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Continental Connections: Changing Temperature, Wind and Precipitation Advance the Postbreeding Roosting Phenology of Avian Aerial Insectivores

Yuting Deng¹  | Birgen Haest² | Maria C. T. D. Belotti¹ | Wenlong Zhao³ | Gustavo Perez³ | Elske K. Tielens⁴ | Daniel R. Sheldon³ | Subhansu Maji³ | Jeffrey F. Kelly^{4,5} | Kyle G. Horton¹ 

¹Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, Colorado, USA | ²Swiss Ornithological Institute, Sempach, Switzerland | ³College of Information and Computer Science, University of Massachusetts, Amherst, Amherst, Massachusetts, USA | ⁴Department of Biology, University of Oklahoma, Norman, Oklahoma, USA | ⁵Oklahoma Biological Survey, University of Oklahoma, Norman, Oklahoma, USA

Correspondence: Yuting Deng (hermione.deng@colostate.edu)

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ABSTRACT

Aim: Migratory birds are under threat by climate change. Successfully conserving them requires knowing which climatic factors drive changes in their migratory behaviour. Weather conditions may directly or indirectly affect the temporally disjointed life history stages of migratory birds, including the breeding, roosting and nonbreeding stages. However, the influences of these broad-scale patterns are often not studied together. Coupling migratory bird movements estimated using weather radar (NEXRAD) with long-term and large-scale environmental data allows us to overcome these spatiotemporal uncertainties. Here, we assess environmental drivers of the phenology of postbreeding roosting of aerial insectivores in the Great Lakes region (USA) by evaluating predictors during the months leading up to roosting across species' ranges.

Location: Northern United States and Canada.

Time Period: 21-year (2000–2020).

Major Taxa Studied: Avian aerial insectivores.

Methods: We conducted a spatially explicit time-window analysis to examine the effects of 17 gridded weather and vegetation variables on swallow peak roosting phenology in the Great Lakes, making minimal ecological assumptions.

Results: We found that peak roosting timing is paced by both local conditions (headwind at 850 hPa) at the Great Lakes and distant conditions (minimum temperature, precipitation rate and specific humidity) at the likely breeding and stopover sites, with warmer temperatures advancing, headwind delaying and high precipitation advancing the phenophases. Time windows selected for the possible breeding and stopover sites are mostly before or around the time of roosting, with one exception during wintertime.

Main Conclusions: Although climatic shifts play a significant role in driving variation in phenology, for migratory species, the proximate driver can originate hundreds to thousands of kilometres away, and potentially months prior. Our study illuminates these far-reaching patterns in aerial insectivores, enhancing our grasp of migration ecology and paving the way for a more comprehensive understanding of hemispheric animal movements.

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1 | Introduction

The direct and indirect impacts of climate and other anthropogenic changes are causing wildlife across the globe to face ever-increasing threats in terms of individual health, altered behaviour, phenology, distribution and population dynamics (Acevedo-Whitehouse and Duffus 2009; Peñuelas et al. 2013; Razgour et al. 2018). Migratory birds navigate hemisphere-scale journeys and live at the forefront of climate change and must adapt through either phenotypic plasticity or microevolution (Moiron et al. 2024). Climate change is increasingly influencing migratory birds' phenology, leading many species to alter their timing of arrival or departure from breeding grounds (Jenni and Kéry 2003; Pearce-Higgins and Green 2012). These shifts, while evident, raise concerns about whether they are sufficient to align with shifting resource availability—a mismatch that could have severe consequences for migratory bird populations (Bairlein 2016; Visser and Both 2005). Therefore, determining which environmental signals are perceived by wildlife, during which period in their life cycle, and at what locations, is an essential step toward unravelling the complexities of climate-induced phenological changes (van de Pol et al. 2016). This understanding is pivotal for understanding how broader ecological processes are being reshaped by climate change (Haest et al. 2018a, 2019, 2021).

Climate-induced phenological changes are particularly complex in long-distance migrants (Miles et al. 2017), due to the diversity of environmental conditions that they experience along the journey. Therefore, it is crucial to adopt approaches that encompass multilocality analyses, capturing the complexities of migration patterns across diverse regions (Haest et al. 2018a, 2019, 2021). Despite this complexity, most studies on the influence of weather on migration phenology use weather variables from migration arrival areas (Gordo 2007). Doing so inherently assumes that migration timing is primarily driven by local conditions rather than by distant conditions at the locations where migration commenced or locations where migrants navigated through. However, both local and distant conditions likely play a role in shaping migration phenology (Cotton 2003). For instance, local temperature conditions at migration stopover sites affect arrival timing for some passerine species migrating between Africa and Europe, particularly those breeding at higher latitudes, who show flexibility in response to local conditions en route (Aharon-Rotman et al. 2022). In contrast, distant conditions at the site where migration commenced can serve as cues for migration initiation, indirectly affecting arrival timing at later stages of migration (Gunnarsson et al. 2006; Shamoun-Baranes et al. 2006). The relative influence of local versus distant conditions can also depend on the scale of movement. For short-distance migration movements, immediate factors like wind conditions or local food availability may have a stronger influence on fine-scale migration timing (Bridge et al. 2010; Eisaguirre et al. 2018). For long-distance movements, distant environmental factors, such as temperature anomalies or precipitation patterns in breeding or nonbreeding grounds, can act as drivers of migration initiation, with effects that propagate over thousands of kilometres (Both and Visser 2001; Studds and Marra 2007). These distinctions highlight the importance of considering the spatial and temporal scale of environmental influences when studying migration phenology.

Large spatial scale climatic variables, such as teleconnections and climate dipoles, have been shown to affect migration patterns (Strong et al. 2015; Zuckerberg et al. 2020). Notably, phenomena like El Niño Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) have been studied for their impact on local ecological changes, including bird spring migration timing and breeding biology (Cotton 2003; Haest et al. 2018a; Huang et al. 2017; Hüppop and Hüppop 2003; Laczi et al. 2019). However, teleconnection patterns, which influence temperature, precipitation, wind, extreme weather and ocean currents, are summarised into single-value indices, making it difficult to attribute these effects to specific source locations (Gordo 2007). This complicates understanding the mechanisms by which climate change-driven shifts in environmental conditions affect different stages of the migration journey. Additionally, timing assumptions are often made when examining the relationship between weather and migration phenology (van de Pol et al. 2016). For instance, predictors are sometimes averaged over extended periods or matched directly with the phenological event. While these approaches have provided valuable insights, they may not always align with the specific biological mechanisms driving phenological events. Advances in tools like sliding window analyses now allow for a more nuanced exploration of these relationships (van de Pol et al. 2016).

More recent work on understanding climate-ecology relationships has moved away from these spatial and temporal assumptions, and instead, steps have been taken to conduct spatially and temporally explicit analyses of several climate conditions (Haest et al. 2018b, 2019, 2020, 2021). Such an exploratory approach allows for the identification of the most likely locations and times of influence and the formulation of data-driven hypotheses on these influences that can then be verified through explicit testing when future data become available. Explicit testing could involve comparing the predicted timing of phenological events based on identified climatic influences with field observations or tracking data to further verify the spatial and temporal relationships between climate and phenology.

Several commonly studied weather variables have been examined in previous research to influence migration phenology by either delaying or advancing its timing. Temperature is among the most studied predictors of changes in phenological events, both across regions and taxa (Gordo 2007; Root et al. 2003). It is a common environmental cue for many organisms to begin their life history events (Schwartz 2013), be it directly (Klinner and Schmaljohann 2020) or indirectly by changing the timing of food resource availability (Both et al. 2004). Warmer surface air temperatures are predicted to advance phenology by increasing insect activity and abundance, providing more favourable foraging conditions earlier in the season (Forrest 2016; Scranton and Amarasekare 2017). Precipitation, in contrast, is hypothesised to have both delaying and advancing effects depending on timing and context. High precipitation can delay phenology by creating poor flight conditions that hinder migration or roosting (Haest et al. 2020), as well as reducing flying insect activity and potentially causing short-term food shortages for aerial insectivores (Cox et al. 2019). However, in arid regions, rainfall can advance phenology by promoting vegetation growth and supporting insect populations, especially when lag effects from soil moisture prolong these favourable conditions (Gordo 2007).

Relative humidity, often correlated with precipitation, influences the availability of water sources, which in turn impacts insect abundance and distribution, ultimately shaping foraging opportunities for obligate insectivores such as swallows and martins (Brown et al. 2002).

Other environmental variables can also serve as drivers of phenological changes in birds. Vegetation phenology, which can be measured by enhanced vegetation index (EVI), can also affect a migratory bird's spring and fall phenology (Adams et al. 2024; Robertson et al. 2024; Youngflesh et al. 2021) as some birds will 'surf' the green wave moving across latitudes. Greener vegetation is hypothesized to cue earlier phenology by providing suitable habitat and food resources (La Sorte and Graham 2021). Wind conditions (speed and direction) are hypothesized to delay or advance phenology depending on their alignment with migratory paths. Favourable tailwinds are expected to advance phenology by facilitating faster migration and reducing energetic costs, whereas headwinds or adverse crosswinds may delay arrival by requiring additional energy or causing stopovers (Gauthreaux et al. 2006; Haest et al. 2020; Horton et al. 2018; Liechti 2006). Finally, surface water temperature is predicted to advance phenology by regulating the emergence of aquatic insects, a key food resource for aerial insectivores. Warmer water temperatures earlier in the season can trigger earlier aquatic insect emergence, thereby supporting earlier roosting or migratory events (Hixson et al. 2015; Twining et al. 2018).

Phenological events, such as shifts in migration timing, influenced by environmental variables that operate across varying spatial and temporal scales, sometimes require large-scale monitoring systems to effectively quantify and understand these patterns. Weather surveillance radar offers a powerful tool for this purpose, enabling the study of phenology across tens of thousands of individuals over extensive spatial areas, sometimes with insights into taxonomic group identities (Deng et al. 2023; Horton et al. 2020; Stepanian and Wainwright 2018). During the postbreeding and premigratory season (Figure 1), some species of swallows aggregate in large numbers at their nocturnal roosting sites and then disperse synchronously before dawn for foraging, leaving a unique donut-shaped signature on radar (Belotti et al. 2023; Laughlin et al. 2013). This offers a unique opportunity to investigate an understudied aspect of swallows' life history, as the daily number of swallows aloft can

be estimated directly from raw radar data (Chilson et al. 2012). From this, phenological metrics describing roosting timing are derived, representing the day of the year when half (or 10%, 25%, 75%, 90%) of the cumulative number of swallows aggregate and emerge at postbreeding roosting sites (Deng et al. 2023). In the Great Lakes region, postbreeding roosts of aerial insectivores are largely composed of Purple Martins (*Progne subis*) and Tree Swallows (*Tachycineta bicolor*), but other swallow species (e.g., Barn Swallow, Bank Swallow and Cliff Swallow) could also mix in (Bridge et al. 2016; Kelly and Pletschet 2018). In the Great Lakes, roosting swallows probably include a combination of local breeders and postbreeding migrants (Fink, Auer, Johnston, Strimas-Mackey, et al. 2020). Therefore, we are expecting far-away teleconnections and short-distance conditions that could both influence the roosting phenology in this region.

With this unique 21-year (2000–2020) weather surveillance radar data set on swallow roosting timing (Deng et al. 2023), we examine the drivers of interannual variation and long-term trends in postbreeding phenology at a large spatial scale. Specifically, we take a spatially explicit time-window analysis approach, free of preconceived assumptions about which location(s) or time window(s) influence migration timing. We seek to answer the following questions: Where, when and to what extent are swallows responding to environmental conditions that drive the observed shift towards earlier roosting phenology in the Great Lakes, and what specific factors are influencing this change? Our findings contribute to a broader understanding of the ecological impacts of climate change on migratory species and provide valuable insights for predicting the effects of future environmental changes.

2 | Materials and Methods

2.1 | Swallow Roosting Phenology Throughout the Great Lakes

Weather surveillance radar can detect and quantify a large number of swallows as they enter the airspace synchronously during dawn during the postbreeding season, with high temporal and spatial resolution. Deng et al. (2023) provide valuable insights into phenological shifts of the roosting swallows in the Great Lakes (defined as longitude -92 to -75 and latitude 41 to 47)

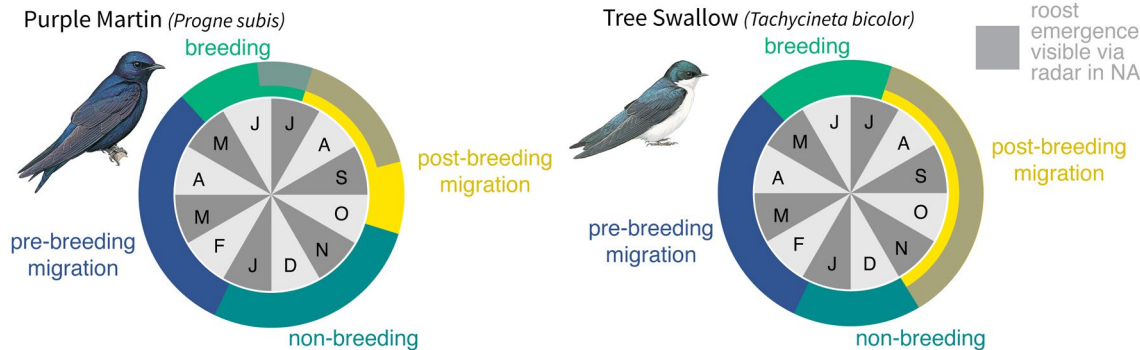


FIGURE 1 | Life cycles of Purple Martin (*Progne subis*) and Tree Swallows (*Tachycineta bicolor*) detected on weather surveillance radar at the Great Lakes. Transparent grey wheel shows the time period in their life history when they form large roosts in North America and can be detected on weather surveillance radar. Months are abbreviated by their first letters on the time wheel.

over 21 consecutive years (2000–2020) using 12 radar stations. The resulting data set generated from radar was used to calculate the peak roosting date (i.e., the 50th percentile date of cumulative passage) of these aerial insectivores in the Great Lakes, which is the biological response in this study.

2.2 | Environmental Data

To determine the mechanisms driving phenological change, we acquired data (Figure 2 and Table S1) from the NCEP Reanalysis I database using the RNCEP R package (Kemp, Emiel van Loon, et al. 2012). These included mean, minimum and maximum daily air temperature, specific humidity at 2m above ground, surface convective precipitation rate, surface precipitation rate, u-wind (east/west) and v-wind (north/south) components during daytime at the 1000, 925 and 850 hPa atmospheric pressure levels. These pressure levels correspond to approximately 100, 750, and 1450 m above sea level (a.s.l.), respectively. We selected the three lowest pressure levels available from the NCEP data set to represent environmental influences across different altitudes, focusing on those most aligned with the typical flight heights of the swallow species studied. Research on swallows and martins indicates that they rarely reach altitudes as high as 2 km during migration, with the majority of their activity occurring at much lower levels (Dreelin et al. 2018; Mateos-Rodríguez and Liechti 2012). Aerial insectivore swallows are known to forage and migrate mainly during the day (Imlay and Taylor 2020). We thus only analysed daytime wind conditions. From the u- and v-wind components, we derived both wind direction and wind assistance (using the *M.Groundspeed* equation in RNCEP) at all three atmospheric pressure levels. Wind direction includes the number of days when wind comes from the reference location (headwind) and wind goes to the reference location (tailwind),

both determined by the wind direction relative to the -45° to $+45^\circ$ angle ranges of the grid cell to reference location direction. The reference location is at the KAPX radar station, which is centrally located in our study area (44.9072° W, -84.7197° N). Wind assistance assumes the animal will adjust its heading and airspeed to achieve different groundspeeds in different flow conditions to achieve complete compensation (Kemp, Shamoun-Baranes, et al. 2012). Here, we defined the preferred ground speed of swallows as 4.97 m/s, which is estimated by the Purple Martins' average migration speed over land presented in a previous GPS tracking study (Lavallée et al. 2021). The preferred direction of movement was defined by pointing from the analysed grid cell to the reference location.

We also acquired Enhanced Vegetation Index (Huete et al. 1994) (EVI) data from MODIS/Terra Vegetation Indices 16-Day L3 Global 1 km SIN Grid V061 (MOD13A2.v061) from 2000 to 2020 and water surface temperature data from MODIS/Aqua Land Surface Temperature/Emissivity 8-Day L3 Global 1 km SIN Grid (MYD11A2.v061) from 2003 to 2020 (limited due to data inavailability). Nine tiles (H09V04, H10V03, H10V04, H11V03, H11V04, H12V03, H12V04, H13V03, H13V04) were downloaded to cover an area similar to the extent of NCEP data. We clipped the Aqua Land Surface Temperature data to the Great Lakes.

To prepare the MODIS data for time-window analysis, we temporally interpolated it to a 1-day resolution and filled in the missing data points in the time series with a generalised additive model (GAM) using the *mgcv* R package (Wood 2001). Due to the high spatial resolution of the original data and computation limitations, we first spatially downsampled the data by a factor of 4 using a mean function. We then modelled the value in each grid cell with ordinal date as the response variable and a tensor product interaction between year and day

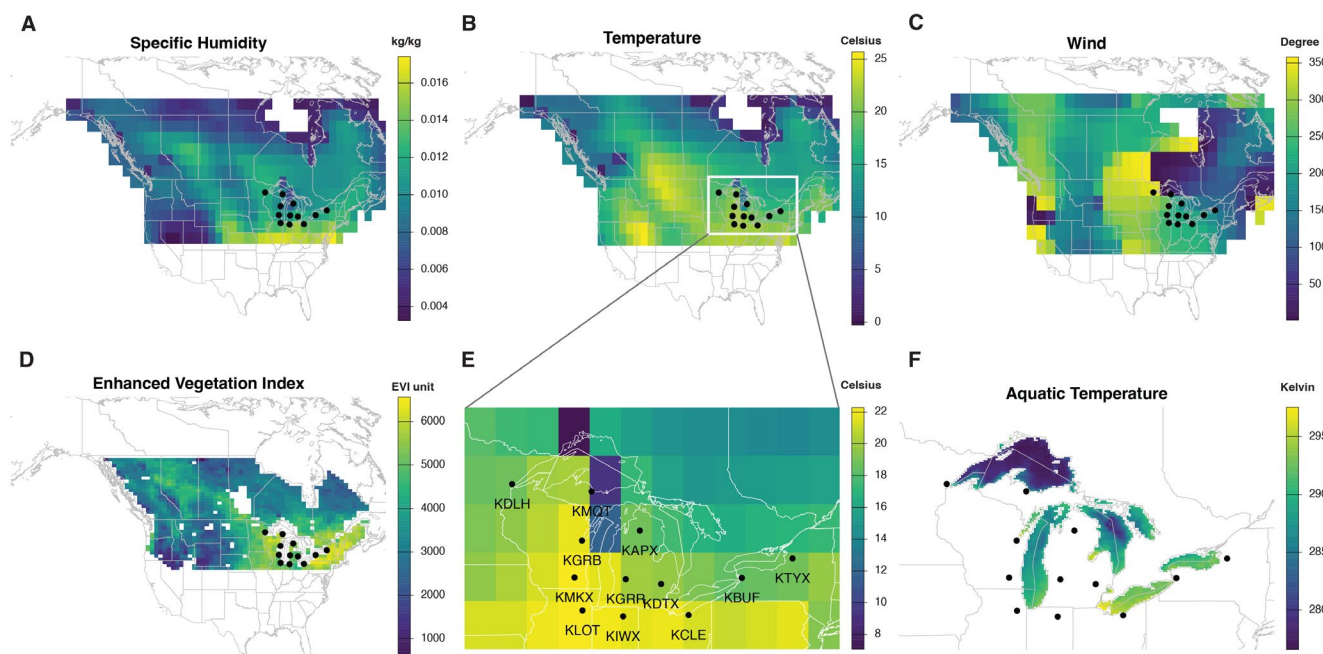


FIGURE 2 | Example input environmental data on July 1st, 2003, showing the resolution and extent of the variables. Black points represent the location of radar stations included in this analysis. (A) Specific humidity at 2 m above ground (kg/kg). (B) Mean air temperature at 2 m above ground (degree Celsius). (C) Wind direction (degree) calculated from u-wind (m/s) and v-wind (m/s). (D) Enhanced vegetation index. (E) Zoomed in location of 12 radar stations across the Great Lakes. (F) Water surface temperature (degree K) zoomed into the Great Lakes region.

of the year as the explanatory variable with a Gaussian distribution. Smooth terms were applied to each variable: cubic regression spline for day of the year and p-splines for year. The number of knots (k) was set to the minimum number of days available in each year. We then further downsampled the interpolated data by a factor of 4 for EVI and 2 for aquatic data using mean functions to ensure the analyses remained computationally efficient. This resulted in a $16\text{ km} \times 16\text{ km}$ resolution final raster product for EVI and $64\text{ km} \times 64\text{ km}$ for aquatic surface temperature over the Great Lakes. All data sets were standardised to the same projection, WGS84 (EPSG: 4326), to maintain spatial consistency.

2.3 | Finding the Influential ‘Environment Variable—Location—Time Window’ Combinations

We conducted per-grid cell time-window analyses to quantify what, when and where environmental conditions influenced swallow premigratory roosting timing in the Great Lakes. The extent of the study area includes latitudes from the southern border of the Great Lakes region to the northern breeding boundary of these roosting swallow species, covering key locations relevant to swallow breeding and postbreeding migration. We followed the methods used in previous literature (Haest et al. 2018b, 2019, 2020, 2021). Broadly, this method works by systematically testing different combinations of environmental variables and locations within their best time windows to quantify their influence on the timing of biological events. In total, we examined 33,369 spatiotemporal environmental variable combinations, encompassing all pixels for all variables across the study area. Ocean masks (not including the Great Lakes) were applied to all the environmental layers to restrict our inference to terrestrial habitats. Given the large number of combinations tested, some spurious relationships are expected; therefore, we applied further steps to refine and identify the most meaningful relationships, as described in the following section.

First, we determined a linear baseline trend model for the roosting phenology by selecting the trend model (among intercept only, linear, quadratic or cubic models) with the lowest second order Akaike information criterion (AICc) value (Anderson and Burnham 2002). By incorporating a linear temporal trend (i.e., year as the independent variable) in the analysis of environmental variables, we mitigate the risk of identifying spurious climate-phenology relationships that could arise from shared year-to-year trends in both phenology and climate (Iler et al. 2016). To ensure the trend model was effective, we verified that the time series was stationary and that the residuals from the detrended data showed no autocorrelation (Haest et al. 2018a). We then performed a time-window analysis independently for each of the environmental variables using the *climwin* R package (Bailey and Van De Pol 2016) on the value of each pixel and using five randomizations to avoid false positives resulting from chance alone. With these five randomizations, we calculated the alternative probability statistics (P_c) to estimate the reliability of the results (van de Pol et al. 2016). We used a P_c cut-off limit of 0.3 to achieve the probability of false negatives less than 0.1 for data with high R^2 (0.40) and less than 0.01 for data with very high

R^2 (0.80), as well as false positives less than 0.2 (Bailey and Van De Pol 2016; van de Pol et al. 2016). The best time-window for each grid cell and variable was determined using ΔAICc , that is, the AICc difference between the testing model and the baseline model. Maps of ΔAICc , R^2 , slope, and visual outputs from the *plotall* function in *climwin* were then generated for all pixels with a $P_c < 0.3$.

We used September 15 as the reference day for the time-window analysis, as by this time, more than 90% of the roosting birds had departed for more southern latitudes (Deng et al. 2023). The minimum time-window length was set to 14 days to reduce the likelihood of overfitting, as very short time windows may capture noise rather than meaningful environmental signals (van de Pol et al. 2016). For wind, the maximum time-window length was limited to 107 days (back to June) to align with the start of the breeding season and postbreeding migration, as wind is a short-term effect and unlikely to persist consistently over extended periods. In contrast, the maximum time window for temperature, precipitation and other variables was set to 258 days (back to January) because these variables tend to have cumulative and longer-term influences on overall environmental conditions, such as habitat suitability or resource availability. We took an absolute time-window approach, as opposed to the relative time window, because we focused on analysing the environmental influence on the roosting swallow population and had the same window for all individuals. For the wind analyses, we set our target location to the reference location. To aggregate statistics within the time window (‘CW_stat’), we employed the slope and mean function for EVI, calculated the number of days going to or coming from the reference location for wind and calculated the mean for wind assistance and temperature, and the sum for precipitation. This process resulted in a single aggregated value for each variable-location-time window-year combination, which was then compared to a single phenology value per year.

Using the output of the per-pixel time-window analyses (i.e., per-weather variable ΔAICc maps of the best time windows), we first, for each of the environmental variables, selected the pixels with the lowest regional ΔAICc using a 9×9 pixel window. Of these, we removed the pixels that had a P_c probability less than 0.3 but were isolated, that is, without any adjacent pixels with a P_c probability of less than 0.3. For further analysis, we no longer included the temporal trend variables in the model since the potential spurious climate-phenology relationships have been accounted for in the earlier steps. From the remaining ‘candidate variables’, we first removed those for which the model with the environmental variable only, that is, without the temporal trend included, was not better (i.e., less than two units of ΔAICc lower) than the intercept-only model. Next, we removed those that had a collinearity of higher than 0.7 with another variable from the remaining ‘candidates’ (Dormann et al. 2013) and a lower ΔAICc value, that is, difference with the base model, than the variable they were highly collinear with. Next, we reduced the number of variables to the top 14 performing variables with the R package *Boruta* (Kursa and Rudnicki 2010), which identifies significantly better predictors by comparing their importance scores (calculated with Random Forest algorithm) to randomly shuffled

shadow variables. In the final step, we performed a variable importance analysis based on three different methods: (1) cumulative AICc weights to identify more important variables by summing multiple models with up to four independent variables (Guthery et al. 2003) using the *MuMIn* R package (2) the Boruta method (Kursa and Rudnicki 2010); and (3) the LMG (Lindeman, Merenda, and Gold) metric (Grömping 2015), which distributes the variance contribution among the predictor variables in linear models and is based on game theory's Shapley value. The final ranking of the variable importance was decided by the mean rank calculated using all three variable importance methods. In cases of disagreements among the three methods, we reran 100 randomizations for the top 14 'environment variable—location—time window' combinations to generate a new ΔAICc value to make sure the result was not due to chance.

For the final assessment of the amount of variance in roosting phenology that was explained by the identified final climate/vegetation variable-location-time combinations, we first repeated the time-window analysis for these variables with a 21-fold cross-validation to decrease the potential of overfitting and the resulting inflated R^2 . For each of these folds, 1 year was left out of the model fitting process, for which a time window was then determined. The k-fold crossvalidation was provided by the *slidingwin* function in the *climwin* package. We chose the maximum number of folds (≤ 21 data points) because the estimation of R^2 improves as the number of folds increases (Bailey and Van De Pol 2016). The final time window-location combinations were still determined through the original analysis without k-fold crossvalidation since it will increase the false-positive rates (Bailey and Van De Pol 2016). The coefficient of partial determination (partial R^2) for the multivariate linear model was calculated for each final signal using the *rsq* R package (Zhang 2022).

2.4 | Trends in Roosting Phenology Explained by Environmental Variables

To examine whether environmental variables that drive inter-annual variations in roosting phenology are also driving overall trends, we calculated the 'overall contributions' made by all the important environmental variable-location-time combinations that have a trend themselves, following the equation (Haest et al. 2019, 2020; McLean et al. 2018):

$$\text{Environment variables' contributions to trend in roosting phenology} = \sum_{i=1}^n \left(\frac{\delta\text{Phenology}}{\delta\text{Env}_i} * \frac{\delta\text{Env}_i}{\delta\text{Year}} \right)$$

where n is the total number of the remaining environmental signals left after the variable selection process; $\frac{\delta\text{Phenology}}{\delta\text{Env}_i}$ the linear regression coefficients; and $\frac{\delta\text{Env}_i}{\delta\text{Year}}$ the trend of the selected environmental variable. The multiplicative propagation of standard errors in trend contribution can be calculated using the chain rule (Taylor 1997):

$$\text{SE}_c = \text{Coef}_c * \sqrt{\left(\frac{\text{SE}_a}{\text{Coef}_a} \right)^2 + \left(\frac{\text{SE}_b}{\text{Coef}_b} \right)^2}$$

2.5 | Comparison to Conventional Approaches Investigating Weather Signals

To determine the effectiveness of our spatiotemporally explicit per-grid-cell time-window analysis, we compared the adjusted R^2 of our final candidates' models with two other approaches that are commonly used to investigate climate-phenology relationships. Both of these approaches use a priori assumptions. The most common 'local, static-time' approach assumes that the climatic impacts on the mean weighted roosting phenology occur at the location and time of observation. For this scenario, we averaged the Great Lake Region local variables from July 1 to September 31 and across space, covering the roosting period at the Great Lakes. The second 'local, dynamic-time' approach assumes climatic impacts occurring at the location of observation but at a flexible time window, so we used the Great Lake Region local variables and dynamic time windows with *climwin* package. We examined all final climate variables except for wind conditions as local wind extraction at the Great Lakes region resulted in no directionality.

Within the local Great Lakes area, we extracted 20 pixels (resolution $1.9047^\circ \times 1.875^\circ$) for each of the final climatic variables (minimum temperature, specific humidity and precipitation rate) because the spatial layers of these variables overlapped with the Great Lakes region for these 20 pixels. This resulted in 60 climate-location combinations for the 'local, dynamic-time' approach.

3 | Results

3.1 | Influential Location-Time-Variable Combinations on Roosting Phenology

We found that five final environmental, location and time-window combinations together explained 89.8% (adjusted R^2) of the inter-annual variation in swallows' premigratory roosting phenology at the Great Lakes. These were composed of a mixture of temperature, wind conditions and precipitation at likely breeding grounds and postbreeding stopover sites (Figure 3).

Each unique variable-location-time combination was examined individually to better understand how specific environmental factors influence roosting phenology across space and time. Among the top five influences, minimum

temperatures and headwind at 850 hPa explained the highest proportion of variance (Table 1). Specifically, minimum temperature ('tmin.2m') in Alberta, Canada between mid-July to mid-August alone explained around 82% of the variance. Higher minimum temperatures at this location advanced the peak roosting timing (slope = -2.79 , SE = 0.30 , $p < 0.0001$). Minimum temperature at coastal New Hampshire and Massachusetts from early May to June also explained 58.8% of variance and was also advancing peak roosting timing (slope = -2.11 , SE = 0.39 , $p < 0.0001$). Wind conditions

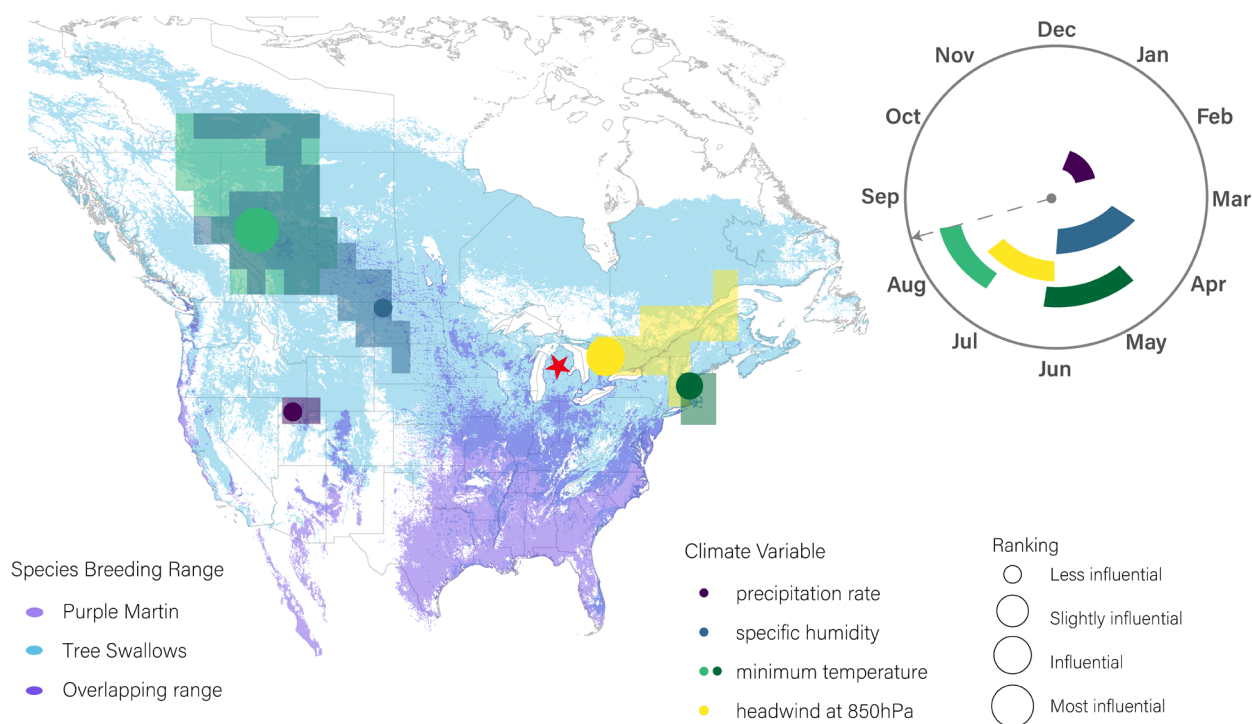


FIGURE 3 | Map and time windows of the most important environmental variables identified to influence the peak postbreeding roosting timing of the aerial insectivores at the Great Lakes. The star marks the centre of the roosting phenomenon detected on radars. Sizes of the marked locations correspond to the final ranking given by the variable importance analysis. The actual influential areas are larger than the representative location we show, represented by the coloured transparent area (based on per-weather variable Δ AICc maps of the best time windows, Map S1). The time-window wheel represents the period of the single best time window for each environmental variable (corresponding colours). The dotted line with arrow points shows the peak roosting timing (August 16th) at the Great Lakes. Breeding abundance maps of Purple Martins (*Progne subis*) and Tree Swallows (*Tachycineta bicolor*) are overlaid, provided by eBird Status and Trends.

(‘WindCF850’) between June to July had a contrasting effect, with headwind from the northeast Great Lakes at the 850 hPa pressure level (1450 m above sea level) resulting in later roosting (slope=0.71, SE=0.12, $p < 0.0001$, adjusted $R^2 = 0.614$). We observed earlier peak roosting timing (slope=−71.068, SE=16.223, $p < 0.001$, adjusted $R^2 = 0.476$) as specific humidity at 2 m above ground (‘shum.2m’) in northern North Dakota from the end of April to June increased. Conversely, we observed later roosting timing as surface precipitation rate (prate.sfc) from the Great Salt Lake area from January to February increased (slope=0.141, SE=0.030, $p < 0.001$, adjusted $R^2 = 0.506$). Accounting for the other variables, the partial R^2 indicated that minimum temperature in Alberta, headwind in the northeast Great Lakes, minimum temperature in coastal New Hampshire and Massachusetts, precipitation rate in the Great Salt Lake area, and specific humidity in the northern North Dakota explained 63.4%, 45.1%, 26.5%, 16.3% and 0.05% of the additional variance, respectively (Table 1).

3.2 | Contributions to the Trend in Roosting Phenology

Over the 2000–2020 study period, only three out of the five final variables showed a temporal trend: minimum temperature at Alberta and coastal New Hampshire/Massachusetts and wind conditions at the northeast of the Great Lakes (Figure 4

and Table 2). We only report trend contributions for these three variables.

Increases in minimum temperature at Alberta advanced roosting phenology at the Great Lakes by 2.52 days, and minimum temperature in coastal New Hampshire/Massachusetts resulted in an advance of 0.84 days over 21 years. A decrease in the headwinds from the roosting location to the northeast Great Lakes may also have contributed to 1.47 days of advance in the roosting phenology.

3.3 | Comparison to Conventional Approaches of Investigating Environmental Drivers on Phenology

None of the examined signals from the ‘local, static-time’ approach showed a significant ($p < 0.05$) relationship with the peak roosting timing. Minimum temperature at the Great Lakes from July to September explained 9.2% of the variances ($p = 0.58$, slope = −0.94, SE=1.69). Averaged across the same space and time period, specific humidity explained 10.9% ($p = 0.61$, slope = −1290, SE=2483) and precipitation rate explained 9.0% ($p = 0.42$, slope = −2.31, SE=2.83) of the variances. The ‘local, dynamic-time’ approach had a normal distribution (Shapiro–Wilk test p value=0.6344) for the adjusted R^2 ranging from 0.25 to 0.67 ($n = 60$, median=0.44, SD=0.094). Only 11.7% of the examined combinations for the dynamic time-window approach had P_c value lower than 0.3, which indicated only a very small number of results being reliable.

TABLE 1 | Identified most influential environmental variables that are likely to influence the peak swallow roosting phenology dates at the Great Lakes, including the identified variable, location, time window (with associated uncertainty), importance ranking and R^2 .

Climate variable	Operation	Pixel number	Location	Interpretation	Window			Mean rank	Adjusted		Partial		K-fold crossvalidation	
					open	close	length							
Minimum temperature	Mean	200	Alberta, Canada	Likely breeding ground and stopover area	Jul 10	Aug 17	38	3	−116.25	54.28	5	0.815	0.634	0.665
Precipitation rate	Sum	233	Great Salt Lake area	Likely breeding ground	Jan 1	Jan 29	28	63	−112.5	40.95	2	0.506	0.163	0.549
Minimum temperature	Mean	518	Coastal New Hampshire and Massachusetts	Likely breeding ground	May 9	Jun 5	27	61	−71.25	42.85	2.3	0.588	0.265	0.254
Specific humidity	Sum	294	Northern North Dakota	Likely passage and stopover area	Apr 23	May 30	37	49	−103.12	48.57	2	0.476	0.005	0.337
Wind coming from Great Lakes	Number of days	294	Northeast Great Lakes	Likely breeding ground	Jun 4	Jun 28	24	45	−80	45	3.7	0.614	0.451	0.244

Note: Window uncertainty means that this percentage of the top models falls within the 95% confidence set.

4 | Discussion

Data integration from weather surveillance radar and satellite-based remote sensing platforms provided a unique opportunity to examine environmental effects on biological events at large spatial and temporal scales. Specifically, we used an intensive per-grid-cell time-window analysis approach to address the current lack of knowledge on the exact location and time of influence on swallows' roosting phenology at the Great Lakes. We found that a mixture of temperature, wind conditions and humidity/precipitation at potential breeding and passage areas during pre-roosting or roosting periods were drivers of migratory phenology, either directly or indirectly—with this approach we were able to explain the vast majority of variance in roosting timing.

From these environmental variables we examined, minimum temperature between mid-July to mid-August at Alberta, Canada was the most important influence on roosting timing at the Great Lakes (Figure 3 and Table 1). This region overlapped both Tree Swallow and Purple Martin breeding locations as highlighted in eBird Status and Trend maps (Figure 3; Fink, Auer, Johnston, Strimas-Mackey, et al. 2020). During the specific time window of temperature influence, 75% of the swallows have emerged from roost locations at the Great Lakes (Deng et al. 2023). This suggests that the minimum temperature in Alberta likely triggers the rapid migration of swallows to the Great Lakes roosting sites, with minimal time lag during this period. For example, increases in minimum temperatures could reflect desiccation of the environment, reducing food availability, resulting in rapid movement out of the region. Alternatively, warmer temperatures can advance insect emergence (McMaster and Wilhelm 1997), which could favour increased food abundance—fueling swallows for an earlier migration at the end of the breeding season. We identified a much weaker influence of minimum temperature in the northeast US (New Hampshire and Massachusetts coastal region) between mid-May to early June (Figure 3 and Table 1), which coincides with the breeding season. This weaker signal may reflect the contribution of breeding or autumn stopover populations in the eastern coastal region to the Great Lakes roosting population. Despite the similar latitude of these regions, tracking data from Tree Swallows have revealed east-to-west movement patterns between the two regions (Knight et al. 2018). In our analyses, we also considered daily mean and maximum temperatures. Although they were not identified as the final influences, their effect was merely excluded because it was highly collinear (Pearson correlation coefficients > 0.7) with minimum temperature and precipitation. This means that we could not statistically separate their effects and hence cannot make a strong conclusion on whether it is indeed minimum, mean or maximum temperature at the breeding grounds that affects postbreeding roosting phenology.

Wind conditions, specifically the frequency of days with headwinds at the 850 hPa pressure level (1450 m a.s.l.) during the migration season in the northeast of the Great Lakes, also had a strong impact on roosting phenology at the Great Lakes. The time window for wind conditions ranged from June to July, that is, the period right before the roosting phenomenon starts in the Great Lakes. As one would expect from a direct wind effect, more days with headwinds during daytime at 850 hPa at the northeastern Great Lakes led to later peak roosting times.

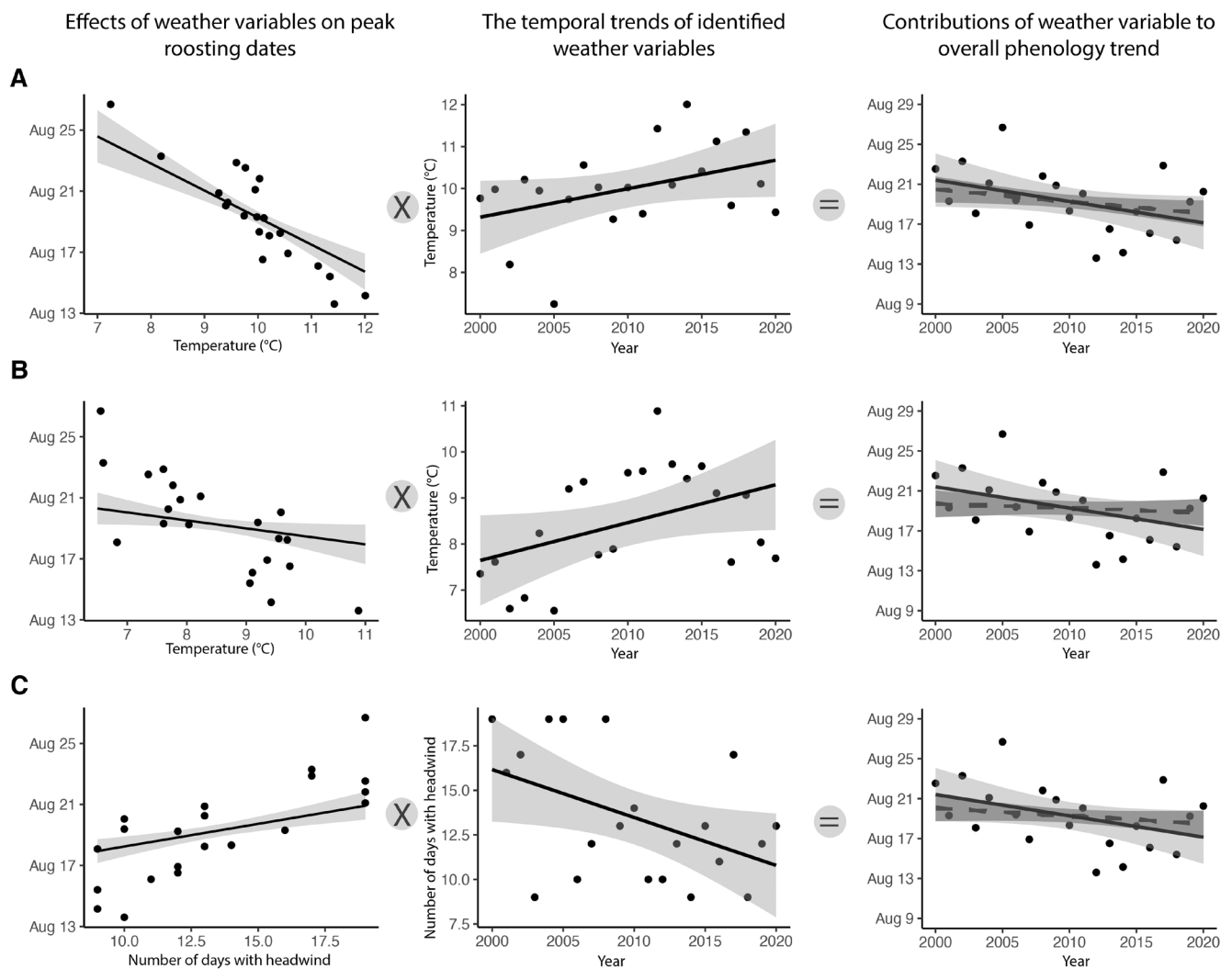


FIGURE 4 | Overview of the correlations between the identified environmental signals and peak roosting timing (the first column); the temporal trends of these signals (the second column); and the resulting contribution to the overall trend of the roosting phenology using the chain rule (the third column). The solid lines on the third column plots represent the trend of roosting phenology over 21 years, and the dotted line shows the calculated contributions to the temporal trend by each signal. Ribbons around each line represent the 95% CI. Three examined signals are (A) Minimum temperature—ID 200—Alberta, Canada. (B) Minimum temperature—ID 518—Coastal New Hampshire and Massachusetts. (C) Wind coming from Great Lakes at 850 hPa—ID 294—Northeast Great Lakes.

TABLE 2 | Trend contributions of three environmental variables to the roosting phenology were calculated based on the chain rule.

Climate variable	Location	dPheno/dClimate		dClimate/dTime		dPheno/dTime	
		Coef.	SE	Coef.	SE	Coef.	SE
Minimum temperature	Alberta, Canada	−1.7735	0.2636	0.0679	0.0356	−0.1204	−0.0656
Minimum temperature	Coastal New Hampshire and Massachusetts	−0.5229	0.2301	0.0821	0.0400	−0.0429	−0.0281
Wind coming from Great Lakes	Northeast Great Lakes	0.2969	0.0702	−0.269	0.1191	−0.0798	−0.0401

Headwind conditions usually require higher energy expenditure from migratory birds, thus delaying swallows' readiness to take off (Liechti 2006). Swallows are very adaptive in terms of migration strategies and sensitive to consistent wind conditions—Tree Swallows do a loop trans-Gulf migration, with a cross-Gulf autumn migration assisted by prevailing wind and circum-Gulf

overland migration in the spring without strong wind assistance (Bradley et al. 2014). Similarly, Purple Martins adjust their spring departure timing from the Yucatán Peninsula across the Gulf of Mexico based on wind speed and direction (Abdulle and Fraser 2018). The Great Lakes themselves serve as a nontrivial ecological barrier and possibly drive swallow populations

breeding in the northeast to migrate through land corridors, which are the space between (1) Lake Erie/Lake Ontario and Lake Huron, and (2) Lake Erie and Lake Ontario. The headwind variable is positioned along these migration corridors, aligning with the swallows' likely flight paths.

Wind at different altitudes also plays a critical part in shaping migration strategies. The detection of headwind influence at the 850 hPa level (1450 m a.s.l.)—a higher altitude than those associated with Tree Swallows and Barn Swallows during the breeding season—suggests that the individuals migrating from the northeast may be predominantly Purple Martins. This is supported by altitude logger data showing that Purple Martins can reach flight altitudes up to 1945 m, compared to 661 m for Tree Swallows and 273 m for Barn Swallows (Dreelin et al. 2018). Alternatively, it is also possible that swallows and martins migrate at higher altitudes than they typically fly during the breeding season, and additional migration altitude studies are needed to gain more insights. Overall, the result suggests that swallows and martins migrating through the Great Lakes often travel at higher altitudes during the day—likely due to a combination of favourable atmospheric conditions over the lakes, the vertical distributions of insect prey, and advantageous flight conditions at higher altitude (Senner et al. 2018; Williamson and Witt 2021).

Following these major influences, specific humidity at the potential breeding grounds and stopover sites of several roosting swallow species (May to June) also had a moderate influence on roosting phenology at the Great Lakes. The region where specific humidity influenced migration phenology extended from Alberta and southern Saskatchewan down to South Dakota (Figure 3 and Map S1). The range overlapped with migration routes of many swallow species, Tree Swallows in particular (Imlay 2018; Imlay et al. 2020; Imlay and Taylor 2020). Specific humidity likely influences a bird's breeding phenology and success through its effects on environmental conditions that impact key reproductive stages, such as nest building, egg laying, incubation, hatching and provisioning (Deeming 2011; Namasivayam-MacDonald et al. 2018). Higher specific humidity can enhance the availability of food resources for insectivorous birds by promoting plant productivity for herbivorous insects (Studds and Marra 2007). For species like Tree Swallows, earlier egg laying during the breeding season has been linked to greater food abundance (Nooker et al. 2005). Evidently, the timing of the breeding season was found to have a carryover effect on the departure timing of the autumn migration in barn swallows (Imlay et al. 2021). This earlier initiation of reproductive activities could cascade into earlier postbreeding migration. Thus, the influence of specific humidity on the timing and success of breeding likely contributes to shifts in the timing of subsequent phenological events.

Precipitation rate at surface (prate.sfc) at the Salt Lake during winter (the month of January) surprisingly showed up in the final candidates as well. There are confirmed distributions of several roosting swallow species in the Salt Lake region, where Purple Martins have a small, isolated breeding and postbreeding range (Fink, Auer, Johnston, Ruiz-Gutierrez, et al. 2020). This result suggests that winter precipitation in the Salt Lake region may influence the timing or condition of early spring migrants, potentially carrying over to the timing of postbreeding roosting

activity observed in the Great Lakes region. Here, a drier winter corresponded to earlier roosting in the summer. This effect was evident in a 57-year study on four swallow species' breeding phenology in Canada: Barn and Tree Swallows experienced time advancements in breeding during warmer winters with reduced snow (i.e., precipitation) due to climate change (Imlay et al. 2018).

Using more localised or time-specific approaches ('local, static-time' and 'local, dynamic-time' frameworks), we were unable to explain much of the observed variance in roosting phenology. These approaches may not always capture the potential lag effects or indirect pathways through which environmental variables can influence phenological events (van de Pol et al. 2016). Migratory species engage in frequent movements, potentially traversing extensive spatial regions throughout their migration season (Berthold 2001). While some studies in migration phenology do account for such complexities, our findings suggest that these dynamics might require further exploration in the context of postbreeding roosting phenology. Much of the current knowledge on environmental drivers of migration phenology stems from observational data, instead of experiments, meaning a priori assumptions have often been propagated over studies. Patterns may seem to be driven by local measures, but there is a probability of obtaining these 'significant' correlations due to spatiotemporally correlated phenomenon (Haest et al. 2018a). Based on our contrasting findings between the a priori approaches and our holistic analysis, we argue that much of the research on the drivers of animal phenology would benefit from a careful examination of assumptions on time, space and types of influences (van de Pol et al. 2016).

While our results explained much of the variance in swallows' postbreeding roosting phenology in the Great Lakes, it is important to acknowledge certain caveats that could affect the interpretation of the results. As many of the environmental variables measured, such as temperature, wind and precipitation, are often correlated both in time and space (Li et al. 2003). For example, wind speed, which is a critical driver of migratory behaviour (Liechti 2006; Nussbaumer et al. 2022), could be indirectly correlated with other variables like temperature and precipitation, leading to potential confounding effects. While our approach allows for some degree of isolation of independent climate and weather effects on phenology, there remains the possibility that some of the relationships we observed could be spurious or influenced by unmeasured covariates. Additionally, our approach of identifying influential pixels does not imply that only these specific locations drive phenology; rather, these pixels represent a broader surrounding area of influence (Figure 3). Future studies incorporating finer-scale biological data and explicitly testing for interactions among predictors could help strengthen confidence in these findings and address remaining uncertainties.

Climate change is a complex and multifaceted phenomenon, operating on a global scale and occurring over extended periods, spanning decades or centuries. While change in migration systems is often gradual in response to climate change, biological responses at times are dramatic. Even within 21 years of our study period, we observed an advance in the peak roosting activity of the swallows at the Great Lakes by 4.75 days (Deng

et al. 2023) due to increasing minimum temperature at potential breeding grounds and less frequent unfavourable wind conditions (Figure 4). In the next 3 decades, we are expecting to see a 2.4°C–2.8°C increase in temperature in this region compared to the historical data (1911–2005) based on CMIP5 (ENSMN) rcp8 model (<https://www.esrl.noaa.gov/psd/ipcc/cmip5/>) and weaker prevailing westerly winds during autumn migration (La Sorte et al. 2019). This suggests that favourable wind conditions for northeastern breeding populations, combined with rising temperatures in northern latitudes where these swallows breed and migrate, could further advance roosting phenology at the Great Lakes. It is also important for future studies to understand whether they are reaching their thermal limits or altering their migration behaviour due to extreme heat or the increasing frequency of heat waves. Overall, trends in many environmental drivers are projected to result in advances in the roosting season at the Great Lakes in the near future, with possible consequences of trophic mismatch, population changes, as well as changing ecosystem functions that aerial insectivores are playing. Studies aiming to investigate climate change impacts on biodiversity, wildlife population and ecosystem functioning are urgently needed in this ever-changing era. As this study shows, if we are going to truly and holistically understand the impacts of climate change, we need to use a broader lens—both in space and time.

Author Contributions

All authors worked to conceive and design this study. Y.D. drafted the manuscript and generated figures. Y.D. and B.H. designed analyses. All authors provided editorial advice, approved the final version of this manuscript and are in agreement to be accountable for all aspects of the work.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data sets generated during and/or analysed during the current study are available at <https://doi.org/10.6084/m9.figshare.25209278.v1>. Data processing codes can be found here: <https://github.com/HermioneDeng/Chap2>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.