

Threat of climate change on a songbird population through its impacts on breeding

Thomas W. Bonnot^{1*}, W. Andrew Cox², Frank R. Thompson³ and Joshua J. Millsbaugh⁴

Understanding global change processes that threaten species viability is critical for assessing vulnerability and deciding on appropriate conservation actions¹. Here we combine individual-based² and metapopulation models to estimate the effects of climate change on annual breeding productivity and population viability up to 2100 of a common forest songbird, the Acadian flycatcher (*Empidonax vireescens*), across the Central Hardwoods ecoregion, a 39.5-million-hectare area of temperate and broadleaf forests in the USA. Our approach integrates local-scale, individual breeding productivity, estimated from empirically derived demographic parameters that vary with landscape and climatic factors (such as forest cover, daily temperature)³, into a dynamic-landscape metapopulation model⁴ that projects growth of the regional population over time. We show that warming temperatures under a worst-case scenario with unabated climate change could reduce breeding productivity to an extent that this currently abundant species will suffer population declines substantial enough to pose a significant risk of quasi-extinction from the region in the twenty-first century. However, we also show that this risk is greatly reduced for scenarios where emissions and warming are curtailed. These results highlight the importance of considering both direct and indirect effects of climate change when assessing the vulnerability of species.

As evidence of climate change impacts on plant and wildlife populations grows, understanding global change processes that threaten species viability may be a necessary precursor to deciding on the most appropriate actions for conservation^{1,5}.

Efforts to identify how climate change will affect species occur across a range of ecological and empirical scales. At the broadest scales, researchers assess range-wide vulnerability for a species or suite of species, often through the use of species distribution (or niche models) and population models. These approaches predict shifts in distribution or changes in population dynamics across large scales based on changes in climate and vegetation^{6,7}, but have been criticized for the lack of relevant processes they consider⁸. For example, distribution models that focus only on climate assume (perhaps erroneously) that species and their habitat/niche necessarily closely track changes in climate^{9,10}. Other recent advances such as dynamic-landscape metapopulation models (DLMPs)⁴ provide a comprehensive and mechanistic approach to modelling both population dynamics and distribution from changes in habitat under climate change, but fail to consider potentially significant and more direct impacts of climate on demographic processes.

The weakness of these approaches is made apparent by the increasing body of evidence that indicates that climate change

directly (and indirectly) affects the demographic parameters that drive population growth. For example, vulnerability in key species traits such as physiological tolerances and diets and habitat can lead to altered demographics¹¹. For many birds, population persistence is sensitive to the rates at which young are produced, which can change as a function of temperature^{3,12}. In the Midwestern USA, greater daily temperatures can reduce nest survival and overall productivity for forest-dwelling songbirds³, probably because of increased predation from snakes and potentially other predators^{13–15}. Studies such as these provide a better mechanistic understanding of how climate change may alter the key demographic rates that contribute to population growth, but scaling up to estimate population-level responses requires a quantitative approach that integrates climate and habitat on a broader scale.

Translating individual-level climate effects into population impacts can be difficult when relationships between climatic variables and demographic parameters occur in the form of empirical findings or statistical models and relate to local temporal and spatial scales¹⁶. For example, survival of individuals and nests is modelled on daily timescales, often as a function of local habitat and daily temperature and precipitation, thus complicating predictions of their fates for an entire region, season or year. Many processes are also subject to variation in the individual traits, behaviours or adaptations that can mitigate impacts^{17,18}. For example, breeding birds often re-nest following successful or failed nests, which might offset the negative impact of increased temperatures on productivity, but the stochastic nature of individual behaviour in these contexts prevents generalizations. Therefore, accurately predicting the impacts of climate change on productivity and population growth will require methods that can model local processes, such as nest survival, under future climates, in a manner that accounts for local factors and individual behaviour and then can be integrated with metapopulation models at broader scales.

Here, we use a two-step process to overcome the challenges of scaling up from individual to population-level impacts of climate change on Acadian flycatchers (*Empidonax vireescens*; hereafter ‘flycatcher’), a common North American passerine, through the year 2100 across a 39.5 million hectare region of temperate and broadleaf forests in the USA known as the Central Hardwoods (Fig. 1). First, we used empirically derived estimates of nest survival and productivity within an individual-based model (IBM) to estimate reproduction of individual birds throughout the region under various scenarios of climate change in this century. We account for individual behaviours, such as re-nesting, that might inadvertently mitigate the impacts on overall productivity. We then integrate those productivity estimates into a DLMP that enables us to project population

¹School of Natural Resources, University of Missouri, Columbia, MO, USA. ²Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, Gainesville, FL, USA. ³Northern Research Station, United States Forest Service, Columbia, MO, USA. ⁴Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, W. A. Franke College of Forestry and Conservation, University of Montana, Missoula, MT, USA.

*e-mail: bonnott@missouri.edu

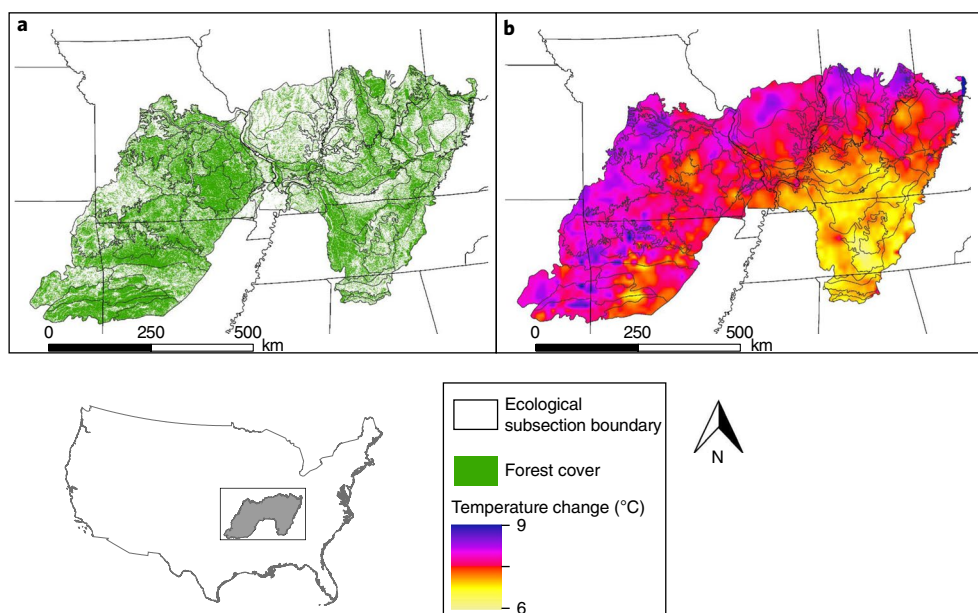


Fig. 1 | Location of the Central Hardwoods region in the USA. a,b, Forest cover (**a**) was integrated with daily downscaled projections of maximum temperature (**b**) during the breeding season from 2010 to 2100 under various climate warming scenarios (GFDL-CM3-8.5, business-as-usual climate, shown) to estimate the annual productivity of Acadian flycatchers across the Central Hardwoods. Ecological subsections were used to stratify the population in the DLMP.

growth while accounting for uncertainty in adult and juvenile survival by considering a range of rates. From these outputs, we predict the risk climate change poses to the flycatcher population.

We found that climate warming reduced flycatcher nest success (defined as the compound probability of a nest surviving the entire 32-day period to fledge young) and annual productivity, posing a significant risk to population viability on a large spatial scale. By the end of the century (2090–2100), breeding season temperatures were projected to increase under all scenarios. A business-as-usual path for emissions (the GFDL-CM3-8.5 scenario) showed a severe 7.55°C warming in the mean daily maximum breeding season temperature across the region by the end of the century, a 25% increase over the recent past (1981–2010) (Fig. 2a). By contrast, emissions in the MRI-CGCM3-2.6 and CanESM2-4.5 scenarios stabilize and then slowly decrease after the middle of the twenty-first century, in line with the mild (1.5°C) and moderate (2°C) increases in daily maximum temperatures targeted under the Intergovernmental Panel on Climate Change (IPCC) 21st session of the Conference of the Parties (COP21) agreement¹⁹. Under these scenarios, estimated productivities averaged between 1.52 and 1.70 fledglings per female per year across the Central Hardwoods in the first decade (Fig. 2b). Annual productivity declined approximately 5% under the MRI-CGCM3-2.6 scenario to approximately 1.6 fledglings per female by 2100. Productivity under the two more severe warming scenarios declined similarly up to 2050 but diverged thereafter. From that point, overall declines in productivity dissipated under the CanESM2-4.5, while productivity continued declining up to 2100 under the GFDL-CM3-8.5 scenario, falling 30% below 2010–2020 levels (Fig. 2b). Our models indicate that under severe warming projections, flycatchers breeding in many areas of the Central Hardwoods would produce <1 fledglings per female per year by 2100 (Fig. 3).

The effects of climate change are often studied for threatened species. However, we found substantial risk facing a species that is still relatively common. We estimated an initial abundance of approximately 4 million breeding females in the population in 2010. Yet, increasingly more severe climate warming impacts on productivity

resulted in increased population declines and elevated risk of local extinction over the next century. We project that flycatchers in the Central Hardwoods under the business-as-usual scenario face a 34% risk of declining to quasi-extinction levels by 2100. That is more than a threefold increase in risk compared to the MRI-CGCM3-2.6 scenario (Table 1 and Supplementary Figs. 1, 2 and 3). Many songbird species are affected by the same communities of predators and, to varying extents, are susceptible to similar temperature effects³. Therefore, not only do our projections highlight the risk of local extinction facing flycatchers, they imply concern for other birds in the community affected by similar processes. Our study is another example of increasingly comprehensive case studies that have identified climate change as an existential threat to entire populations^{20,21}.

Although predictive modelling includes multiple assumptions and uncertainties, a number of points underscore the credibility of this risk. First, reproductive estimates produced by the IBM follow a pattern of warming temperatures and declining nest survival observed over recent decades. Studies that took place in the region from 2000–2010 reported nest success rates of >40% during a decade when average daily maximum temperatures during breeding averaged 29.7°C (Supplementary Fig. 3). Since 2010, however, average daily maximum temperatures have increased to 30.1°C while probabilities of a nest surviving to success approached 30%. Our temperature and nest success projections for 2010–2016 bracket these later values. Second, despite multiple stochastic processes inherent in the model, the severity of declines in productivity and their ultimate effects on population growth tracked warming patterns predicted under each climate scenario, where increased severity of warming produced greater productivity declines and increased risk (Table 1). Even the midcentury asymptote in temperature, inherent in the 4.5 Representative Concentration Pathway (RCP), is evident in individual model results (Fig. 4). These patterns occurred despite holding the landscape (that is, habitat) constant, thus isolating the role of temperature in nest survival, relative to changes in habitat. And finally, we used a population model to translate productivity declines into population impacts that were robust to uncertainty in

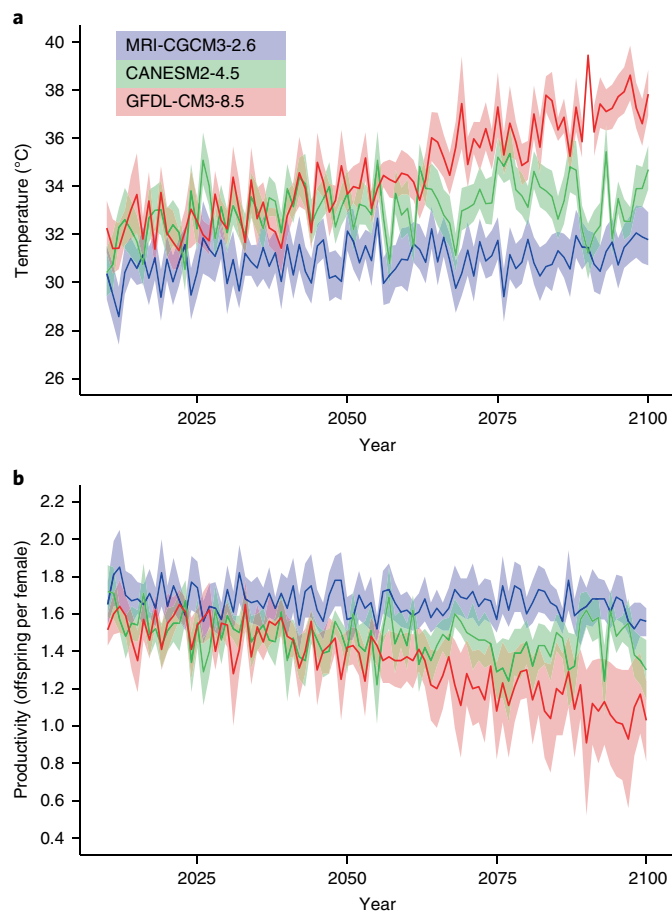


Fig. 2 | Projected mean daily maximum temperatures and estimated mean annual productivity of Acadian flycatchers. a, b, Projected mean daily maximum temperatures during the breeding season (15 May to 15 August) (**a**) and estimated mean annual productivity of Acadian flycatchers (**b**) across the Central Hardwoods from 2010 to 2100 under three scenarios for future climate change. Projections were derived from an IBM that simulated the effects of future temperature and precipitation under mild (MRI-CGCM3-2.6), moderate (CanESM2-4.5) and severe (GFDL-CM3-8.5) climate scenarios on nesting. Mean productivity reflects the average of individual productivity estimates weighted by habitat quality as conveyed through carrying capacity. Shaded ribbons span 1 s.d.

adult and juvenile survival. In actuality, these constraints probably provided an optimistic estimate of risk, as even the lowest survival rates we considered were reasonable based on the current songbird literature. Furthermore, it is possible that these rates will also be negatively affected by climate change, through changes in habitat, phenology, food availability or species interactions^{12,22}. Where data are available, these processes should be considered.

Although changes in overall climate means, variation and extreme events are often the focus when predicting impacts on species, the results from our IBM of flycatcher nesting demonstrate that substantial population impacts can stem from seemingly intricate changes. For example, nest survival declined by >60% despite a smaller 20% increase in mean temperatures under severe climate warming, largely because of the cumulative effects of elevated daily temperatures across the 32-day periods each nest must endure throughout each breeding season (Supplementary Fig. 5). Similar patterns are seen in other ecological processes and systems as well (for example, the effects of weekly temperature extremes on Bobwhite quail survival²³ and consecutive dry days on tree mortality and forest composition²⁴). Thus, changes in climate

patterns can be just as important as changes in magnitude. At the same time, processes such as temperature's influence on nest survival can be offset in complex ways by traits such as behaviour¹⁸. The propensity of Acadian flycatchers to renest following a failed attempt mediated the declines in daily nest survival, resulting in relatively smaller declines in productivity than would have otherwise occurred (Supplementary Fig. 5). This example of phenotypic plasticity demonstrates an adaptive capacity of flycatchers to mitigate climate change impacts¹⁷. These results highlight the nuanced nature of climate impacts and the importance of examining ecological processes at the scales with which they interact with climate.

Certain key assumptions inject uncertainty into our models. First, our projected outcomes are based on past relationships that we applied to future conditions, and it is appropriate to question the stationarity of those processes. The most likely mechanism underlying the temperature effect on nest survival is the increased predation by snakes (a major nest predator in the Central Hardwoods) with increasing ambient temperatures due to increased metabolic rates and mobility^{13,15}. However, declines in nest survival may lessen if snake predation plateaus under climate change as more days exceed temperatures at which snakes begin reducing activity (>35 °C)^{14,15}. By contrast, metabolic requirements also increase for endothermic predators such as small mammals¹³. Climate warming might also affect the demographics and growth of snake populations, which could affect predation levels. We modelled climate's effects assuming a constant landscape. This assumption allowed us to better distinguish the effects of climate change from those of land-use change, but it will certainly be violated. Rather, changes in climate and landscape are likely to interact with other processes to affect nest productivity, alter the amount of available habitat, and impact flycatcher population growth^{12,25}. Furthermore, survival throughout the full annual cycle is a major driver of population change in short-lived species²⁶. Therefore, a more complete assessment requires improved understanding of all demographic processes and their interactions during the breeding, wintering and migration periods under climate change²⁷. Finally, a century is a long time for animals to evolve in response to environmental change and adaptations could play a large role in the long term²⁸. Thus, more information on demographic processes is needed to more comprehensively assess risk to flycatchers.

Despite this uncertainty, a potential drop in population of more than 3.7 million female flycatchers within less than a century constitutes a decline that is both substantial and rapid. Demographics are a critical aspect of assessing vulnerability and designing conservation actions because of the sensitivity and speed at which populations respond to their changes^{22,29}. Our results reinforce this idea and serve as a warning that diligence will be required to identify and manage threats of this nature. Much focus is given to the impacts of climate change on the distribution of habitats⁸. However, we projected flycatcher declines even with adequate habitat, indicating that assessing vulnerability through only the lens of habitat could leave wildlife populations at risk¹. Moreover, these projections question the effectiveness of habitat management alone in conserving populations when demographics are affected. We suggest more attention should be given to the mechanisms by which climate affects vital rates, interspecies interactions, and other demographic processes if we are to have a realistic understanding of the threats facing species and how to address them.

The threat climate warming poses for flycatcher productivity presents a formidable challenge to ensuring the viability of the Central Hardwoods population. However, the more we understand the mechanisms through which climate change threatens populations, the more we increase our ability to plan conservation to address those threats. Habitat restoration for the sake of more habitat may not effectively offset impacts to reproduction. However, restoration that reduces forest fragmentation and decreases edge could reduce predation and

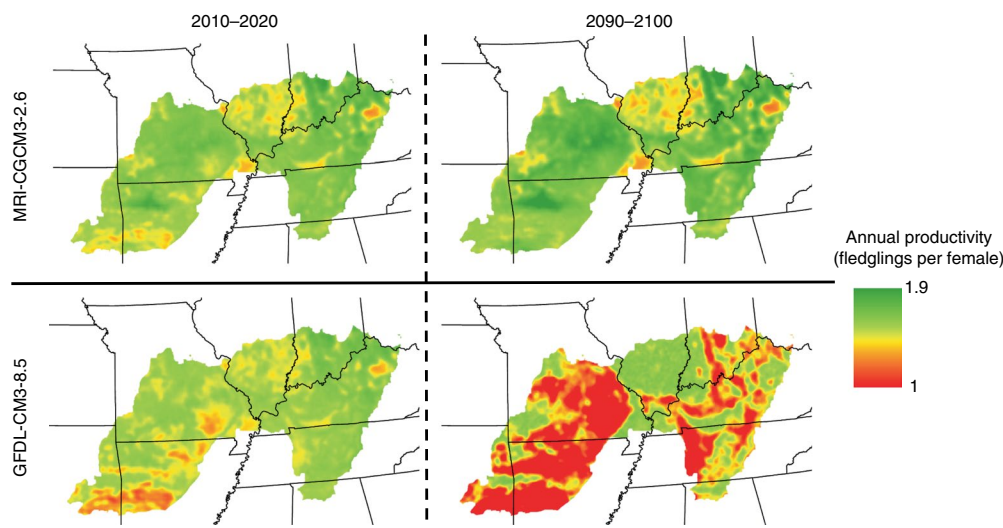


Fig. 3 | Predicted annual productivity for Acadian flycatchers in territories throughout the Central Hardwoods under climate change. Maps indicate spatially explicit changes in annual productivity (averaged over two time periods) under a mild (MRI-CGCM3-2.6) and a severe (GFDL-CM3-8.5) climate change scenario. The greatest declines in productivity under severe warming occurred in landscapes with the most forested habitat (reddened areas of map), thus increasing the impact on population growth.

Table 1 | Estimated risk for the Central Hardwoods population of Acadian flycatchers in the twenty-first century according to different climate scenarios

Climate scenario	Increase in temperature (°C)	Median abundance in 2100	Probability of 95% decline (%)	Probability of quasi-extinction (%)
MRI-CGCM3-2.6	1.1	901,453	56	9
CanESM2-4.5	1.3	441,847	66	30
GFDL-CM3-8.5	5.0	173,301	67	34

Climate scenarios consider combinations of CMIP5 general circulation models and representative concentration pathways (RCPs) to bracket a range of future climate warming, indicated by the average increases in the daily maximum temperatures during the breeding season during the beginning (2010–2016) and end (2090–2100) of the twenty-first century. The scenarios represent mild (MRI-CGCM3-2.6), moderate (CanESM2-4.5) and severe (GFDL-CM3-8.5) levels of climate warming. Risk estimates during this century are pooled across all combinations of adult and juvenile survival and include the median abundance of females in 2100, the probability (%) of female abundance falling below 95% of its initial value, and the probability (%) of quasi-extinction, defined as total females declining below 10,000 individuals (a 99% decline). The initial population began with 3,986,336 females.

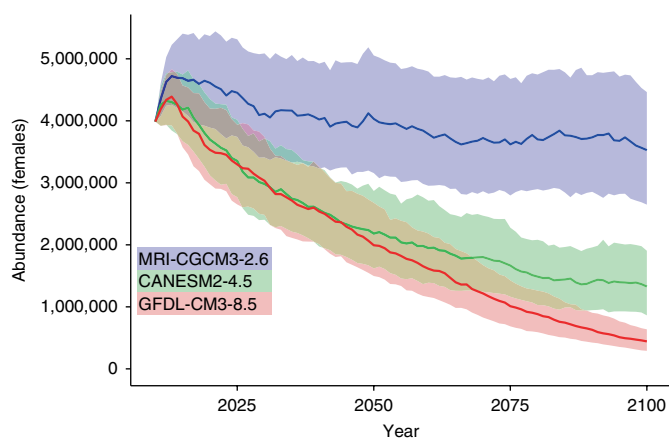


Fig. 4 | Projected declines of the population of Acadian flycatchers in the Central Hardwoods under future climate change. A DLMP was used to examine the impacts of decreased productivity under mild (MRI-CGCM3-2.6), moderate (CanESM2-4.5) and severe (GFDL-CM3-8.5) climate warming. After estimating the carrying capacity and initial distribution across the region, the landscape and habitat were held constant to isolate the effects of temperature on reproduction in driving population declines. The projections shown assume 66% and 46% annual adult and juvenile survival, respectively. Shaded ribbons span the 20th and 80th percentiles.

brood parasitism rates and improve productivity^{29,30}. The scale of this threat could necessitate a comprehensive approach that targets other demographics. For example, analyses have demonstrated the power that reducing mortality can have on songbird populations in this region²⁹. Finally, our projections demonstrated the potential for the flycatcher productivity and population growth to respond if emissions and warming can be curtailed. Therefore, a primary source of uncertainty in the risk facing flycatchers of the Central Hardwoods is the degree of emissions and climate warming that transpires³¹.

Methods

Methods, including statements of data availability and any associated accession codes and references, are available at <https://doi.org/10.1038/s41558-018-0232-8>.

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Author contributions

All authors contributed to the design of the analysis. T.W.B. and W.A.C. developed the individual-based model. T.W.B. developed the metapopulation model and performed the analysis. All authors contributed to drafting of the manuscript.

Additional information

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Methods

Study context. We focused on the population of flycatchers in a 39.5 million ha (395,519 km²) portion of the Central Hardwoods forest in the centre of the USA. The area encompasses portions of 10 states and a variety of vegetation, terrains, soils and climates³². The topography varies from relatively flat Central Till Plains to open hills and irregular plains (for example, Interior Low Plateau), to highly dissected Ozark Highlands. The region supports a diversity of forest ecosystems, including upland oak (*Quercus* spp.)–hickory (*Carya* spp.) forests and oak–pine (*Pinus* spp.) forests, with less common woodlands, glades and savannas. The area is in the Central Interior Broadleaf Forest Province of the Hot Continental Division and the climate has been continental with long, hot summers and cool winters. Mean annual temperatures range from 12 to 16 °C, with the warmer temperatures in the south. Annual precipitation ranges from 115 cm in the northwest to 165 cm in the southeast, occurring mostly in spring and autumn³³.

Acadian flycatchers are long-distance migrants that breed in mature deciduous forests in the forested landscape of the eastern USA³⁴. Usually associated with water and found in bottomland forests, along riparian strips of small and large streams, the species is area-dependent and sensitive to forest fragmentation^{34–36}. It experiences high rates of parasitism by brown-headed cowbirds (*Molothrus ater*) and nest predation in small forest fragments³⁷. Breeding Bird Survey data suggest that Acadian flycatcher populations are relatively common and stable over their range, following declines through the early twentieth century³⁸. Current estimates indicate that the Central Hardwoods population has been growing 1% annually over the last decade.

IBM of productivity. IBMs provide the framework for estimating population-level changes that emerge from individual-level ecological processes involving traits and behaviours². They have been used to model reproduction in songbirds and can account for variability among individuals in nesting behaviour to achieve unbiased estimates of productivity^{39,40}. In our IBM, we applied empirical nest survival models² to spatio-temporal data on habitat and climate under future emissions scenarios to simulate nesting activity across the Central Hardwoods during each breeding season from 2010 to 2100. The model followed individual flycatcher pairs in territories throughout each season on a daily basis as they attempted to successfully nest and produce fledglings. We defined annual productivity as the number of female fledglings produced per breeding female per season. Productivity depended on multiple processes, including (1) the survival of nests for the duration required for broods to fledge, (2) the number of fledglings per brood, (3) the length of the breeding season and (4) the probability of re-nesting as a function of ordinal date and a prior nest's fate. We simulated these processes using empirical models of daily nest survival and brood size for this species.

We modelled nesting activity in territorial grid cells across the Central Hardwoods region during annual breeding seasons. We set the length of breeding season at 93 days (15 May–15 August) based on observations for flycatchers³⁴. We simulated territories using a cell size of 120 m (1.4 ha) to reflect estimates of territory size for the species³⁴. Thus, each cell in the landscape comprised an individual territory. We assumed that birds in each territory began constructing nests on 15 May and allowed 5 days before egg laying. We allotted 3 days for egg laying, 14 days for incubation and 14 days for nestling care. Overall, we assumed nests successfully fledged young on day 32. Re-nesting attempts began 4 days following a failed nest to allow for a new nest to be built, and 7 days following a successful nest to also allow for a short period of post-fledging care by adults before a second brood attempt was initiated. Initiation of a second brood was modelled as a Bernoulli process with a probability based on the day of the year. We estimated this probability by fitting a logistic model between observations of whether or not flycatcher pairs attempted second broods and the day of completion of their first nest using data from ref. ⁴¹. The estimated model demonstrated declines in the propensity to attempt a second brood after June. We allowed an unlimited number of re-nesting attempts until 19 July (<31 days before the end of the season) because flycatchers rarely attempt new nests after mid-July⁴¹ (model code is provided in the Supplementary Information).

We simulated the fates of nests each day based on the probability of nest survival estimated from a model developed by Cox et al.³, who used 20 years of nest-monitoring data on more than 1,000 nests from study sites across a gradient of habitat fragmentation in Missouri, USA, to investigate the relative influence of weather variables and landscape factors on nest survival and brood size. They found that increased temperatures interacted with landscape forest cover and edge density to reduce nest survival according to a logistic exposure model:

$$\begin{aligned} \phi = & -1.4995 + 0.154(\text{Incubation}) + 0.182(\text{Nestling}) \\ & + 10.976(\% \text{ Forest}) + 0.052(\text{Edge}) + \\ & - 0.126(\% \text{ Forest} \times \text{Edge}) + -0.230(\text{Precip}) \\ & + 0.039(\text{MaxTemp}) + 0.008(\text{Day}) + \\ & - 0.127(\% \text{ Forest} \times \text{MaxTemp}) + -0.0001(\text{Edge} \times \text{MaxTemp}) \\ & + 0.001(\% \text{ Forest} \times \text{Edge} \times \text{MaxTemp}) \end{aligned}$$

The negative effect of temperature was greatest in landscapes with high forest cover and low edge densities. They also observed that extreme precipitation events

reduced nest survival. Other factors affecting survival included the day of season and nesting stage (laying, incubation and nestling).

We incorporated daily total precipitation and daily maximum temperature into nest survival using spatially explicit, downscaled climate predictions, based on three combinations of CMIP5 general circulation models and representative concentration pathways (RCPs). We considered the MRI-CGCM3, CanESM2 and GFDL-CM3 models to reflect the increasing sensitivity of summer temperatures¹⁹. We paired these models with the three RCPs that represented +2.6, +4.5 and +8.5 W m⁻² of relative forcing by the end of the century. Thus, we bracketed mild to severe predicted increases in summer temperatures in the region. For example, the GFDL-CM3-8.5 scenario reflects a business-as-usual path and projects a 7.55 °C (25%) increase in the mean daily maximum breeding season temperature across the region by the end of the century (2090–2100) over the recent past (1981–2010) (Fig. 1). By contrast, emissions in the MRI-CGCM3-2.6 and CanESM2-4.5 scenarios stabilize at different points, then slowly decrease after the middle of the twenty-first century²⁴, approaching the respective 1.5 °C and 2 °C increases. We obtained the daily CMIP5 climate projections, downscaled to 1/12th km resolution for the Central Hardwoods region for the period 2010–2100 from the US Department of the Interior (http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/)⁴². For each year, we extracted daily precipitation and daily maximum temperature predictions for each territory on each day during the breeding season. We constrained projected daily maximum temperatures to <38.9 °C (102 °F), the maximum temperature observed by Cox and colleagues³.

In addition to climate, we based nest survival predictions on forest cover and edge density values for each territory, the current stage of nesting, and day of year, because these factors also affect nest survival³. Replicating the original model, we estimated forest cover variables based on National Land Cover Data (NLCD)⁴³. We estimated the percent of forest within 10 km and the density of forest/nonforest edge within 500 m through focal analyses in ArcGIS 10.3 (ESRI 2012). Cox and colleagues chose these variables because they best explain variation in nest predation across fragmented landscapes and proximate to edges³.

We derived stochastic estimates of nest survival (NS_d) on each territory for each day given the surrounding landscape, the predicted temperature and precipitation on that day, the day of year, and the current stage of nesting. We maintained a constant landscape for all future projections because we wanted to focus on the potential effects of climate on a population while controlling for landscape change. We randomly sampled survival predictions (ϕ) from a normal distribution with mean and variances estimated using the nest survival model and its associated variance–covariance matrix on the linear scale. We simulated the fate of the nests as Bernoulli trials by transforming predictions into survival probabilities on the logit scale:

$$NS_d = \frac{e^{\phi}}{1 + e^{\phi}}$$

We estimated brood sizes for completed nests using additional models developed by Cox and colleagues³ that associated the number of young produced in a successful nest with the surrounding forest cover and cowbird parasitism status (whether the nest was parasitized)³. Parasitism status had a pronounced influence on the number of fledglings; flycatchers fledged 36% fewer young in parasitized than in unparasitized nests. Fledging brood size was also lower in less forested landscapes independent of parasitism. We sampled brood sizes from Poisson distributions with means estimated by the brood size model. Because these estimates require specification of the parasitism status of nests, we simulated parasitism across nests as a Bernoulli process with probabilities based on a logistic function that demonstrated increased risk of parasitism with increasing edge density and decreasing forest cover in the surrounding landscape. We constrained Poisson samples to a maximum of four young per nest to reflect the biological limitations of this species³⁴.

We estimated variance in predictions of annual productivity by conducting 10 independent replicates of the IBM in each year. In each replicate, we summed brood sizes across completed nests in each territory (that is, cell) throughout each season and calculated the mean and standard deviation (s.d.) across replicates to project annual productivity and variance throughout the Central Hardwoods from 2010 to 2100 under varying levels of climate change. We programmed the IBM in R v3.0.1 (R Core Team, 2015, <https://www.r-project.org/>; see Supplementary Information for code).

DLMP model. We evaluated the impacts of future productivity under climate change on flycatcher population viability by integrating productivity projections into a DLMP model developed for flycatchers in the Central Hardwoods. This approach provides the means to understand the impacts of climate and landscape change on the viability of wildlife populations by linking local climate, habitat and landscape patterns over time to regional population dynamics⁴. The process centres on the integration of habitat models with climate and landscape data to project species' habitat and demographics over time. Estimates of demographics across the region and over time are summarized within 87 subpopulations, delineated from ecological subsections, to parameterize a metapopulation model that includes stochasticity and uncertainty²⁶ (Supplementary Fig. 1).

Habitat model. Within the DLMP we estimated the distribution of initial abundance (N_0) and carrying capacity (K) of flycatchers using a multiscale Habitat Suitability Index (HSI) model⁴⁴. Habitat suitability models use a conceptual, meta-analytic approach that incorporates published findings across a range of studies to predict suitability sites⁴⁵. Previously developed specifically for the Central Hardwoods, the HSI indexed the suitability of 30×30 m cells based on the habitat attributes of the cell and the surrounding landscape⁴⁴. The model has been independently verified and validated with data from the North American Breeding Bird Survey, a long-term, large-scale bird monitoring programme⁴⁶.

The flycatcher HSI model includes seven variables: landform, landcover type, forest successional age class, distance to water, canopy cover, forest patch size and percent forest in a window of 1 km radius. Suitability first considered combinations of landform, landcover and successional age class on the basis of reported habitat associations with mature stands of bottomland and riparian forests along drainages^{34,44}. The HSI models predict a value between 0 and 1, where 0 represented non-habitat and 1 optimal habitat. An inverse logistic function is used to represent Acadian flycatcher's association with water, where cells greater than 200 m from water presented lower suitability. The model also includes a logistic relationship with canopy cover because of the strong affinity of this species for closed-canopy forests. Finally, an interaction between forest patch size and percent forest within 1 km is used to account for the tradeoff of small habitat patches in predominately forested landscapes and large habitat patches in non-forested landscapes.

We derived landcover and forest data from the 2011 NLCD. We used 2011 canopy cover estimates from the Multi-Resolution Land Characteristics Consortium⁴³. We classified successional age by estimates of tree diameter, derived from imputation techniques on Forest Inventory and Analysis data and MODIS (moderate resolution imaging spectroradiometer) imagery⁴⁷. We used a landform classification derived from a digital elevation model (DEM)⁴⁸ and measured distance to water based on the National Hydrography Dataset⁴⁹.

The model calculates carrying capacity K for each subpopulation (K_p) by first calculating K of each 30×30 m cell (K_c). Although the IBM used a cell size of 120 m, a smaller cell size is used in the DLMP model to capture the habitat and landscape patterns that vary at this resolution. The model assumes bird density reaches its maximum where HSI=1 (implying that densities are highest in the best quality habitat) and declined linearly to zero pairs per ha where HSI=0. We set bird density in the optimal habitat at 1.5 breeding females per ha based on the available literature⁵⁰. We then scaled the density by the area of cells and spatially filtered areas of the landscape that could not support at least one territory, constrained by a maximum territory size (2.84 ha)³⁴. This process more realistically captured the interaction between spatial and resource limitations inherent in estimating K . The model sets initial abundance N_0 as a percentage of K_p based on current knowledge of the status of the population in relation to carrying capacity. We set initial abundances at 30% of K based on recently observed densities^{51,52}. Estimates of K_p are obtained by summing K_c across grid cells within subpopulations (Supplementary Fig. 1). Assuming a constant landscape left K_p unchanged over time.

Reproduction and growth. We used a female-only, Lefkovich matrix model comprising adult and juvenile stages:

$$\begin{bmatrix} F_{y,p} & F_{y,p} \\ S_j & S_a \end{bmatrix}$$

where S_j and S_a are the annual survival rates for juveniles and adults⁵³. Because adult and juvenile survival estimates for flycatchers are sparse and incomplete, we conducted 121 simulations that considered 11 adult rates from 50 to 70% and 11 juvenile rates from 30 to 50%. Based on the range of published estimates for migratory songbirds, we felt these ranges adequately spanned likely flycatcher survival^{54–56}. $F_{y,p}$ is the average of annual productivity estimates produced by the IBM for adult females breeding throughout subpopulation p in year y . The model averages productivity values across all cells in each subsection weighted by the density of pairs they contain, assuming that the relative effect of productivity in an area has on the entire subpopulation is conditional on the proportion of breeding that occurs in that area.

Dispersal. We modelled dispersal in the same way as in ref. ²⁶ by combining assumptions about the proportion of each subpopulation that dispersed with relative estimates of the cell-based movements of those dispersers to the surrounding landscape. The model assumes that dispersal rates are stage-specific, with 90% of juveniles and 10% adults dispersing, and multiplies each subpopulation's stage abundances by their respective dispersal rates to identify the proportion of that population dispersing each year. Exchanges of dispersers among subsections are calculated on a relative basis by summarizing cell-scale movements such that the rate of dispersal from any starting subsection (p) to any destination subsection (p') is calculated as

$$\omega_{p',p} = \sum_{c' \in p'} \sum_{c \in p} K_{c'} m_{c',c}$$

where $K_{c'}$ is the carrying capacity of the destination cell and $m_{c',c}$ is the rate of movement from a starting cell in the starting subsection. Movement to surrounding cells decreased with distance according to a negative exponential function:

$$m_{c',c} = \begin{cases} e^{-\frac{d(c',c)}{b}} & \text{if } d(c',c) > D_{\max} \\ 0 & \text{if } d(c',c) = D_{\max} \end{cases}$$

where $d(c',c)$ is the distance between the starting and destination cells, b is a constant representing the average dispersal range observed for the species, and D_{\max} is the maximum dispersal distance allowed. The average dispersal range is set at 70 km (ref. ⁵⁷), with D_{\max} twice that of b to permit some larger dispersal movements that seemed reasonable for a migratory songbird. Because subpopulations at K could still receive immigrants, the K weighting added a density-dependent component to dispersal. We assumed no dispersal mortality aside from that incorporated into the stage survival rates. Summarizing K -weighted, cell-level movement rates by subsections enables the model to realistically account for distance- and habitat-dependent dispersal among subpopulations as large and irregularly shaped as ecological subsections (Supplementary Fig. 2). Much of the dispersal actually occurred within the same subpopulations.

Density dependence and stochasticity. We programmed the population model in R v3.0.1 and incorporated density dependence, stochasticity and correlation. See Supplementary Information for the R code for the DLMP model. We used a modification to the commonly referred to ceiling density dependence⁵⁸ such that individuals over K in a population were prohibited from breeding but could remain in the population or disperse²⁹, as nonbreeding 'floater' adults are relatively common in passerine populations^{59,60}.

We quantified viability or risk by using Monte Carlo sampling to induce parameter uncertainty and stochasticity in our population dynamics⁶¹. We simulated parameter uncertainty by sampling a different survival rate in each iteration from a beta distribution with mean set as the overall estimate and corresponding variance of 0.005. In each iteration, the rate drawn was used to construct a second beta distribution, from which annual survival could be drawn. We captured environmental stochasticity by basing variances for the second distribution on the amount of temporal variation in survival observed from field data. We assumed that adult and juvenile survival varied annually by 10% and 25%, respectively. Patterns in annual survival rates were correlated among subpopulations at the rate

$$\rho_{ij} = e^{\left(\frac{-D_{ij}}{140}\right)}$$

based on the distance between them (D_{ij}). We also drew annual productivity rates from a lognormal distribution with mean and standard deviation corresponding to the IBM predictions for each subpopulation. In each year we modelled demographic stochasticity by drawing the number of survivors and the number of young produced in each stage each year from binomial and Poisson distributions, respectively. We ran 1,000 simulations for each adult and juvenile survival combination under each climate change scenario.

Data availability. Daily CMIP5 climate projections are available from the US Department of the Interior (http://gdo-dcp.uclnl.org/downscaled_cmip_projections/). The authors declare that all other data supporting the findings of this study are available within this Letter and its Supplementary Information files, or are available from the corresponding author on request. The data sets generated during the current study are available from the corresponding author on reasonable request.

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