trends, with an added error term to explicitly account for the precision of each regional trend estimate, served as the response for all models. "Traits" was any combination of the 22 trait variables from our dataset in a given iteration of a model, specified as fixed effects. We specified BCR as a random intercept to account for intraspecific, spatially explicit differences in regional population trends due to geography. Finally, we specified phylogeny as a random intercept to account for phylogenetic non-independence among species. We created this phylogeny term using a phylogenetic dissimilarity matrix derived from Jetz et al. (2012).

We implemented all Bayesian models using the R package *brms* (Bürkner 2017). Given our dataset of ~5,000 observations, we used 4 Markov chain Monte-Carlo (MCMC) chains, 10,000 warmup and post-warmup iterations each,

TABLE 1. The 22 ecological life history traits considered in our Bayesian analysis, including whether the variable was continuous, ordinal, or categorial as well as a description of what the variable represents and, if relevant, how it was calculated.

Variable	Type	Description	Data source
Insect dependence	**Ordinal**	**Scoring system ranging from 1 to 10 by increments of 0.5 that ranks a species' level of dependence on insects throughout the annual cycle. Low values indicate low dependence on insects.**	**Unpublished dataset, University of Delaware** [a]
Winter geography	Categorical	Major geographical nonbreeding areas for each species, such as Nearctic (e.g., resident North American species), Temperate South America (e.g., obligate long-distance migrants), or Mesoamerica (e.g., species wintering in Mexico or Central America).	Avian Conservation Assessment Database [b]
Primary breeding habitat	Categorical	Breeding habitat designations for each species as defined by the Avian Conservation Assessment Database, such as Wetlands—Tundra or Forest—Temperate Western.	Avian Conservation Assessment Database
Primary nonbreeding habitat	Categorical	Nonbreeding habitat designations for each species as defined by the Avian Conservation Assessment Database, such as Wetlands—Freshwater Marsh or Forest—Tropical Lowland Evergreen.	Avian Conservation Assessment Database
Primary diet	Categorical	Primary dietary guild according to the Handbook of the Birds of the World.	Global Avian Trait Database [c]
BirdLife forest dependency	Ordinal	Species' dependence on areas designated by BirdLife International: low (1), medium (2), high (3), or non-forest species (0).	Global Avian Trait Database
Annual distance migrated	Continuous	Average distance migrated throughout the annual cycle per year measured in kilometers. Calculated by finding the distance between the mean centroids of breeding and nonbreeding range polygons for each species.	Unpublished dataset, Cornell Lab of Ornithology [d]
Passage area	Continuous	Total geographic area of the range where a species is considered migratory or nonresident measured using range polygons from BirdLife International.	Unpublished dataset, Cornell Lab of Ornithology
Resident area	Continuous	Total geographic area of the range where a species is considered resident year-round measured using range polygons from BirdLife International.	Unpublished dataset, Cornell Lab of Ornithology
Dietary breadth	Ordinal	Dietary breadth. Score ranging from 1 to 9, where one point is allocated for each major type of food (e.g., fruit, insects, etc.) known to be consumed by a species at some point during its annual cycle.	Global Avian Trait Database
Habitat breadth	Ordinal	Habitat breadth. Score ranging from 1 to 15, where one point is allocated for each major habitat type a species is known to use at some point in its annual cycle.	Global Avian Trait Database
Foraging layer	Ordinal	Estimated average foraging layer based on available data from Handbook of the Birds of the World: water, ground, ground and understory, understory, understory and mid-level, mid-level, mid-level and high, high, high and canopy, canopy, all layers.	Global Avian Trait Database
Average body mass	Continuous	Average body mass (g) according to the Handbook of the Birds of the World.	Global Avian Trait Database
Nest	Categorical	Preferred nesting site according to the Handbook of the Birds of the World, such as cavity (e.g., woodpeckers), platform (e.g., osprey), or ground (e.g., quail).	Global Avian Trait Database
Average clutch size	Continuous	Estimated average clutch size using data from Handbook of the Birds of the World.	Global Avian Trait Database
Minimum clutch size	Continuous	Minimum clutch size according to Handbook of the Birds of the World.	Global Avian Trait Database
Incubation period	Continuous	Estimated average duration of incubation using data from Handbook of the Birds of the World.	Global Avian Trait Database
Fledgling period	Continuous	Estimated average time until the first nestling fledges using data from Handbook of the Birds of the World.	Global Avian Trait Database
Modeled bird annual survival	Continuous	Estimated annual survival modeled by the Institute for Bird Populations.	Global Avian Trait Database
Modeled bird age at first breeding	Continuous	Estimated age at first breeding modeled by the Institute for Bird Populations.	Global Avian Trait Database
Modeled bird longevity	Continuous	Estimated longevity modeled by the Institute for Bird Populations.	Global Avian Trait Database
Modeled bird generation length	Continuous	Estimated generation length modeled by the Institute for Bird Populations.	Global Avian Trait Database

[a] Tallamy et al. Unpublished dataset.
[b] Partners in Flight (2021).
[c] La Sorte et al. Unpublished dataset.
[d] Sekercioglu et al. Unpublished dataset.

TABLE 2. Candidate model set for determining whether certain ecological traits in addition to constraints for phylogeny and BCR explain variation in regional population trends for North American bird species ranked by LOOIC scores. Top-performing model (model 1) as determined by LOOIC approximation score highlighted in bold.

Model iteration	Model formula	LOOIC score	ΔLOOIC
1	**Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass + LogPopulationSize + HabitatBreadth + DietaryBreadth + ClutchSize + Incubation + Fledgling + Foraging Layer + InsectDependence**	**39,997.3**	0
2	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass + LogPopulationSize + ModeledBirdAnnualSurvival + ModeledBirdAgeAtFirstBreeding + ModeledBirdLongevity + ModeledBirdGenerationLength + ClutchSize + Incubation + Fledgling + InsectDependence	40,024.6	27.3
3	Regional population trend ~ 1|phylogeny + 1|BCR + InsectDependence + DistanceMigrated + LogBodyMass + LogPopulationSize	40,101.8	104.5
4	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated	40,118	120.7
5	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass + LogPopulationSize + PrimaryDiet	40,175	177.7
6	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + InsectDependence + LogBodyMass + HabitatBreadth + DietaryBreadth + ClutchSize + Incubation + Fledgling	40,302.7	305.4
7	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass + LogPopulationSize + PrimaryDiet + ForagingLayer	40,311.9	314.6
8	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass	40,333	335.7
9	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + InsectDependence + LogBodyMass + ClutchSize + Incubation + Fledgling	40,343.3	346
10	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass + LogPopulationSize + ModeledBirdAnnualSurvival + ModeledBirdAgeAtFirstBreeding + ModeledBirdLongevity + ModeledBirdGenerationLength + ClutchSize + Incubation + Fledgling + PrimaryDiet	40,361.7	364.4
11	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + InsectDependence + LogBodyMass + HabitatBreadth + DietaryBreadth + ClutchSize + Incubation + Fledgling + Foraging Layer	40,437.9	440.6
12	Regional population trend ~ 1|phylogeny + 1|BCR + LogPopulationSize + LogBodyMass	40,541.8	544.5
13	Regional population trend ~ 1|phylogeny + 1|BCR + InsectDependence + DistanceMigrated	40,593	595.7
14	Regional population trend ~ 1|phylogeny + 1|BCR + DistanceMigrated + LogBodyMass + ModeledBirdAnnualSurvival + ModeledBirdAgeAtFirstBreeding + ModeledBirdLongevity + ModeledBirdGenerationLength + InsectDependence	40,655.1	657.8
15	Regional population trend ~ 1|phylogeny + 1|BCR [a]	40,664	666.7
16	Regional population trend ~ 1|phylogeny + 1|BCR + InsectDependence + DistanceMigrated + LogBodyMass	40,686.6	689.3
17	Regional population trend ~ 1|phylogeny + 1|BCR + InsectDependence + DistanceMigrated + LogBodyMass + WinterGeography	40,771.1	773.8
18	Regional population trend ~ 1|phylogeny + 1|BCR + WinterGeography	40,793.5	796.2
19	Regional population trend ~ 1|phylogeny + 1|BCR + InsectDependence	40,801.4	804.1
20	Regional population trend ~ 1|phylogeny + 1|BCR + ClutchSize + Incubation + Fledgling + InsectDependence	40,960.9	963.6
21	Regional population trend ~ 1|phylogeny + 1|BCR + PrimaryBreedingHabitat + PrimaryNonbreedingHabitat	Did not converge	Did not converge
22	Regional population trend ~ 1|phylogeny + 1|BCR + WinterGeography + BreedingArea + NonbreedingArea	Did not converge	Did not converge
23	Regional population trend ~ 1|phylogeny + 1|BCR + Nest	Did not converge	Did not converge

[a] Terms for phylogeny and BCR begin with a "1|" to indicate that these are terms specified in the models as random intercepts.

and a thinning interval of 10 to ensure that the effective sample size for each parameter exceeded 400 (Vehtari et al. 2021). We specified weakly informative priors (mean of 0 and standard deviation of 10) for each parameter. We chose these prior values based on an informal sensitivity analysis—lower values for the standard deviation (i.e., SD = 1, SD = 5) influenced parameter estimates from the models, and one of the goals of this analysis was to avoid biasing the model with preconceived notions about how each predictor variable was thought to affect population trends. Finally, for each model we investigated the trace plot to confirm that the chains mixed appropriately and verified that the $\hat{r}$ values for each parameter did not exceed 1.01 to ensure that the model converged successfully (Vehtari et al. 2021). The package *brms* rescales all variables internally, so we did not rescale any variables before modeling. However, *brms* reports unscaled parameter effects, so we rescaled all selected variables by their respective standard deviations after modeling to enable direct comparisons between variables.

After building and running our set of candidate models (Table 2), we ranked models by measuring their predictive accuracy using an approximation of the leave-one-out cross-validation information criterion (LOOIC) with the R package *loo* (Vehtari et al. 2021). The *loo* package allows the user to input multiple candidate models where it then calculates an approximation of the LOOIC score for each model and returns a list ranking the models by their relative LOOIC approximations and thus can be compared like AIC scores (Vehtari et al. 2021). We used this function to select the top-performing candidate model, and checked the *pareto-k* diagnostics to ensure that the majority of the model data had *pareto-k* values under 0.7 (Vehtari et al. 2021). The *pareto-k* diagnostic describes the shape of the generalized Pareto distribution developed using the posterior data of the model, where values below 0.7 indicate that the variance of the Pareto distribution is finite and therefore offers a reliable estimate, and values above 0.7 indicate an infinite variance and therefore an unreliable estimate. We also performed and plotted a posterior predictive check for the top-performing model to visually inspect whether 1,000 draws of simulated response data closely matched our original trend data. Lastly, we summarized and plotted posterior distributions for the marginal effects on regional population trends of each parameter from the top-performing model using the r package *tidybayes* (Kay 2021). For each ecological trait, we created a unique data frame by producing 100 predicted draws of response data for each observation (i.e., species-region combination) for each level of the trait if it was ordinal, or 100 predicted draws for 100 sequential values of the trait if it was continuous, holding all other ecological traits at their respective mean values. We then plotted a mean point interval function to visualize the marginal effect of that particular ecological trait on predicted regional population trends.

We then merged our trend data with a phylogenetic tree containing the 380 species considered in our analysis and plotted a tree showing the relative group trends for major clades of birds as a visual post-hoc to understand if certain groups were driving results of the model. We opted to group regional population trends by family given evidence from Rosenberg et al. (2019) that certain families of birds experienced greater net losses in abundance compared to others. We assigned families to three trend classifications based on their BCR group trend: increasing (i.e., group trend > 1% yr^{-1}), stable (i.e., group trend between –1% yr^{-1} and 1% yr^{-1}), and decreasing (group trend < –1% yr^{-1}). Using the intercept of the phylogenetic control from our top-performing model, we also calculated Pagel's λ (lambda) to estimate the strength of the phylogenetic signal present in our regional population trend data (Pagel 1999). Pagel's λ is one of the core metrics used in comparative evolutionary and ecological studies to infer the degree to which phylogenetic relationships explain the distribution of traits (or in this case, trends) among a group of species. Pagel's λ ranges from 0 to 1, with low values suggesting phylogeny had no effect on regional population trend data and high values suggesting phylogeny alone explained the assortment of regional population trend data among the species considered in our analysis.

To visualize the effect of geography on regional population trends, we calculated mean regional population trends for each BCR with available BBS data, and plotted the resulting BCR map color coded by mean trend estimates.

Next, we conducted a second analysis to determine how the relative effects of ecological traits, phylogeny, and geography, differ in their contribution to explaining variation in regional population trends between major bird orders—specifically, Anseriformes (Ducks), Charadriiformes (Shorebirds), Passeriformes (Songbirds), and Pelecaniformes (Waterbirds). We chose these orders because they cover different key regions of the overall phylogeny and exhibit strong variation in their average regional population trends (see Results). Focusing on the role of ecological traits in predicting regional population trends across all species may miss more intricate relationships between certain groups of birds and phylogeny and geography, making this secondary analysis useful for understanding the overall picture relating population trends and ecological traits, phylogeny, and geography. In order to estimate and compare order-specific effects for ecological traits, phylogeny, and geography, we fit four smaller Bayesian models using the same model formula as described earlier, and based trait selection on the top-performing model (see Results). However, given the smaller number of observations per order (~260–360 for most orders except for Passeriformes), we could not include all of the traits identified by the top-performing model in our order-specific models due to issues with overfitting and nonconvergence despite manipulating the priors, number of iterations, and thinning intervals. Therefore, we chose to include migration distance as an example of a representative ecological trait given (1) it was the ecological trait with the strongest effect on regional trends identified by the top-performing model, and (2) migration distance has broad conceptual relevance to birds across many taxonomic groups. For these order-specific models, we specified migration distance as a fixed effect, and estimated random intercepts for phylogeny and geography. Given our goal was to compare the relative influence of migration distance, phylogeny, and geography in explaining variation in regional population for different orders, we scaled migration distance by its standard deviation prior to modeling. Scaling migration distance by its standard deviation meant the beta parameter estimated by each order-specific model represented the corresponding change in regional population trends for one standard deviation of change in migration distance. Therefore, scaling migration distance allowed for a more meaningful comparison with the random intercepts estimated for phylogeny and geography, which themselves represent the standard deviation of the random effects for these two variables on regional population trends. For each order-specific model, we used the following model structure:

$$\text{regional trend} \mid \text{error} \sim \text{migration distance} + \\ (1 \mid \text{phylogeny}) + (1 \mid \text{geography})$$

where like our first analysis, regional population trends (adjusted by the uncertainty of the estimate, "error") are predicted as a function of a fixed effect for migration distance (i.e., representative ecological trait), a random intercept accounting for differences in population trends due to

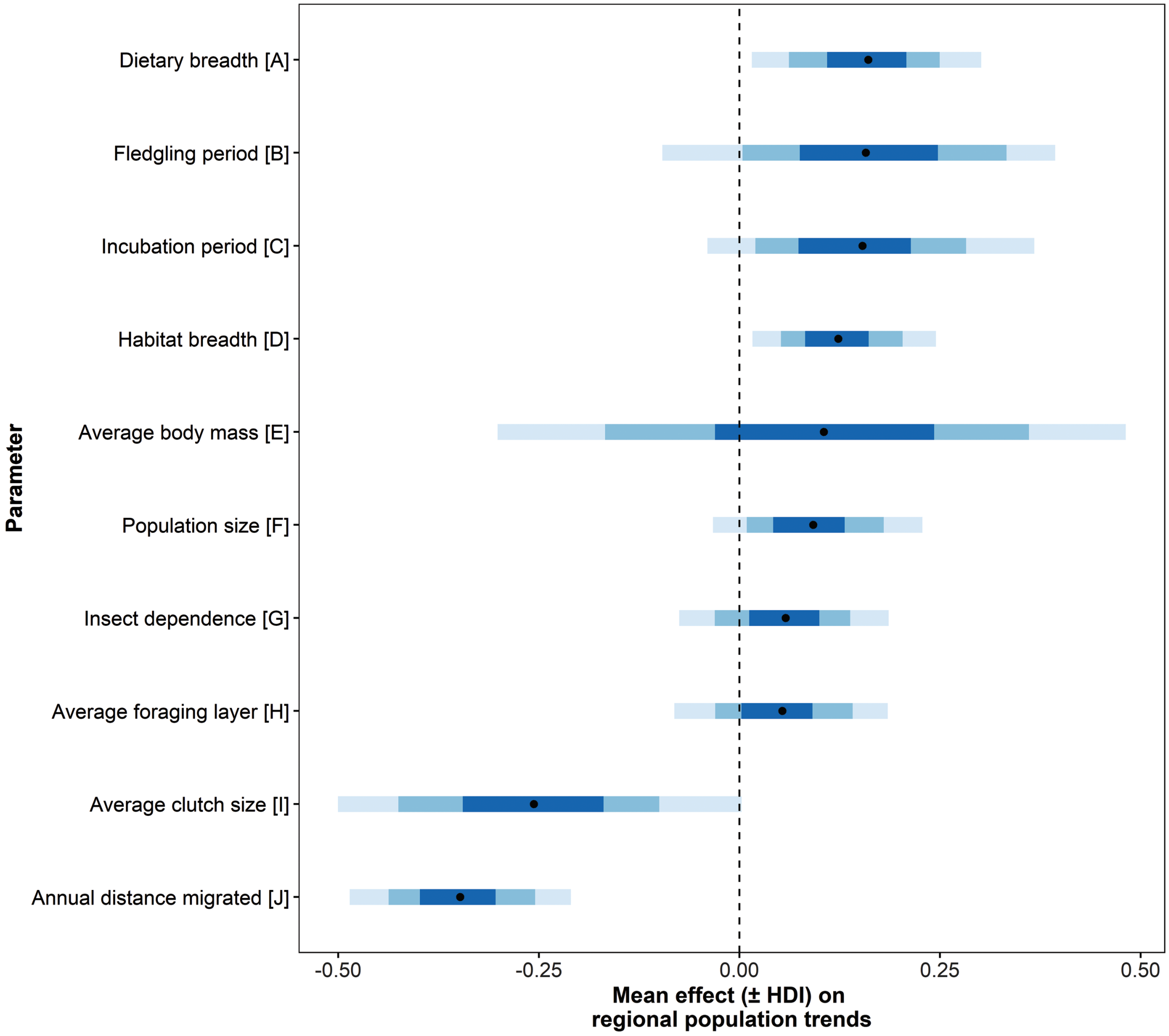

FIGURE 1. Ecological traits explain variation in regional population trends for North American birds. The panel above displays mean parameter effects scaled by standard deviation with high density intervals (HDIs) for each parameter measured in the top-performing Bayesian model. Black dots represent means, and dark blue, blue, and light blue shading represent 50%, 80%, and 95% credible intervals, respectively. Each subsequent labeled subpanel shows individual marginal effects on regional population trends (PRPT, percent change/year) for each observed ecological trait from the top-performing model. Each graph plots a mean point interval function (with 50%, 80%, and 95% credible intervals) estimating the marginal effect of each ecological trait on posterior draws of predicted regional population trends (100 draws per level of the ecological trait for ordinal traits, or 100 draws for 100 sequential values for continuous traits). Plotted points are a subsample (~1% to 10% depending on the trait) of the posterior predicted draws included strictly for visual purposes. These individual observed ecological trait plots illustrate that regional population trends for North American birds are predicted to increase with increasing (**A**) dietary breadth, (**B**) fledgling period (days), (**C**) incubation period (days), (**D**) habitat breadth, (**E**) log-transformed average body mass (g), (**F**) log-transformed population size, (**G**) insect dependence throughout the annual cycle, (**H**) average foraging layer, but are predicted to decrease with increasing (**I**) average clutch size, and (**J**) annual distance migrated throughout the annual cycle (km yr^{-1}). *Figure 1 is continued on the next page.*

phylogenetic dissimilarity between species, and a random intercept accounting for spatially heterogenous differences in population trends due to geography. We ran into multiple issues with convergence for the Anseriformes model which we could not resolve despite manipulating priors, number of chains, number of iterations, and thinning interval. Based on a post-hoc investigation of the Anseriformes model, we reasoned that the convergence issues likely stemmed from the fact that migration distance accounted for nearly zero variation in regional population trends. In other words, the model was tasked with estimating a slope for an ecological trait that may simply not be meaningful for explaining regional population trends for Anseriformes. Given these issues with non-convergence, we opted to remove Anseriformes from the analysis. After modeling Charadriiformes, Passeriformes, and Pelecaniformes, we plotted the resulting effects of migration distance, phylogeny, and geography to visualize their relative influence on explaining variation in regional population trends for each of these three bird orders we modeled.

Finally, curious to further understand how the role of migration distance in influencing regional population trends

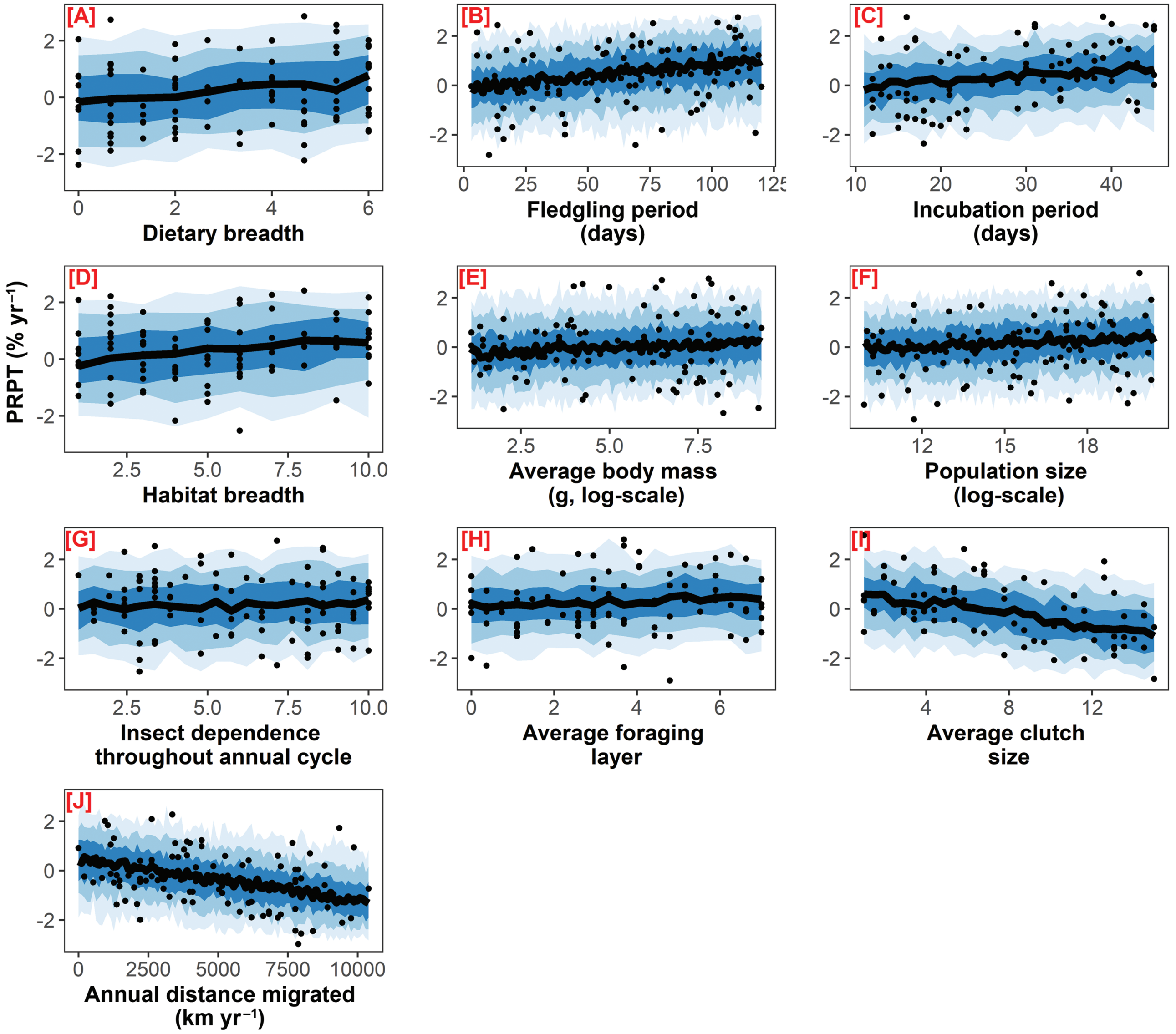

FIGURE 1. Continued

varied with order, we constructed one last model that included all the species in our dataset using the following model syntax:

$$\text{regional trend}\,|\text{error} \sim (1 + \text{migration distance}|\,\text{order}) + (1 \mid \text{phylogeny}) + (1 \mid \text{geography})$$

where the response (regional trends adjusted by error in the estimates) and random intercepts accounting for variation due to phylogeny and geography are the same as prior models in our previous analyses. The key difference in this model is the inclusion of the random slope term migration distance|order. The inclusion of the term allowed us to estimate posterior probability distributions for the effect (i.e., slope) of migration distance on regional trends for every single order represented in our dataset. After running the model, we plotted these posterior probability distributions for each order ranked by increasing slope estimates (i.e., from orders where increasing migration distance has a negative effect on regional population trends to orders where increasing migration distance has a positive effect on regional population trends).

We used R v.4.2.2 for all data preparation, manipulation, analysis, and visualization (R Core Team 2023). All data and R code are available in Dryad (see Stevens et al. 2023).

RESULTS

The Bayesian generalized mixed model with the lowest leave-one-out information criterion approximation score (LOOIC = 39,997.3) identified phylogeny (SD 0.23 ± 0.01) and geography (SD = 0.41 ± 0.06), as well as log-transformed average body mass, insect dependence across the annual cycle, log-transformed population size, average annual distance migrated, habitat breadth, dietary breadth, average clutch size, incubation period, fledgling period, and average foraging layer as important in explaining variation in regional population trends for 380 North American bird species (Figure 1). Highest density credible intervals did not overlap with 0 for dietary breadth, habitat breadth, average clutch size, and annual distance migrated (Figure 1). Ecological traits differed in their individual effects on

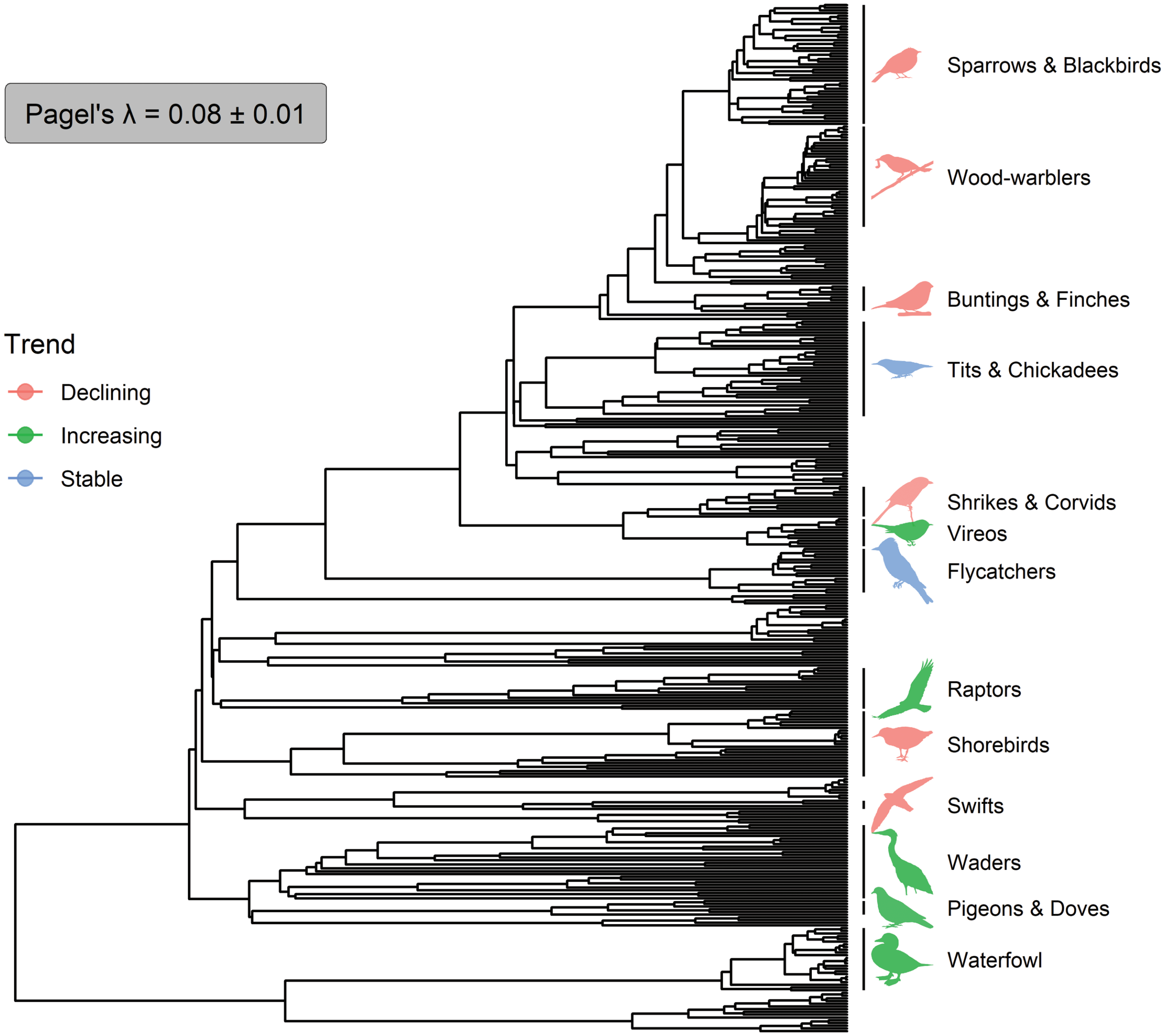

FIGURE 2. A phylogenetic tree merged with regional population trend data for 380 North American bird species highlights variation in average regional population trends between different clades. Images and labels correspond to select clades of birds, and are colored based on the average regional population trend for that group: red indicates a declining trend (< –1%), blue is stable (between –1% and 1%), and green is increasing (>1%). Pagel's λ (lambda) indicates the strength of the phylogenetic signal present in the regional population trend data, where values close to zero indicate a weak phylogenetic effect and values close to one indicate a strong phylogenetic effect.

predicted regional population trends, sampled from the posterior distribution of the top-performing model (Figure 1). Predicted regional population trends were positively associated with increasing dietary breadth (Figure 1A), incubation period (Figure 1B), fledgling period (Figure 1C), habitat breadth (Figure 1D), log-transformed average body mass (Figure 1E), log-transformed population size (Figure 1F), insect dependence across the annual cycle (Figure 1G), and average foraging layer (Figure 1H). Conversely, predicted regional population trends were negatively associated with increasing average clutch size (Figure 1I) and average annual distance migrated (Figure 1J).

A phylogeny merged with trend data revealed clear trajectories for various clades of the 380 species considered in this study (Figure 2). Sparrows and blackbirds, wood-warblers, shorebirds, buntings and finches, swifts, and shrikes and corvids all exhibited group trends of less than –1% yr^{-1}, while raptors, waterfowl, waders, pigeons, vireos, and doves exhibited group trends of over 1% yr^{-1} (Figure 2). Other major clades, such as flycatchers, tits, and chickadees, exhibited intermediate group trends of between –1% and 1% yr^{-1} (Figure 2). Despite this apparent assortment of regional population trends by clade, Pagel's λ was low [λ: mean (SE) = 0.08 (0.01); Figure 2].

Mean regional population trends separated by BCR showed variation along north–south and coastal–interior gradients (Figure 3). The regions with the most negative mean regional population trends (~ –1% yr^{-1}) tended to occur in the extreme latitudes of North America, such as Northwestern interior forest covering Alaska and British Columbia as well as peninsular Florida on the East coast and the Sierra Madre Occidental extending south into Mexico. Conversely, BCRs in the interior of the continent tended to lean toward positive mean regional trends. Our BCR map highlights a band of BCRs with

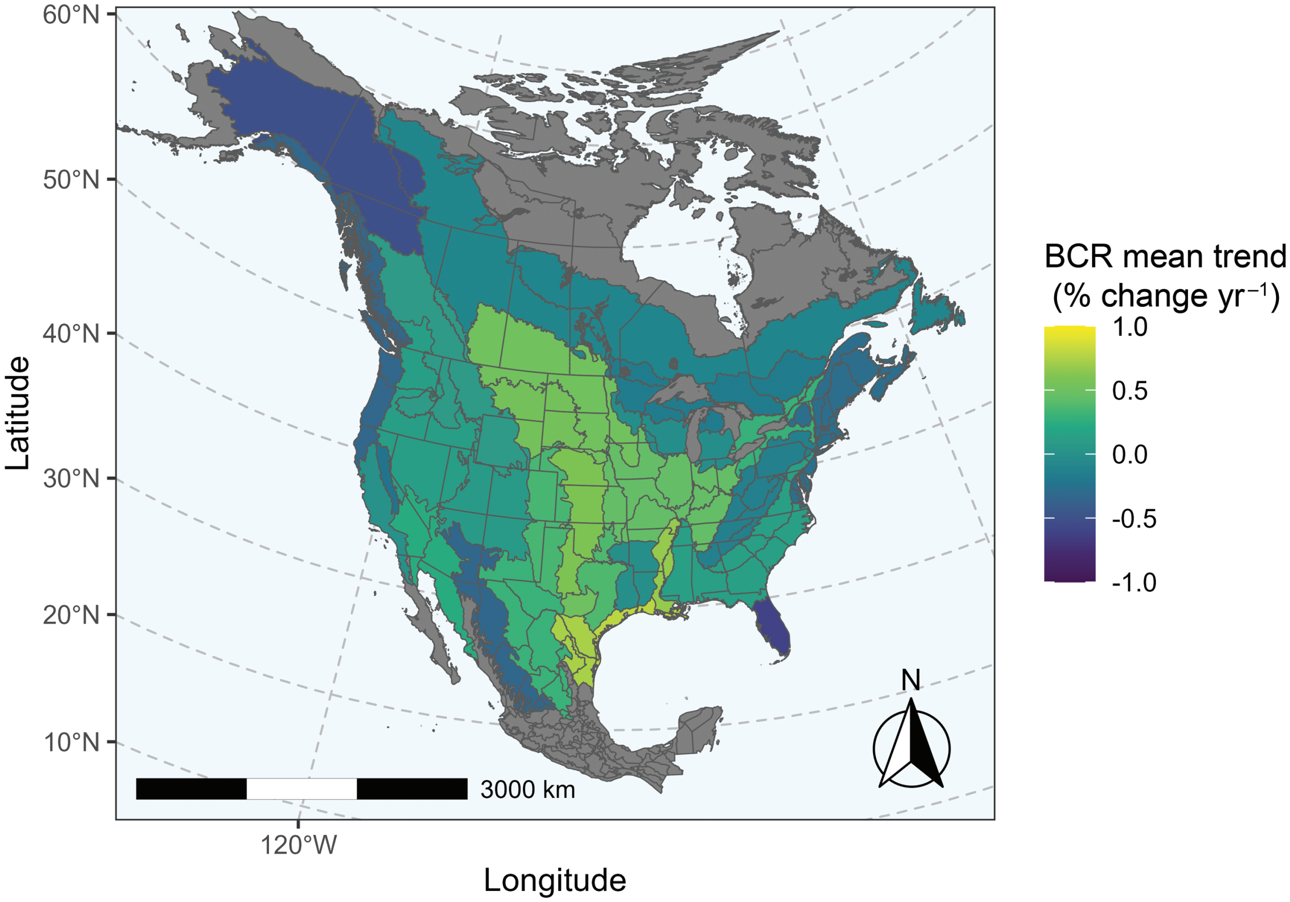

FIGURE 3. Mean regional population trends vary geographically by Bird Conservation Region (BCR), where species occupying regions at more extreme latitudes in North America are more likely to exhibit negative regional population trends. Each colored region represents one BCR and its corresponding mean regional population trend, calculated by averaging the regional population trend for each species with available trend data from that BCR. Darker colors represent more negative mean regional population trends whereas lighter colors represent more positive mean regional population trends. Dark lines indicate BCR boundaries. Gray BCRs represent areas lacking sufficient regional trend estimates for any of the 380 species considered in this analysis.

positive mean regional population trends beginning with the Tamaulipan Brushlands along the Texas-Mexico border and extending up through the Prairie Pothole region.

Individual Bayesian order-specific models for shorebirds, songbirds, and waterbirds revealed that the relative effects of migration distance, phylogeny, and geography, do not impact different orders uniformly (Figure 4). The effect of geography was strongest in explaining variation in regional population trends for shorebirds, whereas migration distance had the strongest effect in explaining regional population trends for songbirds. The effect of phylogeny was relatively low compared to migration distance and geography for all bird orders.

Finally, a global model estimating random slopes for migration distance by order highlighted variation in the role of migration distance in influencing regional population trends among orders (Figure 5). Increasing migration distance appears to negatively affect regional trends for orders including many long-distance migrants such as Apodiformes and Passeriformes.

DISCUSSION

Overall, our results provide evidence that multiple ecological traits correlate with population declines for North American birds. Clearly, understanding the variation in regional population trends is more nuanced than broad effects of geography and phylogeny, instead requiring comprehensive information on species-specific ecology to understand this variation. We were unable to identify a single trait (or pair of traits) that were the primary drivers of variation observed across large geographic and taxonomic scales. Though our analysis identified multiple ecological traits, each trait exhibited a weak individual effect in predicting population trends for all species. However, it appears that increasing migration distance could correspond with more negative regional population trends for particular orders (e.g., songbirds).

Phylogeny and Geography

Our results provide empirical evidence that ecological traits, phylogeny, and geography are associated with regional population trends of North American birds. The effects of phylogeny and geography are consistent with pre-existing knowledge that some variation in demographic trends is due to (1) phylogenetic relationships across different major groups of taxa (Böhning-Gaese and Oberrath 1999) and (2) spatial heterogeneity of the environment, respectively. Our results follow the findings of Rosenberg et al. (2019) who highlighted major net declines in abundance for some clades of birds (e.g.,

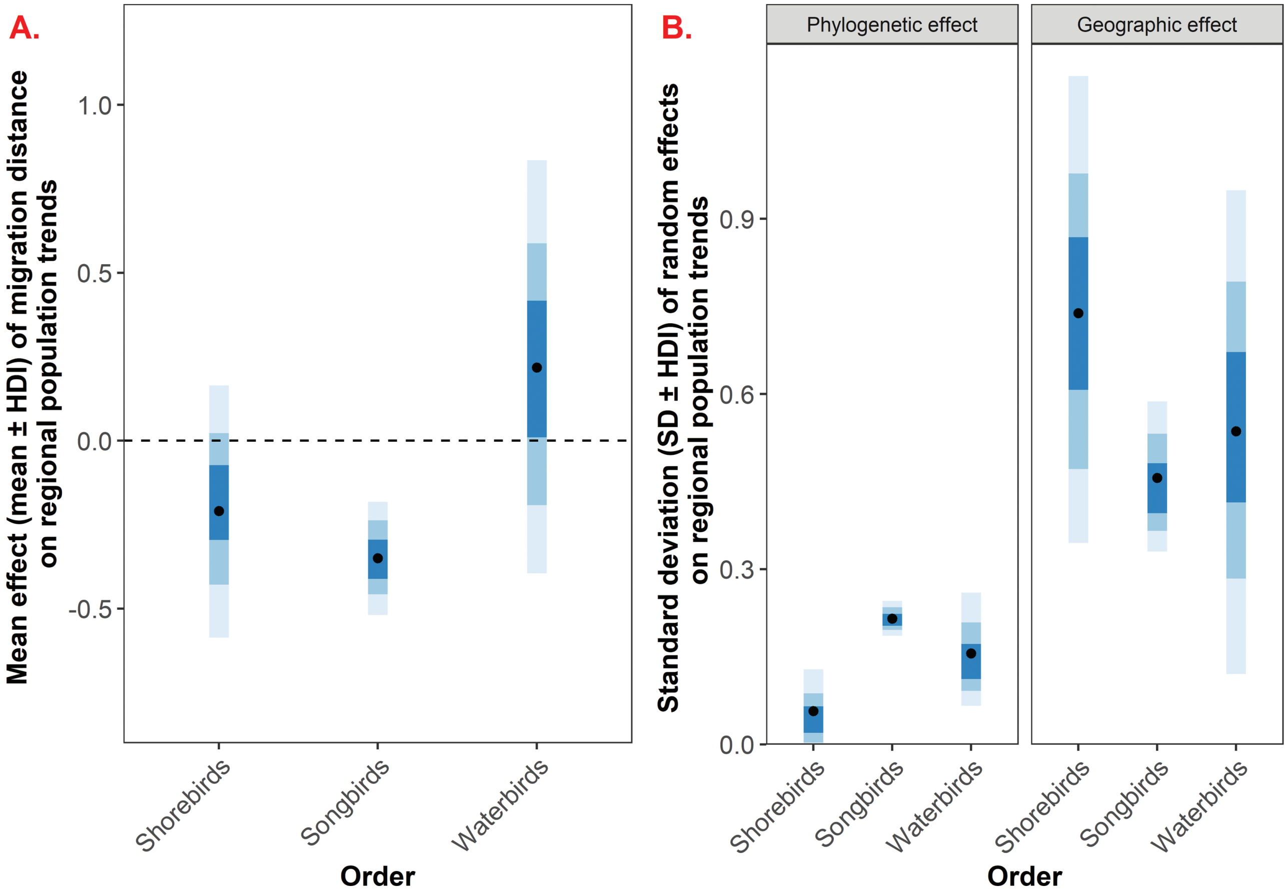

Figure 4. Average annual migration distance, phylogeny, and geography vary in their contribution to explaining variation in regional population trends between three major North American bird orders. Black dots represent mean estimates of standard deviation from each order-specific Bayesian intercept-only model. Dark blue shading, blue shading, and light blue shading represent the 50%, 80%, and 95% highest density intervals (HDIs), respectively, Orders are labeled by their colloquial group names: Charadriiformes (Shorebirds), Passeriformes (Songbirds), and Pelecaniformes (Waterbirds).

shorebirds) as well as for birds occupying particular regions in North America (e.g., grasslands). Additionally, we found notable mean declines for particular clades like sparrows, larks, pipits, blackbirds, wood-warblers, shorebirds, and swifts, and notable mean increases for many large raptors, wading birds, and waterfowl. Finally, similar to Rosenberg et al. (2019), our results highlight the inexplicable success of vireos—obligate long-distance migratory insectivores which, from an ecological traits perspective, we would expect to be declining.

Our map displaying mean regional population trends by BCR revealed intriguing variation along north–south and coastal–interior gradients. Interestingly, Godown and Peterson (2000) identified peninsular Florida and the Sierra Madre Occidental—two of the BCRs exhibiting the most negative mean regional population trends in this study—as hosting the highest concentration of endangered species lacking protection from the National Park system more than two decades ago. More recently, Handel and Sauer (2017) calculated long-term population trends for species occupying BCRs in Alaska—namely, northwestern interior forest, the other BCR in our study with a pronounced mean negative regional trend estimate—and found that species associated with northwestern interior forest habitat (e.g., Olive-sided Flycatcher [*Contopus cooperi*]) showed steep, significant declines from 1993 to 2015. Rosenberg et al. (2019) highlighted boreal and western forests—encompassing BCRs like northwestern interior forest and the boreal hardwood shield—as 2 of the 3 biomes that experienced highest net loss of total bird abundance since 1970, likely driven by massive losses in blackbirds. Rosenberg et al. (2019) also showed that the grassland biome experienced the greatest net loss of birds in North American since 1970. Intriguingly, this result directly contradicts our finding that the BCRs with the most positive mean regional population trends appeared to cluster in the southern and central United States, following a band of BCRs from the Tamaulipan Brushlands and Gulf Coast prairie north through the Prairie Pothole region. One notable distinction between our two analyses is that Rosenberg et al. (2019) focused on net changes in abundance while we focused instead on regional population trends. Therefore, every species is represented equally in our mean trend estimates, whereas in Rosenberg et al. (2019) a few species that suffered major losses in abundance since 1970 could potentially dominate the estimate of net abundance change for a given biome. We suspect that the relative success of waterfowl could be driving the positive mean regional trends for the BCRs covering the Midwestern belt.

Identified Ecological Traits

The three ecological traits we predicted to explain variation in avian declines—average body mass, insect dependence across

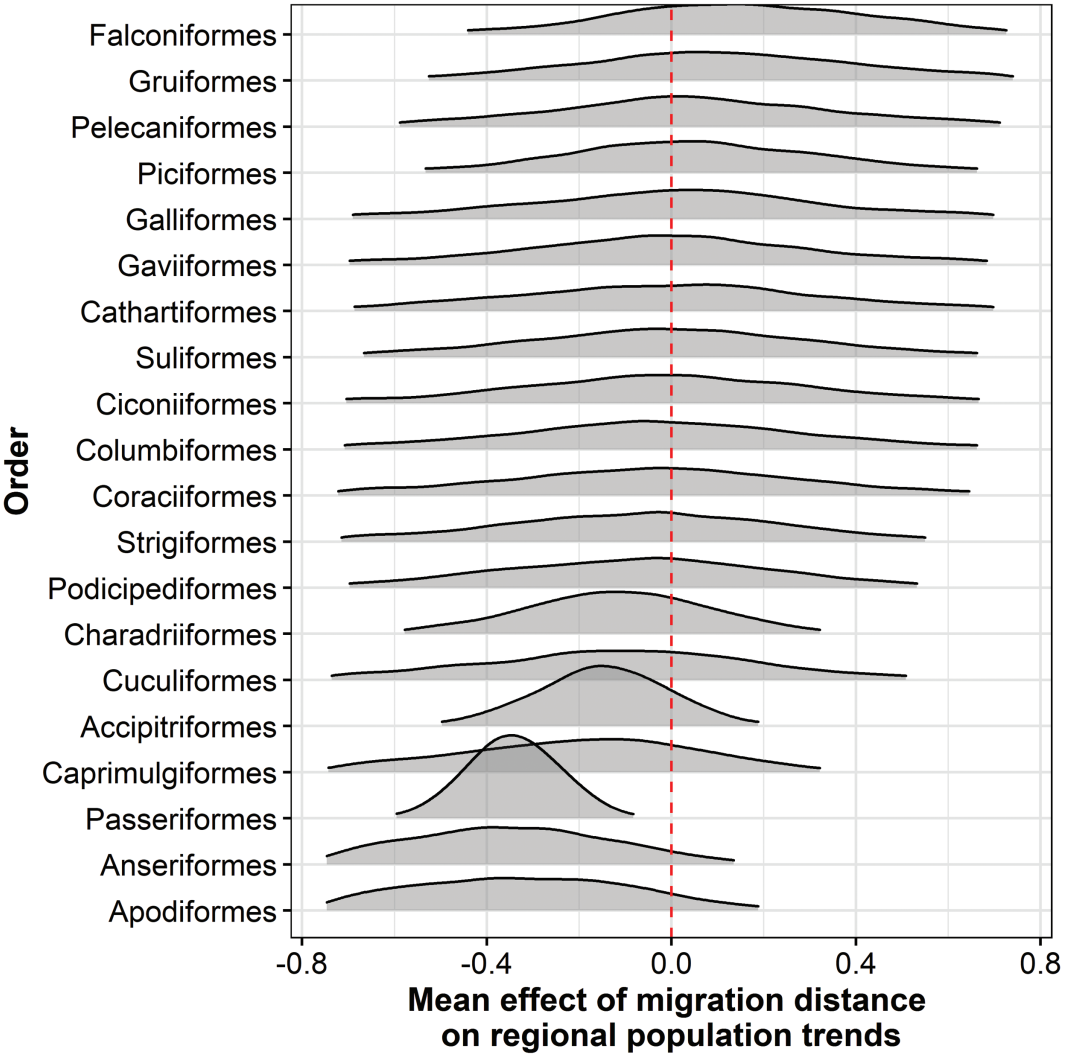

FIGURE 5. Effect of migration distance on regional population trends changes with bird orders in North America. Each curve represents the posterior probability distribution (95% confidence interval) for the order-specific effect of migration distance on regional population trends from a global random slopes Bayesian model accounting for variation due to phylogeny and geography. Orders and their corresponding posterior probability distributions are ranked by increasing mean values (scaled by standard deviation) for the effect of migration distance on regional population trends. The height at any point of a posterior probability curve represents the corresponding density of predicted *x*-values from the model. Dotted red line highlights the *y*-intercept.

the annual cycle, and average annual distance migrated—exhibited signals in predicting regional population trends. The strong, positive effect of average body mass on regional population trends almost certainly reflects the rebounding populations of large-bodied species following successful conservation initiatives implemented in the 20th century. Well-known examples of these rebounding large-bodied species include the recovery of raptors like Bald Eagles following the ban of dichloro-diphenyl-trichloroethane (DDT; Eakle et al. 2015) and ongoing population growth for most waterfowl species due to dedicated attention to wetlands and adaptive harvest management (Anderson et al. 2018). Furthermore, our phylogenetic analysis revealed that clades of large-bodied birds exhibited more positive average regional population trends than other clades, with waders, waterfowl, and raptors all showing positive group trends, underscoring rebounding populations of these groups of birds thanks to intensive management and conservation. Importantly, this relationship between increased average body mass and more positive regional population trends is atypical compared to global trends. Across the world, large-bodied organisms tend to face elevated extinction risk (Atwood et al. 2020), as is the case for large mammals (Cardillo et al. 2005), marine and freshwater fish (Olden et al. 2007), and reptiles, among other groups (Atwood et al. 2020).

Surprisingly, we found that insect dependence throughout the annual cycle had a marginally positive effect on regional population trends. We expected the opposite, mainly due to the hypothesized consequences of ongoing insect loss for birds that depend on insects during all stages of their annual cycle (van Klink et al. 2020). Upon visual inspection of the predicted regional trend data, we noticed that multiple waterfowl species have a moderate insect dependence score—6.5, or "waterbird that eats both insects and vegetation." Given that most waterfowl species in our analysis displayed high regional population trends, these ducks (e.g., Wood Duck [*Aix sponsa*]) could be driving the positive effect for insect dependence in the model. Past research that focused on smaller geographic scales and specialized groups of birds provides some support that higher insect dependence does in fact correlate with avian declines (Tallamy and Shriver 2021; but see Michel et al. 2016). For example, aerial insectivores exhibit steeper population declines than bird species occupying other feeding guilds (Nebel et al. 2010, 2020), insect dependence acts as one of the core factors limiting aerial insectivores during multiple stages of their annual cycles (Spiller and Dettmers 2019), and aerial insectivore declines correlate with ongoing insect loss (Tallamy and Shriver 2021). However, other work has underscored the complexity underlying the relationship between insect loss and aerial insectivores, suggesting that insects do not act as the core limiting factor driving declines for aerial insectivores and other guilds (Michel et al. 2016, Spiller and Dettmers 2019). Overall, insect loss interacts with a myriad of other natural and anthropogenic processes (e.g., climate change) to drive spatiotemporal variation in population change (Michel et al. 2021), so insect dependence likely plays a unique role in influencing regional population trends for different groups of birds.

Regional population trends for North American birds increased with increasing habitat breadth, dietary breadth, and foraging layer, suggesting that species exhibiting higher plasticity in space and resource use are more likely to exhibit positive regional population trends. This result follows work documenting a predictable shift from slower paced specialist life-history strategies to faster paced, generalist ones (Cooke et al. 2019). As one might expect, the capability to use multiple habitat types and rely on a variety of food sources throughout the cycle may confer a demographic advantage, especially in the face of global change. However, this issue is likely scale-dependent. Some evidence suggests that habitat and dietary breadth are more important in predicting bird distributions at a regional scale but lose power at continental scales (Brändle and Brandl 2001).

Our top-performing model also identified a group of reproductive ecological traits—namely, clutch size, incubation period, and fledgling period—as important for predicting regional population trends for North American birds. Specifically, predicted regional population trends increased with incubation and fledgling periods but decreased with increasing clutch size. This result may in part be due to some correlation between body mass and reproductive traits, where larger bodied birds are generally expected to have lower clutch sizes and longer fledgling periods, although these relationships are also influenced heavily by geographic variation in nesting behavior (e.g., tropical versus temperate) and ambient temperature (Martin et al. 2007). Clutch size follows a strong latitudinal gradient, where bird species at higher latitudes consistently have higher average clutch sizes (Jetz et al. 2008). Given more obligate, long-distance migratory birds occur at higher latitudes, clutch size is partially correlated with annual distance migrated, the most important ecological trait for predicting regional population trends identified by our analysis. Moreover, we know particular groups of migratory birds breeding in the boreal forest and arctic tundra like wood-warblers, blackbirds, and shorebirds exhibit some of the steepest annual declines amongst bird species in North America (Rosenberg et al. 2019). These species share higher clutch sizes and shorter incubation and fledgling periods, and therefore could be driving the direction of the parameter effects for these reproductive ecological traits.

Consistent with our predictions, increasing average, annual migration distance corresponded with decreasing regional population trends. In fact, this ecological trait exhibited the strongest magnitude in its effect on regional population trends compared to any other ecological trait in the top-performing model. Our order-specific models further revealed that the negative effect of increasing migration distance seems pronounced for orders with many long-distance migrants; namely, songbirds, swifts, nighthawks and ducks. Globally, long-distance migrant bird species are declining much faster than sedentary species (Sekercioglu 2007; Horns and Şekercioğlu 2018). Between 2007 and 2018, 79% more of the world's long-distance migrant bird species became extinction-prone (i.e., near threatened or threatened with extinction), in contrast to 8% more of the world's sedentary species becoming extinction-prone during the same period (Sekercioglu 2007; Horns and Şekercioğlu 2018). Ultimately, the fitness tradeoff between the greater costs associated with long-distance migrations (e.g., threat exposure and physiological expenditure) and the opportunity to access seasonally abundant resources likely affects each migratory species uniquely (Alerstam 2011, Cheng et al. 2019, Winger and Pegan 2021). Furthermore, previous work suggests that partial migrants (i.e., species where some populations migrate and others do not) were less likely to exhibit population declines than obligate migrants (Gilroy et al. 2016). Despite these species-level differences, however, there is growing evidence suggesting that climate change may be selecting for shorter migration distances via extreme drought conditions in key breeding or nonbreeding regions (Jenni and Kéry 2003, Visser et al. 2009). We note that many species exhibit considerable intraspecific variation in migration distance (Ketterson and Nolan Jr. 1985). Therefore, examining the relationship between demography and migration distance within a species could lead to a more nuanced understanding of this mechanism.

Our predictor variables represent ecological traits that relate to multiple ecological and environmental processes, many of which may also interact synergistically throughout the annual cycle. Therefore, though we were careful to only use variables that we knew were only weakly correlated or not correlated at all in our analysis, the ecological traits we identified surely are not mutually exclusive in their effects on population trends for North American bird species. Previous studies from multiple long-term study systems have demonstrated that myriad processes interact to affect bird species throughout their annual cycle (Norris and Marra 2007, Morrissette et al. 2010, Finch et al. 2014). Additionally, we note that our selection of ecological trait variables likely does not cover all traits that may be relevant to explaining variation in species' population trends, such as data on phenology and migratory connectivity that are not available for all species (Faaborg et al. 2010). Moreover, the coarse resolution of many of our traits almost certainly hinders the predictive capacity of our model to reflect accurate patterns between regional population trends and ecological traits. Particularly for species that occupy expansive geographic ranges, many of the traits considered in our analysis likely do not remain uniform across intraspecific populations (e.g., known differences in diet for different populations of American Robins [*Turdus migratorius*]; Wheelwright 1986).

Implications for Conservation

To date, most conservation efforts have been focused on broad scale habitat protection and threat reduction (Carter et al. 2000). In many cases, protected habitat may be insufficient for vulnerable species conservation, as it is eroded by logistical, political, and socioeconomic factors and constraints (Baldi 2020). As a result, many organizations and governmental agencies resort to determining population and species-focused limiting factors only once species becomes federally listed. Our results highlight that even species which may appear similar based on ecological traits may still experience different population trends, and that these population trends cannot be explained by phylogeny and geography alone. Furthermore, our order-specific analyses revealed that the relative magnitude of the effects of migration distance, phylogeny, and geography differ even between bird orders. We found that the relative effect of migration distance on explaining variation in regional population trends is higher than the effects of phylogeny and geography for songbirds, but that geography outweighs migration distance and phylogeny in its effect on regional population trends for shorebirds. Our global migration distance-order model further underscored the fact that the degree to which migration distance impacts regional population trends is highly variable across orders (e.g., Falconiformes versus Passeriformes). Our results highlight migration distance as just one example of an ecological trait with notable variation in its influence on regional population trends for different groups of North American birds, and, moreover, show that phylogeny and geography can further modulate the effects of ecological traits like migration distance on influencing these regional population trends.

Our results challenge those current conservation management plans in North America that are organized and implemented regionally (e.g., the US Fish and Wildlife regional division system). One notable exception is the success of waterfowl, which continue to exhibit overwhelmingly positive trends across species despite being managed as a group at a regional level (e.g., flyways; Williams et al. 1999). Our post hoc analysis suggests that this success for waterfowl could be due to the strong phylogenetic control operating on regional population trends for ducks, potentially facilitating the implementation of similar conservation strategies and management practices across geographically distinct regions. This differs notably from other major groups like shorebirds, whose regional population trends appear be influenced strongly by geography with little to no effect from phylogenetic differences, or raptors, which seem to be more influenced by ecological traits. Accounting for these order-specific controls on regional population trends should be a priority in conservation planning given that management practices implemented at a range-wide scale will likely only be effective for certain groups of birds (e.g., for waterfowl, but not shorebirds). The link between shared traits and population trends for certain groups also suggests that multi-species conservation plans could be effective if aimed at species that share key ecological traits, like aerial insectivores, for which working groups already exist.

The reality that a complex suite of ecological traits drive variation in population trends for most North American bird species underscores the need to expand current conservation practices towards recovery strategies that encompass both existing biogeographic coverage but also integrate research on single species across their annual cycles. Such strategies include building on existing multiorganizational, species-specific working groups (e.g., Cerulean Warbler Working Group; Dawson et al. 2012), cross-continental conservation plans for declining clades of migratory birds (e.g., Western Hemisphere Shorebird Reserve Network; Niles et al. 2010), and the strengthening of existing policy (e.g., Migratory Bird Treaty Act), research, and management on rapidly declining species and populations before they reach critically low population levels.

Fortunately, some of this transition in conservation strategy has begun. Scientists, wildlife managers, and conservation practitioners across federal, academic, and non-governmental institutions have identified a list of bird species (i.e., species on the brink) likely to be considered for federal listing if no action is taken. The primary goal of this effort—known as the Road to Recovery—is to then identify species-specific limiting factors (R2R 2023). Limiting factors remain unknown for most North American bird species, thus necessitating a carefully planned combination of quantifying migratory connectivity to link populations across their annual cycle, vital rate estimation, full annual cycle population modeling and determination of the drivers of reduced vital rates. Given the longstanding role of birds as sentinels of environmental change (Wormworth and Sekercioglu 2011), improving our understanding on the factors limiting bird populations could also elucidate why we are witnessing widespread declines across taxa worldwide.

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Ethics statement

We did not adhere to any specific institutional or governmental ethics guidelines for this project.

Conflict of interest statement

The authors declare no conflicts of interest.

Author contributions

H.C.S., E.R.B., C.H.S., K.V.R., and P.P.M. conceived the idea for this manuscript, and H.C.S., A.C.S., and V.S. designed the analysis and analyzed the data. H.C.S. wrote the paper. C.H.S., K.V.R., F.A.L., and D.T. contributed crucial datasets for the analysis.

Data availability

Analyses reported in this article can be reproduced using the data provided by Stevens et al. (2023).

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