

## BIRD DECLINE

# Acceleration hotspots of North American birds' decline are associated with agriculture

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Human activities might have accelerated declines of population abundance, but this acceleration remains underexplored. Using 1033 North American Breeding Bird Survey routes, we analyze abundance change and its acceleration for 261 bird species, 54 avian families, and 10 habitats from 1987 to 2021. We show an average continent-wide decline of abundance of all birds per local route, with hotspots of decline in southern and warm parts of North America and hotspots of accelerating decline in the Mid-Atlantic, Midwest, and California, matching patterns of agricultural intensity. Overall, 122 species (47%) exhibit significant declines, of which 63 also show acceleration of this decline, and 67 show declining per-capita growth rate, raising concerns for a large part of North American bird populations. These findings suggest that bird abundance decline is mostly accelerating, with spatial patterns of this acceleration indicating that agricultural intensity may be a driver of this trend.

Human activities such as land use change, agricultural intensification, overexploitation, and pollution have considerably affected ecosystems over the past centuries (1). Temporal changes in local population abundances are closely monitored indicators of this impact (2) and have shown an overall abundance decline across taxa (1, 3). The past century, however, has seen not only the increase but also an acceleration in the increase of human activities, sometimes termed the Great Acceleration (4–6), and a likely acceleration of global vertebrate extinction rates (7–9). We should thus expect a corresponding acceleration in population declines. In essence, although the first-order derivative of population abundance over time for many species appears to be a decline, the second-order derivative (i.e. acceleration or deceleration of this change) has so far only been used to detect year-specific shifts in population trajectories (10–12).

Although examining temporal changes in population abundance is valuable, understanding how these changes evolve over time, particularly in terms of their acceleration, offers deeper ecological insights. Here, the change in abundance over time ( $\Delta N$ , eq. S14) reflects the net increase or decline in the number of individuals throughout a time series (i.e., linear trend of abundance over time), and the yearly growth rate ( $g$ , eq. S11) represents the average difference in absolute abundance from one year to the next. These differences are ecologically significant, as absolute bird numbers are linked to ecosystem services (13). Crucially, change in this growth rate ( $\Delta g$ , eq. S15) represents acceleration or deceleration in abundance change (Fig. 1). For instance, a negative  $\Delta g$  for a population already in decline (i.e., with negative  $\Delta N$ ) indicates an acceleration of the decline (Fig. 1). This second-order derivative remains largely unexplored in large-scale studies of biodiversity trends. Finally, an ecologically fundamental metric is the yearly per capita growth rate ( $r$ , eq. S12), along with its change through time

( $\Delta r$ , eq. S16), which captures how individual contributions to population growth shift over time. Although  $\Delta g$  and  $\Delta r$  are related, they capture different ecological information:  $\Delta g$  reflects the magnitude of the acceleration in absolute numbers of birds and thus reflects the shifting contribution of bird populations to ecosystems. By contrast,  $\Delta r$  is directly linked to underlying demographic processes of per-capita recruitment and loss and also provides a relative measure of acceleration comparable among populations of varying sizes.

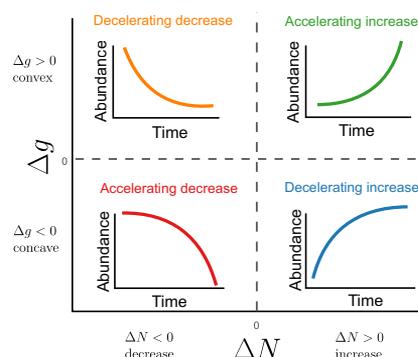
We provide a comprehensive assessment of temporal changes in local population abundances of 261 bird species across North America from 1987 to 2021, focusing on acceleration and deceleration. Using 1033 routes of the North American Breeding Bird Survey (BBS) (14)—a long-term, annual, and standardized monitoring program—and advances in N-mixture population models (15, 16), paired with full Bayesian inference, we exhibit widespread bird abundance declines across North America and pinpoint regions, taxa, and habitats where abundance declines accelerate or decelerate. We then show coincidence of the acceleration hotspots with environmental and anthropogenic variables. The time period of 1987 to 2021, though longer (17) or shorter (18–20) than other studies on bird abundance changes in the US, balances long temporal coverage with broad spatial representation.

## Nationwide decline in abundance

The average change in total bird abundance per route ( $\Delta N$ , eq. S14) is a significant decline of  $\Delta N = -8.94$  individuals per year [95% credible interval (CI) =  $-10.01, -7.88$ ], histogram in Fig. 2A), representing an average loss of 304 birds (out of an average abundance of 2034 in 1987, i.e. 15%) per route from 1987 to 2021. The trends we uncover align with the reported decline of bird abundance across North America (17, 18, 20) and mirror trends in some European bird species (21–27). Of the 1033 routes analyzed here, only 17% (172) experienced a significant increase in total bird abundance whereas 70% (718) experienced a significant decrease (Fig. 2A and figs. S1 and S2A). Using a spatial smoother to show average regional trends not obscured by local variation, we found only seven routes located in regions with increasing abundance (dotted black circle in Fig. 2B) and that bird abundances in FL, TX, LA, and AZ underwent the most pronounced average declines per route.

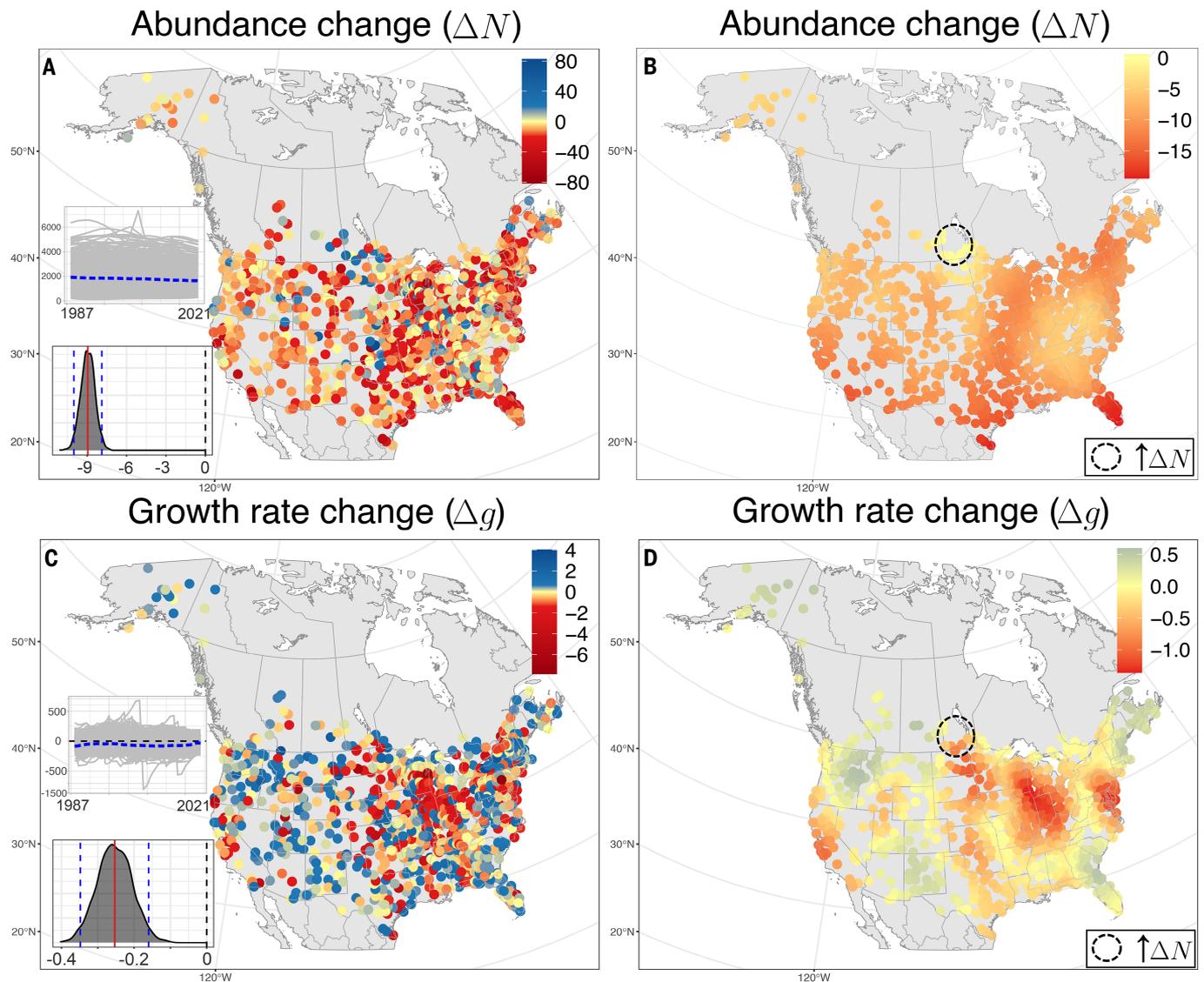
## Regional hotspots of accelerating abundance decline

The average change of  $g$  per route is a significant decline with  $\Delta g = -0.25$  [CI =  $-0.35, -0.16$ ; histogram shown (Fig. 2C)], indicating that the yearly change in abundance (i.e., growth rate  $g$ ) decreased over time (Fig. 2, C and D, fig. S1, B and D, and figs. S2A and S3A). That is, on average, routes experienced a significant acceleration of bird abundance decline. Among the 718 routes with significantly declining abundance,



**Fig. 1. Illustration of acceleration and deceleration of abundance change.** Here,  $\Delta N$  denotes abundance change and  $\Delta g$  (change in yearly growth rate) denotes its acceleration or deceleration. The case in which  $\Delta g = 0$  represents a constant rate of change—that is, no acceleration or deceleration in  $\Delta N$  (i.e., linear trend).

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**Fig. 2. Temporal change of abundance and growth rate.** (A and B) Total changes in bird abundance per route from 1987 to 2021 ( $\Delta N$ ), and (C and D) temporal change of growth rate ( $\Delta g$ ), after correcting for imperfect detection. Maps in (B) and (D) are estimates from the dynamic  $N$ -mixture models, smoothed using a spatial Generalized Additive Model (total var. explained  $R^2$  are 7.62% and 16.5%, respectively); nonsmoothed values are in (A) and (C). Smoothed and nonsmoothed panels share the same fixed color scale. Because abundance is decreasing across most of North America, the red regions in (D) are regional hotspots of acceleration of bird abundance decline. Dashed circles in (B) and (D) mark the only region with positive values of the smoothed  $\Delta N$ . Inset plots (bottom left) show the raw (i.e., not spatially smoothed) changes in abundance and growth rate with the average represented by the blue dashed line;  $y$ -axes in (C) are signed square root transformed. The histograms show the posterior distributions of the average slope; Red vertical lines are means and dashed blue lines are 95% CI.

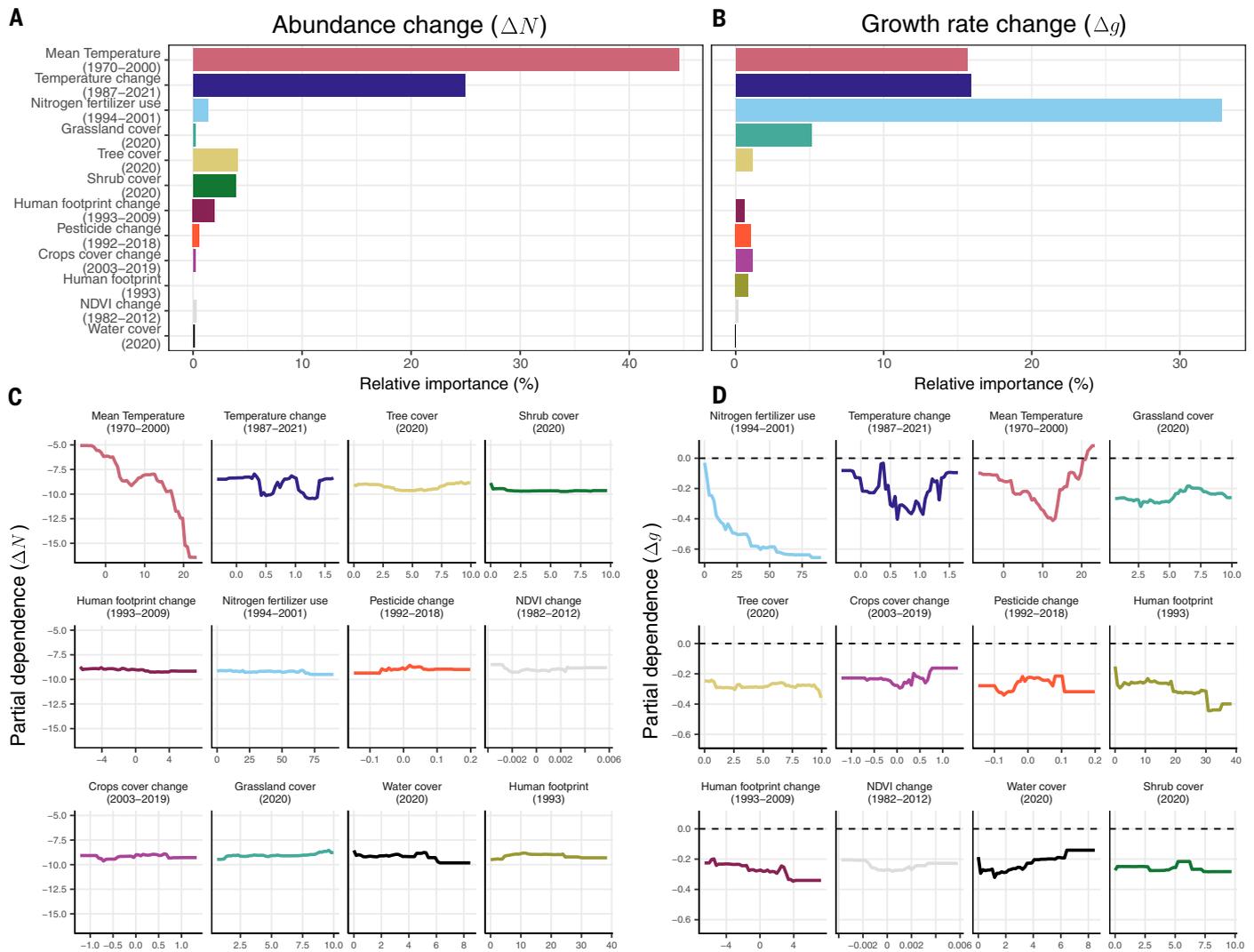
163 routes exhibited a significant negative  $\Delta g$  and 146 a significant positive  $\Delta g$  (raw, not smoothed estimates, Fig. 2C).

Because most of the spatially smoothed  $\Delta N$  is negative (Fig. 2, B and D, outside the black dotted circle), the smoothed map of  $\Delta g$  can be interpreted as average regional acceleration ( $\Delta g < 0$ ) and deceleration ( $\Delta g > 0$ ) of the abundance decline (Fig. 2D, outside the black dotted circle, fig. S1D). Parts of the Mid-Atlantic region of the USA (DE, MD, and NJ), the Midwest (especially IN, OH, KY, IL, WI, MI) and CA had negative smoothed  $\Delta g$ , indicating an acceleration of the decline in abundance (i.e., each year more birds are lost than in the previous year). In these regions, the gap between the number of lost and recruited individuals widens each year, raising concerns about the future of these bird populations. By contrast, YT, SK, AB, NM, AK, Atlantic Canada (NB, PE, and NS), AZ, MT, parts of New England (MA, ME, NH, VT), WA, CO, OR, SC, and parts of GA and Northern FL

showed a positive smoothed  $\Delta g$ , that is, a deceleration (i.e., slow-down) of the abundance decline. All raw spatial patterns of per capita growth rate change  $\Delta r$  were highly correlated with  $\Delta g$  (Spearman's correlation = 0.97, fig. S4), although in contrast to the significant  $\Delta g$ , the average  $\Delta r$  at the continental scale was negative but with 95% CI overlapping zero (figs. S3B and S5). We suggest that this apparent discrepancy is because the mean  $\Delta r$  normalizes absolute change by abundance, allowing weak negative per capita trends to cause acceleration in total population decline.

### Linking patterns of change to environment

We also investigated how raw and smoothed patterns of  $\Delta N$ ,  $\Delta g$ , and  $\Delta r$  correlate with environmental conditions. Changes in bird abundance have been previously linked to specific climates, habitats, land uses, and their temporal change. For instance, grassland and farmland



**Fig. 3. Variable importances and partial dependence plots from best-performing tree-based models explaining changes in spatially smoothed abundance change  $\Delta N$  and growth rate change  $\Delta g$ .** (A) and (B) Variable importance scores scaled to  $R^2$  from XGBoost for  $\Delta N$  (total var. explained  $R^2 = 82.9\%$ ) and for  $\Delta g$  (total var. explained  $R^2 = 75.2\%$ ). (C) and (D) Partial dependence plots ordered from most to least important predictors for  $\Delta N$  and  $\Delta g$ , respectively. Note here that more negative values of  $\Delta g$  indicate accelerated declines in abundance.

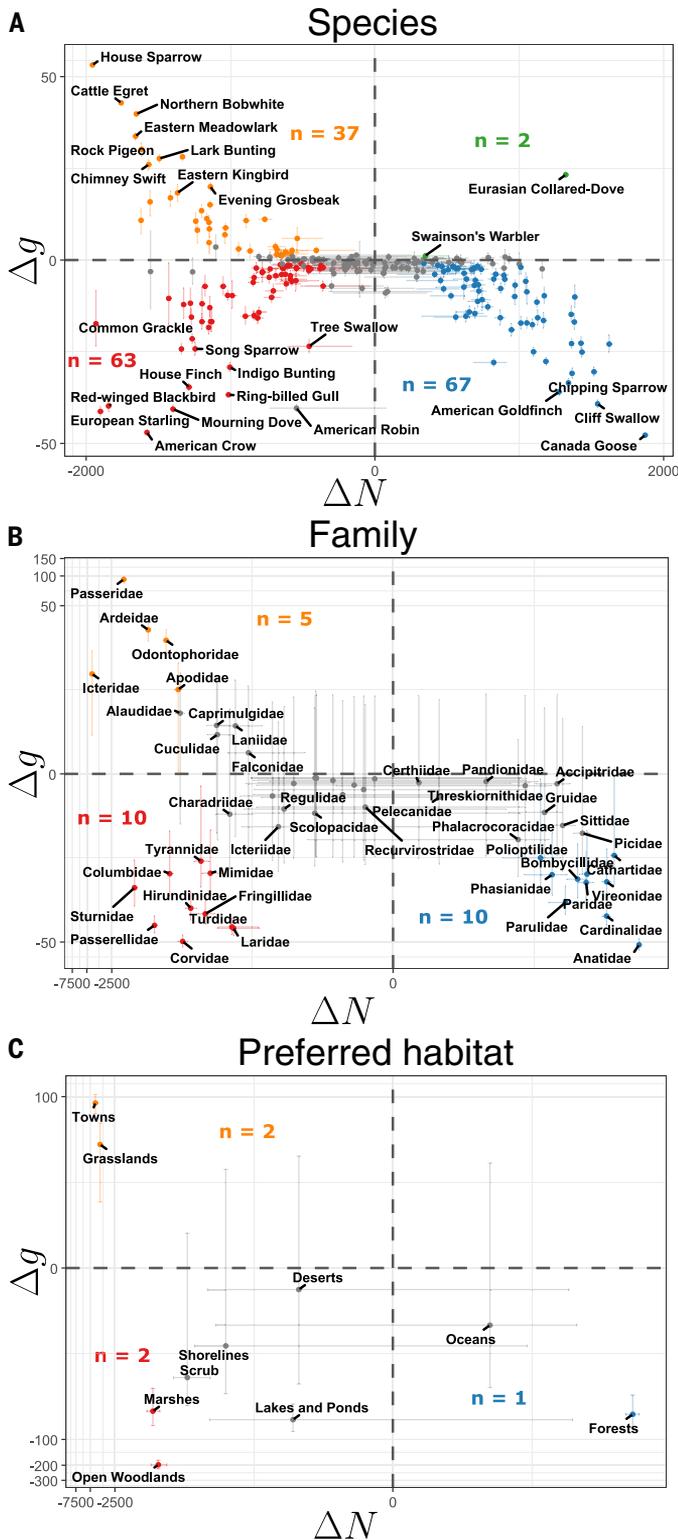
species have been declining in both Europe and the USA (18, 21–27) whereas forest dwellers and species associated with warm climates have either remained stable or increased in some regions of Europe (26–28). Among the important processes previously linked to bird population dynamics are agricultural intensification (21, 23, 26, 29, 30) and changes in land use (21, 22). We amassed 20 predictors representing either static or dynamic patterns of climate, habitats, and human impact in North America, selected 12 of them to minimize collinearity (Fig. 3, figs. S4 and S6, and table S1), and linked them to the raw and smoothed geographic patterns of  $\Delta N$ ,  $\Delta g$ , and  $\Delta r$  using tree-based machine learning algorithms (Random Forest, Boosted Regression Tree, and XGBoost).

The first notable finding is that warm and warming regions coincide with areas of abundance decline ( $\Delta N$ , Fig. 3, A and C, and figs. S7 and S8). This pattern is consistent with the evidence that bird populations are shifting their distributions northward as they track cooler conditions (31). Increases in temperatures have been shown to increase the risk of bird species' extinction as a result of a lack of species adaptability to rapidly changing climatic conditions (32), and consistent

temperature-related responses have been documented across both Europe and North America (33). Our results further support this by showing that areas experiencing greater warming (Fig. 3C) also exhibit stronger abundance declines, suggesting that rising temperatures may be a driver of recent bird population losses.

The second major finding is that the hotspots of negative  $\Delta g$  (and  $\Delta r$ ), i.e., the acceleration of the decline (Fig. 2D and fig. S5B), coincide with areas of high-intensity agriculture—namely those with high fertilizer or pesticide use or large areas of croplands (26) (Fig. 3, B and D, and figs. S7 and S8). These three variables are strongly correlated (fig. S4) and we cannot separate their independent effects, and so we interpret them collectively as indicators of agricultural intensity. The coincidence between agricultural intensity and acceleration of bird abundance decline is concerning, especially given the increases in North American agricultural production, and farm size, during the past 40 years (34).

We also found an interaction between agricultural intensity (i.e., pesticide use, fertilizer use and/or cropland area) and temperature change in their effect on  $\Delta g$  (fig. S9): The negative effect of agricultural



**Fig. 4. Acceleration and deceleration of bird abundance change aggregated across species, families, and habitats.** Each point represents  $\Delta N$  and  $\Delta g$  calculated by aggregating all individuals at the level of (A) a species, (B) a family, and (C) a habitat. Error bars show the 95% CI and gray points indicate nonsignificant acceleration or deceleration (i.e. 95% CI overlaps 0 on either axis). Colors follow the scheme of Fig. 1 (red, accelerating decrease; orange, decelerating decrease; blue, decelerating increase; green, accelerating increase). The number ( $n$ ) of significant points in each quadrant is noted. Axes are pseudo log-transformed for better visual separation.

intensity on  $\Delta g$  is stronger in areas with more pronounced temperature increase. Indeed, agricultural landscapes are known to warm more than natural areas as a result of reduced vegetation cover and altered surface properties (35, 36), which may amplify climate-driven stress on birds (37). Another possible explanation is that intense agricultural practices, through pesticide use and mechanical disturbance, interact with temperature change and thus further reduce food and habitat availability. Also, the nonlinear effects of temperature on  $\Delta g$  (Fig. 3D) indicate that the strongest acceleration of decline occurs around intermediate mean temperatures ( $\sim 10^\circ\text{C}$ ), where bird populations are densest and human activities are most pronounced.

Clearly, the predictors for the acceleration differ from those driving the decline in abundance ( $\Delta N$ ) (Fig. 3, A and C, versus B and D). This suggests that focusing only on the magnitude of the decline may underestimate the impact of agriculture on bird populations, as intense agriculture use can accelerate the abundance decline that may be primarily driven by climate. By contrast, temperature change is the second most important variable explaining  $\Delta N$ ,  $\Delta g$ , and  $\Delta r$ . The fact that we found similar relationships for changes in per capita growth rate ( $\Delta r$ ; fig. S10) suggests that agricultural intensity affects not just total numbers but also the increasing difference between individual survival and recruitment. Given the advances in the estimation of survival and recruitment from abundance time series (15, 16, 38), this is an opportunity for future research.

To our knowledge, this is the first large-scale study that has linked the acceleration of abundance change to the environment. Our findings suggest that such dynamics could represent a critical, yet unexplored, dimension of ecological responses, one that may yield valuable insights if applied to temporal dynamics of metrics such as species richness or turnover. Nonetheless, we also caution that this is a correlative post hoc analysis and that majority of geographic variation in  $\Delta N$ ,  $\Delta g$ , and  $\Delta r$  still remains to be explained. More robust causal analyses, such as quasicausal analytical designs (26, 39) or experiments (40, 41) can help disentangle how agricultural practices affect abundance dynamics.

### Per-species, per-family, and per-habitat analyses

In addition to the geographic variation in total  $\Delta N$ ,  $\Delta g$ , and  $\Delta r$  of all birds per route, we also assessed these metrics across all routes and at different levels of taxonomic aggregation: species, family, and species' preferred habitat (42). Across 261 species, 84 species (32%) showed a significant positive  $\Delta N$ , of which most (67 species) had a significant decelerating increase (Fig. 4A). This is expected, as a sustained accelerating increase in abundance is rapidly physically limited and therefore rare (4, 43, 44). By contrast, the most common trend was a significant decline, observed in 122 species (47%), with more than half of these (63 species, 53%) experiencing a significant acceleration of the decline (Fig. 4A). This indicates that most of the declining species and a quarter of all the species analyzed are undergoing a significant accelerating decline. Additionally, 21 families (39%) show a significant negative  $\Delta N$  (versus 14 positive), of which 10 experienced a significant acceleration of this decline (Fig. 4B). This indicates that most of the declining families are also experiencing an acceleration of the decline, showing that the pattern is not driven by a few taxonomic groups with shared traits or evolutionary histories but is instead widespread across families. At the per capita level, the number of species with negative  $\Delta r$  (67 species, fig. S11B) was comparable to the number with negative  $\Delta g$  whereas only seven species showed positive  $\Delta r$ . This indicates that for most species undergoing declines in total abundance the difference between per-capita recruitment and loss is widening. By contrast, species with positive  $\Delta N$  showed only significant negative  $\Delta r$ , consistent with expectations under logistic growth as populations approach carrying capacity (fig. S11B).

Out of 10 habitats considered here, only forests showed a significant positive  $\Delta N$ , with a decelerating increase (Fig. 4C). Although this increase seemingly contradicts the well-known decline in forest populations in the USA (17, 18, 20), our classification is based on species'

preferred habitats rather than biogeographic regions, as commonly used in previous studies. Consequently, our results of abundance decline across the contiguous US are consistent with those earlier findings whereas the observed increase in forest specialists aligns with other analyses using similar habitat-based classifications in the USA (45) and Europe (26, 28). Conversely, four habitats exhibited significant decline in abundance, with the strongest declines observed for towns, grasslands, marshes, and open woodlands (Fig. 4C and fig. S12). Additionally, two of these habitats, marshes and open woodlands, showed an accelerating decline. These habitats are considerably affected by human activities (46–48), suggesting a link between the acceleration of the decline and anthropogenic pressures such as agricultural intensification and habitat degradation. At the per capita level ( $\Delta r$ ), patterns across families and preferred habitats were consistent with those observed for  $\Delta g$  (fig. S11, C and D).

## Conclusions

Using one of the most comprehensive and standardized bird time series datasets in the world, coupled with a state-of-the-art dynamic N-mixture Bayesian model, we examined the abundance dynamics and acceleration for 261 species over 35 years at the continental scale. Although the hotspots of abundance decline coincide with high and increasing temperatures, the hotspots of accelerated decline coincide with agricultural intensity. These findings highlight the importance of monitoring not only ecological changes but also the second derivative of ecological variables over time. Incorporating acceleration of metrics into conservation assessments could uncover signals of decline that would remain hidden when focusing solely on abundance trends. Our approach could be applied to other taxa and biodiversity metrics, such as occupancy, species richness, or turnover to test for similar acceleration patterns. Finally, our results are concerning, particularly considering accelerating growth in human activities across various sectors such as economy, agriculture, or transportation (4–6, 49–52).

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## SUPPLEMENTARY MATERIALS

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### Editor's summary

Human activities, including dramatic changes to land cover and land use, are known to negatively influence populations of many species. As human populations and technologies have expanded, so has the rate of our influence on ecosystems. Leroy *et al.* investigated whether this "Great Acceleration" has led to increasing abundance changes in birds, one of the most highly studied taxonomic groups. Using data from the North American Breeding Bird Survey, the authors found that about half of the 261 species analyzed showed significant declines from 1987 to 2021, and a quarter showed accelerating declines. Hotspots of accelerating abundance decline were located in regions with high-intensity agriculture (high cropland area, fertilizer use, or pesticide use). —Bianca Lopez

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