Potential breeding distributions of U.S. birds predicted with both short-term variability and long-term average climate data

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Abstract. Climate conditions, such as temperature or precipitation, averaged over several decades strongly affect species distributions, as evidenced by experimental results and a plethora of models demonstrating statistical relations between species occurrences and long-term climate averages. However, long-term averages can conceal climate changes that have occurred in recent decades and may not capture actual species occurrence well because the distributions of species, especially at the edges of their range, are typically dynamic and may respond strongly to short-term climate variability. Our goal here was to test whether bird occurrence models can be predicted by either covariates based on short-term climate variability or on long-term climate averages. We parameterized species distribution models (SDMs) based on either short-term variability or long-term average climate covariates for 320 bird species in the conterminous USA and tested whether any life-history trait-based guilds were particularly sensitive to short-term conditions. Models including short-term climate variability performed well based on their cross-validated area-under-the-curve AUC score (0.85), as did models based on long-term climate averages (0.84). Similarly, both models performed well compared to independent presence/absence data from the North American Breeding Bird Survey (independent AUC of 0.89 and 0.90, respectively). However, models based on short-term variability covariates more accurately classified true absences for most species (73% of true absences classified within the lowest quarter of environmental suitability vs. 68%). In addition, they have the advantage that they can reveal the dynamic relationship between species and their environment because they capture the spatial fluctuations of species potential breeding distributions. With this information, we can identify which species and guilds are sensitive to climate variability, identify sites of high conservation value where climate variability is low, and assess how species' potential distributions may have already shifted due to recent climate change. However, long-term climate averages require less data and processing time and may be more readily available for some areas of interest. Where data on short-term climate variability are not available, long-term climate information is a sufficient predictor of species distributions in many cases. However, short-term climate variability data may provide information not captured with long-term climate data for use in SDMs.

Key words: climate change; guilds; Maxent; North American breeding birds; species distribution model; species range.

Introduction

With temperatures rising and precipitation patterns changing globally, questions about how biodiversity will be affected by climate change are becoming ever more urgent. Addressing this conservation challenge requires accurate predictions about the spatial and temporal dynamics of species distributions. Such predictions are typically based on models that capture the relationships between species observations and measures of their environment, which are then projected onto scenarios of future climate conditions to assess potential changes in distributions (e.g., Peterson et al. 2002, Thuiller 2003, Thomas et al. 2004) and abundances (e.g., VanDerWal et al. 2009, Tôrres et al. 2012). Predominantly, these
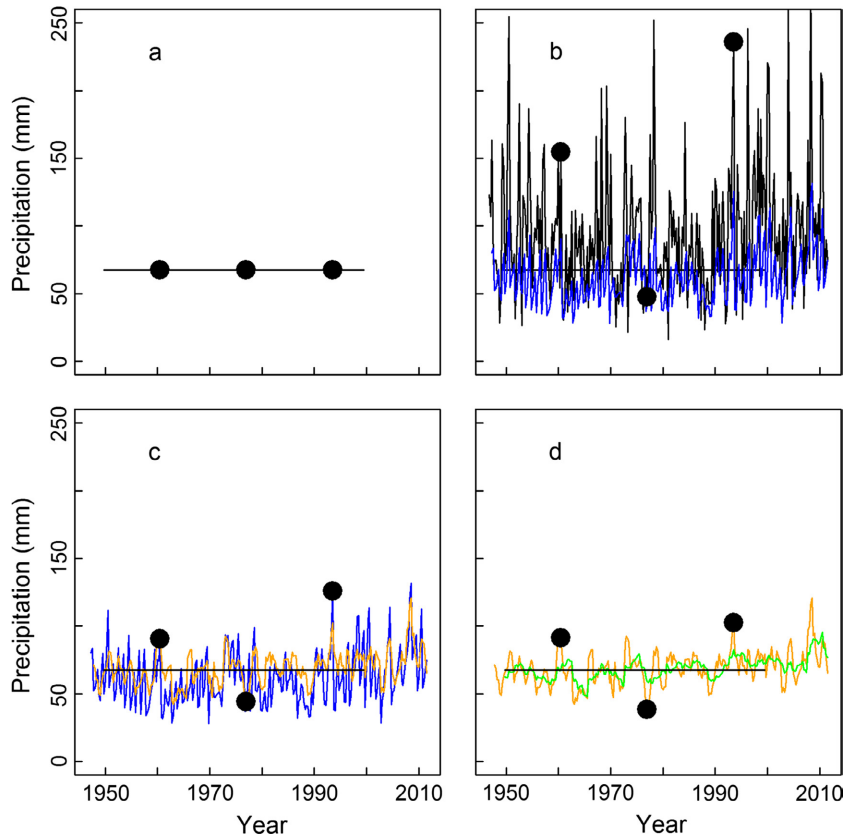
Fig. 1.   Hypothetical species occurrence records (black dots) and actual precipitation from 1950 to 2011 for (a) the long-term climate average (50-yr average; black line), (b) monthly accumulated weather (black line) and intra-annual climate variability (averaged over the preceding six months; blue line), (c) intra-annual climate variability (blue line) and inter-annual climate variability (averaged over the preceding 12 months; orange line), and (d) inter-annual climate variability for 12-month (orange line) and 3-yr (averaged over the preceding 36 months; green line) time lags. Climate variability experienced at each location varies through time, whereas the long-term average (represented in all plots by black line) remains static; the intra- and interannual climate measures reflect the inherent variability of the data, at different temporal scales.

species distribution models (SDMs) represent the environment based on long-term climate averages, such as 30- or 60-yr averages of temperature and precipitation, often summarized seasonally (Pearson and Dawson 2003, Elith and Leathwick 2009). Although rough measures of climate variability, such as standard deviation or coefficient of variation, are sometimes included (see Beaumont et al. 2005), these measures of long-term climate data represent a muted version of the actual variability experienced by species over shorter time scales. As a consequence, long-term climate characterizations may conceal important aspects of how climate affects species. Indeed, both species occurrences and their persistence may depend more on shorter-term climate variability and extreme weather events than on long-term climate averages (Gutschick and BassiriRad 2003, Thompson et al. 2013).

Ultimately, both long-term averages and short-term climate variability may affect the distribution and population dynamics of species (Parmesan et al. 2000, Jentsch et al. 2007, Jentsch and Beierkuhnlein 2008). The abundance, richness, and composition of bird communities changes predictably in response to climate anomalies and short-term variability in regional climate patterns (Albright et al. 2010a, b, 2011). Similarly, fluctuations in bird breeding success (Guthery et al. 2001, Nott et al. 2002, Skagen and Adams 2012), population size and growth rate (Cormont et al. 2011), and reproduction and survival (Becker et al. 1997, Christman 2002, McKechnie and Wolf 2010) are affected by short-term climate events. Indeed, in their lifetime organisms experience weather patterns, i.e., changes over days or weeks, seasonality (predictable changes in averages related to seasons), short-term climate variability, i.e., variability over the course of a few months or years, and long-term climate averages (Fig. 1a, b). Incorporating intra- and interannual climate measures in models is a way to incorporate this variability that would be lost if one were to focus only on long-term averages (Fig. 1). Indeed, some studies have shown that shorter-term annually resolved data characterizing climate variability can predict species distributions well (Zimmermann et al. 2009, Reside et al.

2010, Bateman et al. 2012b, VanDerWal et al. 2013, Fancourt et al. 2015). However, the general performance of predictions based on short-term climate variability relative to long-term averages is not known.

Our goal here was to examine the role of short-term climate variability over months and years and long-term climate averages in predicting bird species distributions in the conterminous USA. We expected the value of long-term climate vs. shorter-term climatic variability to depend on life-history traits of birds. Therefore, our first objective was to explore the sensitivity of distributions of birds with different life-history traits to short-term climate variability. More generally, our objective was to compare the power of the two sets of climate data for explaining avian potential breeding distribution patterns, and we expected that short-term climate variability would provide important insights into biological patterns for bird species that are missed when using long-term climate averages (e.g., 30–60 yr averages).

METHODS

Bird occurrence data

We obtained a total of 21,500,000 bird occurrences for 432 landbird and waterbird species recorded within the conterminous USA from 1950 to 2011 from the Global Biodiversity Information Facility (GBIF; *available online*).[11] GBIF is a free, open-access database that provides species occurrence data from a variety of sources (e.g., citizen science databases, museum collections, survey and monitoring programs, etc.; Beck et al. 2013; please see full list of bird data sources for our study in Appendix S1). From the GBIF bird occurrence data, we excluded species with insufficient data (i.e., fewer than 30 records), records for which no date was reported, and records we suspected of being inaccurate (we checked for spatial errors). Because our climate data are restricted to the conterminous USA, and because we wanted to compare models among species groups, we eliminated species whose breeding range is either exclusively or primarily north or south of the conterminous U.S. border and species nesting off-shore. We restricted our analysis to bird records from the breeding season (April–July), for a total of 7,228,996 unique occurrences of 320 species (Appendix S1: Data S1). We used this data set for both the analysis of short-term climate variability and long-term climate averages so that both analyses had the same presence and background data.

In addition, we obtained bird data for 1967–2011 from the North American Breeding Bird Survey from the USGS North American Breeding Bird Survey website (BBS; *available online*; Pardieck et al. 2015).[12] Sufficient BBS abundance data were available for 281 of the bird species that we modeled. The BBS, an annual bird survey initiated in 1966, is conducted on ~39.4 km routes throughout the USA during the breeding season (Bystrack 1981). The BBS provides bird count data that are not included in GBIF and as such an ideal independent data set to test our model performance. We resampled the route-level BBS abundance data into presence and absence data across all BBS routes in the conterminous USA. For mapping purposes, we also obtained the BBS summer distribution maps of relative abundance estimated over the period 2008–2012 and resampled these into breeding ranges. We downloaded the relative abundance maps for each species as shapefiles from the USGS website (*available online*; Sauer et al. 2012).[13]

Climate data

We obtained monthly climate data summaries including temperature maxima and minima and total precipitation from 1947 to 2011, at 4-km resolution for the conterminous USA, from PRISM Climate Group (*data available online*).[14] We aggregated these monthly climate data into eight annual variables that included mean annual temperature (°C), temperature seasonality (standard deviation × 100), maximum temperature of the warmest month (°C), minimum temperature of the coldest month (°C), annual precipitation (mm), precipitation of the wettest quarter (mm), precipitation of the driest quarter (mm), and precipitation seasonality (coefficient of variation, CV). These eight variables mimic a subset of those offered by BIOCLIM, a subset that has been used successfully in other SDM modeling efforts and has been found to provide maximum climate information while avoiding strongly collinear variables (see Bateman et al. 2012a, c; *data available online*).[15] Annual estimates of these variables were used to derive ~60-yr (1950–2010) averages, and these long-term means served as the eight covariates in the climate average models. Bird locations from GBIF were associated with the eight long-term average covariates based on the PRISM cell where the location record occurred. Multiple resightings of a particular species at the same location over time were associated with an invariant set of the long-term mean climate covariates.

To compare the performance of models based on long-term climate averages with those based on short-term climate variability, we summarized PRISM climate data for three different blocks of time preceding each month. This allowed us to capture intra- (six and 12 month) and interannual (36 month) climate variability, along with time lag effects (as in VanDerWal et al. 2013). For the 12 and 36 months preceding each month from 1950 to 2011 (note, 1947 data are needed to estimate the preceding 36-month covariates for 1950), we calculated all eight climate covariates as defined for the climate average

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[11] http://www.gbif.org/
[12] https://www.pwrc.usgs.gov/bbs/RawData/

[13] http://www.mbr-pwrc.usgs.gov/bbs/shape_ra12.html
[14] http://prism.oregonstate.edu
[15] http://www.worldclim.org/bioclim

modeling. For the six months preceding, we only calculated six covariates, excluding precipitation of the wettest and driest quarter because they are not meaningful half-year data. The six covariates for the six months preceding data were summarized as 6-month trends rather than annual. This yielded a total of 22 short-term climate variability covariates. Bird location records were associated with short-term climate covariates based on when the sighting date fell with respect to the prior 6-, 12-, and 36-month time periods. Therefore, short-term climate variability modeling allowed each unique bird sighting date to be assigned its own short-term climatic conditions.

Modeling

We used maximum entropy modeling (Maxent; Phillips et al. 2006) to predict the distributions of bird species using both short-term and long-term climate covariates. We used Maxent because its' presence-background modeling framework is well suited to data from the GBIF which includes presence records only (Phillips et al. 2006), and Maxent performs well and consistently (Elith et al. 2006, Hijmans and Graham 2006, Elith and Graham 2009). Consistency in performance was essential to our efforts as we were interested in comparing model performance across many species using two fundamentally different sets of covariates (short-term climate variability and long-term climate averages). We did not want the comparison to be confounded by variation in performance that has characterized other modeling approaches (Elith et al. 2006). We used a target-group background (Phillips and Dudik 2008) to estimate Maxent models, where the locations and dates of all birds were the background to account for spatial bias in the sampling of occurrence records of a given species on the assumption that any bias would also be observed in the background points (Phillips and Dudik 2008, Reside et al. 2010). To run Maxent with a target-group background, we used SWD (i.e., samples with data) format, and in doing so, retained duplicate records per grid cell. We parameterized Maxent with default settings (Phillips and Dudik 2008) but removed threshold and hinge features to ensure more ecologically realistic response curves (Bateman et al. 2012c).

We built distribution models using short-term variability and long-term average covariates in turn. We fit the short-term variability model including both intra- and inter-annual climate variability measures (three time-lags; eight variables for 12- and 36-month periods, and six variables for the 6-month periods; total of 22 covariates). In addition, we generated separate short-term variability models using a single time-lag with the 36-month covariates only (model specified with a total of eight covariates). We included the single time-lag model to check whether the larger number of covariates in the initial short-term variability model, which included all three time-lags (22 covariates), affected model performance,

because AUC (area-under-the-curve) can potentially be influenced by the number of covariates and possible overfitting. We built the long-term average model with all eight long-term average covariates included for each species, based on common precedents (Pearson et al. 2002, Thuiller 2004, Warren et al. 2013).

Model evaluation

We evaluated model predictive performance based on 10-fold cross validation (Elith et al. 2011, Bateman et al. 2012c) and considered models above 0.5 as better than random (Raes and ter Steege 2007). Although we could have attempted to conduct this evaluation based on spatially distinct data sets (see Warton et al. 2013) to provide an indication of how well bias had been addressed, the implementation on spatially distinct data sets for 320 species was infeasible due to computational challenges. Therefore, for the purposes of this study, we assumed that any bias in our estimation of AUC based on simple 10-fold cross validation was randomly distributed and our fundamental performance comparison (between the climate covariate data sets) was tenable. To directly compare results across the different models for individual species, we assessed model improvement by assessing difference in AUC scores between short-term variability and long-term average model outputs (as per Reside et al. 2010) using Wilcoxon signed-rank test for related samples (calculated in R, version 2.15.1; R Core Team 2012) and 0.05 as our significance level (Reside et al. 2010).

We conducted model evaluation for all bird species as a whole and for guilds grouped according to broad habitat affinity or life-history traits during the breeding season. Our guilds were based on major habitat type (landbird or waterbird), dietary preference during the breeding season (carnivore, herbivore, invertivore, with landbird and waterbird assessed separately, and omnivore), and foraging habit (aerial, ground, water, bark, upper-canopy, lower-canopy, and floral hover; adapted from De Graaf et al. 1985, Poole 2005: see Appendix S1: Data S1 for groupings). We also analyzed birds by migratory habit (Neotropical, short-distance, permanent resident, and varied [those with elements of more than one migratory habit] adapted from Poole 2005, Albright et al. 2010b). To assess whether there was a significant difference in the predictive power of short-term variability and long-term average models among guilds, we used Kruskal–Wallis nonparametric ANOVA on AUC scores (Reside et al. 2010) calculated in R.

We mapped suitability in geographic space for each species based on both long-term average and short-term variability models. For the short-term variability model, we made projections based on monthly climate data from 1950 to 2011, in order to generate dynamic maps highlighting the spatial distribution of suitable climate through time. We accomplished this by generating monthly sets of all predictor variables, so that each

month/year date combination had a full set of predictors for the 6-, 12-, and 36-month time periods. In addition, we calculated an overall estimate of climate suitability as the average of all monthly climate suitability maps in each grid cell of the potential breeding distribution over the study period. We present dynamic and overall climate suitability maps for three selected species and an animated representation of dynamic climate suitability maps over the entire time period for one species. For the long-term average model, we projected onto the ~60-yr (1950–2010) climate average data.

To visualize how projected distributions match observed breeding ranges, we compared our distribution maps with the BBS derived breeding range maps (see above under *Methods: Bird Occurrence Data*). To quantify how well our projected distributions matched breeding ranges, we calculated independent testing AUC scores based on the rate that surveyed route-level BBS occurrences and absences were correctly predicted by our GBIF based distribution models. AUC scores were calculated using the R package SDMTools (*available online*).[16] For each species, we then calculated the proportion of BBS-derived presences and absences that were correctly predicted across binned values of environmental suitability (logistic output values from of 0–1, binned at the midpoint of each 0.05 increment) for both short-term variability and long-term average models. For the short-term variability model, we matched the month and year of the BBS survey with the environmental suitability of the same month and year. For the long-term average model, only a single value of environmental suitability was available for each BBS route regardless of month and year of survey, and we used that value. Finally, to obtain a measure of true absence rate, we calculated the proportion of absences that occurred in the lowest quarter of the environmental suitability bins for both the short-term variability and long-term average models, which was defined as being equal to or lower than an environmental suitability value of 0.175 for the Maxent logistic output. We then evaluated how well short-term variability models and long-term average models were able to characterize true absences for all species and across guilds.

RESULTS

Short-term variability (22 covariates, three time-lags) and long-term average (eight covariate) models each described the potential breeding distribution of species well, with short-term variability models (AUC 0.86 ± 0.11 SD) exhibiting slightly better model performance (with a mean difference in AUC of 0.02, Wilcoxon signed-rank test, $P < 0.00001$) than long-term climate average (AUC 0.84 ± 0.12 SD). Short-term variability models incorporating only a single time-lag (i.e., an eight-covariate model) exhibited similar model performance as

[16] https://cran.r-project.org/web/packages/SDMTools/SDMTools.pdf

long-term average models, with no difference in AUC detected for 36-month time lag models (AUC 0.84 ± 0.12 SD) indicating that short-term variability characterized the potential breeding distribution of species as well as long-term average regardless of the number of covariates included (i.e., the 22-covariate and eight-covariate models both performed similarly). Model evaluation using 10-fold cross-validation confirmed that both long-term average and short-term variability accurately predict bird species presences (based on testing AUC scores). However, short-term variability models (testing AUC 0.85 ± 0.11 SD) outperformed long-term average models, again slightly (testing AUC 0.84 ± 0.12 SD), with a mean difference in AUC of 0.01 (Wilcoxon signed-rank test, $P < 0.00001$).

Short-term variability models for both landbirds and waterbirds performed similar to long-term average models with cross-validated AUC scores (Kruskal–Wallis ANOVA, $\chi^2 = 0.95$, df = 1, $P = 0.33$; Δ AUC 0.01 ± 0.03 SD for both landbirds and waterbirds). Short-term variability outperformed long-term average models with cross-validation testing in all migratory guilds, but the extent to which this was the case was generally small and differed by guild (Kruskal–Wallis ANOVA, $\chi^2 = 51.06$, df = 3, $P < 0.00001$; Fig. 2), with Neotropical migrants (0.02 mean Δ AUC ± 0.03 SD) showing the biggest differences. This difference was smaller for short-distance migrants (0.01 mean Δ AUC ± 0.02 SD), birds with varied migratory habits (0.01 mean Δ AUC ± 0.02 SD), and negligible for permanent residents (0.00 mean Δ AUC ± 0.02 SD).

Differences in the predictive power of the two types of models also varied among dietary preference guilds (Kruskal–Wallis ANOVA, $\chi^2 = 15.99$ df = 4, $P = 0.003$; Fig. 2). Again, short-term variability models generally performed similarly to long-term average models and outperformed them for landbird invertivores (0.02 mean Δ AUC ± 0.03 SD). Among foraging habit guilds, the magnitude of the differences varied (Kruskal–Wallis ANOVA, $\chi^2 = 32.58$, df = 7, $P < 0.0001$; Fig. 2) and was highest for upper-canopy foragers (0.03 mean Δ AUC ± 0.04 SD), lower-canopy foragers (0.03 mean Δ AUC ± 0.03 SD), and aerial foragers (0.02 mean Δ AUC ± 0.03 SD). Water, bark, ground, and floral hover foragers showed only modest differences in short-term variability and long-term average models of distribution (Fig. 2).

Models for individual species based on short-term variability vs. long-term averages (Fig. 3) did result in different predicted potential breeding distributions in geographical space. Comparisons of these potential breeding distributions with BBS summer distribution maps provided an indication of how well the two types of models predict a given species' breeding range. Model performance based on the independent BBS presence absence data indicated that both short-term variability (independent AUC 0.89 ± 0.10 SD) and long-term average (independent AUC 0.90 ± 0.10 SD) models were able to accurately predict independent data, although here long-term average
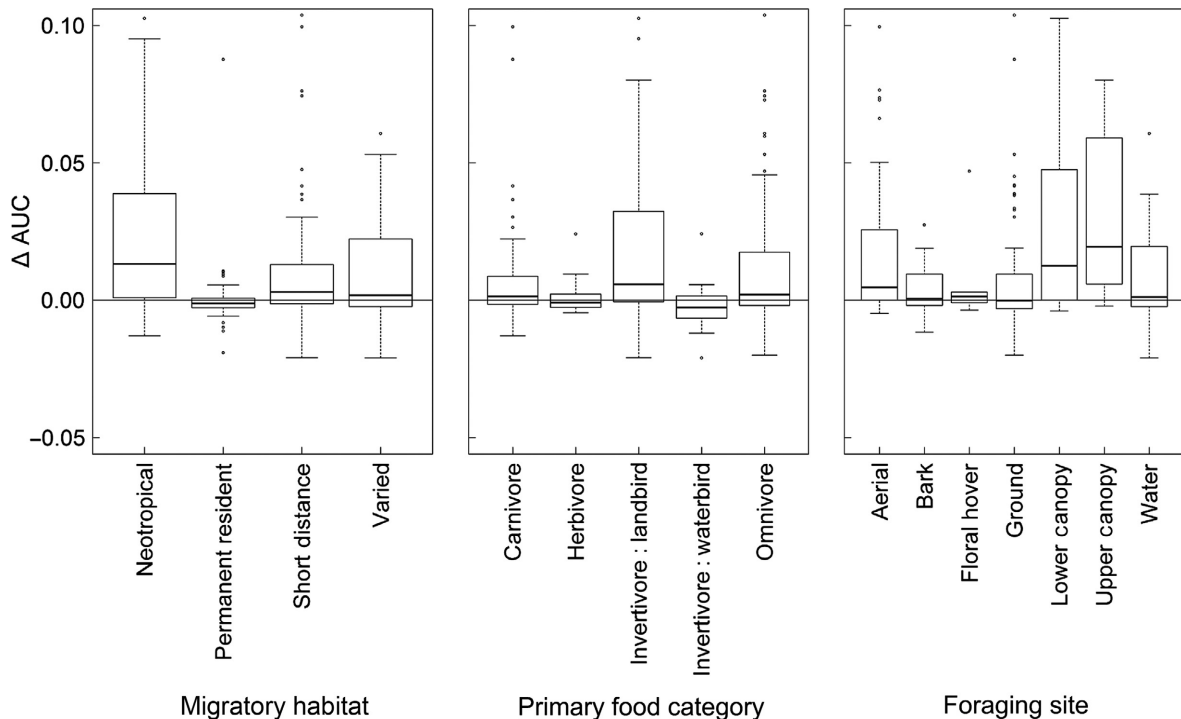
FIG. 2.   Pairwise differences in AUC scores calculated as short-term climate variability model AUC scores minus long-term average model AUC scores. Bird species are grouped by (left panel) migratory habit, (middle panel) primary food category, and (right panel) foraging site. Boxplots were used with default R settings, where the line in the box represents the 5th percentile (median), box end points represent the 25th (lower) and 75th (upper) percentile, and error bars/whiskers extend 1.5 IQRs and are calculated as upper whisker = min(max(x), Q_3 + 1.5 × IQR) lower whisker = max(min(x), Q_1 − 1.5 × IQR) where IQR = Q_3 − Q_1, is the box length.

exhibited slightly better model performance (with a mean difference in AUC of 0.01, Wilcoxon signed-rank test, $P < 0.00001$). Comparisons of AUC scores derived from the independent BBS data revealed no significant differences among any of the guild groupings (broad avian grouping, Kruskal–Wallis ANOVA, $\chi^2 = 0.91$, df = 1, $P = 0.34$; migratory habit, Kruskal–Wallis ANOVA, $\chi^2 = 4.72$, df = 3, $P = 0.19$; primary food category, Kruskal–Wallis ANOVA, $\chi^2 = 5.25$, df = 4, $P = 0.26$; foraging site, Kruskal–Wallis ANOVA, $\chi^2 = 2.75$, df = 6, $P = 0.84$).

For Fox Sparrow (*Passerella iliaca;* Fig. 3a), short-term variability models performed better with both 10-fold cross-validation testing (AUC 0.88 vs. AUC 0.77 for long-term average) and independent testing (AUC 0.93 vs. AUC 0.80 for long-term average) than long-term average models. The long-term average models predicted highly suitable breeding distribution throughout the Great Lakes and Northeastern U.S. regions, but these regions are not within the breeding range of this species. Furthermore, the short-term variability model was better able to identify the independent BBS-based absence data at low environmental suitability than was the long-term average model (93% of true absences identified correctly within the lowest quarter of environmental suitability by short-term variability model vs. only 42% of true absences identified using long-term average model; Fig. 3a; Appendix S1: Data S1). For the Northern Pintail (*Anas acuta*), the short-term variability model with

10-fold cross validation testing performed better than the long-term average model (AUC 0.81 vs. AUC 0.76 for long-term average), however, both independent testing models performed equally well (AUC 0.91 for short-term variability vs. AUC 0.91 for long-term average). Over-prediction of potential breeding distribution by the long-term average model was pronounced for Northern Pintail (Fig. 3b), although less so than for the Fox Sparrow, and, the long-term average model was particularly poor at predicting true absences in areas of very low environmental suitability (43% true absences predicted for the long-term average vs. 75% for the short-term variability model; Fig. 3b; Appendix S1: Data S1). For the Eastern Meadowlark (*Sturnella magna*; Fig. 3c) the long-term average model performed equally well in 10-fold cross-validation testing (AUC 0.74 for both models) and performed better in the independent testing than short-term variability models (AUC 0.90 for the long-term average vs. AUC 0.88 for short-term variability). For the Eastern Meadowlark, the long-term average model correctly predicted a higher proportion of true absences (69%) in the lowest quarter of environmental suitability areas than short-term variability model (67%; Fig. 3c; Appendix S1: Data S1).

We found that short-term variability models were generally better able to characterize low environmental suitability across all species than were long term average-based models (73% vs. 68%, respectively, of 282 species' true
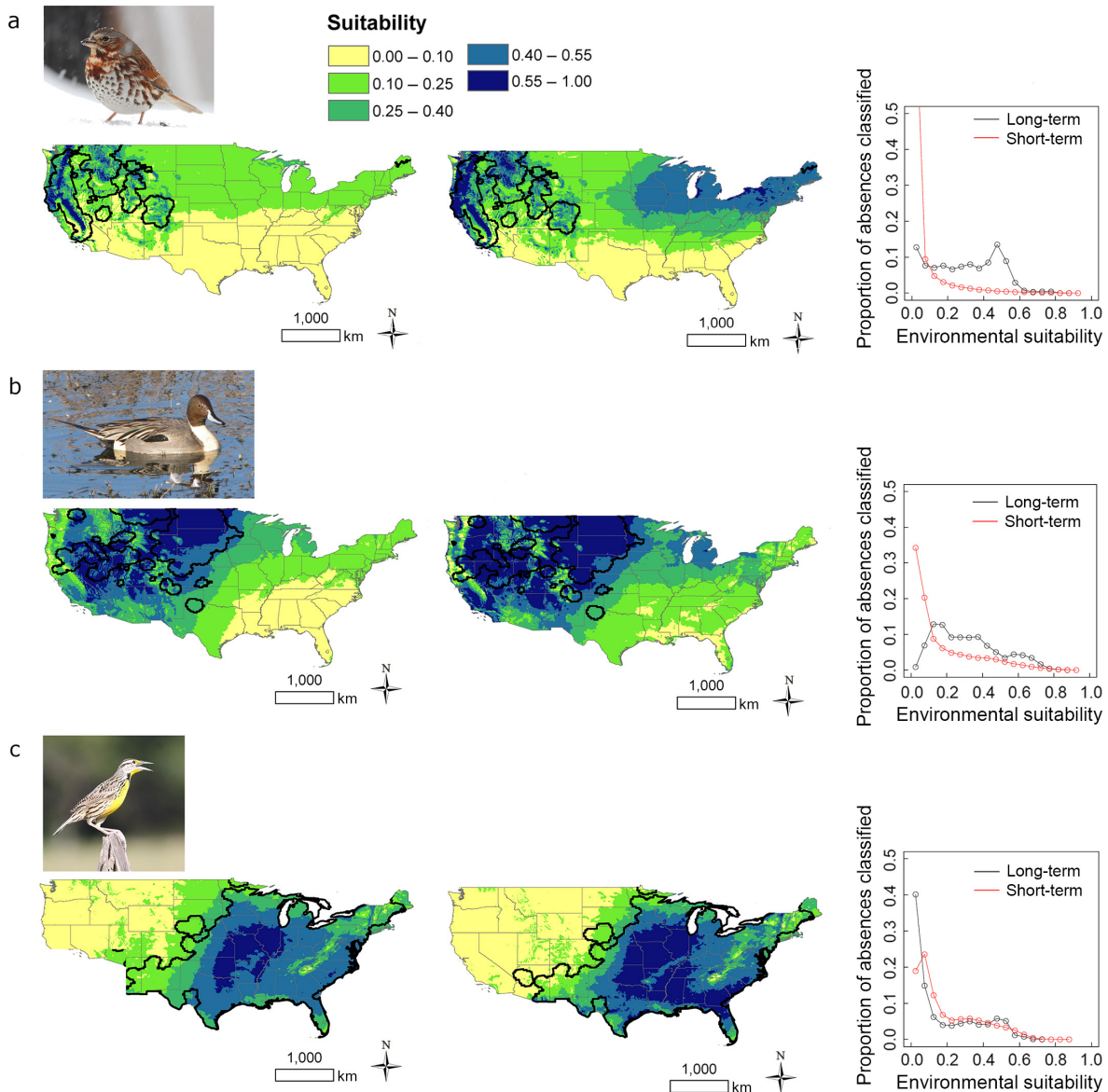
Fig. 3. For (a) Fox Sparrow (*Passerella iliaca*), (b) Northern Pintail (*Anas acuta*), and (c) Eastern Meadowlark (*Sturnella magna*), from left to right, are shown the short-term climate variability model output, the long-term climate averages model output (in both, black polygons depict summer distribution map for 2006–2011 characterized by the North American Breeding Bird Survey), and the proportion of absences correctly predicted by both models over the range of environmental suitability. Species image citations: Fox Sparrow, by permission, from Brian Collins, http://saintcroixbirds.blogspot.com/2013/05/why-we-do-it-part-ii.html; Northern Pintail, by permission, from Luke Fara; Eastern Meadowlark, Photographs by Alastair Rae, licensed under the Creative Commons Attribution-Share Alike 2.0 Generic License, https://commons.wikimedia.org/wiki/Category:Photographs_by_Alastair_Rae

absences were correctly predicted) within the lowest quarter of environmental suitability. Please see Appendix S1: Data S2 for each species, the proportion of absences classified across all environmental suitability values for both the short-term variability and long-term average models. This was particularly so for waterbirds (0.10 Δ proportion of true absences predicted by short-term variability model in relation to long-term average model ± 0.13 SD) compared to landbirds (0.04 Δ proportion of true

absences predicted ± 0.11 SD; Kruskal–Wallis ANOVA, $\chi^2 = 12.59$, df = 1, $P < 0.001$; Fig. 4), as well as for birds that were migratory (neotropical migrants, 0.04 Δ proportion of true absences predicted ± 0.12 SD; short distance migrants, 0.07 Δ proportion of true absences predicted ± 0.14 SD; and varied migratory habit, 0.10 Δ proportion of true absences predicted ± 0.15 SD) compared to permanent resident species (0.02 Δ proportion of true absences predicted ± 0.03 SD; Kruskal–Wallis
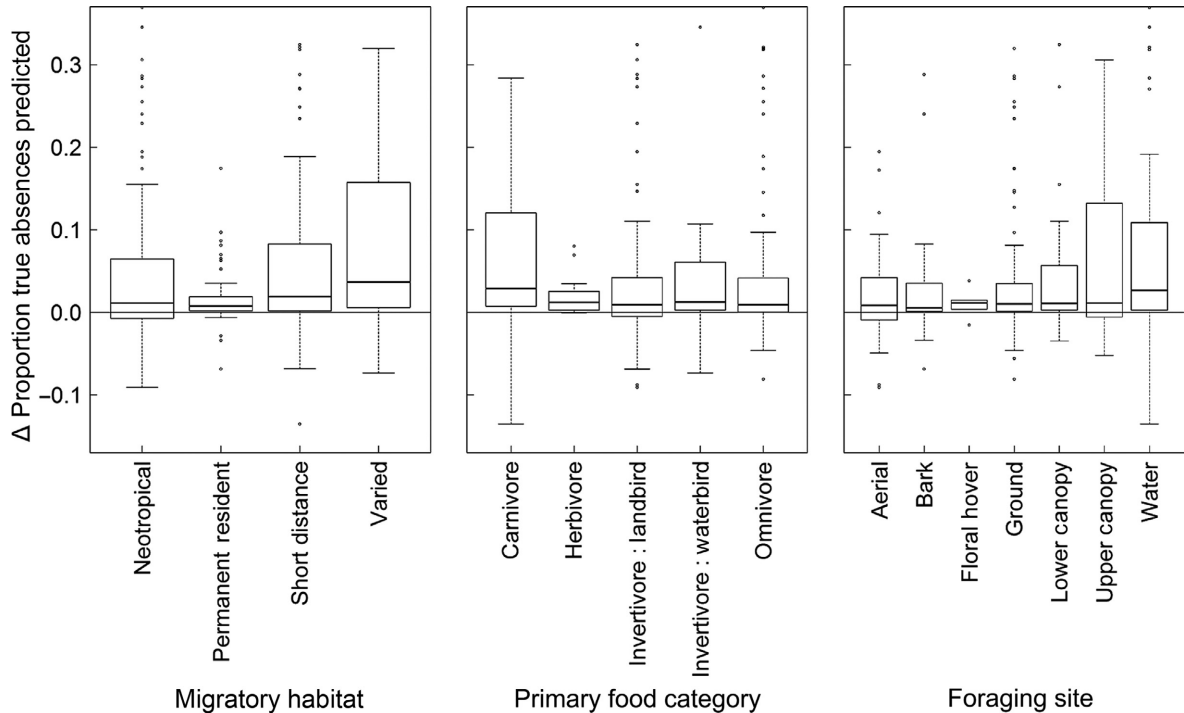
FIG. 4. Pairwise differences in the proportion of true absences correctly predicted in the lowest quarter of environmental suitability calculated as short-term climate variability model AUC scores minus long-term average model AUC scores. Bird species are grouped by (left panel) migratory habit, (middle panel) primary food category, and (right panel) foraging site. Boxplots were used with default R settings, where the line in the box represents the 5th percentile (median), box end points represent the 25th (lower) and 75th (upper) percentile, and error bars/whiskers extend 1.5 IQRs and are calculated as upper whisker = $\min(\max(x)$, $Q_3 + 1.5 \times IQR)$ lower whisker = $\max(\min(x), Q_1 - 1.5 \times IQR)$ where $IQR = Q_3 - Q_1$, is the box length.

ANOVA, $\chi^2 = 7.90$, df = 3, $P < 0.05$; Fig. 4). Although short-term variability models were better able to characterize true absences across all primary food category and foraging site guilds, we found no significant differences among them (Fig. 4). Within two guilds, carnivores and omnivores as well as upper-canopy, water, and lower-canopy foragers all had 5% or more additional true absences correctly predicted by short-term variability model in relation to long-term average model (Fig. 4).

For some species, such as the Pine Siskin (*Spinus pinus*), the short-term variability model-projected breeding distribution varied greatly across the landscape through time (see animation, Appendix S1: Video S1). Short-term variability outperformed long-term average models for this species in both 10-fold cross validation (AUC 0.82 for the short-term variability vs. AUC 0.74 for the long-term average) and independent testing (AUC 0.89 for the short-term variability vs. AUC 0.87 for the long-term average). For this species, the short-term variability model also performed better within areas of lowest environmental suitability with 91% of true absences predicted accurately, whereas the long-term average model only predicted 38% of absences accurately (Appendix S1: Data S1). Monthly predictions of species' potential breeding distributions allow an examination of changes among years, revealing the inter-annual variability inherent in the potential breeding distributions of some species.

DISCUSSION

Our potential breeding distribution analysis showed that both models based on short-term variability and those based on long-term average climate data predicted bird occurrences well. For some species, short-term variability models characterized the potential breeding distribution better, identified true absences more accurately, and provided dynamic information not available from long-term average methods. This reflects the role that climate variability plays in determining the breeding area of many bird species across the USA. However, generally the differences in predictive power were minor, and we suggest that the selection between these types of data should be made with the end goal of the SDM study in mind. Short-term variability data may be necessary for studies that aim to identify variation in species distribution through time, identify species-specific bioclimatic velocity (VanDerWal et al. 2013, Serra-Diaz et al. 2014, Bateman et al. 2016), or to identify spatiotemporal absences of species that are migratory or dynamic in their distribution from year to year. However, short-term variability data are also inherently more complex to analyze and may not be warranted when general distribution patterns are the goal.

We found that in particular the potential breeding distributions of migratory species, upper- and lower-canopy foragers, and landbird invertivores were better

characterized by short-term variability data than long-term average data when evaluated by cross-validation. This pattern was not evident, however, with evaluation based on independent testing data; here, both models performed equally well. Our independent testing data were derived from the BBS data, that only covers a small portion of the USA and represents some species better than others, and did not provide full coverage for all of our species or regions that we modeled using our GBIF data. Therefore, these results are only reflective of a subset of our models. Nevertheless, for species that are well represented in the BBS data, short-term variability models predicted true absences across all guilds better, especially for migratory species and upper-canopy foragers. A likely reason for this pattern is that foraging conditions and resource availability for these guilds are more tightly regulated by local short-term processes than is the case for other guilds. Landbird invertivore migrants that forage in the upper canopies of trees are dependent on a seasonal food supply (e.g., insects), which is governed strongly by short-term climate variability. Population dynamics of many insect species are affected by temperature (Kingsolver 1989) and snow-melt (Boggs and Inouye 2012). Extreme events, such as cold snaps, are negatively associated with insect abundance and hence invertivore landbird species in some years. Therefore, the spatial distribution of invertivore landbird migrant and waterbird species are likely to vary across the landscape according to shorter-term climate conditions and its influence on resource availability (Wolda 1978, McClure 1989, Forister et al. 2010).

On the other hand, we found that permanent resident bird species were characterized equally well by models based on both short-term climate variability and long-term climate averages, including the distribution of true absences for this guild. Permanent residents are less able to shift location in response to climate variability and generally stay within a well-defined range. These species tend to have lower dispersal distances than migrants (Paradis et al. 1998), and many are habitat specialists (e.g., American Dipper, *Cinclus mexicanus* and Pinyon Jay, *Gymnorhinus cyanocephalus*). Together, these traits result in less distributional flexibility than is the case for migrants. Permanent residents may experience greater population responses to climate variability, manifested as fluctuation in abundances, rather than distribution shifts (Roseberry 1962, Graber and Graber 1979, Norris and Elder 1982), especially when a large portion of their range is affected. Alternatively, permanent residents may be more tolerant of weather extremes due to adaptation (Reed et al. 2013).

Other guilds for which models based on short-term variability and long-term climate averages performed equally well included waterbird invertivores and water foragers, floral hoverers, and bark foragers. During the breeding season, occurrences of floral hover species may be less tied to nectar resources influenced by weather and more to local habitat characteristics and presence of conspecifics (Feldman and McGill 2013). Bark foragers have a food

source that is available throughout the annual cycle (Vermunt et al. 2012), and all of these species are permanent residents. For waterbird invertivores and water-foraging species, in particular, it is likely that their primary food sources are less affected by either short-term climate variability or long-term climate averages than by the condition and quality of the water bodies they depend on. However, we did find that short-term variability models predicted true absences for waterbirds and water foraging species better. Waterbirds and water foraging species are tied to seasonally variable and ephemeral wetland habitats (Kreakie et al. 2012), where local weather processes such as precipitation and evapotranspiration directly affect habitat quality in the short-term (Poiani et al. 1995). These species community dynamics can be influenced by extreme events such as high precipitation events, which can reduce water quality for waterbirds, lowering habitat quality for these species (Studds et al. 2012).

In addition to better characterizing true absences, the short-term variability models captured important biological patterns related to climate variability. Fluctuations in a species' geographic distribution can occur over fairly short time periods (Bateman et al. 2012b), and this may be particularly evident for facultative migrants and for opportunistic, nomadic, and irruptive species, which exhibit strong inter-annual fluctuations in their occurrence and abundances (Dean et al. 2009, Newton 2012). The strong fluctuations in potential distribution of the Pine Siskin (Appendix S1: Video S1) could potentially reflect the spatially fluctuating nature of the conifer cone crop, their food source, among years. For this species, the use of short-term data provided a clear advantage in identifying true absences, highlighting that for highly mobile species, climate variability can play an important role identifying where they do not occur in the landscape. The occurrence of a facultative migrant (a species that may or may not migrate depending on environmental conditions) at a given location thus depends on the occurrence of suitable conditions for that species (Newton 2012). This phenomenon can lead to both under-predictions and over-predictions when models are solely based on long-term averages. Under-predictions are observed when the average conditions at a location are unsuitable for a species but occasional years are suitable, whereas over-predictions occur when the average condition of a location are suitable but individual years are not. For Fox Sparrow and Northern Pintail, long-term average models over-predicted suitable breeding distributions and short-term variability models were better able to identify the occasional years when suitable climate conditions occurred outside the most consistent breeding ranges. The average suitability for these species may thus be better captured through an index of consistency in the occurrence of suitable years as predicted by short-term variability models. Locations that consistently experience high-quality conditions are of high conservation value. However, long-term average data

were sufficient or better in predicting breeding distribution for some species, such as the Eastern Meadowlark.

Whereas our focus here was on short- and long-term climate and its relationship to bird potential breeding distributions, we acknowledge that species distributions are also influenced by other factors, such as land cover, vegetation composition and structure, weather extremes such as heat waves and cold snaps occurring over days, and community composition. However, climate does have a strong influence on bird distributions in North America (Jiménez-Valverde et al. 2011), and over the last century birds have tracked their climatic niche (Tingley et al. 2009). As such, it is important to understand the relationship of bird distributions and climate. Ultimately though, an emerging conservation challenge is that future suitable climate for many species may be in areas where land cover has already been strongly altered, eliminating most suitable habitat (Bateman et al. 2016).

Our results demonstrate that both short-term and long-term climate conditions are equally able to predict breeding bird species distributions, suggesting that both capture important factors regulating where species occur and persist in the landscape. Although short-term climate data characterized potential breeding distributions of some bird species in the USA slightly better than long-term averages, the magnitude of this difference was small. In most cases, long-term climate information was a sufficient predictor of species distributions. There is a cost to including short-term climate variability data into SDMs, in that larger amounts of data are required, resulting in longer processing times. In addition, fine-scale historical climate data (e.g., daily or monthly temporal resolution, such as PRISM used here) are required, which may not be available for many areas of interest in climate-biodiversity studies (i.e., much of South America, Asia, Africa, etc.). Furthermore, short-term climate data in SDM have unique limitations, such as being sensitive to changes in station networks and data sources. Lastly, lack of knowledge on the relationship between species and environmental fluctuations such as climate variability, and the necessity of using the same set of variables for all species, among other factors, might mean that even if short-term variability determines species distributions, our approach may not detect it. However, there are exciting possible uses of short-term variability models, such as assessing how species' potential distributions may have already shifted due recent climate change. This is an important question (Thomas and Lennon 1999, Hitch and Leberg 2007, Zuckerberg et al. 2009) that models based on long-term averages cannot address because averages cannot capture recent climate change. The possibility of observing distributional shifts, and the degree of annual variance in these shifts, argues for the use of short-term climate variability in species distribution models. Indeed, bird species have shown multi-directions distribution shifts in respond to recent changes in precipitation and temperature (VanDerWal et al. 2013, Bateman et al. 2016). Given that climate variability data are now available into the future,

short-term variability data could be more easily integrated into SDMs in the future. By gaining an understanding of how both climate variability and climate averages affect bird species within their current ranges and shapes their distribution, ecologists will be better able to gauge and predict the full effects of climate change in the future.

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Supporting Information

Data Availability