



RESEARCH ARTICLE

Effects of climate change on the evolution of Brown Creeper (*Certhia americana*) lineages

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ABSTRACT

Understanding how distributions of species change through time allows evaluation of hypotheses about factors shaping biogeographic patterns and evolutionary trajectories of genetic lineages. Ideally, such studies would assess whether population genetic processes are associated with geographic distribution shifts, loss or gain of distributional area through time, or fragmentation of distributional areas, information that can now be derived via ecological niche modeling. We examined the distributional changes through time in lineages and populations of Brown Creeper (*Certhia americana*), a widespread North American bird, to test biogeographic and population genetic hypotheses. In two populations with genetic support for population bottlenecks, Monterey County in California and the Sierra Madre Oriental in Mexico, ecological niche models indicated range contractions and increased fragmentation since the Last Glacial Maximum (LGM). Projections of niche models to the future suggested continuation of range contractions and fragmentation. Of the 3 major allopatric lineages of Brown Creeper (eastern North America, western North America, and southern North America and Central America), the most stable through time was the southern lineage, which corresponds with increased genetic diversity. The potential geographic distribution of the western lineage has remained stable in size but not location since the LGM, corresponding with a genetic signal of isolation by distance. The eastern lineage experienced range contractions during the LGM, likely resulting in the contemporary lack of genetic structure within the lineage. Finally, there is limited evidence of potential range overlap during the LGM between the western lineage and the other 2 lineages, although the overlap is limited to the Arizona sky islands between the west and south lineages. These results suggest that ecological niche modeling and population genetic data may be used as mutual predictors when investigating phylogeographic patterns and processes.

Keywords: *Certhia*, phylogeography, ecological niche modeling, fragmentation, niche conservatism, population bottleneck

Efectos del cambio climático en la evolución de los linajes de *Certhia americana*

RESUMEN

Entender cómo las distribuciones de las especies cambian a través del tiempo permite la evaluación de hipótesis sobre los factores que modelan los patrones biogeográficos y las trayectorias evolutivas de los linajes genéticos. Idealmente, estos estudios permitirían evaluar si los procesos genéticos poblacionales están asociados con los cambios en las distribuciones geográficas, pérdida o ganancia de área de distribución a través del tiempo, o la fragmentación de áreas de distribución—esta información puede ahora derivarse mediante el modelado del nicho ecológico. Examinamos los cambios en la distribución a través del tiempo en linajes y poblaciones de *Certhia americana*, un ave ampliamente distribuida en América del Norte, para evaluar hipótesis biogeográficas y de genética de poblaciones. En dos poblaciones con evidencia genética de cuellos de botella poblacionales (Condado de Monterrey, California y Sierra Madre Oriental, México), los modelos de nicho ecológico indicaron contracciones del rango y aumento de la fragmentación desde el Último Máximo Glacial (UMG). Las proyecciones a futuro de los modelos de nicho sugirieron la continuación de las contracciones y la fragmentación del rango. De los tres mayores linajes alopatricos de *C. americana* (este de América del Norte, oeste de América del Norte, y sur de América del Norte y América Central), el más estable en el tiempo fue el linaje sur, que corresponde a aumentos en la diversidad genética. La distribución geográfica potencial del linaje del oeste permaneció estable en tamaño pero no en ubicación debido a que el UMG coincidió con una señal genética de aislamiento por distancia. El linaje este experimentó contracciones del rango durante el UMG,

resultando probablemente en la falta contemporánea de estructura genética al interior del linaje. Finalmente, existe poca evidencia de superposición potencial del rango entre el linaje del oeste y los otros dos linajes durante el UMG, aunque está limitado a las islas del cielo de Arizona entre los linajes oeste y sur. Estos resultados sugieren que el modelado del nicho ecológico y los datos genéticos poblacionales pueden ser usados como predictores mutuos cuando se investigan los patrones y procesos filogenéticos.

Palabras clave: *Certhia*, conservadorismo de nicho, cuello de botella poblacional, filogeografía, fragmentación, modelado de nicho ecológico

INTRODUCTION

The spatial distributions of genetic lineages are of paramount concern to the field of phylogeography (Avice 2000). Understanding how distributions change through time, in size, and in other characteristics allows evaluation of hypotheses about factors shaping evolutionary trajectories of multiple genetic lineages. Over the past decade, newly developed methods (e.g., ecological niche modeling) have allowed biologists to characterize a species' existing ecological niche based on known occurrence locality information and associated environmental data. Ecological niche modeling methods can support and enrich genetic data from phylogeographic studies, although for most species these methods are limited to biogeographic (macro), not landscape (micro), scale questions (Guisan and Thuiller 2005) owing to limited data availability (Peterson 2009).

Studies using ecological niche modeling and multilocus genetic data have become more common as more methods and data become available (for examples, see Zink et al. 2013, Walstrom et al. 2012). Multilocus genetic studies allow investigation of population genetic processes such as population expansions, population bottlenecks, and gene flow between evolutionary lineages. Incorporating ecological niche modeling allows testing whether these population genetic processes are associated with distributional shifts (e.g., during Pleistocene glacial cycles; Jezkova et al. 2011), loss (or gain) of potential distributional area through time (Jezkova et al. 2011), or fragmentation of populations (Lim et al. 2011).

Over time, environmental characteristics change, driving landscape changes, as with Pleistocene glacial cycles influencing habitat shifts and changes in North America (e.g., Waltari et al. 2007). Assessing corresponding spatiotemporal shifts in distributions of species via these correlational approaches requires, at least initially, assumptions of niche conservatism through time of the species under investigation, such that species will either track habitat or risk extinction. Thus, in contemporary allopatric species (or lineages), niches must be tested to establish whether they have been conserved over relevant time periods. Here, we focus on niche conservatism, or retained ancestral traits, of large-scale climatic tolerances

(scenopoetic factors) that may limit distributions (Soberón 2007).

Although niches of allopatric species may seem different, they may remain constant (but broad) given the environment(s) available to them. For example, a species inhabiting the eastern deciduous forests of North America may seem, superficially, to inhabit a different niche than a species in North America's western coniferous forests. However, these species may share the same niche characteristics given the suite of environmental characteristics in their geographic region, with different lineages "expressing" different parts of a broad niche.

Recent methods (Warren et al. 2008, McCormack et al. 2010) allow comparison of niches between species by quantitatively considering the available background environment. In addition to niche conservatism or divergence, interpretation of species' niche models should consider the context of the organism's dispersal capabilities and life history characteristics (e.g., Swab et al. 2012), which provide more robust conclusions than simple interpretation of distributional models. For example, in birds, appreciable distances may separate fragmented "islands" of habitat, but the populations may still be effectively connected if dispersal ability is sufficient to link them genetically.

The Brown Creeper (*Certhia americana*; Aves: Certhiidae) is a common and widespread resident of North American mature, old growth coniferous, and mixed coniferous–deciduous forests. Currently considered a single biological species (AOU 1983, Chesser et al. 2013), the Brown Creeper shows significant genetic structure in both mitochondrial DNA (mtDNA; Manthey et al. 2011a) and nuclear DNA (nDNA; Manthey et al. 2011b). Concordant patterns of genetic structure between datasets identify 3 allopatric lineages: southern (southern Arizona south to Honduras), western (western mountain ranges of the United States and Canada), and eastern (eastern forests of United States and Canada). The earliest phylogenetic split in the species separates temperate and subtropical populations, coinciding with the largest difference in morphology (overall body size and coloration; Webster 1986), while morphological differences between eastern and western populations are largely clinal. The basal lineages separated ~1.50 million years (0.80–3.01 MYA highest probability density [HPD]) ago, while the eastern

and western groups within the northern lineage separated ~0.6 MYA (0.37–1.23 MYA HPD) ago (Manthey et al. 2011a, 2011b).

Population genetic data reveal that gene flow between lineages of Brown Creeper is limited, while gene flow within lineages is prevalent (Manthey et al. 2011a, 2011b). Two populations (Monterey County, California, and Sierra Madre Oriental, Mexico) show evidence of population bottlenecks (Manthey et al. 2011a, 2011b). Multiple allopatric lineages, estimates of divergence and gene flow, and varied population genetic patterns (e.g., bottlenecks; Manthey et al. 2011a, 2011b) thus make Brown Creeper populations an excellent system for using ecological niche modeling to illuminate biogeographic processes driving observed evolutionary trajectories.

To investigate how distributional changes have affected the evolution of the Brown Creeper, we created ecological niche models for its 3 lineages and projected them to past (Last Glacial Maximum; LGM) climatic conditions. The goals of this study were to (1) investigate patterns of niche conservatism (or divergence) between lineages; (2) investigate potential distributional overlap between lineages (e.g., did they persist in allopatry during the LGM?); and (3) identify changes in distributional range size, location, and patchiness through time, as they relate to population genetic characteristics.

To examine the effects of distributional changes on population genetic characteristics, we investigated the following null hypotheses: (H1₀) locations with genetic evidence of population bottlenecks have experienced range contractions and increased distributional fragmentation since the LGM and will continue this trend into the future; (H2₀) lineages that have higher inter-population genetic structure will be more stable through time; and (H3₀) evidence of potential geographic connectivity between lineages will be limited.

METHODS

Input Data

Georeferenced data associated with scientific specimens were obtained from ORNIS (<http://olla.berkeley.edu/ornisnet/>), an online portal to data associated with museum specimens in North America, and from the literature (Manthey et al. 2011a). Occurrence points within 10 km of each other were omitted to avoid over-sampling identical and closely neighboring raster cells. After data reduction, 1,557 occurrence points were used, including 659, 281, and 617 points for the eastern, southern, and western lineages, respectively (Appendix Figure 4).

We obtained 19 “bioclimatic” layers from the WorldClim database (Hijmans et al. 2005; www.worldclim.org), which contains worldwide precipitation and temperature information, including minima, maxima, and ranges of

values. Only 11 layers were included in our analyses (Appendix Table 5), however, owing to high correlation between some of the variables ($R > 0.8$). Past environmental layers for the LGM (21,000 years before present) were drawn from model outputs from the Community Climate System Model (CCSM3; Collins et al. 2006) and the Model for Interdisciplinary Research on Climate (MIROC; Nozawa et al. 2005). Additionally, future layers were downloaded for the time periods of the 2020s, 2050s, and 2080s for 3 scenarios of climate change (A1b, A2a, and B2a) using 2 global climate models, the Third Generation Coupled Global Climate Model (CGCM3.1; Environment Canada) and the Hadley Centre Coupled Model (HadCM3; Collins and Tett 2001). These layers were downloaded from the International Centre for Tropical Agriculture (Ramirez and Jarvis 2008).

Ecological Niche Modeling and Testing Niche Conservatism

Occurrence data and environmental layers were analyzed in Maxent (Phillips et al. 2006), which integrates occurrence data with environmental data to identify environmental conditions associated with occurrences. In Maxent, we applied default settings while using 3 occurrence-point datasets based on the eastern, western, and southern groups of Brown Creepers (Appendix Figure 4). Each occurrence dataset included 80% of the original locality data, with 20% excluded for model evaluation. For each lineage, we ran 50 bootstrap replicates to assess effects of occurrence dataset variation on model outputs. The training region for each lineage was defined as any area within 200 km of occurrence points for that lineage; following training, models were projected to the entire continent of North America for LGM, current, and future conditions. Future models were included to assess trends in populations experiencing bottlenecks. Models were thresholded (transformed to binary output) for visualization as inclusive of 90% of the training occurrence data.

Model evaluation was performed using the partial ROC method of Peterson et al. (2008). For each lineage, we ran 1,000 bootstrap replicates, each using 50% of the test data. We ran this analysis twice for each lineage, setting the threshold of acceptable omission error to 10% and 5% for each run; values consistently >1 indicated model performance above null expectations.

Using the environmental niche model testing method ENMTools (Warren et al. 2008), Schoener's *D* statistic (a measure of niche overlap; Schoener 1968) was calculated between each pair of niche models. This statistic calculates the similarity of raster data for each cell and is standardized to provide values between 0 and 1 over the entire extent examined. Higher values indicate a greater amount of overlap between models.

To test niche conservatism, as compared to conditions available across the accessible area, we used ENMTools' Background Similarity Test tool with 100 replicates for each comparison. This test determines whether partially overlapping populations (in this case lineages) are more similar or different from one another than would be expected given the environmental conditions available to each lineage. The available space for each lineage was defined conservatively as sites within 200 km of occurrence points of the lineage. We used this background space as a conservative estimate of environments to each lineage over recent evolutionary time (as compared to a generational dispersal capability). We used a conservative estimate here to reduce the chances of spurious conclusions of niche divergence owing to an overly large background space (Barve et al. 2011).

Output of the background tests included 2 null distributions: the expected values of overlap between lineage A's empirical model and lineage B background models (models of randomly selected points from lineage B's available space), as well as the expected values of overlap between lineage B's empirical model and lineage A background models. If overlap observed between the 2 empirical models fell within these null distributions, we did not reject the null hypothesis that the lineages' niches are no more similar or different than would be expected by chance. Alternatively, empirical overlap less than (or greater than) the null distributions led us to reject the null hypothesis and support niche divergence (or conservatism).

In addition to the ENM background testing method, we used a principal component analysis (PCA) method to test niche similarity compared to available habitat (as described by McCormack et al. 2010). The null hypothesis of this test is that observed niche divergence (D_O) is equal to background environmental divergence (D_{BE}). Niche conservatism is supported if $D_O < D_{BE}$, while niche divergence is supported if D_O is significantly different (t -test) between lineages and $D_O > D_{BE}$. Using all occurrence points and 1,000 background points per lineage (and their associated environmental data values), we performed PCA to obtain principal component axes that describe the environmental variation available to all Brown Creeper lineages. We used as many PCs as were necessary to investigate the majority of the variance in the data (until a PC did not explain 3% of the variance in the data). For each PC, we tested (t -test) whether occurrence data for each lineage differed significantly. T -test significance values were corrected for multiple comparisons using a Bonferroni correction (Miller 1966). Using a custom script in *R*, the mean difference between lineages (i.e. D_O) was compared to the mean difference of a null distribution of background samples (i.e. D_{BE}) for each PC and pairwise comparison of lineages.

Assessing Fragmentation and Range Shifts

When measured within a lineage, as opposed to between lineages as described in the preceding section, the statistic D can be used to measure niche stability through time. In this context, a higher value indicates relatively more stability than a low value, which would indicate less stability through time. Because of this, we used ENMTools to calculate D between time frames within the same lineage (e.g., between the LGM and contemporary models for each lineage).

In addition to testing within lineages, we measured overlap of models for all pairwise comparisons between lineages at LGM and contemporary conditions. These measures assess whether levels of allopatry changed (or will change) between time periods. Additionally, overlap between lineages was assessed by measuring the number of pixels designated as presence for both lineages in each pairwise comparison.

To calculate fragmentation, or the patchiness of potential space for each lineage, we used the following multistep process (similar to number of disjunct core areas [NDCA] statistic; McGarigal et al. 2012). First, we measured total area as the number of pixels in the raster for each model classified as presence in the binary model output. Second, we calculated the total number of patches inclusive of at least 100 pixels. Although this threshold is arbitrary, we applied it because of the high variability in number of small (<100 pixels) patches between contemporary and projected conditions. Next, we determined the number of patches assuming 2 levels of connectivity, 5 km and 10 km, which provided different levels of assumptions regarding the distance that may be trivial to Brown Creepers to traverse between nearby patches on a generational basis. Finally, we calculated patchiness, or fragmentation, as total area divided by the number of patches. All values were reported as relative to contemporary conditions with no dispersal between patches (i.e. values <1 indicate a model less fragmented than the current model and vice versa).

In addition to investigating patterns in the 3 lineages, we also investigated 2 populations that have undergone population bottlenecks (Manthey et al. 2011b). The first of these populations consists of birds from the Sierra Madre Oriental; we defined the area of this population as bounded by a polygon with corners at: (1) 21.67°N, 99.77°W; (2) 21.67°N, 98.20°W; (3) 25.99°N, 99.84°W; and (4) 25.99°N, 101.41°W. The second population investigated is in Monterey County, California, defined as the area within 200 km of the sampled population at 36.33°N, 121.58°W. For these populations, we calculated total area and fragmentation using identical methods to those described in the preceding paragraphs, including future projections as well as LGM projections.

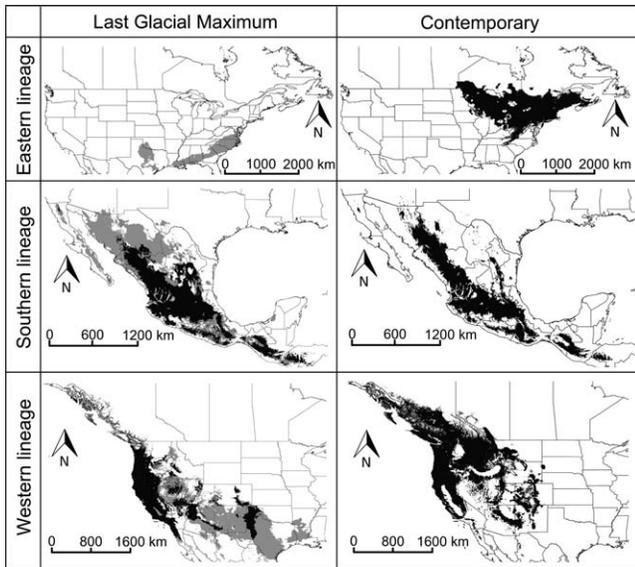


FIGURE 1. Ecological niche models for Last Glacial Maximum and Contemporary periods for the 3 lineages of Brown Creeper (*Certhia americana*). Suitable areas are colored black and gray in maps. For projected models, because 2 different climate models were used for projection, areas with prediction from 1 of 2 models is colored gray, with agreement between both models colored black.

RESULTS

Ecological Niche Models

Ecological niche models of the 3 lineages (Figure 1) accurately reconstructed the breeding range of Brown Creepers. The models performed well, both quantitatively and qualitatively. All area under the curve (AUC) ratios at acceptable omission thresholds of 5% and 10% were >1.5, well above null expectations (Table 1). When compared qualitatively to breeding maps from the North American Breeding Bird Survey, the sum of the 3 lineages seemed nearly identical, aside from a small area in southern Wisconsin which seems to have been overestimated in the model.

Models for the LGM varied between lineages and climate models (Figure 1). While the western and southern lineages were relatively stable between LGM and current conditions (Figure 1 and 2), the eastern lineage experi-

TABLE 1. Range of AUC ratios in the partial ROC testing of the models for each lineage. Omission thresholds of 10% and 5% were used.

	Omission Threshold	
	10%	5%
East	1.66–1.86	1.57–1.81
South	1.86–1.98	1.85–1.98
West	1.65–1.89	1.53–1.87

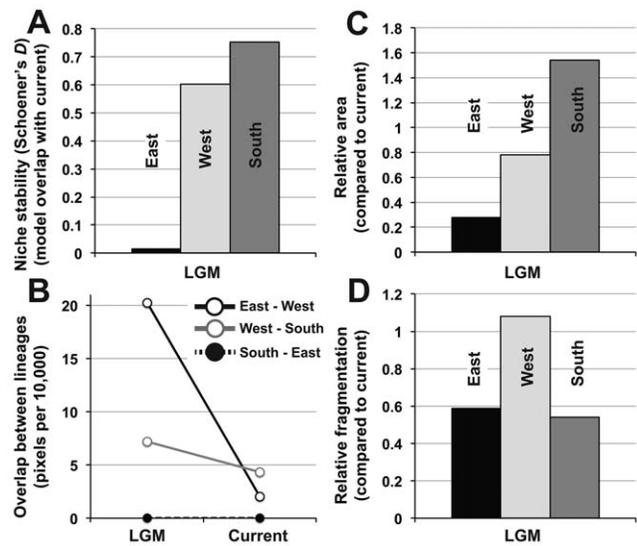


FIGURE 2. Patterns of (A) relative niche stability, (B) overlap between lineages, (C) relative area, and (D) relative fragmentation of Brown Creeper. LGM patterns are the average of the MIROC and CCSM climate model predictions.

enced large shifts in suitable geographic space. Niche models for the LGM differed between climatic models (CCSM and MIROC), mostly in the eastern lineage (Figure 1), where the CCSM model predicted only 2 small refugia in parts of North Carolina and Louisiana, while the MIROC model predicted a wide swath of suitable habitat.

Overlap between lineages showed largely different patterns, both currently and in the past (Figure 2). Overlap was measured using *I*, Schoener’s *D*, and the number of pixels designated as presence (from the binary maps) for both lineages in each pairwise comparison. These measures were all positively correlated ($R^2 > 0.86$, $p < 0.001$, for all pairwise comparisons); therefore, only one is reported in Figure 2. Generally, the southern and eastern lineages have had little geographic overlap through time, especially considering the accessible area to each lineage. The southern and western lineages have had moderate amounts of overlap in northern Mexico, Arizona, and New Mexico (Figures 1 and 2), although this has decreased through time. Lastly, the most varied patterns of overlap through time are between the eastern and western lineages; current overlap is relatively low, but during the LGM there was extensive potential overlap in Texas.

Patterns of Niche Similarity Between Lineages

Niche similarity between lineages was assessed using 2 methods, both of which consider each lineage’s niche within the context of the available environment to that lineage. The first method, which is model-based, identified varied patterns of similarity between lineages (Table 2). There was partial evidence for niche divergence between

TABLE 2. Results of niche divergence testing using a model-based method (Background Similarity Tests) in ENMTools. Observed values of model overlap were compared to overlap between empirical (e.g., West) and replicates of background models (e.g., East_bg). C and D indicate significant patterns of niche conservatism or divergence, respectively. Observed overlap between models was: East–West (0.092), East–South (0.016), and South–West (0.078).

	East_bg	South_bg	West_bg
East	—	0.008–0.011 C ($p < 0.01$)	0.098–0.122 D ($p < 0.01$)
South	0.018–0.022 D ($p < 0.01$)	—	0.066–0.084 NS ($0.11 < p < 0.12$)
West	0.102–0.118 D ($p < 0.01$)	0.054–0.079 C ($p < 0.05$)	—

the eastern and other lineages, while comparisons between the south and west identified patterns of niche conservatism.

Niche similarity was also investigated using a PC-based analysis. PCA identified 5 PCs explaining a modest proportion of the variance in the environmental data of occurrence and background points (~3% or more). In the 2 largest PCs (with ~70% of the variance of the data), patterns of niche conservatism (Table 3) matched those of the model-based method's results in the preceding paragraph. Again, the eastern lineage showed evidence of niche divergence, while comparisons between the west and south lineages identified niche conservatism (Table 3). PCs explaining less variance included varied results of niche divergence and nonsignificant results (Table 3). Because the southern and western lineages remain conserved relative to one another (in model-based and the first 2 PCs), and only comparisons involving the eastern lineage indicate niche divergence, the simplest explanation is differentiation of the eastern lineage from the ancestral trait. This pattern is reinforced in a phylogenetic context because the western and eastern lineages together are sister to the southern lineage, suggesting an ancestral niche more similar to the western and southern lineages.

Spatiotemporal Patterns of Potential Niche Area and Fragmentation

The 3 Brown Creeper lineages show varied patterns of changing relative area and fragmentation when comparing contemporary and LGM models. The 3 lineages have had

varied patterns of expansion or contraction since the LGM (Figure 2C; Table 4). One model for the eastern lineage, the CCSM model of the LGM, indicated relatively no potential habitat (<1% of contemporary area; Figure 1). Because of this, Figure 2C and 2D were edited to include only the MIROC LGM model for the eastern lineage.

Similar to relative area, the 3 lineages showed mixed trends in fragmentation through time; the eastern and southern lineages indicated increased fragmentation since the LGM, while the western lineage indicated slightly decreased fragmentation (Figure 2D; Table 4).

The 2 populations that have experienced a population bottleneck, Monterey County, California, and the Sierra Madre Oriental, showed similar patterns, although they vary in their similarity to the lineage they are nested within (Figure 3; Table 4; Appendix Table 6). These 2 populations exhibited evidence for greatly reduced potential area and much greater fragmentation since the LGM. Under future climate models, both populations will likely undergo range contractions and increased fragmentation of available habitat (Figure 3; Appendix Table 6).

DISCUSSION

Patterns of Niche Conservatism and Divergence

Niche conservatism is commonly observed among recently diverged animal taxa (see review by Peterson 2011). Alternatively, other studies have shown taxon groups to exhibit little or no relationship between ecological similarity and phylogenetic relatedness (e.g., *Anolis* lizards; Losos et al. 2003) or mixed patterns of niche conservatism and divergence between lineages (e.g., *Ephedra* shrubs; Loera et al. 2012).

While visual inspection of the 3 Brown Creeper lineages' niche models suggest they are nonidentical, 2 independent tests accounting for the available background environment for each lineage support varied patterns of niche conservatism and divergence (Tables 2 and 3). Similar patterns have been shown in *Aphelocoma* jays, where niche models of lineages (McCormack et al. 2010) seem visually divergent, but when available background environment is considered have varied patterns of niche conservatism and divergence.

Because the tests of niche similarity identify niche conservatism between the western and southern lineages

TABLE 3. Results of niche divergence testing using a PCA-based method. Observed mean values between lineages are shown above the range of values observed in the background testing replicates (in parentheses). C and D indicate niche conservatism or divergence, respectively. Proportion of variance explained of each principal component is shown in parentheses on the header line.

	PC1 (38.1%)	PC2 (32.0%)	PC3 (13.5%)	PC4 (8.9%)	PC5 (3.7%)
East–South	2.57 D (2.31–2.44)	3.14 C (3.48–3.56)	0.34 D (0.11–0.17)	2.26 D (1.01–1.07)	0.71 D (0.14–0.20)
East–West	2.10 D (1.52–1.62)	0.03 C (0.10–0.16)	1.42 C (1.50–1.56)	1.58 D (0.52–0.58)	0.07 (0.02–0.06)
South–West	0.47 C (0.73–0.87)	3.11 C (3.34–3.42)	1.75 D (1.36–1.43)	0.68 D (0.45–0.53)	0.78 D (0.10–0.16)

TABLE 4. Relative area and fragmentation of each model (compared to current) during the LGM for the 3 lineages and 2 populations (SMO = Sierra Madre Oriental; Monterey = Monterey County, California). All values of relative area and fragmentation are the average of both climate models for each scenario (e.g., CCSM and MIROC models for the LGM). For the eastern lineage, the relative area of the CCSM model was <1% of the current model and was not used in the average because of exponentially increasing fragmentation estimation. Fragmentation is also reported with connectivity between habitat “islands” of 5 km and 10 km relative to present fragmentation with no connectivity.

	Area	Frag	Frag (5 km)	Frag (10 km)
East	0.28	0.59	0.42	0.36
South	1.54	0.54	0.24	0.11
West	0.78	1.08	0.54	0.32
SMO	1.85	0.35	0.25	0.13
Monterey	1.81	0.28	0.28	0.28

(Tables 2 and 3), we are confident in assuming that niches remained similar during the climatic fluctuations of the Pleistocene. Because the eastern lineage exhibits patterns of niche divergence from the western and southern lineages, projections for this lineage should be interpreted with caution. However, niche divergence in this lineage potentially took place over a long time period (e.g., since lineage divergence, or 0.37–1.23 MYA); therefore, projec-

tions since the LGM (~22,000 years before present), a much shorter time scale, still present interpretable data.

Testing Phylogeographic Hypotheses Associating Population Genetics and Distributions

Our first hypothesis (H1₀) stated that populations with genetic evidence of population bottlenecks have experienced range contractions and increased distributional fragmentation since the LGM. The Monterey County, California, population shows decreased potential geographic space and increased fragmentation since the LGM; this provides a mechanism for a current bottleneck in this area, with little-to-no incoming gene flow from other populations in the western lineage. This is in contrast to the LGM models, where the central valley of California would likely have provided suitable climatic conditions for the Brown Creeper (Figure 1), allowing for gene flow between Monterey County and other populations in the western lineage.

Similarly, the Sierra Madre Oriental population has experienced decreased range size and increased fragmentation since the LGM (Figures 1 and 3). Additionally, during the LGM, and in contrast to current conditions, these populations potentially exhibited connectivity with other populations in the southern lineage, likely with populations to the south (e.g., Eje Volcánico Transversal of Central Mexico) based on coalescent analyses (Manthey et al. 2011b). This pattern of elevational expansion in colder climates and contraction during interglacials has been identified in geographic and genetic studies of several pine species (Ledig et al. 2000, González-Astorga et al. 2005) and birds associated with pines (Pygmy Nuthatch [*Sitta pygmaea*] and Steller’s Jay [*Cyanocitta stelleri*]; G.M. Spellman personal communication) of the Sierra Madre Oriental.

Under potential future scenarios, these 2 populations will continue to experience decreases in potential suitable range and increased fragmentation (Figure 3; Appendix Table 6). While similar between both populations, these patterns seem especially drastic under all climate models in the Sierra Madre Oriental (Figure 3) and would likely impact many montane species. Pine species, especially those already exhibiting limited ranges (e.g., Ledig et al. 2000, González-Astorga et al. 2005), as well as species relying on these montane pine forests for habitat (e.g., Pygmy Nuthatch and Steller’s Jay) would likely exhibit similar responses to the changing climate in the Sierra Madre Oriental, necessitating this locality as a target for conservation of the existing pine forest.

Our second hypothesis (H2₀) stated that lineages with higher within-clade genetic structure would have been relatively stable through time. Repeated movement within a lineage would have brought populations together, promoting gene flow and preventing inter-population

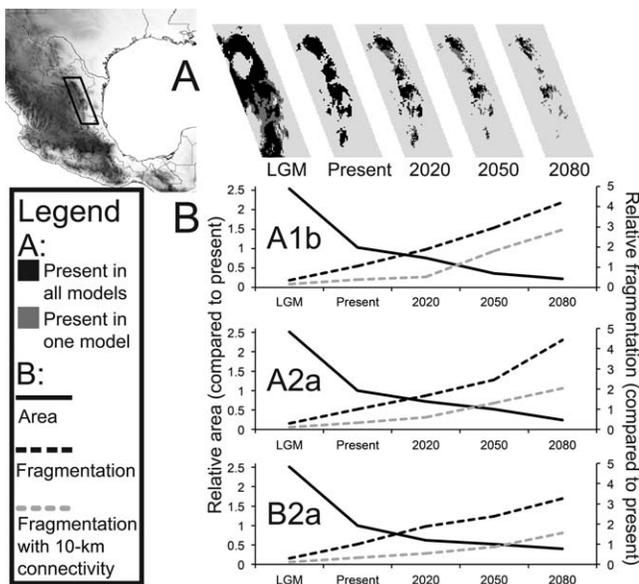


FIGURE 3. Patterns of relative area and fragmentation of niche models for the Sierra Madre Oriental population in Mexico. Inset map shows topography and encased area magnified in part A. (A) Predicted occurrence for projected models; future climate models for the A2a climate scenario; (B) trends of relative area and fragmentation (average of 2 climate models) under the 3 scenarios of future climate change.

divergence. Since the LGM, the southern lineage remained the most spatially stable (Figure 2A) while exhibiting a decrease in potential distributional area (Figure 2C; Table 4). Contemporary populations of southern Brown Creeper live in the sky islands of the major Mexican mountain chains, separated by environments unsuitable for colonization. As expected under H_{20} , the southern lineage exhibits the most private haplotypes or alleles in both mtDNA and nDNA (Manthey et al. 2011a, 2011b). Similarly, within the southern lineage is the largest signal for among-population (rather than within) variation in analysis of molecular variance (AMOVA) analyses (Manthey et al. 2011a). Additionally, the pattern of distributional expansion during the LGM is consistent with expected patterns of elevational shifts in species distributions during Pleistocene climate fluctuations (McCormack et al. 2009). These patterns may suggest that some, or all, southern Brown Creeper populations have undergone population size contractions since the LGM. MtDNA data support a similar pattern; as many (50%) of the populations in the Mexican clade differ significantly from the pattern of an expanding population (Manthey et al. 2011a).

The western lineage remained relatively stable in potential distributional area and fragmentation (Figure 2; Table 4), although less so than the southern lineage; however, Rocky Mountain populations likely experienced displacement (Figure 1). Following glacial retreat, populations of the Rocky Mountains were able to expand toward the current distribution, likely the cause for evidence of isolation by distance in the west (Manthey et al. 2011a). Other species of western North American birds show patterns both similar and contrasting to those of the western Brown Creeper. The Mountain Chickadee (*Poecile gambeli*) was shown to have a similar pattern of movement south and westward during the LGM (Waltari et al. 2007, Manthey et al. 2012). Conversely, the Blue Grouse (*Denragapus obscurus*), which exhibits a similar distribution to Brown Creeper and Mountain Chickadee, underwent range expansion during the LGM (Waltari et al. 2007).

The eastern lineage was the most displaced (Figure 2A) and most fragmented (Figure 2D; Table 4) of all lineages during the LGM, as well as having the largest change in total area between current and LGM conditions (Figure 2C; Table 4). Patterns of displacement and range-area instability likely led to a lack of significant genetic structure seen between contemporary populations (from mtDNA AMOVA analyses; Manthey et al. 2011a). Disparate patterns of stability between the eastern and other lineages (Figure 2A) may be a manifestation of the eastern lineage's relative ease to track suitable climate latitudinally since the LGM; conversely, more montane lineages (western and southern) may have been more likely to track suitable habitat elevationally, as was seen in

modeled climate-change responses of Rocky Mountain and Great Plains bird species (Peterson 2003).

Similar patterns of large changes in area, fragmentation, and displacement during the LGM are found in the eastern lineage of the White-breasted Nuthatch (*Sitta carolinensis*; Walstrom et al. 2012); in this species, there is a lack of significant genetic structure between contemporary populations following post-glacial expansion (Spellman and Klicka 2007, Walstrom et al. 2012) matching the pattern seen in the eastern lineage of the Brown Creeper. Conversely (although comparing only spatial, and not genetic, data), other eastern species show patterns of LGM refugia ranging from a single, tiny refugium (e.g., the pygmy salamander [*Desmogathus wright*]; Waltari et al. 2007) to large and widespread refugia (e.g., red-backed vole [*Myodes gapperi*] and five-lined skink [*Eumeces fasciatus*]; Waltari et al. 2007). This information supports the hypothesis that species with different habitat preferences experienced vastly different responses to the LGM in eastern North America (Soltis et al. 2006).

Finally, we hypothesized (H_{30}) that evidence of potential geographic connectivity between lineages would be limited. Potential overlap between the western and southern lineages, during contemporary and LGM conditions, occurs in Arizona, New Mexico, and northwestern Mexico. While not strong evidence for complete isolation, these patterns suggest connectivity between the western and southern lineages may occur somewhere in the sky islands between the Rocky Mountains and the Sierra Madre Occidental, in the cline between tropical and subtropical forests. This region represents the only known location of hybridization between the Rocky Mountains Brown Creeper (*C. a. montana*) and the Sierra Madre Occidental (*C. a. albescens*) subspecies in the Rincon Mountains of southern Arizona (Marshall 1956).

Similarly, LGM models of eastern and western lineages do not exhibit complete allopatry. During the LGM, a much higher level of overlap occurred between these lineages (Figure 2B), with a potential "bridge" of habitat connecting the lineages in Texas (Figure 1). If this pattern occurred during multiple glacial maxima of the Pleistocene, it could explain diversification of the Brown Creeper into the forests of eastern North America during a period of connectivity (0.37–1.12 MYA). However, a lack of fossil data in *Certhia* precludes verification of whether any *Certhia* were in eastern North America prior to this time period. This pattern of connection in the southern United States during the LGM between the eastern and western lineages (Figure 1) may also explain the persistence of gene flow or retention of ancestral genetic variation observed within these lineages (mtDNA and nDNA structure, but lacking nDNA fixed differences; Manthey et al. 2011b).

The best example of isolation manifested in the ecological niche models occurs in Central America and

southern Mexico. Here, suitable regions in Guatemala, Honduras, and Chiapas, Mexico, are separated from all other regions of the southern lineage by unsuitable regions in the Isthmus of Tehuantepec during contemporary and LGM conditions (Figure 1). This pattern is manifested in genetic data, which show strong, yet shallow, genetic structure in both mtDNA and nDNA (Manthey et al. 2011a, 2011b).

Conclusions

We performed ecological niche modeling on 3 allopatric lineages of Brown Creeper, with additional emphasis on 2 populations with genetic evidence for population bottlenecks. We identified mixed patterns of niche conservatism and divergence between lineages, although only comparisons with the eastern lineage included evidence for niche divergence from other lineages. In the 2 populations with genetic evidence for population bottlenecks, ecological niche models indicated potential geographic distribution range contractions and fragmentation since the LGM, with projections of models into the future suggesting continuation of population contraction and fragmentation. Patterns of genetic differentiation within lineages correspond with geographic and potential size stability since the LGM. The southern lineage has remained relatively stable since the LGM, with a gap at the Isthmus of Tehuantepec between northern and southern populations (current and LGM) manifesting in strong genetic structure across this boundary. The western lineage remained stable in potential distributional size but not geographic space, evident as a pattern of isolation by distance in genetic data. The eastern lineage was the least stable in potential geographic space and location since the LGM, resulting in a lack of any genetic structure with the clade. Together, the genetic and ecological niche modeling data provide synergistic evidence to describe the processes driving the patterns in phylogeographic data.

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Diego Museum of Natural History, University of Alaska Museum of the North, University of British Columbia Beatty Biodiversity Museum, University of California at Los Angeles, University of Michigan Museum of Zoology, and the Yale University Peabody Museum.

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APPENDIX

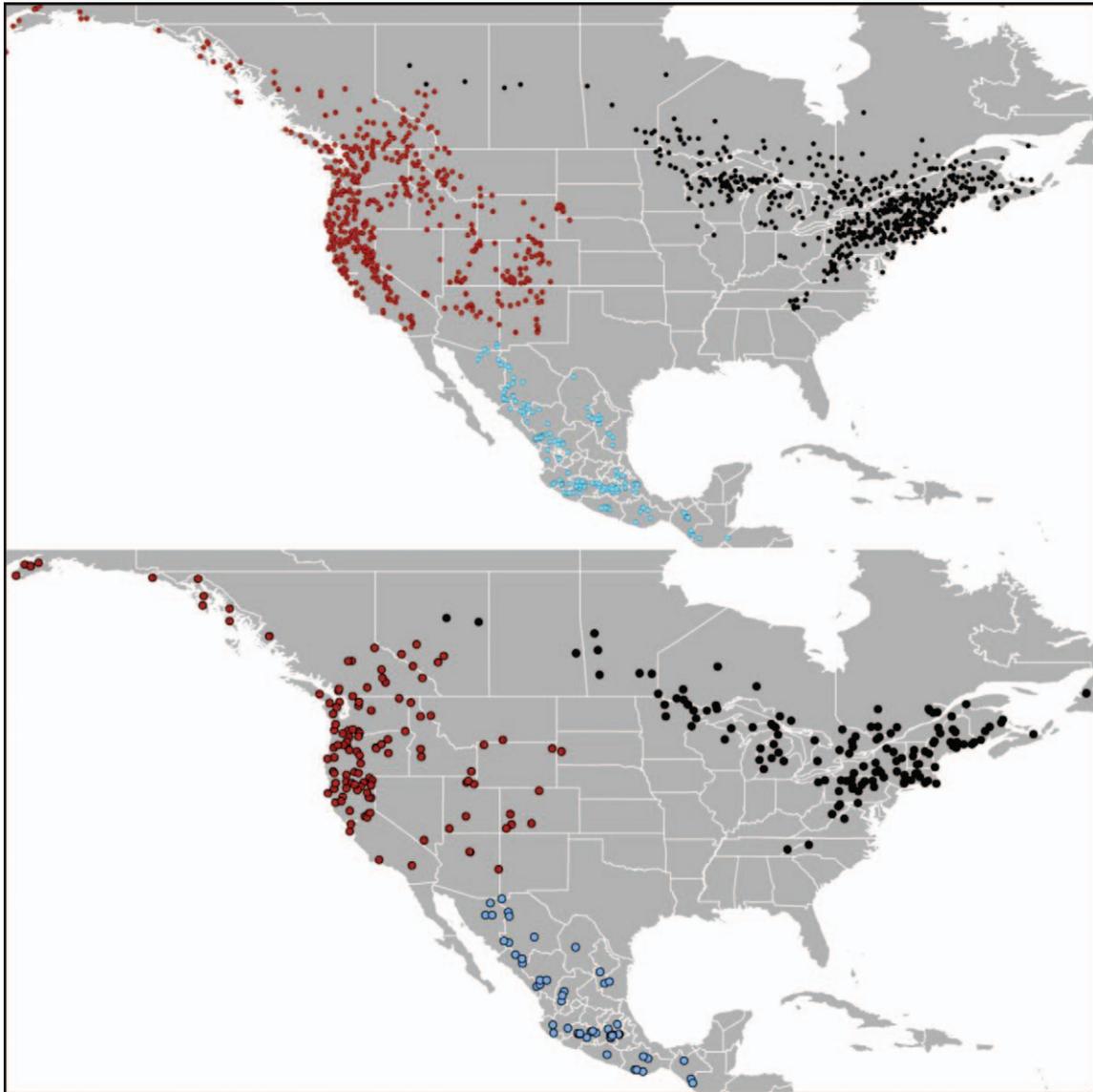


FIGURE 4. Training (above) and testing (below) locality points for the niche models of the eastern (black), western (red), and southern (light blue) lineages.

Appendix Table 5. Environmental layers (“bioclimatic” layers), and their descriptions, used in ecological niche modeling.

Layer	Description
Bio1	Annual mean temperature
Bio2	Monthly temperature range
Bio4	Temperature seasonality
Bio5	Max temperature warmest month
Bio6	Min temperature coldest month
Bio9	Mean temperature driest quarter
Bio12	Annual precipitation
Bio15	Precipitation seasonality
Bio17	Precipitation driest quarter
Bio18	Precipitation warmest quarter
Bio19	Precipitation coldest quarter

Appendix Table 6. Relative area and fragmentation for the two populations with genetic evidence of population bottlenecks. All values are relative to current model with no connectivity.

	Model	Area	Fragmentation	Frag. (5 km conn.)	Frag. (10 km conn.)
Monterey	LGM	1.89	0.18	0.18	0.18
	Current	1	1	0.33	0.33
	2020 A1b	0.69	4.02	1.63	0.71
	2020 A2a	0.66	5.94	3.56	1.19
	2020 B2a	0.67	4.70	2.57	1.01
	2050 A1b	0.50	5.70	3.51	2.85
	2050 A2a	0.59	5.42	3.12	2.56
	2050 B2a	0.59	7.85	4.13	2.56
	2080 A1b	0.33	9.21	5.15	3.76
	2080 A2a	0.75	3.30	2.52	2.35
	2080 B2a	0.59	3.67	3.10	2.26
	Sierra Madre Oriental	LGM	2.52	0.30	0.22
Current		1	1	0.33	0.33
2020 A1b		0.73	1.83	0.70	0.46
2020 A2a		0.72	1.67	0.60	0.60
2020 B2a		0.62	1.88	0.94	0.54
2050 A1b		0.34	2.90	1.96	1.75
2050 A2a		0.52	2.46	1.69	1.31
2050 B2a		0.52	2.39	1.26	0.86
2080 A1b		0.19	4.15	3.42	2.81
2080 A2a		0.24	4.43	2.85	2.03
2080 B2a		0.40	3.25	1.93	1.55