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Demographic consequences of phenological asynchrony for North American songbirds

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Changes in phenology in response to ongoing climate change have been observed in numerous taxa around the world. Differing rates of phenological shifts across trophic levels have led to concerns that ecological interactions may become increasingly decoupled in time, with potential negative consequences for populations. Despite widespread evidence of phenological change and a broad body of supporting theory, large-scale multitaxa evidence for demographic consequences of phenological asynchrony remains elusive. Using data from a continental-scale bird-banding program, we assess the impact of phenological dynamics on avian breeding productivity in 41 species of migratory and resident North American birds breeding in and around forested areas. We find strong evidence for a phenological optimum where breeding productivity decreases in years with both particularly early or late phenology and when breeding occurs early or late relative to local vegetation phenology. Moreover, we demonstrate that landbird breeding phenology did not keep pace with shifts in the timing of vegetation green-up over a recent 18-y period, even though avian breeding phenology has tracked green-up with greater sensitivity than arrival for migratory species. Species whose breeding phenology more closely tracked green-up tend to migrate shorter distances (or are resident over the entire year) and breed earlier in the season. These results showcase the broadest-scale evidence yet of the demographic impacts of phenological change. Future climate change–associated phenological shifts will likely result in a decrease in breeding productivity for most species, given that bird breeding phenology is failing to keep pace with climate change.

phenological mismatch | phenology | demography | green-up | climate change

Significance

Changes in phenology—the timing of seasonal events—are among the most pronounced ecological responses to climate change. Scientists are concerned that differential phenological responses across trophic levels could have negative consequences for animal populations, but widespread evidence is lacking. Here, we present evidence of a link between reproductive productivity and the timing of both bird breeding and the arrival of spring across the North American continent. These findings, which are the broadest yet in extent, in conjunction with evidence that bird phenology is not keeping pace with climate change, suggest that future phenological change will likely result in negative demographic consequences for these birds.

One of the clearest ecological responses to climatic change has been a large-scale shift in the timing of seasonal ecological events, known as phenology (1, 2). Variation in the magnitude and direction of these shifts across taxa and trophic groups has raised concerns that ecological interactions are becoming increasingly decoupled in time (3), with the potential to negatively impact vulnerable species and ecological systems (4). For example, depressed survival or breeding productivity might be expected if organisms mistime their breeding events in such a way that periods of peak resource requirements do not match periods of peak resource availability or favorable environmental conditions (5, 6).

Despite a large body of theoretical work that predicts substantial ecological consequences of phenological change (7–10), empirical evidence of these negative outcomes is mixed (11–13). While several canonical examples of demographic linkages to phenological asynchrony have dominated the literature, such as that between the great tit (*Parus major*) and its principal food resource, the winter moth caterpillar (*Operophtera brumata*) (14, 15), this pattern has not been well demonstrated across broad suites of species. This is particularly true in systems where food web complexity provides substantial substitutability in trophic resources and when considering responses at the population, rather than individual, level. Lack of relevant long-term, multispecies datasets across broad extents has impeded the testing of theoretical predictions at large scales (13, 16), with many studies limited by small spatial and taxonomic scope (12).

Understanding the links between phenology and demographic processes is critical to predicting the future response of species to ongoing climatic change. For North American birds, many of which have undergone large-scale phenological shifts over the last several decades (17–19), this is a topic of particular concern. Findings that avian species are not keeping pace in their migration with the rate of climatic change (20) have motivated concern that precipitous declines in abundance over this time period (21) may be, in part, due to phenological dynamics. Additionally, the demographic consequences of phenological change on the breeding grounds may differ between migratory and resident species, as migratory species are likely more constrained in their ability to adjust their breeding to meet fluctuating phenological conditions.

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Here, we assess how phenological dynamics impact the breeding productivity of 41 species of passerine birds, from long-distance migrants to residents, breeding in and around forested areas across a large portion of the North American continent from 2001 to 2018 (Fig. 1*A* and *SI Appendix*, Table S1). Using data on the phenology of both bird breeding and vegetation green-up, we derived two phenological indices using a principal component analysis (Fig. 1*B*). We quantified annual variation in overall phenology using an Early/Late Index—a measure of an ecosystem's overall phenology in a given year (i.e., the degree to which both bird breeding and green-up were early or late relative to the mean across years for a given location and species). Similarly, we quantified the relative asynchrony between bird breeding and green-up in a given year using an Asynchrony Index (i.e., the difference between bird breeding and green-up relative to the mean difference across years for a given location and species). The Asynchrony Index is a relative measure, so values of 0 indicate average synchrony between bird breeding and green-up, rather than absolute synchrony. These indices allow us to decouple the overall early or late timing of a year from phenological asynchrony. Timing of breeding was estimated from nearly 150,000 captures from the Monitoring Avian Productivity and Survivorship (MAPS) program (22), a continental-scale, constant-effort, bird-banding project with standardized protocols across locations and for the duration of this study. Our metric of location-specific breeding phenology was derived for each species by calculating the average initial capture date of juvenile birds at a banding station. Vegetation green-up, a metric of the onset of spring conditions (23) correlated with the timing of insect food resources for breeding birds (24), was estimated using satellite data (25). Taking this approach, we were able to parse—for every species, year, and location—the effects of early and late years from the effects of asynchrony. Breeding productivity was modeled as the proportion of total unique birds captured that were juveniles for a given species, location, and year, using a binomial distribution. We were able to quantify relationships across our entire bird community using a flexible hierarchical Bayesian approach that incorporated varying intercepts and varying slopes (i.e., random effects) to account for variation across both space and species. This allowed us to focus on the impact of phenological variation across time for a given species–location combination, hereafter species/location. Using our model, we estimated the extent to which these birds are experiencing phenological mismatch, defined as lower breeding productivity for a given species/location under certain phenological conditions. We additionally estimated how closely bird breeding phenology is tracking interannual fluctuations in green-up (i.e., the sensitivity of breeding phenology to green-up), how breeding sensitivity compares to the sensitivity of arrival phenology (20), and how future phenological changes, in response to ongoing climate change, might impact the breeding productivity of these species.

Results and Discussion

Demographic Consequences of Phenology. On average, across the 41 species analyzed in this study, we found that both the Early/Late Index (μ_{β_2} Eq. **4** = −2.41, 89% CI: [−3.55, −1.30], $p(\mu_{\beta_2} < 0) = 1$; *SI Appendix*, Fig. S3) and the Asynchrony Index (μ_{γ_2} Eq. **4** = −2.80, 89% CI: [−3.90, −1.68], $p(\mu_{\gamma_2} < 0) = 1$; *SI Appendix*, Fig. S3) had a hump-shaped (i.e., concave-down) relationship with breeding productivity (Fig. 2 *A* and *B*), indicating local maxima in productivity as a function of relative crosstrophic phenology. Note parameter estimates are on the logit scale. Breeding productivity was maximized for a given species/location: 1) when both bird breeding and green-up were not particularly early or particularly late and 2) when the synchrony between bird breeding and green-up corresponded to relatively average conditions.

This generalizable hump-shaped relationship between breeding productivity and the Early/Late Index illustrates the importance of the overall timing of phenological events in a given year, irrespective of the degree of asynchrony. A demographic peak near average conditions may be due to harsh weather conditions which might be more likely to occur in very early (near the beginning of the breeding season) or very late (near the end of the breeding season) years (26). These weather events might lead to decreased total availability of food resources (27), or have a negative impact on the survival of eggs or young (28, 29). Another possibility is that in these very early or very late years, birds may alter their migratory behaviors in a way that impacts breeding productivity—previous work has shown that increased migration speed to "make-up" for a late overwintering ground departure may be linked to lower survival rates (30). The consequences of these early/late years may differ among regions within a species' range (28), though we are able to assess these impacts only at the range-wide level in this study.

This broad-scale hump-shaped relationship between phenology and breeding productivity is potentially contrary to what has been observed at the individual level, where the earliest breeding

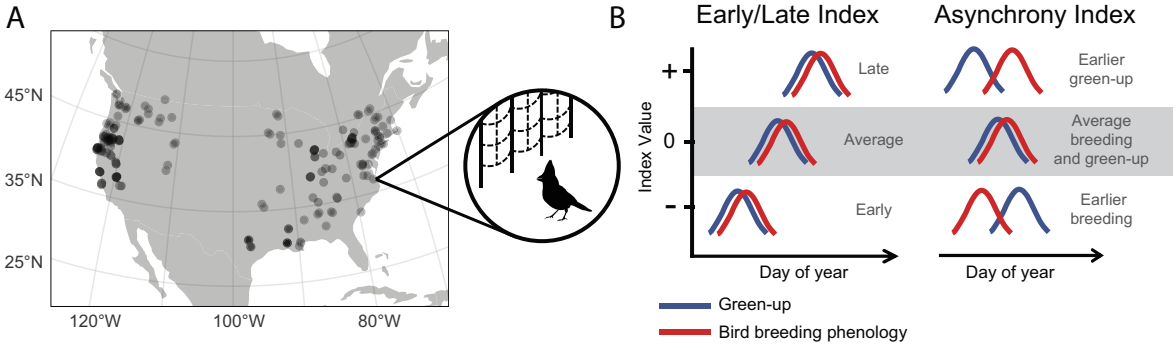

Fig. 1. Bird capture data from across North America combined with satellite remote sensing allow the calculation of crosstrophic phenological indices. (*A*) Points represent bird-banding stations from the Monitoring Avian Productivity and Survivorship Program (n = 179) used in this study. (*B*) Data on bird breeding phenology and satellite-derived vegetation green-up were used to calculate two crosstrophic phenological indices using principal component analysis. The Early/Late Index indicates the degree to which both green-up (blue lines) and bird breeding (red lines) are particularly early (negative Index values) or late (positive Index values), while the Asynchrony Index indicates the degree to which bird breeding is early (negative Index values) or late (positive Index values) relative to green-up for a given species/location. In each case, these indices represent anomalies from average conditions at a given species/location.

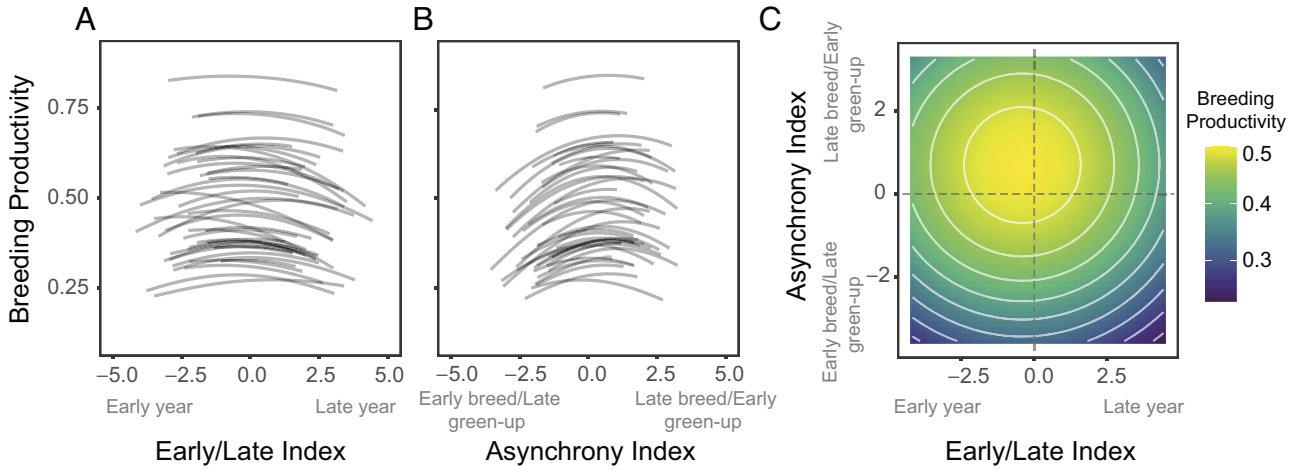

Fig. 2. Both overall phenology and crosstrophic asynchrony impact breeding productivity. Breeding productivity (i.e., the probability that a given captured bird is a juvenile) was modeled as a function of (*A*) whether multitrophic phenology occurred relatively early or late in a given year (Early/Late Index), and (*B*) the degree to which bird and vegetation phenology showed relative asynchrony in a given year (Asynchrony Index). Note the Asynchrony Index is a relative measure, rather than an absolute measure. Each line represents the fitted response for a single species, all derived from one hierarchical model. A one-unit change in the Early/Late Index in the positive direction is equivalent to green-up occurring 4.3 d later and breeding phenology occurring 4.2 d later. A one-unit change in the Asynchrony Index in the positive direction is equivalent to green-up occurring 4.3 d earlier and breeding phenology occurring 4.2 d later. Values for both indices near zero indicate mean conditions (for a given species and location). (*C*) Crossspecies estimate of breeding productivity as a function of both the Early/Late Index and Asynchrony Index illustrates phenological conditions under which productivity is maximized. Yellow regions denote higher breeding productivity, while purple hues represent lower breeding productivity. White contours show isoclines for breeding productivity. Dashed gray lines represent average conditions for each index.

individuals in a given year for a given population tend to have higher breeding productivity (31). Variation in the relative timing of individuals within a population, however, is distinct from the average timing of the population as a whole. The individual-level pattern may arise because individuals that arrive early tend to be intrinsically more fit (31), are able to more readily take advantage of resources compared to individuals that breed later (32), can have more clutches due to a longer breeding season (33), or have some combination of these factors. Of these mechanisms, only the increased capacity to lay more clutches is relevant at the population level. While longer breeding seasons may suggest that earlier years should be better for many species (due to the potential for additional clutches), the hump-shaped relationship to productivity indicates earlier years are not necessarily better (Fig. 2*A*). The potential benefits of early years could be mediated by other factors, including the increased potential for harsh weather events (26). Several species, however, did exhibit a general pattern of increased breeding productivity in earlier years, including northern cardinal (*Cardinalis cardinalis*), Bewick's wren (*Thryomanes bewickii*), and wrentit (*Chamaea fasciata*), notably all resident in the majority of their ranges. The plurality of resident species, however, did not exhibit this pattern (*SI Appendix*, Figs. S1 and S3 and Table S3).

The observed hump-shaped relationship between the Asynchrony Index and breeding productivity is consistent both with ecological theory (34) and studies on individual species of birds (15, 35). Breeding too early or too late relative to the phenology at lower trophic levels will likely result in birds missing a seasonal peak in resource availability (6). While green-up is not a perfect representation of the temporal peak in food resources, the phenology of larval lepidopterans (i.e., caterpillars), which make up the majority of the resources that these focal species rely on to feed their young (36), is associated with temporal fluctuations in vegetation phenology (24). Lepidopterans have been shown to generally track changes in the timing of their plant food resources (37, 38) in order to take advantage of more palatable early growth (39), though variation in the magnitude of responses among prey items might also result in a change in the availability of preferential prey resources (40). In some cases, the phenology of lepidopterans might be advancing even faster than green-up (41, 42), exacerbating the degree of trophic asynchrony over time. Notably, the costs of breeding too early relative to green-up are larger than those of breeding too late relative to green-up (μ_{γ_1} Eq. 4 = 2.75, 89% CI: [1.42, 4.06], $p(\mu_{\beta_2} > 0) = 1$; Fig. 1*B* and *SI Appendix*, Fig. S3). This is consistent with expectations, since the availability and quality of food resources is likely to be somewhat asymmetrically distributed across the season. Early in the spring, invertebrate prey may be limited by processes of insect emergence and development (43), while even after seasonal peaks in prey biomass, continued invertebrate reproductive cycles can sustain avian food resources for multiple broods (44).

Optimal values for the Early/Late Index and Asynchrony Index (i.e., where breeding productivity is maximized) are slightly lower (−0.39) and higher (0.88), respectively, than the mean conditions experienced from 1989 to 2018 (Fig. 1*C* and *SI Appendix*, Fig. S6). In other words, productivity is maximized near (5.5 d earlier for green-up and 2 d later for breeding phenology; *SI Appendix*, Fig. S6), but not directly at, long-term average phenological conditions, as might be expected if we assume that species are optimally adapted to their current environments. Here, optimal phenological conditions would amount to approximately 1% higher breeding productivity compared to the long-term average (*SI Appendix*, Fig. S6). While understanding species-level differences in the location and height of optima is of interest, uncertainty in the species-specific coefficient estimates makes it difficult to robustly assess how these differences might correspond to species' traits (*SI Appendix*, Fig. S3). Past work has suggested that there may be certain evolutionary conditions under which populations would be expected to breed later than the optimum (45, 46). Independent of this expectation, nonoptimally timed breeding may arise due to other factors, including unconsidered constraints that might drive the timing of breeding. That is, there may exist an "adaptive mismatch," whereby individuals miss peak resource availability due to factors that might depress breeding productivity, such as abiotic conditions (47, 48). Another possibility is that the cues that these bird species use to initiate breeding,

such as photoperiod or temperature (49), may not be perfect indicators of optimal environmental conditions.

Our results stand as one of the largest taxonomic- and geographic-scale demonstrations of the importance of phenology for demographic processes. We note, however, that both the Early/Late Index and Asynchrony Index together explained only a relatively modest degree of the temporal variation in breeding productivity (median: 4.9%; species-specific range: 1.8 to 23.5%). The magnitude of this overall effect may be tempered by the diversity of the lepidopteran communities (the primary prey resource for the young of these birds) and the multivoltine nature of many lepidopteran species across North America (50–52). If multiple prey species—or even multiple generations of a single prey species—exist, each having a different phenological "peak" over the course of a given year, resources for predators may effectively be less pulsed—a phenological version of the biodiversity insurance hypothesis (53). Differences in phenological responses among individuals (within populations) may further obscure any potential demographic signal of phenology (54), as we used population-level estimates of both breeding phenology and breeding productivity. Our results, however, highlight the importance of phenology despite the potential buffering effects of prey diversity and variation in phenological responses among individual birds. This evidence suggests that phenological dynamics deserve more widespread consideration alongside the myriad of other factors more universally well known to be important for demographic processes, such as abiotic factors (55) and overall resource availability (56).

Among-Species Sensitivity of Breeding Phenology to Green-Up. Across the 41 species evaluated here, year-to-year advances in bird breeding phenology are not keeping pace with the simultaneous advancement in green-up (Fig. 3). For every 1-d advancement in green-up, the average bird breeding phenology advanced by only 0.28 d on average (μ_θ Eq. **9** = 0.28, 89% CI: [0.25, 0.32], $p(\mu_\theta > 0) = 1$; Fig. 3 and *SI Appendix*, Fig. S4). We call this metric phenological sensitivity, where a sensitivity of one would indicate that fluctuations in bird breeding phenology perfectly match fluctuations in green-up. Interannual variation in breeding phenology (median SD across species = 5.68 d) was similar to that of green-up (5.72 d), in contrast to migration phenology where variation in green-up is larger than variation in bird arrival phenology (20). A large number of factors likely influence when a given individual breeds (57, 58), which may not necessarily be optimal for breeding productivity. Similar to studies of phenological sensitivity of migration phenology to green-up (20), these results show that birds are not responding perfectly to changes in phenology at lower trophic levels, and that the degree of phenological sensitivity varies among species. This interspecific variation in phenological sensitivity could also lead to novel competitive interactions, with potentially negative demographic consequences for some species (59).

While fluctuations in breeding phenology are not keeping pace with green-up, breeding phenology shows higher sensitivity to advancing green-up than does the phenology of migratory arrival on breeding grounds. In this study, the average migratory species advanced its breeding phenology by 0.28 d (mean of species-level posterior means $\widehat{\theta}$ Eq. **10**; 0.32 d when also considering resident species) for every 1-d advance in green-up. By comparison, in a study of some of the same migratory North American birds (20), the average species advanced its migratory arrival timing by only 0.13 d for every 1-d advance in green-up. This differential phenological advancement might be expected, as birds may directly assess conditions on the breeding grounds to determine when to initiate breeding somewhat independently of when they arrive. But, this discrepancy in phenological sensitivity between breeding and arrival also means that the period between arrival and breeding is likely to become compressed as green-up continues to advance in response to warming temperatures. This large-scale pattern is consistent with responses observed for single species in previous work (35, 60). The compression of this period may have further consequences for breeding productivity, as birds need time to establish territories and develop physiologically in preparation for egg-laying and rearing of the young (61, 62).

Species that migrate shorter distances (resident species were considered to have a migratory distance of 0-km) and that breed earlier in the season tended to be those that have higher phenological sensitivity to fluctuations in green-up (β_ζ Eq. **10** = –0.019, 89% CI: [–0.033, –0.004], $p(\beta_{\mu_\gamma} < 0) = 0.98$; Fig. 3*B*). For example, chestnut-backed chickadee (*Poecile rufescens*), a resident

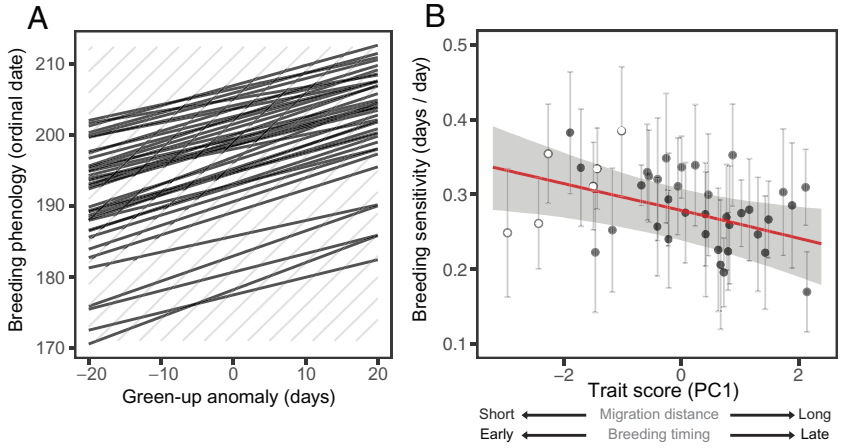

Fig. 3. Bird breeding phenology is not keeping pace with changes in green-up, yet sensitivity to green-up varies predictably across species. (*A*) Average bird breeding phenology for 41 species (black lines) shows a universally slower rate of advancement with green-up anomaly than would be expected under a scenario of perfect synchrony (i.e., 1:1 response; background gray lines). Fitted responses for each species are derived from a single hierarchical model. (*B*) Avian breeding phenology sensitivity to green-up increases as a function of migration distance and average timing of breeding. Species that migrate shorter distances and breed earlier tend to be more sensitive to changes in green-up. Points represent the posterior mean values (μ_θ Eq. **9**), while error bars represent one posterior SD. Open circles represent resident species (migration distance of 0), while closed circles represent migratory species. The red line (and corresponding 89% credible interval) represents the model fit for a phylogenetically controlled regression that also accounts for point-level uncertainty in the response.

species that breeds earlier in the year, had higher phenological sensitivity to green-up, while Swainson's thrush (*Catharus ustulatus*), a migrant that breeds later in the year, exhibited lower breeding sensitivity to green-up (*SI Appendix*, Table S3). The association between shorter migration distance and phenological sensitivity is similar to patterns observed in a prior study examining trait relationships of sensitivity in arrival phenology (20). For sensitivity of arrival timing, this previous work hypothesized that migratory distance is associated with arrival sensitivity because of a disconnect of relevant information regarding the state of phenology between where migration begins and ends. This decoupling may be carried over to the timing of breeding because durations of breeding stages (territory establishment, incubation, brooding, fledgling) are somewhat fixed (63). However, the inability of even resident species to perfectly track changes in green-up (Fig. 3*B* and *SI Appendix*, Table S3) suggests that other cues and/or constraints may prevent birds from breeding at the optimal time, even given complete access to local information.

Demographic Consequences of Continued Climate Change. Predicting how ecosystems will respond to ongoing global change represents one of the major challenges in modern-day environmental science. To interpret our demographic findings in light of future climatic change, we used our estimates of phenological sensitivity and the relationship between phenological dynamics and breeding productivity to predict the demographic effects of future climatic warming. The results show that large-scale shifts in green-up (i.e., a 25-d advance in green-up and subsequent 6.75-d advance in breeding phenology, as calculated using the average crossspecies phenological sensitivity) are expected to result in a 12% decrease in breeding productivity for the average songbird species ($\mu_{\Delta_{P_{pred}}}$ Eq. **13** = −0.12, 89% CI: [−0.20, −0.04], $p(\mu_{\Delta_{P_{pred}}} > 0) = 0.99$; Fig. 4*A*). Some variation among species exists, though productivity is expected to decline for most species given a green-up shift of this magnitude (Fig. 4*B* and *SI Appendix*, Fig. S7). While accurately forecasting the magnitude of phenological change that North American vegetation is likely to exhibit in the future is a challenging task (64, 65), phenological advancement of 25 d is within the bounds of what might be expected by the end of the 21st century. Given average projected temperature increases of 2.8 °C and 5.2 °C for the locations considered in this study under SSP2-4.5 and SSP5-8.5 IPCC scenarios, respectively, and previous estimated advancement rates of vegetation phenology (leaf-out) to temperature of approximately 6 d per °C [based on a synthesis of over 1,500 species (66)], green-up would be expected to advance 18 d and 33 d by 2,100 for the SSP2-4.5 and SSP5-8.5 scenarios, respectively (*SI Appendix*, Table S2).

Considering the importance of extreme weather events for vegetation phenology (67) and evidence that the rate of phenological change may be larger under warmer conditions (64), these estimates of potential phenological change in vegetation may be conservative (68). However, it should be noted that these changes may be buffered by other, poorly understood factors (69). Increasing variability of green-up is also expected over time (70), which may result in more years with poor breeding performance (i.e., further away from optimal values on the productivity landscape; *SI Appendix*, Fig. S6), even without considering a change in the mean timing. Estimates of phenological responses vary considerably across species and space (71, 72), posing challenges for deriving precise projections of phenological change. For this reason, we present our findings in terms of days advancement in green-up, rather than in terms of warming scenarios. To avoid projecting outside the bounds of previously observed conditions, we limit our projections to 25-d advancement in green-up, which is near the limit of phenological conditions observed in this study (*SI Appendix*, Figs. S2 and S5).

While large-scale changes in green-up are likely to result in significant consequences for breeding productivity, smaller-scale phenological shifts (i.e., < 10-d advance in green-up) might result in very little change (Fig. 4*A*). With relatively limited advancement in green-up, breeding phenology is expected to become later relative to green-up (higher Asynchrony Index values), resulting in—at least initially—phenological conditions closer to the optimal values (Fig. 2 and *SI Appendix*, Fig. S6). After this initial demographic boost, however, productivity is expected to rapidly decline (Fig. 4), moving away from optimal values on the productivity landscape (*SI Appendix*, Fig. S6). Interestingly, this observed trajectory of productivity suggests that phenological dynamics are

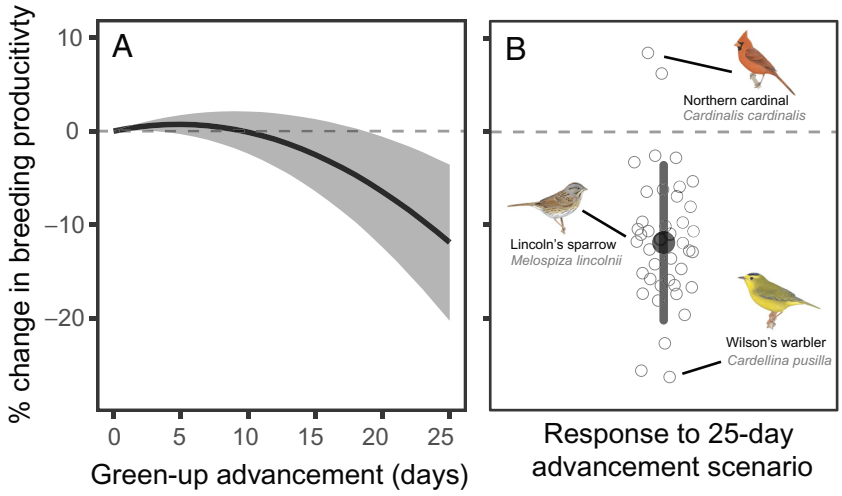

Fig. 4. Increasing green-up advancement is predicted to result in strong productivity declines under future warming scenarios. (*A*) Predicted percent change in breeding productivity given various degrees of advancement in green-up, as would be expected under a continually warming climate. The black line represents the best estimate for the community-wide trajectory, while the gray ribbon represents the 89% CI. Values below the dotted line indicate situations in which breeding productivity declines. A 25-d advancement in green-up is within the bounds of what might be expected by 2,100, given projected changes in temperature. (*B*) Species-specific percent change in breeding productivity under a 25-d advancement in green-up scenario. Each open circle is a species, with the solid dot representing the posterior median and the bar representing the 89% CI. Characteristic species are shown to illustrate average and extreme predicted productivity consequences. Bird illustrations reproduced by permission of Lynx Edicions.

unlikely to have contributed in a major way to large-scale declines observed in North American birds over the last 50 y (21). Conditions prior to the start of large-scale phenological changes that coincided with warming temperatures were likely further from optimal values compared to present day, with more positive values for the Early/Late Index and more negative values for the Asynchrony Index.

Long-term declines in breeding productivity into the future are likely to have consequences for the abundance of the bird species studied here (11), although population-level responses may be buffered by several factors (73–75), including pressures on adult and juvenile survival that might occur across the full annual cycle (76) and differences in demographic responses among individuals in a population (54). Developing a more detailed mechanistic understanding of the impacts of phenological change on demographics will be needed, if we are to forecast how the overall abundance of species will change into the future (16, 58). This understanding will likely require considering tri-trophic dynamics in this system, where the role of the spatiotemporal availability of insects (77) on demography is directly considered.

Conclusion

Characterizing demographic responses to phenological change has important implications for understanding how organisms are likely to respond to future global change. For a set of 41 North American migratory and resident bird species that breed in and around forested areas, we demonstrate that breeding productivity varies in relation to both absolute and relative phenology across trophic levels (Fig. 2), that the timing of avian breeding is not keeping pace with the rate of phenological change (Fig. 3), and consequently, that large-scale climate change–driven advancements in green-up are likely to result in future declines in breeding productivity (Fig. 4). The magnitude of these demographic changes, however, is likely to differ both within and across species, due to spatially varying abiotic environmental change (78), and predictable spatial and taxonomic variation in phenological sensitivity for birds (20) and organisms at other trophic levels (65, 79, 80). Some species, namely those that migrate shorter distances (or are resident) and breed earlier, are likely to be better equipped to cope with phenological changes at lower trophic levels (Fig. 3). Species and populations at high latitudes, on the contrary, may be more at risk, given the elevated rates of climatic change in these regions (81) and concurrent impacts associated with these abiotic changes (82). Those species found in environments with more pulsed resource availability, such as forested environments, are expected to have stronger phenological responses as well (83). Other factors, such as species' capacities to adapt via evolutionary responses (4, 84) or range shifts (28), may also determine the degree to which species might be buffered from the consequences of large-scale phenological change.

Thus far, the limited spatial and taxonomic scope of previous work (12, 13), coupled with the complexities of crosstrophic ecological dynamics, has slowed efforts to assess the importance of changes in phenology and phenological asynchrony at meaningful scales (16). We present evidence for the large-scale importance of phenological dynamics for demographic processes in North American birds and suggest mechanisms that may explain how and why responses to phenological changes vary predictably across species. Accurately assessing species' responses to climate-driven phenological change is an important piece in understanding the large-scale declines in the abundance of many species across the world (85) and in effectively implementing conservation measures to address these changes.

Methods

Bird Capture Data. We characterized bird breeding phenology using data from the MAPS program, a long-term collaborative constant-effort bird-banding program with banding stations located across North America, all following the same systematic sampling protocol (22). Data were obtained from 179 banding stations (Fig. 1*A*) from 2001 to 2018 (though most stations did not continually operate over the entire period). Only stations located at or below 50°N latitude were considered for analysis, to avoid issues with potentially very late breeding seasons at high latitudes. Each banding station consisted of 6 to 20 mist nets operated approximately every 10 d beginning as early as May 1 (start date varying slightly by location) through August 8 (ordinal dates 121 to 220 in a nonleap year) (22), which span the breeding season for most birds in North America. This protocol remained unchanged for the duration of this study. Only records from banding stations where a bird species was determined to be breeding (determined at each station by operators) were used in analyses. Only species/locations/years with at least 15 total captures, at least five of those being juveniles, species/locations with at least 5 y of data, and species with at least 15 locations/y of data were considered. The median number of location/years of data across species was 45 (range 15 to 561), representing 41 species of passerines from 13 different families (*SI Appendix*, Table S1).

Phenological Measures. Bird breeding phenology was calculated using the capture dates of juvenile birds at MAPS stations. This measure of breeding phenology is indicative of the time of year at which young birds are fledging. For each species, at each location, in each year, our metric of breeding phenology was the mean date of first capture across all juveniles captured at that station that year. Following Saracco et al. (86), we exclude subsequent captures of the same individual after its first capture. This metric of phenology differs from other commonly used metrics such as first egg date, which is commonly used for studies which employ nest monitoring–based approaches (e.g., ref. 77). While other approaches have higher precision regarding phenological estimates, our method allowed us to explore phenological dynamics across a very large spatial, temporal, and taxonomic extent while avoiding the intensive sampling required by monitoring studies.

We used green-up ("mid green-up") as our measure of vegetation phenology, derived from the Moderate Resolution Imaging Spectroradiometer Land Cover Dynamics MCD12Q2 product (25). We filtered green-up data by pixel quality, keeping only those characterized as "best" or "good," filtered by forest land cover type, as provided by the MCD12Q1 product (87), and filtered by the number of vegetation cycles, keeping only those pixels with one vegetation cycle to avoid any confounding effects that multiple green-up cycles might have on green-up for a given year. Only locations that had an average of at least 150 valid pixels in a 10-km radius were retained (approximately 12% of the 10-km radius circle around each station), effectively restricting locations to forested areas. Only those locations with green-up estimates that were equal to or later than ordinal day 60 (March 1 in a nonleap year) on average were used, to avoid erroneous green-up estimates and areas that might first "green-up" in the winter season. At each station, green-up estimates that were more than six median absolute deviations (88) away from the median were excluded, to eliminate extreme green-up outliers. The mean green-up value for valid pixels within a 10-km radius of each location was used as a measure of green-up for a given location/year.

Phenological Indices. We decomposed bird breeding phenology and green-up with a principal component analysis (PCA) into two orthogonal indices (Fig. 1*B*), as we were interested in both the overall phenology of a given year and the phenology of bird breeding relative to green-up (i.e., asynchrony). This PCA-based approach parses these two interrelated measures into independent elements, allowing us to decouple the effects of early/late years from differences in the timing of breeding and green-up, which is not possible using the raw metrics. Bird breeding phenology and green-up across years were centered for species/locations, as the optimal absolute difference between breeding and green-up might vary among species and across space. A PCA was conducted on these centered dates for all species/locations. We labeled the two principal components from this analysis as the Early/Late Index (representing a measure of how early or late both green-up and bird breeding were) and the Asynchrony Index (representing a measure of how early or late bird breeding was relative to green-up; *SI Appendix*, Fig. S9). Note that the Asynchrony Index represents relative, rather than absolute, synchrony, so a value of 0 is the average synchrony between bird breeding and green-up for a given species and location.

Modeling the Demographic Response to Phenology. We modeled breeding productivity in a hierarchical Bayesian framework using a binomial distribution, following the procedure used by (86),

$$y_{ijk} \sim binom(N_{ijk},\ p_{ijk}), \quad [1]$$

where y is the number of unique juveniles captured in year i, at location j, for species k, N is the total number of unique birds captured (juveniles plus adults) for that year/location/species, and p is the probability that a given capture is a juvenile. This measure, p, represents an index of reproductive performance, which we refer to throughout as breeding productivity. The total number of captures (N) can be thought of as the "number of trials," while the number of juvenile captures (y) can be thought of as the "number of successes." In using the binomial distribution, variation in the precision of breeding productivity (uncertainty on p) across species/locations/years is explicitly modeled and accounted for when estimating the effect of phenological covariates. We focus on the variation in this metric of productivity over time for a given species/location. Comparing patterns of productivity across space might be challenging, given species- and location-specific factors that impact the detectability of adults or juveniles. However, our analysis is robust to such variation as our models include random intercepts for each species and location to account for expected variation in productivity. Consistency in the sampling protocols at study sites helps to ensure that the detectability of juveniles relative to adults did not change over the study period for a given species/location. A logit link was used to model p as a function of covariates,

$$\begin{aligned}\text{logit}(p_{ijk}) = \alpha_{jk} + \beta_{1_k} \times EL_{ijk} + \beta_{2_k} \times EL_{ijk}^2 + \gamma_{1_k} \times AS_{ijk} + \gamma_{2_k} \\ \times AS_{ijk}^2 + \kappa_k \times EF_{ijk} + \in_{ijk},\end{aligned} \quad [2]$$

where α is the intercept (mean productivity) for each species/station, β_1 is the linear effect of the Early Late Index (EL), β_2 is the quadratic effect of EL, γ_1 is the linear effect of the Asynchrony Index (AS), γ_2 is the quadratic effect of AS, κ is the effect of effort hours (EF), and $\in$ is the residual error term, to account for overdispersion. Here, EL and AS represent the orthogonal polynomials, as produced by the "poly" function in R (89)–a standard practice for polynomial regression (90). Second-order polynomials were used, as ecological theory suggests that we are likely to see a hump-shaped relationship between these phenological metrics and breeding productivity. EF was calculated as the proportion of net-hours (total area of mist nets multiplied by the number of hours that these nets were deployed) during the period where juveniles were captured, excluding the first 2.5% of juvenile captures to remove outliers, following the procedure used by (86). The overdispersion parameter was included to account for residual variation in the model that other parameters did not capture.

Parameter α was modeled as normally distributed,

$$\begin{aligned}\alpha_{jk} &\sim N(\mu_{\alpha_k},\ \sigma_\alpha), \\ \mu_{\alpha_k} &\sim N\ (\mu_{\mu_\alpha},\ \sigma_{\mu_\alpha}),\end{aligned} \quad [3]$$

where μ_α represents the mean breeding productivity for each species, and σ_α is the SD. Parameters μ_{μ_α} and σ_{μ_α} represent the mean and SD of μ_α, respectively. Parameters β_1, β_2, γ_1, and γ_2 were modeled using a multivariate normal,

$$\begin{bmatrix}\beta_{1_k} \\ \beta_{2k} \\ \gamma_{1k} \\ \gamma_{2k}\end{bmatrix} \sim MVN\left(\begin{bmatrix}\mu_{\beta_1} \\ \mu_{\beta_2} \\ \mu_{\gamma_1} \\ \mu_{\gamma_2}\end{bmatrix}, \Sigma\right), \quad [4]$$

where μ_{β_1}, μ_{β_2}, μ_{γ_1}, and μ_{γ_2} represent the means of β_1, β_2, γ_1, and γ_2, respectively, and Σ is a 4 x 4 covariance matrix. Parameter κ was modeled as normally distributed,

$$\kappa_k \sim N(\mu_\kappa,\ \sigma_\kappa), \quad [5]$$

with mean μ_κ and SD σ_κ. Parameter $\in$ was modeled as 0-centered t-distributed,

$$\begin{aligned}\in_{ijk} &\sim t\ (\nu,\ 0,\ \sigma_{\in_k}), \\ \sigma_{\in_k} &\sim N\ (\mu_{\sigma_\in}, \sigma_{\sigma_\in}),\end{aligned} \quad [6]$$

where ν is the degree of freedom parameter which controls the normality of the distribution, and each species gets its own SD, $\sigma_{\hat{a}\in}$, which is itself modeled as normally distributed, with mean $\mu_{\sigma_\in}$ and SD $\sigma_{\sigma_\in}$.

We fit all models using the R package "rstan" to interface with Stan (91) in R (89). We used R package "MCMCvis" (92) to summarize, visualize, and manipulate all Bayesian model output and the "tidyverse" packages (93) for additional data manipulation. For all models, Rhat <= 1.01, the number of effective samples was > 400 for all parameters, and no models had divergent transitions (91). We ran this model for 5,000 iterations, with 2,500 iteration warmup. Graphical posterior predictive checks were used to ensure that the model generated data similar to that used to fit the model (94). Data simulated from the posterior predictive distribution were similar to the observed data (*SI Appendix*, Fig. S8).

We present posterior mean estimates for parameters in the main text, alongside 89% credible intervals, following the procedure used by (95). This choice is arbitrary but provides a way by which to quantify parameter uncertainty without suggesting that Bayesian credible intervals represent tests of statistical significance (which might be suggested by using 95% intervals). We also present the probability of a given parameter being positive (calculated as the proportion of the posterior distribution that is greater than zero) as P (PARAMETER > 0), or negative (the proportion of the posterior distribution that is less than zero) as P (PARAMETER < 0). Values near 0.5 indicate that positive and negative values are equally likely.

Breeding Sensitivity to Green-Up. We modeled breeding phenology as a function of fluctuations in green-up to estimate the phenological sensitivity of these species. We used an observation model to account for the uncertainty in our estimate of breeding phenology, defined as the standard error of the mean (SEM) capture date (σ_{BR}) for each species/location/year. In the cases where all juveniles for a given species/location/year were captured on the same day, an SEM of 1 was used. Breeding phenology (BR) was modeled as normally distributed, with mean η and SD σ_{BR}. Parameter η was modeled as a function of green-up, with each species/location having its own intercept and slope,

$$\begin{aligned}BR_{ijk} &\sim N\ (\eta_{ijk}, \sigma_{BR_{ijk}}), \\ \eta_{ijk} &\sim N\ (\mu_{ijk}, \sigma), \\ \mu_{ijk} &= \alpha_{jk} + \beta_{jk} \times GR_{ijk},\end{aligned} \quad [7]$$

where σ is process error, α is the species-/location-specific intercept, β is the species-/location-specific slope, and GR is green-up for each year i, location j, and species k. Parameters α and β were modeled as normally distributed,

$$\begin{aligned}\alpha_{jk} &\sim N(\mu_{\alpha_k}, \sigma_\alpha), \\ \beta_{jk} &\sim N(\theta_k,\ \sigma_\beta),\end{aligned} \quad [8]$$

with means μ_α and θ, respectively, and SD σ_α and σ_β, respectively. Parameters μ_α and θ were themselves modeled normally, with means μ_{μ_α} and μ_θ and SD σ_{μ_α} and σ_θ respectively,

$$\begin{aligned}\mu_{\alpha_k} &\sim N\ (\mu_{\mu_\alpha},\ \sigma_{\mu_\alpha}), \\ \theta_k &\sim N\ (\mu_\theta,\ \sigma_\theta),\end{aligned} \quad [9]$$

We ran this model for 5,000 iterations with a warmup of 2,500 iterations.

We were interested in the degree to which phenological sensitivity was related to species-level traits (similar to patterns found by Youngflesh et al. (20) for the sensitivity of migration phenology), namely migration distance and mean breeding phenology (i.e., whether species typically breed earlier or later in the year). For each species, we calculated migration distance as the distance between the centroids of the overwinter and breeding ranges, using existing range maps (96). Because these traits covary (correlation coefficient: 0.64), we fit a model to

regress phenological sensitivity on the first principal component (*PC*) of these variables (which represents 82% of the variation in these variables) to avoid issues of collinearity while controlling for phylogenetic relatedness among species. We considered resident species to have a migration distance of 0. We modeled the posterior mean of the estimated phenological sensitivity ($\widehat{\theta}$) of breeding phenology to green-up for each species (θ Eq. **8**) as normally distributed, with the SD represented by the uncertainty in the estimate of phenological sensitivity (posterior SD for θ, denoted as $\sigma_{\widehat{\theta}}$),

$$\begin{aligned}\widehat{\theta_k} &\sim N\ (\mu_{\theta k},\ \sigma_{\widehat{\theta}_k}),\\ \mu_{\theta k} &\sim MVN\ \left(\zeta_k, \Sigma_{\mathrm{PS}} \times \sigma_{PS}\right),\\ \zeta_k &= \alpha_\zeta + \beta_\zeta \times PC_k,\\ \Sigma_{\mathrm{PS}} &= \lambda \times \Sigma_{PD} + (1-\lambda) \times I,\end{aligned} \quad [10]$$

where α_ζ is the intercept, β_ζ is the effect of *PC* on phenological sensitivity, and σ_{PS} is the process error. Parameter Σ_{PD} is a phylogenetic covariance matrix that was standardized so that the diagonal elements are 1, and *I* is an identity matrix. The off-diagonals of this matrix represent the pair-wise phylogenetic distances between species. This matrix was calculated using a consensus phylogenetic tree calculated using the "phytools" package (97) in R, based on 100 phylogenetic trees obtained from BirdTree (98) (www.birdtree.org). Parameter λ is Pagel's lambda (99), which is representative of how the phylogenetic relatedness contributes to variation in μ_θ. Values for Pagel's lambda range between zero and one, with zero being no phylogenetic signal, and one corresponding to variation in μ_θ following a Brownian motion model of evolution (100). We ran this model for 5,000 iterations with a warmup of 2,500 iterations.

Breeding Productivity in Response to Future Changes. We projected how the Early/Late Index and Asynchrony Index are likely to change into the future, given the estimated sensitivity of breeding phenology to green-up and plausible magnitudes of phenological change into the future. To assess likely future changes in green-up, we took estimates of the rate of phenological change for plants from a large-scale meta-analysis (66) and multiplied these values by expected changes in temperature based on CMIP6 climate projections (*SI Appendix*, Table S2). These temperature projections were downscaled estimates from an ensemble of 13 CMIP6 climate models, as outlined by Mahony et al. (101). We downloaded projected temperatures at MAPS stations in the period 2,080 to 2,100 for the SSP2- 4.5 (CO2-stabilization) and SSP5-8.5 (high CO2 emission) scenarios and calculated the projected increase in temperature using historic temperature data from 2001 to 2010. All climate temperature data were obtained from the climatena.ca platform (102). We chose to use a window of 0- to 25-d advancement in green-up over which to assess changes in breeding productivity, as this was within the range of likely future change by the end of the century (*SI Appendix*, Table S2), but also within what has been observed historically over the course of this study (*SI Appendix*, Figs. S2, S5). In this way, we avoid projecting outside the range of observed conditions.

We then assessed how breeding phenology is likely to change in response to hypothetical advances in green-up. For each species, we multiplied estimates for phenological sensitivity (θ Eq. **8**) by 0 to 25 d to get projected advancement in breeding, and then calculated the corresponding Early/Late Index and Asynchrony Index given projected breeding phenology and green-up. Uncertainty in the phenological sensitivity of each species was taken into account by calculating these estimates of each iteration of the posterior for θ. These indices were then used in conjunction with estimates for the species-specific intercept for breeding productivity (μ_α Eq. **3**), and species-specific parameter estimates for the linear and quadratic effects of the Early/Late Index (β_{1_k} and β_{2_k}, respectively Eq. **4**) and Asynchrony Index (γ_{1_k} and γ_{2_k}, respectively Eq. **4**) to estimate breeding productivity,

$$\begin{aligned}logit\left(p_{pred_k}\right) = \mu_{\alpha_k} \times \beta_{1_k} \times EL_{pred_k} + \beta_{2_k} \times EL^2_{pred_k} + \gamma_{1_k}\\ \times AS_{pred_k} + \gamma_{2_k} \times AS^2_{pred_k},\end{aligned} \quad [11]$$

where p_{pred} is the predicted breeding productivity value for species *k* for a given set of predicted Early/Late Index (EL_{pred}) and Asynchrony Index (AS_{pred}) values. Uncertainty in these estimates can be accounted for by calculating estimates over each iteration of the posterior. The same procedure was carried out for the mean response of the community, using the crossspecies estimates,

$$\begin{aligned}logit\left(\mu_{p_{pred}}\right) = \mu_{\mu_\alpha} + \mu_{\beta_1} \times EL_{pred} + \mu_2 \times EL^2_{pred} + \mu_{\gamma_1}\\ \times AS_{pred} + \mu_{\gamma_2} \times AS^2_{pred},\end{aligned} \quad [12]$$

Changes in breeding productivity were calculated as a proportional change from mean conditions; that is, breeding productivity for a given advancement in green-up (ΔX, where *X* is the magnitude of the advancement) minus breeding productivity at mean conditions observed during this study ($\Delta 0$) over the breeding productivity at mean conditions observed during the study:

$$\mu_{\Delta_{p_{pred}}} = \frac{\mu_{p_{pred_{\Delta 25}}} - \mu_{p_{pred_{\Delta 0}}}}{\mu_{p_{pred_{\Delta 0}}}}. \quad [13]$$

Data, Materials, and Software Availability. Data from the Monitoring Avian Productivity and Survivorship (MAPS) program are curated and managed by The Institute for Bird Populations and were queried from the MAPS database on 2019-10-16. Data necessary to fit the models presented here have been deposited in Dryad (https://doi.org/10.5068/D1N09C) (103). All code used to produce analyses are freely available on Github (https://github.com/caseyyoungflesh/phenology_demography) and have been archived on Zenodo (https://doi.org/10.5281/zenodo.8033898) (104).

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