

# Temperate origins of long-distance seasonal migration in New World songbirds

Benjamin M. Winger<sup>a,b,1</sup>, F. Keith Barker<sup>c,d</sup>, and Richard H. Ree<sup>a,b</sup>

<sup>a</sup>Committee on Evolutionary Biology, University of Chicago, Chicago, IL 60637; <sup>b</sup>Life Sciences Section, Integrative Research Center, Field Museum of Natural History, Chicago, IL 60605; and <sup>c</sup>Department of Ecology, Evolution and Behavior and <sup>d</sup>Bell Museum of Natural History, University of Minnesota, St. Paul, MN 55108

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**Migratory species exhibit seasonal variation in their geographic ranges, often inhabiting geographically and ecologically distinct breeding and nonbreeding areas. The complicated geography of seasonal migration has long posed a challenge for inferring the geographic origins of migratory species as well as evolutionary sequences of change in migratory behavior. To address this challenge, we developed a phylogenetic model of the joint evolution of breeding and nonbreeding (winter) ranges and applied it to the inference of biogeographic history in the emberizoid passerine birds. We found 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. This result contrasts with a dominant paradigm that hypothesized migration evolving out of the tropics via shifts of the breeding ranges. We also show that major lineages of tropical, sedentary emberizoids are derived from northern, migratory ancestors. In these lineages, the winter ranges served as a biogeographic conduit for temperate-to-tropical colonization: winter-range shifts toward the tropics during the evolution of long-distance migration often preceded southward shifts of breeding ranges, the loss of migration, and in situ tropical diversification. Meanwhile, the evolution of long-distance migration enabled the persistence of old lineages in North America. These results illuminate how the evolution of seasonal migration has contributed to greater niche conservatism among tropical members of this diverse avian radiation.**

evolution of migration | historical biogeography | dispersal-extinction-cladogenesis | bird migration | tropical niche conservatism

**T**he evolution of seasonal migratory behavior among animals involves a suite of behavioral, physiological, morphological, and neurological adaptations that enable migrants' extraordinary feats of endurance and navigation (1–3). However, the evolution of migration also is an inherently geographic process during which a species' breeding range and nonbreeding range (henceforth, winter range) become physically and ecologically separated (4). Understanding the evolution of migration therefore requires reconciling the fascinating adaptations of migratory individuals with the biogeographic factors that control the shifting boundaries of a species' range (5). The field of historical biogeography has shed considerable light on the geographic histories of organisms (6, 7) but has largely ignored migratory species due to the difficulty of simultaneously reconstructing the evolution of the breeding and winter ranges, which in migratory species are often ecologically disparate and separated by long distances (5). Consequently, progress in our understanding of the evolution of migration has been impeded by a biogeographic conundrum: testing hypotheses on the evolution of migration requires knowledge of the geographic histories of migratory species (4, 8, 9), but the existence of migratory behavior in a lineage confounds our ability to infer these histories (10).

This difficulty in resolving the geographic provenance of migratory species not only has left incomplete our understanding of the geographic histories of many lineages that contain migrants

but also has impaired our ability to discriminate among hypotheses on the selective forces that drive the evolution of migratory behavior. For over a century, the principal dichotomy among hypotheses on the evolution of bird migration has hinged on a question of geographic ancestry: does seasonal migration evolve through a geographic shift of the breeding grounds away from an ancestral year-round range, or via a shift of the wintering grounds (11–13)? The most visible bird migrations occur between breeding regions at temperate latitudes to wintering areas at lower, more tropical latitudes (2). The dominant paradigm in the literature on the evolution of migration has imagined these long-distance migrations as evolving via shifts of the breeding range out of the tropics, driven by increased reproductive success and reduced competition in temperate regions (14–18). An opposing camp has hypothesized that migration evolves when species resident year-round in temperate latitudes shift their winter ranges to lower latitudes to increase survival during the harsh and resource-depleted temperate winters (11, 13, 19). Much debate has occurred over the selective forces that would make a tropical versus temperate ancestry of migratory birds more likely (12, 13). However, due to the absence of historical biogeographic models capable of handling the complex geographic ranges of migratory species, previous studies have had difficulty determining which geographic shifts produced the distributions of migratory species observed today, as well as where migratory lineages originated (4, 8–10, 20, 21).

To address this challenge, we designed a phylogenetic model specifically for inferring the biogeographic history of migratory lineages. Our model is inspired by the dispersal-extinction-cladogenesis

## Significance

**Determining where species arose and how they spread across the globe is paramount to understanding geographic patterns of biodiversity. For migratory organisms, this task has been difficult due to the complex geography of seasonal migration. One longstanding hypothesis is that migratory animals originated in the tropics and that migration evolved through shifts of breeding ranges to temperate regions. We tested this hypothesis in the largest radiation of migratory birds in the Americas, the emberizoid passerines. Contrary to expectations, we found that long-distance migration primarily evolved through evolutionary shifts of geographic range south for the winter out of North America, as opposed to north for the summer. Our results further suggest that seasonal migration promoted colonization of the tropics from North America.**

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<sup>1</sup>To whom correspondence should be addressed. Email: bwinger@uchicago.edu.

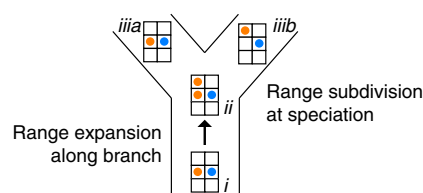
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(DEC) model (22, 23), in which geographic range evolves via discrete events of dispersal and local extinction along phylogenetic branches and via inheritance and subdivision at speciation events. Our model follows similar logic but is novel in jointly considering the evolution of both the breeding and winter range.

The discrete states of our model are presence–absence grids whose cells signify breeding and wintering in three latitudinal regions (*Materials and Methods*). These grids, which we refer to as “dominos,” summarize the ranges of New World bird species in each season (Fig. 1 and Table S1). Ancestor-to-descendant transitions between dominos represent expansion or contraction events of the breeding and/or winter range and describe broad patterns of change in the geography of seasonal migration (Fig. 2 and Fig. S1). We focus on the evolution of long-distance bird migration between summer breeding grounds in temperate North America and winter grounds at subtropical or tropical latitudes. This migratory system, known as Nearctic-Neotropical migration (henceforth, Neotropical migration), involves the largest number of species of any avian migratory system in the New World (24, 25).

Applied to a phylogenetic tree, the domino model enables estimation of ancestral breeding and winter ranges (that is, ancestral dominos), as well as rates of ancestor–descendant transitions between dominos (*Materials and Methods*). Our estimation of transition rates results in an adjacency matrix that describes every possible geographic change throughout phylogenetic history (Fig. 3A). The complexity of this matrix illustrates the principal challenge of inferring the biogeographic histories of migratory species: many different sequences of geographic change could explain the evolution of a given migratory species’ range (5, 26). To overcome this challenge, we used graph theory and network analysis to extract from the rate matrix the dominant pathways of geographic evolutionary change that led to the evolution of Neotropical migration (Fig. 3B and C and *Materials and Methods*).

We applied the model in a study of the largest New World radiation of migratory birds, the emberizoid passerines (superfamily Emberizoidea), for which we had a recent and comprehensive species-level molecular phylogeny (27). This lineage of



**Fig. 2.** Transitions between dominos represent instantaneous expansions or contractions of the range along branches (between *i* and *ii*) or dichotomous subdivision or inheritance at speciation (between *ii* and *iii*). Here, the breeding range has expanded from Middle America to North America (*i* to *ii*) during the evolution of Neotropical migration. A speciation event occurs at *ii*; illustrated here is one possible scenario of range subdivision/inheritance following speciation, resulting in one tropical endemic domino (*iii*a) and one Neotropical migratory domino (*iii*b).

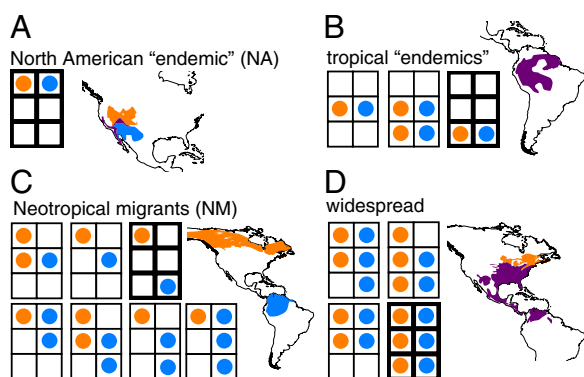
~823 songbird species contains all New World warblers, sparrows, blackbirds, orioles, cardinals, buntings, tanagers, and allies. Most emberizoid diversity is comprised of nonmigratory, tropical species, mirroring the more general global trend of higher species diversity in the tropics than in temperate regions (28). However, all major lineages of Emberizoidea except the Thraupidae (tanagers) also contain Neotropical migrants (species that breed in North America and spend the northern winter in the Neotropics); in total, the group contains 120 species of Neotropical migrants, which together represent 25% of all Neotropical migratory bird species (24).

The ancestral emberizoid is thought to have colonized the Americas via Beringia and thus have a northern origin in the New World (27, 29). However, insight into the group’s biogeographic history in the New World has been complicated by the dilemma of Neotropical migration, particularly because multiple gains and losses of migration are evident throughout emberizoid history (10, 20, 30). Did major emberizoid lineages originate in the tropics, implying that Neotropical migration evolved in these lineages via shifts of the breeding ranges to North America? Or did migratory emberizoid lineages originate in North America and evolve Neotropical migration via shifts of the winter ranges toward the equator? What does the geographic history of Neotropical migration imply for the origins, geographic spread and diversification of this diverse, widespread radiation?

## Results

We used our model to examine the biogeographic events that accompanied gains and losses of Neotropical migration, as well as the influence of Neotropical migration on colonization of the tropics.

**The Evolution of Neotropical Migration.** We reconstructed ancestral states of dominos across a posterior distribution of model parameters (Fig. 4 and *SI Materials and Methods*). We asked whether dominos representing Neotropical migratory species (henceforth, NM dominos) (Fig. 1C) more frequently evolved along a phylogenetic branch from an ancestral domino endemic to North America (henceforth, the NA domino) (Fig. 1A) or from ancestors endemic to the tropics in both breeding and winter range (henceforth, tropical dominos) (Fig. 1B). That is, how often did a lineage starting out in North America or the tropics evolve to a Neotropical migratory condition by the end of its phylogenetic branch? We repeated this tabulation across 1,000 sets of ancestral state reconstructions (*SI Materials and Methods*) and found that Neotropical migration evolved from a North American ancestor along an average of 17.64 branches, and from a tropical ancestor on an average of 8.14 branches. Thus, Neotropical migration evolved significantly more often from North America than from the tropics ( $P < 0.001$ ,  $df = 1,704.5$ , Welch’s *t* test). We also examined how often NM evolved from ancestors with



**Fig. 1.** In the domino model,  $3 \times 2$  grids (“dominos”) describe species’ breeding and winter ranges. Grid rows correspond to latitudinal zones (North America, Middle America and the Caribbean, and South America). Orange dots (left column) and blue dots (right column) indicate whether a species breeds and winters, respectively, in a latitudinal zone. The 15 dominos in this figure describe the distributions of all New World emberizoids and are the tip states in the phylogenetic analysis. We classify dominos according to four distributional patterns: (A) endemic in breeding and winter range to North America, (B) endemic in breeding and winter range to the tropics (Middle and/or South America), (C) migratory between North America and the tropics (Neotropical migration), and (D) widespread in breeding and winter range. Range maps illustrate species distributions that exemplify each of four dominos in bold outline: *Artemisiospiza belli* (A), *Tangara chilensis* (B), *Setophaga striata* (C), *Sturnella magna* (D). Purple in range maps indicates areas of overlap of breeding and winter range.





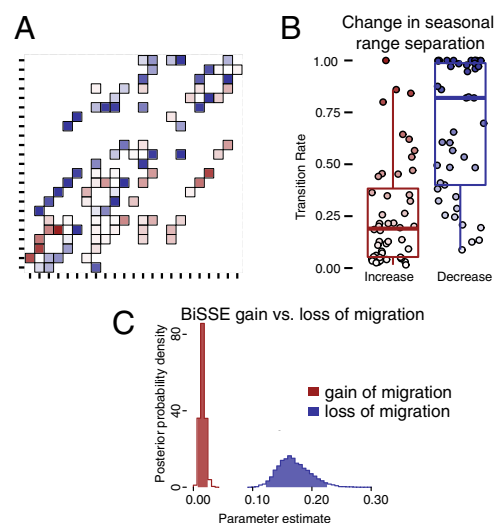
and Fig. S2). Overall, the shortest paths between the NA domino to the NM dominos were significantly shorter than the shortest paths from tropical dominos to NM dominos ( $P < 0.001$ ,  $df = 14.8$ , Welch's  $t$  test) (Fig. 3C). This result supports the inference that shifts of the winter ranges out of North America to tropical latitudes were the dominant geographic process during the evolution of Neotropical migration in Emberizoidea and that Neotropical migration evolved out of the tropics more rarely. This conclusion is further supported by the result of an additional test using the graph theory concept of degree (*SI Materials and Methods* and Fig. S3). Collectively, our analyses indicate that, although both geographic processes have likely occurred, out-of-the-tropics expansions have played a lesser role in the evolution of long-distance Neotropical migration in the Emberizoidea than shifts of winter ranges from North America.

**Loss of Neotropical Migration.** Neotropical migration evolved early in many emberizoid lineages and was subsequently lost (Fig. 4); consequently, a prominent pattern in the phylogeny is that of latitudinal coalescence of breeding and winter ranges and the loss of migration. To calculate the prevalence of loss versus gain of Neotropical migration, we determined which transitions between dominos resulted in an increase of breeding- and winter-range geographic separation (seasonal range separation), and which transitions resulted in a decrease of seasonal range separation (Fig. 5A, Fig. S4, and *Materials and Methods*). Collectively, rates of individual transition parameters that resulted in a decrease of seasonal range separation were significantly higher than rates of transitions resulting in an increase in seasonal range separation ( $P < 0.001$ ,  $df = 84.5$ , Welch's  $t$  test) (Fig. 5B), indicating an overall trend toward loss of migration. We also recovered a trend of loss of migration using existing state-dependent speciation-extinction (SSE) models (31, 32) implemented in Diversitree (33) (*Materials and Methods* and Fig. 5C).

**Tropical Colonization.** Loss of migration in Emberizoidea is associated with a broader trend of temperate to tropical colonization (Fig. S5). The loss of migration was previously documented in one of the major lineages of Emberizoidea (the Parulidae) (20) and at a larger scale among all bird lineages (34), but the geographic pathways leading to loss of migration remained unclear. Here, we used the domino model to explore the influence of Neotropical migration on colonization of the tropics. We asked whether winter-range expansions into the tropics during the evolution of Neotropical migration bolstered subsequent tropical colonization by breeding populations, or, alternatively, whether tropical colonization proceeded more frequently via expansion of resident, nonmigratory ranges (*SI Materials and Methods*). We found that both types of events occurred at high rates (Fig. S6). Therefore, although multiple geographic processes were likely responsible for the colonization of the tropics by emberizoids, our analyses suggest that winter ranges often reached the tropics before breeding ranges and therefore bolstered temperate-to-tropical colonization.

## Discussion

Our study reconciles migratory behavior with geographic origins to untangle a complex geographic history. Despite early invasions of emberizoid lineages such as Thraupidae into tropical latitudes (27, 35), our analyses demonstrate that long-distance migration between North America and the Neotropics evolved primarily via shifts of winter ranges from North America as opposed to breeding-range shifts from tropical latitudes (Figs. 3 and 4). These winter-range shifts occurred most notably in the ancestor to the largest clade of emberizoid migratory birds, Parulidae and Icteridae (starred blue branch in Fig. 4), and repeatedly in the Passerellidae (blue branches, Fig. 4). In contrast, shifts of breeding ranges out of tropical latitudes into North



**Fig. 5.** Loss versus gain of migration. (A) To test whether migration was more often lost than gained, we determined which of the pairwise domino transitions in the adjacency rate matrix represented a decrease (blue) versus an increase (red) of breeding- and winter-range separation (*SI Materials and Methods* and Fig. S4). Both colors are shaded light to dark according to mean transition rate. (B) Boxplots with median and quartile values are overlaid on shaded circles (jittered horizontally) that represent individual rate parameters and correspond to shaded squares in the adjacency matrix in A. Transitions that resulted in decreased separation of breeding and winter range (reduction of migration, blue,  $n = 45$ ) occurred at higher rates than transitions that increased seasonal range separation (red,  $n = 48$ ), indicating an overall trend of loss of migration. (C) We also tested whether migration was more often lost than gained using state-dependent speciation and extinction models. MCMC sampling of the BiSSE model (31, 33) indicates that migration was lost at a significantly higher rate than gained (*SI Materials and Methods*).

America during the evolution of Neotropical migration occurred more rarely and at a lower rate (Fig. 3). Apparent tropical origins of Neotropical migration led to small numbers of migratory species in *Icterus orioles* (Icteridae) (Fig. 4, node 1) and in the Cardinalidae (Fig. 4, nodes 2–4). Notably, neither Neotropical migration nor North American residency has evolved in the largest emberizoid family, the Thraupidae, despite the widespread diversification of this lineage throughout the tropics (35) and the evolution of shorter-distance intratropical migrations in this group (25).

We do not interpret the emergence of Neotropical migration in Emberizoidea as de novo evolution of migratory behavior, as migration in some form likely traces much deeper in the avian tree of life (1, 26, 36). Rather, our study illuminates the geographic origins and history of a major migratory system during the hemisphere-wide radiation of this diverse New World lineage. Our results are striking considering that lineages containing Neotropical migrants have centers of species diversity in the tropics. Previous workers have often cited the taxonomic relationships between nonmigratory, tropical species and temperate migrants as evidence that migration evolved out of the tropics and have suggested myriad selective forces to explain the evolution of long-distance seasonal migration out of the tropics (15, 16, 18). For example, one hypothesis suggested that localized movements that evolve in the tropics, such as the search for ephemeral food resources by frugivores, may be “evolutionary precursors” to long-distance migration (16, 37). That is, these hypotheses suggest that demographic and selective forces operating in tropical breeding regions drive the evolution of long-distance migration out of the tropics. However, our results suggest that traditional out-of-the-tropics hypotheses of bird migration do not

explain the emergence of long-distance migration in the largest lineage of Neotropical migratory birds.

Rather, our results are consistent with hypotheses suggesting that shifts of the winter range are the primary drivers of the evolution of long-distance migration (13, 19, 36, 38). Neotropical migration emerged early in Emberizoid history (Fig. 4), and age estimates for major emberizoid lineages date as far back as the early Miocene (15–20 MyBP), with the split from the sister family to Emberizoidea, the cosmopolitan Fringillidae, dated to the late Oligocene (20–25 MyBP) (29, 39). Thus, early shifts of winter ranges (e.g., starred node, Fig. 4) may have occurred in response to global cooling and increasing seasonality at high latitudes since the late Oligocene (36). As such, early shifts of winter ranges may not represent invasions of tropical habitats as much as tracking of tropical habitat to lower latitudes to escape harsh winter conditions while maintaining breeding at high latitudes (36, 40). Plio-Pleistocene glaciations have clearly served to modify geographic ranges and migratory distances and routes (26, 41, 42) and may have had an influence on more recent shifts of winter ranges out of North America in the Passerellidae (blue branches, Fig. 4). However, recent glacial cycles were not responsible for the initial development of Neotropical migration in Emberizoidea.

The dominant biogeographic pattern throughout emberizoid history is one of colonization of the tropics from the north temperate region (Fig. S5), and our analyses revealed that this colonization occurred via three processes: fragmentation of widespread ranges, expansion of resident ranges of nonmigratory populations from temperate to tropical latitudes, and the expansion of a migratory species' breeding range into a tropical area already occupied by their winter range (Fig. S6). Secondary colonization of North America from the tropics occurred surprisingly rarely, given the high species diversity and deep history of Emberizoidea in the tropics. These results contrast with out-of-the-tropics models for the evolution of the latitudinal diversity gradient (43) and instead are consistent with the hypothesis that tropical species have greater conservatism in ecological niche than temperate species (28, 44). Our results further suggest that, in this diverse radiation of migratory birds, shifts of winter ranges out of North America during the evolution of migration served as a biogeographical conduit that bolstered the establishment of temperate lineages in the tropics and preceded *in situ* tropical diversification. Meanwhile, the evolution of long-distance migration out of North America also enabled the persistence and subsequent diversification of old lineages in temperate North America, by allowing species to escape inhospitable winter conditions each year. Thus, the complex geographic history of seasonal migration has at once promoted colonization of the tropics from the temperate zone and enabled the persistence and diversification of incumbent lineages in temperate, seasonal environments.

## Materials and Methods

**Phylogeny.** We performed analyses on a comprehensive, multilocus species-level molecular phylogeny of the superfamily Emberizoidea, also known as the New World nine-primaried oscines, from Barker et al. (27) (*SI Materials and Methods*).

**Domino Model of Migratory Range Evolution.** We described each species' range as a  $3 \times 2$  matrix (a "domino"), wherein a species' presence or absence is indicated in three geographic areas in both the breeding and nonbreeding (winter) season (Fig. 1). To capture the major biogeographic events relevant to the evolution of long-distance, Neotropical migration, we divided the Western Hemisphere into three geographic regions: North America ( $>29^\circ$  N) Middle America and Caribbean islands ( $<29^\circ$  N,  $>11.5^\circ$  N), and South America. Latitude  $29^\circ$  N represents a transition from a subtropical to a temperate environment; above  $29^\circ$  N latitude, many species migrate south for the northern winter whereas, below this latitudinal line, few species, particularly emberizoids, migrate latitudinally (45). Latitude  $11.5^\circ$  N roughly divides continental South America from Caribbean islands and Central America. See *SI Materials and Methods* for additional details on domino construction.

The pattern of breeding- and winter-range symmetry of each domino indicates breeding- and winter-range overlap and, implicitly, the presence or absence of Neotropical migration, as well as the average length of migratory journeys of the species represented (Table S1). Asymmetrical dominos (Fig. 1C) always represent Neotropical migration whereas symmetrical dominos (Fig. 1A and B) represent nonmigratory or less migratory species (Table S1). The broad latitudinal divisions of dominos do not reflect shorter-distance seasonal migration that may occur within latitudinal regions (25). We prefer this broad-scale approach for testing the hypotheses in this study. Our foci are the major biogeographic events in lineage history that led to the evolution of the Neotropical migratory system, as opposed to the appearance or disappearance of migratory behavior in a population *per se*. Migratory behavior has been shown to sometimes change very rapidly (46) and is sensitive to temporally ephemeral changes, such as range oscillations during North American glacial cycles (26, 41, 42). Conversely, domino states are geographically broad and therefore temporally more stable and appropriate for phylogenetic analysis than are finer geographic state delineations that would capture more nuanced, but fleeting, contemporary details of migratory behavior.

Our model is based on the dispersal-extinction-cladogenesis (DEC) model (22, 23). As in DEC, anagenetic change along a phylogenetic branch in the domino model occurs as a continuous-time Markov process of range expansion (dispersal) and contraction (local extinction), and cladogenetic change occurs via dichotomous subdivision and inheritance of ancestral ranges at speciation events (Fig. 2 and Fig. S7). A series of simple rules govern (i) how geographic range can evolve along a phylogenetic branch in either or both seasons and (ii) how lineage splitting (speciation) can subdivide breeding and winter ranges to yield derived dominos inherited by the daughter lineages (*SI Materials and Methods* and Fig. S1). These rules determine which transitions between dominos are permitted directly.

Anagenetic change is described by the instantaneous rate matrix  $\mu Q$ , where  $\mu$  is the baseline transition rate and  $Q$  is a  $23 \times 23$  matrix (corresponding to the 23 possible dominos) in which off-diagonal entries correspond to parameters that scale  $\mu$  for specific ancestor-descendant pairwise transitions between dominos.  $Q$  is normalized such that the rows of  $\mu Q$  sum to 0. Transition probabilities corresponding to observations of particular dominos at the start and end of a branch of length  $t$  are obtained by matrix exponentiation,  $P(t) = \exp(\mu Q t)$ . These probabilities are used to calculate the likelihood of the tip data, given the phylogeny and a parameterized rate matrix. We modified the familiar pruning algorithm (47) to integrate over subdivision/inheritance scenarios at internal nodes (23).

**Parameter and Ancestral-State Estimation.** The rate matrix  $Q$  contained 128 nonzero off-diagonal entries representing all direct transitions between dominos that we considered to be plausible *a priori*. The relatively large number of these parameters motivated us to follow Lemey et al. (48) in implementing Bayesian stochastic search variable selection as a means of exploring more parsimonious parameterizations of  $Q$ , allowing rates for some transitions—those unsupported by the data—to be zero. We constructed a Markov Chain Monte Carlo (MCMC) analysis in which each permitted rate parameter was treated as an independent discrete variable having three possible values: 0, 0.1, and 1, which can be thought of as "off," "slow," and "fast," respectively. These rate classes scale the base rate of domino evolution  $\mu$  for each permitted ancestor-descendant domino transition and were assigned a uniform prior distribution. We set the prior for  $\mu$  to be gamma-distributed ( $\alpha = \beta = 1$ ). The likelihood function and priors for Metropolis-Hastings sampling were implemented in Python using the PyMC library (49). We ran five independent MCMC analyses for 1.5 million generations each, recording the sampled rate parameters every 1,000 generations after a burn-in period of 150,000 generations. Plots of likelihood and individual rate parameters against generation were visually inspected to assess stationarity and convergence across runs. To calculate a mean transition rate for each permitted parameter, we determined the proportion of MCMC sampled rate parameters that were 0, 0.1, or 1 for each parameter (i.e., the probability of each transition parameter occurring in each rate class). Using these proportions as weights, we calculated a mean rate for each transition parameter as the weighted mean of the three rate classes. To estimate ancestral states, we used the posterior distributions of  $\mu$  and  $Q$  estimated by MCMC to generate a distribution of 1,000 sets of ancestral domino states at internal nodes of the phylogeny (details in *SI Materials and Methods*).

**Network Analysis.** To test hypotheses of migratory range evolution, we treated the adjacency matrix of mean transition rates (Fig. 3A) as a weighted, directed graph (Fig. 3B). The vertices of the graph are the 23 dominos, the edges are the instantaneous transitions between dominos, and the edge weights are the mean transition rates between dominos (Fig. 3B). Treating the matrix as a directed graph allows each permitted ancestor-to-descendant

transition in the rate matrix to be thought of as a link in a path connecting dominos that cannot transition instantaneously to one another. Paths between nonneighboring dominos differ by their weighted length: the sum of the edge weights connecting two vertices. By scaling edge weights such that the highest transition rates indicate the lowest edge weights and vice versa (Fig. S2), we calculated the paths with the lowest weighted length (i.e., shortest path) using the igraph R package (50). That is, we treated paths that minimized the number of links (edges) and maximized transition rates of individual links as the “shortest” and therefore highest rate pathways (Fig. S2). Because each domino differs by some combination of breeding and wintering grid cell occupancy, edges between neighboring vertices in the graph represent expansions or contractions of breeding and/or wintering ranges. Consequently, paths between nonneighboring vertices in the graph represent a cumulative flow of biogeographic change throughout the New World, and the weighted path length indicates the inverse rate of this flow. Our results for path length were not biased by the inherent structure of the transition matrix: when the same tests were repeated with all edges weighted equally, no bias in path lengths was recovered for the alternative scenarios in each test.

**State-Dependent Speciation–Extinction Analyses.** A potentially important aspect of modeling geographic range evolution is the influence of geographic state on speciation or extinction rates; models that consider this influence

have been shown to sometimes produce different estimates of transition rates and ancestral states than models that do not include state-dependent speciation or extinction (SSE) parameters (31, 32). Due to the necessarily high number of geographic states and parameters in the domino model, incorporating SSE parameters in the domino model would be untenable. Therefore, where possible, we tested major conclusions of the domino model individually under SSE models with a series of simpler, binary characters, implemented in Diversitree (33). Using binary characters, we tested rates of gain and loss of migration under the BiSSE (31, 33) and GeoSSE (32) models, and rates of tropical-to-temperate versus temperate-to-tropical dispersal under the GeoSSE model. Detailed SSE methods are provided in *SI Materials and Methods*.

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1. Zink R (2002) Towards a framework for understanding the evolution of avian migration. *J Avian Biol* 33:433–436.
2. Berthold P (2001) *Bird Migration: A General Survey* (Oxford Univ Press, New York), 2nd Ed.
3. Alerstam T, Hedenstrom A, Åkesson S (2003) Long-distance migration: Evolution and determinants. *Oikos* 103:247–260.
4. Joseph L, Lessa E, Christidis L (1999) Phylogeny and biogeography in the evolution of migration: Shorebirds of the Charadrius complex. *J Biogeogr* 26:329–342.
5. Joseph L (2005) *Birds of Two Worlds: The Ecology and Evolution of Bird Migration*, eds Greenberg R, Marra PP (Johns Hopkins Univ Press, Baltimore), pp 18–26.
6. Ronquist F, Sanmartin I (2011) Phylogenetic methods in biogeography. *Annu Rev Ecol Syst* 42:441–464.
7. Ree RH, Sanmartin I (2009) Prospects and challenges for parametric models in historical biogeographical inference. *J Biogeogr* 36:1211–1220.
8. Outlaw D, Voelker G, Mila B, Gorman D (2003) Evolution of long-distance migration in and historical biogeography of Catharus thrushes: A molecular phylogenetic approach. *Auk* 120:299–310.
9. Voelker G, Bowie RCK, Klicka J (2013) Gene trees, species trees and Earth history combine to shed light on the evolution of migration in a model avian system. *Mol Ecol* 22(12):3333–3344.
10. Bryson R, et al. (2014) Diversification across the New World within the “blue” cardinals (Aves: Cardinalidae). *J Biogeogr* 41:587–599.
11. Wallace AR (1874) Migration of Birds. *Nature* 10:459.
12. Salewski V, Bruderer B (2007) The evolution of bird migration—a synthesis. *Naturwissenschaften* 94(4):268–279.
13. Gauthreaux S (1982) *Avian Biology*, eds Farner D, Parkes K, King J (Academic, New York), 6th Ed, pp 93–168.
14. Cox GW (1968) The role of competition in the evolution of migration. *Evolution* 22:180–192.
15. Rappole J, Jones P (2002) Evolution of old and new world migration systems. *Ardea* 90:525–537.
16. Levey D, Stiles F (1992) Evolutionary precursors of long-distance migration: Resource availability and movement patterns in neotropical landbirds. *Am Nat* 140:447–476.
17. Rappole J (1995) *The Ecology of Migrant Birds: A Neotropical Perspective* (Smithsonian Institution Press, Washington, DC).
18. Helbig A (2003) *Avian Migration*, eds Berthold P, Gwinner E, Sonnenschein E (Springer, Berlin), pp 81–95.
19. Bell C (2000) Process in the evolution of bird migration and pattern in avian ecology. *J Avian Biol* 31:258–265.
20. Winger BM, Lovette IJ, Winkler DW (2012) Ancestry and evolution of seasonal migration in the Parulidae. *Proc R Soc B Biol Sci* 279:610–618.
21. Outlaw DC, Voelker G (2006) Phylogenetic tests of hypotheses for the evolution of avian migration: A case study using the Motacillidae. *Auk* 123:455–466.
22. Ree RH, Smith SA (2008) Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst Biol* 57(1):4–14.
23. Ree RH, Moore BR, Webb CO, Donoghue MJ (2005) A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* 59(11):2299–2311.
24. DeGraaf RM, Rappole J (1995) *Neotropical Migratory Birds* (Cornell Univ Press, Ithaca, NY).
25. Jahn A, Levey D, Smith K (2004) Reflections across hemispheres: A system-wide approach to new world bird migration. *Auk* 121:1005–1013.
26. Zink RM (2011) The evolution of avian migration. *Biol J Linn Soc Lond* 104:237–250.
27. Barker FK, Burns KJ, Klicka J, Lanyon SM, Lovette IJ (2013) New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *Auk Ornithol Adv*, in press.
28. Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends Ecol Evol* 19(12):639–644.
29. Barker FK, Cibois A, Schikler P, Feinstein J, Cracraft J (2004) Phylogeny and diversification of the largest avian radiation. *Proc Natl Acad Sci USA* 101(30):11040–11045.
30. Kondo B, Omland K (2007) Ancestral state reconstruction of migration: Multistate analysis reveals rapid changes in New World orioles (*Icterus* spp.). *Auk* 124:410–419.
31. Maddison WP, Midford PE, Otto SP (2007) Estimating a binary character's effect on speciation and extinction. *Syst Biol* 56(5):701–710.
32. Goldberg EE, Lancaster LT, Ree RH (2011) Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst Biol* 60(4):451–465.
33. FitzJohn RG (2012) Diversitree: Comparative phylogenetic analyses of diversification in R. *Methods Ecol Evol* 3:1084–1092.
34. Rolland J, Jiguet F, Jönsson KA, Condamine FL, Morlon H (2014) Settling down of seasonal migrants promotes bird diversification. *Proc R Soc B Biol Sci* 281(1784):20140473.
35. Burns KJ, et al. (2014) Phylogenetics and diversification of tanagers (Passeriformes: Thraupidae), the largest radiation of Neotropical songbirds. *Mol Phylogenet Evol* 75:41–77.
36. Louchart A (2008) Emergence of long distance bird migrations: A new model integrating global climate changes. *Naturwissenschaften* 95(12):1109–1119.
37. Boyle WA, Conway CJ (2007) Why migrate? A test of the evolutionary precursor hypothesis. *Am Nat* 169(3):344–359.
38. Bell C (2005) The origin and development of bird migration: Comments on Rappole and Jones, and an alternative evolutionary model. *Ardea* 93:115–123.
39. Barker FK, Burns KJ, Klicka J, Lanyon SM, Lovette IJ (2013) Going to extremes: Contrasting rates of diversification in a recent radiation of new world passerine birds. *Syst Biol* 62(2):298–320.
40. Hawkins BA, Diniz-Filho JAF, Jaramillo CA, Soeller SA (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *J Biogeogr* 33:770–780.
41. Milá B, Smith TB, Wayne RK (2006) Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution* 60(11):2403–2409.
42. Ruegg KC, Hijmans RJ, Moritz C (2006) Climate change and the origin of migratory pathways in the Swainson's thrush, *Catharus ustulatus*. *J Biogeogr* 33:1172–1182.
43. Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science* 314(5796):102–106.
44. Smith BT, Bryson RW, Jr, Houston DD, Klicka J (2012) An asymmetry in niche conservatism contributes to the latitudinal species diversity gradient in New World vertebrates. *Ecol Lett* 15(11):1318–1325.
45. Cox G (1985) The evolution of avian migration systems between the temperate and tropical regions of the New World. *Am Nat* 126:451–474.
46. Berthold P, Helbig AJ, Mohr G, Querner U (1992) Rapid microevolution of migratory behaviour in a wild bird species. *Nature* 360:668–670.
47. Felsenstein J (1981) Evolutionary trees from gene frequencies and quantitative characters: Finding maximum likelihood estimates. *Evolution* 35:1229–1242.
48. Lemey P, Rambaut A, Drummond AJ, Suchard MA (2009) Bayesian phylogeography finds its roots. *PLoS Comput Biol* 5(9):e1000520.
49. Patil A, Huard D, Fonnesebeck CJ (2010) PyMC: Bayesian stochastic modelling in Python. *J Stat Softw* 35(4):1–81.
50. Csardi G, Nepusz T (2006) The igraph software package for complex network research. *InterJournal Complex Systems*:1695.