Exploring the Spatiotemporal Influence of Climate on American Avian Migration with Random Forests

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Abstract

North and South American Birds have adapted to climatic and ecological patterns to inform their Spring and Fall migration timings. Temperature and precipitation patterns are shifting under anthropogenic climate change, causing downstream effects on plant flowering cycles, insect populations, and habitat availability. Understanding how these cues trigger migration could improve the effectiveness and timing of bird surveys, as well as informing habitat protection and creation efforts to lessen biodiversity loss due to climate change. Here, we employ a modeling approach to explore how climate spatiotemporally affects accuracy of predicting bird occurrence. Specifically, we train an ensemble of random forests on subsets of North and South American climate data to predict distributions of historical bird occurrence probability for passerine bird species in a North American forested region on eBird citizen science surveys from 2008-2018. We further investigate the relevance of each feature, region, and temporal lag for predicting the observed bird occurrence in a forested region in Northeast America, finding that both temperature and precipitation facilitate accurate prediction. For predicting species in October, when many passerines have begun their southward winter migration, we achieve more accurate predictions of bird occurrence using lagged, rather than current, climate features alone to predict communities in October. We also note significant higher random forest feature

importance for some lagged North American climate features than South American features. These results suggest that machine learning models may be useful for identifying spatiotemporal climatic cues that affect migratory behavior. Lastly, we explore the application and limitations of random forests for prediction of future bird occurrence using 2021-2040 climate projections.

Introduction

Across the globe, birds undertake Spring migrations to breeding grounds and Fall migrations to winter in warmer climates. In the Western Hemisphere specifically, many bird species migrate northward from their winter homes in the Southeastern USA, the Caribbean, Mexico, and Central America to breeding grounds in the Northern forests of Canada and the United States each Spring, then again southward in the Fall (1,2). Bird species rely on climatic and ecological conditions such as temperature, pressure, precipitation, and food availability to trigger the timings of their migrations (3–6) in addition to their endogenous rhythms (7–9). However, these climatic and ecological triggers are shifting with climate change. In North America, these are projected to be characterized by warming of northern breeding regions, increased rainfall during Spring migration, and less rainfall in southern regions during non-breeding season (10).

The broad effects of climate change on migrations have already been demonstrated: shifts to earlier Spring first arrival dates (2,6,7,11,12), smaller and more dispersed migratory cohorts (8), and a northward shifts in breeding grounds (13). Bird species will have to adapt behavioral patterns more quickly to these habitat and climatic changes than has been done before anthropogenic climate change began (2). However, the sensitivities to environmental and ecological cues have been genetically shaped by natural selection to correctly time behaviors such as egg laying to the availability of food, and species often over- or under-correct their

timings (5,14). Understanding the fine details of these shifts in behavior is key to conserving biodiversity through the era of climate change. For example, the optimal times and places to conduct bird surveys may shift. Additionally, understanding the climatic and ecological factors underlying changing bird migration behavior could support habitat protection and creation.

Many studies have explored relationships between migration timings and climatic features through linear-based models. For example, linking warmer Spring temperatures in the Northeastern USA to earlier arrivals (7,8), or demonstrating effects of local weather on autumn migration timing and stopovers (15,16). The literature demonstrates clearly that changes in bird migratory behavior are correlated with, and to some degree explained by, the changing climate. Still, many papers (7,8,16) show trends from post-hoc analyses and do not directly use climatic features to predict how migratory patterns may change. Machine learning methods such as random forests can leverage non-linear and complex trends in ecological data (17–19) to model historical trends and make predictions of future behavior. Random forest models are high-performing, efficient to train compared to neural networks under limited data, have built-in feature importance metrics, and have been applied in ecological settings to relate climate and ecological features to biodiversity (18,20) and animal movement and migration (19).

Here, we seek to build upon the existing literature with a predictive modeling approach for species occurrence and migration patterns. Specifically, we use a random forest multi-regression to predict eBird (21) checklist occurrences of common migrating passerine species in a large North American forested region, using monthly averages of climate features (maximum temperature, minimum temperature, and precipitation) across North, Central, and South America as feature sets. By repeating this analysis across lags in the features, we explore which regions and times are critical for predicting species Spring arrival and Fall departure dates in North American forests. Through this approach, we make use of model error and

feature importance metrics to explore which features, at which times and places, are most useful for prediction of migration. We demonstrate that random forest regressors can accurately predict passerine species occurrence, even when presented with limited training data. We also show that lagged temperature and precipitation features are as predictive, and often more predictive, of species occurrence probability than non-lagged features. Finally, we train a random forest regression model on historical data, then project future checklist occurrences using several climate models projections averaged from 2021-2040, comparing our results to the general literature consensus of earlier species Spring arrival times and later Fall departure times due to climate change. The data and Python notebooks required to run these analyses are available online (https://doi.org/10.5281/zenodo.8412210).

Methods

eBird Data

We used the eBird Basic Dataset from 2008-2018 (21) to derive the monthly occurrence rate of bird species across surveys in our study area. The dataset consists of checklists of observed species from citizen scientists, representing an “encounter rate” metric for each target species, which can be thought of as the product of that species’ detectability and occurrence probability (22). We implement several data pre-processing steps to limit spatiotemporal variability in species detectability to create an “apparent distribution” (22) of encounter rate that resembles actual occurrence probability as much as possible: we restrict surveys to forested areas, only consider the most common migrating passerine species, and drop high-effort surveys. To account for increases in eBird usage throughout the study period, we also subsample surveys (23) annually.

Checklists were first filtered to our study area, the Level 2 Ecoregion “Atlantic Highlands” within the Level 1 “Northern Forests” Ecoregion (Fig 1) (24). These Environmental Protection Agency (EPA) Ecoregions seek to aggregate areas of similar plant and animal species, as well as abiotic characteristics such as water availability (25). The “Northern Forests” ecoregion is characterized by extensive boreal forests and lakes (26), as well as extensive coverage by eBird surveys. This spatial aggregation allowed us to limit the number of climate predictor variables in our random forest models and thus more easily study the temporal effects of regional climate on migration.

Checklists were further processed according to methods recommended by Johnston shown to improve the performance of species occupancy and detection models when using eBird data, especially in models with large survey sample sizes (22). Specifically, we included only ‘complete’ checklists, removing any surveys where an unknown species was observed, and thus retaining information on species absence. Surveys with very high effort, specifically those lasting over three hours and traveling more than 5 km, as well as area counts, were excluded to retain spatial information of observations. Group surveys, which contain redundant checklists, were condensed to a single checklist.

We next limited the species of interest to the 50 most common passerine species, as such birds in general have a lower body mass and higher cold sensitivity, which can induce migratory behaviors (27). Of these species, we filtered down to 41 species (mean observations: 3,571, std: 2,044) (Table S1) which are either short-distance or long-distance migrants rather than resident species, based on distribution maps from Birds of the World (28) and expert opinion. To further refine our analysis to only forested regions, we filtered out all checklists with less than 50% surrounding tree cover based on 100m resolution tree cover density data (29). From 2008 until 2018, the number of annual surveys in eBird has greatly increased. To avoid bias in

inferred species richness in later years which have a greater number of surveys, we randomly subsampled 1601 surveys at the annual scale, the number of surveys in 2008 after filtering for forest cover and survey type (Fig S1). We then calculated the percentage of surveys on which each species appears on a monthly scale to create our target features.

Climate Data

To study historical patterns in migration and climate, we utilized WorldClim monthly historical raster data (30) downscaled with WorldClim 2.1 (31) for monthly minimum temperature, maximum temperature, and precipitation at 2.5 minute spatial resolution across North and South America. The raster data were averaged into EPA Level 1 Ecoregions for North and South America (Fig 1A) that fall within typical migration pathways for birds that spend their breeding season in the eBird study region. Features were then individually normalized by setting a mean of 0 and scaling features to unit variance. Each of the three feature sets (maximum temperature, minimum temperature, and precipitation) had a total of 15 features per month, from eight North American Ecoregions and seven South American Ecoregions. One feature set containing all three climate features was also created, with 45 features in total.

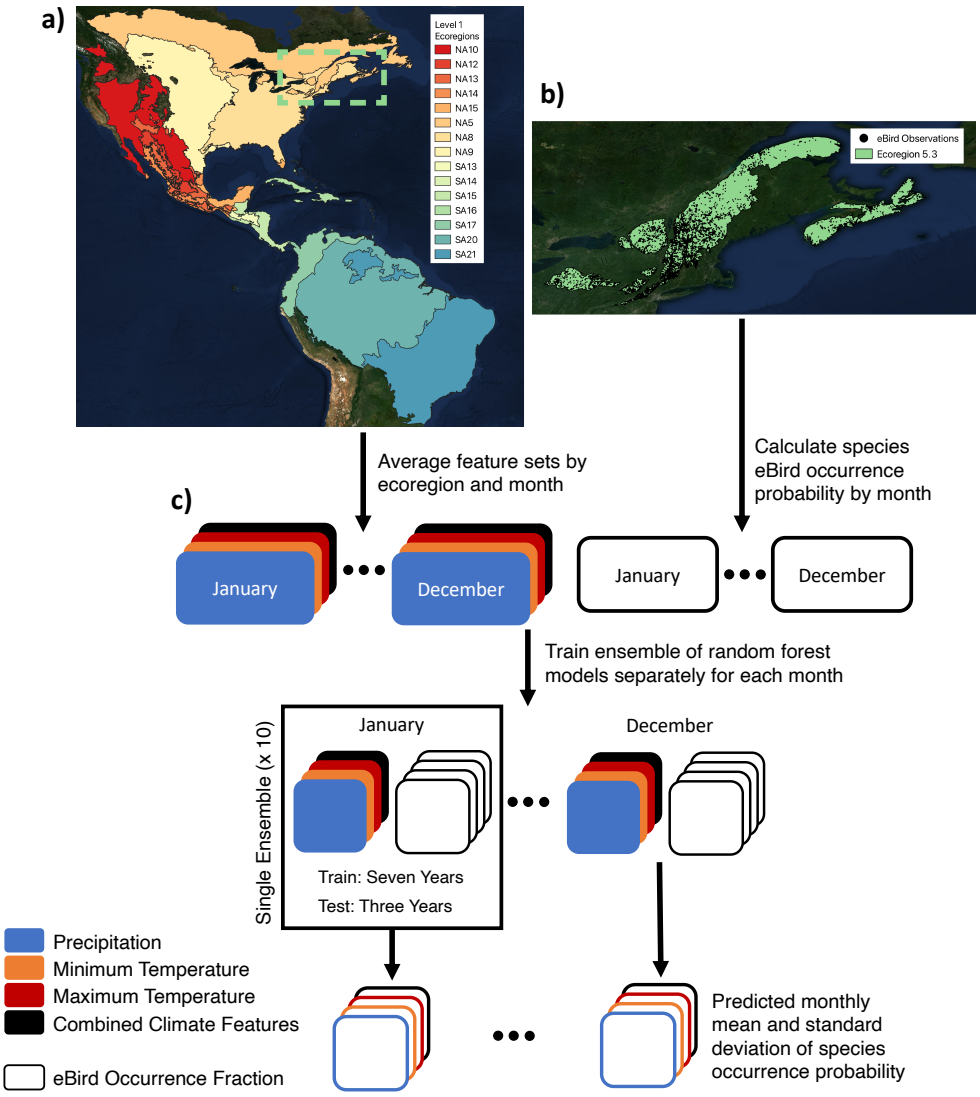

Figure 1: Map of targeted EPA Ecoregions and eBird survey locations. a) North and South American Level 1 Ecoregions for averaging of climate variables. b) The eBird study region Ecoregion 5.3, a subset of Level 1 Ecoregion 5 (NA5), outlined in light green with individual eBird survey coordinates in black. c) Data flow through random forest model ensembles. Monthly climate features are aggregated to the Level 1 Ecoregion spatial scale and monthly eBird species occurrence fractions across checklists are calculated for the Ecoregion 5.3 study region. An ensemble of ten models is trained and tested for each month and climate feature combination to predict checklist occurrence fractions, and the results of the ensemble are then averaged.

Similarly, to generate projected climate features, we utilized WorldClim monthly projected data from the Coupled Model Intercomparison Project Phase 6 (CMIP6) (31), aggregated and

averaged to the same EPA Level 1 Ecoregions. The CMIP6 framework forms the standard for international climate assessments, such as those from the Intergovernmental Panel on Climate Change (32) and includes an ensemble of climate models from various research groups that rely on common historical training data. For each CMIP6 model, we also tested several radiative forcing pathways, dubbed the Shared Socioeconomic Pathways (SSP) (33), which compared the effects of various greenhouse gas emissions scenarios. Due to our use of a standard random forest regressor, which averages across previously seen training samples to make predictions and cannot extrapolate, our projections of species occurrence fall within the bounds of observed species occurrences on eBird checklists from 2008-2018. Still, in order to avoid projecting species occurrence rates in radically different climatic conditions, we limited our study to the 2021-2040 averaged WorldClim datasets. This consists of the mean projected monthly minimum temperature, maximum temperature, and precipitation from 2021 to 2040. We used four CMIP6 models available from WorldClim which performed best on tests comparing probability distributions of projections to historical observations and the regularity of climate fluctuations (34).

Analysis of Historical Avian Migration

We trained Random Forest regressors on the historical climate features to predict the eBird checklist target features (Fig 1C). Twelve ensembles of models were trained in total, one for prediction of eBird checklist occurrences in each month of the year. This separate training of models for each month of the year and lag on the climate feature dataset enabled us to study seasonal patterns in the error rates and feature importance. Each ensemble of models consists of ten 1000-tree Random Forest models trained with varying 30:70 test-train splits across the ten years of data being studied (2009-2018). For example, the first model was trained on 2009, 2010, and 2011 data, and tested on 2012-2018 data, the second model was trained on 2010,

2011, and 2012 data, and tested on 2013-2018 and 2009 data, and so forth. Each model is trained on 7 years x 15 aggregated climate features, or 7 x 45 when using all temperature and precipitation features. This process was then repeated while lagging the climate features from one to six months. For example, the climate features from March were used to train models to predict the checklist occurrences in April, and so forth.

From each group of ten models (an ensemble), we recorded the mean and variance of the test set predictions and mean absolute errors for all species. We also extracted random forest feature importance for each climate feature and Ecoregion. The features ranking highest in importance were those which best split the distribution of target features across all nodes in the decision trees. For a regression problem such as predicting checklist occurrences, this decrease in impurity is related to the reduction of variance that each feature provides when splitting training set samples. These forest importance metrics are relative, and sum to one (35). As these ensembles of models generate distributions of error and feature importance, we were able to compare their performances in Kolmogorov-Smirnov tests. These statistical tests can evaluate whether one distribution is significantly greater or less than another, allowing us to test whether certain features facilitate better model performance based on their errors, or if certain groups of features have higher importance.

Projections of Avian Migration Shifts

We trained scikit-learn random forest multi-regression models (each with 1,000 trees) on the combined data set of 45 climate features aggregated to the Ecoregion scale (minimum temperature, maximum temperature, and precipitation) to predict the target eBird data from 2009-2015. Validation was performed on 2016-2018 data (Fig S4). We then used this model to project on the 2021-2040 monthly average climate projections from the four CMIP6 models (EC-

Earth3-Veg, INM-CM4-8, MPI-ESM1-2-HR, and GISS-E2-1-H.) and four SSP projections (SSP 1, 2, 3, and 5). As with the historical ensemble of models, a separate model was trained to predict each month of the year. Projected species-wise shifts in monthly occurrence probability were calculated by subtracting the mean monthly eBird checklist occurrences (2009-2018) from the mean projected occurrences for each of the four CMIP6 models and four projections.

Results

We found accurate per-species predictions of eBird checklists for the 41 passerines studied (Fig 2A) were made with monthly mean climate data (Fig 2D) as well as with lagged climate data up to 6 months (Fig 2F). Average monthly errors in predictions were generally low across all months and across climate features, ranging from 1.7 to 3.8 percent error in eBird checklist occurrence fraction averaged across all species (Fig 3, Fig S2), with higher errors in the Spring and Summer months when species richness was also higher. We noted a trend in the mean annual error across species where the model tended to under-predict species occurrence fraction in earlier years and over-predict species occurrence fraction in later years (Fig 3A-D). This pattern in error followed a trend in the underlying eBird data; on average, each species in the study occurred on 2.6% fewer eBird checklists from 2009 to 2018 (Fig 2C), a trend apparent for most species (Fig 2 E, G).

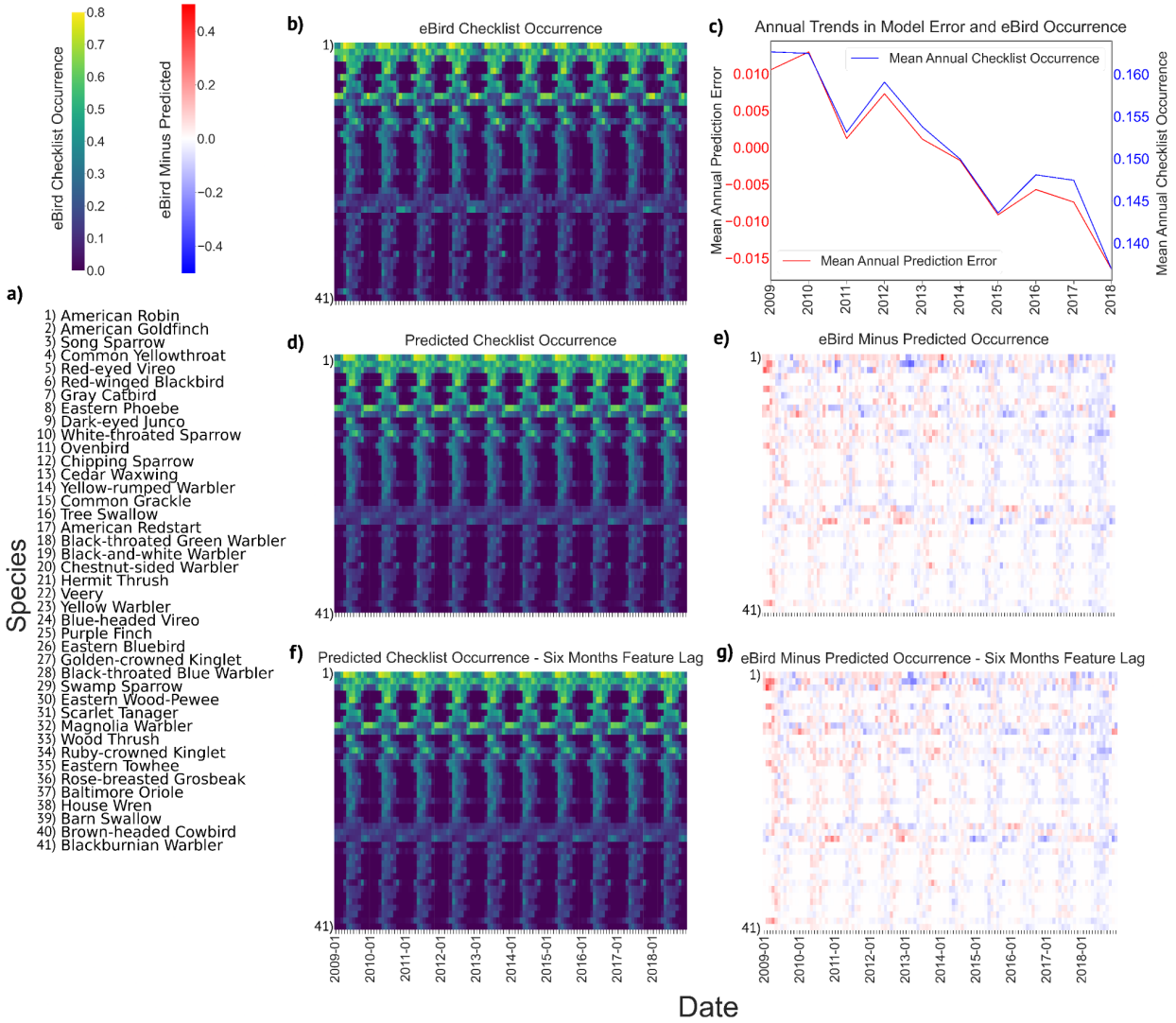

Figure 2: Aggregated climate data supports accurate predictions of eBird species checklist occurrences - a) List of 41 common migrating passerine bird species observed in forested areas of the study region, representing the y-axis of the following heatmaps. b) Actual eBird checklist occurrence fractions for all species. c) Mean annual eBird checklist occurrence across all species (blue) and the mean annual error in occurrence fraction predictions (red) across all species. d) The Random Forest-predicted eBird checklist occurrence fractions for all species utilizing all available climate variables (minimum temperature, maximum temperature, and precipitation), e) eBird checklists minus the predicted checklists using current climate feature sets, showing over-predictions in blue and under-predictions in red, f) predicted eBird checklist occurrences utilizing all climate variables lagged by six months, and g) eBird checklists minus the predicted checklists using six month lagged climate variables.

Figure 3 illustrates the accuracy of the random forest ensembles for prediction of species occurrence fractions, but also how the temporal trends in the underlying eBird features impacted

model performance. The model increasingly tended to overpredict individual species checklist occurrence towards later years in the analysis (Fig 3 C, D). Following this, the derived species richness was also increasingly over-predicted (Fig 3 A, B). Figure 3E and 3F focus on April and October specifically, as these months are transitory periods between breeding and winter seasons (Fig 2B) when migratory species are arriving and departing our study area. We noted higher volatility and no apparent trend in model error for April (Fig 3E). In October, however, the lowest error occurred when climate feature sets were lagged by one to three months (Fig 3F).

We performed Kolmogorov-Smirnov tests on the distributions of errors across the model ensembles to determine whether the lower error of these lagged datasets was significant. After correcting for multiple hypotheses, we found that lagging climate features for two and three months produced significant reductions in model MAE for predicting eBird checklist occurrences in October ($p=0.00981$) (Table S2). No such significant changes in error were found for lagged datasets in April. We applied Kolmogorov-Smirnov tests between distributions of random forest feature importance of the North and South American ecoregions (Fig S5) to determine if the model was identifying relevant regional features. For predicting checklist occurrences in October in our northeastern study region, we found that North American climate features were significantly more important only at a lag of 3 ($p < 0.001$) (Table S2). No significant effects were seen for importance in predicting April occurrences.

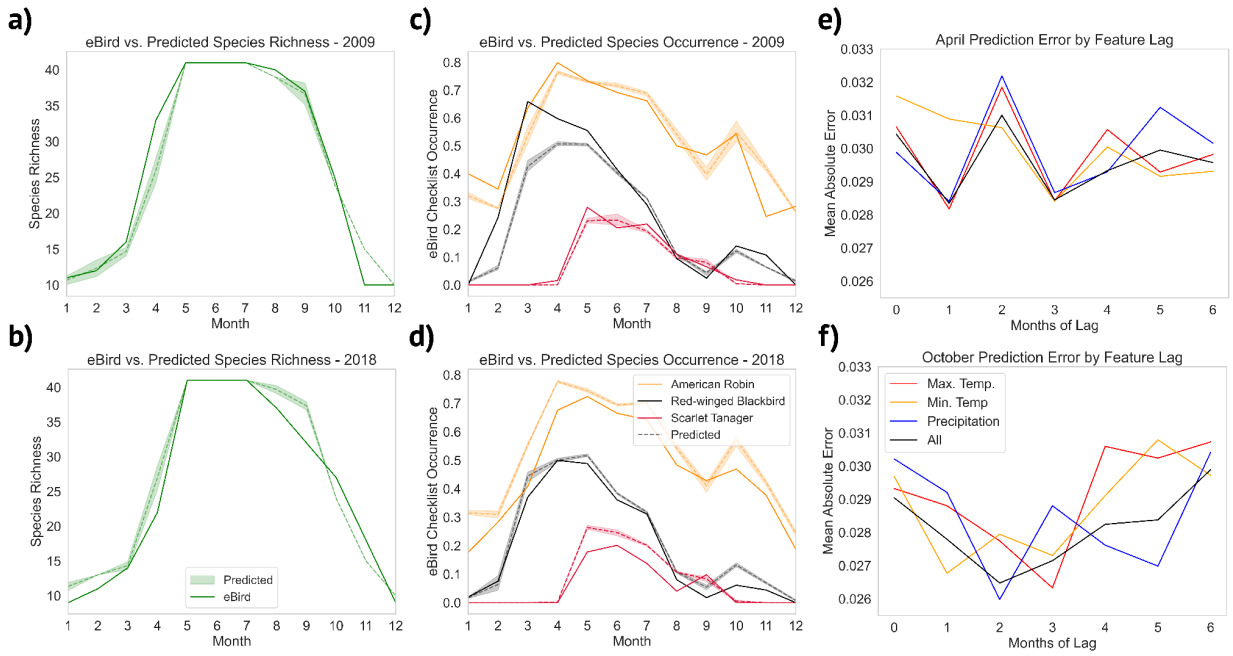

Figure 3: Model predictions across years reveal underlying shifts in eBird species occurrence and strength of lagged climate data for predictions. a) 2009 and b) 2018 eBird species richness versus mean and standard deviation of predicted species richness across the model ensemble. Species richness shown includes all species appearing on more than two percent of actual and predicted eBird checklists. c) 2009 and d) 2018 eBird ground truth versus predicted checklist occurrence fraction, showing mean and standard deviation of predictions across the model ensemble. e) Average random forest mean absolute test set errors by month of feature lag for April and f) October across all species and climate features.

By training on the 2008-2018 eBird checklists with all climate features and testing on CMIP6 climate projections (making broad assumptions of no change in habitat or species abundance), we projected higher positive shifts in checklist occurrence probability for April through August (ranging from 0.36% to 0.75%), with less change projected for Fall months (ranging from 0.011 to 0.19%) (Fig 4A). We found an increase in species occurrence probability across models projected for 25 of 41 species in April (mean: 0.80%), 15 species having a projected decrease (mean: -0.36%), and one species with no change (Fig 4B). Results were more mixed for October, with projected occurrence probability increases for 20 of 41 species (mean: 0.67%), decreases for 19 (mean: -0.46%), and no change for two species (Fig 4C). In contrast to the variation within eBird training data, the variance of occurrence probability for all species was

effectively zero across all four CMIP6 models and four SSP projections tested, indicating that the random forest model consistently reached the bounds of known distributions of checklist occurrences across the available climate training data.

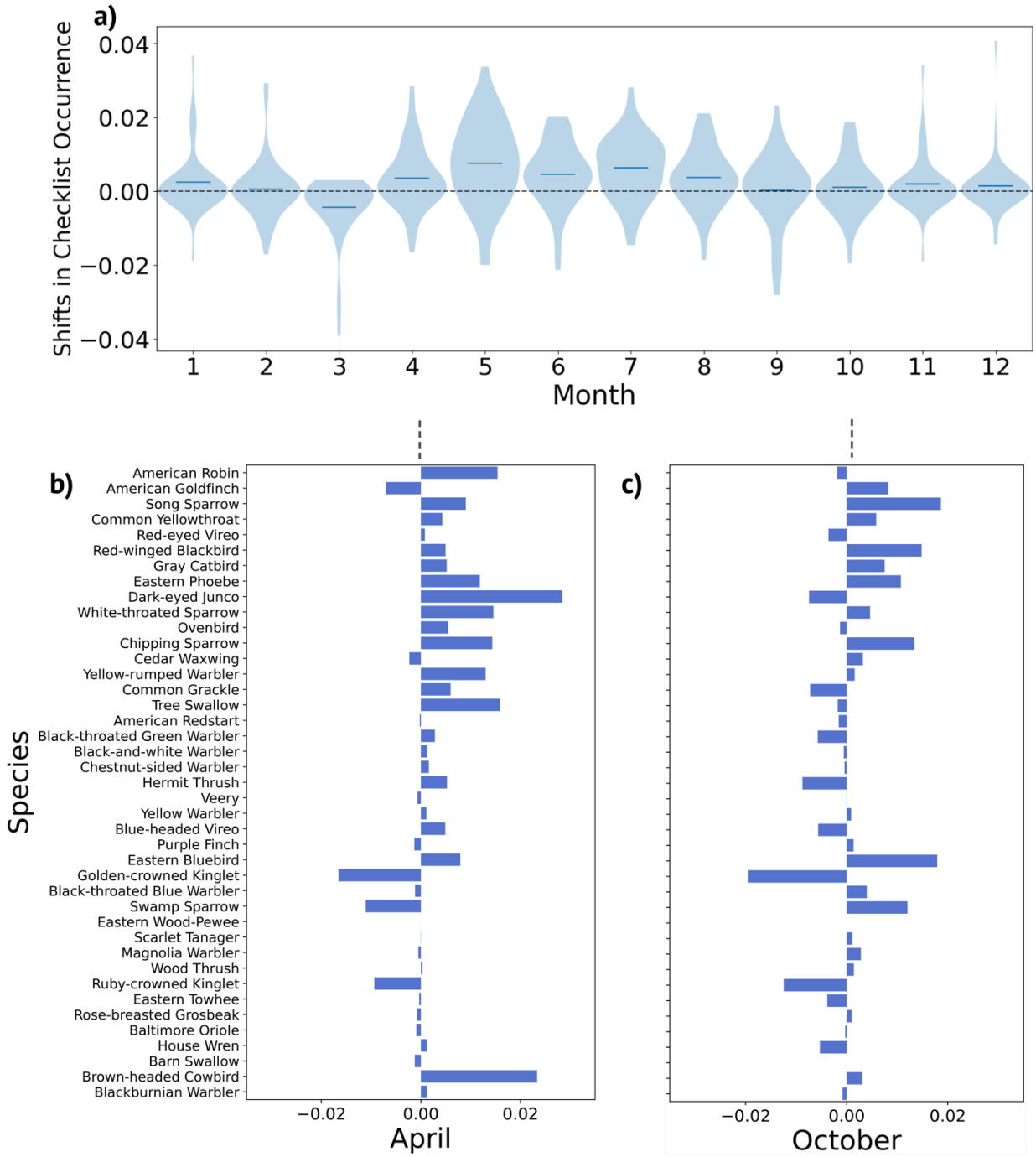

Figure 4: Projections of eBird checklist occurrences from 2021-2040 show earlier Spring occurrence probability for passerine species - a) Violin plot showing mean projected shifts of occurrence probability for 41 passerine species in 2021-2040 compared to historical eBird monthly means from 2008-2018 in Ecoregion 5.3 b) April and c) October per-species difference between mean historical eBird occurrence probability and mean 2021-2040 projected occurrence probability.

Discussion

In this section, we begin by highlighting the effectiveness of aggregated climate features from both North and South America in accurately predicting eBird checklist occurrence probability for 41 passerine species in our North American forest study region, as well as species richness (depicted in Fig 2B and Fig 3 A, B). Importantly, the accuracy of our predictions remained consistent regardless of the specific climate variable chosen as a training feature (as illustrated in Fig 3E, 3F, and Fig S2). Additionally, combining multiple climate features resulted in reduced variability in prediction error (as indicated in Fig 3E, F). Furthermore, we observed that the trend in mean annual model error closely mirrored the trend in mean annual checklist occurrence over time across all species (as shown in Fig 2C). This alignment in error trends might be attributed to underlying patterns of decreasing biodiversity and total bird counts observed during our study period, a phenomenon that has also been documented in previous studies (36,37). It's worth noting that potential errors could also arise from systematic shifts in the accuracy of the underlying eBird data. However, we attempted to mitigate this risk by using randomly selected complete checklists, as recommended by Johnston et al. (2021).

During October, a period when species are actively migrating southward from our study region (as depicted in Fig 3A), we observed a notable reduction in prediction error when climate features were lagged by two or three months, in comparison to using current climate features (as illustrated in Fig 3B, Table S2). The results suggest that our model ensembles may be effectively capturing delayed temporal patterns in climate that influence migratory departure.

Furthermore, in October, the random forest analysis highlighted that North American climate features were significantly more influential than South American features at a lag of three months, indicating that the model may be discerning spatial climate cues contributing to migratory behavior. Conversely, in April, when birds are arriving in our Northern study area from their Southern wintering grounds (as shown in Fig 2B), the model did not identify any statistically significant temporal or spatial differences in prediction error or feature importance.

These findings align with existing research that highlights the influence of time lagged effects of climate on migration triggers (14,38). Our projections of bird species from 2021-2040 were not designed to model future changes in biodiversity and population abundance. Instead, they serve the purpose of exploring how bird species might respond if sudden shifts in climatic conditions were to occur in the near future, such as within the next year. Essentially, we aimed to uncover insights from historical climate and bird migration patterns that could shed light on potential future trends. Furthermore, it's important to note that our approach utilizes a random forest model architecture. As a result, our projections of future species occurrence probability remain constrained within the bounds of the historical training data, rendering them inherently conservative. These projections do not account for factors like changes in land-use and development (10), alterations in the timing of resource availability related to insects and flowering plants (14,38–41), or shifts in inter-species competition (42), all of which affect bird populations and distributions. These aspects are known to exert significant influences on bird populations and distributions.

Despite these limitations, we were still able to discern potential future trends in the timing of bird arrivals and departures, consistent with existing literature and empirical research. Notably, our findings indicate an increased occurrence of species arriving in North American forests during the spring (as depicted in Fig 4B). However, the trends for autumn months were more varied (as shown in Fig 4C), aligning with previous studies (12,16). Several aspects of our results suggest

a higher sensitivity to climate and greater volatility in the Spring migration than the Fall migration. This includes the higher test set error observed in April compared to October (Fig 3 E, F) and the more pronounced and extensive shifts in projected future species occurrences in April and May than in Fall months (as displayed in Fig 4 A-C). It is important to note that test set error for the climate projection model exceeded the training set error (covering the period from 2008 to 2015) and displayed an upward trend from 2016 to 2018 (as presented in Figs S6, 7). This trend culminated in a monthly maximum mean absolute error of 5.3% for August 2018.

The monthly scale of data resolution and the resulting small dataset size in this analysis constrained our ability to employ more deep learning techniques, like recurrent neural networks, which potentially could capture nuanced temporal influences of climate on migration. Nonetheless, the utilization of random forests decision trees offered several advantages, including built-in feature importance methods and the ability to confine future predictions within the bounds of the training dataset. This contrasts with simpler models such as multiple linear regression, which might produce projections outside the historical range.

For future research, there are several avenues to explore for enhancing our understanding of bird migration in relation to climate. One promising direction involves improving the temporal and spatial resolution of the climate datasets, which could enable machine learning models to provide a more comprehensive view of climate influence on migration patterns. Additionally, focusing on factors related to population abundance might yield valuable insights, particularly considering observed decreases in bird populations. Furthermore, incorporating other climate features that are known to affect migrations such as wind speed and direction (as highlighted by (16)) could contribute to a more comprehensive model. Finally, the inclusion of indices derived from satellite data such as normalized difference vegetation and water indices, which are

associated with food availability and drought conditions (as mentioned by (18,43)), could provide a more holistic understanding of the ecological factors impacting bird migrations.

Conclusions

In this study, we present a modeling approach to identify spatiotemporal climate features that influence bird migratory behavior. Our results demonstrate that random forest models trained on these features accurately predicted eBird checklist occurrence probability throughout the year in a northern forested region. Our findings indicate that lagged feature sets were more effective in predicting passerine species occurrence probability in October compared to current climate conditions. The models also assigned greater spatiotemporal importance to North American features over South American features in October, coinciding with the southward migration of species to their wintering sites.

Furthermore, we explored potential future trends in migratory behavior using mean climate projections from CMIP6 for the period 2021-2040. Our results suggest an increased occurrence probability in Spring and Summer months, but a reduced effect in the Fall and Winter. These findings align with existing studies, supporting the hypothesis of a shifting of migratory timings with climate change, characterized by earlier spring arrivals and later autumn departures. Our pilot tests demonstrate that thorough investigation into model performance and feature importance within machine learning models can contribute to our understanding of complex ecological processes.

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Author Contributions

IAB led manuscript writing and methodology design and ran the analyses. VB, MP, KR, and SS advised on methodology design and research questions and made significant contributions to the manuscript. All authors reviewed and approved the manuscript.

Conflicts of Interest

The authors have no conflicts of interest to declare.

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