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Integrating multi-scale terrestrial and atmospheric predictors enhances nocturnal bird migration forecasts

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ABSTRACT

Our ability to forecast the spatial and temporal patterns of ecological processes at continental scales has drastically improved over the past decade. Yet, predicting ecological patterns at broad scales while capturing fine-scale processes is a central challenge of ecological forecasting given the inherent tension between grain and extent, whereby enhancing one often diminishes the other. We leveraged 10 years of terrestrial and atmospheric data (2012–2021) to develop a high-resolution (2.9 × 2.9 km), radar-driven bird migration forecast model for a highly active region of the Mississippi flyway. Based on the suite of candidate models we examined, adding terrestrial predictors improved model performance only marginally, whereas spatially distant atmospheric predictors, particularly air temperature and wind speed from focal and distant regions, were major contributors to our top model, explaining 56% of variation in regional migration activity. Among terrestrial predictors, which ranked considerably lower than atmospheric predictors in terms of variable importance, vegetation phenology, artificial light at night, and percent of forest cover were the most important predictors. Furthermore, we scale this model to demonstrate the capacity to generate real-time, high-resolution forecasts for the continental United States that explained up to 65% of national variation. Our study demonstrates an approach for increasing the resolution of migration forecasts, which could facilitate the integration of radar with other data sources and inform dynamic conservation efforts at a local scale that is more relevant to threats, such as anthropogenic light at night.

Keywords: aeroecology, bird migration, ecological forecasting, machine learning, remote sensing

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LAY SUMMARY

- Current migration forecasts rely solely on local atmospheric conditions and predictions are made at a relatively coarse scale. Yet, the inclusion of additional predictors may increase forecast resolution.
- We integrated terrestrial variables and atmospheric conditions at various scales into an existing radar-driven forecasting approach to significantly enhance the spatial resolution of forecasting outputs.
- By comparing 6 modeling approaches, we demonstrate that integrating these variables improved forecasting performance at a high-resolution of 2.9 × 2.9 km within North America's most active flyway. As a proof of concept, we applied this approach to the entire continental United States, where our model successfully explained up to 65% of variation in migration activity.
- The high-resolution predictions of our new models could facilitate data integration and inform migratory bird conservation efforts at local scales.

Integrar predictores terrestres y atmosféricos de múltiples escalas mejora los pronósticos de migración nocturna de las aves

RESUMEN

Nuestra capacidad para pronosticar patrones espaciales y temporales de procesos ecológicos a escalas continentales ha mejorado drásticamente en la última década. Sin embargo, predecir patrones ecológicos a escalas amplias mientras se capturan procesos de escala fina sigue siendo un desafío central en la predicción ecológica debido a la tensión inherente entre grano y extensión, donde mejorar uno a menudo disminuye

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el otro. Aprovechamos 10 años de datos terrestres y atmosféricos (2012–2021) para desarrollar un modelo de pronóstico de migración de aves de alta resolución (2.9 × 2.9 km) mediado por radar, para una región altamente activa de la ruta migratoria del Mississippi. Basados en un conjunto de modelos candidatos que examinamos, agregar predictores terrestres mejoró el rendimiento del modelo solo de manera marginal, mientras que los predictores atmosféricos espacialmente distantes, en particular la temperatura del aire y la velocidad del viento de regiones focales y distantes, fueron los principales contribuyentes a nuestro mejor modelo, explicando el 56% de la variación en la actividad migratoria regional. Entre los predictores terrestres, que se posicionaron considerablemente más bajos que los predictores atmosféricos en términos de importancia de las variables, la fenología de la vegetación, la luz artificial durante la noche y el porcentaje de cobertura forestal fueron los predictores más importantes. Además, ampliamos este modelo para demostrar la capacidad de generar pronósticos en tiempo real de alta resolución para los Estados Unidos continentales, que explicaron hasta el 65% de la variación nacional. Nuestro estudio brinda un enfoque para aumentar la resolución de los pronósticos de migración, lo que podría facilitar la integración del radar con otras fuentes de datos y colaborar con los esfuerzos de conservación dinámicos a escala local que es más relevante para las amenazas, como la luz artificial nocturna.

Palabras clave: aeroecología, aprendizaje automático, migración de aves, pronósticos ecológicos, teledetección

INTRODUCTION

Our ability to forecast bird migration intensity at a continental scale has the potential to inform dynamic conservation efforts (Horton et al. 2021). Yet, accounting for various scales that influence ecological systems is an established challenge of ecological forecasting (Wiens 1989, Dietze et al. 2018). There is an inherent tradeoff between grain and extent, such that expanding the spatial scope of a forecast typically comes at the cost of capturing fine-scale processes (Levin 1992). Given this, it is generally difficult to make ecological predictions at a broad scale that account for fine-scale variation and provide insight that can be applied to local conservation efforts (Petchey et al. 2015). One application of ecological forecasting that has received considerable attention is the prediction of migratory bird movements, with notable advancements in the development of forecasting systems that leverage decades of weather surveillance radar data to predict nightly migration intensities (Van Doren and Horton 2018, Van Gasteren et al. 2019, Lippert et al. 2022). Many of these systems calculate vertical profiles of activity, which take data across multiple altitudes within more than 200,000 volumes and consolidate them to as few as 30 values that summarize activity within an altitudinal range of interest (Dokter et al. 2019).

Yet, these migration forecasting systems could be further enhanced by incorporating additional geospatial predictors that characterize the terrestrial landscape to provide additional predictive power. Various land cover features such as vegetation phenology (Gordo 2007, Youngflesh et al. 2021) and the amount of canopy cover at the local scale (Buler and Dawson 2014) have been shown to influence spatial and temporal patterns of bird migration, with bird migration advancing to keep up with phenological shifts and relying on forested areas for migratory stopover. However, predictors in current North American radar-driven forecasts like BirdCast (Van Doren and Horton 2018) are solely composed of atmospheric variables, such as wind speed, wind direction, temperature, and sampling variables, such as timing and location of data collection, without incorporating terrestrial landcover variables that may influence where birds take off from and land.

Beyond the incorporation of terrestrial landcover, forecasts could potentially be enhanced by integrating predictors at multiple spatial scales rather than solely relying on local predictors that reflect conditions around each respective radar site that is measuring migration activity. Migration is likely driven by variables across a wide range of spatial scales, and by integrating atmospheric and terrestrial predictors at regional and macro scales, we can potentially enhance the spatial resolution and predictive power to forecast migration intensity, specifically the density of migrants in the airspace 3 hr after sunset, as measured by weather surveillance radar. While many near-term forecasting models use predictors at the local area around a focal point (e.g., Van Doren and Horton 2018) and remain limited by coarse spatial resolution (Dietze et al. 2018), the inclusion of spatially distant predictors or those that reflect conditions at a set range away from a given focal point could capture both environmental cues at broad scales and local conditions, such as temperature (Tøttrup et al. 2010), to enhance model resolution. This concept has been demonstrated by Kranstauber et al. (2022), who developed ensemble models that have leveraged multi-scale predictors to improve bird migration forecasting performance. Such findings strongly suggest that integrating both terrestrial and atmospheric predictors across multiple scales into existing forecasting systems in the continental United States may help explain variance at a smaller spatial grain and effectively enhance the resolution of predictions.

This spatial enhancement could have important implications for both research and conservation applications. For instance, while there have been considerable efforts to integrate Next Generation Weather Radar (NEXRAD) data with crowdsourced occurrence data, such as eBird, to better understand the taxonomic composition of migratory movements (Shipley et al. 2018, Weisshaupt et al. 2021), there is a spatial mismatch between the fine scale of these taxonomic data products and the relatively coarse scale of previous NEXRAD estimates of migration activity (e.g., Haas et al. 2022). Similarly, many pressing global landcover changes, such as urbanization, occur at fine scales that require high spatial resolution to properly investigate in an ecological context (Cadenasso et al. 2007). From a conservation standpoint, there is growing evidence that collisions with human-built structures are a major source of mortality (Loss et al. 2014) and the amount of anthropogenic light at night can influence migrant behavior, attracting and trapping birds in brightly lit areas (Horton et al. 2019). Near-term forecasting of migration events has already demonstrated immense value to conservation practitioners (Horton et al. 2021) and is often used to inform Lights Out campaigns across the United States, which seek to reduce anthropogenic light during periods of intense migration (Burt et al. 2023). However, previous studies have demonstrated that birds respond to point light sources at a remarkably local scale (Van Doren et al. 2017), far beyond the coarse resolution of current forecasts. Relatedly, an increased resolution could help target messaging to the appropriate stakeholders at a local scale, which is a noted barrier to the efficacy of current Lights Out programs and campaigns (Burt et al. 2023). Together, there is a strong motivation to enhance the spatial resolution of these forecasts to both advance research and improve our capacity for effective conservation messaging and decision-making.

Here, our objectives were to enhance the spatial resolution of migration forecasts while maintaining high predictive power by addressing the limitations noted above. Our approach entailed (1) training models on rasters of weather surveillance radar products to capture heterogeneity in nightly migration, (2) integrating terrestrial covariates, and (3) incorporating spatially distant predictors. As a first step, we developed these forecasts within the midwestern United States, the most active flyway in North America. We then scaled up our approach to the full continental United States to test performance across a broad extent and compared our models to existing continental forecast models (Van Doren and Horton, 2018). We predicted that integrating both land cover and distant predictor variables would explain additional variance in observed data and, consequently, improve the prediction of migration intensity.

METHODS

Study System and Overview of Approach

To understand the relationship between bird migration intensity (as measured by radar) and predictor variables, we focused on developing testbed forecasts in the midwestern United States (Figure 1). We chose to focus on a smaller region because of the computational intensity of developing high-resolution forecasts, which required hundreds of gigabytes of data. This region is dominated by low elevation and flat interior plains, and has relatively dense coverage of NEXRAD stations, providing our model with ample measures for training. This region serves as a major flyway for migratory birds (Dokter et al. 2018, Horton et al. 2019). The combination of comprehensive NEXRAD radar coverage, minimal topographical blockage, and high degree of bird migration activity make this an ideal site for developing radar-driven migration forecasting tools. Notably, Van Doren and Horton (2018) reported that models in this region performed relatively well at broad spatial scales ($R^2 > 0.75$). For this focal region, we chose 14 conterminous NEXRAD weather stations in this region (Supplementary Material Table 1). Once developed, we extended our approach to the continental United States to explore the possibility of broadening this approach across the full extent of the NEXRAD system for potential conservation science and outreach. We describe this expanded forecast below in our national-scale forecasting section.

Weather Surveillance Radar Data

We used radar data collected through the NEXRAD network, which is operated by the National Weather Service (NWS), the Federal Aviation Administration (FAA), and the U.S. Air Force. With the contiguous United States, this network consists of 143 high-resolution Doppler weather radars (WSR-88D) that scan 360° at 0.5° azimuthal intervals (e.g., 720 azimuths) and multiple elevation angles (e.g., 0.5°, 1.5° … 4.5°) to actively monitor the airspace every 5–10 min and are accessible through Amazon Web Services (https://registry.opendata.aws/noaa-nexrad/). We downloaded level-II radar scans 2–4 hr after local sunset from 2012 to 2021 (from March 1 to November 15), since this 2-hr period usually encompasses

FIGURE 1. Overview of the study area and sampling methodology. (**A**) Dots represent 143 weather surveillance radar (NEXRAD) stations across the contiguous United States, and the inset box represents our study area. (**B**) A zoomed-in view of our study area, where circular domains represent 14 radar sampling regions. Within these domains, we show 1,287 sampling points (dots) used to collect bird migration observation data and predictor values for training and evaluating our forecast model. Within each circle, the light background represents the radar station coverage after removing clutter and beam blockage. (**C**) A schematic view of our sampling method to collect predictor values from an example focal cell (2.9 × 2.9 km), as well as 150-km distant predictor values in cardinal directions (not drawn to scale).

peak nightly bird migration activity (Farnsworth et al. 2016). These data provide the meteorological base moments of reflectivity, mean radial velocity, and spectrum width, which are commonly used for biological analysis. We downloaded polar volumes (PPIs), or a collection of azimuthal scans for all 14 stations and used the native date and time stamp associated with each radar scan. We used the R package *bioRad* (Dokter et al. 2019) in R version 4.2.2 (R Core Team 2022) to process data and we used the *apply_mistnet* function to filter out precipitation from PPIs and during the construction of vertical profiles of reflectivity (Lin et al. 2019). We used static clutter masks to remove clutter from physical structures (e.g., buildings and wind turbines) and elevational beam blockage (e.g., mountains). Because weather surveillance radars sample at increasing height above ground level with increasing distance from the radar, the biological coverage (and thus migration activity) covaries with distance to radar. Specifically, as the distance from the radar increases, our ability to quantify migrant density decreases, especially beyond 80–100 km, and thus density and distance negatively covary. To reduce this bias, and leverage the spatial information composed within polar volumes, we corrected for range artifacts (Buler and Diehl 2009). To account for errors associated with measures taken at increasing distance from each radar, we range-corrected planned position indicator (PPIs) using the *integrate_to_ppi* function in *bioRad*. We calculated the expected reflectivity at each pixel in each PPI as weighted by the vertical profile of reflectivity. We excluded individual PPI pixels that had range adjustment factors (R) higher than 10. The result of this correction was a range-corrected measure of vertically integrated reflectivity (cm^2 km^{-2}), which we used as a raster of biological activity. For volumes that were labeled as precipitation by MistNet, we changed the reflectivity values to zero. We aggregated the resulting polar volumes to rasters with a grain of 2.9 × 2.9 km.

Weather Reanalysis—North American Regional Reanalysis

We used the North American Regional Reanalysis (NARR) (National Centers for Environmental Prediction/NWS/NOAA/U.S. Department of Commerce 2005) to produce a best estimate of weather conditions that occurred across the Midwest region (Mesinger et al. 2006) on the basis that it is commonly used for similar research across this extent. NARR is a combined model and assimilated dataset of many different atmospheric measurements, reanalyzed to generate continuous continental scale coverage. The NARR model provides 8 daily measurements every 3 hr of variables at 29 pressure levels with a 32-km resolution. We downloaded NARR data from 2012 to 2021, and for each geographic coordinate we only included measurements of the closest 3-hr Coordinated Universal Time (UTC) to the local sunset. We then extracted the following parameters: air temperature (°C), geopotential height (m), zonal and meridional wind components (m s^{-1}), surface pressure (Pa), relative humidity (%), visibility (m), mean sea level pressure (Pa), and total cloud cover (%). For variables available at multiple pressure levels (air temperature and zonal and meridional wind speed), we extracted data from the surface level to 800 hPa at 50 hPa intervals. We have summarized the atmospheric predictor variables included in this study in Table 1.

Weather Forecasts—North American Mesoscale Forecast System

To understand how the model performed in real-time scenarios for nightly migration forecasts, we quantified the performance using true forecasts of atmospheric measures. We used the North American Mesoscale Forecast System (NAM; https://www.ncei.noaa.gov/products/weather-climate-models/north-american-mesoscale), which generates weather forecasts up to 84 hr. In contrast to NARR, NAM is a true forecast and naturally is prone to predictive error. Forecasts are available hourly from 1 to 36 hr and subsequently every 3 hr until hour 84. Forecast models are run every 6 hr. NAM predictions are made on a 12-km grid. We downloaded forecasts from 0 to 6 UTC and extracted the same parameters as for NARR, and matched NAM data to cells within the radar coverage.

Terrestrial Predictors

To understand how terrestrial variables influence migration activity, we selected 3 categories of predictors: land cover, vegetative phenology, and artificial light at night. We extracted terrestrial variables as potential predictors of bird migration activity. We derived land cover data from the MODIS Land Cover Type Product (MCD12Q1 v 6.0; Sulla-Menashe and Friedl 2018). This product comes with 6 different land cover classifications at ~500-m resolution and annual time, of which we used the University of Maryland (UMD) classification scheme. The UMD classification scheme provides 16 classes/types of land cover. For cropland, forest, shrubland, and savanna land cover types, we first summed all associated classes, and then calculated the percent cover at 2.9-km resolution. Specifically, for croplands, we combined the Cropland and Cropland/Natural Vegetation classes. For forest, we combined Evergreen Needleleaf Forests, Evergreen Broadleaf Forests, Deciduous Needleleaf Forests, Deciduous Broadleaf Forests, and Mixed Forests. For shrublands, we combined Closed and Open Shrublands. For Savanna, we combined Savannas and Woody Savannas.

For each of the terrestrial predictors, we aggregated ~500 m cells by 6 × 6 (roughly 2.9 × 2.9 km) cell quadrants and calculated the mean and standard deviation for each resultant cell. Resampling these datasets allowed us to project the data onto roughly the same resolution (2.9 × 2.9 km). We selected this resolution because it is the current resolution of publicly available eBird community science data (Auer et al. 2020, Fink et al. 2020). Since radars do not provide species-specific information, we view eBird as a natural point of future data integration to strengthen insights and conservation actions.

In total, our aggregation process resulted in 9 classes of land cover in our forecasting model using this dataset (Table 1). Additionally, we used the MODIS vegetation index (VI) to measure the mean enhanced vegetation index (EVI) at a ~500-m resolution (Didan et al. 2015). We used the MOD13A1 v6.0 layer to extract EVI. We aggregated EVI values to 2.9-km resolution (roughly 6 × 6 cells) and calculated the mean and standard deviation per grid cell (i.e., generating 2 variables, mean EVI, and SD EVI, using this dataset). Lastly, we used NASA's visible infrared imaging radiometer suite (VIIRS; the "vcm" version of tiled monthly cloud-free Day/Night band composites) dataset as a measure of anthropogenic light at night at a 15 arc second (roughly 500 m) spatial resolution (available at the Colorado School of Mines' Earth

TABLE 1. A list of the sampling, atmospheric, and terrestrial predictor variables used to predict bird migration density with gradient boosted trees.

Predictor	Class of variables	Resolution	Collection metrics	Cardinal directions
Ordinal date	Sampling	–	–	No
Time after sunset	Sampling	–	–	No
Distance from radar	Sampling	–	–	No
Elevation	Sampling	NASADEM (30 m)	–	No
Air temperature	Atmospheric	NARR (32 km) NAM (12 km)	2 m above ground, 800–1,000 hPa	Yes
Geospatial height	Atmospheric	NARR (32 km) NAM (12 km)	Surface	Yes
Pressure	Atmospheric	NARR (32 km) NAM (12 km)	Surface, mean sea level	Yes
Relative humidity	Atmospheric	NARR (32 km) NAM (12 km)	2 m above ground	Yes
Total cloud cover	Atmospheric	NARR (32 km) NAM (12 km)	Entire atmosphere	Yes
Visibility	Atmospheric	NARR (32 km) NAM (12 km)	Surface	Yes
Zonal and meridional wind speed	Atmospheric	NARR (32 km) NAM (12 km)	10 m above ground, 800–1000 hPa	Yes
Enhanced vegetation index (EVI)	Terrestrial	MOD13A1 (500 m)	Aggregated to 2.9 km, and mean and standard deviation collected	No
Visible infrared imaging radiometer suite (VIIRS)	Terrestrial	VIIRS nighttime lights (~500 m at the equator)	Aggregated to 2.9 km, and mean and standard deviation collected	No
Water bodies	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No
Grasslands	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No
Permanent wetlands	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No
Urban and built-up lands	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km, and the relative percentage calculated	No
Non-vegetated lands	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No
Forests	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No
Shrublands	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No
Croplands	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and relative percentage calculated	No
Savannas	Terrestrial	MCD12Q1 (500 m)	Aggregated to 2.9 km and the relative percentage calculated	No

Observation Group webpage: https://eogdata.mines.edu/products/vnl/). We applied the same method as EVI to this dataset and generated 2 new variables, mean and standard deviation values of radiance derived from VIIRS (hereafter "anthropogenic light"). In total, we derived 13 terrestrial predictors to be included in our forecasting model (Table 1).

Supervised Machine Learning

We used gradient boosted trees that predict bird migration activity from atmospheric and terrestrial features. We matched the timestamps of the terrestrial and atmospheric data to the nearest available timestamps of the radar observations, ensuring the data from different sources were temporally coherent. For this supervised learning approach, we divided our data into 3 sets: (1) a training set to train the model with 70% of data, (2) a validation set for hyperparameter tuning (15%), and (3) a test set to evaluate performance (15%). The purpose of this division was to train the model using the training set and to tune the hyperparameters of the model using the validation set. To tune the hyperparameters, we performed a grid search by trying different combinations of parameters, such as the objective for regression application, learning rate, number of trees, max number of leaves in one tree, and maximum depth for the tree model. Specifically, we set an initial learning rate of 0.1, with a maximum tree depth of 30 and 500 leaves per tree. We constrained the minimum number of data points in each leaf to 3,000 and required a minimum gain of 3 to perform a split. Additionally, a minimum sum of 2 for the Hessian in each leaf was imposed. We used a serial tree learner, leveraging 10 computational threads, with a fixed random seed (123) for reproducibility. To enhance generalization, a bagging fraction of 80% was employed, along with a bagging frequency of 5 iterations and a feature fraction of 95%. Early stopping was applied after 7 rounds of no improvement. The importance of features was saved based on split gains, and column-wise processing of features was forced to improve computational efficiency. We used the *LightGBM* package in R (Ke et al. 2017), which employs gradient-based one-sided sampling and exclusive feature bundling to accelerate the training process while maintaining high accuracy.

We randomly selected 1,287 unique points for training our forecasting system from our testbed region (Figure 1). Points were distributed proportional to the coverage of each NEXRAD site (i.e., sites with great blockage and clutter accounted for a smaller proportion of points) with a maximum of 100 points per site. We then extracted the atmospheric and terrestrial predictor values associated with each point. For atmospheric predictor variables, we also extracted spatially distant predictors (i.e., from locations 150 km from each focal point in each cardinal directions; Table 1). We included distant predictors to reflect conditions at a set range away from the focal area to capture the possibility that birds respond to environmental cues at a macroscale. This definition doubles the range of remote predictors used by Kranstauber et al. (2022) and was informed by estimated average flight distance of *Catharus ustulatus* (Swainson's Thrush), which on average flew 265 km per night (Wikelski et al. 2003). Given the large amount of data included in each model, experimenting with multiple scales would have been exceedingly difficult from both a time and computational perspective. In total, we assessed 167 predictor variables associated with each point to train a gradient boosted tree. The final dataset for training and evaluating our machine learning-based forecasting model contained 11,993,543 weather radar scan-derived bird migration estimates collected from 1,287 sampling points from 2,587 nights across 10 years.

For model fitting, we used Root Mean Square Error (RMSE) as a measure of model performance as it measures the average magnitude of the error between predicted and actual values, while also penalizing large errors more heavily than small errors (Morley et al. 2018). To prevent overfitting, we used early stopping and stopped the algorithm after 10 boosting iterations in which performance on the validation set failed to improve the RMSE. We then used the validation dataset to select the best-performing model based on the lowest RMSE. The best combination of model parameters was: regression for the objective, 0.1 for learning rate, 1,000 for number of trees, 500 for maximum number of leaves, and 30 for maximum depth. Finally, we evaluated the performance of the model on the test set to assess its generalization ability.

Description of Six Candidate Models

We created 6 modeling scenarios with varying candidate predictor sets using different combinations of 167 predictor variables to explore 6 hypotheses relating to the importance of atmospheric, terrestrial, and spatially distant predictors in forecasting bird migration density. All atmospheric variables used to develop and evaluate the forecasting system were obtained from NARR. To evaluate our model performance, we performed a 10-fold cross-validation across 10 years of historical data (2012–2021) and calculated the coefficient of determination (R^2) per year. Below, we summarize the details of each model scenario:

Scenario 0: As a null model test, we designed a system to predict bird migration forecast using only sampling variables to understand the extent to which the chosen predictors (ordinal date, hour after sunset, elevation, and distance to radar) can explain the observed variation in bird migration patterns. By isolating the impact of these sampling variables, we aimed to understand the underlying processes driving bird migration better.

Scenario 1: In this scenario, we designed a system similar to Van Doren and Horton (2018), but using the currently enhanced spatial resolution (~2.9×2.9 km), representing the hypothesis that nightly bird migration intensity is best predicted solely by atmospheric predictors. Our scenario one model included 28 atmospheric and sampling predictors associated with the focal area/cell. This scenario was chosen as the benchmark for comparison of improvement as we added more predictor variables to the system. Note that Van Doren and Horton (2018) trained their model on vertical profiles of reflectivity, a product that averages migration intensity across a broad spatial extent (4,417 km^2), whereas our model is trained on considerably smaller spatial extents (9 km^2).

Scenario 2: We added terrestrial variables (i.e., land cover, EVI, and artificial light at night) associated with the focal area to Scenario 1, representing the hypothesis that terrestrial predictors would improve forecasting performance. The model in Scenario 2 included 41 total predictors.

Scenario 3: We added spatially distant terrestrial predictors 150 km away in each cardinal direction to Scenario 2, representing the hypothesis that including terrestrial predictors at multiple scales would increase forecasting performance. This model included 71 total predictors.

Scenario 4: We added spatially distant atmospheric variables 150 km away from the focal pixel in each cardinal direction to Scenario 2, representing the hypothesis that including atmospheric predictors at multiple spatial scales would increase forecasting performance. The model in Scenario 4 included 137 total predictors.

Scenario 5: In the last scenario, we integrated all 167 predictors used across all previous models to represent the hypothesis that including both terrestrial and atmospheric predictors at multiple spatial scales would best predict nocturnal bird migration density.

Across these 6 modeling scenarios, we used the coefficient of determination (R^2) to compare forecasted migration density vs. observed migration density to assess the performance of the models represented in each predictor set. The R^2 value represents the amount of variation in the response variable explained by predictors (Renaud and Victoria-Feser 2010). We selected this metric vs. other available ones (e.g., RMSE and MAE) because R^2 can be used to compare model performance across all stations/regions or time periods, while for other metrics we need to provide ranges throughout the region or time (Chicco et al. 2021).

Regional-Scale Forecasting

We selected Scenario 4 for subsequent regional- and national-scale analyses on the basis of the highest consistent high performance with the fewest additional predictors (see Model performance across 6 candidate predictor sets in Results). Using our validated migration forecasting model, we made predictions across the midwestern region covered by 14 radar stations for 20 nights from 2020 and 2021 (i.e., 10 nights per year). Prior to making predictions, we excluded observations associated with 2020 and 2021 and trained the model on the remaining 9 years.

We selected nights with high and low migration activity and spatial heterogeneity in intensities through the region—

some areas showing visually lower activity than others. We defined "high" and "low" migration nights, using the Live Bird Migration Maps tool from BirdCast (https://birdcast.info/migration-tools/live-migration-maps/). For "high" migration nights, we selected dates during peak migration seasons when migration traffic rates were close to 50,000 birds km^{-1} hr^{-1} over a wide area, indicating widespread and intense migration activity. For "low" migration nights, we chose from dates outside peak migration periods when the migration traffic rates did not reach 2,000 birds km^{-1} hr^{-1}, being often around 500–1,000 individual birds, reflecting minimal migratory activity. By setting these quantitative thresholds based on migration traffic rate values from BirdCast, we ensured that our selection of "high" and "low" migration nights was consistent and representative of typical migration patterns, which helped to evaluate the performance of our model better across different migration intensities.

To forecast bird migration density, we generated 2 sets of prediction maps at 3 hr after local sunset per night for comparison (i.e., 40 maps in total), one using atmospheric variables obtained from the 32-km NARR grids, and another using similar atmospheric variables obtained from the 12-km NAM grids. The archived NAM dataset helped simulate a real-world forecasting event since this system generates weather forecasts up to 84 hr. Last, to standardize distance from radars for forecasting, we assumed that each cell block was 35 km away from a radar station.

National-Scale Forecasting

To simulate a real-world scenario for national-scale forecasting, we randomly selected 2,020 points from all 143 radar stations in the lower 48 states of the United States. The number of sampling points varied based on the coverage area of each radar station; for stations with larger coverage, we sampled more points. We repeated this process 25 times, each time selecting a different set of 2,020 random points and extracting values for the 137 predictors in our scenario 4 with integrated predictors. We used these 25 datasets to train 25 national-scale models, with 70% of the data for training, 15% for validation, and 15% for testing. After training, we applied the process outlined in the preceding section to produce bird migration forecasts using NAM data for the same 20 nights from 2020 to 2021. To create a final national bird migration forecast map, we calculated the average value across the 25 predictions per each 2.9 × 2.9 km cell.

Evaluating Regional and National Model Performance

Similar to Van Doren and Horton (2018), we used R^2 to evaluate regional and national model performance. Additionally, we evaluated the spatial accuracy of our system at the regional scale over areas with no radar coverage, by iteratively removing observational data from each of the 14 radar stations and retraining the model on the remaining data. To evaluate the temporal accuracy of our regional system, we iteratively excluded a year from our 10-year historical dataset (2012–2021), retrained the model on the remaining 9 years, and forecast bird migration density for each observational record per sampling point.

At both scales, we selected 10 nights each from 2020 to 2021 that had moderate-to-high migration activity and spatial heterogeneity in the distribution of migration activity. We calculated the R^2 for each of these 20 nights across the randomly selected unique locations for training. Additionally, we selected 10 of the lowest activity nights in March 2020 to assess model performance on nights with low migration intensity. We used the Van Doren and Horton (2018) model, which uses Global Forecast System (GFS) data, as a comparison point of model performance.

RESULTS

Model Performance Across Six Modeling Scenarios

The median R^2 for Scenario 0 (null model using only sampling variables) was 0.29. Scenario 1 (including atmospheric and sampling variables) yielded a median R^2 of 0.53 (Figure 2). The addition of terrestrial predictors in Scenario 2 resulted in a slight improvement, increasing R^2 from 0.53 to 0.54. The inclusion of spatially distant terrestrial predictors in Scenario 3 did not further increase forecasting performance ($R^2 = 0.54$); however, the inclusion of spatially distant atmospheric predictors in Scenario 4 further improved forecasts ($R^2 = 0.56$). Last, Scenario 5, which included the predictors used across all models performed similarly to Scenario 4 ($R^2 = 0.56$), demonstrating that the addition of spatially distant terrestrial variables does not improve our predictive power for bird migration.

To understand important predictors for bird migration density forecast, we calculated the relative percentage of the gain value provided per predictor in Scenario 4 for both spring (March 1 to June 15) and fall (August 1 to November 15) migration seasons across 10 years. In spring, the top 5 predictors included ordinal date, air temperature at 950 hPa pressure level in the west, distance from radar (km), and meridional wind (north/south component) at 850 and 900 hPa pressure levels to the west. Among terrestrial predictors, the mean value of anthropogenic light (rank 52), percentage of forest cover (rank 53), and the mean value of EVI (rank 55) were the most important variables. In fall, the top 5 predictors included ordinal date, meridional wind of the focal area at 950 hPa pressure level, meridional wind at 950 hPa pressure level in both north and east, and distance from radar (km). Among terrestrial predictors, the mean value of anthropogenic light (rank 37), the mean value of EVI (rank 48), and the percentage of forest cover (rank 52) were the most important variables.

In total, for spring models, atmospheric variables comprised 55.70% of gain, sampling variables comprised 42.85%, and terrestrial variables comprised 1.45%. For fall models, atmospheric variables comprised 70.56% of gain, sampling variables comprised 27.29%, and terrestrial variables comprised 2.15%. We provide a full list of spring and fall feature importance and the relative gain for this model in Supplementary Material Table 2.

Regional Forecasting Spatial and Temporal Accuracy

With regard to spatial accuracy, the median R^2 for withheld stations was 0.58, while R^2 was 0.57 or higher for 10 stations. We did not detect any patterns among stations with higher R^2 rates, such as spatial proximity or overlapping coverage with other stations. With regard to temporal accuracy, the median R^2 across 10 years was 0.56, and we achieved a 0.54 or higher R^2 for 8 years.

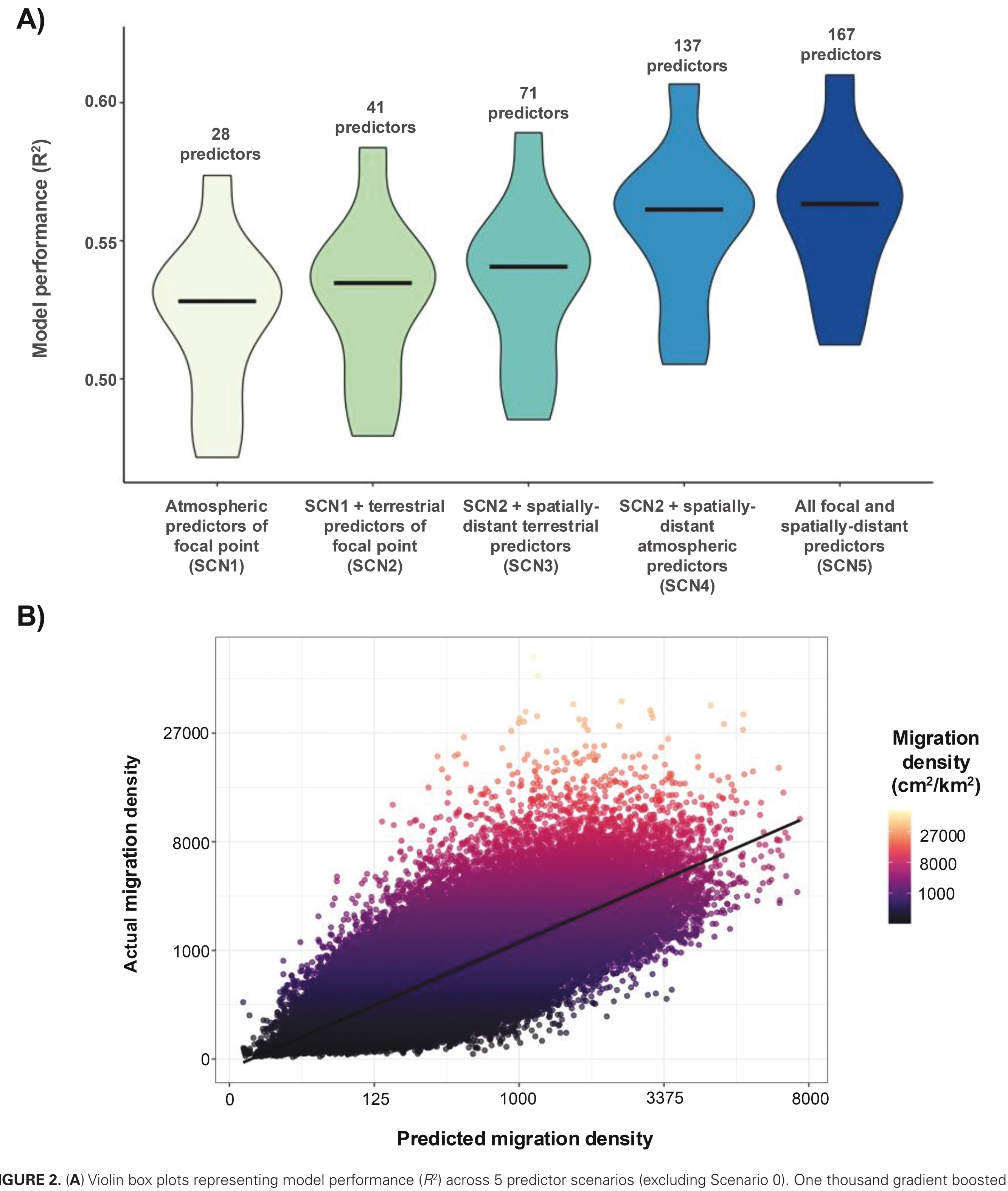

FIGURE 2. (**A**) Violin box plots representing model performance (R^2) across 5 predictor scenarios (excluding Scenario 0). One thousand gradient boosted trees were produced for each predictor set using different combinations of atmospheric and terrestrial predictors at varying scales to predict regional bird migration intensity. (**B**) Scatterplot of observed vs. predicted bird migration density using Scenario 4: we show 10% of points randomly selected from our 2021 holdout experiment (i.e., all data from 2021 excluded during model training). Higher values represent higher migration density and the line represents the best fit.

Forecasts Performance in Capturing Spatial Heterogeneity

Using the NARR and NAM datasets, we generated 2 prediction maps at 3 hr after local sunset per night, calculated R^2 to evaluate our model performance, and averaged prediction values (migration density) across multiple cell blocks to smooth prediction maps. Due to different spatial resolutions in atmospheric datasets, we averaged predictions across 7×7

and 3 × 3 cell blocks to smooth maps for NARR and NAM data, respectively. Median R^2 for forecasting 20 nights using NARR data was 0.43. The R^2 values ranged from 0.01 to 0.70 across selected nights. The median R^2 for NAM data was markedly lower ($R^2 = 0.32$), while the R^2 variation among nights was similar to NARR, ranging from 0.02 to 0.69. For the same night that showed the lowest R^2 rate using both NARR ($R^2 = 0.01$) and NAM ($R^2 = 0.02$) data, the Van Doren and Horton (2018) model also performed relatively low ($R^2 = 0.13$), considering they developed the model on a much coarser resolution.

For the national forecast map, we calculated the average prediction for each cell based on the output from the 25 models using NAM data. The median R^2 for the 25 rounds of training of our national-scale models was 0.73. We evaluated the forecasting performance for each of the 20 nights by computing the R^2 values for all 25 models, and then taking the median R^2 value for each night. Across the 20 nights, the median R^2 values ranged from 0.26 to 0.65, with a median of 0.54. When using NAM data, our national forecast system achieved a higher median R^2 rate ($R^2 = 0.54$) compared to the regional forecast system ($R^2 = 0.32$). On nights of low migration activity, side-by-side visual comparison of our high-resolution forecast system with Van Doren and Horton's (2018) model suggests their performance was, as expected, substantially poorer with a median R^2 of 0.09 (Figure 3).

DISCUSSION

This study sought to enhance forecasts of migratory activity while maintaining high model performance by integrating multi-scale terrestrial and atmospheric predictors. Through this work, we illuminate both the benefits and potential limitations of these integrations. Although terrestrial predictors across multiple scales offered marginal predictive gain, including atmospheric predictors at multiple spatial scales with detailed spatial information from weather surveillance radars enhanced nightly migration forecasts at a continental scale. Ultimately, integrating these variables did allow us to make predictions at high resolution, while maintaining consistently strong forecasting performance across a broad extent. Here, we discuss the implications that our findings and similar high-resolution forecasts may have for data integration and advancing migratory bird conservation.

Surprisingly, terrestrial predictors were not strong predictors of migration intensity, and they only contributed marginally to model performance at both local and distant scales. Notably, elevation was a top 10 predictor in both seasons, which may be partly due to topographic-driven variations in birds reaching a flight height, where they can be detected by radar. Alternatively, migrating birds could be responding to altitudinal conditions driven by the underlying topography, which would be consistent with studies in alpine systems (Katzner et al. 2015, Lindenmayer et al. 2014). Among terrestrial predictors, EVI and forest cover were also

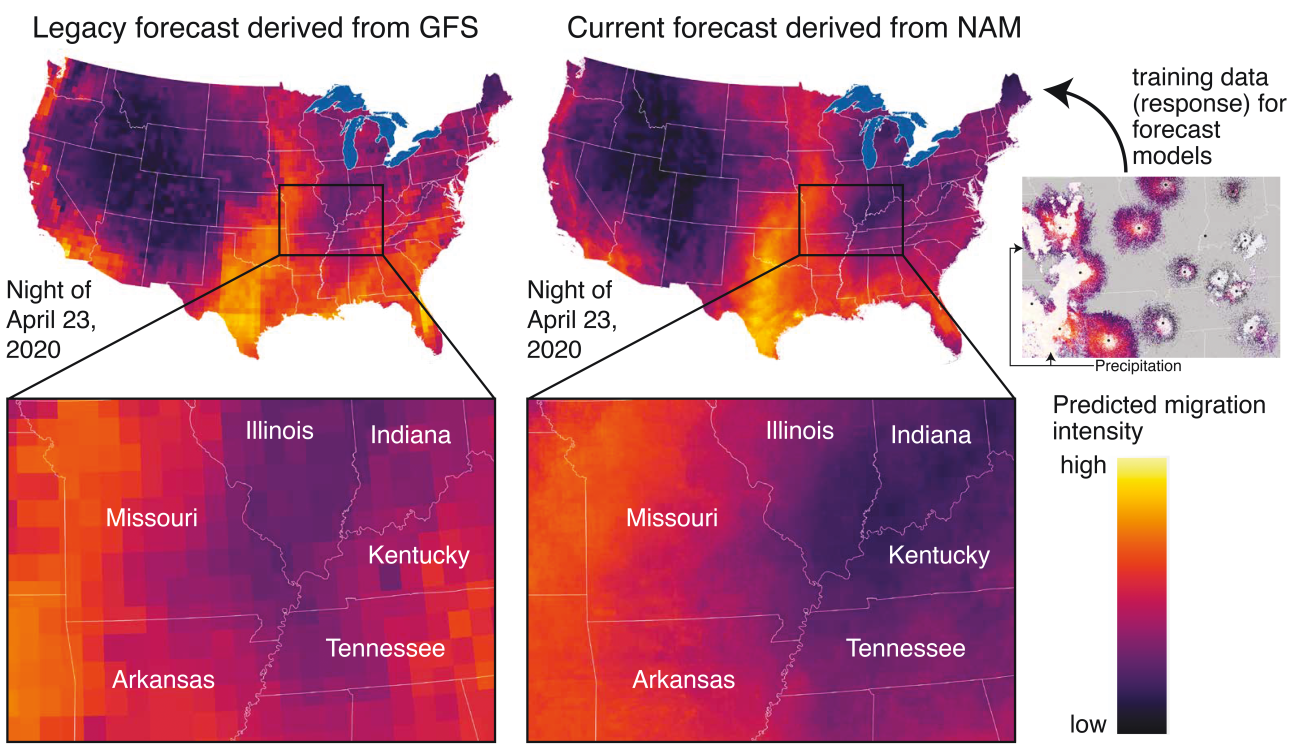

FIGURE 3. Performance comparison of different forecasting models vs. the actual observations of bird migration density for the night of April 23, 2020 in both national- and regional-scale. The upper right corner demonstrates range-corrected radar reflectivity across 14 radar stations. Lighter shades represent higher migration density and darker colors represent lower migration density in cm² km⁻². Areas identified as precipitation are shaded in white; weather contaminated pixels were removed from our analysis. (Left) Migration predictions derived from the framework established by Van Doren and Horton (2018) (accessible on https://birdcast.info/). We show these predictions in their native 0.5° resolution; predictions are solely dependent on atmospheric variables derived from the global forecast system (GFS). (Right) High-resolution forecast of bird migration density using sampling and terrestrial predictors, as well as atmospheric predictors derived from the North American Mesoscale (NAM) Forecast System. The R^2 rates for this night using the NAM dataset were 0.66 and 0.50 for regional and national scales, respectively.

important, which is consistent with previous literature suggesting that vegetation phenology impacts the timing of migration (Kelly et al. 2016) and that forest cover is a strong driver of migratory stopover (Buler and Dawson 2014), but their relative gain was marginal relative to atmospheric predictors. Although this lack of predictive gain contrasted our predictions, we note that our response variable of migration intensity was ultimately a metric of birds aloft. Thus, it is perhaps unsurprising that it was driven largely by atmospheric habitat conditions. Nevertheless, our models were trained on data from 2 to 4 hr after sunset. However, the importance of terrestrial features could increase as birds depart for nocturnal flights and land in stopover or breeding habitats, both of which are periods when their behavior may be more tied to land cover. Therefore, studies that directly incorporate this dynamic nature, for example by comparing the relative importance of terrestrial features at different stages of the night, could provide important insights to inform the appropriate scales, at which terrestrial predictors may best support migration forecasts.

In contrast, integrating spatially distant atmospheric predictors did improve model performance, with many of our top predictors being reflective of distant conditions (150 km from the sampling point). This finding comports with recent work in European systems, which integrated multi-scale predictors into ensemble models to improve forecasting performance (Kranstauber et al. 2022). Additionally, we found a distinct difference in the impact of scale between terrestrial and atmospheric predictors, suggesting that birds respond to atmospheric conditions on a relatively large scale, whereas on-the-ground drivers may have a more localized effect. This finding is consistent with the proposed stopover theory, suggesting that "extrinsic" site effects, or habitat characteristics around a stopover site, are stronger than "intrinsic" effects, or habitat characteristics within a stopover site, with respect to stopover decisions (Martin and Finch 1995). Our findings add to a well-established literature suggesting that bird migration behavior is driven by a multi-scale process (Buler et al. 2007, Sapir et al. 2011, Mellone et al. 2015) and more broadly, highlights the importance of incorporating multiple scales to model macroecological processes, such as bird migration.

Our ability to produce high-resolution migration forecasts across the continental United States that explain up to 65% of variation builds on the work of existing migration forecast efforts (Kranstauber et al. 2022, Lippert et al. 2022, Van Doren and Horton 2018). Given the complex relationship between spatial resolution and model uncertainty (Pogson and Smith 2015), it is difficult to directly compare our model performance to these previous works. However, we do feel that the consistently strong predictive performance of our models at a high resolution is encouraging and addresses long-standing challenges within scaling theory. As stated by Wiens (1989), to understand ecological systems, we must view them "on the appropriate scale." Although bird migration is a hemispheric process, many of the most pressing biological and conservation questions occur at a much more local scale. While radar has played an increasingly large role in studying migration, its insights are typically limited to relatively coarse spatial resolution. The ability to predict migration activity at a 2.9 × 2.9 km resolution across both regional and national scales has widespread implications for research and conservation. We demonstrate that this scale-up approach (Fritsch et al. 2020) may be applicable to ecological forecasting in other systems as a method of integrating multiple scales to assess the scale-dependence of ecological processes (Sandel and Smith 2009). Specific to ornithology, the enhanced resolution produced here could also provide opportunities to elucidate the relationship between migration activity and rapid, fine-scale landcover change processes, such as urbanization (Cadenasso et al. 2007). This high-resolution output could also be coupled with increasingly fine-scale remote sensing datasets (e.g., Zanaga et al. 2022) and species distribution models (e.g., Fink et al. 2020) to advance the integration of radar data with crowdsourced compositional data. Such research could advance our understanding of how the migration of different taxonomic groups may be disproportionately impacted by various predictors (Flack et al. 2022). Furthermore, the enhanced spatial resolution may be more relevant for actionable conservation efforts. Anthropogenic light at night has been found to impact birds far more local scales (Parkins et al. 2015, Van Doren et al. 2021) than the level of operation of current forecasts. Even within a single urban landscape, point sources of anthropogenic light can seriously affect migratory bird behavior and activity (Van Doren et al. 2017). The output demonstrated here could be a step toward more targeted conservation messaging, in particular by incorporating information about migration activity at a scale more relevant to Lights Out programs working with local building owners and residents, which is a well-documented outreach disconnect amongst conservation practitioners (Burt et al. 2023).

Beyond enhancing forecasting resolution, our ability to rank the predictive gain associated with different variables informs us about the relative importance of different drivers of migration that have been identified by previous research. Ordinal date was the top predictor across both seasons, reflecting the strong seasonality of migration (Helm et al. 2013) and internal, endogenous programs that drive migration timing (Åkesson and Helm 2020). Beyond this, we found that atmospheric variables, such as wind speed and air temperature, made up the vast majority of our top predictors across both seasons (Figure 4; Supplementary Material Table 2). The connection between migratory behavior and weather conditions has been recognized for over a century (Smith 1917) and research advancements continue to strengthen our understanding of this relationship. The growing use of radar, for example, has consistently highlighted atmospheric conditions as major predictors of the migration intensity of birds en masse (Shamoun-Baranes et al. 2017, Horton et al. 2021). Work tying individual departure timing to wind regimes (Åkesson and Hedenström 2000) and air pressure (Cooper et al. 2023) have not only supported this notion, but also illuminated additional nuance with respect to variability across age and sex classes. The combination of ordinal date and atmospheric conditions is consistent with a hierarchical migratory decision-making model (Cooper et al. 2023), whereby birds have a broad departure window but rely on weather cues to inform their nightly behavior. The corroboration of these findings suggests that this relationship transcends across scales and investigative approaches (e.g., individuals vs. community assemblages).

There were several limitations of our study that serve as areas that are ripe for additional developments and future experiments. First, we note that our approach could be extended

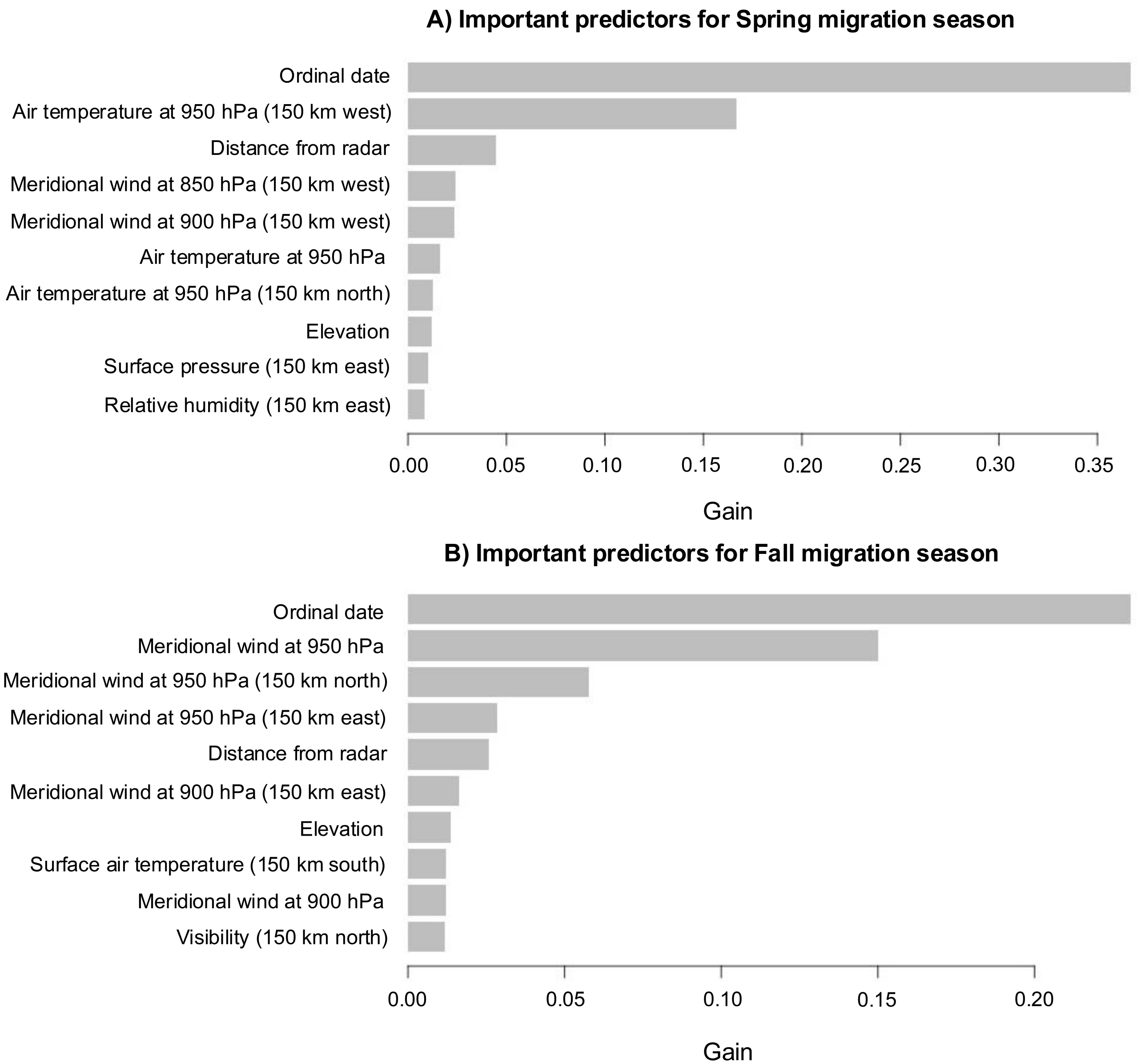

FIGURE 4. Top 10 seasonal (spring and fall) predictors as estimated by model gain, a measure of the relative contribution of the corresponding feature to the model.

to integrate more modern and higher-resolution predictor datasets as they become available. For example, while our models rely on NARR data for weather condition predictions as a comparison point to previous forecasting systems, the integration of recently developed global atmospheric and climate variables estimates, such as ECMWF Reanalysis v5 (Hersbach et al. 2020), which provides 1-hr resolution, could be an exciting opportunity to improve the temporal resolution of model predictions. To some degree, our comparison of GFS- and NAM-derived forecasts demonstrates sensitivity to the resolution of weather forecast inputs (Figure 3). For example, in this comparison, the GFS forecast includes hotspots over Kentucky, Tennessee, and West Virginia that are much more diffuse in the NAM forecast. Nevertheless, GFS provides a base horizontal resolution of ~50 km, whereas NAM pixels are produced at 12 km. While it is difficult to identify what is driving these differences, GFS hotspots may be more diffuse in reality, but NAM fails to detect this heterogeneity. More generally, integrating predictor datasets with high temporal resolution may continue to improve nuanced information during critical time-sensitive events, such as migration initiation at sunset. In sum, although we did not provide an exhaustive exploration of different atmospheric predictor datasets, future studies that address these tradeoffs could be an exciting and valuable direction for migration forecasting. Similarly, our choice to define distant predictors at a range of 150 km was based on relatively limited information on flight distances of migratory birds (Wikelski et al. 2003). As noted above, our definition doubles the range of "remote" predictors used by Kranstauber et al. (2022), highlighting a lack of consensus in the macroscales that may influence migratory bird behavior, and exploring the effect of this range could be explicitly investigated in future forecasting efforts.

Finally, because our goal was to predict migration during the peak within the night (3 hr after local sunset), we were not able to investigate how predictor importance changes over the course of a single night. This may be particularly relevant to dynamic variables that can change rapidly throughout a given night, such as wind speed, air pressure, and the amount of anthropogenic light at night being emitted across a landscape. For instance, terrestrial predictors may rise in importance early and late in the night as migrants emerge or look to land—behaviors that are likely shaped by underlying spatial heterogeneity in resources. On the contrary, atmospheric conditions may better predict migration traffic rates of birds aloft, such as the altitudinal distribution of birds aloft. Future work that seeks to understand the relative importance of different predictors throughout a given night could have important research and applied implications. For example, high-resolution predictions of the specific hours, at which migration will peak over a given area could inform conservation actions, such as reducing anthropogenic light at night during that time window. While this framework has been suggested at the season level (Horton et al. 2021), to our knowledge it has not been explored at a temporal scale within individual nights.

Billions of birds migrate across North America every year and are facing rapid declines (Rosenberg et al. 2019). Our ability to predict when and where they move throughout their full annual cycle is central to inform conservation actions. Here, we provide an enhanced forecasting model that integrates terrestrial and atmospheric predictors at various scales to predict migratory movements of birds aloft at a high resolution. In doing so, we highlight limitations, promising paths forward, and potential data integration and conservation applications of this approach.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

No birds were handled or observed as part of this research, and the authors adhered to the American Ornithological Society code of professional conduct.

Author contributions

M.F.J., A.K., and K.G.H. conceived the project and supervised research; M.F.J., A.K., and K.G.H. designed methods; A.K. and K.G.H. processed and analyzed the data; M.F.J. led the writing; and all authors contributed to the writing and revision process.

Data availability

All data and code to reproduce this study are available at Jiminez et al. (2025).

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