

BIRD DECLINE

North American bird declines are greatest where species are most abundant

Alison Johnston^{1,2*}, Amanda D. Rodewald^{1,3},
 Matt Strimas-Mackey¹, Tom Auer¹, Wesley M. Hochachka¹,
 Andrew N. Stillman¹, Courtney L. Davis¹, Viviana Ruiz-Gutierrez¹,
 Adriaan M. Dokter¹, Eliot T. Miller^{1,4}, Orin Robinson¹,
 Shawn Ligocki¹, Lauren Oldham Jaromczyk¹, Cynthia Crowley¹,
 Christopher L. Wood¹, Daniel Fink¹

Efforts to address declines of North American birds have been constrained by limited availability of fine-scale information about population change. By using participatory science data from eBird, we estimated continental population change and relative abundance at 27-kilometer resolution for 495 bird species from 2007 to 2021. Results revealed high and previously undetected spatial heterogeneity in trends; although 75% of species were declining, 97% of species showed separate areas of significantly increasing and decreasing populations. Populations tended to decline most steeply in strongholds where species were most abundant, yet they fared better where species were least abundant. These high-resolution trends improve our ability to understand population dynamics, prioritize recovery efforts, and guide conservation at a time when action is urgently needed.

Bird communities globally are in crisis, with steep declines of many common species (1–3), and North America is no exception with more than one-quarter of all breeding birds lost since 1970 (4). Long-term indicators of population trends from structured monitoring surveys have documented these declines in bird populations over several decades (4–6). However, charting a pathway to recover populations requires detailed spatial information about population change to identify where populations are most imperiled and the optimal locations for conservation.

Practitioners have long recognized that conservation is most likely to be successful when the scale of information corresponds to the scale of the problem and implementation of actions, which often is on the order of several hectares or square kilometers (7). High-resolution estimates of population trends have a number of advantages for conservation: (i) They can be used to detect localized declines that are obscured at coarser resolutions and thus act as an early warning system; (ii) they can help identify causes of declines because many potential drivers are most readily determined at local or landscape scales (8–11); and (iii) they can inform management, which is typically implemented within sites and local landscapes (12, 13). Access to high-resolution information is especially valuable when resources for conservation are limited, forcing decision-makers to prioritize actions among locations to get the best return on their investments. Unfortunately, even for well-surveyed taxa, such as birds (5, 14), few monitoring programs can provide population trends at both a high resolution and a broad extent (1). We combined recent advances in

analytical methods with open-source participatory science data to generate high-resolution bird population trends and provide a new opportunity to meet these needs in North America (15).

Estimating population trends

In this study, we harnessed participatory science (also known as “citizen science”) data to reveal high-resolution patterns of avian population change across North America. We used 36 million checklists from eBird (16) collected from 2007 to 2021 to estimate population trends for 495 bird species breeding within North America, Central America, and the Caribbean. Each eBird checklist is a list of all birds observed and identified by a participant at a particular time and place. We estimated species trends as the average percent-per-year rate of change in relative abundance from 2007 to 2021 at a $27 \times 27 \text{ km}^2$ spatial resolution across each species’ range. We also produced confidence intervals for the trend estimates for each species within each $27 \times 27 \text{ km}^2$ grid cell (15, 17).

eBird, like most broad-scale participatory science projects, does not have the structured protocols necessary to maintain consistent sampling across space and time. Therefore, to reliably estimate bird population change, it is critical to use a model that separates changes in the bird populations from changes in how people observe birds. Without formally separating these processes, changes to the observation process will bias estimates of bird population trends. To accomplish this separation, we used a causal machine learning trend model designed to control for confounding sources of intra- and interannual variation, including changes in site selection, search effort, and search efficiency (15, 18–21). We assessed the reliability of the trend estimates using an extensive suite of spatially explicit simulations for each species. We used these simulations to assess statistical power and error rates and found high power to reliably detect and delineate spatial variation with low error rates for trends at the 27-km spatial resolution for most North American species. In general, statistical performance was stronger (higher power and lower error rates) among trends with larger magnitudes but did not vary with species’ relative abundance at the 27-km spatial resolution (17). Although we initially modeled trends for 573 species breeding in the region with sufficient data, we only present the results from the 495 deemed to have reliably estimated trends based on results from these species-specific simulations.

The high-resolution trends provide insights into the spatial structure of population dynamics for North American birds. Range-wide population trends indicated population declines for 75% of species and significant population declines for 65% of species. However, there is strong spatial heterogeneity that is invisible when population trends are summarized across species ranges (Fig. 1). Notably, 97% of species experienced both declines and increases in different locations within their ranges, and 67% of species had declines in more than half of their range (Fig. 2). The amount of spatial variation in trends that is obscured by regional summaries is substantial even within smaller Bird Conservation Regions (BCRs) (22), which represent regions with similar ecosystems and bird communities (Fig. 1). Specifically, the range of trend estimates at 27-km resolution within a BCR spanned more than 6% per year for most species (e.g., 27-km resolution trends might range from $\pm 3\%$ per year for a species with a BCR-wide stable trend) (fig. S1).

Birds are declining where they are most abundant

Our most concerning finding was that, for the overwhelming majority of species, the strongest rates of decline occurred in areas where populations were most abundant. By using a linear model that accounted for trend uncertainty with weights and modeled spatial autocorrelation with a Gaussian process, we found a negative association between local rates of population change and population abundances for 83% of species (statistically significant for 73% of species; Fig. 3A). For example, Williamson’s sapsucker (*Sphyrapicus thyroideus*) is considered

¹Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY, USA. ²Centre for Research into Ecological and Environmental Modelling, School of Mathematics and Statistics, University of St Andrews, St Andrews, UK. ³Department of Natural Resources and the Environment, Cornell University, Ithaca, NY, USA. ⁴American Bird Conservancy, The Plains, VA, USA.

*Corresponding author. Email: alison.johnston@st-andrews.ac.uk

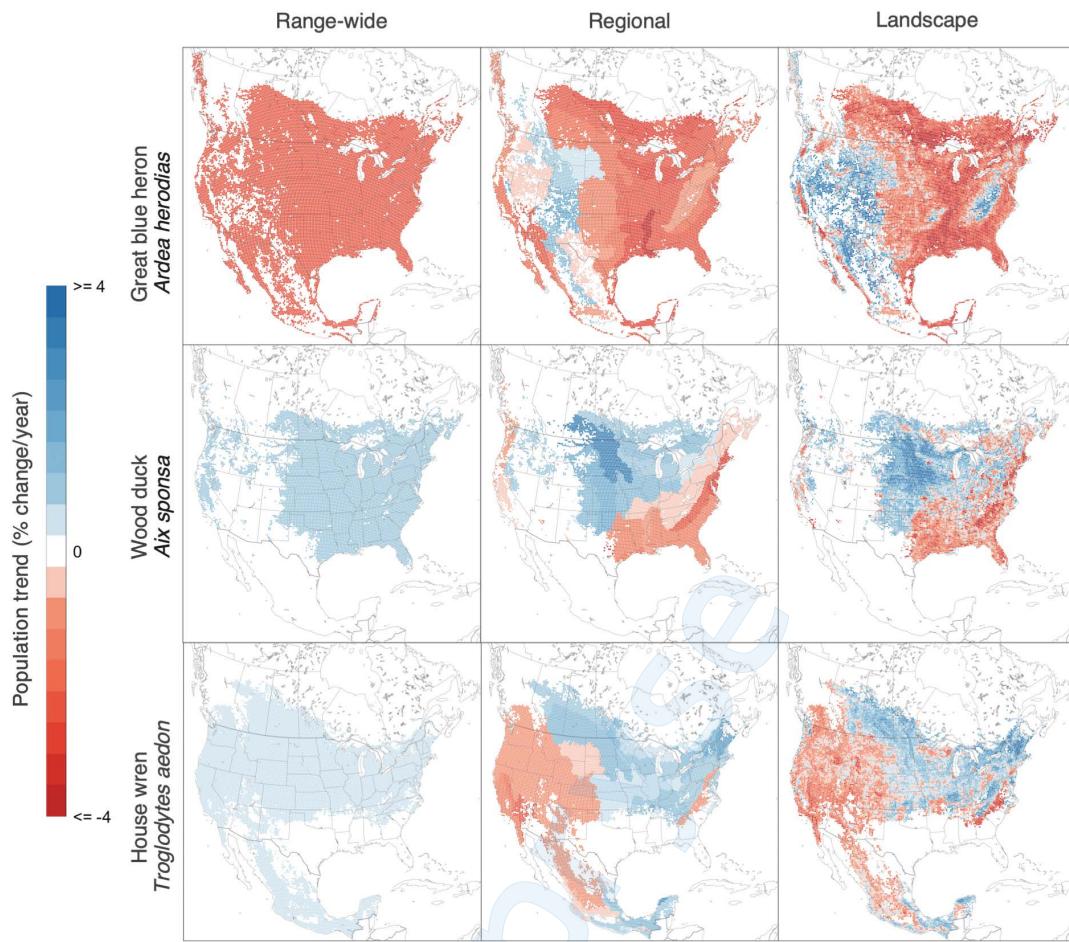


Fig. 1. High trend resolution reveals complexity of population changes from 2007 to 2021. Columns represent range-wide, regional (Bird Conservation Region), and landscape scales ($27 \times 27 \text{ km}^2$ grid cells). Trends are shown for (rows) the great blue heron (*Ardea herodias*), wood duck (*Aix sponsa*), and house wren (*Troglodytes aedon*). Each map shows the annual percent-per-year rate of change in abundance from 2007 to 2021 as averaged across the whole species' range, within BCRs, or within landscapes. All trends in a row were estimated with the same data and models, with outputs aggregated to the different spatial scales. (<https://science.ebird.org/en/status-and-trends/trends-maps>)

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imperiled or vulnerable in more than half of the states and provinces where it breeds (4) and shows declines in remaining strongholds, raising particular concern for its conservation status (Fig. 3A). Positive correlations were evident for 17% of species (significantly positive for 7% of species), such as the yellow-billed cuckoo (*Coccyzus americanus*), whose abundance is increasing in areas where conditions already support high numbers (Fig. 3A). Our study thus builds upon previous alerts of steep declines among the most abundant birds in North America (4) and demonstrates that most species are experiencing declines in regions where each species is itself most abundant.

The negative association between local abundance and local population trend was consistent across communities of species breeding in similar habitats. Classifying species into breeding biome communities and calculating average effects over all species within those biomes, we found that every biome was characterized by negative relationships between relative abundance and trends. The strongest negative associations between local relative abundance and local population trends were evident for species breeding in aridlands and grasslands, which had the highest proportions of species with negative associations (87 and 96%, respectively) (Fig. 3B). In only three cases were species' populations within biomes actually increasing at their lowest abundances (positive intercepts on Fig. 3B): aridland, forest, and habitat generalist species. These positive trends suggest that these communities may be able to respond to environmental fluxes with population increases

where the species are currently at low abundance or even with colonizations of new locations (Fig. 3B). However, the outlook was less hopeful for grassland, wetland and coast, and Arctic tundra species, which had biome averages with no evidence of population growth in areas of low abundance and stronger declines at higher abundances (Fig. 3B). Taken as a whole, the current weight of evidence points toward a worsening situation for North American birds.

To infer the potential mechanisms of the relationship between abundance and trend in relation to core-periphery population dynamics (23), we also explored whether distance to range edge was similarly correlated with local population trend. Consistent with ecological theory (24, 25), most North American birds occur at lower abundance near range edges (26) and/or at higher abundance near the centroids of their ranges (27). We compared linear mixed models to determine whether variation in species trends was more closely associated with abundance or distance to range edge, the two of which were weakly correlated (median correlation coefficient across species $r = 0.54$). Results showed that both intra- and interspecific variation in trends across space were much better explained by species abundance than by distance to range edge, underscoring the ecological rather than geographical nature of this association (17, 23).

These findings emphasize the need to understand and address the causes of recent declines in species' strongholds. Multiple explanations may account for these negative relationships, and we present several

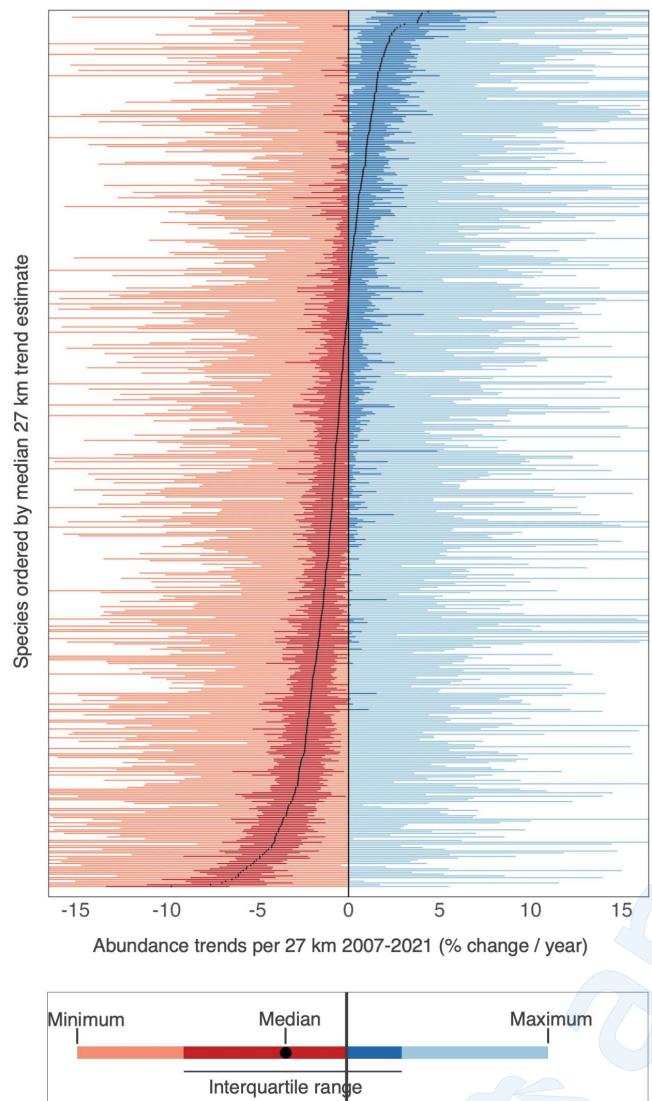


Fig. 2. Most of the 495 species show areas of both increase and decline across their ranges. Each horizontal bar represents a single species, located sequentially in order of their median 27-km resolution trend. The horizontal extent of each bar shows the maximum and minimum of species' 27-km resolution trends across their range. The darker central section of each bar indicates the interquartile range of each species' trends across its range. The median is shown with a black dot. Sixty-seven percent of species have a median trend less than 0 (black dot to the left of the vertical line).

possible interpretations that are not mutually exclusive; indeed, the relevant explanations likely vary across species. First, high-quality sites that could support abundant populations may be more affected by stressors, such as climate change, land conversion, and pollution, than lower-quality sites, where birds are less abundant and may have been previously exposed to any given stressor. Nonequilibrium populations in areas of low abundance also may be less subject to density-dependent mortality and/or reduced breeding success than areas where populations are near carrying capacity (28). Secondly, if areas predicted to have higher abundances are characterized by more suitable and/or stable habitats, then birds in those areas may be selected for slower pace-of-life syndrome ("k" selected) owing to differential environmental selection processes (29–31). This could make these populations less demographically suited to recovery after perturbations. Thirdly, individuals in areas

of low abundance (i.e., range edges or nonideal environments) may be adapted to and/or more resilient to marginal, fluctuating, extreme, or unpredictable conditions, as has been shown for other taxonomic groups (31–33). Individuals adapted to these conditions at distribution edges may be important for population persistence in a changing environment (32). However, species and communities are still decreasing in total population size, suggesting that environmental changes (e.g., climate or land conversion) are outpacing the ability of most species to adapt, leading to potentially irreversible declines in their core ranges (34–36).

Trends among breeding biome communities

The high resolution of the trend estimates allows us to compare range-wide population changes with the proportion of the range experiencing declines. For species with the same population trend, there was high variation in the proportion of the range that was declining (fig. S2). Although 75% of species were declining overall, species declined, on average, across only 60% of their ranges. The proportions of ranges declining were largest for species that breed in Arctic tundra (on average, populations of Arctic-breeding species were declining across 74% of their nonbreeding ranges) and grasslands (70%) but smallest for aridland birds (47%). Declines tended to be worse for species whose trends were estimated during nonbreeding seasons (typically those species that breed further north) (fig. S3). These patterns of decline suggest that biome-level impacts, such as climate change in the Arctic (37), are impacting critical breeding habitats for species. These patterns also point toward opportunities for conservation, as almost all declining species have areas where the population is locally increasing (Fig. 2), demonstrating they have potential for increases in some environmental conditions.

Within species' breeding biomes, we discovered patterns of spatial convergence in species' trends that can be used to identify common areas of community declines and increases (Fig. 4). Grassland species were declining strongly within the core of their ranges, though with small pockets of increase in the Upper Midwest and Arid West of the US (Figs. 3B and 4). This is consistent with the broad-scale changes to agricultural practices throughout the distributions of grassland birds (38). Most communities tended to have both mean declines and the majority of species declining in the Southeast US, the Mississippi Alluvial Valley, parts of the Upper Midwest, the California Central Valley, and the Pacific Northwest (Fig. 4). By contrast, we found many shared patterns of community increases in the Appalachian and western mountains (Fig. 4), particularly at higher elevations in the southern Appalachians, where many species reach their southern range limits (39). Birds associated with aridlands stood out as faring better in Mexico than in the US or Canada. These shared patterns of population change enable us to identify areas of threat and refuge for these communities (40). However, some caution in interpretation is required, as these patterns also reflect changes in community composition across space.

Conservation implications

The fine-scale heterogeneity of population change that we describe in this work highlights the geographic variability in conservation urgency. These trends were estimated over a 14-year period, which provides information about recent population changes while being long enough to reliably reflect population change rather than short-term demographic stochasticity (41). Therefore, this time period has high value for guiding strategically directed conservation action for current drivers of population change (9, 42). The availability of high-resolution trends makes it possible to inform and direct management interventions to specific landscapes where action is most needed and resources are best invested, whether for individual species or groups of species (20, 43, 44). As such, we expect that these trends will be useful to international or multisector partnerships, such as the North American Bird Conservation Initiative, government agencies, not-for-profit

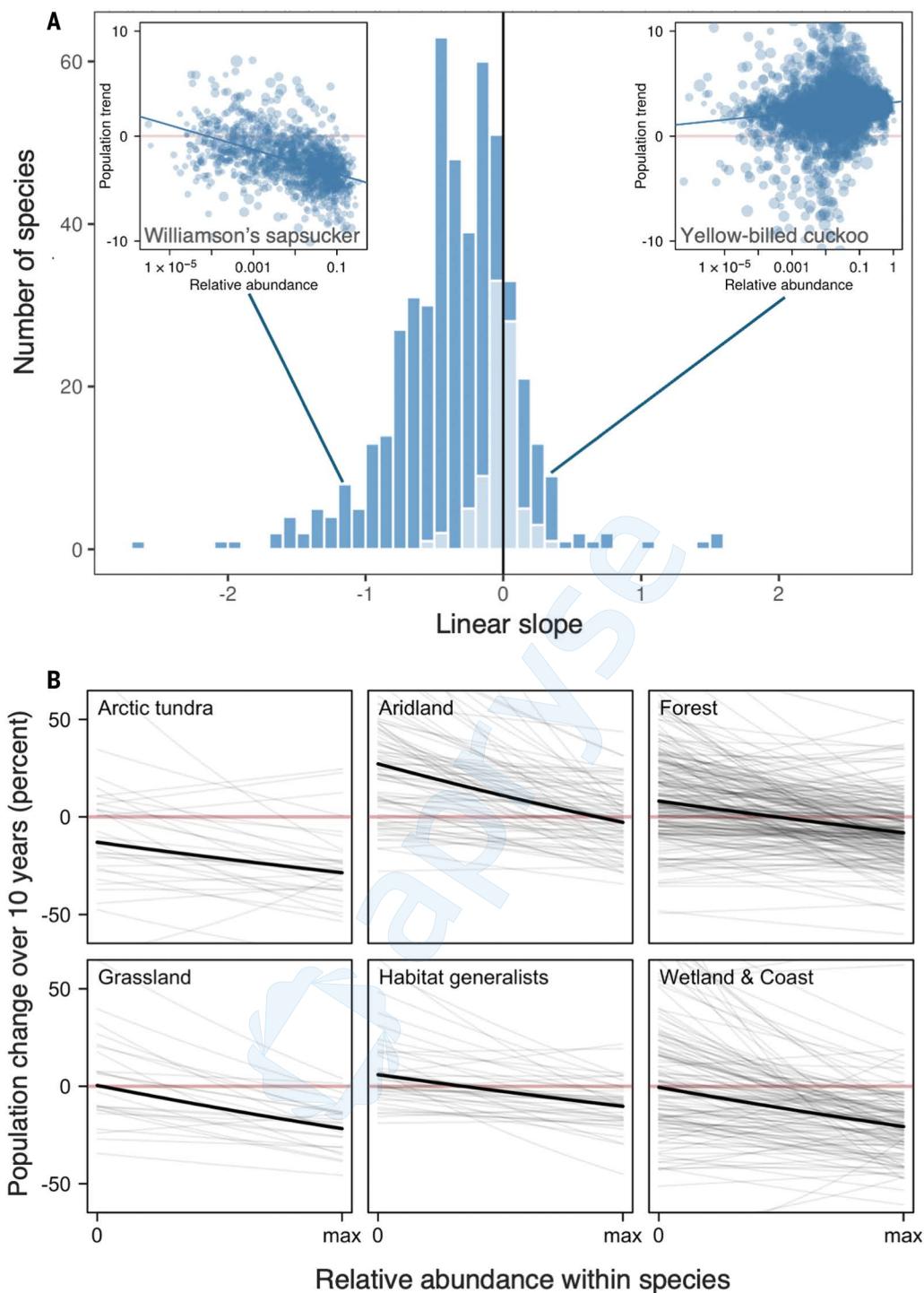


Fig. 3. Most species have a negative correlation between abundance and trend, indicating population declines in areas with highest abundance. (A) The histogram shows species-specific slopes of the fitted relationships between relative abundance and trend at 27-km resolution. Example species with negative (*Williamson's sapsucker*, *Sphyrapicus thyroideus*) and positive (*yellow-billed cuckoo*, *Coccyzus americanus*) relationships are shown in the insets. The vertical black line indicates a slope of zero or no association between abundance and trend. Eighty-three percent of species have negative slopes (to the left of the zero line), and 73% of species have significantly negative slopes (dark blue to the left of the zero line). (B) Most species (thin gray lines) and all community averages of all species breeding in each biome (thick black lines) have negative correlations between population change and abundance at a 27-km resolution. The pale horizontal pink lines indicate zero population change. The models were fit with percent-per-year changes related to \log_{10} abundance, and here we show these trends aggregated to expected population change over a 10-year period. This leads to some nonlinear relationships due to “compound interest” of population changes. Biome effect sizes were calculated as the average of species differences in expected trend (percent per year) between minimum and maximum \log_{10} relative abundance and population trend. These were also aggregated up to estimate 10-year population change, and the average differences in percent population change from minimum to maximum abundance over 10 years within the species in each biome were (in increasing order): Aridlands, -30%; Grassland, -22%; Wetlands and Coast, -20%; Forest, -16%; Habitat Generalist, -16%; and Arctic Tundra, -16%.

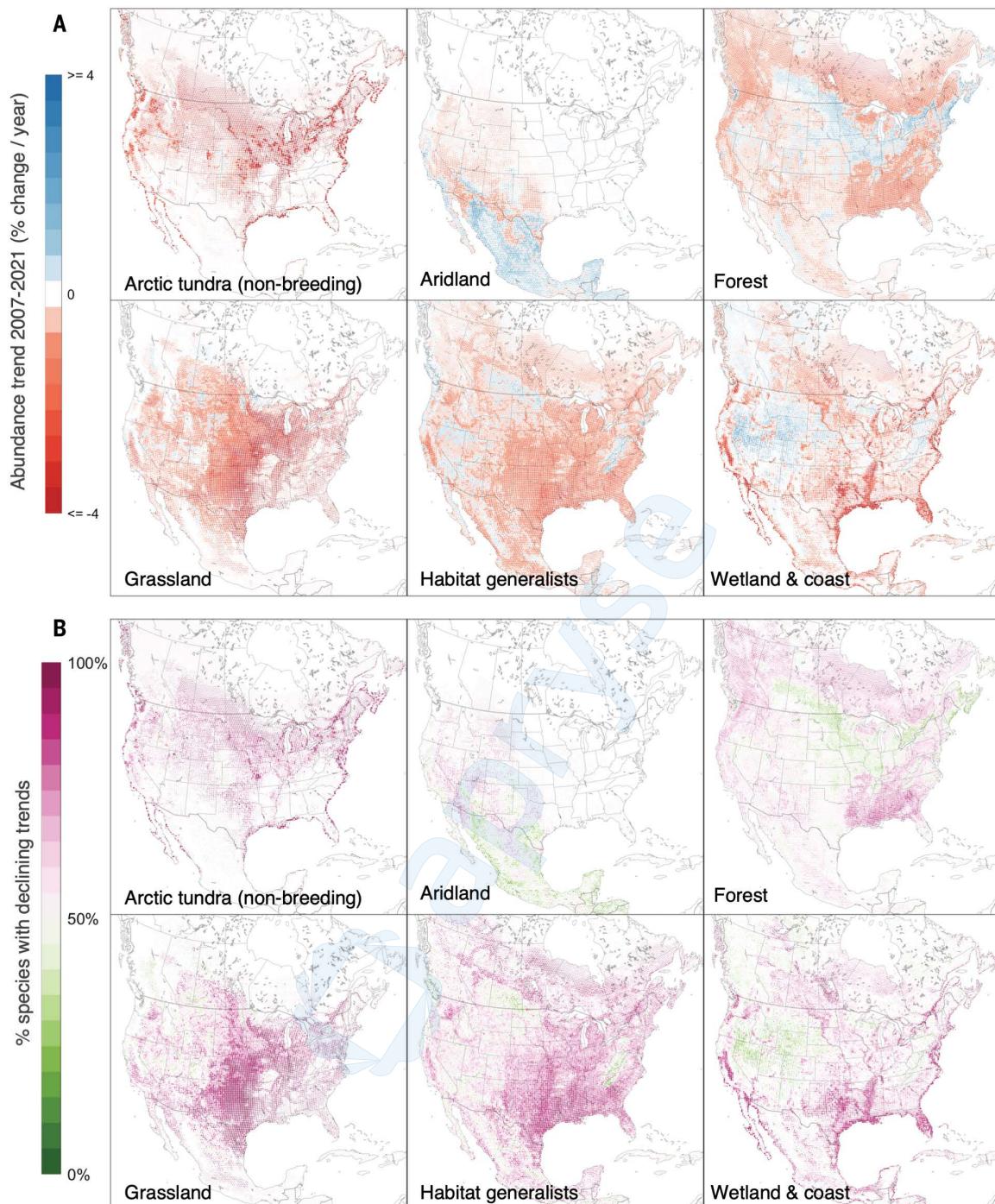


Fig. 4. Landscape-scale patterns of population change were shared among breeding biome communities. (A) Red-blue maps show the mean trend (i.e., annual percent-per-year rate of change in abundance) from 2007 to 2021 (red, decline; blue, increase; darker colors indicate stronger trends) within each $27 \times 27 \text{ km}^2$ grid cell averaged across all species in each of six North American breeding biome communities. (B) Pink-green maps show the percentage of species within each breeding biome community with declining trends (pink, the majority of species declining; green, the majority of species increasing; darker colors indicate larger majorities). Note that all Arctic tundra species have trends estimated in their nonbreeding season. Despite the heterogeneity among trend maps for individual species, the red-blue and pink-green patterns within community-level trends indicate shared patterns of population change among species within breeding biome communities.

organizations, and the private sector, all of which have limited fiscal and human resources to address a multitude of environmental challenges, including the recovery of North American birds.

This study demonstrates how participatory science data and other broad-scale, observational datasets can be leveraged with promising analytical tools to detect, diagnose, and respond to population changes

at ecologically relevant scales. We present high-resolution spatially explicit population trends across a broad geographic extent for most of an entire taxonomic group. The continued expansion of participatory science projects provides opportunities to replicate our approach to trend estimation on other continents and other taxonomic groups. The ability to estimate population trends for hundreds of species at

landscape scales and across an entire continent can advance the ability of scientists, managers, and decision-makers seeking to understand and reverse population declines (44). High-resolution trends, in conjunction with other environmental datasets, can also be used to study the associations with other spatially dependent processes (e.g., management actions, resource availability or change) and provide new insights to better understand the drivers of population change.

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SUPPLEMENTARY MATERIALS

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