Decline of the North American Avifauna

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Abstract: Species extinctions have defined the global biodiversity crisis, but extinction begins with loss in abundance of individuals that can result in compositional and functional changes of ecosystems. Using multiple and independent monitoring networks, we report population losses across much of the North American avifauna over 48 years, including once common species and from most biomes. Integration of range-wide population trajectories and size estimates indicates a net loss approaching 3 billion birds, or 29% of 1970 abundance. A continent-wide weather radar network also reveals a similarly steep decline in biomass passage of migrating birds over a recent 10-year period. This loss of bird abundance signals an urgent need to address threats to avert future avifaunal collapse and associated loss of ecosystem integrity, function and services.

One Sentence Summary: Cumulative loss of nearly three billion birds since 1970, across most North American biomes, signals a pervasive and ongoing avifaunal crisis.
Main Text:

Slowing the loss of biodiversity is one of the defining environmental challenges of the 21st century (1–5). Habitat loss, climate change, unregulated harvest, and other forms of human-caused mortality (6, 7) have contributed to a thousand-fold increase in global extinctions in the Anthropocene compared to the presumed prehuman background rate, with profound effects on ecosystem functioning and services (8). The overwhelming focus on species extinctions, however, has underestimated the extent and consequences of biotic change, by ignoring the loss of abundance within still-common species and in aggregate across large species assemblages (2, 9). Declines in abundance can degrade ecosystem integrity, reducing vital ecological, evolutionary, economic, and social services that organisms provide to their environment (8, 10–15). Given the current pace of global environmental change, quantifying change in species abundances is essential to assess ecosystem impacts. Evaluating the magnitude of declines requires effective long-term monitoring of population sizes and trends, data which are rarely available for most taxa.

Birds are excellent indicators of environmental health and ecosystem integrity (16, 17), and our ability to monitor many species over vast spatial scales far exceeds that of any other animal group. We evaluated population change for 529 species of birds in the continental United States and Canada (76% of breeding species), drawing from multiple standardized bird-monitoring datasets, some of which provide close to fifty years of population data. We integrated range-wide estimates of population size and 48-year population trajectories, along with their associated uncertainty, to quantify net change in numbers of birds across the avifauna over recent decades (18). We also used a network 143 weather radars (NEXRAD) across the contiguous U.S. to estimate long-term changes in nocturnal migratory passage of avian biomass through the airspace in spring from 2007 to 2017. The continuous operation and broad coverage of NEXRAD provide an automated and standardised monitoring tool with unrivaled temporal and spatial extent (19). Radar measures cumulative passage across all nocturnally migrating species, many of which breed in areas north of the contiguous U.S. that are poorly monitored by avian surveys. Radar thus expands the area and the proportion of the migratory avifauna that is sampled relative to ground surveys.

Results from long-term surveys, accounting for both increasing and declining species, reveal a net loss in total abundance of 2.9 billion (95% CI = 2.7–3.1 billion) birds across almost all biomes, a reduction of 29% (95% CI = 27–30%) since 1970 (Figure 1; Table 1). Analysis of NEXRAD data indicate a similarly steep decline in nocturnal passage of migratory biomass, a reduction of 13.6 ± 9.1% since 2007 (Figure 2A). Reduction in biomass passage occurred across the eastern U.S. (Figure 2 C,D), where migration is dominated by large numbers of temperate- and boreal-breeding songbirds; we observed no consistent trend in the Central or Pacific flyway regions (Figure 2B,C,D, Table S5). Two completely different and independent monitoring techniques thus signal major population loss across the continental avifauna.

Species exhibiting declines (57%, 303/529) based on long-term survey data span diverse ecological and taxonomic groups. Across breeding biomes, grassland birds showed the largest magnitude of total population loss since 1970—more than 700 million breeding individuals across 31 species—and the largest proportional loss (53%); 74% of grassland species are declining. (Figure 1; Table 1). All forest biomes experienced large avian loss, with a cumulative reduction of more than 1 billion birds. Wetland birds represent the only biome to show an overall
net gain in numbers (13%), led by a 56% increase in waterfowl populations (Figure 3, Table 1). Surprisingly, we also found a large net loss (63%) across 10 introduced species (Figure 3D,E, Table 1).

A total of 419 native migratory species experienced a net loss of 2.5 billion individuals, whereas 100 native resident species showed a small net increase (26 million). Species overwintering in temperate regions experienced the largest net reduction in abundance (1.4 billion), but proportional loss was greatest among species overwintering in coastal regions (42%), southwestern aridlands (42%), and South America (40%) (Table 1; Figure S1). Shorebirds, most of which migrate long distances to winter along coasts throughout the hemisphere, are experiencing consistent, steep population loss (37%).

More than 90% of the total cumulative loss can be attributed to 12 bird families (Figure 3A), including sparrows, warblers, blackbirds, and finches. Of 67 bird families surveyed, 38 showed a net loss in total abundance, whereas 29 showed gains (Figure 3B), indicating recent changes in avifaunal composition (Table S2). While not optimized for species-level analysis, our model indicates 19 widespread and abundant landbirds (including 2 introduced species) each experienced population reductions of >50 million birds (Data S1). Abundant species also contribute strongly to the migratory passage detected by radar (19), and radar-derived trends provide a fully independent estimate of widespread declines of migratory birds.

Our study documents a long-developing but overlooked biodiversity crisis in North America—the cumulative loss of nearly 3 billion birds across the avifauna. Population loss is not restricted to rare and threatened species, but includes many widespread and common species that may be disproportionately influential components of food webs and ecosystem function. Furthermore, losses among habitat generalists and even introduced species indicate that declining species are not replaced by species that fare well in human-altered landscapes. Increases among waterfowl and a few other groups (e.g., raptors recovering after the banning of DDT) are insufficient to offset large losses among abundant species (Figure 3). Importantly, our population loss estimates are conservative since we estimated loss only in breeding populations. The total loss and impact on communities and ecosystems could be even higher outside the breeding season if we consider the amplifying effect of “missing” reproductive output from these lost breeders.

Extinction of the Passenger Pigeon (*Ectopistes migratorius*), once likely the most numerous bird on the planet, provides a poignant reminder that even abundant species can go extinct rapidly. Systematic monitoring and attention paid to population declines could have alerted society to its pending extinction (20). Today, monitoring data suggest that avian declines will likely continue without targeted conservation action, triggering additional endangered species listings at tremendous financial and social cost. Moreover, because birds provide numerous benefits to ecosystems (e.g., seed dispersal, pollination, pest control) and economies (47 million people spend 9.3 billion U.S. dollars per year through bird-related activities in the U.S. (21)), their population reductions and possible extinctions will have severe direct and indirect consequences (10, 22). Population declines can be reversed, as evidenced by the remarkable recovery of waterfowl populations under adaptive harvest management (23) and the associated allocation of billions of dollars devoted to wetland protection and restoration, providing a model for proactive conservation in other widespread native habitats such as grasslands.
Steep declines in North American birds parallel patterns of avian declines emerging globally (14, 15, 22, 24). In particular, depletion of native grassland bird populations in North America, driven by habitat loss and more toxic pesticide use in both breeding and wintering areas (25), mirrors loss of farmland birds throughout Europe and elsewhere (15). Even declines among introduced species match similar declines within these same species’ native ranges (26). Agricultural intensification and urbanization have been similarly linked to declines in insect diversity and biomass (27), with cascading impacts on birds and other consumers (24, 28, 29). Given that birds are one of the best monitored animal groups, birds may also represent the tip of the iceberg, indicating similar or greater losses in other taxonomic groups (28, 30).

Pervasiveness of avian loss across biomes and bird families suggests multiple and interacting threats. Isolating spatio-temporal limiting factors for individual species and populations will require additional study, however, since migratory species with complex life histories are in contact with many threats throughout their annual cycles. A focus on breeding season biology hampers our ability to understand how seasonal interactions drive population change (31), although recent continent-wide analyses affirm the importance of events during the non-breeding season (19, 32). Targeted research to identify limiting factors must be coupled with effective policies and societal change that emphasize reducing threats to breeding and non-breeding habitats and minimizing avoidable anthropogenic mortality year-round. Endangered species legislation and international treaties, such as the 1916 Migratory Bird Treaty between Canada and the United States, have prevented extinctions and promoted recovery of once-depleted bird species. History shows that conservation action and legislation works. Our results signal an urgent need to address the ongoing threats of habitat loss, agricultural intensification, coastal disturbance, and direct anthropogenic mortality, all exacerbated by climate change, to avert continued biodiversity loss and potential collapse of the continental avifauna.

References and Notes:


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**Data and materials availability:** All data and software are archived and available on Zenodo (DOI 10.5281/zenodo.3218403, 10.5281/zenodo.3369999, 10.5281/zenodo.3370005), and will
be published in future versions of the Avian Conservation Assessment Database (http://pif.birdconservancy.org/ACAD/).

**Supplementary Materials:**

Materials and Methods

Figures S1-S7

Tables S1-S5

External Databases S1-S2

References (33-100)
Figure captions:

Fig. 1. Net population change in North American birds. (A) By integrating population size estimates and trajectories for 529 species (18), we show a net loss of 2.9 billion breeding birds across the continental avifauna since 1970. Gray shading represents ± 95% credible intervals around total estimated loss. Map shows color-coded breeding biomes based on Bird Conservation Regions and land cover classification (18). (B) Net loss of abundance occurred across all major breeding biomes except wetlands (see Table 1). (C) Proportional net population change relative to 1970, ±95% C.I. (D) Proportion of species declining in each biome.

Fig. 2. NEXRAD radar monitoring of nocturnal bird migration across the contiguous U.S. (A) Annual change in biomass passage for the full continental U.S. (black) and (B) the Pacific (green), Central (brown), Mississippi (yellow), and Atlantic (blue) flyways (borders indicated in panel C), with percentage of total biomass passage (migration traffic) for each flyway indicated; Declines are significant only for the full U.S. and the Mississippi and Atlantic flyways (Table S3-5). (C) Single-site trends in seasonal biomass passage at 143 NEXRAD stations in spring (1 Mar – 1 Jul), estimated for the period 2007-2017. Darker red colors indicate higher declines and loss of biomass passage, while blue colors indicate biomass increase. Circle size indicates trend significance, with closed circles being significant at a 95% confidence level. Only areas outside gray shading have a spatially consistent trend signal separated from background variability. (D) 10-year cumulative loss in biomass passage, estimated as the product of a spatially-explicit (generalized additive model) trend, times the surface of average cumulative spring biomass passage.

Fig. 3. Gains and losses across the North American avifauna over the last half century. (A) Bird families were categorized as having a net loss (red) or gain (blue). Total loss of 3.2 billion birds occurred across 38 families; each family with losses greater than 50 million individuals is shown as a proportion of total loss, including two introduced families (gray). Swallows, nightjars, and swifts together show loss within the aerial insectivore guild. (B) 29 families show a total gain of 250 million individual birds; the five families with gains greater than 15 million individuals are shown as a proportion of total gain. Four families of raptors are shown as a single group. Note that combining total gain and total loss yields a net loss of 2.9 billion birds across the entire avifauna. (C) For each individually represented family in B and C, proportional population change within that family is shown. See Table S2 for statistics on each individual family. (D) Left, proportion of species with declining trends and, Right, percentage population change among introduced and each of four management groups (18). A representative species from each group is shown (top to bottom, house sparrow, Passer domesticus; sanderling, Calidris alba; western meadowlark, Sturnella neglecta; green heron, Butorides virescens; and snow goose, Anser caerulescens).
Table 1. Net change in abundance across the North American avifauna, 1970-2017. Species are grouped into native and introduced species, management groups (landbirds, shorebirds, waterbirds, waterfowl), major breeding biomes, and nonbreeding biomes (see Data S1 in (18) for...
assignments and definitions of groups and biomes). Net change in abundance is expressed in millions of breeding individuals, with upper and lower 95% credible intervals (CI) shown. Percentage of species in each group with negative trend trajectories are also noted. Rows colored in red indicate declines and loss; blue rows indicate gains.
Supplementary Materials for

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This PDF file includes:

Materials and Methods
Figs. S1 to S7
Tables S1 to S5
Caption for Data S1
Caption for Data S2

Other Supplementary Materials for this manuscript include the following:

Data S1
Data S2
**Materials and Methods**

**General approach to estimating long-term net population change**

We compiled estimates of long-term population change and current population size for 529 species from a variety of sources (Table S1), as described below. For every species, we selected the most appropriate data sources and assessed the quality of population size and change estimates, based on sampling methodology, range coverage, and precision of the estimates. Our primary source of population change estimates was the North American Breeding Bird Survey (BBS) (33), which provides conservation assessment information for hundreds of bird species (34). For our current analysis we relied on the full trajectory of population change for each species, which we define as the scaled time-series of annual population indices derived from the underlying trend model. Note that using the full trajectory provides much more information on population change than the simple trend value (% change/yr) usually associated with survey data. We used Partners in Flight’s (PIF) recently published population size estimates for North American landbirds (35), and we supplemented these with data from several other surveys (Table S1). Values for all U.S./Canada population size estimates, along with their sources, are provided in Data S1.

After compiling population size and trajectory estimates for all species (Data S1), we integrated these into a single hierarchical Bayesian model that estimates the full time-series (1970-2017) of population sizes for each species and for the overall avifauna. Because some species are better monitored than others, the precision of estimates varied greatly among species (Data S1). To reduce the effects of imprecise species-level estimates on our overall estimates of population change, our model included a hierarchical structure that allowed for estimation of composite change based on shrinkage estimators, in which imprecise species results are shrunk toward species-group means based on common ecological biomes in which they breed and overwinter (see below). For summaries, estimates of net population change were computed for four general management categorizations (shorebirds, landbirds, waterbirds, waterfowl), taxonomic families, and breeding and nonbreeding biomes.

Our hierarchical model of composite change is similar in concept to the bird-group indicator models used to summarize the status of major bird groups at a national level in recent State of the Birds reports in Canada and the United States (36, 37). These indicator models estimate an average population trajectory with respect to a base-year, across species in a group. To this basic group-level model, we added 4 major components: (1) we added a non-parametric smooth to each species estimated population trajectory, accounting for the uncertainty of each annual value, to emphasize the medium- and long-term changes in species populations and reduce the effects of annual fluctuations; (2) we added a second layer to the hierarchical structure to account for influences on each species population trajectory from across the full annual cycle (both nonbreeding and breeding biome); (3) we used the species-level predictions, instead of the group-level trajectories summarized for the State of the Birds reports, as improved estimates of a species population trajectory; and (4) we integrated these improved species trajectories with the species-level population size estimates, to sample the full posterior distribution of population change estimates for each species. The model, an R-script to run it, and all of the orginal data are available on GitHub (https://github.com/AdamCSmithCWS/Rosenberg_et_al).

Data included in the modeling were (1) species (s) population indices by year (y) and associated variances ($\tilde{\sigma}_{xy}$, $\sigma_{\tilde{y}}^{2}$); (2) species population size estimates and associated variances ($\tilde{n}_s$, $\sigma_{n_s}^{2}$); (3) year(s) in which each species population size was estimated (e.g., most PIF
population estimates represent the species mean population size in the years 2006-2015; \( K_s = 10, k_s = 2006 - 2015 \); and (4) information regarding wintering region and breeding biome associations for each species (w = wintering region, b = breeding biome).

Non-parametric smoothing of species’ trajectories, centering, and missing data

We used a generalized additive model (GAM) to smooth each species population trajectory \((\hat{t}_{s,y}, \hat{\sigma}_{s,y}^2)\) before including them in the main model, similar to (38). The GAM smooth allowed us to accommodate the wide variation in the underlying population trajectory data and models across the various datasets; for example, some species trajectories have gaps in the time-series when data were not available in a particular year, but were available before and after, and other trajectories are derived from models that allow annual values to fluctuate completely independently, leading to extreme annual fluctuations in relation to other species. Modeling each species trajectory with a flexible smoother retains the most important medium- and long-term patterns in the species’ population, and reconciles the level of annual variation among species.

We used the R-package mgcv (39) to smooth each species trajectory, using a hierarchical Bayesian GAM that accounted for the uncertainty of each annual index in the trajectory to model most species, and for the few species where published estimates of uncertainty were not available (\(N = 3,\) Trumpeter Swan, Emperior Goose, and American Woodcock), we used a simpler non-Bayesian GAM function from the same package.

The annual predictions from the GAM smooth \((\hat{t}_{s,y}, \hat{\sigma}_{s,y}^2)\) for each species and from each data-source were in different units, e.g., BBS estimates are scaled to the number of birds seen on a single route and CBC estimates are scaled to the number observed in an average count-circle. To allow for the hierarchical structure of the model that pools information across groups of species (e.g., grassland birds that winter in Mexico), each species’ trajectory was re-scaled to a common base-year (1970) and log-transformed.

\[
\hat{\theta}_{s,y} = \ln \left( \frac{t_{s,y}}{t_{s,1970}} \right)
\]

Where, \(\hat{\theta}_{s,y}\) is the log-transformed standardized annual estimate for year \(y\) and species \(s\) \((t_{s,y})\) and represents the status of the species in year-\(y\), as a proportion of the original estimate in the base-year, 1970 \((t_{s,1970})\). We calculated the variance of \(\hat{\theta}_{s,y}\) as the log transformation of the variance of a ratio of two random variables (Cochran 1977, pg. 183), making the simplifying assumption that the annual estimates are independent in time. We acknowledge that this assumption of independent estimates in time is certainly invalid for adjacent years, but becomes more plausible as length of the time-series increases

\[
\hat{\sigma}_{s,y}^2 = \ln \left( 1 + \frac{\hat{\sigma}_{s,y}^2}{\hat{t}_{s,y}^2} + \frac{\hat{\sigma}_{s,1970}^2}{\hat{t}_{s,1970}^2} \right)
\]

For 8% of species (43), population trajectories spanning 1970-2017 were not available. About half have data-sources that started in the early 1970s and most of the remainder have trajectories starting in the 1990s. In these cases, we assumed that the population did not change during the missing years. Years with missing trajectory information at the beginning of the time-series (e.g., no data before 1993 for some boreal species monitored by the BBS) were given
values equal to the first year with data (i.e. a conservative assumption of no overall change) but we increased the estimated variance ($\sigma^2_{\hat{\theta}_{s,y}}$) by the square of the number of years since non-missing data, so that these imputed data would have little overall effect on the final results. For these species and years, because of the extremely high variance and the hierarchical structure of the model, the modeled population trajectories and the annual number of birds were almost entirely determined by the group-level mean trajectories for the other species sharing the same wintering region and breeding biome.

The primary model: population trajectories accounting for nonbreeding and breeding biome

Each species’ estimated status in a given year ($\hat{\theta}_{s,y}$) was treated as a normal random variable with mean $\theta_{s,y}$ and a variance estimated from the species data ($\sigma^2_{\theta_{s,y}}$).

$$\hat{\theta}_{s,y} \sim N\left(\theta_{s,y}, \sigma^2_{\theta_{s,y}}\right)$$

The species status parameter $\theta_{s,y}$ was assumed to be normally distributed, governed by a hyperparameter ($\mu_{w,b,y}$) with year-specific variance ($\sigma^2_{\mu_{y}}$),

$$\theta_{s,y} \sim N\left(\mu_{w,b,y}, \sigma^2_{\mu_{y}}\right)$$

representing mean status for all species with the same combination of wintering range and breeding biome (e.g., all species that winter in South American and breed in the boreal forest). This structure has the effect of shrinking each species population trajectory towards the mean trajectory for species in the same nonbreeding-by-breeding group. The mean trajectories for each group ($\mu_{w,b,y}$) were estimated using an additive sub-model that combined the effects of nonbreeding and breeding biomes. The biome-level components of the additive model were estimated using random-walk time-series for the effects of nonbreeding biomes ($\omega_{w,y}$) and breeding biomes ($\beta_{b,y}$).

$$\mu_{w,b,y} = \omega_{w,y} + \beta_{b,y}$$

$$\omega_{w,y} = N(\omega_{w,y-1}, \sigma^2_{\omega_{w}})$$

$$\omega_{w,1970} = 0$$

$$\beta_{b,y} = N(\beta_{b,y-1}, \sigma^2_{\beta_{y}})$$

$$\beta_{b,1970} = 0$$

The random-walk structure has the effect of slightly smoothing large annual fluctuations in the wintering-group annual means, while also allowing for non-linear temporal changes across the 48-year time series.

Integrating the population sizes and population trajectories

Each species’ population size estimate was incorporated in the model as the mean ($\hat{n}_{s}$) and variance ($\sigma^2_{\hat{n}_{s}}$) of a normal distribution. Random draws from those distributions ($n_{s}$) allowed the model to incorporate the uncertainty around each species’ population estimate. We used the
estimated population sizes and the population trajectories during the relevant years represented by each species’ population estimate to calculate a scaling factor ($\psi_s$) that allowed us to re-scale the species estimated population trajectory ($\theta_{s,y}$) to an estimated number of birds in each year of the time-series ($\nu_{s,y}$). Each population estimate was related to a specific year or range of years; e.g., all PIF population estimates reflect the species’ mean population size between 2006 and 2015 ($K_s = 10, k = 2006 - 2015$). We estimated the scaling factors by averaging the ratio across the relevant span of years, with $K_s = 3$ as a minimum in a few cases where the species’ estimated population reportedly related to a single year.

$$\psi_s = \frac{\sum_{y=1}^{y_k} \left( \frac{n_s}{\exp(\theta_{s,y})} \right)}{K_s}$$

$$\nu_{s,y} = \psi_s \cdot \theta_{s,y}$$

All precision parameters were given diffuse gamma prior distributions, with scale and shape parameters set to 0.001. Formal measures of model fit are difficult to implement for complex hierarchical models, and are generally not presented for analyses of complex surveys (40). We used graphical comparisons between data and predictions (see additional figures available in the data and code repository) to ensure there was no important lack of fit between the model and the data.

**Annual number of birds and overall population change**

We calculated the overall population change by species ($\lambda_s$) using the posterior distribution of the difference between the estimated number of birds in 1970 and the number in 2017. We calculated the estimated number of birds in the North American avifauna for each year ($N_y$) using the posterior distribution of the annual sums of all species estimates. We calculated the overall net change in the North American avifauna using the posterior distribution of the sum of the species-level change estimates ($\Lambda$). Estimates of the annual number of birds ($N_y$) and overall change ($\Lambda$) by family, nonbreeding biome (Figure S1), breeding biome (Figure 1A), and combinations of nonbreeding and breeding biome (Figure S2) were made from the posterior distribution of group-level summaries across all S-species in a group.

$$\lambda_s = \nu_{s,1970} - \nu_{s,2017}$$

$$N_y = \sum_{s=1}^{S} (\nu_{s,y})$$

$$\Lambda = \sum_{s=1}^{S} (\lambda_s)$$

**Sources of Population Trajectories for North American Birds**

We compiled long term population trajectories for 529 species, based on the best available survey data for each species (Table S1; see Data S1 for species-specific information). We note that this compilation reflects standard data sources used by North American bird conservation and management (23, 36, 41–45). We are fortunate that standardized, long-term survey data exist for a majority of North American bird species, perhaps the best-monitored group of organisms.
globally. We used trajectory estimates based on surveys of breeding populations whenever possible; however not all species are well-monitored during the breeding season, and for 18% of species we relied on surveys from migration periods or winter (Table S1). In all cases, trajectories and population estimates for each species were calculated from data during the same season (i.e., breeding to breeding, winter to winter). We could not find credible surveys for estimation of continent-scale trajectories for oceanic birds, many coastal-nesting seabirds, and other rare, secretive, range-restricted or nocturnal species. However, our synthesis includes 76% of species that breed regularly in the continental U.S. and Canada (46), and these species likely account for 95%-99% of total breeding abundance across the North American avifauna (i.e., most species omitted have very small populations in the U.S. and Canada).

For 434 species (82% of 529 species considered) we used trajectories from BBS data, most of which are updated annually and publicly available at https://www.mbr-pwrc.usgs.gov/. For species surveyed by the BBS, a hierarchical model (47) was used to estimate annual indices of abundance. In our hierarchical analysis, annual indices are based on regional fits within states and provinces that are weighted by area and local abundance to accommodate differences in population sizes among strata. For a majority of species (415) we used data from the ‘core’ BBS area from 1970-2017, based on road-based survey routes in the contiguous U.S. and southern Canada. For 19 species with restricted or northern breeding distributions (See Data S1), we used data from an expanded analysis beginning in 1993, including additional BBS routes in Alaska and northern Canada (48). The proportion of each species’ breeding range covered by the BBS is provided in (33), and all metadata and data are available (https://www.pwrc.usgs.gov/bbs/).

Potential limitations or biases in BBS trends (overall rates of change across the trajectories) have been extensively examined and documented (e.g., (33, 49)). In general, there is no evidence to suggest that estimates of population trends from the BBS are systematically biased across large spatial areas or across many species. Published studies that have examined the potential roadside bias in BBS trends have found that the magnitudes of bias in the sampling of habitat-change are generally small, e.g. (50–53), that potential biases vary in space (e.g., contrasting biases in the regions used in (54), or in (55)), and that they vary among species (i.e., if biases exist, some species’ trends may be underestimated and others overestimated, e.g., (55, 56)). Overall, BBS routes survey a reasonably representative sample of the overall habitat in the landscape at the broad spatial and temporal scales, for which the BBS was designed (50).

National Audubon Society Christmas Bird Counts (57) provided trajectory data for 58 species; these are primarily species that breed in northern regions not surveyed by the BBS, but are encountered in CBCs because they spend the non-breeding season primarily within the U.S. and southern Canada. The CBC protocols are less standardized than BBS, but annual winter-season counts in fixed 15-mile diameter circles cover a large portion of the U.S. and Canada, especially in coastal regions. Trajectories from CBC data were estimated using a hierarchical model that controlled for effort (57). Annual indices to compute trajectories from the CBC for the 1970-2017 period were provided to us by Tim Meehan (National Audubon).

Trajectories for 20 species of long-distance migrant shorebirds came from an analysis of migration monitoring surveys carried out across Canada and the United States (58, 59). The shorebird migration surveys used here are part of the International Shorebird Survey, coordinated by Manomet, and the Atlantic Canada and Ontario Shorebird Surveys, coordinated by Environment and Climate Change Canada. Volunteers carry out surveys every 10 days in spring and fall, at sites distributed across Canada and the United States but concentrated primarily in the eastern half of the continent. Analyses of shorebird trajectories from fall count data, 1974-2016,
were carried out using hierarchical Bayesian models similar to those used for the BBS (47), with an additional General Additive Model (GAM) component to describe variation in birds’ abundance during the period of migratory passage. The model assumes that counts follow an overdispersed Poisson distribution, and includes terms for a long-term, log-linear trend, year-effects and site-level abundance. Sites were grouped into biologically relevant regions, and trend terms within each region were estimated as hierarchical random effects distributed around a mean, continental trend. Methods and survey coverage are described in more detail at wildlife-species.canada.ca/bird-status (https://tinyurl.com/yak95ssn). For one shorebird species, American Woodcock, we made use of Singing-ground Survey estimates from the 2017 American Woodcock Status report (60).

For nine species of intensely managed waterfowl we relied on trajectory data from the U.S. Fish and Wildlife Service (USFWS) (61), and trajectories for nine additional waterfowl species came from other species-specific sources (see Table S1, Data S1). Trajectories for many waterfowl species were computed using population estimates from Spring Breeding Ground Surveys, which use a combination of aerial and ground-based counts in late spring, covering 2.0 million square miles in Alaska, Canada, and the northern U.S. (Table c3 in (61)). For a small subset of species, we employed other sources of trajectory information where this resulted in better coverage of North American populations, and/or more current information. For all goose species we relied on estimated trajectories from the same sources of information on population trends reported for North American goose populations by Fox and Leafloor (62); these sources represent the most appropriate survey for each species as determined by experts on goose populations. Finally, for Trumpeter Swans we relied on values in the 2015 North American Trumpeter Swan Survey report (63).

Sources of Population Size Estimates and Variances

We relied on the best available data sources and published estimates of North American breeding population size and variance for all species with credible data (Table S1; Data S1). The largest source of population estimates for our current analysis (65% of species) was the recently published PIF estimates for 344 landbird species (35). The PIF estimates were based on extrapolations from BBS count data from 2006-2015, using previously described methods (64–67). Averaged annual BBS counts were converted to a regional (landscape-scale) abundance estimate through the application of detectability adjustment factors for time-of-day, detection distance, and likelihood of both members of a pair being detected on BBS routes, and extrapolation from BBS count area to area of the region. These regional estimates are calculated for each state, province and territory portion of each Bird Conservation Region (BCR), and then summed across regions to derive U.S.-Canada population estimates. Estimates incorporated uncertainty in the estimation components, resulting in confidence bounds around the final estimates (35). Population estimates are therefore adjusted for detection, account for variation in relative abundance across the species’ range, and are accompanied by a measure of uncertainty. This approach to estimation of total population size has been widely adopted in conservation planning (35), and is considered to be conservative, likely underestimating true population size due to sampling concerns associated with BBS data (67).

The PIF methods for estimating population size have historically been applied only to landbirds (41, 42). For this analysis, we determined that the BBS also provides adequate survey coverage for 46 waterbirds, and 6 waterfowl that otherwise were lacking useful population estimates (see Data S1 for sources by species), and we applied the PIF approach for calculating
population size estimates to data for these species. Adjustment factors used in the estimation of U.S.-Canada population sizes for the current analysis, based on BBS relative abundances, are provided in Table S2. More details on the use of adjustment factors and their ranges of uncertainty for landbirds can be found in (35).

Estimates of population size for many shorebirds and waterfowl came from published sources that rely on other surveys. Estimates for 12 waterfowl species were from the 2017 USFWS Waterfowl Status Report (61) (7 species from traditional area surveys, 2 from eastern survey area, 2 summed from traditional and eastern surveys, and 1 from western survey area) – for these species, we used an average of published estimates across the last 5 years (2013-2017) to smooth out annual variance in population sizes. Estimates for 14 additional waterfowl species were based on a 2007 Seaduck Joint Venture Report (68). All 45 shorebird species estimates were North American population estimates (69) from the Shorebird Flyway Population Database (70).

Other estimates of population size came from species-specific sources (Table S1; Data S1): We used published estimates from Birds of North America (BNA) accounts (71) for 33 species; a Conservation of Arctic Flora and Fauna (CAFF) 2018 report provided current estimates for 7 goose species (62); estimates for 17 landbird species without useful BBS-based estimates were taken from the Avian Conservation Assessment Database ACAD (46, 72), which itself relied on a variety of sources; the 2015 North American Trumpeter Swan Survey (63) was used for Trumpeter Swan, and the Waterbird Population Estimates database (WPE5) provided estimates for Arctic Tern (73).

Most sources of population estimates also provided estimates of variance in population size, which we incorporated into our analysis. For those that did not, we estimated a range of variance based on a description of methods used for population estimation. For example, we applied a range 10% below and above the mean for species if estimates were based on well-designed surveys with good population coverage, versus 75% below and above the mean for species with ballpark estimates and/or low coverage of relevant populations, with an intermediate range of variance if limitations were between those two.

Note that our goal was to compile and use the most current estimates of breeding population size for each species; i.e., the number of breeding adult individuals in the population. We did not attempt to estimate the annual increase in population size due to the influences of reproductive output, as this will likely vary greatly across species and years and be subject to density-dependent effects. Total population size varies throughout the annual cycle, but post-breeding total population could increase as much as four to five times the size of the pre-breeding population size depending on recruitment success of young of the year. Estimating this annual variation for individual species is currently impossible, but it is important to point out that the cumulative impact of population loss on ecosystems throughout the year could be quite significant. Our estimates of population change are therefore conservative.

Assigning species to management and biome categories

For the purpose of summarizing changes in abundance across the North American avifauna, we recognize four broad species categories used for management and conservation planning: Landbirds are defined by Partners in Flight (41, 42) as all birds occupying terrestrial habitats and a few species from primarily terrestrial bird families that use wetland habitats (e.g., Marsh Wren, Cistothorus palustris). The ACAD lists (448) native landbirds breeding in the U.S. and Canada; in this paper we include 366 landbird species with adequate population size and trajectory data, including 9 introduced species. Shorebirds include all sandpipers, plovers, stilts, avocets, and oystercatchers that are considered under the U.S. Shorebird Conservation Partnership
we had adequate data for 45 shorebird species for the current analysis. Waterfowl include all ducks, geese, and swans, which are managed separately under the North American Waterfowl Management Plan; most species have populations that are adaptively managed for sport hunting (23). We had adequate data for 42 species in the current analysis, including 1 introduced species. Other Waterbird species that are not specifically covered by the three plans above are included under the Waterbird Conservation for the Americas initiative (44); these include colonial-nesting seabirds, herons, beach-nesting species and secretive marshbirds. Waterbirds are most poorly represented in our dataset, as many species are poorly monitored. We had adequate data for 77 species in the current analysis.

We assigned each species to a primary breeding biome and a primary nonbreeding biome, using the Avian Conservation Assessment Database. The ACAD provides broad breeding-habitat categories (e.g., forests, grasslands, oceans) derived from similar categories used to develop habitat indicators for State of the Birds reports in the U.S. and Canada (e.g., (36, 45)), as well as more descriptive sub-categories within major habitats (e.g., Temperate Eastern Forest; Desert Scrub, Freshwater Marsh). All category assignments were based on literature review (primarily BNA accounts) or expert knowledge and underwent extensive review as part of the ACAD process (66). Species that use three or more broad habitats in similar importance were considered habitat generalists.

For this paper, we used a combination of Primary Breeding Habitat and Breeding Habitat Description sub-categories defined in the ACAD to derive a single set of unique breeding biome categories across the North American avifauna (shown in Figure 1A), as follows:

- **Wetlands** = freshwater, inland wetlands; does not include coastal marshes or Arctic tundra.
- **Coasts** = all habitats associated with the Coastal zone, including saltmarsh, beach and tidal estuary, mangroves, and rocky cliffs and islands; includes birds that forage primary in the marine zone
- **Tundra** = Alpine tundra and Arctic tundra, including upland and low, seasonally wet tundra
- **Grasslands** = native grassland, prairie, pasture, and agriculture that supports grassland birds
- **Aridlands** = all arid shrub-dominated communities; primarily in southwestern U.S. and northwestern Mexico; includes ACAD sub-categories of sagebrush, chaparral, desert scrub, barren rocky cliffs, and extensions of tropical dry forest (thornscrub) in southern Texas
- **Boreal forest** = "True" boreal forest of Canada and Alaska; note that some boreal-forest birds also use the boreal zone (primarily spruce-fir) of high mountains in the western and northeastern U.S.
- **Eastern forest** = all temperate forest types of eastern U.S. and southeastern Canada (south of the boreal), including northern hardwoods, oak-hickory, pine-oak, southern pine, and bottomland hardwood associations
- **Western forest** = all temperate forest types of western U.S. and Canada (south of the boreal) and extending in high mountains south into northwestern Mexico; includes Pacific Northwest rainforest, all western conifer, oak-dominated, and riparian forests, pinyon-juniper, juniper-oak woodlands of Edward's Plateau, pine-oak and high-elevation conifer forests of northwestern Mexico
- **Forest generalist** = occurs in similar abundance in two or more forest biomes as described above
Habitat Generalist = occurs in similar abundance in three or more major habitat types, usually including forest and non-forest categories.

The ACAD database also lists Primary Wintering Regions, in which a majority of the population of each species spends the stationary nonbreeding period during the boreal winter. For this paper we modified and lumped ACAD regions into broader nonbreeding biome categories, using published range maps and eBird distributional data (https://ebird.org/explore), as follows:

- **Temperate North America** = broad region encompassing all of Canada and most of the U.S., excluding arid regions in the Southwest
- **Southwestern Aridlands** = arid regions of southwestern U.S., northwestern Mexico and Mexican Plateau; included species that winter in arid Chihuahuan grassland habitat
- **Mexico-Central America** = combination of ACAD regions within Mexico and Central America, including Pacific Lowlands, Gulf-Caribbean Lowlands, Mexican Highlands, and species from Central and South American Highlands that winter primarily in Central America
- **South America** = includes South American Lowlands, species from Central and South American Highlands that winter primarily in South America, and Southern Cone ACAD regions
- **Caribbean** = West Indies region, including Cuba, Bahamas, Greater and Lesser Antilles
- **Widespread Neotropical** = occurs in similar numbers in two or more biome regions within the Neotropics
- **Coastal** = coastline habitats throughout the western Hemisphere from Arctic to Atlantic and Pacific Coasts of North, Middle, and South America; eastern Hemisphere coastlines were included to incorporate the main wintering grounds of Pacific Golden-Plover
- **Marine** = littoral zone; area of oceans influenced by continental coastlines; includes bays and deep estuaries (includes a few species that are largely pelagic in the nonbreeding season)
- **Widespread** = occurs in similar abundance in 3 or more nonbreeding biomes, usually encompassing both temperate North American and Neotropical regions
- **Southeast Asia** = overwintering region for Arctic Warbler (and additional Arctic-breeding species not included in the present analysis); note that this nonbreeding biome is not included in summaries presented in Table 1 and Figure S1, but data for Arctic Warbler (Data S1) and included in higher level summaries of population change for all birds, breeding biomes, etc.

**Computing vertical profile time series of birds from NEXRAD radar data**

While designed to monitor meteorological phenomena (e.g., precipitation, tornados, hail), weather radars routinely detect migrating birds. Weather radar infrastructure represents a biological monitoring tool that achieves an unprecedented spatial and temporal coverage for studying bird migration (74). The NEXRAD weather radar network consists of 143 radars in the contiguous US that continuously survey the airspace above the US (75). Each of these radars was used to estimate vertical profiles of birds, which summarize a radar’s scans completed at a given timestep into the amount, speeds, and directions of birds aloft as a function of altitude. Profile data can be used to accurately estimate migratory biomass abundance and its change throughout the year at comprehensive continental scales (19, 77), an approach we extended here to detect long-
term change in migratory passage across the full US. We restricted our analysis to spring data only
(Mar 1 to Jul 1), which is the migratory period closest in time to the breeding bird surveys by BBS.
Also, aerial insects are far less numerous in the airspace in early spring as compared to autumn, therefore the spring period allows us to obtain the clearest bird signal from NEXRAD (see final paragraph of section “Calculating biomass passage from vertical profile time series” below).

Data were obtained from the NOAA-nexrad-level2 public S3 bucket on Amazon Web Services (78). Data were analyzed for the period 2007-2018, the period after the Open RDA deployment in NEXRAD (RDA build 7.0), which was a significant upgrade to the Radar Data Acquisition (RDA) functional area of the WSR-88D. In particular, it implemented Gaussian Model Adaptive Processing (GMAP) (79, 80), replacing and improving over the legacy ground clutter filter (81) by Doppler filtering. We did not include older potentially lower quality data in the analysis to limit the possibility of legacy filter settings affecting our results. Trend analyses (see following sections for details) controlled for two important data acquisition updates, the gradual upgrades to superresolution (2008-2009) and dual-polarization (2010-2013). The superresolution upgrade increased the azimuthal resolution from 1 to 0.5 degree and range resolution from 1 km to 250 m. The dual-polarization upgrade added functionality to receive horizontally and vertically polarized electromagnetic waves independently, which provided additional products that greatly simplify the classification of meteorological and biological scatterers (82).

Night-time polar volumes (level-II data) were processed for all 143 radars in the contiguous US at half-hour interval from 2007-2018 using the vol2bird algorithm (version 0.4.0) (76, 83, 84), available in R-package bioRad (version 0.4.0) (83, 85). Using cloud computing with 1000 parallel cores on Amazon Web Services (AWS) we reduced this computational task of ~4 years on a single CPU to less than a day. Data were processed using the vol2bird algorithm in single-polarization mode (76), which requires radial velocity and reflectivity factor information only and no dual-polarization data. Dual-polarization data became available only after mid-2013, and therefore cannot be used for analyses involving older data. In single-polarization mode, resolution samples with high reflectivity values are masked out (\( \eta \) above 36000 cm\(^2\)/km\(^3\), i.e., 31 dBZ at S-band / 20 dBZ at C-band, cf. algorithm parameter ETAMAX and paragraph 3.2 in (76) ), since such high reflectivities are typically associated with precipitation (76). The algorithm also identifies contiguous areas of direct neighbors (in a queen’s case sense; i.e., diagonal pixels are included as direct neighbors) of reflectivity above 0 dBZ, denoted as reflectivity cells. Cells with a mean reflectivity above 11500 cm\(^2\)/km\(^3\) (i.e., 26 dBZ at S-band / 15 dBZ at C-band, cf. algorithm parameter ETACELL and Zcell in (76)) are masked from the data. Following recommendations for S-band data discussed in (83), we used \( \text{sd_vvp\_threshold}=1 \text{ m/s} \) (cf. Eq. A2 in (76)) and \( \text{STDEV\_CELL}=1 \text{ m/s} \) (cf. Eq. A3 in (76)) to limit masking based on radial velocity texture at S-band.

At S-band, single-polarization mode masks out only the strongest precipitation areas, and weaker precipitation may remain (83) (see Figure S3C/E). Precipitation is generally easily identifiable in vertical profiles by experts, based on high reflectivities extending over a relatively large portion of the altitude column (see Figure S3D). Such precipitation cases stand out from bird migration cases, which are characterized by low reflectivities that typically decrease with altitude (see Figure S3A). We used machine learning to develop a full-profile classifier that automatically identifies precipitation-contaminated profiles, as follows.

Years when dual-polarization data were available (2014-2017) were processed a second time in dual-polarization mode (19, 83), which adequately removes precipitation based on high correlation coefficient values (19, 82). These precipitation-free profile data were paired with the single-polarization profile data. By comparing the precipitation-free reflectivity (\( \eta_{\text{dual\_pol}} \), cf.
Figure S3A) with the total reflectivity including precipitation (\( \eta_{\text{total}} \) derived from reflectivity factor DBZH, cf. Figure S3D), we defined a measure that indicates the range of altitudes H (m) likely containing precipitation, as follows:

\[
H = \sum_{l=1}^{n_{\text{layer}}} \left( \text{if } \eta_{\text{total},l} - \eta_{\text{dualpol},l} > \Delta \text{ then } w_{\text{layer}} \text{ else } 0 \right)
\]

with \( \Delta = 50 \text{ cm}^2 \text{ km}^{-3} \) (corresponding to 3 dBZ at S-band), and \( w_{\text{layer}} \) the width of a single altitude layer (200 m). The value of \( \Delta \) amounts to a fairly low threshold value for classifying potential precipitation, as meteorologists typically assume weak precipitation to start at \( 7 \text{ dBZ} \) (\( 86 \text{ cm}^2 \text{ km}^{-3} \) at a 10 cm S-band wavelength), and therefore the vast majority of rain events will show differences in reflectivity exceeding \( \Delta \). We labelled all single-polarization profiles in the 4-year dataset with their corresponding H value.

Next, we used gradient boosted trees to detect rain-contaminated profiles computed in single-polarization mode automatically in an unsupervised learning approach, using the H value as our labeling of profiles, with higher H values indicating a wider altitudinal range containing precipitation. We used the R implementation of XGBoost, a highly efficient and scalable gradient boosting algorithm, which can deal with complex nonlinear interactions and collinearity among predictors (87, 88). We used default hyperparameter settings of the xgboost algorithm (learning rate eta=0.3, tree depth max_depth=6, min_child_weight=1, gamma=1, colsample_bytree=1, and subsample=1). Full-profile classifiers were trained for each radar separately. Response variable was the range of altitudes with precipitation H. Predictors included total reflectivity factor (DBZH), precipitation-filtered reflectivity in single-polarization mode (eta), ground speed components (u,v), all at each of the 20 profiles altitude layers, as well as day of year (1-366) and time of day (UTC time). Profiles of each radar were randomly assigned to training (75%) and testing (25%) datasets.

Finally, we determined the parameter \( H_{\text{max}} \) as the value of H above which profiles are removed in order to discard precipitation contaminations. The value of \( H_{\text{max}} \) was determined using Figure S4, showing an R-squared measure that quantifies the correspondence between the seasonal migration traffic MT (see next paragraph for definition) of the single-polarization vertical profile time series (with contaminated profiles removed by the full-profile classifier), and the seasonal migration traffic of the reference computed in dual-polarization mode. This R-squared measure amounts to the coefficient of determination of the scatter points in Figure S5 for a given value of \( H_{\text{max}} \). We choose the value of \( H_{\text{max}} = 1600 \text{ m} \), producing the best correspondence between the dual-polarization reference and our new single-polarization method. Gaps in a radar’s profile time series (after removal of rain-contaminated profiles) of less than 4 hours were filled by linearly interpolating between the neighboring profiles directly before and after the gap.

Applying this value of \( H_{\text{max}} \) and the full-profile classifier on the testing dataset, we find a precision to correctly classify a profile as rain-contaminated of 99.2%, and a recall of rain-contaminated cases of 97.4%. Precision and recall (89) did not depend strongly on the value of the \( H_{\text{max}} \) threshold, e.g., for \( H_{\text{max}} = 800 \text{ m} \) we have a precision of 97.0 % and recall of 99.0%. Our classification performance therefore did not depend critically on the adopted value of the \( H_{\text{max}} \) parameter.

Calculating biomass passage from vertical profile time series
Nightly reflectivity traffic (RT) \((83)\) was calculated for the vertical profile time series of each station for each night with the `integrate_profile()` function in bioRad (version 0.4.0) \((83, 85)\), which equals the total reflectivity crossing the radar stations per season per one kilometer transect perpendicular to the ground speed direction of movement. Reflectivity traffic is closely related to the amount of biomass that has passed the radar station \((83)\). It can be converted to migration traffic (MT), the number of individual birds having passed the radar station per km transect, under assumption of radar cross section (RCS) per individual bird, as in \(MT = RT/RCS\). To express RT in a more intuitive unit, we report MT values in figures using a constant seasonal mean RCS = 11 cm\(^2\) for an individual bird. This value was determined in a calibration experiment spanning a full spring and autumn migration season \((76)\), corresponding to passerine-sized birds (10-100 g range) \((90)\), which represents the highest-abundance species group dominating our radar signals \((19)\). As additional quality control for non-avian signals, we only included altitude layers of profiles for which the ground speed direction was in the northward semicircle surrounding a radar, since migratory bird movements in spring are expected to fall within this semicircle.

Spatial interpolations across the contiguous US of nightly migration traffic were estimated by ordinary kriging with a spherical variogram model, using the R package `gstat` \((91)\). We clipped water areas after interpolating, leaving land areas of the contiguous United States. Missing estimates of nightly migration traffic (e.g., due to temporary radar down time) were imputed from nightly kriging-interpolated maps of MT based on operational stations, imputing the MT value at the location of the inactive radars. Parameters of the spherical variogram model were estimated for each night. In cases where the variogram fit did not converge - typically during nights with very limited migration - we used variogram parameters fit to the average seasonal spring migration traffic (partial sill = 0.577, range = 1093 km). Radar availability was very high, therefore only a small percentage of in total 2.8% of nightly MT values were imputed by this procedure.

Total seasonal migration traffic was calculated as the sum of nightly MT values within a season from Mar 1 to Jul 1. Radar seasons were excluded from trend analysis entirely if data availability dropped below 80% in the period 1 Mar – 1 Jul (4.8% of radar seasons for 143 stations during 11 spring seasons).

While traffic rates suppress any non-migratory stationary signals, like those of non-directed foraging movements of insects or bats \((19)\), a small contribution of directed migratory movements of bats or insects could remain in our data. Free-tailed bats in the south are known to show up in radar \((92)\) and have a population size estimated up to 100 million individuals \((93)\), which amounts to up to a few percent of the total migratory passage of several billion birds along the southern border \((19)\). In the North-East - where we observe strongest declines in biomass passage - several migratory tree-dwelling bat species occur, but their population sizes are thought to be smaller than of free-tailed bats. For the period 2013-2017 we have provided earlier a detailed quantitative estimate of the upper limit to the migratory insect contribution to the migratory passage in autumn, when insect abundances are highest. The estimated passage due to insects was 2.1 % (northern US border) – 3.8 % (southern US border) \((19)\). Our current study is conducted in spring when aerial insect abundances are far lower \((94)\), especially in the North East where we observe most declines, and we estimate the insect contribution to the biomass passage to be on the order of a percent or less.

Calculating trends from seasonal biomass passage values

To correct for potential radar sensitivity changes related to radar processing upgrades, we determined the timing of the upgrade to super-resolution and the upgrade to dual-polarization for
each station. Radar seasons for which the upgrade fell within a migration period were excluded from the analysis. The mode of operation was classified as “legacy” (before superresolution upgrade), “superres” (after superresolution upgrade, before dual-polarization upgrade) or “dualpol” (after dual-polarization upgrade), and stored as a factor variable ‘mode’ having three factor levels to denote each mode of operation. Variable ‘mode’ was included in models to correct for changes in operational mode. We also tested for the effect of dual-polarization and superresolution upgrade separately. In these cases, factor variable ‘mode’ was replaced with a logical explanatory variable ‘dualpol’ (true after dual-polarization upgrade, otherwise false) or ‘superres’ (true after superresolution upgrade, otherwise false) in the trend models. The total model candidate set thus contained 4 models, encompassing all combinations of possible corrections for mode of operation, including no correction.

We estimated geographically varying trend patterns using a spatial GAM (95) using the mgcv package in R (39). Seasonal migration traffic was standardized to each radar’s 11-year mean, stored as variable ‘index’. We then modeled the spatial trend using an offset tensor product smooth \(te(lon,lat)\) and a tensor smooth representing a spatially varying linear trend with year \(te(lon,lat,by=year)\) on the linear predictor scale (see Table S3). We used a Gamma distribution with log-link, such that our linear trend smooth term on the linear predictor scale represents a spatially varying annual rate of change \(\mu_{\text{trend}}\) (with standard deviation \(\sigma_{\text{trend}}\)) on the response scale. The Gamma distribution accommodates a small right-skew in our continuous positive response variable and warrants normality of deviance residuals, as inspected using QQ plots. Plots of the spatial trend surfaces estimated for the models in Table S3 are shown in Figure S7.

Changes in seasonal migration traffic (Table S4, Figure 2D) were calculated as the GAM prediction for year 2007 minus 2017 (the proportional loss over 11 years), times the 11-year average seasonal migratory traffic (MT) of each station. The surface of average migratory traffic was obtained from a kriging interpolation of the 11-year mean seasonal MT value for each station (see Figure S6, 2). Average trends for the entire US (see main text and Table S3) were averaged over all pixels of these spatially-explicit decline and loss surfaces across the contiguous US, using arithmetic mean and harmonic mean for calculating mean and variance values, respectively, effectively weighing the trend by passage of biomass. The trend value reported in the main text refers to this biomass-weighted average trend for a model average of all GAM models in our candidate set (listed in Table S3). Models were averaged using package MuMIn (96), which averages models based on AIC (97).

We also estimated continental-wide trends in migratory passage and trends for four flyway regions: Atlantic, Mississippi, Central and Western, following the definitions of the US Fish and Wildlife Service, REF (cf. Figure 2B,C). We fitted generalized linear mixed models using R-package lme4 (98), including radar station as a random offset, and region and the interaction year:region as fixed effects, see Table S4 for model structures and Table S5 for estimated model parameters. Like in the GAM analysis, the candidate model set equaled for 4 models, containing all combinations of possible corrections for operational mode.

Regional biomass passage indices (Figure 2A,B) were calculated as the yearly sum of seasonal migration traffic values MT for the radars within each region, standardized by the sum of seasonal migration traffic values MT for all radars in the network of the first year (2007). Values of regionalized decline rates (Atlantic, Mississippi, Central and Western) in the main text are based on the model average (96) of all GLMs in the candidate set. Reported errors represent standard errors at a 95% confidence level.
Our GAM analysis (Table S3) and GLM analysis (Table S5) both found support for the dual-polarization upgrade affecting the value of MT, but not for the superresolution upgrade: including variable ‘mode’ did not produce a more informative model relative to a model with variable ‘dualpol’ that makes no distinction between “legacy” and “superresolution” data. Effect of the dual-polarization upgrade was a reduction in seasonal migration traffic by a factor 0.85 ± 0.03 (regionalized GLM) or 0.88 ± 0.05 (spatial GAM). Accounting for potential changes in detectability effectively reduced the steepness of decline rates and biomass loss. Both the superresolution and dual-polarization upgrades were designed to prevent changes in detectability and minimize bias effects for meteorological echoes as much as possible, and it is not known whether including correction terms for biological echoes is required. We report versions of the models with and without correction terms such that the effects of these corrections can be compared. By including correction terms, potentially part of the declines in seasonal migration traffic are modelled by the detection-related explanatory variables, and our estimates of decline of models with most information-theoretic support (model 1, model 5) are thus potentially too conservative. Importantly, the presence of an average decline in the passage of migratory biomass is robust to inclusion of correction terms for changes in operational mode of the radar, and even our most conservative rates of decline are alarming.

Supplementary References


Fig. S1. **Net population change in North American migratory birds grouped by non-breeding biome.**

(A) By integrating breeding-season population trajectory and size estimates for 529 species (see Methods), we show the continental avifauna lost > 2.9 billion breeding birds since 1970. Gray shaded region represents ± 95% credible intervals around total estimated loss. Map shows color-coded non-breeding biomes based on primary overwinter distributions of each species (See Methods). (B) Net loss of abundance occurred across all major non-breeding biomes, except Caribbean (see Table 1). (C) Proportional population loss, ±95% C.I. (D) Proportion of species declining in each biome.
Millions of birds in North American population

- Caribbean – Boreal Forest
  - 0.77M lost 3 species

- Caribbean – Eastern Forest
  - 2.8M lost 4 species

- Caribbean – Forest Generalist
  - 9.4M gained 1 species

- Coastal – Arctic Tundra
  - 9.2M lost 14 species

- Coastal – Coasts
  - 0.98M gained 22 species

- Coastal – Wetland
  - 3M lost 8 species

- Introduced – Introduced
  - 390M lost 10 species

- Marine – Arctic Tundra
  - 6.3M lost 7 species

- Marine – Coasts
  - 5.6M lost 14 species
2.6M lost 5 species
88M lost 19 species
52M lost 30 species
9.1M gained 14 species
55M lost 3 species
1.5M lost 5 species
36M gained 7 species
370M lost 7 species

Mexico
−
Central America
−
Western Forest

South America
−
Arctic Tundra

South America
−
Boreal Forest

Mexico
−
Central America
−
Eastern Forest

Mexico
−
Central America
−
Forest Generalist

Mexico
−
Central America
−
Grassland

Marine
−
Wetland

Marine
−
Aridlands

Marine
−
Boreal Forest

Millions of birds in North American population


200 400 600

175 200 225 250 275 300 325 350 375

100 120 140

20 30 40 50 60

1.5M lost 5 species
4.1M gained 14 species
5.9M lost 3 species
8.6M gained 7 species
370M lost 7 species
Widespread – Grassland

Widespread – Western Forest

Widespread – Habitat Generalist

Widespread – Eastern Forest

Widespread – Coasts

Widespread – Arctic Tundra

Widespread – Forest Generalist

Widespread – Widespread – Temperate North America – Western Forest

Temperate North America – Wetland

Millions of birds in North American population
Fig. S2.

Change in number of birds in North America by combined nonbreeding and breeding biomes from 1970–2017. Each panel of the figure shows the 1970–2017 trajectory of summed abundance across the species that share a given combination of nonbreeding and breeding biomes (e.g., the first panel shows the trajectory in summed abundance across the 3 species that winter in the Caribbean and breed in the boreal forest). The panel title indicates the wintering biome followed by the breeding biome; labels within the plots show the estimated change in total abundance in millions (M) of birds between 1970 and 2017, and the number of species included in the group. Colored lines and the colored uncertainty bounds represent the median and 95% C.I. of the posterior distribution from the hierarchical Bayesian model. The panels are sorted by nonbreeding biome and the lines are coloured based on the breeding biome.
Fig. S3.

Example of vertical profile time series for bird density and speed retrieved in dual polarization mode (A, precipitation-free reference) and the final single-polarization product used in the study (B) for the KBGM radar from 28-31 May 2017. The full-profile classifier that screens precipitation uses the reflectivity product obtained in single-polarization mode (C) and the total reflectivity including precipitation (D). Precipitation is characterized by high reflectivities spanning a large part of the vertical air column (see D), as well by cases in which the single-polarization rain filter removes part (but not necessarily all) of the signal (C versus D). The final single-polarization product (B) closely matches the dual-polarization mode reference (A), see also E, black and blue lines closely overlapping).
Fig. S4. Coefficient of determination $R^2$ between full-spring seasonal migration traffic values calculated in single polarization mode (rain-filtered using full-profile classifier) and dual-polarization mode reference ($R^2$ based on n=143 stations * 4 years = 572 points), as a function of the classification threshold $H_{\text{max}}$. The value of $R^2$ peaks at $H_{\text{max}} = 1600$ m.
Fig. S5. Seasonal migration traffic (MT) as estimated in dual-polarization mode and in single-polarization mode (rain-filtered using full-profile classifier) for the years 2014-2017 (n=143 stations * 4 year = 572 points). Solid line equals the y=x line of perfect correspondence. This figure shows MT values for \( H_{\text{max}} = 1600 \) m, which achieves the best correspondence with the dual-polarization reference mode (see Figure S4).
Fig. S6. Cumulated nocturnal migration traffic (biomass passage) MT in spring (1 Mar – 1 Jul) averaged over 11 seasons (2007-2017). Darker colors indicate more migratory biomass passage MT. Values give the numbers of birds passing per 1 km transect perpendicular to the migratory direction per spring season. Radar reflectivity was converted to bird numbers under the assumption of a constant radar cross section of 11 cm$^2$ per bird. Ordinary kriging was used to interpolate between radar stations. Dots indicate locations of radar station sites.
**Fig. S7.** GAM spatial trend surfaces estimated for the models in Table S3 for the period 2007-2017. Darker red colors indicate higher declines and loss of migration traffic (biomass passage) MT, while blue colors indicate migration traffic increase. Gray shaded regions have an annual rate of change $\mu_{\text{trend}}$ that is smaller than twice the standard deviation in the rate of change $\sigma_{\text{trend}}$, i.e. $\mu_{\text{trend}} < 2*\sigma_{\text{trend}}$. Overlaid circles indicate single-site trend estimates (circle color) and their significance (circle area $\sim \log(1/p)$), with closed circles being significant at a 95% confidence level. Single site trends are fits to seasonal migration traffic data of each radar site separately, using a Generalized Linear Model (GLM) with a Gamma distributional family and log-link. Detectability effects as estimated by the GAM were accounted for in the single-site data prior to fitting the GLMs.
Table S1.

Data sources for population size estimates and population trajectories for 529 North American bird species included in the net population change analysis for the present study. We used published sources of data wherever possible, and applied published methods to calculate estimates for the remaining species. Brief description of methodology, time-span, seasonal, and geographic coverage of surveys and other data sources provided, along with number of species for which that source was used and key citations.

<table>
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<tr>
<th>Data source</th>
<th>Years</th>
<th>Season</th>
<th>Methods</th>
<th>Coverage</th>
<th>N Spp. Trajectory</th>
<th>N Spp. Pop</th>
<th>Refs</th>
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<tr>
<td>North American Breeding Bird Survey (BBS)</td>
<td>1970-2017</td>
<td>Breeding</td>
<td>25-mile roadside surveys with 50 3-minute point counts</td>
<td>&gt;4,100 routes in contiguous U.S., southern Canada</td>
<td>415</td>
<td>0</td>
<td>(33, 34, 47)</td>
</tr>
<tr>
<td>North American Breeding Bird Survey (BBS)</td>
<td>1993-2017</td>
<td>Breeding</td>
<td>25-mile roadside surveys with 50 3-minute point counts</td>
<td>Same as above, with additional routes in northern Canada and Alaska</td>
<td>19</td>
<td>0</td>
<td>(48)</td>
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<tr>
<td>Audubon Christmas Bird Count (CBC)</td>
<td>1970-2017</td>
<td>Winter</td>
<td>Non-standard counts within 15-mile diameter circles</td>
<td>1,500-2,000 circles in U.S. and Canada</td>
<td>58</td>
<td>0</td>
<td>(57)</td>
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<tr>
<td>Partners in Flight (PIF) Population Estimates</td>
<td>2006-2015</td>
<td>Breeding</td>
<td>Extrapolation from BBS and other survey count data</td>
<td>Same as BBS, above</td>
<td>0</td>
<td>399*</td>
<td>(35)</td>
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<tr>
<td>Arctic goose surveys (CAFF 2018)</td>
<td>1975-2014</td>
<td>Variable</td>
<td>Aerial or ground surveys or mark-recapture models, depending on species</td>
<td>Continentwide for each species</td>
<td>7</td>
<td>7</td>
<td>(62)</td>
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<td>Shorebird Migration Surveys</td>
<td>1974-2016</td>
<td>Fall</td>
<td>Volunteer-conducted surveys at pre-determined sites</td>
<td>Canada and U.S., concentrated in eastern portion</td>
<td>20</td>
<td>0</td>
<td>(58, 59)</td>
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<td>USFWS Breeding Waterfowl Surveys</td>
<td>1970-2017</td>
<td>Breeding</td>
<td>Aerial surveys corrected for detectability with ground surveys</td>
<td>2.0 million square miles in Alaska, Canada, and northern U.S.</td>
<td>9</td>
<td>13</td>
<td>(61)</td>
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<td>North American Trumpeter Swan Survey</td>
<td>1968-2015</td>
<td>Breeding</td>
<td>Aerial surveys and ground counts</td>
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<td>1</td>
<td>(63)</td>
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<td>American Woodcock Singing Ground Survey</td>
<td>1968-2017</td>
<td>Breeding</td>
<td>3.6-mile roadside routes</td>
<td>1,500 routes in eastern North America</td>
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<td>(60)</td>
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<tr>
<td>2007 Seaduck Joint Venture Report</td>
<td>1970-2007</td>
<td>Variable</td>
<td>Compilation of best available estimates</td>
<td>Continentwide for each species</td>
<td>0</td>
<td>14</td>
<td>(68)</td>
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<tr>
<td>Shorebird Flyway Population Database</td>
<td>2012</td>
<td>Breeding population</td>
<td>Compilation of best available estimates</td>
<td>Continentwide for each species</td>
<td>0</td>
<td>45</td>
<td>(69, 70)</td>
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<td>Birds of North America (BNA) species accounts</td>
<td>1970-2007</td>
<td>Breeding adults</td>
<td>Variable; best for each species</td>
<td>Continentwide for each species</td>
<td>0</td>
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<td>Avian Conservation Assessment Database (ACAD)</td>
<td>Variable</td>
<td>Breeding adults</td>
<td>Variable; compiled from other sources</td>
<td>North American estimates</td>
<td>0</td>
<td>17</td>
<td>(46)</td>
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* Estimates for 344 landbird species provided by (35); identical methods applied to 55 additional non-landbird species in the present study.
Table S2.
Net change in abundance across North American bird families, 1970-2017. Taxonomy and common names of families follow (99); families listed in order of greatest decline. Net change in abundance expressed in millions of breeding individuals, with upper and lower 90% credible intervals (CI) shown. Percentage of species in each group with negative trend trajectories also noted.

<table>
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<tr>
<th>Family</th>
<th>Common Name</th>
<th>N Spp</th>
<th>Net Abundance Change (Millions) &amp; 90% CI</th>
<th>Percent Change &amp; 90% CIs</th>
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<tr>
<td></td>
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<td>Change</td>
<td>UC90</td>
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<td>New World Sparrows</td>
<td>38</td>
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<td>Parulidae</td>
<td>New World Warblers</td>
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<td>-617.5</td>
<td>-737.8</td>
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<tr>
<td>Icteridae</td>
<td>New World Blackbirds</td>
<td>18</td>
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<td>-207.2</td>
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Table S3.
GAM spatial trend analysis and model comparison. AIC gives Akaike’s An Information Criterion. df gives degrees of freedom. Models significantly different according to a Chi-squared likelihood ratio test are labelled by different letters (a,b). Change in biomass traffic was calculated as a spatial mean of the multiplication of spatial trend and kriging-interpolated biomass passage. Changes in biomass traffic are based on spatial averages of the GAM predictions over the contiguous US, as detailed in the text. From left to right: % / yr = annual rate of decline in seasonal migration traffic, % = decline over the period 2007-2017, loss in seasonal migration traffic, p = significance of the te(lon,lat):year trend term. See Figure S7 for plots of the estimated smoothed spatial trend.

<table>
<thead>
<tr>
<th>Model*</th>
<th>Formula</th>
<th>AIC</th>
<th>df</th>
<th>% / yr</th>
<th>%</th>
<th>10^5 birds/km</th>
<th>p</th>
</tr>
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<tbody>
<tr>
<td>1</td>
<td>index ~ te(lon,lat) + te(lon,lat):year + dualpol†</td>
<td>337</td>
<td>10</td>
<td>a</td>
<td>-1.2 ± 0.7</td>
<td>-11.6 ± 5.9</td>
<td>-1.4 ± 1.7</td>
</tr>
<tr>
<td>2</td>
<td>index ~ te(lon,lat) + te(lon,lat):year + mode‡</td>
<td>338</td>
<td>11</td>
<td>a</td>
<td>-1.6 ± 0.8</td>
<td>-14.8 ± 7.2</td>
<td>-1.8 ± 1.9</td>
</tr>
<tr>
<td>3</td>
<td>Index ~ te(lon,lat) + te(lon,lat):year + superres§</td>
<td>342</td>
<td>10</td>
<td>b</td>
<td>-2.9 ± 0.5</td>
<td>-25.6 ± 4.2</td>
<td>-3.2 ± 2.8</td>
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<tr>
<td>4</td>
<td>index ~ te(lon,lat) + te(lon,lat):year (model average)</td>
<td>360</td>
<td>9</td>
<td>c</td>
<td>-3.3 ± 0.6</td>
<td>-28.7 ± 4.1</td>
<td>-3.7 ± 3.1</td>
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</tbody>
</table>

*Family=Gamma(link=log)
†mode is a factor variable with levels “legacy”, “superres” and “dualpol”, distinguishing the three time periods in which the radar acquired legacy, super-resolution and dual-polarization data. Note that the dual-polarization upgrade occurred after the super-resolution upgrade, and dual-polarization data includes super-resolution.
‡dualpol is a logical variable that is true after the dual-polarization upgrade, and false before
§superres is a logical variable that is true after the superresolution upgrade, and false before
Table S4.

Model comparison of regionalized generalized mixed models, differentiating in four geographic flyway regions: Atlantic, Mississippi, Central and Western (see Fig. XXX). AIC gives Akaike’s An Information Criterion, df degrees of freedom. Models significantly different according to a Chi-squared likelihood ratio test are labelled by different letters (a,b). We found support for an effect of dual-polarization upgrade on detected biomass passage (cf. model 5), but not for additional correction for the superresolution upgrade (model 6 did not improve over model 5). See Table S5 for fixed effect estimates.

<table>
<thead>
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<th>Model</th>
<th>Formula</th>
<th>AIC</th>
<th>df</th>
<th>letter</th>
</tr>
</thead>
<tbody>
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<td>5</td>
<td>index ~ region + year:flyway + (1</td>
<td>radar) + dualpol†</td>
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<td>11</td>
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<tr>
<td>6</td>
<td>index ~ region + year:flyway + (1</td>
<td>radar) + mode‡</td>
<td>340</td>
<td>12</td>
</tr>
<tr>
<td>7</td>
<td>Index ~ region + year:flyway + (1</td>
<td>radar) + superres</td>
<td>343</td>
<td>11</td>
</tr>
<tr>
<td>8</td>
<td>Index ~ region + year:flyway + (1</td>
<td>radar)</td>
<td>361</td>
<td>10</td>
</tr>
</tbody>
</table>

†Family=Gamma(link=log)
‡mode is a factor variable with levels “legacy”, “superres” and “dualpol”, distinguishing the three time periods in which the radar acquired legacy, super-resolution and dual-polarization data. Note that the dual-polarization upgrade occurred after the super-resolution upgrade, and dual-polarization data includes super-resolution.
§dualpol is a logical variable that is true after the dual-polarization upgrade, and false before
$superres is a logical variable that is true after the superresolution upgrade, and false before
Table S5.

Parameter estimates of temporal and detection-related fixed effects, based on generalized mixed models differentiating in three geographic regions: west (lon < -105°), central (-105° < lon < -95°) and east (lon > -95°). Estimates of change in migratory biomass traffic are expressed as percentages change per year. Explanatory variable year was scaled to zero at 2007. Significant model terms are highlighted in bold. See Table S4 for model comparisons.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed effect</th>
<th>Estimate</th>
<th>Unit</th>
<th>t</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>5</td>
<td>year:flyway_Atlantic</td>
<td>-3.0 ± 0.6</td>
<td>%/yr</td>
<td>-4.7</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>5</td>
<td>year:flyway_Mississippi</td>
<td>-2.7 ± 0.6</td>
<td>%/yr</td>
<td>-4.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>5</td>
<td>year:flyway_Central</td>
<td>0.6 ± 0.6</td>
<td>%/yr</td>
<td>1.0</td>
<td>0.3</td>
</tr>
<tr>
<td>5</td>
<td>year:flyway_Pacific</td>
<td>0.2 ± 0.6</td>
<td>%/yr</td>
<td>0.3</td>
<td>0.8</td>
</tr>
<tr>
<td>5</td>
<td>dualpol=TRUE</td>
<td>-16 ± 3</td>
<td>%</td>
<td>-5.0</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6</td>
<td>year:flyway_Atlantic</td>
<td>-3.4 ± 0.7</td>
<td>%/yr</td>
<td>-4.5</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6</td>
<td>year:flyway_Mississippi</td>
<td>-3.0 ± 0.7</td>
<td>%/yr</td>
<td>-4.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>6</td>
<td>year:flyway_Central</td>
<td>0.2 ± 0.7</td>
<td>%/yr</td>
<td>0.3</td>
<td>0.7</td>
</tr>
<tr>
<td>6</td>
<td>year:flyway_Pacific</td>
<td>0.1 ± 0.8</td>
<td>%/yr</td>
<td>-0.2</td>
<td>0.9</td>
</tr>
<tr>
<td>6</td>
<td>mode=&quot;superres&quot;</td>
<td>25 ± 27</td>
<td>%</td>
<td>0.9</td>
<td>0.4</td>
</tr>
<tr>
<td>6</td>
<td>mode=&quot;dualpol&quot;</td>
<td>-12 ± 5</td>
<td>%</td>
<td>-2.4</td>
<td>0.02</td>
</tr>
<tr>
<td>7</td>
<td>year:flyway_Atlantic</td>
<td>-4.7 ± 0.5</td>
<td>%/yr</td>
<td>-9.9</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>7</td>
<td>year:flyway_Mississippi</td>
<td>-4.4 ± 0.4</td>
<td>%/yr</td>
<td>-10.2</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>7</td>
<td>year:flyway_Central</td>
<td>-1.2 ± 0.4</td>
<td>%/yr</td>
<td>-2.7</td>
<td>0.007</td>
</tr>
<tr>
<td>7</td>
<td>year:flyway_Pacific</td>
<td>-1.5 ± 0.5</td>
<td>%/yr</td>
<td>-3.0</td>
<td>0.003</td>
</tr>
<tr>
<td>7</td>
<td>superres=TRUE</td>
<td>8 ± 2</td>
<td>%</td>
<td>4.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>8</td>
<td>year:flyway_Atlantic</td>
<td>-5.2 ± 0.5</td>
<td>%/yr</td>
<td>-10.9</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>8</td>
<td>year:flyway_Mississippi</td>
<td>-4.8 ± 0.4</td>
<td>%/yr</td>
<td>-11.3</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>8</td>
<td>year:flyway_Central</td>
<td>-1.5 ± 0.4</td>
<td>%/yr</td>
<td>-3.5</td>
<td>0.0004</td>
</tr>
<tr>
<td>8</td>
<td>year:flyway_Pacific</td>
<td>-1.9 ± 0.5</td>
<td>%/yr</td>
<td>-3.8</td>
<td>0.0001</td>
</tr>
<tr>
<td>5-8 (average)†</td>
<td>year:flyway_Atlantic</td>
<td>-3.2 ± 0.8</td>
<td>%/yr</td>
<td>4.1*</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>5-8 (average)†</td>
<td>year:flyway_Mississippi</td>
<td>-2.9 ± 0.7</td>
<td>%/yr</td>
<td>3.9*</td>
<td>0.0001</td>
</tr>
<tr>
<td>5-8 (average)†</td>
<td>year:flyway_Central</td>
<td>0.4 ± 0.8</td>
<td>%/yr</td>
<td>0.5*</td>
<td>0.6</td>
</tr>
<tr>
<td>5-8 (average)†</td>
<td>year:flyway_Pacific</td>
<td>0.3 ± 0.8</td>
<td>%/yr</td>
<td>0.0*</td>
<td>1.0</td>
</tr>
</tbody>
</table>

* z value instead of t value
† showing full model-averaged coefficients for temporal fixed effects only
Data S1. (separate file)
Species-specific data and results for analysis of net population change in the North American avifauna. Included are 529 species with common and scientific names, taxonomic sort number (100), bird family, species group and biome assignments, absolute and proportional changes in abundance with associated variance, start and end-year population estimates with variance, and source data for population size estimates and population trajectories for each species. A separate worksheet in the same file contains definitions of each column header.

Data S2. (separate file)
Species-specific adjustment factors used in the calculation of Partners in Flight (PIF) population size estimates based on BBS count data. Included are 399 species, including 344 landbird species previously published in (35), and 55 additional non-landbird species for which we estimated population size using identical methods. Unrounded population size estimates (PopUsCa) are the same as in Data S1, and are provided here for easy reference. Adjustment factors are further defined and described in (35).