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Shifting Gears in a Shifting Climate: Birds Adjust Migration Speed in Response to Spring Vegetation Green-Up

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ABSTRACT

Aim: Investigate whether birds use vegetation green-up, a measure of spring arrival, as a cue to shift their migration speed in response to climate change by examining: (1) how green-up moves in the landscape, (2) how bird migratory speed responds to green-up, (3) how species traits affect migratory speed and (4) how migration speed affects arrival time at breeding sites.
Location: Eastern North America.
Time Period: 2002 to 2017.
Major Taxa Studied: Fifty-five species of eastern North American Passerines.
Methods: We calculated speed at the migration front using arrival dates derived from 16 years of eBird data with a linear regression. Similarly, we calculated the advancement speed of forest vegetation green-up using satellite data. Green-up effects on bird speed were tested using generalised additive models.
Results: On average, songbirds migrate northward during spring at a mean speed of 63 km/day. We observed strong non-linear effects of latitude, with bird migration speed accelerated and green-up speed slowed as the distance from the equator increased. Annual and spatial variation in bird migration speed depended on the local green-up date and how quickly green-up was advancing northward: years with earlier and faster green-up were associated with higher migration speeds. Bird arrival relative to green-up was strongly influenced by two variables: how early green-up was and how fast birds were migrating.
Main Conclusions: The variation of bird migration speed with green-up suggests birds can shift migration speed to 'catch up' with earlier springs. However, the stronger effect of green-up date compared to migration speed suggests that birds do not fully compensate for arrival time by simply migrating more quickly. Climate change will likely outpace birds' ability to speed up their migration and adapt to new phenological regimes.

1 | Introduction

Seasonal migration enables species to track their climatic niche in space and time as one strategy to adapt to changing local environmental conditions (Winger et al. 2019). To be successful, migratory species must be able to travel long distances and time migration to co-occur with seasonal resource needs across their life cycle (Alerstam et al. 2003; Thorup et al. 2017). Migration

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allows birds to maximise their time in favourable habitats by tracking vegetation phenology and resource availability between and across continents (Thorup et al. 2017; Winkler et al. 2014). However, climate change has created a new challenge for migratory species as it modifies the optimal timing and speed at which seasonal migrations must occur to match shifting environments. Our ability to determine what these effects are depends on our ability to quantify continental-scale migratory movements.

Birds' capacity to time their seasonal movements between breeding and wintering grounds results from their ability to process a combination of exogenous (environmental) and endogenous (circannual rhythms) cues (Cohen et al. 2012). Birds track seasonal fluctuations in weather and resource availability, aligning their migration phenology to the conditions in their breeding and wintering grounds (Stanley et al. 2012; Studds and Marra 2011; Thorup et al. 2017). Environmental factors exhibit variation from year to year, offering fine-scale information to individuals and, consequently, allowing for some degree of flexibility in the pace of migration: individuals are collecting and using information in real time (Åkesson and Helm 2020). On the other hand, reliance on internal clocks and cues that do not vary from year to year, such as photoperiod, can result in relatively rigid migration timing (Gwinner 1996; Packmor et al. 2020). The inflexibility and precision of endogenous migration triggers may be adaptive in constant climate scenarios where generations of birds have been selected for optimum arrival dates (Gwinner 1996; Newton 2012). However, endogenous mechanisms may also prevent species' adaptation to altered climate conditions as they require evolution to track the rate of environmental change (Quintero and Wiens 2013; Radchuk et al. 2019). If that is not possible, species' abilities to perceive phenological changes in the environment and flexibility to adjust migratory behaviour will determine responses to shifting climates.

As the result of a warming climate, spring arrival—measured by events such as plant budburst—has gotten earlier over time (Allstadt et al. 2015; Walther et al. 2002). In the past decades, green-up in the US has advanced around 2.5 days per decade (Jiang et al. 2023). Shifts in plant phenology may have cascading effects across trophic levels by altering bottom-up trophic interactions among taxa, resulting in a temporal asynchrony between the availability of resources and consumers' needs (Price 2002; Rosenblatt and Schmitz 2016). Fitness can be maximised when organisms match reproduction timing with the peak food availability; for birds, raising chicks under optimal conditions can increase reproductive success (Youngflesh et al. 2023). Moreover, migration energy costs make food availability in stopover locations also crucial for individual survival and migration completion (Drent et al. 2007). The rate of energy expenditure during flights is greater than the rate of energy accumulation in stopover sites for songbirds (Alerstam and Lindström 1990), directly impacting survival during migration (Baker et al. 2004; Newton 2007). Energy reserves are especially crucial for migrants crossing large inhospitable habitats (deserts and oceans): exhausted birds can settle on the ocean's surface, soak and become unable to fly again (Newton 2007). Migrant deaths due to cold weather are also associated with individuals who are light in weight and with almost no fat reserves, and it is hypothesised they starve to death or die from hypothermia (examples in Whitmore et al. 1977; Marcström and Mascher 1979).

Birds can adjust arrival time at breeding grounds in two ways: (1) by changing when they first depart from overwintering grounds to begin migration and (2) by altering how quickly they migrate through adjustments in flight speed and stop-over duration. The ability of species to alter overwintering departure time is reliant on a combination of photoperiod, circannual rhythms and local environmental conditions that cue migration (Dawson et al. 2001; Marra et al. 2005; Studds and Marra 2011). In addition, the quality of overwintering habitats plays a critical role in individuals' physical condition and, consequently, when they can start migration (Marra et al. 1998). Because environmental cues in the overwintering grounds might not accurately represent what is happening in the breeding grounds (especially for long-distance migrants), cues for initializing spring migration may not be reliable indicators of the optimal departure time. For example, the Northern wheatear (*Oenanthe oenanthe*), a long-distance European-breeding migrant, was found to use fewer extrinsic cues to inform the departure time from stop-over sites than two medium-distance migrants (Alerstam and Lindström 1990; Packmor et al. 2020).

Much of birds' ability to respond to exogenous cues to change their overall migration speed should be related to stopover ecology. Birds have multiple opportunities to adjust arrival time at breeding grounds in response to environmental cues by choosing to leave or stay at stopover grounds, allowing them to track shifting phenology due to climate change (Both 2010; Packmor et al. 2020; Winkler et al. 2014). Stopover sites represent important places where birds gather information about how fast they should be moving, in addition to refuelling energy reserves (Linscott and Senner 2021). However, the ability to shorten or lengthen stop-over duration is constrained by a combination of weather, food availability and individual energetic conditions (Goymann et al. 2010; Marra et al. 2005). The importance of stopovers for resting and refuelling may create energetic limits on an individual's ability to increase migration speed in years when green-up is earlier than expected (Schmaljohann and Both 2017).

Over the last decade, migratory birds in the eastern flyway of North America have begun arriving increasingly later in their breeding grounds relative to when vegetation green-up occurs (Buskirk et al. 2009; Mayor et al. 2017; Youngflesh et al. 2021; Zelt et al. 2017; Zimova et al. 2021). Despite evincing the greatest adjustments to arrival dates, Eastern temperate birds have been falling behind green-up in their breeding habitats (Mayor et al. 2017), which ultimately affects population demography (Youngflesh et al. 2023). Given that the departure from wintering sites is strongly influenced by endogenous factors and that birds do not have accurate information on relevant climatic conditions at the breeding sites while on the overwintering grounds, changes in migratory speed represent a vital mechanism for ensuring that migration and arrival at breeding sites are synchronised with the seasonal availability of resources. Although speed decisions are made at the individual level, it is currently not feasible to track millions of birds individually across many years and an entire continent. By leveraging a dataset with extensive temporal and spatial coverage (such as the eBird database used by Youngflesh et al. 2021 and this study), combined with smaller-scale studies tracking individual birds, we can enhance our understanding of bird migration phenology.

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Combining these two approaches represents a significant convergence of information, yielding a comprehensive understanding of migratory patterns.

Here, we investigate how bird migratory speed affects species' timely arrival on their breeding grounds in the face of climate change. We focus on how vegetation green-up is moving North in the green wave (Question 1), and whether birds are using these green-up cues to modify their migratory speed while moving North during spring migration (Question 2). We also investigate which bird traits might be associated with species' abilities to shift their migratory speeds (Question 3), and the relative importance of vegetation green-up timing, when migration begins and migration speed in determining bird arrival time (Question 4). We predict that birds are using green-up in the surrounding environment as a cue to inform their migration pace, with birds and green-up moving North synchronously (Models 1 and 2). We also expect that different species vary in their ability to perceive and track green-up cues (Model 3), and that both bird migratory speed and green-up are affecting how early or late birds are (Model 4).

2 | Methods

2.1 | Dataset and Arrival Date Estimates

We quantified songbird migration front speed by estimating the velocity at which bird arrival progressed across eastern North America for 55 migratory Passerine species that breed in this area. Our speed metric quantifies the leading edge of the migration wave, and it estimates when the first migrants of a species arrive on a cell (the half-maximum date of the distribution arrival of birds is used by Youngflesh et al. 2021). Our speed metric is comprised not only of a combination of flight speed and time spent at stopover sites but also of populations that might possess distinct migration strategies (e.g., leapfrog, chain, telescopic) within the same species (Newton 2024).

Using bird arrival and plant green-up dates from Youngflesh et al. (2021), we estimated species-specific migration speed across a grid of 73 hexagonal equal-sized cells (Icosahedral Snyder Equal Area projection with an aperture of 3; distance between cell centres of 285 km; per-cell area of ~70,000 km^2) that spanned 33° of latitude using estimates for 16 years (2002 to 2017, Figure 1, Table S1). Cell size and arrangement followed Youngflesh et al. (2021), where data was aggregated within a cell large enough to allow robust estimates of phenology while maintaining geographic specificity. Bird arrival dates were estimated by Youngflesh et al. (2021) using logistic generalised additive models (GAMs) applied to data from eBird (Sullivan et al. 2014). The speed of vegetation green-up (green-up velocity across space, i.e., 'green-wave', O'Leary et al. 2020) was calculated using green-up dates estimated from the Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Dynamics MCD12Q2 v.6 data product (Friedl and Gray 2019). Bird arrival date for each cell was defined as the half-maximum value of the distribution of arrival dates, and vegetation green-up date as the mean of 'mid-green-up' values of the pixels in a cell.

2.2 | Estimating Velocity of Bird Arrival and Green-Up

The local velocity for bird arrival and vegetation green-up date was estimated for each grid cell in each year by comparing bird arrival and green-up dates to adjacent cells. We estimated the slope and direction of change from one cell to its neighbours

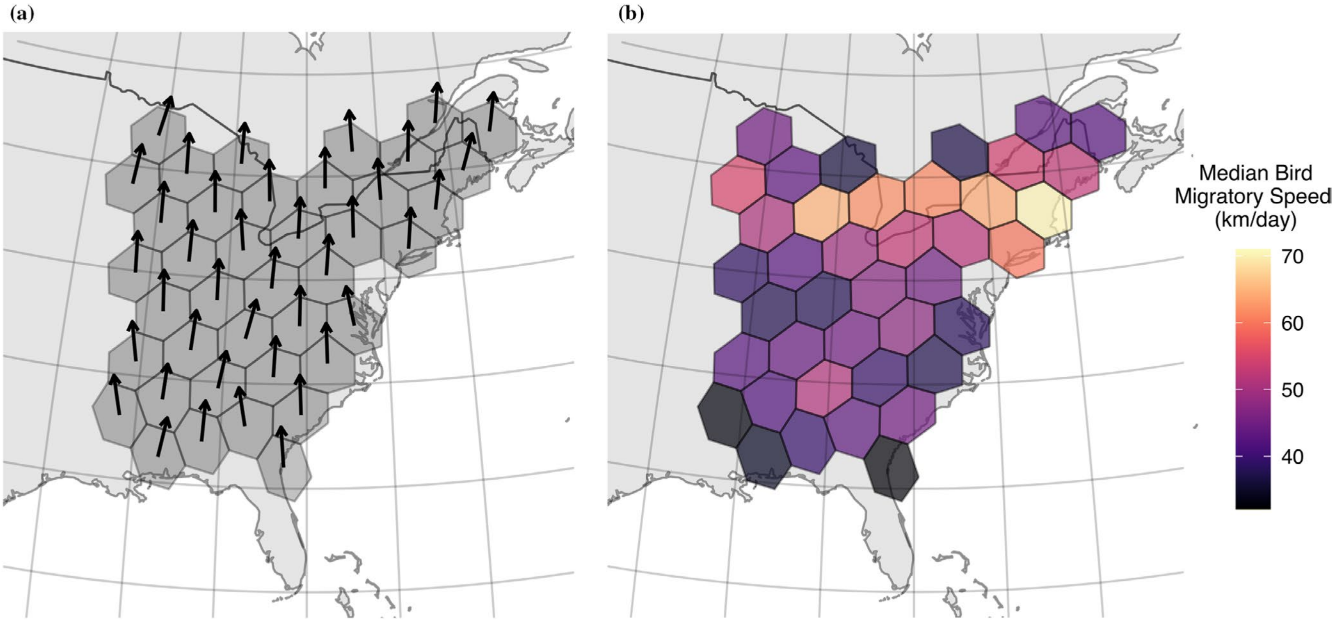

FIGURE 1 | Bird migration velocity (direction (a) and speed (b)) in the Eastern flyway in North America. (a) Arrows represent median bird migration direction according to latitude across years (2002 to 2017) for all species combined. Birds are mostly moving north, as seen in the arrows showing migration direction. (b) Median bird migration speed according to latitude across years (2002 to 2017) for all species combined is represented in the shades of purple and yellow. Birds move faster in higher latitudes as seen by the yellow-coloured cells in the plot in the north. Species have different occurrence ranges and data available for different cells and years, the migration speed and direction in a cell might represent different sets of species.

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using linear regressions (details in Figure S1). We selected only hexagonal cells with a minimum of five neighbours with data and estimated the intercept and slope of the linear regression using cell centre coordinates of its neighbour cells as the predictor variables (longitude and latitude, spatial coordinates measured in km) and the bird-arrival or green-up dates as the response variable. Thus, the estimated coefficients were the rate at which arrival dates changed with respect to geographic location. The *x* and *y* coefficient estimates of the regression line were used to calculate two values: the angle of the vector measuring the direction of travel (0° to 360°) and the magnitude of the arrival dates change (days/km, using the Pythagorean Theorem, see Figure S1). We then converted the magnitude (days/km) to a measure of speed by taking the inverse of the slope to have it in km/day. These estimates of direction and magnitude of speed quantify, for birds, the movement of the migration front rather than the average movement rates of single individuals and, for forested habitats, the rate at which green-up progresses across the landscape. We emphasise that our speed metric represents the combination of stopover and in-flight time for a subset of the first migrants arriving at a location. By measuring the speed of the migration front, we can assess how species might shift migratory behaviours to track the green wave while en route. Even though Youngflesh et al. (2021) had arrival date estimates for 56 species of birds, only 55 species had enough adjacent cells that we could use for estimating speed (the eastern towhee, *Pipilo erythrophthalmus*, was removed).

In addition to cell and year-specific migration and green-up date front speeds (hereafter, migration speed and green-up speed) and directions, we also calculated the bird-arrival date relative to the green-up date (hereafter relative arrival), defined as the green-up date minus the bird-arrival date for each species in each year in each cell. Relative arrival is a measure of how far ahead or behind birds were in relation to vegetation phenology in a given year at a given cell location. Our standard speed measure quantifies speed using adjacent cells, integrating previous, current and future (neighbouring cells) speeds of migration and green-up progression in space.

We were also interested in quantifying the migration speed only prior to arrival at a grid cell, to evaluate how fast the migration was moving. To do this, we calculated the mean bird speed prior to arrival, which describes how fast the migration wave was moving before reaching a cell in a given year. We used the distance from each cell centres to the first cell in which a species arrived in a given year and divided it by the difference in time (days) between their detection in each cell (Figure S2).

To quantify annual deviations in bird and green-up metrics, we calculated annual anomalies for all variables in each cell (i.e., the difference between each annual value and the average value across all years). This allowed us to quantify annual variation while controlling for average differences among cells (spatial component) and species in the metrics. Only cells with a minimum of 8 years of data were included in any anomaly calculation. For example, for the green-up date, an anomaly value of zero represents the average green-up date for a cell between the 16 years of sampling; negative values would represent early green-up years, and positive values, late green-up years. When calculating anomalies for speed measurements, we first took the base-ten logarithm of the estimates, making these anomalies relative on the log scale.

2.3 | Species Traits

We gathered trait data from the literature, including species body mass (grams), migratory sensitivity (an estimate of the number of days arrival date changes per one-day change in green-up progression, calculated for each species in each cell), overwinter latitude (degrees) and hand-wing index (HWI, proxy for wing shape) (Table S2). We sought to determine whether species traits were related to bird migration speed differences. All these traits have been previously associated with either changes in migration speed, arrival dates at breeding and wintering sites, or dispersal ability (La Sorte et al. 2013; La Sorte and Graham 2021; Sheard et al. 2020; Usui et al. 2017; Youngflesh et al. 2021). To create an additional species trait, we calculated first-arrival dates, defined as the mean arrival date for a species in all migratory cells located under 35° North latitude within our study area (North America). This date represents the southernmost part of each species' migration range that we measured, which we used as a proxy for when species first arrived as migrants in the United States. We used this metric to characterise species as early- or late-arriving migrants because we do not have direct information about departing dates from the overwinter grounds outside of our study area. We recognise that this metric can also be influenced by bird migration speed between overwintering sites and arrival in the U.S., but we believe it characterises an important aspect of species migration. We also calculated annual anomalies for first-arrival dates to quantify the degree to which a species arrived earlier or later than average in a given year. Lastly, for each species, each cell was classified as part of the migratory or breeding range, or both.

We removed two extreme outlier estimates for a species in a year in a cell from our bird migration speed estimates with values that exceeded 3000 km/day (the Blackburnian warbler *Setophaga fusca* and the black-throated blue warbler *Setophaga caerulescens* in 2012 al latitude 42°), which are values substantially larger than what has been recorded for Passerines (Payevsky 2013). This occurred because estimated arrival times for the set of cells (a given cell plus its six neighbours) were so similar that the linear regression slope for arrival dates was close to zero. The small slope value, close to zero, makes its inverse values quite large (Equation S7 in Figure S1). These were likely the result of two overwintering populations converging on a single migratory point along the migratory route.

2.4 | Analysis and Model Fitting

To test the relationships between migration speed and our covariates of interest, we fit linear mixed models (LMMs) and generalised additive models (GAMs) to our data. GAMs relax the assumption of strict linearity between the response and the predictors, using smooth functions to describe the relationship between them. GAMs can also incorporate fixed and random effects like traditional linear mixed models. We used non-linear

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terms (tabletop smoother) to describe how latitude was related to our response variables. We also incorporated linear random effects into the model to account for variation between years and species, and for a species in a cell, since the effect of a cell might vary by species (spatial coverage of all species is not identical). We modelled all the predictors (i.e., anomalies and species traits) as fixed linear effects because we did not have a priori predictions for non-linear responses to the dependent variables. All models were fit using R (Version 4.1.0, R Core Team [2022]) and the 'gam' function from the 'mgcv' package (Wood 2017), using a restricted maximum likelihood algorithm (REML) which is numerically more stable than using maximum likelihood (Wood 2017). Maximum likelihood estimators are preferred to fit GAMs because they are less prone to local minima when compared to other criteria, such as generalised cross-validation (GCV). We used the base-ten logarithm of the speed in all models to minimise the skewness of the distribution of speed values. We fit four separate regression models, each associated with one of four primary research questions. The four regression models differed in the response and explanatory variables, allowing us to quantify different aspects of migration speed and its relationship to green-up.

2.4.1 | Question 1: How Does Green-Up Speed Vary With Latitude?

Model 1 quantifies how green-up speed is influenced by latitude. We did this by fitting a GAM with green-up speed as the response variable, latitude as the predictor (smooth term) and both cell ID and year as random intercepts (Equation S2).

2.4.2 | Question 2: Do Birds Change Migration Speed in Response to the Timing and Speed of Vegetation Green-Up?

We examined whether birds adjust migration speed in response to green-up across space within years (Model 2). We fit a GAM estimating how bird migration speed ($\log_{10}$(km/day)) varied in response to three linear terms: annual anomalies (within a cell) of (1) green-up date and (2) green-up speed and (3) the location of each cell within the species range (migratory versus breeding range; Equation S1). We expect birds to travel faster in their migratory ranges, and slower at the breeding range to assess habitat quality and establish territories. Cells that included both migration and breeding range were classified as breeding cells. Because migratory cells are at lower latitudes compared to breeding cells, and relative speed changes as birds and green-up (Model 1, above) move north, we included latitude in this model as a predictor variable (smooth term). We controlled for differences among species, years and species by cell by including random intercepts for these variables.

2.4.3 | Question 3: Are Species Traits Associated With Bird Migration Speed?

Next, we wished to determine which bird traits are most related to among-species variation in average migratory speed. Model 3 estimated how bird migration speed ($\log_{10}$ (km/day)) was linearly affected by five species traits previously hypothesised to influence bird migratory speed and timing (Equation S3): migratory sensitivity, first arrival date, body mass, overwinter latitude and hand-wing index (Table S2, see *Species traits* for details). All trait predictor variables were scaled (average subtracted and divided by the standard deviation) to fit the model. The relationship between bird migration speed and latitude was again modelled using a smooth term to account for non-linearity. We included random intercepts for species, years and species in a cell to account for differences that naturally occur within those variables (Table 1). To determine whether a phylogenetic signal was present in the residuals (which would indicate the influence of shared evolutionary history on our results), we calculated Blomberg's K (Blomberg et al. 2003) using the *picante* R package (Kembel et al. 2010) in a *post hoc* analysis. We found no strong evidence of the influence of shared ancestry in our results for the set of species we analysed.

For nine species with data in the literature, we also combined the existing estimates of average migration distance and flight speed with our estimates of bird migration front speed (our metric incorporates time both spent in flight and at stopover sites). We then calculated the percentage of time that birds stay at stopover sites (Table S3). We estimate that 92% of migration time is spent in stopover sites, not actively flying.

2.4.4 | Question 4: What Explains Among-Year Variation in Bird Relative Arrival Dates?

In any given year, birds may arrive earlier or later relative to the timing of local green-up as compared to other years (controlling for species and location). Our final goal was to determine to which degree relative arrival was influenced by three different components of migration: (1) when birds first arrive in our study area, (2) how fast birds migrate from the time they arrive in the study area until they arrive at the grid cell of interest and (3) when green-up occurred at a given location in that year (Equation S4). These three factors represent three ways birds may arrive earlier relative to green-up in a given year: they may start migrating earlier, they may migrate faster, or green-up may be late. We decompose the influence of these three factors to determine the relative importance of each in explaining the among-year variation in relative arrival. Model 4 was a linear mixed model (random effects model) with the relative arrival anomaly as the response variable and fixed effects as the anomaly of bird first-arrival date, the anomaly of bird migration speed prior to arrival, and the anomaly of the green-up date (Table 1). We scaled each of our predictors to have a standard deviation of 1, allowing us to quantify the relative contribution of each factor in explaining variation based on the effect size of the response. We again included species and species in a cell as random effects and only included cells in the breeding range of the species. While anomalies in the green-up date might be thought to be related to bird speed prior to arrival and to bird first-arrival date, correlation coefficients were quite low (Spearman <0.2), suggesting that any relationship among the three variables is not confounding inference (Graham 2003).

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TABLE 1 | Generalised additive models and their response variables, predictors and results. Coefficient estimates and confidence intervals are shown for the linear fixed effects of the four models that investigated variation in bird migratory and green-up speed. For the random effects and smooth terms, we show how much variance they are explaining, as well as the residual variance estimate. Bold estimates indicate coefficient estimates with 95% confidence intervals that do not overlap zero in the fixed effects; for the non-linear and non-fixed effects, bold font indicates a p-value smaller than 0.05 in the likelihood ratio test that uses a reference distribution to test a null hypothesis (that the variance is 0) using the estimated degrees of freedom and maximum degrees of freedom for each term.

		Linear fixed terms			Smooth and random effects		
Model	**Response**	**Coefficient**	**Estimate**	**Confidence intervals (95%)**	**Coefficient**	**Variance**	**Effect type**
Model 1 ($n=1301$)	Vegetation green-up speed (km/day, log scale)	**Intercept**	**3.777**	**(3.636: 3.917)**	**Latitude**	**0.076**	**Smooth (table-top)**
					Year	0	Random intercept
					Cell Id	**0.413**	**Random intercept**
					Residual Variance	0.094	
Model 2 ($n=6418$)	Bird migration speed (km/day, log scale)	**Intercept**	**3.933**	**(3.868: 3.996)**	**Latitude**	**0.182**	**Smooth (table-top)**
		Green-up date anomaly	**−0.549**	**(−0.770: −0.327)**	Year	0	Random intercept
		Green-up speed anomaly	**0.088**	**(0.041: 0.134)**	**Species_cell**	**0.282**	**Random intercept**
		Migratory cell	**0.130**	**(0.055: 0.205)**	**Species**	**0.215**	**Random intercept**
		Green-up date anomaly: Migratory cell (true)	0.172	(−0.429: 0.773)	Residual Variance	0.152	
		Green-up speed anomaly: Migratory cell (true)	0.069	(−0.057: 0.195)			
Model 3 ($n=4026$)	Bird migration speed (km/day, log scale)	Intercept	3.8023	(2.021: 5.584)	**Latitude**	**0.991**	**Smooth (table-top)**
		Species sensitivity	0.119	(−0.034: 0.203)	Year	0.036	Random intercept
		Species first arrival date	**0.203**	**(0.110: 0.295)**	**Species_cell**	**0.705**	**Random intercept**
		Body mass	0.099	(−0.012: 0.211)	**Species**	**0.833**	**Random intercept**
		Wintering latitude	0.098	(−0.022: 0.217)	Residual Variance	0.154	
		Hand-wing index	0.147	(−0.032: 0.327)			
Model 4 ($n=4909$)	Anomaly on bird relative arrival date	**Intercept**	**−0.206**	**(−0.127: −0.082)**	Species_cell	0	Random intercept
		Bird speed prior to arrival (z-score)	**0.023**	**(0.001: 0.045)**	**Species**	**0.164**	**Random intercept**
		Bird first-arrival (z-score)	**−0.033**	**(−0.053: −0.014)**	Residual Variance	0.405	
		Green-up date (z-score)	**0.454**	**(0.432: 0.476)**			

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3 | Results

We estimated the mean bird migration speed of 55 species that breed in the Eastern US across 40 hexagonal equal-area cells, including bird migration speed data from a mean of 18 (ranging from one to 38) cells per species, and 18 (ranging from zero to 46) species per cell—with a total of 6521unique species-cell-year speed estimates (Table S1). We conducted a sensitivity analysis to test whether extreme arrival dates or variation in the number of neighbouring observations influenced our speed estimates. Results showed no evidence of bias, indicating that our estimates were robust to these factors (Figure S4). Bird migration speed estimates ranged from 7.1 to 1434.3 km/day for a species in a cell, with a mean of 62.5 and a median of 48.4 km/day (Figures 1b and 2). The eastern wood pewee (*Contopus virens*) exhibited near-average speed relative to all species, moving on average at 59.1 km/day. The species with the slowest mean speed was the tree swallow (*Tachycineta bicolor*), migrating at 36 km/day, whereas the fastest migrant was the willow flycatcher (*Empidonax traillii*), migrating at 102 km/day (Table S2). As expected, the general estimated direction of bird migration was nearly north, with the mode of migration front direction deviating west by five degrees and the mean east by three degrees (Figure 1a and Figure S3).

3.1 | Effect of Latitude on Green-Up and Migration Speed

On average, migration speed increased with latitude: birds accelerated as they moved north (Model 2; Figures 1b and 3, Table 1). The effect of latitude was the same on migratory and breeding ranges, but the baseline bird migration speed in the migratory range was higher (Table 1). The average difference in speed between the southern (< 36.7° north) and northern (> 36.7° north) halves of our study area (start and end of migration) was 8 km/day. There was more variation in migration speed among species than among years within cells. Green-up speed had the opposite pattern across latitude: speed decreased as the latitude increased, with a difference of around 20 km/day between the southern and northern halves of our study area (Model 1; Figure 3, Table 1). Comparing the magnitude of speeds, green-up speed is faster than bird migration speed at most latitudes (Figure 3).

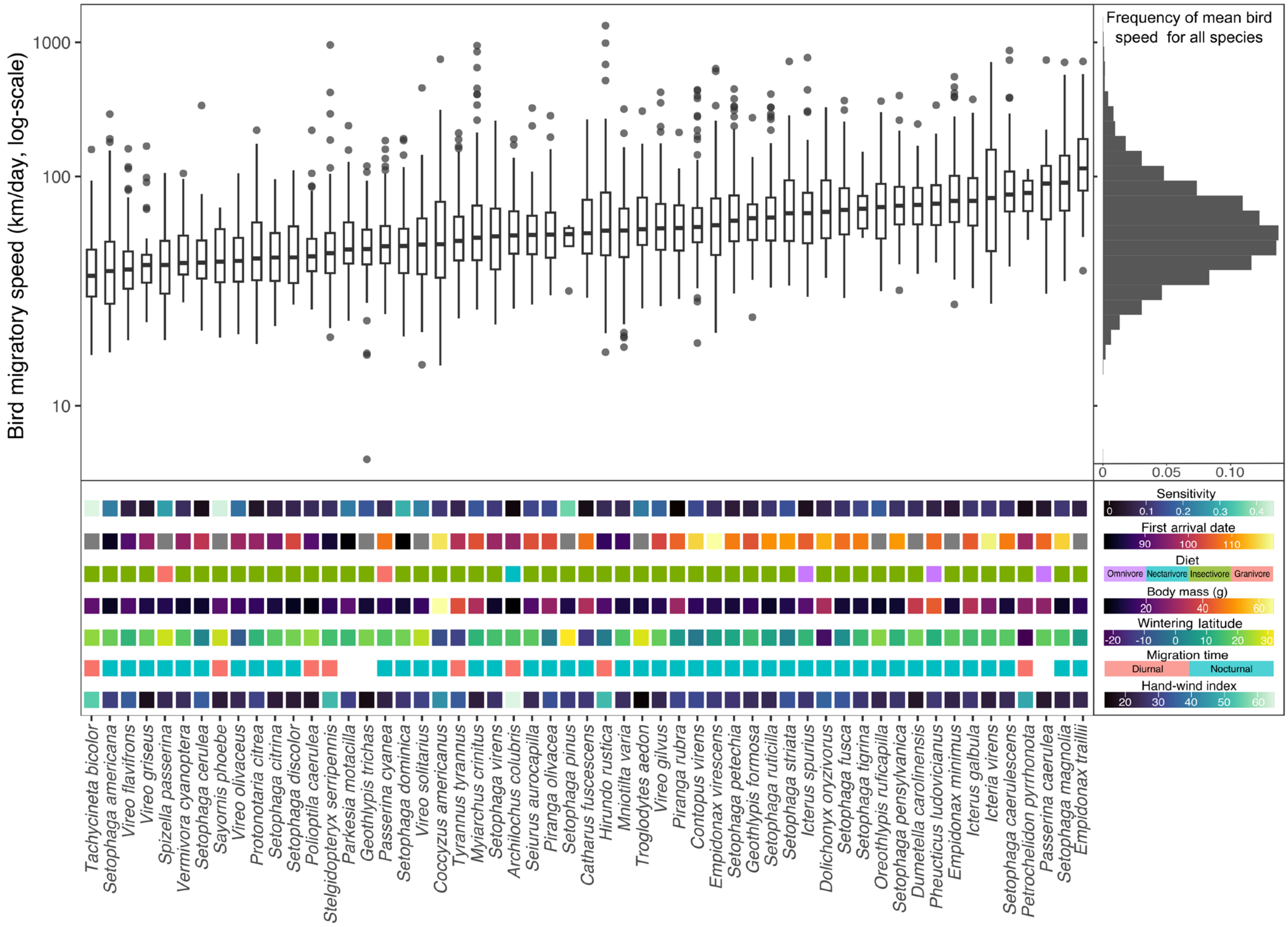

FIGURE 2 | Species and trait-specific bird front migration speed (km/day). Bird migration speed estimates in the Eastern flyway in North America for each species grouped mean estimates distribution (histogram, log scale *y*-axis). Each boxplot represents a species in a year and a cell (25th and 75th percentiles), and species are ordered according to their median speed. The squares on the bottom represent the data used in model 3 to estimate bird migration speed (details in Table 1, legend on the bottom right), except for species diet and migration time. Both variables were removed from the model due to the lack of many species in each category.

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3.2 | Green-Up Effects on Bird Migration Speed

We found evidence that birds adjust migration speed in response to cues from vegetation green-up information while en route (Model 2, Table 1): in early green-up years, birds move faster compared to years when green-up is late (−0.55, ±0.11 [effect size ± SE], Table 1, Figure 4a). The effect was relatively small, with a ~5% increase in bird speed for each day green-up was early. Across the whole study area, green-up varied between years from around −10 days (i.e., 10 days earlier) to 10 days late. For example, the eastern wood pewee in its migratory range was predicted to migrate at 63 km/day on an average green-up date year. When green-up was 10 days early, the predicted speed was 76 km/day, and in late green-up years (anomaly green-up date equals 10), it was 52 km/day.

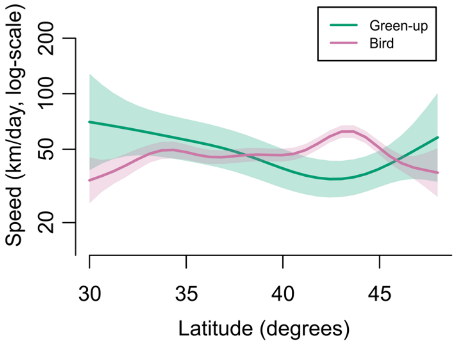

FIGURE 3 | Mean bird migration speed (in pink, log(km/day)) varying according to latitude estimated by model 2 (details on Table 1). Vegetation green-up speed varied according to latitude (in green, log(km/day)) according to model 1. Bird speed tends to increase with latitude, while green-up speed decreases with latitude in the Eastern flyway in North America. Lines represent mean estimate, and the shaded region the 95% confidence interval.

Anomalies in green-up speed also influenced bird migration speed: faster green-up speed was correlated with faster migration speed (0.09 ± 0.02, Figure 4b). The relationship was positive in both the migratory and breeding ranges, but birds migrated faster on average in the migratory range (0.13 ± 0.04 change in speed from breeding to migratory range, Figure 4c and Table 1). The migration speed of the eastern wood pewee, for example, on an average green-up speed year (green-up speed around 60 km/day, zero green-up speed anomaly) on its migratory range was 63 km/day, whereas in fast green-up years (0.7 green-up speed anomaly) speed was 70.5 km/day and in slow green-up years (−0.7 green-up speed anomaly) bird migration speed was 56.2 km/day.

3.3 | Species Traits and Migration Speed

Model 3 showed support for one species-specific trait being related to bird migration speed: species' first arrival date (Table 1). We found that species that arrive earlier in the US move slower on average than species that arrive later in the season: the log$_{10}$(speed) increased by 2% for every 1 day later a species arrived later (Figure 5).

3.4 | Bird Relative Arrival

Both bird migration speed prior to arrival and green-up date had a strong effect on arrival (Figure 6, Table 1). Faster bird migration speed prior to arrival was associated with earlier relative arrival. Birds moved faster in years when they were ahead of

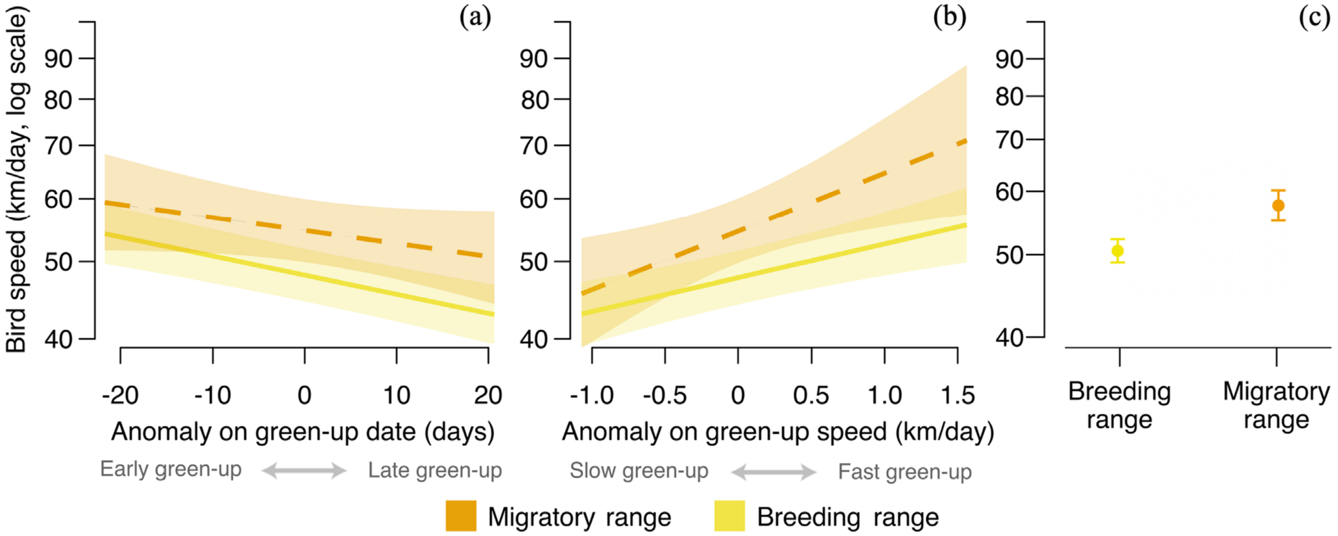

FIGURE 4 | Effect of vegetation green-up on bird migration speed (km/day) in the breeding (yellow and solid) and migratory range (orange and dashed) Eastern flyway in North America (model 2). Lines (a, b) and dots (c) represent the mean estimate and the shaded areas (a, b) and whiskers (c) represent the 95% confidence interval. (a) Anomaly in green-up date (ordinal day, scaled) effect on bird migration speed. Early green-up years were associated with a faster migration pace. (b) Anomaly in green-up speed (km/day, base 10 logarithm and scaled) effect on bird migration speed. Fast green-up years were associated with a fast migration pace. (c) Bird migration speed varied according to bird range type. Birds moved slower in breeding cells than in migratory cells.

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time: for each increase of one standard deviation (112.9 km/day) of bird migration speed prior to arrival, the anomaly on bird relative arrival increased by 0.32 ± 0.01 days (positive lag values, pink line on Figure 6). Late green-up years were also associated with the timing of arrival, with birds 0.56 ± 0.01 days ahead of green-up (green line in Figure 6) for each 13 days green-up was late. The effect of bird first arrival on bird relative arrival was negligible compared to the other covariates (0.02 ± 0.01). Comparing the effect of bird migration speed prior to arrival and green-up date, we find a substantial difference in the magnitude of their impact: green-up date had the greatest (almost double) effect on the degree to which birds were ahead or behind green-up, compared to bird migration speed prior to arrival. While changes in bird migration speed are greatly helping birds in adjusting their arrival relative to green-up, these shifts were less important in determining the relative timing of arrival than when green-up occurs.

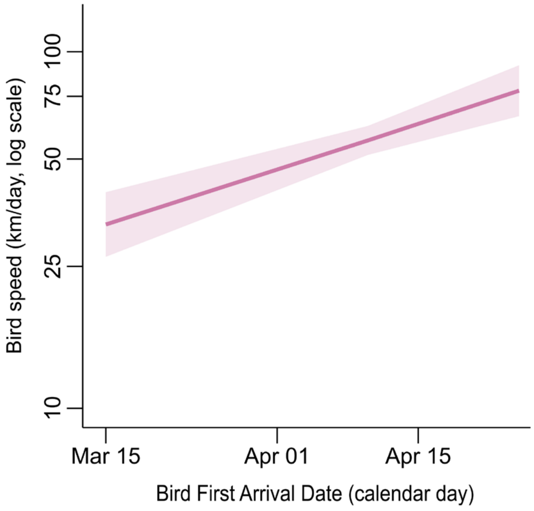

FIGURE 5 | Bird traits that influenced migration speed in the Eastern flyway in North America. The pink line indicates the average relationships, while the shaded area indicates the 0.95 confidence interval. The first arrival date was positively associated with bird migration speed, with birds migrating faster when they arrive later.

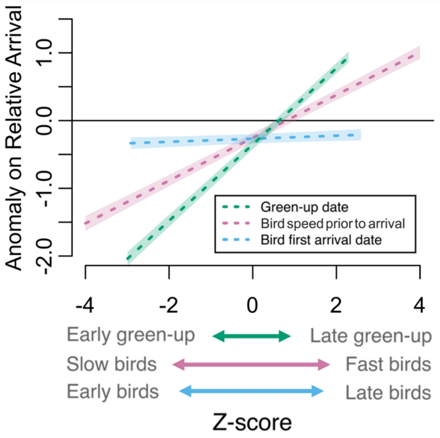

FIGURE 6 | Coefficient effects of model 4 (details in Table 1) on anomaly on bird relative arrival (vegetation green-up arrival date minus bird arrival date, scaled). Positive values of anomaly on relative arrival (y-axis) represent birds arriving earlier than green-up, whereas negative values represent birds arriving behind green-up. The green dashed line represents the effect of the green-up date z-score on the relative arrival anomaly. Early green-up years are strongly associated with birds arriving relatively later than average, relative to green-up. The pink dashed line represents the effect of bird migration speed prior to arrival (km/day, z-score) on relative arrival anomaly. Birds are migrating slower on average (negative z-score), they are late in relation to green-up. The blue dashed line shows the effect of the first-arrival date (ordinal date z-score) on anomalies on relative arrival anomaly. First-arrival date and anomalies in relative arrival presented a very weak relationship. Even though both the green-up date and bird migration speed prior to arrival were associated with relative arrival anomaly, the effect size of the green-up date was almost twice the effect of bird migration speed prior to arrival.

4 | Discussion

By harnessing a large global database of bird observation data, extensive remotely sensed satellite data for vegetation phenology, and a robust statistical modelling framework, we were able to simultaneously quantify how the timing of spring vegetation phenology influences the speed and timing of bird migration for 55 species of birds. Specifically, we show that overall migration speed changes in response to the timing of spring vegetation green-up and the speed at which the spring green-wave progresses northward, suggesting that birds use exogenous cues to inform their seasonal movements en route. Finally, we show that annual differences in when birds arrive on their breeding grounds relative to green-up are largely due to differences in the speed at which they migrate, rather than when their migration started in our study area. These results provide unique insights into a key component of the avian life cycle with implications for understanding how these species can respond to climate change in the future.

Even though our data do not allow us to account for distinct migration strategies (Newton 2024) when estimating speed, it still provides important insights into how the species-level migration vanguard assesses green-up information to decide when to move. Continental-level studies trade off fine-scale population and individual-level data for vast amounts of spatial, temporal and taxonomic information. Combining our results with smaller studies that focused on single species and individuals provides a powerful approach to understanding these complex migration strategies. The leading edge of migration can reflect well species' abilities to follow green-up: advancing migration while ensuring that the first migrants arriving will have access to food resources and favourable weather is key for individuals' safety.

4.1 | Bird Migratory and Green-Up Speeds

Latitude is a primary driver of climate, vegetation and phenology, even though the local topography also modifies green-up phenology (O'Leary et al. 2020). We found that latitude was a strong predictor of the speed of both bird migration and green-up. Bird migration front speed generally increased with latitude, suggesting birds are accelerating their migration while they move North to arrive earlier (Covino 2020; Horton et al. 2019). However, it may also be possible that populations (within a species) that

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move further north migrate faster than populations that stop in the south. Our study area encompasses the whole Eastern flyway in North America, so we acknowledge that evaluating such a large spatial extent comes with limitations; results should be interpreted in the context of the first wave of migrants (surfing the green-wave, Van der Graaf et al. 2006) and in conjunction with individual-level studies.

Migration speed is mainly dictated by the amount of time individuals stay at a stopover site. Based on estimated flight speed, we estimate that, on average, 92% of total migration time is spent resting or feeding at stopover sites and not actively in flight. This is similar to other estimates of 85% (Hedenström and Alerstam 1997), 80% (Green et al. 2002) and 70% (Schmaljohann et al. 2012). Increases in migratory speed, therefore, are likely to occur primarily via the amount of time spent at a stopover site, rather than the flight speed during migration (Hedenström and Alerstam 1997). Birds, therefore, have several opportunities to decide when to leave or stay in a stopover site, enabling them to fine-tune their migration timing and track plant green-up.

A combination of favourable environmental conditions for flight (wind speed and direction) and individual status (fat storage and resting state) influences bird decisions to leave a stopover site (Dossman et al. 2016; Roques et al. 2022; Schmaljohann et al. 2012). Decisions of when to leave are likely associated with cues in the landscape that inform the environmental conditions at the breeding sites, combined with an individual's ability to accumulate resources rapidly and recommence migration (Marra et al. 2005). Several studies looking at fat storage at stopover sites found a strong association with departure, with lean migrants staying longer (Arizaga et al. 2011; Dossman et al. 2016; Goymann et al. 2010; Moore and Kerlinger 1987). Energy constraints, therefore, might limit the maximum speed at which migration can occur.

The migration pace of many birds has been associated with when migration begins (González et al. 2020; Matyjasiak 2013). In our study, we found similar results for bird first arrival date: species that arrived earlier in North America migrated slower. The negative relationship between bird first arrival and migration speed at the species level might represent a mechanism to ensure arrival at the optimal time (Youngflesh et al. 2021), while the positive relationship between bird migration speed and green-up date and speed is possibly assisting birds with tuning the migration progression once birds arrive in the continent. Early arrival might result in individuals experiencing unfavourable weather conditions and starvation; these costs represent a big risk to individuals that arrive too early, especially in higher latitudes (Rotics et al. 2018; Youngflesh et al. 2023).

4.2 | Responses to the Phenological Component of Global Change

Even though birds are able to change their migration speed in response to phenological cues in the vegetation, shifts in speed are probably not sufficient for birds to arrive at the optimal time in abnormally early or late green-up years. This is similar to findings in European migratory birds (Schmaljohann and Both 2017). The speed of bird migration played a larger role in explaining variation in relative arrival compared to when the birds first arrived in the southern end of our study area, suggesting that migration speed plays a major role in arrival time. Even though the bird first arrival date plays an important role in migration speed, birds might have limited access to environmental cues when migration starts, once they are very far from the breeding sites, and the use of fixed endogenous cues provides a single opportunity to choose a departing date.

While faster migration might allow birds to compensate for early green-up years and we showed that they can tune speed with the surrounding environment, it may also come with survival costs. In a study tracking migrating American redstarts (*Setophaga ruticilla*), late arrivers migrated faster but experienced a 6.3% reduction in survival (Dossman et al. 2023). Energetic costs limit how much birds can speed up in early and fast green-up years while still surviving migration. Costs can be especially high for long-distance migrants, which start migration further away from their breeding grounds and have less access to information regarding environmental conditions of the breeding and stopover sites at the beginning of their journey. If migration speed is already close to its maximum limit, as the relationship between fast migration and high mortality indicates, birds might have limited potential to adapt to climate change by switching their migratory phenology with speed changes (Nilsson et al. 2013).

The extent to which species are able to speed up migration and perceive phenological changes poses a challenge for migratory birds responding to changing phenology. Changes in neither migratory (Youngflesh et al. 2021) nor breeding phenology (Youngflesh et al. 2023) are matching the rapid pace of climate change. This is likely due to the limited capacity that birds have to adjust their migratory speed en route and the role that endogenous factors play in driving the phenological dynamics. This is concerning, given the demographic consequences that phenological mismatch may have (Youngflesh et al. 2023). The impacts of sustained phenological change at lower trophic levels will be compounded by the occurrence of extreme weather events, such as storms and heat waves, which are expected to increase in the next decades (Coumou and Rahmstorf 2012; Easterling et al. 2000; Palmer et al. 2017; van de Pol et al. 2017). These have been shown to impact phenological events, which can cause as many phenological shifts in the vegetation as one decade of gradual warming (Jentsch et al. 2009) in addition to directly depleting food supplies, resulting in higher rates of mortality and potentially forcing migration before individuals are physiologically ready (Yang et al. 2021).

Birds are experiencing an increasingly unpredictable and variable climate. Given that mitigating strategies, such as changes in migratory speed, have a limited capacity to respond to rapid climatic changes, tracking ideal environmental conditions might require evolutionary adaptations to endogenous responses. Unfortunately, these may evolve at slower rates than the changes in the landscape are happening. The evidence for evolutionary responses is still limited (Charmantier and Gienapp 2014) and appears to be variable according to the system evaluated (e.g., Sheldon et al. 2003; Gienapp et al. 2006; Visser 2008; Buskirk et al. 2012; Helm et al. 2019; Zimova et al. 2021). Adaptive responses are unlikely to be enough to counteract the rapid pace of phenological changes individuals will experience in the future (Radchuk et al. 2019).

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Our results have direct implications for the conservation of migratory bird diversity in Eastern North America. While birds show some plasticity in adjusting migration pace, this flexibility has limits—particularly when green-up occurs unusually early. Coupled with the slow pace of climate change mitigation through policy and behaviour, migratory birds face constrained options. Mismatches between migration timing and peak resource availability at stopover and breeding sites may reduce reproductive success and survival (Youngflesh et al. 2023). Conservation efforts should therefore prioritise the protection and management of key stopover habitats that allow birds to adjust their pace en route and buffer against phenological mismatches (Mehlman et al. 2005). High-quality and abundant stopover sites can support timely arrivals at breeding grounds by providing birds with the resources needed to either resume migration quickly or pause until conditions are favourable.

Author Contributions

D.A.W.M. lead the conceptualization of the study. B.R.A. lead the analysis. B.R.A., C.Y., D.A.W.M. and M.T. interpreted the results. B.R.A. wrote the original draft. B.R.A., C.Y., D.A.W.M. and M.T. reviewed and edited the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data and code used in this study are available at Dryad (https://doi.org/10.5061/dryad.ttdz08m6w) and GitHub (github.com/br-amaral/BirdMigrationSpe). The original bird occurrence data are available on eBird (https://ebird.org). The original green-up (MCD12Q2) and land cover (MCD12Q1) data are available on the NASA/USGS Land Processes Distributed Active Archive Center (https://lpdaac.usgs.gov/). The original bird arrival dates and green-up date estimates used in this study are publicly available at Zenodo (10.5281/zenodo.4549909).

Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70033.

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