AVIAN ECOLOGY

Agriculture and hot temperatures interactively erode the nest success of habitat generalist birds across the United States

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Habitat conversion and climate change are fundamental drivers of biodiversity loss worldwide but are often analyzed in isolation. We used a continental-scale, decades-long database of more than 150,000 bird nesting attempts to explore how extreme heat affects avian reproduction in forests, grasslands, and agricultural and developed areas across the US. We found that in forests, extreme heat increased nest success, but birds nesting in agricultural settings were less likely to successfully fledge young when temperatures reached anomalously high levels. Species that build exposed cup nests and species of higher conservation concern were particularly vulnerable to maximum temperature anomalies in agricultural settings. Finally, future projections suggested that ongoing climate change may exacerbate the negative effects of habitat conversion on avian nesting success, thereby compromising conservation efforts in human-dominated landscapes.

Habitat conversion is the primary driver of terrestrial biodiversity loss, and climate change is projected to cause widespread extirpations (1, 2). However, the effects of habitat conversion and climate change are often analyzed in isolation even though the fate of many species will ultimately depend on how they interact (3). For example, many forms of habitat conversion (e.g., agricultural or urban expansion) remove insulating tree canopies or other complex microhabitats, thereby exposing organisms to warmer maximum and/or cooler minimum temperatures [i.e., reducing thermal buffering (4)]. Indeed, temperatures in agricultural settings regularly attain levels >10°C higher than in nearby natural habitats (5). Other stressors related to human land use may increase the sensitivity of biodiversity to heat; for example, pesticide use and low vegetation complexity may reduce insect prey availability, limiting food and water available for thermoregulation (6). In addition, trees may protect understory species from heavy rains and retain moisture, buffering against drought (4). Thus, as temperatures warm and precipitation regimes shift, climate change may cause cities and farms to become even less hospitable, undermining efforts to safeguard biodiversity in human-dominated landscapes (7).

Birds may be particularly sensitive to temperature extremes, because species with altricial young are ectothermic for the first few weeks of life, and extreme temperatures can divert energy from growth to thermoregulation (8). Although the effects of cold snaps on avian reproduction are well documented (9, 10), recent work suggests that high temperatures can also reduce avian survival (11–13) and even cause community collapse (13). Temperature extremes may limit species persistence more than long-term increases in average temperatures (14), and variations in microclimate buffering can thus influence bird distributions (15).

Unfortunately, understanding the interactive effects of climate and land-use change on species persistence requires demographic data that are difficult to obtain over large spatiotemporal scales (3). Thus, our knowledge of how climate and land-use change interactively affect species is mostly restricted to changes in species distributions and/or abundances (4, 16). Project NestWatch, a citizen-science nest-monitoring program organized by the Cornell Laboratory of Ornithology, offers a rare opportunity to explore how temperature extremes and land use interact to affect avian nesting success at a national scale. Using their data, we analyzed 152,863 nesting attempts by 58 bird species across 23 years (1998 to 2020) and 37,869 sites in four land-use types within the conterminous US: forests, open natural habitats, agricultural settings, and developed areas [table S1 (17)]. We used GridMET (18) to measure temperature extremes during each nesting attempt by calculating temperature anomalies, which we defined as the average maximum (or minimum) temperatures during the 45 days after each nesting attempt's date of first egg relative to conditions during the same date range over a historical reference period (1980 to 2000).

Our work was guided by four questions. First, how do the effects of temperature on nesting success vary across land-cover types? We hypothesized that maximum temperature anomalies would reduce success in open, human-dominated habitats with fewer thermally buffered areas. We also quantified precipitation anomalies during nesting, hypothesizing that extreme events would also reduce success in open, human-dominated habitats. Second, are some species more vulnerable to the interactive effects of habitat conversion and climate change than others? We predicted that species that build exposed nests (as opposed to cavity nests) and species of higher conservation concern would be the most sensitive to climate and land-use interactions. Third, are the effects of temperature and land cover consistent across species' ranges? We predicted that maximum temperature anomalies would disproportionately affect nesting success in agricultural areas within warmer regions. Finally, looking forward across the 21st century, how will nesting success likely change across space, time, and alternative climate change scenarios? We hypothesized that declines would be pronounced in agricultural settings, grassland, and developed areas, but not in forests.

The interactive effects of climate and land cover could arise from individuals of the same species varying in their temperature responses across land-cover types (e.g., if some provide more thermal buffering than others) or from shifts in species composition (e.g., if agriculture-associated species are more thermally sensitive than forest-associated species). To determine whether thermal buffering in some land-cover types increases avian resilience against heat waves, we focused on habitat generalist species that could conceivably exhibit different responses to heat waves in different land-cover types. Additionally, we modeled climate and land-use interactions using both generalized linear mixed models (GLMMs) that integrate within- and across-species effects and Bayesian models that only consider variation within species (17).

Climate and land-cover interactions
Interactions between maximum temperature anomalies and land-cover type

Across both modeling frameworks, we found that the effects of maximum temperature extremes on avian nesting success differed among land-use types (P < 0.001 for GLMM; Bayesian confidence interval: agricultural settings, –0.21 to –0.01; forests, 0.03 to 0.15; Fig. 1 and tables S2 to S5). In agricultural settings, the probability of successfully fledging at least one offspring declined by 6% (from 75 to 69%) between nests that experienced cooler versus warmer maximum temperature anomalies (i.e., 2 SDs lower versus 2 SDs higher than mean historical temperatures). Only considering within-species

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effects produced a similar decline (i.e., an 8% decline of the same temperature range in the Bayesian model). In developed areas, the probability of success declined by only 2% from cooler to warmer maximum temperature anomalies (not significant in the Bayesian model). One reason for the more muted decline might be that nests in "developed areas" were often in residential areas that can have high tree cover, not in city centers that may be subject to particularly extreme heat island effects. By contrast, only 1.5% of agricultural sites were in plantations with tree canopies (table S6). As a result, developed areas had higher canopy cover than both agricultural and natural open sites (mean cover: developed, 21%; agricultural, 11%; natural open, 17.6%). Future work could profitably focus on using temperature loggers to link nesting success to local microclimates rather than the coarser air temperature measurements analyzed here.

Although temperature increases in forests have been previously shown to reduce nest productivity through increased predation (19), we found that reproductive success increased in forests by 5% across the same temperature range (6% in the Bayesian model). Why might this be? First, because tree canopies may keep nests cool, adults nesting in forests could be released from thermoregulatory care when temperatures increase, allowing them to spend more time foraging (20). Increased temperatures in cold microclimates might also reduce the reproductive cost of time spent off the nest (21). Maximum temperature anomalies could also drive phenological shifts that improve forest-nesting birds' access to food resources [e.g., by increasing insect abundance earlier in the season (22)]. Critically, the positive relationship between nesting success and maximum temperature anomalies in forests does not suggest that climate change is benefiting forest birds, because warming temperatures may be decreasing other demographic parameters (e.g., adult and/or juvenile survival).

Finally, in natural open habitats, nest success exhibited a nonlinear relationship with maximum temperature anomalies, peaking at an intermediate value (in the Bayesian model, no relationship with temperature was observed). One explanation is that grassland species could be adapted to temperature regimes in open-canopied environments, but too much deviation from historical norms (in either direction) may decrease success. Indeed, most nests in natural open habitats were in grasslands or prairies (~85% of attempts; table S6).

Our finding that the effects of temperature extremes on nesting success vary across land-use types persisted when additionally accounting for latitude, elevation, nest predation, spatial autocorrelation, extreme observations, the scale of landscape cover composition, and nests in more thermally buffered agri-
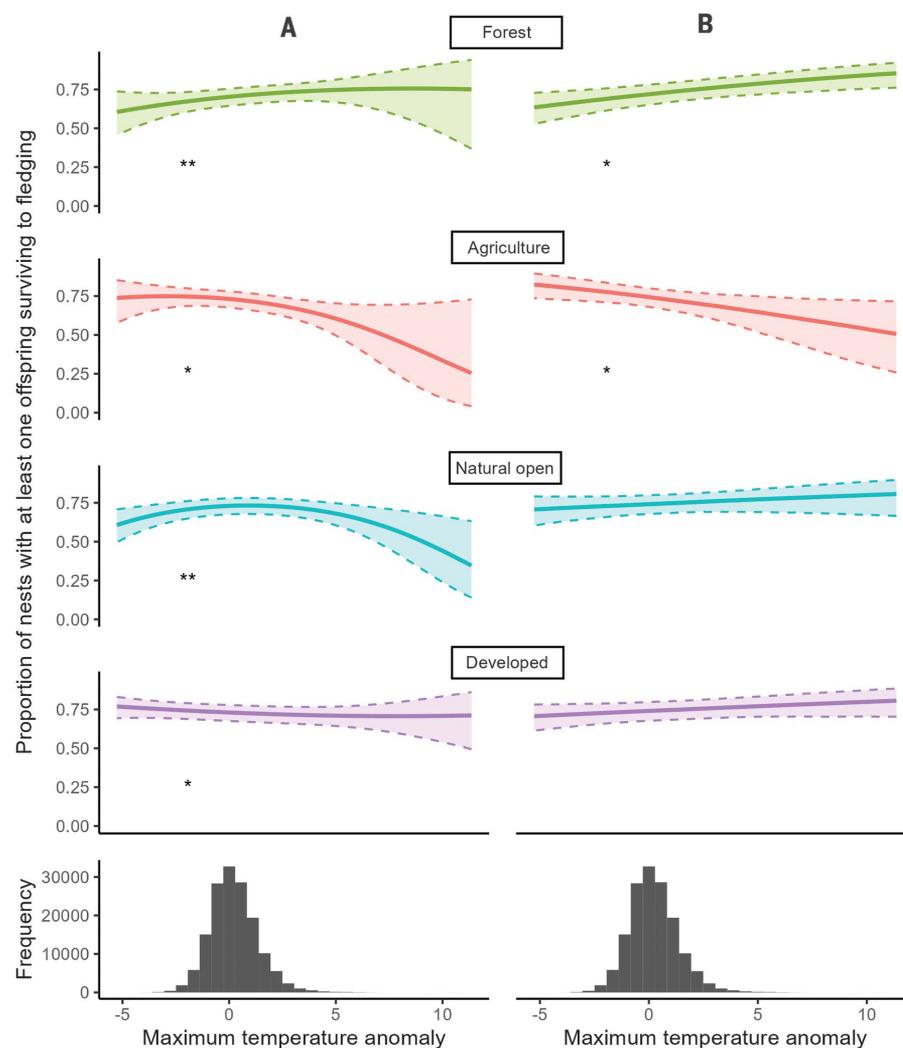
Fig. 1. Maximum temperature extremes reduce avian nesting success in agricultural settings but increase it in forests. For nests in each land-use type, panels present the relationship between maximum temperature anomalies 45 days after lay date as z-scores relative to historical temperatures (17) and the predicted proportion of nests with at least one offspring surviving to fledging. Solid lines indicate model predictions; shaded regions represent 95% confidence regions. Histograms in the bottom panels depict the distribution of maximum temperature anomalies across all nesting attempts. (**A**) Results from GLMMs combining within- and among-species variations in response to temperature. Asterisks indicate the level of significance in each land use. *$P < 0.05$; **$P < 0.01$. The quadratic effect of maximum temperature anomaly is only significant in natural open land cover. (**B**) Results from a Bayesian analysis that only assesses the effects of temperatures within species (i.e., factoring out changes in species composition among land-cover types). Asterisks indicate that the 95% Bayesian confidence interval did not overlap zero.

cultural habitats [table S7 and fig. S1 (17)]. Birds were also not more sensitive to temperature anomalies in agricultural settings because of differences in air temperature among land-use types (fig. S2).

Interactions among minimum temperature anomaly, precipitation, and land cover

Unlike maximum temperatures, the effects of other climate variables exhibited much less variation among land-cover types (tables S2, S3, and S8). First, the linear effect of minimum temperature anomalies did not vary among

land-cover types ($P = 0.28$). However, the quadratic effect did so marginally ($P = 0.05$), with nesting success exhibiting a more convex relationship with minimum temperature anomaly in forests and a more linear relationship in the other land-cover types. Second, precipitation over the prior year also exhibited no variation in linear effects on nesting success across land-cover types ($P = 0.19$). However, the quadratic effect again varied (table S3 and S8), exhibiting a more convex relationship in forests and a more linear effect in the other land-cover types. Finally, the linear effect of precipitation anomalies

Fig. 2. Interactive effects of temperature extremes and land use are exacerbated for species of higher conservation concern and for cup-nesting species in agricultural settings. (**A**) Maximum temperature anomalies 45 days after lay date on the proportion of nests with at least one fledging (i.e., nest success) in each land-use type and for species of varying levels of conservation concern. Colored lines depict predictions for species of varying levels of conservation concern, represented by: house sparrow (*Passer domesticus*; score level 4, lowest concern), barn swallow (*Hirundo rustica*, level 8), chestnut-backed chickadee (*Poecile rufescens*, level 12), and oak titmouse (*Baeolophus inornatus*; score level 15, highest concern). (**B**) Maximum temperature anomaly effects on birds nesting in cavities (blue) versus cup nests (red). Asterisks indicate the level of significance of the interaction between maximum temperature anomalies and species' conservation scores or nest types in each land use. $+P < 0.1$, $*P < 0.05$, $**P < 0.01$.
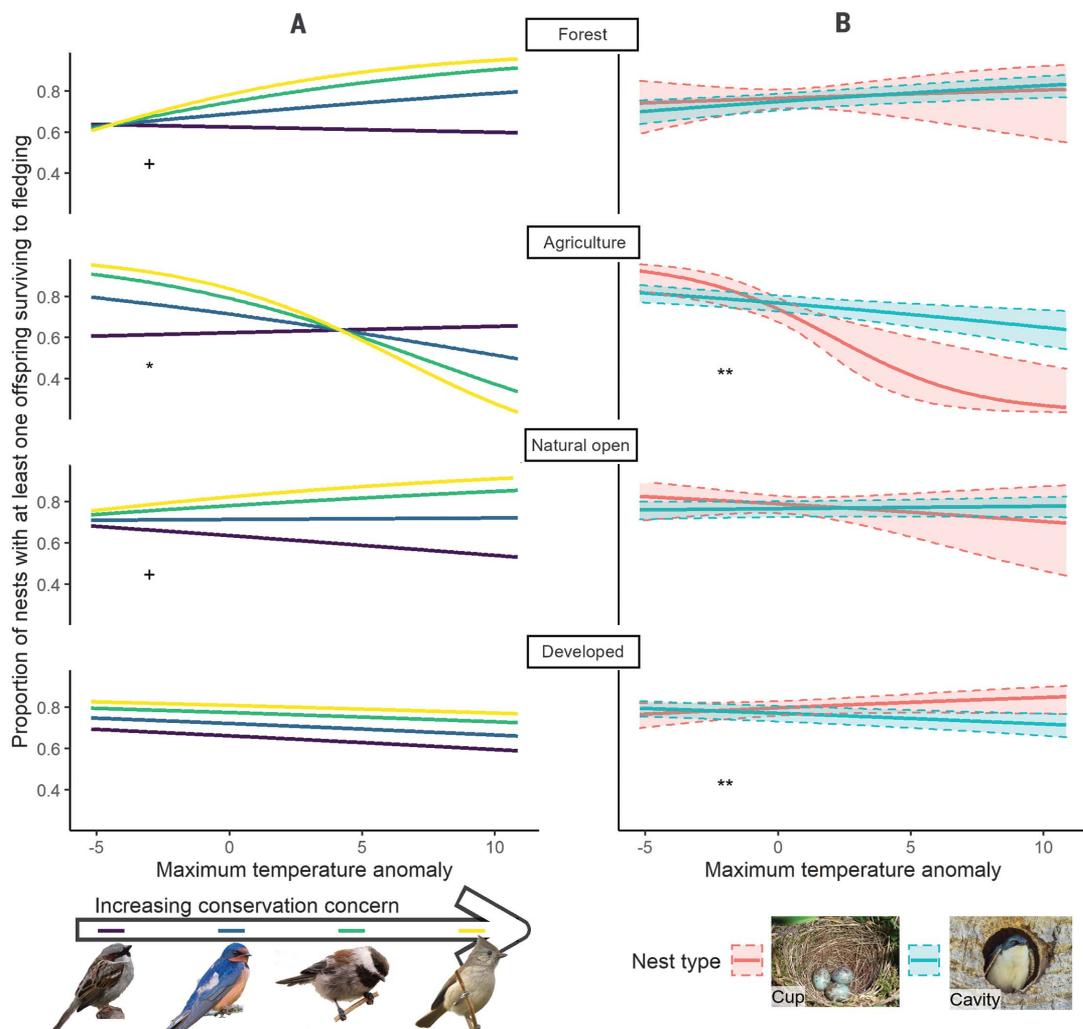
during nesting varied by land-cover type, but with smaller effect sizes than maximum temperature anomalies ($P < 0.001$; fig. S3 and tables S3, S8, and S9). Specifically, higher precipitation during nesting was associated with higher success in agricultural settings, decreased success in forests, and small effects in other land-cover types. This suggests that birds in agricultural settings may suffer even more when precipitation is low and temperatures are high.

Identifying species sensitive to climate and land-cover interactions

The negative effects of maximum temperature anomalies on avian reproduction in agricultural settings and the positive effects in forests were generally consistent across species, but were not consistent across species in other land-cover types (fig. S4 and table S5). Multiple mechanisms may explain these trends. First, temperature extremes in agricultural settings could induce physiological stress and require nestlings to expend energy on thermoregulation rather than growth or to suffer water costs and dehydration (8). Second, maximum

temperature anomalies may affect birds indirectly, for example, by reducing arthropod prey abundance or adult foraging efficiency in agricultural settings but not in natural habitats with microclimate refugia (23, 24). Indeed, arthropods are particularly sensitive to climate warming in agricultural settings but are more buffered in natural habitats (25).

Nest type

Identifying traits that explain variations in species' responses to maximum temperature anomalies might provide insight into the underlying mechanisms. We found that cup nests in agricultural settings experienced particularly severe declines in nest success with higher maximum temperatures ($P = 0.005$; Fig. 2 and tables S10 to S12). Cup nests are less thermally buffered than cavity nests, suggesting that maximum temperature anomalies may indeed reduce nesting success directly [i.e., through avian physiology (26)]. We also found similar results when comparing nests in human-constructed nest boxes with other nests (fig. S5 and tables S10 to S12); however, because 99% of cavity nests

were also in nest boxes, these two comparisons are functionally equivalent. This finding suggests that the effect sizes of the temperature and land-use interactions reported above may be conservative given the dominance of artificial nest box observations in the database (table S1).

Conservation concern

Species of higher conservation concern [as defined by (27)] were also more vulnerable to maximum temperature anomalies in agricultural settings and more successful in forests ($P = 0.027$; Fig. 2 and tables S10 to S12). This again suggests that the effect sizes reported above may be conservative for rarer, less frequently sampled species. For example, in agricultural settings, GLMMs predicted that hotter maximum temperature anomalies would decrease nest success by 15% (from 90 to 75%; maximum temperatures ± 2 SDs) for species of highest conservation concern but increase success by 1% for species of low concern. Because species of conservation concern are often already sensitive to anthropogenic land uses (28), they
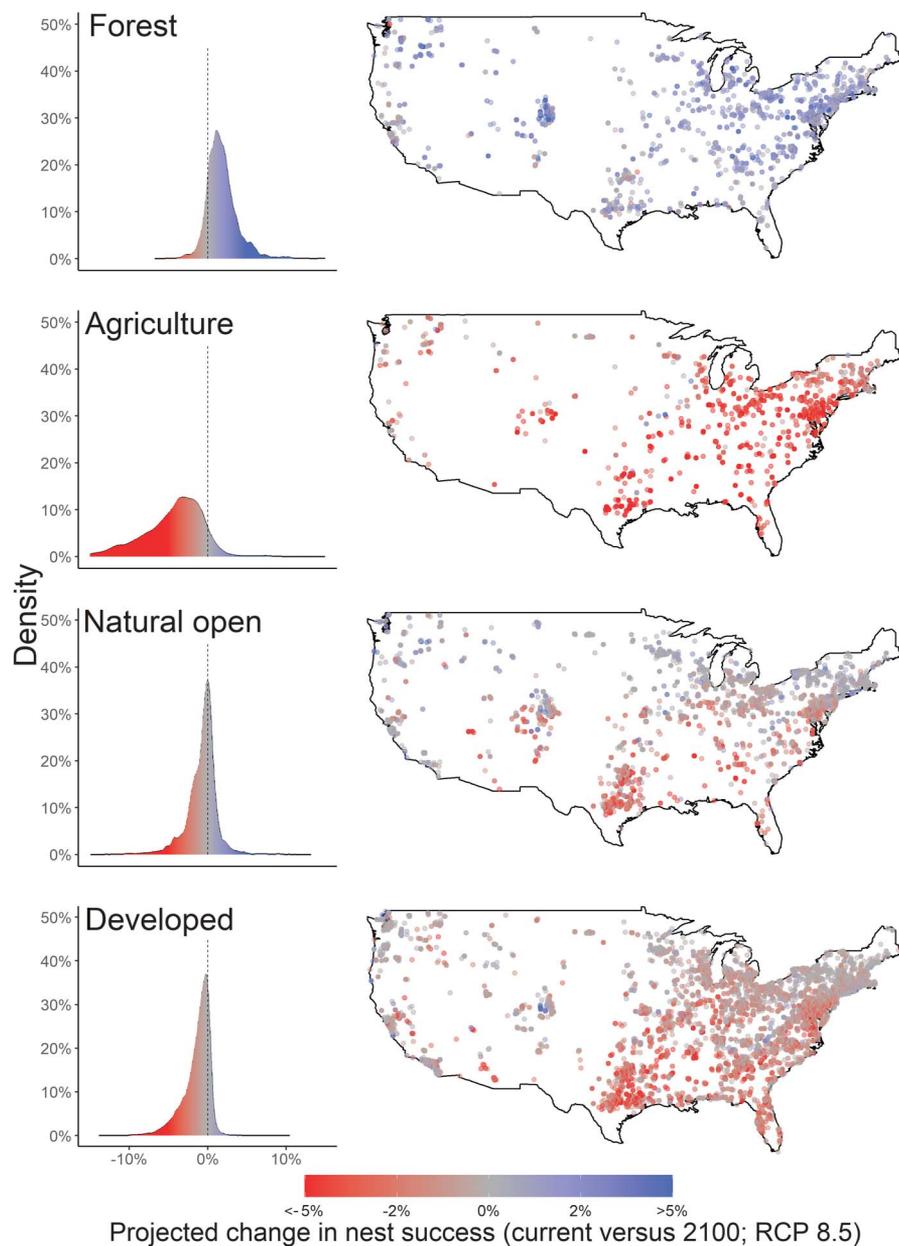
Fig. 3. Climate change is expected to decrease nesting success in agricultural settings but increase it in forests. Density diagrams (left) depict how the probability of successfully fledging at least one offspring is predicted to change by 2100 under a high-emissions scenario (RCP 8.5) across sites for each land-use type. Maps depict the spatial distribution of predicted changes; dark blue, red, and gray points indicate sites where nesting success is expected to increase by 5% or more, decrease by 5% or more, or remain largely unchanged, respectively. Points and histograms represent average predictions across five climate models (17).

may simply be unable to cope when temperatures increase in marginal environments.

Thermal limits

Avian reproduction is expected to be most sensitive to temperature extremes in regions that experience temperatures near species' thermal limits (29). To examine spatial variation in species' responses to maximum temperature ano-

malies and land use, we calculated site temperature baselines in four ways, including approaches that quantify temperatures in absolute terms and relative to temperature variability across each species' geographic range (17). Although nest success was more sensitive to maximum temperature anomalies in warmer regions ($P < 0.001$ for three of four measures; fig. S6 and tables S13 and S14), the interactive

effect of maximum temperature anomalies and land-use types was consistent across regions: In both hot and cold regions, maximum temperature anomalies were the most harmful in agricultural settings ($P \geq 0.6$; tables S13 and S15).

Future climate change scenarios

Our results suggest that bird species nesting in agricultural settings may be more vulnerable to climate change than those in forests. Leveraging five global climate models and multiple climate change scenarios [representative concentration pathways (RCPs)], we used our models to explore how nest success would change if each nesting attempt in our dataset instead occurred with the climate conditions of 2040 to 2059 or 2080 to 2099 (Fig. 3, fig. S7A, and table S16). These analyses implicitly assume that nesting phenology is fixed in time, even though some birds can shift to earlier breeding times to track climate niches (29). Therefore, these results should be considered a sensitivity analysis rather than explicit predictions. Climatic uncertainty for agricultural settings was slightly higher than for the other land-cover types, especially in the southeastern US (figs. S7B and S8), but we suspect that climatic uncertainty may have constrained the projected effect sizes. Statistical uncertainty exceeded climatic uncertainty (figs. S7C and S8). Our models suggest that nesting success in agricultural settings would decline by an additional 4.41% by 2100 if greenhouse gas emissions maintain their current rate of increase (RCP 8.5), whereas success in forests would increase by 1.78%. By contrast, if emissions were reduced (RCP 4.5), then nesting success in agricultural settings would decline by only 1.14% and success in forests would increase by 1.07% (fig. S7A and table S16). Thus, if emissions are curtailed, then birds nesting in human-dominated areas would likely be more successful over the long term.

Conclusions

Our results highlight the vulnerability of birds nesting in agricultural settings to temperature extremes and may offer insight into mechanisms underlying North American bird declines (30). They also align with recent findings from Europe suggesting that climate change may be causing larger population declines in generalist, farmland-associated birds compared with specialist, woodland-associated species (31). Maintaining forest patches in anthropogenic landscapes may thus increase avian resilience to extreme climatic events (32). An important caveat is that the species studied here are habitat generalists. Enhancing forest cover in naturally open land covers could harm grassland-obligate birds, which might be able to leverage habitat heterogeneity in natural grasslands to find thermally buffered areas (33). Nonetheless, for other species, erecting

sun-shielded or insulated nest boxes in shaded locations (*34*), conserving forest patches, and/or planting scattered trees in human-dominated landscapes may help species cope with climate change–driven temperature extremes by providing thermal buffering (*35*), especially for the species of conservation concern studied here.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Figs. S1 to S8
Tables S1 to S16
References (*38–49*)

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Editor's summary

Habitat transformation into agricultural and urban land uses is expanding and is accompanied by warming temperatures and increasing climate extremes. These dual stresses may interact to affect animal fitness because forests can buffer extreme temperatures more than open habitats such as agricultural lands. Using data from the citizen science program Project NestWatch, Lauck *et al.* examined how extreme heat influences birds' fledgling success in forests, grassland, developed areas, and agricultural lands across the continental US. They found different effects of extreme heat in different land uses. Birds nesting in agricultural lands had lower fledgling success at extreme warm temperatures, but the opposite was true in forests. Future warming will likely negatively affect bird reproduction in human-dominated areas, especially among species of conservation concern. —BEL

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