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

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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

The 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

(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. 3*A*). 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. 3 *B* 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
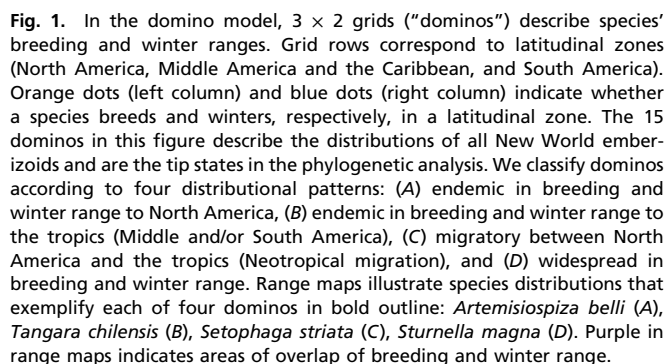

Fig. 2. Transitions between dominos represent instantaneous expansions or contractions of the range along branches (between *i* and *ii*) or dichotomous subdivision or inheritance at speciation (between *ii* and *iii*). Here, the breeding range has expanded from Middle America to North America (*i* to *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 (*iiia*) and one Neotropical migratory domino (*iiib*).

~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. 1*C*) more frequently evolved along a phylogenetic branch from an ancestral domino endemic to North America in both the breeding and winter range (henceforth, the NA domino) (Fig. 1*A*) or from ancestors endemic to the tropics in both breeding and winter range (henceforth, tropical dominos) (Fig. 1*B*). 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 × 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.

Fig. 3. Network analysis. The instantaneous transition rates in the model can be summarized as a 23 × 23 adjacency matrix (*A*). Axis ticks represent the 23 dominos as ancestor (*x*) and descendant (*y*) states; three example dominos representing tropical, Neotropical migratory (NM), and North American (NA) states are shown on axes. Outlined squares represent permitted direct pairwise transitions; white space indicates pairwise transitions that are not permitted instantaneously. Permitted transitions are shaded on a gradient corresponding to estimated mean rate, from 0 (white) to 1.0 (black). For hypothesis testing, we treated the adjacency matrix of transition rates in *A* as a weighted, directed graph (*B*) wherein each node (circles) represents one of 23 dominos, each edge (arrows) represents a transition (corresponding to outlined squares in *A*), and edge weights (thickness) correspond to mean transition rate. A reduced set of nodes is shown here for illustrative purposes. To test how Neotropical migration evolved, we calculated weighted path lengths between the NA domino (Fig. 1*A*) and each of the NM dominos (Fig. 1*C*), and between each of the tropical dominos (Fig. 1*B*) and the NM dominos (Fig. 1*C*). One possible path from NA to a NM domino is depicted in *B* with blue arrows, indicating shifts of the winter range, and from a tropical domino to the same NM domino with orange arrows, indicating shifts of the breeding range. (*C*) Boxplots with median and quartile values show that the shortest paths from NA to the NM dominos (blue, *n* = 7) were shorter than shortest paths from tropical to NM dominos (orange, *n* = 21). Shorter weighted paths indicate higher rate sequences of range evolution (*Materials and Methods* and Fig. S2); therefore, winter-range shifts from North America had a more dominant influence on the evolution of Neotropical migration than breeding-range shifts from the tropics.

widespread distributions but found these occurrences to be negligible (less than two branches). This result implies that shifts of the winter range out of North America were more prevalent than shifts of the breeding range out of the tropics in the evolution of Neotropical migration.

The ancestral state reconstructions permit only coarse-grained summaries of evolutionary change on specific branches of the phylogeny. To obtain a more nuanced understanding of trends in range evolution, we constructed an adjacency matrix that describes the mean ancestor–descendant transition rates between pairs of dominos (*Materials and Methods* and Fig. 3*A*). We then performed network analyses on the matrix's corresponding graph to infer the dominant sequences of geographic evolution

that occurred throughout the phylogeny (Fig. 3). To test whether Neotropical migration evolved via shifts of breeding range out of the tropics versus shifts of winter ranges out of North America, we calculated the shortest weighted paths (*Materials and Methods*, Fig. 3*B*, and Fig. S2) between the NA domino (Fig. 1*A*) and each NM domino (Fig. 1*C*). The shortest weighted paths between the NA domino and the NM dominos involve incremental shifts of the winter range toward the tropics (Fig. 3*B* and Fig. S2). We then calculated the shortest paths between the tropical dominos (Fig. 1*B*) and each of the NM dominos (Fig. 1*C*). These paths involve shifts of the breeding range out of the tropics (Fig. 3*B*). Shorter paths indicate higher rate and therefore more dominant pathways of geographic change (*Materials and Methods*

Fig. 4. The phylogeny of the New World Emberizoidea (27). Branches are colored according to the most frequent ancestral state reconstructed at the beginning and end of each branch in 1,000 ancestral state estimates (*Materials and Methods* and *SI Materials and Methods*). Dashed gray lines indicate a widespread domino (Fig. 1*D*); solid gray a tropical domino (Fig. 1*B*); black the North American (NA) domino (Fig 1*A*). Blue indicates branches that are NA at the beginning and Neotropical migratory (NM) at the end of the branch (i.e., evolved NM via a shift of the winter range); orange indicates branches that are tropical at the beginning and NM at the end (i.e., evolved NM via a shift of the breeding range). Pink indicates an NM domino at the beginning and end of a branch. Pink lines at the tips are scaled according to average migratory distances of each contemporary NM species. The starred blue branch shows that NM evolved in the ancestor to the largest lineage of migratory emberizoids via a winter-range shift out of NA. Numbers refer to taxa that were inferred to have evolved migration via a breeding-range shift out of the tropics (see *Results*). Thraupidae is the largest family but does not contain Neotropical migrants.

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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
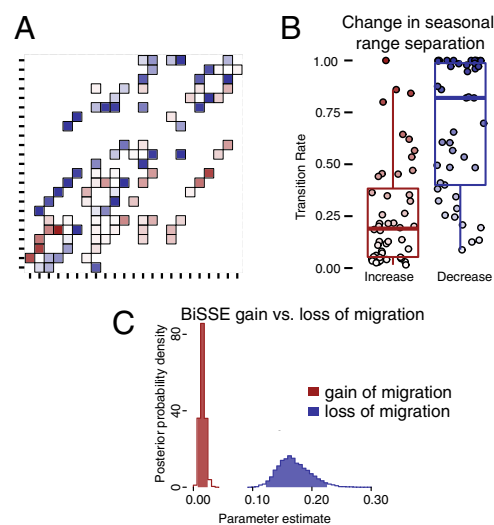
Fig. 5. Loss versus gain of migration. (*A*) To test whether migration was more often lost than gained, we determined which of the pairwise domino transitions in the adjacency rate matrix represented a decrease (blue) versus an increase (red) of breeding- and winter-range separation (*SI Materials and 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 × 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° N) Middle America and Caribbean islands (<29° N, >11.5° N), and South America. Latitude 29° N represents a transition from a subtropical to a temperate environment; above 29° 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° 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. 1 A 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 μQ, where μ is the baseline transition rate and Q is a 23×23 matrix (corresponding to the 23 possible dominos) in which off-diagonal entries correspond to parameters that scale μ for specific ancestor–descendant pairwise transitions between dominos. Q is normalized such that the rows of μQ 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 μ for each permitted ancestor–descendant domino transition and were assigned a uniform prior distribution. We set the prior for μ 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 μ 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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Supporting Information

Winger et al. 10.1073/pnas.1405000111

SI Materials and Methods

Phylogeny. The phylogeny used in this study is a multilocus molecular phylogeny from Barker et al. (1) that represents the most complete species level phylogeny constructed for the Emberizoidea. Molecular data from over 95% of recognized emberizoid species were included, and all relationships relevant to transitions in migratory behavior or biogeographic change are represented. As described in Barker et al. (1), we performed analyses in this study on a maximum clade credibility tree generated from a pseudoposterior distribution of 1,000 supertrees (1). These supertrees were constructed using a planned supertree approach that integrated a multilocus, genus-level backbone tree—the Species Tree of Barker et al. (2)—with comprehensive, multilocus species-level phylogenies of major emberizoid lineages (3–6). The phylogeny is scaled in absolute time using external calibrations (2).

We pruned the monophyletic group of 41 species of buntings endemic to the Old World (the Emberizidae *sensu stricto*) (2) from the tree before analyses; all remaining species are endemic to the New World, except for two arctic breeding species with Holarctic distributions (*Calcarius lapponicus* and *Plectrophenax nivalis*) and three thraupid species endemic to Tristan da Cunha.

Designation of Dominos. Dominos are 3×2 grids with at least one cell occupied in each column; mathematically there are 49 possible unique dominos. We determined each emberizoid species' domino by extracting latitudinal boundaries of breeding and winter ranges from shapefiles of range maps available online (7) and confirming latitudes with additional references (8, 9). We required ranges to extend across the latitudinal thresholds by at least three degrees to be designated as present in that region.

Fifteen unique dominos are required to depict the geographic distributions of all emberizoids (Fig. 1; dominos 1–15 in Table S1), and the remaining possible dominos do not exist among emberizoids. However, we included an additional 8 dominos that we considered to be possible transitional states (Table S1). Dominos 16–18 (Table S1) describe the ranges of other New World migratory passerine birds, and dominos 19 and 20 represent ranges that could conceivably occur with minor adjustments to extant ranges. Dominos 21–23 indicate breeding in North and South America but not Middle America. Although species with such dramatically disjunct populations do not exist among emberizoids, we include these three dominos as possible transitional states. These transitional states enable in the model the possibility of a migratory "drop-off," in which migratory populations wintering in South America form an isolated breeding population in the wintering region and undergo subsequent speciation from the migratory ancestor, to form both tropical resident and migratory daughters (Fig. S1C) (10–12).

Rules Governing Transitions Between Dominos. The transition matrix (Fig. 3A) describes the instantaneous transitions permitted between pairs of dominos. There are $23^2 = 529$ possible pairwise combinations of dominos. However, a series of simple rules based on the biology of geographic range evolution (13) and avian migration in the New World limits our transition matrix to 128 instantaneous transitions. The rules for anagenetic change are as follows. Both breeding and winter range can expand and contract separately or in unison into neighboring domino cells. However, the breeding range cannot expand or contract to result in breeding-range occupancy in cells south of the winter range (Fig. S1A). Likewise, winter range cannot occupy cells north of the

breeding range. Although migrations from southern breeding grounds to more northern winter grounds occur within South America or locally within other regions (14), such migrations do not occur across the broad geographic regions of dominos among terrestrial birds (9, 15). Therefore, breeding-range expansion to the south requires a simultaneous southward expansion of the winter range, and winter-range expansions north always involve a simultaneous northward expansion of the breeding range (Fig. S1A). However, breeding range can expand or contract to the north without change in the winter range, and winter range can expand or contract to the south without change to breeding range. Ranges cannot jump between nonneighboring cells; for example, a winter-range shift from North America to South America requires intermediate transitions (Fig. S1B). The only exception to this rule is during "migratory drop-offs" in which a species already wintering in South America begins breeding there as well (Fig. S1C).

During speciation, ancestral ranges can be inherited or fragmented, but the entire ancestral range must be cumulatively present in the daughters (speciation can fragment ranges and cause range reduction in one daughter, but it cannot instantaneously eliminate a portion of the ancestor's range in both daughters). Migratory (asymmetrical) dominos cannot be created instantaneously at speciation from nonmigratory (symmetrical) dominos. Our model includes changes that can happen only at speciation events. However, if speciation occurred along a branch and one daughter lineage goes extinct, a signature of speciation is not left on the phylogeny, as the branch appears nonbifurcating (16). Therefore, we allowed cladogenetic subdivision to occur at nodes (visible speciation events), as well as along branches at "hidden" speciation events (Fig. S7).

Calculation of Increase vs. Decrease of Range Separation. To determine whether breeding and winter ranges tended to coalesce or separate from ancestor to descendant throughout emberizoid history, we defined a metric that determines the "seasonal range separation" of a domino. For example, a domino with both breeding and winter range wholly in North America would have no range separation whereas a domino breeding only in North America and wintering only in South America has high range separation. The seasonal range separation of dominos varies from 0 to 4 and was calculated as the quantity of cells occupied in the breeding season but not in winter, plus the quantity of cells occupied in the winter but not in the breeding season. Unoccupied cells separating breeding and wintering distribution also count toward the sum (Fig. S4A and Table S1). This discrete separation metric corresponds well to the average migratory distances of extant emberizoid species that were coded as each domino (Fig. S4A). We then calculated the difference in range separation between ancestor and descendant dominos in each permitted transition; transitions with a negative value indicate increases in seasonal range separation, and vice versa (Fig. S4B). In Fig. 3, transitions in red represent negative ancestor–descendant range-separation differences (increase of seasonal range separation), and transitions in blue represent positive ancestor–descendant disparity differences (decreases of seasonal range separation).

Ancestral-State Estimation. We generated a posterior probability distribution of ancestral states. In this context, "ancestral state" refers to the scenario of range subdivision and inheritance at the node: that is, the ancestral domino (the state of the lineage immediately before splitting) and the derived dominos inherited

by the two daughter species. For each posterior sample of μ and **Q** from the Markov Chain Monte Carlo (MCMC) runs, the conditional likelihoods of ancestral states given the observed dominos at descendant leaf nodes were computed for each internal node using the pruning algorithm of (17). These likelihoods were used to compute the maximum-likelihood set of ancestral states for μ and **Q**, first at the root node (i.e., the state with highest conditional likelihood), and then by a recursive preorder traversal of the phylogeny, selecting the state with highest likelihood given the domino at the start of the node's ancestral (subtending) branch. Two hundred samples of ancestral states were computed from each of the five MCMC runs, for a total of 1,000 sets of ancestral states.

Degree Test. We performed an additional test of the biogeographic pathways involved in the evolution of Neotropical migration using the graph theory concept of degree. The weighted degree is a measure of the strength of connections of one vertex to neighboring vertices in a graph. We first reduced the graph of instantaneous transitions to only those transitions between dominos that resulted in an increase in geographic separation of the breeding and winter range (see *Calculation of Increase vs. Decrease of Range Separation*). Within this reduced graph, we calculated the weighted out-degree of the North American endemic domino and the tropical endemic dominos, using the graph.strength function in igraph (18). Because the reduced graph includes only transitions that result in an increase in separation of breeding and winter range, the out-degree of a domino in this graph indicates the rate at which direct transitions out of this state resulted in increases in separation of breeding and winter ranges. The shortest path analysis (*Materials and Methods* and Fig. 3) explored sequences of change between nonneighboring vertices, and individual transitions were not required to increase seasonal range separation as long as the net change along the path resulted in increased seasonal range separation. Conversely, the degree test explored only transitions between neighboring vertices, but every transition was required to increase seasonal range separation. The degree test supports our conclusions from the shortest path analysis that winter-range shifts were the dominant process during the evolution of Neotropical migration (Fig. S3).

Domino Analysis of Pathways to Tropical Colonization. To explore how the tropics were colonized by year-round resident emberizoids, we identified all direct ancestor-to-descendant domino transitions that involved a shift of the breeding range from North America to Middle America, or Middle America to South America. We then identified which of these transitions involved a simultaneous shift of the breeding and winter range into an unoccupied region (i.e., an expansion of a resident, year-round range into more tropical latitudes) and which transitions involved a shift of a migratory species' breeding range into a tropical area already occupied by their winter range. Both types of events occurred at high rates (Fig. S6).

State-Dependent Speciation-Extinction Analyses. The results of the domino model indicate that migration evolved early in emberizoid history and that breeding and winter ranges of emberizoids tended to evolve greater overlap throughout subsequent lineage history rather than evolve separation—that is, migration tended to be lost rather than gained. To further test this conclusion under models with state-dependent speciation and extinction (SSE) components, we modeled the evolution of migratory behavior using the BiSSE model (19), implemented in the R package Diversitree (20). Following Winger et al. (21), we modeled migratory behavior as a binary character indicating presence or absence of migration in a species. Some emberizoid species have both migratory and sedentary populations so we created two binary characters in which polymorphic species were coded either as migratory or sedentary. The geographic-state speciation and extinction (GeoSSE) (22) model enables coding of a binary character in which tips are permitted to occur in both states. Therefore, we coded a migration character in GeoSSE in which states were migratory, sedentary, or both migratory and sedentary. Across all character codings, migration was always lost at a higher rate than gained; therefore, we present here only the results of the BiSSE migration character in which polymorphic species were treated as migratory.

We also used GeoSSE to examine rates of tropical to north temperate versus north temperate to tropical dispersal of breeding range. We coded three characters in which breeding distributions were coded as north, south, or on both sides of three latitudinal thresholds: respectively, 11.5° N, 23.5° N, and 29° N. These three characters reflect three estimates of dispersal between more temperate, northern and more tropical, southern latitudes.
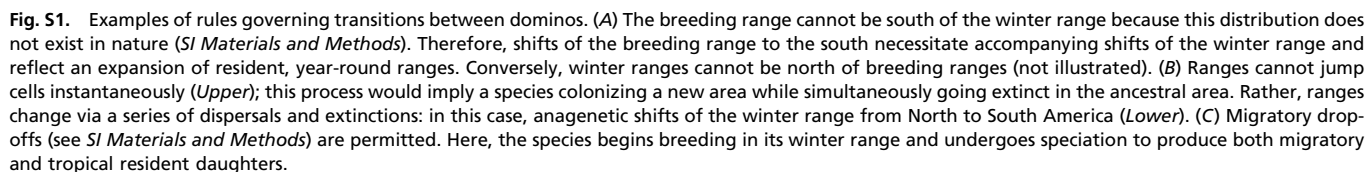
Following Winger et al. (21), we tested a series of nested models in which diversification, speciation, and transition rates were variously constrained. For the BiSSE characters, the full parameter models—which include state-dependent speciation and extinction parameters—provided a significantly better fit to the data than constrained models and thus were used for parameter estimation below. For the GeoSSE characters, some constrained models provided a slightly better fit to the data than the full model, but the parameter estimates relevant to this study were similar using the full and constrained models; so, for simplicity, we present here the results of the full GeoSSE model. To account for model uncertainty for the migratory character and three latitudinal characters, we sampled rates estimated in BiSSE and GeoSSE using an MCMC approach implemented in Diversitree (20). We ran the MCMC chain for 20,000 generations, discarding the first 10,000 generations as burn-in.

Consistent with the domino model, the SSE models estimated a higher rate of loss of migration than gain of migration (Fig. 5), as well as higher rates of north temperate-to-tropical dispersal than tropical-to-north temperate dispersal (Fig. S5). Ratios of northern-to-southern dispersal were most extreme when 29° N was used as the latitudinal boundary and most subtle when 11° N was used (Fig. S5). This result indicates high rates of dispersal from North America into Middle America and lower dispersal from Middle America into South America.
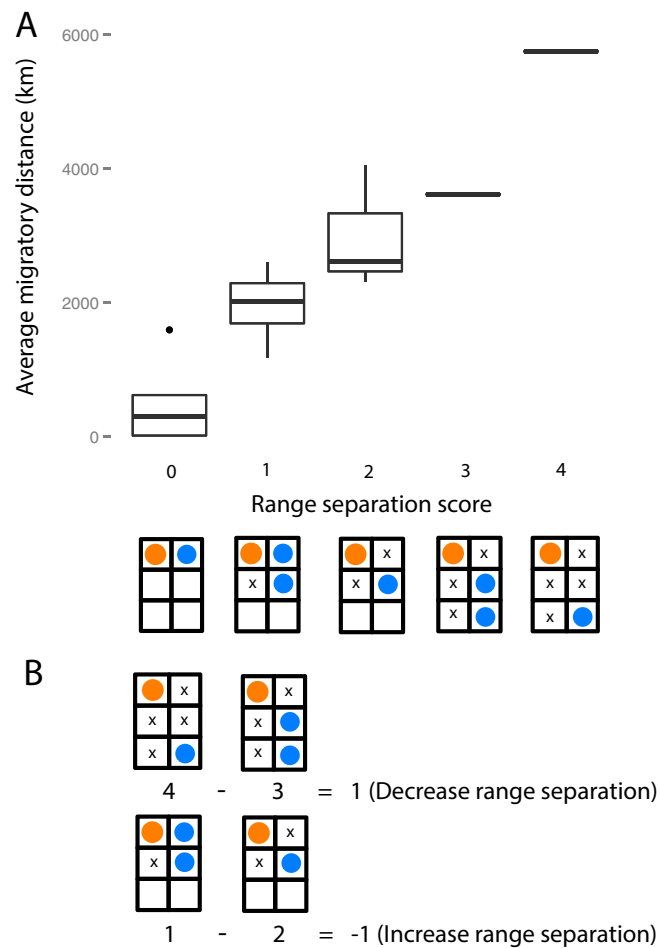
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22. Goldberg EE, Lancaster LT, Ree RH (2011) Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Syst Biol* 60(4):451–465.

Fig. S1. Examples of rules governing transitions between dominos. (*A*) The breeding range cannot be south of the winter range because this distribution does not exist in nature (*SI Materials and Methods*). Therefore, shifts of the breeding range to the south necessitate accompanying shifts of the winter range and reflect an expansion of resident, year-round ranges. Conversely, winter ranges cannot be north of breeding ranges (not illustrated). (*B*) Ranges cannot jump cells instantaneously (*Upper*); this process would imply a species colonizing a new area while simultaneously going extinct in the ancestral area. Rather, ranges change via a series of dispersals and extinctions: in this case, anagenetic shifts of the winter range from North to South America (*Lower*). (*C*) Migratory drop-offs (see *SI Materials and Methods*) are permitted. Here, the species begins breeding in its winter range and undergoes speciation to produce both migratory and tropical resident daughters.

Path length = (1.0 - 0.797) + (1.0 - 0.615) + (1.0 - 1.0) = **0.588**

Path length = (1.0 - 0.046) = **0.954**

Fig. S2. Shortest path analysis. We calculated the shortest paths as those that minimize the number of transitions between vertices in the graph of transition rates (Fig. 3*B*), while maximizing rates of each transition. To calculate these shortest paths, we weighted edges in the graph as 1 minus mean transition rate; this weighting assigns the lowest weights to the highest rates, and vice versa, and results in the shortest paths being those with the fewest transitions with the highest rates. For example, the shortest path between the NA endemic and an NM descendant that breeds in North and Middle America and winters in Middle America requires three instantaneous transitions (mean transition rates listed above arrows). The shortest path to the same migratory descendant from an ancestor endemic to Middle America requires only one transition. However, despite the higher number of transitions required in the top pathway, the rates of each transition from the NA endemic are higher, and consequently the summed path length (0.588) is shorter than the path from the tropical endemic. We therefore infer the top path to have been more influential in geographic range evolution of emberizoids.

Fig. S3. Boxplots with median and quartile values summarize the weighted out-degree from the three tropical dominos (Fig. 1*C*) and the NA domino (Fig. 1*A*) in the reduced transition graph representing only ancestor–descendant transitions that result in increased separation of breeding and winter range (*SI Materials and Methods*). The out-degree for the NA domino ($n = 1$) is higher than any out-degree for tropical dominos ($n = 3$), indicating a higher influence of shifts of the winter range out of North America in the evolution of Neotropical migration.

Fig. S4. Increase versus decrease of breeding- and winter-range separation. (*A*) Dominos below the plot illustrate examples of each of five scores of seasonal range separation (*SI Materials and Methods*); an "x" indicates cells that count toward the tally of seasonal range-separation scores, and sum to 0, 1, 2, 3, and 4, respectively, in each separation score. Higher range-separation scores indicate longer-distance Neotropical migration, as shown in the boxplots with median and quartile values, which summarize migratory distance of all emberizoid species with dominos in each class of separation scores. Migratory distances were calculated as Great Circle Distances between centroids of breeding and winter ranges. The seasonal range-separation score for each domino is listed in Table S1. (*B*) The difference in range-separation scores between ancestor to descendant indicates whether range separation decreased (positive score, *Upper* example) or increased (negative score, *Lower* example).
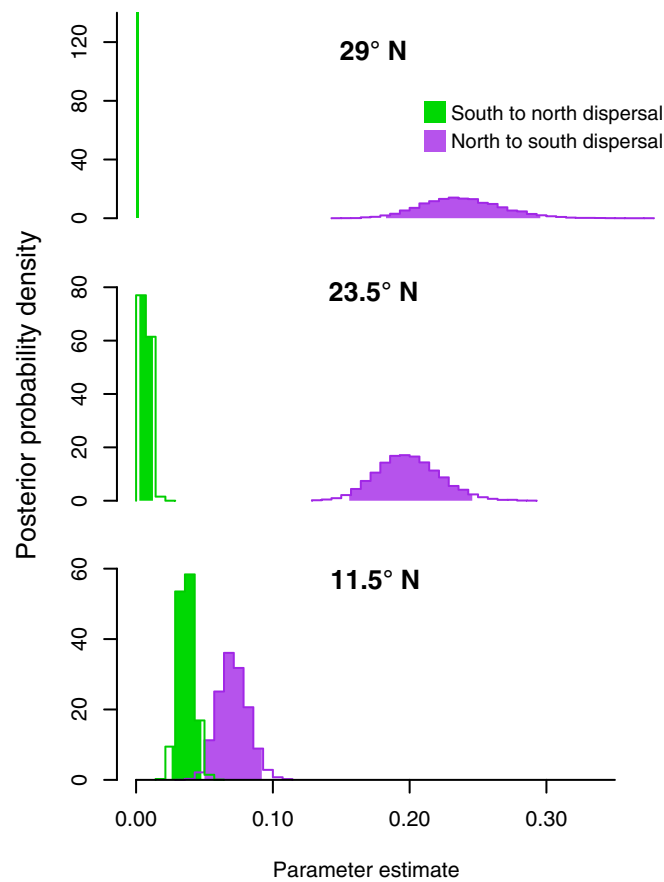
Fig. S5. Plots of estimated rate parameters from 10,000 generations of MCMC sampling using the GeoSSE model (22) to test temperate-to-tropical versus tropical-to-temperate colonization (*SI Materials and Methods*). Dispersal south across 29° N reflects dispersal from North America toward more subtropical and tropical latitudes; this boundary corresponds with the latitude in the Mexican plateau and in central Florida where many species change migratory behavior (*Materials and Methods*). Dispersal south across 23.5° N reflects dispersal into the true (latitudinally defined) tropics from the north temperate and north subtropical region. Dispersal across 11.5° N roughly corresponds to the dispersal in and out of South America. Rates of dispersal from north to south are higher than rates of dispersal from south to north at all thresholds; lopsided rates of dispersal decrease in severity as the threshold is moved south.
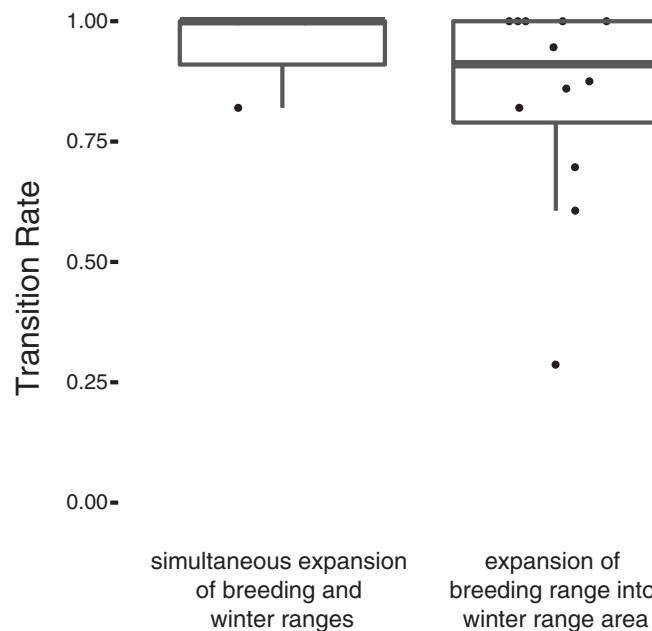
Fig. S6. Boxplots with median and quartile values are overlain on points representing rates of ancestor–descendant transitions between pairs of dominos that resulted in colonization of the tropics (Middle or South America) by the breeding range. We tested two processes: the simultaneous southward expansion of breeding and winter ranges (i.e., year-round resident ranges) from North America to Middle America and Middle America to South America (*Left*, n = 3), and the expansion of migratory species' breeding range into tropical areas already occupied by their wintering range (*Right*, n = 12). Each point represents a transition parameter, and points are jittered horizontally for visual purposes. Both processes occurred at high rates (*Results*).
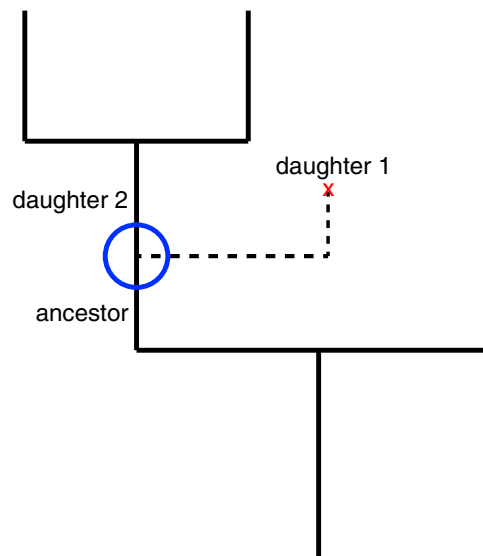

Fig. S7. Change at hidden speciation events. Certain domino transitions can occur only during cladogenesis, when ancestral ranges are subdivided between two daughters (Fig. 2). However, if a speciation event occurred (at blue circle) and one daughter went extinct (daughter 1), then the signature of this speciation event would not be present in the phylogeny and only anagenetic processes would be modeled. Therefore, we allow for hidden speciation events (for example, at blue circle) to occur along branches, such that the ancestor–descendant transition along a branch could represent a cladogenetic process.

Table S1. Reference table of the 23 dominos in the model

Domino no.	Domino	No. of emberizoid species	Migratory distance, km	Separation score	Class	Example species (family)
1		16	1,594	0	NA	*Passerela iliaca* (Passerellidae)
2		21	2,187	1	NM	*Setophaga palmarum* (Parulidae)
3		3	4,049	2	NM	*Mniotilta varia* (Parulidae)
4		11	2,315	2	NM	*Setophaga kirtlandii* (Parulidae)
5		18	3,617	3	NM	*Pheucticus ludovicianus* (Cardinalidae)
6		9	5,752	4	NM	*Dolichonyx oryzivorus* (Icteridae)
7		10	1,183	1	NM	*Cardellina rubrifrons* (Parulidae)
8		8	2,621	2	NM	*Icterus spurius* (Icteridae)
9		2	1,861	1	W	*Piranga flava* (Cardinalidae)
10		2	2,606	1	W	*Setophaga coronata* (Parulidae)
11		4	572	0	W	*Quiscalus mexicanus* (Icteridae)
12		25	638	0	W	*Cardinalis cardinalis* (Cardinalidae)
13		99	12	0	T	*Passerina rositae* (Cardinalidae)
14		56	13	0	T	*Haplospiza rustica* (Thraupidae)
15		451	24	0	T	*Ramphocelus carbo* (Thraupidae)
16		0	—	3	—	*Myiodynastes luteiventris* (Tyrannidae; not emberizoid)
17		0	—	1	—	*Vireo altilocus* (Vireonidae; not emberizoid)

Table S1. Cont.

Domino no.	Domino	No. of emberizoid species	Migratory distance, km	Separation score	Class	Example species (family)
18		0	—	1	—	*Vireo flavoviridis* (Vireonidae; not emberizoid)
19		0	—	2	—	?
20		0	—	2	—	?
21		0	—	1	—	("Drop-off")
22		0	—	2	—	("Drop-off")
23		0	—	0	—	("Drop-off")

Domino no., indices for dominos are listed for convenience in *SI Materials and Methods*; no. of emberizoid species, the number of species of extant or recently extinct emberizoids whose ranges are described by each domino (*Materials and Methods*); migratory distance, great circle distances between the centroids of breeding and winter ranges of each domino extracted from digital shapefiles and averaged across every emberizoid species represented by each domino; separation score, an integer index from 0 to 4 describing the separation of breeding and wintering range of each domino (*SI Materials and Methods* and Fig. S4); class, the four classifications of dominos in Fig. 1 used for analyses; example species, an example of an emberizoid species typifying each domino for dominos 1–15 (those present in the data) and other migratory passerines for dominos 16–18. Species representing dominos 19 and 20 were not found. Dominos 21–23 represent transitional states, or migratory "drop-offs" (*SI Materials and Methods*). NA, endemic to North America in breeding and winter range; NM, Neotropical migrant; T, endemic to the tropics in breeding and winter range; W, widespread.