Decline of the North American avifauna

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.

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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 thousandfold 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 that 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 data sets, some of which provide close to 50 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 of 143 weather radars (NEXRAD) across the contiguous United States 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 standardized 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 United States 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% credible interval (CI) = 2.7–3.1 billion] birds across almost all biomes, a reduction of 29% (95% CIs = 27–30%) since 1970 (Fig. 1 and Table 1). Analysis of NEXRAD data indicates a similarly steep decline in nocturnal passage of migratory biomass, a reduction of 13.6 ± 9.1% since 2007 (Fig. 2A). Reduction in biomass passage occurred across the eastern United States (Fig. 2, C and 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 (Fig. 2, B to D, and table S5). Two completely different and independent monitoring techniques thus signal major population loss across the continental avifauna.

Species exhibiting declines (57%, 303 out of 529 species) on the basis of 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. (Fig. 1 and 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 (Fig. 3 and Table 1). Unexpectedly, we also found a large net loss (63%) across 10 introduced species (Fig. 3, D and E, and 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 and fig. 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 (Fig. 3A), including sparrows, warblers, blackbirds, and finches. Of 67 bird families surveyed, 38 showed a net loss in total abundance, whereas 29 showed gains (Fig. 3B), indicating recent changes in avifaunal composition (table S2). Although not optimized for species-level analysis, our model indicates that 19 widespread and abundant land birds (including two 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.

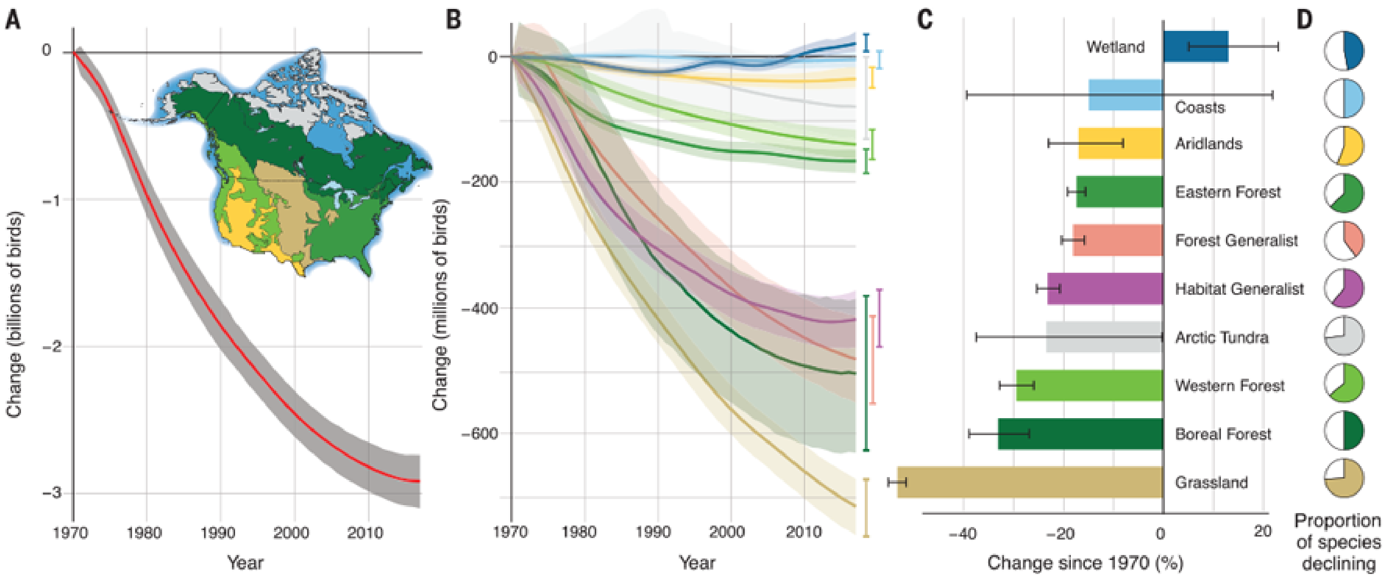

Fig. 1. Net population change in North American birds. (A) By integrating population size estimates and trajectories for 529 species (18), we show a net loss of 2.9 billion breeding birds across the continental avifauna since 1970. Gray shading represents the 95% credible interval (CI) around total estimated 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% CI. (**D**) Proportion of species declining in each biome.

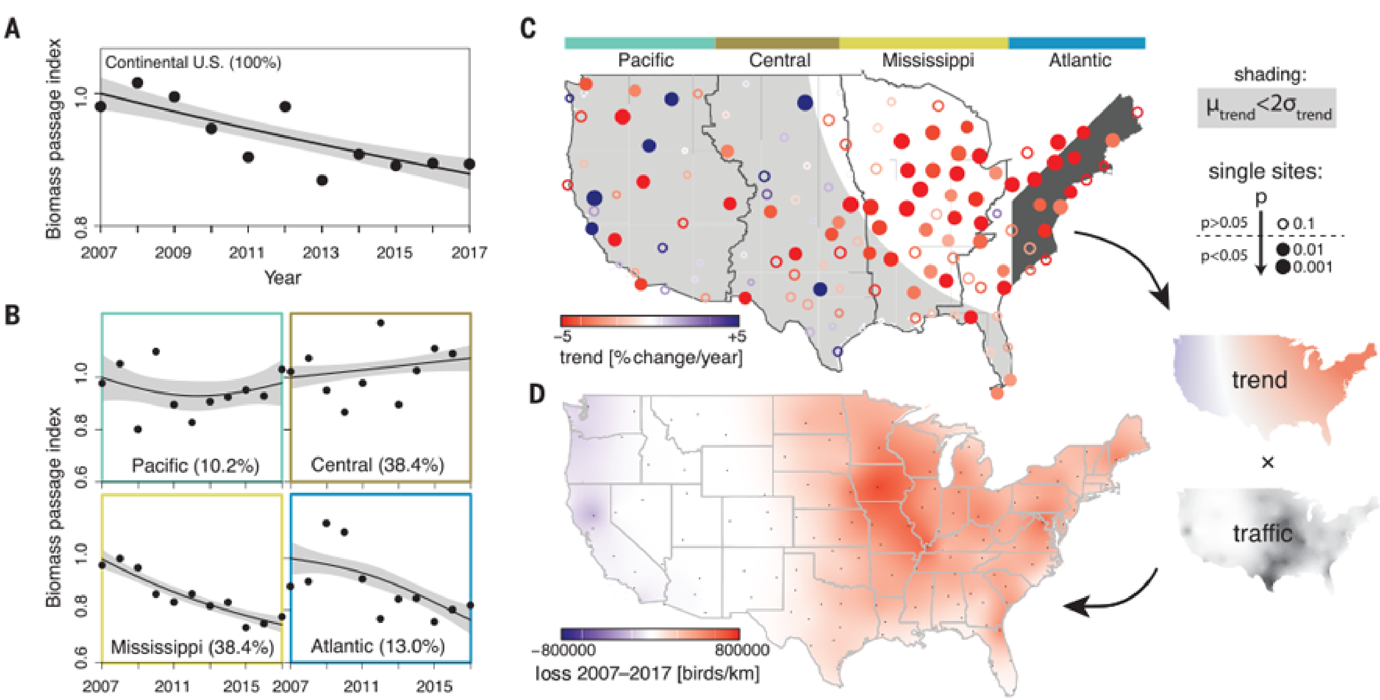

Fig. 2. NEXRAD radar monitoring of nocturnal bird migration across the contiguous United States. (A) Annual change in biomass passage for the full

continental United States (black) and (**B**) the Pacific (green), Central (brown), Mississippi (yellow), and Atlantic (blue) flyways [borders indicated in (C)], with percentage of total biomass passage (migration traffic) for each flyway indicated; declines are significant only for the full United States and the Mississippi and Atlantic flyways (tables S3 to S5). (**C**) Single-site trends in seasonal biomass passage at 143 NEXRAD stations in spring (1 March to 1 July), estimated for the period 2007–2017. Darker red colors indicate higher declines and loss of biomass passage, whereas 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**) Ten-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.

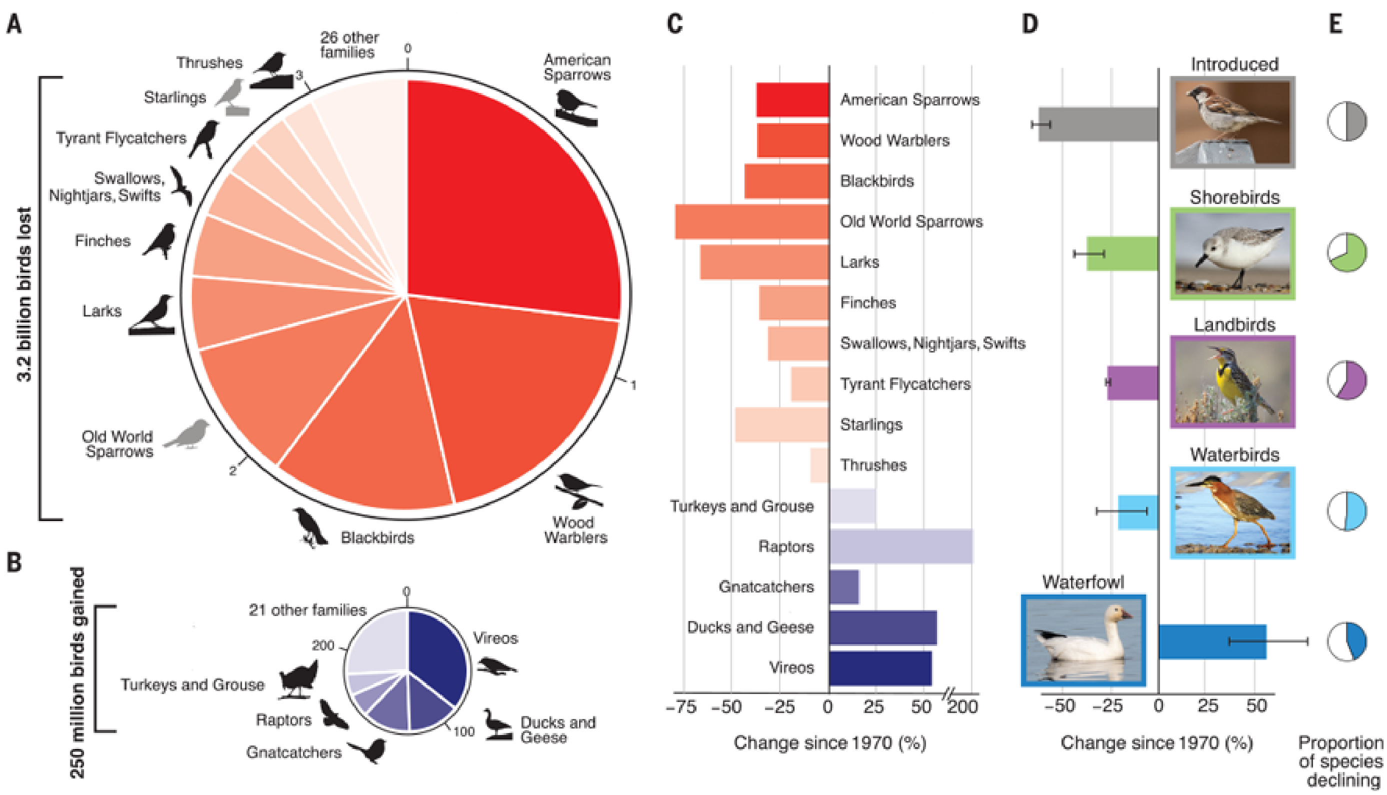

Fig. 3. Gains and losses across the North American avifauna over the past half-century. (A) Bird families were categorized as having a net loss (red) or gain (blue). Total loss of 3.2 billion birds occurred across 38 families; each family with losses greater than 50 million individuals is shown as a proportion of total loss, including two introduced families (gray). Swallows, nightjars, and swifts together show loss within the aerial insectivore guild. (**B**) Twenty-nine 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**) 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*). (**E**) Proportion of species with declining trends.

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 (Fig. 3). Notably, our population loss estimates are conservative because 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 [47million people spend U.S.$9.3 billion per year through birdrelated activities in the United States (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 exceptional 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 bird populations 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 foreshadow a much larger problem, indicating similar or greater losses in other taxonomic groups (28, 30).

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 bounds of each 95% credible interval (CI) shown. Percentage of species in each group with negative trend trajectories is also noted. Values in bold indicate declines and loss; those in italics indicate gains.

Species group	No. of species	Net abundance change (millions) and 95% CIs			Percent change and 95% CIs			Proportion species in decline
		Change	LC95	UC95	Change	LC95	UC95	
Species summary								
All N. Am. species	529	**−2,911.9**	−3,097.5	−2,732.9	**−28.8%**	−30.2%	−27.3%	57.3%
All native species	519	**−2,521.0**	−2,698.5	−2,347.6	**−26.5%**	−28.0%	−24.9%	57.4%
Introduced species	10	**−391.6**	−442.3	−336.6	**−62.9%**	−66.5%	−56.4%	50.0%
Native migratory species	419	**−2,547.7**	−2,723.7	−2,374.5	**−28.3%**	−29.8%	−26.7%	58.2%
Native resident species	100	*26.3*	7.3	46.9	*5.3%*	1.4%	9.6%	54.0%
Landbirds	357	**−2,516.5**	−2,692.2	−2,346.0	**−27.1%**	−28.6%	−25.5%	58.8%
Shorebirds	44	**−17.1**	−21.8	−12.6	**−37.4%**	−45.0%	−28.8%	68.2%
Waterbirds	77	**−22.5**	−37.8	−6.3	**−21.5%**	−33.1%	−6.2%	51.9%
Waterfowl	41	*34.8*	24.5	48.3	*56.0%*	37.9%	79.4%	43.9%
Aerial insectivores	26	**−156.8**	−183.8	−127.0	**−31.8%**	−36.4%	−26.1%	73.1%
Breeding biome								
Grassland	31	**−717.5**	−763.9	−673.3	**−53.3%**	−55.1%	−51.5%	74.2%
Boreal forest	34	**−500.7**	−627.1	−381.0	**−33.1%**	−38.9%	−26.9%	50.0%
Forest generalist	40	**−482.2**	−552.5	−413.4	**−18.1%**	−20.4%	−15.8%	40.0%
Habitat generalist	38	**−417.3**	−462.1	−371.3	**−23.1%**	−25.4%	−20.7%	60.5%
Eastern forest	63	**−166.7**	−185.8	−147.7	**−17.4%**	−19.2%	−15.6%	63.5%
Western forest	67	**−139.7**	−163.8	−116.1	**−29.5%**	−32.8%	−26.0%	64.2%
Arctic tundra	51	**−79.9**	−131.2	−0.7	**−23.4%**	−37.5%	−0.2%	56.5%
Aridlands	62	**−35.6**	−49.7	−17.0	**−17.0%**	−23.0%	−8.1%	56.5%
Coasts	38	−6.1	−18.9	8.5	−15.0%	−39.4%	21.9%	50.0%
Wetlands	95	*20.6*	8.3	35.3	*13.0%*	5.1%	23.0%	47.4%
Nonbreeding biome								
Temperate N. America	192	**−1,413.0**	−1,521.5	−1,292.3	**−27.4%**	−29.3%	−25.3%	55.2%
South America	41	**−537.4**	−651.1	−432.6	**−40.1%**	−45.2%	−34.6%	75.6%
Southwestern aridlands	50	**−238.1**	−261.2	−215.6	**−41.9%**	−44.5%	−39.2%	74.0%
Mexico–Central America	76	**−155.3**	−187.8	−122.0	**−15.5%**	−18.3%	−12.6%	52.6%
Widespread neotropical	22	**−126.0**	−171.2	−86.1	**−26.8%**	−33.4%	−19.3%	45.5%
Widespread	60	−31.6	−63.1	1.6	−3.7%	−7.4%	0.2%	43.3%
Marine	26	**−16.3**	−29.7	−1.2	**−30.8%**	−49.1%	−2.5%	61.5%
Coastal	44	**−11.0**	−14.9	−6.7	**−42.0%**	−51.8%	−26.7%	68.2%
Caribbean	8	−6.0	1.4	−15.7	12.1%	−2.8%	31.7%	25.0%

Pervasiveness of avian loss across biomes and bird families suggests multiple and interacting threats. Isolating spatiotemporal limiting factors for individual species and populations will require additional study, however, because 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 nonbreeding 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 nonbreeding 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 work. 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.

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SUPPLEMENTARY MATERIALS

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