Phenological synchronization of seasonal bird migration with vegetation greenness across dietary guilds

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Funding information

The Wolf Creek Charitable Foundation, National Science Foundation (ABI sustaining: DBI-
1939187).

Abstract

1. The seasonal movement of animals has been linked to seasonal variation in ecological productivity, and it has been hypothesized that primary consumers synchronize migration with vegetation phenology. Within temperate regions of the Northern Hemisphere, herbivorous bird species often track the phenology of vegetation greenness during spring migration. Phenological synchronization with vegetation greenness by migratory birds in other dietary guilds, across the full extent of their annual distributions during both spring and autumn migration, has not been explored.

2. Here, we document population-level associations with a remotely sensed measure of vegetation greenness for 230 North American migratory bird species in seven dietary guilds across the full annual cycle using eBird occurrence information for the combined period 2006-2018.

3. Evidence of phenological synchronization was strongest for omnivores, herbivores, herbivore-granivores, and granivores during spring and autumn migration, except for omnivores in the west during spring migration. Strong evidence also occurred for insectivores during spring migration and carnivores during spring and autumn migration that migrated across the entire breadth of the continent. The level of evidence declined for insectivores in the west and east during spring migration, and for nectarivores in the west during spring and autumn migration. This was followed by insectivores in the east during autumn migration, insectivores in the west and the center of the continent during spring and autumn migration, and carnivores in the west during spring migration. The weakest evidence occurred for carnivores in the west during autumn migration.

4. We found broad support across an array of dietary guilds for phenological coupling between vegetation greenness and seasonal bird migration within North America. As vegetation phenology within the region responds to climate change, our results highlight the potential for many migratory bird species to encounter phenological mismatches. Our findings emphasize the need to better understand the environmental cues that regulate migratory behavior across dietary guilds, consumer levels, and migration tactics.

KEYWORDS

eBird, green-wave hypothesis, phenological synchronization, phenological tracking, seasonal bird migration, vegetation greenness

1 | INTRODUCTION

The seasonal movements of animals often correspond to seasonal variation in ecological productivity (Milner-Gulland, Fryxell & Sinclair 2011; Dingle 2014), which can enhance foraging opportunities across the annual cycle (Armstrong *et al.* 2016). One example is migratory birds whose seasonal movements promote associations with resource surpluses within temperate regions of the Northern Hemisphere (Somveille, Rodrigues & Manica 2015). A well-studied example is large-bodied herbivorous bird species, primarily species of geese, whose movements during spring migration are often synchronized with vegetation green-up (van der Graaf *et al.* 2006; Duriez *et al.* 2009; van Wijk *et al.* 2012; Shariatinajafabadi *et al.* 2014; Shariati Najafabadi *et al.* 2015; Si *et al.* 2015; Kölzsch *et al.* 2016). Young vegetation in the spring is more nutritious and contains fewer physical and chemical defenses (Feeny 1970; Feeny 1976; Boege & Marquis 2005). Herbivorous bird species likely benefit during migration by tracking the emergence of these energy rich resources (Drent, Ebbinge & Weijand 1978; Owen 1980). Tracking this “green wave” of vegetation productivity during migration may also benefit some secondary consumers. Spring green-up often corresponds with the emergence of insect populations (Feeny 1970; Feeny 1976; van Asch & Visser 2007), and the phenological synchronization between plants and insects may extend to include the migration of insectivorous bird species (La Sorte *et al.* 2014a; Thorup *et al.* 2017). The degree to which birds in other dietary guilds at similar or higher consumer levels synchronize migration with vegetation phenology during both spring and autumn migration has not been fully explored. If the influence of the “green wave” is pervasive, changes in vegetation phenology may have a cascading influence across migratory bird species. Here, we evaluate if the phenology of vegetation greenness is coupled with the seasonal movements of migratory birds by contrasting seasonal

associations with vegetation greenness across dietary guilds and consumer levels for a large number of migratory bird species.

Two approaches have been used to study how migratory birds associate with vegetation greenness across space and time, both of which rely on remotely sensed measures of vegetation greenness. The first associates movement patterns of individually tracked birds, and has found positive associations during spring migration with vegetation green-up for herbivores (Shariatina Najafabadi *et al.* 2014; Shariati Najafabadi *et al.* 2015) and insectivores (Thorup *et al.* 2017). While detailed information about migration is obtained from this approach, it is typically limited to a few individuals from a limited number of species over short time periods. The second approach uses observations compiled by citizen-science programs to document population-level associations. This approach has demonstrated that insectivores track vegetation green-up during spring migration and vegetation senescence during autumn migration (La Sorte *et al.* 2014a). While lacking individual continuity, the citizen science approach can be used to document general associations for many species simultaneously at broad spatial extents.

Here, we document the association between bird populations and a remotely sensed measure of vegetation greenness for 230 North American migratory bird species in seven dietary guilds across the annual cycle within the Western Hemisphere using occurrence information from the eBird citizen-science database (Sullivan *et al.* 2014). While these data have been used to assess associations with vegetation greenness during a portion of the annual cycle within North America (La Sorte *et al.* 2014a), we now have sufficient information to consider the full annual cycle across the entire Western Hemisphere. We use daily patterns of bird occurrence compiled over a 13-year period (2006 to 2018) to document species' observed associations with vegetation greenness by year. To provide a context to determine how species are 'sampling'

vegetation greenness across the annual cycle, we use species' daily patterns of occurrence to extract the minimum and maximum annual associations with vegetation greenness (see Figure 1). To provide a framework to test the level of evidence for phenological synchronization during spring and autumn migration, we extract the instantaneous rate of change in EVI by day across the annual cycle (see Figure 1).

The seasonal movements of migratory birds occur across a latitudinal gradient of vegetation greenness characterized by high seasonality on temperate breeding grounds and low seasonality on tropical and sub-tropical non-breeding grounds (see Figure 1). When navigating between these two regions, migratory birds can encounter a range of conditions depending on migration timing and speed. Under strong phenological synchronization, we expect associations with vegetation greenness to increase above non-breeding season levels during spring migration and decrease towards non-breeding season levels during autumn migration (see Figure 1). In other words, we expect migratory bird populations to track the seasonal pulse of vegetation greenness within temperature regions, maintaining or exceeding non-breeding season associations. Alternatively, under weak phenological synchronization, migratory bird populations fail to track this seasonal pulse in vegetation greenness, resulting in associations during migration that fall below non-breeding season associations (see Figure 1). In this situation, associations with vegetation greenness only increase during the breeding season when the migratory population is established on the breeding grounds.

Based on this framework, we can generate expectations for migratory bird species based on their trophic and dietary classifications. For primary consumers such as herbivores where phenological synchronization would provide direct nutritional benefits, we expect strong synchronization during spring and autumn migration. For secondary consumers, whose prey base

is synchronized with vegetation phenology, such as insectivores and some omnivores, we expect similar or weaker phenological synchronization. With tertiary consumers, such as carnivores where synchronization with vegetation phenology would provide few apparent nutritional benefits, we expect weak phenological synchronization. We would also expect weak phenological synchronization to occur when migrants must navigate large ecological barriers to migration, such as deserts, mountains, or oceans (Henningsson & Alerstam 2005) where tracking vegetation greenness is not feasible (Wang *et al.* 2019). The primary barrier to migration in the Western Hemisphere is the Gulf of Mexico (Stevenson 1957), whose effects should be evident during early spring and late autumn migration for species that migrate through central or eastern North America (Cohen *et al.* 2015; La Sorte & Fink 2017). By testing these predictions, our goal is to document how phenological synchronization varies across avian life-history strategies. As vegetation phenology responds to global warming within temperate regions of the Northern Hemisphere (Cleland *et al.* 2007; Richardson *et al.* 2013), this information will advance our understanding of the implications of these changes for the region's migratory bird populations.

2 | MATERIALS AND METHODS

2.1 | Vegetation greenness

We estimated vegetation greenness using the Enhanced Vegetation Index (EVI) (Huete, Justice & Liu 1994) from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument (Justice *et al.* 1998) onboard the Terra (MOD13A2 V.006) (Didan 2015a) and Aqua satellites (MYD13A2 V.006) (Didan 2015b). EVI measures canopy greenness, a composite property of canopy structure, leaf area, and canopy chlorophyll content while minimizing soil and atmosphere influences (Myneni *et al.* 1995). Unlike the Normalized Vegetation Index (NDVI),

139 EVI is less prone to saturation in temperate and tropical forests (Xiao *et al.* 2004; Huete *et al.*
140 2006). EVI is more responsive to canopy structural variations including leaf area index, canopy
141 type, plant physiognomy, and canopy architecture (Gao *et al.* 2000; Huete *et al.* 2002). EVI has
142 been shown to correlate well with gross primary production (GPP) across temperate biomes in
143 North America (Rahman *et al.* 2005). Outside of temperate and tropical forests, EVI has been
144 found to be sensitive to spatial and temporal variation in vegetation amount and condition (Huete
145 *et al.* 2002). We used EVI estimates rendered at a 1×1 km spatial resolution and 16-day
146 composite periods during the interval from 2006 to 2018. The Terra and Aqua satellites in
147 combination provide EVI estimates at eight-day intervals. We averaged the EVI values at a $10 \times$
148 10 km spatial resolution (Figure S1). We then interpolated daily EVI values for each year using
149 generalized additive models (GAM) (Wood 2017) with a cyclic penalized cubic regression spline
150 to smoothly join the first day and last day of each year. We retained the native MODIS
151 sinusoidal map projection throughout our analysis.

153 **2.2 | Bird occurrence**

154 We compiled bird occurrence information from the eBird database (Sullivan *et al.* 2014) from 1
155 January 2006 to 31 December 2018 within the Western Hemisphere. eBird contains bird
156 observations in checklist format where species detected by sight or sound are recorded during a
157 sampling event. eBird represents a semi-structured database where each observer selects a
158 predefined sampling protocol and survey effort is determined by the observer. We combined
159 occurrence information across checklists that were identified as a group sampling event. A total
160 of 28,520,138 checklists were available for analysis within our study area containing a total of
161 4,577 unique species.

We summarized eBird occurrence information by day across each year by calculating species' frequency of occurrence within each 10×10 km pixel for each day and year. Specifically, for pixels that contained eBird checklists, we divided the total number of checklists where the species was observed by the total number of checklists submitted in each pixel (see Figure 2a for an example). We estimated seasonal patterns of movement for each species using the following procedure. Applying the geographic coordinates of the center of each 10×10 km pixel, we calculated each species' weighted geographic center of occurrence by day and year using species' frequency of occurrence in each pixel as a weighting factor (see Figure 2b for an example). We summarized the latitudinal location of species' centers of occurrence by day across the annual cycle using generalized additive mixed models (GAMM)(Wood 2017). We included the intercept for year as a random effect and we used a cyclic penalized cubic regression spline to smoothly join the first day and last day of each year. We estimated seasonal migration phenology for each species by extracting the daily predicted values of latitude from the GAMM fits (see Figure 2b for an example). We used the first derivative of the predicted values from the GAMM fits to then calculate the instantaneous rate of change in latitude by day (latitudinal speed; see Figure 2c for an example). Changes in latitudinal speed across the annual cycle allowed us to separate peak migration periods from sedentary periods. Here, the maximum (positive) latitudinal speed captured the height of spring migration, and the minimum (negative) latitudinal speed captures the height of autumn migration (see Figure 2d-e for an example).

We selected species for analysis using the following procedure. We first removed species that occurred primarily within marine environments and species that lacked eBird occurrence information for a significant portion of the annual cycle (see Figure 2b for an example). We then selected species whose breeding range map centers were located north of the tropics (24°N

latitude) and whose breeding and non-breeding range maps intersected less than 50%. This procedure resulted in a total of 237 species for analysis (Table S1). We estimated the geographic centers and the percent overlap of species' breeding and non-breeding ranges using NatureServe range maps (Ridgely *et al.* 2007). We selected range maps because they provide geographic summaries of extent of occurrence (Gaston 1991), allowing us to estimate these parameters consistently across species. We first converted the range map polygons to equal-area hexagons with a cell size of 49,811 km², generated using a icosahedral discrete global grid system based on a Fuller icosahedral projection using an aperture 4 hexagon partition method (Sahr, White & Kimerling 2003; Sahr 2011). The equal-area hexagon cells provide a uniform spatial summary of the range maps polygons across the surface of the earth. We then calculated species' geographic center of occurrence by averaging the geographic coordinates of the hexagon cell-centers that occurred within each species' non-breeding and breeding range polygons. We only considered hexagon cells that contained greater than 10% terrestrial (non-marine) surface area in these calculations. We estimated the percent overlap between the breeding and non-breeding ranges using the number of hexagon cells classified as breeding, non-breeding, or both.

We accounted for differences in broad-scale migratory behavior in our analysis by classifying the 237 species based on their dominant migration flyway association in North America. We first identified all of the 10 × 10 km pixels between 24° and 50° N latitude where the frequency of occurrence for each species during any day of the year was greater than zero. We then used the majority rule (proportion >50%) to classify each species into one of the three migration flyway categories: western (west of the 103rd meridian), central (between the 103rd and 90th meridian), and eastern (east of the 90th meridian)(La Sorte *et al.* 2014b). We designated a

fourth category, all flyways, for species that occurred equally across the three flyway categories (Figure S2).

We used the dominant category from Wilman *et al.* (2014) to classify each species' dietary guild (Table S1). We eliminated seven species from two dietary guilds (piscivore and frugivore) whose combined classification of migration flyway and dietary guild contained less than three representatives. This final step resulted in a total of 230 species for analysis in four flyway designations: western ($n = 58$), central ($n = 12$), eastern ($n = 92$), and all ($n = 68$). These species were distributed across seven dietary guilds: insectivore ($n = 148$), nectarivore ($n = 6$), omnivore ($n = 28$), herbivore ($n = 13$), herbivore-granivore ($n = 8$), granivore ($n = 16$), and carnivore ($n = 11$; Table S1). When combined, the 230 species occurred in 16 unique combinations of flyway designation and dietary guild (Table S1).

2.3 | Associations with vegetation greenness

We quantified the association between species' occurrence and vegetation greenness using the following procedure. We first calculated the weighted mean EVI by day and year for the 10×10 km pixels where each species occurred using species' frequency of occurrence within the pixels as a weighting factor. We then averaged these values by day across years. To provide a context for interpreting the observed EVI associations, we extracted the annual minimum and maximum EVI associations using the average EVI for each day of the year based on species' daily patterns of occurrence within the 10×10 km pixels (see Figure 2d for an example). This minimum/maximum envelop captures the full range of conditions that exist across species' annual distributions (see Fig. 1). We summarized species observed EVI associations by calculating the instantaneous rate of change in EVI by day using the first derivative of the

predicted values from the GAM fit of EVI by day (see Figure 2e for an example). We summarized these EVI associations across the annual cycle for species in each migration flyway and species in each migration flyway/dietary guild combination using GAMM with species included as a random effect. We used 100 bootstrap replicates to provide a visual summary of uncertainty in the GAMM fits. This procedure involves sampling species with replacement in each migration flyway and in each migration flyway/dietary guild combination, and then reimplementing the GAMM analysis.

We used a bootstrap procedure applied to species' GAMM predicted values for species in each migration flyway and in each migration flyway/dietary guild combination to test the level of evidence for phenological synchronization (Figure 1). First, we split the GAMM predicted values for each species into their “spring” and “autumn” components based on the day during the breeding season when the predicted values crossed zero on the y-axis (see Figure 1 and Figure 2e for an example). We then calculated a weighted ratio for each seasonal component. For the spring component, we calculated the ratio of the sum of the positive predicted values in the spring divided by the sum of the absolute value of all of the predicted values in the spring, each multiplied by the migration speed estimated for each day. The ratio for each species has the form

$$\frac{\sum_{i=1}^a x_i s_i, \text{ for } x_i > 0}{\sum_{j=1}^b |y_j| s_j}$$

where x_i is the predicted value for day i during the spring component for the a days containing positive predicted values, s_i is migration speed on day i , y_j is the predicted value for day j across all b days of the spring component, and s_j is migration speed on day j . For the autumn component, we calculated the ratio of the sum of the absolute value of the negative values in the autumn divided by the sum of the absolute value of all of the predicted values in the autumn,

each multiplied by the migration speed estimated for each day and negative one. The ratio for each species has the form

$$\frac{\sum_{i=1}^a |x_i| s_i (-1), \text{ for } x_i < 0}{\sum_{j=1}^b |y_j| s_j (-1)}$$

where x_i is the negative predicted value for day i during the autumn component for the a days containing negative predicted values, s_i is migration speed on day i , y_j is the predicted value for day j across all b days of the autumn component, and s_j is migration speed on day j . We estimated 95% confidence intervals for the ratios using a bootstrap procedure where we randomly sampled species with replacement 9,999 times and regenerated the GAMM predicted values and test statistic for each iteration.

We used the ratio and the bootstrap 95% confidence intervals to classify the level of evidence for phenological synchronization based on six designations. From high to low evidence, the designations were defined as: (1) a ratio greater than 0.75 and the 95% confidence interval does not include 0.75; (2) a ratio greater than 0.75 and the 95% confidence interval includes 0.75; (3) a ratio greater than 0.5 and the 95% confidence interval does not include 0.5; (4) a ratio greater than 0.5 and the 95% confidence interval includes 0.5; (5) a ratio greater than 0.25 and the 95% confidence does not include 0.25; and (6) a ratio is greater than 0.25 and the 95% confidence interval includes 0.25.

All analyses were conducted in R, version 3.6.0 (R Development Core Team 2020). We implemented GAM using the `mgcv` library (Wood 2017), GAMM using the `gamm4` library (Wood & Scheipl 2020), and we estimated first derivatives using the `features` library (Varadhan 2015).

3 | RESULTS

Across flyway designations, observed EVI associations were lower on average during the non-breeding season and higher on average during the breeding season (Figure 3a-d). These differences were weaker for species in the western flyway (Figure 3a) and stronger for species in the eastern flyway (Figure 3c). The range between the maximum and minimum annual EVI associations were very similar on average across the annual cycle for species in the western flyway (Figure 3a), and increased on average during the breeding season for species in the remaining three flyway designations (Figure 3b-d). The maximum annual EVI association during the breeding season exceeded on average the maximum annual EVI association during the non-breeding season only for species in the eastern flyway (Figure 3c). For all four flyway designations, observed EVI associations during migration did not decline substantially below the observed EVI associations during the non-breeding season (Figure 3a-d).

The instantaneous rate of change in EVI by day when examined across flyway designations (Figure 3e-h) contained different levels of evidence for phenological synchronization. Evidence was strongest for the all flyway designation during the spring and autumn (Figure 3h, Table 1), followed by the western flyway in the spring (Figure 3e, Table 1) and the eastern flyway in the spring and autumn (Figure 3g, Table 1). Evidence was weaker in the central flyway in the spring and autumn (Figure 3f, Table 1) followed by the western flyway in the autumn (Figure 3e, Table 1).

When the observed EVI associations and annual minimum and maximum EVI associations were examined based on migration flyway and dietary guild combinations, different patterns were evident (Figure 4) from those documented at the flyway level (Figure 3a-d). Within the eastern flyway, insectivores presented the greatest range between the maximum and

minimum annual EVI associations during the breeding and non-breeding seasons (Figure 4c). The range between the minimum and maximum annual EVI associations for omnivores (Figure 4g) and especially herbivore-granivores (Figure 4j) in the eastern flyway remained large across the entire annual cycle. The narrowest range between the minimum and maximum annual EVI associations occurred for insectivores (Figure 4a) and especially nectarivores (Figure 4e) in the western flyway. The observed EVI associations during the breeding season for nectarivores in the western flyway were lower than the annual maximum EVI association on their non-breeding grounds (Figure 4e).

The instantaneous rate of change in EVI by day when summarized by migration flyway and dietary guild combination (Figure 5) presented different levels of evidence for phenological synchronization. The evidence was strongest for omnivores, herbivores, herbivore-granivores, and granivores during spring and autumn migration (Figure 5g-n, Table 1), with the exception of omnivores in the western flyway during spring migration (Figure 5f, Table 1). Evidence was also strongest for insectivores in the all flyway designation during spring migration (Figure 5d, Table 1) and carnivores in the all flyway designation during spring and autumn migration (Figure 5p, Table 1). Evidence was weaker for insectivores in the western (Figure 5a, Table 1) and eastern flyways (Figure 5c, Table 1) during spring migration, and for nectarivores in the western flyway during spring and autumn migration (Figure 5e, Table 1). Evidence was weaker still for insectivores in the eastern flyway during autumn migration (Figure 5c, Table 1). This was followed by insectivores in the western flyway (Figure 5a, Table 1) and central flyway during spring and autumn migration (Figure 5b, Table 1), and carnivores in the western flyway during spring migration (Figure 5o, Table 1). Evidence was weakest for carnivores in the western flyway during autumn migration (Figure 5o, Table 1).

320

321 4 | DISCUSSION

322 In this study, we evaluated how 230 North American migratory bird species associate with
323 vegetation greenness across the full annual cycle within the Western Hemisphere. Our analysis
324 identified different associations with vegetation greenness and different levels of evidence for
325 phenological synchronization during spring and autumn migration by flyway and flyway/dietary
326 guild combinations. As expected, herbivores presented the strongest evidence for phenological
327 synchronization during spring and autumn migration. Granivores, herbivore-granivore,
328 omnivores, and carnivores also presented in most cases strong evidence for phenological
329 synchronization during spring and autumn migration. Evidence of phenological synchronization
330 was weakest for insectivores during spring and autumn migration that migrate through the
331 eastern and especially central portions of the continent, and insectivores and carnivores that
332 migrate through the western portion of the continent during spring and especially autumn
333 migration. In total, our results suggest migration and vegetation phenology are broadly congruent
334 across a range of dietary guilds, consumer levels, and migration tactics. Any changes in
335 vegetation phenology could therefore have far-reaching implications for the region's migratory
336 bird populations.

337 Weak evidence for phenological synchronization documented for insectivores in the
338 central and eastern migration flyways diverged from our expectations. Although phenological
339 synchronization appears to occur for these species within the contiguous USA (La Sorte *et al.*
340 2014a), these findings suggest strong synchronization does not occur south of this region. These
341 findings could be related to the presence of a large ecological barrier to migration, the Gulf of
342 Mexico, where tracking vegetation greenness is likely not feasible during migration. Current

evidence suggests the phenology of vegetation greenness north and south of the Gulf of Mexico is poorly correlated (Cohen *et al.* 2015) and the arrival of migrants along the north coast of the Gulf of Mexico in the spring has not been affected by recent climate change (Cohen *et al.* 2015; Horton *et al.* 2019).

Weaker evidence for insectivores and nectivores that migrate in the western portion of the continent could be related to the use of looped migration trajectories. These trajectories place these species at higher elevations in the autumn (La Sorte *et al.* 2014a; Supp *et al.* 2015) where levels of vegetation greenness are lower (see Figure S1). The phenology of flowers and insects within these montane environments are regulated by temperature and the timing of snowmelt (Forrest & Thomson 2011). Thus, insectivores and nectivores in the autumn are likely tracking the occurrence of flowers and insects along elevational gradients as they move south. The weak associations for insectivores could also be a result of the molting of flight feathers during autumn migration, which is more common for passerine species that migrate in the western portion of the continent (Leu & Thompson 2002; Rohwer, Butler & Froehlich 2005).

Carnivores that migrate in the western portion of the continent presented the weakest evidence for phenological synchronization, especially in the autumn. These findings follow our expectations where carnivores would gain little apparent benefit through phenological synchronization. This finding contrasts with carnivores that migrate across the full extent of the North American continent, which showed strong evidence for phenological synchronization. The carnivores in the western flyway are mostly large-bodied species that prey primarily on small to medium sized mammals, whereas carnivores that migrate across the entire continent have a range of body sizes and prey on insects, birds, and mammals (see Table S1). Our findings therefore

suggest the benefits of phenological synchronization are weakest for carnivores in the west that prey on larger bodied mammals.

The mechanism underlying phenological synchronization for herbivores (van der Graaf *et al.* 2006; Duriez *et al.* 2009; van Wijk *et al.* 2012; Shariatinajafabadi *et al.* 2014; Shariati Najafabadi *et al.* 2015; Si *et al.* 2015; Kölzsch *et al.* 2016) and insectivores (La Sorte *et al.* 2014a; Thorup *et al.* 2017) has been previously explored. Most work has focused on spring migration where phenological synchronization is thought to enhance associations with young vegetation and emerging insect populations. The presence of similar associations for species whose diets deviate from plants and insects could be related to other ecological or environmental factors that are connected to or correlated with vegetation phenology. For example, the phenology of other vegetation features that occur in close association with vegetation green-up in the spring (Rathcke & Lacey 1985) may provide food resources for omnivores and granivores. Other ecosystem components whose phenologies correspond with vegetation green-up and senescence, such as small mammal hibernation (Williams *et al.* 2014), may play a role for some species, such as omnivores and carnivores. For omnivores and carnivores that prey on birds, phenological synchronization may occur as they track migrating bird populations. During autumn migration, the ripening of fruits and seeds (Rathcke & Lacey 1985) can provide resources for species whose diets expand during autumn migration (Berthold 1976; Bairlein 1990; Bairlein & Gwinner 1994). Alternatively, the environmental factors that control vegetation green-up and senescence could similarly influence migration. Vegetation green-up in the spring is controlled by changes in temperature and precipitation (Chen 2017), whereas the senescence of vegetation in the autumn is controlled by temperature and photoperiod, with photoperiod having a stronger influence at higher latitudes and temperature at lower latitudes (Lang *et al.*

2019). Thus, if plants and birds rely on similar environmental cues, such as photoperiod at higher latitudes in the autumn (Winkler *et al.* 2014), our findings suggest similar patterns of phenological tracking can occur.

As expected, species occurred on their temperate breeding grounds when vegetation greenness was at its annual maximum. However, we found the opposite pattern when species occurred on their non-breeding grounds. Here, vegetation greenness was close to its annual minimum. This outcome was more pronounced for species that migrate outside the western flyway, which as a group tend to winter further south (see Figure S2). Seasonality in vegetation greenness in the tropics and subtropics is inherently low (see Figure S1), but the annual minimum in these regions is typically higher than the annual minimum in northern temperate regions.

We found that associations with vegetation greenness on the breeding grounds tended to be higher than the associations on the non-breeding ground. Similar to findings for the world's migratory birds (Zurell *et al.* 2018a), these results suggest that productivity levels encountered during the breeding and non-breeding seasons are not necessarily the same. We also found that these differences were greatest for species that migrate and breed in eastern North America. These findings emphasize the role of eastern deciduous forests (Figure S1) as a critical habitat for the continent's migratory bird species during migration and the breeding season (Rabenold 1993).

Current evidence suggests that vegetation phenology is responding to global climate change (Cleland *et al.* 2007; Richardson *et al.* 2013). In the Northern Hemisphere, this includes earlier spring phenology (Schwartz, Ahas & Aasa 2006; Jeong *et al.* 2011) and longer growing seasons (Richardson *et al.* 2006). The effects of climate change on autumn phenology has been

less well studied (Gallinat, Primack & Wagner 2015). However, phenological responses are thought to be occurring at lower latitudes where temperature more directly controls vegetation phenology (Lang *et al.* 2019). Current evidence suggests short-distance migrants are responding more effectively than long-distance migrants to changes in vegetation phenology (Usui, Butchart & Phillimore 2017). Species that migrate and breed in central and eastern North America tend to migrate longer distances (Figure S2), and climate change in these regions is resulting in earlier springs, longer growing seasons, and delayed autumns (Jeong *et al.* 2011; Dragoni & Rahman 2012; Gaertner *et al.* 2019), which could increase the risk of population declines for these species.

Our approach necessarily contains uncertainties that could affect our results. This includes uncertainty in our estimates of vegetation greenness, species' daily patterns of occurrence, and dietary guild. The variance generated by these sources of uncertainty are more likely to affect our results and conclusions when sample sizes (the number of species) are small. As more bird occurrence data become available across the globe (La Sorte & Somveille 2020), it will be valuable to explore similar questions across a larger number of species and a greater diversity of dietary guilds. It would also be valuable to explore these questions for species that migrate outside of the Western Hemisphere.

In this study, we identified phenological synchronization with vegetation greenness as a general correlate of migration phenology for diverse array of dietary guilds, trophic levels, and migration tactics. Exceptions were likely due to the presence of large ecological barriers to migration and the use of high elevation habitats in the autumn. Any changes in vegetation phenology could therefore impact many of the region's migratory bird populations, which would add to the challenges these species already face under global change (Zurell *et al.* 2018b;

Rosenberg *et al.* 2019). Our findings emphasize the need to better understand the environmental cues that regulate migratory behavior and the implications for migratory bird populations if these cues were to change. Our approach underscores the unique potential created by citizen-science to study the patterns and drivers of natural systems at broad spatial extents.

ACKNOWLEDGEMENTS

We thank E.B. Pereira and four anonymous reviewers for constructive suggestions on an earlier draft, S. Kelling and the eBird team for their support, and the many eBird participants for their contributions.

AUTHORS' CONTRIBUTIONS

F.A.L. and C.H.G. conceived of the study. F.A.L. compiled the data, designed and implemented the analysis, and drafted the manuscript. C.H.G. contributed suggestions and text to subsequent drafts.

DATA AVAILABILITY STATEMENT

The bird occurrence data is available from eBird (ebird.org). The vegetation greenness data (MODIS EVI) is available from the NASA lpdaac server (lpdaac.usgs.gov).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at
the end of the article.

Table 1. Ratios with bootstrapped 95% confidence intervals for the spring and autumn components of the annual cycle by migration flyway and migration flyway/dietary guild combinations (see Table S1). The level of evidence for phenological synchronization based on six designations, from high to low evidence: (1) the ratio is greater than 0.75 and the 95% confidence interval does not include 0.75; (2) the ratio is greater than 0.75 and the 95% confidence interval includes 0.75; (3) the ratio is greater than 0.5 and the 95% confidence interval does not include 0.5; (4) the ratio is greater than 0.5 and the 95% confidence interval includes 0.5; (5) the ratio is greater than 0.25 and the 95% confidence does not include 0.25; and (6) the ratio is greater than 0.25 and the 95% confidence interval includes 0.25. Note that not all six designations occur in the table.

Flyway	Diet	Component	Ratio (95% CI)	Designation
Western		Spring	0.952 (0.773, 1.000)	1
Western		Autumn	0.779 (0.550, 0.964)	2
Central		Spring	0.967 (0.614, 1.000)	2
Central		Autumn	0.893 (0.403, 1.000)	2
Eastern		Spring	0.932 (0.868, 0.978)	1
Eastern		Autumn	0.911 (0.832, 0.973)	1
All		Spring	1.000 (0.999, 1.000)	1
All		Autumn	1.000 (1.000, 1.000)	1
Western	Insectivore	Spring	0.817 (0.576, 1.000)	2
Western	Insectivore	Autumn	0.608 (0.373, 0.904)	4
Central	Insectivore	Spring	0.697 (0.000, 0.984)	4
Central	Insectivore	Autumn	0.551 (0.000, 0.975)	4
Eastern	Insectivore	Spring	0.877 (0.800, 0.936)	2
Eastern	Insectivore	Autumn	0.821 (0.732, 0.899)	3
All	Insectivore	Spring	1.000 (0.919, 1.000)	1
All	Insectivore	Autumn	0.985 (0.768, 1.000)	1
Western	Nectarivore	Spring	0.987 (0.562, 1.000)	2
Western	Nectarivore	Autumn	0.835 (0.310, 0.953)	2
Western	Omnivore	Spring	0.988 (0.674, 1.000)	2
Western	Omnivore	Autumn	1.000 (0.505, 1.000)	2
Eastern	Omnivore	Spring	1.000 (0.933, 1.000)	1
Eastern	Omnivore	Autumn	1.000 (1.000, 1.000)	1
All	Omnivore	Spring	1.000 (0.994, 1.000)	1
All	Omnivore	Autumn	1.000 (1.000, 1.000)	1
All	Herbivore	Spring	1.000 (0.997, 1.000)	1

All	Herbivore	Autumn	1.000 (1.000, 1.000)	1
Eastern	Herbivore, Granivore	Spring	1.000 (1.000, 1.000)	1
Eastern	Herbivore, Granivore	Autumn	1.000 (1.000, 1.000)	1
All	Herbivore, Granivore	Spring	1.000 (1.000, 1.000)	1
All	Herbivore, Granivore	Autumn	1.000 (1.000, 1.000)	1
Western	Granivore	Spring	1.000 (0.919, 1.000)	1
Western	Granivore	Autumn	1.000 (0.970, 1.000)	1
Central	Granivore	Spring	1.000 (0.559, 1.000)	2
Central	Granivore	Autumn	1.000 (0.792, 1.000)	1
All	Granivore	Spring	1.000 (1.000, 1.000)	1
All	Granivore	Autumn	1.000 (1.000, 1.000)	1
Western	Carnivore	Spring	0.730 (0.009, 1.000)	4
Western	Carnivore	Autumn	0.258 (0.005, 1.000)	6
All	Carnivore	Spring	1.000 (1.000, 1.000)	1
All	Carnivore	Autumn	1.000 (1.000, 1.000)	1

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Figure 1. Conceptual figure demonstrating how (a) observed associations with the MODIS enhanced vegetation index (EVI) are defined across the annual cycle under strong and weak phenological synchronization with vegetation greenness. The blue polygon represents the annual maximum and minimum EVI associations. (b) The observed EVI associations under strong and weak phenological synchronization converted to instantaneous rate of change in EVI by day.

Figure 2. (a) Occurrences information for the Black-and-white Warbler (*Mniotilta varia*) during the combined period 2006 to 2018. (b) The latitude of the geographic center of occurrence by day for each year. The fitted line is from a generalized additive mixed model with year included as a random effect. (c) The instantaneous rate of change in latitude by day (latitudinal speed) derived from the fitted line in (b). (d) The observed association with the MODIS enhanced vegetation index (EVI; black line) and the annual maximum and minimum EVI associations (gray polygon). (e) The instantaneous rate of change in EVI by day derived from the observed associations with EVI in (d). The vertical colored bands in (d, e) correspond to the latitudinal speed (red = positive; blue = negative) shown in (c). Bright red bands indicate the species in undertaking spring migration. Bright blue bands indicate the species in undertaking autumn migration.

Figure 3. (a-d) Observed associations (solid lines) with the MODIS enhanced vegetation index (EVI) and the annual maximum and minimum EVI associations (dashed lines) for 230 migratory bird species organized by migration flyway. (e-h) The instantaneous rate of change in the observed EVI associations for 230 migratory bird species organized by migration flyway (bottom row). The flyway designations include Western ($n = 58$), Central ($n = 12$), Eastern ($n = 92$), and species that migrate in All flyways ($n = 68$; Table S1). The fitted lines were estimated using generalized additive mixed models (GAMM) with species included as a random effect. The

vertical bands correspond to the average latitudinal speed of species in each flyway (red = positive; blue = negative). Bright red bands indicate the species in undertaking spring migration. Bright blue bands indicate the species in undertaking autumn migration. The grey lines are 100 bootstrap replicas used to estimate uncertainty in the GAMM fits.

Figure 4. Observed associations (solid lines) with the MODIS enhanced vegetation index (EVI) and the annual maximum and minimum EVI associations (dashed lines) for 230 migratory bird species by migration flyway and dietary guild combination (see Table S1). The migration flyway designations include Western, Central, Eastern, and species that migrate in All flyways. The fitted lines were estimated using generalized additive mixed models (GAMM) with species included as a random effect. The vertical bands correspond to the average latitudinal speed of species in each flyway (red = positive; blue = negative). Bright red bands indicate the species in undertaking spring migration. Bright blue bands indicate the species in undertaking autumn migration. The grey lines are 100 bootstrap replicas used to estimate uncertainty in the GAMM fits.

Figure 5. The instantaneous rate of change in the observed associations with the MODIS enhanced vegetation index (EVI) across the annual cycle for 230 migratory bird species by migration flyway and dietary guild combination (see Table S1). The migration flyways include Western, Central, Eastern, and species that migrate in All flyways. The fitted lines were estimated using generalized additive mixed models (GAMM) with species included as a random effect. The vertical bands correspond to the average latitudinal speed of species in each flyway (red = positive; blue = negative). Bright red bands indicate the species in undertaking spring migration. Bright blue bands indicate the species in undertaking autumn migration. The grey lines are 100 bootstrap replicas used to estimate uncertainty in the GAMM fits.

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5