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NICHE CONSERVATISM AND DISJUNCT POPULATIONS: A CASE STUDY WITH PAINTED BUNTINGS (*PASSERINA CIRIS*)

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Abstract.—Painted Buntings (*Passerina ciris*) breed in a variety of habitats across the southern United States; however, a 500-km gap divides the species into eastern and western populations with dramatically different molting schedules. By contrast, the closely related Indigo Bunting (*P. cyanea*) is syntopic with Painted Buntings, but its range includes the 500-km gap. To date, no well-supported hypothesis explains the gap in the range of Painted Buntings. We used MaxEnt to describe ecological niches of both species and performed comparative analyses of model results to evaluate niche similarity between the two Painted Bunting breeding populations and the range gap. All present-day niche models for both species predicted a single contiguous breeding range, which suggests that the gap in the Painted Bunting range is not bioclimatic in origin. Comparative analyses of the three different environments suggest little bioclimatic divergence. Distribution models during the Last Glacial Maximum suggest that Painted Buntings likely bred as far north as ~28°N latitude, with two disjunct populations in what are now Florida and northern Mexico. Although alternatives exist, the most parsimonious explanation is that the Gulf of Mexico serves as a migratory divide and there are fitness costs to birds attempting to fly around or over the Gulf to reach their molting or wintering grounds. This was a primary factor contributing to the origin of the current allopatric breeding distribution. Historical distribution models imply that the species may not have filled the 500-km gap as their breeding range expanded northward; divergent molting schedules may reinforce the existing range disjunction. *Received 14 August 2012, accepted 5 December 2012.*

Key words: breeding biology, distribution, migrant songbirds, migration, molt, *Passerina ciris*.

Conservatismo de Nicho y Poblaciones Disyuntas: *Passerina ciris* como Caso de Estudio

Resumen.—*Passerina ciris* se reproduce en una variedad de hábitats a través del sur de los Estados Unidos; sin embargo, una brecha de 500 km divide la especie en poblaciones del oriente y el occidente, las cuales presentan patrones de muda dramáticamente diferentes. En contraste, la especie cercanamente relacionada *Passerina cyanea* está es sintópica con *P. ciris*, pero su distribución incluye la brecha de 500 km. Hasta la fecha, ninguna hipótesis bien sustentada explica la brecha en la distribución de *P. ciris*. Usamos MaxEnt para describir los nichos ecológicos de ambas especies e hicimos análisis comparativos de los modelos resultantes para evaluar la similitud del nicho entre las dos poblaciones de *P. ciris* y la brecha en su distribución. Todos los modelos de nicho basados en condiciones del presente para ambas especies predijeron una distribución reproductiva continua, lo que sugiere que la brecha en la distribución de *P. ciris* no es de origen bioclimático. Análisis comparativos de tres ambientes diferentes sugieren poca divergencia bioclimática. Los modelos de distribución durante el último máximo glacial sugieren que *P. ciris* probablemente se reproducía hasta ~28°N de latitud, con dos poblaciones disyuntas en lo que ahora es Florida y el norte de México. Aunque existen alternativas, la explicación más parsimoniosa es que el golfo de México sirve como división migratoria y que hay costos en la aptitud para las aves que intentan volar alrededor o a través del golfo para alcanzar sus terrenos de muda o invernada. Este fue un factor primario que contribuyó al origen de la distribución alopátrica actual. Los modelos de distribución histórica implican que la especie pudo no haber llenado la brecha de 500 km conforme su distribución reproductivo se expandió hacia el norte; los patrones de muda divergentes podrían reforzar la disyunción existente.

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A species' distribution is the spatial portion of the environment in which a population can meet the basic requirements for persistence. These distributions often lie within a temporal context. That is, distribution patterns often change seasonally in response to available resources such as food, suitable roosting sites, predators, and bioclimatic constraints that drive the periodicity of such resources. Some of these annual movements can be quite dramatic (Alerstam 1993). Migratory movements of many species are related to annual phenological events associated with annual temperature and precipitation patterns that drive the seasonality of primary production.

Ecological niche models (ENMs) are a means of visualizing the relationship between known species occurrence data and abiotic factors (i.e., environmental or ecological data) to understand a species' fundamental niche (Soberón and Peterson 2005). Ecological niche models may predict relatively high suitability of regions where the species is absent, which suggests that biotic factors such as competition, dispersal, energetic constraints, or other unknown factors may limit a species' presence. In contrast to ENMs, species distribution models (SDMs) model the realized niche of a species. In SDMs, abiotic, biotic, and dispersal factors are incorporated because these factors already affect the known distributional range. A thorough discussion of the conceptual differences between ENMs and SDMs is provided in Peterson et al. (2008, 2011).

The Painted Bunting (*Passerina ciris*), a small migratory songbird, occurs in two isolated, regional populations. The larger population breeds in the southern Midwest of the United States, and the smaller eastern population breeds along the Atlantic coast. Indigo Buntings (*P. cyanea*) have a continuous distribution in eastern North America. The two Painted Bunting populations are separated by a gap of >500 km throughout most of Alabama and Mississippi. Painted Buntings can exploit diverse landscape types as they occur in riparian zones, sparsely forested areas, and shrublands across a variety of ecoregions and forest types (Lowther et al. 1999). They feed on small seeds and terrestrial invertebrates and are capable of adjusting their feeding behavior efficiently in accordance with local resource availability (Lowther et al. 1999, Fudickar 2007).

An interesting aspect of Painted Bunting natural history is that the molt and migration strategies of eastern and western populations are markedly different. Western birds begin fall migration in late July and August, and most individuals travel to stopover sites in northwestern Mexico, where they undergo a complete prebasic molt before moving farther south for the winter (Thompson 1991, Rohwer et al. 2009, Bridge et al. 2011). By contrast, the eastern population molts on the breeding grounds and migrates to wintering areas in southern Florida and the Caribbean only in late September or October (Thompson 1991). The role, if any, of different migration timing and routes in explaining the gap in the breeding range of the Painted Bunting remains unclear.

Although landscapes vary greatly along the Atlantic coastal plain, no obvious geographic or climatological feature excludes Painted Buntings from the gap area. At least some areas within the gap region appear to meet the basic requirements of Painted Buntings, so their absence from this area is puzzling, especially given that similar species (e.g., Indigo Buntings; Payne 2006) have continuous distributions that span the area between the eastern and western populations of Painted Buntings.

One possible explanation for this gap is that a particular combination of landscape variables in this area results in an unsuitable breeding habitat; some combination of conditions in the gap region may lie outside the ecological niche of the Painted Bunting. We investigated this possibility using ecological niche modeling, which characterizes the set of landscape and climatological factors under which a species can maintain populations (Elith et al. 2006). Although this approach is limited by the relatively few dimensions of the niche that can be characterized on similar spatial scales such as land use and climatic variables, niche models often produce accurate predictions of species' distributions (Raxworthy et al. 2007) and have been used to locate previously unknown areas of suitable habitat that have proved to hold substantial populations (Raxworthy et al. 2003, Menon et al. 2010).

Recent genetic analysis of Painted Buntings has suggested that the eastern and western populations may be emerging species (Herr et al. 2011); there has been little or no measurable gene flow between the two populations over the past 25,000 to 115,000 years. Recent reviews of the literature suggest that over evolutionary time, coarse-grained Grinnellian niches tend to be conserved in many species from individual life spans up to tens or hundreds of thousands of years (Wiens and Graham 2005, Peterson 2011). It is unlikely, therefore, that any considerable ecological niche differentiation has occurred in Painted or Indigo buntings since the Last Glacial Maximum (LGM), and it is even possible that niche conservatism drives the origin of migration in response to climatic shifts (Martínez-Meyer et al. 2004). Two distinct variations exist on the niche conservatism theme: (1) sister taxa are compared in a phylogenetic context to determine whether taxa are more similar than expected from random divergence (Losos et al. 2003), and (2) single species' conservatism is evaluated across spatial and temporal domains (Martínez-Meyer et al. 2004, Broennimann et al. 2007). Current distributions are invariably related to historical distributions, and niche modeling can estimate a species' potential distribution in recent geological time scales (Carstens and Richards 2007, Waltari et al. 2007). Determining the relative extent of the species' historical range can provide insight into the role that geographic barriers play in speciation events in migratory species.

In the present study, we employed niche modeling in a novel context. We exploited an abundance of occurrence data to evaluate the suitability of an area where the species of interest is known to be absent. In effect, we sought to determine whether climatic variation across landscapes could help explain the absence of Painted Buntings from portions of the southern coastal plains of the United States. For comparison we also model the ecological niche of the closely related Indigo Bunting, which has a continuous range. We used several modeling approaches to evaluate how both present-day and historical niche parameters are related to the unusual disjunct distribution of Painted Buntings.

Our first objective was to evaluate the potential for accurate prediction of the distribution of the Painted Bunting: to this end, we generated niche models for breeding distributions, and also for the eastern and western breeding populations separately. Next, we evaluated the degree to which the two breeding populations occur under common environmental circumstances. We reasoned that the extent of the areas within the gap classified as suitable habitat by these models would indicate whether climatic factors were a sufficient explanation of the gap, or whether we should consider other explanations. We further explored the Painted and Indigo buntings' niches over the past 21,000 years (i.e., since the LGM), to evaluate the potential role of historical contingency as a determinant of the current range of these species.

Combining this historical perspective, present-day niche models, and the known current species distributions inspires a number of explanations for the gap in the Painted Bunting's distribution, as well as insights into the bioclimatic factors that determine suitability of habitat for this species.

METHODS

Model Data

Locality data.—Our first objective was to understand the distribution gap in the breeding range of Painted Buntings across the United States by comparing ecological niches of western and eastern breeding populations and the region of the gap between them. We considered occurrence records from 15 May through 15 August to be representative of the breeding period (Lowther et al. 1999); occurrences outside this period were excluded from breeding-season analysis.

We based our ecological niche models on occurrence points for Painted and Indigo buntings obtained from the online Global Biodiversity Information Facility (GBIF) in September 2011. The GBIF collects occurrence data from multiple databases, including the Avian Knowledge Network, eBIRD, and Project Feeder Watch among many other sources. The original data query contained 29,093 and 154,056 records for Painted and Indigo buntings, from which we removed outliers from areas not considered to be a normal part of each species range (e.g., Minnesota, Washington, etc. for Painted Buntings), which might be sightings of vagrants or possibly misidentifications. Because models using only presence data can be affected by sample selection bias (Phillips et al. 2009) and spatial autocorrelation, we created a 0.0416°-resolution grid in which we included only a single randomly selected occurrence point per cell. This spatial filtering yielded 4,503 unique points from throughout the year for Painted Buntings and 15,670 unique points for Indigo Buntings. This stratification enhanced our ability to model the unbiased potential distribution of the species and avoid a prediction biased by sampling effort (Soberón and Nakamura 2009).

Environmental data.—We examined potential distributions across North America and the Neotropics from northwestern Canada south to Guyana (138.22°W, 52.60°W and 60.38°N, 6.87°N). For present-day analysis, we used subsets of the 19 variables from the BIOCLIM data set (Table 1), which contains bioclimatic data based on average weather-station data from 1960–2000. Data layers were used at a pixel size of 0.041667° square, which yielded a 2,087 × 1,340 pixel grid, with 2,628,345 pixels containing data points for all variables. Previous results from MaxEnt variable importance tests suggested that land use, slope, and aspect provided little useful information to our modeling effort, and these were omitted from further analyses. We projected niche models based on current climate conditions onto the corresponding set of bioclimatic variables for the Last Glacial Maximum; these were generated from the Model for Interdisciplinary Research on Climate (MIROC) and Community Climate Systems Model (CCSM3). We interpret these projections as estimates of breeding distributions during the LGM 21,000 years before present. The LGM data were obtained from the Paleoclimate Modeling Intercomparison Project Phase 2 (PMIP2) and used in the same spatial resolution as other environmental data.

TABLE 1. Predictor variables used in modeling the seasonal niches of Painted and Indigo buntings, with abbreviations and relative rank of different variables used in niche models of the two species' breeding ranges.

Variable	Abbreviation	Relative rank [a]
Annual mean temperature	1	3
Mean diurnal range	2	17
Isothermality	3	6
Temperature seasonality	4	8
Maximum temperature of warmest month	5	4
Minimum temperature of coldest month [b]	6	5
Temperature annual range	7	9
Mean temperature of wettest quarter	8	10
Mean temperature of driest quarter	9	7
Mean temperature of warmest quarter	10	1
Mean temperature of coldest quarter [b]	11	2
Annual precipitation	12	15
Precipitation of wettest month	13	11
Precipitation of driest month	14	13
Precipitation seasonality	15	20
Precipitation of wettest quarter [b]	16	16
Precipitation of driest quarter	17	12
Precipitation of warmest quarter [b]	18	19
Precipitation of coldest quarter	19	18
Land use [b]	LAND	22
Aspect [b]	ASP	23
Elevation [b]	ELE	14
Slope [b]	SLO	21

[a] Determined using MaxEnt jacknife text of variable importance.

[b] Not used in final models because of low modeling significance, high correlation with other variables, or lack of biological meaning.

Model Construction

Autopredictions.—We selected a series of 17 models that included model predictor variables that have been shown to be related to the ecological range limits of migratory birds including Painted Buntings (Root 1988a, b; Tingley et al. 2009). Initially, to test for variable significance, we used the MaxEnt jacknife function to measure the relative contribution of individual variables to a model. We included only variables that had pairwise Pearson correlation coefficients (Supplemental Table 1; see Acknowledgments) of <0.85 for the breeding season.

Allopredictions.—To test for a bioclimatic basis for the gap in the Painted Bunting's range, we used the three best models from those included in our autoprediction modeling. We selected random training points from within the eastern population and western populations. We then tested the suitability of these points based on the model parameters from the allopatric potion of the range (i.e., eastern sample points tested with western model and vice versa). This crossover approach provided an opportunity to test inter-predictability of the two populations based on spatially unbiased testing–training data.

Paleopredictions.—Because our alloprediction models were able to accurately characterize the eastern and western ranges of Painted and Indigo buntings (see below), we tested for evidence of a historical explanation for the disjunction. Creating predictive models for periods for which it is impossible to collect verification data for presence–absence statistics is a subjective exercise (Elith et al. 2011). We worked to ameliorate this

TABLE 2. Current breeding-range model evaluation for Painted Buntings (PABU) and Indigo Buntings (INBU). Results of model selection from 17 different combinations of variables that each have a proposed relation to the breeding ranges of Painted and Indigo buntings. Each variable has a pairwise Pearson correlation coefficient <0.85.

		Model selection rankings [b]			
Model	Variables [a]	PABU all	PABU east	PABU west	INBU all
1	1, 2, 10, 13	1 (1)	13	7	11
2	1, 10, 13, 14	6	6	2 (2)	9
3	4, 7, 10, 12, 15	13	5	13	4 (1)
4	1, 5, 7, 8, 9, 12, 15	2 (2)	16	4	6
5	1, 4, 7, 10, 12, 15	9	17	10	5
6	1, 2, 10, 12, 13, 14	4	10	3 (3)	7
7	2, 7, 8, 9, 10, 12, 15	11	15	6	2 (4)
8	3, 4, 7, 8, 9, 12, 15	15	14	16	12
9	1, 2, 7, 8, 9, 10, 12, 15	8	12	8	1 (3)
10	2, 7, 8, 9, 12, 15, 17	10	11	11	13
11	3, 4, 10, 12, 15	16	4	15	3 (2)
12	3, 4, 7, 8, 9	12	1 (1)	14	17
13	3, 4, 10, 15	14	7	12	14
14	3, 4, 13, 14	17	2 (3)	17	15
15	1, 5, 12, 15	5	8	1 (1)	10
16	1, 2, 7, 12, 15	7	3 (2)	9	8
17	1, 2, 10, 13, 14	3 (3)	9	5	16

[a] Variable numbers correspond with abbreviations outlined in Table 1.

[b] Model quality ranks evaluated by corrected Akaike's information criterion; numbers in parentheses are rankings according to the Bayesian information criterion.

subjectivity by establishing first which models showed the greatest predictability in the present era and then used the same set of models for historical projections assuming climatic niche conservation. For modeling the LGM breeding ranges, we used the three best models evaluated from model selection for each season (see Tables 2 and 3).

TABLE 3. Comparative results of niche model predictions. Evaluations of model allopredictability are evaluated using the average of three best models from model selection and the calculation of the partial receiver operating characteristic–area under curve (ROC–AUC) scores.

		Partial ROC scores			Student's *t*-test	
Model	Test points [a]	AUC at 0.95 [b]	null AUC at 0.5	AUC Ratio [c]	*P*	α
Painted Bunting both	East and west	0.90	0.49	1.84	<0.0001	0.05
Painted Bunting western	East	0.93	0.49	1.87	<0.0001	0.05
Painted Bunting east	West	0.18	0.17	1.07	<0.001	0.05
Indigo Bunting	All	0.89	0.48	1.85	<0.0001	0.05

[a] Occurrence points were randomly divided into subsets for use in either model training or testing.

[b] 0.95 corresponds to an error of omission of 5%.

[c] The AUC ratio; a score of 2.0 = perfect and 1.0 = random.

Model Evaluation

Model building (parameters).—We modeled ecological niches using the maximum entropy (MaxEnt) algorithm, version 3.3.1 (Phillips et al. 2006), a machine learning method that has demonstrated accuracy in estimating ecological niches of species (Elith et al. 2010). For each model, we performed 10 cross-validated replicates on subsets of known occurrence points for training. We allocated the algorithm a maximum of 2,500 iterations to converge, and we left all parameters at the default settings except for paleoclimatic models; we used a regularization multiplier set to default and 2.5 to fit more generalized models. Regularization allows species-specific tuning of model outputs, which minimizes potential overfitting when projecting to novel regions or climates and creates models that are a compromise between sensitivity and specificity (Anderson and Gonzalez 2011).

Given the absence of obvious "hard" barriers to dispersal of the species (with the exception of the Atlantic Ocean), we chose to use a background spatial extent that encompassed current seasonal ranges as well as regions ≤200 km outside the known range that were not separated by geographic barriers and that could have been a component of the fundamental niche (see Fig. 1). That is, we tested a hypothesis of "M," in the biotic–abiotic–movement (BAM) framework of Soberón and Peterson (2005), as described by Barve et al. (2011). The spatial extent for our background polygon was the area from which we drew random points to evaluate climatic niche similarity for each population. Because the movement of individuals within a breeding season is unlikely to be >200 km, the use of this background spatial extent is justified.

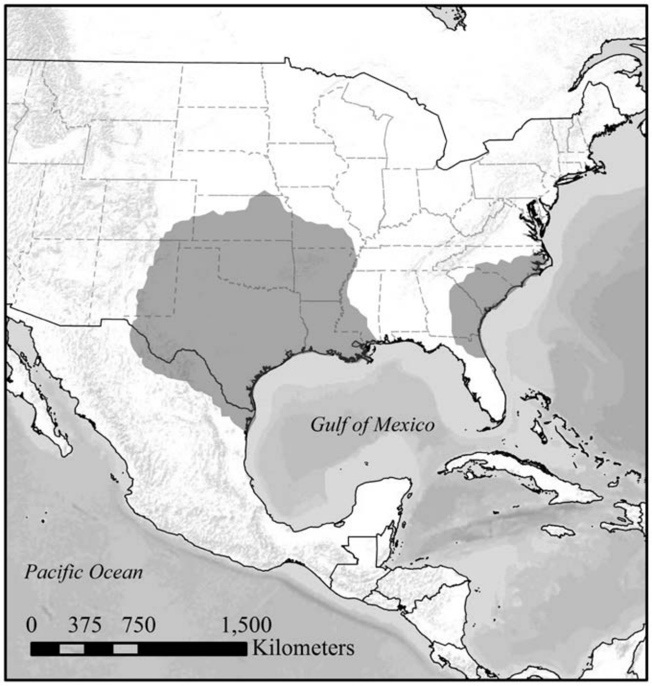

FIG. 1. Sampling envelope for background similarity tests of breeding-season populations. We calculated a 200-km buffer around current occurrence points to draw random test points for background similarity tests.

Model selection and comparison.—To evaluate model quality, we used the model selection tool within the ENMTools package (Warren et al. 2010). That tool evaluates complexity and generates Akaike's information criterion (AIC), corrected Akaike's information criterion (AIC_c), and Bayesian information criterion (BIC) scores for each model. We used these information criteria to select the best models. The three models with the lowest AIC_c scores were then compared using identical training–testing locality data between runs, to create a partial receiver operating characteristic–area under curve (ROC–AUC) statistic that we used to compare the explanatory power among similar models (Peterson et al. 2008). AIC_c was the most robust statistic for testing the model selection functions in ENMTools for ecological niche models (Warren et al. 2010).

Partial tests of receiver operator characteristics.—Traditional ROC analyses are not appropriate for evaluating niche models (Lobo et al. 2008, Peterson et al. 2008) or their predictive performance. We followed recommendations by Peterson et al. (2008) for calculating partial ROC scores, using a predefined expected error threshold of $E = 5\%$. We chose an omission error tolerance of 5% because of the potential noise associated with using publicly submitted occurrence records, in which misclassification, vagrants, and geolocation errors are possible. Depending on the study design and intent, errors of omission are more relevant in comparisons determining model quality than errors of commission (Anderson et al. 2003). The methodology we followed allows us to define the minimum acceptable sensitivity and evaluate model performance above this threshold. We allocated 1,000 iterations for calculating a partial version of the AUC (Hanley and McNeil 1982). We express the results as a ratio of the observed ROC curve to random expectations, where both are truncated to the area delimited by the error threshold. When using partial ROCs, only the portion of the area in the ROC curve where the model predictions are relevant is used in the calculation of a score (Peterson et al. 2008). Therefore, the null expectations for the model were <0.5. We report partial ROC scores as a ratio of the observed expectations to random, with a range of scores between zero and 2.0, where 1.0 is random expectation.

Niche similarity tests.—To test whether the ecological niches of the current eastern and western breeding ranges were more similar than expected by chance alone, we used the niche background similarity tests in the ENMTools package, version 1.3 (Warren et al. 2008, 2010). Allopatric populations rarely encompass identical distributions of environmental variables, and these two populations would be expected to be more similar than by chance alone, making the niche identity test inappropriate. The background similarity test circumvents this difficulty by creating a null distribution of the ENM differences between a population and a set of occurrence points selected at random from an allopatric area that should be accessible to the population of interest. We then used ENMTools to calculate niche similarity metrics *I* and Schoener's *D* (Warren et al. 2008). We compared these observed similarity values with the distribution of values of random replicates.

Comparison of niches in multivariate space.—We performed a principal component analysis (PCA) using the variables identified through model selection as components of the best-fit model. For this analysis, we selected 24 random occurrence points from each population (24 random points in gap region). To illustrate the comparison of the eastern and western populations along with the gap regions, we plotted the bioclimatic parameters associated with different regions in multivariate space (Fig. 2).

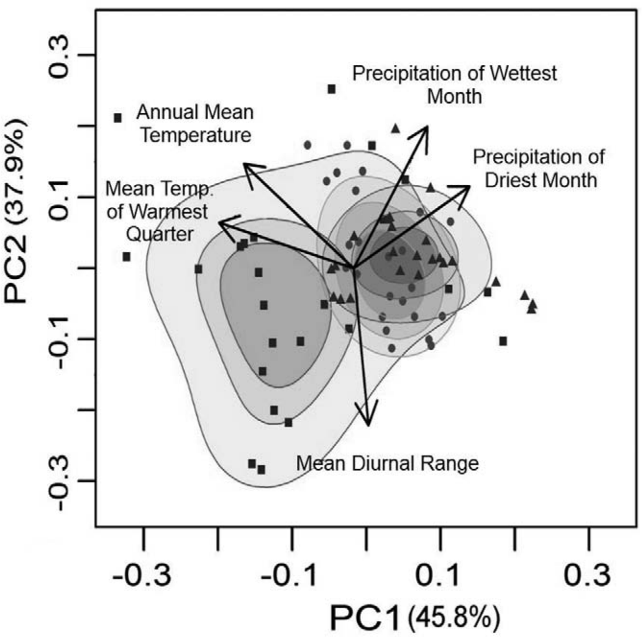

Fig. 2. Multivariate bioclimatic niche space of the three study regions. The occurrence data from western and eastern populations and the "gap" region are represented by squares, circles, and triangles, respectively. The climatic niche of the "gap" region overlaps the eastern population's points and lies within some of the western populations' sample points. The principal component (PC) analysis accounts for 83.7% of the total variation within the data set on the first two axes. The contour lines represent the nonparametric bivariate distribution of the sample occurrence data representing 0.25, 0.50, and 0.75 probability densities from outside of centroid inward. Climatic predictors used for this illustration are the best cumulative predictors for both the western and eastern populations, not as individual models.

Results

Current Climate

Autoprediction.—All three best models, based on AIC_c and BIC scores, were highly statistically significant for both Painted and Indigo buntings (Tables 2 and 3; Supplemental Tables 3, 4, and 5 [see Acknowledgments]). In each of these cases, a partial ROC curve for each model performed significantly better than random expectations (Student's t-test, $P < 0.001$, $\alpha = 0.05$), with average AUC ratios of 1.84 for Painted Buntings and 1.85 for Indigo Buntings. Predictions from these models suggest that bioclimatic divergence is not a sufficient explanation for the breeding-range gap in Painted Buntings. Much of the coastal plain of Alabama, Mississippi, and the panhandle of Florida were within the range of suitable scores. If the suitability threshold was raised, evidence of a gap began to emerge in the coastal plain between the eastern

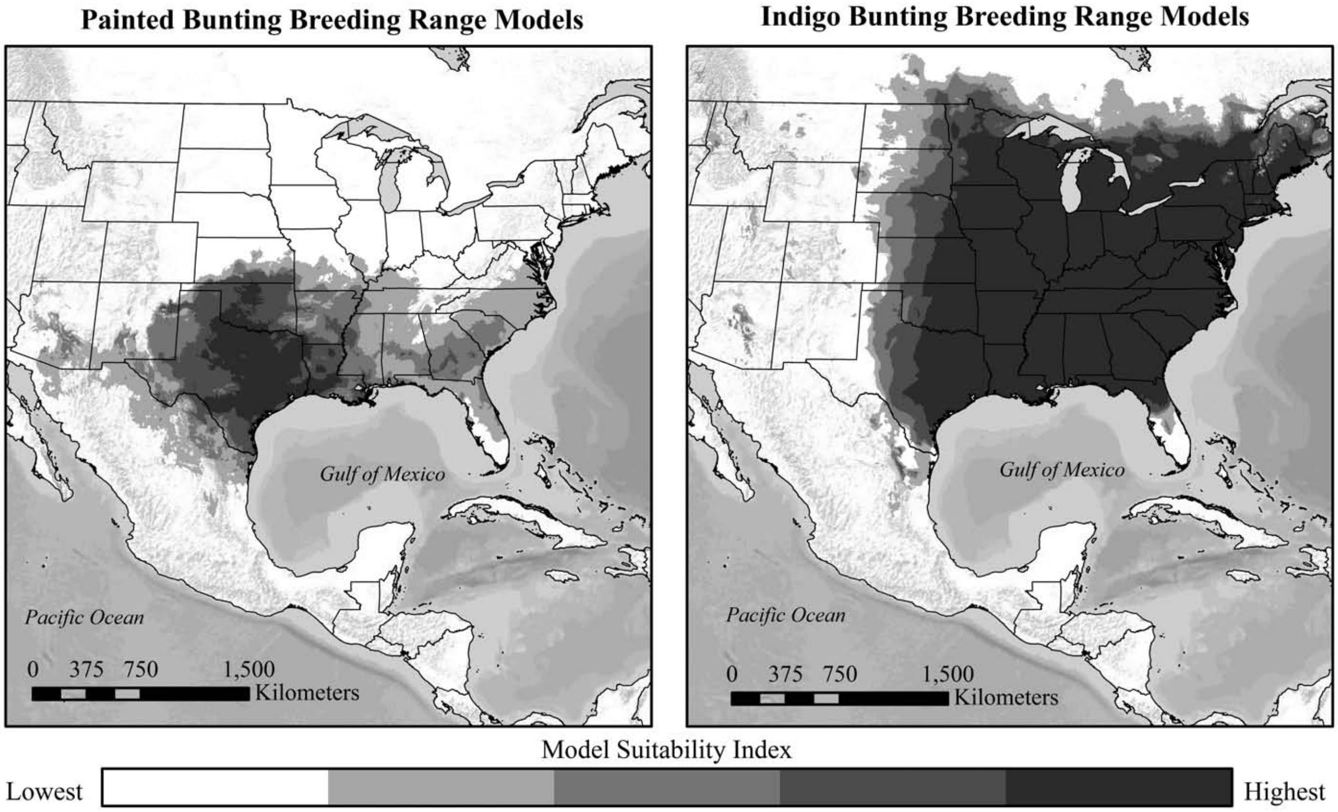

FIG. 3. Maps of breeding ranges using the entire range of occurrence points for Painted and Indigo buntings. We used climate data calculated from current occurrence points to predict the breeding distribution of each species. Each map represents the average of the three best models determined using model selection. The Indigo Bunting model accurately predicts the known breeding range; however, the Painted Bunting model suggests bioclimatic suitability within the known gap region where the species is absent. Scale is at equator in Mollweide projection.

and western populations (Fig. 3); however, the size of the area predicted as suitable also decreased in the region where the species is known to be present. These models suggest that the size and location of the present breeding range gap are not correlated with current bioclimatic patterns.

Alloprediction (*Painted Bunting only*).—When we used the western population for calibration and the eastern population for evaluation, the partial AUC ratio was 1.87 (Student's *t*-test, $P < 0.0001$, $\alpha = 0.05$). The region predicted to be suitable extended along the coasts of the Gulf of Mexico and Atlantic Ocean in the areas where the eastern breeding population resides. These models did not show any evidence of a gap in the species distribution (Fig. 4). However, the results were dissimilar when we used the eastern breeding population for calibration and the western population for evaluation. The best model predicted little of the western population's current range with a partial ROC score of 1.07. However, the similarity between the two distributions was still statistically significant (Student's *t*-test, $P < 0.001$, $\alpha = 0.05$). This model was, nonetheless, consistent with the model calibrated on the western range in identifying ample suitability across the gap along the Gulf of Mexico (Fig. 5).

Niche similarity tests (*Painted Bunting only*).—When we used the eastern population for calibration and the western population for evaluation, both niche metrics were significant (Student's *t*-test; I: $P < 0.001$; D: $P < 0.001$; $\alpha = 0.05$), indicating unexpected similarity given the landscapes on which the two populations are distributed. In the reciprocal prediction, comparing the western occurrence points to the points drawn at random from the eastern background, one of the niche metrics indicated significant similarity (Student's *t*-test; I: $P < 0.001$; $\alpha = 0.05$), whereas the other approached significance (Student's *t*-test; D: $P = 0.085$; $\alpha = 0.05$). These results suggest little niche differentiation in bioclimatic factors between these two populations, and that they occupy similar niches.

Principal component analysis of different regions (Painted Bunting only).—Climatic predictors used in the PCA were the best cumulative predictors for both the western and eastern population, not as individual models. The predictors used were annual mean temperature, mean diurnal range, mean temperature of the warmest quarter, precipitation of the wettest month, and precipitation of the driest month (Table 4). The first axis, which accounted for 45.8% of the variation, was a contrast of mean annual temperature and mean temperature during the warmest quarter with precipitation in the driest month; positive scores represented sites with low temperatures but high precipitation. The second axis contrasted precipitation in the wettest month with mean annual temperature and mean diurnal range in temperature. It accounted for an additional 37.9% of the variation,

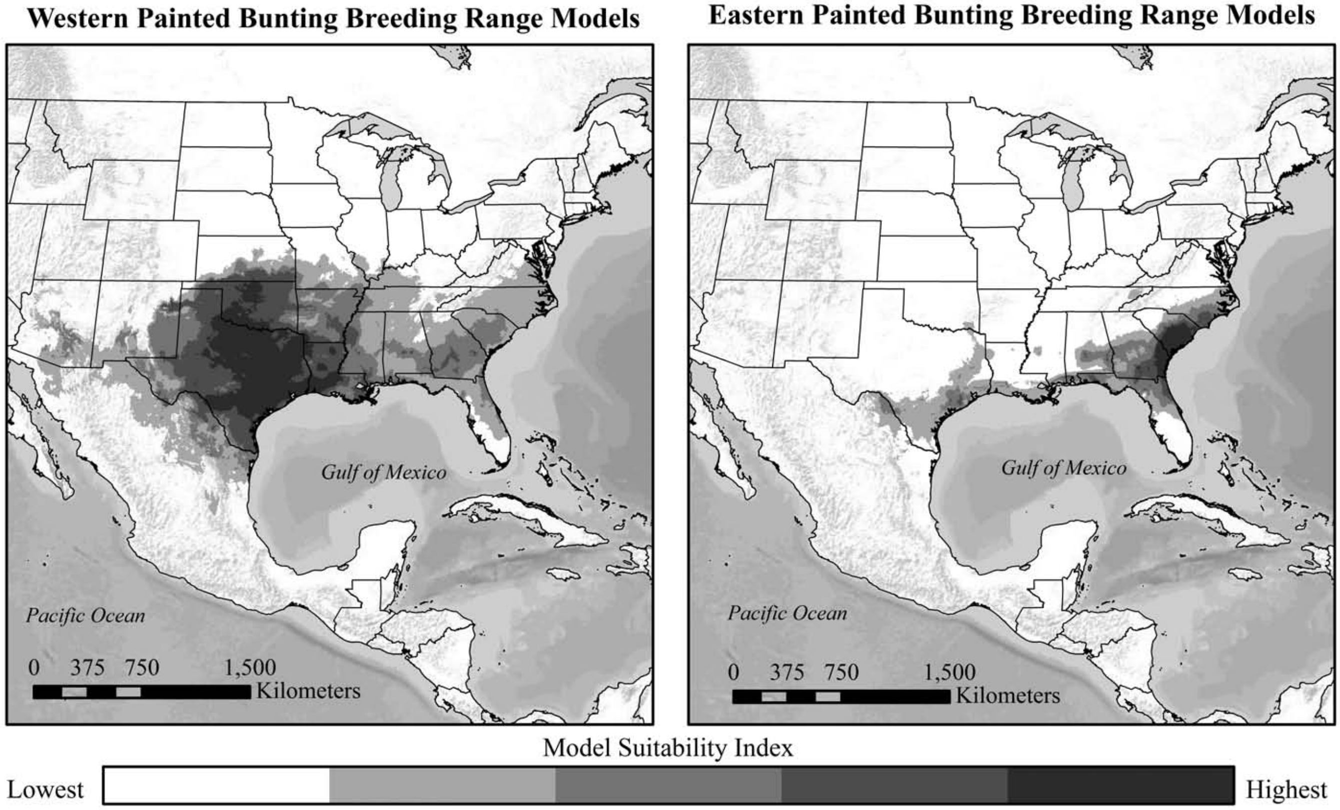

FIG. 4. Maps of predicted current breeding range derived from models based on breeding populations' western (left) and eastern (right) occurrence data. We used climate data calculated from current occurrence points to create models that predict the extent of the gap in the breeding distribution along the Gulf of Mexico coast. Each map represents the average of the best three models determined by model selection. Each model predicted a considerable suitable area across the known gap in the breeding distribution, providing no evidence of a climatic explanation for the gap. Scale is at equator in Mollweide projection.

with positive values being indicative of sites with high precipitation and high mean annual temperature, but low diurnal range in temperature (Table 4). We focus on just these two axes because they accounted for ~84% of the total variation. The region of the gap and eastern population overlapped almost entirely in multivariate space (Fig. 1), and many of the points from the eastern edge of the western population were in this multivariate space envelope. The western population covers a much larger geographic region experiencing a wider range of climatic conditions than the eastern population, and some of these points lie outside the climate envelopes of the eastern population and range gap in multivariate space.

TABLE 4. Factor loadings from the principal component analysis of the climatic predictor variables used in ecological niche modeling.

Variable	Abbreviation	PC1	PC2
Cumulative proportion		45.8%	83.7%
Annual mean temperature	1	−0.49	0.41
Mean diurnal range	2	0.07	−0.62
Mean temperature of warmest quarter	10	−0.61	0.18
Precipitation of wettest month	13	0.33	0.56
Precipitation of driest month	14	0.52	0.32

Historical Climate

Niche conservatism in many species suggests that using current climatic variables that accurately modeled breeding distributions may be useful for creating predictions based on paleoclimatic models (Martínez-Meyer et al. 2004, Waltari et al. 2007, Peterson and Nyári 2008). The CCSM3 and MIROC models for both species of buntings provided similar results for both seasonal predictions; the MIROC outputs were somewhat more conservative in estimating the species' range. Both LGM predictions of Painted Bunting breeding ranges showed a marked contraction in the extent of the western distribution that was not evident in the eastern distribution (Fig. 4). This discrepancy most likely results from maritime effects on climate in the coastal range of the eastern population, whereas the western population experienced a decidedly continental climate that has changed more over time. For Indigo Buntings, there is a marked contraction of their breeding range with their northern limit around 34°N; however, there was no indication of the existence of disjunct populations.

DISCUSSION

Breeding-range disjunction in the Painted Bunting.—All the niche models used to test autopredictions indicated that the area

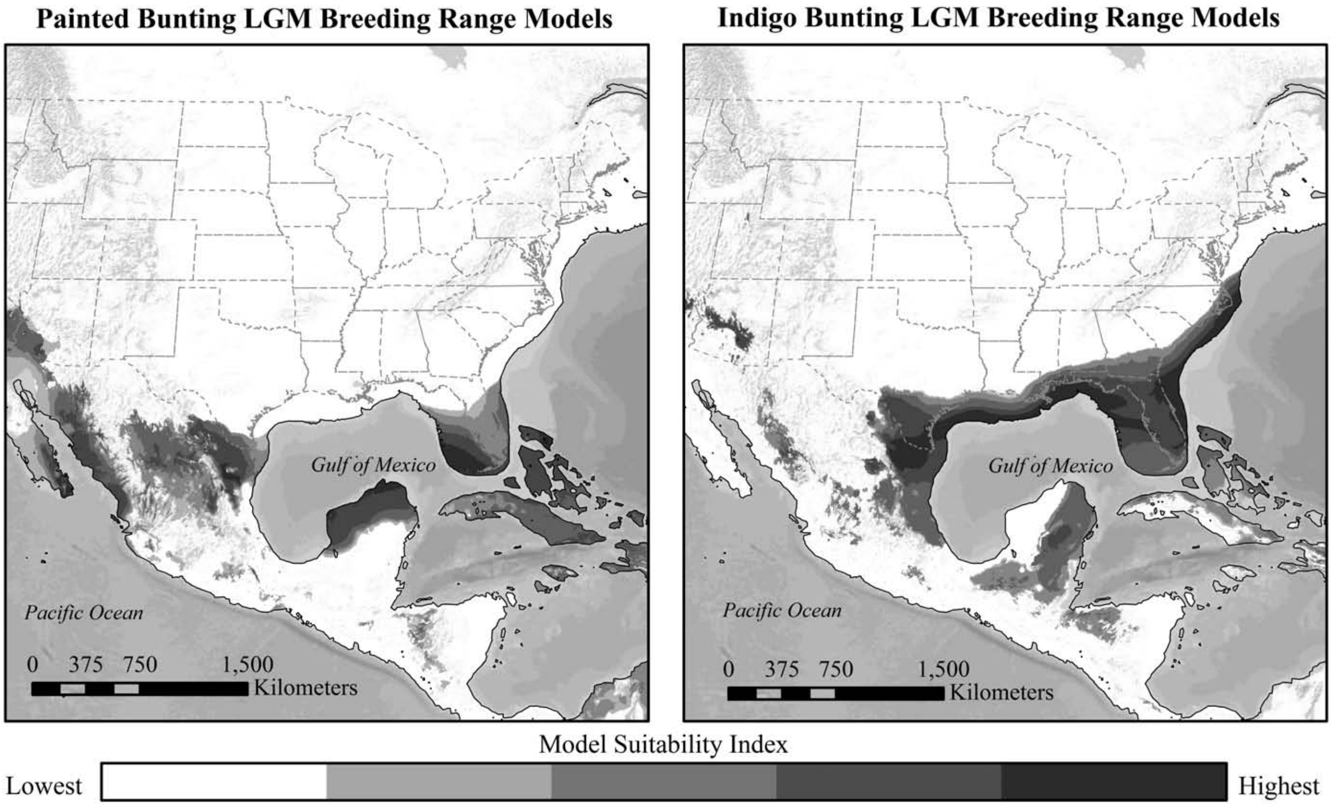

Fig. 5. Map of results of averaged MIROC and CCSM (see text) model paleo-projections at the Last Glacial Maximum (LGM) for Painted and Indigo buntings. Predicted breeding and wintering ranges were based on models that projected climate variables from current population ranges onto LGM conditions. For Painted Buntings, the regions of highest suitability are strongly divided into small groups on either side of the Gulf coast, whereas that for Indigo Buntings is continuous above the Gulf of Mexico. Considering the divergent molting schedules in present Painted Buntings, it is interesting that the region to which the western population migrates after breeding in northwest Mexico is predicted as being highly suitable. Depicted sea levels are from estimates during LGM conditions. Scale is at equator in Mollweide projection.

constituting the gap in the breeding range is bioclimatically suitable for Painted Buntings. When we made the suitability threshold more stringent, a gap began to emerge in the distribution predicted along the coastal plain, but this elevated threshold also significantly reduced the correspondence between model prediction of suitable habitat and the area where the species actually occurs. Model predictions varied with regard to how much of the known gap area was predicted to be suitable, but all model predictions included a substantial portion of the gap as suitable area (Fig. 3). The results of the background similarity test suggest that eastern and western breeding populations occupy bioclimatic niches that are more similar than expected at random. That is, there was no evidence of divergence along bioclimatic niche axes between eastern and western Painted Buntings. Niche model predictions based on occurrence data pooled from the entire breeding range identified the entirety of the gap in the breeding range as suitable.

Alternative explanations for the gap.—Ecological niche models usually do not incorporate interaction effects, biotic relationships (e.g., competition), and other unknown biological factors. For example, predator and parasite distributions may play an important role in shaping the life histories of migratory birds, yet such factors are generally not an explicit part of a distribution model (Folstad et al. 1991, Ydenberg et al. 2007). Consequently, niche models are typically an estimate of the fundamental niche rather than the realized niche of a species (Soberón and Peterson 2005). However, recent theory suggests that biotic interactions are manifested at much finer spatial scales than climatic variables (Soberón and Nakamura 2009). This effect has been termed the "Eltonian noise hypothesis" (Soberón and Nakamura 2009, Peterson et al. 2011) and has the potential to explain the good performance of niche models in predicting distributions in spite of not explicitly including biotic variables.

Moreover, details of species' responses even to abiotic factors may be missed. For example, for migratory species, understanding the temporal dynamics of the niche may be crucial for understanding distributions during the stationary phases of the annual cycle, and niche models do not often characterize seasonal changes in both breeding and wintering areas (Nakazawa et al. 2004). Carryover effects from one season to another are common (Marra and Holberton 1998), and it is unclear how best to incorporate such effects into niche models.

Nonetheless, results from our traditional niche-modeling approach imply that perhaps we need to look beyond basic breeding-season bioclimatic variables to understand the odd distribution of the Painted Bunting. Although numerous explanations are possible, here we explore several aspects of the species' natural history that may be relevant to the known gap in their distribution.

The different migration routes of the two Painted Bunting populations suggest that perhaps the Gulf of Mexico has served as a migratory divide as the species' breeding range has expanded north since the LGM. A migratory divide is a biogeographic feature that creates assortative breeding in adjacent or syntopic populations or subspecies. Expansion of either the western or eastern population into the known gap region may entail increased fitness costs associated with migration distance or difficulties associated with navigating longer or more complex migration routes. The striking population-based differences in molt strategy (eastern Painted Buntings undergo basic molt on the breeding grounds, and western Painted Buntings are molt migrants) only makes the possibility of the Gulf of Mexico operating as a migratory divide more likely. Two explanations that seem most likely are that either (1) in the present day, circumnavigation or crossing the Gulf of Mexico may be difficult; or (2) populations confined to separate migratory refugia at the LGM have not yet expanded to fill the region of the gap (i.e., non-equilibrated effects). Modeling of non-equilibrated effects in European tree species has suggested that postglacial expansion of ranges is strongly controlled by geographic dispersal constraints as well as climate, reinforcing the notion that present-day ranges may not be representative of modeled potential ranges because of limitations other than climatic envelopes (Svenning and Skov 2004, Svenning et al. 2006).

Moreover, as suggested by studies of Blackcaps (*Sylvia atricapilla*), interbreeding of individuals from eastern and western populations might produce offspring with "intermediate" migration behavior or molt strategies (Rohwer et al. 2005), which would likely impart low fitness to these individuals (Helbig 1991, 1996; Berthold et al. 1992). Although migratory divides are uncommon, clear examples of this phenomenon include Greenish Warblers (*Phylloscopus trochiloides*), Common Rosefinches (*Carpodacus erythinus*), Swainson's Thrushes (*Catharus ustulatus*) in the Pacific Northwest (Ruegg and Smith 2002), and Siberian Stonechats (*Saxicola maura*) that circumnavigate the Gobi Desert (Irwin et al. 2005). Because eastern and western Painted Bunting populations are not known to come into contact, it is possible that they are separated by a migratory divide associated with the Gulf of Mexico and the timing and location of molt during the annual cycle.

Our paleoclimate-based niche model projections suggest that the historical breeding range for Painted Buntings was considerably farther south than the current range, such that the bulk of suitable breeding habitat occurred at roughly the same latitudes as the Gulf of Mexico (Fig. 5). As a result, the historical breeding range likely divided into eastern and western segments around the Gulf of Mexico. It is thus possible that the present-day split in the Painted Bunting populations originated in the Pleistocene when the Gulf of Mexico divided the species' breeding range during globally cool periods. As the species presumably shifted its breeding range northward following LGM, the divided populations may have remained separate, given the length of migratory movements required, giving rise to the isolated eastern and western breeding ranges and the mysterious gap. There is higher haplotype diversity in the western population than the eastern population and no measurable gene flow between the coastal and interior population over the past 25,000–115,000 years (Herr et al. 2011). This time range corresponds most recently with the LGM and extends back to the interglacial optimum that occurred during the Late Pleistocene, known as the Eemian Stage, approximately 114 to 131 thousand years ago. It is interesting that the models showed a potential range expansion in the western population but not the eastern, and that genetic evidence (Herr et al. 2011) suggests greater haplotype diversity within the western population.

The breeding range of the Painted Bunting is unusual among migratory passerines because it is disjunct. Moreover, population trends in the western range tend to vary from increasing trends to strong negative trajectories, whereas population trends of eastern populations are stable or declining (Sauer et al. 2011), to the point where the population is at risk of localized extirpation (Rich et al. 2004). Given the lack of a clear difference in the bioclimatic factors associated with niche suitability across the range in most of our models (Fig. 1), it seems that climatic differences are unlikely to explain these differences in population trajectory. Comparative studies of migratory life histories and population connectivity (e.g., Webster et al. 2002) across the range of the Painted Bunting would provide useful insights into the factors that create different population trajectories.

The ecological niche of the Painted Bunting spans the known distributional gap, and the ecological niches of eastern and western populations are largely conserved. This strong niche conservatism allowed us to explore the role of paleoclimatic effects in the disjunct nature of these two populations. The Gulf of Mexico could have served as a migratory barrier during northward expansion after the Pleistocene and provided the isolation necessary for these two populations to diverge in molting and migration schedules in response to their exposure to different environments.

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