EVOLUTIONARY ECOLOGY

Glaciation as a migratory switch

Robert M. Zink[1]* and Aubrey S. Gardner[2]

Migratory behavior in birds is evolutionarily plastic, but it is unclear how this behavior responded during glacial cycles. One view is that at glacial maxima, species simply shifted their breeding ranges south of glacial ice and remained migratory. To test this hypothesis, we constructed ecological niche models for breeding and wintering ranges of 56 species, finding that 70% of currently long-distance North American migrant species likely lacked suitable breeding habitat in North America at the Last Glacial Maximum (LGM), and we hypothesized that they reverted to the ancestral state of being tropical sedentary residents. A smaller percentage of short-distance migrants (27%) experienced altered migratory behavior at the LGM, although the ranges of all species were shifted southward, as traditionally envisioned. We suggest that many species oscillate between sedentary and migratory strategies with each glacial cycle acting as an adaptive switch. Thus, range shifts occur more frequently than speciation events and are inadequately depicted by phylogenetic reconstructions. We suggest that reconstructing the evolutionary history of traits, such as migratory behavior, is best served by using ranges at glacial maxima. A phylogeny of warblers strongly predicted LGM, but not present distributions, and suggested that migration was re-expressed from three tropical centers of warbler diversity. Understanding of evolutionary history will be improved when reconstructions use distributions relevant to the time of character transitions.

INTRODUCTION

Observations in historic times reveal that species ranges expand and contract on decadal scales. Reconstructions of the distributions of Northern Hemisphere glaciers led to the conclusion that species ranges were necessarily fluid over millennial scales because thousands of square kilometers of landscape that provided suitable habitat during interglacials were ice-covered during glacial maxima (1). Despite our extensive understanding of glacial history, many evolutionary reconstructions do not adequately account for glacial-induced range shifts. For example, it is usually assumed (2–4) that migratory behavior in birds evolved in once-sedentary tropical species in which populations expanded northward following glacial retreat, eventually reaching an environmental threshold caused by seasonal climatic deterioration and reduction of the food supply, which triggered an annual postbreeding migration southward back to ancestral tropical areas. Components of this "southern home hypothesis" (SHH) include (i) a fitness advantage to individuals that migrate, (ii) establishment of an intermediate partially migratory population, and (iii) the concomitant northward advance of the southern breeding limit, creating a sizeable gap between the breeding and wintering areas. The SHH is attractive because it could explain how birds hatched in far-north temperate forests successfully survive their first winters in markedly differing tropical forests; ecologically speaking, they are "returning home" (5, 6) and do not need to evolve a new set of adaptations to tropical biotic and abiotic conditions (7), unlike requirements for the alternative "northern home" hypothesis (2, 3). A fundamental question concerns how glacial cycles influence the expression of migratory behavior.

Traditional interpretations typically have implied that at glacial maxima, north-temperate migratory species shifted their breeding grounds to localized southerly glacial refugia but remained migratory, migrating shorter distances to the same wintering areas. Winger *et al.* [(8), p. 12119] suggested that "Plio-Pleistocene glaciations have clearly served to modify geographic ranges and migratory distances and

routes…" Given the rapidity with which migration can be expressed or suppressed both experimentally and in natural situations (9), an alternative to a southern shift in breeding ranges is that species ceased migratory behavior at glacial maxima and reverted to being tropical sedentary residents (10). With the transition to the next interglacial and the environmental amelioration of areas previously occupied during the previous interglacial, migratory behavior would be re-expressed. Species whose durations span multiple glacial cycles would experience multiple oscillations between migratory and sedentary behavior, with glaciation being the adaptive switch. To our knowledge, this has not been previously proposed.

Niche modeling and LGM breeding distributions

We constructed climatic ecological niche models (11) for breeding and wintering ranges independently at the present and at the Last Glacial Maximum (LGM; 21,000 years before present) for a taxonomically diverse set of 56 long-distance migrant (LDM) or short-distance migrant (SDM) species to determine whether LGM breeding ranges existed in North America (appendix S1). Species were chosen to (i) represent a well-sampled phylogeny (8, 12, 13) and (ii) provide taxonomic breadth. This exercise assumes, as have hundreds of published studies [for example, the study of Peterson *et al.* (14)], that species' fundamental ecological niches have been conserved since the LGM. However, whether a species is present in an area depends on both the climatic regime and suitable habitat, and in some instances, a climate niche model suggests appropriate climatic conditions, but habitat reconstructions suggest an inappropriate habitat. Thus, we consulted maps of the approximate distribution of major vegetation types at the LGM (15) to check whether climate niche models predict presence in areas of inappropriate vegetation. We classified species as LDMs or SDMs; the distinction is somewhat subjective, but in general, for the latter, there is a relatively short distance between breeding and wintering areas (2). If a species' predicted LGM breeding ranges were lacking or very small and wintering ranges equal to or greater than at the present, we inferred that the species switched from migratory to sedentary. We reasoned that very small populations coupled with the costs of migration would prevent persistence over tens of thousands of generations in the Northern Hemisphere during glacial maxima.
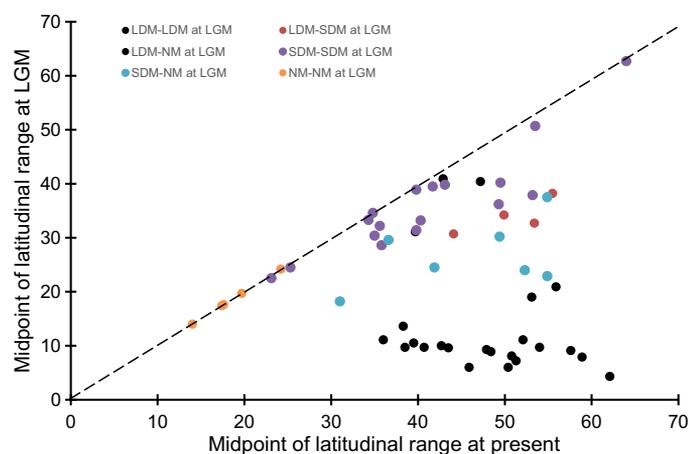
[1]School of Natural Resources, School of Biological Sciences, and University of Nebraska State Museum, University of Nebraska-Lincoln, Lincoln, NE 68583, USA. [2]Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108, USA.
*Corresponding author. Email: rzink2@unl.edu

Given that many species winter in the tropics and are presumed to have once been tropical sedentary breeding residents, we assume that resumption of tropical breeding not only is feasible but also provides a fitness advantage to individuals that cease migration at glacial maxima. It is not possible at the present to predict ranges at glacial maxima that predate the LGM, but we assume that if migratory status changed between the LGM and the present, then it would have been similarly labile across older glacial-interglacial transitions.

RESULTS

The ranges of all species were either consistent with those at the present or shifted southward, often considerably (Fig. 1). Although this general result has long been appreciated (1), our results provide a more explicit demonstration that not all species ranges during glacial maxima, such as the LGM, were displaced southward by a consistent degree. For 20 of 29 (69%) LDMs, we estimated a North American range at the LGM that was nonexistent or insufficient to support breeding populations (Table 1 and Figs. 2 and 3). For these species (for example, Fig. 3), the winter ranges at the LGM were equal to or greater in extent than present wintering ranges. Hence, we concluded that these species reverted to being tropical sedentary (that is, nonmigratory) breeders at the LGM, owing to the lack of suitable breeding habitat in southern North America, despite extended land area owing to lowered sea level. Although many species exhibit an apparently disjunct LGM wintering distribution (see maps in appendix S1), which could imply intratropical migration (either north to south or vice versa), the habitat in western South America was deemed unsuitable for forest-dwelling species [see maps by Ray and Adams (15)], and we did not consider this as a viable LGM winter breeding area. We found that a relatively high percentage of western breeding migrants of both thrushes and warblers remained migratory during the LGM (Fig. 2 and appendix S1), suggesting a difference between species in eastern and western North America. For SDMs, we found that 17 of 22 (77%) species apparently remained migratory through the last glacial cycle. Overall, 63% of LDMs or SDMs altered their migratory behavior during the LGM. Most of those

that apparently retained migratory strategies were classified as SDMs, perhaps supporting the role of this intermediate migration strategy in the SHH.

DISCUSSION

Experimental studies have shown that migratory behavior can be suppressed or expressed in just a few generations (9, 16–18), revealing considerable plasticity. The direction of migration can also be altered in a few generations in captivity and in the wild (9). Thus, once the physiological migration machinery has evolved, glaciation is a switch that can lead to adaptive shifts from migratory to sedentary behavior depending on the phase of the glacial cycle. These behavioral switches would not have been instantaneous but would have been on the same time scale as shifting glacial environments. However, transitions from warm interglacials to cold glacial maxima occurred gradually, whereas transitions from cold glacial maxima to warm interglacials occurred very quickly (19). Therefore, the ability of birds to rapidly shift migratory strategy would be adaptive. Results presented herein suggest that migratory behavior is a labile character and was likely suppressed at glacial maxima and re-expressed during interglacial periods, concomitant with major shifts in breeding ranges. Thus, shifts in a species' ranges and the resulting effects on migratory strategies occur with a higher frequency than speciation events. In essence, what we propose is that the processes involved in the SHH model can be repeated multiple times over the course of a species' history, as opposed to occurring only once in a lineage.

To explore the ecology of distributions for each species and season, we tallied the three bioclim variables that were the top contributors for each species' model. All the 19 climate layers were within the top three of at least one species, and across the 56 species, no two species had the same top three most important climate layers for either breeding and nonbreeding periods, showing that a diversity of climate layers influence distributions across species (appendix S2). The climate layers most frequently in the top three most important factors were as follows: annual mean temperature, isothermality, temperature seasonality, maximum temperature of the warmest month, mean temperature of the warmest quarter, precipitation of the warmest quarter for breeding ranges, temperature seasonality, temperature annual range, mean temperature of the coldest quarter, precipitation seasonality, precipitation of the wettest month, isothermality, and precipitation of the warmest quarter (table S1). Thus, temperature measures contributed most to breeding ranges, and temperature and precipitation contributed most to wintering ranges.

Given that niche models depend on their own set of assumptions (20), it is possible that more extensive suitable areas were present at the LGM but are underrepresented in the current environment, upon

Fig. 1. Plot of midpoint of current range versus midpoint of estimated LGM range derived from niche modeling (LDM-LDM represents species that was an LDM at both periods). All points are at or below the dashed line, which represents the expectation if ranges at the two time periods were the same and shows that although most species' ranges were shifted south at the LGM, it was not to a consistent degree. Many long-distance migratory species have LGM ranges centered well south of the current range.

Table 1. Summary of changes in migration status between the condition at the present and that at the LGM. See appendix S2.

LGM	Present		
	LDM	SDM	Not migratory
LDM	3	0	0
SDM	4	17	0
Not migratory	20	7	5
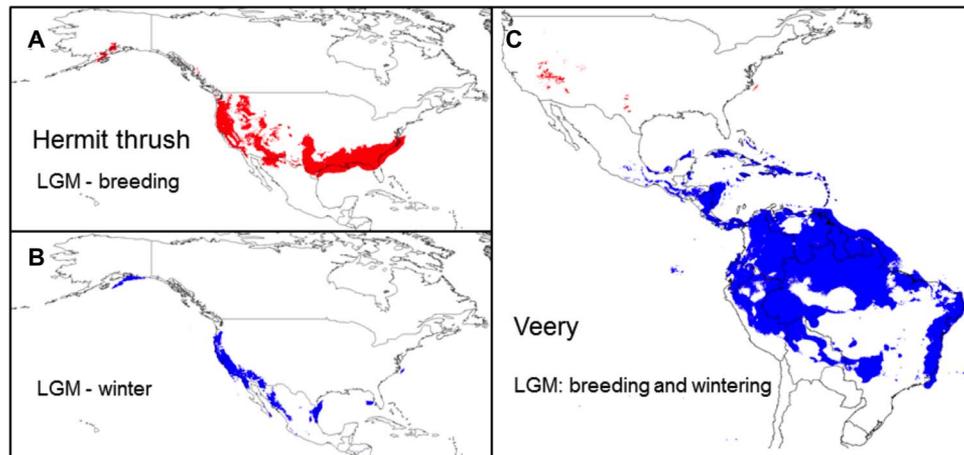
Fig. 2. Examples of predicted breeding (red) and wintering (blue) distributions at the LGM for the hermit thrush (*Catharus guttatus*) and veery (*Catharus fuscescens*). The hermit thrush apparently maintained migratory status at the LGM (**A** and **B**), whereas too little predicted breeding area is present for the veery (**C**) to have maintained breeding populations in North America, and it is inferred that this species became a tropical sedentary resident during this glacial maximum. See fig. S17 for the regions thought to consist of unsuitable habitat at the LGM.
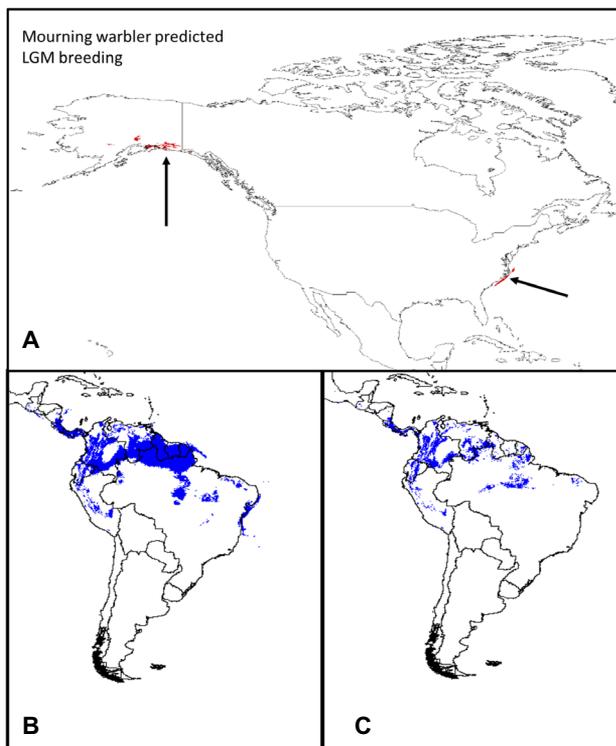
Fig. 3. Example of a species for which too little predicted distribution existed at the LGM to allow breeding in (and migration to and from) North America, but for which predicted winter distribution was substantial, suggesting that the species adopted a sedentary tropical range during the glacial advance. Breeding distribution estimated by ecological niche modeling for mourning warbler (*Geothlypis philadelphia*) at the LGM (**A**), showing two small predicted areas (arrows) considered unlikely to be a sufficient area for breeding throughout a glacial period (and habitat in Beringia was not suitable), and wintering distributions at the LGM (**B**) and the present (**C**), showing an expanded winter range at the LGM.

which the model is based, thereby leading to underprediction of habitable area (*21*). We explored this issue by rerunning models with differing climate layers but found no changes to our results (see Materials and Methods). Furthermore, the amount of available habitat predicted by models of plant species distributions (*22*) also suggests that LGM populations would be very small and likely not viable for the duration of an interglacial period. Because the niche models built on climatic niches of current breeding populations did not predict presence in Central or South America at the LGM, it suggests a major climatic niche shift for breeding populations at each major phase of the glacial cycle (which are extended processes themselves). However, given that many migrant species spend most of their annual cycle in the tropics, it is not likely an insurmountable problem to (re)initiate breeding on the ancestral wintering grounds during glacial maxima, as has been suggested for Nearctic species that might breed secondarily along southward migratory routes (*23*). Furthermore, many but not all tropical habitats were more, not less, extensive at the LGM (*24*), supporting the notion of an expanded area for tropical breeding in species for which migration was suppressed during glacial maxima.

Effects of oscillating migratory status on phylogenetic reconstruction of migration in New World warblers

Hypotheses about the evolution of avian migration can be tested by plotting the distribution of migratory behavior on a phylogenetic tree (*25, 26*). If the SHH was the dominant mode for the evolution of migration, one should observe a consistent transition from sedentary to migratory. However, phylogenetic tests mostly using parsimony found no consistent support for any particular migration hypothesis (*10*), which could result from several factors. First, the hypothesis might apply to only some species. Second, reconstruction methods, such as parsimony mapping (*25*), restrict multiple changes along branches, which might be unrealistic given the species durations that span multiple glacial cycles (*10, 26*). That is, if migration is expressed and suppressed at the temporal scale of glacial cycles, reconstruction methods should reveal that changes in character state (migratory and sedentary) occur much more frequently than speciation events.

We reconstructed the history of migratory behavior on a phylogenetic tree (*12, 13*) for a clade of 23 North American wood warblers using

two starting conditions, present and inferred LGM migratory states. Given that range shifts occur more frequently than speciation events, the goal was to assess whether assuming ranges representing an interglacial or a glacial maximum influenced reconstruction of the expression of migratory behavior (we assumed that there were no changes in phylogenetic topology over the past 21,000 years). We used stochastic character mapping (27) to assess the temporal history of migratory behavior because it allows character-state transitions along individual branches. Assuming the present state (Fig. 4A), several species show switches in state since their last common ancestor, and overall, there were two transitions from sedentary to SDM, two from SDM to sedentary, four from SDM to LDM, four from LDM to SDM, and three from LDM to sedentary. Most of these transitions were in accordance with the expectation that short-distance migration is an intermediate step. Assuming the LGM state (Fig. 4B), a different series of transitions inferred, with seven sedentary to SDM, four SDM to sedentary, two SDM to LDM, two LDM to sedentary, and one sedentary to LDM. Again, there were few transitions that excluded the SDM condition. Although it is not surprising that different starting conditions affect the reconstructed history of migration, the reconstruction based on the present migration state (Fig. 4A) underestimates the frequency of recent transitions to sedentary compared to estimates based on niche models. For example, along the branch leading to *Setophaga magnolia*, there are several hypothesized switches in both reconstructions; however, the species lineage has existed for more than 2 million years (28), which spans the Pleistocene. During the first part of the Pleistocene, glacial cycles were on a scale of 41,000 years, but during the middle Pleistocene, glacial cycles shifted to 100,000-year scales (29). Thus, it is clear that *S. magnolia* has persisted across many glacial cycles, and if we are correct in asserting a reversion to sedentary tropical life history during glacial advances, the number of switches between migratory states is well underestimated by both reconstruction methods. More sophisticated models are needed to capture the apparent high frequency

of switches between migratory and sedentary behavior, and we suggest that using LGM ranges to reconstruct migratory history is more appropriate.

If breeding ranges and, hence, migratory status differ across phases of the glacial cycle, implications exist for other evolutionary inferences concerning migration. Winger *et al.* (13) concluded that "losses of migration have been at least as prevalent as gains throughout the history of Parulidae." Given the likelihood that the history of migration is underestimated on our trees, it is not possible to test this hypothesis. Winger *et al.* (8) suggested that "seasonal migration between breeding ranges in North America and winter ranges in the Neotropics evolved primarily via shifts of winter ranges toward the tropics from ancestral ranges in North America" and that "seasonal migration promoted colonization of the tropics from North America." First, we assume that they mean that the expression rather than the evolutionary origin of migration is what occurred. Second, their analysis was based on a phylogenetic "domino" model that consisted of three latitudinal bands representing North America, Mesoamerica plus the Caribbean, and South America, and two columns representing breeding and wintering, in which they scored transitions from area to area. However, their analysis implicitly assumes that each latitudinal band was equally habitable at all times, which seems unlikely given our understanding of the geography of glacial distributions and the results of our niche models. We suggest that seasonal migration promoted colonization of North America from the tropics.

Ancestral areas and the re-expression of migratory behavior

Frequent shifts in species' ranges across glacial cycles have implications for inferring locations of ancestral areas (30), which provide an additional perspective on the expression of migratory behavior. We coded the geographic breeding ranges for the 23 warbler species (13) at the present and at the LGM and independently inferred ancestral areas and the number of vicariant and dispersal events using statistical
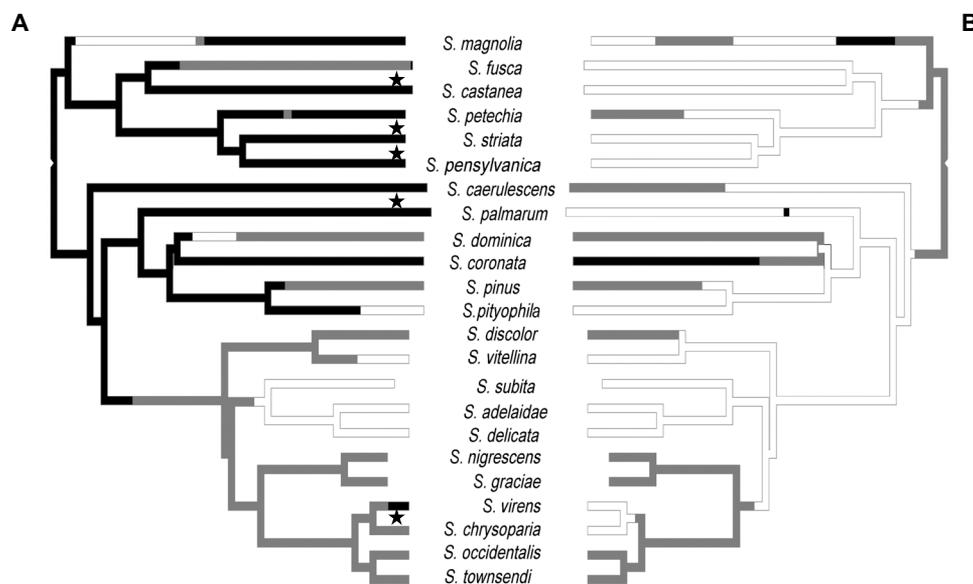
Fig. 4. Mapping migratory behavior on a phylogenetic tree to infer evolutionary transitions between migratory states. Reconstructed history (13) of sedentary (white), SDM (gray), and LDM (black) assuming the present (**A**) or the LGM migratory state (**B**) using stochastic character mapping. Stars indicate positions along the branches where niche modeling suggested a switch in state at the LGM but was not reconstructed by the model. The two hypotheses suggest different frequencies of transitions among states, showing that reconstruction of migratory behavior must account for the potential of transitions occurring on a temporal scale of glacial cycles and not speciation events.

dispersal-vicariance analysis (*31*) in the software Rasp2 (*32*). It is apparent that LGM distributions have a striking phylogenetic signal (Fig. 5), whereas no such relationship is apparent in the reconstruction based on present distributions (which are usually used in these reconstructions). Assuming present ranges as terminal states, the first split of the ancestral area was between northern and eastern North America, with a subsequent complex biogeographic history entailing 11 vicariant events. In the companion analysis, three major areas on the phylogeny, South America, Central America, and the Caribbean, were centers of LGM diversity. An initial dichotomy suggested that South America and the Caribbean were the first two areas to diverge via vicariance. Overall, there were five estimated vicariant events. We suggest that re-expression of migration at the onset of the current interglacial stemmed from these three centers of LGM diversity, which is not apparent in the reconstruction based on current ranges. We consider this support for the notion that investigation of evolutionary history might best use reconstructed LGM ranges because they represent the most likely areas (and times) where changes in migratory behavior and speciation occurred. Of course, it is usually not possible to match particular evolutionary events to a given glacial advance, but our analysis suggests that using present distributions as the starting point in evolutionary reconstructions could be likely misleading.

CONCLUSIONS

In retrospect, it has been widely acknowledged that species ranges shifted during glacial maxima. Even highly sedentary animals, such as salamanders, were forced to move long distances during glacial maxima to novel areas (*33*). How these observations alone have been insufficient to influence assumptions behind evolutionary reconstructions is puzzling. We provide one of the first empirical demonstrations of

Fig. 5. Phylogenetic hypothesis of warbler relationships [from the study of Winger et al. (*13*)] showing reconstructed ancestral areas based on distributions at the LGM (left) and the present (right). Colors indicate different areas, and stars mark inferred vicariant events. Key to areas: A (North America), B (northern North America), C (western North America), D (eastern North America), E (southern North America), F (Central America), G (South America), H (Sonoran Desert), I (central Texas), and J (Caribbean).

the variable nature and magnitude of range shifts at glacial maxima. These range shifts have implications for evolutionary reconstructions. In the case of avian migration, we are proposing a modification of a model often used to explain the "evolution" of migration. That is, we are proposing no new mechanisms, only that the expression and suppression of migration occur multiple times with a given species lineage, driven by whatever life history strategy produces the highest fitness at that time. The onset and termination of glacial cycles act as an adaptive switch. We believe that this better describes the evolution of migratory behavior in birds. Our results also have implications for other types of evolutionary reconstructions. For example, it is often assumed that lineage divergence and speciation occurs during glacial maxima when displaced populations are isolated in refugia. Because range shifts occur more frequently than speciation events, phylogenetic reconstructions of speciation [for example, the study of Weir and Schluter (*34*)] might have greater validity if they used distributions that better approximate those at glacial maxima, because these more likely represent species ranges at the time that speciation occurred.

MATERIALS AND METHODS

Unique breeding and wintering locality records were obtained from the Breeding Bird Survey (accessed at www.pwrc.usgs.gov/bbs), ORNIS2 (http://ornis2.ornisnet.org/), and the Global Biodiversity Information Facility (www.gbif.org) data site, and these were used to produce ecological niche models separately for breeding and wintering populations using Maxent (version 3.3.3k) (*35*). Wintering records were limited to those from December to January to avoid potential migrant individuals. Breeding and wintering models were obtained for both the present and the LGM (Community Climate System Model). The 19 bioclim layers (*36*) for the New World were used to develop the niche models. Climate layers were not trimmed to constrain the model to locality points because our goal was to discover geographic regions where the species might have occurred during the LGM winter, and constraining the evaluated area would prevent finding areas that are outside the "expected" ranges. We performed some runs of Maxent with trimmed climate layers, but they had no effect on the results; therefore, each species was evaluated under the same climate envelope.

It is well known that the climate layers are correlated, and many solutions had been proposed to mitigate redundancy. Some authors computed correlation coefficients among climate layers and eliminated those that were highly correlated. However, this makes little statistical sense unless correlation coefficients are extremely high because there is residual variation that can be important, especially across many ecologically different species, such as analyzed here. In appendix S2, we show that all climate variables were important for at least one species, and no two species range estimates were based on the same layers.

Hence, for each data set, we followed Brown and Knowles (*37*) and performed three replicates of Maxent and, based on the average of these, selected the bioclim layers that contributed >5% to the model, and reran Maxent with these layers only for a total of 10 times; the average of the 10 runs was taken. Maxent outputs a measure of the overall performance of the model, estimated as the area under the receiver operating characteristic curve (AUC). AUC values higher than 0.5 indicate a better predictive ability, with a value of 1 indicating a perfect prediction. Here, niche models estimated under current climate conditions had mean test AUC values of >0.85, indicating a very good ability to discriminate between presence and absence locations.

Bioclim variables represent annual variation, and it is possible that including climate data from outside the temporal window a species occupies, a given area could bias the results. Some had advocated excluding climate data from parts of the year when the species is absent from an area (38). We suggested that this is inappropriate for several reasons: First, in many species, birds of different sexes and ages leave the breeding or wintering grounds at different times and over an extended period, and it would be arbitrary to pick a single time interval. Second, in our opinion, climate models for birds do an excellent job of predicting avian distributions because they are keyed in to the major features of vegetation, which determines whether birds occur in an area or not. Vegetation only grows in an area if the climate is suitable for 12 months of the year, and for this reason, we felt that using the annual climate layers is the most appropriate. That is, if birds are keying in on vegetation/habitat features, and vegetation/habitat is a product of annual patterns of temperature, precipitation, and seasonality, then it is appropriate to include all the climate layers.

Nonetheless, to explore the effects of using layers representing the entire year, models using only bioclim layers 5, 8, 10, 13, 16, and 18 (representing periods when the species were likely in North America) were repeated for 10 species (Canada warbler, chestnut-sided warbler, Cape May warbler, Tennessee warbler, golden-winged warbler, Kentucky warbler, blackpoll warbler, blackburnian warbler, veery, and gray-cheeked thrush) that we estimated to be absent from North America at the LGM. None of these models suggested different results, and the results are not shown.

We recognized that multiple opinions exist on how best to construct and interpret niche models. Some of the variation in opinion stemmed from the goals of a particular project, such as identifying precise distributions. Because our main goal in this study was to ascertain whether sufficient predicted breeding areas occurred in North America during the LGM, the precise limits were not as important as the areal extent of the predicted areas. Thus, as long as the predicted distribution was approximately 10% or less of the current breeding distribution, we assumed that a species would not be successful in sustaining breeding populations in small areas in southern North America across the duration of a glacial maximum; many species showed no suitable area at the LGM.

Models were displayed in DIVA-GIS and maps produced of distributional presence/absence using the equal test sensitivity and specificity threshold produced in Maxent; although this threshold is typically larger than others, the "fixed cumulative value 10" was also evaluated and did not alter our conclusions. Maxent's auto-features and the default regularization multiplier parameter (1.0) were used, except that the number of iterations was increased to 1500 to allow the program to reach the default convergence threshold, and the option "extrapolate" was not used.

We recognized that multiple ways exist to optimize character states on trees, but our goal was to ask whether generalizations resulting from present-day migratory status are retained if the state at the LGM is assumed. We also recognized that migration per se is not a "character" but rather a composite of different physiological conditions, including hyperplasia, migratory restlessness (Zugunruhe), and navigational ability (10). For the warbler data set (13), we reconstructed the history of migration on phylogenetic trees using stochastic character mapping (27) because it allows character-state transitions along individual branches in the software Mesquite (39), assuming an estimated migratory status at the LGM (and assuming that currently sedentary species also were sedentary at the LGM). Huelsenbeck et al. (27) noted that

this method is "an application of Nielsen's (2002) method for mapping characters under continuous-time Markov models that is fundamentally different from the parsimony method," and that "more than a single change is allowed on a branch and the probability of a change on a branch increases with its length." Therefore, we used this method instead of a parsimony-based method.

We coded the warbler tree as to geographic range at the present and inferred at the LGM and used the default settings in the program Rasp2 (32) to infer the ancestral areas and the number of dispersal and vicariant events. Rasp2 is an event-based biogeographic method assuming vicariance as a null hypothesis with costs assessed costs for dispersal and extinction [see the study of Fernando et al. (30) for additional details]. We designated 10 areas: North America, northern North America, western North America, eastern North America, southern North America, Central America, South America, Sonoran Desert, Central Texas, and the Caribbean. All areas were assigned to the outgroup, and the maximum number of areas in ancestral distributions was set to four.

SUPPLEMENTARY MATERIALS

fig. S21B. Blue-winged warbler predicted wintering distribution at the LGM.

fig. S22. Golden-winged warbler (*Vermivora chrysoptera*) predicted wintering distribution at the LGM.

fig. S23A. Tennessee warbler (*Oreothlypis peregrina*) predicted breeding distribution at the LGM.

fig. S23B. Tennessee warbler predicted wintering distribution at the LGM.

fig. S24. Connecticut warbler (*Oporonis agilis*) predicted wintering distribution at the LGM.

fig. S25. Mourning warbler (*Geothlypis philadelphia*) predicted wintering distribution at the LGM.

fig. S26. Kentucky warbler (*Geothlypis formosa*) predicted wintering distribution at the LGM.

fig. S27A. Blackpoll warbler (*S. striata*) predicted breeding distribution at the LGM.

fig. S27B. Blackpoll warbler predicted wintering distribution at the LGM.

fig. S28. Magnolia warbler (*S. magnolia*) predicted wintering distribution at the LGM.

fig. S29. Cape May warbler (*S. tigrina*) predicted wintering distribution at the LGM.

fig. S30. Bay-breasted warbler (*S. castanea*) predicted wintering distribution at the LGM.

fig. S31. Blackburnian warbler (*S. fusca*) predicted wintering distribution at the LGM.

fig. S32. Chestnut-sided warbler (*S. pensylvanica*) predicted wintering distribution at the LGM.

fig. S33A. Palm warbler (*S. palmarum*) predicted breeding distribution at the LGM.

fig. S33B. Palm warbler predicted wintering distribution at the LGM.

fig. S34. Black-throated green warbler (*S. virens*) predicted wintering distribution at the LGM.

fig. S35. Canada warbler (*Cardellina canadensis*) predicted wintering distribution at the LGM.

fig. S36A. Wilson's warbler (*Cardellina pusilla*) predicted breeding distribution at the LGM.

fig. S36B. Wilson's warbler predicted wintering distribution at the LGM.

fig. S37A. Hermit thrush (*Catharus guttatus*) predicted breeding distribution at the LGM.

fig. S37B. Hermit thrush predicted wintering distribution at the LGM.

fig. S38A. Hooded oriole (*Icterus cucullatus nelsoni*) predicted breeding distribution at the LGM.

fig. S38B. Hooded oriole predicted wintering distribution at the LGM.

fig. S39A. Abeile's oriole (*Icturus abellei*) predicted breeding distribution at the LGM.

fig. S39B. Abeile's oriole predicted wintering distribution at the LGM.

fig. S40A. Lucy's warbler (*Oreothlypis luciae*) predicted breeding distribution at the LGM.

fig. S40B. Lucy's warbler predicted wintering distribution at the LGM.

fig. S41A. Yellow-throated warbler (*S. dominica*) predicted breeding distribution at the LGM.

fig. S41B. Yellow-throated warbler (*S. dominica*) predicted wintering distribution at the LGM.

fig. S42A. Pine warbler (*S. pinus*) predicted breeding distribution at the LGM.

fig. S42B. Pine warbler predicted wintering distribution at the LGM.

fig. S43A. Black-throated gray warbler (*S. nigrescens*) predicted breeding distribution at the LGM.

fig. S43B. Black-throated gray warbler predicted wintering distribution at the LGM.

fig. S44A. Hermit warbler (*S. occidentalis*) predicted breeding distribution at the LGM.

fig. S44B. Hermit warbler predicted wintering distribution at the LGM.

fig. S45A. Townsend's warbler (*S. townsendi*) predicted breeding distribution at the LGM.

fig. S45B. Townsend's warbler predicted wintering distribution at the LGM.

fig. S46A. Grace's warbler (*S. graciae*) predicted breeding distribution at LGM.

fig. S46B. Grace's warbler predicted wintering distribution at the LGM.

fig. S47A. Common yellowthroat (*Geothlypis trichas*) predicted breeding distribution at the LGM.

fig. S47B. Common yellowthroat predicted wintering distribution at the LGM.

fig. S48. Golden-cheeked warbler (*S. chrysoparia*) predicted wintering distribution at the LGM.

fig. S49. Prairie warbler (*S. discolor*) predicted wintering distribution at the LGM.

fig. S50A. Swamp sparrow (*Melospiza georgiana*) predicted breeding distribution at the LGM.

fig. S50B. Swamp sparrow predicted wintering distribution at the LGM.

fig. S51. Song sparrow (*Melospiza melodia*; eastern migratory populations only) predicted wintering distribution at the LGM.

appendix S2. Species studied, migratory status at present and LGM, samples sizes, latitudinal midpoint of ranges at present and LGM, and climate layers important in distribution models.

REFERENCES AND NOTES

1. E. C. Pielou, *After the Ice Age: The Return of Life to Glaciated North America* (University of Chicago Press, 2008).

2. J. H. Rappole, *The Ecology of Migrant Birds: A Neotropical Perspective* (Smithsonian Institution Scholarly Press, 1995).

3. J. H. Rappole, *The Avian Migrant: The Biology of Bird Migration* (Columbia Univ. Press, 2013).

4. P. Berthold, A comprehensive theory for the evolution, control and adaptability of avian migration. *Ostrich* **70**, 1–11 (1999).

5. B. Milá, T. B. Smith, R. K. Wayne. Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution* **60**, 2403–2409 (2006).

6. L. Joseph, E. P. Lessa, L. Christidis, Phylogeny and biogeography in the evolution of migration: Shorebirds of the *Charadrius* complex. *J. Biogeogr.* **26**, 329–342 (1999).

7. A. Louchart, Emergence of long distance bird migrations: A new model integrating global climate changes. *Naturwissenschaften* **95**, 1109–1119 (2008).

8. B. M. Winger, F. K. Barker, R. H. Ree, Temperate origins of long-distance seasonal migration in New World songbirds. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 12115–12120 (2014).

9. P. Berthold, A. J. Helbig, G. Mohr, U. Querner, Rapid microevolution of migratory behaviour in a wild bird species. *Nature* **360**, 668–670 (1992).

10. R. M. Zink, The evolution of avian migration. *Biol. J. Linn. Soc.* **104**, 237–250 (2011).

11. A. T. Peterson, Predicting species' geographic distributions based on ecological niche modeling. *Condor* **103**, 599–605 (2001).

12. I. J. Lovette, E. Bermingham, Explosive speciation in the New World Dendroica warblers. *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 1629–1636 (1999).

13. B. M. Winger, I. J. Lovette, D. W. Winkler, Ancestry and evolution of seasonal migration in the Parulidae. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 610–618 (2012).

14. A. T. Peterson, J. Soberón, V. Sánchez-Cordero, Conservatism of ecological niches in evolutionary time. *Science* **285**, 1265–1267 (1999).

15. N. Ray, J. Adams, A GIS-based vegetation map of the world at the Last Glacial Maximum (25,000-15,000 BP). *Internet Archaeol.* **11**, 1–44 (2001).

16. B. Helm, E. Gwinner, Migratory restlessness in an equatorial nonmigratory bird. *PLOS Biol.* **4**, e110 (2006).

17. J. C. Mueller, F. Pulido, B. Kempenaers, Identification of a gene associated with avian migratory behavior. *Proc. R. Soc. Lond. B Biol. Sci.* **278**, 2848–2856 (2011).

18. K. P. Able, J. R. Belthoff, Rapid 'evolution' of migratory behaviour in the introduced house finch of eastern North America. *Proc. R. Soc. Lond. B Biol. Sci.* **265**, 2063–2071 (1998).

19. P. U. Clark, R. B. Alley, D. Pollard, Northern hemisphere ice-sheet influences on global climate change. *Science* **286**, 1104–1111 (1999).

20. M. B. Araújo, A. T. Peterson, Uses and misuses of bioclimatic envelope modeling. *Ecology* **93**, 1527–1539 (2012).

21. P. B. Pearman, C. F. Randin, O. Broennimann, P. Vittoz, W. O. van der Knaap, R. Engler, G. Le Lay, N. E. Zimmermann, A. Guisan, Prediction of plant species distributions across six millennia. *Ecol. Lett.* **11**, 357–369 (2008).

22. J. W. Williams, *Quaternary Vegetation Distributions. Encyclopedia of Paleoclimatology and Ancient Environments* (Springer, 2009), pp. 856–862.

23. S. Rohwer, K. A. Hobson, V. G. Rohwer, Migratory double breeding in Neotropical migrant birds. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 19050–19055 (2009).

24. Y. L. R. Leite, L. P. Costa, A. C. Loss, R. G. Rocha, H. Batalha-Filho, A. C. Bastos, V. S. Quaresma, V. Fagundes, R. Paresque, M. Passamani, R. Pardini, Neotropical forest expansion during the last glacial period challenges refuge hypothesis. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 1008–1013 (2016).

25. D. C. Outlaw, G. Voelker, Phylogenetic tests of hypotheses for the evolution of avian migration: A case study using the Motacillidae. *Auk* **123**, 455–466 (2006).

26. G. Voelker, R. C. Bowie, J. Klicka, Gene trees, species trees and Earth history combine to shed light on the evolution of migration in a model avian system. *Mol. Ecol.* **22**, 3333–3344 (2013).

27. J. P. Huelsenbeck, R. Nielsen, J. P. Bollback, Stochastic mapping of morphological characters. *Syst. Biol.* **52**, 131–158 (2003).

28. F. K. Barker, K. J. Burns, J. Klicka, S. M. Lanyon, I. J. Lovette. New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *Auk* **132**, 333–348 (2015).

29. I. Daruka, P. D. Ditlevsen, A conceptual model for glacial cycles and the middle Pleistocene transition. *Clim. Dynam.* **46**, 29–40 (2016).

30. S. W. Fernando, A. T. Peterson, S.-H. Li, Reconstructing the geographic origin of the New World jays. *Neotrop. Biodivers.* **3**, 80–92 (2017).

31. Y. Yu, A. J. Harris, X. He. S-DIVA (Statistical Dispersal-Vicariance Analysis): A tool for inferring biogeographic histories. *Mol. Phylogenet. Evol.* **56**, 848–850 (2010).

32. Y. Yu, A. J. Harris, C. Blair, X. He, RASP (Reconstruct Ancestral State in Phylogenies): A tool for historical biogeography. *Mol. Phylogenet. Evol.* **87**, 46–49 (2015).

33. D. R. Vieites, M.-S. Min, D. B. Wake, Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 19903–19907 (2007).

34. J. T. Weir, D. Schluter, The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574–1576 (2007).

35. S. J. Phillips, R. P. Anderson, R. E. Schapire, Maximum entropy modeling of species geographic distributions. *Ecol. Mod.* **190**, 231–259 (2006).

36. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).

37. J. L. Brown, L. L. Knowles. Spatially explicit models of dynamic histories: Examination of the genetic consequences of Pleistocene glaciation and recent climate change on the American Pika. *Mol. Ecol.* **21**, 3757–3775 (2012).

38. Y. Nakazawa, A. T. Peterson, E. Martínez-Meyer, A. G. Navarro-Sigüenza. Seasonal niches of Nearctic-Neotropical migratory birds: Implications for the evolution of migration. *Auk* **121**, 610–618 (2004).
39. W. P. Maddison, D. R. Maddison, Mesquite: A modular system for evolutionary analysis. Version 3.04 (2015); http://mesquiteproject.org/.

Citation: R. M. Zink, A. S. Gardner, Glaciation as a migratory switch. *Sci. Adv.* **3**, e1603133 (2017).

Science Advances

Glaciation as a migratory switch

Robert M. Zink and Aubrey S. Gardner

ARTICLE TOOLS	http://advances.sciencemag.org/content/3/9/e1603133
SUPPLEMENTARY MATERIALS	http://advances.sciencemag.org/content/suppl/2017/09/18/3.9.e1603133.DC1
REFERENCES	This article cites 34 articles, 7 of which you can access for free http://advances.sciencemag.org/content/3/9/e1603133#BIBL
PERMISSIONS	http://www.sciencemag.org/help/reprints-and-permissions

Use of this article is subject to the Terms of Service