

A Framework for Simultaneous Tests of Abiotic, Biotic, and Historical Drivers of Species Distributions: Empirical Tests for North American Wood Warblers Based on Climate and Pollen

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ABSTRACT: Understanding how abiotic, biotic, and historical factors shape species distributions remains a central question in ecology, but studies linking biotic factors to continental-scale patterns remain scarce. Here, we present a novel framework for simultaneously testing patterns expected when abiotic, biotic, or historical factors drive species range limits. We use ecological niche models to produce empirical estimates of the “biotic, abiotic, and movement” paradigm (BAM diagrams), which previously has been used only theoretically. On the basis of climatic and pollen data as well as explicit consideration of dispersal limitations, we implement the framework for a group of North American birds (*Oreothlypis* warblers) with clear habitat associations. Because the pollen-based predictor variables characterize vegetation, they represent biotic factors needed by each bird species. Although continental-scale patterns of distribution are traditionally attributed to abiotic factors, only one species matched the hypothesis of solely abiotic drivers. In contrast, pollen-based models indicate biotic drivers for two species, correctly predicting their absence in climatically suitable areas. These results highlight the feasibility of considering and quantifying the potential effects of biotic interactions on species ranges, especially when interactions can be decoupled from abiotic factors. Furthermore, the availability of pollen data now and in the Holocene highlights the potential of these data to be used to predict range shifts of other organisms tightly dependent on particular vegetation types.

Keywords: BAM diagram, ecological niche models, geographical distribution, *Oreothlypis*, palynology, species distribution models.

Introduction

Understanding how abiotic, biotic, and historical factors interact to shape species distributions has been and remains a central question in ecology, evolution, and conservation biology (Gaston 2009; Sexton et al. 2009). Investigating the role played by climatic factors, in particular, has been greatly facilitated by the development of species distribution modeling (SDM) and ecological niche modeling (ENM) methods that aim to characterize the ecological space in which a species occurs and identify geographical areas of climatic suitability (Peterson et al. 2011). However, despite calls for such considerations, studies linking abiotic, biotic, and historical factors simultaneously to continental-scale distributional patterns remain scarce (reviewed in Wisz et al. 2013 and Araújo and Rozenfeld 2014).

Climatic factors have been demonstrated to limit species distributions using both correlative (Lima et al. 2007) and physiological (Parker and Andrews 2007) studies, but other factors also shape species' geographical ranges. Specifically, at a given time a species might occupy either all or a fraction of the geographical space in which conditions are favorable. For example, transplant experiments in monkey flowers in western North America showed that these species occupy the entire altitudinal range in which they can grow within that geographical region (Angert and Schemske 2005). However, such cases of a species in “distributional equilibrium” (when it occupies all areas in a region with favorable conditions) are not the norm (Araújo and Pearson 2005). The extent of distributional “disequilibrium” (when

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a portion of a species' potential range is not occupied) depends on such factors as colonization history, dispersal ability, biogeographical barriers, biotic interactions, and human impacts (Peterson et al. 1999; Araújo and Pearson 2005; Svenning et al. 2008; Hara 2010; Fløjgaard et al. 2011).

Whereas modeling abiotic suitability (e.g., based on climatic variables) has received great attention, the effect of biotic interactions on large-scale distributional patterns has been hypothesized to be encapsulated by the abiotic conditions in which the species occur (Eltonian noise hypothesis; Soberón and Nakamura 2009). In this case, only fine-scale patterns of the distribution of the species can be attributed to the effects of biotic interactions (Pearson and Dawson 2003; Peterson et al. 2011). Nevertheless, many studies have linked biotic interactions to range limits (reviewed in Wisz et al. 2013 and Louthan et al. 2015), and simulation analyses suggest that patterns resulting from positive biotic interactions (i.e., mutualism and commensalism) manifest across all scales (Araújo and Rozenfeld 2014). As called for recently, integration of biotic interactors into ENMs represents a necessary key advance, especially given the pressing need to forecast the effects of anthropogenic climate and land use change on species distributions (Anderson 2013 and references therein; Blois et al. 2013).

The conceptual BAM ("biotic, abiotic, and movement") framework of factors (fig. 1; Soberón and Peterson 2005; Peterson 2008; Peterson et al. 2011) formally describes the regions in which a species occurs as the intersection of areas that meet certain ecological and historical requirements. In it, the area of a continent or other geographical study region is depicted as a Venn diagram (fig. 1) in which a geographical region (G) is divided into three overlapping sets: first, areas with abiotic conditions in which the species can exist, denoted set A; second, areas in which the biotic composition includes interacting species that are necessary for the focal species and excludes prohibitive ones, denoted set B; and third, areas where the species is not limited by geographical barriers to movement (i.e., dispersal), denoted set M (note later extensions to demographically related restrictions in small areas of suitable conditions; Anderson 2013). Different configurations of the BAM diagram are commonly used to illustrate, from a theoretical point of view, how each of these classes of factors (abiotic, biotic, and movement) or changes in them determine species ranges (e.g., Peterson 2008; Peterson et al. 2011, fig. 3.5). However, despite a recent surge in studies investigating the role played by biotic interactors in determining species ranges by including biotic variables as additional predictor vari-

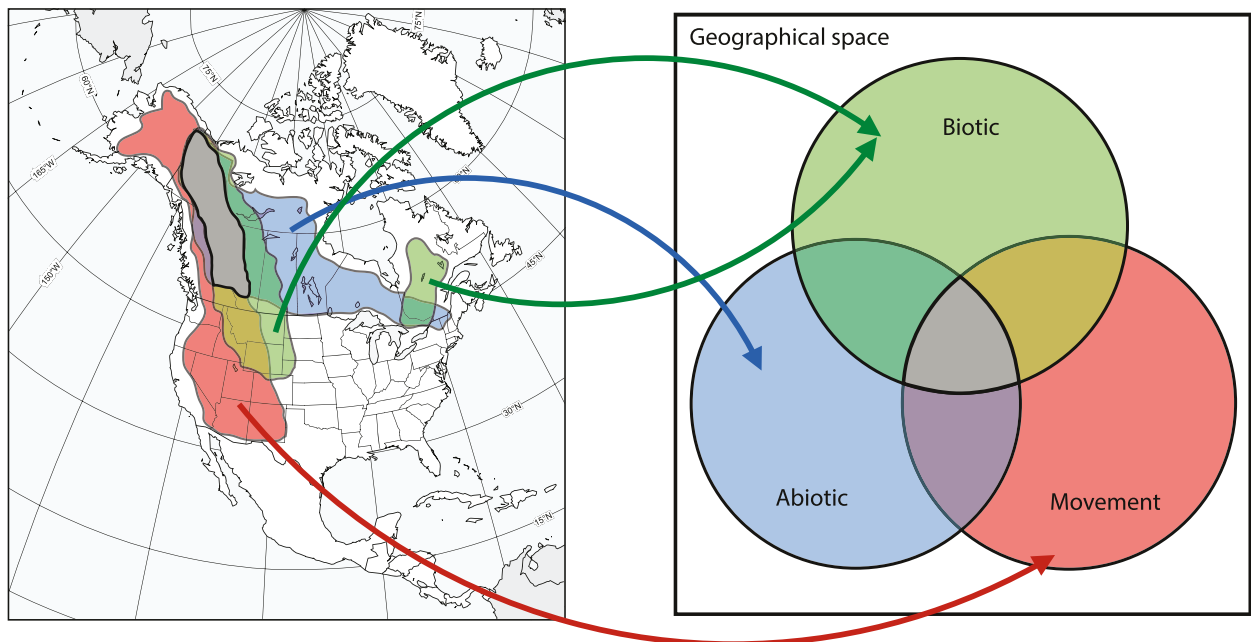


Figure 1: BAM ("biotic, abiotic, and movement") diagram representing the geographical areas where certain ecological and historical conditions required by a hypothetical species are met. The blue area (A) represents the regions in which the abiotic conditions are suitable for the species. The green area (B) represents the regions in which a suitable combination of interacting species occurs. The red area (M) indicates the regions that have been available for a species (e.g., no barriers to dispersal). Areas in the darkest gray match the species' need for all three factors. G represents the total geographical area of the study region. Note that the different sets in the right panel represent a rearrangement of the areas in the map on the left and therefore still represent the extent of suitability in geographical space. Modified from Soberón and Peterson (2005).

ables (Anderson 2017), an empirical approach to simultaneously modeling and mapping the areas that are suitable for a species based on abiotic, biotic, and movement-related factors remains lacking.

Here, we provide such a framework for empirically disentangling the effects these classes of factors have on species ranges and apply it to the breeding ranges of a group of North American wood warblers (Parulidae). For six species of the genus *Oreothlypis*, we modeled necessary abiotic and biotic conditions by including predictor variables that fall into these categories (climatic conditions and palynological data, respectively); we then identified the suitable geographical areas in North America using these models and taking current dispersal limitations into account. Importantly, wood warblers show a strong association with the forest types in which they occur, particularly during the breeding season (Curson et al. 1994; Curson 2010), indicating that the availability of a particular vegetational composition (e.g., one that can be characterized with palynological data) may limit their distributions. Here, the quantification of environmentally suitable areas is not intended to characterize the complete set of abiotic or biotic factors limiting these species distributions but rather to illustrate the feasibility of applying the framework by using examples very likely to affect the species distributions (climate and pollen/vegetation). For instance, interactions with other organisms, such as competition, predation, or parasitism, would not be captured by climatic or palynological data. Hence, the current analyses directly address only one possible kind of critical biotic limitation.

Pollen data have great potential for understanding species range limits across space and time (Maguire et al. 2015), and we use them in a novel way here. Generally, such data are used only in models of the plants themselves (e.g., McGuire and Davis 2013; Blois et al. 2014; Yannic et al. 2014), and their capacity to predict other species distributions (in comparison with climatic and other abiotic variables) has not been tested. Importantly, it is reasonable to assume in this system that vegetational composition is not affected by the presence of the wood warblers themselves and thus can be used as a predictor in correlative ENMs (i.e., the pollen data represent unlinked or scenopoeitic factors sensu Soberón 2007; see also Anderson 2017). Furthermore, because the bird-plant interaction is assumed to be positive-neutral (analogous to commensalism, in which the effects on the presence or abundance of the species is unidirectional), it can be expected to manifest in a species' geographical range at regional and continental scales (Araújo and Rozenfeld 2014). Notably, if this bird-plant relationship quantified on the basis of pollen data affects species ranges at continental scales, it would constitute a new way to model species distributions across both space and time (Maguire et al. 2015).

Framework for Simultaneous Testing

ENMs based on these two largely independent sources of environmental information (climate and pollen), along with explicit consideration of regions accessible to each species (without internal barriers to dispersal), allow for tests of abiotic versus biotic limits to species distributions. Specifically, the following three scenarios exist for ENMs generated within a geographical region delimited to reflect areas without internal dispersal barriers. In the first scenario, if a species' distribution is limited by climatic factors, biotically suitable areas should exist outside the range of the species, with the species occurring only in the more restricted, climatically suitable areas (fig. 2A). Conversely, in the second scenario, if biotic factors (i.e., vegetational composition) are limiting, some areas outside the distribution would be climatically suitable, and the species would occur only in a smaller set of biotically suitable areas (fig. 2B). Alternatively, in the third scenario, if abiotically and biotically suitable areas are congruent, it is not possible (with correlative analyses) to disentangle their relative importance to the limits of a species' distribution (including the possibility that the Eltonian noise hypothesis is true). In this latter case, the species would occupy all suitable areas (i.e., be at distributional equilibrium; fig. 2C). Additionally, a fourth scenario is expected if dispersal restrictions (or other factors not captured by the climatic or pollen data sets) are limiting. In that case, the species would not be present in all suitable areas of the continent but rather would be present in only those areas within the region lacking internal barriers to dispersal (fig. 2D). The latter two scenarios (fig. 2C, 2D) represent cases in which climate and pollen-based ENMs would have similar predictions. However, incongruence is expected in the former two scenarios (fig. 2A, 2B); in these cases, the areas predicted by the models made on the basis of the limiting variable class (climate or pollen) would be most similar to ENMs built using both sets of variables together.

Methods

Focal Species

We obtained records for six of the seven North American species of *Oreothlypis* wood warblers (Lovette et al. 2010): the orange-crowned warbler (*O. celata*), Virginia's warbler (*O. virginiae*), the Tennessee warbler (*O. peregrina*), Lucy's warbler (*O. luciae*), the Nashville warbler (*O. ruficapilla*), and the Calaveras warbler (*O. ridgwayi*). The geographical ranges of these species cover almost all forest types in North America; some species, such as the orange-crowned warbler, are broadly distributed, whereas others, such as Virginia's warbler, are found in narrow montane habitats. Although the Nashville and Calaveras warblers have traditionally been considered conspecific, molecular data indi-

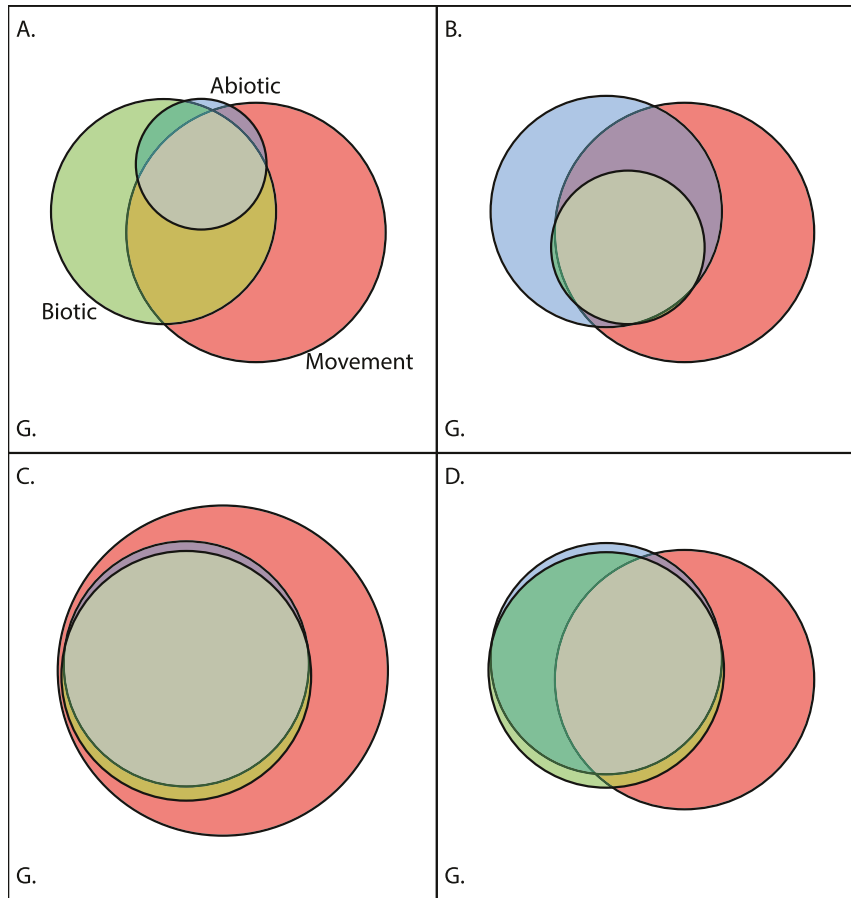


Figure 2: Hypothetical scenarios under which abiotic and biotic factors may limit species distributions represented by different configurations of the BAM ("biotic, abiotic, and movement") diagram. *A*, Predicted configuration if a species' distribution is limited by abiotic factors. *B*, Predicted configuration if biotic factors are limiting. *C*, Predicted distribution if both of these factors limit the species' distribution. *D*, Predicted configuration if "movement" restrictions or other factors not captured by the biotic or abiotic variables are limiting, beyond the confounded effects of abiotic and biotic factors. The lower panels represent configurations in which biotically and abiotically suitable areas are congruent.

cate that they show substantial differentiation and might not even be each other's closest relative (Weir and Schluter 2004). Because of the paucity of locality and palynological data for the Colima warbler (*O. crissalis*), it was not included in the study.

Environmental Variables

We used two sources of variables to describe the environmental niche of each species. First, the scenopoetic abiotic factors were based on climatic data from WorldClim (Hijmans et al. 2005) that were interpolated from monthly data from meteorological stations across the globe. The complete WorldClim data set includes 19 bioclimatic variables; of these, eight that describe the average, extremes, and variability of temperature and precipitation were employed in this study (table 1).

The second source of variables, related to scenopoetic biotic requirements (see above) of each species, was derived from present palynological data (Late Quaternary North American Vegetation Dynamics Data; Williams et al. 2004) in which the relative abundances of 55 plant taxa were sampled from lake deposit pollen and interpolated on a geographical grid. Pollen data from Williams et al. (2004) were identified to various taxonomic levels; therefore, they required further classification into 15 derived variables in which the pollen percentages of each taxon were pooled together as plant functional groups (tables 1, S1; tables S1, S2 are available online; based on Williams et al. 1998). Key assumptions are that palynological data at this resolution reflect the vegetation in the proximity of the lakes in which the pollen was deposited (Sugita 2007) and that the pollen-vegetation relationship is the same across the continent. It is worth noting that more complex pollen-vegetation models (e.g., Dawson

Table 1: Biotic and abiotic variables included as environmental predictors

Climatic variables (abiotic factors)		Pollen variables (biotic factors)	
Bioclimatic variable	Variable code	Functional group	Abbreviation
Annual mean temperature	BIO1	Boreal conifer	BorCon
Temperature seasonality	BIO4	Cool temperate conifer	CoolTempCon
Maximum temperature of warmest month	BIO5	Eurythermic conifer	EuryCon
Minimum temperature of coldest month	BIO6	Boreal summer green	BorSumGre
Annual precipitation	BIO12	Cool temperate summer green	CoolTempSumGre
Precipitation of wettest month	BIO13	Temperate summer green	TempSumGre
Precipitation of driest month	BIO14	Warm temperate summer green	WarmTempSumGre
Precipitation seasonality	BIO15	Warm temperate evergreen	WarmTempEvGreen
		Shrubs	Shrubs
		Sedge	Sedge
		Forbs	Forbs
		Grass	Grass
		Holly and Ericaceae	AqEric
		Legumes	Legumes
		<i>Selaginella</i>	Selagi

et al. 2016 and references therein) have been developed, but their application has been at more localized areas than the continental scale.

Both data sets were projected from their original format into a longitude-latitude WGS84 projection with a 0.5° resolution and an extent covering North America using the raster (Hijmans 2017) and rgdal (Bivand et al. 2017) packages in R 3.1.3 (R Core Team 2014). Because data from pollen deposits were sparse and to avoid excessive interpolation across geography, not all cells in North America were included in the original generation of the pollen data (Williams et al. 2004). Therefore, areas for which climatic data were available but pollen data were not were not used in this study.

Locality Data

Presence records for each of the species were obtained from the eBird database (Sullivan et al. 2009). The total number of records for each species ranged from ~18,000 to 415,000. We restricted analyses to the portion of records that were observed during 2 months of the breeding season (June 15 to August 15) and that fell within 100 km of the estimated breeding distribution of each respective species (available at <http://www.natureserve.org/>; Ridgely et al. 2007). The total unique localities ranged from ~2,300 to 22,000 per species. Because of the coarse resolution of the environmental data and substantial aggregation of records around highly sampled areas, only one locality per cell was used, for a total of 84–1,087 unique cells recorded per species.

Study Region

ENMs are built on the assumption that environmental variables used to model the niche (or others correlated with

them) are the only factors limiting the geographical distribution within the training area (Peterson et al. 2011). To meet this expectation (see the noise assumptions of Anderson [2013]), the region from which environmental data are drawn should be restricted to areas in which there are no biogeographical restrictions to the presence of the species (i.e., within which no dispersal barriers exist; M in fig. 1). Additionally, the study region should not include areas in which unexamined biotic factors limit the species' distribution (outside B in fig. 1; Anderson and Raza 2010). In these parapatrically distributed wood warblers, competitive interactions with close relatives likely restrict the distributions of some species that come into geographical contact (Anderson et al. 2002; Krosby and Rohwer 2010).

To build distribution models that match these assumptions, we defined species-specific training areas (red area in fig. 3A and panel A of figs. S1–S5; figs. S1–S8 are available online) through a two-step process. First, we excluded regions to which the species likely has not had the opportunity to disperse by defining an area including the known breeding distribution of each species based on its breeding range (Ridgely et al. 2007) with a 500-km buffer. Second, we took into account the possible effect of interspecific competition by excluding areas in which other nonsympatric species of this group occur (again using the same range polygons). The resulting study regions for each species represent areas in which the species can be expected to be in environmental equilibrium with respect to the variables used in the models.

Because the eBird presence locality data were highly biased (i.e., toward grid cells in more accessible areas and closer to urban centers that have been more heavily sampled), we addressed the potential effect of geographical sampling differences on the ENMs. To do so, background

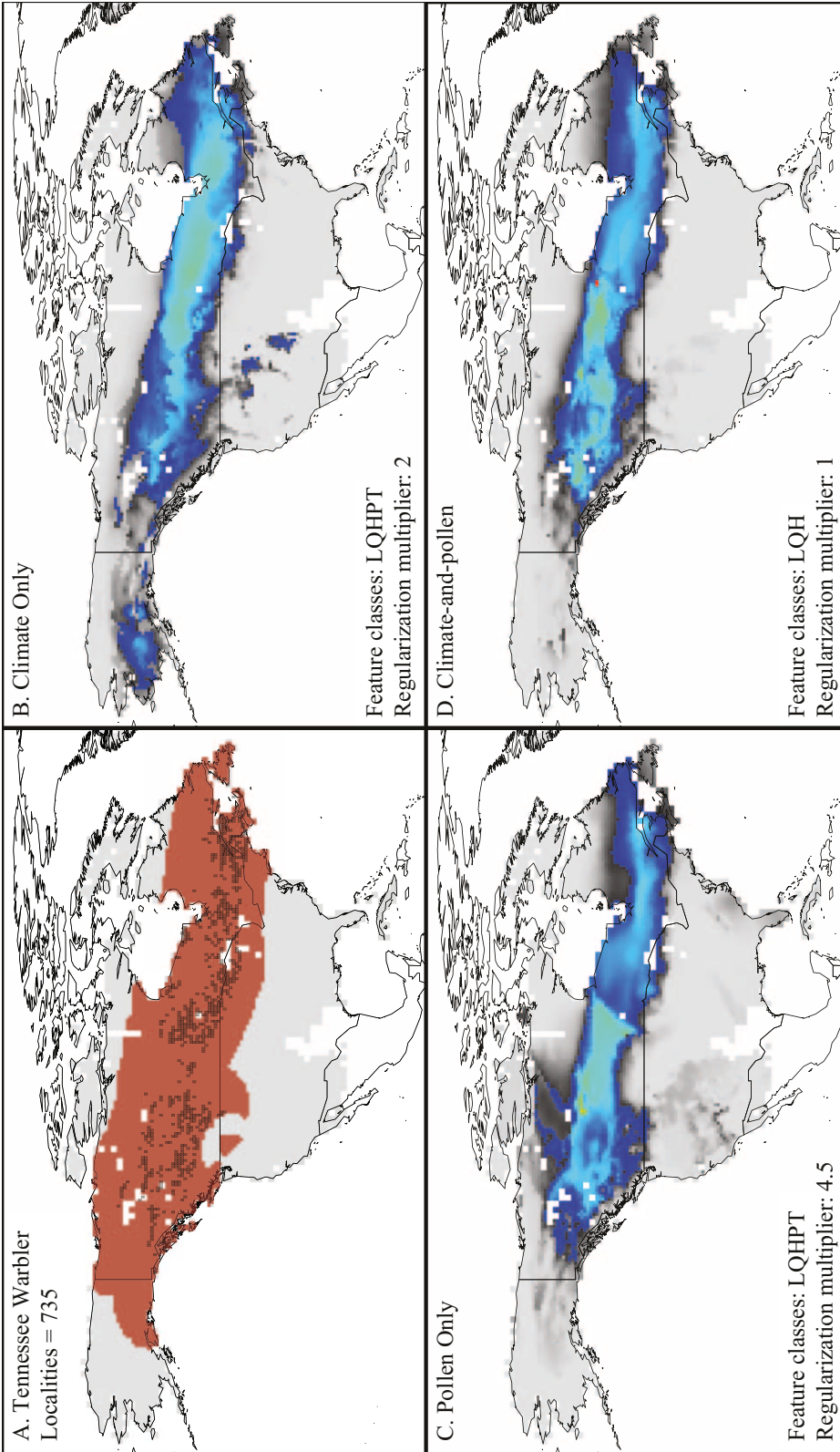


Figure 3: Input data and Maxent ecological niche model (ENM) projections to all of North America for the Tennessee warbler. A, Unique cells sampled for the species (points), with the red area indicating the region from which the background data were drawn (red set in fig. 5D). B, Abiotically suitable areas predicted by ENMs based on climate-only variables (blue set in fig. 5D). C, Biotically suitable areas predicted by ENMs based on pollen-only variables (green set in fig. 5D). D, Areas predicted to be suitable with ENMs based on both climatic and pollen data. For B–D, light to dark grays represent relative suitability below the respective 10% omission rate thresholds, and cold to warm colors show increasing suitability above those thresholds. Letters for feature classes stand for linear (L), quadratic (Q), hinge (H), product (P), and threshold (T). Similar figures for all other species appear in the supplemental material (figs. S1–S5).

data used to train the model should be proportional to the sampling effort that led to the presence locality data (Phillips et al. 2009). To produce such a data set, we first created a sampling effort raster in which the value of each cell was the number of times it had been sampled based on the entire eBird data set for the same dates as the occurrence data. Background data were then selected by sampling without replacement 70% of the cells within the background area defined for each species, where the probability of a cell being sampled was proportional to the number of sampling events in that cell (weighted target group approach of Anderson 2003). There are two reasons for sampling background data without replacement here. First, only one locality record per cell was used in the presence data set. Second, if the probability of sampling *with* replacement had been proportional to the sampling effort, a computationally unfeasible amount of background points would be required to capture a representative portion of the ecological space (because the number of sampling events in some cells was orders of magnitude larger than in others).

Model Selection and Projection

ENMs were made in Maxent 3.3.3.k (Phillips et al. 2006), using the dismo package (Hijmans et al. 2017) in R 3.13. To select key species-specific settings related to model complexity for Maxent, we used the ENMeval R package (Muscarella et al. 2014) to build and evaluate multiple candidate models with various combinations of the regularization multiplier and feature classes allowed (see below). We used the block partitioning method of ENMeval, in which the study area was partitioned into four spatial bins, three of which were used to train the model in each iteration while the remaining one was withheld for evaluation.

Niche models were built with three sets of variables: (1) climate only, (2) pollen only, and (3) both climate and pollen. For each of the three sets of variables, 180 total models were made per species. These models were built using 60 different combinations of settings in which two factors varied: the complexity of the feature classes included and the regularization multiplier. We employed all of the combinations of feature classes provided by ENMeval and regularization multipliers from 1 to 5 in intervals of 0.5 units. The best model was selected under two sequential conditions: information criteria and transferability. First, to select the best-performing settings, only the candidate models within two units of the lowest corrected Akaike information criterion (AICc) score (Warren et al. 2008) were considered. Second, when more than one model had a Δ AICc lower than 2, the one with the lowest difference between training and testing AUC (area under the curve) was selected to maximize geographical transferability (Warren and Seifert 2011; Radosavljevic and Anderson 2014). Importantly, metrics cal-

culated on the withheld bin are subject to being artifactually over- or underestimated because evaluation localities remain spatially biased (whereas the resulting model was corrected for bias using the weighted target group approach). Thus, we favored AICc over other performance metrics because it is calculated on the unpartitioned, corrected model.

For each of the models, we quantified the number of parameters used by Maxent as a measure of complexity (Warren and Seifert 2011). It is worth noting that model selection based on the lowest AICc (see above) penalizes parameter-rich ENMs (Warren and Seifert 2011; Muscarella et al. 2014). Additionally, to assess model performance and transferability, the omission rate metric was calculated (using the “10% training omission” threshold, OR10). This metric calculates the proportion of test localities with suitability values below the 10% training suitability threshold. Under perfect transferability, the OR10 value is expected to be 0.10. Therefore, values larger than that indicate that the ENMs built with the training data predict presences in the testing data set less adequately than those models showing OR10 at or below 0.10. The settings selected for each species (for each environmental data set) were then used to build ENMs using the full (unpartitioned) presence and background data.

For each species, the final ENMs based on each of the three sets of variables were projected onto the entire continent, therefore estimating all environmentally suitable areas in North America regardless of whether the species actually occurs there. Projections into nonanalog environments (conditions present in North America but not within the training area of a particular species) were made by allowing Maxent to extrapolate responses beyond the range of the variables in an unconstrained manner (i.e., not “clamping”; Elith et al. 2011). To evaluate to what extent suitability patterns projected by ENMs were affected by extrapolation into nonanalogous environments, we identified areas in the continent in which at least one variable that contributed to the model ($\lambda > 0$) fell outside its training range. To examine the individual contribution of each variable, response curves of ENMs were examined using Maxent’s explain tool (Elith et al. 2010).

Environmental Variable Correlations

Unlike regression-based techniques, in which highly correlated variables could produce spurious results due to overfitting or collinearity, Maxent is built to handle highly correlated variables by excluding predictors with redundant information from the final model, via regularization (Elith et al. 2011). However, to assess the extent to which congruences between the resulting models are an outcome of correlation of the environmental data, we calculated the pairwise Pearson product-moment correlation coefficients among the climatic variables and pollen functional groups

as well as between variables in the two data sources, across all cells in the continent. These pairwise comparisons were visualized using the R package *corrplot* (Wei and Simko 2017).

Distance Matrix and Multidimensional Scaling

To examine the overall congruence of the various species' ENMs, we computed a distance matrix among all resulting projections. Suitability maps of all species based on each of the three sets of variables were compared pairwise among species. The distance between two raster grids was equal to $1 - \text{Schoener's } D$ (Schoener 1968; Warren et al. 2008), calculated using the *nicheOverlap* function in *dismo* (Hijmans et al. 2016). The value of the comparison of two maps ranges between 0 and 1, with identical maps having a value of 0 and very dissimilar maps having a value close to 1. To visualize these distances in a two-dimensional space, we then performed a nonmetric multidimensional scaling analysis using the *vegan* package (Oksanen et al. 2016) in R.

Empirical BAM Diagrams

We tested the predictions outlined in the introduction by examining results via empirical BAM quantifications and visualizations. To compute BAM diagrams for each species, we first defined the total biotically and abiotically suitable regions by applying a 10% training omission rate threshold to the continental projections of the climate-only and pollen-only models (sets A and B, respectively, in BAM; Pearson 2004; Peterson et al. 2011). As mentioned earlier, we approximated the “movement” (set M) of BAM as the species-specific area from which the background data were drawn for each species. We subsequently calculated the total area deemed suitable by both climate and pollen (via the separate models) as well as their overlap using the raster package in R. Euler diagrams depicting the relationships among the “biotic, abiotic, and movement” areas were first calculated in R and then illustrated using the BAM diagram script deposited in Dryad (<https://dx.doi.org/10.5061/dryad.q3b45>; Sanín and Anderson 2018).

Results

Model Selection and Evaluation

The best-performing settings (lowest AICc models) varied greatly across species and the set of variables used (figs. 3, S1–S5). Feature classes used were consistent within a species, increasing in complexity in species with more occurrence records and larger geographical ranges. The regularization multiplier varied within species, without any clear pattern for each set of environmental variables.

Models for narrowly distributed species (Lucy's, Virginia's, Tennessee, and Nashville warblers; OR10 range, 0.12–0.35) had better performance in terms of transferability than did those with more heterogeneous environmental conditions across the species' range (Calaveras and orange-crowned warblers; OR10 range, 0.31–0.82), which generally resulted in more complex and over-fit ENMs. While these values might be caused by uncorrected spatial bias in evaluation localities (see above), they could also be the result of violating the assumption of stationarity among the geographically independent evaluations bins (Murphy and Lovett-Doust 2007; Radosavljevic and Anderson 2014). Model evaluation metrics estimated for every model built have been uploaded to Dryad (<https://dx.doi.org/10.5061/dryad.q3b45>; Sanín and Anderson 2018).

Environmental Variable Correlations

The absolute values of the Pearson's correlation coefficients were highest between bioclimatic variables, with eight (28.6%; bold blue grid squares in fig. S6) of those pairwise combinations showing substantial correlation (magnitude greater than 0.75). As expected, bioclimatic variables derived related to temperature were highly correlated, and so were those derived from precipitation. Likewise, six comparisons between pairs of functional group variables were highly correlated (bold green grid squares in fig. S6). Notably, however, comparisons for pairs of functional group versus bioclimatic variables were considerably less correlated, with only one pair showing a correlation greater than 0.75 (bold black grid square in fig. S6).

Geographical Concordance of Abiotic and Biotic Suitability

The final maps of environmental suitability based on models built with three different sets of variables (climate only, pollen only, and both pollen and climate) for each species indicated various patterns of geographical concordance but with few complications of nonanalog environments. For example, the suitable conditions in North America for the Tennessee warbler for the three sets of environmental data differ: climate only (fig. 3B), pollen only (fig. 3C), and both climate and pollen (fig. 3D; corresponding maps for all other species can be found in figs. S1–S5). As expected, models built with climate and pollen together predicted a more restricted distribution of suitability than did models built with either separately. The extent of suitable area predicted in nonanalogous environments was negligible for most models (mean, 2.6%; range, 0%–18%; figs. S7, S8), with the exception of the climate-only model for Virginia's warbler, which predicted as climatically suitable areas in the

eastern United States in which the precipitation of the driest month was higher than the range found in the area in which the ENM was trained.

The extent to which abiotically and biotically suitable areas overlapped when projected to the full extent of North America varied greatly across taxa. Congruent with the predictions of geographic correspondence (nonindependence) between biotic and abiotic factors (Eltonian noise hypothesis; fig. 2C, 2D), the respective climate-only and pollen-only models were virtually identical in orange-crowned, Nashville, Tennessee, and Lucy's warblers (fig. 4). However, climate-only and pollen-only models were conspicuously different from each other (and from the pollen-and-climate models) for Virginia's and Calaveras warblers (orange and yellow symbols, respectively, in fig. 4). Notably, for these species two opposing patterns were recovered regarding their similar-

ity (quantified distance) to the climate-and-pollen models. On one hand, the pollen-only model for Virginia's warbler was closer to its climate-and-pollen model, congruent with the prediction of biotic limits to its distribution (fig. 2B). On the other hand, for the Calaveras warbler (fig. 2A), the climate-only model was more similar to the one based on both climate and pollen, consistent with limiting climatic factors.

Empirical BAM Diagrams

The patterns described above were reflected in the BAM diagrams constructed for each species based on ENMs, which also include quantification of movement-related factors (fig. 5). Suitable areas predicted by pollen and climatic variables separately overlapped broadly for orange-crowned, Nashville,

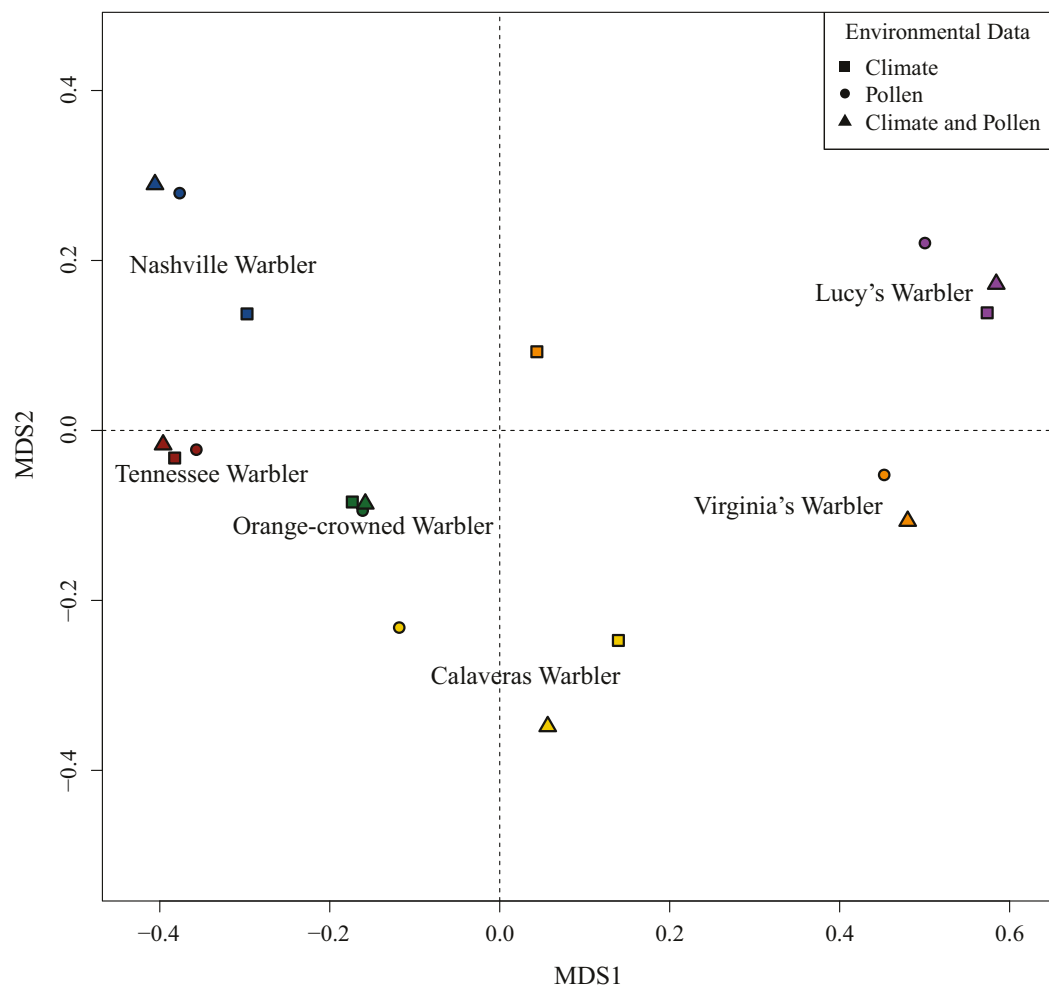


Figure 4: Multidimensional scaling plot showing the relationship among the projected suitable areas for all species of warblers examined in this study. This plot visualizes the overall distances ($1 - \text{Schoener's } D$) between climate-only ecological niche models (ENMs; squares), pollen-only ENMs (circles), and climate-and-pollen ENMs (triangles) for each species (different colors).

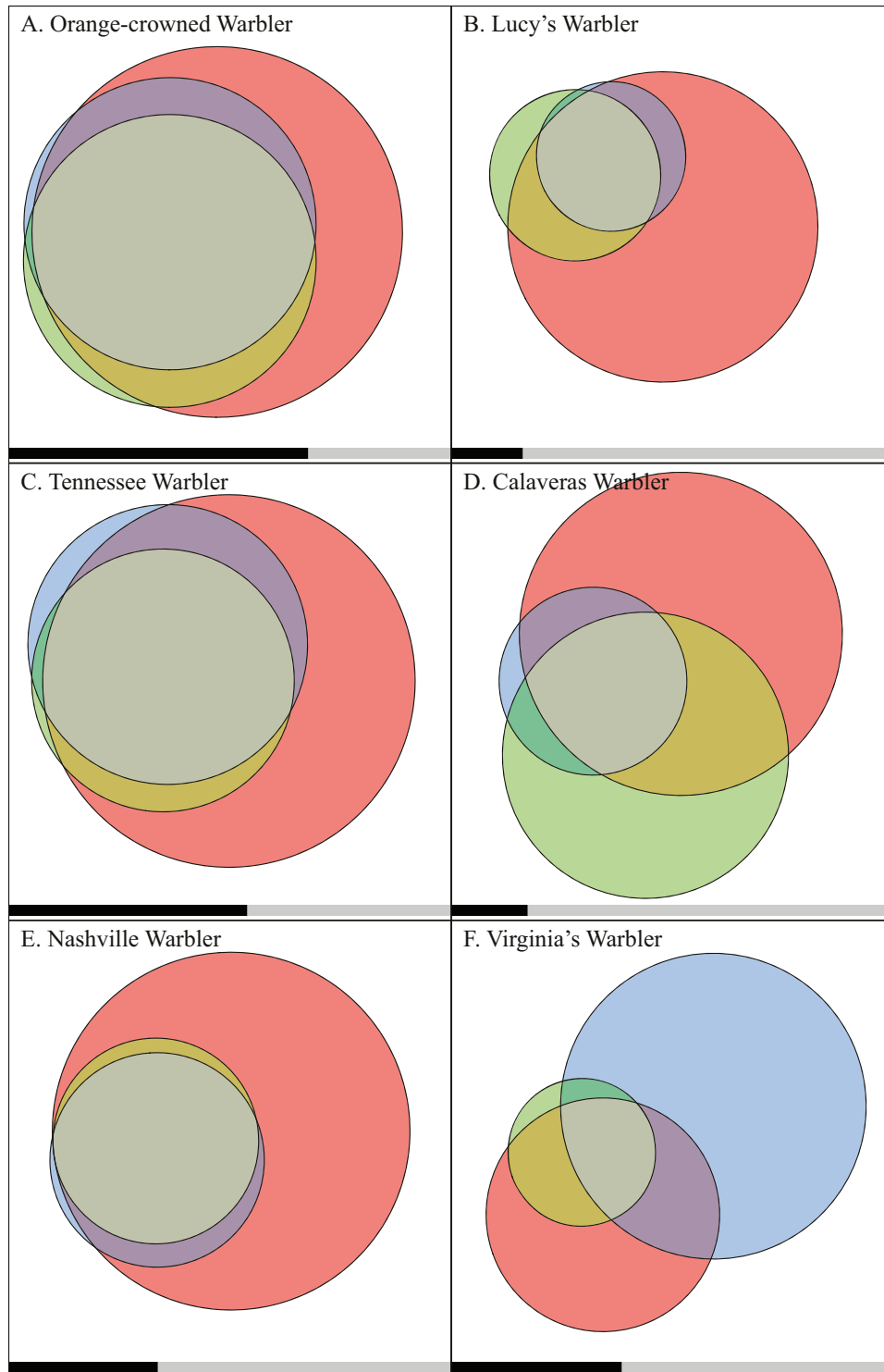


Figure 5: Empirical BAM (“biotic, abiotic, and movement”) diagrams calculated for each species of warbler examined in this study. Blue areas represent abiotically suitable regions based on climate-only ecological niche models (ENMs). Green areas represent biotically suitable regions based on pollen-only ENMs. Red areas represent available areas within which movement-related factors are not expected to be limiting (see text). The length of the black bar at the bottom of each diagram is proportional to the total area of the union of A, B, and M, indicating the “zoom” for each species relative to the whole of North America (the sum of the black bar and the gray bar).

Tennessee, and Lucy's warblers (fig. 5A–5C, 5E). For those species, when ENMs were projected to North America, areas abiotically and biotically suitable outside the training area (M) of the species were scarce. This is consistent with the scenario of distributional equilibrium (fig. 2C), in which the most important factor (or its correlate) limiting the species' distribution in the continent is included in the ENMs, and the species occupies all suitable areas.

In contrast, areas from which Virginia's warbler (fig. S5) is absent in the eastern United States were predicted to be climatically suitable. Concordant with the scenario of biotic limitations (fig. 2B), suitable areas based on pollen data were largely restricted to the vicinity of presence records for this species (fig. 5F). In particular, the high relative abundance of two plant functional groups related to mixed and deciduous forest account for the low suitability in the east. Reflecting the difference in forest composition among these areas, Virginia's warbler was associated with a large representation (more than 40% of relative pollen abundance) of the "eurythermic conifer" functional group species (such as junipers of the Cupressaceae family; table S1). In contrast, areas in which either "temperate summer green" or "warm temperate evergreen" represented more than 15% of the relative pollen abundance were estimated as not suitable.

Alternatively and consistent with abiotic limits to distributions (fig. 2A), the Calaveras warbler's climate-based ENM predicted a more restricted area than the one based on pollen, which indicated suitability in southwestern Canada, where the species is absent (fig. 5D). These biotically suitable areas experience unsuitably low temperatures and higher temperature seasonality than the modeled tolerances of the Calaveras warbler.

Importantly, cases like the Tennessee warbler suggest that species do not perfectly match just one of the hypothetical scenarios in figure 2 across all of its distribution. This species does not occur in western Alaska, where biotic factors seemed to be limiting (figs. 3, 5C). In this case, the abundance of boreal conifers was the variable that contributed the most to the model (as determined by this variable having the largest lambda weight in the ENM). Specifically, only areas in which pollen of species classified as "boreal conifers" accounted for more than 20% of the palynological composition were considered as suitable for it. Low suitability in western Alaska is explained by the change of a community dominated by boreal conifers into one with a large representation of "cool temperature summer green" plants west and north of the northern Rocky Mountains.

Discussion

As possible limits to species distributions, abiotic and biotic factors have often been treated as alternatives (e.g.,

Cumming 2002), but the current results indicate the utility of comparing models based on them separately and together. Although bioclimatic variables and those for pollen functional groups had low correlation coefficients (fig. S6C), pollen-only and climate-only models broadly overlapped for most of the taxa. Thus, abiotic and biotic factors are not geographically independent of each other for these species. Furthermore, for four species—orange-crowned, Lucy's, Tennessee, and Nashville warblers—most biotically suitable areas are also climatically suitable (and vice versa), which suggests that the plant communities in which these species occur are strongly associated with climate. While this pattern is congruent with the Eltonian noise hypothesis (Peterson et al. 2011) for this set of biotic factors, our results do not imply that this is the mechanism behind the geographical coincidence of climatically and vegetationally suitable areas.

Using climate and pollen data simultaneously produced the closest predictions to the actual geographical range for models when projected to the entire continent, but with only slight improvements over models made with one or the other (depending on the species involved; triangles in fig. 4). Additionally, with the exception of the Calaveras warbler, all species occurred across most of the abiotically and biotically suitable areas available on the continent, which suggests distributional equilibrium for them in North America. This pattern was also supported by the empirical BAM diagrams (fig. 5), in which nearly no abiotically and biotically suitable areas (the intersection of A and B in fig. 5) were outside the available areas for each species (M), except for the Calaveras warbler.

At odds with the view that abiotic factors constitute the primary limitations for species distributions at a continental scale (Pearson and Dawson 2003), only one of the six taxa examined (the Calaveras warbler) exhibited a pattern consistent with solely climatic limitation within areas accessible to it. Specifically, the models identified low minimum temperatures and high temperature seasonality as putative limiting factors (fig. 2A). Importantly, however, the role played by climate in shaping a species' geographical range cannot be discounted in those species for which independent models based on either climate or pollen had similar predictions. Moreover, climatic factors could play an indirect role through other biotic factors not explicitly examined here. For example, the availability of prey species (Price and Gross 2000), the availability of host species (Gutiérrez et al. 2005; Bozick and Real 2015), or the lack of competition (Taniguchi and Nakano 2000; Gutiérrez et al. 2014) or disease (Lips et al. 2008) could ultimately depend on the climatic limitations of the interacting species. In such a case, the effect of these interactions on a focal species' distribution would also be captured by the climatic variables used as long as the interactor occurred in distributional equilibrium with climate within the study region examined (Anderson 2013, 2017).

Furthermore, biotic data alone clearly provided relevant information not accounted for in climate-only ENMs for at least two species. For Virginia's warbler and to a lesser extent the Tennessee warbler, climatic models predicted more regions outside a species' distribution to be suitable than did the pollen data set. For Virginia's warbler—a species specialized to pinyon-juniper woodlands (Curson et al. 1994; Curson 2010)—climatically suitable areas in eastern North America, where this forest type does not occur, did not contain a high enough abundance of the conifer species required by this species. Importantly, the climatic suitability in this case is contingent on the ENM extrapolation into a portion of the areas in which less extreme droughts occur compared with those in which the model was trained. Similarly, for the Tennessee warbler (which during its breeding season is strongly associated with its primary prey item, the spruce budworm; Patten and Burger 1998; McMartin et al. 2002), the dominance of species in the functional group “cool temperature summer green” in northwestern Alaska resulted in low biotic suitability, as opposed to the boreal conifer-dominated areas where it is distributed. That pollen-based models correctly predict low suitability for the species in climatically suitable areas suggests that these biotic factors (i.e., plant species) could have been affected by similar historical events as the focal wood warbler species. Historical processes such as postglaciation range expansion, the inability to cross geographical barriers (i.e., the Rocky Mountains), or vicariant events would affect fauna and flora simultaneously (yet likely in idiosyncratic ways), but modern climate would not reflect these patterns.

This study provides a novel framework for testing patterns expected regarding the drivers of species' range limits at a continental scale. By estimating BAM diagrams empirically (the “biotic, abiotic, and movement” paradigm; Soberón and Peterson 2005), we evaluated the importance of abiotic, biotic, and movement-related limits to species distributions, harnessing a framework that previously had been used only theoretically. The putative mechanisms uncovered by the present correlative analyses should now be tested via experimental studies (Peterson et al. 2015). Additionally, future uses of this framework can include consideration of other classes of biotic interactions (e.g., predators, mutualists, and parasites; Giannini et al. 2013) when such interactors are not themselves affected by the focal species (i.e., they are scenopoetic; Soberón 2007; Anderson 2017). This framework is particularly well suited for systems in which the presence of an organism is essential to the occurrence of the focal species (e.g., phytophagous insects and their host plants or parasites and their hosts). Extensions of this paradigm should be developed for assessing the role played by biotic interactions on species ranges when populations of both species are linked (affect-

ing each other), which represents a current limitation to correlative SDMs (Anderson 2017). Finally, these results highlight the importance of considering the potential effects of biotic interactions when ENMs are projected across time or space and used as tools for policy making regarding issues such as invasive species and climate change (Sax et al. 2013; Louthan et al. 2015) or for biogeographical analyses (Kozak et al. 2008) in which the availability of palynological data now and in the Holocene (Maguire et al. 2015) highlights the potential of these data to be used to predict range shifts of other organisms tightly dependent on particular vegetation types.

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