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Novel measures of continental-scale avian migration phenology related to proximate environmental cues

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Abstract. Rapid changes in seasonal avian migrations provide compelling examples of biotic response to climate change. Seasonal waves of land surface phenology and temperature are thought to be primary exogenous cues that migrants use to fine tune migration timing. Exploration of the role that these cues play in regulating migration timing requires better spatial, temporal, and taxonomic sampling than is typically available. We analyze weather surveillance radar (WSR) and eBird citizen science data in an effort to understand the macroscale relationships among migration phenology, seasonal waves of land surface phenology and seasonality of temperature. We demonstrate that both WSR and eBird data provide similar estimates of migration timing at local (within 100 km) and macro scales (>20° of latitude). These measures of avian phenology were positively correlated with spring temperatures and land surface phenology (extended spring index of first leaf date), which followed a south to north wave. Start-of-spring, estimated from a remotely sensed index of vegetation greenness, did not show the expected pattern from south to north and appears unlikely to be a useful exogenous migration cue within the study region. Future analyses of WSR and eBird data have the potential to provide high-resolution phenology data that may be useful in understanding spatiotemporal dynamics of migration systems and the response of these systems to climate change.

Key words: aeroecology; eBird; green wave; migration; thermal wave; weather radar.

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INTRODUCTION

Change in avian migration phenology is a flagship example of biological impacts of climate change (Morisette et al. 2009). Migrant songbirds are arriving earlier on breeding grounds in response to warmer spring temperatures in Europe and North America (Butler 2003, Jonzen et al. 2006, Lehikoinen et al. 2010). Measures of winter precipitation and temperature are also correlated with advancing spring migration phenology (Saino et al. 2004, 2010, Studds and Marra 2007, McKellar et al. 2013). Advances in arrival timing are generally consistent with advances in timing of passage of migrants en route (Van Buskirk et al. 2009, Saino et al. 2010). Within the en route period, migrants appear to adjust their migration timing based on conditions at a variety of spatial and temporal scales (Marra et al. 2005, Tottrup et al. 2006*a*, *b*, 2010, Tøttrup et al. 2012, Renfrew et al. 2013). Despite numerous studies, our inference about migration phenology remains tied to either idiosyncratic long-term studies at single sites or extensive research efforts on few well-known species (Margary 1926, Stewart et al. 1952, Dunn and Winkler 1999, Root et al. 2003, Both et al. 2004, Marra et al. 2005, Parmesan 2006, Miller-Rushing et al. 2008, Van Buskirk et al. 2009).

Migration timing, as an individual-based phenotypic trait, emerges from the interaction of an endogenous annual cycle entrained by day length and variable exogenous environmental cues (Gwinner 1977). Temperature and land surface phenology are thought to be among the most critical variable exogenous environmental cues impacting migration timing. Temperature has consistently been associated with shifts in migration phenology for well-studied species in Europe and North America (Dunn and Winkler 1999, Both et al. 2004, Marra et al. 2005). Evidence that migrants adjust their timing en route in response to land surface phenology is less consistent. Typically, macroscale land surface phenology is measured using satellite radiometry (e.g., normalized difference vegetation index [NDVI; Tucker 1979]). Vegetation indices and other proxies of land surface phenology (Marra et al. 2005) are typically used as a proxy for food availability, which may be more closely related to vegetation dynamics than to temperature. We investigate both traditional NDVI and a recently modified extended spring first leaf index in this context (Schwartz et al. 2013, Ault et al. 2015).

At the species level, there is relatively consistent evidence that en route migrants in Europe respond to variation in land surface phenology (Thorup et al. 2007, Bauer et al. 2008, Saino et al. 2010, Tøttrup et al. 2012, Shariatinajafabadi et al. 2014, Si et al. 2015), but the evidence for a similar response at the species level in temperate North America is equivocal (Renfrew et al. 2013, Paxton et al. 2014, Cohen et al. 2015). This difference may well be related to the lower latitudes associated with the North American studies. Recent studies of North American avian migration systems, however, suggest that migration timing is associated with remotely sensed indices of vegetation greening (La Sorte et al. 2014, 2015). Inconsistent results among studies fuels concerns that our understanding of migration phenology and its link to climate change is primarily phenomenological rather than mechanistic (Knudsen et al. 2011), which limits our ability to forecast changes in migration timing in response to global change (Winkler et al. 2014). To move beyond phenomenological explanations, we need new data sources that can be used to test specific predictions about how migrants should respond to variation in temperature and vegetation phenology. This need is a primary motivating factor for this research. Examining spatiotemporal variation in migration timing relative to spring temperature and land surface phenology may yield insights into the mechanisms that drive dynamics of en masse arrival times of migrants. However, analyses of this type require data with better spatial and temporal coverage than is presently available. A primary objective of this study is to examine the novel data sources for developing new metrics of macroscale patterns in migration phenology that could be used to assess associations between migration phenology and potential migration cues.

Our exploration of the associations among migration timing and environmental cues is informed by several long-standing hypotheses about these relationships. The general notion that environmental factors govern the timing of annual northward spring migration is at least thousands of years old (Thompson 1910). The specific hypothesis that primary productivity regulates these northward movements has been termed the green wave hypothesis (Drent et al. 1978). For convenience, we refer to the parallel hypothesis based on ambient temperature as the "thermal wave hypothesis." Many studies have evaluated whether avian migration phenology is consistent with use of the green or thermal wave as a timing cue. Despite this history, the wave hypotheses are poorly and inconsistently described in the literature. We suggest that the wave hypotheses share two basic assumptions. First, the purported migration cue must show a seasonal increase locally (i.e., at the spatial grain size). That is, vegetation must green up in the spring (green wave) or the temperature must get warmer (thermal wave). This assumption is well supported in the literature for both temperature and land surface phenology (e.g., Schwartz 1998). The second assumption is that these local seasonal patterns must be part of a geographical wave, in the case of Nearctic–Neotropic migrants in spring, we expect a wave of greenness (and temperature) to move from south to north, but in other regions, waves might move in other directions. If this condition is also met, then it is plausible that migrants are either constrained by the progression of the wave or that local conditions could be a good predictor of conditions further north. In either case, the wave would be a useful cue for migration timing. However, if these conditions are not met at a macroscale, it is difficult to understand how these exogenous cues could be useful in timing migration. Within the United States, there is no strong evidence for a generalized south to north green wave as typically measured using remotely sensed vegetation indices (White et al. 2009). However, it is less clear whether geographical gradients in green-up occur within particular regions associated with regional migration systems. To examine this question directly, we compare novel measures of migration timing to broadscale patterns in green-up of vegetation and warm-up of temperatures to assess the degree of correspondence among them within the eastern United States.

The motivation for developing new measures of songbird migration timing is that it is very challenging to address macro-ecological questions with existing migration phenology data. Existing data on migration timing come primarily from short-term or, more rarely, long-term field studies of local populations (Lehikoinen et al. 2010). These data are typically collected at migration banding stations, biological field stations, or local to regional monitoring networks. Our approach relies on two continental observation networks: one based on human observers (eBird; Sullivan et al. 2009) and one based on radar remote sensing of birds (weather surveillance radars [WSRs]; Crum and Alberty 1993, Gauthreaux and Belser 1998, Buler and Dawson 2014, Horton et al. 2015). These data are appropriate for developing new measures for examining the phenology of migration systems. That is, we are primarily interested in understanding factors governing the timing of nocturnal migration systems overall rather than in examining species-level patterns. eBird data have been used to estimate migrant arrival dates at particular locations and occurrence-weighted migration speeds (LaSorte et al. 2013). Observation networks have been used to estimate arrival dates of short-distance migrants (Zuckerberg et al. 2015). Building upon this work, we apply a similar analysis framework to eBird data to quantify seasonal patterns in species richness of nocturnal migrants. Despite a long history of using WSRs in ornithology (Eastwood 1967, Diehl and Larkin 2005, Gauthreaux and Belser 2003, Shamoun-Baranes et al. 2014), we are not aware of any studies that use WSR data measure macroscale migration phenology that could be used to examine potential exogenous cues linking changes in phenology to changes in climate.

METHODS

Radar data

We retrieved and analyzed level II radar data from 03:00 UTC to 08:00 UTC for the period January through June of 2013 for each of 32 radars (Fig. 1).

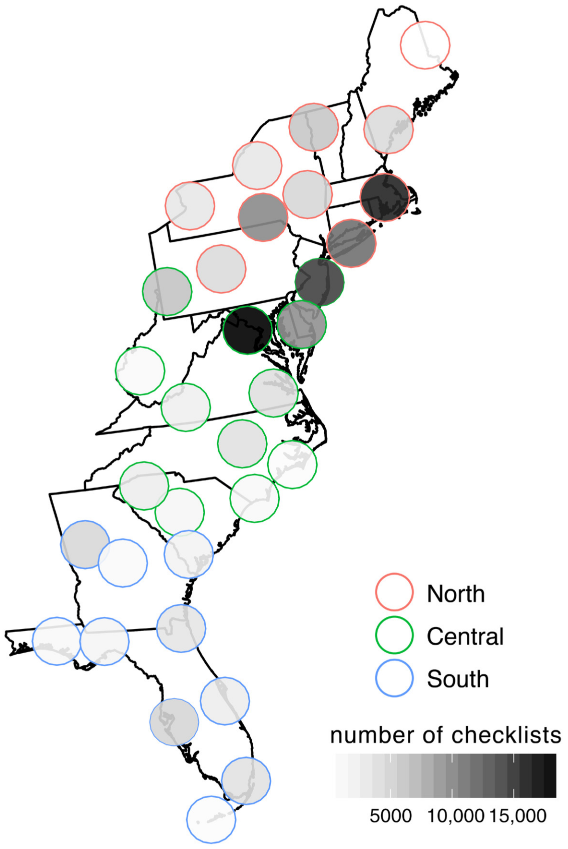

Fig. 1. Locations of 32 weather surveillance radars (WSRs) and density of eBird checklists (shading) within 100 km of those radars in spring of 2013. WSR and eBird data were divided into north, central, and south regions.

This time period was chosen to minimize the influence of dusk ascent (Buler and Dawson 2014) and dawn descent of migrants (Van Doren et al. 2016). We chose to censor data from the beginning and ending of nightly migratory flights because we were primarily interested in a measure of nightly migration intensity, that is, total amount of birds aloft. During the ascent and descent periods, only a fraction of the night's migrants would be airborne, which could bias our index. We used data from the lowest elevation angle sweep (0.5°) of each radar scan, consisting of either 360 or 720 azimuths (1° or 0.5° wedges). The minimum sampling height of the radar increases with distance from the radar. We did not modify the radar data in an effort to adjust for sampling height. Adjustments for sampling height can be important in comparing fine spatial variation in density of birds aloft (Buler and Diehl 2009). However, we did not think this height adjustment would improve our index of nightly migration intensity at the larger scale of 100 km radii around individual radars, and thus, we did not apply an adjustment.

Radar sampling units were 250-m distance intervals along each azimuth from the radar, known as pulse volumes. We used data from pulse volumes that were within 100 km of the radar (392 pulse volumes per azimuth). Sweeps occurred once in every 5 to 10 minutes at each radar, resulting in a total of 234,007 radar sweeps within our analysis period. We filtered these data to retain signal from migrating birds, but not weather. Our filtering process was a modification of the hydrometeor classification algorithm of Park et al. (2009), combined with a static ground clutter mask. Ground clutter masks were generated for each radar to filter consistently low and high values of reflectivity, as these values are typically associated with ground clutter. The major changes to the classification algorithm included the removal of the radial velocity and correlation coefficient thresholds, as well as a widening of the membership functions for reflectivity factor (Z in units of $\text{mm}^6 \cdot \text{mm}^{-3}$, hereafter referred to as reflectivity) and differential reflectivity (ZDR in units of dBZ). These changes enabled proper biological classification during heavy migratory movements at the expense of worse classifications within meteorological categories. That is, our classification algorithm did not perform as well as the original algorithm in distinguishing among meteorological scatters (rain vs. sleet vs. hail), but was better at distinguishing between meteorological phenomena and biological scatters. If filtering decreased the number of samples (individual pulse volumes) remaining per sweep to less than 2000, we omitted the sweep from further analysis. To gauge the effectiveness of our filtering, we visually inspected thousands of images of the censored data; the vast majority of the analyzed reflectivity corresponded to easily recognizable patterns attributable to bird migration (Stepanian and Horton 2015).

We calculated mean reflectivity of each sweep using pulse volumes (as defined above) as our sampling unit. We then calculated the mean reflectivity across sweeps for each night. We interpret this mean as a measure of nightly intensity of bird migration. We then fit a generalized additive model (GAM) with a spline smoothing function to the 6 months of daily data for each radar to smooth between-day variation. We extracted the smoothed reflectivity estimates for each day and the date associated with the seasonal peak in smoothed reflectivity for each radar. Because the smoothed reflectivity values were highly variable among radars, we normalized these data across radars using a z-score standardization. We fit GAMs to these normalized daily radar data to examine seasonal phenology in migration intensity by grouping radars into south, central, and north regions (Fig. 1).

eBird data

We compiled eBird checklists from 2013 for areas within 80 km of the 32 radars and extracted occurrence information for 182 species of nocturnal migrants (Table 1). We selected complete checklists using stationary and traveling protocols and restricted checklists to land-based observations between 26° and 48° N latitude. We limited traveling counts to distances less than 8.1 km and restricted all observations to less than 180 min in observation duration. To reduce redundant sampling, we removed all but one set of observations conducted at the same location on the same calendar date. From these checklists, we then determined the number of nocturnal migrant species encountered each day (species richness $\cdot$ $\text{day}^{-1} \cdot \text{radar}^{-1}$). We used a total of 196,071 checklists, which contained approximately 1.2 million occurrences. Because daily richness values

Table 1. Frequency at which taxa of nocturnal migrant birds were represented in eBird data used to estimate phenology of migration.

Order	Percentage of total	Family (common name)	No. species	Percentage of total
Podicipediformes	1.86	Podicipedidae (grebes)	4	1.86
Pelecaniformes	5.78	Ardeidae (herons, egrets, and bitterns)	9	5.78
Anseriforme	14.99	Anatidae (ducks, geese, and waterfowl)	26	14.99
Gruiformes	2.10	Rallidae (rails, gallinules, and coots)	8	2.10
Charadriiformes	7.32	Charadriidae (plovers and lapwings)	4	2.57
		Scolopacidae (sandpipers and allies)	19	4.19
		Laridae (gulls, terns, and skimmers)	3	0.56
Cuculiformes	0.45	Cuculidae (cuckoos)	2	0.45
Strigiformes	0.03	Strigidae (owls)	1	0.03
Caprimulgiformes	0.20	Caprimulgidae (nightjars and allies)	3	0.20
Apodiformes	0.73	Trochilidae (hummingbirds)	1	0.73
Piciformes	0.79	Picidae (woodpeckers)	1	0.79
Passeriformes	65.74	Tyrannidae (tyrant flycatchers)	11	6.85
		Vireonidae (vireos)	6	3.87
		Sittidae (nuthatches)	1	1.25
		Certhiidae (treecreepers)	1	0.66
		Troglodytidae (wrens)	4	2.02
		Regulidae (kinglets)	2	1.90
		Polioptilidae (gnatcatchers)	1	1.79
		Turdidae (thrushes and allies)	6	2.18
		Mimidae (mockingbirds and thrashers)	2	4.10
		Parulidae (New World warblers)	36	18.34
		Cardinalidae (cardinals and allies)	7	2.94
		Emberizidae (buntings and New World sparrows)	19	17.13
		Calcariidae (longspurs and snow buntings)	1	0.10
		Icteridae (troupials and allies)	3	2.03
		Fringillidae (siskins, crossbills, and allies)	1	0.57

remained highly variable within and among radars we normalized these data to a daily richness index using the same z-score standardization. To determine peak richness dates, we fit a GAM for each radar domain and geographical region (i.e., south, central, and north; Fig. 1). Day of year was the explanatory variable, and migration intensity was the response variable.

Land surface phenology data

Many methods have been applied to vegetation indices derived via remote sensing to estimate start-of-spring dates. It was not the purpose of this study to evaluate these methods. Rather, we chose to apply commonly used methods to provide a comparison with our new estimate of migration phenology. We used two common data sources to estimate spring land surface phenology. We first calculated the start-of-spring based on NDVI data for the area around each radar following the midpoint pixel method of White et al. (2009). This method is often used in geographical and biological sciences to determine the start-of-spring and has been cited hundreds of times. Start-of-spring date determined with this method has been referred to as the green wave index in a study focused on bird migration (Shariatinajafabadi et al. 2014).

In brief, we used the 16-day composite MODIS product from within 80 km of each radar site (MCD43C4; http://glovis.usgs.gov/). To avoid phenology biases introduced by cropland, we excluded all areas (0.05 degree pixels) that were dominated by crops by removing pixels identified as "croplands" in the MOD12C1 data product. For all other pixels, we determined a start-of-spring date. We averaged start-of-spring dates for pixels within 80 km of each radar (Fig. 1). The second approach we used for estimating start-of-spring dates was an extended start-of-spring index (SI-x) developed based on weather conditions needed for leaf out of a lilac (*Syringa chinensis*) and two species of honey suckle (*Lonicera tatarica* and *L. korolkowii*; Ault et al. 2015). These data were processed in the same manner as the NDVI data.

Temperature data

To examine the seasonality of temperatures relative to that of the green wave and bird phenology, we extracted 2013 temperature data for radar locations from PRISM (http://www.prism.oregonstate.edu/). We explored several temperature thresholds for analysis (e.g., 0°C, 5°C, and 10°C) and found that they generate largely parallel relationships. For this analysis, we focus on the 5°C temperature threshold, but this value is arbitrary with respect to avian migratory phenology. For each radar, we identified the latest spring date on which the average minimum nighttime temperature within 80 km of each radar site dipped below 5°C.

We compared latitudinal trends in peak migration intensity as measured with radar and peak species richness from eBird with those in spring temperatures and land surface phenology. We were interested in whether radar and eBird data provide similar estimates of migration phenology at the macroscale and whether these estimates of phenology were consistent with reliance on a green wave or thermal wave as a primary migration cue. For each data set, we aggregated data by radar site and used the latitude of the radar sites in analyses.

RESULTS

There were clear phenological peaks in nocturnal migration intensity based on radar data analysis at both the individual radar and the regional scale. Among regions, these peaks occurred in the expected sequence with the southern radar peak occurring first (26 April), central peak second (12 May), and northern peak last (18 May; Fig. 2a). Similarly, species richness of nocturnal migrants peaked in the same progression as that of migration intensity (Fig. 2b) and the timing of these peaks also had a similar progression as the timing of peaks in migration intensity. Each eBird-based peak was within 5 days of the peak estimated from the radar data: 24 April in the south, 7 May in the central, and 17 May in the north region. Interestingly, total richness was much higher in the northern region suggesting that nocturnal migrants were more diverse at northern latitudes. There was no obvious increase in migration intensity associated with the increased diversity in the northern region, which perhaps suggests the increase in diversity does not change the system-level phenology from south to north across the migratory flyway.

Daily radar and eBird migration estimates were more strongly correlated during peak migration months than outside of the migration season (Fig. 3). The correlation between radar and eBird was strongest in May ($r = 0.53$, $P < 0.001$, slope = 0.24), and this relationship is significant from March through June (all $r > 0.18$ and $P < 0.001$). In contrast, this relationship was not significant in January or February. In addition, the total increase in migration intensity across the spring was evident in both reflectivity and richness indices as the shift in location of the fit lines among months (Fig. 3). Finally, the latitudinal pattern in timing of peak migration intensity, peak species richness, and temperature across the spring all have similar positive slopes (Fig. 4). When examined on a radar-by-radar basis, the peak dates in migration intensity (radar) and migratory richness (eBird) were strongly correlated ($r = 0.76$, $P < 0.001$). In addition, temperature ($r = 0.48$, $P = 0.018$), start-of-spring ($r = -0.61$, $P = 0.002$), and spring index ($r = 0.76$, $P < 0.001$) are all significantly correlated with peaks in migration intensity as well as with eBird measures of migrant richness (temperature $r = 0.73$, $P < 0.001$; start-of-spring $r = -0.44$, $P = 0.018$; spring index $r = 0.73$, $P < 0.001$).

Start-of-spring dates based on NDVI data were similar to those reported by White et al. (2009) and were not positively associated with latitude or migration phenology as would be required to form a green wave. Rather, in this case, start-of-spring was significantly negatively related to latitude. Start-of-spring dates based on the extended spring index did exhibit the expected green wave from south to north and seem like a plausible link between temperature and plant phenology that could be perceived by migrants.

DISCUSSION

Both radar- and eBird-based methods of quantifying phenology produced expected seasonal peaks within local domains and across >20° of

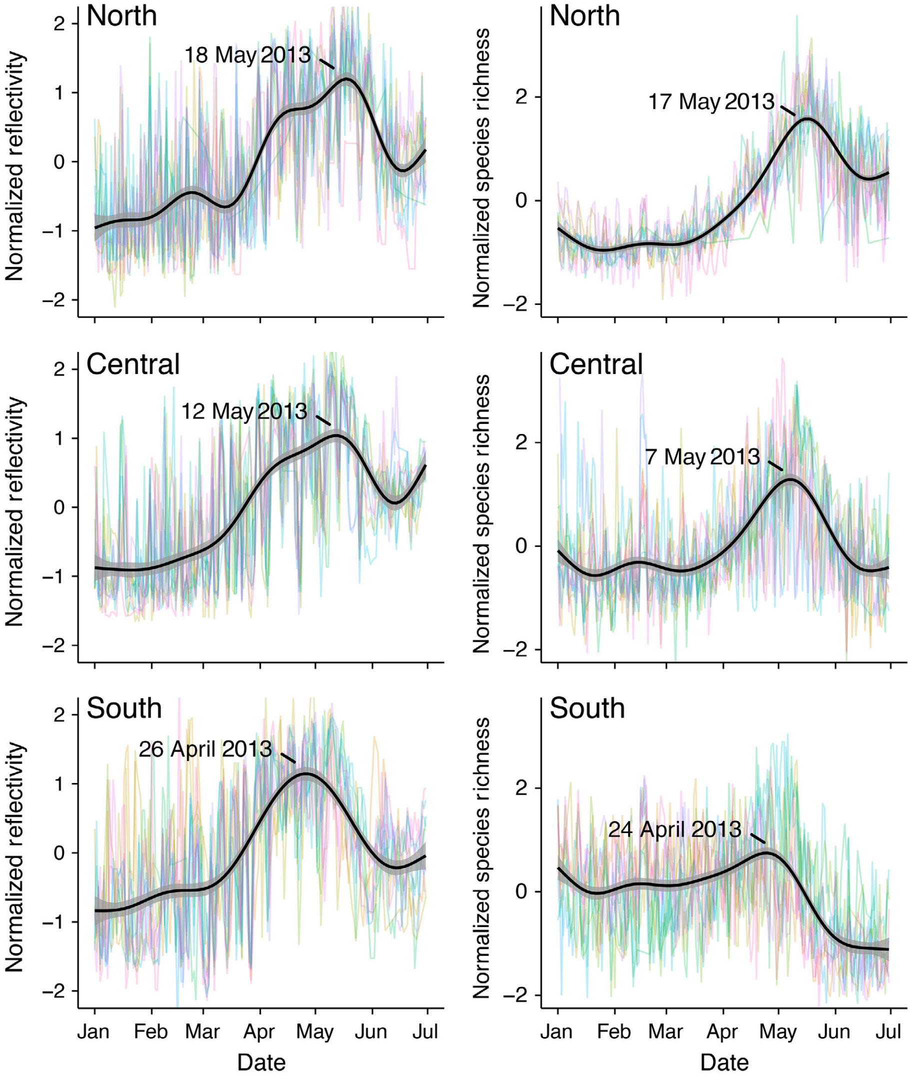

Fig. 2. Generalized additive model fits to radar-based measure of nocturnal migration intensity (normalized reflectivity) in the northern, central, and southern regions of the eastern United States (left). Number of species on eBird checklists (normalized species richness) in those same regions (right); both variables are plotted against date. Note the similarity in the peak dates labeled on each plot. Gray shading is the 95% confidence interval around each fit, and colored transparent lines represent daily measures at each individual radar.

latitude. There were positive trends in the dates for peak migration intensity, peak species richness, temperature, and the extended spring index across latitudes. There was no positive trend in start-of-spring dates derived from NDVI across latitude, and, in fact, the trend had a significantly negative slope (Fig. 4). Based on these results, it seems unlikely that nocturnal migrants could be responding to changes in primary productivity as reflected in these start-of-spring dates. There are, however, myriad possible methods of filtering and analyzing NDVI data, some of which may produce a positive trend with latitude. We are not aware of any a priori reason to suspect that a different method would produce a meaningful large-scale migration cue. Start-of-spring dates based on the relatively recently revised extended spring index did produce a latitudinal pattern consistent with a green wave. There was also a predictable thermal wave that could be a

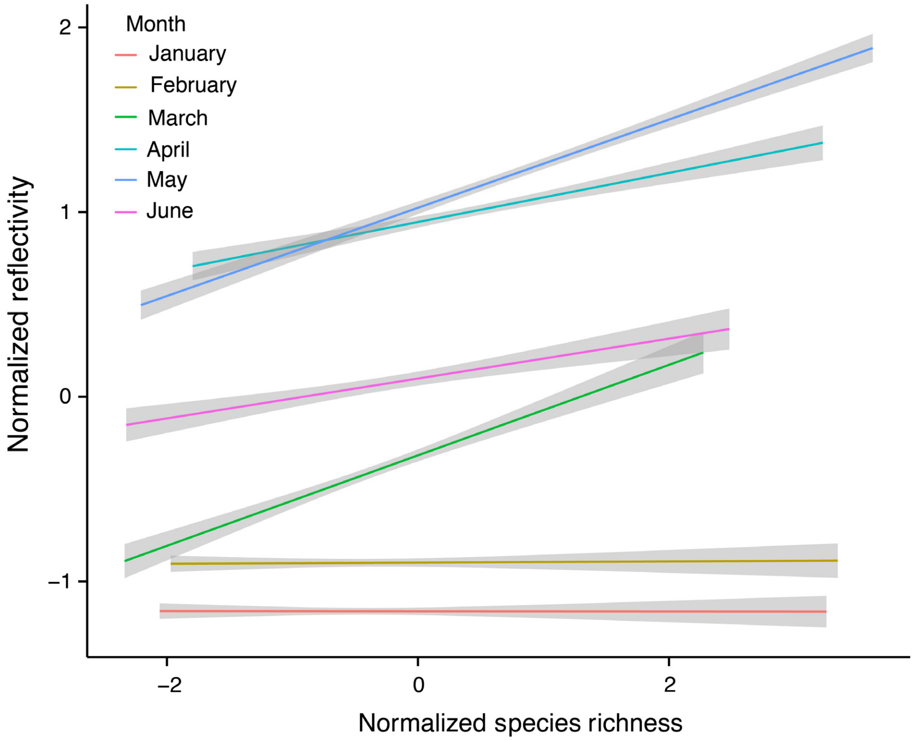

Fig. 3. Radar-based migratory intensity (normalized reflectivity) plotted against species richness for January through June of 2013. Lines are least squares fits to daily samples taken at each of 32 radars in the eastern United States. Note the slopes of the correlations increase in each month from February through May. The relationships are significant for March through June (January, $r = 0.0$, slope = 0.0, $P = 0.92$; February, $r = 0.0$, slope = 0.0, $P = 0.64$; March, $r = 0.32$, slope = 0.26, $P < 0.01$; April, $r = 0.26$, slope = 00.14, $P < 0.01$; May, $r = 0.53$, slope = 0.25, $P < 0.01$; June, $r = 0.17$, slope = 0.11, $P < 0.01$). Shaded regions are 95% confidence intervals of the regression lines.

useful exogenous cue in timing migration for all trophic levels (Cohen et al. 2012).

The finding that land surface phenology, as measured through NDVI, is unlikely to be a useful exogenous migration cue in temperate North America is consistent with the existing literature. Most studies that find correspondence between migration timing and a green wave in vegetation are from northern Europe (Thorup et al. 2007, Bauer et al. 2008, Saino et al. 2010, Tøttrup et al. 2012, Shariatinajafabadi et al. 2014, Si et al. 2015). These studies are much further north than our study region where a green wave is likely to exist and be a prominent feature of the progress of spring. Studies from the North American temperate zone and elsewhere have more consistently supported a correspondence between migration timing and temperature than with land surface phenology (Dunn and Winkler 1999, Marra et al. 2005, van Wijk et al. 2012, Renfrew et al. 2013, Paxton et al. 2014, Cohen et al. 2015). Lack of pattern in the NDVI data at temperate latitudes in North America suggests that inconsistent findings among avian studies in North America may be due, at least in part, to the absence of a seasonal wave in the start-of-season index. Another potential reason for conflicting findings among these studies is related to the scale of analysis. When viewed locally, there is both an increase in greenness across the spring and an increase in abundance of migrants at most locations. That is, at the local scale, these variables are correlated. However, as our results show, this relationship does not exist at broader spatial extents. Some of the inconsistency in the role of vegetation phenology (NDVI and enhanced vegetation index) as a cue for migration phenology might be resolved by relying more on the spring index (SI-x) in future research.

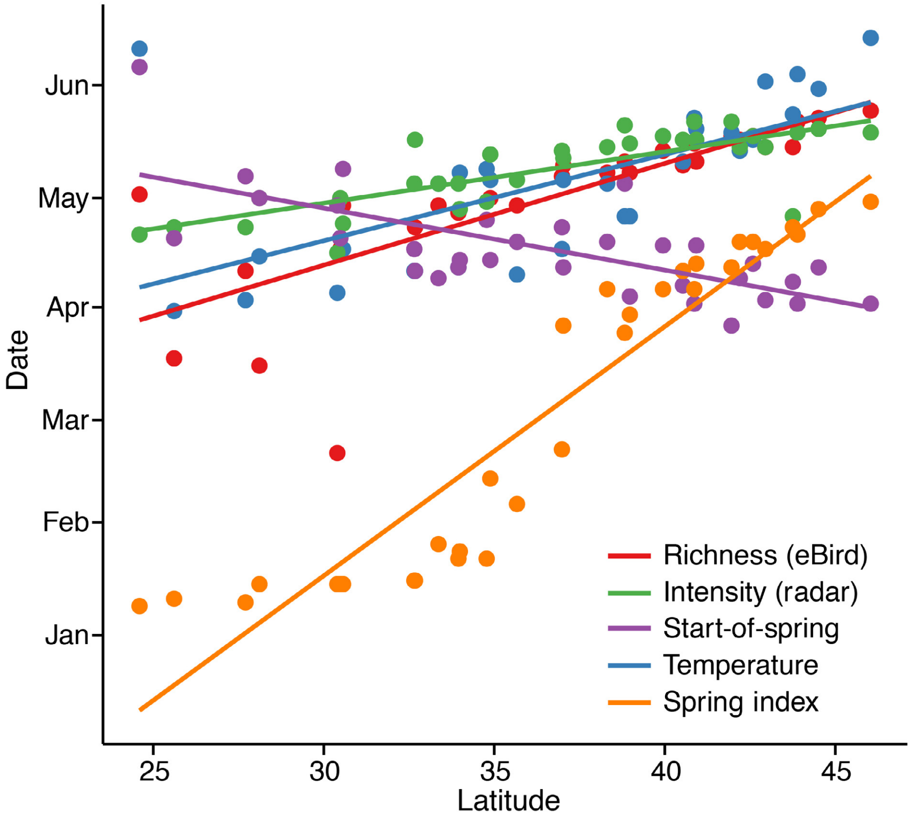

Fig. 4. Dates of peak radar-based intensity of migration ($r = 0.78$, slope = 1.46, $P < 0.001$), species richness of migrants (eBird-based, $r = 0.78$, slope = 2.73, $P < 0.001$), start-of-spring (normalized difference vegetation index-based, $r = -0.71$, slope = –1.70, $P < 0.001$), extended spring index (SI-x, $r = 0.94$, slope = 6.84, $P < 0.001$), and temperature (last day to dip below 5°C, $r = 0.66$, slope 2.37, $P < 0.001$) all plotted against latitude of the sampling locations for 2013. Note that the phenology of migration intensity, migrant richness, temperature, and the extended spring index are significantly positively related to latitude in the spring as expected, whereas start-of-spring does not follow this pattern.

We cannot infer from our results how en route migrants are using exogenous cues, but two hypotheses seem likely: (1) exogenous cues at a stopover location might be predictive of conditions further north; (2) exogenous cues locally might actively constrain movements northward (e.g., critical thermal temperatures). The first possibility is consistent with observations that long-distance migrants rely more on endogenous cycles and fixed cues (e.g., day length) than short-distance migrants because the predictive power of exogenous cues declines rapidly with distance (Hagan et al. 1991). The second possibility is consistent with the widely held notion that temperature has a primary role in setting northern range limits (Dobzhansky 1950, MacArthur 1972, Root 1988, Brown et al. 1996). Understanding the specific mechanisms that link use of exogenous cues to migration timing is key to forecasting biotic responses to global change. Future analysis of radar- and eBird-based phenologies at finer spatial scales might well be able to separate the mechanism we have proposed. For example, finer examination of the variation in migratory flow of biodiversity traits (e.g., body size, diet, migration distance) could reveal how exogenous cues differentially impact migration of biodiversity across time and space. This variation could be used to test predictions that distinguish the predictive-cue hypothesis from the northern temperature-limit hypothesis described above. An additional consideration is that our analysis does not examine the role of synoptic weather in driving the periodicity of migration flow. The interaction between pulses of weather and pulses of migrants is likely to explain a significant amount of variation in migratory phenology (Vansteelant et al. 2015).

Both WSR and eBird data have considerable potential to reveal the phenology of the mass flow of avian migration. The correspondence between peak migration dates across latitudes in these data encourages us to think about how to extend analyses across spatial scales. In addition, we are interested in trying to parse these data further to examine whether the spatiotemporal variation in traits of species on eBird checklists is more or less associated with spatiotemporal variation in reflectivity. The potential to associate migration of biodiversity traits (diet, body mass, migration distance, social system) with the biomass sampling capabilities of the WSR is one of the more promising aspects of this particular analysis method. In the cases we present, the correspondence of the two methods suggests that information being gathered by both sampling networks is consistent with regard to the phenology of migrant birds, which makes it possible to leverage the strengths of each system to compensate for weaknesses in the other. In particular, the strength of the WSR system is standardized effort, which is the weakness of the eBird system. In contrast, the lack of biodiversity trait data from WSRs can be compensated for with eBird data. The major impediment to such integrated analyses is data processing. While the pace of data acquisition, screening, and processing is faster than ever before, it remains the limiting step in using radar data for biological applications. Nonetheless, this is a promising approach to addressing the future challenges of understanding the dynamics responses of migration systems to environmental change from fine spatiotemporal grain to large spatiotemporal extents.

The correspondence between migration intensity as measured with WSRs and the density of birds on the ground has been a topic of considerable interest and debate (DiGaudio et al. 2008, Peckford and Taylor 2008, Fischer et al. 2012*a*, *b*, Horton et al. 2015). Past results have been mixed with some studies finding correspondence and others finding no relationship. One source of uncertainty is the degree to which scale of the ground surveys matches data collected by the radars. Our results suggest that, at the macroscale, there is a correlation between birds on the ground and those in the air on the subsequent night. There is high variation in counts on a daily basis making daily forecasts unlikely to be precise. Nonetheless, at the macroscale and seasonal time frame, these data are a promising resource for asking fundamental ecological questions.

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