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Current Biology

Avian traits link divergent population responses to environmental change across North America

Highlights

- Local populations of all species are increasing, decreasing, or stable over time
- Within-species trends track changes in local climate, land cover, and pollution
- Species differ widely in sensitivity to different forms of environmental change
- Thermal, visual, aerial, vocal, and life-history traits explain species sensitivities

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In brief

Jennings et al. show that local bird population trends across North America are shaped by multiple forms of environmental change, including light pollution, air quality, climate, and urbanization. Species' responses depended on traits, revealing why some birds are more vulnerable than others and highlighting conservation actions that can be implemented.

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Avian traits link divergent population responses to environmental change across North America

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SUMMARY

Birds are in decline globally. However, at finer spatial scales, species often exhibit notable geographic variation in how their populations are changing. Understanding why population trends vary within and across species remains a gap that impedes conservation. Here, we leverage over ½ million bird captures from 356 North American banding stations to derive temporal trends in local abundance and productivity for 46 species and examine whether 11 dimensions of environmental change explain geographic variation in species' population trends. We found that all species had local populations that were increasing, decreasing, or stable. Critically, we show that geographic variation in abundance and productivity trends is linked to changes in the local environment. While individual species vary markedly in their responses to different forms of environmental change, trait-based explanations reveal why this variation exists. Specifically, visual capabilities, aerial lifestyle, thermal niche, vocal characteristics, and life-history traits explain demographic responses to changes in light pollution, air pollution, temperature, human population, and land cover, respectively. These results support recent links between ecological traits and responses to global change, and by elucidating these relationships, we provide key information to forecast how understudied species will respond to environmental change. Furthermore, by identifying the most relevant forms of environmental change to individual species and where their populations are impacted, our results can inform policy. Importantly, multiple forms of environmental change in this study can be mitigated within local municipalities with existing solutions, indicating that high-impact conservation actions that have positive consequences for birds are within reach.

INTRODUCTION

Human-caused biodiversity declines continue to be a critical global environmental challenge.[1–3] Recently, Rosenberg et al.[4] reported a loss of nearly 3 billion birds across almost every North American biome. Five years on, the majority of North American birds continue to decline.[5] Although documentation of these staggering losses has spurred a heightened concern for birds and biodiversity,[6–8] the analytical focus on biome-level trends employed by many studies is both too coarse to inform conservation efforts at the smaller spatial scales where wildlife management typically occurs and too general to inform species-specific mitigation strategies. Recent efforts have attempted to address these issues by mapping abundance trends at finer spatial scales, revealing marked spatial heterogeneity within species.[9] While this represents an important advance, critical knowledge gaps persist. Namely, we have a limited understanding of how changes in demographic parameters, such as reproductive output and recruitment, underlie widespread declines in abundance. Furthermore, the types of environmental change that drive population change often remain unidentified, even though this information is crucial to mitigate biodiversity loss. Given the exceptional morphological and functional diversity of birds,[10,11] species are likely to exhibit striking differences in their responses to various forms of environmental change, and approaches that scaffold species-specific analyses with comparative methods can reveal why this variation exists. Moreover, because there is significant spatial variation in the type and intensity of different human activities, we need measurements of environmental change and the resulting demographic responses by birds at finer organizational scales.

Here, we addressed these needs by linking spatial variation in local population trends for 46 species with spatial variation in 11 dimensions of local-scale environmental change (STAR Methods; Table S1). To do so, we leveraged 596,325 bird captures from 356 Monitoring Avian Population and Survivorship (MAPS) stations with time series as long as 27 years (Figure 1A). Specifically, we quantified how breeding season adult abundance and productivity have changed over time at all stations occupied by each species (STAR Methods). While abundance provides a general measure of overall population status, productivity reflects the outcome of reproductive attempts and is a specific measure of local demographic performance (i.e., a vital rate) that captures one potential driver of population change. Thus, the joint evaluation of abundance and productivity allowed us to provide stronger inferences about

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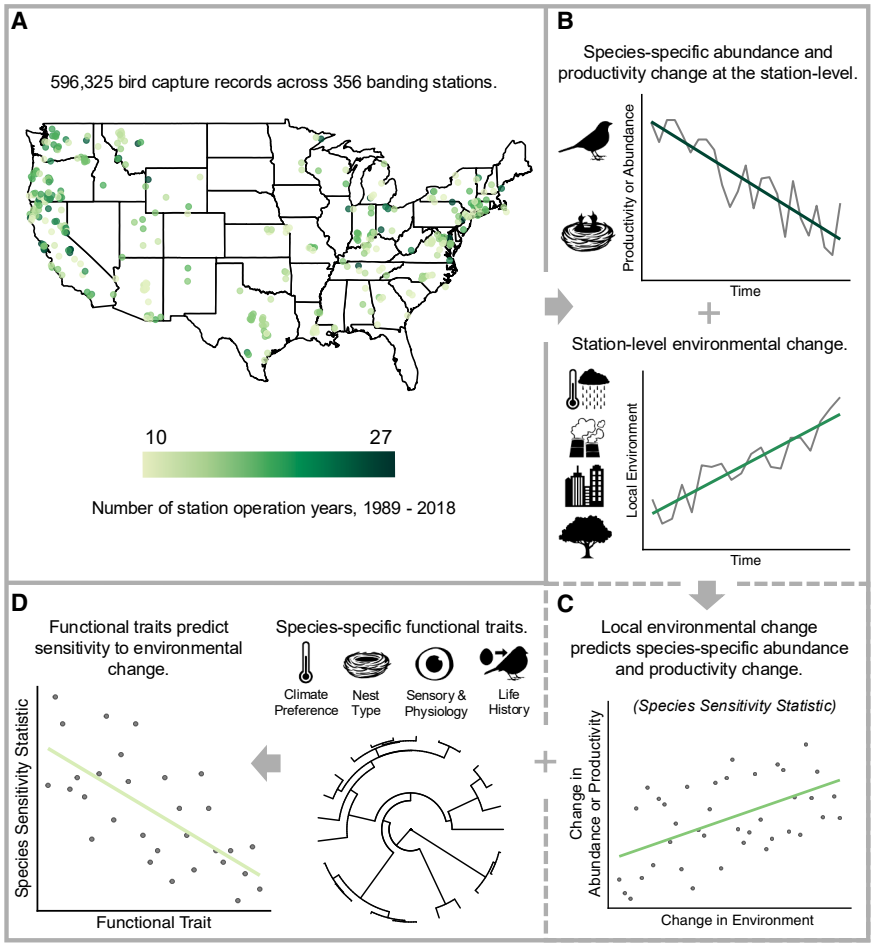

Figure 1. Study design and methodology

(A) We retained MAPS banding stations within the contiguous United States that operated for a minimum of 10 years (light green points), with no breaks in operation longer than 5 years. Stations had an average operation length of 15 years, with a maximum of 27 years (dark green points).

(B) Generalized Poisson distributions were fitted using breeding season adult capture counts across years to quantify species-specific abundance change at occupied stations, and species-specific productivity across time was quantified using linear (Gaussian) models. We used linear models to measure local temporal changes in 11 climate, pollution, urbanization, and habitat variables at a 1 km^2 resolution for each station.

(C) Species change statistics and environmental change statistics were used in spatially explicit linear models to determine species-level sensitivities to environmental change.

(D) Phylogenetically informed generalized linear models (PGLSs) were fitted using species sensitivity statistics and species-specific trait data to predict how traits influence species' responses to environmental and anthropogenic change. We examined 11 traits across four broad categories: climate preference, nest type, sensory and physiological traits, and life history.

See also Table S1.

the mechanisms underlying population trends. We also quantified temporal environmental changes at each station (e.g., air quality, light pollution, temperature, precipitation, and landcover; Figure 1B). To do so, we estimated the temporal change in abundance, productivity, and environmental conditions using t-statistics. The advantage of the t-statistic as a measure of change over time is that it quantifies trend magnitude relative to estimation uncertainty, allowing us to distinguish strong, reproducible directional change in population metrics or environmental conditions from imprecise estimates. We then used the measures of temporal change in abundance and productivity as response variables and measures of environmental change as predictor variables in a series of spatially explicit models to determine for each species which, if any, types of local environmental change explain variation in local productivity and abundance trends across their range (Figure 1C). These models provided species-specific sensitivity statistics that capture how responsive a species is to each form of environmental change (e.g., sensitivity to changes in precipitation; Figure 1C). Importantly, by estimating the effect of each form of environmental change within the same model, while also carefully checking models for multicollinearity, we were able to parse the relative influence of each form of environmental change. Finally, to understand why species vary in the magnitude and direction of their responses to the various types of environmental change, we implemented phylogenetically informed models that link species traits to variation in species-specific environmental sensitivities, which were represented by the t-statistics from the previous step that integrate both the magnitude and precision of the estimated influence of each environmental variable on abundance or productivity (Figure 1D; STAR Methods; Table 1). Collectively, this framework couples high-resolution temporal trends for bird populations and their environments at local scales to identify which aspects of environmental change explain spatial variation in population trends and illustrates that functional traits can explain variation among species in their responses to environmental change.

RESULTS AND DISCUSSION

Species respond to different forms of environmental change

At odds with Rosenberg et al.'s report[4] of a loss of 3 billion birds in North America, but confirming the heterogeneity in population trends recently highlighted by Johnston et al.,[9] we found that all species had abundance and productivity trends that were increasing, decreasing, or stable at the local level (Figure 2A; Data S1; Table S2). For the 27 species in our analysis with both measures of population change, we found only two species where changes in abundance and productivity were positively correlated and one with a negative correlation (Table S2). In all three cases, the correlations were quite weak ($\leq|0.3|$; Table S2). The predominance of no or weak correlations

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Table 1. Complete list of hypothesized relationships between functional traits and species environmental sensitivities that were tested in this study

Trait group/functional trait	Trait description	Sensitivity statistic	Prediction	Explanation
Climate preferences				
Species temperature index[12]	average temperature within each species' summer (breeding) range (°C)	maximum temperature minimum temperature	positive positive	species with warmer thermal niches will have stronger positive population trends in response to increasing maximum and minimum temperatures compared with species that have cooler thermal preferences
Annual precipitation[13]	average rainfall within each species' range (mm)	precipitation	positive	species that prefer wetter areas will exhibit positive population trends in response to increasing rainfall compared with those that inhabit drier areas
Nest				
Location[14,15]	species classified as using either on-ground or above-ground nests	impervious surface human footprint human population density	ground < above ground	species that use ground nests will exhibit stronger negative population trends in response to increasing levels of urbanization than those that nest above the ground due to the lack of suitable substrates for ground nests in urban areas and the elevated risk of disturbance and predation
Structure[14,15]	species classified as using either open or enclosed nests	impervious surface human footprint human population density	open < closed	species that use open nests may be more vulnerable to anthropogenic stressors and novel predators and will exhibit stronger negative population trends with increasing urbanization than species that use enclosed nests
Sensory and physiology				
Peak vocal frequency[16]	vocal frequency of the maximum amplitude within each species' song (kHz)	impervious surface human footprint human population density	positive	Species with low-frequency vocalizations will exhibit stronger negative population trends in response to increasing urbanization than species with higher-frequency vocalizations as they will experience greater masking of vocal communication in the presence of anthropogenic noise. We used change in urbanization as a proxy for change in noise levels.
Dim-light vision[17–20]; this study	ratio of the corneal diameter (mm) to the transverse diameter of the eye (mm)	nighttime light	positive	species that see better under low-light conditions may benefit from increases in light pollution by extending their temporal niche and will exhibit stronger positive population trends compared with species that have reduced dim-light vision

(*Continued on next page*)

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Table 1. ***Continued***

Trait group/functional trait	Trait description	Sensitivity statistic	Prediction	Explanation
Aerobic power[21]	ratio of log-transformed heart mass (g) to log-transformed body mass (g)	ozone nitrogen dioxide fine particulate matter	negative	species with larger heart mass to body mass ratios (greater aerobic power) will be more sensitive to increasing air pollution and will exhibit more negative population trends relative to species with lower aerobic power
Aerial lifestyle[11]	represented by the hand-wing index (HWI), which is an index of wing pointedness	ozone nitrogen dioxide fine particulate matter	negative	species with higher HWI values, which reflects a more active and aerobically challenging lifestyle,[13,22] will be more sensitive to increasing air pollution and will exhibit more negative population trends relative to species with lower HWI values
Life history				
Longevity[23]	maximum lifespan in years for each species	impervious surface human footprint human population density	positive	species with greater longevity will be more likely to show increasing population trends in response to increases in urbanization compared with those that have shorter lifespans
Brood value[23,24]	the relative value of each reproductive event, such that species with fewer lifetime breeding attempts have higher brood values	impervious surface human footprint human population density	negative	species with lower brood values will exhibit stronger positive population trends in response to increasing urbanization compared with species with higher brood values because they spread the risk over more attempts and may be better able to adapt to the novel pressures associated with urban areas
Clutch size[24]	number of eggs laid in a clutch by each species	impervious surface human footprint human population density	positive	species with larger clutch sizes will be associated with more positive population trends in response to increasing urbanization compared with species that have lower clutch sizes because their faster pace of life may facilitate rapid adaptation to the novel conditions created by urbanization

Sources for trait data denoted by superscript numbers. See also Table S4 for full results.

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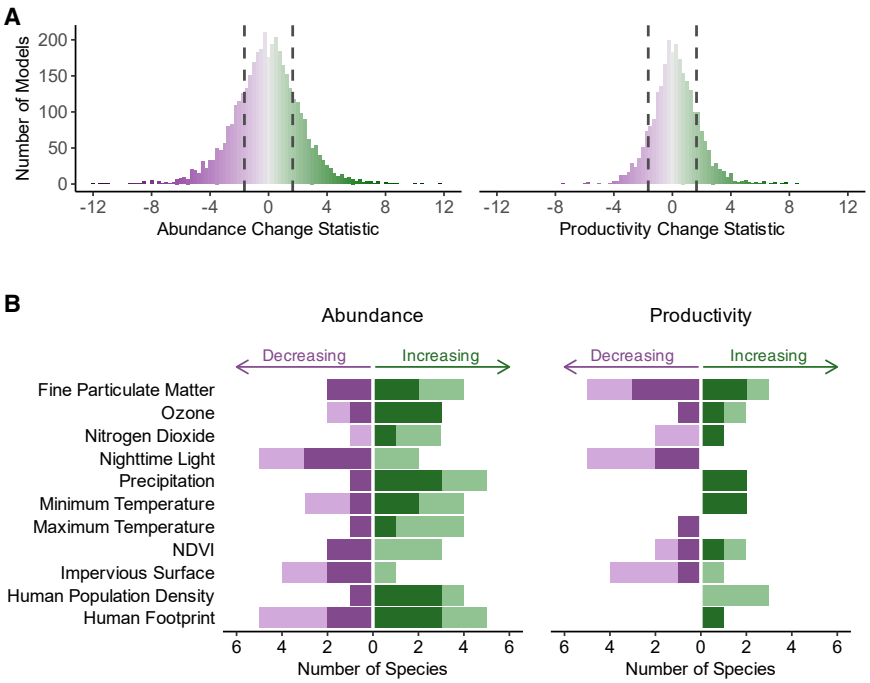

Figure 2. Strength of population change over time and links to forms of environmental change

(A) Pooled local temporal trends in abundance (left) and productivity (right) across all stations and species reveal a relatively balanced distribution of populations with declines or increases in abundance or productivity. Dashed lines reflect t-statistics of −1.65 or 1.65, which indicate a relationship where the 90% CIs do not overlap zero.

(B) Species-level spatially explicit models linked local variation in abundance and productivity trends to 11 forms of environmental change. Dark and light colors reflect 95% and 90% CIs that do not overlap zero.

See also Data S1, S2, and S3 and Tables S2 and S3.

between local trends in abundance and productivity across species underscores that these population demographic metrics are not tightly coupled for our study and instead reflect distinct aspects of population change. Furthermore, while many species had local populations that varied in their degree of spatial separation from a few kilometers up to thousands of kilometers, evidence of spatial autocorrelation within the abundance or productivity trends for each species was rare and weak when present (Mantel r < |0.15| for all species; Table S3). This implies that the population trends measured at each station are likely the product of local environmental variation rather than regional trends in population trajectories.

No single form of environmental change was the dominant driver of changes in local abundance and productivity across species. Unsurprisingly, given variation in niches and traits, we detected substantial variation among species' responses to the different forms of environmental change, with 35/46 species exhibiting pronounced environmental sensitivities (90% confidence interval [CI] does not overlap zero; Figure 2B). Despite considerable variation among species' responses to different forms of environmental change, changes in artificial night lighting, air pollution, urbanization, and climate were linked to strong responses among multiple species (Figure 2B). Below, we provide an overview and examples of responses to each of these forms of environmental change, then describe how trait and life-history variation are linked to species-specific variation in their sensitivities to different forms of environmental change.

Responses to brighter nights

Strong increases in artificial light at night occurred at ~50% of stations (Data S2), corroborating reports of brightening night skies across North America.[25] Local abundance or productivity trajectories were strongly linked to changes in night lighting for ¼ of species (n = 12). For nearly all, local productivity or abundance declined in areas where night lighting increased the most (n = 10). This pattern included species where the intensity of night lighting at individual stations has both decreased and increased over time (Chipping Sparrow [*Spizella passerina*] abundance, β = −1.247, 95% CI = −2.011, −0.483; Wilson's Warbler [*Cardellina pusilla*] abundance, β = −0.528, CI = −0.920, −0.136; Figure 3A; Data S3). It also encompassed species where night lighting has increased at most stations within their breeding range, such as the Yellow-breasted Chat (*Icteria virens*; productivity, β = −0.611, CI = −1.131, −0.090) and the Carolina Wren (*Thryothorus ludovicianus*; abundance, β = −0.635, CI = −1.238, −0.032; Figure 3A; Data S3). Interestingly, evidence suggests that Carolina Wrens increase their clutch sizes when exposed to more night lighting,[26] perhaps supporting the notion that artificial lighting can increase usable daylength and allow breeding birds to support larger broods (i.e., daylength hypotheses).[27] Yet our data-rich trends suggest that any potential benefits of night lighting are potentially outweighed by costs that ultimately influence population densities.

While many species exhibited declining populations in response to increases in night lighting, this pattern was not universal (Figure 2B). We found that how well species can see in low light explained their sensitivities to night lighting such that species with better dim light vision tend to decline in abundance with increasing light pollution, while the abundances of species with poorer vision in low light were unresponsive to night lighting changes (β = −6.972, CI = −13.792, −0.152, λ = 0.000; Figure 4A). This finding corroborates recent research that has identified variation in avian eye dimensions as a functional trait that is associated with multiple niche axes[28,29] and explains changes in breeding phenology and success in response to light pollution.[26] In light-polluted areas, readily available and effective mitigation strategies[30,31] may be critical to population persistence, and our findings suggest that reducing unnecessary illumination may be particularly beneficial for species with sensitive dim-light vision.

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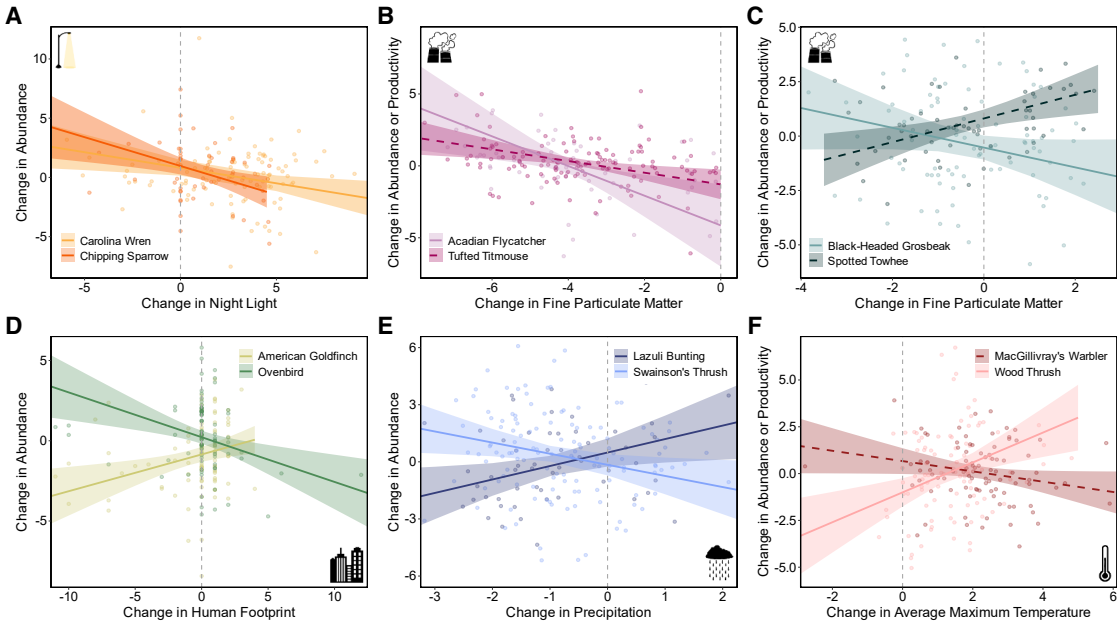

Figure 3. Species sensitivity to environmental change

(A) Local changes in light pollution negatively covaried with the magnitude of change in population abundance such that local areas that have become darker have experienced increases in population abundance and those that have become brighter have experienced declines in abundance. A similar negative covariance predominated for productivity (Figure 2B).

(B) Air pollution, measured as fine particulate matter, has improved over time at nearly all MAPS stations for birds with breeding ranges in eastern North America (Data S2), and both population abundance and productivity have improved with greater declines in air pollution.

(C) However, for species with ranges in western North America, where temporal trends in air quality are much more heterogeneous (Data S2), changes in abundance and productivity have been mixed.

(D–F) Species were mixed in their relationships to changes in the human footprint index, precipitation, and average maximum temperature, but variation in (D) and (F) was linked to functional traits (Figures 5 and S1; Table S4).

In (B)–(D) and (F), solid lines reflect abundance trends and dashed lines reflect productivity trends. In all panels, data points represent t-statistics for environmental and population trends at individual stations, and lines and shading reflect marginal effects and 95% CIs.

See also Data S2 and S3.

Responses to air quality

Air quality, measured as changes in ozone, fine particulate matter (PM2.5), and nitrogen dioxide, improved at most stations, likely due to the Clean Air Act, which has regulated airborne emissions in the United States since the 1960s.[32] Changes in air pollutants were strongly linked to population changes for 21 species. Similar to the relationships detected with changes in light pollution, responses to air pollutants were variable. One clear pattern is that air quality has improved across eastern North America (Data S2), and a number of species with ranges restricted to this area have population trajectories that are improving most where air pollution has declined most strongly. For instance, the abundance of Acadian Flycatchers (*Empidonax virescens*) increased where PM2.5 has decreased sharply

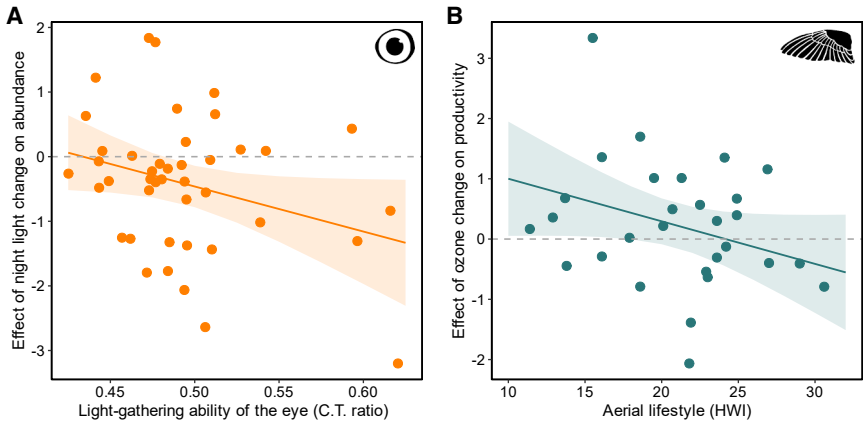

Figure 4. Light sensitivity and aerial lifestyle explain sensitivities to light and air pollution

(A) Species with better dim light vision (i.e., light-gathering ability of the eye) tend to decline in abundance with increases in night lighting.

(B) Aerial lifestyle negatively covaried with sensitivity to ozone such that species that tend to be less frequent fliers tended to experience minor increases in productivity with increases in ozone, but those that are frequent fliers experienced minor decreases in productivity with increases in ozone. In all panels, *y* axis units are t-statistics, data points represent individual species, and solid lines and shading reflect model-estimated marginal effects and 95% CIs.

See also Figure S1 and Tables S4 and S6.

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(abundance, $\beta = -2.013$, CI = −3.389, −0.637; Figure 3B; Data S3). Similarly, the productivity of Tufted Titmice (*Baeolophus bicolor*) has increased where PM2.5 has declined most strongly (productivity, $\beta = -0.702$, CI = −1.162, −0.242; Figure 3B; Data S3).

Smoke from frequent and intense wildfires is driving increased particulate matter across the West,[33] and increases in PM2.5 were common at western MAPS stations (Data S2). We observed mixed population responses to changes in particulate matter for species with western distributions. For instance, Black-headed Grosbeaks (*Pheucticus melanocephalus*) exhibited increased abundance at the stations with the largest improvements in air quality but declined at stations where PM2.5 had gone up ($\beta = -0.776$, CI = −1.447, −0.106; Figure 3C; Data S3). By contrast, Oregon juncos (*Junco hyemalis oreganus*) and spotted towhees (*Pipilo maculatus*) increased their productivity in the areas where air quality has declined the most (Oregon junco, $\beta = 0.327$, CI = 0.024, 0.630; spotted towhee, $\beta = 0.786$, CI = 0.265, 1.308; Figure 3C; Data S3). While this pattern initially seems puzzling, many of the stations with increasing PM2.5 are in habitats that may offer advantages for breeding birds that currently outweigh any negative impacts from air pollution. While protected areas may offer some obvious advantages that could outweigh costs associated with air pollution, other advantages may come through breeding in cities. Increases in breeding Oregon juncos within cities are well documented,[34,35] and spotted towhees are known to regularly nest in urban areas.[36]

Over half the species that were responsive to changes in air pollutants employ active foraging tactics such as sallying and gleaning. We predicted that aerobically active species would be more sensitive to air pollution and thus would exhibit stronger population changes than less aerobically active species. To test this idea, we used two proxies of aerobic activity. The first was aerial lifestyle, reflected by species-specific values for the hand-wing index.[11,13,22] The second was species-specific heart masses while controlling for body size because larger hearts enable greater aerobic power (i.e., they move more oxygenated blood per heartbeat) and allow species to employ more energetically demanding modes of flight.[21] We found that species that use flight more during their daily routines exhibited declines in productivity in areas with increasing levels of ozone, while the productivity of species with less active lives was stable or increasing in response to higher ozone, but the uncertainty around this estimated effect was slightly higher than for other traits ($\beta = -0.071$, CI = −0.147, 0.005, $\lambda = 0.000$; Figure 4B). That we detect decreased productivity in response to increases in air pollution but not abundance suggests that breeding adults of species with more flight-intensive foraging behaviors may struggle to adequately provision their young when exposed to elevated levels of ozone, leading to reduced reproductive success. However, we found no support for a link between variation in heart mass and species' sensitivities to any of the three types of air pollution (Table S4). This trait may be a better predictor of sensitivity to air pollution during periods of high respiratory demand, like migration. While the impacts of air pollution on birds have only recently begun to garner attention, polluted air is associated with reduced body condition,[37] disrupted movements,[38,39] and less diverse dawn soundscapes.[40] As almost one-half of the species in our analysis were sensitive to changes in air pollution, our results underscore the need for further studies to examine the effects of airborne pollutants on birds.

Responses to climate change

Climatic changes were evident across MAPS stations, with maximum and minimum temperatures increasing at the vast majority of locations, while changes in precipitation promoted wetter and drier conditions in the East and West, respectively (Data S2). Changes in climate were more often associated with changes in abundance than changes in productivity (14 versus 5 species; Figure 2B). Yet, across both types of population change, wetter and/or warmer conditions were often linked with increased productivity or abundance (Figure 2B). For instance, Wood Thrush (*Hylocichla mustelina*) local abundance increased in areas where temperatures have gone up over time and declined in areas that have become cooler (maximum temperature, $\beta = 0.891$, CI = 0.377, 1.405; Figure 3F; Data S3). Additionally, Lazuli Bunting (*Passerina amoena*) abundance increased in areas that have become wetter and declined at stations that have become drier (precipitation, $\beta = 0.822$, CI = 0.004, 1.639; Figure 3E; Data S3). Fewer species showed the opposite pattern, but one exemplar was the MacGillivray's Warbler (*Geothlypis tolmiei*). In this species, cooler temperatures were associated with increases in local productivity, and decreases in productivity were coupled with warming (maximum temperature, $\beta = -0.402$, CI = −0.781, −0.024; Figure 3F; Data S3), possibly because it is a more montane species in most of its range[41] and thus has a relatively cool thermal niche.

The heterogeneous abundance responses to changes in maximum temperature observed across species were explained by species' temperature indices. This trait reflects thermal preferences using the mean summer temperature within each species' breeding range.[12,42] Species with high temperature indices tended to increase in abundance in areas that have become consistently warmer, but the abundance of species that prefer lower temperatures tended not to change in a consistent direction with local changes in temperature ($\beta = 0.089$, CI = 0.026, 0.153, $\lambda = 0.000$; Figure 5A). That the abundances of only certain species respond consistently to local temperature trajectories supports findings that the composition of breeding bird communities is changing but not at a sufficient pace to keep up with warming.[42] Importantly, a key contribution of our study is that variable population-level responses are linked to thermal regimes associated with species' historic ranges and that the only species benefiting from warmer local conditions are those with ranges that experience higher temperatures. Recent evidence suggests that shifts in phenology to track climate preferences temporally may be more common among North American birds than geographical shifts.[43] Whether the changes in abundance documented here reflect geographical shifts northward or up in elevation reported recently[44] will require further study. Additional key unknowns are whether variation among species in phenological responses is also related to their thermal preferences and whether phenological and abundance responses to temperature trajectories are linked.

Responses to land cover change

Changes in land cover or human activity were linked to strong positive and negative changes in abundance and productivity

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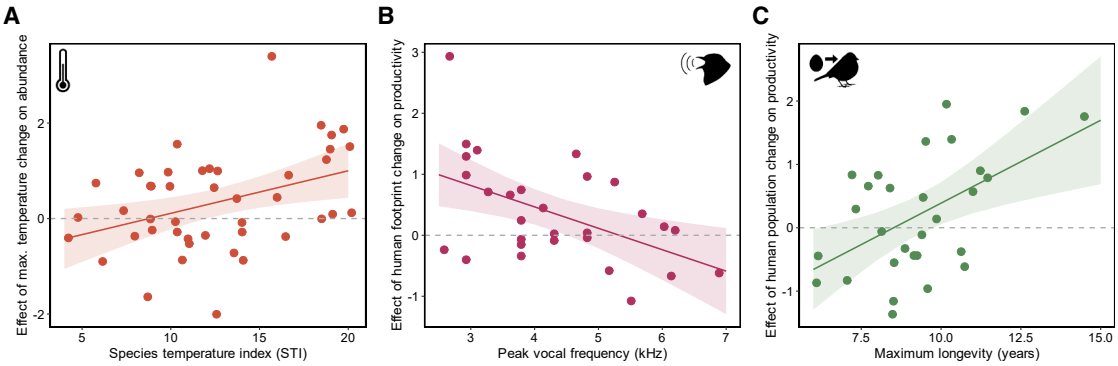

Figure 5. Thermal, vocal, and life-history traits explain sensitivities to environmental change

(A) Increases in the species temperature index were associated with an increase in local abundance with rising local maximum temperatures.

(B) Birds with low-frequency vocalizations tended to experience greater productivity with increases in the human footprint index.

(C) Longer lifespan was associated with higher productivity in response to growth in the human population. In all panels, *y* axis units are t-statistics, data points represent individual species, and solid lines and shading reflect model-estimated effects and 95% CIs.

See also Figure S1 and Table S4.

(Figure 2B). Species associated with human-modified areas, including the American Goldfinch (*Spinus tristis*) and American Robin (*Turdus migratorius*), decreased in abundance in areas where the human footprint index has declined over time but maintained stable populations where the human footprint index has increased (American Goldfinch, β = 0.686, CI = 0.210, 1.161; Figure 3D; American Robin, β = 0.424, CI = 0.096, 0.751; Data S3). Many species also exhibited the opposite pattern, showing positive responses where human impact has gone down and declines in abundance or productivity in locations that have become more urbanized (e.g., ovenbird [*Seiurus aurocapilla*] abundance, $\beta = -0.719$, CI = −1.161, −0.276; Figure 3D; Data S3).

Several traits were linked to species-specific sensitivities to changes in human impact (Table S4). We found that sensitivities to changes in the human footprint index and human population density both negatively covaried with vocal frequency. Specifically, species with lower-frequency vocalizations tended to exhibit increased productivity at stations where the human footprint index and human population have increased over time (human footprint, $\beta = -0.351$, CI = −0.580, −0.122, λ = 0.000; Figure 5B; human population, $\beta = -0.302$, CI = −0.573, −0.032, λ = 0.000; Figure S1). The explanation for the negative relationship between vocal frequency and these forms of environmental change is not clear. The patterns cannot be explained by the link between vocal frequency and body size because body size was found to be uninformative in models when included as a predictor variable alongside vocal frequency (Table S4). Additionally, assuming both increases in human population and the human footprint positively covary with human-made noise, these results contrast with considerable evidence suggesting birds with low-frequency vocalizations avoid urban areas[45] or decline in abundance in more urbanized, noisy locations.[46–48] However, an important difference is that we find a relationship between vocal frequency and changes in productivity in response to urbanization, rather than the abundance-related changes detected by past studies. In this study, changes in abundance and productivity within each species were rarely correlated (Table S2), so it is not surprising that we uncovered patterns associated with productivity that differ from those previously reported for abundance. One plausible explanation is that the link to vocal frequency may reflect variation in hearing sensitivities across frequencies, as the two are considered broadly correlated.[49,50] Yet birds also listen for non-communication tasks such as locating threats and food. It is possible that the ability to hear cues from nest predators in noisy conditions is dependent on auditory sensitivities, where those with better low-frequency hearing detect and respond to threats, and those with higher frequency hearing may have trouble hearing and responding to these sounds. Regardless, because our finding aligns with a reduced avoidance of anthropogenic noise among birds with better hearing sensitivity for lower-frequency sounds,[48] studies that consider auditory function beyond conspecific communication in the context of noise will be needed. Quantifying hearing function across more species will be necessary to determine whether hearing metrics outperform vocal features in explaining responses to noisy human activities. Finally, although we report a link between species-specific acoustic channels and responses to human impacts, we did not quantify changes in environmental acoustics directly, and variation in vocal frequencies may reflect latent traits important to explaining responses to other aspects of environmental change reflected by changes in the human footprint index and human population.

Life-history variation was also linked to sensitivities to changes in human impact. Suggestive that species on the slower end of the life-history continuum are better suited to coping with human disturbance, we found species with longer lifespans and more breeding attempts across their lifetime (lower brood values) had local populations that increased in productivity in response to human population growth (longevity, β = 0.262, CI = 0.101, 0.422, λ = 0.000; Figure 5C; brood value, $\beta = -0.983$, CI = −1.677, −0.290, λ = 0.000; Figure S1). However, populations of species with larger clutch sizes tended to experience increases in productivity in locations with larger increases in anthropogenic impervious surfaces (β = 0.454, CI = 0.034, 0.875, λ = 0.000; Figure S1), implying that species on the opposite end of the life-history continuum may also exploit certain forms of human-caused environmental change. Interestingly, a recent global study detected similar mixed results between life-history traits and birds' abilities to tolerate urbanization.[51]

Life histories are often defined by optimization across several axes.[52] Larger clutches, which are routinely associated with urban-adapted birds,[51,53] may allow populations to quickly respond to rapid urbanization, while longevity could offer another avenue by allowing more reproductive attempts.

Conservation implications

This study shows how aggregating local-scale monitoring data can explain geographically heterogeneous population trends while identifying which forms of environmental change are most important to mitigate for individual species. By operating at spatial scales relevant to practical management, our results provide clear guidance for conservation action in two key ways. First, we reveal species-specific sensitivities to multiple dimensions of environmental change, which can guide targeted interventions at the local scale to improve population outcomes. Second, our trait-based analyses illuminate why species differ in these sensitivities and enable forecasting of likely responses for data-limited species based on their traits and life histories. Together, these findings add critical nuance to reported continental-scale declines[4,5] by linking environmental conditions to demographic trajectories and confirming substantial geographic variation in population change.[9] Importantly, these insights emerge from evaluating both abundance and productivity. However, they have necessarily been drawn from analyses of the species most commonly caught at MAPS stations. These results are highly relevant given that declines in North American avifauna are driven disproportionately by reductions in common species.[54] Yet we also caution that rare species might exhibit different patterns than those represented by common species. Nevertheless, our trait-based framework provides a critical pathway for extending inference beyond data-rich taxa to anticipate responses by less common species.

Mitigating biodiversity loss due to human activities must occur across scales. Managing climate change requires global solutions, while reducing air pollution necessitates policies at the landscape to regional scales. However, 65% of species studied had sensitivities to environmental variables that can be effectively managed at the scale of municipalities, such as light pollution, anthropogenic impervious surfaces, and other features of urbanization. As we pursue solutions that must be implemented at broad spatial scales, we should not lose sight of the real improvements that can be made for bird populations and other dimensions of biodiversity with local-scale policies.

RESOURCE AVAILABILITY

Lead contact

Requests for further information should be directed to and will be fulfilled by the lead contact, Clinton Francis (cdfanci@calpoly.edu).

Materials availability

This study did not generate any new materials.

Data and code availability

- All datasets used can be downloaded from the original sources listed in the key resources table or accessed from the Zenodo repository listed in the key resources table.
- All original code has been deposited in the Zenodo repository listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

All authors conceived of the project. S.L.J. and E.M.M. led the analyses. S.L.J. and C.D.F. provided project supervision. All authors contributed to writing the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Station-level abundance, productivity and environmental trends; species-level environmental sensitivities	This paper	Zenodo: https://doi.org/10.5281/zenodo.20331205
MAPS data	Institute for Bird Populations	https://ibp-maps-data-exploration-tool.org/app/maps
Fine particulate matter (PM2.5)	Di et al.[55]	https://doi.org/10.1016/j.envint.2019.104909
Ozone	Requia et al.[56]	https://doi.org/10.1021/acs.est.0c01791
Nitrogen dioxide	Di et al.[57]	https://doi.org/10.1021/acs.est.9b03358
Normalized Difference Vegetation Index (NDVI) Composites	USGS Earth Resources Observation and Science Center	https://doi.org/10.5066/F7707ZKN
DAYMET: precipitation and minimum and maximum temperature	Thornton et al.[58]	https://doi.org/10.3334/ORNLDAAC/2131
Human footprint	Venter et al.[59]	https://doi.org/10.1038/sdata.2016.67
Human population density	Center for International Earth Science Information Network	https://doi.org/10.7927/H4F47M65
Nighttime light	Li et al.[60]	https://doi.org/10.1038/s41597-020-0510-y
Urban impervious surface	Dewitz and USGS[61]	https://doi.org/10.5066/P9KZCM54
Species temperature index	Lehikoinen et al.[12]	https://doi.org/10.1111/1365-2656.13433
Average annual precipitation within each species' range	Sheard et al.[13]	https://doi.org/10.1038/s41467-020-16313-6
Nesting location and structure	Sheard et al.[14]; Chia et al.[15]	https://doi.org/10.1098/rstb.2022.0147; https://doi.org/10.1038/s41597-023-02837-1
Peak vocal frequency	Mikula et al.[16]	https://doi.org/10.1111/ele.13662
Dim light vision	Ausprey and Ritland[20]; Moore et al.[18,19]; Wilson et al.[17]; This study	https://doi.org/10.5061/dryad.3xsj3txq7; https://doi.org/10.1007/s00359-012-0790-6; https://doi.org/10.1242/jeb.108613; https://doi.org/10.1111/gcb.15663; Zenodo: https://doi.org/10.5281/zenodo.20331205
Aerobic power	Nespolo et al.[21]	https://doi.org/10.1242/jeb.162693
Hand-wing index	Tobias et al.[11]	https://doi.org/10.1111/ele.13898
Maximum lifespan (longevity)	Bird et al.[23]	https://doi.org/10.1111/cobi.13486
Brood value	Bird et al.[23]; Myhrvold et al.[24]	https://doi.org/10.1111/cobi.13486; https://doi.org/10.1890/15-0846R.1
Clutch size	Myhrvold et al.[24]	https://doi.org/10.1890/15-0846R.1
Software and algorithms		
Code supporting all analyses	This study	Zenodo: https://doi.org/10.5281/zenodo.20331205

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

The full MAPS dataset was downloaded from the MAPS Data Exploration Tool (https://ibp-maps-data-exploration-tool.org/app/maps). Sources for environmental data and traits are listed in the key resources table and additional details are provided below.

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METHOD DETAILS

Measures Of Population Change

We obtained bird capture records from the Monitoring Avian Productivity and Survivorship (MAPS) Program; a long-term, cooperative effort coordinated by the Institute for Bird Populations (IBP) that measures population and demographic parameters for North American birds. MAPS is a network of banding stations distributed across the US and Canada where trained, permitted individuals perform standardized bird monitoring during the breeding season to gather information about the abundance, age, sex, body condition, and reproductive status of the local species. MAPS stations have operated since 1989, and the available data at the time of our analysis extended through 2018 and consisted of 1.9 million capture records from 1259 stations.

We used these data to measure how the populations of individual species changed over time at each MAPS banding station. Sufficiently long time series are needed to have the statistical power required to accurately quantify population change. A recent analysis of 842 vertebrate population time series, 89% of which were birds, found that 10 years was the minimum length to detect population trends in the majority of datasets.[62] Accordingly, we retained stations with at least 10 years of data and no breaks in operation that were longer than 5 years. As most of the species caught at MAPS stations are passerines that can breed in their second year, each year of data is approximately equivalent to a generation time, and thus each station's time series was greater than or equal to 10 generations. We also removed banding stations that fell outside the contiguous United States as several of the environmental data sources used in our analysis were limited to this range. After applying these steps, 356 stations remained that had an average operating length of 15 years (range: 10 to 27 years; Figure 1A).

We further processed the capture data from the remaining banding stations to remove duplicate records from individuals that were recorded more than once in a given year. Birds of unknown age were also dropped, and we classified all remaining individuals as either hatch year birds that were born that year or as adults in their second year or older that were potentially breeding. In another processing step, to maintain consistency with current taxonomy used by the MAPS Program, we combined records for Pacific-slope and Cordilleran Flycatcher to reflect the current naming of these previously-separated species as the Western Flycatcher (*Empidonax difficilis*). MAPS protocols classify captures of Yellow-rumped Warbler (*Setophaga coronata*) into the Audubon's (*Setophaga coronata auduboni*) and Myrtle subspecies (*Setophaga coronata coronata*). They also differentiate Dark-eyed Juncos (*Junco hyemalis*) into six races. We maintained these classifications rather than combining subspecies or races. However, only Audubon's Warbler (*Setophaga coronata auduboni*) and Oregon Dark-eyed Junco (*Junco hyemalis oreganus*) had sufficient sample sizes to be retained in our analyses. Finally, MAPS includes an identifier for each capture record that marks it as reliable for productivity and survivorship analyses, so we filtered the data to ensure all remaining birds met this criterion. In total, 881,170 capture records from 347 species remained, with 583,962 adults and 297,208 hatch-year birds.

We summed the number of adults and hatch-year birds of each species that were caught during each operation year at each station. These data were used to obtain two measures of population change: adult abundance and productivity (Figure 1B). We quantified adult abundance as the total number of unique adults in each year, and we calculated productivity, a measure of reproductive output, as the ratio of the total number of unique hatch-year birds to the total number of adults. We assigned a productivity value of zero to all years where no hatch-year birds of a particular species were recorded. For stations with years where both adults and hatch-year birds of a species were captured, we calculated productivity as the ratio of the number of hatch-year birds to the number of adult birds. In years where one or more hatch-year birds and no adults were detected, we assumed that breeding adults were in fact present in the surrounding area but had evaded capture in the mist nets. For these records, we adjusted the adult count to equal one, and calculated productivity using the same ratio. While a pair of individuals is required to produce offspring in birds, mist netting efforts typically do not capture all adults breeding within an area.[63] Therefore, we took a conservative approach that accounted for the possibility of missed detections by setting adult abundance as one rather than two.

It was not unusual for a species to be detected infrequently at a particular station, resulting in only a few years with positive values for adult abundance and/or productivity. We applied several thresholds to ensure that we did not measure population change for species at stations where the data were highly zero-inflated. For adult abundance, we retained species at stations that met the following two criteria: 1) the total number of adults was equal to or exceeded the number of years of data for the station, and 2) the number of years with positive values for adult abundance (> 0 captures) was greater than or equal to 1/3 of the number of operation years. For example, stations with 15 years of data required 15 or more capture records for adults of a particular species, and at least 5 of the 15 years had to have positive counts. Similarly, for the productivity models we kept only species at stations that had positive productivity values in 1/3 or more of the station's operation years. After applying these thresholds, the mean percentage of years with non-zero values within each species-station time series was 83% for adult abundance and 64% for productivity. Finally, we confirmed the remaining capture records belonged to locally breeding species using an identifier included in the MAPS data.

Using these data, we fit models to measure the degree of species-specific change in adult abundance and productivity at each MAPS station over time. The measure of population change, either abundance or productivity, served as the response variable in each model and year was the explanatory variable. We also included log-transformed monitoring effort as an offset because analyses routinely account for effort when using constant-effort mist-netting data and variation in effort exists.[64–66] While all MAPS stations complete a standardized protocol to enable reliable estimates of population demographics, total effort at each station may vary slightly from year to year for a number of reasons (e.g., weather impacting the monitoring schedule). The monitoring effort value summarized the number of netting hours completed at a station across each year of operation and was calculated based on the size and number of mist nets, and the number of hours each net was in use.

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We quantified the two types of population change using different modelling approaches. Count variables, such as adult abundance, are often characterized by overdispersion, so we examined the mean-variance relationship for each abundance model. We found that many models were overdispersed (n = 5102), a moderate number were underdispersed (lower variance than the mean, n = 818), and some had equal mean-variance (n = 269). Due to the variation in the degree of dispersion across models, we compared two discrete distributions that can account for both over- or under-dispersion: Generalized Poisson[67] and Conway-Maxwell-Poisson.[68] We fit models to estimate change in adult abundance over time using both distributions and examined the number of models that successfully converged. Models were implemented using the *glmmTMB function* from the glmmTMB package in R.[69] We also compared the Akaike information criterion (AIC) associated with each model using both distributions as a measure of model fit. The two approaches produced similar results overall, but many more models converged (6173 vs 5008) and a larger number had improved model fit (evaluated as a lower AIC score; 2563 vs 2444) when using the Generalized Poisson distribution compared with the Conway-Maxwell Poisson distribution. Based on these results, we proceeded with the Generalized Poisson distribution. Our goal was to find a model distribution that worked well across the majority of abundance models; however, because optimizing and validating thousands of models individually was not feasible, we obtained parameter estimates from each model using 1000 bootstrapped replicates with replacement to produce robust estimates of uncertainty. This process was computational-intensive, so we used the Technology Infrastructure for Data Exploration (TIDE) computational core facility at San Diego State University to complete this step. From these models, we retained the median estimates for the slope, t-statistic, and standard error from the bootstrap replicates. We used median estimates to reflect the central tendency for these metrics because it is more robust to the influence of rare extreme values (i.e., outliers) and for asymmetrical distributions. In total, we measured trends in adult abundance for 6173 species-station combinations from 233 species and 356 banding stations.

We quantified the change in productivity over time, a continuous variable, using linear (Gaussian) models, which was a distribution that worked across productivity models when productivity values were log(x+1) transformed to account for the fact that they were right skewed and contained zeros. As with the abundance models, the parameter estimates were bootstrapped using 1000 replicates of the data with replacement, and we kept the median estimates for the slope, t-statistic, and standard error across the bootstrap replicates for each model. We obtained 4791 species-station productivity trends from 225 species and 355 banding stations.

In subsequent analyses, we retained species that had abundance or productivity trends from at least 50 stations. Consequently, these species represent common birds that typically have large geographic distributions across the contiguous United States. In total, 46 species remained; 44 with trends for adult abundance (n = 3932 species-station trends) and 29 with trends for productivity (n = 2557 species-station trends). These trends were derived from 596,325 unique captures.

Prior to subsequent analyses, we checked two assumptions of our approach. First, we tested our assumption that abundance and productivity trends reflect different properties of population dynamics. We obtained the Pearson's correlation coefficient as a measure of the degree of correlation between the productivity and abundance trends for the 27 species that had both trends and found little evidence of correlations between them (see results and discussion and Table S2). Second, we tested our assumption that station-level variation in abundance or productivity does not reflect broader regional trends. Unsurprisingly, MAPS stations are not evenly distributed across North America (Figure 1A). This resulted in many species having abundance and productivity trends from stations that vary widely in their proximity to another MAPS station (from < 5 km to up to 1000s of km apart). We used Mantel tests to examine the degree of spatial autocorrelation within each species' abundance and/or productivity trends using a matrix of pairwise distances between MAPS stations (measured in meters) and a matrix of pairwise differences in the species' abundance or productivity trends at each station. We found little evidence of spatial autocorrelation that would be present if larger regional dynamics were responsible for the changes in abundance and productivity (see results and discussion and Table S3).

Measures of Anthropogenic and Climate Change

We obtained publicly available geospatial layers for 11 environmental variables that were used to measure climate and anthropogenic change at the MAPS stations over time (Figure 1B). These variables included human population density, human footprint, urban imperviousness, normalized difference vegetation index (NDVI, a measure of vegetation greenness), nighttime light pollution, three climate variables including precipitation, maximum temperature, and minimum temperature, and three measures of air quality — ozone, fine particulate matter (PM 2.5), and nitrogen dioxide. Nitrogen dioxide and fine particulate matter both have direct physiological and behavioral effects on birds,[70] and elevated ozone levels have been linked to avian population declines in North America and Europe.[71,72] See Table S1 for a full list of the sources and details for these datasets.

If needed, we adjusted the spatial resolution of the geospatial layers to be 1 km^2. Many were already at this resolution and required no further modification (see Table S1). When necessary, we reprojected the geographic coordinates of the MAPS station locations to match the projection of the geospatial data and we extracted the values from the geospatial layers in the 1 km-by-1 km grid cell where each MAPS station was located. The range size of the species in our analysis during the breeding season is typically smaller than 1 km^2 (Table S5), so this area reflects the environmental change that occurred in the core use area of most birds recorded at a station.

The various environmental variables differed in their temporal duration and resolution. We sought to measure each environmental variable over the same span of available capture data from the MAPS program. However, some environmental variables did not align perfectly (see Table S1). For instance, data were only available for PM2.5, ozone and nitrogen dioxide from 2000-2016. In these cases, we assumed that magnitude and precision of environmental change was representative of how conditions have changed across years represented by the capture data. To better match the temporal resolution among datasets, additional processing was often required to estimate environmental change at each station with an approach that matched our measures of population

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change. Nighttime light was the only environmental variable that had annual values available across consecutive years. Multiple variables had a higher temporal resolution, such as daily or monthly values that we used to produce annual values; this included the air quality measures (PM 2.5, ozone, nitrogen dioxide; daily values), climate variables (precipitation, maximum and minimum temperature; daily values), and NDVI (14-day composites). Importantly, these particular variables can exhibit large fluctuations over short time scales. This means that the conditions during the non-breeding season may not reflect the conditions experienced by birds during the MAPS stations operation period, particularly as many species are migratory and arrive in the area of the MAPS station in spring. Furthermore, the MAPS stations are distributed across varying latitudes and elevations, and certain stations consistently open later in the year than others (i.e., only performing 8 of the 10 standardized MAPS sampling periods). Rather than using data from all available dates to calculate an average value for each year, we accounted for these two types of variability by finding the typical operating season for each station across all the years the station had been active. We then calculated the average for a given year of operation for each variable using only the dates that fell during the typical operating period of each station. For example, a low elevation station in a temperate climate that operated between May and August used data from these four months to find the average values for each environmental variable per operation year. In contrast, a station at higher elevation with an alpine climate that had a shorter operating season from June and August only used data from 3 months to calculate the average values for environmental variables per operation year.

After obtaining annual values, we fit a linear model to each station to measure the change over time at each location and we obtained estimates for the parameters using 1000 bootstrap replicates of the data. As with the population change models, we kept the median estimates for the slope, t-statistic, and standard error across the bootstrap replicates for each model. We were not able to obtain annual values for the three urbanization variables – urban imperviousness, human population density, and human footprint – which were only available at coarser temporal scales (e.g., one layer for every 5 years; see Table S1). For these variables, we calculated change at each station as the difference between the most recent value and the oldest available value.

QUANTIFICATION AND STATISTICAL ANALYSIS

Species' Sensitivity To Local Environmental Change

From the population and environmental change models, we extracted the t-statistic. This variable is the ratio of the slope and the standard error of the slope. For our models, it captures the magnitude of either population or environmental change and adjusts it based on the degree of uncertainty. The t-statistics representing local trends in abundance, productivity and environmental change were highly correlated with the slope estimates (mean = 0.893, range = 0.795 to 0.962), suggesting that this metric adequately reflected the direction and magnitude of change while accounting for uncertainty in the estimate. For context, a t-statistic with an absolute value of 1.96 or higher reflects a relationship where the 95% CI does not overlap zero, and t-statistics with absolute values between 1.65 and 1.94 indicate a relationship where the 90% CI does not overlap zero. We considered all relationships where the 90% CI did not overlap zero as evidence for a link between the form of environmental change and the change in abundance or productivity. These model or "change" statistics served as the inputs for the next stage of our analysis.

We fit spatial linear models to determine whether the local population trends for species were explained by local environmental change (Figure 1C). In each single-species model, the response variable was the population change model statistics for either productivity or adult abundance from all MAPS stations where a species occurred. The 11 station-specific measures of environmental change were the explanatory variables, which were centered and scaled to improve model performance and interpretation. Inclusion of all 11 forms of environmental change was necessary for parsing the relative influence of each on spatial variation in abundance and productivity trends. Additionally, we included a Matérn spatial correlation structure based on the geographic coordinates of the stations as a random effect that accounted for the spatial structure of the data. All models were implemented using the *splm* function in the spmodel package in R.[73]

We examined residual diagnostic plots to evaluate each model. Additionally, because many of the 11 forms of environmental change have the potential to covary, we inspected all models for issues of multicollinearity by calculating variance inflation factors using the *vif* function in the R package car.[74] We assessed potential issues of multicollinearity if VIF > 10.[17,26,75] VIF scores were ≤ 3 for 97.6% and 96.3% of all variables across the abundance and productivity models, respectively. Only one model had VIF values > 10. The abundance model for Hermit Thrush (*Catharus guttatus*) had a VIF = 13.5 for change in human population and 11.5 for change in anthropogenic impervious surface. We reran the model without change in human population and also without change in anthropogenic impervious surface. In both cases, the reduced models did not result in parameter estimates that would change the interpretation of model results, thus we kept the original full model.[17,26]

As in previous steps, we retained the model t-statistics and used them as inputs into a subsequent series of models. These values reflect the magnitude and direction of the relationship between a measure of population change (abundance or productivity) and one of the 11 types of environmental change while adjusting for the degree of uncertainty in the estimate. We consider these values "sensitivity statistics" that represent how a species' productivity or abundance responds to a particular type of environmental change (e.g., sensitivity to change in artificial night lighting).

Trait-Based Models

We selected 11 ecological traits that fell under four broad categories that may explain the variation in how different species responded to environmental change: climate preferences, nest traits, sensory and physiological traits, and life history. We identified

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the potential relationships between the types of environmental change and the selected ecological traits, and we generated *a priori* predictions about the form the relationship would take (see Table 1 for complete information about the selected traits and associated predictions that were tested). For some trait categories we had two or more traits that were used as predictor variables for the same environmental sensitivity. For sensitivities to the three measures of air pollution, we used both aerobic power and aerial lifestyle, which were weakly correlated (r = 0.24). We also used three life history variables as predictors to explain variation in sensitivities to changes in impervious surface, human footprint and human population density. Among the three variables, longevity and clutch size were weakly and negatively correlated (r = -0.33), clutch size and brood value were weakly positively related (r = 0.25) and brood value and longevity were more strongly negatively related (-0.71). This final relationship is unsurprising because longevity is used to calculate brood value.[76] Despite the strong relationship between brood value and longevity, each variable reflects unique aspects of life history variation that could prove useful in explaining variation in sensitivities to environmental change.

We obtained the vast majority of traits from existing databases (Table 1). However, to increase trait information for a proxy for variation in dim light vision, quantified as the ratio of the corneal diameter (mm) to the transverse diameter (mm) of the eye (C.T. ratio), we measured 92 skeletal specimens representing 27 species at the Natural History Museum of Los Angeles County, the Field Museum of Natural History in Chicago, the University of Washington Burke Museum of Natural History and Culture, the California Academy of Science, and the University of California at Berkeley Museum of Vertebrate Zoology (Table S6). We followed the methods of Wolf and Francis.[77] Briefly, using digital calipers sensitive to 0.01 mm, we measured the transverse diameter of the eye orbit from the middle of the quadratojugal to the point on the orbit rim directly opposite and we quantified the corneal diameter by measuring the inner diameter of the sclerotic ring. We measured each morphological dimension three times for accuracy and used the mean values of these repeated measurements to reflect eye geometries for a C.T. ratio per specimen. For subsequent analyses, we calculated a mean C.T. ratio per species when measurements were available from more than one specimen (85% of 27 species).

Trait information was available at the species level rather than the subspecies or race level, so we used trait values for Yellow-rumped Warbler (*Setophaga coronata*) for the Audubon's warbler subspecies and values for Dark-eyed Junco (*Junco hyemalis*) for Oregon Junco. We had complete trait information for all 46 species in our analyses, with the exception of the C.T. ratio, which was unavailable for four species, and the ratio of log-transformed heart mass to log-transformed body mass (HM:BM ratio), a proxy for aerobic activity, which was missing for 13 species. We examined the degree of phylogenetic signal, measured as Pagel's lambda (λ),[78] across all the species available in the C.T. ratio (n = 1417 species) and HM:BM ratio (n = 920 species) databases to evaluate the potential to impute values for the missing species. Imputation methods perform poorly when the phylogenetic signal for a trait is low (e.g., $\lambda < 0.7$)[79]; therefore, we did not impute values for the species missing C.T. ratios where $\lambda = 0.54$. There was a strong phylogenetic signal for log-transformed heart mass ($\lambda = 0.99$), so we used the *impute* function in the R package funspace[80] to obtain values for the missing species. This approach decomposes the provided phylogeny into eigenvectors that are used as predictor variables along with the available trait values in a random forest model. We combined the imputed log-transformed heart masses with log-transformed body mass data from Tobias et al.[11] to obtain HM:BM for the 13 species. Finally, the Brown-headed Cowbird (*Molothrus ater*) was one of the species with adult abundance models, but as they are a brood parasite, we removed this species from all models relating to nests and life history traits.

We used phylogenetically-informed generalized linear models (PGLS) to examine the relationships between species' traits and their population responses to environmental change (Figure 1C). In these models, the species-specific responses to a particular measure of environmental change were used as the response variable, and the species-specific traits were the explanatory variables. Each model incorporated a pruned consensus tree[81] and estimated Pagel's lambda (λ) as a measure of phylogenetic signal in the relationship between the response variable and predictor variable. We fit PGLS models using the *gls* function in the R package nlme.[82,83] When a model estimated a value for λ outside the range of zero to 1, we fixed λ at the nearest boundary (either 0 or 1) and reran the model. We considered models with and without log-transformed body mass as a covariate to account for potential relationships between species' size and the trait of interest, and used a likelihood ratio test to identify the model with greater support. We evaluated model fit using residual plots.

We identified strong effects as those where the 95% CI did not overlap zero. We also report relationships where the 90% CI did not overlap zero that have slightly lower precision associated with the estimated effect. The only exception to this approach was for the Mantel tests that were used to examine spatial autocorrelation within the species' abundance or productivity trends. This output of the Mantel test does not provide a confidence interval, so we report p-values and use alpha of 0.05 to identify important relationships. All analyses were performed with the R programming language (R Core Team 2025; version 4.4.3) and implemented via the RStudio integrated development environment (Posit team 2025; version 2025.05.0+496).